Journal
of
Northwest Atlantic
Fishery Science

Volume 53
2022

Posted online January 2023
Northwest Atlantic Fisheries Organization

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ISSN: 0250-4408

Journal of Northwest Atlantic Fishery Science

Scientific publications by ICNAF and NAFO have been in existence since ICNAF began in 1949 with the ICNAF Special Publication series dealing with proceedings of scientific symposia. The ICNAF Research Bulletin was started in 1964 to provide a means of publishing results of scientific research relevant to ICNAF. The *ICNAF Research Bulletin* was terminated in September 1979 after the issue of Number 14. The first volume of the NAFO *Journal of Northwest Atlantic Fishery Science* was published in December 1980, after NAFO came into force replacing ICNAF in 1979.

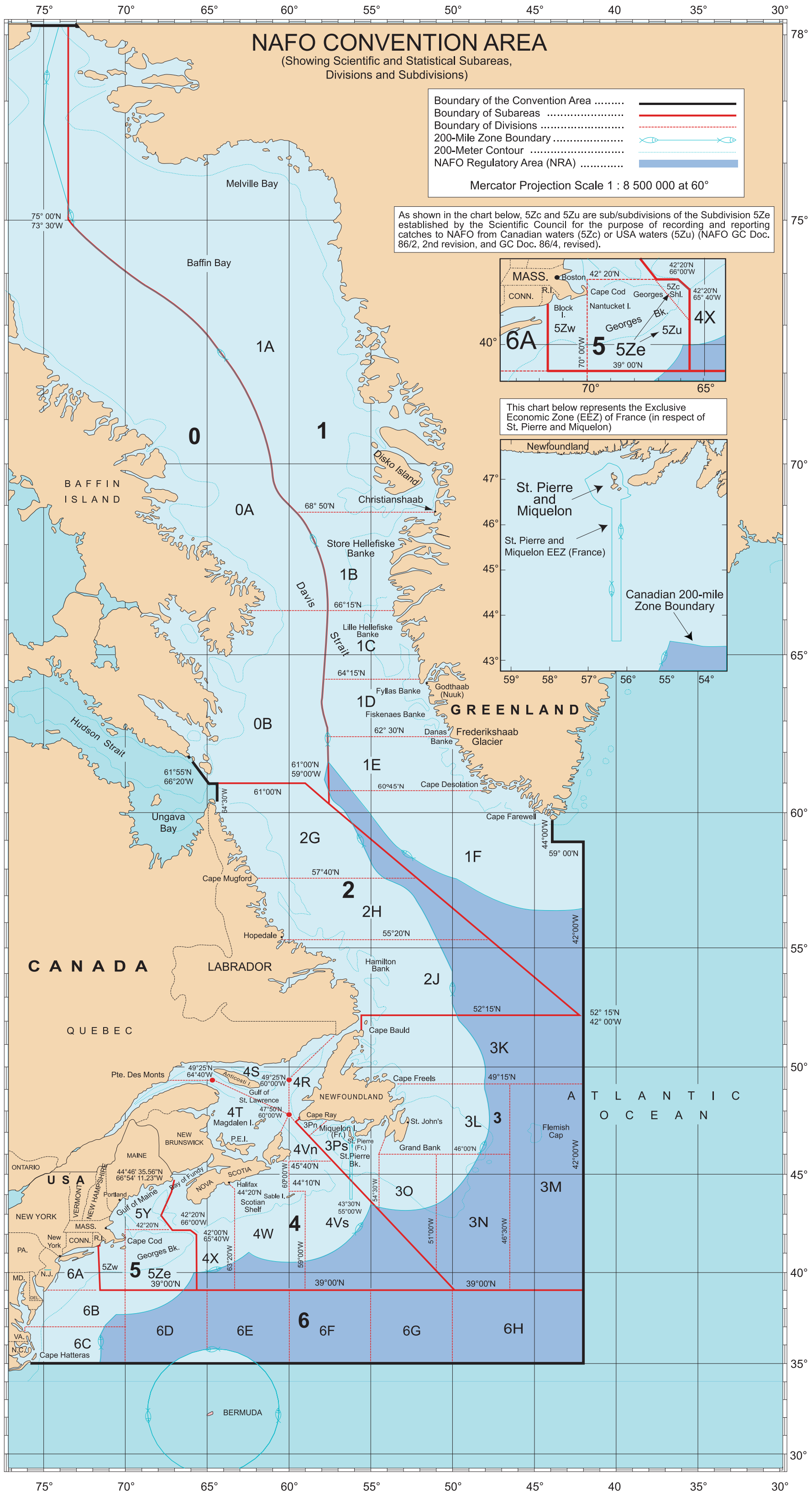
The Northwest Atlantic fisheries have a rich history, and a great deal of research has been sponsored and encouraged by NAFO and its predecessor ICNAF. NAFO has been a leader amongst international organizations in the application of science to fishery management and in the regulation of fisheries in areas beyond national jurisdiction. In accordance with its mandate to disseminate information on fisheries research to the scientific community, the Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, which contains peer-reviewed primary papers, and NAFO Scientific Council Studies, which contains unrefereed papers of topical interest and importance to the Scientific Council. Lists of these and other NAFO publications are given on the back of this issue.

Editorial Policy

The Journal provides an international forum for the primary publication of original research papers, with emphasis on environmental, biological, economic and social science aspects of fisheries and their interactions with marine habitats and ecosystems. While the Journal is intended to be regional in scope, papers of general applicability, and methodological and review papers, irrespective of region, are considered. Space is available for notes and letters to the editor to facilitate scientific discussion of published papers. Both practical and theoretical papers are eligible. All papers are peer-reviewed to determine their suitability for primary publication. Associate Editors arrange for the peer-reviews and ensure that the papers accepted for publication meet the high standards required for the Journal. Manuscripts approved for publication are accepted with the understanding that they are not copyrighted, published or submitted elsewhere except in abstract form. There are no page charges.

Editorial Board

The Scientific Council of NAFO publishes the *Journal of Northwest Atlantic Fishery Science*, containing peer-reviewed primary literature detailing original research of relevance to fisheries science and management in the Northwest Atlantic Ocean. Articles are published electronically under a Creative Commons (Canada) 2.5 license and https://creativecommons.org/licenses/by/2.5/ca/, and are freely available at https://journal.nafo.int. NAFO Scientific Council has resolved to produce annual or bi-annual online volumes and these represent a compilation of the web based articles published throughout the year. Additionally, the journal supports the use of digital object identifiers (doi) for electronic media and encourages others to support this initiative. The citations are now downloadable to various reference software platforms. The journal is also indexed in the Aquatic Sciences and Fisheries Abstracts (ASFA) database.



NAFO CONVENTION AREA

(Showing Scientific and Statistical Subareas, Divisions and Subdivisions)

Boundary of the Convention Area	▬
Boundary of Subareas	▬
Boundary of Divisions	- - -
200-Mile Zone Boundary	⟷
200-Meter Contour	······
NAFO Regulatory Area (NRA)	▬

Mercator Projection Scale 1 : 8 500 000 at 60°

As shown in the chart below, 5Zc and 5Zu are sub/subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).

This chart below represents the Exclusive Economic Zone (EEZ) of France (in respect of St. Pierre and Miquelon)

June 2015

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J. Northw. Atl. Fish. Sci., Vol. 53: 1–18 Publication (Upload) date: 19 Apr 2022

Interdisciplinary stock identification of North Atlantic porbeagle (*Lamna nasus*)

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Haugen, J.B., Skomal, G.B., Curtis, T.H., and Cadrin, S.X. 2022. Interdisciplinary stock identification of North Atlantic porbeagle (*Lamna nasus*). *J. Northw. Atl. Fish. Sci.*, 53**:** 1–18. https://doi.org/10.2960/J.v53.m732

Abstract

We conducted an interdisciplinary review of available information (*i.e.*, genetics, life-history, and movement) to evaluate the stock structure of a previously targeted shark species, the porbeagle (*Lamna nasus*), in the North Atlantic. Most available information supports the conclusion that porbeagle consist of a single genetic population in the North Atlantic, which is relevant for determining species conservation status. However, the observed movement rates between the Northwest, Northeast Atlantic, and the Mediterranean appear to be low enough to consider separate spatial units for stock assessment and fishery management. The review reveals different interpretations among the organizations involved with the conservation, management, and assessments of porbeagle in the North Atlantic regarding biological population and stock boundaries. Differences in the spatial definition of management units among management organizations may pose an impediment to conserving porbeagle populations and achieving management objectives. We recommend an increased collaboration between organizations involved in highly migratory shark species as it would be beneficial for data collection, data inclusiveness, the robustness of assessments, and provide clarity for fishery managers, scientists, and the public on stocks and status. This review demonstrates that the interdisciplinary approach to stock identification is particularly valuable for data-limited species because no single approach typically has enough information to be definitive. Clearly defining management units that reflect the biological populations of porbeagle in the North Atlantic is expected to reduce uncertainty in stock assessments and help achieve current management and conservation goals of rebuilding North Atlantic porbeagle stocks.

Keywords: data-limited species; fisheries management; highly migratory species; regional fisheries management organizations; stock assessment; shark conservation

Introduction

Stock assessments inform fisheries management and conservation of threatened populations, but conventional stock assessment models assume the identification of self-sustaining populations that have negligible connectivity with other populations (Eagle *et al.,* 2008). Therefore, differences between population boundaries and spatial management units can pose a problem for achieving management objectives (Kerr *et al.,* 2017). For fisheries management purposes, stocks are considered discrete units, and each stock can be exploited independently (Cadrin *et al.,* 2014). One main assumption in a stock assessment is that the assessed stock is a closed population with little to no emigration from or immigration into the stock area (Hilborn and Walters, 1992). If this assumption is violated, the model results may be less accurate (Begg, 2004; Cope and Punt, 2011; Punt *et al.,* 2015; Goethel *et al,.* 2016; Jardim *et al.,* 2018) and these inaccuracies have led to several fishery management failures (Cadrin, 2020). Stock identification examines the unit stock assumption used in these assessments, which is an important aspect of any stock assessment.

Stock identification also plays an important role in species conservation. Conservation of threatened species requires the identification of biological populations, which are more precisely defined using an ecological paradigm (*e.g.*, “a group of individuals sufficiently isolated that immigration does not substantially affect the population dynamics or extinction risk over a 100-year time frame”) (Hanski and Gilpin, 1996) or an evolutionary paradigm (*e.g.*, “a group of interbreeding individuals that exist together in time and space”) (Hedrick, 2000; Waples and Gaggiotti, 2006). To evaluate species conservation status and extinction risk, it is necessary to account for all population components so that each can be conserved and recovered (Ryman *et al.,* 1995) while identifying any components that are ‘evolutionarily significant,’ such that their loss would be a permanent reduction in biodiversity (Waples, 1995). For example, stock identity is important for a species, or “distinct population segment,” being listed under the U.S. Endangered Species Act (Eagle *et al.,* 2008).

Managing highly migratory species is challenging because of their broad-scale movements across international jurisdictions (Campana, 2016; Harrison *et al.,* 2018). Due to the highly migratory behavior of many sharks, the identification of stock boundaries and the amount of mixing between adjacent stocks are important aspects to assure accurate assessments and management. However, stock identification of fish stocks and the exploration of alternative stock structures have often been historically ignored in stock assessments for teleost fish (Cadrin, *et al.,* 2014), and elasmobranchs and other data-limited species (Hammer and Zimmerman, 2014).

The interdisciplinary assessment of life-history traits, environmental signals, genetic analyses, and movement studies has been successfully used for several species (*e.g.*, Atlantic horse mackerel, *Trachurus trachurus*, Abaunza *et al.,* 2008; beaked redfish, *Sebastes mentella*, Cadrin *et al.,* 2010; yellowtail flounder, *Limanada ferruginea*, Cadrin 2010; winter flounder, *Pseudopleuronectes americanus*, DeCelles and Cadrin, 2011; Atlantic cod, *Gadus morhua*, Zemeckis *et al.,* 2014). The use of multiple data sources can be complementary and provides more certainty in the results. This is particularly important for data-limited elasmobranch species in which stock identity is typically based on simple life history characteristics and spatio-temporal information from fishery statistics (*e.g.*, seasonal and geographic patterns in landings; Begg, 2004). Results from these data-limited approaches can then help re-design future research for more definitive inferences of stock identity.

Although stock structure of porbeagle (*Lamna nasus*) has previously been examined (ICCAT/ICES, 2009; ICCAT, 2020; Curtis *et al.,* 2016), an interdisciplinary assessment of porbeagle can provide more holistic information about intraspecific stock structure and boundaries as there are still discrepancies of stock boundaries, biological populations, and management units between government and non-governmental organizations for stock assessment, fishery management and species conservation (Table 1). The porbeagle is distributed across the North Atlantic Ocean and Mediterranean Sea (Fig. 1). The distribution is considered to be continuous across the North Atlantic, with a discrete distribution in the southern hemisphere (Compagno, 2001; Semba *et al.,* 2013; Curtis *et al.,* 2016). Porbeagle is commonly found on continental shelves and shelf edges in relatively cold waters (<18˚C) (Campana *et al.,* 2002a; Skomal *et al.,* 2021). Porbeagles were first targeted by fisheries in the Northeast Atlantic in the 1920s, but the fishery was closed in 2010 due to overfishing (ICCAT/ICES, 2009). The much smaller Northwest Atlantic porbeagle fishery started in 1961, and both stocks were considered overfished in the 2009 and 2020 stock assessments (ICCAT/ICES, 2009). Few porbeagles have been caught in the Mediterranean (Ferretti *et al.,* 2008) and Mediterranean data are not included in porbeagle stock assessments, nor is there a separate stock assessment for Mediterranean porbeagle (ICCAT, 2020; Fig. 2)

As is typical of highly migratory species management, there are multiple national and international organizations, countries, and regions that take part in fishery management and conservation of porbeagle (Table 1). The International Council for the Exploration of the Sea (ICES) provides management advice on porbeagle fisheries in the Northeast Atlantic (excluding the Mediterranean), whereas the International Commission for the Conservation of Atlantic Tunas (ICCAT) collects data, reports annual catches, conducts stock assessments, and provides advice on tuna and tuna-like fisheries where porbeagle are caught in the entire North Atlantic and Mediterranean. The Northwest Atlantic Fisheries Organization (NAFO), a Regional Fisheries Management Organization (RFMO), is not regularly involved in the management of Northwest Atlantic porbeagle fisheries but has contributed with advice upon request in the past (Campana and Gibson, 2008). The Canada Department of Fisheries and Oceans (DFO) manages porbeagle fisheries in Canadian waters, and the U.S. National Marine Fisheries Service (NMFS) manages porbeagle fisheries in the United States. Northeast Atlantic fisheries are managed by the European Common Fisheries Policy in the European Union (E.U.) and by individual non-EU countries. The Northeast

Atlantic Fisheries Commission (NEAFC) is the RFMO for the Northeast Atlantic, and the General Fisheries Commission for the Mediterranean (GFCM) is the RFMO for the Mediterranean. In addition to these management organizations, there are several conservation organizations and treaties that are involved in the management and conservation of highly migratory sharks in the North Atlantic, and several nations have independent mandates for species conservation. There is presently little collaboration among management organizations, conservation organizations, and countries within regional organizations, and fisheries management varies greatly among European countries and between the U.S. and Canada (Campana, 2016; Cameron *et al.,* 2019). There are several examples in the last 20 years where management advice, management actions, and conservation actions for the same stocks have been uncoordinated and, in some cases, contradicting (Fig. 3).

Different stock definitions and boundaries among fishery management or conservation organizations can hinder the success of fishery management and the ability to achieve conservation goals. Therefore, refining the terminology and finding agreement on stock boundaries among parties for the North Atlantic porbeagle is expected to improve collaboration among parties and increase the effectiveness of fishery management, the performance of stock assessments and conservation assessments of this overexploited, highly migratory species. The objectives of this study were to 1) provide a comprehensive review of the information available on North Atlantic porbeagle stock structure using diverse stock identification approaches; 2) evaluate if current stock delineations reflect biological populations; and 3) consider the extent to which the misalignment of stock identification could impact stock assessments, conservation assessments, and management.

Table 1: Organizations involved with porbeagle conservation and management in the North Atlantic and their identified stocks, populations, and management units. Abbreviations: Convention on International Trade in Endangered Species (CITES), Canada Department of Fisheries and Oceans (DFO), International Union for the Conservation of Nature (IUCN), International Council for the Exploration of the Sea (ICES), International Commission for the Conservation of Atlantic Tunas (ICCAT), Northwest Atlantic Fisheries Organization (NAFO), National Oceanic and Atmospheric Administration (NOAA Fisheries).

Organization	Identified stocks, populations, or units	Source	Terminology used
CITES	1. Northwest Atlantic 2. Northeast Atlantic 3. Mediterranean Sea 4. Southwest Atlantic 5. Southern Ocean	CITES, 2013	Stocks
DFO	1. Northwest Atlantic	O'Boyle *et al.,* 1998; Campana *et al.,* 2012	Stock
IUCN	1. Northwest Atlantic 2. Northeast Atlantic 3. Mediterranean Sea 4. South Atlantic	Stevens *et al.,* 2006; Rigby *et al.,* 2018	Subpopulations in North Atlantic Metapopulation in South Atlantic/ Southern Ocean with an unknown number of subpopulations
ICCAT and ICES	1. Northwest Atlantic 2. Northeast Atlantic 3. Mediterranean Sea 4. Southwest Atlantic 5. Southeast Atlantic	ICCAT/ICES, 2009;	Stocks. Northeast Atlantic not including the Mediterranean Sea
ICCAT	1. Northwest Atlantic 2. Northeast Atlantic 3. Mediterranean Sea* 4. Southwest Atlantic 5. Southeast Atlantic	ICCAT, 2016; ICCAT, 2020	Management units; Stocks; Statistical areas
NAFO	1. Northwest Atlantic	Campana and Gibson, 2008	Stock
NOAA Fisheries	1. Northern Hemisphere 2. Southern Hemisphere 3. Northwest Atlantic	Curtis *et al.,* 2016	Distinct population segments; Stocks

* Mediterranean catches are reported in the most recent stock assessment, but 'left apart for future consideration' (ICCAT 2020).

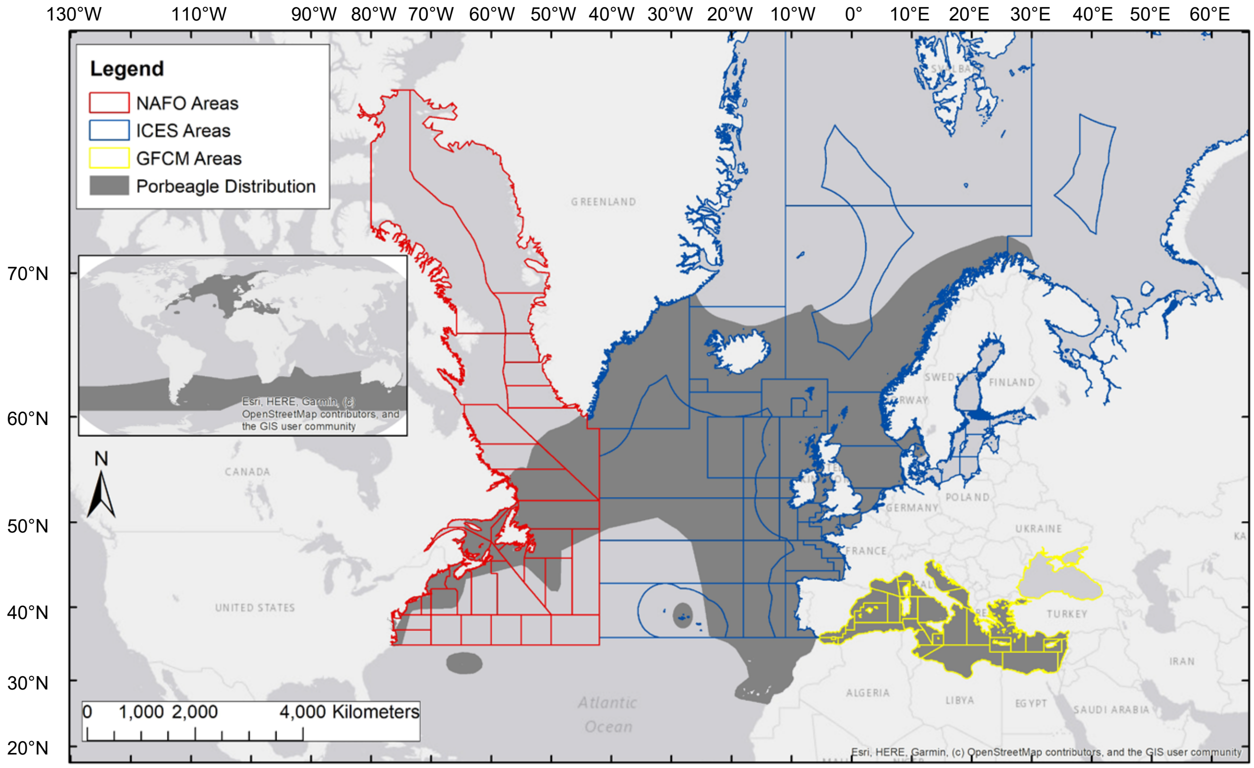

Fig. 1. Worldwide (insert) and North Atlantic distribution of porbeagle (grey www.iucnredlist.org) in relation to statistical reporting areas for the three regional management units. Discontinuous distributions in the North Atlantic result from data gaps and do not indicate discrete population segments.

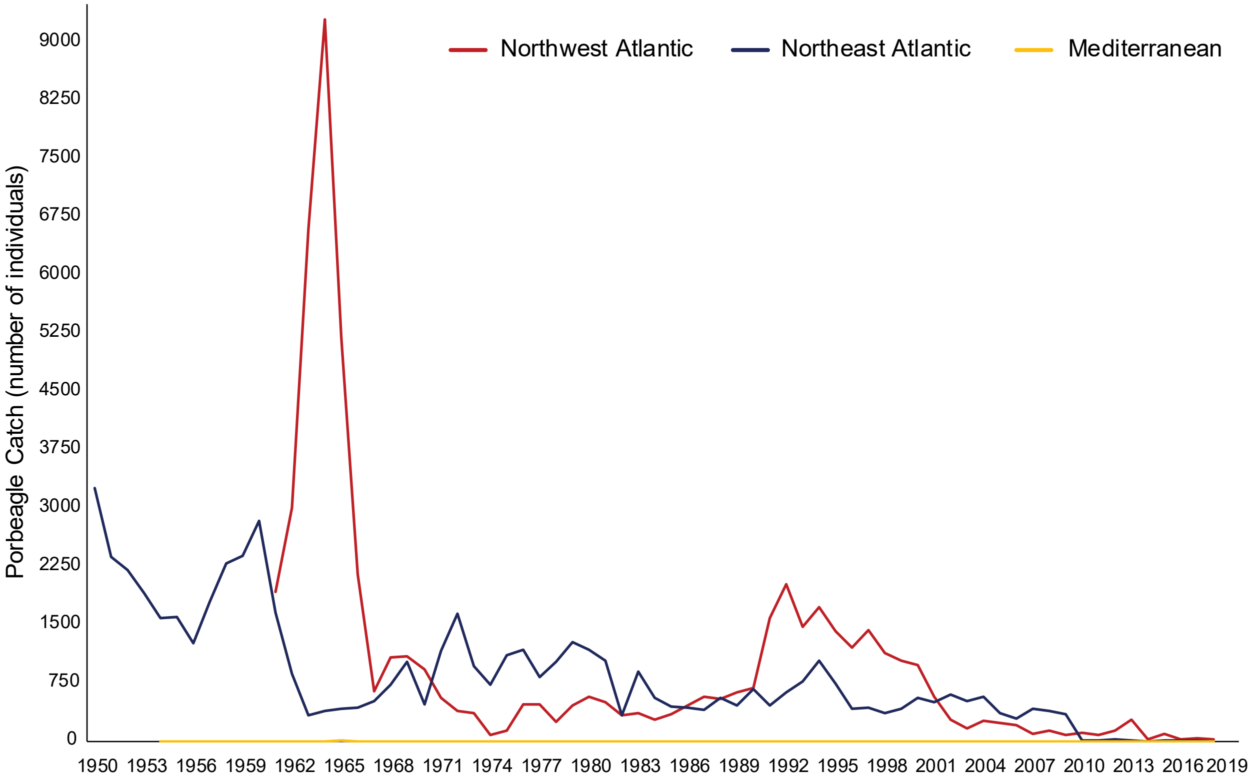

Fig. 2. Historical porbeagle catch in the Northwest Atlantic, Northeast Atlantic, and the Mediterranean regions. Data from ICCAT 2020.

Porbeagle Stock Identification Information

Genetic analyses

The investigation of genetic diversity within and among populations is valuable for species with depleted abundance like the porbeagle (Testerman, 2014). Both nuclear DNA and mitochondrial DNA analyses can be useful molecular techniques to identify stock structure (Antoniou and Magoulas, 2014; Mariani and Bekkevold, 2014). The population structure of porbeagle was investigated in the North and South Atlantic using the nucleotide sequence of mitochondrial DNA by (Kitamura and Matsunaga, 2010). Based on four sharks sampled off Nova Scotia and 49 sampled in the South Atlantic from 1992–2007, the authors found greater nucleotide diversity in the Nova Scotian samples. They attributed these findings to larger effective population size or different breeding populations in the North Atlantic (*e.g.*, Northwest and Northeast Atlantic breeding populations), noting that some of the tissue samples were >20 years old and porbeagle abundance was greater in the 1990s than when the samples were analyzed (Kitamura and Matsunaga, 2010). Kitamura and Matsunaga (2010) concluded that the gene flow of porbeagles between the North Atlantic and South Atlantic is restricted, and conservation efforts should consider them to be separate populations. However, with samples only in the Northwest Atlantic, this study could not infer any stock structure in the North Atlantic.

The genetic structure of porbeagles from the Northern and Southern hemispheres, including genetic differences within the North Atlantic, was further investigated by (Testerman, 2014). This study used a mitochondrial control region from 224 porbeagles collected at one site in the Northwest Atlantic ($n = 40$; off Canada), two sites in

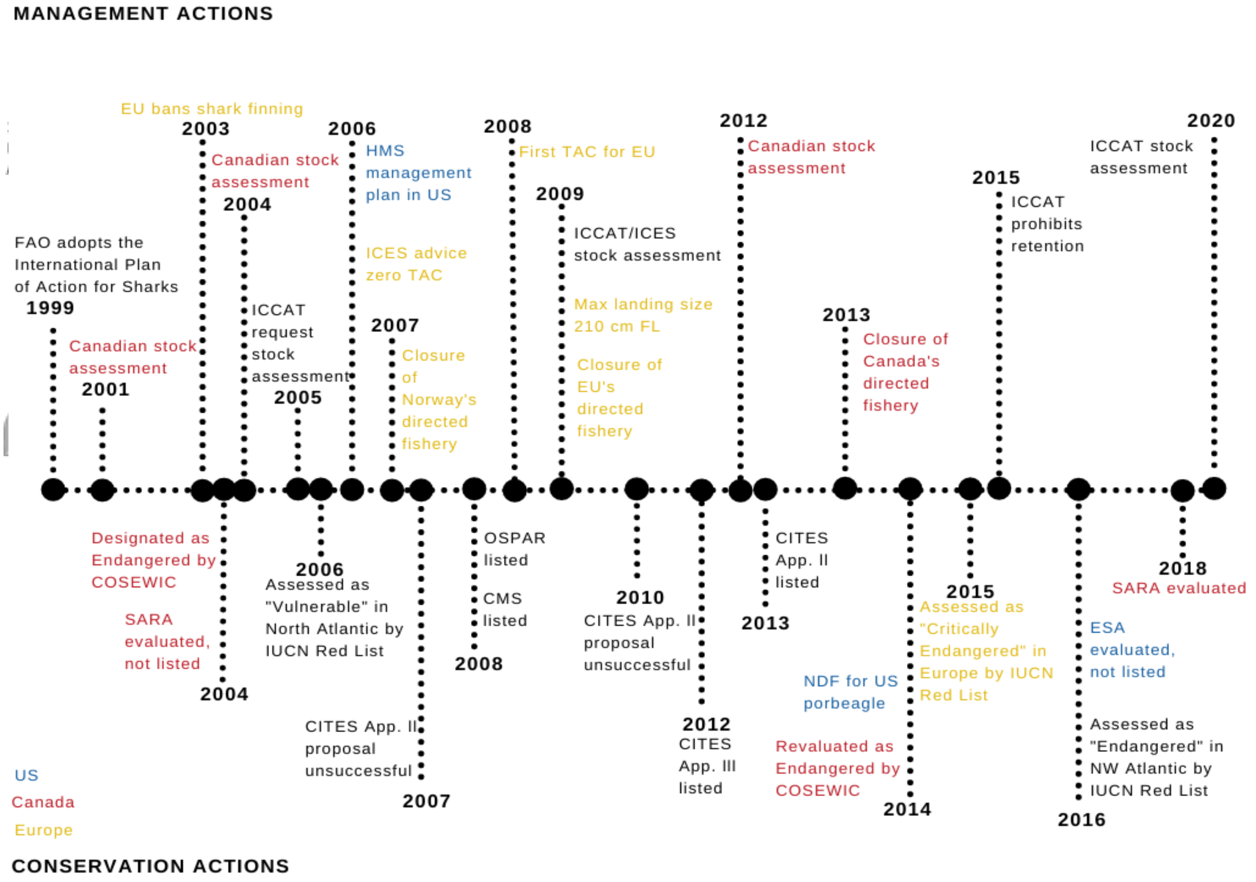

Fig. 3. Timeline of the development of major management (top) and conservation (bottom) actions related to porbeagle in the North Atlantic. Abbreviations: FAO: Food and Agriculture Organization, E.U.: European Union, COSEWIC: Committee on the Status of Endangered Wildlife in Canada, SARA: Species at Risk Act, ICCAT: International Commission for the Conservation of Atlantic Tunas, HMS: Highly Migratory Species, CITES: Convention on International Trade in Endangered Species, ICES: International Council for the Exploration of the Sea, TAC: Total Allowable Catch, FL: Fork length, OSPAR: Oslo-Paris Convention, CMS: Convention on Migratory Species, NDF: Non-Detrimental Finding, ESA: Endangered Species Act, IUCN: International Union for Conservation of Nature.

the Northeast Atlantic (*n* = 35; off Denmark and the United Kingdom), and five sites in the Southern hemisphere (*n* = 149; off Chile, the Falkland Islands, South Africa, Tasmania, and New Zealand). Similar to the results of Kitamura and Matsunaga (2010), Testerman (2014) found significant genetic differences and no genetic connectivity between the northern and southern hemispheres, and the results represented the greatest intraspecific genetic diversity for any shark species measured to date. Temperature preferences of porbeagle sharks (<18°C; Skomal *et al.,* 2021) suggest that equatorial seas are too warm for porbeagles, thereby forming a barrier between the hemispheres (Kitamura and Matsunaga, 2010; Testerman, 2014), although recent evidence suggests porbeagles may occupy equatorial waters (ICCAT, 2020). Other shark species that predominantly inhabit temperate waters transit the equator via deep tropical waters (*e.g.*, basking shark; Skomal *et al.,* 2009), genetic analyses from two studies using different genetic markers, when coupled with existing distribution and movement data (see below), suggest that porbeagle movement may be limited by warm equatorial surface waters.

Testerman (2014) also found no genetic differences between porbeagles sampled from the Northwest and Northeast Atlantic. Assuming a 13-year generation time, reproductive mixing by 2–12 migrating porbeagle sharks between the Northwest and Northeast Atlantic every year, or 30–150 migrants per generation, is sufficient gene flow for genetic structure to be of similar character (Testerman, 2014). A recent and more comprehensive analysis of mitochondrial DNA confirms two separate populations in the North Atlantic and southern hemisphere and no genetic structure within the North Atlantic (*n* = 70 northwest Atlantic, *n* = 99 northeast Atlantic, *n* = 2 Mediterranean markets; González *et al.,* 2021).

These results are indicative of an anti-equatorial distribution with genetically divergent northern and southern hemisphere stocks (Kitamura and Matsunaga, 2010; Testerman, 2014; González *et al.,* 2021). No genetic differences between porbeagles sampled in the Northwest and Northeast Atlantic have been found, but the genetic structure of this species in the Mediterranean is based on only two market samples with an unknown location of capture. There appears to be enough reproductive mixing across the Atlantic to promote gene flow, and the lack of genetic structure suggests that Northwest and Northeast Atlantic porbeagle are not reproductively isolated and may form a single evolutionary significant unit. However, a much greater mixing rate between the east and west might be needed to replenish depleted stocks (Waples, 1998). To improve the certainty of stock structure in the North Atlantic, genetic studies of porbeagle with samples from Canada and the U.S. in the Northwest Atlantic, in addition to samples from various locations in the Northeast Atlantic and the Mediterranean, should be analyzed in conjunction with other stock identification methods (*i.e.*, biological, conventional, and electronic tags).

Life-history traits

Life-history traits are one of the oldest tools used to inform management of a fishery resource, largely because they are relatively inexpensive and easy to sample (Begg, 2004). Therefore, life history attributes are generally the most accessible and robust information for data-limited species such as the porbeagle. The three groupings of life-history parameters that are commonly used for stock identification are 1) age, size, growth, and mortality; 2) reproduction, maturity, fecundity, and recruitment; and 3) spatial distribution and abundance (McBride, 2014). Many of these traits are routinely sampled for stock assessment and are available for stock identification. Life-history traits are phenotypic, so geographic variation can reflect genetic or environmental differences.

Growth and maturity

Although porbeagles are distributed across the North Atlantic, information on life-history traits varies greatly between regions. The Northwest Atlantic is relatively well-sampled, and there are some samples from the Northeast Atlantic but few samples from the Mediterranean (Table 2). Validated growth studies have been published for porbeagle in the Northwest Atlantic, but there are no comparable studies in the Northeast Atlantic. The former comprises two studies that sampled porbeagle from U.S. and Canadian waters, including lengths and vertebrae for age determination. Aasen (1963) sampled porbeagles in 1961 from Georges Bank, the Gulf of Maine, the eastern Scotian Shelf, and St. Pierre Bank, and Natanson *et al.* (2002) sampled between 1966 and 1999 from Massachusetts to the Grand Banks. Their growth estimates were similar (*e.g.*, estimates of asymptotic length were not significantly different). Vertebral band pair counts produced maximum ages of 25 and 24 years for males and females, respectively (Natanson *et al.,* 2002), which are similar to the maximum age estimated using bomb radiocarbon (26 years, Campana *et al.,* (2002b)). However, these could represent minimum estimates of longevity because of uncertainties in vertebral aging techniques (Natanson *et al.,* 2018); calculated longevity estimates were as high as 46 years in an unfished population (Natanson *et al.,* 2002).

Another metric that stock assessments rely on is size or age at maturity. The length at maturity for porbeagles in the Northwest Atlantic ranges from 173 to 216 cm total length (T.L.) for males (Aasen 1963; Jensen *et al.,* 2002) and 155 to 269 cm T.L. for females (Bigelow and Schroeder, 1948; Aasen 1963; Jensen *et al.,* 2002). The estimated size at 50% maturity of Canadian and U.S. porbeagle mature is 198 cm T.L. and 246 cm T.L. for males and females, respectively (Jensen *et al.,* 2002). Based on fewer observations, the porbeagle in the Northeast Atlantic matures at smaller sizes and reaches a smaller maximum size than those in the west (Table 2), and length at 50% maturity is 191 cm T.L. for males and 226 cm T.L. for females (Hennache and Jung, 2010). Age at maturity for porbeagle in the Northwest Atlantic is 13 years for females and 8 years for males (Jensen *et al.,* 2002; Natanson *et al.,* 2002), but there are no age estimates for comparison in the Northeast Atlantic.

Sex ratios

The reported sex ratios of porbeagle in the three regions of the North Atlantic were statistically tested for significant deviances from 1:1 the sex ratios using a G-test (Sokal and Rohlf, 2012). The proportion of males has been reported as 0.46 in the Northwest Atlantic ($n = 122$, Aasen, 1963), 0.43 in the Northeast Atlantic ($n = 1368$, Gauld, 1989), and 0.33 in the Mediterranean ($n = 15$, Storai *et al.,* 2005). Based on these data, all areas have female-biased sex ratios that significantly deviate from the expected 1:1 male: female ratio ($P < 0.01$). However, no significant differences were found among the three areas ($P = 0.25$). The Mediterranean has a low sample size compared to the other areas, but excluding the Mediterranean did not result in significant differences in sex ratios between the Northeast and Northwest ($P = 0.28$). Despite the significant female-bias in sex ratios within each population, the result may not be ecologically significant because the differences are relatively small. Further, as the data are fisheries-dependent, the detectable differences could be biased by the effort deployed, time of year, or area of operation of the fishery.

Although these results suggest that all regions in the North Atlantic (Northwest, Northeast, and Mediterranean)

Table 2: Life–history parameters for the porbeagle in the Northwest Atlantic, Northeast Atlantic, and the Mediterranean Sea. Lengths are reported as total length (T.L.). *Fork length reported in the source was converted to T.L. using https://apps–nefsc.fisheries.noaa.gov/loranconv/shark/calc.html.

Parameter	Northwest Atlantic	Source	Northeast Atlantic	Source	Mediterranean Sea	Source
Max length (cm T.L.)	M:262 F:~370 M:262 F:317	Compagno, 2001 ICCAT/ICES, 2009	M: 281* F: 312*	Gauld, 1989	M: min 206 F: min ~250	Storai *et al.,* 2005
Length at maturity (cm T.L.)	M:183–208* F: 236–360* M:173–216* F:216–269* F:155*	Jensen *et al.,* 2002; Aasen, 1963 Bigelow and Schroeder, 1948	M:190 F:223	Hennache and Jung, 2010		
Longevity (yr)	>26 M: 25 F: 24–46	Campana *et al.,* 2002b; Natanson *et al.,* 2002	>23	ICCAT/ ICES, 2009		
Gestation period (months)	8–9	Jensen *et al.,* 2002; Aasen 1963	>12	Gauld, 1989		
Mean litter size (pups)	3.9	Jensen *et al.,* 2002	3.7	Gauld, 1989		

have had sex ratios favoring female sharks, a more recent estimate in the Northeast Atlantic indicates that the overall male to female sex ratio has increased to 0.84 (Hennache and Jung, 2010). Male bias was apparent in certain locations, like the St. Georges Channel (male: female 0.84) in the Irish Sea and north in the Gulf of Gascogne (male: female 0.85). However, in the waters off the southern tip of Ireland, there were fewer females than males, with a sex ratio of 1.35 (Hennache and Jung, 2010). These areas are in close proximity, and the difference in sex ratios can be influenced by time of year and environmental conditions, particularly in conjunction with parturition. Porbeagles segregate by size and sex (Aasen, 1963; Compagno, 2001; Natanson *et al.,* 2019), so differences among sex ratio samples may not represent the population. Instead, these differences at specific locations can help identify important nursery areas in conjunction with movement studies.

Mating, gestation, and nursery areas

In the Northwest Atlantic, mating is thought to occur from September to December, the gestation period is estimated to be eight to nine months (Aasen, 1963; Jensen *et al.,* 2002), and parturition occurs between April and June (Aasen, 1963; O'Boyle *et al.,* 1998; Jensen *et al.,* 2002). Natanson *et al.* (2019) suggested that porbeagles have a biennial instead of an annual reproductive cycle based on the examination of ovaries, which were unlikely to be ready for a new litter in the fall after giving birth in the spring of the same year. In the Northeast Atlantic, Gauld (1989) inferred a mating season of December–January, a gestation period of >12 months based on two distinct size groups of embryos in females caught in December-February, and parturition in the summer/autumn. The mean number of embryos in each porbeagle litter was 3.7 pups in the Northeast Atlantic, which is similar to the reported mean litter size of 3.9 pups in the Northwest Atlantic (Gauld, 1989; Jensen *et al.,* 2002).

Parturition and nursery areas for North Atlantic porbeagle are not well understood. However, investigations of site fidelity from tagging studies, the capture of gravid females, and changes in sex ratios have improved our knowledge of locations for potential biologically important areas in the North Atlantic. In the Northwest Atlantic, the observation of mature, ovulating, or gravid females and females with mating scars from September–December on the Scotian Shelf and Grand Banks suggests that these areas are mating grounds for the porbeagle (Jensen *et al.,* 2002). Georges Bank has also been suggested as a mating ground-based on high catches of mature females in the summer (Campana *et al.,* 2010). However, Natanson *et al.* (2019) noted, with regard to that study, that no males were caught, biological samples were not collected, and these mature females were part of a reproductively resting population on Georges Bank. The Sargasso Sea south of 35°N has been suggested to be a parturition area based on seasonal north-south migrations undertaken by large females in the summer (Campana *et al.,* 2010). However, given the resting population of females in the Stellwagen/Georges Bank area and the lack of biological data, Natanson *et al.,* (2019) concluded that females do not migrate to the Sargasso Sea for pupping because they were only assumed to be gravid and did not transit mating grounds before moving south. Previous studies (Bigelow and Schroeder, 1948; Jensen *et al.,* 2002; Kohler *et al.,* 2002) and ongoing research in the Gulf of Maine indicate that pregnant females remain in the Gulf of Maine, and young-of-the-year porbeagles spend approximately the first two years of their lives in that area, where they make offshore migrations to the Gulf Stream in the winter, and move inshore in the summer (Skomal *et al.,* 2021; Anderson *et al.,* 2021).

In the Northeast Atlantic, recent studies suggest that porbeagles may use temperate waters in the Bay of Biscay as a potential nursery ground (Saunders *et al.,* 2011; Biais *et al.,* 2017). In the Mediterranean, an examination of 33 porbeagle caught in Italian waters from 1871–2004 revealed both juveniles and mature porbeagles (Storai *et al.,* 2005). The authors hypothesized that porbeagles do not reproduce in Italian waters but in other areas of the Mediterranean (Storai *et al.,* 2005). However, the Adriatic Sea has been interpreted as an important mating area (southern-middle open waters of the Adriatic Sea), pupping area (middle of the Adriatic Sea), and nursery area (middle-northern Adriatic Sea) areas based on size, sex, and maturity of the captured porbeagles (Soldo, 2006; Scacco *et al.,* 2012; Lipej *et al.,* 2016). A 104 cm T.L. male porbeagle was recently caught in December by fishermen in the northern Adriatic Sea, the first record of this species in Slovenian waters (Lipej *et al.,* 2016). These studies confirm the rarity of porbeagles in the Mediterranean but indicate that juvenile porbeagles are present in the Mediterranean throughout the year. Furthermore, the IUCN has suggested that the Mediterranean includes nursery areas for porbeagle with few adult sharks occupying the area year-round (Stevens *et al.,* 2006; Rigby *et al.,* 2018), and a recent review found no evidence that the Mediterranean porbeagle is isolated from the Northeast Atlantic (Curtis *et al.,* 2016), inferring that there is likely connectivity between these two regions. However, additional research is needed to address the questions of connectivity in the Northeast/Mediterranean and potential nursery areas for porbeagle in the North Atlantic.

Shark nursery areas are thought to be driven by factors such as food availability and shelter from predators (Branstetter, 1990). Heupel *et al.* (2007) suggested the following quantifiable criteria to delineate such areas: 1) a higher density of sharks than the surrounding areas; 2) the sharks remain or return for an extended period; and 3) the area is used repeatedly across years. No study to date has quantified porbeagle nursery areas in the North Atlantic using the suggested criteria, which help separate nursery areas from other areas where juvenile sharks have been documented to occur. Although there are several studies showing site fidelity and large porbeagle aggregations (*e.g.*, Pade *et al.,* 2009; Biais *et al.,* 2017; Haugen and Papastamatiou 2019), the occurrence of juvenile sharks or aggregating sharks in an area is not necessarily equivalent to a nursery area (Heupel *et al.,* 2007).

Collectively, these studies suggest similar rates of growth and maturation among areas but some minor differences in other reproductive traits, such as mating season, gestation period, and parturition between the western and eastern regions in the North Atlantic. As suggested by Curtis *et al.* (2016), porbeagles appear to be relatively uncommon in the Mediterranean, and it may represent a fringe of its Northeast Atlantic range. Most studies on phenotypic traits of porbeagle in the North Atlantic have focused on the Northwest Atlantic, with a data gap in life-history studies for the remaining regions. The life history information available for porbeagles in U.S. and Canadian waters suggests no difference between the two areas, suggesting that U.S. and Canadian porbeagles are part of the same biological population. However, none of the studies have explicitly investigated differences between Canadian and U.S. porbeagle, and most studies pooled samples from both countries.

Differences in size at maturity can be affected by fishing pressure. Cassoff *et al.* (2007) estimated the age at maturity for Northwest Atlantic porbeagle to be 8–7 years for males and 19–14 years for females when the population was unfished (1961–1963). The size at maturity of males decreased (from 179–174 cm curved fork length) after large declines in abundance due to fishing, but there was no change in female size at maturity (216 cm curved fork length) (Cassoff *et al.,* 2007). Therefore, morphological traits, such as size at a certain life stage, can vary between regions based on environmental conditions, like density dependence and selection. Although both sides of the Atlantic have experienced large declines in abundance, the Northeast Atlantic porbeagle has had much greater removals, which may explain some of the differences in growth between the east and west (ICCAT/ICES, 2009). The sample composition (*e.g.*, size range), capture location, time of year of sample collection, and aging methodology can also affect the outcome when sample sizes are small. Research to examine the differences in the abundance, age, size, growth, mortality, reproduction, maturity, fecundity, and recruitment of porbeagle in the Northeast Atlantic and Mediterranean is needed.

Movement and tagging information

Recoveries of conventional tags and information from electronic tags can be used to empirically determine mixing between groups of fish and to investigate dispersal and residency patterns. For highly migratory species, acoustic and satellite telemetry tags are particularly useful to assess movement between stocks, but electronic tagging information has historically rarely been used for stock identification purposes (DeCelles and Zemeckis, 2014).

Both satellite archival and conventional tags have been used to investigate porbeagle movement in the North Atlantic. Collectively, the published literature has information retrieved from 322 porbeagles tagged from 1961–2020 (total tagged = 3044; Table 3). The NMFS Cooperative Shark Tagging Program provides porbeagle data from the longest-running conventional shark tagging program (Kohler and Turner, 2020). Of 1754 porbeagles tagged in the Northwest and Northeast Atlantic during 1962–2013, 178 (9.8%) fish were recaptured (Kohler and Turner 2020). Several porbeagles were recaptured in a different nation's Exclusive Economic Zone than from where they were tagged (Fig. 4). The average tag deployment was three years, with a mean distance traveled of 424 km (Kohler and Turner, 2020). All of the conventional tagging studies conducted to date in the North Atlantic, representing 261 (8.8%) recaptures from 2971 tags, indicated site fidelity to the Atlantic region where the shark was tagged.

Pop-up satellite archival transmitting (PSAT) tags have been used to investigate migratory routes and habitat preferences of porbeagle in the Northwest Atlantic. PSATs attached to 17 porbeagles on Georges Bank showed minimum linear movements ranging from 937 to 3310 km over track durations of 120 to 360 days; all of the sharks remained in the western North Atlantic from the Gulf of Maine, the Scotian Shelf, on George's Bank, and in the deep, oceanic waters off the continental shelf along the edge of, and within, the Gulf Stream (Skomal *et al.,* 2021). The results indicated broad, seasonally-dependent vertical and horizontal movements of porbeagles in the Northwest Atlantic with most of their time (97%) in temperatures ranging from 6–20°C (Skomal *et al.,* 2021). This study also showed that porbeagles move routinely from the U.S. Exclusive Economic Zone (EEZ) into Canadian waters and that they spend a significant amount of their time in the high seas outside of any EEZ (Kohler and Turner, 2020; Skomal *et al.,* 2021; Fig. 5).

The only documented transatlantic crossing by a porbeagle was a female shark conventionally tagged in Irish waters in 1972 and recaptured on the Grand Banks outside of Canada ten years later, a distance of approximately 3300 km (Cameron *et al.,* 2018). The longest estimated travel distance for one shark in 365 days was 13–352 km (Biais *et al.,* 2017). In the Northeast Atlantic, multiple studies suggested short-term residency in coastal waters (*i.e.*, Celtic Sea, English Channel, Bay of Biscay) during the summer months and long-term site fidelity based on porbeagles returning to the same areas (Irish waters) for multiple years (Pade *et al.,* 2009; Saunders *et al.,* 2011; Biais *et al.,* 2017; Cameron *et al.,* 2019).

Tagging studies have also recorded porbeagle sharks moving near or past the current Northeast Atlantic jurisdictional boundaries. Out of nine sharks PSAT-tagged in the Bay of Biscay, one traveled south of the Northeast Atlantic stock border (36°N) to 33°N, while another tag popped off at 31°W close to the east/west boundary in the Atlantic (Biais *et al.,* 2017). Bendall *et al.* (2013) tagged 14 porbeagle sharks with PSAT tags around the British Isles, where two sharks made extensive movements from the tagging locations. One shark migrated south towards the Strait of Gibraltar, and the other traveled far west into the central Atlantic Ocean. The tag popped up at ~40°W, only 2° east of the western border between the Northwest and Northeast Atlantic, the furthest a tagged porbeagle has traveled from the U.K. (Bendall *et al.,* 2013). Out of three porbeagles (one male, two female) tagged Northwest of Ireland, the male porbeagle migrated south towards Morocco and past the southern boundary of the Northeast Atlantic management unit to 33°N (Saunders *et al.,* 2011). The shark was between Morocco and Madeira when the tag popped off. The two female sharks spent most of their time on the continental shelf outside of Western Ireland near a high abundance of Atlantic mackerel (*Scomber scombrus*) in the region.

Table 3: Movement studies of North Atlantic porbeagle. N.A. indicates not applicable or that information was not available in the source.

Tag type	#Fish Tagged	#Tags/ Data Retrieved	Location	Max Time at Liberty	Max Distance Travelled	Source
Conventional	8	0	Northeast Canada	NA	NA	Burnett *et al.,* 1987
Conventional	268	9	Ireland	10.8 yr	3300 km	Cameron *et al.,* 2018, 2019
Conventional	1754	178	Northwest Atlantic; Northeast Atlantic	16.8 yr	2252 km	Kohler and Turner, 2020
Conventional	26	8	Northeast Atlantic	13 yr	2370 km	Stevens, 1990
Conventional	3	0	Southern Coast of England	NA	NA	Kohler and Turner, 2001
Conventional	92	>1	Maine and Nova Scotia Northwest Atlantic	69 days	1259 km	Aasen, 1963
Conventional	8	0	Celtic Sea, north of Ireland, Bay of Biscay	NA	NA	Bendall *et al.,* 2013
Conventional	542	53	Northwest Atlantic	NA	NA	Campana *et al.,* 1999
Conventional	270	12	Northeast Canada	NA	NA	O'Boyle *et al.,* 1998
Archival	12	9	Bay of Biscay	1 yr	2408 km	Biais *et al.,* 2017
Archival	3	3	Ireland	122 days	>2400 km	Saunders *et al.,* 2011
Archival	4	4	Southwest United Kingdom	90 days	596 km	Pade *et al.,* 2009
Archival	20	17	Northeast USA	1 yr	8200 km	Skomal *et al.,* 2021
Archival	20	15	Celtic Sea, north of Ireland, Bay of Biscay	NA	NA	Bendall *et al.,* 2013
Archival	14	13	Northwest Atlantic	246 days	975 km	Anderson *et al.,* 2021

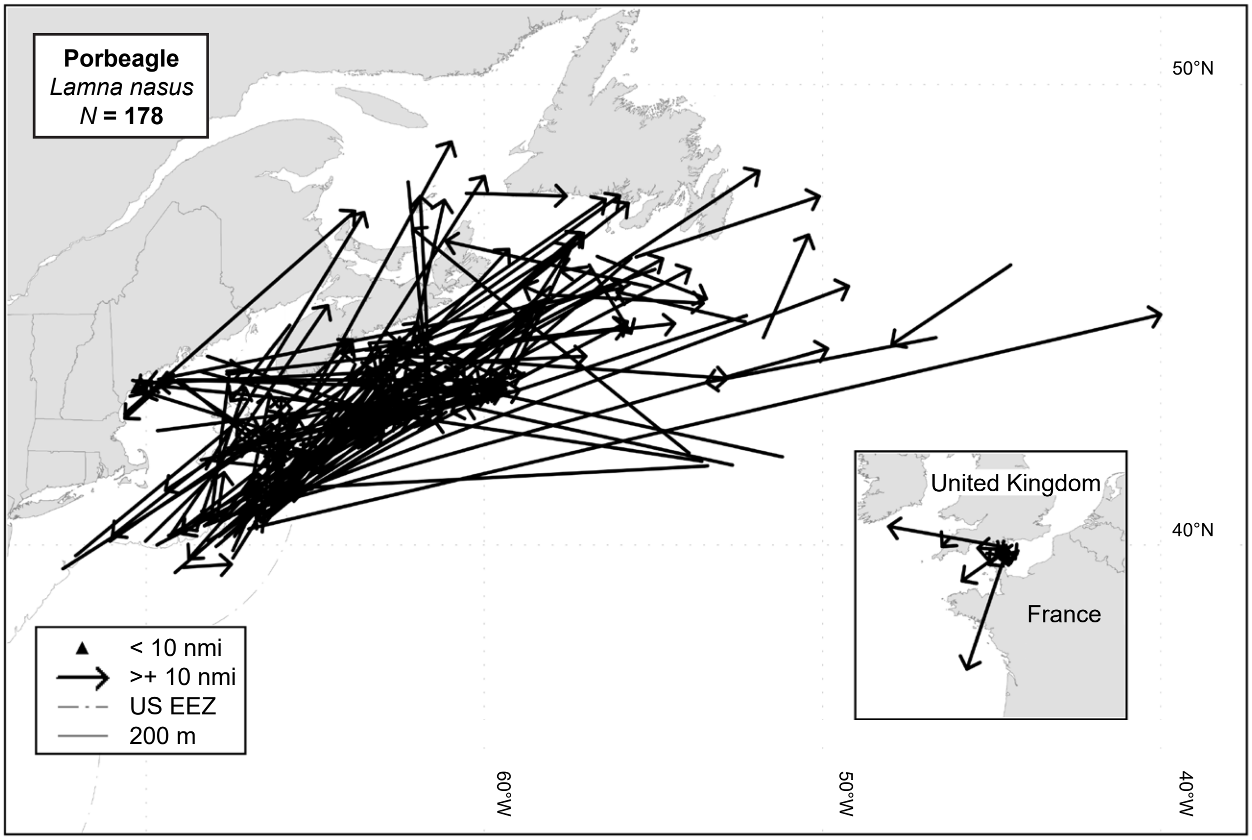

Fig. 4. Distribution of porbeagle tagged and recaptured in the Cooperative Shark Tagging Program 1962–2013. (Figure 31a from Kohler and Turner 2020).

Tagging studies confirm that porbeagles have large home ranges and are capable of long-distance migrations. Porbeagle distribution in the Northeast Atlantic ranges at least from the North Sea to Morocco and south of the entrance to the Mediterranean Sea, past the current management unit for the Northeast Atlantic porbeagle. Distribution in the Northwest Atlantic ranges from Canada to the Sargasso Sea, with several studies observing porbeagle movements between the U.S. and Canada. Information from tagging suggests a low rate of movement between the northeast and northwest Atlantic, with one porbeagle tagged in Irish waters and recaptured on the Grand Banks ten years later (Cameron *et al.,* 2018) from a total of 346 conventional tag recaptures (ICES, 2022), and location estimates from several archival tag deployments that indicate movement across the ICES-NAFO boundary (42°W) from porbeagle tagged in the Bay of Biscay (ICES, 2022) and off the British Isles (ICES, 2022). There are no observed movements between the Northeast Atlantic and Mediterranean, and a thermal habitat barrier may limit movement between those areas (ICES, 2022). To further investigate the mixing potential between the Northeast Atlantic and the Mediterranean, fine-scale movement patterns between the waters outside of Northwest Africa and the Mediterranean should be investigated.

Discussion

Interdisciplinary synthesis

Best practices in stock identification involve an interdisciplinary synthesis of all available information to determine the most plausible paradigms of population structure in which information from different approaches is integrated conceptually and geographically (Begg, 2004; Cadrin *et al.,* 2014). Information on distribution, movement, and geographic variation from advanced technologies can be reconciled with previous information from traditional methods to define spatial population structure. Considering all available information on life history, genetics, and movement of porbeagle in the North Atlantic, there appears to be a single genetic population of porbeagle in the Northern hemisphere, with a low frequency of transatlantic movements. However,

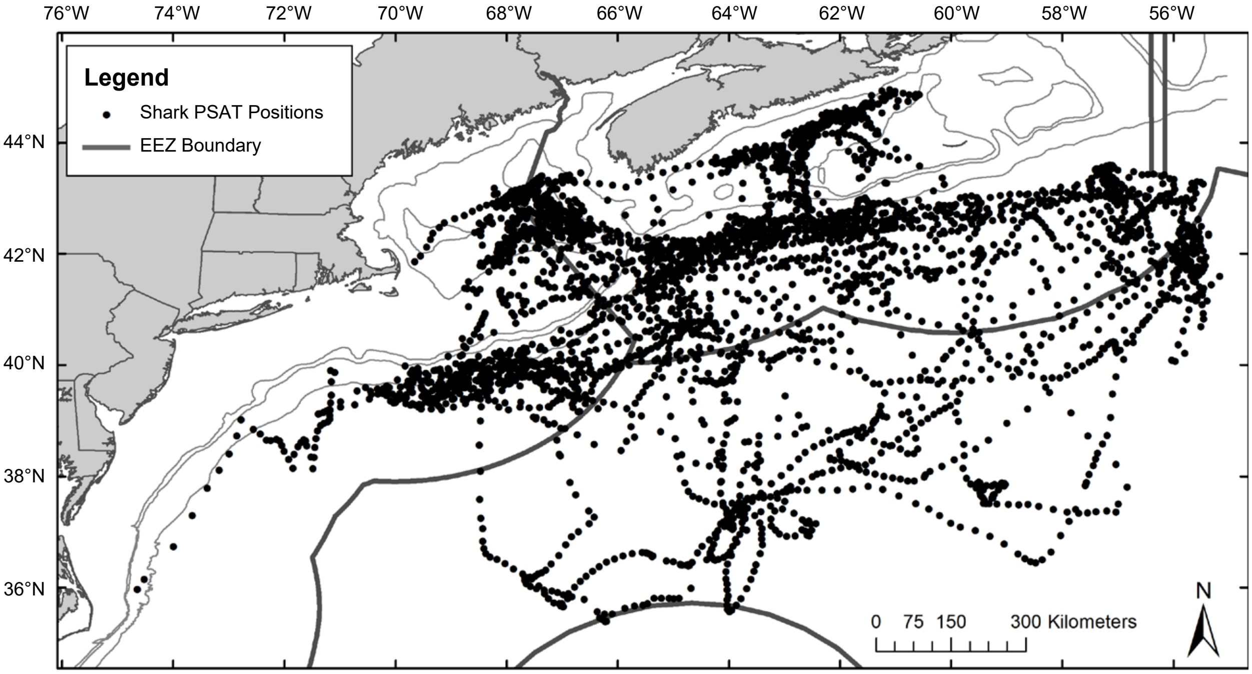

Fig. 5 PSAT positions from 17 porbeagles tagged by (Skomal *et al.* 2021) on the Northeast U.S. continental shelf and Exclusive Economic Zones for Canada and the U.S.

low movement rates and some phenotypic differences between the Northwest Atlantic and the Northeast Atlantic suggest two semi-distinct stocks that are demographically independent on ecological timescales. Therefore, the U.S. definition of a single distinct population segment in the North Atlantic (Curtis *et al.,* 2016) is consistent with the inference of a single genetic population. The Northeast Atlantic and Mediterranean management units defined by ICES/ICCAT, GFCM, CITES, and IUCN may not reflect the single biological population in the North Atlantic but may be appropriate for stock assessment and fishery management because of low mixing rates with the Northwest Atlantic areas. Similarly, the NAFO and Canadian definition of a Northwest Atlantic porbeagle stock (*e.g.*, Campana and Gibson 2008; Campana *et al.,* 2012) may be appropriate because of low mixing rates with the Northeast Atlantic.

The available information on porbeagle stock structure in the Northwest Atlantic indicates that U.S. and Canadian porbeagle are part of the same biological population. Life history traits suggest relatively homogeneous traits within the Northwest Atlantic and some differences with the Northeast Atlantic (*e.g.*, gestation period; Table 2). Possible nursery grounds for this population are in U.S. waters (Georges Bank and the Gulf of Maine) and Canadian waters (Scotian shelf and Grand Bank region). Substantial movement across the U.S. EEZ from multiple studies (Kohler and Turner, 2020; Skomal *et al.,* 2021), and no difference in life-history and genetics, indicates that porbeagles in the Northwest Atlantic are part of the same stock, as is currently assumed in NAFO, ICES, ICCAT, and Canadian stock assessments (Campana and Gibson, 2008; ICCAT/ICES, 2009; Campana *et al.,* 2015). There is currently no evidence of subpopulation structure within the Northwest Atlantic, although U.S. and Canadian fisheries have been managed differently over time.

There is no strong evidence of the stock identity of the Mediterranean porbeagle. Porbeagles are rarely encountered in the Mediterranean, but the area is part of their distribution. Therefore, hypotheses about the most likely stock structure in the Northeast Atlantic and the Mediterranean need to be tested with more information on geographic variation and mixing. Based on this review, particularly the Mediterranean genetic samples and Curtis *et al.* (2016), we hypothesize that the Mediterranean porbeagle is not a separate population from the Northeast Atlantic stock. We found no evidence that the Mediterranean porbeagle is a separate biological population or stock, as evaluated by CITES (CITES, 2013), and there are no indicators that IUCN's evaluation of the Mediterranean porbeagle as a subpopulation in the Northeast Atlantic is more appropriate. Observations of young of the year and mature sharks in the Mediterranean and the inference of a nursery ground for Northeast

Atlantic porbeagle imply some connectivity between the areas (Storai *et al.,* 2005; Soldo, 2006; Stevens *et al.,* 2006; Scacco *et al.,* 2012; Lipej *et al.,* 2016). Since there is no evidence of a separate Mediterranean porbeagle stock, we argue that there is no population structure in the Mediterranean unless evidence of structure is presented. Therefore, we suggest one biological population of porbeagle in the Northeast Atlantic with some sharks utilizing the Mediterranean habitat. However, the lack of observed movements and apparent thermal habitat barrier between the Northeast Atlantic and the Mediterranean Sea may justify separate stock assessment units (ICES 2022).

Mixing between Northwest and Northeast Atlantic

Empirical evidence from movement and tagging studies suggests that Northwest and Northeast Atlantic porbeagle mixing rates are low. There is only one observation of an individual shark making a transatlantic crossing from Ireland to Canada (Cameron *et al.,* 2018), a PSAT deployment from the British Isles suggested movement to the Flemish Cap (45°W; ICES, 2022), another PSAT tag deployed off Ireland in summer popped off in winter in the central Atlantic (Bendall *et al.,* 2013), and several PSAT tags deployed in the Bay of Biscay and the Celtic Sea had winter positions in the central Atlantic (ICES, 2022). Despite the few observed transatlantic movements, the species is capable of broad latitudinal migrations, and the distance between Europe and North America is within their observed movements. Although most published movement studies for North Atlantic porbeagle provide evidence for the separation of Northwest and Northeast Atlantic stocks, sample sizes were relatively small, and tracking was too brief (up to one year) to make general inferences on a population level. Larger sample sizes of returned tags from conventionally tagged porbeagles and an increased number of satellite-tagged porbeagles may reveal more transatlantic crossings.

There is no genetic evidence of separate stocks in the Northwest and Northeast, and few individuals making the transatlantic crossing every year would be needed for sufficient gene flow between the two regions (Testerman, 2014). Although there have only been a few transatlantic movements documented, tagging studies cannot alone determine with certainty that reproductive isolation exists. These migration numbers are based on estimated longevity; therefore, changes in longevity will impact the number of individuals needed to make transatlantic migrations each year to have sufficient gene flow for there to not be genetic differentiation of porbeagles in the North Atlantic (Testerman, 2014). More importantly, the low estimate of individuals crossing the Atlantic and reproducing on the other side per year is not likely enough for recruitment, recolonization, or rebuilding within fishery management or conservation timelines.

Movement studies indicated that porbeagles are capable of movements over great distances (Table 3), but the scope of the current tagging studies appears to be too small to empirically identify the mixing that would support the estimated gene flow. One possible mechanism for gene flow between the Northwest and Northeast Atlantic could be the result of a shared pupping area in the central Atlantic with random recruits to either side of the Atlantic Ocean (Campana *et al.,* 2010). However, this hypothesis requires further investigation, including improved delineation of parturition areas as well as movements of neonate porbeagles (Natanson *et al.,* 2019). Due to uncertainty in pupping and nursery areas, low gene flow and recruitment, limited movement studies, and some demographic independence in phenotypic traits between the Northwest and Northeast Atlantic, the use of one eastern and one western stock of North Atlantic porbeagle is appropriate.

Historical, current, and future management

Perceptions of appropriate spatial units for species conservation or fishery management vary among organizations involved in fisheries management and conservation of highly migratory sharks in the North Atlantic. Communication among organizations and consideration of all available information is needed to achieve a holistic view of the complexity of managing highly migratory sharks in the North Atlantic. An interdisciplinary approach to assessing the stock structure of porbeagle and other highly migratory sharks can provide increased certainty in the results since different approaches may provide results of the same magnitude (Cadrin *et al.,* 2014).

Despite the overwhelming evidence of a shared porbeagle stock between Canada and the U.S., fisheries management for the species has varied greatly between the countries over the years. Although Canada has harvested much larger quantities of porbeagle before the closure of their directed fishery in 2013, the U.S. has more consistently allowed low numbers of porbeagle to be harvested. Canada started exploiting porbeagle in the 1990s, provided descriptive stock assessments in the mid-1990s (Hurley, 1995; O'Boyle *et al.,* 1998), and provided an analytical assessment of porbeagle in 1999 (Campana *et al.,* 1999). The 1999 stock assessment produced a catch rate standardization model and yield per recruit analysis using landings, lengths, and tagging data from Norwegian, Canadian, and U.S. vessels in the Northwest

Atlantic. The main assumption (supported by the tagging data) was that the Northwest Atlantic porbeagle was one transboundary stock between the U.S. and Canada and international NAFO waters (NAFO areas 2-6; Campana *et al.,* 1999). Canada has since continued to produce assessments of porbeagle to inform Canadian management of the species. All Canadian assessments have assumed that U.S., Canadian, and NAFO porbeagle is one stock (Campana *et al.,* 1999, 2001, 2002a, 2012, 2015). The U.S. has not conducted its own stock assessment for porbeagle, but U.S. management and stock status determinations of the species have relied on the ICCAT/ICES (2009; 2020) stock assessments for Northwest Atlantic porbeagle. Current management strategies and quotas differ between the U.S. and Canada, so increased communication and collaboration between the country's management organizations (DFO and NMFS) and RMFOs would be beneficial for the success of shared conservation goals. For example, coordinated quotas could reduce recovery time for the current stock, better account for domestic bycatch, and prevent overfishing in the future. Coordinating management of the shared porbeagle stock would be seen as a precautionary approach to international management of a shared transboundary stock. According to ICCAT advice, which the U.S. follows for porbeagle fishery management, "precautionary management measures should be considered for shark stocks where there is the greatest biological vulnerability and conservation concern, and for which there are few data and/or greater uncertainty in assessment results" (ICCAT, 2015). Therefore, broader joint management of the resource should be considered, and the Northwest Atlantic porbeagle should continue to be assessed as one single transboundary stock in U.S., Canadian, and adjacent high seas waters.

The 2009 stock assessment of North Atlantic porbeagle did not include Mediterranean data (ICCAT/ICES, 2009), and the 2020 assessment included Mediterranean catches but set them apart for future consideration (ICCAT, 2020). Based on this comprehensive review of information available on the North Atlantic porbeagle stock structure, excluding the Mediterranean from the Northeast Atlantic porbeagle stock assessment may be a mismatch between biological population structure and management units in the Northeast Atlantic. Although there is little reported catch in the Mediterranean, and they are not expected to have a large influence on stock assessment results, this mismatch could negatively impact fisheries management. The justification given for excluding Mediterranean porbeagle data in the 2020 ICCAT stock assessment for Northeast Atlantic porbeagle was to follow the same format for stock boundaries and assessments as ICCAT does for blue shark (*Prionace glauca*) and shortfin mako (*Isurus oxyrinchus*) stock assessments (ICCAT, 2020). However, blue sharks and shortfin mako sharks have different life history characteristics and migration patterns compared to the porbeagle (Kohler *et al.,* 2002; Campana, 2016). As this review has shown, there is no biological or ecological justification to consider the Mediterranean porbeagle a separate stock from the Northeast Atlantic. Accurate stock identification can help reduce uncertainty in the stock assessment as more data may become available (*i.e.*, Mediterranean data) for the data-limited Northeast Atlantic porbeagle. Therefore, future stock assessments should consider the inclusion of catch and effort data on Mediterranean porbeagle from ICCAT and GFCM in the assessment of Northeast Atlantic porbeagle. Re-defining current management units to better reflect biological populations in the Northeast Atlantic would benefit porbeagle stock assessments and potentially reduce data collection requirements for each unit.

Given the current conservation and management situation for North Atlantic porbeagle (*i.e.*, very low commercial landings, CITES-listed), data availability is a limiting factor for future stock assessments and conservation assessments. Stock assessments rely on commercial fishery catch per unit effort (CPUE) time-series data when available and, in data-limited situations, age or length-frequency data to assess reference points, if the stock is overfished, and make predictions about levels of fishing mortality the stock can sustain in the future (Bowlby and Cortes, 2020; ICCAT, 2020). With few commercial porbeagle landings and inconsistent reporting of discards, obtaining representative CPUE series may be challenging, however, new assessment models have been explored (Bowlby and Cortes, 2020; Cortes *et al.,* 2020). Additionally, data collection from bycatch in fisheries not traditionally included in porbeagle stock assessments (*i.e.*, coastal bottom trawls and gillnets) and CPUE from recreationally caught porbeagle may help mitigate some of the data loss from current management and conservation regulations. With little data available, correct stock structure becomes more important as it can reduce data requirements in some situations (*i.e.*, Mediterranean as discussed above). These, and other, research recommendations were included in ICCAT's 2020 porbeagle assessment.

RFMOs provide the most appropriate processes for international stock assessments of highly migratory species like the porbeagle as they have the ability to unify countries and organizations to create a holistic overview of each species' biology, ecology, and data needs. While ICCAT, an RFMO focusing on Atlantic tuna fisheries, has been the main arena for highly migratory species stock assessments, other RFMOs such as NAFO, NEAFC, and GFCM could take a more prominent role to improve stock assessments of highly migratory species. For example, in the Northwest Atlantic, this would entail inviting the USA (NMFS), Canada (DFO), and the high seas fisheries (ICCAT) to the table for porbeagle stock assessments hosted by NAFO. In the Northeast Atlantic, a combined host of NEAFC and GFCM, inviting both ICES and ICCAT to contribute, would allow for a more complete assessment of the Northeast Atlantic porbeagle. Increased collaboration between these organizations would be beneficial for data collection, data inclusiveness (*i.e.*, non-tuna and non-pelagic fisheries), the robustness of assessments, and clarity for fishery managers, scientists, and the general public on porbeagle stocks and status.

The management structure of highly migratory species in the North Atlantic has several organizations (*i.e.*, NEAFC, NAFO, GFCM, E.U., ICES, NMFS, DFO, and ICCAT) working on advice, fisheries management, and conservation, and their different jurisdictions may not represent the biological populations of each highly migratory species. The need for an improved international management strategy has been suggested in previous studies (Campana, 2016; Cameron *et al.,* 2019). This review supports the conclusion of previous findings that increased collaboration between the fishery management organizations in the North Atlantic can contribute to improved management, assessments, and conservation of data-limited highly migratory species. Additionally, we provide clear evidence for the most likely stock structure of porbeagle in the North Atlantic and recommend international stock assessments of highly migratory species like the porbeagle to be hosted by overarching RFMOs. No single source of data can provide enough insight for a highly migratory and data-limited species, so interdisciplinary and interagency approaches are particularly well-suited for improving stock identification. Until more research is devoted to interdisciplinary stock identification of porbeagle, this review may serve as a starting point to achieve consistency in the number of stocks, biological population boundaries, and management units amongst organizations working with management, assessments, and conservation.

Acknowledgments

Thank you to Thomas Heimann, Alex Hansell, and Pingguo He, who provided valuable comments on earlier versions of this manuscript. This research was funded by the Andrew E. and G. Norman Wigeland Fund and the Stolt-Nielsen Fund via the American Scandinavian Foundation and the University of Massachusetts, Dartmouth. We would also like to thank the scientists in ICES, WGEF, and WKELASMO that provided valuable information and the reviewers and editor for their constructive feedback and guidance in improving the quality of the final manuscript.

References

Aasen, O. 1963. Length and growth of the Porbeagle (*Lamna nasus*, Bonnaterre) in the North West Atlantic. Fiskeridirektoratets Havforskningsinstitutt 20–37.

Abaunza, P., Murta, A. G., Campbell, N., *et al.* 2008. Considerations on sampling strategies for an holistic approach to stock identification: The example of the HOMSIR project. *Fisheries Research*, **89**: 104–113. https://doi.org/10.1016/j.fishres.2007.09.020

Anderson, B., Bowlby, H., Natanson, L., *et al.* 2021. Preliminary estimate of post-release survival of immature porbeagles caught with rod-and-reel in the Northwest Atlantic Ocean. *Mar. Ecol. Prog. Ser.* **660**: 153–159. https://doi.org/10.3354/meps13603

Antoniou, A., and Magoulas, A. 2014. Application of mitochondrial DNA in stock identification. *In*: S.X. Cadrin, L.A. Kerr, and S. Mariani (Eds.), Stock Identification Methods: Applications in Fisheries Science, 2nd ed., p. 257–285. Elsevier Academic Press, London. https://doi.org/10.1016/B978-0-12-397003-9.00013-8

Begg, G. A. 2004. Life history parameters. *In*: S.X. Cadrin, K.D. Friedland, and J.R. Waldman (Eds.), Stock Identification Methods: Applications in Fishery Science, 1st ed.. Elsevier Academic Press, London, p. 119–150. https://doi.org/10.1016/B978-012154351-8/50007-1

Bendall, Victoria, J., Ellis, Jim R., Hetherington, Stuart J., *et al.* 2013. Preliminary observations on the biology and movements of porbeagle (*Lamna nasus*) around the British Isles. *Collect. Vol. Sci. Pap. ICCAT*, **69**: 1702–1722

Biais, G., Coupeau, Y., Séret, B., *et al.* 2017. Return migration patterns of porbeagle shark (*Lamna nasus*) in the Northeast Atlantic: implications for stock range and structure. *ICES Journal of Marine Science*, **74**: 1268–1276. https://doi.org/10.1093/icesjms/fsw233

Bigelow, H. B., and Schroeder, W. C. 1948. Fishes of the Western North Atlantic. Part 1. Lancelets, cyclostomes, sharks. *Mem. Sears Found. Marine Research*. https://doi.org/10.2307/j.ctvbcd08p.6

Bowlby, H. D., and Cortes, E. 2020. An incidental catch model for porbeagle assessment and status evaluation

Cadrin, S. X. 2010. Interdisciplinary Analysis of Yellowtail Flounder Stock Structure off New England. *Reviews in Fisheries Science*, **18**: 281–299. https://doi.org/10.1080/10641262.2010.506251

Cadrin, S. X. 2020. Defining spatial structure for fishery stock assessment. *Fisheries Research*, **221**: 105397. https://doi.org/10.1016/j.fishres.2019.105397

Cadrin, S. X., Bernreuther, M., Danielsdottir, A. K., *et al.* 2010. Population structure of beaked redfish, *Sebastes mentella*: evidence of divergence associated with different habitats. *ICES Journal of Marine Science*, **67**: 1617–1630. https://doi.org/10.1093/icesjms/fsq046

Cadrin, S. X., Kerr, L. A., Mariani, S. 2014. Stock Identification Methods: An Overview. *In* S.X. Cadrin, L.A. Kerr, and S. Mariani.(Eds.), Stock Identification Methods: Applications in Fisheries Science. 2nd ed. p. 1–5 Elsevier Academic Press, London. https://doi.org/10.1016/B978-0-12-397003-9.00001-1

Cameron, L. W. J., Roche, W., Green, P., *et al*. 2018. Transatlantic movement in porbeagle sharks, *Lamna nasus*. *Fisheries Research*, **207**: 25–27. https://doi.org/10.1016/j.fishres.2018.05.014

Cameron, L. W. J., Roche, W. K., Houghton, J. D. R., and Mensink, P. J. 2019. Population structure and spatial distribution of porbeagles (*Lamna nasus*) in Irish waters. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsz046

Campana, S. E. 2016. Transboundary movements, unmonitored fishing mortality, and ineffective international fisheries management pose risks for pelagic sharks in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.*, **73**: 1599–1607. https://doi.org/10.1139/cjfas-2015-0502

Campana, S. E., Fowler, M., Houlihan, D., *et al.* 2015. Recovery Potential Assessment for Porbeagle (*Lamna nasus*) in Atlantic Canada

Campana, S. E., and Gibson, J. 2008. Catch and Stock Status of Porbeagle Shark (*Lamna nasus*) in the Northwest Atlantic to 2007. *NAFO SCR Doc.* 08/36. Serial No. N5537

Campana, S. E, Gibson, J., Fowler, M., *et al.* 2012. Population dynamics of Northwest Atlantic porbeagle (*Lamna nasus*), with an assessment of status and projections for recovery. *Canadian Science Advisory Secretariat Research Document*, 2012/096

Campana, S. E., Joyce, W., and Fowler, M. 2010. Subtropical pupping ground for a cold-water shark. *Can. J. Fish. Aquat. Sci.*, **67**: 769–773. https://doi.org/10.1139/F10-020

Campana, S. E., Joyce, W., Marks, L., *et al.* 2002a Population Dynamics of the Porbeagle in the Northwest Atlantic Ocean. *North American Journal of Fisheries Management*, **22**: 106–121. https://doi.org/10.1577/1548-8675(2002)022%3C0106:PDOTPI%3E2.0.CO;2

Campana, S. E., Joyce, W., Marks, L., Harley, S. 2001. Analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic, with estimates of long-term sustainable yield. *Canadian Stock Assessment Research Document*, 2001/067.

Campana, S. E., Marks, L, Joyce W, *et al.* 1999. An analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic. *Canadian Stock Assessment Research Document*, 1999/158.

Campana, S. E. , Natanson, L. J., Myklevoll, S. 2002b. Bomb dating and age determination of large pelagic sharks. *Can. J. Fish. Aquat. Sci.*, **59**: 450–455. https://doi.org/10.1139/f02-027

Cassoff, R. M., Campana, S. E., and Myklevoll, S. 2007. Changes in baseline growth and maturation parameters of Northwest Atlantic porbeagle following heavy exploitation. *Can. J. Fish. Aquat. Sci.*, **64**: 19–29. https://doi.org/10.1139/f06-167

CITES, 2013. Proposal for inclusion of *Lamna nasus* (Bonnaterre, 1788) in Appendix II in accordance with Article II 2(a).

Compagno, L. J. 2001. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Bullhead, mackeral and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes), FAO Species Catalogue for Fishery Purposes No. 1, **Vol. 2,** 269p.

Cope, J. M., and Punt, A. E. 2011. Reconciling stock assessment and management scales under conditions of spatially varying catch histories. *Fisheries Research*, **107(1–3)**, 22–38. https://doi.org/10.1016/j.fishres.2010.10.002

Cortes E, Bowlby, H. D., Carlson, J., *et al.* 2020. Preliminary sustainability assessment for fishing effects (SAFE) of pelagic longline fisheries on porbeagle sharks and identification of F-based biological reference points

Curtis, T. H., Laporte, S., Cortes, E, DuBeck, G., and McCandless, C. 2016. Status review report: Porbeagle Shark (*Lamna nasus*). Final Report to National Marine Fisheries Service, Office of Protected Resources. February 2016. 56p.

DeCelles, G. R., and Cadrin, S. X. 2011. An Interdisciplinary Assessment of Winter Flounder (*Pseudopleuronectes americanus*) Stock Structure. *J. Northw. Atl. Fish. Sci.*, **43**: 103–120. https://doi.org/10.2960/J.v43.m673

DeCelles, G. R., and Zemeckis, D. R. 2014. Acoustic and radio telemetry. *In*: S.X. Cadrin, L.A. Kerr, and S. Mariani (Eds.), Stock Identification Methods: Applications in Fisheries Science, 2nd ed., p. 397–428. Elsevier Academic Press, London. https://doi.org/10.1016/B978-0-12-397003-9.00017-5

Eagle, T. C., Cadrin, S. X., Caldwell M. E., *et al.* 2008. Conservation units of managed fish, threatened or endangered species, and marine mammals. *NOAA Technical Memorandum* NMFS-OPR-37, p. 108

Gauld, J. 1989. Records of porbeagles landed in Scotland, with observations on the biology, distribution and exploitation of the species. Scottish Fisheries Research Report Number 45, p. 16

Goethel, D. R., Kerr, L. A., and Cadrin, S. X. 2016. Incorporating spatial population structure into the assessment–management interface of marine resources. *In*: C.T.T. Edwards and D.J. Dankel. (Eds.), Management science in fisheries: an introduction to simulation-based methods. New York, p. 319–347

González, M. T., Sepúlveda, F. A., Zárate, P. M., *et al.* 2020. Regional population genetics and global phylogeography of the endangered highly migratory shark Lamna nasus: Implications for fishery management and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* **31: 3** 620–634. https://doi.org/10.1002/aqc.3455

Hammer, C., and Zimmerman, C. 2014. The Role of Stock Identification in Formulating Fishery Management Advice. *In*: Cadrin, S.X., Friedland, K.D., and Waldman, J. (Eds.), Stock Identification Methods. Elsevier Academic Press, p. 631–658. https://doi.org/10.1016/B978-012154351-8/50031-9

Hanski, I., and Gilpin, M. 1996. Metapopulation Dynamics, Ecology, Genetics, and Evolution. Academic Press, New York

Harrison, A.-L., and Costa, D. P., Winship, A. J., *et al.* 2018. The political biogeography of migratory marine predators. *Nat. Ecol. Evol.*, **2**: 1571–1578. https://doi.org/10.1038/s41559-018-0646-8

Haugen, J. B., and Papastamatiou, Y. 2019. Observation of a porbeagle shark (*Lamna nasus*) aggregation at a North Sea oil platform. *J. Fish. Biol.*, **95(6)** 1496–1499. https://doi.org/10.1111/jfb.14149

Hedrick, P. W. 2000. Genetics of Populations, 2nd ed. Jones and Bartlett, Sudbury, Massachusetts.

Hennache, C., and Jung, A. 2010. Étude de la pêche palangrière de requin-taupe de l'ile d'Yeu. Association pour l'étude et la conservation des sélaciens (APECS).

Heupel, M., Carlson, J., and Simpfendorfer, C. 2007. Shark nursery areas: concepts, definition, characterization and assumptions. *Mar. Ecol. Prog. Ser.* **337**: 287–297. https://doi.org/10.3354/meps337287

Hilborn, R., and Walters, C. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York

ICCAT. 2020. Report of the 2020 porbeagle shark stock assessment meeting. 15–22 June 2020.

ICCAT. 2015. Recommendation by ICCAT on porbeagle caught in association with ICCAT fisheries. Rec 15-06.

ICCAT/ICES. 2009. Report of the 2009 porbeagle stock assessment meeting

ICES. 2022. Benchmark workshop for selected elasmobranch stocks (WKELASMO). February (online) 2022.

Jardim, E., Eero, M., Silva, A., *et al.* 2018. Testing spatial heterogeneity with stock assessment models. PLoS ONE 13:e0190791. https://doi.org/10.1371/journal.pone.0190791

Jensen, C., Natanson, L. J., Pratt, H., *et al.* 2002. The reproductive biology of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Fishery Bulletin*, **100**: 727–738

Kitamura, T., and Matsunaga, H. 2010. Population structure of porbeagle (*Lamna nasus*) in the Atlantic Ocean as inferred from mitochondrial DNA control region sequences. *Collective volume of scientific papers International Commission for the Conservation of Atlantic Tunas*, **65**: 2082–2087.

Kohler, N, Turner, P. A, Hoey, J. J, *et al.* 2002. Tag and recapture data for three pelagic shark species, blue shark (*Prionace glauca*), shortfin mako (*Isurus oxyrinchus*), and porbeagle (*Lamna nasus*) in the North Atlantic Ocean. *Collective volume of scientific papers International Commission for the Conservation of Atlantic Tunas*, **54**: 1231–1260.

Kohler, N. E., and Turner, P. A. 2020. Distributions and Movements of Atlantic Shark Species: A 52-Year Retrospective Atlas of Mark and Recapture Data. *Marine Fisheries Review*, **81**: 1–93. https://doi.org/10.7755/MFR.81.2.1

Lipej, L., Uhan, J., Mavrič, B., and Vujčić-Karlo, S. 2016. A record of porbeagle, *Lamna nasus* (Bonnaterre, 1788), in the Gulf of Trieste with discussion on its occurrence in the Adriatic Sea. *Acta Adriatica*, **57**: 305–314

Mariani, S., and Bekkevold, D. 2014. The nuclear genome: Neutral and adaptive markers in fisheries. *In*: S.X. Cadrin, L.A. Kerr, and S. Mariani (Eds.), Stock Identification Methods: Applications in Fisheries Science, 2nd ed., p. 297–320. Elsevier Academic Press, London. https://doi.org/10.1016/B978-0-12-397003-9.00014-X

McBride, R. S. 2014. The continuing role of life history parameters to identify stock structure. *In*: S.X. Cadrin, L.A. Kerr, and S. Mariani (Eds.), Stock Identification Methods: Applications in Fisheries Science, 2nd ed., p.77–96. Elsevier Academic Press, London. https://doi.org/10.1016/B978-0-12-397003-9.00005-9

Natanson, L. J., Deacy, B. M., Joyce, W., and Sulikowski, J. 2019. Presence of a resting population of female porbeagles (*Lamna nasus*), indicating a biennial reproductive cycle, in the western North Atlantic Ocean. *Fishery Bulletin*, **117**: 70–77. https://doi.org/10.7755/FB.117.1-2.8

Natanson, L. J., Mello, J., and Campana, S. E. 2002. Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. *Collect. Vol. Sci. Pap. ICCAT*, **54**: 1261–1279

Natanson, L. J., Skomal, G. B., Hoffmann, S. L., *et al.* 2018. Age and growth of sharks: do vertebral band pairs record age? *Mar. Freshwater Res.*, **69**: 1440. https://doi.org/10.1071/MF17279

O'Boyle, R. N., Fowler, G. M., and Hurley, P. C. F., *et al.* 1998. Update on the status of NAFO SA 3-6 porbeagle shark, *Lamna nasus*. *Canadian Stock Assessment Secretariat Research Document*, 98/41.

Pade, N. G., Queiroz, N., Humphries, N. E., *et al.* 2009. First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology*, **370**: 64–74. https://doi.org/10.1016/j.jembe.2008.12.002

Punt, A. E., Haddon, M., and Tuck, G. N. 2015. Which assessment configurations perform best in the face of spatial heterogeneity in fishing mortality, growth and recruitment? A case study based on pink ling in Australia. *Fisheries Research*, **168**: 85–99. https://doi.org/10.1016/j.fishres.2015.04.002

Rigby, C.L., Barreto, R., and Carlson, J., *et al.* 2018. *Lamna nasus*: The IUCN Red List of Threatened Species 2019 Global

Ryman, N., Utter, F., and Laikre, L. 1995. Protection of intraspecific biodiversity of exploited fishes. *Rev. Fish. Biol. Fisheries*, **5**: 417. https://doi.org/10.1007/BF01103814

Saunders, R. A., Royer, F., and Clarke, M. W. 2011. Winter migration and diving behaviour of porbeagle shark, *Lamna nasus*, in the Northeast Atlantic. *ICES Journal of Marine Science*, **68**: 166–174. https://doi.org/10.1093/icesjms/fsq145

Scacco, U, Consalvo, I., DiMuccio, S., and Tunesi, L. 2012. On the by-catch of two porbeagle sharks *Lamna nasus* in the central Adriatic Sea. *Mar. Biodivers. Rec.* **5**: e61. https://doi.org/10.1017/S1755267212000127

Semba, Y., Yokawa, K., Matsunaga, H., and Shono, H. 2013. Distribution and trend in abundance of the porbeagle (*Lamna nasus*) in the southern hemisphere. *Mar. Freshwater*

Res., **64**: 518. https://doi.org/10.1071/MF12272

Skomal, G., Marshall, H., Galuardi, B., *et al.* 2021. Horizontal and vertical movement patterns and habitat use of juvenile Porbeagles (*Lamna nasus*) in the Western North Atlantic. *Front. Mar. Sci.*, **8**: 624158. https://doi.org/10.3389/fmars.2021.624158

Skomal, G. B., Zeeman, S. I., Chisholm, J. H., *et al.* 2009. Transequatorial Migrations by Basking Sharks in the Western Atlantic Ocean. *Current Biology*, **19**: 1019–1022. https://doi.org/10.1016/j.cub.2009.04.019

Sokal, R. R., Rohlf, F. J. 2012. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co. New York.

Soldo, A. 2006. Status of the sharks in the Adriatic. *In*: N., Basusta, C. Keskin, F. Serena and B. Seret (Eds.), The proceedings of the International Workshop on Mediterranean Cartilaginous Fish with Emphasis on Southern and Eastern Mediterranean, Istanbul, Turkey, p. 128–134

Stevens, J. D., Fowler S.L., Soldo, A, *et al.* 2006. *Lamna nasus* (Northwest Atlantic population). In IUCN Red List of Threatened Species

Storai, T., Celona, A., Zuffa M., and De Maddalena, A. 2005. On the occurrence of the porbeagle, *Lamna nasus* (Bonnaterre, 1788) (Chondrichthyes: Lamnidae), off Italian coasts (northern and central Mediterranean Sea): A historical survey. *Annales Ser. Hist. Nat.*, **15**: 195–202.

Testerman, C. B. 2014. Molecular Ecology of Globally Distributed Sharks. Doctoral dissertation.

Waples, R. S. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. *In*: Nielsen J.L. (Ed.), Evolution and the aquatic ecosystem: defining unique units in population conservation, American Fisheries Society, Bethesda, MD., p. 8–27.

Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, **89**: 438–450. https://doi.org/10.1093/jhered/89.5.438

Waples, R. S., and Gaggiotti O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity: *Molecular Ecology,* **15**: 1419–1439. https://doi.org/10.1111/j.1365-294X.2006.02890.x

Zemeckis, D. R., Martins, D., Kerr L. A., and Cadrin S. X. 2014. Stock identification of Atlantic cod (*Gadus morhua*) in U.S. waters: an interdisciplinary approach. *ICES Journal of Marine Science*, **71**: 1490–1506. https://doi.org/10.1093/icesjms/fsu032

J. Northw. Atl. Fish. Sci., Vol. 53: 19–34 Publication (Upload) date: 08 Aug 2022

Review of tagging studies on Atlantic herring (*Clupea harengus*) in relation to transboundary movement in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic

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Tobin-van den Heuvel, G.A., van den Heuvel, M.R, Deroba, J.J., and Barrett, T.J. 2022. Review of tagging studies on Atlantic herring (*Clupea harengus*) in relation to transboundary movement in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic. *J. Northw. Atl. Fish. Sci.*, **53**: 19–34. https://doi.org/10.2960/J.v53.m734

Abstract

The management of Atlantic herring in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic (NAFO areas 4WX5YZ) assumes separate stocks in Canadian and US waters; however, herring landed in the weir fishery in southwest New Brunswick (SWNB) are assumed to be of US origin for management purposes. The present study is a review of tagging studies that have been conducted on herring since the 1950s in NAFO areas 4WX5YZ. The tagging data show consistent patterns over time. Juvenile herring in the coastal Gulf of Maine and SWNB nursery areas generally show only movements between these two areas. These nursery areas are believed to include herring that hatched from the US and Canadian spawning grounds, contrary to the current management assumption for the weir fishery in SWNB. As herring mature, they are understood to primarily return to their natal spawning area. The tagging data show mixing of adults from different spawning grounds (including transboundary mixing) during the summer feeding and overwintering seasons. Canadian spawners have been observed to overwinter in New England and US spawners have been observed to overwinter in Nova Scotia. Herring tagged on Canadian spawning grounds have been recaptured in the SWNB weir fishery, refuting the assumption that all herring landed in this fishery are of US origin. The tagging data suggest that the weir fishery comprises a mix of herring hatched from spawning grounds in Canada and the US. The biases associated with recapture data from tagging programs precludes estimation of any proportions of stock mixing. Alternative methods for evaluating stock structure in NAFO areas 4WX5YZ are recommended.

Keywords: juvenile herring; migration; overwintering; stock structure; weir fishery

Introduction

Stock structure of Atlantic herring (*Clupea harengus*; hereafter, herring) is complex and stocks have generally been defined in the Western Atlantic based on Northwest Atlantic Fisheries Organization (NAFO) divisions (Melvin *et al.,* 2009). Stock in this context refers to a group of fish sufficiently isolated from other groups so as to allow for fisheries management. Each stock has multiple spawning areas that result in reproductively isolated subpopulations and there is mixing among adjacent stocks during feeding and overwintering migrations (McQuinn, 1997; Stephenson *et al.,* 2009). Each stock spawns in specific locations at known times (Geffen, 2009; Melvin *et al.,* 2009). The assumption that herring exhibit spawning-area fidelity (Stobo, 1982; McQuinn, 1997) has been the basis of the definition of herring stocks and fisheries management (Stephenson *et al.,* 1993), but the degree of natal homing versus genetic exchange among spawning assemblages within a metapopulation remains a source of uncertainty (Brophy *et al.,* 2006; Stephenson *et al.,* 2009). Herring stock structure for fisheries management in the Bay of Fundy/Gulf of Maine/Scotian Shelf region of the Northwest Atlantic (NAFO areas 4WX5YZ) is complicated by the life history of herring, where annual long distance migrations occur to adult feeding and overwintering areas where there is overlap of multiple sub-populations from different spawning areas (Stephenson *et al.,* 2009). In NAFO areas 4WX5YZ, at least seven major spawning areas have been characterized (Fig. 1). The timing of spawning varies from May to November with the degree of spring spawning increasing with latitude, but the majority of spawning (~90%) occurs in autumn (Wuenschel and Deroba, 2019). These spawning time differences (spring vs. autumn) provide a further basis for reproductive stock separation (Melvin *et al.,* 2009).

The Canadian herring fishery in NAFO areas 4VWX5YZ is managed as five different units: Southwest Nova Scotia/Bay of Fundy (SWNS/BoF), offshore Scotian Shelf, coastal Nova Scotia (NS), Southwest New Brunswick (SWNB) “migrant juveniles” (nearshore fishery), and Georges Bank. The SWNS/BoF management area makes up the majority (75% over the last 10 years) of the 4VWX landings (DFO, 2020a). The SWNS/BoF herring fishery is managed by an annual total allowable catch (TAC). The SWNB “migrant juvenile” fishery (hereafter, “SWNB weir fishery”) overlaps spatially with the SWNS/BoF management unit, but consists only of nearshore landings by weir, trap nets, and shut-offs in SWNB. The SWNB weir fishery is effort controlled and the landings are not included towards the TAC for the SWNB/BoF management unit (DFO, 2020b).

The SWNB weir fishery landings are primarily juveniles and for decades have been assumed for management purposes to be dominated by “migrant juveniles” from the Gulf of Maine (GoM) and Georges Bank spawning

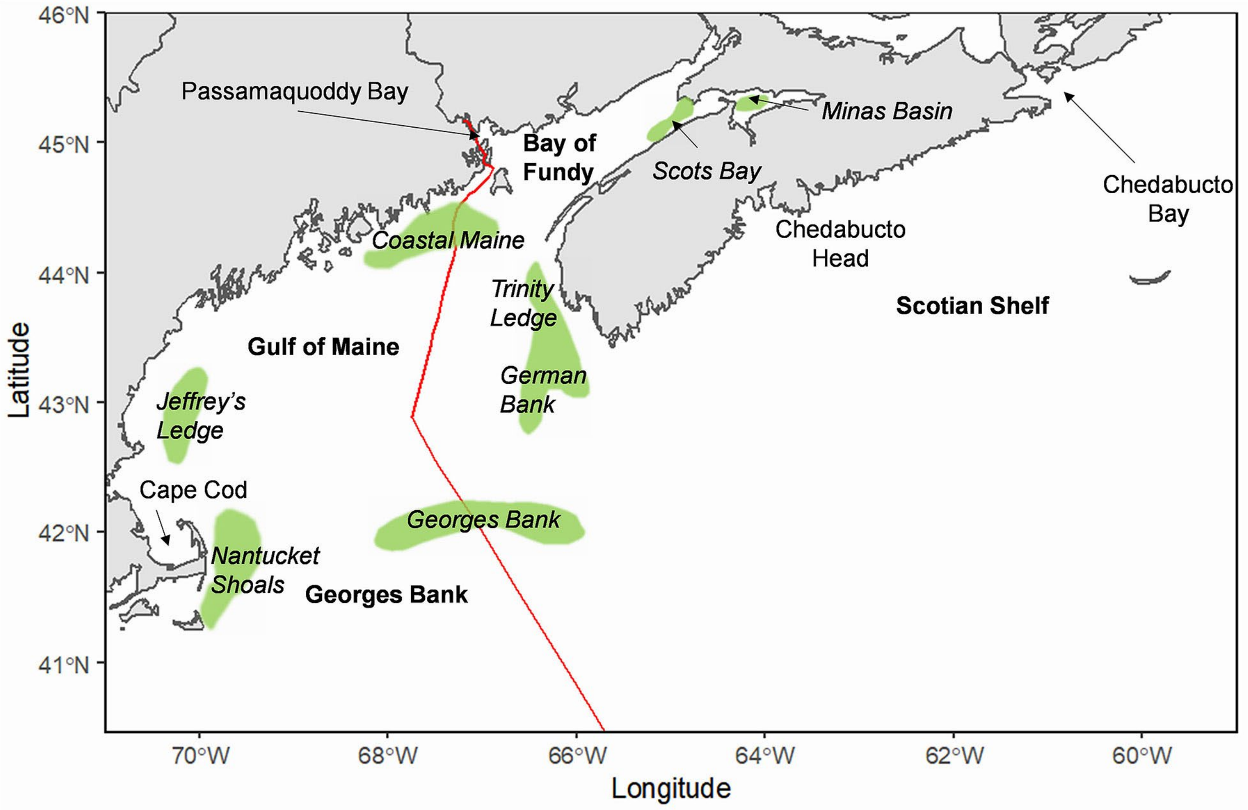

Fig. 1. Map of the study area showing the Bay of Fundy, Gulf of Maine, Scotian Shelf and areas referenced in this review. Major spawning areas in green based on Stephenson *et al.* (1993) although there are spatial variations in the spawning areas reported in other studies (*e.g.*, Waring 1981; Tupper *et al.* 1998; Overholtz *et al.* 2004; Stephenson *et al.* 2009). The Canada/US border is in red.

components of the US stock (Stephenson *et al.,* 1993; DFO, 1999, 2000; NFSC, 2012). This assumption dates back to at least the 1970s when it was hypothesized that juvenile abundance in SWNB may indicate future recruitment to the Georges Bank fishery (ICNAF, 1973). The assumption listed in the 1999 Fisheries and Oceans Canada (DFO) stock status report for NAFO areas 4VWX5Z herring was that all juvenile herring from the SWNB weir fishery originate from the US coastal complex which at the time was considered at high abundance (DFO, 1999). In the most recent 4VWX assessment, all juvenile and adult herring landed in the SWNB weir fishery are excluded from the SWNS/BoF TAC and assumed, although not explicitly stated, to originate from the US spawning components (DFO, 2020a).

The US herring fishery in NAFO areas 5YZ is managed as four different units. Quota management begins with the specification of a stock-wide, annual, overfishing limit (OFL) that corresponds to the catch that would result from applying the fishing mortality rate associated with maximum sustainable yield or a proxy. The OFL is then reduced to account for scientific uncertainty, which results in the annual, allowable biological catch (ABC). The ABC is further reduced to account for management uncertainty, which results in the stock-wide, annual catch limit (ACL). The SWNB weir catches are assumed to be fish from the US stock, but the effort controls used to manage the SWNB weir fishery can create fluctuations in catch that are difficult to anticipate. To account for these fluctuations during US quota setting, a recent (usually 10 year) average of the SWNB weir catches is subtracted from the ABC as part of management uncertainty, resulting in the ACL. The stock-wide ACL is then subdivided into four management areas with the intention of avoiding overfishing in each sub-stock. The biomass of the US stock has decreased in recent years and the ABC has been reduced such that the SWNB weir catches have approached 50% of the ABC. The assumption of the SWNB weir catches being US fish now has a strong influence on ACLs.

The scientific characterization of herring stocks and management units in NAFO areas 4WX5YZ has been almost exclusively examined through tagging studies for the past several decades (*e.g.*, ICNAF, 1976; Stephenson *et al.,* 1993; DFO, 2007; NFSC, 2012). The number of herring tagged in NAFO areas 4WX5YZ exceeds 750 000 individuals. Tagging studies have focused on both nearshore juvenile herring, overwintering herring, and spawning adults. Tagging studies have used a wide variety of gear and fisheries for capture and recovery and an equally diverse array of timing and duration of study. The present study is a synthesis of all data to date on tagging studies in NAFO areas 4WX5YZ to address two main objectives related to the management of herring fisheries: 1) evaluate the assumption that herring landed in the Canadian weir fishery in SWNB are of US origin, and 2) evaluate transboundary movement and the degree of movement of herring among management units in NAFO areas 4WX5YZ.

Materials and Methods

Data from tagging studies in NAFO areas 4WX5YZ were assembled and synthesized. The studies consisted of peer-reviewed publications, government reports, and unpublished data. The synthesis of tagging study data presented a number of challenges due to the age/life-stage tagged, varying geographic resolution, duration of each study, capture methods, inconsistencies in return collection, and inconsistencies in calculation of the reporting metrics. In order to provide an interpretable synthesis of these data, all tagging and recapture locations were reassigned to consistent geographic zones. Spawning areas are distinct and given the importance of spawning areas in defining populations, these were included in the geographic resolution (each tag return area typically held a distinct spawning area). Wherever possible, the boundaries of the NAFO areas were used as the initial basis of tagging zones (Fig. 2). One of the objectives of this study relates to transboundary movement so the Canada-US border was used to define tagging area boundaries (Fig. 2, shown in red). The exception to this is in the area of the disputed "gray zone" were the 4X5Y NAFO boundary was used to delineate zones and the Canadian portion of Georges Bank was included in the Georges Bank zone. As NAFO area 4X encompasses a number of distinct herring spawning areas, the tagging boundary designations IX and X agreed upon by the US National Marine Fisheries Service and DFO (Stobo, 1982, Creaser *et al.,* 1984) were used to distinguish SWNB (X), the upper BoF (IX) from the remainder of NAFO area 4X. While scientists have agreed upon 14 tagging zones (Creaser *et al.,* 1984), six of which are in the GoM, these were largely aggregated within the NAFO areas to simplify results for the purposes of this review. Given the geographic scope of this review and the rarity of far northern and eastern tag recoveries, NAFO areas 4VW were considered as one zone. The resultant divisions provide seven geographic zones for evaluation of tagging data. These geographic zones are referred to as New England, encompassing the area to the southwest of 5Z (5Zw and 6), Georges Bank (5Z) which encompasses both Georges Bank and Nantucket Shoals spawning zones, GoM (5Y), which encompasses the Jeffery's Ledge and Coastal Maine spawning areas, SWNB (4X-X) into which the Coastal Maine spawning area extends and includes

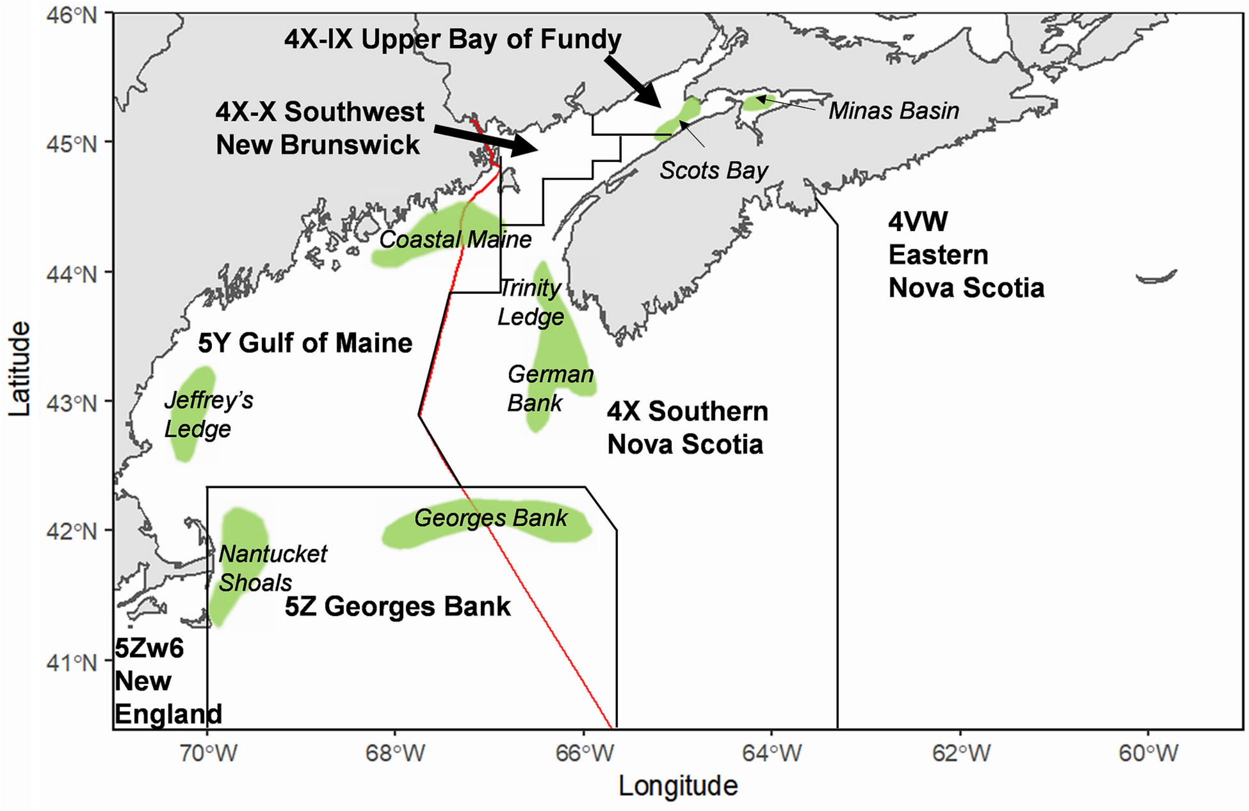

Fig. 2. Map showing the seven tagging zone delineations based on NAFO area divisions. The Canada/US border is in red. Major spawning areas in green based on Stephenson *et al*. (1993) although there are spatial variations in the spawning areas reported in other studies (*e.g.*, Waring 1981; Tupper *et al*. 1998; Overholtz *et al*. 2004; Stephenson *et al*. 2009).

the SWNB weir fishery, upper BoF (4X-IX) that has the Scots Bay and Minas Basin spawning areas, Southern NS (remainder of 4X) with the German Bank and Trinity Ledge spawning areas, and Eastern NS (4VW; Fig. 2).

Although tagging studies included multiple tagging locations within a geographic zone, the tagging locations were aggregated to one of the seven geographic zones. Each study is reported by the zone for which the tags were applied. Dates of recapture and time at large are important in the evaluation of individual studies, these vary substantially from study to study and are reported for each study to aid in interpretation of the tag return data. Tagging studies often use an effective recovery time period (*e.g.*, number of days) when presenting results because tagging efforts are likely to recapture tagged individuals within short periods after tagging. The effective recovery time period reported for each study is the initial period of time during which recaptures are ignored in the results. For the studies in this review, this varied from 0 to 14 days and could not be adjusted to a consistent value. The percentage of tag recoveries reported in the results are the effective recoveries and ignore the recaptures before the effective recovery time period.

Results

Herring movement in the Bay of Fundy and Gulf of Maine 1957 and 1958

The movement of immature herring was examined in the southern part of the BoF and the western part of the GoM in 1957 and 1958 (McKenzie and Tibbo, 1961). Results of the 1957 tagging studies were also reported in McKenzie and Scud (1958) and McKenzie and Tibbo (1958) but are reported for the combined study (McKenzie and Tibbo, 1961). All herring were obtained from nearshore weirs and seines and were implanted with opercular tags. The overall mean length of herring tagged in 1958 was 14.1 cm and was thought to represent age 1 to 3 (juvenile) herring.

Herring were tagged at 42 locations and more than half of those locations were located in SWNB. Two sampling locations (Loring Cove and Gleason Cove) were in

US waters but within Passamaquoddy Bay (Fig. 1), so were considered in the SWNB zone, consistent with the geographic zones defined in other tagging studies in the GoM (*e.g.*, Creaser and Libby, 1988). Effective recovery time was not applied to recapture data, so a significant proportion of recaptures were in the initial weeks after tagging. Tagging was conducted between March and October in each year and more than 95% of recaptures were within eight weeks of tag deployment. The total duration of recapture efforts was approximately six months. Herring were also tagged at two locations in Southern NS. Of the 1 126 herring tagged in NS, none were recovered. Of 73 188 tags applied in SWNB, 2 644 (3.6% recovery) tags were recovered with 99.8% of recaptures in SWNB and only 0.2% in GoM (Table 1). Of the 26 786 herring tagged south of the US-Canadian border, 146 (0.55% recovery) tags were recovered with 91.1% in GoM and only 8.9% in SWNB (Table 1). In both Maine and New Brunswick, a general northerly pattern of movement was observed and herring were typically recaptured in locations in close proximity to initial capture (approximately one-third recaptured within 20 km).

Juvenile herring movement along Coastal Maine 1960

Watson (1963) tagged 8 303 juvenile herring between May and October 1960 along the Maine coast (GoM) using spaghetti tags. The average time to recovery was 18 days, and no effective recovery time was used. Recaptures were reported up to September 1962 and 109 tag returns (94% of recoveries) were in GoM and 7 tag returns (6.0% of recoveries) in SWNB (Table 1). The longest distance between mark and recapture was approximately 90 km and the longest recovery time was 391 days.

Movements of mixed (juvenile/adult) herring tagged in the Bay of Fundy 1973–1974

A total of 24 140 herring were tagged near Grand Manan (November to December 1973 and June 1974) and Campobello Island (July 1974) using T-bar anchor tags or dart tags (Stobo *et al.,* 1975; Stobo, 1976). Fish tagged in 1973 were from the purse seine fishery and in 1974 from the weir fishery. The length range was 13 to 30 cm and included juvenile and adults. An effective recovery time of 14 days was used and tagging returns

Table 1. Summary of tag returns (percentage of returns by zone) from studies that tagged only juvenile herring. Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded.

Reference	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	1957–58	1957–58	73 188	2 644	3.6	0			0.2	99.8			
1	1957–58	1957–58	26 786	146	0.55	0			91.1	8.9			
1	1957–58	1957–58	1 126	0	0	0						0	
2	1960	1960–62	8 303	116	1.4	0			94.0	6.0			
3	1976–78	1976–80	4 463	17	0.38	14			82.4	17.6			
4	1976–78	1976–81	37 664	1 642	4.4	14		0.3	96.5	3.0		0.2	
4	1976–78	1976–81	3 700	107	2.9	14	1.0			98.1	1.0		
5	1980–82	1980–84	48 324	1 973	4.1	14			98.5	1.4		0.1	
5	1981–82	1981–84	9 635	260	2.7	14			3.7	95.5		0.8	
6	1982	1983–85	7 161	97	1.4	14				100			
6	1983	1983–85	7 923	61	0.77	14			92.3	7.7			
7	1999	1999–03	1 389	4	0.28	Unknown			75.0	25.0			
7	1999–02	1999–03	27 818	389	0.95	Unknown		0.4	1.5	89.1	0.4	7.9	0.8
8	2002–04	2002–04	76 957	1 986	2.6	4	0.2	0.1	1.3	93.1	1.2	4.2	
8	2003–04	2003–04	1 230	4	0.33	4				25.0		75.0	

[1]McKenzie and Tibbo 1961, [2]Watson 1963, [3]Waring 1981, [4]Creaser *et al.* 1984, [5]Creaser and Libby 1988, [6]Creaser and Libby 1986, [7]Mouland *et al.* 2003, [8]Waters and Clark 2005.

were reported until March 1976. The return rate was 4.2% (1 020 tags) with 94.1% in SWNB, just under 3% in each of GoM and Southern NS, and 0.3% in each of Eastern NS (overwintering in Chedabucto Bay) and Georges Bank (Table 2).

Herring movement of spawning and overwintering life stages in the Gulf of Maine and Georges Bank 1976–1978.

From 1976 to 1978 adult herring collected from fixed gears were tagged in US waters in both the GoM and Georges Bank and juveniles were tagged in coastal Maine area using T-bar anchor tags (Waring, 1981). Tagging was primarily conducted from September to November for spawning adults, May for migrating/overwintering fish, and February or August for juveniles and tag returns were recorded in all months of the year. Tags were recovered in fish processing plants in Canada, the US, and Europe and tagging results were combined across years. Recoveries were reported after 14 days (effective recovery time) after tagging until the end of 1980.

Herring tagged in spawning condition were recaptured in adjacent areas, although recaptures from Georges Bank were low due to a fishery closure at the time making estimates unreliable (Table 3). Of 29 693 tags applied to GoM spawning herring, there were 302 recaptures (~1% recovery) with 97.3 % of the recaptures in GoM and less than 1.7% migrating north to SWNB, and 1% south to New England (Table 3). For Georges Bank tags, the effective recovery was 0.05% of 30 346 tags with returns from only Georges Bank (82.4%) and GoM (17.6%).

Herring tagged in May that were assumed by Waring (1981) to be migrating/overwintering showed a substantially different pattern of movement than herring tagged in spawning condition. Of the 10 973 herring tagged in the GoM, there were 509 recaptures (4.6% recovery rate) with approximately half of the recaptures in GoM with the next highest percentage (35.4%) captured in SWNB and the remaining recaptures were in New England or NS, as far north as Chedabucto Bay, NS (an overwintering area) (Table 2). No herring tagged in the Georges Bank zone in May (tagged in the Great South Channel and assumed by Waring (1981) to be migrating/overwintering) were recaptured on Georges Bank, likely due to the absence of a fishery at the time. Most of the recaptures from the Georges Bank tagging were in the GoM zone, though there were recaptures in SWNB, Southern NS, and New England.

Of 4 463 juvenile herring tagged in Coastal Maine, the effective recovery was 0.38% with 82.4% of recoveries in GoM and 17.6% in SWNB (Table 1).

Table 2. Summary of tag returns (percentage of returns by zone) from studies that tagged mixed (adult/juvenile) herring or herring identified as overwintering (OW), summer feeding adults (A–Feed), or autumn migrating adults (Mig). Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded.

Reference	Group	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	Mixed	1973–74	1973–76	24 140	1 020	4.2	14		0.3	2.5	94.1		2.8	0.3
2	OW	1976–78	1976–80	10 973	509	4.6	14	0.8		50.5	35.4		12.8	0.6
2	Mixed	1976–78	1976–80	22 882	268	1.2	14	5.2	0	84.3	8.2		2.2	
3	Mixed	1976–78	1976–81	4 800	177	3.7	14	0.7		93.3	5.9			
3	A–Feed	1976–78	1976–81	11 723	475	4.1	14	2.7		67.4	26.1	0.2	3.2	0.4
4	A–Feed/Mig	1980–82	1980–84	22 033	711	3.2	14	0.3		81.6	13.8		4.4	
5	OW	1999–02	1999–03	46 152	389	0.84	Unknown	0.5			8.2	4.1	37.5	49.6
6	OW	2003–06	2003–07	45 411	144	0.32	0	23.6		37.5	6.9	3.5	28.5	

[1]Stobo *et al.* 1975 with updates from Stobo 1976, [2]Waring 1981, [3]Creaser *et al.* 1984, [4]Creaser and Libby 1986, [5]Mouland *et al.* 2003, [6]Kanwit 2006.

Table 3. Summary of tag returns (percentage of returns by zone) from studies that tagged only spawning herring. Tagging zones are abbreviated as NE: New England, GB: Georges Bank, GoM: Gulf of Maine, SWNB: Southwest New Brunswick, UBoF: Upper Bay of Fundy, SNS: Southern Nova Scotia, and ENS: Eastern Nova Scotia. Returns from the zone of tagging are shaded. Tagging areas are abbreviated as "E Shore" = Eastern Shore Nova Scotia, "Ger Bank" = German Bank, GB: Georges Bank, GoM: Gulf of Maine. Returns from the zone of tagging are shaded.

Reference	Tagging Area	Tagging Dates	Recovery Dates	N Tagged	N Returned	Effective Recovery (%)	Effective Recovery (days)	NE	GB	GoM	SWNB	UBoF	SNS	ENS
1	GoM	1976–78	1976–80	29 693	302	1.0	14	1.0		97.3	1.7			
2	GB	1976–78	1976–80	30 346	14	0.05	14		82.4	17.6				
2	Ger Bank	1974	1974–81	23 938	393	1.6	14		0.8	13.2	16.5	5.3	48.6	15.5
2	Ger Bank	1977	1977–81	54 266	750	1.4	14		0.3	5.7	5.9	3.3	43.9	40.9
3	GoM	1980	1980–82	990	11	1.1	14			100				
3	SWNB	1980	1980–80	692	21	3.0	14			19.0	81.0			
4	E Shore	1998–01	1998–03	1 941	3	0.15	Unknown						33.3	66.6
4	SNS	1998–01	1998–03	24 175	107	0.45	Unknown			3.7	1.9		90.7	3.7
4	Scots Bay	1998–01	1998–03	4 908	31	0.63	Unknown				6.4	71.0	19.4	3.2
5	GoM	2003–06	2003–07	40 150	139	0.35	0	8.6	4.3	72.7	3.6	1.4	9.4	
5	GB	2005	2005–07	10 325	9	0.09	0	66.7	0	22.2				11.1
6	Scots Bay	2005	2005	5 047	151	3.0	2			3.1	31.0	60.5	5.4	
6	Ger Bank	2005	2005	8 580	52	0.61	2				17.0		80.9	2.1
7	Ger Bank	2009	2009–11	10 334	86	0.83	2			1.2	1.2		96.4	1.2
8	Ger Bank	2010	2010–11	6 036	36	0.60	2						80.6	19.4
8	Ger Bank	2011	2011–12	6 623	57	0.86	2			1.8			98.2	

[1]Waring 1981, [2]Stobo 1982, [3]Creaser and Libby 1988, [4]Mouland *et al.* 2003, [5]Kanwit 2006, [6]Clark 2006, [7]Maxner *et al.* 2010 with updates from DFO unpublished data,[8]Melvin *et al.* 2014 with updates from DFO unpublished data.

Herring movement from the German Bank spawning area 1974 and 1977.

Herring collected by purse seine and fixed gears were tagged using T-bar anchor tags on German Bank (off southwest NS) in two separate events in August 1974 and August to September 1977 (Stobo, 1982). The intent of the study was to tag ripe and running herring on the spawning area, but the 1974 component of the study captured and tagged substantial numbers of ripe herring that were not running. Recapture efforts focused on all potential fisheries including weir, gillnet, and purse seines. Recovery efforts were reported up to 7 years after tagging and the effective recovery time used was 14 days. Recaptures were reported by season (summer or winter). The 1974 and 1977 studies are examined independently as they were separate efforts. Of the 23 938 herring tagged in 1974, the effective recovery was 1.6% with approximately half of the recaptures in Southern NS, approximately 15% were captured in each of Eastern NS, GoM, and SWNB, 5.3% in the upper BoF, and less than 1% in Georges Bank (Table 3). The 1977 study differed from the 1974 tagging effort in that of the 54 266 herring tagged (1.4% effective recovery), 40.9% of the recaptures were in Eastern NS (Table 3) and small number of recaptures (3 to 6%) were documented in the upper BoF, SWNB, and the GoM, while Georges Bank recaptures were again less than 1% of the total (Table 3).

Herring tagging in Gulf of Maine coastal waters 1976–1978

A tagging study in the GoM was divided into and summarized according to 1-year-old juveniles, summer feeding adults, or mixed (adult/juveniles) (Creaser *et al.,* 1984). Tagging was conducted using T-bar anchor tags. Recoveries were reported by quarter of the year and were observed in all quarters and an effective recovery time of 14 days was applied to the recapture data.

Of 34 664 juvenile herring tagged in GoM, the effective recovery was 4.4% with 96.5% of recoveries in GoM, 3.0% in SWNB, and 0.3% in Georges Bank (Table 1). In SWNB, 3 700 juvenile herring were tagged and the effective recovery was 2.6% with 98.1% of recoveries in SWNB, 1.0% in each of the upper BoF and New England (Table 1).

A total of 4 800 summer feeding adult herring (Table 2) were tagged in GoM and the effective recovery was 3.7% with 93.3 of recaptured in GoM, 5.9% in SWNB, and 0.7% in New England (Table 2). Tagging of summer feeding adult herring (11 723 tags) demonstrated that fish had a much higher probability of leaving the GoM as more than one quarter of the 475 recoveries were from SWNB, approximately 3% from each of New England and Southern NS, and a single fish (0.2%) from the upper BoF, and two fish (0.4%) from Eastern NS near Cape Breton (Table 2).

Herring tagging in Gulf of Maine coastal waters 1980–1982

The tagging study by Creaser *et al.* (1984) in the GoM was repeated in 1980–1982 (Creaser and Libby, 1988). Results were summarized according to 1-year-old juveniles and summer feeding adults (Creaser and Libby, 1988). The authors expressed tag recoveries as a ratio of tags to 1000 metric tons (mt) of catch per geographic area. In order to provide comparable numbers for comparison to other studies in this review, the actual number of tags recovered in each geographic area was calculated using the total catch and tag ratio data provided. Tag ratios reported as < 0.05 tags/1000 mt were substituted with 0.025 tags/mt (*i.e.*, half the reporting limit) for estimation of counts, resulting in counts of either 1 or 2 recaptures. Tagging was conducted in the summer months using T-bar anchor tags. Recoveries were reported by quarter of the year and were observed in all quarters and an effective recovery time period of 14 days was used.

Tagging of summer feeding juvenile herring (48 324 tags; 4.1% effective recovery) revealed that while the vast majority (98.5%) were recaptured in GoM waters, there was movement to SWNB (1.4%) and Southern NS (0.1%) (Table 1). A smaller tagging effort (9 635 tags; 2.7% effective recovery) targeted juveniles in the SWNB weir fishery, and the only recoveries outside of SWNB were from the GoM (Table 1).

Consistent with the 1976–78 tagging study, summer feeding and autumn migrating adult herring demonstrated that fish had a much higher probability of leaving the GoM compared to juveniles. Of 22 033 tags, 711 were recovered (3.2%) with 13.8% from SWNB, 4.4% from Southern NS, and 0.3% from New England (Table 2). A small number of adult herring in spawning condition were tagged in GoM (990 tags) and SWNB (692 tags) in 1980. A total of 11 GoM tags (1.1%) were recovered, all in GoM, and a total of 21 SWNB tags (3.0%) were recovered with 81% in SWNB and 19% in GoM (Table 3).

Herring tagging in New Brunswick and Gulf of Maine coastal waters 1982–1983.

Age-1 herring were targeted for tagging using T-bar anchor tags in SWNB and GoM nearshore fisheries using seines or weirs in late August to October in 1982 and 1983 (Creaser and Libby, 1986). The age-1 herring tagged in 1982 were not reported in the previous section (Creaser and Libby, 1988). The effective recapture time reported was 14 days. Tag recoveries were reported by quarter of the year. Recoveries were reported in all quarters and only recorded up to 1985. A total of 7 161 herring were tagged in SWNB and all 97 recaptures were in SWNB. Of the 7 923 herring tagged in the GoM, 7.7% were recaptured in SWNB (Table 1).

Herring tagging in 4VWX from 1998 to 2003

Tagging studies using T-bar anchor tags were conducted on both nearshore and spawning herring as part of a large tagging effort that occurred between 1998 and 2003 (Mouland *et al.,* 2003). The studies are divided into the nearshore fishery (largely captured in the SWNB weir fishery), an overwintering herring study, herring captured on spawning grounds, and herring tagged along coastal Maine. Updates to this tagging study were documented in Waters and Clark (2005) and returns presented here include all of those tag return updates, and it is not clear whether an effective recovery date was not applied.

Tagged juveniles were released near Jeffrey's Ledge (GoM) in 1999 (study initially described in Waters *et al*., 2000). A total of 1 389 juvenile and pre-spawning herring were tagged and 3 tags were recovered in coastal Maine and one in SWNB (Table 1). A number of distinct tagging efforts were made from the SWNB weir fishery. The first consisted of tagging 27 818 juvenile (1- to 3-year-old) herring captured in weirs in 1999 and 2002. This study was a preliminary study for the NB weir project launched later (Waters and Clark, 2005). Herring returns (0.95% recovery) up to 2003 were recorded and 89.1% were recaptured in SWNB. The greatest movement was to Southern NS (7.9%) with small numbers of fish recaptured in Georges Bank, GoM, Upper BoF, and Eastern NS (Table 1).

A total of 46 152 overwintering herring were tagged in the Eastern NS zone, either at Chebucto Head or Chedabucto Bay (Fig. 1) from 1999–2002. While Chebucto Head was the dividing line between the Eastern and Southern NS zones used herein, it was considered as Eastern NS for the purposes of this review. The effective recovery rate was 0.84% and half of the recaptures were in Eastern NS, 37.5% in Southern NS, 4.1% in upper BoF and 8.2% in SWNB, and a few recaptures in New England (Table 3). A total of 31 024 spawning herring were tagged on German Bank and Trinity Ledge (Southern NS), Scots Bay, and Eastern Shore (Eastern NS). The effective recovery ranged from 0.15 to 0.63% among zones. Scots Bay herring were mostly recaptured in that zone but did move to the three other Canadian zones as well (Table 3). Very few herring were tagged at Eastern Shore (1 941) and only one tag was recovered outside of the tagging zone in Southern NS. The majority of fish (24 175) were tagged on German Bank and Trinity Ledge (Southern NS; Fig. 2) and 72.7% of recaptures were in this zone and recaptures were observed in all other zones with the exceptions of Eastern NS (Table 3).

Weir herring tagging project 2002–2004

A larger NB weir tagging study (Waters and Clark, 2005) followed the preliminary NB weir study that was conducted from 1998 to 2001. A total of 75 440 primarily juvenile herring were tagged using T-bar anchor tags in SWNB weirs from August to November 2002, May to October 2003, and May to October 2004. An additional 2 517 herring were tagged near Grand Manan (SWNB) in the autumn and spring purse seine fishery and these data are included in the overall summary for SWNB. Recaptures were reported to the end of 2004 and the effective recovery rate was 2.6%. More than 90% of recaptures were in SWNB, 4.3% in Southern NS, 1.3% in GoM, 1.2% in upper BoF, and a few recaptures in Georges Bank and New England. A small number of herring (1 230) were also tagged in the NS weir fishery as part of this study. Of the four recovered tags, three were recaptured in the Southern NS area and one in SWNB.

US Herring tagging project 2003–2006

Adult herring in pre-spawning condition were tagged using T-bar anchor tags in the GoM (2003–2006) and Georges Bank (2005) zones from July to October and in the New England zone (2003–2006) zone from January to April. Herring were assumed to be representative of the spawning stocks in the GoM and Georges Bank zones and of overwintering herring in the New England zone (Kanwit, 2006; Kanwit and Libby, 2009). The targeted size for tagging was age 3+ and herring were tagged from the purse seine and midwater trawl fisheries. No effective recovery time was applied and recoveries were reported until May 2007.

Of 45 411 overwintering herring tagged in New England, the return rate was 0.32% with the highest returns in GoM (37.5%), Southern NS (28.5%), and New England (23.6%). Returns were also observed in SWNB and as far as Scots Bay in the upper BoF (Table 2). For pre-spawning herring, in GoM, 40 150 tags were applied with a recovery of 0.35%. Returns were 72.7% in GoM and returns were observed in all zones (with the exception on Eastern NS) in low proportions (Table 3). For pre-spawning herring, on Georges Bank, 10 325 tags were applied with a low recovery of 0.09% or 9 individual tags. Returns were biased due to little directed fishing effort on Georges Bank but the returns showed recoveries in GoM, New England, and overwintering in Eastern NS (Table 3).

Migration of herring captured at the Scots Bay and German Bank spawning areas in 2005

In a study conducted in 2005, Clark (2006) examined the movement of herring from the Scots Bay (upper BoF; 5 047 tags) and German Bank (Southern NS; 8 580 tags) spawning areas. T-bar anchor tags were used and herring were tagged from the purse seine fishery. As tagging was performed at different intervals, the reproductive stage ranged from spawning to spent. Effective recovery time was set at two days and as there were four and five tagging efforts at Scots Bay and German Bank, respectively, spanning more than one month, this effort biased recaptures at the spawning locations. Effective recovery was 3.0% for Scots Bay and 0.61% for German Bank. Outside of the tagging zone, the recaptures were relatively high in SWNB (31% and 17% for Scots Bay and German Bank, respectively), Scots Bay recoveries were also in GoM (3.1%) and southern NS (5.4%) and 2.1% of German Bank recoveries were in Eastern NS (Table 3).

Tagging of herring on the German Bank spawning ground 2009–2011

A tagging program using T-bar anchor tags was conducted on the German Bank spawning ground in cooperation with the commercial purse seine fishery in 2009, 2010, and 2011 (Maxner *et al.,* 2010; Melvin *et al.,* 2014, updates from DFO unpublished data). A total of 23 047 tags were applied in 2009 to 2011 and recapture was documented for the period up until the end of 2019. Effective recovery time was set at 2 days and effective recoveries were 0.60 to 0.86% among years. The majority (93.9%) of returned tags were recovered in Southern NS (Table 3). Two tags (3.8%) were recovered in the GoM, eight tags (4.5%) in Eastern NS, and one tag (0.6%) near Grand Manan in SWNB. The focus of these tagging events was for evaluating turnover on the German Bank spawning ground so recoveries from the tagging area are strongly biased.

Data summary

More than 750 000 tagged herring were released in NAFO areas 4WX5YZ since the 1950s and more than 15 000 tag returns were reported (Tables 1–3). Results were tabulated as juveniles (Table 1), mixed (adult/juvenile), overwintering or adult summer feeding/ autumn migrating (Table 2), or spawning adults (Table 3). While results are not always consistent, even between replicated studies (*e.g.*, Stobo, 1982), there is a general trend for juvenile herring to have limited movements, and adult herring to move more widely, and in greater numbers. In particular, juvenile herring tagged in coastal GoM and the SWNB weir fishery showed little movement, or tended only to move between the GoM and SWNB zones (*e.g.*, MacKenzie and Tibbo, 1961; Waring, 1981, Creaser and Libby, 1986, 1988; Table 1). In contrast, spawning herring (Table 3) and mixed (adult/juvenile) and overwintering, and adult feeding/migrating herring (Table 2) generally moved among several tagging zones. In particular, the two studies of Stobo (1982) where more than half of tagged fish were captured outside of the tagged zone and the study by Kanwit (2006) that showed herring from US spawning grounds overwintering in Canadian waters and herring from Canadian spawning grounds overwintering in US waters.

Discussion

Extensive tagging studies over the past seven decades in NAFO areas 4WX5YZ have provided considerable insight of herring movement between fishery management areas. The basis of herring management is that different sub-populations are formed by spawning aggregations, and that there is a reasonable amount of homing to maintain those population structures (Stephenson *et al.,* 2009). This is supported by tagging studies with herring in ripe and running condition tagged on spawning grounds only being recovered from the same spawning ground in subsequent years (Stobo, 1987; Wheeler and Winters, 1984; Stephenson *et al.*, 2009; Melvin *et al.,* 2014). Further support for the hypothesis of homing is that there was no colonization of Georges Bank by the adjacent GoM spawning areas after it collapsed in 1977 (Grosslein, 1987) and little recovery of Trinity Ledge following a collapse in the late 1980s (Stephenson *et al.,* 2009), despite adjacent spawning areas (GoM and German Bank, respectively) remaining occupied.

While sub-populations are separated at spawning, they also appear to remain separated for the first few months of larval life (Grosslein, 1987; Sinclair *et al.*, 1981). The evidence in the literature is that herring larvae from SWNS/BoF spawning areas are generally retained in the SWNS/BoF area (Sinclair and Iles, 1985; Bradford and Iles, 1993; Stephenson *et al.,* 2009; Stephenson *et al.,* 2015) and vertical migration has been proposed as the mechanism for larval retention in the BoF (Stephenson and Power, 1989). In the GoM, larval herring move inshore and metamorphose into juvenile herring in the spring (Overholtz *et al.,* 2004). It is believed that they only travel small distances until autumn when they move offshore to overwinter near the bottom before returning inshore in the spring as age two and recruit to the weir fishery (Overholtz *et al.,* 2004).

Juvenile herring have been captured in weirs for more than a century in the SWNB area (DFO, 2020b). The assumption that juvenile herring from SWNB are associated with GoM and Georges Bank adults dates back to at least 1973 and it was hypothesized that juvenile abundance in SWNB may indicate future recruitment to the Georges Bank fishery (ICNAF, 1973). Meristic studies by Anthony and Waring (1980; cited in Overholtz *et al.,* 2004) suggested juvenile herring populations in coastal Maine and SWNB were augmented by juveniles from Georges Bank. Further support for a link between US spawning components and the SWNB weir fishery were based on studies of age-1 length frequency distributions in SWNS (Messieh, 1970; Koeller, 1979). Observed changes in juvenile growth in SWNB in the 1980s was coincident with the collapse of the Georges Bank fishery which suggested a link between the two areas pre-collapse (Sinclair *et al.,* 1981). Sinclair *et al.* (1981) did, however, suggest that there is mixing of GoM and SWNS juveniles along the coast of Maine and in the BoF and this is the earliest report that a portion of the juveniles in SWNB may be from SWNS spawning grounds. The Georges Bank fishery was large in the 1960s and early 1970s and juveniles from the Georges Bank spawning area may have historically dominated the SWNB weir landings; however, the relative abundance of different spawning components of herring in NAFO areas 4WX5YZ today is much different, with greater abundance in SWNS/BoF than in GoM and Georges Bank. Messieh (1970) examined monthly length frequency distribution of age-1 herring in Passamaquoddy Bay from 1965 to 1968 and identified three different size groups that corresponded to spring, summer, and autumn spawners. He suggested that at least one group was from the GoM based on water circulation patterns. Koeller (1979) also examined length-frequency distributions of juvenile herring along the NB side of the BoF. He also found three unique length-frequency distributions of age-1 herring and suggested mixed aggregations of juvenile herring in the BoF from at least 3 different spawning areas. It has been recognized for decades that the coastal Maine and SWNB areas are a juvenile nursery for multiple spawning areas including SWNS (Sinclair *et al.,* 1981); however, the current management of herring in the US and Canada assumes that herring from the SWNB weir fishery originate from the GoM and Georges Bank spawning stocks.

Since the 1950s a substantial number of the tagging studies on juvenile herring have been conducted in the GoM and SWNB areas (McKenzie and Tibbo, 1961; Creaser and Libby 1986; Mouland *et al.,* 2003; Waters and Clark, 2005) because this is the juvenile nursery area in NAFO areas 4WX5YZ. The results of those studies consistently show relatively short distance movements of juvenile herring, and the US studies showed that juvenile recaptures outside of the GoM were predominately in SWNB. Many of the tagging locations of juveniles in the GoM studies were close to the GoM/SWNB zone boundary, so movements between zones are relatively short distances in many cases. Tupper *et al.* (1998) and Overholtz *et al.* (2004) speculated that the coastal GoM and SWNB areas serve as the juvenile nursery area for many spawning components in the region (*i.e.*, Georges Bank, GoM, and Southern NS). The coastal GoM and SWNB areas are the primary juvenile nursery areas in the SWNS/BoF area so juvenile herring that were hatched on the primary spawning grounds in SWNS/BoF (*i.e.*, German Bank and Scots Bay) are most likely in the SWNB/coastal Maine areas (Tupper *et al.,* 1998). Adult herring tagged on Canadian spawning grounds and overwintering areas from 1998–2002 were recaptured in the SWNB weir fishery (Waters and Clark, 2005) providing evidence that herring from Canadian spawning grounds are landed in the SWNB weir fishery. Adult herring tagged during the spawning season on German Bank were recovered in the SWNB weir fishery (Clark, 2006), and herring tagged from the purse seine fishery in SWNB that count towards the TAC for the SWNS/BoF fishery were also recovered in the SWNB weir fishery (DFO, unpublished data).

The 2006 Transboundary Assessment Review Committee (TRAC, 2006) considered the tagging information from Waters and Clark (2005) and did conclude that there is a mix of Scotian Shelf and GoM spawners in the SWNB weir fishery but noted that there is no way to estimate the proportion of herring from each stock area. Similarly, the 2006 assessment team for 4VWX herring concluded that the Waters and Clark (2005) tagging data easily refute the hypothesis that herring landed in the SWNB weir fishery are all of US origin. Despite these results, the most recent US (NFSC, 2018) and Canadian (DFO, 2020a) assessment reports assume all SWNB weir fishery landings (adult and juvenile) are from the US stock (GoM and Georges Bank spawning components).

Tagging studies of adult spawning herring have been conducted on all the primary spawning populations within NAFO areas 4WX5YZ and show a much different result than juvenile tagging studies. Adult herring undergo substantial migrations from their spawning areas to summer feeding and overwintering areas in all the zones examined herein within one season after spawning. There was no overall directional trend in the movement of adult herring and patterns have even been observed to change from year to year. This lack of overall directional trend in the movement and variation among years may be related to several factors including: differences in fishing patterns, changes in environmental conditions, and changes in the relative abundance of different spawning components over time and these make efforts to account for herring stock structure in assessment and management difficult. Attempts to develop a two-area (GoM and Georges Bank) stock assessment model in the US failed because of lack of information to estimate movement rates between the areas (NFSC, 2018). The two-area model, however, did not incorporate any tagging data and such data are necessary to reliably estimate movement parameters (Goethel *et al.*, 2019). Correctly estimating movement rates in stock assessments has been shown to be more important than correctly identifying the underlying population structure (*e.g.*, meta-population versus natal homing; Goethel *et al.*, 2019; Bosley *et al.*, 2022). Given the interannual variation in movement rates for herring, continued consideration of multi-area stock assessments will likely require periodically (*e.g.*, 2–3 years) conducting tagging studies to ensure accurate and precise estimation of movement rates, which would require a substantial amount of resources to implement (Goethel *et al.*, 2019).

The Kanwit (2006) tagging study provided some insight into migrations. Recoveries showed a clear pattern of short term residency within 100 days of tagging, longer distance migrations to other zones after 100 days, and recoveries were close to the tagging location around one year after tagging. Scots Bay is known to be a spawning ground and not a feeding or overwintering area. Recaptures at Scots Bay from herring tagged in GoM and New England suggest that these fish were feeding or overwintering in US waters and spawning in the upper BoF. Similarly, a tag recovered in the Chedabucto Bay area of NS in the winter from tagging on Georges Bank suggests overwintering of US fish in Canadian waters.

Overall, the pattern of herring movement from tagging studies is consistent with the conceptual figure of herring stock structure (Fig. 3) that was proposed by Stephenson *et al.* (2009). Herring spawn in discrete areas and that is well established (Overholtz *et al.,* 2004; Melvin *et al.,* 2009). The question of larval drift from those spawning areas has been addressed by a number of studies reviewed by Stephenson *et al.* (2009) and the consensus was that there is limited larval movement away from the spawning grounds; however, there is some overlap of larval retention areas from different spawning grounds (*e.g.*, German Bank and Scots Bay; Stephenson *et al.,* 2015) consistent with the Stephenson *et al.* (2009) conceptual figure (Fig. 3). The tagging data reviewed in the present study support a

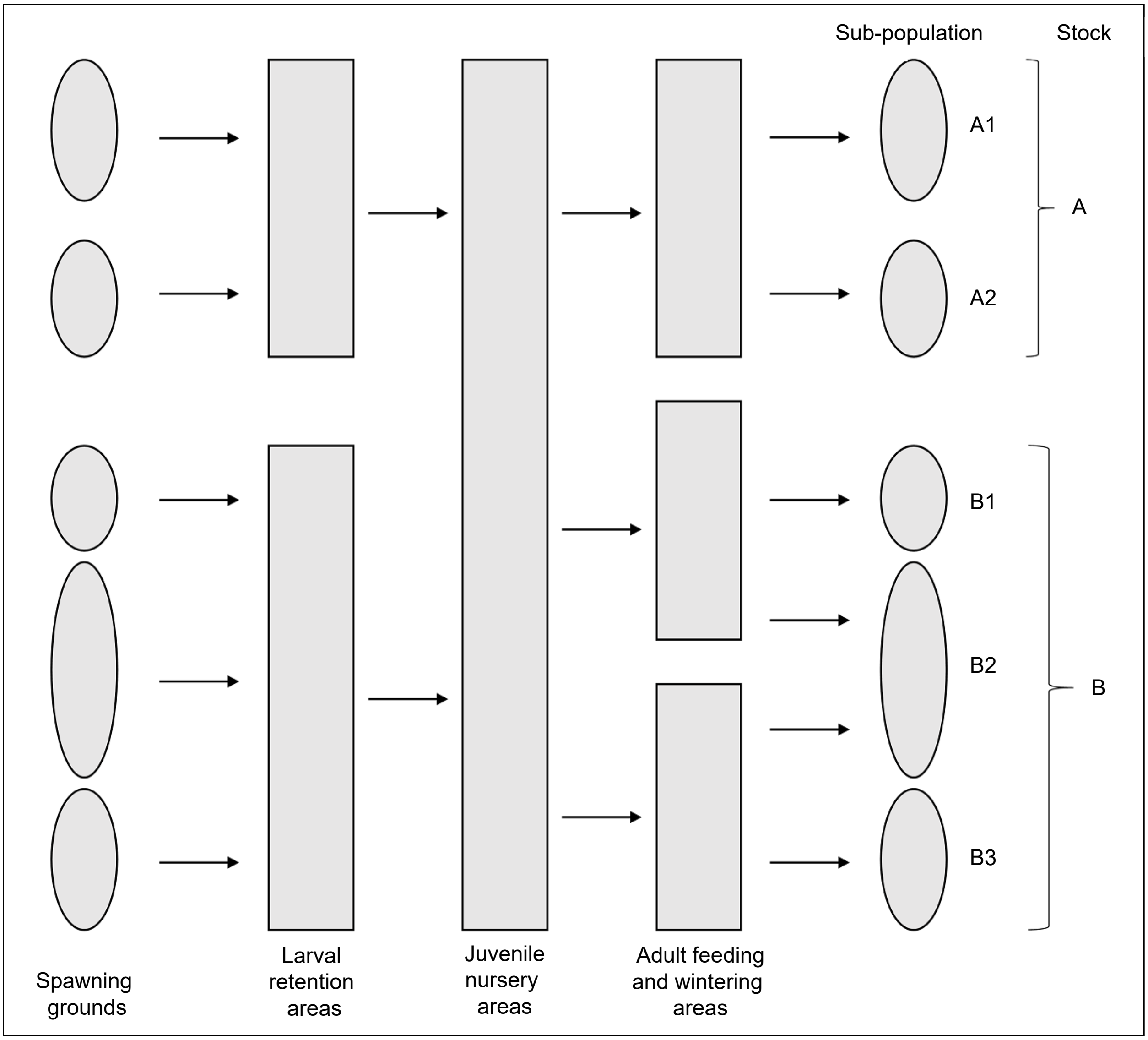

Fig. 3. Conceptual diagram of herring sub-population overlap, modified from Stephenson *et al*. (2009).

common juvenile nursery area in NAFO areas 4WX5YZ with limited movements and as herring become sexually mature, longer distance movements occur and support the overlap of adult feeding and overwintering areas from adjacent sub-populations. The spawning of individuals at the same location in multiple years has been documented, a necessary, but not sufficient condition to prove homing to natal spawning grounds.

There are limitations of tagging studies to evaluate population structure in NAFO areas 4WX5YZ. No tagging study can follow herring from larvae to adult to evaluate the level of homing to the natal spawning grounds. The inability to tag small herring also precludes any studies on fidelity to natal spawning grounds (Tupper *et al.,* 1998). Different tagging methods (*e.g.*, opercular tags, T-bar anchor tags) were used in the studies summarized in this review. The choice of tagging method can result in different mortality rates of tagged individuals (Nakashima and Winters, 1984). The shedding of tags over time and the differential rates among tagging methods can also bias the recapture data (Nakashima and Winters, 1984). Collection method (*e.g.*, purse seine vs. weir) and experience of the tagger are also expected to influence tagging survival. The interpretation of tagging data in any quantitative sense is limited due to the biases in tag returns. Methods to adjust tag return data (*e.g.*, catch-weight, Creaser and Libby, 1988) to account for probability of recapture can remove some of the bias, but the targeting nature of fishing fleets, costs associated with travel to offshore fishing grounds (*e.g.*, Georges Bank and offshore Scotian Shelf), and closure of fishing areas (*e.g.*, spawning areas in the GoM) will always bias the tag return data. In the context of stock assessments, parameters can be estimated in some cases to account for some biases in tag-recapture data (*e.g.*, non-random mixing of tagged fish), and this should be considered if such stock assessments are developed (Goethel *et al.*, 2019). The tagging studies are also strongly biased towards short-term recaptures. For example, only 20% of tag returns had a recovery time of more than 30 days and only 5.2% of tag returns had a recovery time of more than 300 days from DFO studies conducted since 2009 (DFO, unpublished data). Additional challenges with tagging data are uncertainty with recapture location (*e.g.*, when a tag is discovered months after recapture in frozen bait), different return rates depending on market (processed fish vs. bait fish), and hesitancy in reporting transboundary tags (DFO, 2007).

Alternative methods for evaluating stock structure in NAFO areas 4WX5YZ have been explored but research has been limited. Herring in Georges Bank to Cape Cod were shown to have fewer pectoral rays than herring from the coastal GoM and NS (Anthony and Waring, 1980), differences in parasites have been observed between sub-populations (reviewed in Tupper *et al.,* 1998), and some genetic studies have been conducted but variation was insufficient to distinguish between sub-populations (*e.g.*, Kornfield *et al.,* 1982; McPherson *et al.,* 2003), with the exception of differences between spring and autumn spawners. More recent research in Europe on herring stock structure, has utilized several alternative techniques to tagging, including genetics (*e.g.*, Bekkevold *et al.,* 2011; Lamichhaney *et al.,* 2012, 2017), otolith microchemistry (*e.g.*, Geffen *et al.,* 2011; Moll *et al.,* 2019), growth patterns in otoliths, (*e.g.*, Brophy and Danilowicz, 2002), and otolith shape (Libungan *et al.,* 2015) to further elucidate population structure. Acoustic tags have been successful used to track movement of herring (*e.g.*, Eggers *et al.,* 2015; Langård *et al.,* 2015) and may serve as an alternative to traditional tagging methods. Lamichhaney *et al.* (2012) compared over 400 000 single nucleotide polymorphisms in herring from the northern Atlantic and the Baltic Sea. High variability was found in several thousand of those polymorphisms and clearly distinguished Baltic from north Atlantic Herring, supporting that Baltic herring are a subspecies. Another recent study of Baltic Sea herring used otolith microchemistry to characterize herring natal areas (Moll *et al.,* 2019). Otoliths deposit minerals over time and those minerals provide a unique fingerprint of specific regions. These techniques are not restricted to determining natal origin as the habitat history of the entire life of a fish is documented within the otolith. The use of such techniques has advanced knowledge of Eastern Atlantic herring populations well beyond what is known of Western Atlantic populations.

Conclusions

Over 60 years of herring tagging studies have been conducted in the BoF/GoM/Scotian Shelf region (NAFO areas 4XW5YZ) and show generally consistent results indicating short distance movement of juvenile herring in coastal Maine and SWNB and movements of mature herring from their natal spawning grounds to shared feeding and overwintering areas in adjacent geographic zones, including transboundary movement. Although there has been evidence for decades to suggest that juvenile herring from coastal Maine and SWNB are from the SWNS/BoF, GoM, and Georges Bank spawning areas, management assumptions of the SWNB weir fishery have not changed and current management is based on the hypothesis that all herring (juvenile and adult) landed in the SWNB weir fishery are of US (spawning grounds) origin. Although in the 1960s and early 1970s, the Georges Bank fishery was large and juveniles from the Georges Bank spawning area may have dominated the SWNB weir landings, the spatial distribution of herring today is much different, with greater abundance in SWNS/BoF than in GoM and Georges Banks. Recent tagging studies continue to support the hypothesis that juvenile herring in SWNB are from a mix of spawning areas in NAFO areas 4XW5YZ and the proportion of mixing is unknown. There are limitations to the evaluation of tagging data (*e.g.*, from biases due to fishery timing and location) and limitations to the comparisons among tagging studies due to different methodology, experimental design, and changes in the spatial distribution and relative abundance of herring over time. Further traditional tagging studies are unlikely to add substantially to the present knowledge. Further research using alternative methods such as well-developed genetic and microchemistry techniques may be the most promising means to significantly advance our understanding of stock structure in NAFO areas 4XW5YZ.

Acknowledgements

The authors thank Michelle Greenlaw, Alex Hansell, Rabindra Singh, Robert Stephenson, two anonymous reviewers, and the editor for providing comments that greatly improved this manuscript.

References

Anthony, V. C., and Waring, G. 1980. The assessment and management of the Georges Bank herring fishery. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer,* **177**: 72–111.

Bekkevold, D., Clausen, L. A. W., Mariani, S., André, C., Hatfield, E. M. C., Torstensen, E., Ryman, N., Carvalho, G. R., and Ruzzante, D. E. 2011. Genetic mixed-stock analysis of Atlantic herring populations in a mixed feeding area. *Marine Ecology Progress Series*, **442**: 187–199. https://doi.org/10.3354/meps09352

Bosley, K. M., Schueller, A. M., Goethel, D. R., Hanselman, D. H., Fenske, K. H., Berger, A.M., Deroba, J. J., and Langseth, B. J. 2022. Finding the perfect mismatch: Evaluating misspecification of population structure within spatially explicit integrated population models. *Fish and Fisheries*, **23**: 294–315. https://doi.org/10.1111/faf.12616

Bradford, R. G., and Iles, T. D. 1993. Retention of herring *Clupea harengus* larvae inside Minas Basin, inner Bay of Fundy. *Canadian Journal of Zoology*. **71**: 56–63. https://doi.org/10.1139/z93-009

Brophy, D., and Danilowicz, B. S. 2002. Tracing populations of Atlantic herring (*Clupea harengus* L.) in the Irish and Celtic Seas using otolith microstructure. *ICES Journal of Marine Science*, **59**: 1305–1313. https://doi.org/10.1006/jmsc.2002.1304

Brophy, D., Danilowicz, B. S., and King, P. A. 2006. Spawning season fidelity in sympatric populations of Atlantic herring (*Clupea harengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **63**: 607–616. https://doi.org/10.1139/f05-235

Clark, K. J. 2006. An examination of turnover rate of herring on the spawning grounds of Scots Bay and German Bank using tagging data. *Canadian Science Advisory Secretariat Research Document,* 2006/47.

Creaser, E. P., and Libby, D. A. 1986. Tagging of age 1 herring (*Clupea harengus* L.) and their movement along the Maine and New Brunswick coasts. *Journal of the Northwest Atlantic Fishery Science*, **7**: 43–46. https://doi.org/10.2960/J.v7.a5

Creaser, E. P., and Libby, D. A. 1988. Seasonal movements of juvenile and adult herring (*Clupea harengus* L.) tagged along the Maine and New Hampshire coasts in 1976–82. *Journal of the Northwest Atlantic Fishery Science*, **8**: 33–42. https://doi.org/10.2960/J.v8.a4

Creaser, E. P., Libby, D. A., and Speirs, G. D. 1984. Seasonal movements of juvenile and adult herring, *Clupea harengus* L., tagged along the Maine coast. *Journal of the Northwest Atlantic Fishery Science*, **5**: 74–78. https://doi.org/10.2960/J.v5.a9

[DFO] Fisheries and Oceans Canada. 1999. 4VWX and 5Z herring. *DFO Science Stock Status Report*, B3-05(1999). https://waves-vagues.dfo-mpo.gc.ca/Library/237778.pdf

2000. 4VWX herring. *DFO Science Stock Status Report*, B3-03(2000). https://waves-vagues.dfo-mpo.gc.ca/Library/244634.pdf

2007. Proceedings of the Maritimes provinces regional advisory process on the assessment framework for 4VWX herring stocks: 31 October - 1 November 2006 and 9 - 11 January 2007. *DFO Canadian Science Advisory Secretariat Proceedings Series*, 2007/002. https://waves-vagues.dfo-mpo.gc.ca/Library/327841.pdf

2020a. Stock status update of 4VWX herring for the 2019/2020 fishing season. *Canadian Science Advisory Secretariat Science Response*, 2020/050. https://www.dfo-mpo.gc.ca/csas-sccs/Publications/ScR-RS/2020/2020_050-eng.pdf

2020b. Atlantic herring in the Maritimes Region. *Fisheries and Oceans Canada Integrated Fisheries Management Plan*. https://www.dfo-mpo.gc.ca/fisheries-peches/ifmp-gmp/herring-hareng/2020/index-eng.html

Eggers, F., Moland Olsen, E., Moland, E., and Slotte, A. 2015. Individual habitat transitions of Atlantic herring *Clupea harengus* in a human-modified coastal system. *Marine Ecology Progress Series*, **520**: 245–256. https://doi.org/10.3354/meps11103

Geffen, A. J. 2009. Advances in herring biology: from simple to complex, coping with plasticity and adaptability. *ICES Journal of Marine Science*, **66**: 1688–1695. https://doi.org/10.1093/icesjms/fsp028

Geffen, A. J., Nash, R. D., and Dickey-Collas, M. 2011. Characterization of herring populations west of the British Isles: an investigation of mixing based on otolith microchemistry. *ICES Journal of Marine Science*, **68**: 1447–1458. https://doi.org/10.1093/icesjms/fsr051

Goethel, D. R., Bosley, K. M., Hanselman, D. H., Berger, A. M., Deroba, J. J., Langseth, B. J., and Schueller, A. M. 2019.

Exploring the utility of different tag-recovery experimental designs for use in spatially explicit, tag-integrated stock assessment models. *Fisheries Research*, **219**: https://doi.org/10.1016/j.fishres.2019.105320

Grosslein, M. D. 1987. Synopsis of knowledge of the recruitment process for Atlantic herring (*Clupea harengus*), with special reference to Georges Bank. *NAFO Scientific Council Studies*, **11**: 91–108.

[ICNAF] International Commission for the Northwest Atlantic Fisheries. 1973. Report of standing committee on research and statistics, August 1973. App. II. Report of the Herring working group. *ICNAF Redbook*, 1976, Part I: 31–49. https://www.nafo.int/Portals/0/PDFs/icnaf/ICNAF-rb/redbook-1973-pt1.pdf

1976. Report of standing committee on research and statistics, January 1976. App. II. Report of the Herring working group. *ICNAF Redbook,* 1976, Part I: 35–50. https://www.nafo.int/icnaf/library/rb/redbook-1976.pdf

Kanwit, K. 2006. Atlantic herring tagging: insights into migration and movement. Results from the 2003–2006 Project. https://apps-nefsc.fisheries.noaa.gov/coopresearch/pdfs/Herring_Tagging_Final_Report.pdf

Kanwit, J. K., and Libby, D. A. 2009. Seasonal movements of Atlantic herring (*Clupea harengus*): results from a four year tagging study conducted in the Gulf of Maine and Southern New England. *Journal of Northwest Atlantic Fishery Science*, **40**: 29-39. https://doi.org/10.2960/J.v40.m577

Koeller, P. 1979. Distribution and movements of herring in the Bay of Fundy from juvenile surveys. *CAFSAC Research Document* No, 79/32. https://publications.gc.ca/collections/collection_2019/mpo-dfo/Fs70-8-79-32-eng.pdf

Kornfield, I., Sidell, B. D., and Gagnon, P. S. 1982. Stock definition in Atlantic herring (*Clupea harengus harengus*): genetic evidence for discrete autumn and spring spawning populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **39**: 1610–1621. https://doi.org/10.1139/f82-217

Lamichhaneya, S., Martinez Barrioa, A., Rafatia, N., Sundströma, G., Rubina, C.-J., Gilberta, E. R., Berglunda, J., Wetterbomb, A., Laikrec, L., Webstera, M. T., Grabherra, M., Rymanc, N., and Andersson, L. 2012. Population-scale sequencing reveals genetic differentiation due to local adaptation in Atlantic herring. *Proceedings of the National Academy of Science*. **109**: 19345–19350. https://doi.org/10.1073/pnas.1216128109

Lamichhaneya, S., Fuentes-Pardo, A.P., Rafati, N., Ryman, N., McCracken, G.R., Bourne, C., Singh, R., Ruzzante, D.E., and Andersson, L. 2017. Parallel adaptive evolution of geographically distant herring populations on both sides of the North Atlantic Ocean. *Proceedings of the National Academy of Science*, **114**: E3452-E3461. https://doi.org/10.1073/pnas.1617728114

Langård, L., Skaret, G., Helge Jensen, K., Johannessen, A., Slotte, A., Nøttestad, L., and Fernö, A. 2015. Tracking individual herring within a semi-enclosed coastal marine ecosystem: 3-dimensional dynamics from pre- to post-spawning. *Marine Ecology Progress Series*, **518**: 267–279. https://doi.org/10.3354/meps11065

Libungan, L. A., Óskarsson, G. J., Slotte, A., Jacobsen, J. A., and Pálsson, S. 2015. Otolith shape: a population marker for Atlantic herring *Clupea harengus*. *Journal of Fish Biology,* 86: 1377–1395. https://doi.org/10.1111/jfb.12647

Maxner, E. E., Melvin, G. D., and Power, M. J. 2010. The 2009 German Bank spawning ground tagging turnover rates. *Canadian Science Advisory Secretariat Research Document*, 2010/110. https://waves-vagues.dfo-mpo.gc.ca/Library/343751.pdf

McKenzie, R. A., and Skud, B. E. 1958. Herring migrations in the Passamaquoddy region. *Journal of the Fisheries Research Board of Canada*, **15**: 1329–1343. https://doi.org/10.1139/f58-072

McKenzie, R. A., and Tibbo, S. N. 1958. Herring tagged in the Bay of Fundy (June to August 1957). *Fisheries Research Board of Canada Atlantic Progress Report*, No. 70. pp.10–25.

McKenzie, R. A., and Tibbo, S. N. 1961. Herring movements in the Bay of Fundy and Gulf of Maine 1957 and 1958. *Journal of the Fisheries Research Board of Canada*, **18**: 221–252. https://doi.org/10.1139/f61-016

McPherson, A. A., Stephenson, R. L., and Taggart, C. T. 2003. Genetically different Atlantic herring *Clupea harengus* spawning waves. *Marine Ecology Progress Series,* **247**: 303–309. https://doi.org/10.3354/meps247303

McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. *Reviews in Fish Biology and Fisheries*, **7**: 297–329. https://doi.org/10.1023/A:1018491828875

Melvin, G. D., Stephenson, R. L., and Power, M. J. 2009. Oscillating reproductive strategies of herring in the western Atlantic in response to changing environmental conditions. *ICES Journal of Marine Science*, **66**: 1784–1792. https://doi.org/10.1093/icesjms/fsp173

Melvin, G. D., Martin, R., and Power, M. J. 2014. Estimating German Bank and Scots Bay herring spawning ground turnover rates from tag returns. *Canadian Science Advisory Secretariat Research Document*, 2014/068. https://waves-vagues.dfo-mpo.gc.ca/Library/360164.pdf

Messieh, S. N. 1970. Immature herring populations in the Bay of Fundy. *International Commission for the Northwest Fisheries Research Bulletin*, **7**: 59–66.

Moll, D., Kotterba, P., Jochum K.P., von Nordheim, L., and Polte, P. 2019. Elemental inventory in fish otoliths reflects natal origin of Atlantic herring (*Clupea harengus*) from Baltic Sea juvenile areas. *Frontiers in Marine Science*, **6**. https://doi.org/10.3389/fmars.2019.00191

Mouland, N. E., Clark, K. J., Melvin, G.D., and Annis, L. M. 2003. A summary of herring tagging in 4VWX, 1998 to 2003. *Canadian Science Advisory Secretariat Research Document*, 2003/43. https://waves-vagues.dfo-mpo.gc.ca/Library/281656.pdf

Nakashima, B. S., and Winters, G. H. 1984. Selection of external tags for marking Atlantic herring (*Cuplea harengus harengus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **41**: 1341–1348. https://doi.org/10.1139/f84-164

[NFSC] Northeast Fisheries Science Center. 2012. 54th Northeast regional stock assessment workshop (54th SAW). *Northeast Fisheries Science Center Reference Document*, 12–18.

2018. 65th northeast regional stock assessment workshop

(65th SAW). *Northeast Fisheries Science Center Reference Document*, 18–11. https://doi.org/10.25923/zapm-ga75

Overholtz, W. J., Jacobson, L. D., Melvin, G. D., Cieri, M., Power, M., Libby, D., and Clark, K. 2004. Stock assessment of the Gulf of Maine - Georges Bank Atlantic herring complex, 2003. *Northeast Fisheries Science Center Reference Document*, 04–06. http://www.asmfc.org/uploads/file/finalTRACReport2003(NEFSC04-06).pdf

Sinclair, A., Sinclair, M., and Iles, T. D. 1981. An analysis of some biological characteristics of the 4X juvenile-herring fishery. *Proceedings of the Nova Scotian Institute of Science,* 31: 155-171.

Sinclair, M., and Iles, T. D. 1985. Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. *Canadian Journal of Fisheries and Aquatic Sciences*, **42**: 880–887. https://doi.org/10.1139/f85-112

Stephenson, R. L., and Power, M. J. 1989. Observations on herring larvae retained in the Bay of Fundy: variability in vertical movement and position of the patch edge. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, **191**: 177–183.

Stephenson, R. L., Lane, B. E., Aldous, D. G., and Nowak, R. 1993. Management of the 4WX Atlantic herring (*Clupea harengus*) fishery: an evaluation of recent events. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**: 2742–2757. https://doi.org/10.1139/f93-299

Stephenson, R. L., Melvin, G. D., and Power, M. J. 2009. Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence. *ICES Journal of Marine Sciences*, **66**: 1733–1739. https://doi.org/10.1093/icesjms/fsp189

Stephenson, R. L., Power, M. J., Laffan, S. W., and Suthers, I. M. 2015. Tests of larval retention in a tidally energetic environment reveal the complexity of the spatial structure in herring populations. *Fisheries Oceanography*, **24**: 553–570. https://doi.org/10.1111/fog.12129

Stobo, W. T. 1976. Movements of herring tagged in the Bay of Fundy - update. *ICNAF Research Document*, 76/VI/48. https://www.nafo.int/Portals/0/PDFs/icnaf/docs/1976/res-76-48.pdf

1982. Tagging studies on Scotian Shelf herring. *NAFO SCR Doc.* 82/IX/108. https://www.nafo.int/Portals/0/PDFs/sc/1982/scr-82-108.pdf

1987. Atlantic herring (*Clupea harengus*) movement along the Scotian Shelf and management considerations. In Proceedings of the Conference on Forage Fishes of the Southeastern Bering Sea, Anchorage, Alaska, 4–5 November 1986, pp. 75-85. US Department of the Interior, Minerals Management Services, Alaska OCS Region, *MMS Report*, 87–0017. 122 pp.

Stobo, W. T., Scott, J. S., and Hunt, J. J. 1975. Movements of herring tagged in the Bay of Fundy. *ICNAF Research Document*, **76/VI/48**. https://www.nafo.int/Portals/0/PDFs/icnaf/docs/1975/res-38.pdf

[TRAC] Transboundary Resources Assessment Committee. 2006. Proceedings of the Maritime Provinces Regional Advisory Process on the Assessment Framework for 4VWX Herring Stocks. *Canadian Science Advisory Secretariat Proceedings Series*, 2007/002.

Tupper, M. H., Anthony, V. C., Chenoweth, S. B., and MacCluen, H. A. 1998. Biology and assessment of Gulf of Maine herring stocks. *Gulf of Maine Aquarium,* 104 pp.

Waring, G. T. 1981. Results of the international herring tagging program conducted by USA in the Gulf of Maine, Georges Bank and contiguous waters from 1976-78. NAFO SCR DOC. 81/IX/122. https://www.nafo.int/Portals/0/PDFs/sc/1981/scr81-122.pdf

Waters, C. L., Stephenson, R. L., Clark, K. J., Fife, F. J., Power, M. J., and Melvin, G. D. 2000. Report of the PRC/DFO 4VWX herring and mackeral tagging program. *Canadian Science Advisory Secretariat Research Document*, 2000/67. https://publications.gc.ca/collections/collection_2015/mpo-dfo/Fs70-1-2000-067-eng.pdf

Waters, C. L., and Clark, K. J. 2005. 2005 summary of the weir herring tagging project, with an update of the HSC/PRC/DFO herring tagging program. Canadian Science Advisory Secretariat Research Document 2005/25. https://waves-vagues.dfo-mpo.gc.ca/Library/321050.pdf

Watson, J. E. 1963. A method for tagging immature herring. United States Department of the Interior Fish and Wildlife Service. *Special Scientific Report - Fisheries*, **No. 451**. https://spo.nmfs.noaa.gov/sites/default/files/legacy-pdfs/SSRF451.pdf

Wheeler, J. P., and Winters, G. H. 1984. Summary of herring tagging experiments conducted along the east and southeast coasts on Newfoundland, 1974–81. *Canadian Data Report of Fisheries and Aquatic Sciences*, **No. 439**. 22pp. https://publications.gc.ca/collections/collection_2013/mpo-dfo/Fs97-13-439-eng.pdf

Wuenschel, M. J., and Deroba, J. J. 2019. The reproductive biology of female Atlantic herring in U.S. waters: validating classification schemes for assessing the importance of spring and skipped spawning. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, **11**: 487–505. https://doi.org/10.1002/mcf2.10099

J. Northw. Atl. Fish. Sci., Vol. 53: 35–45 Publication (Upload) date: 08 Sep 2022

The feeding ecology of striped bass and the role of ontogeny

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Murphy Jr., R.D., Nelson, G.A., and Grabowski, J.H. 2022. The feeding ecology of striped bass and the role of ontogeny. *J. Northw. Atl. Fish. Sci.*, **53:** 35–45. https://doi.org/10.2960/J.v53.m737

Abstract

Amidst constantly changing biotic and abiotic conditions, a more thorough understanding of the ecological consequences of dynamic predator-prey interactions will likely enable increasingly sustainable fisheries management. This study assessed the diet of striped bass, a generalist marine predator in coastal Massachusetts that feed on a variety of prey species and impose top-down pressure on other important fishery species, such as the American lobster and Atlantic menhaden. We explored the role of ontogeny using both stomach content and stable isotope analyses. Empirical results from 158 striped bass collected in northern Massachusetts revealed that striped bass in this area may have shifted from feeding predominantly on Atlantic menhaden in the late 1990s and early 2000s to Atlantic mackerel in this study. Stable isotope data suggested that the diet of striped bass is significantly linked with ontogeny: larger fish feed more heavily on benthic prey, particularly in the latter half of their seasonal residency in Massachusetts. Our study suggests that large striped bass gain an energetic advantage, as indicated by a liver somatic index, by feeding on benthic prey, possibly due to decreased foraging costs. Collectively, this work illustrates the ability of predatory fish to capitalize on the variability of forage fish populations, but highlights the importance of invertebrate prey for large striped bass and proposes underlying mechanisms driving ontogenetic diet switches from piscivory to benthivory.

Keywords: striped bass (*Morone saxatilis*), ontogenic diet switch, predator-prey interactions, stomach content analysis, stable isotope analysis

Introduction

Comprehensive knowledge of predator-prey interactions is an important underpinning of ecosystem approaches to fisheries management, which is increasingly receiving attention (*e.g.*, North Pacific Fishery Management Council 2019). Further, temporal variability in species distributions, abundances, and size-frequencies necessitates that we routinely monitor ecosystems and the consequences of changing predator-prey interactions (Hilborn *et al.,* 2017). For example, predators can have strong top-down effects on prey populations and alter ecosystems (Denno and Lewis, 2009). They exert control over the distribution of species (Connell, 1961), mediate trophic cascades (Carpenter *et al.,* 1985), and control the flow of nutrients within food webs (Trussell *et al.,* 2006; Hawlena and Schmitz, 2010). Conversely, the availability of prey can fundamentally affect predators (Sherwood *et al.,* 2002). For instance, along the coast of Canada, declining capelin (*Mallotus villosus*) availability (an important prey species) may have contributed to reduced lipid storage and spawning potential in Atlantic cod (*Gadus morhua*) (Sherwood *et al.,* 2007). There is growing evidence, however, that the reliance of a predator population on forage fish abundance is largely context-dependent. Hilborn and colleagues (2017) argued that forage fish abundance rarely has a measurable impact on predator abundance in U.S. fisheries, in part because predators may exhibit significant behavioral plasticity and modify their feeding to account for the natural variability of prey populations.

An important step in investigating predator-prey interactions involves characterizing the suite of factors that can alter prey selection (Juanes *et al.,* 1994). Optimal Foraging Theory (OFT) suggests that a predator will select prey items by balancing the costs of energy acquisition and consumption relative to the intake of energy. More specifically, OFT predicts that predators will select prey that maximize the difference between the energetic value of the prey and the energetic cost of pursuing, attacking, and handling the prey (Pyke *et al.,* 1977). However, other factors may prevent predators from consuming optimal prey, including the presence of competitors (intra- and inter-specific competition), avoidance of their own predators, and morphological limitations such as gape width (Hughes, 1990; Hambright, 1991; Einfalt and Wahl, 1997). For instance, Milinksi (1982) found that sticklebacks consumed fewer optimal prey items in the presence of superior intra-specific competitors. Additionally, optimal prey may change as predators grow, as they may "switch" to consuming a completely new, often larger prey type (*i.e.*, an ontogenetic diet shift) to overcome the aerobic and anaerobic costs of prey consumption (Townsend and Winfield, 1985; Sherwood *et al.,* 2002). Fluctuations in the abundance of prey populations may, however, drive predators to consume less energy-dense but more abundant prey, leading to declines in predator condition (Sherwood *et al.,* 2007).

In the western Atlantic, significant historic and more recent fluctuations in the abundance of both striped bass (*Morone saxatilis*) and their prey emphasize that predator-prey interactions are dynamic (Hill *et al.,* 1989; Atlantic States Marine Fisheries Commission, 2014). The striped bass is a highly mobile and generalist predator that typically spawns in western Atlantic, mid-coast United States estuaries and brackish habitats and migrates north during the spring and summer where they feed heavily on economically valuable prey species like the American lobster (*Homarus americanus*) and Atlantic menhaden (*Brevoortia tyrannus*) (Bigelow *et al.,* 1953, Boreman *et al.,* 1987; Nelson *et al.,* 2003). However, striped bass also consumed large quantities of the Blueback herring (*Alosa aestivalis*) (Greene *et al.,* 2009), which has since declined in many coastal and riverine ecosystems (Atlantic States Marine Fisheries Commission, 2017). Striped bass may have shifted their diet in the late 1990s towards other *Clupeid* prey that were still prevalent like the Atlantic menhaden (Nelson *et al.,* 2003). Our ability to sustainably manage both striped bass and their prey populations amidst such dynamic ecosystems will require a holistic understanding of the causes and consequences of these interactions across space and time.

Our study explored the feeding ecology and potential role of ontogeny in striped bass during their spring and summer migration into Massachusetts (MA) where they consume a variety of prey items from zooplankton and fish to large invertebrates, such as the American lobster and green crab (*Carcinus maenas*) (Chapoton and Sykes, 1961; Manooch, 1973; Nelson *et al.,* 2003). Striped bass spawn and spend the majority of the year in the western Atlantic, mid-coast United States, and the vast majority of studies on striped bass feeding ecology have been conducted in the southern half of their range, such as the Chesapeake Bay (Dovel, 1968; Gardinier and Hoff, 1982; Dunning *et al.,* 1997; Griffin and Margraf, 2003). By and large, these studies indicate that juveniles feed on zooplankton and small crustaceans, while adult striped bass are predominately piscivorous, but may also consume a small proportion of invertebrate prey (Manooch, 1973; Gardinier and Hoff, 1982; Griffin and Margraf, 2003; Overton *et al.,* 2009). In contrast to these studies, Nelson *et al.* (2003, 2006) conducted an extensive diet study on striped bass collected between 1997–2000, whereby half of the collected fish were from the North Shore region of coastal MA. Their results suggested that as striped bass grow, they rely more heavily on benthic decapod prey, while smaller adults feed more on forage fish. This apparent ontogenetic diet shift may have other consequences on striped bass since crustaceans, such as American lobsters, may generate proportionally less energy per gram wet weight as compared to forage fish such as Atlantic herring, *Clupea harrengus* (Nelson *et al.,* 2006). Crustaceans also require more time for predatory fish to digest them (Langton and Center, 1982) and, as such, may represent a suboptimal prey choice. The mechanisms for this potential ontogenetic prey shift are unclear, along with the degree to which suboptimal prey consumption influences the condition and growth of striped bass (Sherwood *et al.,* 2002).

To assess the diet of striped bass in northern MA, we conducted stomach content and stable isotope analyses. Traditional stomach content analysis can result in precise identification of prey species but offers only a recent snapshot of what an individual has been consuming. An alternative approach, utilizing stable isotopic ratios in predator tissue, provides an approximate yet more holistic metric because it examines the assimilation of consumed prey into predator biomass. The stable isotope ratios of nitrogen (δ^{14}N / δ^{15}N) indicate trophic position due to the predictable enrichment of nitrogen for predators relative to their prey (Fry, 1988; Post, 2002). Conversely, the stable isotope ratios of carbon (δ^{13}C / δ^{12}C) do not fractionate as much between trophic levels, and thus indicate benthic versus pelagic feeding due to differences in the enrichment of carbon isotopes at the base of the food chain (Post, 2002). As such, our study used stomach content and stable isotope analyses to identify important prey taxa, evaluate the role of ontogeny, and explore whether diet metrics correlate with predator condition. Thus, we used this approach to explore possible mechanisms underlying diet transitions in striped bass.

Materials and Methods

All methods were approved by Northeastern University's Institutional Animal Care and Use Committee. From 2012 to 2016, striped bass were collected via rod-and-reel from the North Shore region of MA between Nahant and Gloucester, centralized around Salem Sound (Fig. 1; n = 158, total length (TL) range = 41.3cm–111.8cm, mean = 77.4cm). Once caught, fish were euthanized via pithing, and TL and fork length of a fish were measured to the nearest tenth of a cm, and fish were placed on ice. A small white muscle plug was extracted from an area 1–3cm below the first dorsal fin for stable isotope analysis and was immediately placed in foil and frozen.

In the laboratory, stomach contents were extracted, and prey items were identified to the lowest taxon possible. The number of individuals by species and the weight (g) of each species were recorded. Prey specimens in good condition (*i.e.*, not digested) were saved and frozen for stable isotope analysis. Samples for stable isotope analysis were taken internally from prey as to reduce the likelihood of contamination. Multiple metrics were used to examine the importance of prey taxon for striped bass. First, empty stomachs were removed from further stomach content analysis (these fish were included in stable isotope analyses, however). Percent weight (W) is a useful metric for comparing the relative energetic value of prey, especially when individuals from different taxa are of disparate sizes (Zale *et al.,* 2012). Percent weight was calculated as the fraction of the total weight of an individual taxon by the total weight of stomach contents for all fish with non-empty stomachs. To determine how often striped bass consumed particular prey, we calculated the frequency of occurrence (F) for each prey item: the fraction of stomachs with an individual taxon by the total number of non-empty stomachs. Both W and F metrics were determined for all striped bass and by size category, whereby fish with non-empty stomachs were separated based on those below and above the mean TL (mean TL was calculated based on non-empty stomachs). To examine the importance of forage fish versus benthic decapods, the following prey items were classified as benthic decapods: Jonah crabs (*Cancer borealis),* rock crabs, green crabs, unclassified crabs *(Cancridae),* unclassified decapods (*Decapod),* Asian shore crabs *(Hemigrapsus sanguineus),* and American lobsters. While sand shrimp (*Crangon septemspinosa*) is of the Order Decapoda, we did not classify it as a benthic decapod given its propensity to swim off the substrate, and the different striped bass attack strategies used to consume Sand shrimp versus other, larger benthic decapods (note, only two Sand shrimp were found in striped bass stomachs in our study).

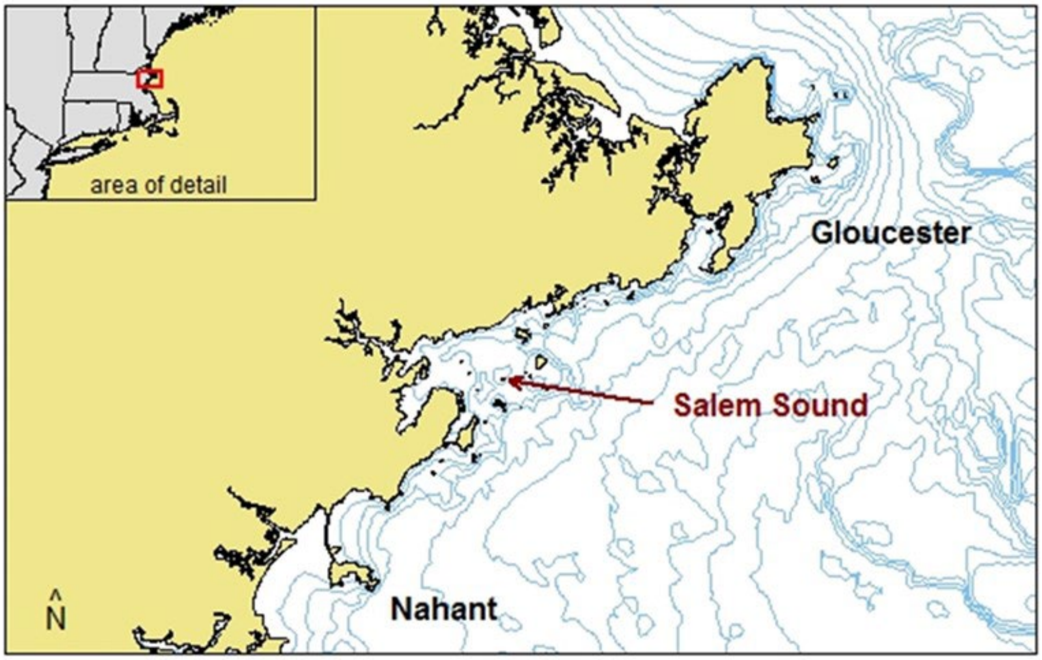

Fig. 1. Study area where striped bass were collected from 2012–2016 with inset map of Massachusetts.

To further explore the role of ontogeny in diet, stable isotope analysis was used as a longer-term approximation of predator diet because it measures prey that have been assimilated into muscle and other tissues (Post, 2002). Using sterile techniques, a small internal plug from each frozen sample was collected internally to avoid contamination. Each sample was then dried for 48 hours at 45°C and subsequently ground to a homogenous powder using a sterilized mortar and pestle. Samples were then weighed, placed in tin caps, and packed for shipment. All samples, including 10% duplicates (*i.e.*, separate sub-samples were taken from the same tissue to examine variation between replicate pairs), were sent to the Colorado Plateau Laboratories to be analyzed. Since lipid content can influence isotopic carbon signatures, prey and predator samples (Post *et al.,* 2007) were lipid-corrected by using methods of Skinner *et al.* (2016). As such, lipid percentages were generated based on a formula from Post *et al.* (2007), which was used as an input in another formula from Kiljunen *et al.* (2006) to correct $\delta^{13}C$ values (hereby called $\delta^{13}C'$).

To estimate predator condition, two metrics were utilized. Liver somatic index (*LSI*) was calculated for each fish as: $LSI = wet\ liver\ weight\ /\ wet\ body\ weight\ *\ 100$ (Adams and McLean, 1985). An individual fish's *LSI* should be closely correlated with health since excess energy is stored as glycogen in the liver, typically after periods of high prey consumption (Hoque *et al.,* 1998). Thus, higher relative *LSI* values should indicate a healthier individual with greater energy stores. To explore the effects of diet on striped bass relative body size, the Relative Condition Factor (K_n) was used, which is standardized to account for allometric growth (Le Cren, 1951). Here, individual fish weight (*w*) was divided by the length specific mean weight (*w'*) of striped bass in MA such that $K_n = w / w'$. Length specific mean weight was calculated according to the MA striped bass Monitoring Report for 2014: $log_{10}(W_p) = -3.455 + 3.001 * log_{10}(L_i)$, where W_p is weight in pounds (1 pound = 454 grams) and *Li* is the total length in inches (1 inch = 2.54 cm) (Nelson, 2015).

Statistical Analysis

Linear regression models were used to explore the potential relationships between striped bass stable isotopic values for $\delta^{13}C'$ and $\delta^{15}N$ and striped bass TL and the day of year (day). We also examined the relationships between response variables, *LSI* and K_n, and potential predictors, striped bass TL and $\delta^{13}C'$, as a proxy for benthic feeding using linear regression models. As such, the four models were as follows; (1) $\delta^{13}C' = f\ (striped\ bass\ TL\ *\ day)$; (2) $\delta^{15}N = f\ (striped\ bass\ TL\ *\ day)$; (3) $LSI = f\ (striped\ bass\ TL\ *\ \delta^{13}C')$; (4) $K_n = f\ (striped\ bass\ TL\ *\ \delta^{13}C')$. All data were modeled as normally-distributed errors (Gaussian GLM) in R (R Core Team, 2020) and models included an interactive term between covariate predictors. Assumptions of residual normality were assessed using normal quantiles plots, while homoscedasticity was inspected using residuals versus fitted values plots. Regression terms were deemed significant at $\alpha \leq 0.05$.

Results

Atlantic mackerel, *Scomber scrombrus*, was the most important prey item by weight (42.8%), followed by American lobster (19.9%), unclassified fish prey (10.3%), and Menhaden (7.0%), while several other species were of much lower importance (Fig. 2). Frequency of occurrence of unclassified fish prey (33.3%), Atlantic mackerel (17.7%), American lobster (16.7%), and rock crabs, *Cancer irroratus*, (16.7%) were higher than other prey taxa consumed by striped bass (Table 1, Fig. 2a). When aggregated by size, small striped bass (*i.e.*, those below the 76.54cm mean TL for non-empty fish) and large striped bass had consumed a similar amount of fish prey, representing 79.5% and 61.2% of their diet by weight, and were found in 58.8% and 64.7% of non-empty stomachs, respectively (Fig. 2b). Conversely, large striped bass consumed more benthic decapods by weight (35.5%) and more frequently (51%) compared to small striped bass (13.2% and 35.3%, respectively). Examination of all striped bass (*i.e.*, those with prey in their stomachs and those with empty stomachs) revealed that the large and small fish had empty stomachs 39% and 32% of the time, respectively.

Stable isotope analysis revealed little variation between replicate pairs (mean of absolute differences between pairs) for striped bass muscle samples ($\delta^{13}C' = 0.19‰$, $\delta^{15}N = 0.20‰$, $n = 15$). Striped bass stable isotopic values were adjusted to account for trophic fractionation between predator and prey ($\delta^{13}C' = +0.8‰$, $\delta^{15}N = +3.4‰$, Fig. 3a) and then for plotting purposes and to visually compare striped bass to their prey, mean isotopic values for striped bass were plotted alongside prey values (Fig. 3b) (Zanden and Rasmussen, 2001). Both species of prey fish, Atlantic herring and Atlantic mackerel, had the highest $\delta^{15}N$ and lowest $\delta^{13}C'$ values among prey, indicating that they represent a higher trophic level and consume a more pelagic food source than crustacean prey. Meanwhile, the two crab species, green crab and rock crab, and the American lobster were of a lower trophic level and $\delta^{13}C'$ was highly enriched, indicating that these species represent benthic prey consumed by striped bass (Fig. 3a).

A model of stable carbon isotopes revealed a significant interaction between TL and day (degrees of freedom (DF)

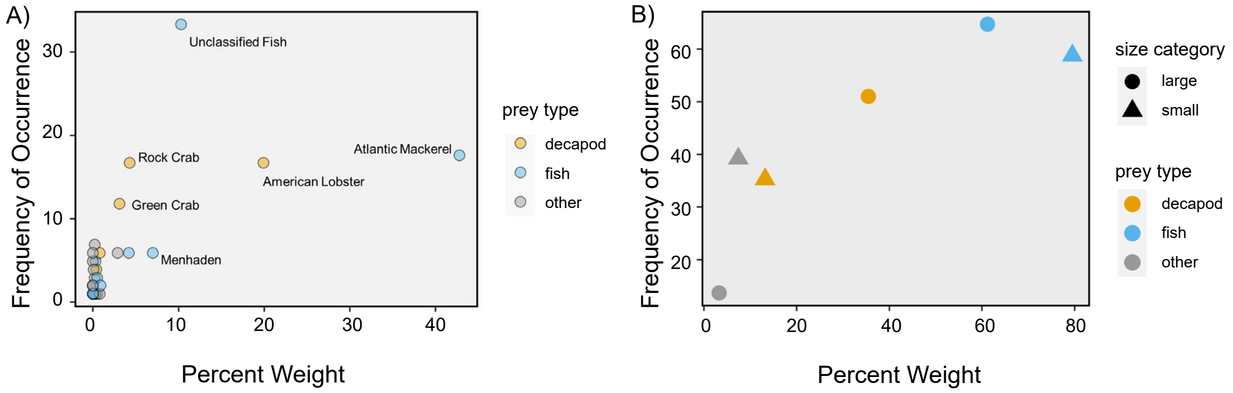

Fig. 2. Plots of prey taxon importance for striped bass collected along the north shore of Massachusetts from 2012–2016. **A**) Plot of stomach content data from all striped bass with the most important prey items by weight and frequency of occurrence are labeled. **B**) Stomach content data summarized by prey type for striped bass below (small = triangle points) and above (large = circle) points the mean total length (76.54cm). Points in both plots are coloured by prey type.

= 151, t-value = 2.456, p-value = 0.015; Fig. 4a). To aid in the visualization of this significant interaction, we conducted linear regression and quantified the slopes for the relationship between δ^{13}C' and day for striped bass whose length was ±1 standard deviation from the mean, which revealed a positive slope for larger fish and negative slope for smaller fish (Fig. 4b). TL and day were not significantly related to δ^{15}N (DF = 151, TL: $t = -1.173$, $p = 0.243$; day: $t = -1.863$, $p = 0.064$; TL x day: $t = 1.569$, $p = 0.119$).

Examination of condition indices revealed significant interactions between stable carbon isotopic values, TL, and *LSI* (DF = 147, $t = 2.593$, $p = 0.011$; Fig. 5a). Again, we used linear regression to quantify the slopes for the relationship between *LSI* and δ^{13}C' for striped bass whose length was ±1 standard deviation from the mean to aid in result interpretation. This revealed a positive slope for larger fish and negative slope for smaller fish (Fig. 5b). Lastly, K_n was not significantly related to δ^{13}C' and TL (DF = 148, δ^{13}C': $t = -1.731$, $p = 0.09$; TL: $t = 1.798$, $p = 0.074$; TL x δ^{13}C': $t = 1.707$, $p = 0.09$).

Discussion

Our results indicated that striped bass in the North Shore region of MA maintain a diet high in Atlantic mackerel, which is in contrast to research two decades earlier that suggested striped bass diets were dominated by Atlantic

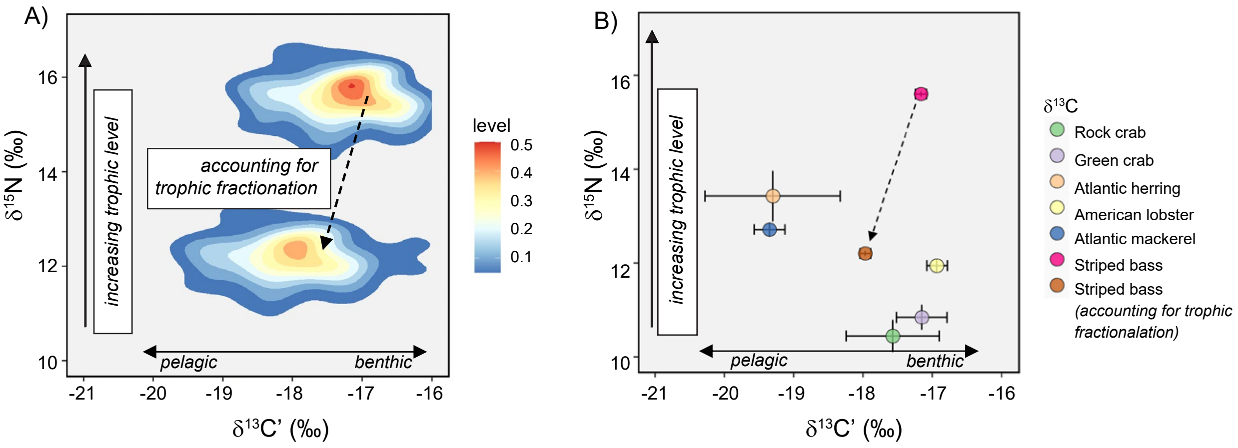

Fig. 3. Prey and striped bass stable isotopic values. Carbon stable isotopic values were lipid corrected and striped bass values are displayed with and without a correction for trophic fractionation. **A**) Mean stable isotopic values for important prey taxa and striped bass. **B**) Density plot for striped bass stable isotopic values showing the distribution of data.

Table 1. Summary of stomach contents by prey of Striped bass collected along the north shore of Massachusetts from 2012–2016. Note that the weight of one Atlantic herring (*Clupea harrengus*) was lost, so the average weight of all other Atlantic herring was used as a proxy. In one other case, the weight of an unclassified fish (highly digested) was lost, so the weight of another unclassified fish of identical morphology (from a Striped bass caught on the same day), as recorded in a lab notebook, was used as a proxy.

taxon	total number of individuals	percent number	total weight (g)	percent weight	number of times in stomach	frequency of occurrence
Ammodytes americanus	8	0.7	16	0.3	5	4.9
Amphipoda uncl	86	7.9	2	0.0	5	4.9
Brevoortia tyrannus	6	0.6	331	7.0	6	5.9
Cancer borealis	6	0.6	25	0.5	1	1.0
Cancer irroratus	32	2.9	203	4.3	17	16.7
Cancridae uncl	6	0.6	40	0.8	6	5.9
Carcinus maenas	18	1.7	145	3.1	12	11.8
Cephalopoda	7	0.6	138	2.9	6	5.9
Clupea harengus	14	1.3	198	4.2	6	5.9
Crangon septemspinosa	2	0.2	1	0.0	2	2.0
Caprellidae	56	5.2	1	0.0	1	1.0
Decapod uncl	1	0.1	3	0.1	1	1.0
Ensis directus	1	0.1	0	0.0	1	1.0
Etrumeus teres	1	0.1	16	0.3	1	1.0
Euphausiidae	1	0.1	0	0.0	1	1.0
Gammaridae	488	44.9	10	0.2	7	6.9
Gastropod	11	1.0	12	0.2	3	2.9
Hemigrapsus sanguineus	8	0.7	17	0.4	4	3.9
Homarus americanus	28	2.6	937	19.9	17	16.7
Idotea sp.	12	1.1	2	0.0	2	2.0
Idotea baltica	12	1.1	2	0.0	6	5.9
Melanogrammus aeglefinus	1	0.1	3	0.1	1	1.0
Mytilus edulis	167	15.4	5	0.1	4	3.9
Nereis virens	7	0.6	38	0.8	1	1.0
Osmerus mordax	1	0.1	2	0.0	1	1.0
Osteichthyes uncl	65	6.0	486	10.3	34	33.3
Pholis sp.	6	0.6	22	0.5	3	2.9
Scomber scombrus	31	2.9	2 019	42.8	18	17.6
Tautogolabrus adspersus	2	0.2	41	0.9	2	2.0
Unclassified organism	2	0.2	0	0.0	2	2.0
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menhaden (Nelson *et al.,* 2003). The occurrence of Atlantic mackerel in striped bass diets increased over 10-fold, potentially indicating a major shift in local availability of forage fish. As opportunistic predators, striped bass appeared to have capitalized on the local variability of forage fish populations (Hilborn *et al.,* 2017). Additionally, Nelson *et al.* (2003) found that striped bass similar in size to those sampled in this study consumed predominantly Atlantic menhaden in the later summer months, which is when this forage fish typically migrates into nearshore waters along coastal MA. Anecdotal evidence suggests that Atlantic menhaden abundances in Salem Sound have been very low in recent years, whereas there was a considerable uptick in Atlantic mackerel spawning-stock-biomass and total biomass directly following the Nelson *et al.* (2003) diet study (42nd Northeast Regional Stock Assessment Workshop, 2006).

Stomach content analysis revealed that the American lobster may also be a critical prey item, and was the most important invertebrate taxa by weight, highlighting an interaction with another vital New England fishery. Catch of American lobster in MA was valued at over $82 million in 2016, second only to Sea scallops (MA Division of Marine Fisheries Annual Report, 2016). Rock crabs were consumed at similar rates but are much smaller and thus likely represent a lesser energy source. This finding agrees with Nelson *et al.* (2003) in their study of adult striped bass throughout MA from 1997–2000, where crustaceans were found to represent ~45% of striped bass diet by weight within the North Shore region. While fish in our study consumed a slightly smaller proportion of crustaceans, the overall consumption of juvenile American lobster remained high.

Analysis of stable isotopes offers a more holistic examination of diet ontogeny as we could sample all fish (including fish with empty stomachs) and because isotopic signatures integrate across longer periods (Post, 2002). As indicated by stable carbon isotopic signatures, striped bass consumed organisms from both benthic and pelagic environments during the beginning of the spring/summer migration into MA. As the summer progressed, large striped bass bass relied heavily on benthic prey. Given the time lag between prey consumption and assimilation into muscle tissue (Buchheister and Latour*,* 2010), it is plausible that large striped bass feed primarily on pelagic food sources before their immediate arrival into MA, followed by a switch to benthic prey in MA where there is higher availability of crustaceans such as American lobsters (Thunberg, 2007).

This ontogenetic diet switch is somewhat counterintuitive given that fish prey offers more energy per gram wet weight (Steimle and Terranova, 1985) and since crustaceans, like the American lobster, are partly composed of chitin (Boßelmann *et al.,* 2007), an organic material that is harder to digest than soft flesh. Analysis of striped bass *LSI* provides insight into possible explanations. Specifically, feeding on benthic organisms was slightly negatively

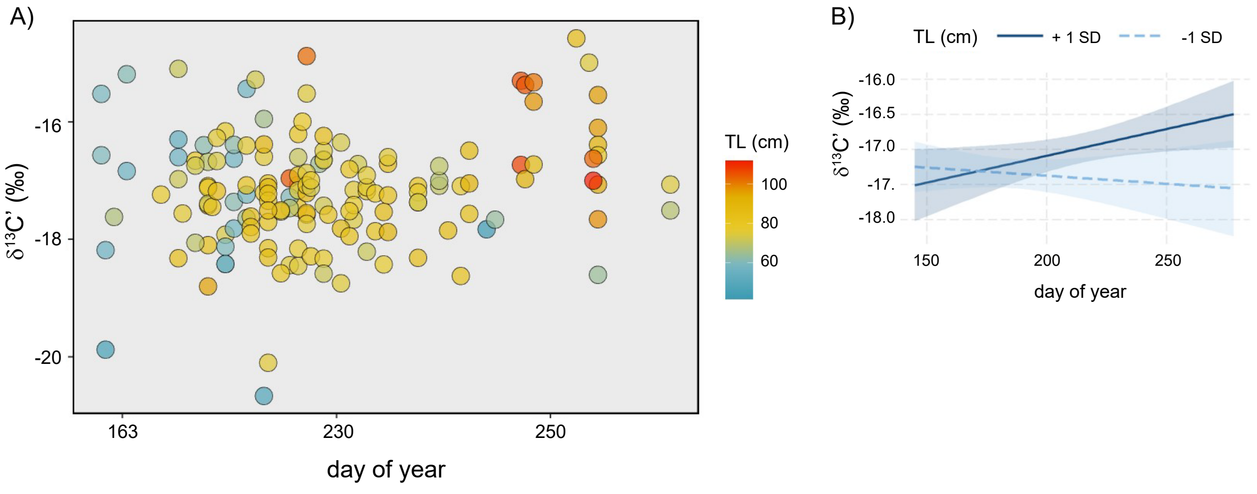

Fig. 4. Carbon isotopic values from the white muscle of striped bass collected along the north shore of Massachusetts from 2012–2016 (n = 155). Carbon isotopic values are compared to striped bass total length (TL) and the day of the year that each fish was caught. **A**) Points are coloured according to striped bass TL. **B**) Linear regression slopes for the relationship between carbon and day of year for striped bass whose length is +1 Standard Deviation (SD) from the mean (solid dark blue line) and -1 SD from the mean (dotted light blue line). Shaded regions represent 95% confidence intervals.

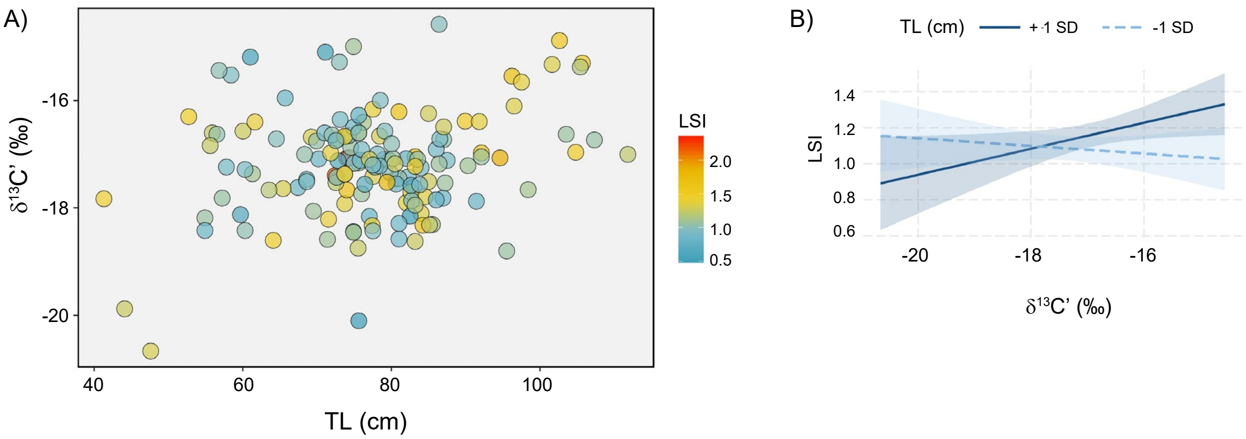

Fig. 5. Liver Somatic Index (LSI) compared to carbon isotopic values from the white muscle of striped bass collected along the north shore of Massachusetts from 2012–2016 (n = 151). Carbon isotopic values are compared to striped bass total length and LSI. **A**) Points are coloured according to LSI. **B**) Linear regression slopes for the relationship between δ^{13}C' and LSI for striped bass whose length is +1 Standard Deviation (SD) from the mean (solid dark blue line) and -1 SD from the mean (dotted light blue line). Shaded regions represent 95% confidence intervals.

correlated with the condition of small striped bass, as their livers weighed less relative to those of their pelagic-feeding counterparts. Conversely, benthic feeding seemed to significantly favour larger striped bass such that fish that fed on benthic prey items had larger livers, indicating that benthic feeding may allow these predators to build up better energy reserves. Given that striped bass experience decelerating growth by length, but their weight increases exponentially with age, large striped bass must propel a relatively heavier body through the w ater to capture prey. Chasing after fast-moving forage fish is thus potentially associated with high attack and pursuit costs for larger striped bass, while smaller, more streamlined individuals may be more capable of efficiently searching for and capturing forage fish. This finding is supported by work from a lake ecosystem, where pelagic Eurasian perch, *Perca fluviatilis*, were more streamlined than Eurasian perch feeding in the littoral zone (Quevedo *et al.,* 2009).

By consuming benthic decapod prey that are slower than forage fish and potentially easier to capture, large striped bass may be able to reduce the energetic costs associated with capturing prey; which aligns with OFT (Pyke *et al.,* 1977). This feeding strategy would allow striped bass to acquire increased energy reserves, as suggested by our *LSI* analysis. Similarly, work by Sherwood *et al.* (2002) suggested that the burst speed required to capture prey is an important component of foraging activity costs. In a lake ecosystem, the authors measured the lactate dehydrogenase levels in the white muscle of yellow perch, *Perca flavescens*, which is a proxy for anaerobic metabolism and burst swimming activity. Predatory Yellow perch that exhibited ontogenetic variation in diet and shifted from consuming zooplankton to benthic invertebrates at first and later to large prey fish were able to reduce their anaerobic activity costs in a step-wise fashion with each diet switch. By resetting their activity costs after each ontogenetic prey switch, these fish were able to maintain growth and prevent a bioenergetic bottleneck. It is plausible that large striped bass switch to feeding more heavily on American lobsters and other large crustacean prey to reduce the metabolic costs of foraging. However, our findings do not rule out other explanations for this ontogenetic transition toward benthic invertebrates. For example, it is possible that smaller striped bass would benefit from consuming benthic invertebrates but are unable to due to morphological challenges (*e.g.*, limited gape size) or resource competition from larger individuals.

Collectively, our study illustrates the significance of ontogenetic diet transitions for predatory fish, whereby the apparent transition to benthic decapods by large striped bass highlights that diversity in prey availability is important for maintaining predator condition with growth. We provide explanations for the energetic basis for this diet ontogeny in striped bass that would be supported by OFT. Specifically, stomach content and stable isotope analyses suggest that diet is driven partly by ontogenetic processes, such that large striped bass may benefit energetically from the consumption of large crustaceans over forage fish prey. A proposed mechanism for this ontogenetic shift from piscivory to benthivory follows that smaller, more streamlined striped bass likely benefit from the consumption of energetically rich forage fish. Conversely, large striped bass may suffer from increased attacking or searching costs associated with pelagic feeding and, as such, likely transition to benthic feeding, as suggested by enhancement in condition. Future experimental, comparative, and modeling studies should continue to unpack these mechanisms, providing additional insights into the complex relationships between predator and prey. Moreover, this study illustrates the variability of some predator-prey interactions over time but suggests that OFT can help to anticipate the consequences of fluctuating species abundances and size-frequency, spatial, and temporal distributions.

Acknowledgments

We would like to thank Kelsey Schultz, Joe Carracappa, Suzanne Kent, and Christopher Baillie for helping with our laboratory and fieldwork. Randy Sigler and the members of his fishing camp provided numerous striped bass samples, for which we are very grateful. Greg Veprek always went out of his way to bring us on his boat to collect samples and we are extremely grateful for his generosity. We also thank two blind reviewers whose feedback greatly improved our manuscript.

References

42nd Northeast Regional Stock Assessment Workshop. 2006. 42nd SAW assessment summary report (Ed.), *In* N. F. S. C. U.S. Dep. Commer.

Adams, S., and McLean, R. 1985. Estimation of largemouth bass, *Micropterus salmoides* Lacépède, growth using the liver somatic index and physiological variables*. *Journal of Fish Biology*, **26**: 111–126. https://doi.org/10.1111/j.1095-8649.1985.tb04248.x

Atlantic States Marine Fisheries Commission. 2014. Addendum IV to Amendment 6 to the Atlantic Striped Bass Interstate Fishery Management Plan.

Atlantic States Marine Fisheries Commission. 2017. River herring stock assessment update volume II: state-specific reports.

Bigelow, H. B., and Schroeder, W. C. 1953. Fishes of the Gulf of Maine. US Government Printing Office Washington, DC.

Boreman, J., Lewis, R. R., and Dadswell, M. 1987. Atlantic coastal migration of striped bass. *In* Common strategies of anadromous and catadromous fishes. *American Fisheries Society, Symposium 1*. **1**: 331–339

Boßelmann, F., Romano, P., Fabritius, H., Raabe, D., and Epple, M. 2007. The composition of the exoskeleton of two crustacea: The American lobster *Homarus americanus* and the edible crab *Cancer pagurus*. *Thermochimica Acta*, **463**: 65–68. https://doi.org/10.1016/j.tca.2007.07.018

Buchheister, A., and Latour, R. J. 2010. Turnover and fractionation of carbon and nitrogen stable isotopes in tissues of a migratory coastal predator, summer flounder (*Paralichthys dentatus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**: 445–461. https://doi.org/10.1139/F09-196

Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. *BioScience*: 634–639. https://doi.org/10.2307/1309989

Chapoton, R. B., and Sykes, J. E. 1961. Atlantic coast migration of large striped bass as evidenced by fisheries and tagging. *Transactions of the American Fisheries Society*, **90**:13–20. https://doi.org/10.1577/1548-8659(1961)90[13:ACMOLS]2.0.CO;2

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs **31**: 61–104. https://doi.org/10.2307/1950746

Denno, R. F., and Lewis, D. 2009. Predator-prey interactions. The Princeton Guide to Ecology. Princeton University press, UK. https://doi.org/10.1515/9781400833023.202

Dovel, W. L. 1968. Predation by striped bass as a possible influence on population size of the Atlantic croaker. *Transactions of the American Fisheries Society,* **97**: 313–319. https://doi.org/10.1577/1548-8659(1968)97[313:PBSBAA]2.0.CO;2

Dunning, D. J., Waldman, J. R., Ross, Q. E., and Mattson, M. T. 1997. Use of Atlantic tomcod and other prey by striped bass in the lower Hudson River estuary during winter. *Transactions of the American Fisheries Society,* **126**: 857–861. https://doi.org/10.1577/1548-8659(1997)126%3C0857:UOATAO%3E2.3.CO;2

Einfalt, L. M., and Wahl, D. H. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. *Canadian Journal of Fisheries and Aquatic Sciences,* **54**: 2618–2626. https://doi.org/10.1139/f97-172

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnology and Oceanography*, **33**: 1182–1190. https://doi.org/10.4319/lo.1988.33.5.1182

Gardinier, M. N., and Hoff, T. B. 1982. Diet of striped bass in the Hudson River Estuary [*Morone saxatilis*, New York]. *New York Fish and Game Journal*, **29**: 152–165

Greene, K. E., Zimmerman, J. L., Laney, R. W., and Thomas-Blate, J. C. 2009. Atlantic coast diadromous fish habitat: a review of utilization, threats, recommendations for conservation, and research needs. *Atlantic States Marine Fisheries Commission Habitat Management Series*, **464**, 276.

Griffin, J., and Margraf, F. 2003. The diet of Chesapeake Bay striped bass in the late 1950s. *Fisheries Management and Ecology,* **10**: 323–328. https://doi.org/10.1046/j.1365-2400.2003.00367.x

Hambright, K. D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society*, **120**: 500–508. https://doi.org/10.1577/1548-8659(1991)120%3C0500:EAOPSB%3E2.3.CO;2

Hawlena, D., and Schmitz, O. J. 2010. Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *Proceedings of the National Academy of Sciences,* **107**: 15503–15507. https://doi.org/10.1073/pnas.1009300107

Hilborn, R., R. Amoroso, O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., and Walters, C. J. 2017. When does fishing forage species affect their predators? *Fisheries Research*, **191**: 211–221. https://doi.org/10.1016/j.fishres.2017.01.008

Hill, J., Evans, J. W., and Van Den Avyle, M. J. 1989. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Atlantic). Striped bass. DTIC Document. https://doi.org/10.21236/ADA226928

Hoque, M., Yusoff, F., Law, T., and Syed, M. 1998. Effect of hydrogen sulphide on liver somatic index and Fulton's condition factor in *Mystus nemurus*. *Journal of Fish Biology,* **52**: 23–30. https://doi.org/10.1111/j.1095-8649.1998.tb01549.x

Hughes, R. N. 1990. Behavioural mechanisms of food selection. Springer-Verlag GmbH & Co. KG. https://doi.org/10.1007/978-3-642-75118-9

Juanes, F., Stouder, D., and Feller, K. 1994. What determines prey size selectivity in piscivorous fishes. *In* Stouder D. J, Fresh, K. L., and Feller R. J. (Eds.), *Theory and application in fish feeding ecology*. pp. 79–100, Carolina University Press, Columbia.

Kiljunen, M., Grey, J. Sinisalo, T., Harrod, C., Immonen, H., and Jones, R. I. 2006. A revised model for lipid-normalizing δ^{13}C values from aquatic organisms, with implications for isotope mixing models. *Journal of Applied Ecology,* **43**: 1213–1222. https://doi.org/10.1111/j.1365-2664.2006.01224.x

Langton, R. W., and Center, N. F. 1982. A review of methods used for estimating gut evacuation rates and calculating daily ration for fish. Ref. Doc:77–07.

Le Cren, E. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *The Journal of Animal Ecology*, **2:2**: 201–219. https://doi.org/10.2307/1540

Manooch, C. S. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. *Chesapeake Science*, **14**: 73–86. https://doi.org/10.2307/1350872

Massachusetts Division of Marine Fisheries. 2016. Annual Report 2016. Department of Fish and Game. https://www.mass.gov/files/documents/2017/08/30/2016-dmf-annual-report.pdf

Milinski, M. 1982. Optimal foraging: the influence of intraspecific competition on diet selection. Behavioral Ecology and Sociobiology **11**:109-115. https://doi.org/10.1007/BF00300099

Nelson, G. 2015. Massachusetts Striped Bass Monitoring Report for 2014. Massachusetts Division of Marine Fisheries TR-62.

Nelson, G. A., Chase, B. C., and Stockwell, J. 2003. Food habits of striped bass (*Morone saxatilis*) in coastal waters of Massachusetts. *Journal of Northwest Atlantic Fishery Science*, **32**: 1–25. https://doi.org/10.2960/J.v32.a1

Nelson, G. A., Chase, B. C., and Stockwell, J. 2006. Population consumption of fish and invertebrate prey by striped bass (*Morone saxatilis*) from coastal waters of northern Massachusetts, USA. *Journal of Northwest Atlantic Fishery Science,* **36**: 111–126. https://doi.org/10.2960/J.v36.m576

North Pacific Fishery Management Council. 2019. Bering Sea Fishery Ecosystem Plan.

Overton, A. S., Margraf, F. J., and May, E. B. 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. *Transactions of the American Fisheries Society,* **138**: 915–926. https://doi.org/10.1577/T07-261.1

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**:703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., and Montana, C. G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, **152**: 179–189. https://doi.org/10.1007/s00442-006-0630-x

Pyke, G. H., Pulliam, H. R. and Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, **52**: 137–154. https://doi.org/10.1086/409852

Quevedo, M., Svanbäck, R., and Eklöv, P.. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology*, **90**: 2263–2274. https://doi.org/10.1890/07-1580.1

R Core Team. 2020. R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Austria, 2015. ISBN 3-900051-07-0: URL http://www.R-project.org.

Sherwood, G. D., Pazzia, I., Moeser, A. Hontela, A., and Rasmussen, J. B. 2002. Shifting gears: enzymatic evidence for the energetic advantage of switching diet in wild-living fish. *Canadian Journal of Fisheries and Aquatic Sciences,* **59**: 229–241. https://doi.org/10.1139/f02-001

Sherwood, G. D., Rideout, R. M., Fudge, S. B., and Rose, G. A. 2007. Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): insights from stable carbon isotopes (δ^{13}C). *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**: 2794–2809. https://doi.org/10.1016/j.dsr2.2007.08.007

Skinner, M. M., Martin, A. A., and Moore, B. C. 2016. Is lipid correction necessary in the stable isotope analysis of fish tissues? *Rapid Communications in Mass Spectrometry,* **30**: 881–889. https://doi.org/10.1002/rcm.7480

Steimle, F., and Terranova, R. J. 1985. Energy equivalents of marine organisms from the continental shelf of the temperate Northwest Atlantic. *Journal of Northwest Atlantic Fishery Science*, **6**: 117–124. https://doi.org/10.2960/J.v6.a11

Thunberg, E. M. 2007. Demographic and economic trends in the northeastern United States lobster (*Homarus americanus*) fishery, 1970–2005. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northeast Fisheries Science Center.

Townsend, C. R., and Winfield, I. J. 1985. The application of optimal foraging theory to feeding behaviour in fish. *Fish energetics*. Springer, pp. 67–98. https://doi.org/10.1007/978-94-011-7918-8_3

Trussell, G. C., Ewanchuk, P. J., and Matassa, C. M. 2006. The fear of being eaten reduces energy transfer in a simple food chain. *Ecology*, **87**: 2979–2984.

Zale, A. V., Parrish, D. L. and Sutton, T. M. 2012. Fisheries techniques. American Fisheries Society.

Zanden, M., and Rasmussen, J. B. 2001. Variation in $\delta^{15}N$ and $\delta^{13}C$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography*, **46**: 2061–2066. https://doi.org/10.4319/lo.2001.46.8.2061

J. Northw. Atl. Fish. Sci., Vol. 53: 47–56 Publication (Upload) date: 13 Sep 2022

Limited temporal variability in natural mortality for juvenile American plaice on the Grand Bank of Newfoundland

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Robertson, M.D., Regular, P.M., and Cadigan, N. 2022. Limited temporal variability in natural mortality for juvenile American plaice on the Grand Bank of Newfoundland. *J. Northw. Atl. Fish. Sci.*, **53**: 47–56. https:doi.org//10.2960/J.v53.m738

Abstract

Increases in natural mortality have been suggested as a potential driver for both the collapse and lack of recovery for the American plaice (*Hippoglossoides platessoides*) population on the Grand Bank of Newfoundland in NAFO Divisions 3LNO. However, natural mortality is among the most difficult parameters to estimate since it can be confounded with other parameters and model misspecifications. One method used to avoid this confounding involves modeling unfished components of a population where total mortality and natural mortality are equal. Here, we use a state-space metapopulation dynamics model to investigate whether there is evidence that natural mortality rates for unfished juvenile American plaice have varied since the population collapse. In addition, our model examined the degree of synchrony in age-1 recruitment signals between each management Division. The best fitting model included temporal variability in natural mortality rates, but estimates did not frequently differ from zero. This indicates that change in natural mortality rates is not an important driver of current juvenile 3LNO American plaice stock dynamics. Instead, this model identified that juvenile stock dynamics were mainly affected by variations in age-1 recruitment. Furthermore, a correlation analysis of the temporal variations in recruitment showed that trends were somewhat dissimilar between NAFO Divisions 3L and 3NO. Overall, although increases in M have been suggested by recent studies, we did not find strong evidence for this in juvenile fish.

Keywords: cohort dynamics, population dynamics, recruitment, spatiotemporal, state-space models

Introduction

Increases in natural mortality rates (M's) have been suggested as a potential driver for both the collapse and lack of recovery for the American plaice (*Hippoglossoides platessoides*) population on the Grand Bank of Newfoundland in NAFO Divisions 3LNO (Morgan and Brodie, 2001; COSEWIC, 2009; Morgan *et al.*, 2011; Perreault *et al.*, 2020). In fact, in the most recent run of the ADAPT model for this stock (Wheeland *et al.*, 2021) and in previously accepted models (*e.g.* Wheeland *et al.*, 2018), the assumed M was increased from 0.2 to 0.53 for all ages from 1989 to 1996. In the late 1980's – early 1990's 3LNO American plaice collapsed, and despite a moratorium on directed commercial fishing since 1994, the population has yet to recover (Fig. 1; Wheeland *et al.*, 2021). Despite an expectation that the collapse and lack of recovery were mainly driven by overfishing (directed fishing for the collapse, and bycatch for the lack of recovery), population dynamics models have indicated that known catches are unlikely to account for observed increases in total mortality rates (Z) both during and after the collapse (Morgan and Brodie, 2001; Perreault *et al.*, 2020). Such increases in Z have consequently been, at least partially, attributed to shifts in M. These shifts are hypothesized to be linked to particularly low bottom-water temperatures that covered the Grand Bank during this time-period (Morgan, 1992; Walsh *et al.*, 2004; Robertson, *et al.* 2021); however, direct estimation of the temporal variability in M and its drivers has yet to occur.

Although M is often considered to be one of the most important parameters in a fish stock assessment model, it is also among the most difficult parameters to estimate using commonly available data (Punt *et al.*, 2021). It can be confounded with survey gear selectivity and fishing mortality rates (Pope *et al.*, 2021). Even when M can be estimated numerically, it may be confounded or aliased with other model misspecifications and M estimates may then be unreliable. There are two main methods capable of avoiding the confounding issue. The first is integration of additional data that can inform M estimates. This usually involves tagging data (*e.g.* Pine, Pollock, High- tower, Kwak, and Rice, 2003; Cadigan, 2015), but there are recent examples that used fish condition indices (*e.g.* Regular *et al.*, 2022). Another approach involves exami- nations of unfished components of a population (Myers and Cadigan, 1993a, 1993b; Gudmundsson, 2004; Zhang *et al.*, 2020). Although 3LNO American plaice lack a time- series of mark-recapture data (but see Morgan (1996) for a tagging experiment), this stock benefits from having research surveys that catch a wide range of ages, includ- ing juvenile age-classes (ages 1–5) that are too small to be captured by the fishery. Survey indices of these age- classes provide a means to examine trends in M for the juvenile component of this population since their Z and M should be equal.

Here we use a state-space metapopulation dynamics model to investigate whether there is evidence that American plaice juvenile M has varied since the population collapse. This model is applied to juvenile (ages 1–5) abundance indices on the Newfoundland Grand Bank since 1995. American plaice have spatiotemporally varying, sexually dimorphic growth with juveniles growing from approximately 5 to 20 cm, female maturation occurring around age eight, and male maturation occurring around age four in recent years in NAFO divisions 3LNO (Zheng *et al.*, 2020a, 2020b). A previous use of this model assessed juvenile cod M around Newfoundland and Labrador, where both cohort strength and M were found to vary across space and time (Zhang *et al.*, 2020). Here, we limited our analysis to one stock on the Grand Bank, but allowed for separate estimates in each management division due to previous findings of divisional-level recruitment asynchrony (Kumar *et al.*, 2019).

Materials and Methods

Metapopulation dynamics process model

The model used here was developed by Zhang *et al.* (2020) and a more detailed description can be found there. Briefly, this model framework uses age-based survey indices of

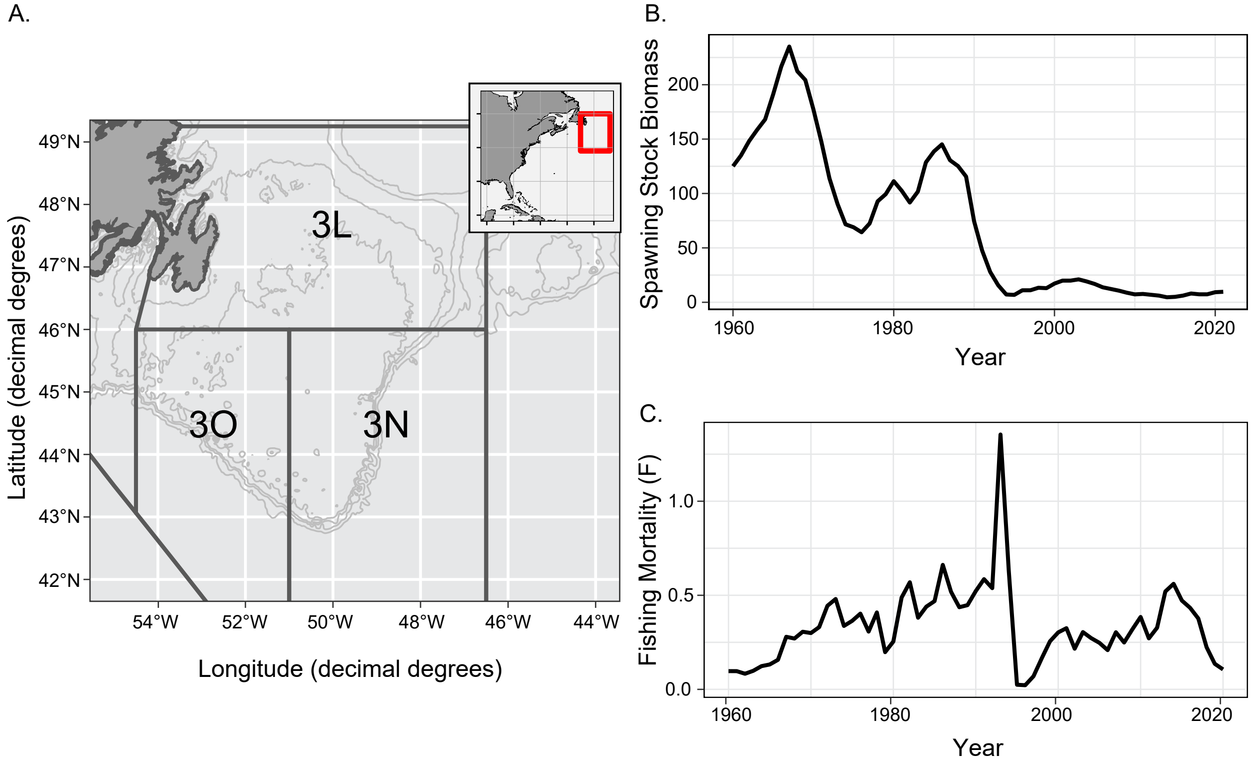

Fig. 1. Map of NAFO Divisions 3LNO (**A**) and estimates of recent spawning stock biomass (**B**) and fishing mortality (**C**) from the most recent run of the stock assessment model (Wheeland *et al.* 2021). Light grey lines in panel A represent bathymetric contours at 100, 200, 400, and 1000m depth. Spawning stock biomass estimates are in the 1000s of tons and estimates of fishing mortality are the average estimates for ages 9–14.

unfished juvenile fish abundance to estimate changes in juvenile M and cohort strength within metapopulation units. The model is based on the common cohort population model, $N_{a,y} = N_{a-1,y-1}\exp\left(-M_{a-1,y-1}\right)$, where $N_{a,y}$ represents stock abundance at age *a* in year *y* and $M_{a,y}$ is the natural mortality rate. We assume that $M_{a,y}$ can be modelled in terms of age- and year-effects, $M_{a,y} = M_a + \delta_y$, where M_a ($a = 0,\ldots,A$) is the overall level of juvenile mortality at age *a* and δ_y ($y = 0,\ldots,Y$) is the annual deviation $M_{a,y} - M_a$ that we assume is common for all juvenile ages. If $c = y - a$ indicates the cohort and $n_{a,y} = \log\left(N_{a,y}\right)$, then we can show through recursive applications of the basic cohort model that

$$n_{a,c} = n_{0,c} - \sum_{i=0}^{a-1}\left(M_i + \delta_{c+i}\right), \qquad a > 0. \tag{1}$$

We model δ_y for $y = 1,\ldots,Y$ using a stationary Gaussian autoregressive process with a correlation parameter φ_δ and stationary variance $\sigma_\delta^2/\left(1-\varphi_\delta^2\right)$:

$$\delta_0 \sim N\left(0, \tfrac{\sigma_\delta^2}{1-\varphi_\delta^2}\right),\ \delta_y\middle|\delta_{y-1} \sim N\left(\varphi_\delta\delta_{y-1}, \sigma_\delta^2\right), y = 1,\ldots,Y. \tag{2}$$

Note that $\delta_y\middle|\delta_{y-1}$ denotes the distribution of δ_y conditional on the value δ_{y-1}, and $\sigma_\delta^2 = Var\left(\delta_y|\delta_{y-1}\right) \le Var\left(\delta_y\right)$.

In addition, we model the time-series of the initial cohort abundance ($n_{0,c}$; *i.e.* recruits) using an intercept plus a Gaussian autoregressive cohort effect (γ_c),

$$n_{0,c} = n_0 + \gamma_c, \tag{3}$$

where

$$\gamma_0 \sim N\left(0, \tfrac{\sigma_\gamma^2}{1-\varphi_\gamma^2}\right), \gamma_c\middle|\gamma_{c-1} \sim N\left(\varphi_\gamma\gamma_{c-1}, \sigma_\gamma^2\right),\ c = 1,\ldots,C \tag{4}$$

Observation model

Our model is based on bottom trawl research survey indices $\left(I_{s,a,y}\right)$, where s denotes the survey, a denotes the age, and y denotes the year. Each age-class in the surveys is expected to have unique catchability $\left(Q_{s,a}\right)$ which is based on gear selectivity and availability of fish at different ages (and sizes) to the survey. Our basic observation model is

$$I_{s,a,y} \approx Q_{s,a}N_{s,a,y}\exp\left\{-f_s\left(M_{s,a}+\delta_{s,y}\right)\right\},$$

where f_s is the fraction of the year that survey *s* occurs and the $\exp\left\{-f_s\left(M_{s,a}+\delta_{s,y}\right)\right\}$ term simply projects beginning of year abundance ($N_{s,a,y}$) to the survivors at the time of the survey. We collect all of the *M* deviations and cohort abundance random effects into the set $\Psi = \left\{\delta_y, \gamma_c; y = 1,\ldots,Y, c = 1,\ldots,C\right\}$. Let $q_{s,a} = \log\left(Q_{s,a}\right)$ and define $\mu_{s,a,y} = E\left\{\log\left(I_{s,a,y}\right)\middle|\Psi\right\}$ to be the statistical expected value of $\log\left(I_{s,a,y}\right)$ given all the random effects. The expectations are

$$\mu_{s,a=0,y=c} = q_{s,0}^* + n_{s,0,c} - f_s\delta_{s,c}, \tag{5}$$

and

$$\mu_{s,a,y=c+a} = q_{s,a}^* + n_{s,0,c} - \sum_{i=0}^{a-1}\left(\delta_{s,c+i} - f_s\delta_{s,c+a}\right), \qquad a > 0, \tag{6}$$

where $q_{s,0}^* = q_{s,0} - f_sM_{s,0}$ and $q_{s,a}^* = q_{s,a} - \sum_{i=0}^{a-1}M_{s,i} - f_sM_{s,a}$. As described in Zhang *et al.* (2020), the $q_{s,a}$ and $M_{s,a}$ values are completely confounded, therefore we cannot directly estimate $M_{s,a}$ without additional information on $q_{s,a}$. As a result, we estimate their combined effect, $q_{s,a}^*$.

The survey index observation equation is

$$\log\left(I_{s,a,y}\right) = \mu_{s,a,y} + \tau_{s,y} + \varepsilon_{s,a,y}, \tag{7}$$

where $\tau_{s,y}$ and $\varepsilon_{s,a,c}$ are normally distributed $\left[i.e.\ \tau_{s,y} \overset{iid}{\sim} N\left(0, \sigma_{s,\tau}^2\right)\right]$ survey measurement errors. The random year-effects ($\tau_{s,y}$) allow for measurement errors to be correlated across ages within surveys and years, which is common for survey indices of juvenile ages. However, these errors are independent for different years and surveys. Due to this structure, these year-effects will only affect estimates in a particular year, rather than having a cumulative effect on cohort dynamics like the temporal deviations in M. Furthermore, $q_{s,a=5}^*$ is constrained to be zero for each survey to eliminate the confounding between the values of $q_{s,a}^*$ and $n_{s,0,c}$ in Equation (6). Finally, we estimate between-survey and unstructured correlations in both $M_{s,a,y}$ and $n_{s,0,c}$, which is described in Zhang *et al.* (2020). These correlations represent the metapopulation aspect of the model, where population processes may be similar among NAFO divisions. These correlations were examined with a hierarchical cluster analysis using the `hclust` function in R on the Pearson dissimilarity between surveys.

Data

We used six relative abundance indices of juvenile (ages 1–5) American plaice from stratified random research bottom-trawl surveys in NAFO Divisions 3LNO. These surveys were conducted in the spring (~April – June) and fall (~ October – November) and were separated based on NAFO Divisions (*i.e.* spring 3L, spring 3N, spring, 3O, fall 3L, fall 3N, and fall 3O). We limited the time-series for our analysis to spring surveys conducted after 1996 and fall surveys after 1995 due to low catchability of age 1 American plaice with the bottom trawl gear used in prior years (Morgan *et al.*, 1998). Surveys were not completed in some years and any indices with zero or very small values (*i.e.* <e^{-5}) were not used (see SM. Fig. 1).

Model fitting

We examined thirteen parameterizations of the model, with varying numbers of random effects (γ_c, $\tau_{s,y}$, δ_c) to determine which components were necessary to account for the variability in the sampled survey indices (Table 1). In addition to sequentially adding components, we tested various correlation structures to identify if cohort effects or M deviations varied across space and season. Model selection was completed using a combination of Akaike's information criterion (AIC), Bayesian information criterion (BIC), and examinations of residuals. BIC measures goodness-of-fit, while AIC is a measure of prediction accuracy (Soper, 2002). We used the Template Model Builder (TMB, Kristensen *et al.,* 2016) package in R (R Core Team, 2018) to evaluate the negative logarithms of the marginal likelihoods (nll) of these models and the data, and to evaluate the nll gradients to improve estimation. Further, we used the R function nlminb() to find the maximum likelihood estimates. Model convergence was evaluated by ensuring that the nll gradient for all parameters was <10^{-4} and that the Hessian matrix was positive definite at the maximum-likelihood estimates.

Results

Our model comparisons indicated that the model with the best fit was model M5 which had cohort and year-effects, as well as M deviations that were shared across Divisions (Table 1). Model M5 fit the data well, with no observable trends in residual plots (see SM. Figs. 6–16). This model was an improvement over the simpler model M4, and had no survey year-effects in standardized residuals (SM. Figs. 2 and 3). M4 had clear residual year-effects (SM. Fig. 2) that were substantially reduced in M5, although a similar trend of small magnitude remained (SM. Fig. 3). M5 included spatial and temporal variability in cohort effects (Fig. 1). Despite 3LNO being managed as a single stock, our model selection process showed substantial improvements in estimates when cohort effects were allowed to vary by Division and season (Table 1). The temporal trends indicated that in NAFO Division 3L, cohort effects decreased until 1996, increased after this until 2012, and have since declined somewhat steadily. Meanwhile, there was much less of a trend in NAFO Divisions 3NO, where cohort effects generally oscillated around a mean with a period of around 5–6 years. The similarity in cohort effect trends between 3N and 3O was identified in the spatial cohort effect correlation matrix (Fig. 2) where 3N and 3O surveys always had a high correlation with each another (>0.9). Meanwhile, the correlations between cohort strength derived from 3L surveys and those in 3N and 3O were often lower (≤0.5). This was further illustrated using a cluster analysis that identified that the cohort effects for 3NO were dissimilar from the cohort effects for 3L (Fig. 3).

Model M5 indicated that accounting for M deviations was necessary to produce the best fits to the survey indices.

Table 1. Model names, descriptions and comparisons using AIC and BIC. + represents effects that were included, while a blank space indicates that the effect was not included. The subscript *d* indicates that the effect was only allowed to vary by Division rather than by survey (*i.e.* season and Division). k is the number of parameters, nll is the negative log-likelihood and the Δ columns represent the difference in the number of criterion points from the model with the lowest respective criterion points. The bolded row (M5) indicates the model that we determined to have the best fit.

Model	$\boldsymbol{n_{0,c}}$	$\boldsymbol{n_{s,0,c}}$	$\boldsymbol{\tau_{s,y}}$	$\boldsymbol{\delta_c}$	$\boldsymbol{\delta_{d,c}}$	$\boldsymbol{\delta_{d,c}}$ Corr.	$\boldsymbol{\delta_{s,c}}$	$\boldsymbol{\delta_{s,c}}$ Corr.	k	nll	AIC	**Δ**AIC	BIC	**Δ**BIC
M1	+								53	834	1773	272	2011	232
M2		+							58	763	1642	141	1902	123
M3		+	+						60	706	1532	31	1801	22
M4		+		+					60	709	1538	37	1807	28
M5		**+**	**+**	**+**					**62**	**689**	**1501**	**0**	**1779**	**0**
M6		+			+				62	714	1551	50	1829	50
M7		+	+		+				64	696	1520	19	1807	28
M8		+			+	+			65	702	1533	32	1825	46
M9		+	+		+	+			67	687	1508	7	1809	30
M10		+					+		65	737	1604	103	1895	116
M11		+	+				+		67	702	1537	36	1838	59
M12		+					+	+	80	692	1544	43	1902	123
M13		+	+				+	+	82	683	1529	28	1897	118

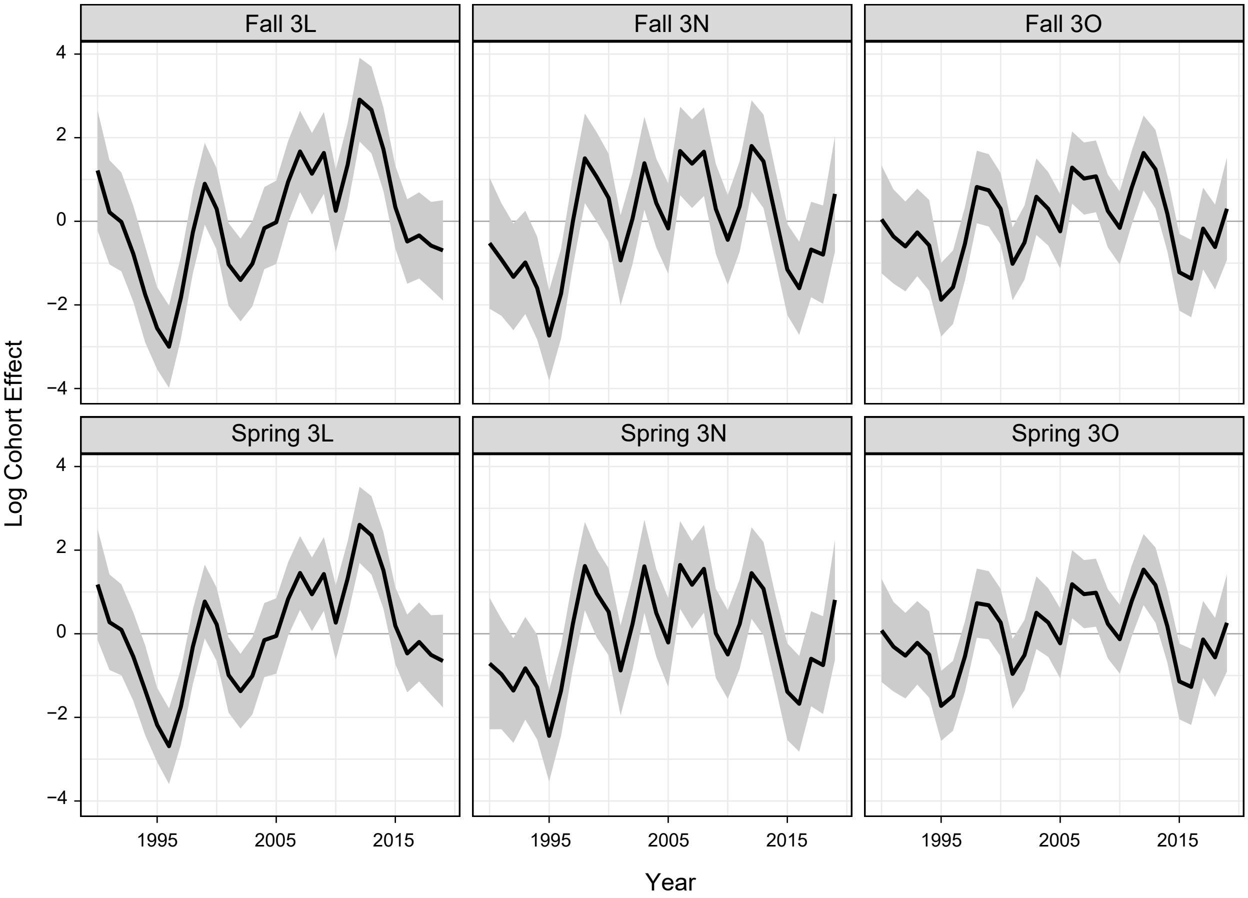

Fig. 2. Time-series of cohort effect deviations estimated for each survey index using model M5. The black lines represent the point-estimates while the shaded grey area represents the 95% confidence intervals.

M5 had the simplest formulation of M deviations, where they were assumed to be equal across NAFO Divisions 3LNO (Table 1). Therefore, unlike cohort effects, our results indicate that M deviations may not vary by Division or season and may be driven by a larger scale process. Finally, despite improving model fit, the estimates of M deviations only differed significantly from zero in four years: 1999, 2005, 2015, and 2016 (Fig. 4). At the extreme, the estimates suggest M's in 2015–16 were slightly more than double those in 1999–2000. Estimated changes in M were much smaller in other years.

Discussion

We applied a state-space metapopulation dynamics model to identify whether American plaice juvenile natural mortality rates (M's) have affected stock dynamics since the population collapse. Our model comparison identified that estimating temporal variability in M improved the model fit to juvenile 3LNO American plaice survey indices which indicates that temporal variability in M may influence the dynamics of the unfished portion of the stock. The best fitting model included spatial cohort and survey year-effects, along with non-spatial M deviations. Although this best fitting model included temporal M deviations, estimates were rarely significantly different from zero. The limited variation in these M deviations in comparison to the larger magnitude variations in age-1 recruitment indicated that juvenile stock dynamics were mainly affected by recruitment. Furthermore, temporal variations in cohort effects were more dissimilar between NAFO Divisions 3L and 3NO, implying that drivers of age-1 recruitment may differ between these regions.

Recent analyses have indicated that current assumptions about M in 3LNO American plaice stock assessments underestimate its impact on the slow recovery for this stock (Perreault *et al.*, 2020; Wheeland, 2021). Here, we observed that estimating temporal variability in juvenile M improved estimates of juvenile stock dynamics. However, annual M deviations were rarely significantly different from zero, indicating that the variation is less important compared to spatial and temporal variations in cohort strength. This finding matches results from a previous cohort model used for this stock that assessed the potential for changes in M graphically rather than modelling it as we have done here (Kumar *et al.,* 2019). Furthermore, this finding matches broader findings that demersal fish juvenile natural mortality tends to show limited temporal variability (Myers and Cadigan, 1993a; Gudmundsson, 2004). The limited variability in juvenile M may affect our ability to understand the drivers of current stock assessment problems for this stock. For example, our findings differ from a recent exploration of M deviations where there was an indication that accounting for temporal change in M at young ages would help reduce retrospective patterns (Perreault *et al.,* 2020). This difference in magnitude of influence of natural mortality may have been generated by M deviations at young ages producing better fits by reducing recruitment variance since the Perreault *et al.* (2020) model formulation did not include an M deviation variance penalty like the model employed here. Overall, although increases in M have been suggested by recent studies, we did not find strong evidence for this in juvenile fish.

We did not find evidence of large changes in juvenile M since the fishing moratorium in 1995 but this does not mean that high juvenile M is not a factor in the delayed recovery of the stock. It is possible that recent M's are much higher than those prior to 1995. However, our model and the available survey data only allow the estimation of M deviations which cannot inform the magnitude of M to provide any direct indication of whether current M is high relative to expected levels of juvenile M. As a result, investigating how juvenile M has varied pre- and post-collapse would require a longer historical time series. Since Fall survey indices are only available since 1990,

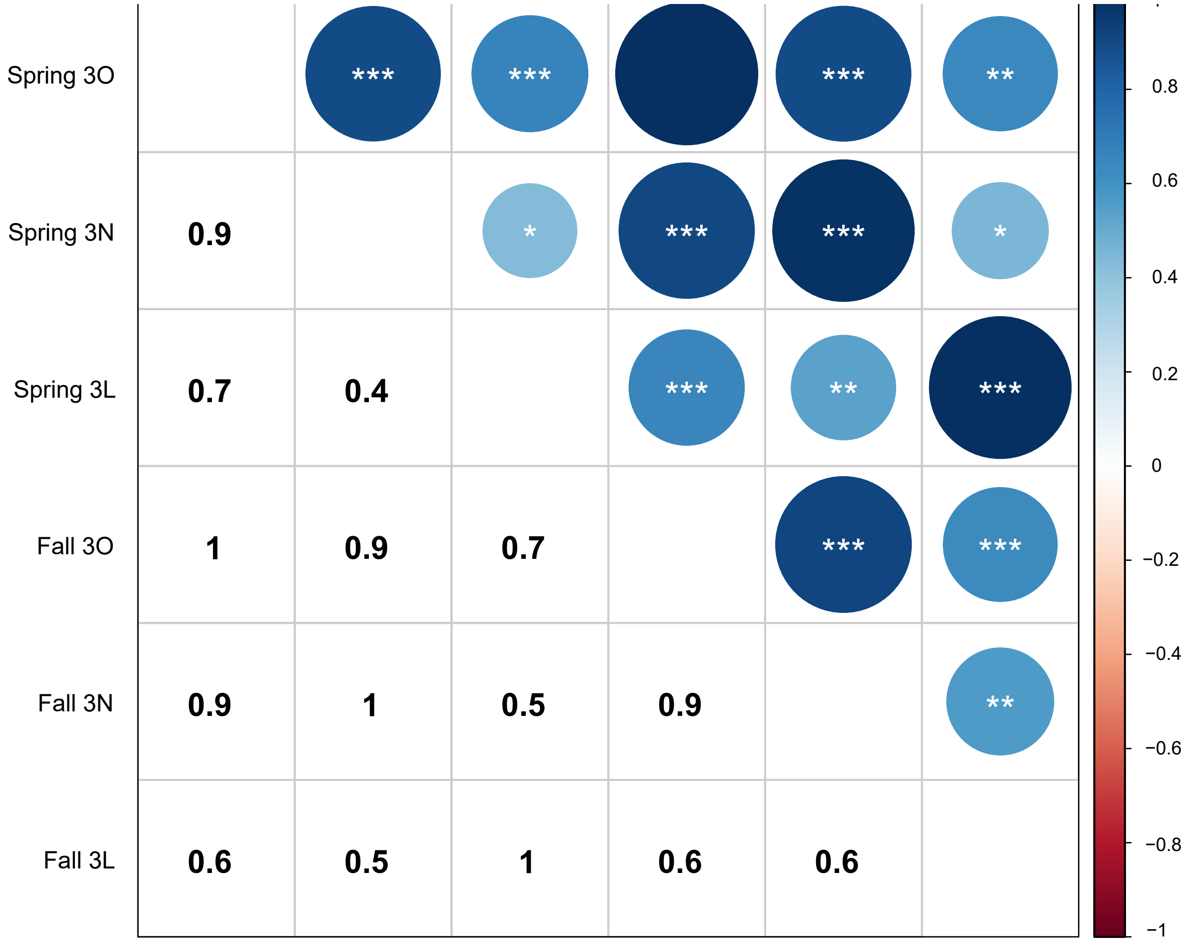

Fig. 3. Spatial correlations of the cohort effects between the six survey indices from model M5. The size and darkness of the circles indicate the magnitude of the correlations. The stars indicate significance, where more stars represent lower *p*-values (1 star = $P < 0.05$, 3 stars = $P < 0.01$).

they cannot provide much information about pre-collapse M. Spring survey indices go back to 1985, but the survey trawl used in the Spring during 1985–1995 had a larger mesh size than the current trawl and indices for age 1–2 seem less reliable. They include many zeroes that we cannot use in the current model formulation. Although Spring indices at ages 3–5 are more reliable, it would be difficult to differentiate between a change in M and year-effects with survey indices for only three ages. Hence, extending our model back to the mid-1980s does not seem useful. Our juvenile metapopulation dynamics model is only practically useful with indices produced by surveys that are effective at monitoring juveniles, such as the current DFO bottom trawl surveys that use the Campelen trawl.

Unlike the cohort effect, there was little evidence of differences in juvenile M across NAFO Divisions, indicating that the main driver(s) of mortality is likely a large scale process. Large-scale processes affecting juvenile M could include bottom-up processes like bottom-water temperature or prey availability, or top-down processes like predation or competition. Regardless of the particular driver, it is interesting that the spatiotemporal structure of M and age-1 recruitment (*e.g.* cohort effects) differed. Although differences in the spatial scales affecting different aspects of population dynamics are likely inherent in many populations (*i.e.* Levin, 1992) recognizing these differences can produce an improved mechanistic understanding of the observed patterns.

The cohort strength effects for juvenile 3LNO American plaice are much larger than the effects of time-varying M. This finding is not particularly novel since understanding recruitment dynamics has been at the core of fisheries science for over a century due to its large influence on population dynamics (*e.g.*, Houde, 2008). However, in a recent analysis of juvenile Atlantic cod dynamics around Newfoundland and Labrador, oscillations with a similar period to those estimated here were identified in both M deviations and cohort effects (Zhang *et al.*, 2020). Fur- thermore, these oscillations are similar to estimates of weight-at-length (an indicator of condition and potentiallystarvation induced mortality) for 3Ps Atlantic cod (Cadigan *et al.*, 2022). The 3Ps Atlantic cod model estimates were compared to regional drivers and significant cor- relations were identified for oceanographic (*e.g.* bottom water temperature), basal food web (*e.g.* zooplankton), and direct prey abundance (3LNO Northern sand lance (*Ammodytes dubius*)). Therefore, it is possible that Atlantic cod and American plaice recruitment and/or M are affected by similar environmental and/or trophic mechanisms.

In addition to the influence of age-1 recruitment, we also observed a substantial influence of survey year-effects on model estimates. Survey year-effects are used to ac- count for correlated observation error among ages in a particular survey that can occur for a variety of unknown reasons (Myers and Cadigan, 1995). For example, catchability may vary annually depending on environmental conditions, there may be anomalous sets accounting for a majority of catch, or there could be differences in how survey crew handles the fishing gear. Additionally, the survey year-effects may be necessary to account for stock distributional shifts (Swain and Sinclair, 1994; Swain and Benoit, 2003). Accounting for these year-effects is important when modelling juvenile dynamics based on survey indices; however, their source(s) remains speculative.

There is substantial evidence that M varies with body size and age, often by orders of magnitude over the life cycle (Lorenzen *et al.* 2022). Although our metapopulation dynamics model was based on separate age-dependent M's for each metapopulation, we assumed that annual deviations in M were the same for all ages even though the absolute value of M could differ substantially among ages. Yet, this simplifying assumption may be unrealistic. For example, if M at age 1 is 2.0 and M at age 5 is 0.3 then it is possible that annual M deviations at age 2 are larger than at age 5. However, additive M deviations have a multiplicative effect on cohort survival; that is, if $M_{a,y} = M_a + \delta_y$ then $N_{a+1,y+1} = N_{a-1,y-1} \exp\left(-M_a\right) \exp\left(-\delta_{y-1}\right)$. If annual M deviations are multiplicative in nature then a more realistic M model would be $M_{a,y} = M_a \exp\left(\delta_y\right)$ or log $\left(M_{a,y}\right) = \log(M_a) + \delta_y$ (Cadigan, 2015; Stock and Miller, 2021). Using the approximation $\exp\left(\delta_y\right) \approx 1 + \delta_y$, then $M_{a,y} = M_a \exp\left(\delta_y\right) \approx M_a + M_a \delta_y$. Note that if δ_y is normally distributed with mean zero and stationary variance $\sigma_\delta^2/(1 - \varphi_\delta^2)$ then $M_a \delta_y$ also is also normally distributed with mean zero but with stationary variance $M_a^2 \sigma_\delta^2/(1 - \varphi_\delta^2)$. As a result, the necessity for using multiplicative rather than additive M deviations for a population where M_a decreases with age could be explored by examining whether there is higher residual variation at younger ages in an additive M deviation model. This is exactly the pattern we found (see SM. Fig. 4). However, it is also possible that the $\varepsilon_{s,a,c}$ survey measurement error variances (see Equation 7) are higher at younger ages, which is another possible model misspecification. The within-survey variance of the indices may indicate if the patterns in SM. Fig. 4 are consistent with sampling variability or not, but these sampling variances were not available to us. Therefore, given the current data, these effects are confounded and we cannot identify whether the observed residual variance pattern is the result of process or observation error. Finally, implementing a model with multiplicative M deviations

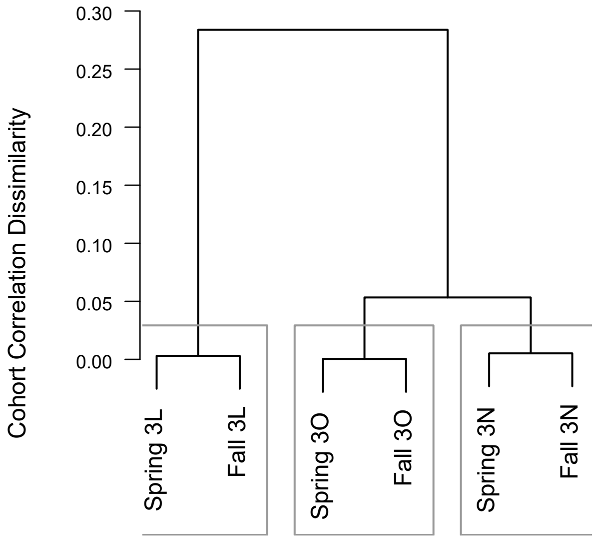

Fig. 4. Dendrogram of a dissimilarity matrix of the spatial correlations of cohort effects in model M5.

would also require that we specify the age pattern in M's. However, we are unsure why the residual variation in SM. Fig. 4 usually increases at age 5 but sometimes at age 4. These are areas that require further research.

We identified that the recruitment trends appear to differ between NAFO Divisions 3L and 3NO despite these management Divisions comprising the same stock. Similar results were found in a different cohort model used for American plaice stocks throughout all of Newfoundland and Labrador (NAFO Divisions 2J3KLNOPs; Kumar *et al.,* 2019). The spatial extent of management on the Grand Bank varies by species. Yellowtail flounder and American plaice are the only two species whose management occurs across NAFO Divisions 3LNO, whereas other species are managed separately between 3L and 3NO (*e.g.* 2J3KL vs. 3NO Atlantic cod). Previous studies have argued that American plaice in NAFO Division 3L differ from those in 3NO (see review by Brodie, 2002). These arguments have stemmed from various lines of evidence including differences in growth and maturity (Zheng *et al.,* 2020b), in divisional research surveys indicating different trends in abundance, and as a result of the general

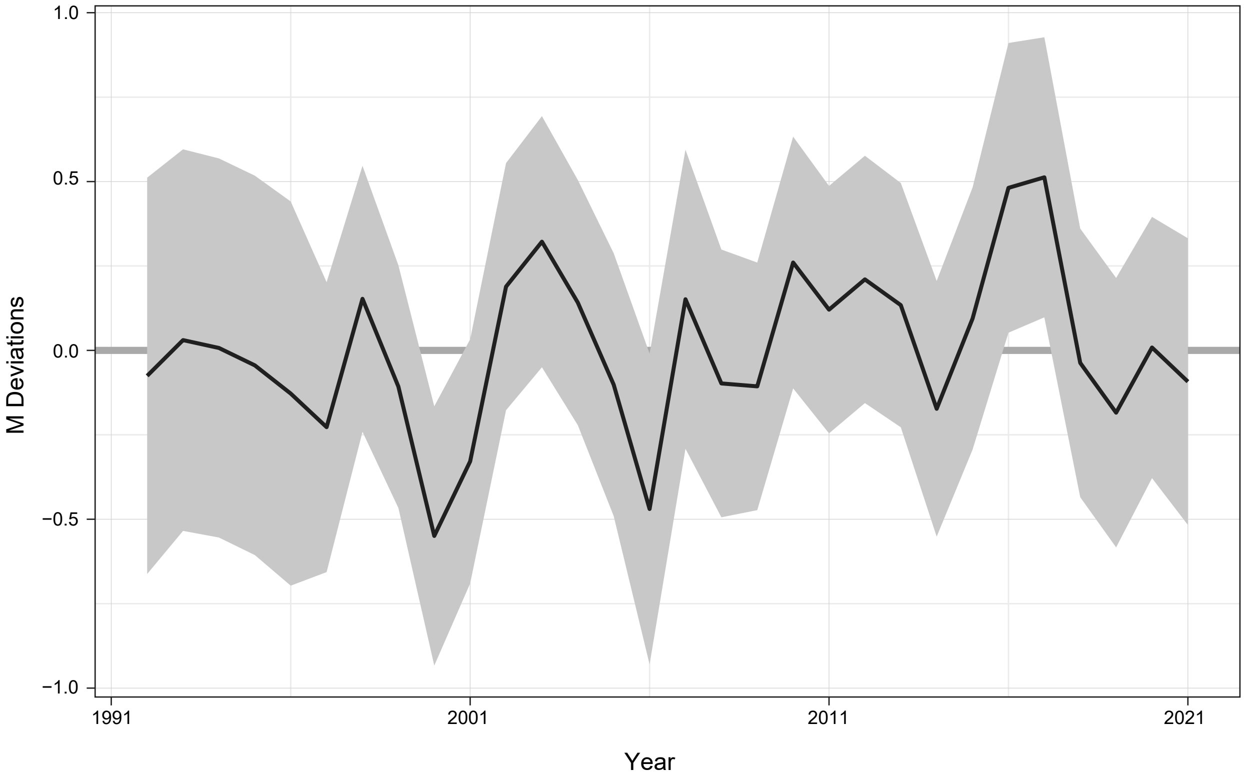

Fig. 5 Time-series of annual natural mortality rate deviations from model M5. The black line represents the point-estimates and the shaded grey area represents 95% confidence intervals.

sedentary nature of American plaice in this region (Pitt 1969; Morgan 1996). Since incorrect delineation of stock spatial structure can affect estimates of productivity and in turn affect management decision-making (*e.g.* Kerr *et al.* 2017), further work on addressing this question for 3LNO American plaice is warranted.

Acknowledgements

Research funding to N.C. and M.D.R. was provided by the Ocean Frontier Institute, through an award from the Canada First Research Excellence Fund. Research funding to M.D.R was provided by the Vanier Canada Graduate Scholarship. Research funding to N.C. was provided by the Ocean Choice International Industry Research Chair program at the Marine Institute of Memorial University of Newfoundland. We also thank the Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, the many people involved in the collection and processing of these data.

References

Brodie, W. B. 2002. American Plaice *Hippoglossoides platessoides* on the Grand Bank (NAFO Divisions 3LNO) – a Review of Stock Structure in Relation to Assessment of the Stock.

Cadigan, N. G. 2015. A state-space stock assessment model for northern cod, including under-reported catches and variable natural mortality rates. *Can. J. Fish. Aquat. Sci.* 73(2): 296–308. https://doi.org/10.1139/cjfas-2015-0047

Cadigan, N. G., Robertson, M. D., Nirmalkanna, K., and Zheng, N. 2022. The complex relationship between weight and length of Atlantic cod off the south coast of Newfoundland. *Can. J. Fish. Aquat. Sci.*: 1–33. https://doi. org/10.1139/cjfas-2021-0325.

COSEWIC. 2009. COSEWIC assessment and status report on the American Plaice *Hippoglossoides platessoides*, Maritime population, Newfoundland and Labrador population and Arctic population, in Canada. Ottawa.

Gudmundsson, G. 2004. Time-series analysis of abundance indices of young fish. *ICES J. Mar. Sci.* 61: 176–183. https://doi.org/10.1016/j.icesjms.2003.12.001

Houde, E. D. 2008. Emerging from Hjort's shadow. *J. Northwest Atl. Fish. Sci.* 41: 53–70. https://doi.org/10.2960/J.v41.m634.

Kerr, L. A., Hintzen, N. T., Cadrin, S. X., Clausen, L. W., Dickeycollas, M., Goethel, D. R., Hatfield, E. M. C., Kritzer, J. P., and Nash, R. D. M. 2017. Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES J. Mar. Sci.* 74(6): 1708–1722. https://doi.org/10.1093/icesjms/fsw188.

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., and Bell, B. 2016. TMB: Automatic Differentiation and Laplace Approximation. *J. Stat. Softw.* 70(5): 21. https://doi.org/10.18637/jss.v070.i05.

Kumar, R., Cadigan, N.G., and Morgan, M. J. 2019. Recruitment synchrony in spatially structured Newfoundland and Labrador populations of American plaice (*Hippoglossoides platessoides*). *Fish. Res.* 211(May 2018): 91–99. Elsevier. https://doi.org/10.1016/j.fishres.2018.10.027.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology, 73(6): 1943–1967. https://doi.org/10.2307/1941447.

Lorenzen, K., Camp, E. V, and Garlock, T. M. 2022. Natural mortality and body size in fish populations. *Fish. Res.* 252: 106327. Elsevier B.V. https://doi.org/10.1016/j.fishres.2022.106327

Morgan, M., and Brodie, W. 2001. An Exploration of Virtual Population Analyses for Divisions 3LNO American Plaice. *NAFO SCR Doc.*, No. 4, Serial No. 4368, 20 p.

Morgan, M., Brodie, W., Bowering, W., Maddock Parsons, D., and Orr, D. 1998. Results of Data Conversions for American Plaice in Div. 3LNO from Comparative Fishing Trials Between the Engel Otter Trawl and the Campelen 1800 Shrimp Trawl. *NAFO SCR Doc.*, No. 70, Serial No. 3062, 10 p.

Morgan, M. J. 1992. Low-Temperature Tolerance of American Plaice in Relation to Declines in Abundance. *Trans. Am. Fish. Soc.* 121: 399–402. https://doi.org/10.1577/1548-8659(1992)121%3C0399:LTOAPI%3E2.3.CO;2

Morgan, M. J. 1996. Preliminary results of tagging experiments on American plaice in NAFO Divs. 3LNO. *NAFO SCR Doc.*, No. 61, Serial No. 2737, 13 p.

Morgan, M. J., Bailey, J., Healey, B. P., Maddock Parsons, D., and Rideout, R. 2011. Recovery potential assessment of American Plaice (*Hippoglossoides platessoides*) in Newfoundland and Labrador. DFO *Can. Sci. Advis. Sec. Res. Doc.* 2011/047.

Myers, R. A., and Cadigan, N. C. 1993a. Is juvenile natural mortality in marine demersal fish variable? *Can. J. Fish. Aquat. Sci.* 50: 1591–1598. https://doi.org/10.1139/f93-180

1993b. Density-dependent juvenile mortality in marine demersal fish. *Can. J. Fish. Aquat. Sci.* 50: 1576–1590. https://doi.org/10.1139/f93-179

1995. Statistical-Analysis of Catch-at-Age Data with Correlated Errors. *Can. J. Fish. Aquat. Sci.* 52(6): 1265–1273. https://doi.org/10.1139/f95-123.

Perreault, A. M. J., Wheeland, L. J., and Morgan, M. J. 2020. A state-space stock assessment model for American plaice on the Grand Bank of Newfoundland. *J. Northwest Atl. Fish. Sci.* 51: 45–104. https://doi.org/10.2960/J.v51.m727

Pine, W. E., Pollock, K. H., Hightower, J. E., Kwak, T. J., and Rice, J. A. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries*. 28(10): 10–23. https://doi.org/10.1577/1548-8446(2003)28[10:AROTMF]2.0.CO;2

Pitt, T. K. 1969. Migrations of American Plaice on the Grand Bank and in St. Mary's Bay, 1954, 1959, and 1961. *J. Fish. Res. Board Canada.* 26: 1301–1319. https://doi.org/10.1139/f69-115

Pope, J. G., Gislason, H., Rice, J. C., and Daan, N. 2021.

Scrabbling around for understanding of natural mortality. *Fish. Res.* 240: 105952. Elsevier B.V. https://doi.org/10.1016/j.fishres.2021.105952

Punt, A. E., Castillo-Jordan, C., Hamel, O. S., Cope, J. M., Maunder, M. N., and Ianelli, J. N. 2021. Consequences of error in natural mortality and its estimation in stock assessment models. *Fish. Res.*, 233: 105759. https://doi.org/10.1016/j.fishres.2020.105759

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.r-project.org/.

Regular, P. M., Buren, A. D., Dwyer, K. S., Cadigan, N. G., Gregory, R. S., Koen-alonso, M., Rideout, R. M., Robertson, G. J., Robertson, M. D., Stenson, G. B., Wheeland, L. J., and Zhang, F. 2022. Indexing starvation mortality to assess its role in the population regulation of Northern cod. *Fish. Res.*, 247: 106180. Elsevier B.V. https://doi.org/10.1016/j. fishres.2021.106180

Robertson, M. D., Gao, J., Regular, P. M., Morgan, M. J., and Zhang, F. 2021. Lagged recovery of fish spatial distributions following a cold - water perturbation. *Sci. Rep.*: 1–11. Nature Publishing Group UK. https://doi.org/10.1038/s41598-021-89066-x

Sober, E. 2002. Instrumentalism, parsimony, and the Akaike framework. *Philosophy of Science*, 69(S3), S112-S123. https://doi.org/10.1086/341839

Stock, B. C., and Miller, T. J. 2021. The Woods Hole Assessment Model (WHAM): A general state-space assessment framework that incorporates time- and age-varying processes via random effects and links to environmental covariates. *Fish. Res.*, 240(105967). Elsevier B.V. https://doi.org/10.1016/j.fishres.2021.105967.

Swain, D. P., and Benoit, H. P. 2003. Accounting for length- and depth-dependent diel variation in catchability of fish and invertebrates in an annual bottom-trawl survey. *ICES J. Mar. Sci.*, 60: 1298–1317. https://doi.org/10.1016/S1054-3139(03)00124-3

Swain, D. P., and Sinclair, A. F. 1994. Distribution and Catchability: What is the Appropriate Measure of Distribution? *Can. J. Fish. Aquat. Sci.*, 51: 1046–1054. https://doi.org/10.1139/f94-104

Walsh, S. J., Simpson, M., and Morgan, M. J. 2004. Continental shelf nurseries and recruitment variability in American plaice and yellowtail flounder on the Grand Bank: Insights into stock resiliency. J. Sea Res., 51(3–4): 271–286. https://doi.org/10.1016/j.seares.2003.10.003

Wheeland, L. 2021. An exploration of the impact of natural mortality assumptions in a Virtual Population Analysis for Divisions 3LNO American Plaice. *NAFO SCR Doc.*, No. 025, Serial No. 7193, 16 p.

Wheeland, L., Dwyer, K., Kumar, R., Rideout, R., Perreault, A., and Rogers, B. 2021. Assessment of American plaice in Div. 3LNO. *NAFO SCR Doc.*, No. 035, Serial No. 7204, 63 p.

Wheeland, L., Dwyer, K., Morgan, J., Rideout, R., and Rogers, R. 2018. Assessment of American Plaice in Div. 3LNO. NAFO SCS Doc., No. 039, Serial No. N6829, 77 p.

Zhang, F., Rideout, R., and Cadigan, N. 2020. Spatiotemporal variations in juvenile mortality and cohort strength of Atlantic cod (Gadus morhua) off Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.*, 77(3): 625–635. https://doi.org/10.1139/cjfas-2019-0156

Zheng, N., Cadigan, N. G., and Morgan, M. 2020a. A spatiotemporal Richards–Schnute growth model and its estimation when data are collected through length-stratified sampling. Environ. Ecol. Stat., 27(3): 415–446. https://doi.org/10.1007/s10651-020-00450-8

Zheng, N., Robertson, M., Cadigan, N., Zhang, F., Morgan, J., and Wheeland, L. 2020b. Spatiotemporal variation in maturation : A case study with American plaice (*Hippoglossoides platessoides*) on the Grand Bank off Newfoundland. *Can. J. Fish. Aquat. Sci.*, 77(10): 1688–1699. https://doi.org/10.1139/cjfas-2020-0017

J. Northw. Atl. Fish. Sci., Vol. 53: 57–77 Publication (Upload) date: 17 Oct. 2022

Evaluating growth dimorphism, maturation, and skip spawning of Atlantic halibut in the Gulf of Maine using a collaborative research approach

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McBride, R.S., Maynard, G.A., Elzey, S.P., Hennen, D.R., Tholke, E.K. Runnebaum, J.M. and McGuire, C.H. 2022. Evaluating growth dimorphism, maturation, and skip spawning of Atlantic halibut in the Gulf of Maine using a collaborative research approach. *J. Northw. Atl. Fish. Sci.*, **53:** 57–77. https://doi.org/10.2960/J.v53.m736

Abstract

The data-limited nature of Atlantic halibut (*Hippoglossus hippoglossus*) in U.S. waters hampers evaluation of what may be a slow but steady rebuilding pattern. Here, we collaborate with the commercial fishery to design and implement a multi-gear sampling program that collected 100s of biological samples from throughout the Gulf of Maine in a five-year period, 2014–2018. Examination of sectioned otoliths revealed a maximum age of 12 years (females) and 13 years (males); in comparison, Atlantic halibut as old as 40–50 years have been collected elsewhere in the western North Atlantic. Growth modeling confirmed sexual dimorphism, with a larger asymptotic length (L_∞) for females (214 cm fork length [FL]) than males (195 cm FL). Estimates of median female length at maturity, L_{50}, of 128 cm FL (124–132 cm, 95% confidence limits), and median female age at maturity, A_{50}, of 9.6 years old (9.0–10.8 years), were longer and older than previous reports for the Gulf of Maine, likely resulting from our use of histological instead of macroscopic methods to classify maturity. Histology demonstrated that vitellogenesis initiated in individuals in spring, nearly a year prior to spawning, which allowed us to identify first-time (primiparous) spawners and provided the first potential evidence of skip spawning for this species. Finally, an index was developed to track the proportion of potentially mature females in the fishery, which showed an increasing trend; this qualitative tool may prove useful in a data-limited environment for evaluating the relative stock status of Atlantic halibut.

Keywords: age, cooperative research, life history, reproduction, *Hippoglossus hippoglossus*

Introduction

The current stock status of Atlantic halibut, *Hippoglossus hippoglossus*, in U.S. waters is unknown but is considered well below target levels based on qualitative evaluation of the stock and historical evidence of much higher abundance (Blaylock and Legault, 2012; Hennen, 2020). Bottom trawls exhibit relatively poor catchability for Atlantic halibut, and persistently low catches in standardized fishery-independent bottom trawl surveys in U.S. waters confounds the detection of abundance trends (Hovgård and Riget, 1992; Zwanenburg *et al.*, 2003; Rago, 2018; DFO, 2020). Evidence of rebuilding is limited but includes: 1) managed fishery catches that have steadily increased from about 40 metric tons (mt) annually during the fishing years 2002–2004 to about 140 mt during 2017–2019, and 2) a time series of commercial catch standardized to fishing effort that shows a stable or slightly increasing trend (Hansell *et al*., 2020). In contrast to the U.S. situation, Atlantic halibut in Canadian waters are certified by the Marine Stewardship Council. Much higher landings are reported, between 2500 and 4100 mt each year since 2010 (DFO, 2020), and the value of this fishery in Canada has increased seven-fold since the early 2000s (Shackell *et al*., 2021).

Atlantic halibut are managed and assessed independently by the United States and Canada with conflicting evidence these stocks may (Kersula and Seitz, 2019; Liu *et al.*, 2019) or may not (Seitz *et al*., 2016; Shackell *et al*., 2016) be connected. Recent genomic evidence suggests two genotypic stocks in the western North Atlantic: one across the North American continental shelf region and another in the semi-enclosed Gulf of St. Lawrence (Kess *et al*., 2021). Such genetic structure is overlaid by additional spatial structure in life history traits and migratory contingents (Shackell *et al.*, 2021).

U.S. Atlantic halibut is likely to remain data limited, for some time, regarding assessment and management. Life history traits typically provide useful context for such data-limited situations. For example, heavily overfished stocks are characterized by size and age truncation, with corresponding loss in reproductive potential (Hixon *et al*., 2014; Barnett *et al*., 2017). In the case of Atlantic halibut, females can live to 38 and males to 50 years (Armsworthy and Campana, 2010), but in U.S. waters, Sigourney *et al*., (2006) observed few fish older than 13 years.

Confounding a direct interpretation of age truncation as a result of fishing pressure, Atlantic halibut exhibit broad geographic variability in life history traits. Growth rates are faster and sizes at maturity are smaller in warmer, southern waters (Armsworthy and Campana, 2010; Shackell *et al*., 2019; Shackell *et al*., 2021). Atlantic halibut in the Gulf of Maine may experience faster growth rates because of higher temperatures than in most Canadian waters, and they appear to exhibit sexual dimorphism as evident in most flatfish species, but growth modeling of fish captured in the Gulf of Maine has not been reported in the literature (Sigourney *et al*., 2006; Shackell *et al*., 2019).

Some aspects of Atlantic halibut reproduction are not well understood in U.S. waters but general reproductive principles are known based on halibut from other areas. Atlantic halibut is an iteroparous, batch spawner with group-synchronous oocyte development with respect to vitellogenesis (Norberg *et al*., 1991; Neilson *et al*., 1993). The final stages of oocyte maturation appear to begin in January – indicating the initiation of winter spawning – becoming transparent and reaching sizes of 2.3–3.4 mm (Haug and Gulliksen, 1988). Haug and Gulliksen (1988) estimated annual fecundity of Atlantic halibut to range from 0.5 to 7.0 million eggs for females from 132 to 195 cm total length. Elevated temperatures have been demonstrated to delay spawning and reduce quantity and quality of eggs for Atlantic halibut (Brown *et al*., 2006).

In this study, we provide new life history parameters for Atlantic halibut at the southern range of its geographic distribution in the western North Atlantic. We overcame a chronic issue of low sample sizes by partnering with fishermen, and used a variety of fishing gears, which resulted in large numbers of fish of all sizes, both sexes, and year round throughout the Gulf of Maine (Read and Hartley, 2006; Fairclough *et al*., 2014; Thiel *et al*., 2014). We used best practices for ageing fish, including a direct comparison of thin-sectioned otoliths to whole otoliths (Karlson *et al*., 2013). We also applied gonad histology as a best practice to evaluate reproductive maturity and to reveal evidence of primiparity and skip spawning (Rideout and Tomkiewicz, 2011; McBride *et al*., 2013). Finally, to aid in future evaluation of the population, we propose the use of an index that approximates the proportion of mature females in the fishery, as a qualitative tool for evaluating the relative stock status.

Materials and methods

Collaborative sampling

A collaborative research approach between federal, state, and industry partners sampled Atlantic halibut throughout the Gulf of Maine. The largest single so urce of biological samples came from a novel, collaborative fishery-dependent sampling program lead by the Cape Cod Commercial Fishermen's Alliance (CCCFA) and The Nature Conservancy (TNC), who used multiple bottom-tending gear types (trawl, longline, and gillnet), fishing predominantly east of Cape Cod (Fig. 1; sample sizes tabulated in Supplemental Materials). Fishermen were compensated for each complete halibut sample, under conditions set forth in an Exempted Fishing Permit (EFP) by NOAA fisheries, and issued to 23 collaborating fishing businesses. Researchers trained collaborating fishermen through in-person training sessions, written protocols, and with a 'how-to' video https://www.youtube.com/watch?v=XhMV9e3UA14 (CCCFA, 2018) recorded by participating fishermen. Fishermen were provided sampling kits including tools, datasheets, a spring scale, and various sampling containers. Northeast multispecies regulations limit fishermen to landing one legal sized (> 41 inches, 104 cm) halibut per trip; under the EFP, the number of samples per day was increased to five in order to maximize sample collection, although it was extremely rare to receive five samples from a single trip.

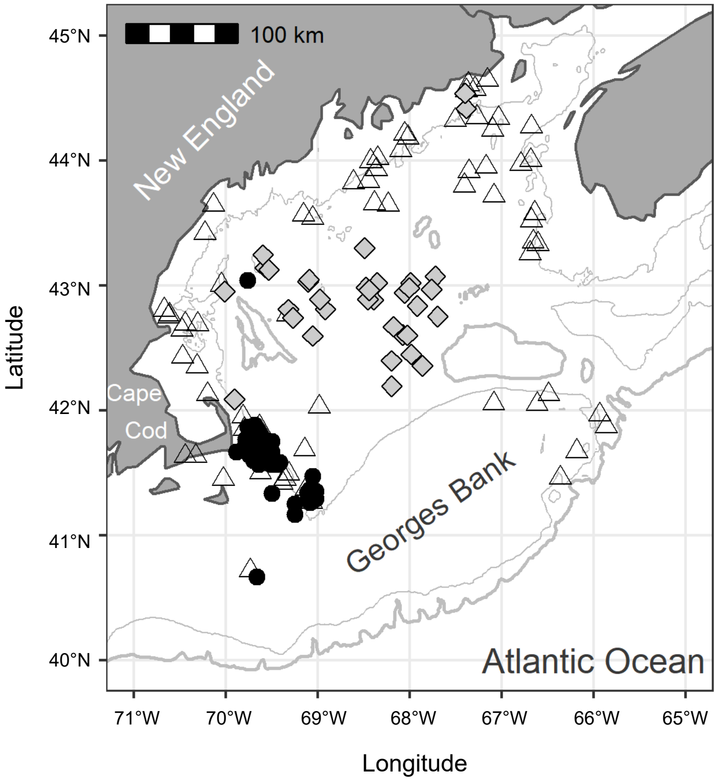

Fig. 1. Atlantic halibut (*Hippoglossus hippoglossus*) were collected throughout the Gulf of Maine, as depicted here for females used in the reproductive analyses. This plot of individuals collected identifies the multiple fishing gears used: bottom trawls (open triangles), gillnets (solid circles), and longlines (gray diamonds). A single fish collected by rod and reel is not shown. The North American continent is in dark gray, and the 100 m and 250 m isobaths are outlined in the thin and thick gray profiles, respectively. The entire scale bar is 100 km. See Supplemental Materials for sample sizes by source, gear, month, and year.

Additional halibut were obtained from several other sources: Maine's commercial fishery; the Maine and New Hampshire inshore bottom trawl survey; the Northeast Fisheries Science Center's (NEFSC) Ecosystem Survey Branch bottom trawl survey (Politis *et al*. 2014); the NEFSC's Cooperative Research Branch (CRB) bottom longline survey (McElroy *et al*. 2019); an industry-based bottom trawl survey in partnership with the Massachusetts Division of Marine Fisheries; and lastly, the NEFSC CRB Study Fleet Program.

Fish were collected as early as 2014–16, and sampling rates increased markedly in 2017–18 as a result of the partnership with CCCFA and TNC. Fish were collected in all months of the year except March during the 5-year period 2014–2018 (Supplemental Materials).

Fish were initially processed at sea and samples were stored on ice to be processed and preserved in the laboratory within 48 hours. Fork length (FL) was measured and reported to the nearest 1 cm. Total mass (TM) was measured to the nearest 1 g by fishery-independent sources or 500 g by fishery-dependent sources, and reported in kg. Ovary mass (OM) was recorded to the nearest g, and the gonadosomatic index was calculated as GSI = OM/(TM-OM) × 100. Sagittal otoliths were excised and stored dry in envelopes for ageing. Approximately 1 cm3 piece of tissue was excised from the middle of the ovary and fixed in 10% neutral-buffered formalin for gonad histology.

Otolith ageing

Age determinations were made on whole sagittal otoliths prior to sectioning for subsequent determinations. Halibut sagittal otoliths differ slightly in shape between the eyed side of the fish and the blind side. When possible, both otoliths from each fish were examined side by side. The asymmetrical (eyed side) otolith tends to be thinner and wider which yields clearer annuli during whole otolith ageing. Whole otoliths were immersed in mineral oil and the distal surface was examined with reflected light. Oil was wiped off after ageing to prevent clearing of the otoliths.

After each sample had been aged whole, the otoliths were embedded in epoxy and thin sectioned through the core with a low-speed diamond wafering saw. These sections were then affixed to glass microscope slides and examined either with reflected (Fig. 2) or transmitted light. The age readers preferred the use of reflected light, except in the oldest fish where increased magnification was needed. The symmetrical otolith was preferred for age determination of thin sections as they are thicker, yielding to better separation of annuli in the primary reading plane along the edge of the sulcal groove.

All structures (n = 421) were assigned an age by two independent readers, with no knowledge of fish size, sex, or previously assigned ages. For structures in which there was disagreement in age between readers, a third joint reading was conducted to reach a consensus age. If a consensus could not be reached, the sample was discarded.

Although otolith ageing with a thin section method has been validated by Armsworthy and Campana (2010), we had not aged this species previously, so we compared ages from surface reads of whole otoliths to sectioned otoliths, and a subsample (n = 92) of the otoliths (whole and sectioned) was aged twice by each reader to assess within reader precision. Estimates of age precision included coefficient of variation (Chang, 1982), percent agreement, and percent agreement + 1 year. Precision estimates were generated between readers (n = 327) and within readers (n = 92) for a subset of the structures. Tests of symmetry (Bowker's, Evans and Hoenig's, McNemar's, as described by McBride [2015]) were performed using the FSA package in R (Ogle *et al*., Version 0.8.30, 2020). Due to difficulty reading whole otoliths and very low reader confidence, consensus ages were only reached for the subset of whole otoliths.

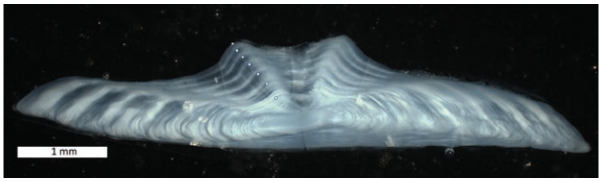

Fig. 2: Cross section of an Atlantic halibut (*Hippoglossus hippoglossus*) otolith viewed with reflected light. This individual was captured in May with the translucent zone nearly complete at the edge. Counting the edge, this fish was determined to be age 7 (annuli and edge marked with white dots on left side of the sulcus).

Final age assignments were based on the number of annuli counted on the sectioned otoliths, the capture date, and the amount of otolith growth after the final completed annulus. This grouped all fish spawned in a given calendar year into the same age group. A birthdate of December 1st was used, based on the literature and evidence presented herein, to calculate biological ages for use in growth modeling.

The von Bertalanffy and Gompertz growth models were evaluated for sex-specific growth of Atlantic halibut. Models were varied to allow each combination of model parameters to be fixed or variable between sexes. Size and age data of 93 males and 297 females were fit to both models and evaluated using Akaike's Information Criterion (AIC) within R software (version 3.6.3) (Supplemental materials).

Our ability to evaluate gear bias was limited by small sample sizes for long line and rod and reel. However, length at age for ages 4–8 were compared between gillnet-captured fish and bottom-trawl-captured fish using Student's t tests.

Chapman-Robson mortality estimates were calculated using the FSA package in R (Ogle *et al*., Version 0.8.30, 2020). Mortality was calculated with all data combined, by sex, and by gear, including 95% confidence intervals.

Ovarian Histology and Oocyte Staging

Subsamples of fixed ovarian tissue were trimmed to < 4 mm thickness, placed in a cassette, and returned to formalin until histology processing. These subsamples were prepared using standard paraffin embedding techniques (McBride *et al*., 2013), including sectioning the tissue using a rotary microtome set to 5 µm, mounting on microscope slides, and staining with Schiffs-Mallory trichrome. Histology slides were viewed (20–400x) on a monitor using a microscope and digital camera.

Descriptions for oocyte stages, including post-ovulatory follicles (POFs) and oocyte atresia, were modified from Neilson *et al*. (1993) for Atlantic halibut; Kennedy *et al*. (2011) for Greenland halibut, *Reinhardtius hippoglossoides*; Press *et al*. (2014) for winter flounder, *Pseudopleuronectes americanus*; and Fish (2020) for Pacific halibut, *Hippoglossus stenolepis* (See also Supplemental Materials). At their most advanced, primary growth (PG) germ cells were small (< 200 µm) with nucleoli scattered along the periphery of the nucleus (Fig. 3). Development of early cortical alveoli (EC) in the germ cell were the first cytoplasmic inclusions noted, appearing initially as scattered, unstained vacuoles on the periphery of the cell. A late cortical alveoli (LC) germ cell stage was recognized once a biphasic dark-light ring of inclusions developed around the periphery of the cytoplasm. An early vitellogenesis (V1) stage emerged as orange inclusions appeared proximal to the outer ring of cortical alveoli. Vitellogenic inclusions spread until the cytoplasm was 'fully yolked' (V2). Histology plate images were scanned using the Grundium Ocus slide scanner and images were taken using Aperio ImageScope software (Figs. 3, 4).

Evidence of oocyte maturation — either migration or breakdown of the nucleus or hydration of the cell — was not observed. Evidence of ovulation was rare, with only the oldest stages of post-ovulatory follicles observed. Follicular atresia was identified as early (alpha) or late (beta), and ranked by extent, but offered little additional information to classify maturity. Tunica (gonad wall) thickness was measured to the nearest micron, as an index of maturity, when present in the histology section. Measurement of the tunica occurred at an intact section of the tissue, away from edges caused by excision of the tissue (see Fig. 4 and Supplemental Materials).

Later, we refer to oocyte stage-specific maximum oocyte diameters. These were measured from images of approximately 300 oocytes per female suspended in water, as captured using a microscope and camera (Leica M26 scope

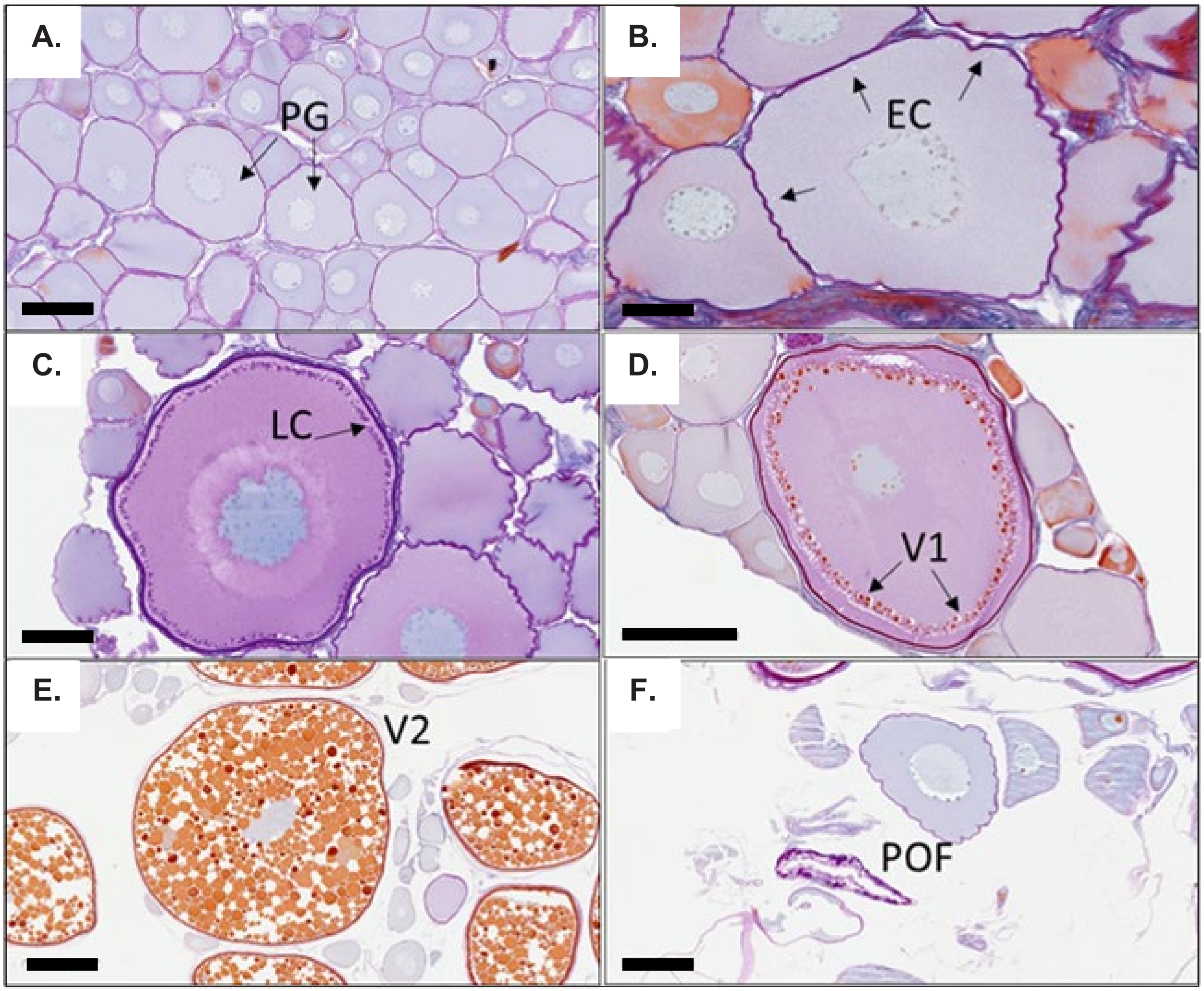

Fig. 3. Images of primary and secondary oocyte development of Atlantic halibut (*Hippoglossus hippoglossus*). **A**) An immature fish with primary growth (PG) oocytes, **B**) early development of cortical alveoli (EC) in the cytoplasm, **C**) late development of cortical alveoli (LC) in the cytoplasm, **D**) early development of yolk (V1), **E**) full development of yolk (V2), and **F**) an older post-ovulatory follicle (POF). Scale bars are 100 microns (A, C, F), 70 microns (B); 200 microns (D), or 400 microns (E).

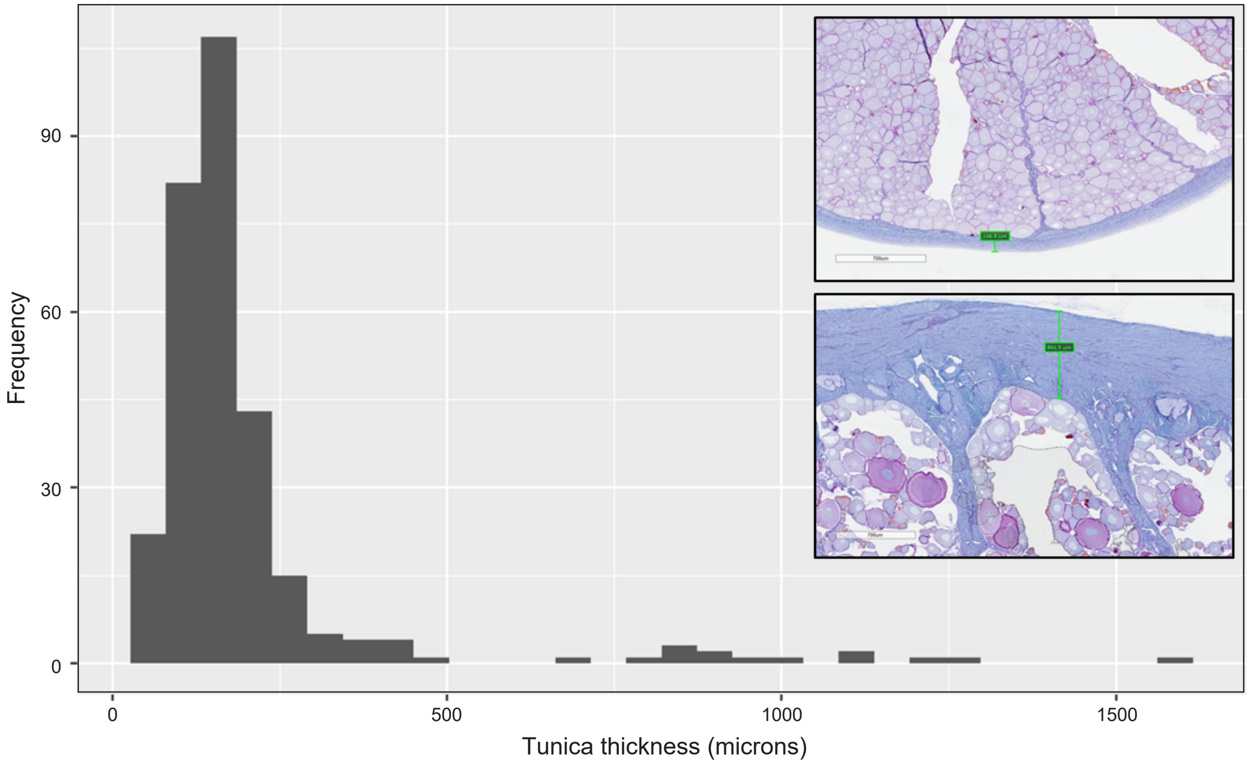

Fig. 4. Frequency of female Atlantic halibut (*Hippoglossus hippoglossus*) tunica (gonad wall) thickness, measured from histology slides of ovarian tissue. The threshold for maturity based on tunica thickness was ≥ 500µ. Specific images are inset of (top) an immature fish showing thin tunica (137µ), and (bottom) a mature fish with thick tunica (842µ). The scale bar in both photomicrographs is 700µ.

and Leica DFC295 camera). Image analysis software (ImageJ with the plugin ObjectJ) was used to manually measure the oocyte diameters. The most advanced oocyte stage (MAOS) of these whole oocytes was identified from a paired sample of ovarian histology.

Maturity classification, ageing, and modelling

Maturity was classified following criteria initially developed for Greenland halibut (Kennedy *et al*., 2011) and winter flounder (Press *et al*., 2014). In the former, vitellogenesis required more than a year to complete, whereas in the latter, vitellogenesis started 10–12 months prior to spawning. Atlantic halibut were classified as immature if they did not have vitellogenic oocytes, any POFs, or a thin tunica (< 500 µ). They were classified as mature if they had vitellogenic oocytes (MAOS V1 or V2), POFs of any age, or a thick tunica. The use of a thick or thin tunica is directed at distinguishing all immature classes from resting fish, the latter of which is a mature class and often confused with immature fish macroscopically (*e.g.*, McBride *et al*., 2013). Support of the specific threshold of 500 µm is presented elsewhere in this paper (Fig. 4).

The binomial, logistic model — logit (mature) = $e^{a+bX}/(1+e^{a+bX})$ — was used to estimate maturity parameters, where a and b are estimated and X is length or age. Confidence limits (95%) were estimated by bootstrapping the data using the sizeMat package in R (Torrejon-Magallanes, 2020).

Changes in Proportion Mature Over Time

In the absence of an effective fishery-independent survey for Atlantic halibut in U.S. waters, fishery-dependent data have been used for stock assessment (Hennen, 2020). In particular, commercial discard rates have been used as an index of abundance. As discarded fish are typically small, a new index was developed to track the proportion of fish landed larger than the L_{50}, determined herein as 128 cm, as measured by port samplers.

Atlantic halibut regulations in the United States have restricted fishermen to one landed fish per trip since 1999, and the minimum size of retention was adjusted from 36 to 41 inches (91.4, 104 cm) in 2009, which starts our time series. In practice, this results in some unknown degree of highgrading where the largest fish encountered is the most likely to be landed. Therefore, the size composition of landed fish may be reasonably indicative of trends in the average maximum size of fish encountered. The annual proportions were estimated as the proportion of fish larger than the L_{50} estimate, using U.S. catches since 2009, and the time series was fit with a generalized linear model (GLM). The data are binomially distributed, where fish $> L_{50}$ were given a 1 and fish $< L_{50}$ were given a 0. The model used year to predict the proportion mature.

Comparing the proportion mature in the Canadian Scotian shelf (4WXZ) stock of Atlantic halibut to the U.S. stock was of interest as the CA stock is relatively data rich and has increased over recent years (DFO, 2020). Fixed station longline survey data from area 4WXZ was also fit to a GLM using year to predict proportion $> L_{50}$. Survey data in this case were preferred as there is reason to believe that the selectivity of fishers in area 4WXZ has changed, in order to better target larger Atlantic halibut (den Heyer pers. com).

Results

Collaborative, multigear sampling

Atlantic halibut were collected throughout the Gulf of Maine (Fig. 1). Bottom trawls collected Atlantic halibut in all years, 2014–2018, all around the Gulf of Maine, in both U.S. and Canadian waters, with some samples on the northeast peak of Georges Bank and offshore of southern New England (Supplemental Materials). Gillnets operated by the CCCFA focused their fishing offshore of Cape Cod, sampling in 2017–18. Longline sampling collected Atlantic halibut in all years, primarily in the deeper portions of the Gulf of Maine.

A wide size range of fish was collected, and the size ranges differed between gears. Fish caught by bottom trawl had the smallest median size (84 cm fork length), but the widest range of sizes (30–171 cm; *n* = 118; Fig. 5). Fish caught by gillnet had the narrowest inter-quartile range, and the longline gear had the highest median. Although, longline gear is typically used to target larger Atlantic halibut in commercial fisheries of the Gulf of Maine and Scotian Shelf, the longlines used here were rigged for groundfish (cod, haddock, pollock) with small (12/0 size) hooks and squid bait, as compared to the larger 16/0 hooks, and half herring bait preferred by commercial halibut fishermen. The sex composition from the CCCFA catch east of Cape Cod were overwhelmingly female: only 27 of the 234 halibut with confirmed sex identification were male (88% female).

Age and growth

Atlantic halibut was a difficult-to-age species, even for Reader 1, who had more experience with otoliths than Reader 2. With whole otoliths, both readers agreed that they had very low confidence, and the results presented a mix of low precision and bias (Table 1). Whole otoliths yielded younger ages than sectioned otoliths across most age classes (Table 2). The opacity of the whole otoliths reduced the visibility of the annuli laid down in the first few years of life.

Table 1. Precision estimates for Atlantic halibut (*Hippoglossus hippoglossus*) ages. Sample size (*n*), Chang's coefficient of variation (CV), percent agreement, percent agreement within 1 year (% within 1), and symmetry test (Evans Hoenig) significance are reported. The results between all tests of symmetry were largely the same, so only the results from Evans and Hoenig's test is shown (ns denotes no significance and * denotes $P < 0.05$), as recommended by McBride (2015).

	Method and read	***n***	**%CV**	**% agreement**	**% within 1**	**Evans Hoenig**
Within Reader	Whole, Reader 1	92	16.52	39.1	82.6	*
	Whole, Reader 2	92	15.73	39.1	84.8	*
	Sectioned, Reader 1	92	7.97	53.8	95.7	ns
	Sectioned, Reader 2	92	16.87	18.3	75.0	*
Between Reader	Whole, first reading	327	11.85	44.2	85.3	ns
	Whole, second reading	92	8.25	63.0	97.9	*
	Sectioned, first reading	92	11.41	40.9	97.2	*
	Sectioned, second reading	327	10.64	47.4	88.1	ns

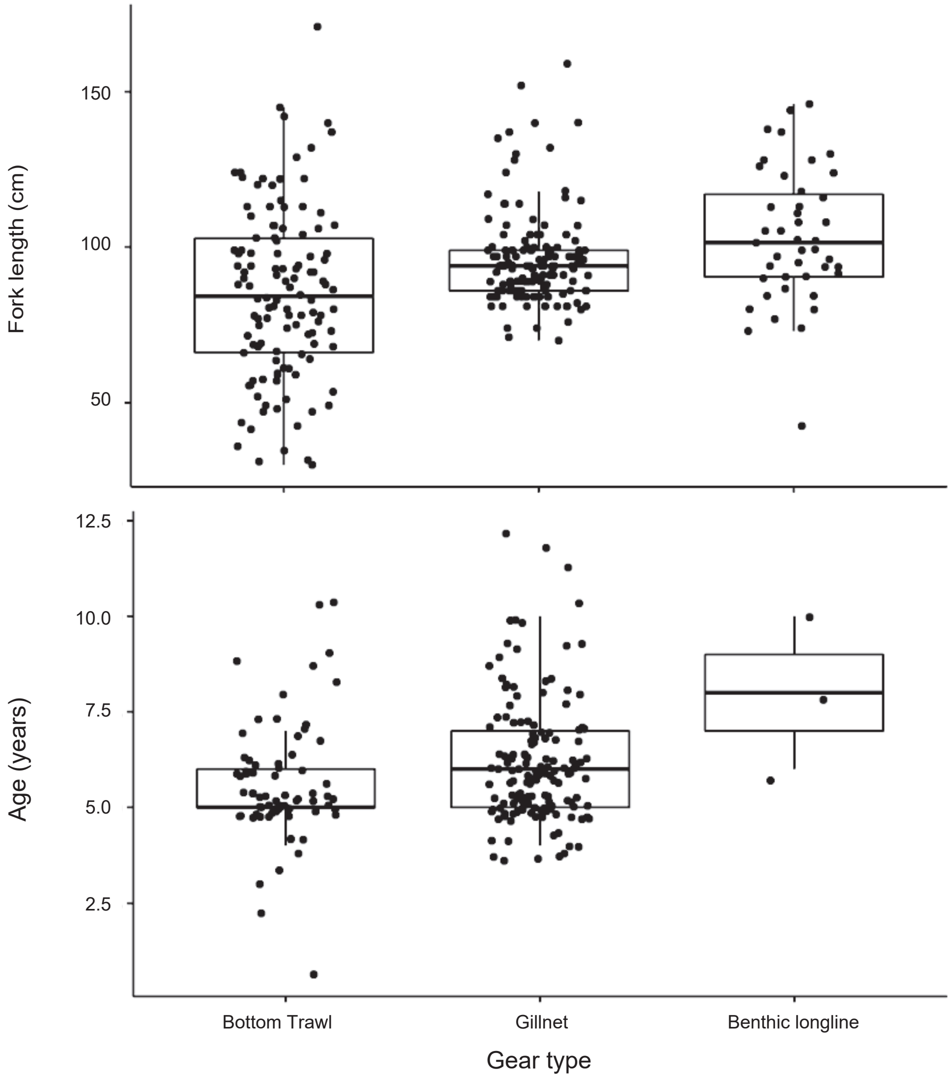

Fig. 5. Sizes (top) and ages (bottom) of female Atlantic halibut (*Hippoglossus hippoglossus*) used for reproductive analyses. Both size and age differed significantly by gear type (Kruskal-Wallis test, $P < 0.001$). Data are plotted as jittered points overlaid on a box-whisker plot, where the median is surrounded by a box of the inter-quartile range (IQR), and the whiskers are an additional 1.5 times the interquartile range. A single fish (130 cm fork length) collected by rod and reel is not shown.

Neither reader had specific experience ageing this species before, and precision and bias improved from the first to second reads, particularly with sectioned otoliths (Table 1; %CV, Evans Hoenig test). With sectioned otoliths, Reader 2 exhibited bias between reads where Reader 1 did not (Table 1; Evans Hoenig test). This was likely due to the experience level of the readers.

Atlantic halibut were assigned ages from 0 to 13 years. Average age of females was slightly older (5.8 years; 5.6–6.0 years) [mean; 95% confidence limits] than males (4.5; 4.0–5.0). Despite this, the maximum recorded age of males (13 years, $n = 52$) was slightly older than that of females (12 years, $n = 247$) (Fig. 6).

By gear, bottom trawls captured the largest age range (0–10 years; Fig. 6). Gillnets captured older fish but ages were truncated at the low range (4–13 years). The other gears had smaller sample sizes and the ages were within 2–11 years.

Table 2. Age frequency table of Atlantic halibut (*Hippoglossus hippoglossus*) ages from sectioned and whole otoliths. Grey boxes represent agreement between structures.

	Sectioned otolith age									
Whole otolith age	0	1	2	3	4	5	6	7	8	9
9									1	
8									1	1
7								1	3	
6							5	4	3	
5						19	10	3		
4					4	18	3			
3					10	1				
2										
1	4	2								
0	3									

Atlantic halibut demonstrated dimorphic growth between sexes. In terms of model selection, the von Bertalanffy model allowing only L_∞ to vary by sex had the lowest AIC value (Table 3). Although minimal differences were seen in AIC values between the von Bertalanffy model and the Gompertz model allowing for sexual dimorphic growth, the von Bertalanffy estimated a more realistic t_0 value. The final selected model for length (L, cm) at age (t, yr) was $L_t = 195(1 - e^{-0.093(t-0.217)})$ for males and $L_t = 214(1 - e^{-0.093(t-0.217)})$ for females (Model vB5, Table 4, Fig. 7). Females were predicted with this model to be 1.3 cm larger at age one, 6.8 cm larger at age five, 11.3 cm larger at age 10, and 14.2 cm larger at age 15 (ΔL_∞ = 19 cm between sexes).

The Chapman-Robson estimate of total mortality (Z) for all data combined was 0.60 (95% confidence limit = 0.52–0.69) for ages five and older (Table 5). Estimates of Z varied by gear and sex from a low of 0.60 (0.51–0.69) for females to a high of 0.66 (0.54–0.79) for males.

Student's t-tests revealed significant differences in length at age between gillnet captured fish and bottom trawl captured fish. Halibut aged 4 and 5 captured with a gillnet were larger than fish captured with a bottom trawl. The inverse relationship was true for ages 7 and 8.

Oogenesis

Oocyte development required several years. Primary growth (PG) oocytes were observed, as the most advanced oocyte stage, in females as young as one year old and as small as 30 cm (sample sizes, $n_{\text{aged}} = 197$, $n_{\text{total}} = 261$). Further steps in oocyte development took at least four more years. Early development of cortical alveoli (EC) first appeared in females as young as five yr. and as small as 64 cm ($n_{\text{aged}} = 7$, $n_{\text{total}} = 14$), and late development of cortical alveoli (LC) first appeared in females as young as six yr. and as small as 102 cm ($n_{\text{aged}} = 7$, $n_{\text{total}} = 15$). First development of secondary, vitellogenic (V1) oocytes appeared in females as young as nine yr. and as small as 117 cm ($n_{\text{aged}} = 1$, $n_{\text{total}} = 6$), and full development of vitellogenesis (V2) first appeared in females as young as nine yr. and as small as 81 cm ($n_{\text{aged}} = 9$, $n_{\text{total}} = 17$).

An advancing cohort of vitellogenic oocytes emerged in spring and grew rapidly in the following months, creating a bimodal distribution of oocyte sizes that is characteristic of group synchronous development of vitellogenic oocytes (Table 6; Supplemental Materials). Maximum sizes of different oocyte stages were: 671 µm (LC), 828 µm (V1), 1873 µm (V2), as measured from whole oocytes (see also Supplemental Materials for oocyte diameters measured from gonad histology of individual females). The emergence and advance of a vitellogenic cohort of oocytes was also evident in monthly plots of the GSI, when the ovarian weight relative to the ovary-free female weight maximized in October at 8.5% (Fig. 8).

Indications of spawning were rare and indirect. The reset of GSI values after November, suggested a likely winter spawning season (Fig. 8). No females were observed to be actively spawning, either with oocytes advanced to nucleus migration or hydration of the oocyte (Fig. 9). No females appeared in a spent condition, either with ovaries containing relatively fresh POFs, extensive atretic yolked oocytes, residual eggs in the lumen, or a mix of these traits. Only two females had any POFs at all, and while these were unambiguously recognizable as a two-layered structure with a collapsed lumen, they were well degraded and not new (Fig. 3).

Maturity and Skipping

The median length at maturity, L_{50}, was 128 cm, with 95% confidence limits between 124 and 132 cm FL (Fig. 10). The median age at maturity, A_{50}, was 9.6 years old, with 95% confidence limits between 9.0 and 10.8 years (Fig. 10).

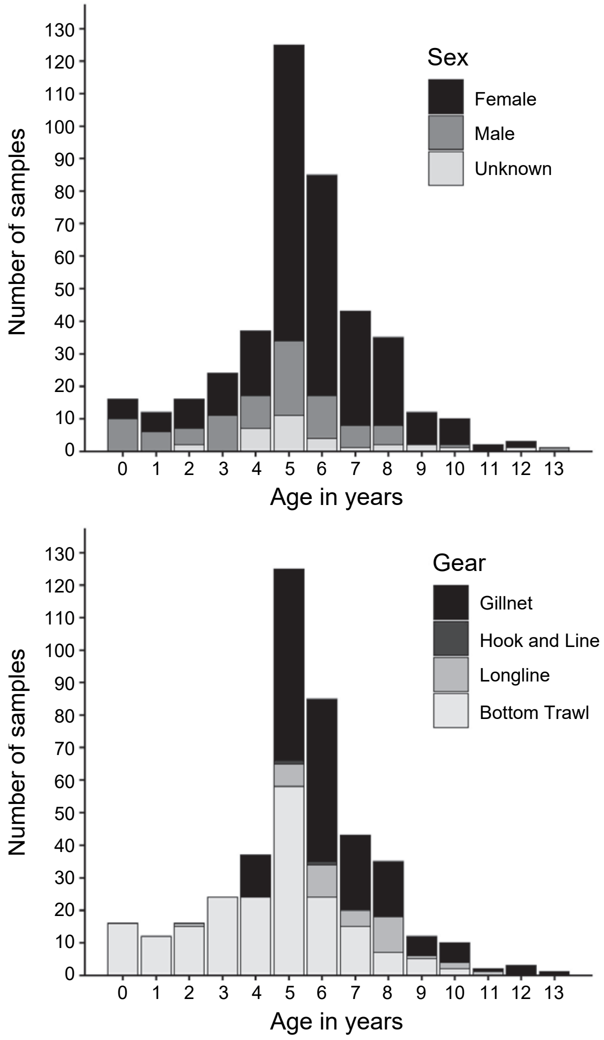

Fig. 6. Atlantic halibut (*Hippoglossus hippoglossus*) age frequency by sex (top) and gear (bottom).

Not all mature fish (*i.e.*, with evidence that they had spawned in the past) had traits to indicate they were preparing to spawn in the next spawning season (*i.e.*, skip spawners). One of 24 females identified as mature was large (135 cm FL), with a thick ovarian wall (1230 µ), but its most advanced oocyte stage was previtellogenic (LC). At the time it was caught, in late July, this resting fish was likely skipping that year's spawning cycle. This sample indicates the skipping rate among mature females was 4.2%. This estimate may be biased (low) because we did not exclude any females collected in November–December, when Atlantic halibut migrate to the continental slope (see Discussion).

A second skip spawner was detected using a different selection method. Again, skipping implies that a fish has spawned in the past, so first we selected females with a thick tunica (> 500 µm). And skipping implies the spawning frequency is mis-specified (in this case every year). Finally, to check for spawning capable ovaries among fish prior to the spawning migration to continental slope waters undertaken by this species, we selected females in the month of October, which precedes the spawning period. These criteria resulted in four females, 117–145 cm FL, each with thick tunicas (685–1000 µm). Three had spawning capable ovaries: an advanced cohort of fully yolked oocytes (MAOS: V2, GSI = 5.0 – 8.5), which would predict that they would ovulate in the approaching winter spawning period. However, the smallest mature female (117 cm FL, 900 µm tunica thickness) was not prepared to spawn within a few months (MAOS: V1, GSI =0.95). This very small sample indicated the skipping rate among mature females was 25%. This estimate may be biased (high) because it assumes that the individual diagnosed as a skipper could not advance in vitellogenesis sufficiently from fall to winter to spawn, which is likely based on other northern flatfishes, but an assumption based on limited sample sizes in our study.

The two skippers observed here, both aged as nine years old, were classified as mature females that are not part of the spawning stock in that reproductive cycle. One of them appeared as resting, with no evidence advancing a vitellogenic cohort of oocytes at time of capture in July, while the other female was developing, but it showed only early signs of vitellogenesis in October, with no evidence it was prepared to ovulate eggs in the winter spawning period that was imminent.

We also considered that we could identify first-time spawners, or primiparous females, based on evidence that the advance of a vitellogenic cohort of oocytes may proceed most of the year in advance of the spawning season, when in combination with immature fish having a thin tunica. One fish could be identified as a first-time spawner by these combined criteria: A female with both a thin tunica (374 µm) and a MAOS of V1 was 122 cm FL, unknown age, caught in April, with a modest gonad to body ratio (GSI = 0.96). Five of the six females with a MAOS of V1 were caught in April–May (Table 6), suggesting a pronounced seasonality initiating vitellogenesis (except for the skip spawner that initiated vitellogenesis in October, as mentioned in the preceding paragraph). This isolated example of a primiparous female was among the group of 24 mature females, representing 4.2% of the mature fish.

Changes in Proportion Mature Over Time

The proportion of fish larger than the L_{50} = 128 cm has increased since 2009 in both the U.S. and Canadian Scotian shelf stocks (Fig. 11). For the U.S. stock, this proportion

Table 3. Multiple growth models were fit to the length and age data of Atlantic halibut (*Hippoglossus hippoglossus*). Model parameters were allowed to vary between sexes in different combinations. Degrees of freedom and AIC values are shown AIC.1 denotes the difference in AIC values from the best fit model.

model type	**sex variable parameters**	**df**	**AIC**	**AIC.1**	**model.seq**
Gompertz	L_∞, G, X	7	3936	1.60	Go1
	G, X	6	3937	3.17	Go2
	L_∞, X	6	3935	1.21	Go3
	L_∞, G	6	3936	1.96	Go4
	L_∞	5	3935	0.75	Go5
	G	5	3936	1.50	Go6
	X	5	3937	2.46	Go7
	none	4	3937	2.82	Go8
von Bertalanffy	L_∞, K, T_0	7	3937	2.98	vB1
	K, T_0	6	3937	2.79	vB2
	L_∞, T_0	6	3936	2.11	vB3
	L_∞, K	6	3935	1.00	vB4
	L_∞	5	3934	0.00	vB5
	K	5	3936	1.39	vB6
	T_0	5	3938	3.76	vB7
	none	4	3939	4.29	vB8

has been increasing at a rate of approximately 18% per year (where year is a significant predictor of the odds of proportion mature, with a coefficient of 0.173 [$P < 0.001$], and $e^{0.173} = 1.18$ or 19%). The trend in the Canadian data is less dramatic, but based on more data (*n* = 6 091 lengths vs. 1 244 for the US). In the Canadian data, year predicts proportion mature with a coefficient of 0.0825 [$P < 0.001$], representing an annual increase in the odds of proportion mature of about 9%.

Discussion

Collaborating with commercial harvesters during their operational fishing trips increased sample sizes, numbers of large fish, and spatiotemporal coverage. In terms of life history, this allowed updated, reasonably precise estimates of dimorphic growth and patterns of reproduction and maturity by Atlantic halibut in the Gulf of Maine. This study also showed an increase in the proportion of mature fish in both the U.S. and Canadian Scotian Shelf stocks, providing some hope for rebuilding the U.S. stock.

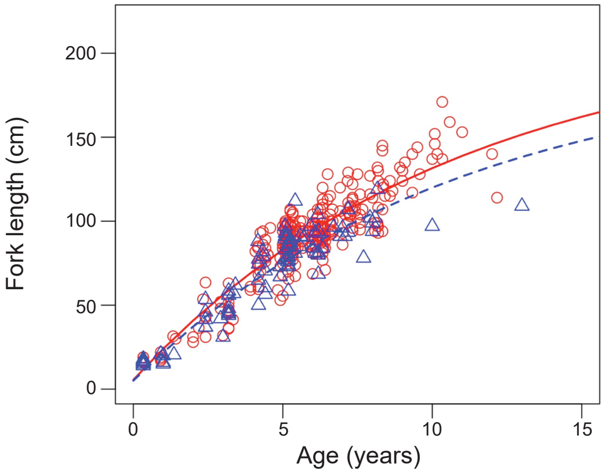

Fig. 7. Atlantic halibut (*Hippoglossus hippoglossus*) growth. Red circles represent females, blue triangles males. Red solid line (female) and blue dashed line (male) are the growth curves as plotted by model vB5 (see Tables 3, 4).

Table 4. Model parameters for the von Bertalanffy model with separate asymptotic maximum lengths for each sex (*i.e.,* $L_\infty F$, the female asymptotic maximum length), accounting for sexual dimorphism of Atlantic halibut (*Hippoglossus hippoglossus*). These parameters are for model vB5 from Table 3.

	Estimate	Std. Error	t value	Pr(>|t|)	95% LCI	95%UCI
$L_\infty F$	214.0	44.02	4.860	0.000	127.5	300.5
K	0.093	0.030	3.079	0.002	0.034	0.152
t_0	0.217	0.342	0.636	0.525	-0.454	0.889
$L_\infty M$	195.2	41.04	4.760	0.000	114.5	275.8

Collaborative Research

We characterize our partnership with commercial fishermen as 'collaborative,' rather than merely 'cooperative,' in that the fishermen were involved in all aspects of the project from forming the research question, to developing sampling methods, to collecting biological samples and reviewing results (Yochum *et al*., 2011). During the project design phase fishermen accurately projected the number of samples they as a group could deliver over two years, which increased the annual sample number from 18 per year in 2014–2016, to over 100 per year in 2017–2018. This resulted in an overall yield of 197 females, 63% of all female Atlantic halibut samples collected for the study. Our study was not designed to address the issue of highly skewed sex ratios in the commercial catch, but we note our results were very similar to the 4F:1M ratio reported in retained catches of Pacific halibut, so this does not appear to be unexpected (Loher *et al*., 2022). In a separate study, Hansell *et al*. (2020) also collaborated with Maine fishermen to develop a time series of standardized catch of Atlantic halibut, which serves as an index of abundance to track trends in population abundance of this data-limited fishery.

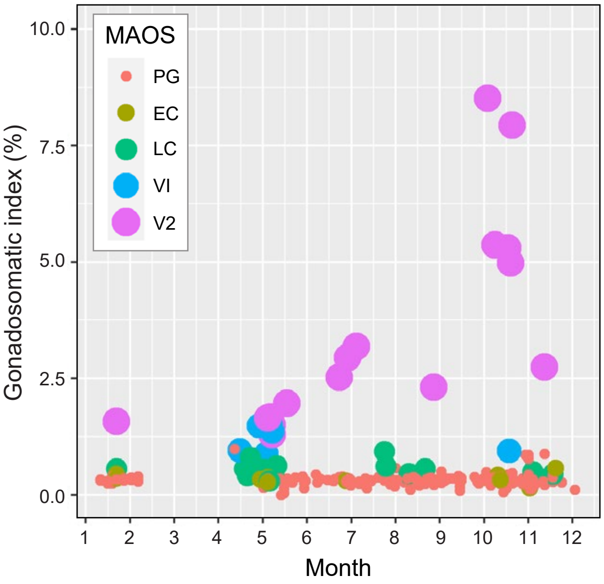

Fig. 8. Seasonal patterns of the gonadosomatic index of female Atlantic halibut (*Hippoglossus hippoglossus*) individuals. The most advanced oocyte stage (MAOS) of each female is indicated by color and increasing symbol size denotes more advanced oogenesis (see Fig. 3 for oocyte stages). Monthly tick marks indicate the first of each month (1 = January 1, all years of data pooled).

Working with commercial fishermen was a highly cost-effective approach to collect biological samples for a relatively rare species like Atlantic halibut, where fishermen landed 0–5 fish per day under an exempted fishing permit. The cost of chartering fishing vessels to target Atlantic halibut would have been prohibitively expensive considering the low daily catch and absence of a targeted fishery. Through the collaborative development of the project, fishermen agreed to financial reimbursement per complete sample, which was designed to compensate fishermen for the cost of carefully completing the biological sampling and sample delivery, while at the same time not being so high that fishermen would be tempted to target Atlantic halibut for the funds.

Age and growth

Atlantic halibut collected for ageing in this study were of size (14–171 cm) and age ranges (0–13 years) similar to those seen by Sigourney *et al.* (2006), whose samples came from a similar geographic region; in fact, many of Sigourney *et al.*'s samples came from the same federal bottom trawl survey which has been ongoing since the 1960s. We report ageing error rates transparently but find no comparable reports of ageing error in the literature

Table 5. Chapman-Robson total mortality estimates and confidence intervals for Atlantic halibut (*Hippoglossus hippoglossus*) captured in this study. Ages five and older were used for mortality estimates. Samples of all fish were also subset by sex and the dominant fishing gears.

Sample	Z	95% LCI	95% UCI
All fish	0.60	0.52	0.69
Female	0.60	0.51	0.69
Male	0.66	0.54	0.79
gillnet	0.61	0.51	0.70
trawl	0.62	0.46	0.77

to evaluate the relative precision in ageing this species among studies. Moreso, there are other factors that affect maximum sizes and ages in growth studies of Atlantic halibut. In particular, Armsworthy and Campana (2010) reported larger (232 cm) and older (50 years) Atlantic halibut from Canadian waters. But their larger maximum size and age may be at least partly an artifact of much larger sample size, because they examined 2 000 thin-sectioned otoliths, selected from an archive of about 65 000 fish. When sample sizes are larger, often, so is the size and age range. Also, their methods describe a post-stratification procedure of this archive (*e.g.*, five fish per 3-cm length bin), which over represents larger and older fish relative to sampling the entire catch as we did here. Finally, the majority of their samples were from longline gear (83%), whereas the majority of our samples were from bottom trawl and gillnet gear (86%; Supplemental Materials). Longline gear catch more faster growing fish than bottom trawls (Armsworthy and Campana, 2010; Sigourney *et al*., 2006), whereas gillnets exhibit dome selectivity (*e.g.*, in this study gillnets did not capture any fish younger than age four, and age four and age five fish were larger at age than those captured by bottom trawl). Other specific gear configurations (*e.g.*, hook size on longlines) confound simple comparisons of different samples, as well. These factors, together with the rebuilt condition of Atlantic halibut in Canadian waters, all contribute to much larger and older fish in the Armsworthy and Campana (2010) report. As a historical benchmark, a halibut larger than 300 kg was caught in the Gulf of Maine in 1917 (Klein-MacPhee, 2002), whereas our largest fish, 171 cm FL, was 10 years old and weighed 44.5 kg.

Consistent with previously published work (Armsworthy and Campana, 2010; Sigourney *et al*., 2006; Bowering, 1986; Shackell *et al*., 2019), female Atlantic halibut in this study grew larger than males. The asymptotic length (L_∞) parameter fit better when modeled separately by sex, with reasonable precision considering the relatively small sample size of the largest fish. Such sexual dimorphism in growth of Atlantic halibut increases the variance of size at age in unsexed samples. Our estimations of asymptotic lengths (214 cm for females and 195 cm for males) were smaller than those produced by Armsworthy and Campana (2010) (232 cm F, 175 cm M). This is not surprising given the differences in sampling design, gear configurations, and Atlantic halibut longevity in U.S. versus Canadian waters.

Given the opportunistic sampling nature of this study in both the gear used and the area sampled, mortality estimates are preliminary. The migratory nature of Atlantic halibut, coupled with the lack of very large, reproductively active individuals in our samples, suggests that our sampling efforts were not inclusive of the whole stock. The absence of those largest individuals likely biased our mortality estimates high. Two tagging studies on the Scotian Shelf and Grand Banks of the western North Atlantic Ocean showed lower total mortality estimates of Atlantic halibut: 0.37–0.46 (years: 2007–2009), or 0.24 (males, year 2009) and 0.41 (females, year 2009) (den Heyer *et al*., 2013; Trzcinski and Bowen, 2016). However, lower total mortality is expected in Canada, where the fishery is certified by the Marine Stewardship Council.

Table 6. Seasonality of reproductive development among female Atlantic halibut (*Hippoglossus hippoglossus*), indicated as the number of fish by most advanced oocyte stage (MAOS) captured each month. See text for characterization of oocyte stages.

MAOS	Month												
	1	2	3	4	5	6	7	8	9	10	11	12	Sum
PG	16	10	0	4	34	22	26	31	24	53	42	1	263
EC	2	0	0	1	6	1	0	0	0	2	2	0	14
LC	1	0	0	3	4	1	2	2	0	0	2	0	15
V1	0	0	0	2	3	0	0	0	0	1	0	0	6
V2	1	0	0	0	5	2	2	1	0	5	1	0	17
Sum	20	10	0	10	52	26	30	34	24	61	47	1	315

Reproduction and maturity

The results from gonad histology were consistent with previous characterizations of Atlantic halibut as iteroparous with group-synchronous oocyte development with respect to vitellogenesis (Haug and Gulliksen, 1988, Neilson *et al*., 1993). In particular, we document a prolonged period of vitellogenesis (months), first-time maturing females (primiparity), repeat spawners (iteroparity), and new evidence of mature females skipping spawning. Fig. 9 integrates the published maturity scheme used by the Northeast Fisheries Science Center (NEFSC; Burnett *et al*, 1988), which is based entirely on macroscopic characters, with the processes of oogenesis and ovarian microstructure informed by gonad histology. In our region, the relative rarity of Atlantic halibut in the NEFSC bottom trawl survey is a challenge for quality assurance of training staff on at-sea maturity determinations of this

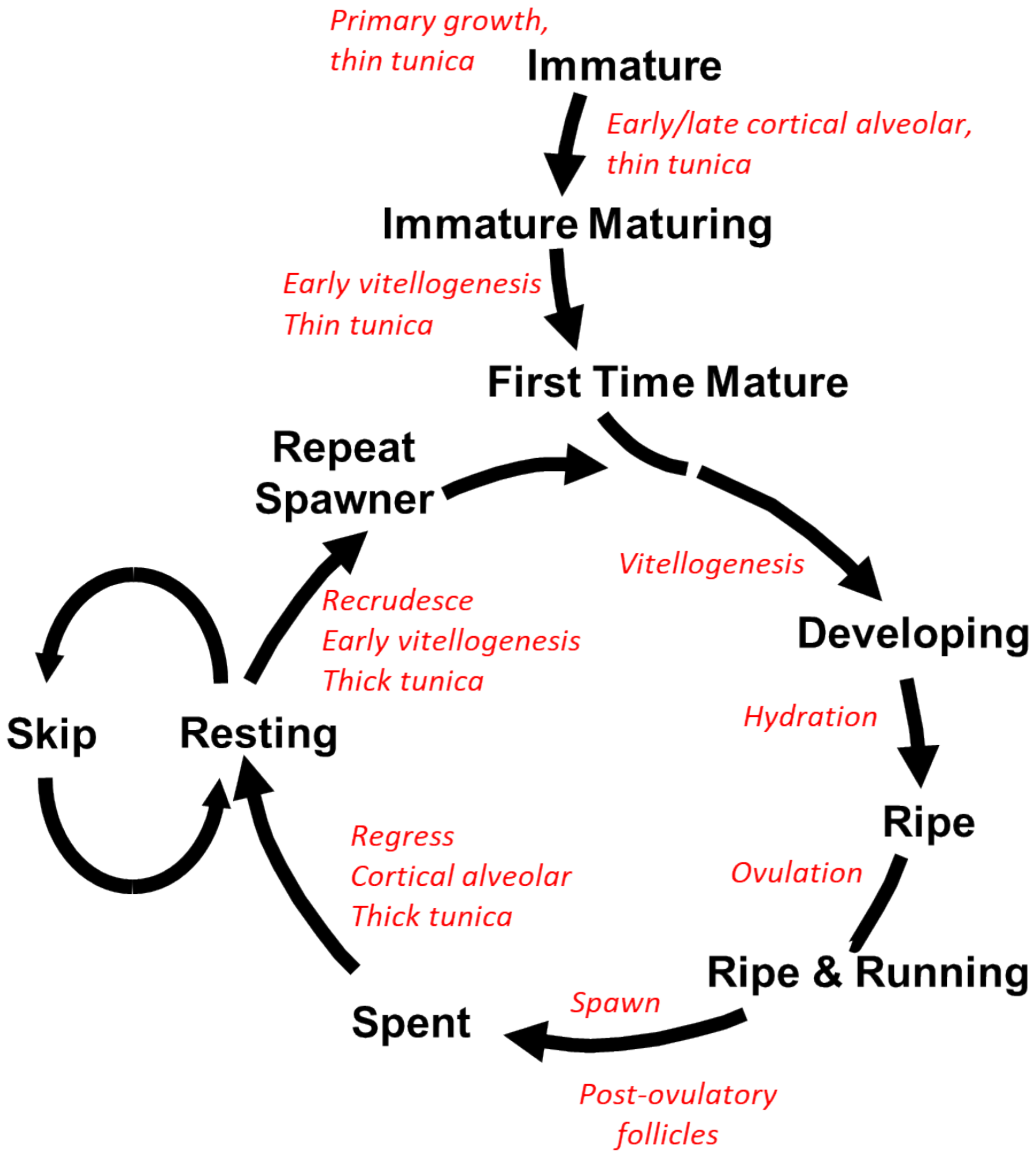

Fig. 9. Proposed maturity classification scheme for female Atlantic halibut (*Hippoglossus hippoglossus*), with major maturity classes in bold and histological features in *italics*. Both the immature and immature maturing classes showed no prospect of spawning within a year or any past spawning. Spawning capable (ripe), actively spawning (ripe and running), or immediately post-spawn (spent) were not observed in this study.

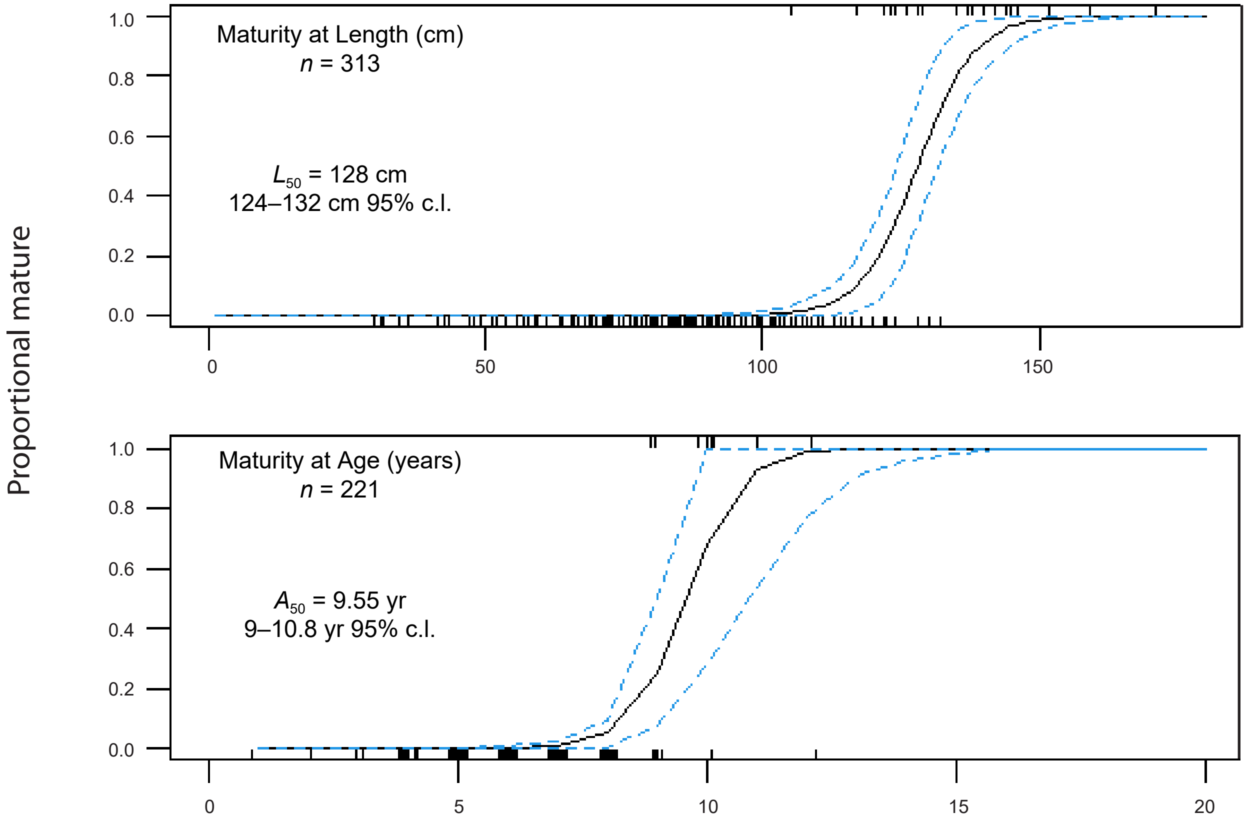

Fig. 10. Proportion mature as a function of length (top) and age (bottom) for female Atlantic halibut (*Hippoglossus hippoglossus*). The solid line is the predicted ogive, dashed (blue) line are the 95% confidence limits (c.l.). The tick marks on each x-axis indicate the individual sizes or ages (jittered) of mature (upper axis) and immature (lower axis) and *n* = the total number of individuals.

species. This updated scheme (Fig. 9) will be used together with a photographic catalog of whole gonad images (see Supplemental Materials) as part of this training.

The median length at female maturity, L_{50} = 128 cm FL, was longer than previous reports for Atlantic halibut in the Gulf of Maine, and the median age at maturity, A_{50} = 9.5 years old, was older, too (Shackell *et al.* 2021; their Fig. 7). The most direct geographic comparison of size or age at maturity would be that of Sigourney *et al.* (2006), who reported female L_{50} = 103 (4.8 SE) cm and A_{50} = 7.3 (0.41 SE) yr. for Atlantic halibut from the Gulf of Maine collected during 1977–2001. A changing, in this case increasing, median size or age at maturity between Signourney *et al.*'s and our results could well be representative of this population as maturation schedules can change with changes in fishing pressure (Rørvik *et al.*, 2021) and indices indicate a level or increasing population size (Hansell *et al.*, 2020). However, as the Gulf of Maine Atlantic halibut population is data-limited, we are not able to address this directly. Older collections from fishing grounds offshore of Nova Scotia demonstrate smaller maturity: L_{50} = 116 (2.2 SE) cm during 1947 (McCracken, 1958) and L_{50} = 107 (5.2 SE) cm during 1959–1963 (Kohler, 1967). McCracken (1958) estimated a similar age at maturity, at roughly 10–12 years. The several decade differences between some of these studies, and an expectation that maturation is not time-invariant, confounds simple geographic comparisons (but see Shackell *et al.* 2021 who assemble such a comparison).

The differences in maturity schedules are also likely the result of our use of ovarian histology, whereas previous reports used macroscopic methods. Our ability to be more precise about the presence of vitellogenesis, likely increases the estimate of age at maturity by one year. Oogenesis proceeded slowly in Atlantic halibut, with only pre-vitellogenic growth stages observed among females < 9 years old in our samples. Vitellogenesis unfolded over most of the year preceding spawning, much like shown for Pacific halibut by Fish *et al.* (2022). We postulate this creates a situation, when the ovary is viewed macroscopically, that some fish with MAOS = LC are confused as resting and erroneously classified as mature, as the case for other regional flatfish such as winter flounder (McBride *et al*., 2013). Using gonad histology, where the tunica thickness can be accurately determined, can distinguish immature and mature individuals. Given the potential for measurement bias between histological and macroscopic studies, a conservative conclusion is that the mean age and size at maturity of female Atlantic halibut in the Gulf of Maine and around Nova Scotia has been fairly stable at 7–12 years and 100–130 cm.

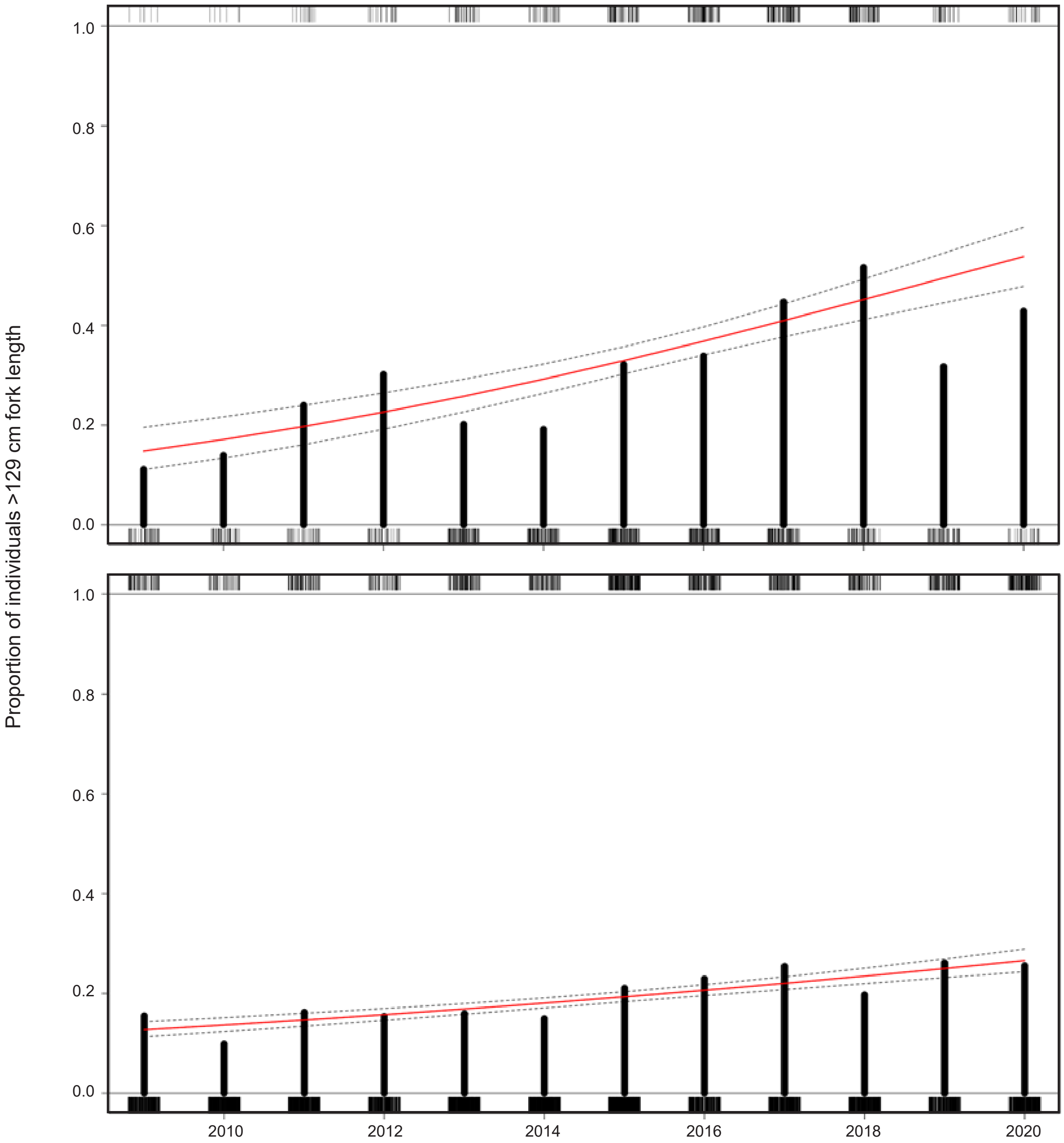

Fig. 11. Proportion mature of Atlantic halibut (*Hippoglossus hippoglossus*) in U.S. landed commercial catch (above) and Canadian longline fixed station survey (below). The bars are the proportion of fish with (length > 129 cm), the rug plots represent sample size and the red line is the fit from a binomial family GLM to the binary (0 ≤ 129 cm and 1 > 129 cm) dataset for each group. The dotted lines are the 95% confidence intervals.

Details of oocyte maturation and ovulation were not observed directly, presumably because Atlantic halibut migrate to the continental slope, outside of our sampling range, to spawn. Liu *et al*. (2019) observed tagged halibut in the Gulf of Maine making long-distance movements suggesting a spawning migration. These fish move to the Northeast Channel off Georges Bank, where neither fishing nor fishery-independent surveys takes place, explaining why we did not collect spawning halibut. Liu *et al*. did not observe abrupt ascents, which could be interpreted as spawning activity, but halibut were in these deep, presumptive spawning habitats during winter, from January to May.

Further east, in the Gulf of St. Lawrence, spawning occurred at depths of 200 m or deeper during winter, from mid-December to late-April with a peak in mid-February (Le Bris *et al*., 2018; Gatti *et al*., 2020). Still further east, in deep (800–1000 m) waters south of the Grand Banks, Armsworthy *et al*. (2014) report abrupt ascents, interpreted as spawning rises, during later autumn – early winter, from October to January. In the eastern Atlantic, the spawning season is so predictable (December–March) that the halibut gillnet fishery in Norway has been prohibited during parts of January–February since the 1950s (Godø and Haug, 1988; Haug and Gulliksen, 1988).

On the other American coast, Pacific halibut have been collected on their spawning grounds, with multiple lines of evidence of winter spawning seasonality (January–February). Evidence of spawning includes the appearance of POFs, and a more complete characterization of oogenesis and gonad maturation (*e.g.*, maximum oocyte size = 2.0 –2.5 mm, a maximum reported GSI of 15% for females; Fish *et al*., 2020, 2022).

Presumably, mature U.S. Atlantic halibut females that remain in our sampling range during the spawning season are skip spawners, but this requires additional, precise information about their spawning migration and an ability to capture them across these habitats (Rodgveller *et al*. 2016). Instead, we interrogated two samples for which we considered immature and mature females should be well mixed. Both skip spawners detected were, not surprisingly, young (9-year-old fish). Skip spawning is more likely among smaller and younger fish that may be energetically challenged compared to larger and more experienced females (Burton, 1994; Rideout and Tomkiewicz, 2011; Tronbøl *et al*., 2022). The calculations presented herein assume a prolonged period of vitellogenesis, which appears supported by our data, and a winter spawning period, which is consistently demonstrated by a number of studies reviewed in the previous paragraphs. Both samples used for these calculations were small, and therefore preliminary, but of interest as the first estimates for this species.

Accuracy in skip spawning rates is important for correctly specifying the spawning stock biomass in stock assessments, when not all mature fish spawn as expected. Electronic tagging data is a complementary tool that could contribute to evaluating skip spawning rates for halibut. Tagging data for Pacific halibut suggest that approximately 10% of mature fish are skip spawning (Loher and Seitz, 2008). The number of fish tagged and released in our region is increasing, which should soon reveal more about Atlantic halibut spawning times, frequencies (*e.g.*, skipping), and the behaviors of spawning contingents in U.S. and neighboring waters (W. DeVoe, State of Maine, pers. comm.). Multiple lines of evidence about skip spawning are needed for robust estimates of skipping rates in different populations of halibut species.

Management Implications

The U.S. Atlantic halibut stock has been depleted for at least a century (Grasso, 2008). Recent U.S. stock assessments have shown evidence of modest population increases over the last decade, and as evident herein, the proportion of mature fish in both U.S. and Canada waters has increased over the same period. These coupled trends are an indicator of an increase in reproductive potential. Now that an estimate of size at maturity exists, it is reasonably cost effective to continue to track the proportion of fish above this size as a proxy for mature females, which could be a useful qualitative assessment tool for this data-limited stock. However, it is important to understand the fishery context for using such an approach because alternative interpretations exist. For example, an increase of proportion mature in an increasing stock is contra-indicative of high fishing pressure, whereas an increase of proportion mature in a stable or decreasing stock may be indicative of recent recruitment failure.

Comparing the proportion mature between spatially adjacent stocks may be of some interest as well. In this case, we compared the proportion mature in U.S. waters to the Canadian Scotian Shelf population, within the Gulf of Maine (Fig. 1). Proportion mature is increasing in both areas, although the trend is less defined in the Canadian data. Several factors may drive the differences in magnitude of trend between the areas. The Canadian data are survey based, while the U.S. data are from commercially landed fish. Current U.S. regulations stipulate that only one Atlantic halibut per trip can be landed, which equates to a tendency for the largest fish encountered to be landed and all others discarded. The Canadian data are measurements of all fish encountered on the survey. The selectivities associated with the two data sets are therefore quite different and may influence results. The Canadian stock has been stable or increasing for many years and supports a large and valuable fishery. The U.S. stock has been depleted for a century and has not supported a directed fishery for most of that period. Therefore, the scope for stock increase (*i.e.* the distance from theoretical carrying capacity) in the U.S. is probably much greater. Finally, the extent of movement between the two areas is unknown and it is possible that some mature fish from Canada have relocated to U.S. waters, which might potentially affect the proportion mature in each area.

Alternatively, size composition of discarded fish from U.S. fishery observer data could be used to compare the U.S. and Canadian stocks. Unfortunately, Atlantic halibut encounter rates in the United States remain low, observer coverage of longline gear (the gear most likely to capture large Atlantic halibut) is low (generally < 10%; Hogan *et al.*, 2019), and there are very few mature fish among the discarded Atlantic halibut length data over the time period concerned (n = 6 fish). There is some possibility of using the kept fish from U.S. observer data, but there are far more Atlantic halibut observations in the landings data and combining the two introduces the possibility of double counting. Ideally, the U.S. data would come from a fishery independent survey, as the Canadian data does –which removes the possibility of spatial bias commonly associated with fishery dependent data (Paloheimo and Dickie, 1964) – but U.S. surveys do not sample Atlantic halibut well (Hennen, 2015).

A truncated age distribution is a common symptom of a stock in poor condition (Hilborn and Peterman, 1996). This describes a situation in which a disproportionate amount of the mature fish have been removed, leaving mostly young and immature fish in the population. This situation is dire for any stock, as mature fish supply the reproductive material for future recruitment. In this sense, a high proportion of mature fish might indicate a healthy stock. When a fishery targets immature fish, they can be removed before reproducing, which can reduce reproductive potential, as for example, when a large year class of fish is fished down before reaching maturity. When a fishery targets mature fish, the effect depends on the contribution of each age class to reproductive value (Kindvater *et al.*, 2016; Marshall *et al*., 2021). Overall, we are cautious about simple interpretations of proportion mature as an indicator of stock health. Nonetheless, an increasing trend of proportion mature together with an increasing trend of stock size is generally an indicator of a healthy stock and relatively low mortality. As there is evidence that both the U.S. and Scotian shelf Atlantic halibut stocks are increasing (Rago, 2018; DFO, 2020), our new observations of an increase of proportions mature indicates an increase in the reproductive potential of each stock.

Acknowledgements

We begin by thanking our collaborative fishing partners, particularly harvesters working with the Cape Cod Commercial Fishermen's Alliance (CCCFA; B. Eldridge, B. Hopkins, B. McCann, J. Amaru, W. Amaru, N. Muto, E. Hesse, J. Nash, G. Connors and G. Walinski) who conceptualized and helped design this project and provided the majority of halibut samples, as well as others in Maine and those involved in the Northeast Fisheries Science Center's (NEFSC) study fleet. We also appreciate the efforts of all hands participating in fishery-independent sampling, who produced a steady stream of samples from the NEFSC's bottom trawl survey and bottom longline survey, as well as samples by surveys operated by the State of Maine and Massachusetts' Division of Marine Fisheries (MDMF). Specific individuals that facilitated collecting from these sources included: G. Gianesin, W. Hoffman, M. Kersula C. Bank, D. McElroy, and D. St. Amand. We also thank the following: G. Skomal, W. Hoffman (MDMF) for fieldwork logistics; E. Koob, C. Draghetti (MDMF) for contributions to ageing; R. Marshall (The Nature Conservancy [TNC]/CCCFA) for designing and administering the commercial sampling scheme; Melissa Sanderson (CCCFA) for supporting shoreside sampling and logistics; M. Wuenschel (NEFSC) for contributions to the maturity work; S. Talmage NOAA's Greater Atlantic Regional Fisheries Office) for facilitating fishing access to the commercial fleet; J. Akin (TNC) for administering this award from NOAA. This project was funded by NOAA Fisheries' Saltonstall-Kennedy Grant Program (Award 16GAR057 to TNC) with additional funding and in-kind match from TNC.

References

Armsworthy, S. L., and Campana, S. E. 2010. Age determination, bomb-radiocarbon validation and growth of Atlantic halibut (*Hippoglossus hippoglossus*) from the Northwest Atlantic. *Environmental Biology of Fishes,* **89**: 279–295. https://link.springer.com/article/10.1007/s10641-010-9696-8.

Armsworthy, S. L., Trzcinski, M. K., and Campana, S. E. 2014. Movements, environmental associations, and presumed spawning locations of Atlantic halibut (*Hippoglossus hippoglossus*) in the northwest Atlantic determined using archival satellite pop-up tags. *Marine Biology,* **161**: 645–656. https://doi.org/10.1007/s00227-013-2367-5

Barnett, L. A. K., Branch, T. A., Ranasinghe, R. A., and Essington, T. E. 2017. Old-growth fishes become scarce under fishing. *Current Biology,* **27**: 2843–2848. https://doi.org/10.1016/j.cub.2017.07.069.

Blaylock, J., and Legault, C. M. 2012. Atlantic halibut. *In* Assessment or Data Updates of 13 Northeast Groundfish Stocks through 2010. *Northeast Fisheries Science Center Reference Document* 12-06*,* https://repository.library.noaa.gov/view/noaa/4060.

Bowering, W. R. 1986. The distribution, age, growth and sexual maturity of Atlantic halibut (*Hippoglossus hippoglossus*) in the Newfoundland and Labrador area of the northwest Atlantic. *Canadian Fisheries and Aquatic Sciences Technical Report* No 1432: 34. http://publications.gc.ca/site/eng/456903/publication.html.

Brown, N. P., Shields, R. J., and Bromage, N. R. 2006. The influence of water temperature on spawning patterns and egg quality in the Atlantic halibut (*Hippoglossus hippoglossus* L.). *Aquaculture*, **261**(3): 993–1002. https://doi.org/10.1016/j.aquaculture.2006.08.025

Burnett, J., O'Brien, L., Mayo, R. K., Darde, J. A., and Bohan, M. 1989. Finfish maturity sampling and classification schemes used during Northeast Fisheries Center bottom trawl surveys, 1963–89. Woods Hole (MA): *NOAA Technical Memorandum NMFS-F/NEC*-76: 1–14. https://repository.library.noaa.gov/view/noaa/5951

Burton, M. P. M. 1994. A critical period for nutritional control of early gametogenesis in female winter flounder, *Pseudopleuronectes americanus* (Pisces: Teleostei). *Journal of Zoology,* **233**: 405–415. https://doi.org/10.1111/J.1469-7998.1994.TB05273.X.

CCCFA [Cape Cod Commercial Fishermen's Alliance]. 2018. Halibut Biological Sampling. https://www.youtube.com/watch?v=XhMV9e3UA14

Chang, W. Y. B. 1982. A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences,* **39**: 1208–1210. https://doi.org/10.1139/f82-158.

DFO, (Department of Fisheries and Oceans, Canada). 2020. Stock status update of Atlantic halibut (*Hippoglossus hippoglossus*) on the Scotian Shelf and Southern Grand Banks in NAFO Divisions 3NOPs4VWX5Zc. *DFO Canadian Science Advisory Secretariat, Science Response*. https://waves-vagues.dfo-mpo.gc.ca/Library/40884454.pdf.

Fairclough, D. V., Brown, J. I., Carlish, B. J., Crisafulli, B. M., and Keay, I. S. 2014. Breathing life into fisheries stock assessments with citizen science. *Scientific Reports,* **4**: 7249. https://doi.org/10.1038/srep07249.

Fish, T., Wolf, N., Harris, B. P., and Planas, J. V. 2020. A comprehensive description of oocyte developmental stages in Pacific halibut, *Hippoglossus stenolepis*. *Journal of Fish Biology,* **97**: 1880–1885. https://onlinelibrary.wiley.com/doi/abs/10.1111/jfb.14551.

Fish, T. M., Wolf, N., Smeltz, T. S., Harris, B. P., and Planas, J. V. 2022 accepted. Reproductive biology of female Pacific halibut (*Hippoglossus stenolepis*) in the Gulf of Alaska. *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2022.801759

Gatti, P., Robert, D., Fisher, J. A. D., Marshall, R. C., and Le Bris, A. 2020. Stock-scale electronic tracking of Atlantic halibut reveals summer site fidelity and winter mixing on common spawning grounds. *ICES Journal of Marine Science,* https://doi.org/10.1093/icesjms/fsaa162

Grasso, G. M. 2008. What appeared limitless plenty: The rise and fall of the nineteenth-century Atlantic halibut fishery. *Environmental History,* **1**3: 66–91. www.jstor.org/stable/25473194.

Godø, O. R,, and Haug, T. 1988. Tagging and recapture of Atlantic Halibut (*Hippoglossus hippoglossus*) in Norwegian waters. *ICES Journal of Marine Science,* **44**(2):169–179. https://doi.org/10.1093/icesjms/44.2.169

Hansell, A. C., DeCelles, G. R., Kersula, M. E., and Cadrin, S. X. 2020. Incorporating harvesters' knowledge into an index of abundance for Atlantic halibut in the northwest Atlantic. *Transactions of the American Fisheries Society,* **149**: 741–752. https://doi.org/10.1002/tafs.10268.

Haug, T., and Gulliksen, B. 1988. Fecundity and oocyte sizes in ovaries of female Atlantic halibut, *Hippoglossus hippoglossus* (L). *Sarsia*, 73(4):259–261. https://doi.org/10.1080/00364827.1988.10413411

Hennen, D. 2015. Atlantic halibut. *In* Operational Assessment of 20 Northeast Groundfish Stocks, Updated Through 2014. *Northeast Fisheries Science Center Ref Doc 15-24,* https://repository.library.noaa.gov/view/noaa/5293.

2020. Atlantic halibut. *In* Operational Assessment of 14 Northeast Groundfish Stocks, Updated through 2018. *Northeast Fisheries Science Center Reference Document,* Prepublication document, https://s3.amazonaws.com/nefmc.org/8_Prepublication-NE-GrndfshOp-Assessment-1-7-2020-revision.pdf.

Hilborn, R. M., and Peterman, R. M. 1996. The development of scientific advice with incomplete information in the context of the Precautionary Approach. *FAO Fisheries Technical Paper*. http://www.fao.org/3/w1238e/W1238E04.htm.

den Heyer, C. E., Schwarz, C. J., and Trzcinski, M. K. 2013. Fishing and natural mortality rates of Atlantic halibut estimated from multiyear tagging and life history. *Transactions of the American Fisheries Society,* **142**: 690–702. https://doi.org/10.1080/00028487.2012.760482.

Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science: Journal du Conseil,* 71: 2171–2185. https://doi.org/10.1093/icesjms/fst200.

Hovgård, H., and Riget, F. F. 1992. Comparison of longline and trawl selectivity in cod surveys off West Greenland. *Fisheries Research,* **13**: 323–333. https://doi.org/10.1016/0165-7836(92)90085-8.

Karlson, S., Michalsen, K., and Folkvord, A. 2013. Age determination of Atlantic halibut (*Hippoglossus hippoglossus* L.) along the coast of Norway: status and improvements. *ICES Journal of Marine Science: Journal du Conseil,* **70**: 50–55. http://doi.org/10.1093/icesjms/fss174.

Kennedy, J., Gundersen, A. C., Høines, A. S., and Kjesbu, O. S. 2011. Greenland halibut (*Reinhardtius hippoglossoides*) spawn annually but successive cohorts of oocytes develop over 2 years, complicating correct assessment of maturity. *Canadian Journal of Fisheries and Aquatic Sciences,* **68**: 201–209. https://doi.org/10.1139/F10-149.

Kersula, M., and Seitz, A. 2019. Diverse migratory behaviors of Atlantic halibut (*Hippoglossus hippoglossus*, L.) based on the 2000–2017 Maine halibut tagging program. *Journal of Northwest Atlantic Fishery Science,* **49**: 13–24. https://doi.org/10.2960/J.v50.m719.

Kess, T., Einfeldt A. L., Wringe, B., Lehnert, S. J., Layton, K. K. S., McBride, M. C., Robert, D., Fisher ,J., Le Bris ,A., den Heyer, C., Shackell, N., Ruzzante, D. E., Bentzen, P., and Bradbury, I. R. 2021. A putative structural variant and environmental variation associated with genomic divergence across the Northwest Atlantic in Atlantic Halibut. *ICES Journal of Marine Science,* **78**: 2371–2384. https://doi.org/10.1093/icesjms/fsab061.

Kindsvater, H. K., Mangel, M., Reynolds, J. D., and Dulvy, N. K. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecology and Evolution,* **6**: 2125–2138. https://doi.org/10.1002/ece3.2012.

Klein-MacPhee, G. 2002. Righteye flounders. Family Pleuronectidae. *In* B.B. Collette and G. Klein-MacPhee (Eds.), Bigelow and Schroeder's *Fishes of the Gulf of Maine*, 3rd ed. Smithsonian Institution Press. pp. 560–587.

Kohler, A. C. 1967. Size at maturity, spawning season, and food of Atlantic halibut. *Journal of the Fisheries Research Board of Canada,* **24**: 53–66. https://doi.org/10.1139/f67-006.

Le Bris, A., Fisher, J. A. D., Murphy, H. M., Galbraith, P. S., Castonguay, M., Loher T., and Robert ,D. 2018. Migration patterns and putative spawning habitats of Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence revealed by geolocation of pop-up satellite archival tags. *ICES Journal of Marine Science*, **75**: 135–147. https://doi.org/10.1093/icesjms/fsx098

Liu, C., Bank, C., Kersula, M., Cowles, G. W., Zemeckis, D. R., Cadrin, S. X., and McGuire, C. 2019. Movements of Atlantic halibut in the Gulf of Maine based on geolocation. *ICES Journal of Marine Science,* **76**: 2020–2032. https://doi.org/10.1093/icesjms/fsz169.

Loher, T., McCarthy, O., Sadorus, L. L., Erikson, L. M., Simeon, A., Drinan, D. P., Hauser, L., Planas, J. V., and Stewart, I. J. 2022. A Test of Deriving Sex-Composition Data for the Directed Pacific Halibut Fishery via At-Sea Marking. *Marine and Coastal Fisheries* **14**(4): e10218. https://doi.org/10.1002/mcf2.10218

Loher, T., and Seitz, A. C. 2008. Characterization of active spawning season and depth for eastern Pacific halibut (*Hippoglossus stenolepis*), and evidence of probable skipped spawning. *Journal of Northwest Atlantic Fishery Science,* **41**: 23–36. https://doi.org/10.2960/J.v41.m617.

Marshall, D., Bode, M., Mangel, M., Arlinghaus, R., and Dick, E. 2021. Reproductive hyperallometry and managing the world's fisheries. *Proceedings of the National Academy of Sciences,* **118**: e2100695118. https://doi.org/10.1073/pnas.2100695118.

McBride, R. S. 2015. Diagnosis of paired age agreement: a simulation of accuracy and precision effects. *ICES Journal of Marine Science: Journal du Conseil,* **72**: 2149–2167. https://doi.org/10.1093/icesjms/fsv047.

McBride, R. S., Wuenschel, M. J., Nitschke, P., Thornton, G., and King, J. R. 2013. Latitudinal and stock-specific variation in size- and age-at-maturity of female winter flounder, *Pseudopleuronectes americanus*, as determined with gonad histology. *Journal of Sea Research,* **75**: 41–51. https://doi.org/10.1016/j.seares.2012.04.005.

McCracken, F. D. 1958. On the biology and fishery of the Canadian Atlantic halibut, *Hippoglossus hippoglossus* L. *Journal of the Fisheries Research Board of Canada,* **15**: 1269–1311. http://dx.doi.org/10.1139/f58-070.

McElroy, W. D., O'Brien, L., Blaylock, J., Martin, M. H., Rago, P. J., Hoey, J. J., and Sheremet, V. A. 2019. Design, Implementation, and Results of a Cooperative Research Gulf of Maine Longline Survey, 2014–2017. *NOAA Technical Memorandum NMFS-NE-249*. https://doi.org/10.25923/2sgn-mx62.

Neilson, J. D., Kearney, J. F., Perley, P., and Sampson, H. 1993. Reproductive biology of Atlantic halibut (*Hippoglossus hippoglossus*) in Canadian waters. *Canadian Journal of Fisheries and Aquatic Sciences,* **50**: 551–563. http://www.nrcresearchpress.com/doi/abs/10.1139/f93-064#.V45zEjFvk1s.

Norberg, B., Valkner, V., Huse, J., Karlsen, I., and Grung, G. L. 1991. Ovulatory Rhythms and Egg Viability in the Atlantic Halibut (*Hippoglossus hippoglossus*). *Aquaculture*, **97**(4): 365–371. https://doi.org/10.1016/0044-8486(91)90328-5

Ogle, D. H., Wheeler, P., and Dinno, A. 2020. FSA, version 0.8.30, https://github.com/droglenc/FSA.

Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer,* **155**: 152–163. https://www.ices.dk/sites/pub/Publication%20Reports/Marine%20Science%20Symposia/Phase%202/Rapport%20et%20Proces-Verbaux%20des%20Reunions%20-%20Volume%20155%20-%201964%20-%20Partie%2031%20de%2043.pdf.

Politis, P. J., Galbraith, J. K., Kostovick, P., and Brown, R. W. 2014. Northeast Fisheries Science Center Bottom Trawl Survey Protocols for the NOAA Ship Henry B. Bigelow. *Northeast Fisheries Science Center Reference Document 14-06*: [Accessed February 2021]. https://repository.library.noaa.gov/view/noaa/4825.

Press, Y. K., McBride, R. S., and Wuenschel, M. J.2014. Time course of oocyte development in winter flounder (*Pseudopleuronectes americanus*) and spawning seasonality for the Gulf of Maine, Georges Bank, and Southern New England stocks. *Journal of Fish Biology,* **85**: 421–445. http://onlinelibrary.wiley.com/doi/10.1111/jfb.12431/full.

Rago, P. J. 2018. Halibut Assessment Report for 2017. *Prepared for the New England Fishery Management Council.* http://s3.amazonaws.com/nefmc.org/Halibut–Assessment–Report–draft–12–01–2017.pdf.

Read, A. N., and Hartley, T. W., (Editors). 2006. Partnerships for a common purpose: Cooperative fisheries research and management. Bethesda, MD: American Fisheries Society. https://doi.org/10.47886/9781888569858.ch31

Rideout, R. M., and Tomkiewicz, J. 2011. Skipped spawning in fishes: more common than you might think. *Marine and Coastal Fisheries,* **3**: 176–189. http://www.tandfonline.com/doi/abs/10.1080/19425120.2011.556943.

Rodgveller, C., Stark, J., Echave, K., and Hulson, P. 2016. Age at maturity, skipped spawning, and fecundity of female sablefish (*Anoplopoma fimbria*) during the spawning season. *Fishery Bulletin*, **114**: 89–102. https://doi.org/10.7755/FB.114.1.8.

Rørvik, C, Bogstad, B, Ottersen, G, and Kjesbu, O. 2021. Long-term interplay between harvest regimes and biophysical conditions may lead to persistent changes in age-at-sexual maturity of Northeast Arctic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, **79**: 576–586. https://doi.org/10.1139/cjfas-2021-0068

Seitz, A. C., Evans, M. D., Courtney, M. B., and Kanwit, J. K. 2016. Continental shelf residency by adult Atlantic halibut electronic tagged in the Gulf of Maine. *Journal of Northwest Atlantic Fishery Science,* **48**: 33–40. https://doi.org/10.2960/J.v48.m713.

Shackell, N. L., Ferguson, K. J., denHeyer, C. E., Brickman, D., Wang, Z., and Ransier, K. T. 2019. Growing degree-day influences growth rate and length of maturity of Northwest Atlantic halibut (*Hippoglossus hippoglossus* L.) across the southern stock domain. *Journal of Northwest Atlantic Fishery Science,* **50**: 25–35. https://doi.org/10.2960/J.v50.m716.

Shackell, N. L., Fisher, J. A. D., den Heyer, C. E., Hennen, D. R., Seitz, A. C., Le Bris, A., Robert, D., Kersula, M. E., Cadrin, S. X., McBride, R. S., McGuire, C. H., Kess, T., Ransier, K. T., Liu, C., Czich, A., and Frank, K. T. 2021. Spatial ecology of Atlantic halibut across the northwest Atlantic: A recovering species in an era of climate change. *Reviews in Fisheries Science & Aquaculture*: 1–25. https://doi.org/10.1080/23308249.2021.1948502.

Shackell, N. L., Frank, K. T., Nye, J. A., and den Heyer, C. E. 2016. A transboundary dilemma: dichotomous designations of Atlantic halibut status in the Northwest Atlantic. *ICES Journal of Marine Science: Journal du Conseil*. https://doi.org/10.1093/icesjms/fsw042.

Sigourney, D. B., Ross, M. R., Brodziak, J., and Burnett, J. 2006. Length at age, sexual maturity and distribution of Atlantic halibut, *Hippoglossus hippoglossus* L., off the Northeast USA. *Journal of Northwest Atlantic Fishery Science,* **36**: 81–90. https://doi.org/10.2960/J.v36.m574.

Thiel, M., Penna-Diaz, M. A., Luna-Jorquera, G., Salas, S., Sellanes, J., and Stotz, W. 2014. Citizen scientists and marine research: volunteer participants, their contributions, and projection for the future. *In* R.N. Hughes, D.J. Hughes, and I.P. Smith (Eds.) *Oceanography and Marine Biology: An Annual Review*, **Vol 52**: CRC Press-Taylor and Francis Group. pp: 257–314. https://doi.org/10.1201/b17143-6

Torrejon-Magallanes, J. 2020. https://github.com/ejosymart/sizeMat.

Tronbøl, F., Johannesen, E., Alix, M., dos Santos Schmidt, T. C., Charitonidou, K., Folkvord, A., and Kjesbu, O. S. 2022. Tracking oocyte development and the timing of skipped spawning for north-east Arctic haddock (*Melanogrammus aeglefinus*). *Journal of Fish Biology* **100**(6): 1464–1474. https://doi.org/10.1111/jfb.15057

Trzcinski, M. K., and Bowen, W. D. 2016. The recovery of Atlantic halibut: a large, long-lived, and exploited marine predator. *ICES Journal of Marine Science: Journal du Conseil,* **73**: 1104–1114. https://doi.org/10.1093/icesjms/fsv266.

Yochum, N., Starr, R. M., and Wendt, D. E. 2011. Utilizing fishermen knowledge and expertise: Keys to success for collaborative fisheries research. *Fisheries,* **36**: 593–605.

Zwanenburg, K., Wilson, S., Branton, R., and Brien, P. 2003. Halibut on the Scotian Shelf and the Southern Grand Banks – Current estimates of population status. *Bedford Institute of Oceanography, Research Document* 2003/046, Dartmouth, NS: 34 pp.

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No. 41, 2008 (Report of the Greenland Halibut (*Reinhardtius hippoglossoides*) Age Determination Workshop)	Online only	
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The Journal is for the primary publication of original practical and theoretical research that is unpublished and is not being submitted for publication elsewhere. While it is intended to be regional in scope, papers of general applicability and methodology may be considered. Space is also provided for notes, letters to the editor and notices. Each paper is assigned to an Associate Editor of the Journal's Editorial Board, and is normally reviewed by two referees regarding suitability as a primary publication.

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The Studies publishes papers which are of topical interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards or general applicability required by the Journal. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Standing Committee on Publications. Studies papers are not peer reviewed.

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The paper should be in English. The sequence should be: Title, Abstract, Text, References, Tables and Figures.

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The paper should start with the title, followed by the name(s), address(es) and emails of the author(s) including professional affiliation, and any related footnotes.

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In general, the text should be organized into Introduction, Materials and Methods, Results, Discussion, and Acknowledgements. Authors should be guided by the organization of papers that have been published in the NAFO Journal or Studies.

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Examples:

King, M. 1995. Fisheries biology, assessment and management. Fishing News Books, UK, 341 p.

Crowder, L.B., and Murawski, S.A. 1998. Fisheries by-catch: implications for management. *Fisheries*, **23**: 8–16. doi:10.1577/1548-8446(1998)023<0008:FBIFM>2.0.CO;2

Ávila de Melo, A. M., Power, D. , and Alpoim, R. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc.*, No. 52, Serial No. N5138, 19 p.

Text citations of the above would be (King, 1995; Crowder and Murawski, 1998; Ávila de Melo *et al.*, MS 2005). The surnames of two authors may be used in a citation, but *et al.* should be used for more than two authors. The citation of mimeographed reports and meeting documents should contain the abbreviation "MS". Abbreviations of periodicals can be found ftp://ftp.fao.org/fi/asfa/Monitoring_List/MASTER.txt . The Digital Object Identifier (doi) should be included if available. http://www.crossref.org/freeTextQuery/ can be used to checked this.

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