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Journal of Northwest Atlantic Fishery Science

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

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

Editorial Policy

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

Editorial Board

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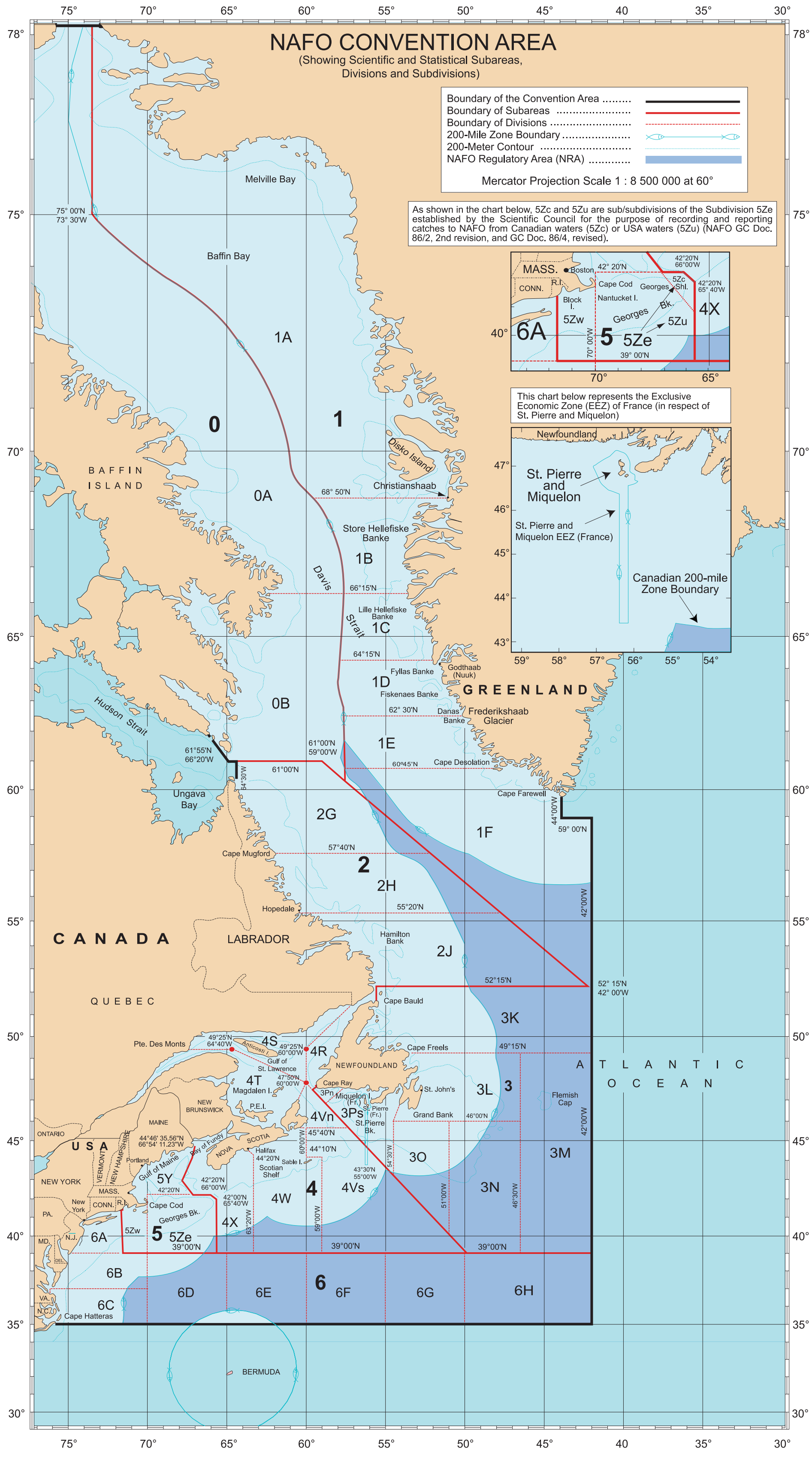

NAFO CONVENTION AREA
(Showing Scientific and Statistical Subareas, Divisions and Subdivisions)
Boundary of the Convention Area
Boundary of Subareas
Boundary of Divisions
200-Mile Zone Boundary
200-Meter Contour
NAFO Regulatory Area (NRA)
Mercator Projection Scale 1 : 8 500 000 at 60°
As shown in the chart below, 5Zc and 5Zu are sub/subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).
This chart below represents the Exclusive Economic Zone (EEZ) of France (in respect of St. Pierre and Miquelon)
St. Pierre and Miquelon
St. Pierre and Miquelon EEZ (France)
Canadian 200-mile Zone Boundary
Newfoundland
Melville Bay
Baffin Bay
BAFFIN ISLAND
Disko Island
Christianshaab
Store Hellefiske Banke
Davis Strait
Lille Hellefiske Banke
Fyllas Banke
Godthaab (Nuuk)
Fiskenaes Banke
Danas Banke
Frederikshaab Glacier
Cape Desolation
Cape Farewell
GREENLAND
Hudson Strait
Ungava Bay
Cape Mugford
Hopedale
Hamilton Bank
CANADA
LABRADOR
QUEBEC
Cape Bauld
Pte. Des Monts
Anticosti I.
Gulf of St. Lawrence
Magdalen I.
P.E.I.
NEW BRUNSWICK
NEWFOUNDLAND
Cape Freels
Cape Ray
St. John's
Miquelon I. (Fr.)
St. Pierre (Fr.)
St. Pierre Bk.
Grand Bank
Flemish Cap
ATLANTIC OCEAN
MAINE
ONTARIO
USA
VERMONT
NEW HAMPSHIRE
NEW YORK
MASS.
CONN.
R.I.
PA.
N.J.
MD.
DEL.
VA.
N.C.
Boston
Portland
Gulf of Maine
Bay of Fundy
NOVA SCOTIA
Halifax
Sable I.
Scotian Shelf
Cape Cod
Nantucket I.
Block I.
Georges Bk.
Georges Shl.
Cape Hatteras
BERMUDA
0 1 2 3 4 5 6
0A 0B 1A 1B 1C 1D 1E 1F 2G 2H 2J 3K 3L 3M 3N 3O 3Pn 3Ps 4R 4S 4T 4Vn 4Vs 4W 4X 5Y 5Zw 5Ze 5Zc 5Zu 6A 6B 6C 6D 6E 6F 6G 6H
75° 00'N 73° 30'W
68° 50'N
66°15'N
64°15'N
62° 30'N
60°45'N
61°55'N 66°20'W
61°00'N 59°00'W
61°00'N
59° 00'N
44°00'W
57°40'N
55°20'N
42°00'W
52°15'N
52° 15'N 42° 00'W
49°25'N 64°40'W
49°25'N 60°00'W
47°50'N 60°00'W
49°15'N
46°00'N
45°40'N
44°10'N
43°30'N 55°00'W
54°30'W
51°00'W
46°30'W
44°46' 35.56"N 66°54' 11.23"W
42°20'N 66°00'W
42°20'N
42°00'N 65°40'W
42° 20'N
42°20'N 65° 40'W
63°20'W
59°00'W
60°00'W
39°00'N
39° 00'N
70° 00'W
78° 75° 70° 65° 60° 55° 50° 45° 40° 35° 30°
June 2015

Dynamics of indigenous rock crab (*Cancer irroratus*) and invasive Green Crab (*Carcinus maenas*) populations during invasion of a southern Newfoundland estuary

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Abstract

Little literature exists on green crab (*Carcinus maenas*) and particularly rock crab (*Cancer irroratus*) in Newfoundland (Canada) waters. In this study, we document demographic composition for the two species upon invasion of green crab into the North Harbour, St. Mary's Bay, estuary, an area previously only occupied by rock crab and undergoing progressive warming. Using data collected via a citizens science approach, we address objectives of documenting the rate of change in speciation upon green crab invasion in the estuary and providing novel data on basic life history processes for rock crab and green crab in Newfoundland waters. The study shows a rapid proportional switch in species composition in the estuary upon green crab invasion, with green crab increasing from a proportion of 0 to 0.75 of collected samples within three years of being detected. Novel data on rock crab suggest overall consistencies with life history processes as described in the broader literature, including presence of molting periods centred near May and August, a shallow water mating migration in fall, and a similar size-at-instar structure as crab along the eastern United States. Novel data on green crab biology suggests the St. Mary's Bay population has similar life history attributes as the original invading population in Newfoundland, including spring-summer spawning and an inferred paucity of molting in fall. Allometric carapace relationships of the North Harbour green crab are the same as those described in the Pacific and northeast Atlantic oceans. The size structure of green crab in the North Harbour estuary has broadened in the three years since initial detection with increased presence of large crab beyond the supposed size-at-maturity in recent years.

Keywords: Citizens Science, Green Crab, Invasive Species, Newfoundland, Rock Crab

Introduction

Rock crab (*Cancer irroratus*) and green crab (*Carcinus maenas*) are similar species that occupy similar habitats. Both species have large ranges. Newfoundland represents the northern limit for both species in the Northwest Atlantic, with rock crab spanning as far south as Florida (Squires, 1990) and green crab as far south as Virginia (Kingsley, 1879). Within these expansive ranges, both species show considerable plasticity in phenotypic traits to enhance survival and reproduction across a broad spectrum of localized environmental conditions. As ocean warming has progressed in recent decades, both species have invaded new northern territories. Green crab expanded into Newfoundland waters circa 2007 (Best, 2017) and rock crab were first reported in Icelandic waters in 2006 (Gíslason *et al.*, 2021). As invasions have ensued, interactions between the two species have become more commonplace.

In Newfoundland, rock crab is an indigenous species that is found in shallow near-to-shore waters off all coasts. However, despite its commonality and supporting a fishery averaging 80 t per year from 2007 to 2019 (DFO, 2025a), the species has received very little historic research focus and little is known about its basic biology. There is no known information on growth or mortality rates or interactions within the Newfoundland marine ecosystem (DFO, 2025a). Generally, from our observations, we purport they are found on gravelly or rocky shoreline areas (*i.e.* 0–20 m depth) of bays and estuaries, often in conjunction with kelp or eelgrass beds.

Green crab is an invasive species in Newfoundland, initially found in Placentia Bay on Newfoundland's south coast, with further expansions in distribution since confirmed along the south and west coasts (DFO, 2025b). Expansion within Newfoundland waters includes into portions of St. Mary's Bay (Lehnert *et al.*, 2018). This particularly adaptive species is a widespread invader of all continents except Antarctica (Young and Elliott, 2020). Green crab can inhabit a wide range of habitats but highest abundances of juveniles can often be found in sheltered shoreline areas where the intertidal zone consists of rocky substrate and sea grass beds (Klassen and Locke, 2007). Green crab are also adaptive to a wide range of temperature and salinity conditions. The population originally discovered in Placentia Bay is thought to be a cold tolerant hybridized variant with lineages from populations in Nova Scotia and Iceland/Norway (Blakeslee *et al.*, 2010; Jeffrey *et al.*, 2017).

Our study site is the North Harbour estuary in St. Mary's Bay, Newfoundland (Fig. 1). The estuary is formed where the North Harbour river empties into St. Mary's Bay. The estuary widens as it extends seaward, but just south of our study beach a spit of land intrudes into the estuary and creates a calm, sheltered embayment. The shoreline consists of small rock and cobble, and there are eelgrass beds located just below the low water mark. From our observations, the estuary itself is overall shallow (*i.e.* < 10 m depth) and features muddy bottom in the mid portions of it. Salmonids, scallops, and rock crab are among the most common species found in the area.

In this study, we utilize a six-year time series of data consisting of measurements of crab shells taken from opportunistic collections from the North Harbour beach. During this period we documented the first occurrence of

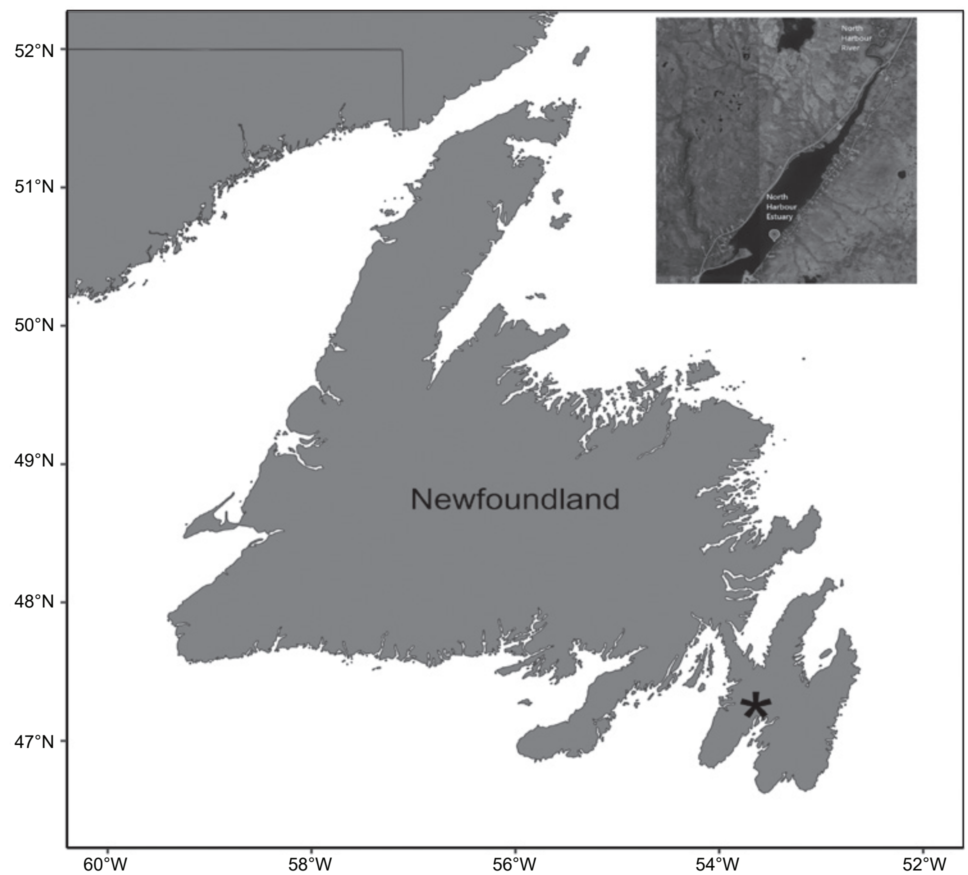

Fig. 1. Map of island of Newfoundland and study area. Black star (~ 47N/-54W) denotes sampling location in the North Harbour estuary. Inset shows North Harbour estuary with pin below name showing location of the sampling beach. Inset originally made in Google Earth, earth.google.com/web/.

invasive green crab into the estuary. Our objectives are to document the rate of change in speciation of the crab community in the North Harbour estuary upon invasion by green crab, and to provide inferences on basic life history traits of rock crab and green crab in the area. These observations constitute some of the first published biological information on rock crab in Newfoundland.

Methods

We began opportunistically collecting and measuring rock crab shells washed up along an approximately 500 m stretch of beach in North Harbour, St. Mary's Bay, Newfoundland (Fig. 1), in 2019. We measured the shells, both cast dorsal carapaces and whole animals, to one-eighth of an inch (3.2 mm) for carapace width (CW) and carapace length (CL) using a standard tape measure, with both measurements made to the tips of spines. We subjectively assigned shell deterioration to a scale of 1 to 3, by units of 0.5, as a proxy for time on the beach. Bleached (white colouration, dry appearance) shells were scored a 1 and freshest (dark colouration, wet appearance) shells were scored a 3.

We continued collecting and measuring rock crab shells in the same fashion on opportunistic trips to the beach over the 2020–2024 period (Table 1), standardizing the area covered by limiting collections to a portion of the beach confined by landmarks at both ends. In 2021, the first green crab shell was found on the beach, thus we expanded our collections and measurements to green crab, with all measurements taken in the same way as for the rock crab.

Our collections were intended to be a thorough census of the shells on the beach during any given sampling event, but we deem it likely that shells were missed in all or some collection events. Accordingly, and further considering that the time period between collections was variable, we focused population demographic analyses on proportion rather than absolute abundances. Population demographic assessments consisted of examinations of annual proportion of shells collected by species as well as annual width-frequency distributions by species. Mean CW and standard deviations were plotted for each species by sampling event to investigate structural change over time. CW and CL were converted to millimetres for all analyses.

To examine allometric growth relationships between CW and CL morphometrics, we produced scatter plots of the measurements by year. Initial analysis fitting the annual distributions with linear regressions showed little difference in either species, thus the data were pooled for fitting linear regressions to them to estimate allometric relationships.

Table 1. Dates of shell collections for Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) in the North Harbour estuary. Note blank date entries indicate shell collections taken with no date recorded.

Year	Month	Day	# Green Crab	# Rock Crab
2019				9
2020				10
2021	6	19		8
2021	6	20		9
2021	8	29	1	4
2022	5	22		11
2022	6	29	1	57
2022	8	7	19	4
2022	8	20	2	6
2022	8	27	9	2
2022	10	2	7	13
2023	4	22		1
2023	5	6		2
2023	5	20	1	5
2023	6	23		10
2023			58	
2024	5	19	2	22
2024	6	8	2	5
2024	7	27	57	1
2024	8	31	39	2
2024				2

As a proxy to estimate molt timing in any given year we calculated the proportion of fresh shells (scored as 2 or higher in our visual subjective index) for individual sampling events for both species, with a high proportion interpreted as being indicative of recent molting.

To qualitatively interpret the effect that temperature could have in affecting rate of speciation change, molt timing, or growth rate differences, we downloaded sea surface data from the European Union Copernicus Marine Service (CMS) ocean climate database (*i.e.* "GLORYS"), accessing the Operational Mercator Global Ocean Reanalysis (OMGOR, 2025; https://doi.org/10.48670/moi-00021) monthly data at 1/12 of a degree confined to a spatial area bound by -53.8 to -53.4W and 47.0 to 47.2N. Monthly means across stations spanning a period from November 2017 to November 2024 were plotted and fit with a linear regression to assess trends in water temperature adjacent to the beach during the study period.

Results

The annual proportion of rock crab shells observed in sample collections shifted from 1 to about 0.25 from 2020 to 2023 as relative green crab prevalence inversely increased (Fig. 2).

The majority of rock crab collected ranged from 45 to 90 mm CW (Fig. 2). There was high variability in modal patterns both across and within years, although dominant peaks appeared at about 60–62 mm CW, and 75–76 mm CW, with lower peaks at about 70–71 mm CW and 80 mm CW. The dominant 60–62 mm CW concentration reflected catches in 2021 and 2023, with the secondary 70–71 mm concentration bolstered by 2019 and 2024 samples and the 80 mm concentration notable in 2020 and 2022 catches (Fig. 3).

The majority of green crab collected were below 45 mm CW (Fig. 3), with a primary concentration ranging about 20–25 mm CW present in all three years of collections. The population structure appeared to broaden in 2024, with a secondary concentration centred near 38 mm CW and increasing prominence in concentrations of larger crab near 52 and 75 mm CW (Fig. 4).

Mean sizes of rock crab in individual sampling events varied without trend over the study period while mean sizes of green crab systematically increased, doubling from 22.1 mm CW on Aug. 7, 2022 to 44.5 mm CW on June 8, 2024 (Fig. 5).

There were no clear differences in CW-CL relationships across year for either species (Fig. 6). For both species, linear regressions fit to pooled data fit well, with a R^2 of 0.93 for green crab and a R^2 of 0.89 for rock crab. For green crab, CWs were on average 29% larger than CLs (slope of 1.29) while for rock crab CWs were on average 37% larger than CLs (slope of 1.37).

The proportion of fresh shells in the rock crab samples were at 1 in August in 2021 and 2022 and May in 2023 and 2024, suggesting molting periods at about these months (Fig. 7). The proportion of fresh shells in the green crab samples was near one in most collection periods, suggesting frequent molting. However, there were exceptions to high proportions of fresh shells in green crab samples during collections in August 2022 and July and August in 2024. This suggests a paucity of molting in mid- to late summer in the green crab.

Sea surface temperatures consistently peaked in August and were lowest in March preceding and throughout the study period (Fig. 8). The temperature trend in the linear regression gradually increased at a rate of 0.00033 degrees per month (slope=0.000331) over the study period. The initial Nov. 2017 estimate of 9.75°C was 0.25°C below the terminal Nov. 2024 estimate of 10°C.

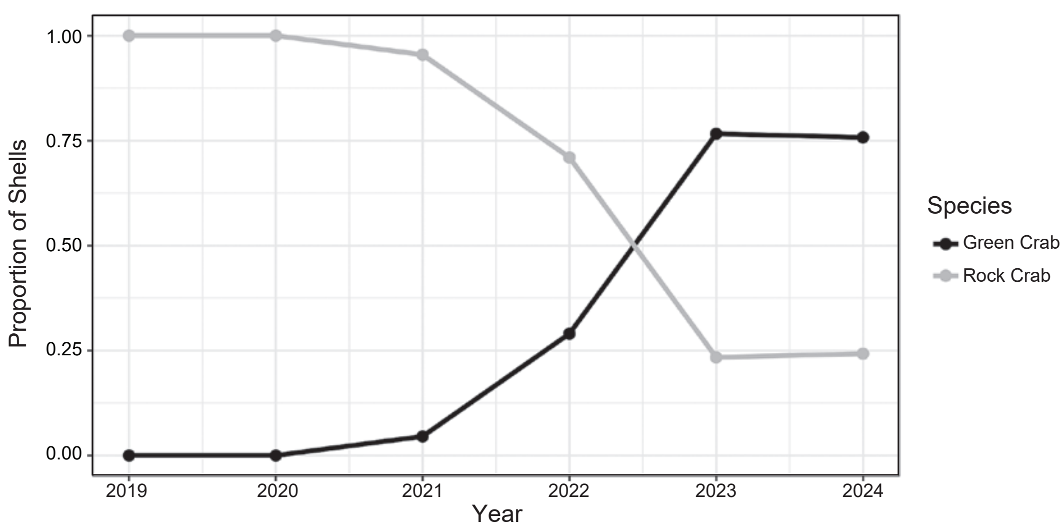

Fig. 2. Proportion of samples collected by year for Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) in the North Harbour estuary.

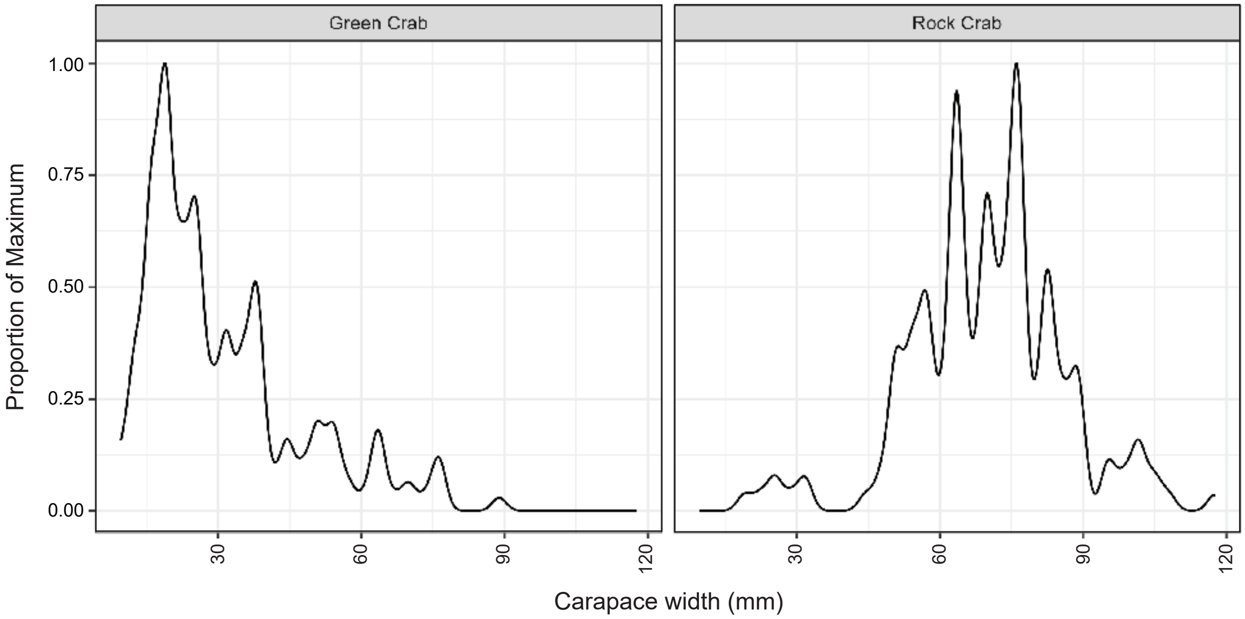

Fig. 3. Pooled width-freqency distributions for Green Crab (*Carcinus maenas)* and Rock Crab (*Carcinus maenas*) in the North Harbour estuary during 2019–2024. Y-axis proportionally scaled to the maximum.

Discussion

Species interactions

Invasive green crab have substantially altered composition of the crab community in the North Harbour estuary in recent years, with a proportional switch in measured species composition from 0 to 0.75 within three years (2021–2023) of being detected. However, given the non-systematic nature of our collection design and inability to examine absolute abundances of crab, we cannot determine the extent to which this switch in ratio represents an increase in abundance of green crab versus a decrease in rock crab abundance.

In terms of interspecific interactions, green crab are generally considered the more aggressive of the two species, as testament by their widespread success as an alien invader (Klassen and Locke, 2007). However, there is literature to suggest that both green and rock crab can be superior competitors upon invasions. For example, in laboratory observations on crab from Newfoundland, Matheson and Gagnon (2012) suggested that green crab can reduce foraging success of small rock crab, particularly in warm water. However, conversely, upon rock crab invasion into Icelandic waters, Gíslason *et al.* (2021) documented how rock crab were able to become more abundant than the indigenous green crab on soft substrates in years following invasion. In a combined laboratory and field experiment in Prince Edward Island, Belair and Miron (2009) showed that interspecific competition did not affect predation rates or stomach contents for either species, and suggested they tend to avoid each other and can coexist in the wild. More recently, Rossong (2016) noted moderate overlap in habitat and prey preference between the two species in Placentia Bay. In terms of rock crab resilience to green crab presence in the North Harbour estuary, it is important to note that as in Placentia Bay there may be partial habitat partitioning between the two species, and that distributional shifts toward deeper water are a known response of rock crab to green crab invasions (Therriault *et al.*, 2008; Rossong, 2016). Species biology for rock crab is such that they tend to occupy deeper water outside of their reproductive periods (Rebach, 1987; Gendron, 2001), thus a more restricted confinement to deeper habitats could be an outcome for rock crab upon the increased presence of green crab near the beach. Rossong (2016) highlighted that the density of green crab was ultimately the factor that would regulate the extent of food availability and shelter loss for rock crab.

Interactions of green crab with rock crab in shoreline areas are likely to be highest during fall months when rock crab are seeking shallow water for reproduction (Rebach, 1987). However, in terms of predation mortality, it would not be intuitive to expect a substantial direct mortality on rock crab under current population structure in the North Harbour estuary. For example, to-date there has been a notable low proportion of large animals observed in the burgeoning green crab population, with the average size of observed rock crab much larger than green crab.

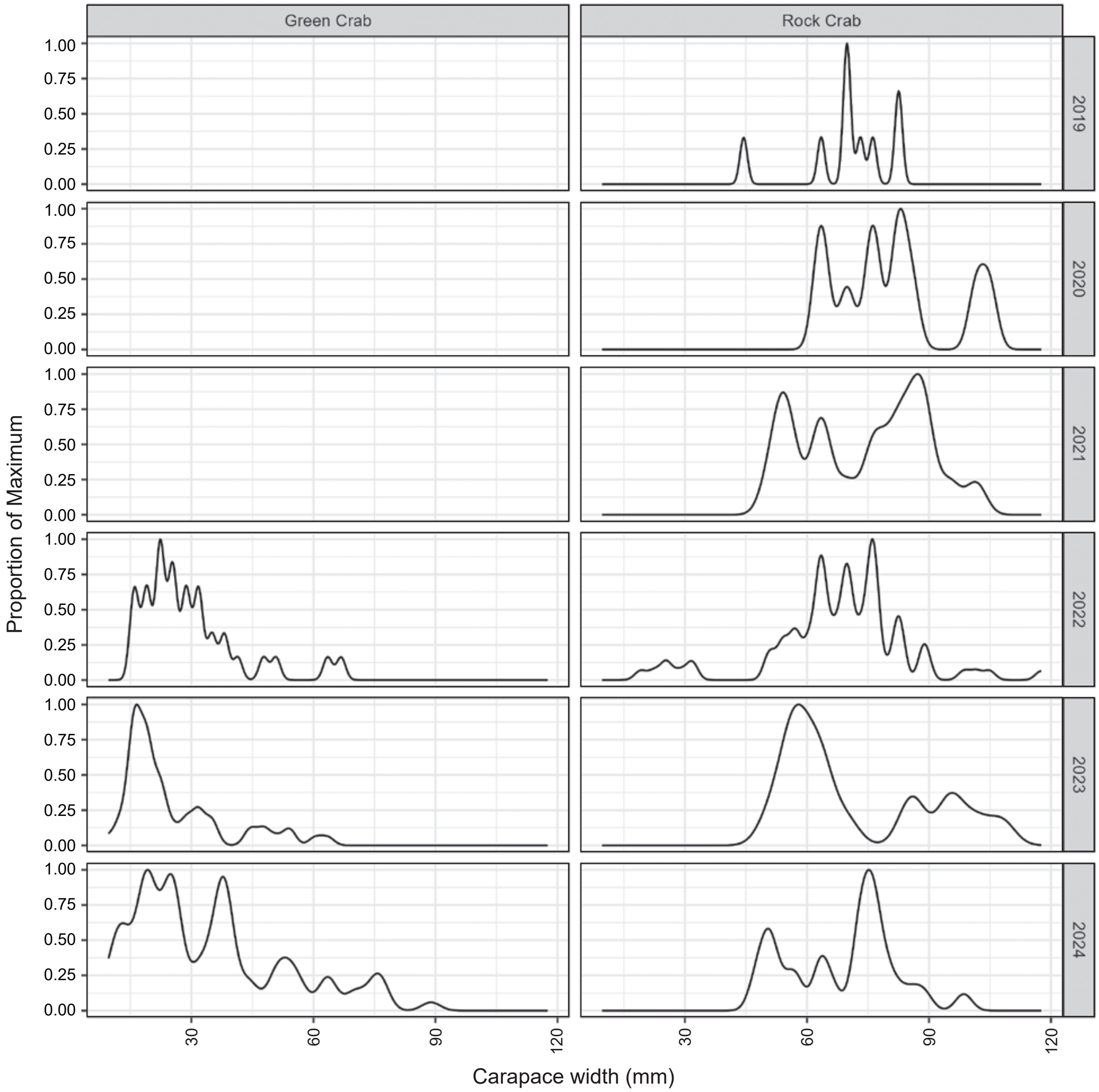

Fig. 4. Annual width-freqency distributions for samples of Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) collected in the North Harbour estuary. Y-axis proportionally scaled to the maximum.

Despite more time and further observations necessary to assess the extent to which the indigenous rock crab population has been or will be affected by invasive green crab, the expectation is that green crab and associated elevated interspecific competition are in the North Harbour estuary to stay. The physical habitat appears very suitable. For example, the estuarine low flow conditions featuring rock cobble shoreline and dense patches of near-to-shore eelgrass are all positive features for green crab habitat. Moreover, the warming conditions bolster the suitability of habitat for the species.

At this point, one major unknown on the future success of green crab revolves around reproduction dynamics. It is noteworthy that none of our collections were knowingly sexually mature animals, thus the extent to which recruitment is produced from localized spawning versus exogenous factors is unknown. Nonetheless, the progressively broadening size structure of animals in the green crab population would align with increasing potential for localized spawning and increasingly firm establishment of the population.

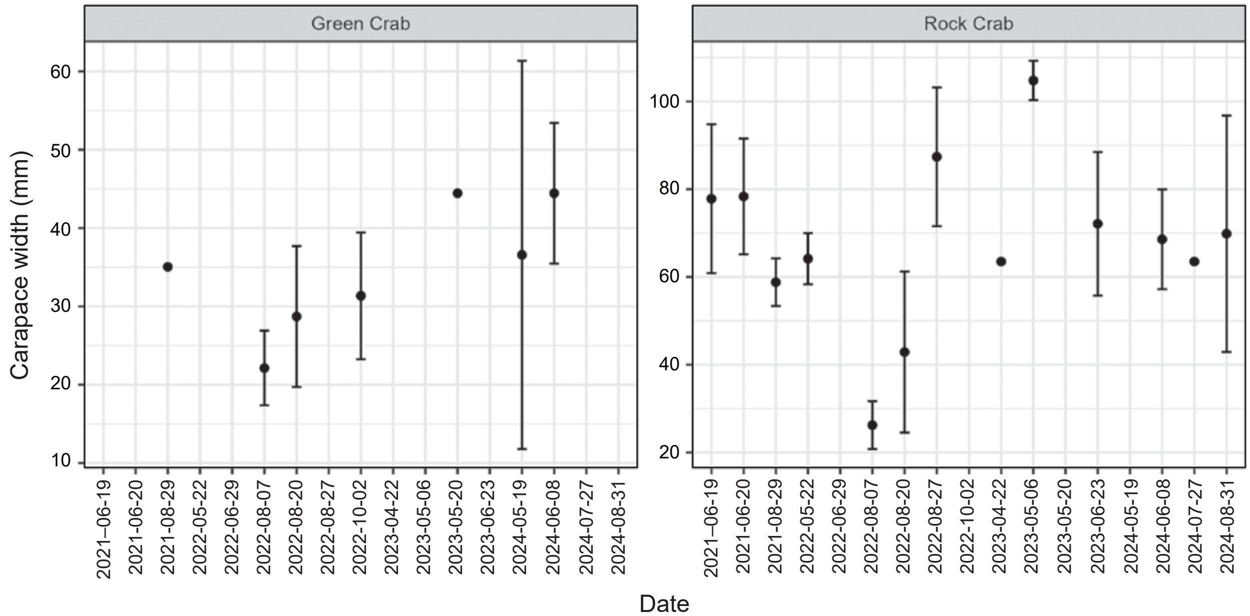

Fig. 5. Mean CW size and one standard deviation for Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) samples from the North Harbour estuary by collection date. Note collection days in 2019 and 2020 were not recorded.

Rock crab population demographics

Rock crab in Newfoundland are at the northern limit of their North American range distribution, and despite being distributed around the entire island, very little information on their basic biology in Newfoundland waters exists. Our results offer insights into their basic biology, and ultimately show overall consistencies with what is known in the broader literature from other areas. For example, there are two known molting periods in rock crab, one for males well before the fall to ensure their shells are hardened before mating, and one for females prior to reproduction in fall to ensure a soft-shell condition during mating (Page, 2002). Our inference of molting periods centred near May and August align with both processes. Moreover, the absence of crab below about 45 mm CW

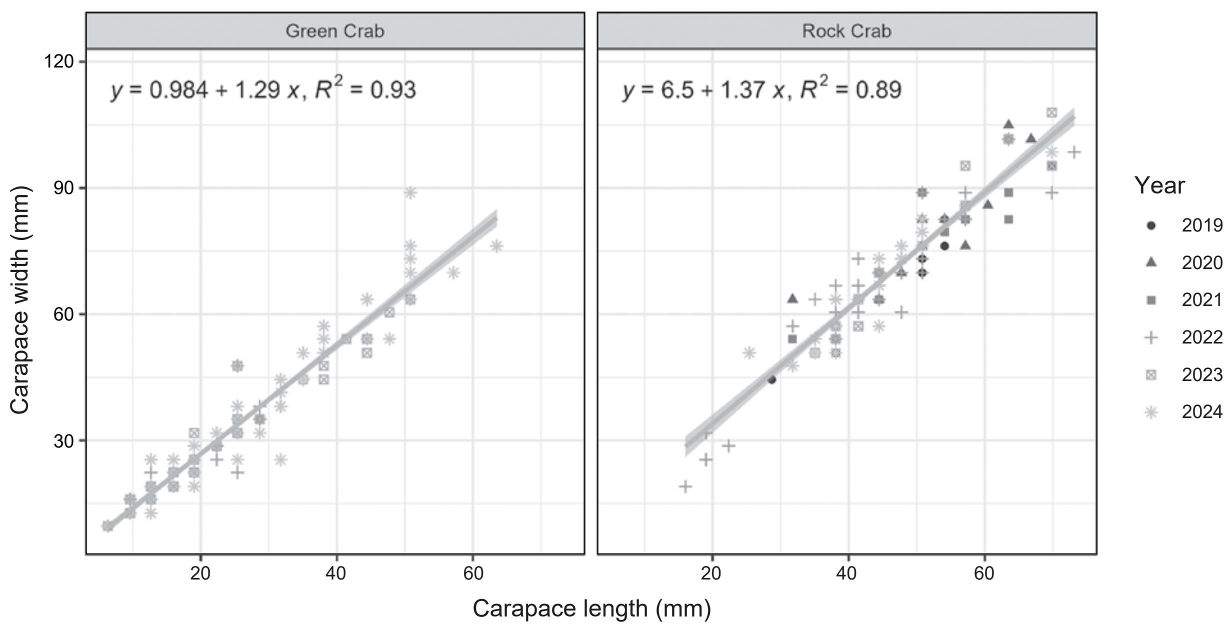

Fig. 6. Allometric relationships between carapace width and carapace length by year for Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) samples from the North Harbour estuary. Linear regression fit to pooled data.

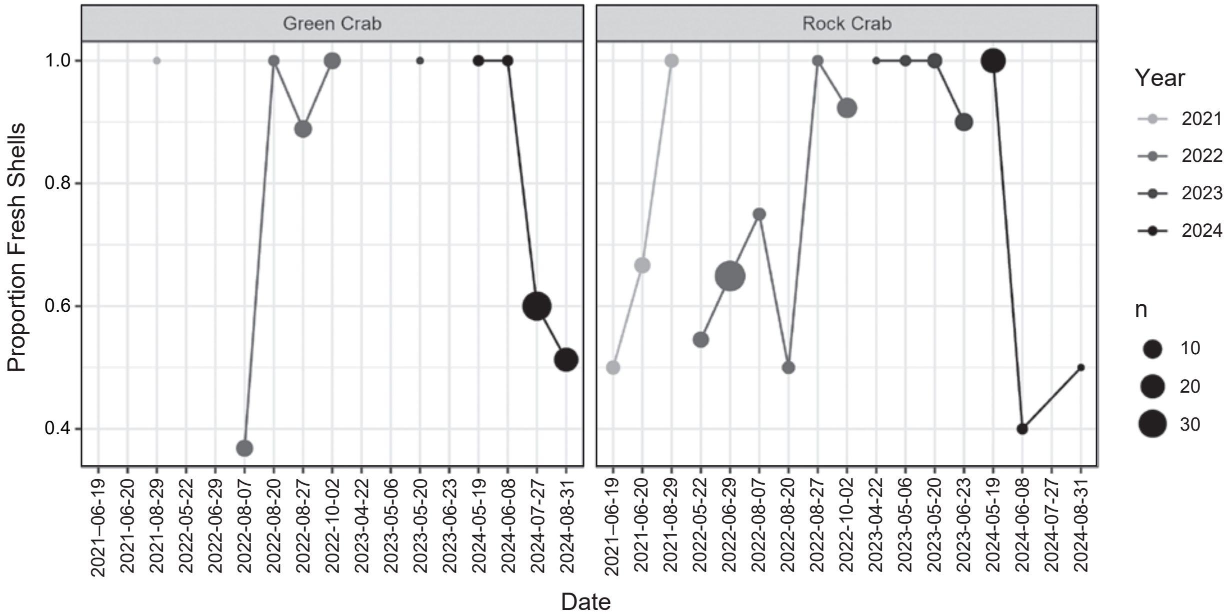

Fig. 7. Proportion of fresh shells in the samples for Green Crab (*Carcinus maenas*) and Rock Crab (*Carcinus maenas*) in the North Harbour estuary by collection date. Bubbles denote sample size and shaded gray colours partition years ranging from 2021 in lightest gray to 2024 in black.

in our samples suggests we may have been tracking a deep-shallow water mating migration. To elaborate, sexual maturity in other Atlantic provinces can occur at sizes of 55–60 mm CW for females and 70 mm CW for males (Squires, 1990), and mature crab are known to move into shallow water in fall for mating (Rebach, 1987). Accordingly, our late summer molting period inference coupled with a size distribution indicative of dominance by sexually mature crab suggests this migration toward the shoreline for mating was being tracked in our shell collections. As the crab can grow to about 40 mm CW within two years (Squires, 1990), it is apparent that our collections poorly captured frequently molting young crab, thus we infer they are distributed further from the beach in deeper habitats.

With respect to growth, our patterns of concentration in rock crab width-frequency distributions reflected interannual variability, but there were dominant concentrations at about 60–62 mm CW and 75–76 mm CW and secondary concentrations at 70–71 mm CW and 80 mm CW in the data. Little is known about size-at-instar in rock crab, but Bigford (1979) estimated modal CW sizes of 66 and 80 mm for instar X and IX males and modal CW sizes of 61, 71, and 80 mm CW for instars X, XI, and XII in females from New England. They showed primary modes near 60 and 85 mm CW in males and 55 and 85 mm CW in females ranging from Cape Cod to Cape Hatteras and 75 mm CW in males and 65 mm CW in females from North Carolina. Notwithstanding variability in our samples, as well as spatiotemporal differentiation in growth rates,

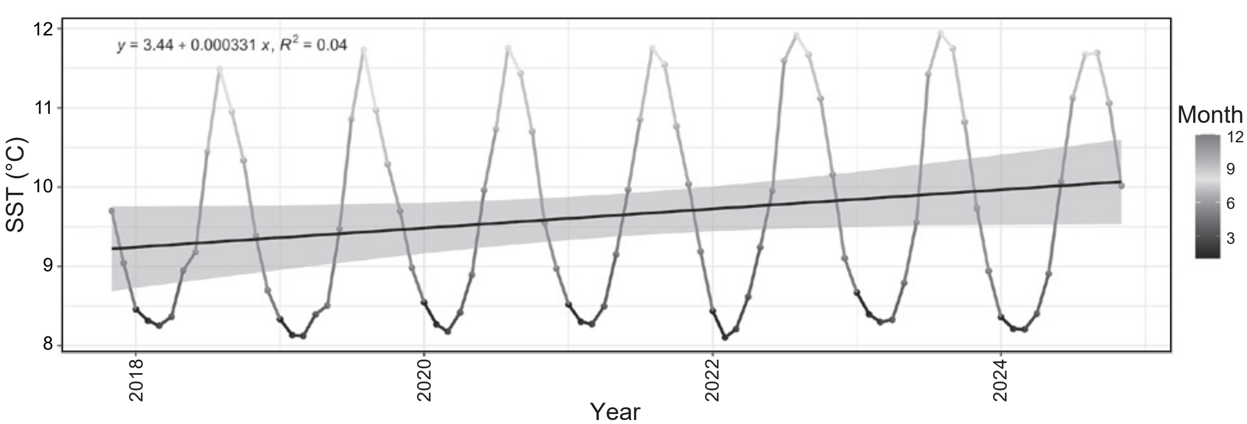

Fig. 8. Monthly sea surface temperature index near North Harbour sampling location from Nov. 2017 to Nov. 2024. Months denoted by colour shading with January in black and August lightest gray shade. Linear regression fit to monthly values. Data acquired from GLORYS satellite observations.

the inference is that our dominant concentrations and overall size structure roughly align with crab of instars X to XII for both sexes identified from other areas. An assumption that instar sizes from the eastern seaboard of the Untied States align with those in our study population is strengthened by no obvious growth pattern changes or relationships coinciding with increasing temperatures occurring in our study area.

Green crab population demographics

Green crab are known to exhibit a high degree of spatiotemporal variability in growth and reproductive patterns (Souza *et al.*, 2011). Our samples of green crab were dominated by small crab and fresh shells, suggesting we were collecting young, frequently molting crab. In Maine, Berrill (1982) reported that crab settled in late summer to mid fall and grew to 5.5 mm CW by their first winter and 13–25 mm CW by their second winter, with sexual maturation thereafter at 2–3 years old. In adjacent Placentia Bay (NL), Best *et al.* (2017) estimated males and females to mature at 32 mm and 37 mm CW respectively and to spawn in June–July.

If patterns held, the dominant 20–25 mm CW concentration we observed in all three years of our samples would be expected to be crab in their second year of life. By extension, the secondary and higher level concentrations observed in 2024 would be expected to be both older crab and those large enough to be sexually mature. Like many crab species, female green crab molt before mating, thus lack of fresh shells in beach samples in July-August would suggest mating is not taking place in late summer or early fall. This would align with observations of Best *et al.* (2017) who determined females in Placentia Bay spawned during June–July, with August and September representing a period when recovery of spent females is common. The reproductive cycle was thought to be annual, with copulation typical in spring. Intuitively, our observations would appear to suggest that the North Harbour estuary population of green crab has similar life history dynamics as those in neighbouring Placentia Bay. Indeed, green crab found near the mouth of St. Mary's Bay have been determined to be genetically akin to those in Placentia Bay (Lehnert *et al.*, 2018).

Despite a broadening of size structure progressively occurring in the green crab population, the relationship of CW to CL held across crab sizes, with CW being roughly 30% higher than CL in most crab and following a linear relationship across the size spectrum. This finding closely reflects observations of the species for sixteen reports from areas of the Pacific and Northeast Atlantic oceans (Clark *et al.*, 2001) as well as the US eastern seaboard and Nova Scotia (Squires, 1990). Accordingly, despite plasticity differences in life history dynamics to adapt to the subarctic conditions in Newfoundland versus in other green crab populations (Best *et al.*, 2017), our data determine that shell morphometrics are the same.

Summary

Citizen science can be a convenient way to collect meaningful data on marine populations without need for extensive equipment or high capital investments. Herein, using a common tape measure and a simple visual shell aging index, we are able to provide novel insights into rock crab and green crab biology in Newfoundland. Our findings show that green crab invasions into existing rock crab habitats can be rapid and document basic rock crab life history processes in Newfoundland waters. We infer that St. Mary's Bay rock crab have spring and summer molting periods, undertake deep to shallow water migrations, and have instar size structure and shell morphometrics akin to other Northwest Atlantic populations. For green crab, our data infer a June–July spawning period and similar size structure to the neighbouring Placentia Bay green crab populations, and confirm near-identical shell morphometrics to most Pacific and Atlantic stocks. For both species, allometric growth relationships remained constant over the study period with no obvious differentiation influenced by warming. Overall, these results highlight that despite occupying unique northern and subarctic habitats, life history attributes of these two brachyuryan crab species are similar to those occurring in more temperate areas of their expansive ranges. Such citizen science initiatives can fulfill a key need to document changes in speciation and biology within poorly monitored marine ecosystems as warming ensues.

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Movement and behaviour of Atlantic Halibut (*Hippoglossus hippoglossus*) in a juvenile hotspot detected by a passive moored acoustic receiver grid and active wave gliders

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Abstract

Novel acoustic receiver applications have recently enabled the monitoring of movements of migratory oceanic species. One such species is the Atlantic Halibut, a commercially important deep-water flatfish that exhibits complex migratory behaviours throughout the Northwest Atlantic Ocean. Here we set up a 144 km^2 receiver grid (n = 24 VR4 receivers) in an important halibut hotspot on the Scotian Shelf and tagged 245 halibut with V13 and V16 tags from 2020–22. Receiver performance was assessed using a Receiver Efficiency Index, indicating that the deeper eastern side of the array was an area of high relative importance for future receiver deployments. Many halibut remained in consistent, localized areas over several years, occasionally making short movements into deeper water. We were also able to assess the post-release behaviour of four recaptured pre-tagged halibut within the grid array, indicating a brief period of hyperactivity and an eventual return to their previously observed behaviours. Wave gliders surveyed the grid site annually from 2021–23 to compare the efficacy of active tracking to stationary arrays for future halibut telemetry projects. Two of three tracking missions were disrupted by environmental disturbances, but results from the 2023 tracking mission indicated that the glider was able to detect more individual halibut than the stationary array in the same time frame. However, the short duration of the glider missions precluded their ability to identify movement and migratory patterns. Here we report lessons learned to streamline future project design for open ocean telemetry and halibut acoustic tracking.

Keywords: Acoustic telemetry, Scotian Shelf, commercial fishery, fish tracking

Introduction

Acoustic telemetry has revolutionized the way researchers collect movement data on aquatic species and has ushered in a "golden era" of animal tracking (Hussey *et al.*, 2015; Hays *et al.*, 2019). This technology has since grown as a fisheries conservation tool and provides data that are used to address a growing diversity of management objectives (Matley *et al.,* 2022), including informing fishery quota decisions (Brownscombe *et al.,* 2019), delineating protected areas (Hussey *et al.,* 2017; Martín *et al.,* 2020), and determining rates of natural mortality (Whitlock *et al.,* 2022).

Receiver array geometry is a key consideration for studies addressing management issues because acoustic receivers define the observable study area for tagged organisms. As a result, studies typically monitor aquatic animals in geographically confined systems such as lakes (Hayden *et al.,* 2014; Futia *et al.,* 2024), rivers (Andrews *et al.,* 2018; Burns *et al.,* 2023), and estuaries (Stokesbury *et al.,* 2016; Hollema *et al.,* 2017) to maintain receiver proximity.

Similarly, monitoring animals that traverse predictable marine routes through bottlenecks such as Atlantic Bluefin Tuna (*Thunnus thynnus*) migrations through the Cabot Strait (Block *et al.,* 2019) is also a common approach to maximize detectability.

Receiver arrays are often arranged into a series of lines or "gates" that bisect corridors (Lacroix *et al.,* 2004) and, if paired, can provide a measure of directional movement (Jackson, 2011). Grid deployments, while less common, can help determine fine scale habitat use in a consistent and unbiased way while allowing researchers to distinguish between unused habitat and the absence of data (Kraus *et al.,* 2018). Grid arrays are often positioned in land-bound areas like bays to best monitor patterns of residency and departures of tagged individuals (Hussey *et al.,* 2017; Kraus *et al.,* 2018). Grid deployments are occasionally used in open ocean regions to monitor areas of known ecological significance for the study species, such as known spawning locations (Zemeckis *et al.,* 2014). However, there is no configuration of acoustic receivers that is universally appropriate for all studies or locations.

Acoustic telemetry can be logistically challenging for tracking highly mobile species in open ocean settings, particularly when their migratory behaviours and pathways are poorly understood (Jacoby and Piper, 2025). Increasingly, drifters (Sanderson *et al.,* 2023) and mobile autonomous vehicles such as wave gliders are being fitted with acoustic receivers and used to actively track tagged animals (Lembke *et al.,* 2018; Ennasr *et al.,* 2020; Masmitja *et al.,* 2020; Cypher *et al.,* 2023), providing flexible monitoring coverage beyond the scope of traditional fixed arrays. These new technologies are beginning to provide critical information on migratory oceanic fishes such as Atlantic Halibut (*Hippoglossus hippoglossus* L., 1758).

The Atlantic Halibut is a large and long-lived flatfish found in the boreal and subarctic waters of the Atlantic Ocean (Trumble*,* 1993). Atlantic Halibut were historically fished to near collapse but have since recovered to healthy abundances in Canadian waters (COSEWIC, 2011; Trzcinski and Bowen, 2016). This is currently Atlantic Canada's most valuable groundfish species (Fisheries and Oceans Canada, 2025), and considerable efforts have been made by regulatory bodies and industry partners to increase ecological research and establish proactive management strategies. Extensive mark-recapture and satellite tagging of Atlantic Halibut in the Northwest Atlantic (NWA) has revealed that they exhibit diverse migratory behaviours (or "contingents"; Secor, 1999; Ransier *et al.,* 2024) and generally spawn in the winter in deep, continental shelf slope regions (den Heyer *et al.,* 2012; Armsworthy *et al.,* 2014; Kersula and Seitz, 2019; James *et al.,* 2020; Ransier *et al.,* 2024).

Several key knowledge gaps surrounding Atlantic Halibut movement remain, because while informative, these prior methods of tagging have limitations. Conventional tagging only reveals the net movement of a halibut between two points and is limited to areas and times where the fishery operates. Satellite tagging has so far occurred only on adult halibut large enough to support the large, cumbersome tags, therefore only representing the commercially exploitable size class (> 81 cm). Furthermore, satellite tags are restricted to short deployment lengths, so they are not well suited to monitor multi-year site fidelity. This project was established to address these knowledge gaps and was the first to track Atlantic Halibut (hereafter "halibut") using acoustic telemetry in Canada. Acoustic tags are much smaller than satellite tags with long battery life spanning up to a decade. Tracking challenges included setting up acoustic monitoring infrastructure in deep, borderless habitats and contending with the diverse and wide-ranging migratory behaviours of halibut that are not well established. To deal with these challenges, a large, non-overlapping offshore receiver grid was deployed in an important juvenile halibut hotspot to provide a consistent measure of presence and residency over a large area. The extent of our monitoring capability was expanded through a collaboration with the Ocean Tracking Network (OTN; O'Dor and Stokesbury, 2009) which allowed us to detect halibut migration and dispersal beyond our study site. We paired this stationary grid with autonomous wave glider tracking to assess the efficacy of active tracking for future halibut telemetry projects in regions with or without moored receivers. In this paper, we investigate 1) the efficiency of our open-ocean grid array, 2) the movement and behaviours of tagged halibut within the array, and 3) a comparative assessment using mobile glider-based tracking for monitoring halibut.

Methods

Study site

This study took place in the Gully region on the Scotian Shelf off Nova Scotia, Canada (Fig. 1). The Gully is the largest submarine canyon on the east coast of North America measuring >40 km long, 16 km wide, and with depths >2 500 m (Rutherford and Breeze 2002), part of which became Atlantic Canada's first Marine Protected Area in 2004. The Gully region has highly complex physical oceanographic processes due to the bathymetrical features of the canyon, highly variable tides, and influences from both the continental shelf and slope hydrodynamics (Han *et al*. 2002). North of the Gully lies a shallower basin known as the Trough, located between Banquereau and Sable Island Bank approximately 40 km east of Sable Island, Nova Scotia (Lat 43.980945°, Long -59.033243°; Northwest Atlantic Fisheries Organization [NAFO] Division 4Vs; Fig. 1). This area funnels down into the Gully and is a site of persistently high juvenile halibut

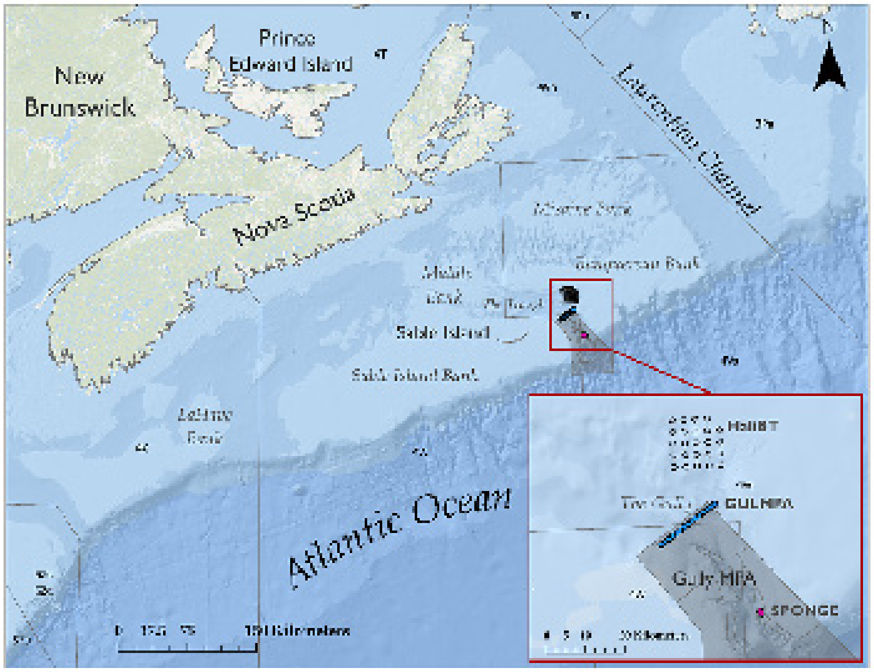

Fig. 1. Map of the Scotian Shelf showing the Northwest Atlantic Fisheries Organization divisions and select offshore banks. The shaded grey area represents the Gully Marine Protected Area and the inset map shows three key acoustic receiver arrays extending throughout the Gully and the Trough: Halibut Bio-Tracking (HaliBT) array (grey dots), Gully Marine Protected Area (GULMPA) array (blue dots), and the Ocean Tracking Network Sponge Ground Landers (SPONGE) array (pink dots).

abundance (Boudreau *et al*., 2017). The northeastern tip of the Trough was the deployment site for the Halibut Bio-Tracking (HaliBT) array (Fig. 1). Approximately 10 km to the south of this location lies a line of receivers ~17 km across that bisects the northern border of the Gully Marine Protected Area (GULMPA), and a final cluster of receivers that is part of the OTN Sponge Ground Landers array (SPONGE; Fig. 1) is located a further ~27 km down into the protected area of the canyon.

Acoustic receiver deployment

In September 2020, 25 VR4-UWM acoustic receivers (Innovasea Systems, Inc) were deployed from a chartered vessel in the northeastern tip of the Gully at the Trough (Lat 44.35398, Long -59.12491), 65 km northeast of Sable Island (Fig. 1). The receivers were deployed to construct a 5 by 5 square grid with units spaced at equidistant 3 km intervals creating a 12 km by 12 km monitoring array covering ~144 km^2. Due to logistical challenges at sea, one receiver was not deployed, leaving a gap in receiver coverage in the northeastern corner of the grid (Fig. 1). Receivers were each moored by a 91 kg steel plate anchor attached to an Innovasea Ascent™ Acoustic Release 2 (AR2) with 5/16″ Dyneema rope. Moored receivers floated 2 m above the seafloor suspended by an 18″ diameter rigid trawl float providing 26 kg of buoyancy. When triggered, the AR2s allowed the receivers to float to the surface at the end of the study, leaving the sacrificial mooring behind. The array spanned depths from 86–210 m and was retrieved on 31 May 2024 after ~3 years and 8 months of deployment.

Sentinel and range test tag deployment

Sentinel V13-1H tags (n = 5; 60–180 s ping rate, 152 db) were deployed in June 2021 within the array using moorings that suspended them 6 m above the seafloor. These tags provided continuous reference points for detection range for both fixed receivers and mobile glider-mounted receivers. In June 2022, temperature-sensing V13T-1H tags (n = 6, 60–180 s ping rate, 152 db) were deployed 3 m above the seafloor throughout the array at ~20 m depth increments (86–208 m) near receivers to transmit temperature measurements at depth to produce a temperature profile of the seafloor across the bathymetric grade of the area.

Additionally, a range test was set up to the west of the HaliBT array using Innovasea's V16-6x tags configured with a fixed transmission delay. In 2021, two range test stations were deployed from a research vessel at 221 m and

95 m depth. These were later approached by the glider in a star-shaped pattern. In 2022, two new range test tags were deployed from a fishing vessel in 210 m and 135 m depth for the glider to conduct range tests in a spiral pattern.

Bathymetry and mapping

Ten metre resolution multibeam bathymetry data for the HaliBT array were accessed from the Canadian Hydrographic Service Non-Navigational (CHS NONNA) bathymetric data portal. These data were interpolated to produce contours in ReefMaster (ReefMaster Software Ltd., 2021) then rasterized and plotted in ArcGIS Pro (ESRI 2024). Maps were made in ArcGIS Pro (ESRI, 2024) and R (R Core Team, 2024), the latter using bathymetric data from the marmap package (Pante and Simon-Bouhet, 2013).

Atlantic Halibut capture and tagging

Atlantic Halibut were captured from a chartered commercial fishing vessel employing commercial bottom-longline gear in the HaliBT array. Halibut between 40–65 cm FL (fork length) were surgically tagged with V13-1H acoustic tags while halibut > 65 cm FL were tagged with a larger V16-4H tag (See Table 1 for tag specifications). All halibut were also tagged with two Floy tags as an external marker. Tagged halibut were then released immediately near their capture location. Tagging occurred in September of 2020 and June of 2021 and 2022.

Telemetry data acquisition

Data from moored acoustic receivers were retrieved through a remote download link using a benthos VM4 modem towed behind a Liquid Robotics SV2 or SV3 autonomous wave glider sub (Fig. 2) operated by Coastal Environmental Observation Technology and Research (CEOTR). Data passed to the glider from the benthos modem were sent back to shore over the Iridium Router-Based Unrestricted Digital Internetworking Connectivity Solutions (RUDICS) satellite network and were also stored internally on the glider. Glider download missions occurred annually in the autumn from 2021–23.

Acoustic telemetry data were also collected via mobile glider tracking using a Liquid Robotics SV3 wave glider (Fig. 2). In 2021, the glider was equipped with two Vemco Mobile Transceivers (VMT; one mounted on the bottom of the float, the other on the bottom of the sub) and one VR2C (mounted on the sub) for the tracking surveys. In 2022, the glider was equipped with 1) the prototype Innovasea Mobile-RX receiver with the head oriented just forward of the bow of the sub, 2) a VMT, and 3) a VR2C positioned at the aft end of the sub with the head pointed downward. In 2023, the glider was equipped with two VMTs on the sub (one pointing up and the other pointing down) and a VM4 mounted on a towfish, pointing downward (Fig. 2). The towfish was towed between 10–12 m behind and 7–10 m below the sub. The glider recorded detections of tagged halibut in the study area along pre-programmed North-South and East-West "lawnmower" pattern transects travelled annually from 2021–23.

HaliBT array receiver efficiency

In ideal conditions in deep water with low turbidity, sandy substrate, and low currents, transmission signals from the highest-powered tags available (V16-5H) can propagate to 1 200 m (Loher *et al.,* 2017). We did not pursue a dedicated receiver range test in our study area due to the challenging logistics of this location, however, the transmission range in our study was suspected to be lower due to our lower-powered tags, the complex bathymetry in the HaliBT array, and the potentially strong tidal currents occurring in the Gully. Another method of assessing the performance of an array is the Receiver Efficiency Index (REI), introduced by Ellis *et al.* (2019). This index is a composite measure of relative importance of each receiver in an array, incorporating ratios of detections and individuals at each receiver, while also inherently incorporating differences in receiver range (Kendall *et al.,* 2021). The resulting indices can help identify redundant or low-value stations to inform future array configurations that will maximize efficiency while allowing an array to be maintained with fewer stations (Ellis *et al.,* 2019). We used the following equation developed by Ellis *et al*. (2019):

$$REI_r = \frac{T_r}{T_a} * \frac{S_r}{S_a} * \frac{DD_r}{DD_a} * \frac{D_r}{D_a}$$

where r is an individual receiver and a is the whole array, T = number of tag IDs in the study, S = number of species, DD = detection days, and D = number of days a specific receiver was deployed within the array. Given that halibut are the only species of interest for the study and that all

Table 1. Specifications of acoustic tags deployed in Atlantic Halibut (*Hippoglossus hippoglossus*) in the Gully region of Nova Scotia in 2020–22. Power is measured in underwater decibels (dB re 1 μPa at 1 m) and weight is measured in water.

Tag type	Freq. (kHz)	Tag life (d)	Power (dB)	Min delay (s)	Max delay (s)	L (mm)	W (g)
V13-1H	69	632	152	60	180	36	6.3
V16-4H	69	2 435	158	60	180	68	10.3

receivers have the same deployment period, both S_r/S_a (the proportion of species in the array detected at each receiver) and D_r/D_a were set to 1.

Detection data analysis and visualization

Detection data downloaded from the HaliBT array and collected by the wave gliders were accessed through the OTN data portal. Detection data and project metadata were managed and visualized in the R programming environment RStudio (R Core Team, 2024).

Glider tracking analysis

Glider tracks and glider-based detections of tagged halibut were superimposed in R. The timing of each glider transect pass (*e.g.*, North-South, East-West) and the associated detections were limited to when the glider was in the array conducting the dedicated tracking surveys. To compare relative detection rates between the mobile glider and the stationary receiver array, detections made by the HaliBT array were subset to only include those which overlapped temporally with glider occurrence in the fixed array. Number of detections and unique tag IDs detected were tallied for both tracking methods for the duration of each directional survey.

Glider range test

The maximum distance at which the glider detected each sentinel tag deployed within the fixed array was calculated in ArcGIS Pro. Since sentinel tags were the same model and configuration as the smallest halibut tags, this was considered a within-array glider range test proxy and an appropriate measure of detection distance of the halibut.

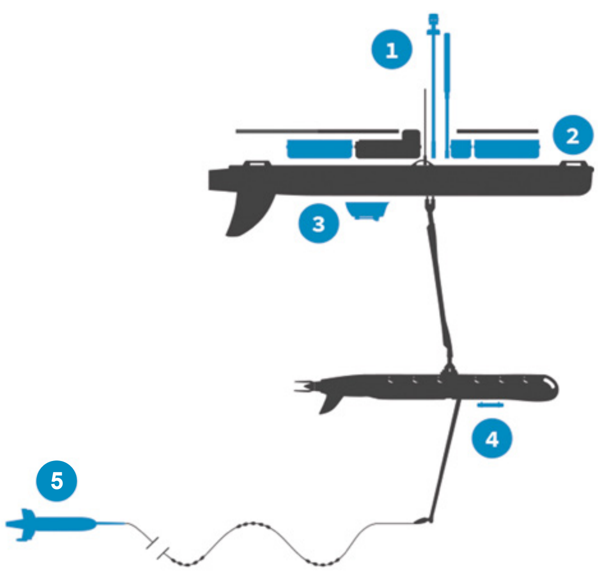

Fig. 2. Schematic of a Liquid Robotics SV3 Wave Glider showing **1**) weather, wave, and communication masts, **2**) batteries and computer, **3**) float sensor mounting, **4**) sub sensor mounting, and **5**) towbody sensor mounting.

Results

Atlantic Halibut length distribution

Fork lengths of tagged halibut ranged from 50 cm to 141 cm and the mean varied by tagging year (Table 2).

Table 2. Summary of fork lengths of tagged Atlantic Halibut (*Hippoglossus hippoglossus)* by tagging year.

Tagging year	*n*	Mean fork length (cm) ± SD
2020	7	95.4 ± *25.9*
2021	138	75.7 ± 12.7
2021	100	77.9 ± 15.8

Detections by yearly release group

Seven halibut tagged in September 2020 were captured and released on Banquereau, outside the study area. Five of those halibut were not detected on the array. Of the two individuals detected, one large halibut (110 cm) passed through the HaliBT array briefly on 23 Dec 2020, then again on 24 Jan 2021. The second smaller halibut (69 cm) was not detected until over two years after release when it was observed in the array over two days in January 2022 (Table 3; Fig. 3).

The 2021 release group (n = 138) was at large for approximately 2 years and 11 months as of the May 2024 HaliBT array retrieval mission (Table 1). Transmissions of V13 tags (n = 70) were projected to have ceased by March 2023, but likely stopped transmitting in April 2023 based on available data. V16 tags (n = 68) are projected to continue transmitting until February 2028 (Table 1). Four halibut from this release group have been reported harvested, one by the DFO groundfish survey trawl in July 2023 near the HaliBT array, one at an unknown time and location in early 2023 by a fishing vessel, the third on the continental shelf edge below Sable Island in March 2024, and the fourth off the coast of Saint Pierre and Miquelon in May 2024.

The 2022 release group (n = 100) was at large for approximately 1 year and 11 months as of the May 2024 HaliBT array retrieval mission. Transmissions of V13 tags (n = 50) ceased in March 2024 and transmissions of V16 tags (n = 50) are projected to stop by February 2029. Two tagged halibut from this group were reported to have been harvested at an unknown time and location in early 2023 by fishing vessels.

Table 3. Summary of detections of tagged Atlantic Halibut (*Hippoglossus hippoglossus*) made by the Halibut Bio-Tracking (HaliBT) receiver array.

Release group	Tag type	Number tagged	Total number detected	Number detected by year				Individual detection count range (n)	Detections/ fish (median)	Range of days individuals were detected in study (n)	Days detected/ fish (median)	Number of receivers/ fish (median)
				2021	2022	2023	2024					
2020	V16	7	2	1	1	NA	NA	19–21	20	1–2	1.5	2.5
2021	V13	70	69	67	50	14	NA	5–33 192	920	1–204	31	7
	V16	68	67	65	49	33	20	10–165 899	2 601	1–505	56	8
2022	V13	50	50	NA	50	29	10	2–11 944	553	1–229	22	5
	V16	50	47	NA	47	30	23	7–14 581	1 034	1–200	26	7

All but five halibut in the 2021/2022 release groups were detected by the HaliBT array at least once following release (Table 3). Numbers of tagged halibut present in the array varied month by month with peaks in the summer (exclusive of tagging efforts) and lows in the winter (Fig. 3). Halibut display a variety of migratory behaviours which may account for the variability in the number of detections and the number of days each individual halibut was detected in the array. A subgroup of halibut was present within the HaliBT array year-round, termed residents.

Glider tracking

Glider tracking missions had variable success over the years. In 2021, the glider had to be manoeuvred off course multiple times to avoid vessels and approaching hurricanes. Upon the glider's return to the HaliBT array to begin the final transect, navigational control was lost and the glider drifted into the Gully MPA where it was retrieved. Extensive damage to the thruster and rudder complex resulting from a shark bite rendered the unit disabled.

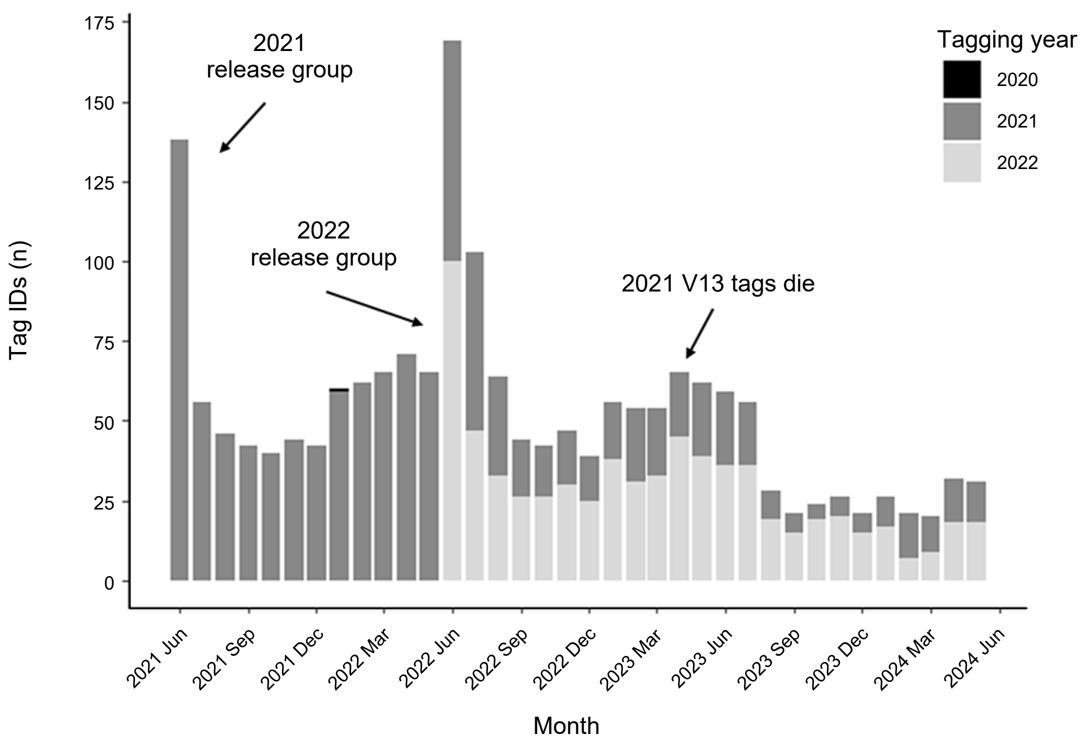

Fig. 3. Number of tagged Atlantic Halibut (*Hippoglossus hippoglossus*) present in the Halibut Bio-Tracking (HaliBT) receiver array by month from June 2021 to May 2024.

In 2022, the first North-South glider transect was interrupted when it was re-routed to avoid the approach of the Category 3 Hurricane Fiona. Hurricane Fiona transitioned to a large, powerful post-tropical storm upon arrival in Atlantic Canada with record-breaking drops in barometric pressure. In the turbulence on 24 September 2022, the glider's umbilical tether detached, losing both the sub and all receiver packages. Sensor readings are unreliable following peak hurricane activity, but at the time of the incapacitation, the glider measured ~ 15 m wave heights and 111–148 km/h winds. The catastrophically damaged glider float drifted north and was retrieved, but no acoustic detection data were salvaged from this mission.

In 2023, the glider had to be routed out of the array during the first East-West transect to avoid the approaching Hurricane Idalia. When wave heights exceeded 4 m during the first North-South transect, the glider was held in a bowtie course to best handle the energetic sea state (Fig. 4). Other deviations from the transects during the survey occurred when the glider was avoiding vessel traffic, but otherwise, the survey was completed without major issues. The survey ran from 28 August 2023 to 5 October 2023 and consisted of a total of 42 East-West passes and 42 North-South passes, averaging 1.0 knot with a maximum of 3.1 knots attained during that time. The downward-pointing VM4 logged most of the detections (n = 1 624) and the downward-pointing VMT logged only 372 detections during the tracking transects (Fig. 4). The upward-pointing VMT logged no detections, likely due to its proximity to and orientation toward surface turbulence.

The glider, performing a "lawnmower" search pattern, consistently detected more individual halibut tag IDs than the HaliBT array during each transect period, but the HaliBT array made more detections overall during the same period, likely due to the simultaneous recording of its 24 receivers and consistent detection of nearby halibut that may have undertaken little movement for some time (Table 4). However, the HaliBT array occasionally detected halibut that were not detected by the glider.

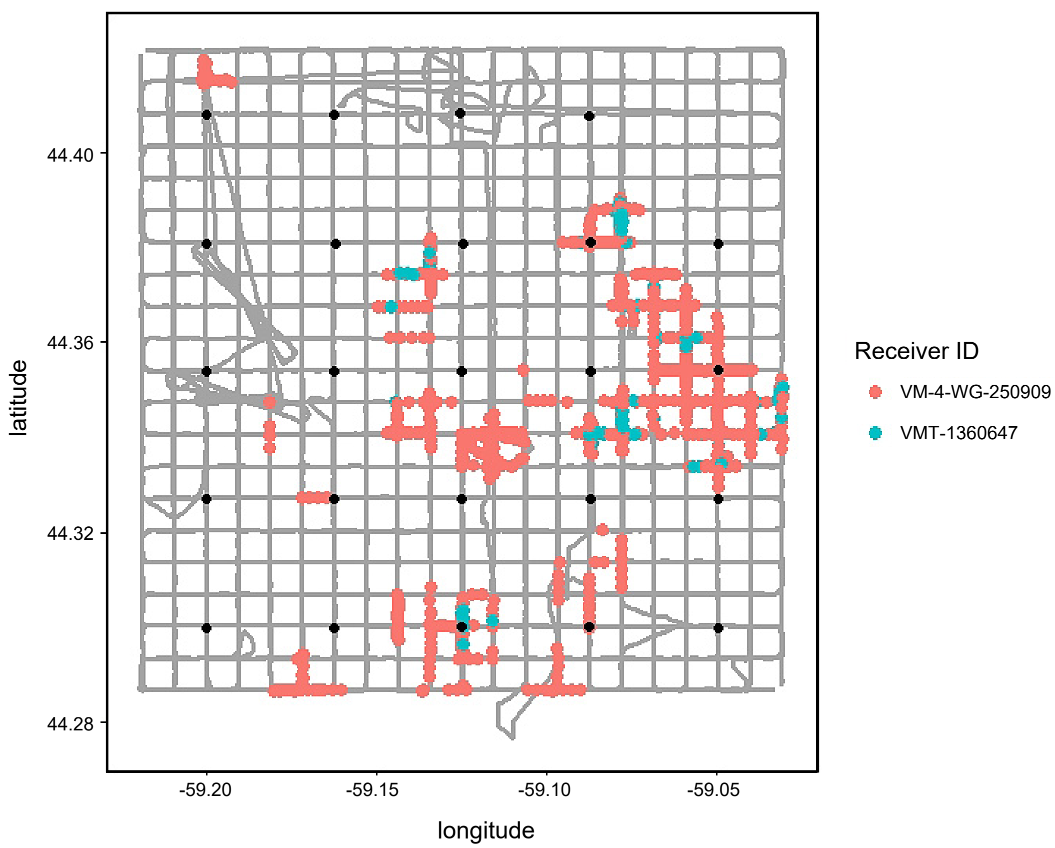

Fig. 4. Detections of tagged Atlantic Halibut (*Hippoglossus hippoglossus*) made by an SV3 wave glider during a tracking survey in 2023. The grey line indicates glider path, the black points are the Halibut Bio-Tracking array receiver locations, and the coloured dots are detections of tagged fish coloured by the receiver mounted on the glider that made each detection. The VM4 unit (red detection points) collected 1,624 detections and the downward-pointing VMT (blue detection points) collected 372.

Table 4. Comparative detections made by an SV3 wave glider and the stationary HaliBT receiver array across four transect periods in 2023.

		EW-1	NS-1	EW-2	NS-2
Glider	Unique tag IDs	20	24	22	27
	Total detections	340	537	609	469
HaliBT array	Unique tag IDs	12	11	9	16
	Total detections	2 730	5 863	4 471	4 404
	Common tag IDs	10	11	7	13

Eighteen halibut were detected by the glider in all four survey transects, but only eleven of those halibut were also detected by the HaliBT array in that time (Fig. 5). This disparity indicates that the gaps between receivers in the HaliBT array allow many halibut to occupy space in the array where they are undetected, but also that these gaps can be filled in on occasion by glider tracking.

HaliBT array receiver efficiency

REI values were highest in the eastern side of the array, with station 15 (Lat 44.35413, Long -59.04956; 142 m depth; Fig. 6) having the highest index of 0.583 (Table 5). The high indices in this region likely relate to denser and more resident aggregations of halibut. Stations with REI > 0.2 may be the best candidates for maintaining receivers in future tracking efforts. Most glider detections of halibut occurred in similar locations as the HaliBT receivers with the highest REI values (Fig. 4; Fig. 6). This may indicate that the eastern side of the array supports a local abundance of halibut and not just high REI values resulting from better acoustic transmission conditions than other areas. Although neighbouring receiver stations were only 3 km apart, the REIs of stations immediately surrounding station 15 dropped by half or more, possibly indicating particularly high detection range at station 15. Halibut were detected on the most days at station 15 (604 total detection days, 95% of entire monitoring period), whereas they were detected on the fewest days at station 23 (Lat 44.40825, Long -59.12527; Fig. 6) at 105 m (18 total detection days, 3% of monitoring period, Table 5).

Station 6 (Lat 44.32701, Long -59.049548; 166 m depth; Fig. 6) was found washed up on Sable Island (~65 km southwest of the original receiver location) on 11 April 2023. The last detection logged by the unit occurred on March 27, 2023. REI was only calculated until the end of March 2023 to best represent when the entire array was still in place.

Glider detection range

The SV3 wave glider's detection range was highly variable. The distances at first detection of the sentinel tags within the array varied by location, the highest being 893 m at the deepest station (208 m) and the lowest being 553 m at the shallowest station (86 m; Fig. 7).

Halibut movement and habitat use in the HaliBT array

Halibut were generally only detected on a small number of HaliBT receivers out of the available 24 (Table 3), indicating discrete use of the study area. The regions of the array that were most visited by halibut were around the shallow point extending down the middle rather than the deepest station, suggesting that the halibut aggregated around major structure throughout the study period (Fig. 6). Many halibut were transient and/or seasonal visitors to the HaliBT array, but some displayed resident behaviour, enabling a closer look into spatial use of the area. Residents remained in the Gully region year-round, with most generally staying in the vicinity of the HaliBT array. The locations of 18 residents from the 2021 release group were plotted as an example due to the long tag deployment time and their tendency to stay within the array (Fig. 8). Halibut in the 2021 resident group tended to remain in one consistent location for extended periods but often made short forays south and then back (Fig. 8). Very few halibut ventured into the shallowest northern edge of the array (receiver stations 21–24; Fig. 8). Even halibut that were not necessarily resident to the area remained relatively stationary when present, as evidenced by glider tracking (Fig. 5). Eighteen of the halibut were detected during every transect during the 2023 glider survey, all of which showed little to no movement during the 39-day survey period (Fig. 5). All of the eighteen halibut were active over the years, including making seasonal movements and venturing deeper into the Gully as monitored by the GULMPA receiver line (Fig. 9).

The HaliBT array provided an unexpected opportunity to assess catch-and-release (C&R) survival and post-release movement. On 22 June 2022, during the final tagging trip of the project in the HaliBT array, four halibut were caught on the longline and identified as previously tagged individuals based on their healed incisions and Floy tags. Those halibut ranged from 53–82 cm at the time of tagging

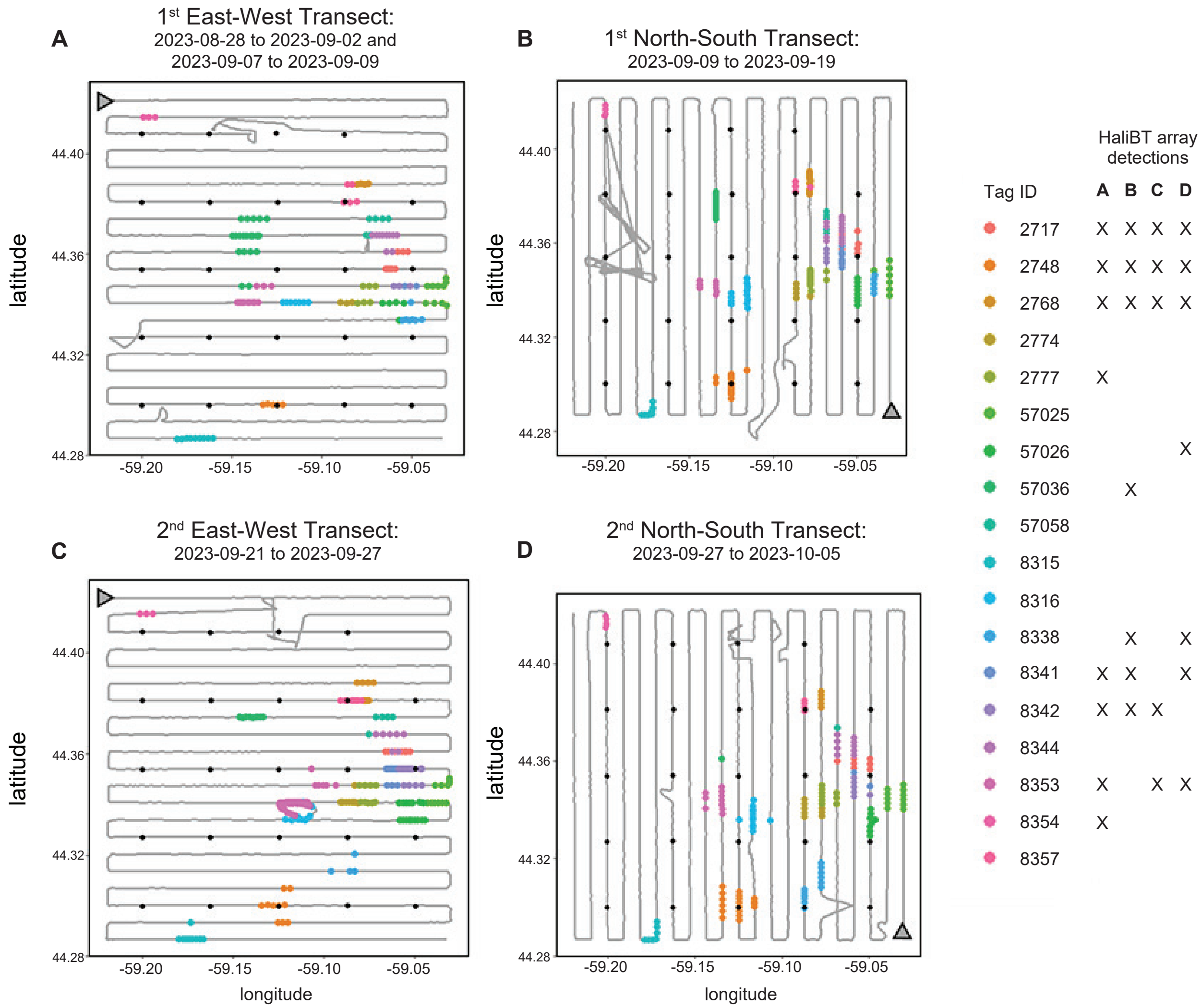

Fig. 5. Detections of acoustic tagged Atlantic Halibut (*Hippoglossus hippoglossus*; n = 18) that were detected in all transect passes in 2023 by an SV3 wave glider. The grey line indicates the glider path, the grey arrow indicates the initial glider direction, the black points are Halibut Bio-Tracking (HaliBT) array receiver locations, and coloured points indicate individual halibut tag IDs. The columns next to the legend indicate which tag IDs were also detected by the HaliBT array, marked by an x in the corresponding transect pass.

and all followed the expected growth rate of ~10 cm/year (Fisheries and Oceans Canada, 2020), suggesting they were in good health. These halibut were handled the same way as they are in the commercial fishery (*e.g.* gaffed through the mouth, brought on deck, and measured) and once their Floy tag information was recorded, they were released overboard as would halibut under the commercial retention size (~ 5–8 minutes total handling time).

In the month leading up to their capture, all four halibut were detected only at station 15. After C&R, tag ID 47676 (seasonal migrant showing summer site fidelity to the HaliBT array; 76 cm at time of tagging) was not detected anywhere for 19 days until it was detected by an external receiver line at the border of the GULMPA 17 km away. This halibut then returned to the HaliBT array to resume activity between several stations (Fig. 10 B). Similarly, tag ID 47 644 (resident, 53 cm at time of tagging) was undetected post-release for 15 days, then was detected regularly back at station 15. Tag ID 2716 (seasonal migrant to the HaliBT array; 82 cm at time of tagging) was detected in consistent 6-day intervals in the month leading up to the C&R event, then went undetected for 25 days until it was detected again on several stations in the HaliBT array. Tag ID 47 635 (resident, 60 cm at time of tagging) was detected at station 6 immediately south of station 15 after release, then went undetected for 13 days until it was detected on one day by the GULMPA line. It was detected again by the GULMPA line nearly three months later, then back in the HaliBT array resuming regular resident behaviour. A similar gap in detection occurred in 2021 after this individual was first captured, tagged, and released (Fig. 10 A).

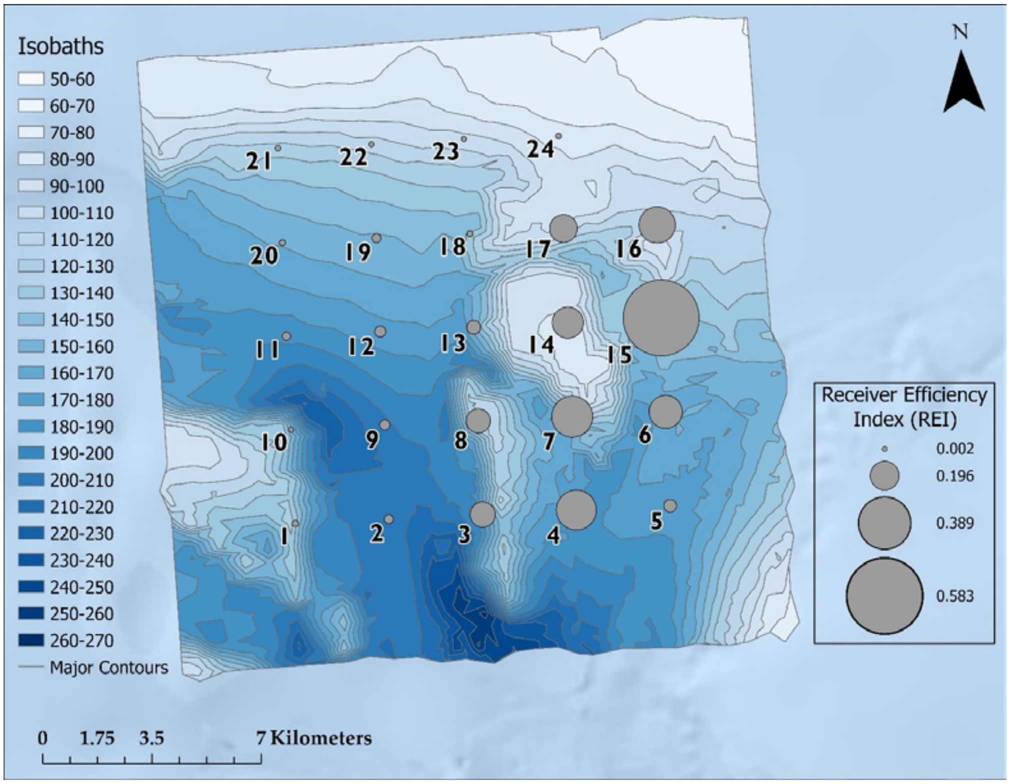

Fig.6. Receiver efficiency indices (REI) of each acoustic receiver location (grey dots labelled with station number) within the Halibut Bio-Tracking array in the Trough at the northern tip of the Gully along the Scotian Shelf. Size of dots indicates value of REI for each receiver, calculated from September 2020–March 2023.

Discussion

In this study, we examined the efficacy of using an open ocean receiver grid and paired wave gliders to track halibut on the Scotian Shelf while comparing both methods in situ. The grid receiver array positioned over a known halibut aggregation area proved to be a successful method of monitoring multi-year halibut behaviour. The large spatial coverage of the array revealed that the deeper eastern channel was an area of higher halibut density, as described by the commercial fishermen who suggested that the tagging efforts be carried out in that location. These observations may help guide future localized studies of habitat ecological linkages to substrate type and prey composition. This array design facilitated a unique opportunity to assess the effectiveness of mobile glider tracking, observe small-scale movements of halibut for extended periods of time, and observe how halibut behave post catch-and-release.

Efficacy of an open-ocean receiver grid

The HaliBT array collected >900 000 detections of tagged halibut and provided important and detailed data on the poorly described movement behaviours of halibut, both on the scale of a few kilometers and on a broader scale when connected with other nearby receiver arrays in the Gully ecosystem and other areas through the OTN. Though this type of array design is particularly effective for fish that display high site fidelity like halibut, the HaliBT array also detected tag IDs associated with 14 other acoustic tracking projects linked through the OTN that monitored a variety of migratory pelagic species including Atlantic Bluefin Tuna, Atlantic Salmon (*Salmo salar*), and Leatherback Sea Turtles (*Dermochelys coriacea*). This underscores the broader application that large oceanic grid arrays can offer to the collaborative tracking community.

Feasibility of mobile glider tracking

Autonomous gliders travelling in set transects over the HaliBT array detected a higher number of acoustically tagged halibut than did the fixed array in the same time frame. Similar results were found in another offshore groundfish study that used gliders to augment fixed arrays (Zemeckis *et al.,* 2019). However, several halibut that were detected by the fixed array were not detected by the glider.

Table 5. Receiver efficiency indices (REI_r), total unique tag IDs detected (T_r), and total detection days (DD_r) of each acoustic receiver station in the Halibut Bio-Tracking (HaliBT) array from July 2021–March 2023.

Station	Lat	Lon	Depth (m)	T_r	DD_r	REI_r
1	44.29999	-59.20012	154.6	16	112	0.013
2	44.29999	-59.16257	208.6	42	115	0.034
3	44.30003	-59.12489	161.0	74	318	0.167
4	44.30005	-59.08727	183.0	145	279	0.287
5	44.30000	-59.04963	179.2	76	121	0.065
6	44.32701	-59.04955	168.7	127	257	0.231
7	44.32697	-59.08713	153.7	113	369	0.296
8	44.32704	-59.12487	121.0	62	362	0.159
9	44.32710	-59.16244	206.8	46	134	0.044
10	44.32702	-59.20008	141.3	16	31	0.004
11	44.35396	-59.20020	192.2	33	114	0.027
12	44.35401	-59.16247	179.7	46	156	0.051
13	44.35397	-59.12491	176.4	62	166	0.073
14	44.35403	-59.08710	91.0	64	475	0.216
15	44.35413	-59.04956	141.6	136	604	0.583
16	44.38089	-59.04938	114.9	76	480	0.259
17	44.38112	-59.08707	101.4	64	414	0.188
18	44.38092	-59.12463	149.0	30	47	0.010
19	44.38092	-59.16222	152.1	40	124	0.035
20	44.38089	-59.20010	163.1	22	67	0.010
21	44.40805	-59.20012	127.4	15	57	0.006
22	44.40795	-59.16254	117.1	22	25	0.004
23	44.40825	-59.12527	105.6	15	18	0.002
24	44.40778	-59.08723	86.0	23	46	0.008

The continual tracking over the study area for approximately one month emphasized how localized halibut can be for extended periods and provided finer-scale detections than were available from the widely spaced array. Using sentinel tags at different depths in the array, we found that the detection range of the glider varied considerably by up to 340 m between locations. Considering that the largest detection range was at the deepest station and the smallest detection range occurred at the shallowest station, there are likely many factors affecting the glider's detection range, including wave action and other ambient noise (How and De Lestang, 2012) and thermocline structure (Huveneers *et al.,* 2016). The detection range we report here is specific to the short time that the glider was in the array and would likely change based on seasons and the physical oceanography at a given time. Although we did not explicitly investigate these relationships in this study, environmental conditions that could impact sound transmission such as thermocline displacement (O'Brien and Secor, 2021) and wind-driven turbulence (Gjelland and Hedger, 2013) should be taken into consideration in future projects. In the 2023 glider survey, most detections were made by the tow-behind VM4 unit which was oriented pointing downward. This orientation biases the VM4 to pick up signals from below, which was likely advantageous in our study as halibut are generally benthic, but this configuration may not be as effective for tracking pelagic fishes.

In addition to the lawnmower-pattern surveys used in our study, the use of gliders can greatly extend the monitoring coverage of a study site by travelling the perimeter of a fixed array or filling in gaps between receiver arrays. Unfortunately, the success of glider missions is unpredictable, as demonstrated by the shark attack in 2021 and the damage inflicted by Hurricane Fiona in 2022, resulting in the loss of several receivers and the collected data. Although gliders are autonomous, weather conditions and

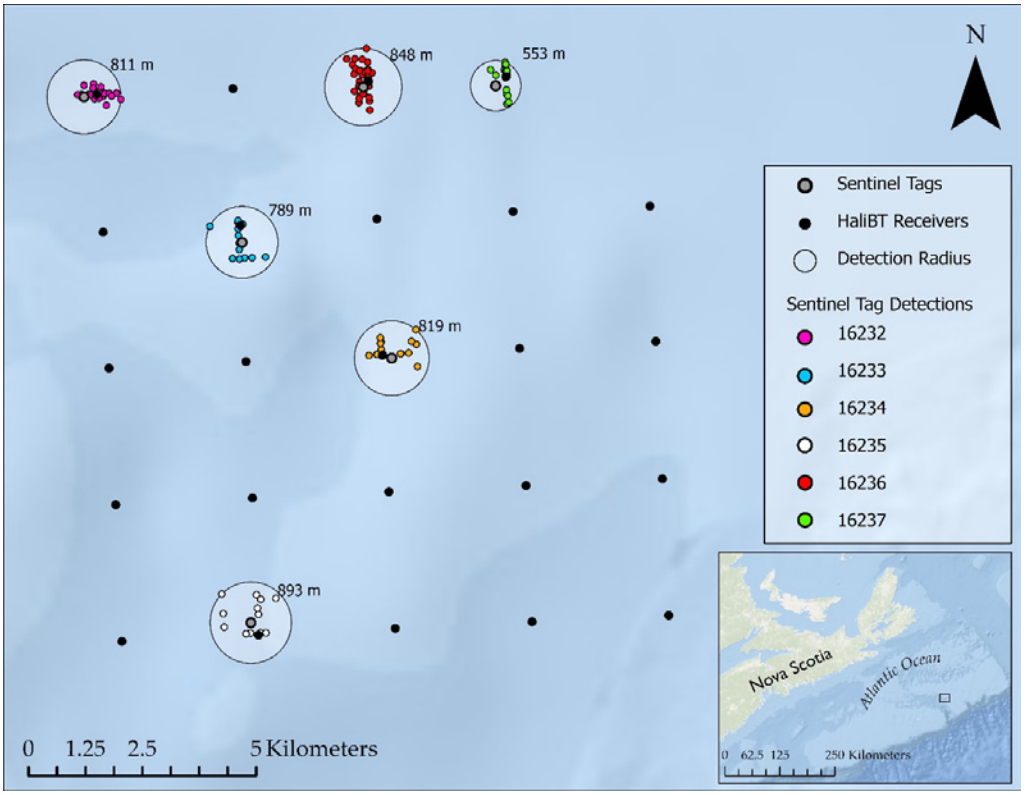

Fig. 7. Detections of each sentinel tag made by an SV3 wave glider during the 2023 tracking transects over the Halibut Bio-Tracking (HaliBT) receiver array. Circles indicate the radius of the furthest detection of each tag.

glider status must be monitored closely by a team of pilots during surveys. Further, discontinuous and infrequent glider surveys over an area of interest are likely to miss important nuances in fish movement, such as seasonal migration. For example, tagged halibut in this study area that exhibited seasonal migratory behaviour regularly spent extended periods in the HaliBT array, but left in the late fall, likely to migrate to their winter spawning grounds. Using data acquired from the short-term glider surveys alone, it was not possible to distinguish residents from migrants. Given these limitations, glider tracking may not be an appropriate standalone substitute for fixed receiver arrays except in locations with heavy fishing pressure or with protected benthic ecosystems where fixed moorings are not possible. The scope of the research question may also influence the utility of glider tracking, where there would be an advantage for detecting short-term events like spawning aggregations.

Mobile tracking has also been used to identify fish mortalities (*i.e.*, sedentary tag IDs) in tagging studies using both VR100 receivers by boat (Chavarie *et al.,* 2022) and by autonomous wave gliders (Zemeckis *et al.,* 2019) under the assumption that in many cases, cessation of horizontal movement during repeated surveys over the area is indicative of death (Klinard and Matley, 2020). Although identifying mortalities was not a goal of this project, it was noted that many tagged halibut did not move at all during the entirety of the 39-day glider survey, which normally would suggest a mortality event. However, the long-term stationary receiver detections of those same halibut revealed extensive activity in the HaliBT array and beyond but over a much longer timescale than the glider survey. The use of gliders for detecting mortalities may therefore be impractical for flatfish species like Atlantic Halibut that can be both highly mobile and can remain in one place for extended periods.

Catch-and-release survival

Assessing the behaviour and survival of fish following a C&R event is rarely possible independent of tagging effects and tagging mortality and is difficult to do without a well-established receiver array. The recapture of four previously-tagged halibut within the HaliBT array provided a glimpse into the survival and behaviour of halibut post-release, facilitated by the extensive coverage of a grid array. Though the sample size is insufficient to provide an estimate of mortality, the significant number of detections from the tagged halibut in this study suggests that survival

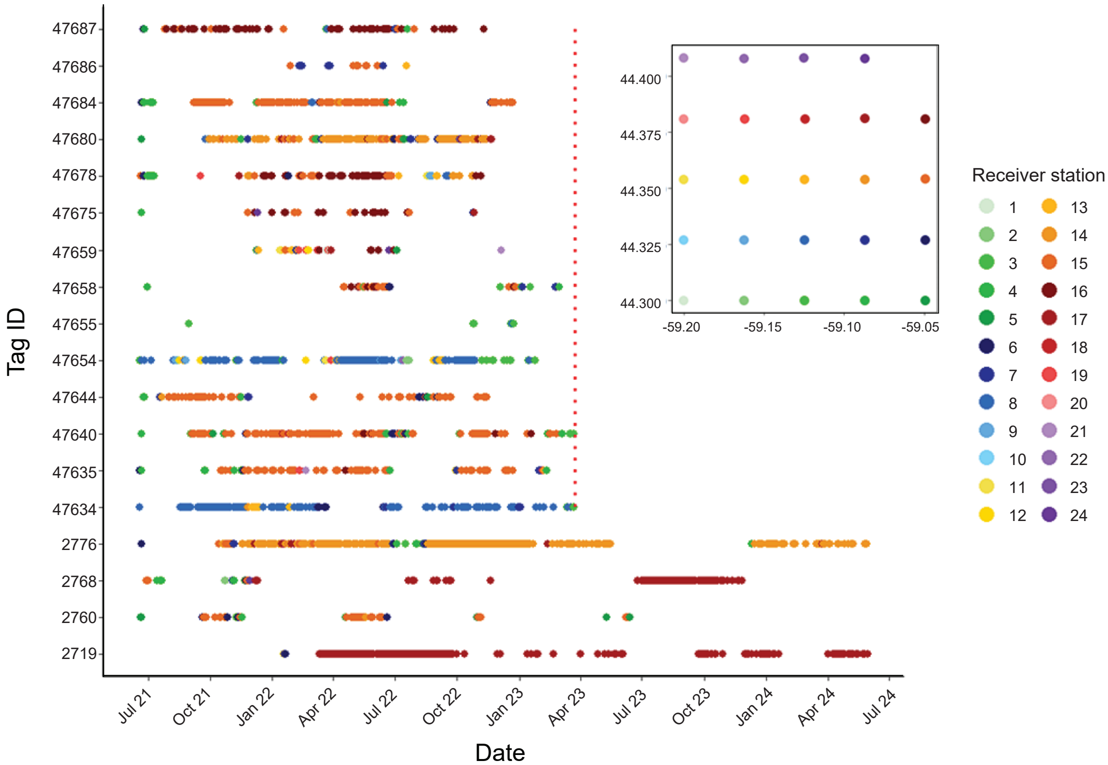

Fig. 8. Detections of resident Atlantic Halibut (*Hippoglossus hippoglossus*; n = 18) from the 2021 release group in the Halibut Bio-Tracking (HaliBT) array from June 2021–May 2024. Dots are detections coloured by receiver station. The inset grid map indicates locations of each receiver station by colour. The dashed red line indicates the estimated tag death date for V13 tags. Detections on other nearby receiver arrays are not shown.

of halibut is high following capture, tagging, and release. Similarly, previous studies have found that post-release survival of halibut (both Atlantic and Pacific *Hippoglossus stenolepis*) captured by longline is high following standard fishing practices and quick handling (Neilson *et al.,* 1989; Kaimmer and Trumble, 1998). The recaptured halibut in this study had good body condition, healed incisions, and normal growth rates a year post-tagging, and the detections following recapture in 2022 indicated survival and an eventual return to regular behaviour. All halibut went undetected for some time after recapture and release and two were detected further down the Gully canyon on the GULMPA line before returning to the HaliBT array. This suggests that halibut might undergo a flight response after release as is documented in other species, such as post-release downstream movements of otherwise upstream-swimming Atlantic Salmon (Mäkinen *et al.,* 2000). Other fish species captured by angling have been found to undergo a period of hyperactivity after release followed by a period of low activity (Cooke *et al.,* 2000; Gurshin and Szedlmayer, 2004). Catch-and-release effects from angling have been previously assessed in Atlantic Halibut using electronic tags (Ferter *et al.,* 2016), but the small sample size, high rates of external tag shedding, and the assumption that mortality is defined by a cessation of vertical movement in that exploratory project limited the conclusions that could be drawn from the results.

The recapture events within the HaliBT array presented the opportunity to monitor the movements of pre-tagged halibut post-release after being captured by longline and handled as they would in a commercial fishery. Although C&R may have elicited a flight response, all halibut eventually returned to their original capture location. Halibut have already been found to display remarkable site fidelity (James *et al.,* 2020), but these detections in the receiver grid demonstrated that halibut returned to their exact location even after a stressful capture event. Furthermore, catch-and-release did not alter the overall migratory behaviour of these halibut, as residents continued to occupy the HaliBT array upon their return and seasonal migrants continued to depart the array during the presumed spawning season, as was found in a similar observation reported for pre-tagged Atlantic Cod (*Gadus morhua;* Ferter *et al.,* 2015). Given that the Trough and Gully receive considerable fishing pressure (Rutherford and Breeze, 2002) and that this region in particular supports undersized halibut (Boudreau *et al*., 2017), it is possible that halibut are captured many times before they are legally harvested. However, these few instances

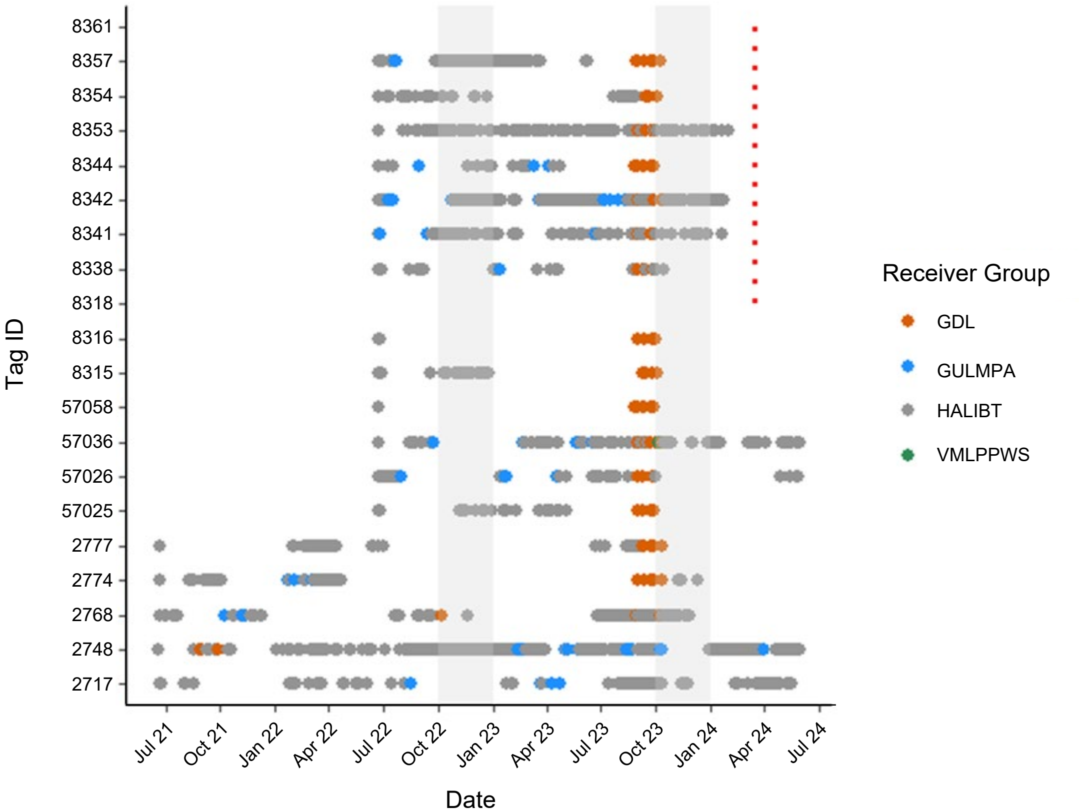

Fig. 9. Detections over the study period (July 2021–March 2024) of acoustic tagged Atlantic Halibut (*Hippoglossus hippoglossus*; n = 18) that were detected in every transect pass in 2023 by an SV3 wave glider (GDL). Detections are coloured by the receiver array upon which they were collected (Halibut Bio-Tracking [HaliBT] array, the Gully Marine Protected Area [GULMPA] array, a mobile transceiver-tagged seal[VMLPPWS], or a wave glider). Shaded grey horizontal bars indicate presumed winter spawning time.

of a true C&R event suggest that the short-term survival and overall migratory behaviours of halibut may not be significantly impacted by release from a longline when the fish are in good condition and handling time is short.

Future halibut tracking considerations

The high REI values in the deep eastern channel in the HaliBT array indicate a high relative importance of that area for the tagged halibut in our study and suggest that it may be valuable and effective to maintain deployments of a small number of receivers in that region for future long-term halibut monitoring. This observation was supported by the glider tracking survey, which revealed that most halibut were found on that deep eastern side, thereby indicating that the REI values in this study were not just a matter of detection efficiency but also localized density. In the future, it may be beneficial to test mooring receivers higher in the water column and pointing downward to maintain improved line-of-signal with benthic-oriented tagged fish such as halibut (Long *et al.,* 2023) and to reduce shadowing effects of complex bathymetry.

Glider tracking offers some potential advantages for examining halibut spatial ecology that were not explored in the scope of this project. The number, exact locations, and characteristics of halibut spawning sites are still undescribed in the NWA, which presents a major management challenge. While recent PSAT studies have begun to address the spawning site knowledge gap (see Le Bris *et al.,* 2018; Liu *et al.,* 2019; Ransier *et al.,* 2024), very few archived data packages have been retrieved from the Eastern Scotian Shelf. Acoustic tags present a distinct advantage over PSATs in the ease and cost-effectiveness of deploying more tags with a battery life that may extend up to a decade. Additionally, acoustic tags can be deployed on smaller fish than PSATs, which can reveal the migratory behaviours of that understudied demographic. However, halibut often make use of habitat that is deeper than acoustic receivers can be maintained and sufficient coverage along the edge of the continental shelf slopes where halibut are presumed to spawn is not feasible. Autonomous gliders are powerful tools for searching for tagged fish in the open ocean (Oliver *et al.,* 2013) and can be adaptively routed to follow tagged individuals (Cypher

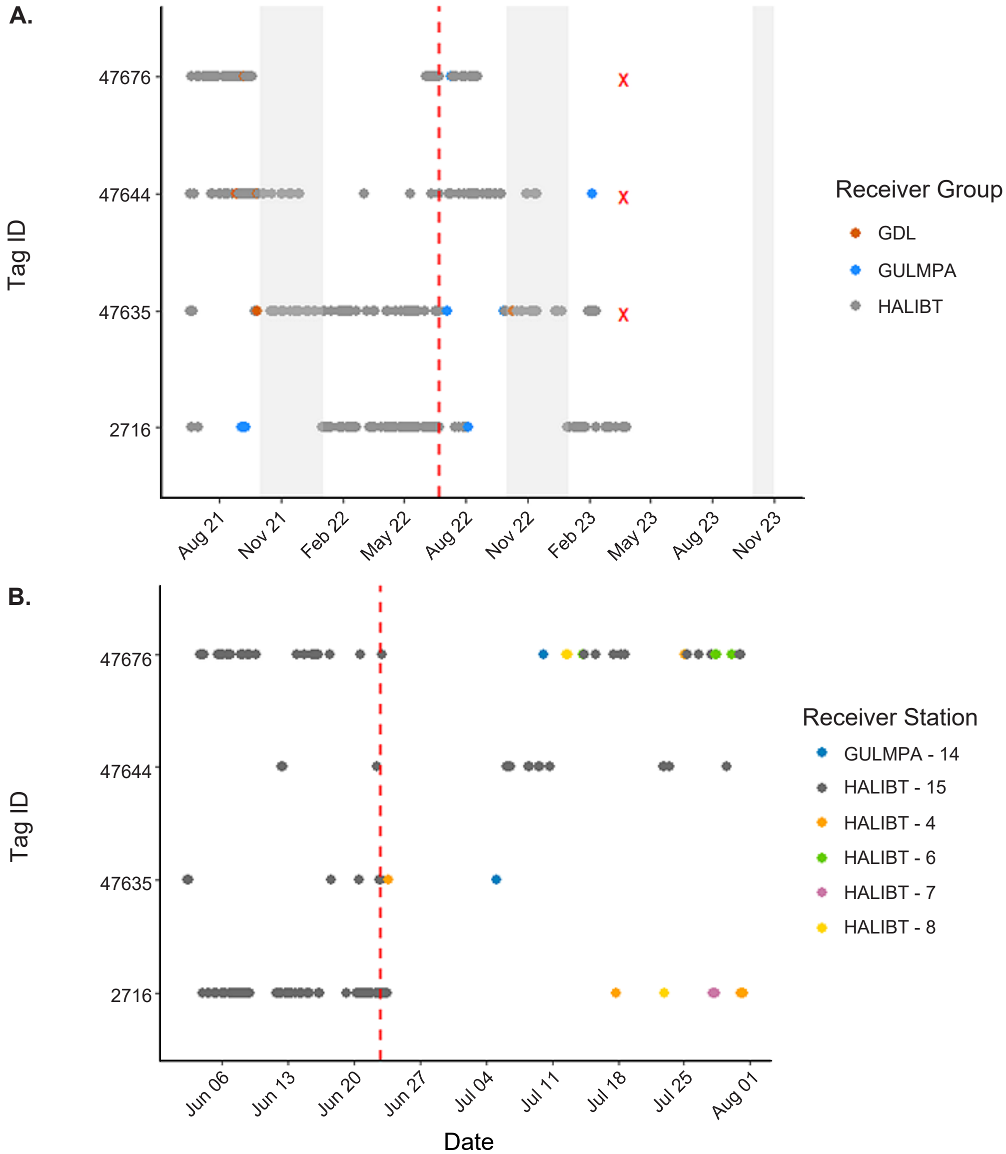

Fig. 10. Detections of Atlantic Halibut (*Hippoglossus hippoglossus*) acoustically tagged in 2021 and recaptured in 2022 (n = 4). Panel **A** shows the detections of each fish over the entire study period (June 2021–March 2024), where dots indicate detections coloured by the receiver group (the Halibut Bio-Tracking [HaliBT] array, Gully Marine Protected Area [GULMPA] array, and a wave glider [GDL]), grey horizontal bars indicate presumed spawning period (Oct–Jan), and red crosses indicate estimated tag death dates for V13 tags. Panel **B** shows the short-term (June–Aug 2022) detections of the same halibut by receiver station. In both plots, the dashed red line indicates June 22nd, the date of the catch-and-release event in 2022.

et al., 2023). Many halibut in this project were absent from the HaliBT array during the presumed spawning season but were found to return at regular annual intervals. Given this information, it may be possible to send gliders to search continental shelf edges near the HaliBT array for tagged fish in the winter to determine Scotian Shelf halibut spawning sites. Due to the challenges of operating wave gliders in the winter, namely low light levels and frequent rough conditions, other types of gliders such as the subsurface Teledyne Webb Research Slocum glider could be explored for this purpose.

Conclusion

In recent years, methods of monitoring acoustically tagged species have evolved, allowing researchers to approach their studies in new ways. Open ocean receiver grids can help identify movements of understudied marine species in a small area but are in some cases impractical for wide-ranging transient species. Our study demonstrates how beneficial these grid arrays can be for investigating both the small-scale movements of halibut and their long-term migratory patterns. However, the success of our grid array is due to the decades of data from the commercial fishery and government surveys indicating that our study site is an area of persistent halibut aggregation, and we emphasize that the establishment of open-ocean grid arrays in areas without similar long-term aggregations may not be as successful.

Autonomous wave gliders are not only able to remotely offload data from offshore receivers but can also act as mobile tracking platforms. We found that gliders were able to detect more tagged halibut in the array than the stationary receivers in the same time frame but were unable to determine long-term nuances in halibut behaviour. By presenting the successes and challenges of our monitoring methods, we hope to inform future telemetry research, particularly of halibut and other offshore species.

Acknowledgements

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Collapse, recovery and collapse of an important fishery

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Abstract

Georges Bank is a shallow plateau off the coast of New England that has supported productive fisheries for centuries. One of these fisheries targeted yellowtail flounder (*Limanda ferruginea*), which at its peak caught over 21 000 mt a year. However, the stock has fluctuated, with periods of high abundance (1970s and 2000s) and low stock size (1990s and 2020s). A review published twenty years ago documented the collapse of the stock in the 1990s and subsequent recovery in the 2000s, hypothesizing the major reason for recovery was bilateral science and successfully coordinated management intervention. Unfortunately, by the time that review was published, the stock had started to decrease again and collapsed in the 2010s. We provide an updated historical review of the fishery and past stock assessments. We conduct new analyses of empirical indicators of spatial distribution and growth for Georges Bank yellowtail flounder and project the stock into the future using the most recent stock assessment. Results suggest that fishing was the likely cause of initial stock depletion while environmental changes, particularly bottom temperature, has limited recovery in recent years. Projections suggest that the population can increase in the future but its ability to increase is related to bottom temperature on Georges Bank. These results give insight into the dynamics an iconic New England fishery and stock, as well as, provide a unique opportunity to study the fluctuations of a stock through multiple periods of recovery and collapse.

Key words: Environment, Overfishing, Stock Assessment, Yellowtail flounder

Introduction

A fishery collapse occurs when a fish population declines so substantially that it can no longer sustain a fishery. Fishery collapses can negatively affect marine habitat, the economy and cause cultural disruption. Historically, the most common hypothesis for a collapse was overfishing, where excessive removals reduced the stock causing reproductive impairment (Roughgarden and Smith, 1996; Pauly *et al.,* 2005). Technological advances in the 20th century allowed commercial fisheries to harvest many marine resourses at unstainable rates. For example, the Northwest Atlantic cod fishery off of Newfoundland was one of the world's most productive fisheries. However, the introduction of large factory trawlers at the conclusion of World War II led to unstainable removals and the collapse of the fishery in the 1990s (Hutchings and Myers, 1994). Similarly, New England's groundfish industry collapsed on Georges Bank with the introduction of factory trawlers in the 1960s and 1970s (Fogarty and Murawski, 1998).

Overfishing is often attributed as the primary cause of stock depletion, but changes in the environment can also lead to reductions in fish productivity. For example, the collapse of the Pacific sardine fishery in the 1940s (Jacobson and MacCall, 1995) and the Peruvian anchoveta fishery in the 1970s (Pauly and Tsukayama, 1987) were hypothesized to be the result of a combination of fishing and changes in sea surface temperatures. The collapse of the Southern New England lobster fishery has been attributed to warming water temperatures linked to shell disease (Glenn and Pugh, 2006). Fisheries collapses have also been attributed to other factors including political interventions, inaccurate science, distant water fishing fleets, changes in natural predator abundance, and the environment (Mullon *et al.,* 2005).

Georges Bank is a shallow plateau (40 000 km^2) located off the coast of New England, separated to the north and south by deep channels (Fig. 1). The Bank has been subject to many environmental fluctuations that are predicted to continue into the future (Fogarty and Murawski, 1998; Wainwright *et al.,* 1993; Mountain and Kane, 2010). This region is characterized by high productivity that has supported fisheries for centuries (Fogarty and Murawski, 1998). The yellowtail flounder fishery on Georges Bank

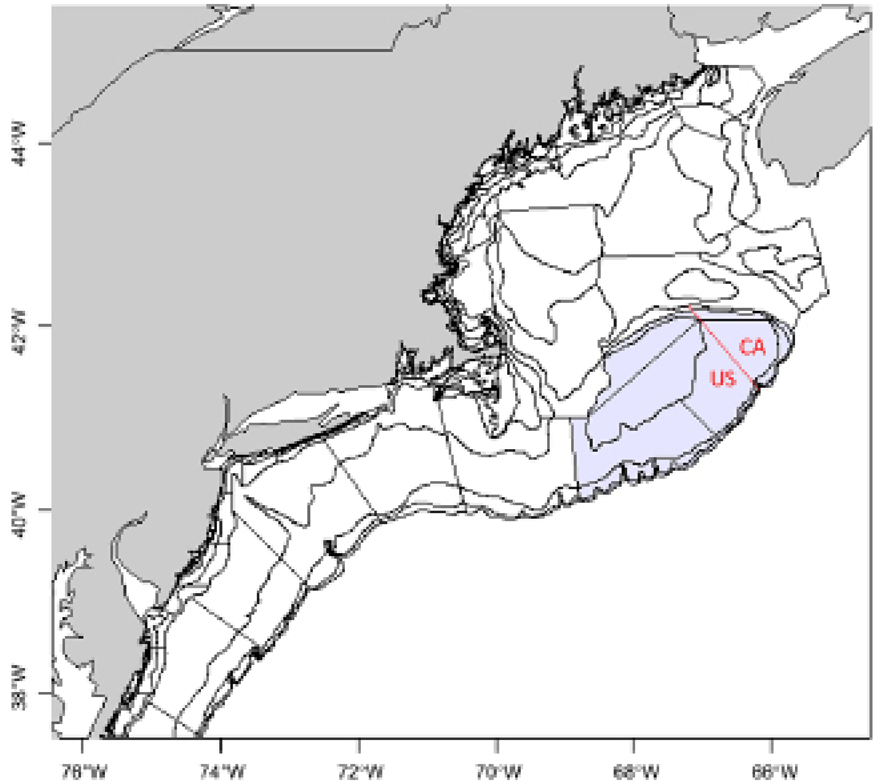

Fig. 1. Georges Bank, the Hague line (marked in red) separates the bank between US and Canadian territorial waters. The blue shaded area is Georges Bank and the bathymetric lines represent different survey strata used by the Northeast Fisheries Science Center bottom trawl survey.

started in the 1930s and was considered one of the principal groundfish stocks. Fisheries targeted primarily cod, haddock and yellowtail flounder on the Bank and the area was open to international fishing until 1977. However, by the 1990s overfishing had led to the collapse of the industry (Fogarty and Murawski, 1998; Stone *et al.,* 2004).

Stone *et al.* (2004) documented the collapse of the Georges Bank yellowtail flounder fishery and its subsequent recovery. Their work examined empirical indicators of distribution shifts, age-structure, and trends of exploitation and biomass, demonstrating that the stock was capable of rapid recovery in response to international collaboration and fisheries regulations. However, by the time the paper was published, the stock was already starting to decline again despite continued international collaboration (Stone and Legault, 2005; NEFSC, 2024). In more recent years, stock biomass has been at an all-time low despite these continued regulations and international collaborations. Therefore, reinvestigation of the potential drivers of the Georges Bank yellowtail flounder fishery collapses is needed to understand why bi-lateral science and management did not prevent the second collapse. Understanding drivers of the different collapses can be used to inform management for improved rebuilding plans.

We review available information as well as conduct updated analyses to assess the primary drivers of the initial fishery collapse, subsequent recovery and following collapse of the Georges Bank yellowtail flounder fishery. A historical review of the Georges Bank fishery and stock assessments are provided to understand potential anthropogenic drivers that could cause the different collapses. We also review the most recent stock assessment (NEFSC, 2024) that incorporates process error and environmental covariates, which allows for the direct comparison of fishery and environmental impacts on the population. We conduct new analyses of empirical trends of spatial distribution and growth to determine if these have changed over time. We also use the most recent stock assessment to estimate new projections to see how the stock might change in the future. Results provide valuable information on yellowtail flounder and provide information on the primary drivers of the two different collapses of the yellowtail flounder fishery.

The fishery

A New England fishery for yellowtail flounder developed in the 1930s, coincident with a decline in winter flounder abundance (Royce *et al.,* 1959; Lux, 1964). Yellowtail were caught in otter trawls targeting other groundfish species and scallops. The fishery for yellowtail flounder was historically divided into Southern New England, Georges Bank, and Cape Cod (Lux, 1964). Fishing effort shifted from Southern New England to Georges Bank in the 1940s leading to landings increasing by over 700% by the end of the decade (Royce *et al.,* 1959; Fig. 2). By 1940, New Bedford, Massachusetts had become the principal port for landing flatfishes because of industry infrastructure and proximity to fishing grounds. From 1940–1961 over one-half of all US yellowtail were landed in New Bedford, Massachusetts (Lux, 1964). Landings decreased in the 1950s, possibly from a warming environment (Royce *et al.,* 1959; Lux, 1964; Lux and Nichy, 1969; Sissenwine, 1974).

In the 1960s and early 1970s, distant water fleets targeted Georges Bank groundfish and herring (Fig. 2). During this time fishery removals increased, reaching an all-time high of roughly 21 000 mt in the late 1960s and early 1970s (Fig. 2). Despite regulations developed by the International Commission for the Northwest Atlantic Fisheries (*e.g.*, minimum mesh sizes, minimum fish sizes, spawning closures, annual quotas) decreases in catch were being associated with too much fishing (Kulka, 2012; Brown and Hennemuth, 1971; Sissenwine, 1977).

The US Magnuson-Stevens Act established an exclusive economic zone, excluded distant-water fisheries, and formed regional fishery management councils in 1976. An initial management plan was adopted in 1977 that relied on total allowable catches (TACs), but there was limited enforcement of quotas. Fishing removals decreased somewhat in the early 1980s (Brown *et al.,* 1980; Clark *et al.,* 1981) although misreporting among the stock areas was considered a problem. Increases in mesh size in 1982 and 1983 also contributed to an increase in biomass (McBride and Clark, 1983), but effort was still considered to be too high (Overholtz and Murawski, 1985). In 1984, a maritime boundary was established splitting Georges Bank between the US and Canada. Canada did not have a directed fishery for yellowtail until 1993 (Stone *et al.,* 2004).

Multiple management changes occurred in the 1990s for US and Canada that included limitations on fishing effort (*i.e.*, limited days at sea), increased minimum mesh size regulations, and year-round area closures. A Canadian fishery developed to target yellowtail flounder on eastern Georges Bank in the 1990s, and the US fleet was temporarily allowed access to a closed area to target yellowtail flounder in 2004 (Stone and Legault, 2005). Access to this closed area is a primary reason why fishery

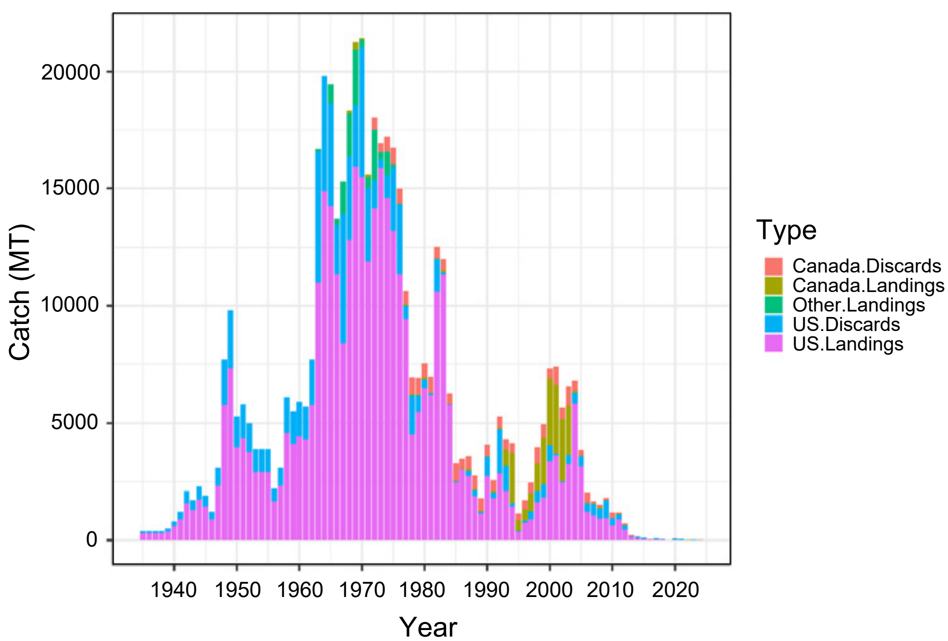

Fig. 2. Catch of yellowtail flounder by disposition on Georges Bank.

catches increased in the early 2000s. However, by 2010 fishery catch started to decline (Fig. 2). Since this decrease, yellowtail has had a limited market and is primarily caught as bycatch in the scallop fishery (NEFSC, 2024). The scallop fishery is the second most lucrative fishery in the region and high catches of yellowtail flounder can lead to accountability measures that closed scallop fisheries in some years (O'Keefe and DeCelles, 2013).

Population assessments

Early stock assessments of Georges Bank yellowtail flounder relied on catch curves, tagging experiments, and a detailed understanding of the fishing fleets operating at the time (Brown *et al.,* 1980). These assessments consistently estimated high fishing mortality rates, relative to natural mortality (M = 0.2), but suggested that fishing had a limited impact on the stock. Early analyses of population dynamics also suggested that temperature could play an important role in stock abundance (Royce *et al.,* 1959; Lux, 1964; Lux and Nichy, 1969). The first analytical stock assessment for Georges Bank yellowtail flounder found high fishing mortality and low stock abundance in the 1980s (NEFSC, 1989). Subsequent assessments found similar results (NEFSC, 1991; NEFSC, 1994), and concluded the stock had collapsed by the mid 1990s (NEFSC, 1994). Canadian catch was first incorporated in the assessment in 1996, but did not change the perception of the stock (Gavaris *et al.,* 1996). The effect of strong management measures (*e.g.*, reduced days-at-sea, increased minimum mesh size, year-round closed areas) were detected by the end of the 1990s by virtual population analysis and surplus production models that both estimated an increase in stock biomass (Cadrin *et al.,* 1999; Stone *et al.,* 2004).

The Transboundary Resources Assessment Committee (TRAC), a joint US-Canadian scientific body, conducted its first joint assessment of Georges Bank yellowtail flounder in 1998 using a virtual population analysis (Neilson and Cadrin, 1998). Retrospective patterns that revised previous stock estimates downward and increased fishing mortality estimates appeared in 2000 (NDWG, 2000) and continued in subsequent assessments (NEFSC, 2002; Stone and Legault, 2003; Legault and Stone, 2004). There were diagnostic problems with the stock assessment in the early 2000s and 2010s with these issues becoming severe in the 2010s. In 2014, the analytical assessment was rejected in favor of an empirical approach that relied on survey trends (O'Brien and Clark, 2014). Catch advice was initially derived from area-swept survey biomass and a target exploitation rate but was revised to a constant quota, conditional on survey biomass remaining within predefined bounds (O'Brien and Clark, 2014). In 2024, a peer review panel supported the recommendation to use a state-space model, the Woods Hole Assessment Model (WHAM, Stock and Miller, 2021), to assess the stock at the conclusion of a multiyear research track assessment (aka benchmark assessment, NEFSC, 2024).

Spatial distribution

A common theory in ecology is that population abundance is positively correlated with spatial range (MacCall, 1990; Holt *et al.,* 1997). As a population decreases, it can contract to preferred habitat (Shackell *et al.,* 2005). Spatial contractions can make it easier for fisheries to target a resource and can violate a common assumption that catch rates are proportional to abundance. Catch rates can stay high or stable in the concentrated areas while population abundance declines (Erisman *et al.,* 2011). Fish can also shift their distribution in response to changing ocean conditions (Nye *et al.,* 2009; Pinsky *et al.,* 2013). We conducted new analyses of the spatial distribution of yellowtail flounder using fisheries independent surveys to examine if spatial distribution changed.

Fisheries surveys are a common tool to explore spatial distributions of marine fishes because they have consistent spatio-temporal sampling. Three fisheries independent surveys cover the entire Georges Bank stock area: Fisheries and Oceans Canada winter survey (DFO, since 1987), and the Northeast Fisheries Science Center (NEFSC) spring and fall surveys (since 1968 and 1963, respectively). All three surveys are based on a stratified random design. The same stratified-mean indices of relative abundance that are derived for stock assessment were used to explore trends in relative abundance. Maps were created to explore visual changes in spatial use. A Gini index (Woillez *et al.,* 2007) was used to measure the spatial distribution for the three different surveys. The Gini index provides a measure of spatial aggregation, with lower values indicate wider distribution and higher values indicate higher concentrations. A Gini index does not provide fine scale measurements of changes in center of gravity or effective area occupied. A loess smoother was fit to the Gini coefficients from each survey to inform long-term trends. The analyses conducted here use a terminal year of 2022, which is the last year in the most recent stock assessment.

High catch rates in the fall and spring NEFSC surveys occurred in the 1960s and early 1970s, catch rates were low in all three surveys in the 1980s and early 1990s, catch rates increased from the late 1990s to early 2010s, with high abundance in the southeast portion of Georges Bank. Two high values for the DFO survey in 2008 and 2009 resulted from large catches in single tows creating high uncertainty for these estimates (Figs. 3–4). Catch rates decreased again after 2010 (Figs. 3–4). The loess smoothers of the Gini coefficients shows an increasing trend for all three surveys, indicating the yellowtail flounder are becoming more concentrated in specific habitat on Georges Bank. The loess trend shows an increase in coefficient values for all three surveys until the early 2000s, with the highest Gini coefficients for the NEFSC spring and DFO survey occurring during that time period. However, since the early 2000s the Gini coefficients continue to increase for the NEFSC fall survey

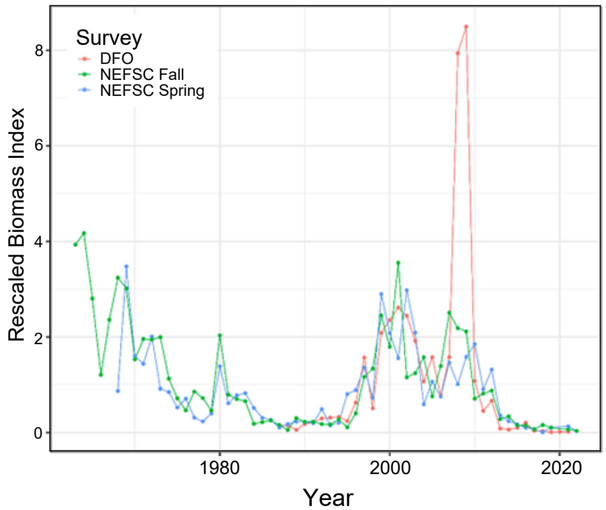

Fig. 3. Annual relative biomass estimates from the three surveys that cover Georges Bank. Results were scaled to the mean for comparison.

and decline for the other two surveys, suggesting seasonal differences in distribution (Fig. 5).

Size and growth

Size and growth information are important for understanding the population dynamics of a stock and can be used as empirical indicators to inform fisheries management. For example, a lack of smaller fish can indicate reduced recruitment. In contrast, fewer larger fish may indicate slower growth, or higher natural or fishing mortality (Miranda *et al.,* 2024). Empirical length and age data are available for the entire time series for both the NEFSC spring and fall surveys. However, individual weights were not collected on the NEFSC surveys until 1995. Empirical age data is available from the DFO survey since 2004. We produced new analyses of trends in size and growth. These analyses focus on ages one through six, because few fish older than age six were caught in the fisheries and surveys. The stock assessment aggregates these ages into an age-6+ group (NEFSC, 2024). Analyses focused on trends in mean length and mean weight to understand temporal trends in growth. These inputs are commonly used in stock assessment and provide indications about changes in growth.

Mean length at age trends from the NEFSC spring survey suggest older fish were smaller towards the end of the time series (Fig. 6). In the fall survey, mean size at age decreased for most ages in the 1990s followed by an increase. In both seasons, age classes had more overlapping mean size towards the end of the time series compared to the beginning (Figs. 6–7). The DFO time series shows a contraction in mean length with similarities between ages two and age-6+ (Fig. 6). Additionally, no age-one fish were caught since 2019. Trends in mean weight at age show a decreasing trend in weight at age for older fish in the NEFSC spring and DFO surveys. At the end of the time series there is less variability in weight at age between ages from all three surveys (Fig. 7). The number of biological samples are lower in recent years due to reduced catch rates in all three surveys (Fig. 4).

Temporal trends in the environment, recruitment, biomass, and fishing mortality

We reviewed the most recent stock assessment for Georges Bank yellowtail flounder and used the results to explore temporal trends. The most recent stock assessment applied the Woods Hole Assessment Model (WHAM), which is an age-structured model that allows for the inclusion of environmental variables and process error on different population dynamic processes (Stock and Miller, 2021). The stock assessment time series starts in 1973 with a terminal year of 2022. The assessment performed well with no major diagnostic issues. The model includes time varying selectivity to account for management and targeting changes. The assessment model estimates random effects for abundance at age transitions to account for annual changes in survival. A Beverton-Holt stock recruit relationship was used to model recruitment with changes in the stock recruit parameters informed by a stock specific bottom water temperature time series. This relationship assumes that recruitment is impacted by both stock size and bottom temperature (Supplemental material; NEFSC, 2024).

Environmental trends were thoroughly reviewed during the research track stock assessment using a multi-faceted approach that involved a literature review, exploratory analyses, and exploration within the stock assessment (Kittel *et al.,* 2024; NEFSC, 2024). For Georges Bank yellowtail flounder, this approach hypothesized that water temperature was likely influencing natural mortality or recruitment (Kittel *et al.,* 2024; NEFSC, 2024). An annual time series for Georges Bank was derived from a data product that interpolates monthly bottom temperature at relatively high spatial resolution (Du Pontavice *et al.,* 2023). Stock assessment model diagnostics (*e.g.*, convergence, residuals, Mohn's rho predictive performance) supported using the bottom temperature covariate to estimate changes in the parameters of the Beverton-Holt stock recruit relationship (NEFSC, 2024). Conversely, model diagnostics did not support including a covariate to estimate time varying natural mortality (Supplemental material; NEFSC, 2024).

The stock assessment model fit to the bottom water temperature time series shows that the coldest water temperatures were in the 1970s and early 2000s (Fig. 8). During this same time, recruitment was estimated to be higher (Figs. 8–9). In contrast, bottom water temperature

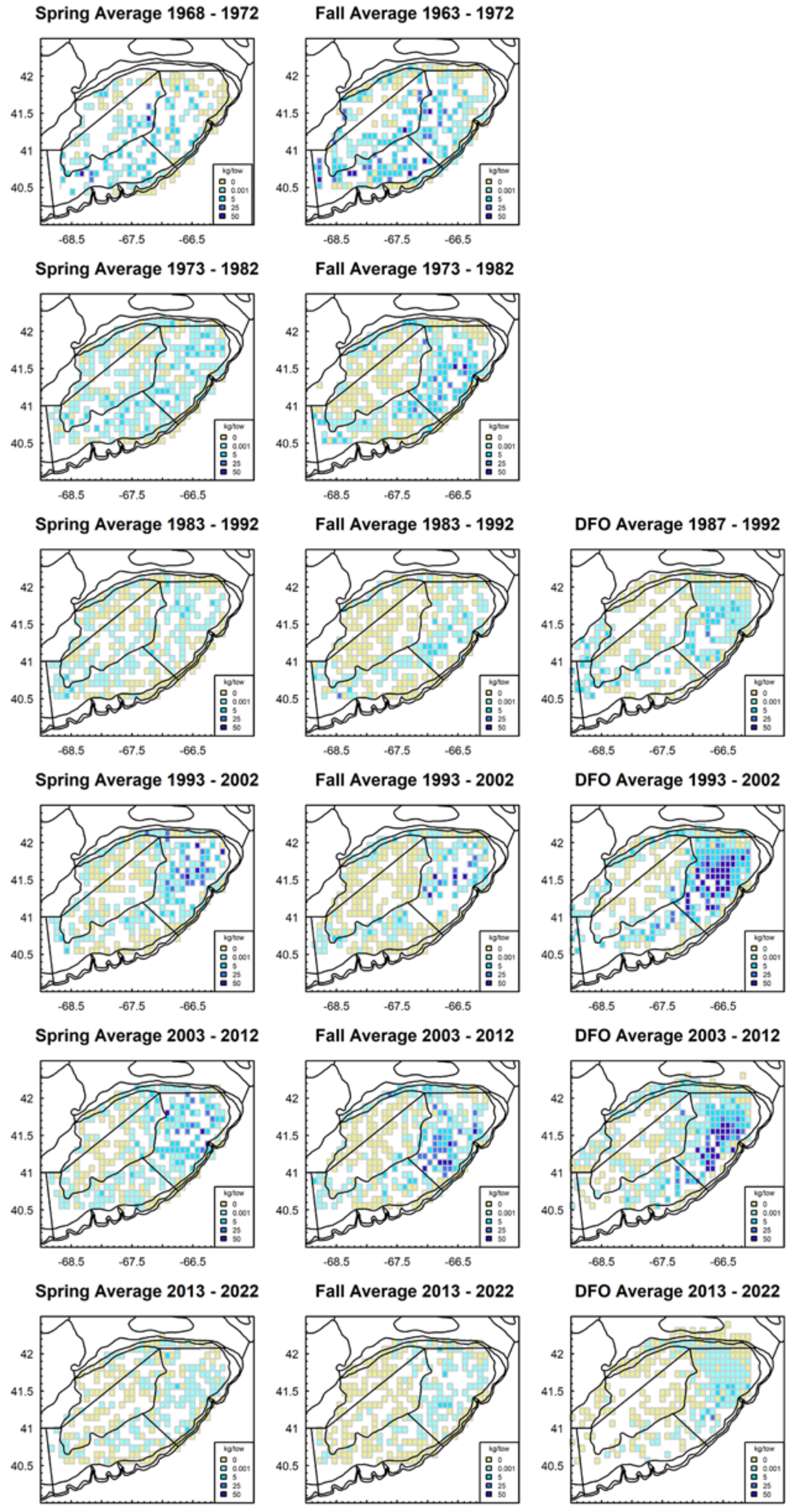

Fig. 4. The spatial distribution of survey catches on Georges Bank. Blue squares represent areas of high yellowtail flounder biomass per tow while yellow squares represent low biomass per tow.

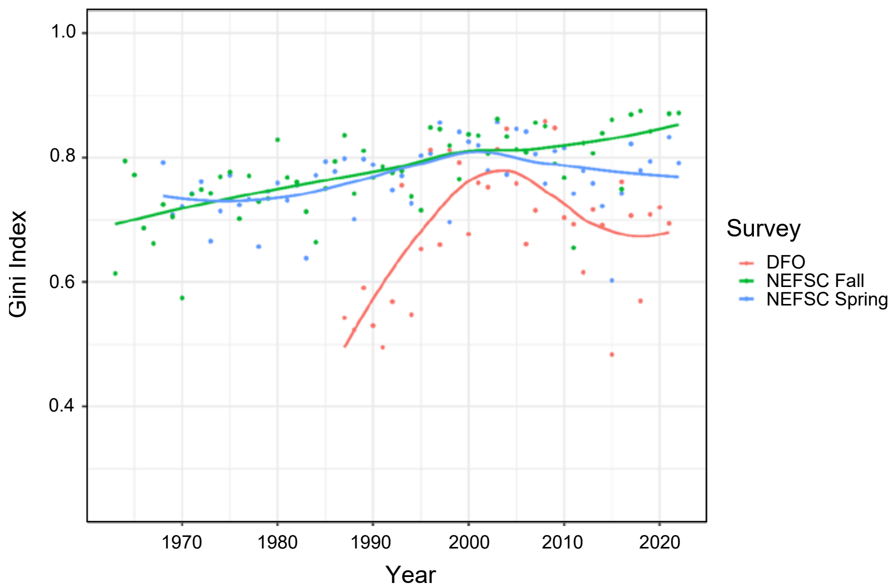

Fig. 5. Gini coefficient for Georges Bank yellowtail flounder surveys. The coloured lines are loess smoothers for the corresponding surveys.

started to warm around 2010 and has been warmest since 2015 (Fig. 8). During this time period, recruitment was estimated to be low (Figs. 8–9).

Annual maximum sustainable yield reference points (SSB_{msy}, F_{msy}, and R_{msy}) derived from equilibrium expectations for annual conditions and their relationship to temporal trends in spawning stock biomass, fishing mortality and recruitment show distinct periods of productivity and overexploitation. Spawning stock biomass is estimated to be high and above the reference point at the beginning of the time series followed by decreases in the 1980s and continued low values until the mid 1990s (Fig. 9). In the 1980s and 1990s spawning stock biomass was below the reference point, indicating that the stock was overfished (Fig. 9). Recruitment was high in the 1970s, followed by lower levels of recruitment in the 1980s–1990s, with some productive years (Fig. 9). Fishing mortality was high until the mid 1990s, suggesting that overfishing was occurring during this time. Following this reduction, spawning stock biomass and recruitment increased in the early 2000s when overfishing was no longer occurring. Fishing mortality has remained low since the end of the 1990s, except for a brief increase in the mid 2000s, which is associated with increases in US and Canadian fishing effort. Overfishing has not occurred since the 2004 closed-area access program. By the 2010s, spawning stock biomass and recruitment started to decrease despite reduced fishing effort and catch. Spawning stock biomass, recruitment and fishing effort have remained low since 2010 (Fig. 9).

Future projections

The stock assessment model can be used to project the stock into the future. Short-term projections (3-year) were used to inform future fishing quotas. In this study, we used the stock assessment model to conduct long term projections to explore if the stock could recover in the future. Projection trends were compared to maximum sustainable yield reference points that were calculated based on current environmental conditions. Current conditions of the stock were used in the projection period: weight at age (2-year average), natural mortality (constant), fleet selectivity (with 1st order autoregressive process error), maturity (constant), recruitment and bottom temperature (NEFSC, 2024). Future bottom temperatures were not available but they are needed to inform recruitment in the projection period. Two methods of estimating bottom temperature in the projection period were explored, a 1st order autoregressive process and recent mean. The recent recruitment period was determined using a changepoint analysis and was assumed to be from 2009–2022 (NEFSC, 2024). Under both scenarios the stock was projected 100 years into the future assuming the fishing mortality rate from the last year of the assessment.

For the autoregressive process on bottom temperature, bottom temperature slowly cools from the terminal year estimate (2022) to the time series mean. The average bottom temperature from the recent recruitment period estimated warmer bottom water in the projection period. Assuming colder bottom temperatures in the projection

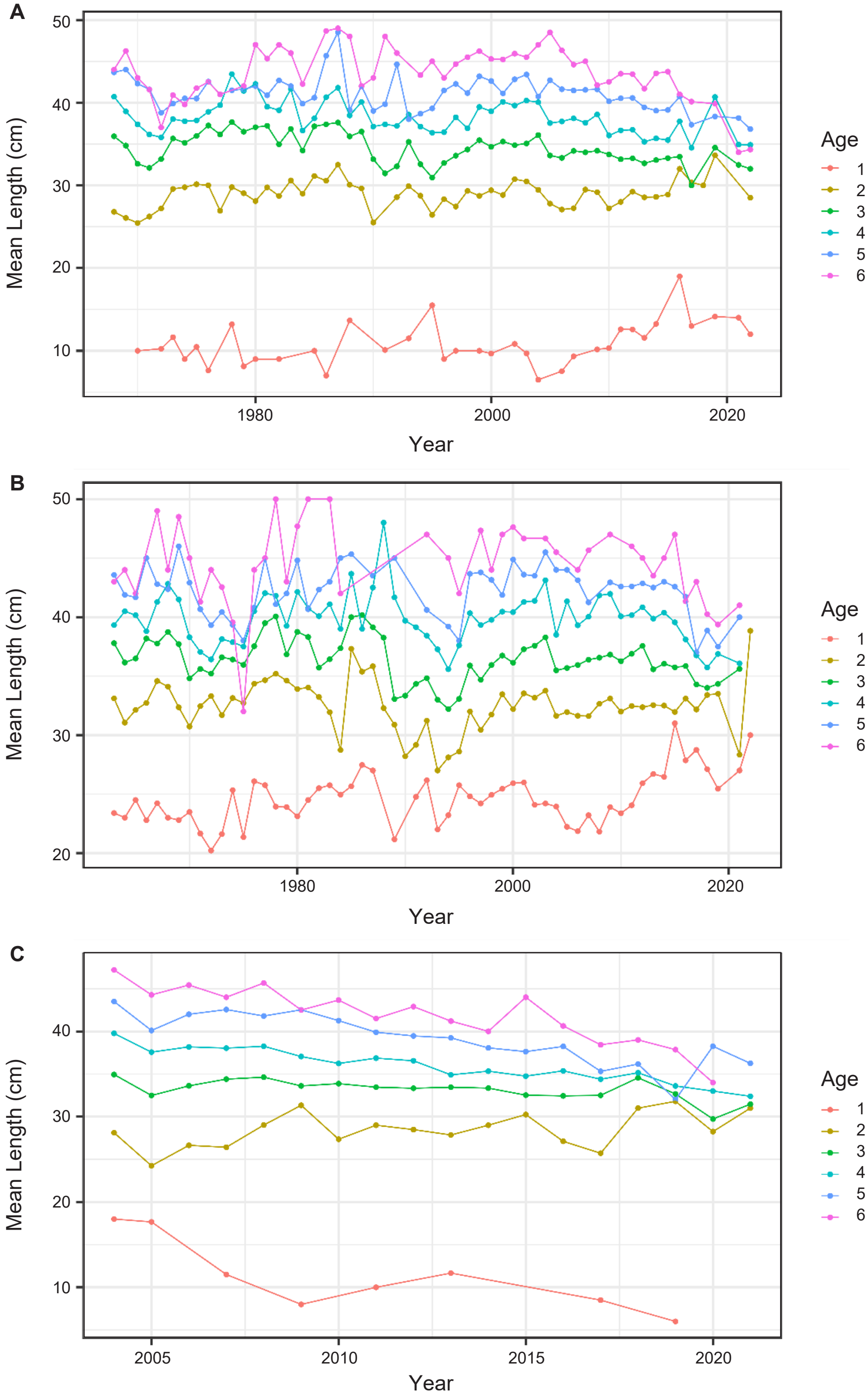

Fig. 6. Georges Bank yellowtail flounder trends in mean length at age for each survey and season: NEFSC spring (**A**) , NEFSC fall (**B**), DFO (**C**).

period allowed recruitment and biomass to be higher in the projection period (Fig. 10). Under both scenarios, the stock size was able to increase above SSB_{msy} in the future, suggesting that despite current low population size the stock has the ability to recover under different environmental conditions. However, this recovery is still below historical high estimates from the 1970s and 2000s (Fig. 10). Thus, it is unlikely that Georges Bank yellowtail will support a level of fishery removals that have historically been taken from this stock.

Discussion

A review of biomass trends from the most recent stock assessment suggests biomass was high in the 1970s, followed by decreases in the 1980–90s, with the stock declared collapsed in 1994. Biomass increased in the 2000s with biomass above SSB_{msy} for large periods of the early 2000s followed by subsequent decreases to all-time lows in the 2020s, indicating the stock had collapsed again. Fishing mortality was high through the mid 1990s followed by a subsequent decrease with some fluctuations through the 2020s.

Stone *et al.* (2004) hypothesized that the primary driver of stock collapse in the 1990s was overfishing, and subsequent recovery in the early 2000s was due to effective bi-lateral science and coordinated management. The results presented here support those hypotheses with the most recent assessment estimating a sharp decline in fishing mortality in the mid 1990s. These reductions are likely due to the implementation of TACs, closed areas, decreased days-at-sea, and increases in mesh size (Stone *et al.,* 2004). The implementation of bi-lateral science and precautionary management during this time also likely benefited the stock and fishery. Subsequent decreases since 2010 are likely due to different factors because similar management measures remain. Thus, it is unlikely that fishing is the primary driver of stock dynamics in recent years (Fig. 9).

Over the last several decades, variability in ocean conditions have been well documented on Georges Bank, with observed changes in salinity, temperature, and predator/prey abundance (Wallace *et al.,* 2018; Tsou and Collie, 2001; Mountain and Kane, 2010). Changing environmental conditions were suggested to have possibly led to reduced recruitment of Georges Bank yellowtail flounder in the 1980s and early 1990s (Stone *et al.,* 2004). A review of the stock assessment model suggests that bottom water temperature impacts recruitment (Fig. 8). Estimated water temperatures from the stock assessment suggest slightly colder water temperatures in the 1970s, warmer temperatures in the 1980/1990s followed by colder temperatures in the 2000s. These fluctuations in cold water temperature coincide with periods of improved recruitment and subsequent larger stock size (Figs. 8–9). Additionally, warmer temperatures since 2010 are the primary reason stock size remains low despite low fishing mortality (Figs. 8–9).

Temperature can impact multiple aspects of recruitment including timing, egg viability, food availability, larval growth and mortality (Takade-Heumacher *et. al.*, 2014). It is unclear what the specific mechanism is for Georges Bank yellowtail flounder. However, it has long been hypothesized that warm temperatures could lead to reduced recruitment (Royce *et al.,* 1959; Lux, 1964; Lux and Nichy, 1969). Previous research, has linked recruitment deviations to water temperature for yellowtail founder on Georges Bank (Brodziak and O'Brien, 2005; Takade-Heumacher *et al.,* 2014) and the adjacent stock in southern New England (Sissenwine, 1974, 1977; Sullivan *et al.,* 2005).

For yellowtail flounder, the majority of research exploring changing ocean conditions have focused on the Southern New England stock. This population is thought to be most susceptible because it is at the Southern extent of the species range (Hare *et al.,* 2016). Unlike the Georges Bank stock, abundance of the Southern New England stock has been decreasing since the 1980s with no signs of recovery (NEFSC, 2024). Previous research applications of the stock assessment have used a cold pool index to improve recruitment estimation, which measures the spatial extent and persistence of cold bottom water across the mid-Atlantic bight (Miller *et al.,* 2016; Xu *et al.,* 2017). The most recent stock assessment currently uses the Gulf Stream index to estimate deviations in recruitment, which measures the latitude above average of the Gulf Stream position (NEFSC, 2024). The Gulf of Maine/Cape Cod stock is the northernmost yellowtail flounder stock in the US and no environmental indicators are currently included in the stock assessment. However, it is hypothesized that fish might be shifting deeper in this region to account for changes in water temperature (Nye *et al.,* 2009).

On Georges Bank, new analyses of spatial distribution suggest that yellowtail flounder were most widely distributed in the 1970s, which corresponds to a period of high stock size (Figs. 4,5,9). However, since then there has been a steady contraction in spatial range (Fig. 4). During the periods of highest stock size in the 2000s, the DFO and to a lesser extent the spring NEFSC survey suggest that there was a restriction in spatial use, with fish occupying less habitat (Figs. 4, 5). Large spatial contractions like this can make the population especially vulnerable to fishing, but fishing mortality rates were not high at these times (Erisman *et al.,* 2011, Fig. 9). The "Basin Hypothesis" has been suggested for yellowtail flounder on the Grand Bank and Georges Bank (Pereria *et al.,* 2012; Adams *et al.,* 2018), which theorizes that when population abundance is high yellowtail occupy a wide range of habitats (MacCall, 1990). The Gini coefficients provide

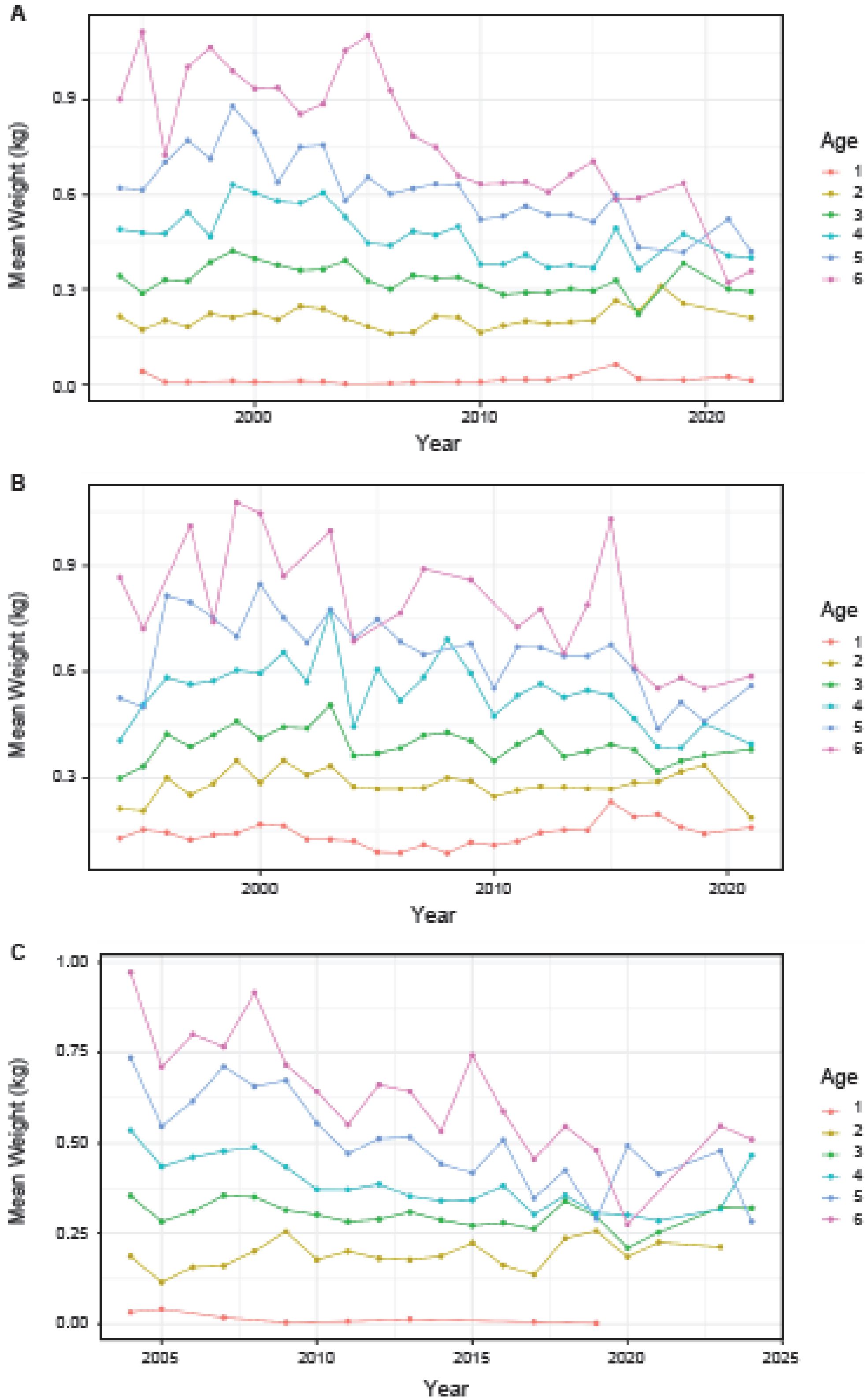

Fig. 7. Georges Bank yellowtail flounder trends in mean weight at age for each survey and season: NEFSC spring (**A**), NEFSC fall (**B**), DFO (**C**).

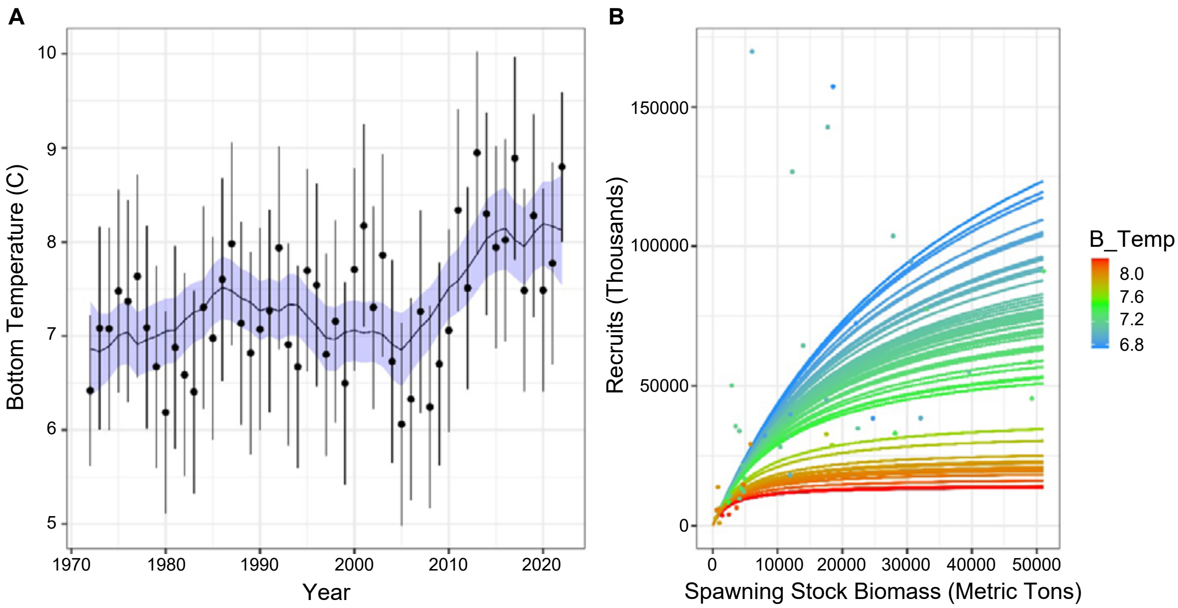

Fig. 8. Bottom water temperature (**A**) used in the stock assessment model to predict recruitment. The horizontal black line is the stock assessment model fit to bottom temperature while the blue is the 90% confidence intervals. Black dots are the observed bottom temperature and confidence limits are the associated standard deviations. The Beverton-Holt stock recruit relationship (**B**) influenced by water temperature and used to estimate recruitment.

a measure of spatial dispersion; however, the results vary among the seasonal surveys. The Gini coefficients suggest that in the fall NEFSC survey yellowtail flounder are occupying less habitat at lower population sizes. The opposite trend occurs in the spring with the NEFSC and DFO surveys estimating fish are occupying less habitat at larger population sizes in the early 2000s (Fig. 5). It is possible that these differences could be due to seasonal environmental conditions, especially because the Spring NEFSC and DFO sample at a similar time of year. Additionally, differences could be due to changes in size structure between the different surveys. The conflict in results, and the use of a single spatial metric, prevent confirmation of the "Basin Hypothesis". Future research should consider additional spatial metrics (*e.g.*, center of gravity, Moran, 1950) and could look to link environmental covariates to dispersion metrics.

Thermal preferences could be altering the spatial use of yellowtail flounder on Georges Bank. The optimal temperature for yellowtail flounder on Georges Bank is hypothesized to be roughly 7°C (Hyun *et al.,* 2014). Since 2009, the average bottom water temperature on Georges Bank has been warmer than 7°C (Fig. 8). This suggests future work should consider exploring time varying availability and spatial distribution shifts of yellowtail flounder. Spatial shifts could be incorporated into future stock assessments with time varying catchability and/or selectivity parameters or the use of spatio-temporal models to standardize survey data (Wilberg *et al.,* 2009; Cao *et al.,* 2017).

Length data from the NEFSC spring and fall survey cover the periods of high stock size (1970s and 2000s) and low stock size (1990s and 2010s). Mean length tended to be larger when the stock was larger and smaller when the stock was lower. Additionally at lower stock biomass, mean length at age one is more similar to mean length at age two (Fig. 6). All length and weight information indicates that fish have been shorter and lighter than they were historically and there is more overlap in size among adjacent ages, indicating reduced growth (Figs. 6–7). Observed changes in size at age could be the result of environmental factors, such as changes in water temperature or prey composition. Future work should explore potential drivers of observed changes in size.

Growth is an important component of stock productivity because natural mortality and reproductive potential usually scale with size. Fish that are larger are less likely to be eaten and produce more offspring (Miranda, *et al.,* 2024). Typically, fishing gear releases small fish and retains larger fish, which can influence the size structure of the population (Enberg *et al.,* 2012). The environment can also influence growth, with restrictions in thermal range possibly negatively affecting growth (Boltaña *et al.,* 2017). Reduced growth, low stock size and reduced fishing at the end of the time series suggest that density dependent factors are not influencing growth for Georges Bank yellowtail.

New long-term projections from this study suggest that the Georges Bank yellowtail flounder stock can increase again

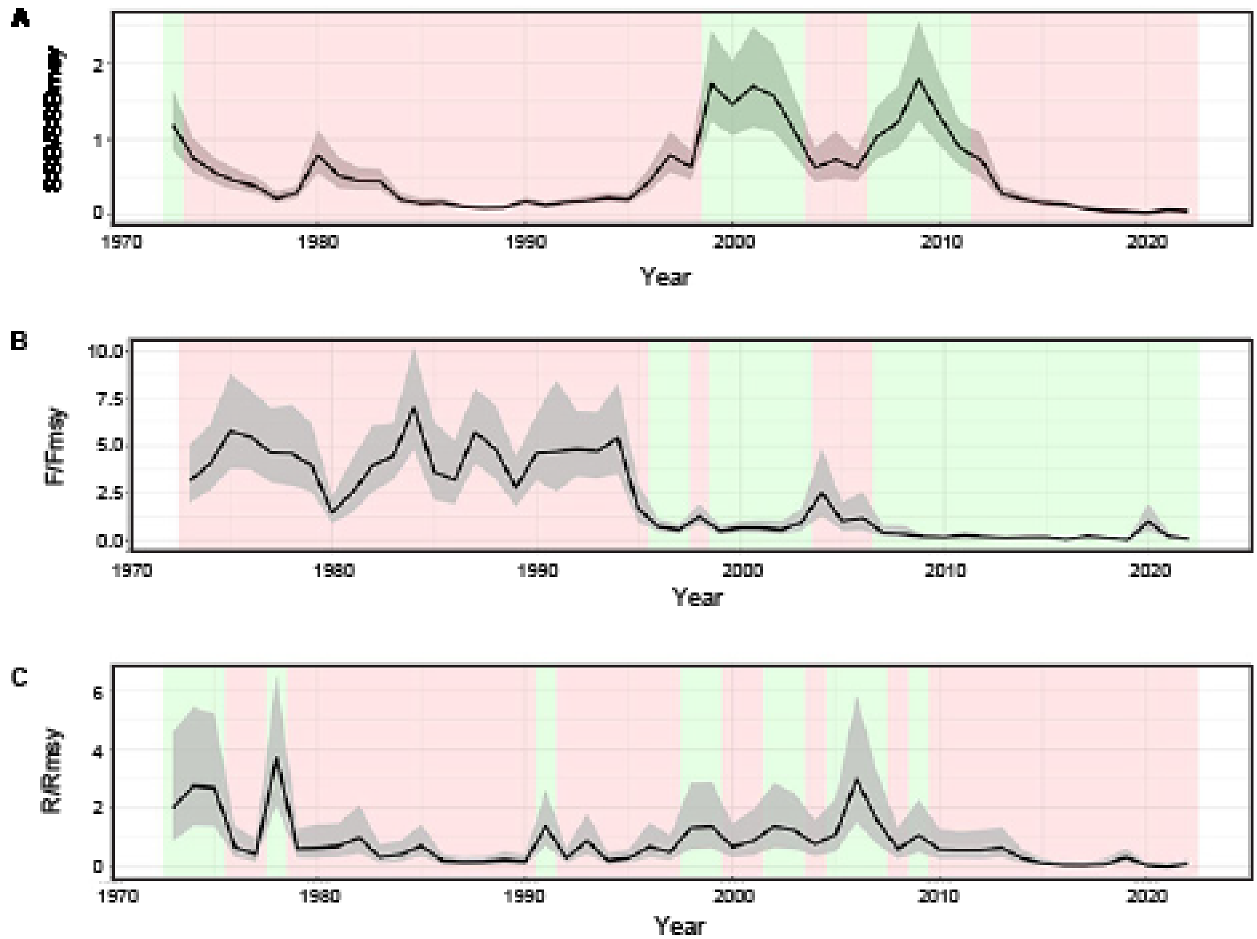

Fig. 9. Spawning stock biomass, recruitment and fishing mortality trends relative to reference points for Georges Bank yellowtail flounder. Shaded grey areas are the 90% confidence intervals. Red areas highlight times where R and SSB are below the reference point and F is above the reference point, while green highlight the opposite. Annual maximum sustainable yield reference points are used to determine status.

in the future. The rate and extent of increase will be based on biology, fishing mortality and bottom temperature. Based on the current assessment, colder bottom temperatures will allow the stock to increase faster and support larger stock sizes. More work is needed on how to treat bottom water temperature in the projection period. Especially since short term projections are often used to inform fisheries management. For example, it is probably not appropriate to assume the most recent conditions (2009–2022) will hold in the future. Additionally, the autocorrelated temperature projection allows the first several years in the projection period to be correlated with terminal year estimates of bottom temperature. This might be appropriate for short-term projections, but over the long-term bottom temperature reverts back to the mean of the entire time series. For long term predictions, neither approach is realistic given the dynamic nature of Georges Bank and predictions of future ocean conditions (Wallace *et al.,* 2018; Cheng *et al.,* 2022). WHAM can fit to future estimates of a covariate in the projection period, but this information is not available for the bottom temperature time series used in the assessment (Du Pontavice *et al.,* 2023). Thus, future work should explore using climate projections in the stock assessment projection period.

Several take home lessons can be learned from the collapses of the Georges Bank yellowtail fishery. Lesson 1: Overfishing can drive a fishery collapse but international collaboration and strong management can drive a recovery. This is observed by the fishery collapse in 1994 being driven by overfishing and the subsequent international collaborations on stock assessment (*e.g.*, TRAC) and strong fishery management measures (*e.g.*, days at sea, changes in mesh size) rebuilding the stock in the early 2000s. Lesson 2: Changing environment conditions can override effective management. Despite continued international collaboration and effective management still being in place the stock collapsed again in 2010. A review of the most recent stock assessment suggests that the second collapse was due to warming water temperatures. Lesson 3: The importance of exploring environmental data in stock assessment. Advances in stock assessment modeling (*e.g.*, WHAM) allowed for the direct incorporation of environmental

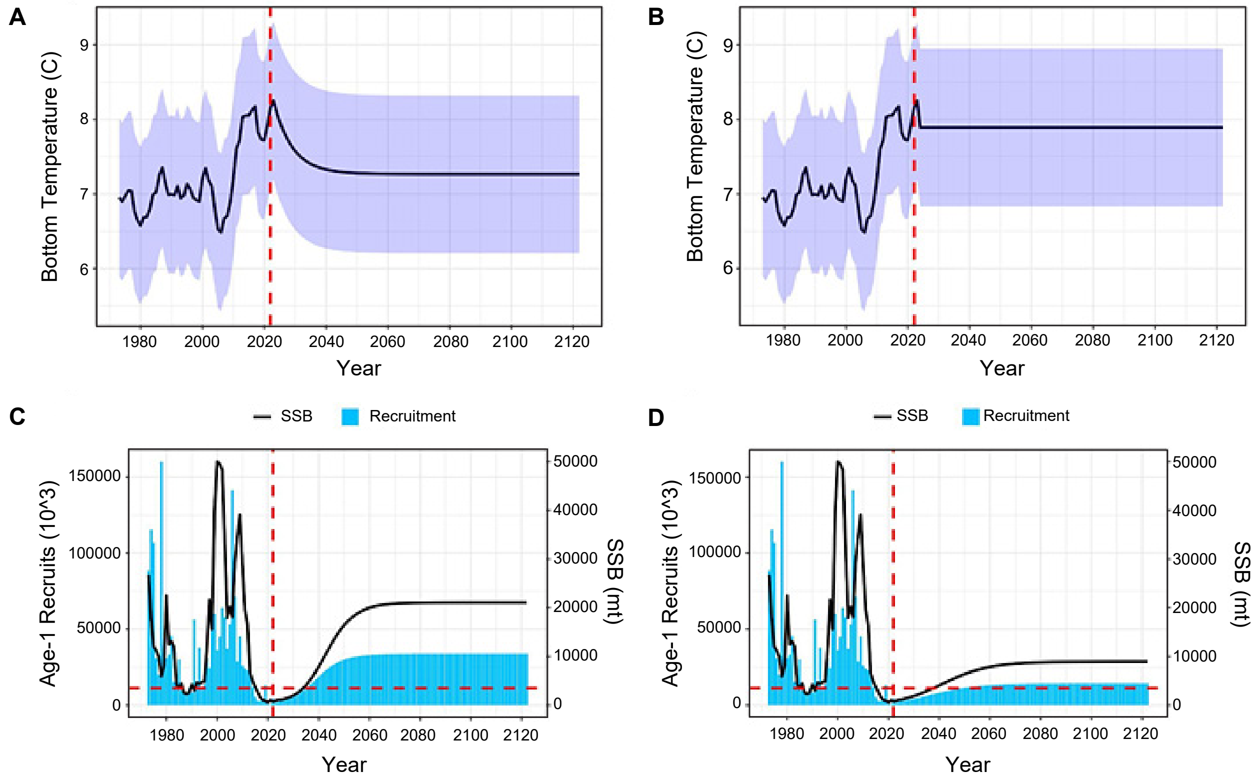

Fig. 10. Long-term projections (100 year) of the Georges Bank stock assuming an AR1 process on bottom temperature (**A, C**) and current conditions (**B, D**; mean: 2009:2022). The vertical dashed red line is the final year of the assessment, while the horizontal dashed red line is the current SSB_{msy} reference point.

variables to determine mechanistic links of the different collapses. Being able to include environmental variables directly into the stock assessment makes it easier to communicate results to stakeholders and managers. Thus, we recommend other stock assessments explore environmental drivers on population dynamic processes. Lesson 4: Stock recovery can still occur under current environmental conditions but the stock will not be able to support historic levels of fishing. Scientists and managers need to adapt expectations (*e.g.*, biological reference points) to account for these changes. Ultimately, the collapses of Georges Bank yellowtail flounder serve as a valuable case study, highlighting that fishery collapses can be caused by different factors and the importance of understanding the impact of fishing as well as a changing environment.

Acknowledgements

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Statistical Bulletin - *Available FREE online at https://www.nafo.int/Library/Science-Council/Statistical-Bulletin*

Complete statistical data have been published in the Statistical Bulletin since 1951. The printed version of the statistics were discontinued after Vol. 49 - 1999. The electronic **STATLANT 21B** database is updated regularly as new information becomes available.

Information for Preparing Manuscripts for NAFO Scientific Publications

Journal of Northwest Atlantic Fishery Science
The *Journal of Northwest Atlantic Fishery Science* is a journal containing peer-reviewed publications which focus on **environmental, biological, economic and social science aspects** of living marine resources and ecosystems of the northwest Atlantic Ocean. **Inter-disciplinary** fishery-related papers and contributions of **general applicability to fisheries science** are also published.

NAFO Scientific Council Studies
The following instructions apply to manuscripts submitted for publication in the *Journal* and the *Scientific Council Studies* series. Papers published in the *Studies* series are not peer-reviewed. Rather, the *Studies* series includes papers which are of interest and importance to the current and future activities of the Scientific Council, but which do not meet the high standards required by the *Journal*. Such papers have usually been presented as research documents at Scientific Council meetings and nominated for publication by the Scientific Council's Standing Committee on Publications.

Instructions
All manuscripts should be submitted in English (British spelling) as a Word document (**Times New Roman 10 point font**) that is double-spaced with page and line numbering throughout. Referees are not asked to conduct English language editing so please have your manuscript reviewed for such, if necessary, prior to submittal. Manuscripts should not exceed 20 pages (double-spaced), not including tables and figures. Measurements should be specified in metric units and SI unit rules and styles conventions should be used for units and abbreviations. Please use the day-month-year format for dates.

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Abstract: The Abstract should be an informative, concise summary of the manuscript but should not exceed 300 words in length.

Keywords: The Keywords section should include four to five keywords, listed alphabetically, that are useful search terms for the article.

The text should be sequentially organized into the following sections: Introduction, Materials and Methods, Results, Discussion, and Acknowledgments. Authors should be guided by the organization of papers that have been published in the NAFO Journal or Studies.

1. **Introduction:** The Introduction section should include the purpose and rationale of the study and any background information necessary for the reader to understand the study topic. Text citations should list references by date rather than alphabetically.

2. **Materials and Methods:** The Materials and Methods section should describe in sufficient detail the methods used, so as to enable other scientists to evaluate or replicate the work.

3. **Results:** The Results section should answer the questions evolving from the purpose of the study in a comprehensive manner in an orderly and coherent sequence, with supporting tables and figures.

4. **Discussion:** The Discussion section should explain the main contributions from the study, with appropriate interpretation of the results focusing on the problem or hypothesis. Comparisons with other studies should be included here.

5. **Acknowledgements:** The Acknowledgements section should be limited to the names of individuals who provided significant scientific and technical support, including reviews, during the preparation of the manuscript, and the names of agencies which provided financial support.

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Journal:
Pares, P., and Britain, B. 1965. Predator–prey behaviour of herring (*Clupea harengus albertus*). *International Journal of Applied Biology*, 24: 132–135.

Book:
Havfrue, D. L. 1990. Ecological implications of genetic mutation. *In* F. Ray, and O. Lith (Eds.), *Studies in Parthenogenesis*, 2nd ed., pp. 282–289. Thalassa Press, London.

Meeting document:
Ávila de Melo, A. M., D. Power and R. Alpoim. MS 2005. An assessment of the status of the redfish in NAFO Division 3LN, *NAFO SCR Doc*., No. 52, Serial No. 5138, 19 p.

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Articles may include supplementary materials and are displayed as is in a separate document next to the main article, in a PDF format.

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All tables and figures must be cited in the text and numbered consecutively within the text. Figure captions should be included, double-spaced, on a separate page. Each table and figure should have a concise descriptive caption. Figures should be submitted in black and white. Colour figures and photographs are acceptable only if colour is essential to the content. **Each table and figure should be submitted separately or as zipped files. See table for guidance. We prefer .wmf, .emf, .ps, .eps files for vector figures. Raster images such as photos, pictures, maps can be in .jpeg, .png, .tiff formats and should be 300 ppi (high resolution).**

Format	Driver	Notes
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PNG	png	Portable Network Graphic; used for screens only; doesn't resize
TIFF	tif	Tagged Image File Format; can be used for print; raster image; doesn’t resize
SVG	svg	Scalable Vector Graphic; easily resizable; can be used for vectors; web only
AI	.ai	Adobe Illustrator; easily resizable; can be used for vectors
EPS	.eps	Encapsulated Postscript; easily resizable; can be used for vectors
EMF	.emf	Enhanced Windows Metafile; best choice with Word; easily resizable; can be used for vectors
WMF	win.metafile	Windows Metafile Format only; best choice with Word; easily resizable; can be used for vectors
PDF	pdf	Portable Document File; best choice with pdflatex; easily resizable; can be used for vectors
PS	postscript	Best choice with latex and Open Office; easily resizable; can be used for vectors

Green highlight – raster format; blue highlight – vector format

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