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REVIEW

Spatial Ecology of Atlantic Halibut across the Northwest Atlantic: A Recovering Species in an Era of Climate Change

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ABSTRACT

Interactions between spatial dynamics and stock structure in marine fishes have largely focused on stocks in decline; stock structure is rarely re-visited for expanding species. Here, the spatial ecology of Atlantic halibut (*Hippoglossus hippoglossus L.*), managed as four stocks in the Northwest Atlantic, is reviewed. Halibut collapsed under high exploitation in the mid-19th century, but the Canadian fisheries value has increased seven-fold since the early 2000s. Atlantic halibut's thermal habitat has increased due to warming, possibly contributing to its expansion. Genomic evidence differentiates two populations in the four management units, whereas there is non-genetic spatial structure within each of the stock boundaries. There are different core juvenile areas and a diversity of spawning migration patterns influenced by timing, fish size, maturity state, and distance between summer-feeding and over-wintering habitats. From tagging studies, multiple estimates of median distance at recapture (~3-90 km) are much less than the spatial domain of each stock. Growth rates are faster in the warmer south, as predicted by growing degree day. The current perspective of Atlantic halibut spatial structure is that there are two distinct populations, and within each, there are subpopulations composed of multiple migratory contingents. The level of mixing on common spawning grounds both among and within subpopulations is only partly understood.

KEYWORDS
Atlantic halibut; climate change; spatial structure; spatial ecology; electronic tagging

Introduction

Associations between spatial dynamics, stock structure, and changing abundances in exploited marine fishes have largely been based on knowledge of stocks in decline (Berkeley et al. 2004; Ciannelli et al. 2013; Reuchlin-Hugenholtz et al. 2015, 2016). There is less research on stock structure for species expanding at their geographic range margins in association with changing ocean conditions (Shackell et al. 2014; Fredston-Hermann et al. 2020; Fredston et al. 2021), for those recovering from past declines (Shackell et al., 2005), or for species for which stock boundaries were established during low-abundance periods. These themes intersect in the rapidly-expanding body of research on Atlantic halibut (*Hippoglossus hippoglossus* L.). Atlantic halibut's life history traits of slow growth and late maturation contributed to its collapse under high exploitation in the mid-19th century United States (U.S.) fisheries (Grasso 2008). Yet in Canada, biomass estimates of Atlantic halibut have increased rapidly since the early 2000s, and may now be stabilizing (DFO 2019b, 2019c). Correspondingly, Atlantic halibut has recently supported exponentially-increasing regional landings (Figure 1A). The economic value of Canadian Atlantic halibut fisheries increased seven-fold over the past two decades and recently accounted for 33%

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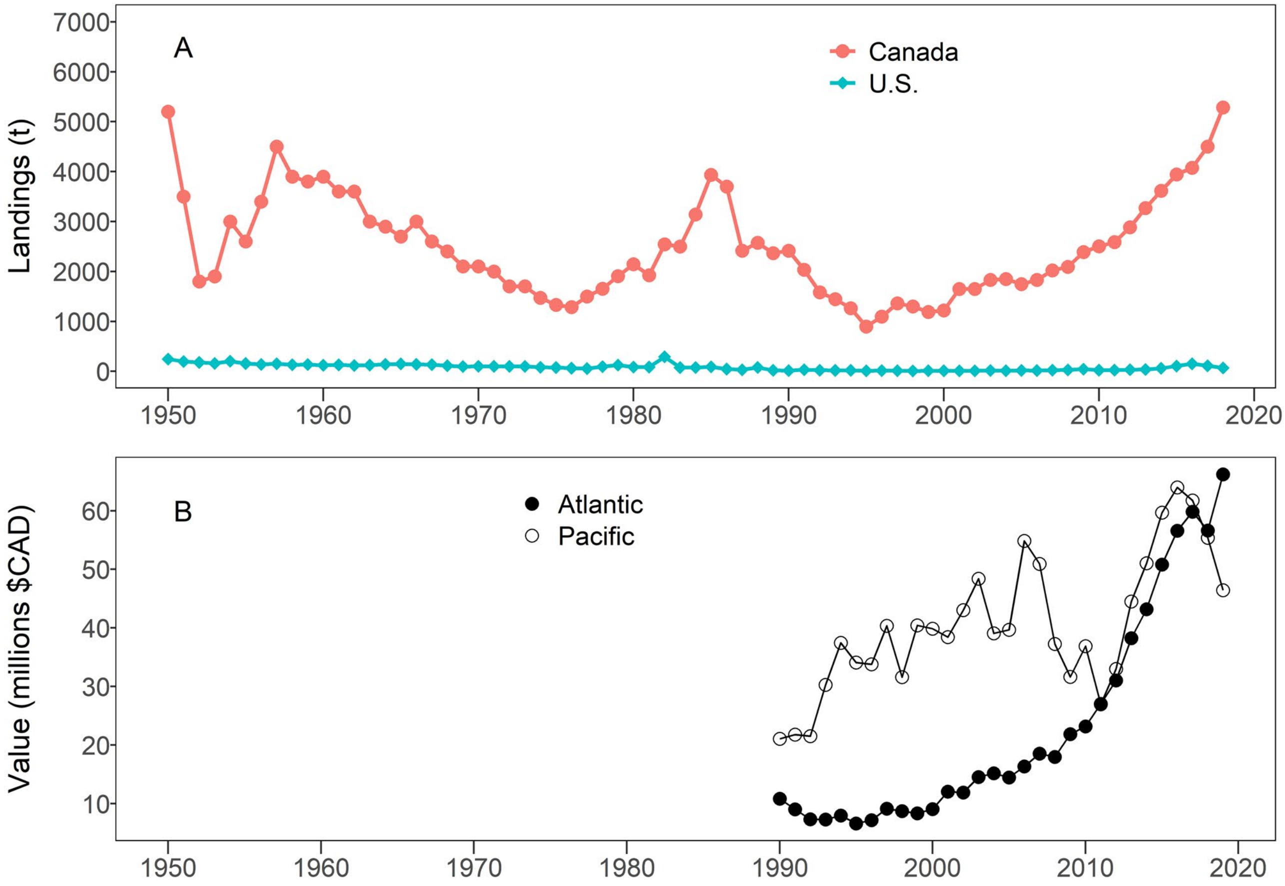

Figure 1. (A) FAO Atlantic halibut landings (t) by two nations (http://www.fao.org/fishery/statistics/global-capture-production/en). (B) Landings values of Pacific halibut (open symbols) and Atlantic halibut (closed symbols) within Canadian fisheries from 1990 to 2019, illustrating the exponential rise in Atlantic halibut landings values over the past two decades (DFO 2019a landings data, $CAD).

of the total landed value of Canadian Atlantic groundfish (DFO 2019a). Atlantic halibut has even recently exceeded the total landed value of the lucrative Canadian Pacific halibut *(Hippoglossus stenolepis)* fishery (Figure 1B). The spatial and economic scales of Atlantic halibut and its fisheries are raising new ecological and management questions about fisheries sustainability—questions that are increasingly suited to regional and international collaborations.

Atlantic halibut is a large cold-water flatfish ranging throughout the north Atlantic as far north as Svalbard, Norway, and Greenland and as far south as the Bay of Biscay, France, and Virginia, U.S. Atlantic halibut has never been common south of 40°N in the western Atlantic (Figure 2) (Goode and Collins 1887; Robins and Ray 1986; Haug 1990; Cargnelli et al. 1999). Atlantic halibut can grow to a maximum length of 3 m. Females reach a much larger size (~300 cm) than males (~189 cm) (McCracken 1958; Bowering 1986; Trumble 1993; Sigourney et al. 2006; Ray and Robins 2016). Females also mature at a larger size (103-125 cm) and age (7-13 years) than males (55-80 cm and 5-12 years, respectively), and their longevity is ~ 38-50 years (Armsworthy and Campana 2010; Armsworthy et al. 2014). Atlantic halibut are thought to batch spawn on continental slopes from late winter to early spring, eggs are bathypelagic (suspended at midwater depths) for 13-20 days, and larvae are pelagic for approximately 90 days before settling to benthic nursery habitats (Cargnelli et al. 1999).

With the collapse of dominant groundfishes in the early 1990s (Boreman et al. 1997), the increase of Atlantic halibut throughout most of its range, and its extremely high value per unit weight ($11.90 CAD per kg vs. an average of $1.49 CAD among 11 other Atlantic groundfish categories), Atlantic halibut is now the second most valuable groundfish species in Canada despite accounting for only 7% of the volume of Atlantic groundfish landings (DFO 2019a). Compared to other groundfishes in the Northwest Atlantic, there has been little research focused on Atlantic halibut (Neilson et al. 1993; Trumble 1993) but their recent recovery has initiated a revival in

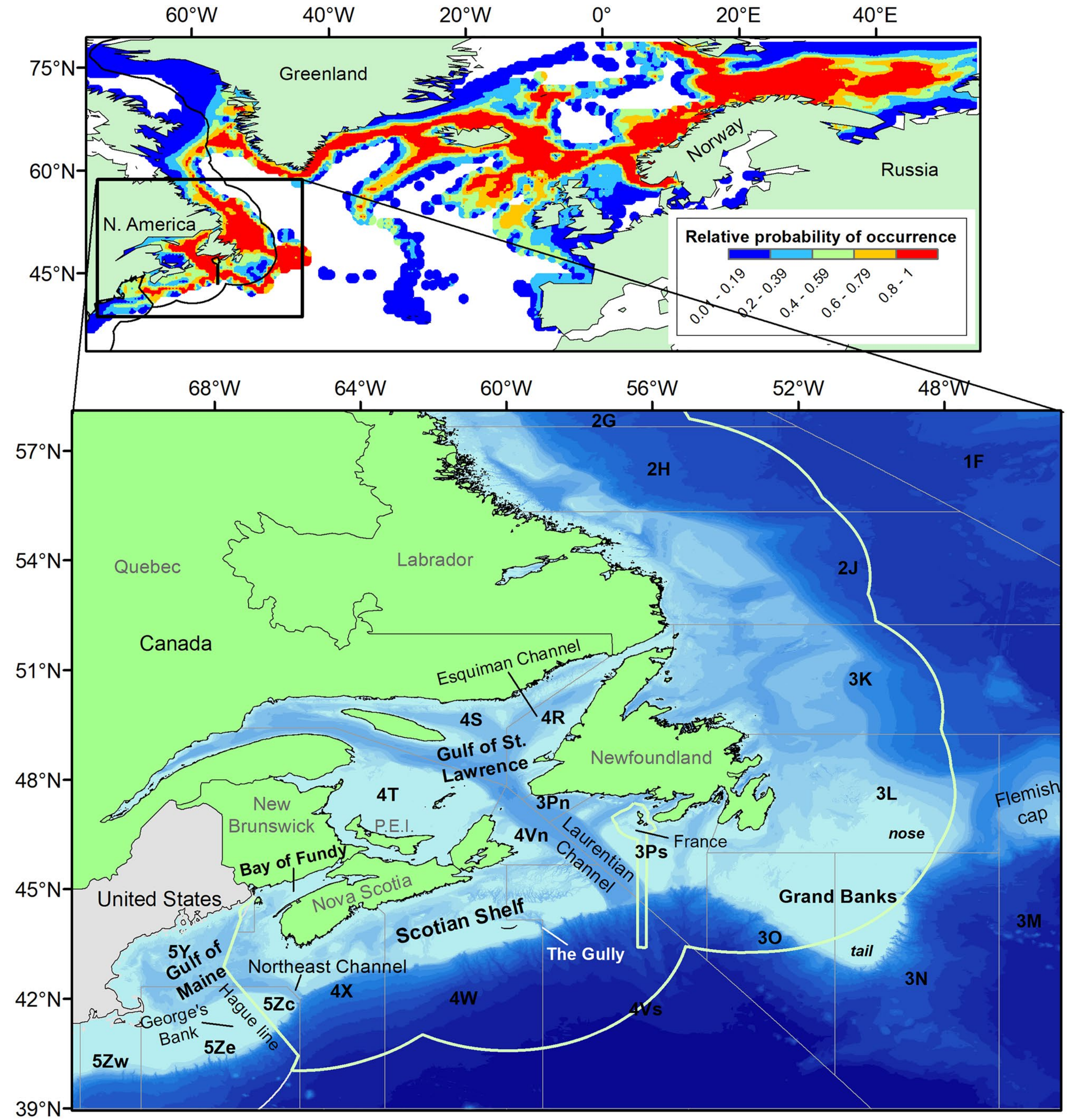

Figure 2. Atlantic halibut distribution across the North Atlantic (www.aquamaps.org) (top panel) and the Northwest Atlantic showing the Northwest Atlantic Fisheries Organization (NAFO) divisions typically used to manage fish stocks (bottom panel). The Gulf of St. Lawrence stock comprises NAFO divisions 4RST. The Scotian Shelf-Grand Banks stock comprises NAFO divisions 3NOPs4VWX5Zc. The Gulf of Maine-Georges Bank stock comprises NAFO divisions 5YZe.

Atlantic halibut research in Canada and the U.S. Given the recent increase in Atlantic halibut abundance throughout the Northwest Atlantic basin and increased scientific effort, available information on stock structure, spatial ecology, and implications for management in an era of climate change is reviewed. Key outstanding research questions are identified that, if answered, would support the sustainable management of Atlantic halibut in a dynamic environmental regime.

Early Atlantic halibut fisheries

In the late 1700s, Atlantic halibut were considered a nuisance and were routinely discarded in the New England Atlantic cod (*Gadus morhua*) fishery (Goode and Collins 1887; Grasso 2008). The taste of salted Atlantic halibut was then not well-liked. Atlantic halibut became a more popular food choice with the expansion of the railroad system and the advent of increased access to ice for the fresh fish markets in the late 1830s. By the time Atlantic halibut became a targeted species starting in the 1840-1850s, they were already somewhat depleted (Grasso 2008). In the early half of the 1800s, they were abundant inshore throughout Massachusetts Bay, but were soon fished out once a commercial fishery was established. The fishery then shifted offshore, and by 1850, stocks had been severely depleted on Georges Bank (Bigelow and Schroeder 1953). American harvesters, at that time, were allowed access to Canadian waters (Lear 1998) and moved sequentially northward into Canada, focusing first on southern areas but then fishing as far north as the Canadian Arctic in 1866 (Trumble 1993; Grasso 2008). While the American fishery had collapsed by the 1940s, the fishery continued in Canada where Atlantic halibut were considered a secondary species to the principal target groundfish species of Atlantic cod and haddock (*Melanogrammus aeglefinus*) (McKenzie 1946; Grasso 2008). The Atlantic halibut fishery declined in the Gulf of St. Lawrence in the 1970s (DFO 2019b) and on the Canadian continental shelf in the late 1980s (Trzcinski and Bowen 2016). Since the early 2000s, Atlantic halibut abundance has been increasing (Cox et al. 2016; Trzcinski and Bowen 2016; DFO 2019b; Hansell et al. 2020), but is still not as abundant, particularly nearshore, as described in the early 1800s (Grasso 2008).

Current stock and national jurisdictional boundaries

In the Northwest Atlantic there are four spatial management units managed independently by three nations, the U.S., Canada, and France. Within U.S. and Canadian waters there is the implicit assumption of a single stock in each management unit as defined by Northwest Atlantic Fisheries Organization (NAFO). In Canada, there are two Atlantic halibut stocks: one in the Gulf of St. Lawrence (NAFO Divisions 4RST) and the other on the Scotian Shelf-Grand Banks (NAFO Divisions 3NOPs4VWX5Zc; Figure 2). The establishment of the two Canadian management units was based on different broad-scale demographic rates between the two units (Neilson et al. 1987), and tagging studies that have shown little exchange between the Gulf of St. Lawrence and the Scotian Shelf-Grand Banks (Stobo et al. 1988). In the U.S., there is a Gulf of Maine-Georges Bank stock (NAFO Divisions 5YZe; Figure 2). Atlantic halibut distribution extends beyond national jurisdictions into international High Seas regulatory areas. France harvests Atlantic halibut within the Exclusive Economic Zone (EEZ) of the Saint-Pierre and Miquelon archipelago, a French territory just south of Newfoundland (Figure 2). Canada and France signed an agreement on their Mutual Fishing Relations in 1972. The agreement was amended in 1994, which delineated the current French EEZ, located within NAFO division 3Ps and 4Vs and surrounded by the Canadian EEZ. To date, Atlantic halibut is not included in the agreement, and the French TAC is currently set independently of the Canadian stock assessment. Whether Atlantic halibut within the French EEZ are a separate stock or are part of the Scotian Shelf-Grand Banks stock complex has not been investigated.

Further south, Atlantic halibut distribution extends across the "Hague Line", established by the International Court of Justice in The Hague, Netherlands, in 1984 as the nautical international border between the U.S. and Canada (Figure 2). The Hague Line divides a natural ecosystem wherein most marine resources are managed separately by each nation, with the exception of three species: Atlantic cod, haddock, and yellowtail flounder (*Limanda ferruginea*) which are jointly managed through bilateral provisions (Koubrak and VanderZwaag 2020). Canada and the U.S. assess the status of Atlantic halibut separately within their respective jurisdictions. On the U.S. side of the Hague Line, the Gulf of Maine-Georges Bank stock has been difficult to assess using fishery-independent survey data. As there is high uncertainty in the American survey indices, there have been recent efforts to derive information from fishery-dependent data. These data have shown a stable or small increase in catch per unit effort (CPUE) in known Atlantic halibut habitat within the U.S. (Hansell et al. 2020). Although there is some indication of stock rebuilding from surveys and CPUE of Atlantic halibut in U.S. waters, the stock is still considered depleted and is currently listed as a "Species of Concern" under the U.S. Endangered Species Act (NMFS 2004; Kocik 2015). In contrast, the Canadian Atlantic halibut fishery for the adjacent Scotian Shelf-Grand Banks stock was certified in 2013 as sustainable by the Marine Stewardship Council ("http://www.msc.org/"). Shackell et al. (2016) explored these divergent perspectives by examining six fishery-independent surveys conducted from 1965 to 2014, during which both sides of the border had been sampled within the same survey. Over the time series, juvenile Atlantic halibut abundance was on average five times greater on the Canadian side, despite comparable amounts of suitable habitat. The persistent differences in abundance and trends between Canada and the U.S. may reflect fine-scale spatial population structure between U.S. and Canadian management units.

Unit stock

A "stock" forms the spatial unit for fishery management and differs from a "population". A population can be defined as a self-sustaining, genetically-distinct group of organisms of a particular species in a geographic area (Waples and Gaggiotti 2006). The definition of a fish "stock" is loosely based on that of a population but is further defined so that stock productivity can be accurately estimated (Cadrin 2020). Broadly, a unit stock can be considered to be a group of fish of a particular species across a geographic domain with homogenous demographics and dynamics (age/size structure, recruitment, reproductive potential, population growth rate, carrying capacity) that result from individual-level parameters (growth, maturation, reproduction, survival). The unit stock assumption typically assumes no movement of fish to or from adjacent areas; decreases in abundance are interpreted as mortality and increases in abundance are interpreted as locally-spawned recruitment.

There has long been an emphasis on finding genetic differences as indicators of reproductive isolation, but a genetically homogenous group of fish might include more than one stock if they exhibit phenotypic or behavioral variation in response to their spatial distribution across a heterogeneous seascape (Booke 1981). A population may be comprised of spatially, phenotypically, or behaviorally separate subpopulations, where subpopulation is herein defined as "… an arbitrary spatially-delimited subset of individuals from within a population" (Wells 1995). The assumption of uniform parameters is important to the demographic models used to estimate the amount of fish production that can be fished without harming future productivity of that fish stock. The combination of inaccurately-delineated stock boundaries combined with serial overfishing, such as that for Atlantic halibut in the 1800s in the New England area (Grasso 2008), can lead to depletion of populations and loss of subpopulations. Contemporary examples of serial overfishing and loss of local subpopulations (Hutchings 1996; Smedbol and Wroblewski 2002; Ames 2004; Ciannelli et al. 2013; Reuchlin-Hugenholtz et al. 2015) have highlighted the importance of accounting for the spatial structure of a unit stock (Cadrin et al. 2020).

Setting the stage: a dynamic environmental regime

"In thinking about population or stocks of fish, there is unfortunately a tendency to consider them static entities… Yet a real understanding of the distribution of stocks of fish can only be gained if they are considered plastic and transient" (Wise and Jensen 1960). The definition of a unit stock does not necessarily imply a static spatial unit, because spatial boundaries can vary over time (Begg et al. 1999). Dynamic stock boundaries may involve expanding or contracting distributions that are related to changes in stock abundance and habitat (MacCall 1990). Climate change and shifting distributions may also be factors in dynamic stock boundaries (Perry et al. 2005; Link et al. 2011). Generally, Atlantic halibut have been observed from −0.92 °C to 19 °C; their preferred temperature range is ~ 2 °C-11 °C (Kaschner et al. 2019) and bottom temperatures have been warming at a rate of ~2 °C per decade since ~2005 in the Gulf of Maine and on the Scotian Shelf (Brickman et al. 2018) and at depth (>200 m) in the Gulf of St. Lawrence (Galbraith et al. 2020).

Czich (2020) used a high-resolution ocean model (Brickman et al. 2018) to estimate the area of preferred temperature (>2.5 °C) and depth (25-400 m) habitat of juvenile (<80cm) Atlantic halibut from 1990 to 2018, based on temperature preferences derived from research vessel surveys (French et al. 2018). The area of preferred thermal habitat within NAFO zones is increasing in parts of the Atlantic basin (Figure 3) with the greatest increase in preferred habitat occurring in southern Newfoundland (NAFO Divs. 3NOPsPn), ranging from ~18 to 92% increase, on the eastern Scotian Shelf (NAFO Divs. 4VsVnW), ranging from ~12 to 60% and at ~17% in the northeastern Gulf of St. Lawrence (NAFO Divs. 4 R) (Figure 3A). Preferred habitat has not increased appreciably in the southern warmer area of the domain (NAFO Divs. 4X5YZew) and declined in the most northeastern parts of the domain (NAFO Divs. 3KL) ranging from −17% to −35%, due to local decreases in bottom temperature (Brickman et al. 2018). Preferred habitat has increased most in three divisions where the volume of preferred habitat had been relatively low (Figure 3B). This expansion in available habitat, associated with warmer bottom water in much of the range, may have played a role in the increase in Atlantic halibut abundance, but the geographic pattern of occurrence suggests that other factors have also contributed.

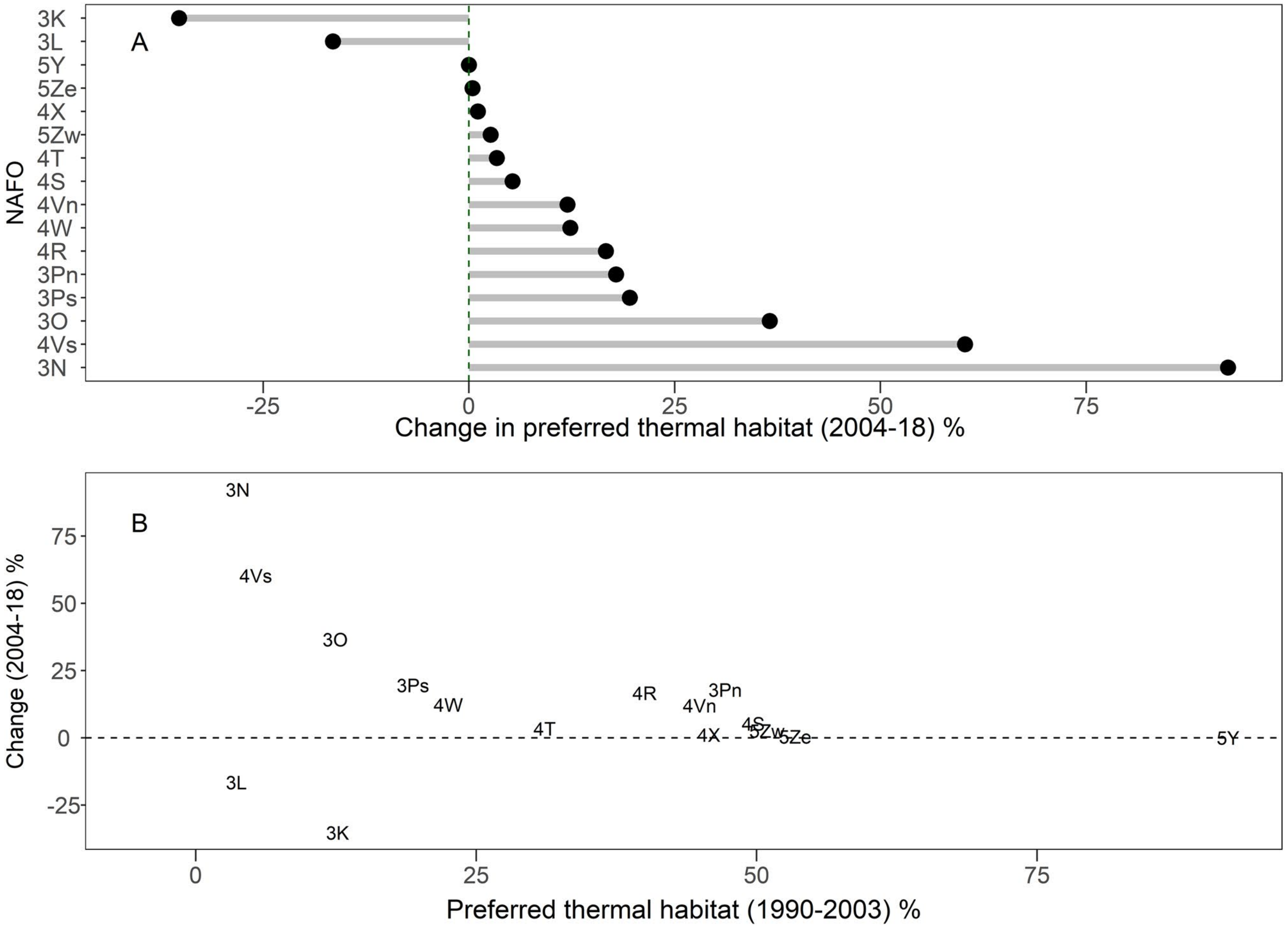

Figure 3. (A) NAFO divisions in increasing order of the percent change in preferred thermal habitat of Atlantic halibut in a recent period. (B) Percent change in preferred thermal habitat of Atlantic halibut in a recent period (2004-2018) relative to an older period (1990 to 2003), plotted against the proportion of preferred thermal habitat in the older period, for each NAFO division. NAFO divisions 4S, 5Zw, and 5Ze labels are overlapping. Preferred thermal habitat was estimated using cumulative distribution functions of temperature and depth from research vessel survey data (see Czich 2020 and French et al. 2018).

Review of existing information related to stock identification

Genetic

Genetic variation sufficient to produce genetically-distinct populations reflects the effects of local adaptation on an evolutionary time scale (Hohenlohe et al. 2021). There are subtle but meaningful genetic differences between Atlantic halibut in the semi-enclosed sea of the Gulf of St. Lawrence and on the Atlantic continental shelf, but there are no detectable differences between the Scotian Shelf-Grand Banks and Gulf of Maine-Georges Bank stocks across the continental shelf (Kess et al. forthcoming). Most of the genetic divergence occurs among individuals through a region of elevated divergence and linkage, consistent with a chromosomal rearrangement; this genomic region exhibits no spatial variation, but may be associated with cryptic variation within stocks(Kess et al. 2020). Demographic reconstructions have identified a decline in abundance from a period of high diversity ~11,000 years ago following the last glacial period (Kess et al., forthcoming). The results confirm the validity of the current management division between Gulf of St. Lawrence and Scotian Shelf-Grand Banks stocks and emphasizes the need for further investigation of demographic spatial structure across the Hague Line.

As explained above, serial depletion of patches within a single population can occur due to differential fishing effort across the seascape (Ciannelli et al. (2013). Further, genetic differences are definitive of distinct populations, but a genetically homogenous group of fish might be more than one stock if they exhibit phenotypic or behavioral differences in response to an environmentally-heterogeneous seascape (Booke 1981) or exhibit behavioral-segregation mechanisms. Phenotypic differences can arise and vary on shorter than evolutionary time scales and this would affect the assumption of uniform life history trait parameters (growth, survival, age-at-maturation, fecundity) in the stock assessment population model. For example, although Pacific halibut is genetically homogeneous throughout large parts of its range (e.g., the Gulf of Alaska through the Bering Sea), it demonstrates a pattern of variation in individual-level life history parameters on a geographic gradient. This may result from a low rate of genetic mixing among areas that is insufficient to lead to genetic population structure, but sufficient to lead to spatial population structure through differences in life history traits (Seitz et al. 2017). Finally, segregation within a heterogeneous landscape can yield multiple stocks even if no discernible phenotypic divergence is apparent. Behavioral isolation/segregation can occur over time scales that are too short to derive genetic divergence, but still invoke stock structure that requires more-complex management strategies. That is, a metapopulation can be genetically uniform but spatially structured with largely independent dynamics within that structure. Below, spatial structure is further examined.

Overview of spatial distribution and connectivity

Fish are rarely distributed uniformly across a large seascape; their spatial structure is often determined by habitat preferences at each life history stage (Stephenson et al. 2001; Hare and Richardson 2014). Commonly observed spatially-structured populations can be assigned into four major categories: sympatric (genetically distinct populations that spatially overlap), allopatric (spatially discrete and genetically isolated), spatially complex (local subpopulations with weak genetic connectivity), and panmictic (mixed across seascape and genetically homogenous (Ciannelli et al. 2013). Demographic models of a unit stock typically assume uniform parameters to estimate the amount of fish production that can be fished without harming future productivity of that fish stock. Although homogeneous vital rates are important for stock assessment, conserving subpopulations across the seascape is equally important. Considering a spatially-complex resource to be a simple unit stock can lead to management failure, even if the subpopulations have similar vital rates, because individual subpopulations are vulnerable to depletion (Hutchings 1996; Smedbol and Wroblewski 2002; Ames 2004; Ciannelli et al. 2013; Reuchlin-Hugenholtz et al. 2015). Preservation of subpopulation structure can be vital to the recovery of stocks following disturbance or depletion and increase their resilience in the face of environmental change.

There is only a general knowledge of the size at which pre-reproductive Atlantic halibut become mature. Size is used to loosely distinguish between juveniles and adults. Adults are considered too large to catch in regional research vessel trawl surveys. Smaller, putative juveniles on the other hand, cannot outswim the trawls and are routinely collected in research vessel trawl surveys across the northwest Atlantic (Boudreau et al. 2017). Because the surveys vary in sample intensity, gear, and temporal coverage, probability of occurrence data were gridded to gain a general impression of juvenile halibut distribution (Figure 4). Juvenile halibut are distributed throughout the region but more prevalent in the northern Gulf of St. Lawrence (NAFO Divisions 4RS) and on the Scotian Shelf (NAFO Divisions 4VWX). Boudreau et al. (2017) further analyzed juvenile Atlantic halibut distribution based on a Bayesian hierarchical spatio-temporal approach that can be used to estimate parameters of relevance to spatial stock structure: connectivity and persistence (Carson et al. 2017). The spatial structure of juvenile Atlantic halibut was modeled across the basin in three time periods, corresponding to specific fisheries management regimes. The first period (1978-1989) corresponded to the establishment of the national exclusive economic zones (EEZs) and the start of a regulated Atlantic halibut fishery in Canada in 1988. The second period (1990-2003) corresponded to the start of the northern Gulf of St. Lawrence research vessel survey and widespread fisheries moratoria on collapsed groundfishes (Newfoundland Atlantic cod fishery in 1992, Gulf of St. Lawrence Atlantic cod in 1993, Eastern Scotian Shelf groundfish fishery in 1994). The third period (2004-2013) corresponded to an increase in juvenile Atlantic halibut abundance across the region. The goal was to determine whether there was an identifiable spatial structure (Boudreau et al. 2017). There were two areas of high-density juvenile abundance that persisted through all three periods, whereas two other high-density areas on the southern Grand Banks did not persist, despite the increased abundance and landings throughout Canadian waters (Figure 5). Connectivity (assessed as coherence of temporal patterns across space) was estimated to be 250 km, an order of magnitude less than the distance from one border of the Scotian Shelf-Grand Banks management units to the other (~2,000 km) . The smaller ~250 km scale of coherent temporal patterns suggests a more complex population structure than previously thought, but this does not preclude dispersal and mixing at older ages across a broader stock complex. A similar approach has recently been

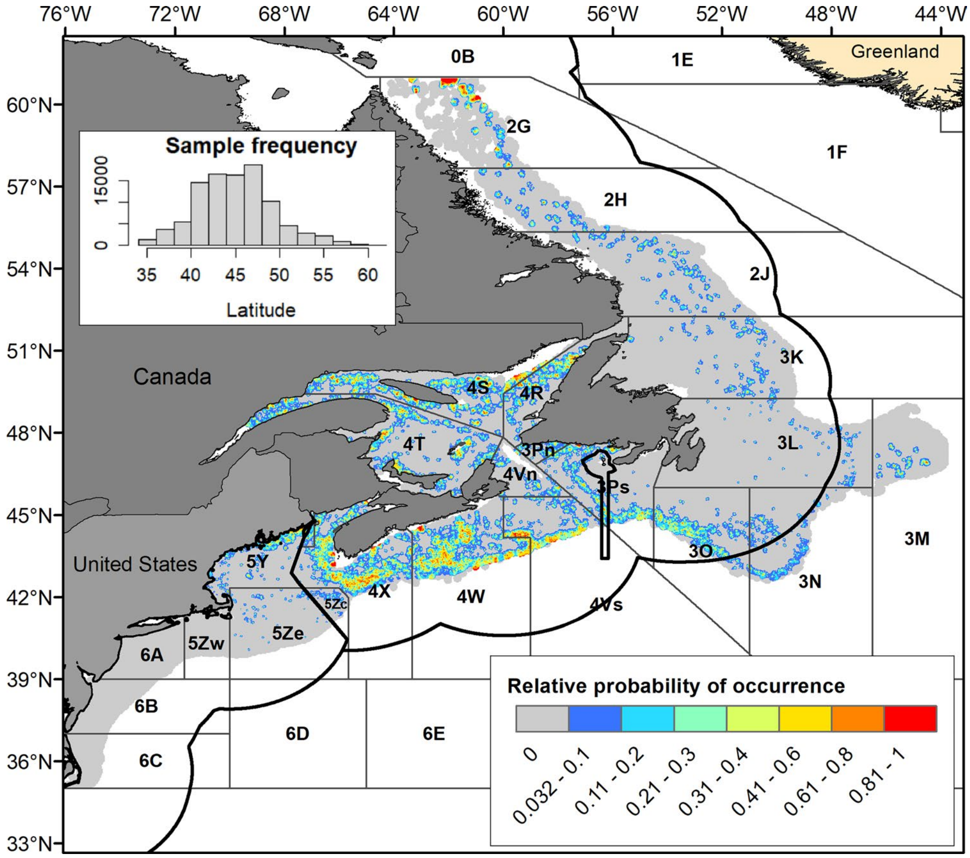

Figure 4. Probability of occurrence of juvenile (<80cm) Atlantic halibut in research vessel trawl surveys across the Atlantic basin covering the period 1970-2013 (see Boudreau et al. 2017 for survey details).

used on Pacific halibut and has potential to monitor changes in an increasingly-dynamic environment (Webster et al. 2020).

Further evidence of a spatially-complex structure was derived from a habitat suitability model. French et al. (2018) estimated the proportion of preferred juvenile Atlantic halibut habitat within each NAFO zone (Figure 2). There was a strong relationship between the amount of preferred juvenile Atlantic halibut habitat and fishery landings within NAFO divisions. NAFO divisions that had more juvenile habitat yielded higher landings, both in contemporary times and historically, using recorded landings from the 1950s, as documented by McCracken (1958). The results were consistent with the "Nursery-zone size" hypothesis that proposed that the amount of juvenile habitat sets an upper limit to adult production (Iles and Sinclair 1982; Rijnsdorp et al. 1992; Gibson 1994; Beverton 1995; Sundblad et al. 2014; Wilson et al. 2016).

Movement and migration

The current perspective of Atlantic halibut movement and migration is derived from the combination of conventional and electronic tagging studies, which provide different knowledge. Conventional tagging studies typically characterize the group-level distance traveled from site of release, the distribution of distance at recapture, and the median distance at recapture. Historical conventional tagging studies suggest largely resident populations with a small proportion migrating long distances, where the median distance at recapture from conventional tagging studies varies across the domain (3-90 km, summarized in Figure 6) (McCracken 1958; Stobo et al. 1988; Kanwit 2007; den Heyer et al. 2013; Kersula and Seitz 2019).

Electronic tagging studies characterize detailed movement of individuals, and even more detailed if archival tags are retrieved and allow for analysis at higher temporal resolution (Fisher et al. 2017), allowing insight into fine-scale behavior. Progress in the last decade in electronic tagging technologies has revealed a variety of migratory behaviors through the reconstruction of migration tracks using geolocation models (Seitz et al. 2017; Le Bris et al. 2018; Liu et al. 2019; Gatti et al. 2020; James et al. 2020; Gatti et al. 2021). Within the Gulf of St. Lawrence, 62 pop-up satellite archival tags (PSATs) placed on Atlantic halibut have

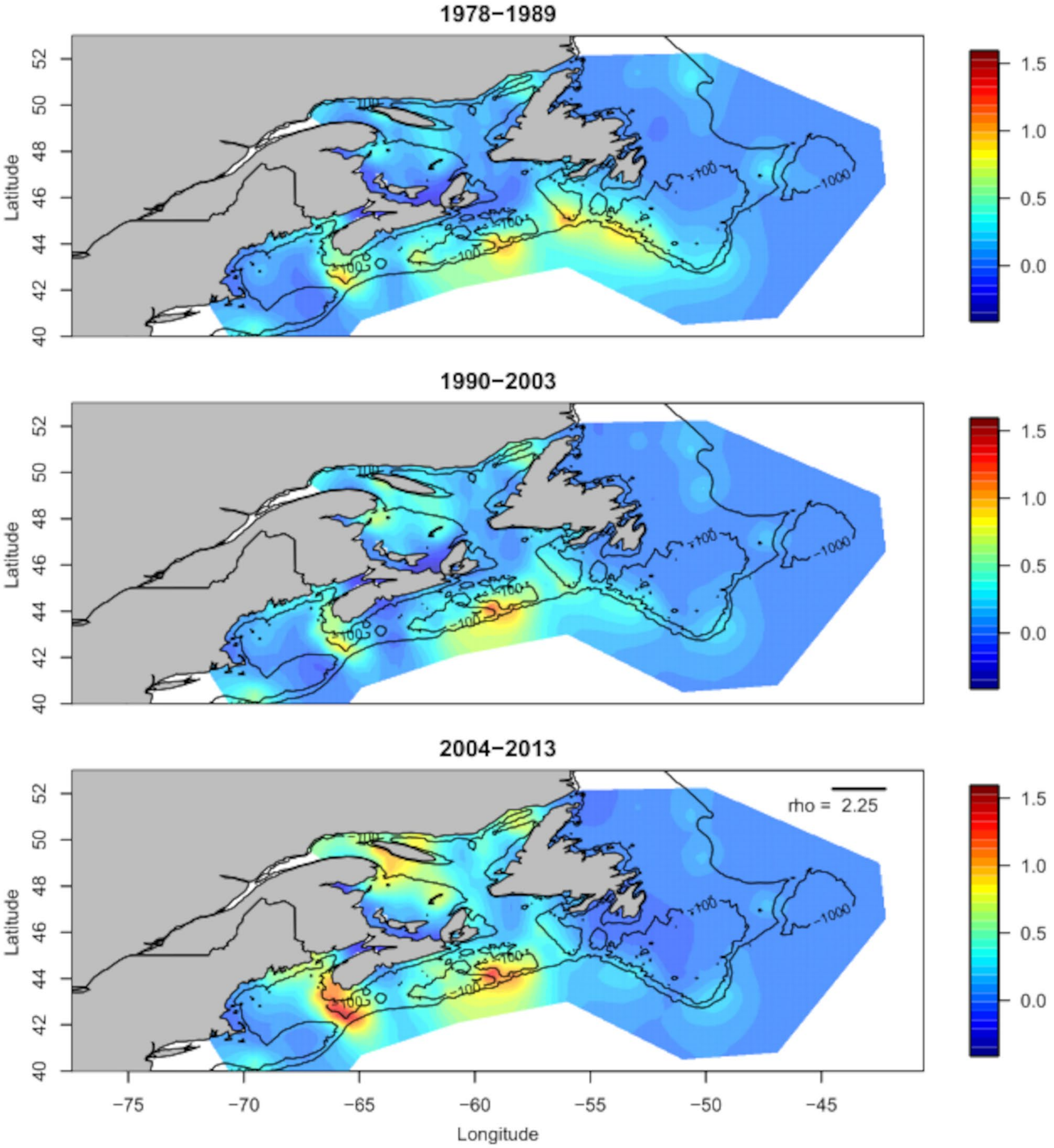

Figure 5. Random fields of juvenile Atlantic halibut abundance of the penultimate model by fisheries management time period, the model parameter connectivity, ρ (rho), is drawn and printed on the bottom map, units are degrees Latitude. A model was fit for three time periods, corresponding to three fisheries management regimes on the Scotian Shelf. The color scale illustrates the random latent field (log abundance), and all three panels are the same scale. The log abundance for panel (a) time period (1) 1978–1989 ranged from −0.30 to 1.07 with a mean of 0.16, for (b) (2) 1990 to 2003; ranged from −0.37 to 1.27 with a mean of 0.15, and (c) (3) 2004–2013; ranged from −0.25 to 1.55 with a mean of 0.21. Bathymetric contours illustrate the 100 and 1,000 m depths representing the continental shelf and larger banks. Figure is reprinted from Boudreau et al. (2017). © 2017 The Authors. Ecology and Evolution published by John Wiley & Sons Ltd.

been recaptured over multiple years, providing complete archived datasets with high temporal resolution (Gatti et al. 2020). Groups of Atlantic halibut were tracked from five locations in the summer, to a common channel in the winter, where they exhibited spawning rises. The tagged Atlantic halibut were then tracked back to their home sites the following summer, documenting summer site fidelity, and suggesting strong

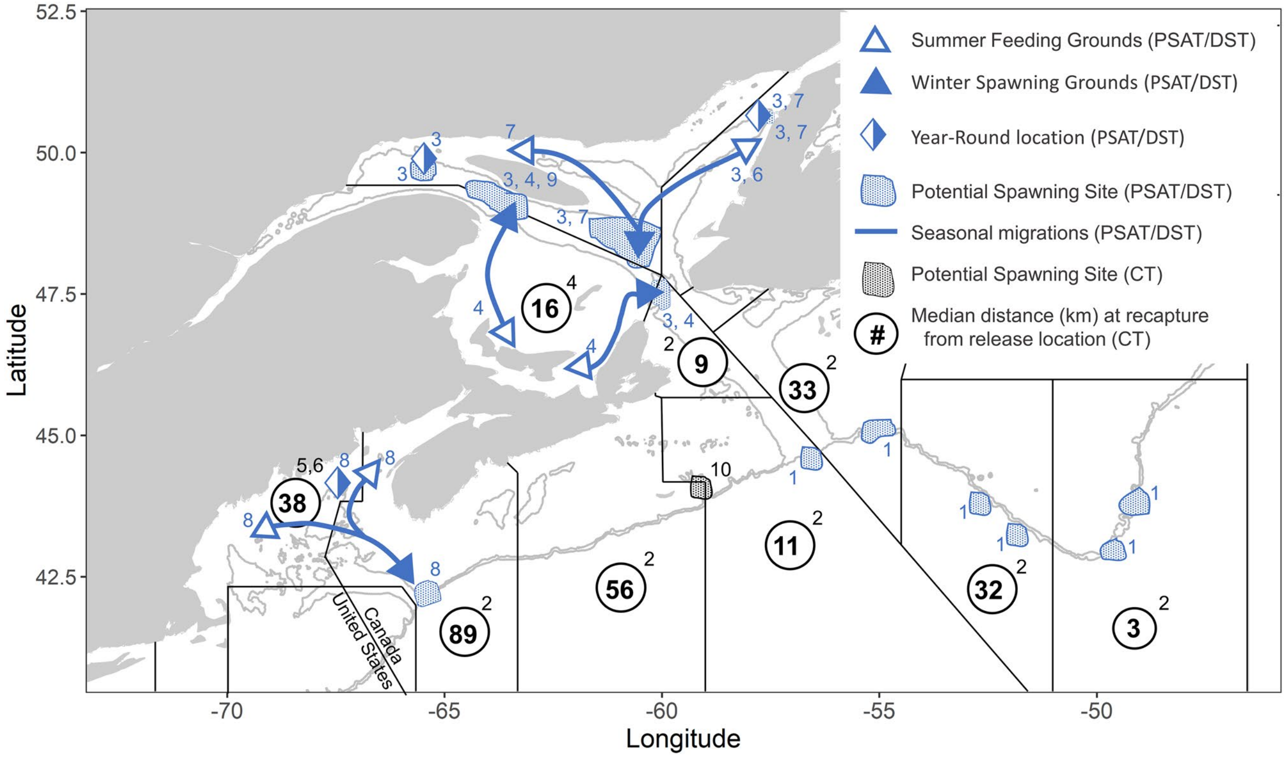

Figure 6. Summary of conventional and electronic archival tagging studies on Atlantic halibut in the Northwest Atlantic. PSAT: pop-up satellite archival tags; DST: data storage tags; CT: conventional tagging. Sources: 1. Armsworthy et al. (2014); 2. den Heyer et al. (2013); 3. Gatti et al. (2020); 4. James et al. (2020); 5. Kanwit (2007); 6. Kersula and Seitz (2019); 7. Le Bris et al. (2018); 8. Liu et al. (2019); 9. McCracken (1958); 10. Stobo et al. (1988).

multi-year fidelity. Among sites, the distance traveled ranged from 3 to 324 km, with a median of 27 km. Although the groups differed in the summer feeding habitats, some groups shared common winter spawning habitats. On the Scotian Shelf-Grand Banks, 14 fish were tracked by PSATs (Armsworthy et al. 2014). The majority of fish did not stray more than 120 km between tagging and tag-reporting locations. These fish exhibited a seasonal pattern of wintering at depth on the continental slope and moving toward the continental shelf in the summer. Four mature fish moved <25 km and may have been resident or skipped spawners. In the Gulf of Maine, 35 fish were tracked by PSAT and recaptured data storage tags (DST) (Liu et al. 2019). The majority (80%) remained within the Gulf of Maine and the linear displacement of 50% of tagged fish was <60km. Two fish migrated from different sites to a common channel, where they resided for the winter (Seitz et al. 2016). Although more PSAT information is needed, the higher propensity of resident behavior of Atlantic halibut observed in the Gulf of Maine (Seitz et al. 2016; Liu et al. 2019) than in Canadian waters is similar to patterns observed in fjords in Norway for Atlantic halibut (Seitz et al. 2014) and in the inside waters of southeast Alaska for Pacific halibut (Nielsen and Seitz 2017).

Atlantic halibut appear to conform to the “Contingent theory” first proposed by Clark (1968) and further developed by Secor (1999). The contingent theory proposes that groups of fish in a population (contingents) exhibit common migration pathways as a result of environmental cues at early life stages or adaptive behavior at later life stages (Lowerre-Barbieri et al. 2014). Contingent structure leads to a diversity of migration patterns within an area or population. Both long and short-distance migrations and year-long residency have been observed for Atlantic halibut both within the Gulf of Maine (Seitz et al. 2016; Kersula and Seitz 2019; Liu et al. 2019) and the Gulf of St. Lawrence (Le Bris et al. 2018; Gatti et al. 2020; James et al. 2020). Migratory diversity is even observed at the scale of the tagging location. For instance, there has been a year-round residency and an 800-km migration observed from Atlantic halibut tagged the same day at the same location in the north-east Gulf of St. Lawrence (Gatti et al. 2020). Atlantic halibut tagged at the same location within a few days of each other in the southern Gulf of St. Lawrence have also demonstrated different migration routes and separate winter spawning areas (James et al. 2020).

The commonality among tagging studies includes partial migration (Kerr and Secor 2012; Dingle 2014), in which seasonal migratory contingents overwinter on the continental slope and return to inshore foraging sites for summer, resident contingents that do not move significantly, and a small minority of fish that are recaptured at extreme distances from where they were conventionally tagged. The seasonal migrations have displayed variation in timing, likely influenced by fish size, maturity state, and the geographic distance between summer feeding areas and available wintering habitats, resulting in a diversity of migration patterns (Gatti et al. 2020). Importantly, seasonal migrations are assumed, and in many instances shown, to be spawning migrations.

Spawning behavior

Prior to electronic archival tagging, general observations across the region supported the inference that Atlantic halibut spawned on the continental slope and along the deepwater margins of offshore banks, with most spawning occurring from November to April (McCracken 1958; Kohler 1967; Neilson et al. 1993) (Figure 6). Observations of spawning Atlantic halibut on the eastern Scotian Shelf and in the eastern Gulf of Maine have been inferred or observed from April to early September spawning from Georges Bank to the Grand Banks, with some geographic variation (late spring off Greenland; summer off the U.S., and in September on the Scotian Shelf) at depths of 300-400 m. These spawning depths are shallower than has been observed off Europe (Bigelow and Schroeder 1953).

The advent of electronic archival tags has offered new opportunities to identify putative spawning behavior from the recorded high-resolution depth times series (Fisher et al. 2017), from which distinct spawning rises can be detected (Murphy et al. 2017; Le Bris et al. 2018). Early utilization of PSATs on Atlantic halibut revealed that fish on the Grand Banks and south of Newfoundland spawn at depths of 450-1050 m from October through February (Armsworthy et al. 2014), most likely on the continental slope. Following that work, a stock-wide electronic tagging study was completed across the Gulf of St. Lawrence, in which more than 100 PSATs were deployed. Using the archived time-series of 40 physically-recovered PSATs, Gatti et al. (2020) showed that spawning occurs primarily from January to March with a peak in mid-February at multiple locations within the 250-500 m depth range. Presumed spawning locations form a network of local bathymetric depressions within the deep channels of the Gulf of St. Lawrence, in which Atlantic halibut convene from disparate summer feeding grounds (Figure 6). A detailed characterization of Gulf of St. Lawrence Atlantic halibut spawning behavior from the same recovered PSATs revealed that Atlantic halibut engage in distinct rapid, 3-202 minute (median of 21 min) rises off the seafloor of an amplitude ranging between 25 and 284 m (Marshall 2020). Supporting earlier evidence for batch spawning (Methven et al. 1992), female Atlantic halibut performed between 5 and 13 spawning rises (median of 7) with a median between-rise interval of 3.15 days (Marshall 2020), which corresponds to the time necessary for female Atlantic halibut to hydrate sequential egg batches (Finn et al. 2002).

In U.S. waters, data from two electronically-tagged fish at locations more than 150 km apart within the inshore Gulf of Maine showed movement to a shared location on the continental slope edge in 800-1200 m depths off the Northeast Channel in Canadian waters from December to April (Liu et al. 2019). Although spawning rises were not observed, potentially because of the coarse data resolution (Fisher et al. 2017), recent returns of tags from Atlantic halibut in the Gulf of Maine have allowed access to high-resolution archived data and provided evidence for spawning rises in the same Northeast Channel slope location and further along the Scotian Shelf. (W. Devoe, personal communication Maine Department of Marine Resources, Nobleboro, Maine, U.S.).

These studies provide glimpses of common patterns as well as diversity in spawning behavior. To date, it is known that maturity status can induce variation in migration patterns within a contingent. Within a given contingent, Atlantic halibut exhibiting spawning rises have been shown to migrate further and deeper in the winter than non-spawners (Gatti et al. 2020). In both Pacific halibut (Seitz et al. 2005; 2011; 2017) and Atlantic halibut (Seitz et al. 2014; 2016), a considerable proportion of fish with >95% probability of being mature do not show evidence of occupying deep water spawning grounds on the continental slope, nor undertaking distinct spawning rises during the winter. The most parsimonious explanation for this observation is "skipped-spawning" behavior (Loher and Seitz 2008), which is not unexpected as many long-lived, cold-water fishes skip spawning (Burton 1999; Rideout et al. 2005). Alternative explanations for mature Atlantic and Pacific halibut foregoing a trip to relatively deep water in the winter for spawning is an unobserved spawning behavior in shallow continental shelf waters in which distinct spawning rises off the sea floor are not undertaken (Loher and Seitz 2008), or that mature fish are not ripe or ripe/running as has been observed across the Gulf of Maine (R. McBride, unpublished data). The evidence of skipped spawning in Atlantic halibut is currently limited and remains to be explicitly demonstrated. At this stage, a relatively small fraction of electronically-tagged fish are assumed to be representative of the behavior of the spawning population; the perspective will only become clearer with further research.

Early life history

Early life history of Atlantic halibut remains largely unknown. After release from spawning rises, eggs rise and become bathypelagic (Haug et al. 1984; Collette and Klein-Macphee 2002). Throughout the northwest Atlantic, the dispersal of eggs and larvae in slope waters would generally be affected by the predominant current, the cold Labrador current that follows the shelf break southerly through the Cabot Strait and around the Grand Banks, and to a lesser extent, the north-flowing warm Gulf Stream. Details however, are unknown. Several spawning grounds have been identified (Figure 6) but there has been no formal analysis of the likely advection pathways from spawning to nursery grounds (but see basic ecological questions section below). Indeed, few larvae have ever been reported in ichthyoplankton collections in the Northwest Atlantic. In U.S. waters and on the western Scotian Shelf, only two larvae have been observed: these were collected off eastern Maine and on Georges Bank (Cargnelli et al. 1999). Only five Atlantic halibut larvae were found in the extensive monthly Scotian Shelf Ichthyoplankton Program (1976-1982) and Fisheries Ecology Program (1983-1985) (Neilson et al. 1993). In the Gulf of St. Lawrence, the historical ichthyoplankton composition and abundance databases only contains 17 occurrences of Atlantic halibut, captured between 1972 and 2014 (P. Ouellet, Fisheries and Oceans Canada, pers. comm.). It may be that larvae are generally located in deep water or off the continental shelf, which is not sampled by regular plankton surveys. Alternatively, the concentration of spawning adults has been relatively low historically, therefore the likelihood of sampling eggs or larvae may have been practically nil. Wild larval observations remain so rare that morphological descriptions of individuals alone have merited publication (Bergstad and Gordon 1993; van der Meeren et al. 2013). Estimates for size and age-at-settlement range from 34 to 100 mm (Haug 1990) and about a year of age (Nickerson 1978). Shallow benthic habitat at 20-60 m depth have been observed as nursery areas for Atlantic halibut off Norway (Haug 1990). The persistent juvenile hotspots that have been identified on shallow banks suggest they are important nursery areas (Boudreau et al. 2017).

Life history trait variation

A wide range of species have larger body size in colder climatic regimes at large geographic/latitudinal scales (Angilletta et al. 2004). This pattern, known as Bergmann's rule, was determined to be true, on average, for 326 marine fish species along a thermal biogeographic cline in the Northwest Atlantic, prior to the collapse of Atlantic cod in the early 1990s (Fisher et al. 2010). Among species, the evolution of life history traits (e.g. fecundity, growth, size at maturity, body size, life span) is influenced by how the environment affects survival, reproduction, and the tradeoffs among life history traits (Stearns 2000). Within species, variation in life history traits can arise from populations residing in different environmental regimes or demonstrate phenotypic plasticity, which is the capacity of one genotype to be expressed as multiple phenotypes in response to the local environment (DeWitt et al. 1998) and has been observed in Pacific halibut (Stewart and Martell 2014; Seitz et al. 2017). There can be a genetic basis of intra-species variation. Chromosomal rearrangements in Atlantic cod (*Gadus morhua*) are associated with different behavior and migration patterns (Kess et al. 2019) that reflect local adaptation to fine-scale ecological variation (Kess et al. 2019; 2020). Variation in traits is often observed along thermal clines, and may occur because temperature has such a profound effect on biological rates. Often, there is a tradeoff between faster growth in early stages in warmer water that results in a smaller size/age at maturity, as has been observed, for example, in Atlantic cod (Thorsen et al. 2010).

Regarding size-at-age, Armsworthy and Campana (2010) were the first to note that there were small yet significant differences in growth in both sexes of Atlantic halibut between the warmer Scotian Shelf and cooler southern Grand Banks. Consistent with their study, Shackell et al. (2019) used tagging data and showed that growth rates of both males and females at 90 cm were greater in the southern warmer divisions (NAFO Div. 4X/4W) than in the northern colder divisions (NAFO Div. 3N/3Ps) (Figure 7A). In both studies, there was considerable variation in growth observations, partially attributed to sampling error.

Median age-at-maturity (AM50%) estimates also exhibit a spatial trend, as reexamined using data transcribed from original reports (Figure 7B). Two studies provided parameters as estimated using a probit

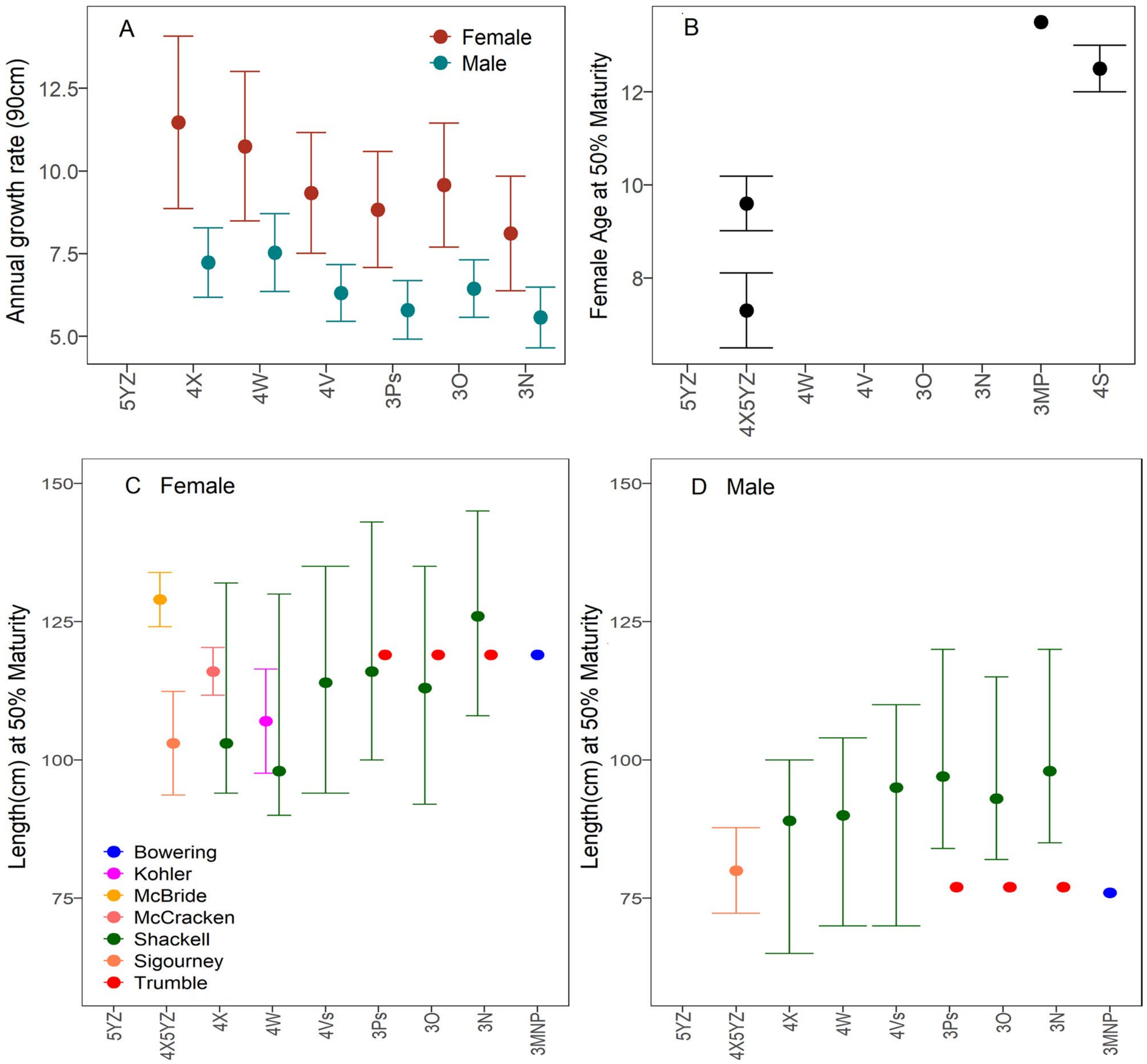

Figure 7. (A) Annual growth rate at 90 cm fork length of Atlantic halibut males and females estimated from fish tagged and recaptured within the NAFO division (Shackell et al. 2019). (B) Female age at 50% maturity. (C) Female and (D) male lengths at 50% maturity compiled from different studies using different methods over different time periods: (McCracken 1958; Kohler 1967; Bowering 1986; Trumble 1993; Sigourney et al. 2006; Shackell et al. 2019) and R. McBride, (unpublished data; NOAA Fisheries, Northeast Fisheries Science Center, Woods Hole, MA 02543, USA). 95% confidence intervals are shown where available.

binomial model (Bowering 1986; Sigourney et al. 2006). Two other studies reported tabulated data from which estimates were derived using a logistic binomial model (McCracken 1958; Kohler 1967). Consistent with the latitudinal trend, the AM50% exhibited a pattern of younger ages in the Gulf of Maine (7.3, 9.6 years) to older ages in the Gulf of St. Lawrence (12-13 years) (McCracken 1958) and offshore of Newfoundland (13.5 years) (Bowering 1986) (Figure 7B).

Finally, median length-at-maturity (LM50%) estimates depict a spatial trend, when observers classified maturity using macroscopic characters. Shackell et al. (2019) used a mixed model to estimate maturity status as a function of length and growing degree days (the integral of the number of days and temperature above a threshold) of Atlantic halibut sampled across the Scotian Shelf-Grand Banks region. Predicted probabilities of being mature of all samples were then aggregated by NAFO division. Shackell et al. (2019) showed that LM50% was smaller for both sexes in the southern division than in the northern divisions (Figure 7 C,D). There was considerable variation in the observer data. In most mixed model frameworks, only the fixed and random sources of uncertainty are reported, Shackell et al. (2019) also included the residual variance, in recognition of the inherent noise. These probabilistic estimates could not be used for prediction given the considerable overlap in confidence intervals. The magnitude of the confidence intervals partly reflects the quality of the observer dataset used for maturity status classification. The female LM50% estimated in Shackell et al. (2019) were consistent with historical studies throughout the stock domain (Bowering 1986; Trumble 1993; Sigourney et al. 2006) (Figure 7C).

An outlier population regarding this clinal trend in LM50% was identified by unpublished data that used gonad histology to classify maturity in the Gulf of Maine (R. McBride, included in Figure 7C). Gonad histology reveals that females start yolk provisioning of germ cells (i.e., vitellogenesis) a year before spawning, so the use of histology reveals females that are physiologically but not functionally mature. Specifically, females maturing for the first time can be identified during a period that brackets the spawning season (October to May in the Gulf of Maine) using two histological criteria: initiation of vitellogenesis (commonly said to be partially yolked) as the most advanced oocyte stage, together with a thin gonad wall (tunica). Such primiparous fish are distinguished from multiparous (repeat spawners), which have a thick tunica (greater than 500 microns), and since they are not capable of spawning within the current season, they are not part of the spawning stock biomass. Quality assurance that these primiparous fish are classified correctly by the lower-cost macroscopic method, in reference to at least a subset of fish processed with gonad histology, is recommended for future research and monitoring.

Excluding the one population surveyed with this histological method, the data are suggestive of latitudinal trends in both sexes for LM50% as well (Figure 7C and D). Nonetheless, these results have been obtained by a variety of researchers employing a variety of methods, from a few studies that span many decades, all of which makes these trends difficult to confirm or accurately characterize (Figure 7). This handful of studies occurred from the 1940s to 2010s; some variation could be the result of different periods of environmental productivity or fishing pressure. Importantly, there are differences in methods, such as the use of macroscopic or microscopic traits to determine maturity, or the use of a probit or logistic function for modeling the maturity ogive, and in some cases, modest sample sizes that led to uncertainty in estimates. Updates with gonad histology throughout the geographic range appear warranted to reduce uncertainty in the spatial variation and to evaluate if there has been change over time given the variability in the thermal regime and the population size. Comparisons of recent and historical studies will always remain a challenge, ongoing monitoring of new and conventional indices are still needed to detect spatio-temporal changes.

The large observed variation in size-at-age is not solely due to methodology. In general, exploited stocks exhibit large variability in weight-at age; a meta-analysis of 91 exploited stocks showed that roughly 2/3 of the variability was explained by age, year (environmental), and cohort (density dependence) effects (Thorson and Minte-Vera 2016). Large temporal and spatial changes in size-at-age in Pacific halibut have been attributed to a combination of not yet fully understood effects of cohort density dependence, prey availability, and selective fishing which complicates the stock assessment process (Stewart and Martell 2014). Variation in life history traits has implications for stock assessment processes that often assume constant parameters (Lowerre-Barbieri et al. 2011). Spatial and temporal variability in size-at-age among and within regions has consequences for stock assessments of Atlantic halibut across its range and would suggest the need to incorporate this uncertainty in the stock assessment method.

Synthesis of recent studies on Atlantic halibut spatial structure

More than a decade ago, Ciannelli et al. (2008) suggested that spatial fisheries ecology will advance along two routes: 1) multidisciplinary studies spanning ecosystems and life stages, and 2) the development and application of new methodologies to address interactions between spatial and abundance dynamics. Recent research on Atlantic halibut has followed both of these routes while Atlantic halibut landings have grown to their highest level in the past 70 years in Canada and 40 years in the U.S. under precautionary quotas (Figure 1). The expansion of the resource and associated increases in fishery production and research interests continue to facilitate collaborations that now explore spatial aspects across the entire Atlantic halibut life-cycle and spanning the Northwest Atlantic range.

Multidisciplinary studies have both challenged and bolstered earlier ideas of Atlantic halibut population spatial structure. Early conventional tagging, published more than 60 years ago, indicated that the Gulf of St. Lawrence and Scotian Shelf-Grand Banks stocks were unique (McCracken 1958). This interpretation provided patterns that informed the spatial extent of Canadian assessment and management jurisdictions decades later (Stobo et al. 1988) and have persisted since. Recent genomic analyses presented evidence of a weak genetic structure throughout most of the Atlantic halibut's domain but differences were sufficient to support the current large-scale division for stock assessment between the Gulf of St. Lawrence and the Scotian Shelf-Grand Banks (Kess et al. forthcoming). Within stocks, however, juvenile Atlantic halibut are spatially structured, exhibiting persistent core juvenile areas where the average connectivity, assessed as the coherence of temporal patterns across space, was an order of magnitude less than the unit stock area assumed for the largest Scotian Shelf-Grand Banks stock (Boudreau et al. 2017). The size of these juvenile core areas was related to adult landings, supporting the nursery-zone size hypothesis (French et al. 2018).

Spatial structure has been clearly documented in adult Atlantic halibut. The wealth of both PSAT and conventional tagging studies conducted in recent decades has shed new light on the diversity of migration patterns in Atlantic halibut as well as the potential drivers of that diversity. Seasonal migratory contingents overwinter on continental slopes and return to foraging sites in the summer. Few individuals are recaptured at extreme distances from where they were conventionally tagged, and individuals in a more-resident contingent remain in the general tagging area. Seasonal migrations are likely spawning and feeding migrations, influenced by variation in timing, fish size, state, and distance to slope, resulting in partial migration. Even within stocks, there are clear patterns of different groups demonstrating spawning migrations (Gatti et al. 2020). Across all studies, it remains unclear whether non-migratory individuals are skipped spawners, or all their needs, including spawning habitat, are met within their home site.

The current perspective of Atlantic halibut spatial structure in Canadian waters is that there are two distinct populations, one in the Gulf of St. Lawrence, the other in Scotian Shelf-Grand Banks. Within each region, there are subpopulations, composed of contingents. Migratory contingents within subpopulations may have discrete feeding areas but share common spawning sites, but the level of mixing on common spawning grounds both among and within subpopulations is only partly understood (Figure 8). In the context of fishery management, the Atlantic halibut resource is a stock complex, composed of sub-stocks with variation in demographic rates within a regional stock. Growth rate is faster in warmer water in southern part of domain, where age-at-maturity, and possibly length-at-maturity, is lower/smaller suggesting phenotypic variation across the seascape. Note that

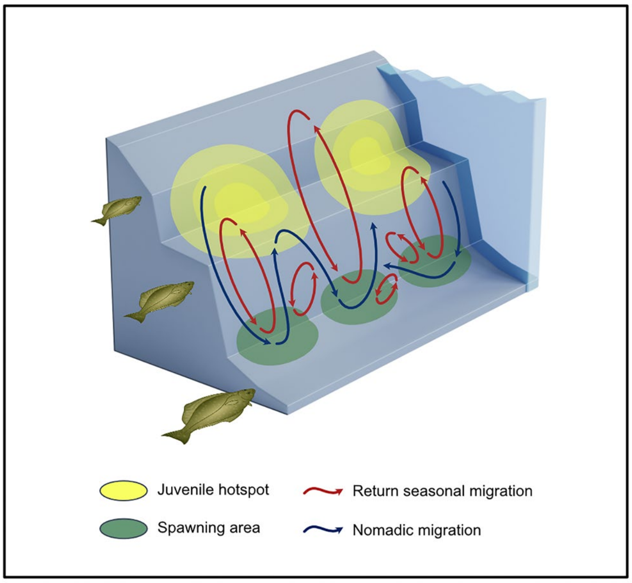

Figure 8. Schematic life cycle of Atlantic halibut. The yellow areas indicate juvenile hotspots with the lighter yellow concentric circles indicating the ontogenetic shift of Atlantic halibut to a broader distribution including greater depths in channels and at the continental shelf edge. The green areas indicate spawning areas. The red arrows depict return migration between foraging and spawning areas. The blue arrows depict alternative nomadic adult migration with potential movement between spawning areas or different foraging areas.

Pacific halibut are assessed on a coast-wide scale, partly because of a lack of genetic structure which may be eroded even by very low levels of exchange among areas, during larval to adult phases, over long time scales. Pacific halibut from several areas in the Bering Sea and Gulf of Alaska show differences in life history parameters, adults from different areas largely do not mix on common spawning grounds (Seitz et al. 2017), and weak genetic structure does exist where spatial segregation mechanisms are relatively strong (Drinan et al. 2016). Sub-structure should be accounted for in spatial management, because fishery pressure acts on much shorter timescales than genetic exchange and evolution (Seitz et al. 2017).

Spatial ecology research questions

Despite the recent Atlantic halibut research, several unanswered questions remain. The fishing industry has been critical to the success of the Atlantic halibut research both in Canada and the U.S. Harvester knowledge and at-sea experience have been instrumental in the logistics and economic feasibility of offshore conventional and electronic tag deployment and recoveries in the U.S. and Canada. The DFO-industry collaborative survey on the Scotian Shelf and Southern Grand Banks has provided an index of biomass and served as a platform for collection of biological samples. A similar collaborative survey has been recently (2017) established in the Gulf of St. Lawrence. Knowledge of life histories within the Gulf of Maine have been greatly aided by the participation and leadership of harvesters in a range of projects, including conventional tagging (Kanwit 2007; Kersula and Seitz 2019), electronic tagging (Seitz et al. 2016; Liu et al. 2019), and an experimental longline survey that informed length-at-age and sexual maturity for the area (Sigourney et al. 2006).

Harvester knowledge has been integrated into spatial analyses through interviews and considerations of covariates to better explain spatial variability in Atlantic halibut catch rates (Hansell et al. 2020), it has been used to identify the timing and locations of migrations, spawning areas, and interactions with other ocean industries (Marshall 2020). Infrequent adult Atlantic halibut encounters in U.S. waters required scientists to adapt their field protocols to train fishermen to deploy PSATs during normal fishing operations (Liu et al. 2019). Population modeling and stock assessment of other reemerging Northwest Atlantic fisheries have been aided by including harvester information (Duplisea 2018), demonstrating its utility to inform inputs and decisions with stock assessments. Major research questions are described below, by category, and questions are itemized where possible.

Basic ecological questions

Climate change

Juvenile Atlantic halibut's thermal habitat availability has increased in the northern part of the domain but habitat is not the sole factor in their expansion. The recent and projected climate-change induced expansion of juvenile Atlantic halibut in the Northwest Atlantic is being further examined to provide insight into the effect of climate change on Atlantic halibut stocks and the implications of these changes in distribution on stock management, but the concern extends to other parts of the life cycle. Deep continental shelf, slope, and channels are used as spawning habitats (Armsworthy et al. 2014; Gatti et al. 2020) yet those same depths have recently shown warming toward their highest temperatures on record (Galbraith et al. 2020) and there is indication that the timing of halibut spawning may be advanced under warming conditions (Marshall 2020). Ecosystem changes may be linked to the interaction of the warm, saline Gulf Stream and the cold, oxygen-rich Labrador Current, and specifically to the stronger influx of Gulf Stream water at the tail of the Grand Banks that started around 2008 (Brickman et al. 2018; Neto et al. 2021). There is concern for both current and future temperature and oxygen saturation levels in deep waters and their potential effects on different life stages of Atlantic halibut and other species, as well as changes in phenology and ocean currents that could impact recruitment processes.

Spatial structure and spawning migration

Prior to technological advances in refrigeration, transportation and communication played roles in the demise of mid-19th century U.S. Atlantic halibut fisheries (Grasso 2008). In contrast, advances in electronic tag development, satellite tracking and recovery of floating tags at-sea (Fisher et al. 2017), evolving population genomic techniques (Kess et al. forthcoming), and spatial geolocation methodologies to model and validate individual Atlantic halibut movements (Gatti et al. 2021) together illustrate the current 'golden age' of animal biologging and movement research (Wilmers et al. 2015). This is permitting new ecological, behavioral, and physiological questions to be asked of deep-water, large-bodied, migratory Atlantic halibut. When early tagging studies were initiated on adult Atlantic halibut, it was during periods where the noted dual constraints of low fish abundance and high fish value severely limited tagging operations, e.g. Jensen and Wise (1961). Given increases in Atlantic halibut abundance, adults can now quite easily be targeted for tagging, while their economic importance drives requests from industry and regulators for more information (Shackell et al. 2016; Kersula and Seitz 2019), including:

1. Spatial structure across the continental shelf. Analysis of more electronic tagging will help resolve the diversity of seasonal migrations and contribute to a comprehensive synthesis.
2. Identification and delineation of spawning areas. There are few electronic archival studies on the Scotian Shelf where knowledge of spawning is relatively less than elsewhere, e.g. the Gully (Figure 2).
3. Formation of migratory contingents. When does an individual Atlantic halibut adopt the migratory cycle of a specific contingent: is it following settlement in a specific area at the post-larvae stage or is it following ontogenetic movement from a nursery area to the adult habitat?
4. Spawning site fidelity and philopatry. In this review, evidence is provided of summer feeding site fidelity and homing in Atlantic halibut, as is common for Pacific halibut (Loher 2008; Nielsen et al. 2014; Nielsen and Seitz 2017) but spawning site fidelity has not been fully examined. Does the same fish return to the same locations to spawn for multiple years, or move between sites or even current stock boundaries. Does a fish that originated in a spawning rise off the Laurentian Channel usually go to the same site/area to spawn when it is mature? Do Atlantic halibut follow the same migratory patterns and paths across years within their lives? How many of these are shared within a population versus unique?
5. Evaluation of skipped spawning. Many long-lived cold water fishes show some degree of skip-spawning (Rideout and Tomkiewicz 2011) and there is recent evidence in the Gulf of Maine (McBride, unpublished data) but what proportion of resident fish observed in PSAT studies are skipping spawners?
6. Effect of climate change on migration. The understanding of Atlantic halibut spatial ecology is based on past and current periods: how will spatial ecology change as the climate changes, as food availability changes, and as fishing behavior changes?

Benthic habitat

There is an association between juvenile Atlantic halibut and sediment size (Shackell et al. 2016), but benthic habitat in the larger perspective is not well understood. Harvesters recognize the importance of bottom type to Atlantic halibut catch rates, but there still needs to be an appropriate approach to mapping and testing the association between Atlantic halibut at different life stages and bottom types (Hansell et al. 2020).

Early life history

There is little information on what happens between the spawning and juvenile stages. Based on the PSAT-derived locations in the Gulf St. Lawrence, spawning areas are currently being used as the origins to model egg- and larval-stage drift based on regional ocean modeling informed by the temperature-specific stage durations and densities of Atlantic halibut early life stages (C. Dufresne et al., University of Quebec at Rimouski, *unpublished data*). Such models may inform the spatial locations of future surveys targeting collection of the elusive early life stages. At the post-settlement life-stage, ongoing research in the Gulf of St. Lawrence is analyzing Atlantic halibut otolith microchemistry, including collections of juvenile fish and analyses of otolith margin chemistry to map chemical variability across Atlantic halibut habitats to reveal likely locations of nursery areas and ontogenetic movement patterns (P. Sirois et al. University of Quebec at Chicoutimi, *unpublished data*). Similar otolith microchemistry approaches in other deep-water species within this region have revealed seasonal migration patterns within and between species (Campana et al. 2007). In combination with analyses of spatial variability in juveniles and adults enabled through survey data, habitat availability, tagging data, and genetic data studies, these emerging analyses of early life stages have the potential to inform future Atlantic halibut population dynamics models that include the entire life cycle (Eckman 1997). Knowledge would also be enhanced by further research on:

1. Larval advection patterns throughout the region.
2. Effects of climate on nursery production and extent.
3. Investigation into the links between oceanographic forcing and recruitment strength as translated through the larval phase.

Life history trait variation and sexual dimorphism

A mix of studies suggest a clinal variation in age, maturity, and growth rate, but are not confirmatory. Further work is needed. Currently, an expanded otolith collection to estimate growth variation across the Scotian Shelf-Grand Banks region is underway and should provide insight into spatio-temporal variation in growth (A. Perreault, Fisheries and Marine Institute of Memorial University, *unpublished data*). The estimation of maturity schedules is also problematic due to quality of data and methodology. Further work using gonad histology is needed to refine the estimation of maturity schedules. Finally, the sexual dimorphism is size-related and occurs around age 10 (Armsworthy and Campana 2010). It could be argued males and females have similar ecological roles until that age. The large size achieved by the females may allow for them to access different prey, and avoid predators so there may be differences in natural mortality between sexes. As well there would be a difference in the catchability by commercial fleets and hence, differences in fishing mortality. The consequences of sexual dimorphism on mortality are typically accounted for in the stock assessment process, however changes in the thermal environment and the density of halibut may impact the maturity schedule, and should be investigated further.

Fishery management questions

Transboundary stocks

The spatial structure of Atlantic halibut is currently of particular interest across the Hague Line separating Canada and the U.S. (Figure 2). In U.S. waters, insufficient data prevent any regular assessment approach and the quota is considered conservative (Rago 2017; Hansell et al. 2020). U.S. fisheries management has relied heavily on input controls, including a limit of one fish per day in federal waters, and limits on season, hooks, and total fish in the directed Maine state waters fishery, where these input controls have become increasingly more stringent each year (https://www.maine.gov/dmr/laws-regulations/regulations/index.html). Both Canadian stocks are deemed healthy and there is limited mixing between them (den Heyer et al. 2012) so any mixing among Canadian stocks is not a concern for fishery management. Mixing between the U.S.-managed portion of the Gulf of Maine and the Scotian Shelf-Grand Banks presents more of a challenge. The total allowable catch (TAC) for 2020 in the Gulf of Saint Lawrence was 1492 Mt, it was 5507 Mt for the Scotian Shelf-Grand Banks stock, but was only 106 Mt for the U.S. stock (NMFS forthcoming).

Shackell et al. (2016) observed connectivity in temporal abundance trends between the eastern Gulf of Maine and the Scotian Shelf. Conventional tagging data also indicate connectivity between the eastern Gulf of Maine and Canada. At least 28-43% of fish tagged in the U.S. portion of the Gulf of Maine spent some time in adjacent Canadian waters, exposed to the Canadian fishery, as evidenced by fishery-dependent tag returns (Kanwit 2007; Kersula and Seitz 2019). Further, fish that were electronically-tagged in U.S. waters during summer within the Gulf of Maine over-wintered in Canadian waters off the Northeast Channel slope (Liu et al. 2019), raising the question as to the extent of mixing and what is the danger to the relatively smaller biomass in the U.S. if there is movement to and from Canadian waters?

If the precautionary TACs are approximately proportional to stock size, the Scotian Shelf-Grand Banks stock should be expected to be 50 times larger than the U.S. stock, and even a relatively small amount of mixing from Canada's stock would be a considerable source of biomass for the U.S. stock. A Canadian conventional tagging program reported 0.6% of the recaptures were from U.S. waters (den Heyer et al. 2012), which would account for roughly a third of the U.S. catch. Conversely, the 43% of returns from Canada reported from the U.S. conventional tagging program (Kersula and Seitz 2019) represents a substantial proportion of fishing mortality for the U.S. stock unit. Given the lower biomass in the U.S. compared to Canadian waters, the U.S. stock is unlikely to be a source for the Scotian Shelf-Grand Banks stock that would affect population dynamics for the Canadian stock. Fishing mortality for fish originating in the U.S. but caught in Canadian waters greatly complicates management of this unit stock.

The wisdom of continuing to manage the U.S. as a separate unit stock from Scotian Shelf-Grand Banks while there is substantial mixing between the two has increasingly been called into question when there is already an established process (TRAC) regularly used to assess and manage cross-boundary stocks (Shackell et al. 2016; Kersula and Seitz 2019). Recent advances in the understanding of the spatial complexity of stocks across the Northwest Atlantic may promote a finer-scale approach to management in order to avoid loss of this complexity and associated productivity (Boudreau et al. 2017; Shackell et al. 2019; Gatti et al. 2020; James et al. 2020). This is especially relevant to the eastern Gulf of Maine and adjacent Canadian waters because Atlantic halibut are not limited by the border between United States and Canadian territorial waters. A more appropriate boundary might reflect the larger Gulf of Maine in order to encompass spawning sites and the majority of known movements (Kersula and Seitz 2019; Liu et al. 2019). These findings raise important research questions about stock boundaries, including:

1. How much does movement among and between the Gulf of St. Lawrence, the Scotian Shelf-Grand Banks, and Gulf of Maine matter to regional productivity trends, and to the different assessment and management processes? Consider that two out of three stocks are healthy, growing stocks, where movement between the two may be less consequential, while the Gulf of Maine is still historically diminished, fishing mortality outside of the Gulf of Maine will have more of an impact on that population component.
2. What is the level of fishing mortality of a stock outside of the "stock boundary"?
3. When does the mortality occurring outside of this boundary start to have more influence over stock dynamics than the fishing mortality within?

Research stock assessment questions

Once a spatial structure has been defined, the question is then: how can spatial structure be incorporated into the stock assessment process? The inclusion of spatial structure into the stock assessment process has long been recognized as important, but has become increasingly possible with advanced technology and improved methodologies over the last 20-30 years (Punt 2019; Cadrin et al. 2020). With respect to Atlantic halibut, the principal motivations are to improve the stock assessment and reduce uncertainty through, for example, accounting for spatially varying rates of biological parameters, such as growth, fecundity, maturity, natural mortality, and/or migration rates among core patches. Equal motivation is provided by the notion that fishing is not uniformly-distributed across a stock domain, and that both natural biological spatial variation as well as spatial distribution and selectivity of the fishing fleet must be considered to avoid local overfishing (Bosley et al. 2019; Punt 2019).

There is a variety of stock assessment approaches designed to accommodate spatial structure. The Pacific halibut annual stock assessment has accounted for spatial differences (Stewart et al. 2021) by modeling areas as separate 'fleets' within the broader stock assessment (Waterhouse et al. 2014). This approach can accommodate spatial differences in growth and selectivity. If there are regional surveys available, the relative biomass index can be used to spatially distribute the fishery yield in proportion to that biomass. The Pacific halibut stock assessment currently uses a coast-wide approach that does not explicitly model movement rates, but accounts for temporal trends in different management areas by apportioning fishery yield among them based on relative survey biomass(IPHC 2021b). Both of these approaches represent intermediate steps between a simple stock assessment model that assumes homogeneous demographic rates and a complex spatially structured assessment model.

Mis-specification of spatial dynamics can be further mitigated using Management Strategy Evaluation (MSE). Uncertainty around abundance in the Pacific halibut assessment is incorporated as variance in an operating model for an MSE used for policy analysis (IPHC 2021a). The MSE allows for exploration of strategies for dealing with uncertainty, which reduces the need for high cost information such as precise estimates of migration rates between management areas.

In this review, evidence was provided of demographic differences across the Northwest Atlantic, different seasonal movement patterns and consequently, different spatial vulnerability to international fleets. None of those complexities would be fully represented using intermediate options. At this stage, exploratory stock assessment modeling, including spatial structure and movement, may be too complex or uncertain for supporting fishery-management advice. Still, exploratory models fit to the available data can provide valuable information to condition spatial operating models for testing alternative management procedures (Goethel et al. 2016; Carruthers and Butterworth 2018).

The complexity of Atlantic halibut behavior and spatial structure suggests that revised stock boundaries may not account for meaningful connectivity among regions. Therefore, a spatially-structured stock assessment may be appropriate (Cadrin et al. 2020) and there are approaches to explore the effects of spatial structure (Mestre et al. 2016). Considering the variability in data availability among regions, an integrated modeling approach will be needed to fit to data where and when it is available, at broad spatial scales and finer scales (Maunder and Punt 2013; Berger et al. 2017). One of the first steps toward spatial assessment is to compile all assessment data (e.g., catch, indices, size/age composition, maturity/fecundity, tagging, environmental covariates) according to the most plausible stock units and strata. The inventory of data by plausible stocks and strata is informative for assessment model decisions about spatial scope and structure, and supports a range of spatial assessment approaches.

An important corollary step would be a thorough comparison between Atlantic and Pacific halibut research and management. Atlantic halibut is often compared with Pacific halibut because there is much to be learned from the rich research and management history in the Pacific. Atlantic and Pacific halibut are morphologically similar, and only confirmed to be separate species in the 1980s (Haug 1990). Indeed, the counter-current movement hypothesis proposed by Stobo et al. (1988) relied heavily on the larger, analogous body of research on Pacific halibut, made possible through the International Pacific Halibut Commission (IPHC) that was established in 1923. and began regulating the fishery in 1928, making it one of the first internationally managed fisheries in the world (Clark 2008).

The Pacific halibut fishery has been monitored for nearly a century. The extended time series itself presents a challenge to many typical assumptions in stock assessments, such as time invariant growth or selectivity at age, which are increasingly unrealistic for long time series. The IPHC currently manages Pacific halibut as a well-mixed, coast-wide stock (Stewart and Martell 2014), following the assumption of population-level panmixia (Stewart and Martell 2015). Nonetheless, emerging evidence indicates that this view may not be entirely accurate on a large scale as Pacific halibut exhibit homing (Loher 2008), summer feeding site fidelity (Nielsen and Seitz 2017), limited mixing of adults on common spawning areas from different summer feeding areas at a basin-scale (Seitz et al. 2017), and evidence of internal genetic structure (Drinan et al. 2016). These findings from Pacific halibut map well onto the emerging views of Atlantic halibut movements and seasonal migrations at the stock-scale (Gatti et al. 2020). Perhaps more importantly, Pacific halibut research continues to provide some of the theoretical and methodological foundations that have aided research programs on the ecological aspects of Atlantic halibut, summarized herein, and it is reasonable to assume that similar behaviors displayed by Atlantic halibut, such as limited movement by some adults (Seitz et al. 2014; 2016), may affect its stock structure.

In closing, the stock assessment process can typically afford many assumptions under a relatively constant environmental regime. Climate change introduces a greater and consistently dynamic regime. There is now a greater impetus for basic ecological research to understand the mechanisms, so that response to changes in drivers can be anticipated. Combined with promising new approaches to ecological research, spatial stock assessments, and management strategy evaluations, Atlantic halibut research is well-positioned to contribute important knowledge for managing in dynamic environments.

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