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A review of the importance of various areas for northern contingent West-Atlantic mackerel spawning

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The southern Gulf of St. Lawrence (sGSL) is considered to be the dominant spawning area of northern contingent West-Atlantic mackerel (*Scomber scombrus*). This premise underlies our basic understanding of the stock and its assessment. Because there are however indications of spawning outside the sGSL, we aimed to review the potential importance of various external regions for spawning, based on a weight of evidence approach. Fundamentally, important spawning areas can only exist where there is evidence of a considerable spawning stock biomass being present when environmental conditions are suitable for spawning. This should lead to direct observations of significant egg and larval densities. Based on an ensemble of evidence (migration patterns, environmental conditions, and ichthyoplankton observations), we investigated the dominance of the sGSL for northern contingent mackerel spawning. Elsewhere, such as on the Scotian Shelf, where mackerel starts its spring migration, there is evidence of minor but relatively consistent egg production. Spawning off Newfoundland, where mackerel can migrate to later in the year, appears sporadic and highly variable in intensity. This review should alleviate some of the uncertainty associated with the mackerel stock assessments and be a baseline to further our knowledge on mackerel spatial spawning dynamics.

Keywords: egg production, Gulf of St. Lawrence, *Scomber scombrus*, spawning habitat, weight of evidence.

Introduction

Stock assessments are based on a range of assumptions about a population's structure and dynamics, a fishery, and data quality (e.g. Hilborn and Walters, 1992). Incorrect assumptions might have significant consequences for both the stock and the management of the fishery (e.g. Walters and Maguire, 1996). Status indicators (e.g. abundance/biomass indices) are often the pillars of an assessment and rely on the fundamental assumption that they are proportional to the overall stock trend. However, many scientific surveys do not cover the full distribution range of the monitored stock attribute (e.g. egg production, recruits abundance or adult biomass). For instance, surveys can have unintended gaps in certain years (e.g. because of technical problems) or might consistently exclude specific zones (e.g. inaccessible near-shore waters, Brehmer *et al.*, 2006). When survey coverage is poor, the proportionality assumption can be violated when there are directional changes in the distribution of the monitored stock attribute relative to the survey area, creating bias (e.g. Breivik *et al.*, 2021). A stock assessment, therefore, requires validation that a survey covers an appropriate and consistent part of the entire stock, based on fishery-dependent or -independent data.

Both the Canadian and US Atlantic mackerel (*Scomber scombrus*) assessments rely heavily on the premise that the southern Gulf of St. Lawrence (sGSL) annual egg survey samples a substantial and stable proportion of northern contingent egg production (NEFSC, 2018; Smith *et al.*, 2020) and therefore adequately tracks changes in spawning stock biomass (SSB, see egg production methods; Bernal *et al.*, 2012). The assumption that the sGSL is the dominant spawning area of northern contingent mackerel dates back to the seminal work of Sette (1943, 1950). He noted that there are two main spawning areas in the West Atlantic, that is, one in the sGSL (for the northern contingent) and the other in the Western Gulf of Maine and offshore of southern New England (for the southern contingent). Since this work and the establishment of an annual egg survey in each spawning area to estimate SSB, the assumption that the sGSL is sufficiently dominant in terms of spawning to be representative of fluctuations in SSB of the entire northern contingent has never been investigated. Consequently, the frequent observations of young-of-the-year or spawning females outside the sGSL have challenged this assumption, in particular during the last decade when egg production in the sGSL has been low (DFO, 2021; Supplementary Figure S1). This challenge represents a concern for the validity of the stock assessment and could directly affect scientific advice that supports fisheries management decisions.

The ideal approach to determine the importance and stability of the sGSL for northern contingent mackerel egg production through time would be to conduct a dedicated survey covering most of the Eastern Canadian shelf and the GSL over several years (Figure 1). Such an approach is logistically and economically unrealistic. However, a weight of evidence approach based on all available data, directly or indirectly indicative of mackerel reproduction in each region could provide valuable information to achieve our goal. A weight of evidence approach transparently integrates various sources of qualitative and quantitative information to determine the support for different hypotheses, and is generally used when a single unequivocal piece of information is missing (see Hardy *et al.*, 2017). In the present case, the hypothesis being

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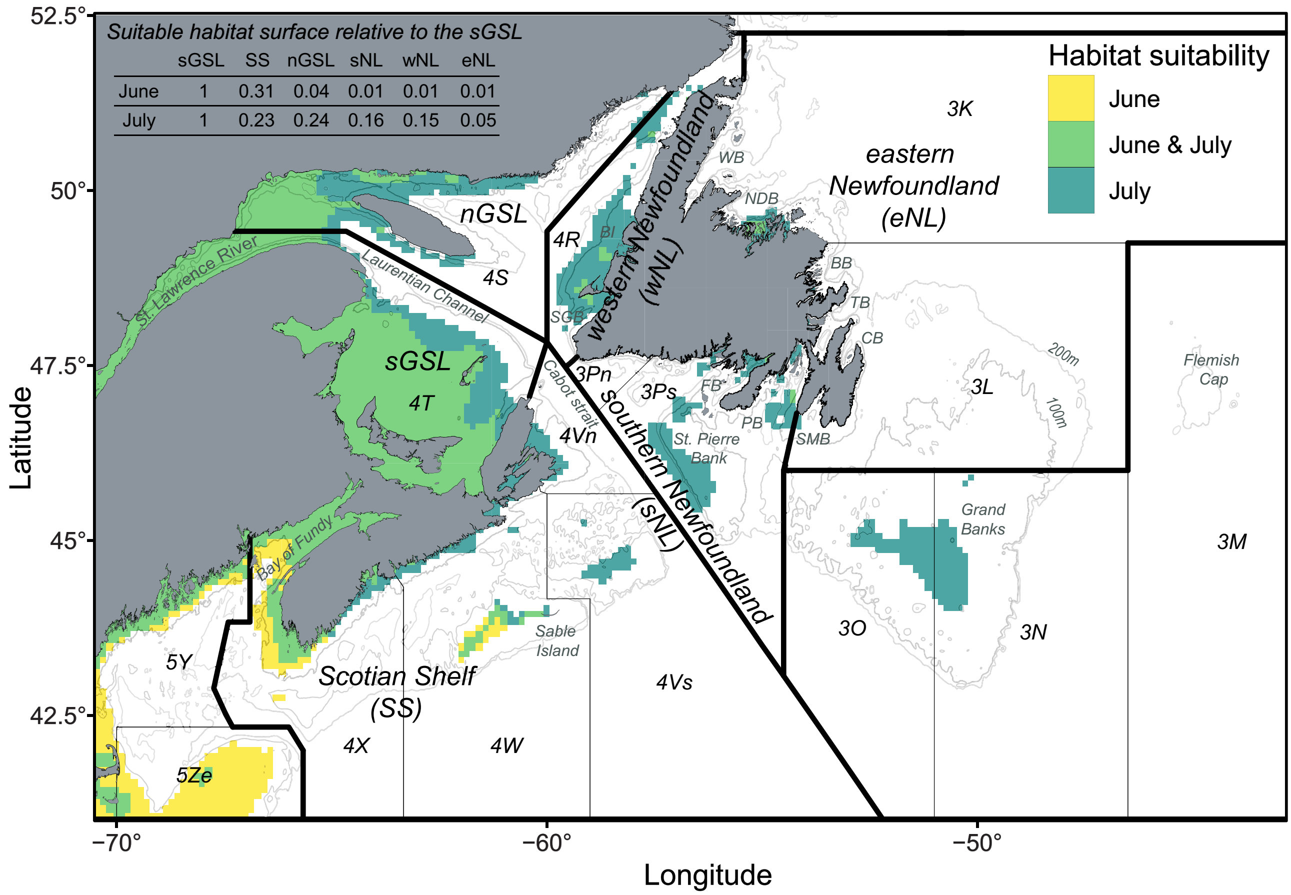

Figure 1. Map of eastern Canadian waters of the Atlantic Ocean (GSL = Gulf of St. Lawrence). Large-scale regions discussed in the paper are indicated (sGSL = southern GSL, Scotian Shelf, nGSL = northern GSL, southern Newfoundland, western Newfoundland and eastern Newfoundland), as well as the NAFO (Northwest Atlantic Fisheries Organization) areas upon which they are based. Predicted mackerel spawning habitat suitability in June–July is shown in colours (1999–2012, data from Mbaye *et al.*, 2020). The suitable habitat surface of each region relative to the sGSL is provided in the table (calculations excluded the Bay of Fundy and the St. Lawrence River). Newfoundland bays are abbreviated. (WB = White Bay, NDB = Notre Dame Bay, BB = Bonavista Bay, TB = Trinity Bay, CB = Conception Bay, SMB = St. Mary's Bay, PB = Placentia Bay, FB = Fortune Bay, SGB = St. George's Bay, and BI = Bay of Islands)

evaluated using this weight of evidence approach is the presence of important spawning activity outside the sGSL. The approach considers the reliability, relevance, and consistency of the observations from a broad range of indicators of spawning activities. Substantial spawning would occur in any given region only if a large biomass of fish in spawning condition is consistently present over several weeks across a large area. Synchronously to gonad maturation, environmental conditions should also be suitable for spawning over sufficiently large spatial and temporal scales, including interannual stability. This indirect evidence of the timing and the location of spawning adults and suitable habitat should provide an order of magnitude of spawning that can be expected for any given region. Whether or not a potentially important spawning habitat is realized can then be validated by direct observations of eggs or larvae, collected opportunistically, or through directed surveys. In summary, important spill-over or shifts in spawning towards other regions (e.g. the Scotian Shelf or waters around Newfoundland; Figure 1) would be expected only if there is evidence of a large biomass of spawning northern contingent fish in these areas during the reproductive season (e.g. when catches are large), when their environmental conditions are suitable for spawning, or there are observations of high densities of mackerel eggs or larvae.

In this study, we aimed to evaluate a key assumption of the West-Atlantic mackerel assessments, that is, that the sGSL is the main spawning area for the northern contingent. The evidence available on mackerel spawning migration and location is highly diverse, often unpublished and typically limited to the grey literature. By reviewing this body of evidence from different sources, we assessed the relative importance of different regions as mackerel spawning areas and also gained a more holistic understanding of northern contingent mackerel spawning dynamics. For reviews focusing on the ecology of West-Atlantic mackerel, we refer readers to Sette (1943, 1950) and Studholme *et al.* (1999).

Review of the evidence

Prior to the start of this review, we determined the pieces of evidence (POE) that are essential to assess the relative importance of different regions in terms of mackerel spawning (Table 1). POE were classified in three categories based on (1) the presence of adults in spawning condition (indirect

Table 1. Summary of POE presented, including their definition, the metric used to summarize information, the figures in which data are shown and the data source (see Annex 1 for further details). (AZMP = Atlantic Zone Monitoring Programme)

POE no.	POE	Metric	Figure	Data source
POE-1	Presence of adults:			
POE-1.1	in large biomass	Median biomass landed per trip in June–July of 1995–2019.	Figure 2 (weekly landings), Figure 3 (annual landings)	commercial landings
POE-1.2	interannual stability	Percentage of years (1995–2019) in which landings in June–July were at least 1% of the annual regional total.	Figure 2 (weekly landings), Figure 3 (annual landings)	commercial landings
POE-1.3	during a long period	Number of weeks in June–July with landings exceeding 1% of the annual regional total, averaged over all years (1995–2019).	Figure 2 (weekly landings)	commercial landings
POE-1.4	across a large space	Percentage of harbours used in June–July of a given year relative to all harbours used that year, averaged over all years (1995–2019).	Not plotted	commercial landings
POE-1.5	in the spawning phase	Percentage of spawners observed per week in June–July, averaged over all years (1973–2020)	Figure 2 (maturity data)	commercial sampling
POE-2	Spawning habitat suitability:			
POE-2.1	interannual stability	Percentage of years (1981–2019) with regional SST suitable for spawning during at least 2 weeks during June–July	Figure 2 (SST)	AZMP
POE-2.2	during a long period	Average number of weeks (1981–2019) over which SST is suitable for spawning in June–July	Figure 2 (SST), Figure 1	AZMP
POE-2.3	across a large space	Predicted suitable habitat surface averaged over June–July, excluding the estuary and the Bay of Fundy (1990–2015)	Figure 1	(Mbaye *et al.*, 2020)
POE-3	Direct evidence of spawning:			
POE-3.1	eggs	Median observed egg densities over all years (1979–2018) and samples from June to July, excluding zeros (n/m^2)	Figure 3 (egg densities)	Ichthyoplankton surveys
POE-3.2	larvae	Median observed larval densities over all years (1979–2018) and samples from June to August, excluding zeros (n/m^2)	Figure 3 (larval densities)	Ichthyoplankton surveys

evidence), (2) the spawning habitat suitability defined by environmental conditions (indirect evidence), and (3) the occurrence and density of eggs and larvae (direct evidence). Details on the data presented as evidence are provided in Annex 1.

Firstly, as egg production and SSB are directly related through fecundity, a large biomass of adults is expected to be present in a region with important spawning activity (POE-1.1), each year (POE-1.2), during a relatively long period (POE-1.3), and across a relatively large space (POE-1.4), during the reproductive season (June–July). A significant fraction of this biomass should be spawning (POE-1.5). Because there are no dedicated scientific surveys targeting adult mackerel in Canadian waters, we explicitly assumed that the timing and amount of landings of the competitive commercial fishery in each region under consideration would represent a reliable proxy for the arrival and presence of mackerel in the different regions. In this fishery, fishermen compete against each other for a share of the catch, possibly resulting in fish being landed as soon and for as long as they are present, until the total allowable catch is reached and the fishery closes. Evidence to support the assumption that landings can be a proxy for mackerel presence across the regions is provided with a review of mackerel migratory patterns first, which should also serve as baseline information to understand where and when mackerel would be spawning. Maturity data is collected each year through a standard port sampling programme and is used to determine the fraction of biomass present that could be spawning. As an example of this first category of evidence, we would expect the Scotian Shelf or waters off Newfoundland to be potentially important for spawning relative to the sGSL if its fishery was or became comparatively active (POE-1.1) every year (POE-1.2) over multiple weeks (POE-1.3) across most of the area (POE-1.4) during the spawning season, when we would observe that a large portion of fish landed is actively spawning (POE-1.5).

Secondly, environmental conditions should be suitable for spawning during the reproductive season (June–July). Suitable environmental conditions must be observed on a recurrent basis (interannual stability; POE-2.1) over a substantial period (POE-2.2) and area (POE-2.3). Available evidence includes model-based predictions of spawning habitat suitability (Mbaye *et al.*, 2020; Figures 1 and 2) as well as environmental data. As an example of this second category of evidence, we would expect the Scotian Shelf or Newfoundland waters to be potentially important for spawning relative to the sGSL only if environmental conditions are consistently (POE-2.1) suitable for spawning over significant timeframes (POE-2.2) and spaces (POE-2.3) during the spawning season.

Thirdly, the evaluation of the relative importance of regions as spawning areas based on indirect evidence (the presence of spawning adults and habitat suitability), could be confirmed with direct observations of eggs (POE-3.1) or larvae

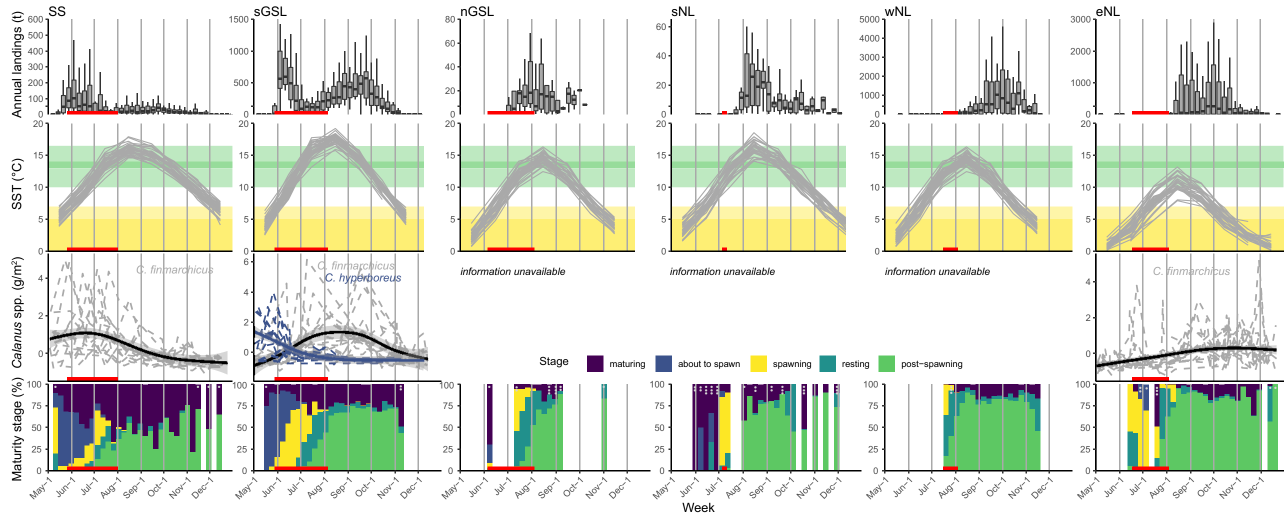

Figure 2. Summary of seasonal information available by region in support of our understanding of spawning areas. Upper row: weekly boxplots of total regional landings (each observation is one year; 1995–2019). Second row: annual sea surface temperatures SST) by month with an indication of mackerel's overall lower thermal limit (yellow) and lower thermal preference (light yellow), as well as favoured (green) and optimal (dark green) spawning temperatures (1981–2019). Third row: density of copepods (grey = *Calanus finmarchicus*, blue = *Calanus hyperboreus*) available for mackerel in the upper water column (0–100 m) annually (dashed lines) and over the available timeframe (solid lines: gam smoother; 1999–2012). Fourth row: weekly percentage of adult fish in a given maturity stage across all samples available over 1973–2020 (port sampling programme) with indication of the number of samples (number of dots) when samples size <4. The red horizontal line indicates the weeks in which 95% of all spawning individuals have been found. (sGSL = southern Gulf of St. Lawrence, SS = Scotian Shelf, nGSL = northern Gulf of St. Lawrence, sNL = southern Newfoundland, wNL = western Newfoundland, and eNL = eastern Newfoundland)

(POE-3.2) obtained from various ichthyoplankton surveys. The presence of young-of-the-year fish was not considered because of an absence of data (targeted by neither the fishery nor scientific surveys). As an example of this third category of evidence, we would except the Scotian Shelf or Newfoundland waters to be important for spawning relative to the sGSL if there are observations of significant densities of eggs (POE-3.1) or larvae (POE-3.2).

Migratory patterns

To assess potential mackerel spawning areas and their relative importance, we first reviewed mackerel's spring and early summer migration pattern and occurrence. The aim of this section is to provide evidence in support of the use of landings data as a proxy of the relative presence of mackerel in each region during the year, and thus of the migration of the bulk of the stock, in the absence of a dedicated survey targeting adult mackerel. The review was performed in relation to the seasonal patterns in physical and biological environmental conditions as migrations of widely distributed pelagic fishes are strongly environmentally driven (e.g. Trenkel *et al.*, 2014). Finally, results from tagging studies as well as regional age-structure information were also used in support of the assumption that the annual transition in relative landings across regions is an adequate proxy of mackerel's main migration patterns.

Scotian shelf, southern and northern Gulf of St. Lawrence

In most years, the mackerel fishery in Canada begins around mid-May (Figure 2, first row), when fish initiate their spring inshore migrations on the Scotian Shelf from their offshore overwintering areas (SS, here defined as zone 4VWX of the NAFO). By early June, fishing activity shifts towards the sGSL (NAFO 4T) to subsequently develop in the northern GSL (nGSL, NAFO 4S) in July.

Both small- and large-scale mackerel movements have traditionally been associated with SST changes (e.g. Castonguay *et al.*, 1992; Castonguay and Gilbert, 1995; Radlinski *et al.*, 2013). Experimental data demonstrates that mackerel actively avoid water temperatures below 5–6°C and prefer those between 7.3 and 15.8°C (Olla *et al.*, 1975, 1976). There is also a considerable amount of field evidence that demonstrates that, with some exceptions, mackerel avoid temperatures below 6–7°C and have an optimum above this threshold (e.g. Sette, 1950; D'Amours and Castonguay, 1992; D'Amours and Grégoire, 1992; Bruneau and Grégoire, 2011; Overholtz *et al.*, 2011).

Mackerel are first caught on the SS in spring, after migration from its deep offshore wintering areas (e.g. Bruneau and Grégoire, 2011), when SST reaches 7°C (Figure 2-SS; similar to the southern contingent, see Goode *et al.*, 1883; Sette, 1950). This close association between migrations and surface water reaching a minimum threshold around 7–8°C is also observed in the sGSL (Figure 2-sGSL; Galbraith and Grégoire, 2015; 7.5°C, Ware and Lambert, 1985). For the northern Gulf (Figure 2-nGSL), information on the drivers of large-scale migrations is missing, but small-scale inshore movements of mackerel were shown to be associated with wind-forced advections of water masses with temperatures ≥7.5°C (Castonguay *et al.*, 1992).

Spring warming removes the temperature barrier for mackerel in the upper water column, but is also associated with changes in the zooplankton community. Mackerel have a wide dietary range (e.g. copepods, decapods, and fish), of which the composition can vary considerably as a function of location, season, and time of the day, amongst other elements (Grégoire and Castonguay, 1989; Myers and Pepin, 1994; Macy *et al.*, 1998; Darbyson *et al.*, 2003). However, copepods are generally dominant, especially in currently dominating younger fish (DFO, 2021), and there is an apparent synchrony between copepod development and mackerel landings. The dominant copepod species on the SS in spring (*C. finmarchicus*) develops earlier than in all other regions, with its biomass peaking around May (Casault *et al.*, 2020), which matches with the expansion of the fishery (Figure 2-SS). When *C. finmarchicus* becomes less abundant (around the end of July), landings on the SS decrease again (Figure 2-SS). The timing of migration into the sGSL is likewise associated with the development of the plankton community and hence food availability (Figure 2-sGSL). In June, when mackerel are present for spawning, total zooplankton biomass in the sGSL is often highest (Blais *et al.*, 2021). During that period, the *Calanus* biomass in the region (in contrast to all other regions) is dominated by the arctic *C. hyperboreus*, an important prey (Darbyson *et al.*, 2003) shown to drive variations in mackerel spawning location (Brosset *et al.*, 2020). The later developing and dominant copepod species (*C. finmarchicus*) is more available to mackerel from July to September, when the fishery expands again (Figure 2-sGSL).

The seasonal match between the landing patterns and mackerel's known temperature and dietary needs (Figure 2, first three rows), as well as the competitiveness of the fishery, indicates that it is unlikely that a large proportion of the northern contingent would be present in a region (SS, sGSL nGSL) when landings are very low or absent. Seasonality in regional landings over the last decades is also not significantly influenced by fishery closures, which happened only from 2016 onwards and no earlier than fall. The start and end of the fisheries are flexible (Supplementary Figure S2), and we are not aware of important drivers other than the presence of mackerel. Landings further track the bulk of mackerel as the age structure of the catches from the SS and the sGSL is characterized by the same large cohorts and recent age truncation (Supplementary Figure S3). Individuals tagged along the SS (Sette, 1950; Mackay, 1967; Beckett *et al.*, 1974; Stobo, 1976; Waters *et al.*, 2000) in early summer also remained in the area or migrated to the sGSL (see Supplementary Figure S4 for a summary of all tagging studies).

Southern, western and eastern Newfoundland

Fishing in southern (sNL, NAFO 3P), eastern (eNL, NAFO 3KL), and western (wNL, NAFO 4R) Newfoundland generally does not start before early August (Figure 2, first row). The fisheries around Newfoundland thus usually develop later than those along the SS, sGSL and nGSL, despite that SST earlier in the summer can already be above the lower physiological threshold in some years (Figure 2, Newfoundland columns). The presence of mackerel in larger numbers later in summer is however coherent with expected large-scale northwards feeding migrations towards areas with better feeding opportunities, typical of several pelagic species (Nøttestad *et al.*, 1999). The important role of prey availability in mackerel distribution and migration might explain why, despite non-limiting SST in especially near-shore areas earlier in the season (e.g. Colbourne *et al.*, 2015), mackerel appear most abundant later on, when zooplankton biomass increases (Figure 2-eNL; Maillet and Pepin, 2005; Johnson *et al.*, 2008). The end of the fishery coincides with a decrease in SST below the mackerel's thermal tolerance and the return of *C. finmarchicus* to dormancy in deeper waters (Figure 2-eNL; Johnson *et al.*, 2008).

Mackerel landings in Newfoundland can change dramatically from one year to another, a pattern diverging from that observed on the SS and in the sGSL (Figure 3, bar plots), where landings vary more clearly in response to changes in stock biomass (Supplementary Figure S1) and fishing effort. These large variations in landings in Newfoundland have been related to changes in environmental conditions (Parsons and Hodder, 1970; Moores *et al.*, 1974; Smith *et al.*, 2020) and the presence of substantial year classes. For instance, Moores *et al.* (1975) reported that after 1880, mackerel virtually disappeared from Newfoundland waters only to become more abundant during a period of warmer conditions (the mid-1940s). Increases in landings around 1985, 1991, and 2001–2010, on the other hand, coincided with the development of a strong year class (1982, 1988, and 1999, respectively; Supplementary Figure S3, DFO, 2021). The percentage of landings in the Newfoundland regions relative to those elsewhere have also been linked to SST, differential food availability between regions, and stock characteristics (Smith *et al.*, 2020). Although the lack of georeferenced fishery data for northern contingent mackerel has so far precluded a detailed study on species distribution and associated potential drivers, an effect of temperature as well as food availability and stock size and structure should be expected as they are key drivers of the distribution of the northeast Atlantic mackerel stock and the northwest Atlantic southern contingent (Jansen and Gislason, 2011; Overholtz *et al.*, 2011; Jansen *et al.*, 2012; Utne *et al.*, 2012; Radlinski *et al.*, 2013; Van Der Kooij *et al.*, 2016; Nikolioudakis *et al.*, 2019). Therefore, although variations in fishing effort inevitably affect the amounts caught, large-amplitude fluctuations in annual landings are likely highly associated with substantial changes in mackerel biomass in the (at least near-shore) waters surrounding Newfoundland.

The contrasting patterns in landings between the SS and sGSL on one hand and Newfoundland on the other hand could theoretically be explained by the presence of a large biomass in Newfoundland that does, to a certain extent, diverge from the major component (e.g. potentially spawning around Newfoundland). However, this appears unlikely as tagging studies showed that there is clear migration between all regions (Supplementary Figure S4), the age composition of fish landed in Newfoundland is very similar to those landed in the sGSL and SS (Supplementary Figure S3), and there is currently no evidence for genetic differentiation of Newfoundland mackerel. The only noteworthy discrepancy between Newfoundland catches and those in the sGSL and SS is the relative poverty of age-1 fish in the Newfoundland landings. Because fishery selectivity for age-1 fish in Newfoundland is not expected to be significantly lower than in other regions (DFO, 2007), this regional difference might be caused by a relatively lower abundance of age-1 fish in the region. This is in line with studies on East-Atlantic mackerel that showed that older and larger and mackerel initiate their feeding migration earlier, move further north, and stay longer in their summer foraging habitats (Eltink, 1987; Nøttestad *et al.*, 1999; Uriarte *et al.*, 2001; Jansen and Gislason, 2011). It is also consistent with the earlier arrival and reproduction of older and larger fish in spawning areas (Dawson, 1986; Eltink, 1987). For northern contingent mackerel, such age-based migration has also been established at multiple phases of their route; larger fish appear to arrive first on the SS (Mackay, 1967), older and more fecund fish are present first in the sGSL (Pelletier, 1986) and old mackerel arrive also first in Newfoundland (Moores *et al.*, 1974). Hence, despite that the fraction of the contingent that moves to Newfoundland can vary dramat-

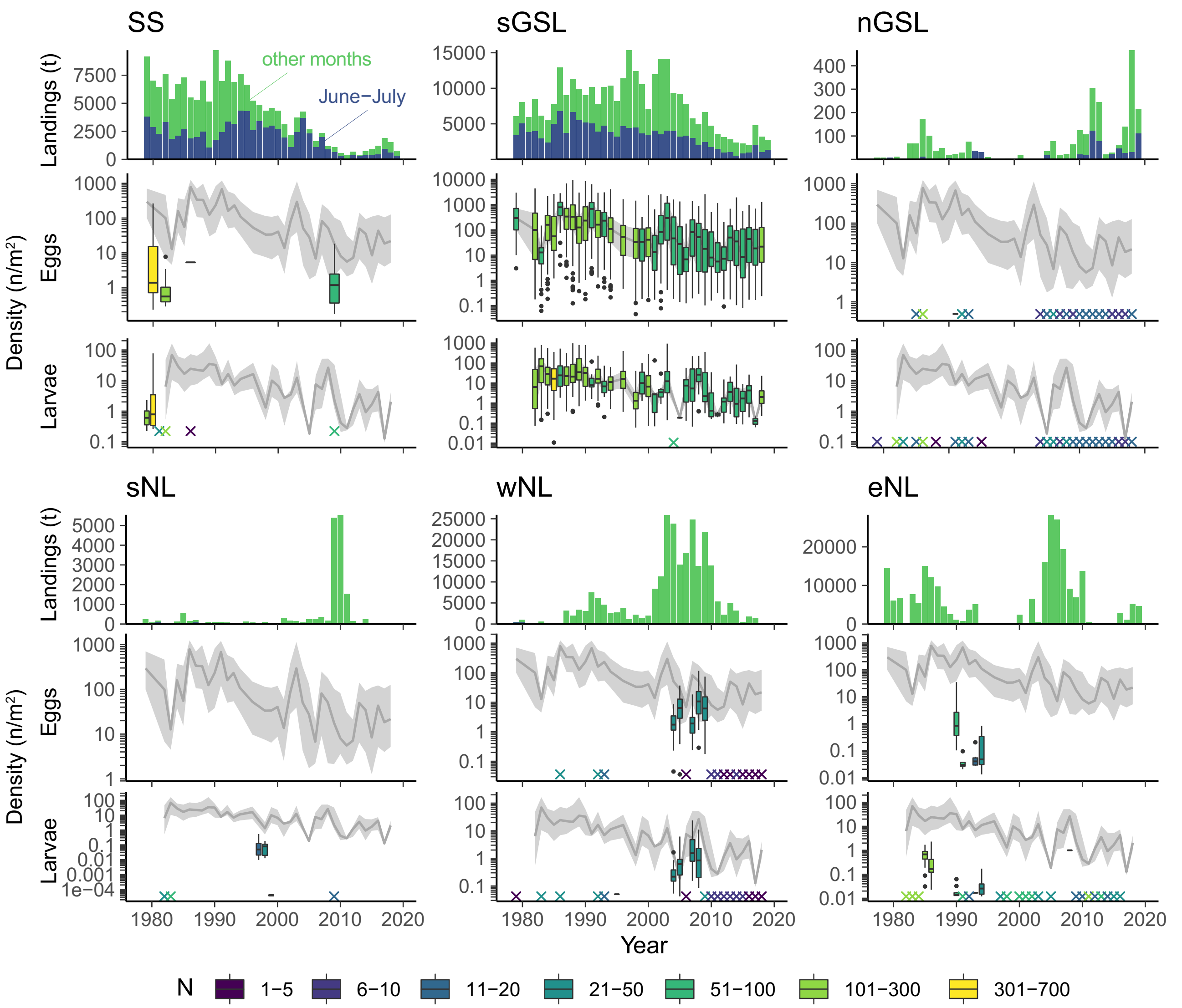

Figure 3. Summary of interannual information available by region in support of our understanding of spawning areas and migrations. Barplots show regional landings, with an indication of whether these were made in June–July (blue) or other months (green). Boxplots show egg (upper panels) and larval (lower panels) densities observed during regional ichthyoplankton surveys in June–July or June–August, respectively (1979–2018; the grey ribbon corresponds to the quantile values of the sGSL; the colour scale indicates the number of samples available; crosses indicate zeros). (sGSL = southern Gulf of St. Lawrence, SS = Scotian Shelf, nGSL = northern Gulf of St. Lawrence, sNL = southern Newfoundland, wNL = western Newfoundland, and eNL = eastern Newfoundland)

ically between years, all evidence suggests that this is a group of fish derived from the main spawning component, with the possible exception of immature fish that are thought to separate and migrate mostly to SS waters from the sGSL (Kulka, 1977).

Our conclusion, based on all the available evidence described above is that landings of this competitive fishery are likely a reasonable proxy for the presence and relative abundance of mackerel across eastern Canadian waters.

Regional spawning patterns

Evidence from seminal work on mackerel

We start by reviewing the information available prior to the official start of the mackerel egg survey in the sGSL in 1979. Goode *et al.* (1883) provided anecdotal observations of spawning along the coast of Nova Scotia, in the sGSL (mostly near the end of June), and on the northeast coast of Newfoundland (end of June), with the sGSL postulated as possibly being the main spawning area. Knowledge on the location and timing of mackerel spawning in Atlantic Canada waters improved greatly thereafter with more than a century of ichthyoplankton sampling. The Canadian Fisheries Expedition of 1914–1915 (Hjort, 1914; Dannevig, 1919), which covered the GSL, the SS, and sNL in June and August, was the first large-scale scientific ichthyoplankton survey in the area (Supplementary Figure S5). Mackerel eggs were almost exclusively observed in the sGSL, with only three eggs sampled on the SS (June 1914). This observation of low egg densities on the SS was corroborated during May-July of 1922 (Sparks, 1929, explained in Sette, 1943; Supplementary Figure S5). During the first survey in the north-eastern GSL and wNL, mackerel eggs and larvae were only identified in Cabot Strait, but the timing of the survey in late summer might have influenced this result (August-September, Supplementary Figure S5, Pinhey, 1926; Huntsman *et al.*, 1954). About two decades later, a low number of eggs was found off wNL (unknown month, Bay of Islands; Sette, 1943). Subsequent evidence also

		sGSL	SS	nGSL	sNL	wNL	eNL
Presence of adults:							
in large biomass	POE−1.1	1 (524 kg)	0.4 (227 kg)	0.2 (106 kg)	0.3 (154 kg)	0.3 (154 kg)	0.2 (98 kg)
interannual stability	POE−1.2	1 (100 % of years)	1 (100 % of years)	0.7 (71 % of years)	0.5 (53 % of years)	0.3 (29 % of years)	0.1 (12 % of years)
during a long period	POE−1.3	1 (9 weeks)	1 (9 weeks)	0.3 (2.6 weeks)	0.3 (2.3 weeks)	0.3 (2.6 weeks)	0.3 (2.3 weeks)
across a large space	POE−1.4	1 (83 % of harbours)	0.7 (62 % of harbours)	0.7 (61 % of harbours)	0.4 (32 % of harbours)	0.3 (27 % of harbours)	0.2 (14 % of harbours)
in the spawning phase	POE−1.5	1 (34 % spawners)	0.5 (16 % spawners)				
Spawning habitat suitability:							
interannual stability	POE−2.1	1 (100 % of years)	1 (100 % of years)	0.9 (95 % of years)	1 (100 % of years)	0.9 (95 % of years)	0.4 (38 % of years)
during a long period	POE−2.2	0.9 (5.2 weeks)	1 (5.8 weeks)	0.7 (4.2 weeks)	0.8 (4.7 weeks)	0.7 (4.2 weeks)	0.4 (2.1 weeks)
across a large space	POE−2.3	1 (65233 km2)	0.3 (17842 km2)	0.2 (9904 km2)	0.1 (6076 km2)	0.1 (5730 km2)	0 (1872 km2)
Direct evidence of spawning:							
eggs	POE−3.1	1 (73.2 n/m2)	0 (1.1 n/m2)	0 (0.5 n/m2)		0.1 (4.2 n/m2)	0 (0.4 n/m2)
larvae	POE−3.2	1 (13.7 n/m2)	0.1 (0.7 n/m2)		0 (0.1 n/m2)	0.1 (0.7 n/m2)	0 (0.2 n/m2)

Figure 4. Summary of the POE. The metric for each region expressed as a fraction of the cross-regional maximum is shown on top. Values for each metric are given in parentheses. (sGSL = southern Gulf of St. Lawrence, SS = Scotian Shelf, nGSL = northern Gulf of St. Lawrence, sNL = southern Newfoundland, wNL = western Newfoundland, and eNL = eastern Newfoundland)

pointed towards mackerel spawning being absent or low and sporadic around Newfoundland, as inferred from the presence of young-of-the-year and (pre-) spawning mackerel (Conception Bay in November 1968, Placentia Bay in July 1970; Parsons and Hodder, 1970). In 1964, another Canadian sampling programme (Kennedy and Powles, 1964; Supplementary Figure S5) with a larger temporal coverage determined that mackerel eggs were mainly present in the sGSL in June (compared to May and July), and it was noted for the third time that eggs were present on the SS, albeit in low density. A variety of ichthyoplankton records from 1954 to 1978, including the experimental stages of the sGSL mackerel egg survey and generally covering the GSL and the SS (DFO databases; Supplementary Figure S5), confirmed previous observations; in the sGSL much larger egg densities are observed than on the SS in June–July. Although there are no additional surveys that covered the areas around Newfoundland, the insignificance of the mackerel fishery in these waters during extended periods, perceived to be because of low fish abundance (Moores *et al.*, 1975), supported the idea that spawning should mainly occur in more southern areas.

The above observations lead to the still prevailing assumption that the sGSL is the dominant spawning site, albeit that mackerel is not restricted to it.

Evidence from 1979 to the present

We discuss all POE following the structure of Table 1. Our findings are summarized in Figure 4 and are detailed in the text below. Because our goal is to investigate the assumption that the sGSL represents the main spawning area for northern contingent mackerel, we examine the evidence for this region first as a reference for all other regions, which will then be reviewed and compared based on the seasonal migration pattern of this stock.

Southern Gulf of St. Lawrence

Presence of adults

When spawning occurs in June–July, mackerel are clearly present in the sGSL (POE-1 of Figure 4, Figure 2-sGSL, and Figure 3-sGSL). Weekly landings are high (POE-1.1) every year (POE-1.2). Mackerel are targeted over a vast area (POE-1.4) and during a long period (POE-1.3), as the fishery is active in the large majority of ports and during all of June–July with a peak in the first three weeks of June, which overlaps in large part with the duration of the spawning period over the last decade (peaking around the 21st of June, see Brosset *et al.*, 2020).

A large fraction of adults present in the sGSL in June–July is also in spawning condition (POE-1.5). The presence, timing, and consistency of spawning can be described using gonad maturity data routinely determined from samples collected by a commercial port sampling programme during the fishing season. Across all 48 years for which data were available (1973–2020), 38% of the fish analysed during the weeks of June–July (see Figure 2-sGSL, last row) were spawners (1747 samples with 56 476 fish). The period during which spawners can be observed in the sGSL ranges from May 28 to August 5 (99% of all individuals for which maturity stage has ever been determined), but they are most prominent near the end of June and early July, in accordance with the peak spawning date, as estimated from gonadal development (around June 21st; Brosset *et al.*, 2020). During these peak weeks, the percentage of spawners observed in samples was almost consistently over 50%. There is therefore robust evidence that the overall probability to observe spawning fish in the sGSL is high (% of spawning individuals in combination with the overall presence of adults approximated by landings; POE-1).

Spawning habitat suitability

Mbaye *et al.* (2020) predicted that mackerel spawning habitat suitability (Figure 1) is consistently optimal (POE-2.1) for most of June–July (POE-2.2) across the sGSL (POE-2.3) (POE-2 of Figure 4). SST in the sGSL in early June quickly increases to become suitable for spawning as mackerel migrate into the region (Figure 2-sGSL). Spawning in the area occurs when SST is between 10 and 16.5°C, with an optimum between 13 and 14°C (Mbaye *et al.*, 2020; Ware and Lambert, 1985). These optimal SST values for spawning are similar to those determined for North-East Atlantic mackerel (e.g. Brunel *et al.*, 2018). They also correspond to the temperature range maximizing mackerel egg survival rates (9–17°C, Lockwood and Nichols, 1977; 11–21°C, Worley, 1933).

Direct evidence of spawning

From 1979 onwards, the sGSL was recognized as the main spawning area of the northern contingent and has been surveyed for mackerel eggs almost annually around the period of peak spawning (June; Figure 3-sGSL). Therefore, there is ample evidence that egg and larval densities in the area are and remain conspicuous (POE-3.1 and POE-3.2). Over the entire time-series (1979–2018), eggs were recorded in at least 50% of the stations and densities were commonly above 10 eggs/m^2, with magnitudes of 1000 eggs/m^2 occasionally reached (Figure 3-sGSL, Supplementary Figure S6). When larvae were present in the samples, their densities often exceeded 1 larvae/m^2 (Figure 3-sGSL, Supplementary Figure S6). The observations of significant egg and larval densities have also been very consistent. For example, even when the egg survey was delayed, lower yet important egg densities were observed (e.g. in 2006, when the median survey date was estimated to have been about 20 d after peak spawning). During the last decades, when egg production and thus estimated stock biomass were lower (aligning with landings and catch-at-age data; DFO, 2021; Supplementary Figure S1), egg densities also remained high relative to values observed elsewhere.

Scotian Shelf

Presence of adults

Over at least the last 35 years (1985–2019), the bulk of mackerel catches on the SS was landed from mid-May to early July (Figure 2-SS). Mackerel are thus present in large biomass (POE-1.1) during multiple weeks (POE-1.3) along the entire shelf (POE-1.4) every year (POE-1.2) (POE-1 of Figure 4). Although the landings per trip (POE-1.1) and percentage of harbours used (POE-1.4) on the SS in June–July are smaller than in the sGSL (Figure 4), this might be due to differences in fishing effort.

Similar to the sGSL, landings can be high throughout June (Figure 2-SS); however, the presence of most individual fish is likely much shorter (POE-1.3) because mackerel migration from the SS to the sGSL is thought to happen swiftly. First, mackerel already start migrating from the area through the southern part of Cabot Strait to enter the sGSL (Castonguay and Gilbert, 1995) near the end of May (D'Amours and Castonguay, 1992; Castonguay and Beaulieu, 1993), which is generally less than two to three weeks after the spring migration from the offshore overwintering areas to the SS started (mid-May). The migration through Cabot Strait has, for five specific years (1989–1993), been shown to occur over approximately the first three weeks of June (D'Amours and Castonguay, 1992; Castonguay and Beaulieu, 1993; Castonguay and Gilbert, 1995). D'Amours and Castonguay (1992) also noted that the Cabot Strait migration should involve the bulk of the stock as the age structure of local catches matched that of the entire stock. Thus, early in the spawning season, the majority of the northern contingent might already be in the sGSL, where landings increase sharply (Figure 2-sGSL, first row). Additional evidence for the short residence time of mackerel in SS waters includes the rapid changes in demographic structure. Sette (1950) for instance noticed clear shifts in length-distribution between late May and mid-June. The large proportion of individuals in the area that are about to spawn relative to those that are in the spawning phase (Figure 2-SS, last row) also indicates that many pre-spawners move out of the area before the gonads can develop further. Hence, relative to the sGSL, the period over which mackerel are present on the SS is likely shorter.

Maturity-stage based evidence for the SS confirms that only a small but consistent amount of eggs is likely produced annually in the region. Fish in a pre- or post-spawning phase are largely dominant (Figure 2-SS, last row) and the percentage of spawners observed in the region in June–July is less than half the value of the sGSL (POE-1.5: Figure 4). Interestingly, the observation of spawners has, very similarly to the sGSL, always been limited to the period from May 26 to August 1 (99% of all 25489 individuals ever analysed). The largest fraction of spawning females was likewise present from the end of June to the beginning of July, when the bulk of the population likely already migrated towards another area (see previous paragraphs).

Spawning habitat suitability

Even though environmental conditions on the SS in spring are generally adequate for mackerel migration, Mbaye *et al.* (2020) predicted SST to be suboptimal for spawning in June and July (POE-2) in nearly the entire area (POE-1.3). Relative to the sGSL, the available suitable habitat in both months is about three-to-four times smaller (Figure 4), more fragmented, and mostly limited to the very near-shore (Figure 1). When SST becomes optimal for spawning (roughly mid-July), the vast majority of mackerel likely left the area (Figure 2-SS). Thus, because most fish are probably present only during a short time period during which environmental conditions are not suitable for spawning, the area is not expected to be of significant importance. Future environmental conditions in the region are also not projected to lead to significant changes in spawning habitat suitability (Mbaye *et al.*, 2020). The prevailing environmental conditions, although restrictive for reproduction when the bulk of the contingent is present, do however not completely exclude spawning in the area. SST later in the season, closer to shore or locally offshore (because of local solar heating, etc.; D'Amours and Castonguay, 1992), can still be warm enough (e.g. around Sable Island), especially if mackerel would spawn near its lower thermal preference limit.

Direct evidence of spawning

The presence of spawning on the SS can be validated by field observations (Figure 3-SS). Ichthyoplankton surveys in June–July have been performed only during five years since 1979, but with a great spatial coverage and standardized gear. During any of those years (1979, 1980, 1981, 1982, and 2009), mackerel eggs and larvae were observed in relatively low densities (Figure 4 and Figure 3. 3-SS; POE-3.1 and 3.2) and with a patchy spatial pattern (Supplementary Figure S7). This is in accordance with observations before 1979 (see section "Evidence from seminal work on mackerel"), which therefore suggests long-term stability in the patterns described. The relative importance of the SS in terms of mackerel egg production was quantified in 2009 (Grégoire *et al.*, 2012). It was concluded that the low egg production measured in only a small proportion of stations (~30%) excluded the possibility that a significant proportion of the stock would spawn on the SS, which matches observations based on maturity data, the known migratory patterns, and environmental conditions.

Northern Gulf of St. Lawrence

Presence of adults

Fishing in the nGSL (defined here as NAFO area 4S) generally only picks up in early or mid-July (Figure 2-nGSL). Adults are thus generally present only during about three weeks near the end of the spawning season (POE-1.3). Fishing in June–July is also much less intense than in other regions (POE-1.1), with important variations from year to year relative to the sGSL (POE-1.2, Figure 3-nGSL) and limited in space (POE-1.4) (POE-1 of Figure 4). Although the North Shore of the GSL is long and landings have so far been recorded in many harbours, mackerel fishing in June–July appears to be mostly opportunistic in many locations, especially those nearest to the sGSL. The fishery dynamics are thus more indicative of a transitional and opportunistic occupancy of the area by a low total mackerel biomass.

In the rare nGSL fishery samples from June or July, the majority of individuals were in a resting or post-spawning phase, and only some spawning individuals have been identified (POE-1.5; Figure 2-nGSL, last row). Thus, based on the low SSB in the region, it can only be expected that a very low amount of eggs might on occasion be produced in this region.

Spawning habitat suitability

Only near-shore environmental conditions (about 20% of the sGSL surface) in July should in theory be suitable for spawning (Figure 1, Mbaye *et al.*, 2020). Therefore, on average, both the temporal (POE-1.2) and spatial (POE-1.3) availability of spawning habitat are considerably less than in the sGSL (POE-2 of Figure 4). There are also years in which the overall SST in the region has been suitable yet suboptimal throughout the spawning season (POE-1.1; Figure 2-nGSL, second row). The areas predicted to be most favourable for spawning are also those that are the least important for the fishery, and hence are likely the ones less visited by mackerel.

Direct evidence of spawning

Ichthyoplankton data from the nGSL was collected during many years and by various surveys (not targeting mackerel). With the exception of one sample, no mackerel eggs or larvae were ever found (Figure 3-nGSL, Supplementary Figure S8), which is in sharp contrast with the sGSL. These observations match the expectations based on the presence of adults and spawning habitat suitability. The northern GSL was to our knowledge never mentioned as a potentially significant spawning area of mackerel in the literature or by anyone involved in the fishery; the observations presented here do not provide evidence to reconsider this understanding, and this area will not be further discussed.

Southern Newfoundland

Presence of adults

The sNL mackerel fishery is of limited intensity in June–July (POE-1.1) similar to the nGSL, as it develops much later than the sGSL fishery (POE-1.3) (Figure 2-sNL). Fishing in June–July is limited in its spatial extent (POE-1.4) and fluctuates heavily from year to year (POE-1.2) (Figure 2-sNL and Figure 3-sNL, POE 1 of Figure 4). The first landings of the season (since 1995) have generally been recorded in August, although during some years the commercial fishery started in July. There is therefore no indication that, relative to the sGSL, there is an important (spawning) biomass present in sNL in June and July.

Because fishing in June–July is relatively scarce, maturity data is rare for this period. Most of the information on the maturity stage of adults in sNL has been collected between the second week of August to September, when the fishery is most active (Figure 2-sNL, last row). As for all other regions, samples from this period never contained spawning fish. The maturity stage of mackerel in sNL in June–July (POE-1.5) has only been determined during four years (1986, 1990, 1991, and 2019). When spawning mackerel were present, they dominated the samples. Moores *et al.* (1974) described the same pattern in earlier years (1970–1973), that is, the majority of mackerel in July samples were fish in the spawning stage, whereas fish sampled in late July-early August were mainly in the spent or recovering maturity stage.

Spawning habitat suitability

Mbaye *et al.* (2020) predicted that SST should on average only be suitable for spawning near the end of the spawning season (July; POE-2.2) and over several small and disconnected areas representing in total only 16% of the suitable habitat in the sGSL in July (POE-2.3): the large bays (mostly Placentia and St. Mary's Bay) and around St. Pierre Bank (south of Saint Pierre and Miquelon, Figure 1). Mackerel, which do not appear abundant in the area in July, thus have relatively limited opportunity in space and time to spawn.

Direct evidence of spawning

Ichthyoplankton data to validate the expectations of occasional minor spawning is limited yet confirmative (Figure 3-sNL, Supplementary Figure S9, POE-3 of Figure 4). During three years of surveys (1982, 1983, and 2009), there were no eggs (POE-3.1) or larvae (POE-3.2) observed when and where they might have been expected based on habitat suitability (Supplementary Figure S9). Larvae have nonetheless been observed in late July and mostly August in Placentia Bay during 1997–1999, albeit again in very low densities (max = 0.53 larvae/m^2) compared to the sGSL.

Western Newfoundland

Presence of adults

The commercial fishery in the wNL usually does not start before August and peaks in September or October (Figure 2-wNL). Only small amounts of fish have exceptionally been landed prior to August, indicating that mackerel are much less abundant during the reproductive season, especially relative to the sGSL (POE-1.1 to 1.4, see Figure 4). Although fish can be present earlier in the year (e.g. Moores *et al.*, 1974, 1975), all available evidence suggests that this biomass is low. As for other regions around Newfoundland, there is thus a mismatch between the period of high mackerel biomass (approximated by the timing of the fishery; generally starting no earlier than august) and the timing of spawning (June–July). Combined with the fact that landings in the wNL are more variable from year to year compared to the sGSL and the SS (Figure 3-wNL, POE-1.2), it can be expected that, if spawning occurs, such activity is less likely to be stable over time.

The few samples available from wNL for which the maturity stage has been determined in July date back to 1985, 1987, 1989, and 1990 (Figure 2-wNL). The majority of those fish from late July were in the resting or post-spawning phase (POE-1.5). Hence, the same pattern exists in the wNL as in most other regions outside the sGSL; when fish are present in July, some will be in the spawning phase, but because the overall biomass of mackerel is likely low, it is unlikely that a significant proportion of the stock is spawning in this region.

Spawning habitat suitability

The shelf off wNL is the largest area around Newfoundland that was predicted to be suitable for spawning (Figure 1, Mbaye *et al.*, 2020). Relative to the sGSL, the available potential spawning habitat is about 10 times smaller (POE-2.3) and about one week shorter (POE-2.2). There are also years when SST was unsuitable for spawning over most of the area, suggesting a lower stability in spawning habitat suitability relative to the sGSL (Figure 2-wNL, 2nd row; POE-2.1). No major changes in habitat suitability are expected for the future (Mbaye *et al.*, 2020).

Direct evidence of spawning

The wNL region was intensively surveyed for fish eggs and larvae during five years using the same protocol as the sGSL mackerel egg survey (2004, 2005, and 2007–2009; Grégoire *et al.*, 2006). Relative to the sGSL, smaller but notable densities of eggs (POE-3.1, on average 17% of egg densities in the sGSL during the 5 years indicated) and larvae (POE-3.2) were found at most of the stations, covering most of the shelf but less than 10% of the sGSL egg survey area (Figure 3-wNL, Supplementary Figure S10).

Eastern Newfoundland

Presence of adults

Commercial fishing along eNL happens generally later relative to sNL and wNL (Figure 2). The fishery is mostly active around September and October (POE-1.1 and 1.3), and the rare landings that occur before August are restricted to a few areas (POE-1.4). Landings in eNL also showed the largest interannual variability across all regions (POE-1.2), likely because of density and environmentally driven variations in the seasonal migration (see section “migratory patterns”). The described migration pattern (late summer presence, large interannual variability) thus makes it presently unlikely that a large mass of mackerel spawns in eNL in July (see POE-1 of Figure 4).

Because the fishery is generally not active in eNL in July, the biological characteristics of fish present at that time have again only rarely been described (only in 1984 and 1989; Figure 2-eNL, last row). The few existing July samples included nonetheless individuals in the spawning phase (POE-1.5). Although spawners have been found during the first days of August, this was as in most regions, an exceptional occurrence (corroborating Moores *et al.*, 1974). There is no evidence of spawning after early August.

Spawning habitat suitability

The environmental conditions in eNL are essentially only suitable for spawning during about 2 weeks near the end of the season (POE-2.2, Figure 2-eNL 3rd row), with optima constrained to certain bays (POE-2.3, Figure 1), and only during some years (POE-2.1) (see POE-2 of Figure 4). Relative to the sGSL, the interannual stability, duration, and area of spawning habitat suitability are the lowest of all regions (Figure 4).

Direct evidence of spawning

The eNL region is characterized by several large bays. Plankton surveys (Figure 3-eNL, Supplementary Figure S11) were performed frequently in Conception Bay (1985–1986, 1990–1994, 1997–1998, 2003, 2005, 2011, and 2013) and Trinity Bay (1982–1986, 1987, 2000–2002, and 2008–2015), and more sporadically in Bonavista Bay (1982–1997), Notre Dame Bay and White Bay (2015–2016). Only the latter two bays were covered specifically to quantify mackerel spawning in these areas (survey details in Shikon *et al.*, 2019), but no eggs or larvae were observed in July or August. Although all other surveys targeted other species, they occurred when indications of mackerel spawning could be expected (mostly July to August) and covered entire bays (Supplementary Figure S10). Over 200 samples from eNL were analysed during the last decades, but mackerel larvae (species-specific egg data is mostly unavailable) have only been observed sporadically in some years (Trinity and Conception bays, July and August) and in very low densities (max. = 2.3 larvae/m^2; Figure 3-eNL, 3rd row; POE-3.1 and 3.2). This contrasts with observations in the sGSL were densities are orders of magnitude greater.

The Grand Banks

Because the Canadian mackerel fishery is operating in nearshore areas, there is unfortunately little information about the Grand Banks, off south-eastern Newfoundland (Figure 1). This region is however sufficiently shallow and warm in July to, in theory, be suitable for mackerel spawning at the end of the reproductive season (Figure 1, Mbaye *et al.*, 2020). The offshore areas have nonetheless historically been of interest to the USSR and oil and gas companies. Between 1958 and 1983, the USSR conducted intensive ichthyoplankton surveys off eNL, the Grand Banks, and the Flemish Cap (Supplementary Figure S4). Although ichthyoplankton sampling was generally done over multiple months and years, no mackerel eggs or larvae were ever found between May and September (Flemish Cap, Serebryakov *et al.*, 1984) or their presence was not worthy of mention (off eastern Newfoundland and the Grand Banks, Serebryakov, 1963). The absence of eggs and larvae on the Grand Banks was confirmed by industry in 1980 (large-scale monthly ichthyoplankton sampling programme, Supplementary Figure S4; Bonnyman, 1981).

Discussion and conclusion

The review demonstrates that the sGSL has been and is still the main spawning area of the Northwest Atlantic mackerel northern contingent. Although spawning activity has been observed in other regions, both indirect and direct evidence indicate that it is likely of much lesser amplitude compared to the sGSL. A large body of evidence leads to this conclusion (summarized in Figure 4), but most important is the coherence between all relevant factors in the sGSL (migration patterns, direct observations, environmental and physical conditions), which is not observed in any other region of Atlantic Canada.

A key consideration in the research needed to quantify the relative importance of various potential spawning areas is time; there is only a short window over which spawning can occur, so during this moment there needs to be a match between conditions that support a large number of mackerel and those that are favourable for spawning. The period over which mackerel are physiologically ready to spawn, as evidenced by the presence of actively spawning females across all regions over several decades, is essentially restricted to June and July. Wherever mackerel are caught during those two months, at least some spawning females are commonly present, albeit in varying proportions. This persistency in reproductive development is also visible in the date of peak spawning. Over the last 36 years (1982–2017), spawning in the sGSL was estimated to have peaked around June 21, at the summer solstice (with peak spawning having a 12 d window from June 15 to June 26, excluding three exceptional years; Brosset *et al.*, 2020). There has been no clear shift over time or a detectable link to an environmental or population driver (e.g. increasing SST, population mean age; Brosset *et al.*, 2020). This contrasts with East-Atlantic mackerel, where the timing of spawning is clearly shifting (Jansen and Gislason, 2011; ICES, 2021a). Because of the short and unshifted spawning window of northern contingent mackerel, spawning areas can thus only exist where a large biomass of fish is observed or expected for at least some weeks in June–July and during which environmental conditions are also optimal for spawning.

Evidence based on fishery and environmental data shows that there is no region other than the sGSL where conditions appear as optimal for adults and spawning during June–July (Figure 4). For the SS, we discussed how large quantities of fish migrate rapidly through the area in the first half of the spawning season as maturing fish and when environmental conditions are mostly unfavourable for spawning. It is therefore unlikely to be an important spawning site. This matches observations made during multiple ichthyoplankton surveys carried out over the last century, during which insignificant egg production was detected, albeit consistently so. There is no indication of any major shifts in the potential spawning importance of this region during the last decades (e.g. timing of the fishery, environmental conditions). The wNL shelf, on the other hand, is not a spring migratory route, and could because of its relative geographic proximity to the sGSL be an easier spillover location for spawners, although both regions are separated by the Laurentian Channel. The spawning habitat suitability of the wNL shelf is nevertheless substantially more restricted in space and time compared to the sGSL, and when surface waters reach suitable temperatures in July, the arrival of adults appears still in progress. Eggs and larvae have however, been found in relatively larger numbers in years when the fishery was very successful. Because of the large interannual variability in landings, it is unclear how stable this pattern is across years. In sNL and especially eNL, large biomasses of mackerel in June or July have so far generally not been encountered or expected, the available suitable spawning habitat is restricted to bays and near-shore areas, and the relative presence of mackerel each year seems to be too variable for some degree of spawning site fidelity to exist. Spawning in these regions has only been observed in small to trivial quantities and is therefore likely opportunistic. This holds true even in warmer years and when the stock was estimated to have been in a healthy state (e.g. mid-2000s).

The importance of the wNL as a spawning area for mackerel relative to the sGSL was evaluated in terms of SSB for five years (2004, 2005, and 2007–2009) by Grégoire *et al.* (2013). Under the assumptions that fish that spawned in this area did not release any batches elsewhere and did so with the same daily pattern as in the sGSL (i.e. the proportion of fish spawning each day is identical), they estimated that the SSB associated with this locally observed egg production was considerably smaller than what was estimated for the sGSL in the same years. True SSB would likely be lower under more realistic assumptions about the proportion of fish spawning each day of the survey, as most spawning in the wNL should occur later and over a shorter period relative to the sGSL (based on spawning habitat suitability and the absence of eggs in most June samples). Additionally, the survey occurred during years when stock biomass was high and the fishery was particularly successful, although not remarkably earlier (Supplementary Figure S2). Thus, although spawning can clearly take place along the wNL in nonnegligible but considerably smaller numbers than in the sGSL, a new survey would be needed during colder years or years of low SSB to determine the stability of this spawning area.

The weight of evidence approach used here to review mackerel spawning areas and migrations is useful when an unequivocal source of information (here, a pan-regional mackerel egg survey) is unavailable or incomplete. Multiple POE were instead provided, which are individually insufficient to address the question, but when combined can provide a pragmatic answer (e.g. Swain *et al.*, 2011; Cánovas-Molina *et al.*, 2021). The combination and overall quality of our review thus relies on some scientific judgement of the quality, nature, and consistency of each POE. Therefore, to further advance our knowledge about mackerel spawning sites in the absence of a large-scale ichthyoplankton survey, each POE could be improved in terms of its quality or corroborated for consistency. For instance, mackerel migration patterns could be studied further in the absence of fishery data (e.g. through a combination of individual-based and spatial modelling), variations in landings across regions could be analysed in greater depth, or additional ichthyoplankton data could be collected.

The evidence presented in this review supports the dominance of the sGSL for mackerel spawning; however, it also demonstrated that mackerel can spawn over a much larger area, albeit in limited numbers. Within Canadian waters, this potential plasticity in spawning location is still poorly understood. Given that mackerel are batch-spawners, it is unclear whether they might produce separate batches along their migratory route across the various regions, whether individual fish move to certain areas and spawn all batches locally, or whether a combination of both tactics is used. The existence of multiple spawning locations, despite being minor, also leads to questions about the nature of individuals reproducing outside the main area. For example, how do these individuals differ from the majority, and is there some degree of homing? This question is further complicated by shifting environmental conditions and potentially migration patterns. Additionally, some degree of egg or larval drift between areas (e.g. from the sGSL to the wNL) cannot be excluded based on surface currents (e.g. Lavoie *et al.*, 2016; Tamtare *et al.*, 2021), and analyses of ichthyoplankton transport or local stages would be necessary to explore this possibility. The present review should serve as a baseline to help future research directed to answer these questions.

Many of the highlighted unknowns are largely unable to be informed by knowledge from other mackerel stocks, despite that the West-Atlantic southern contingent and East-Atlantic mackerel are likewise monitored with an egg survey. There are key ecological differences. For example, East-Atlantic mackerel generally spawn in open waters around the shelf edge, whereas West-Atlantic mackerel spawn on the shelf. Within Canadian waters, there are clear barriers between the various potential spawning areas, which is also in contrast to the other stocks (excluding the Mediterranean). Because the spawning habitat of these other stocks is generally a spatial continuum, small-scale dynamics (e.g. distribution of batches spawned by a single individual, egg and larval drift between subareas) are of lesser concern. Additionally, spawning areas, migrations, and dynamics depend on several regionally divergent factors such as bathymetry, oceanographic and environmental conditions, and stock size and composition. Currently, there is at least about an order of magnitude of difference in SSB between the large East-Atlantic stock and the smaller West-Atlantic stock; moreover in the West-Atlantic, the northern contingent SSB is about an order of magnitude larger than that of the southern contingent (Richardson *et al.*, 2020; DFO, 2021; ICES, 2021b). As a result, shifts in spawning distribution differ between regions (westward for the northern contingent, north-eastward for the southern contingent and northward in the East-Atlantic; Trenkel et al., Brosset *et al.*, 2020; Richardson *et al.*, 2020), as does the timing of spawning and spawning habitat size of each stock, so that work is often done on a very different scale.

Clearly, there are still some knowledge gaps in our mechanistic understanding of mackerel spawning migrations in Canadian waters. There is however a sufficiently large and coherent ensemble of evidence (e.g. Figure 4) that demonstrates that the sGSL is the dominant spawning area, and that estimates of egg production for this region should be representative of overall stock trend. This is especially true as the recent decline in sGSL egg production (more than an order of magnitude) exceeds any uncertainty associated with the spatial coverage of the survey. Because egg production methods are used for a variety of stocks worldwide (Bernal *et al.*, 2012), our review framework could also be applied to other stocks where there is some uncertainty around the representativeness of the monitored area for spawning.

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Supplementary Material

Supplementary material is available at *ICESJMS* online.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

EVB and SP contributed to the conception of the paper and designed the data analysis. EVB and PP were responsible for the collection of data. EVB conducted the data analysis. All authors contributed to the interpretation of results. EVB led the writing of the manuscript and all authors contributed to writing and editing the manuscript and approved the final draft.

Data availability statement

The data underlying this article will be shared upon reasonable request to the corresponding author.

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