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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.

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Editorial Board

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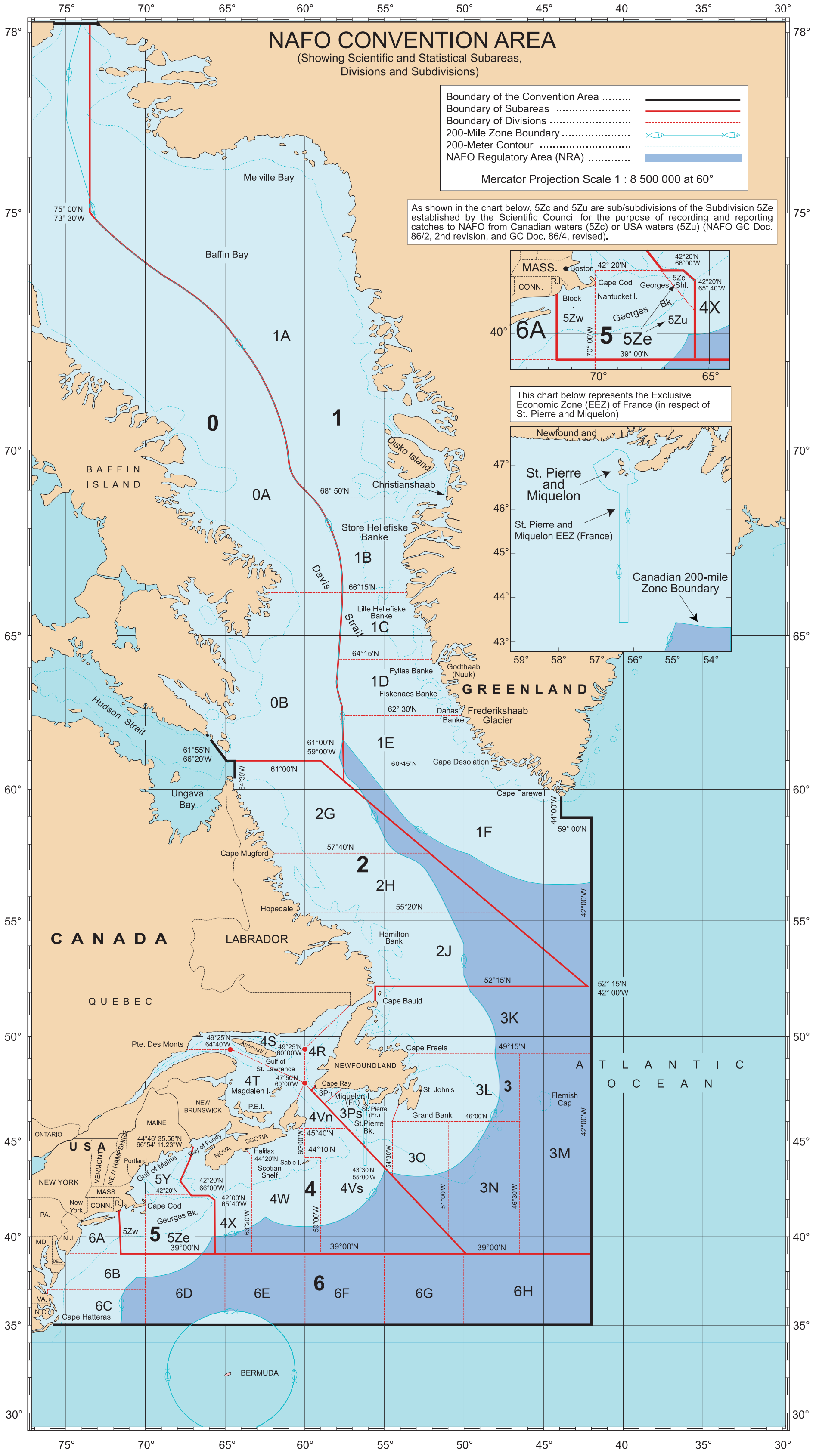

As shown in the chart below, 5Zc and 5Zu are sub/subdivisions of the Subdivision 5Ze established by the Scientific Council for the purpose of recording and reporting catches to NAFO from Canadian waters (5Zc) or USA waters (5Zu) (NAFO GC Doc. 86/2, 2nd revision, and GC Doc. 86/4, revised).

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

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How the collection of fish length data using electronic monitoring video review measures up to current methods used on a fishery-independent survey

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Abstract

Electronic monitoring (EM) systems are tools that can generate fisheries survey data when at-sea challenges such as on-deck logistics, workload capacity, or deployment interruptions prevent staff from fulfilling their duties. We sought to validate EM's specific utility in collecting fish lengths at a comparable resolution to those collected at sea during a fishery-independent survey, the Gulf of Maine Bottom Longline Survey. We also examined whether measurement accuracy was influenced by tail morphology and length type (fork, total, and stretched total) by selecting individuals from six anatomically variable species. Individuals were measured twice: Survey-based length measurements, L_S, were recorded using an electronic measuring board and EM-based length measurements, L_E, were visually estimated using a color-coded EM measuring strip during video review. Paired Wilcoxon signed rank tests determined significant differences between the L_S and L_E distributions for all species overall, and for individual species Atlantic cod, cusk, haddock, and spiny dogfish but not thorny skate or white hake. Kolmogorov-Smirnov tests detected no difference between the distributions of L_S and L_E, overall and for each species. Examination of the differences between L_S and L_E for every individual, L_D, indicated that the EM-based method slightly over-estimated lengths (μ = 0.89 mm). Linear regression indicated that the effect of extreme small or great lengths on absolute L_D was present only for Atlantic cod where L_D increased as fish length decreased. Pairwise comparisons of L_D among fish length types indicated that fork and stretched total length measurements were overestimated by the EM-based method (μ = 2.39 mm, 3.09 mm, respectively) and this was significantly more than total length (μ = 0.04 mm). We demonstrated that collection of fish lengths using video review could be an adequate substitution for collecting lengths by hand, though it is at the discretion of the end users to determine whether these length differences exceed the acceptable range. These results have particular applications to small scale survey operations, research, and the fishery-dependent sector.

Keywords: fisheries management, Gulf of Maine, fish morphology, subsample analyses

Introduction

Over the last two decades, electronic monitoring (EM) systems have been increasingly implemented in worldwide fishery-dependent data collection and fisheries management (van Helmond *et al.*, 2020). These systems tend to consist of a central control unit, GPS, mechanical sensors, and video cameras that record footage of fishing activity (McElderry, 2008). The resulting video can be reviewed to collect fishery-dependent data, supplementing or replacing on-board observers. EM systems may be preferable to on-board observers when a vessel's size or configuration is not suited to host an additional person, when there is a need for simultaneous viewing of multiple angles of activity, or when observation periods extend beyond reasonable human capabilities. EM systems are also deployed to validate fishing location and duration, identify protected species interactions, and document regulatory compliance.

Fishery-independent surveys present a unique platform for experimental testing, but challenges around increased staff workload or staff deployment exist. Camera systems can solve these problems by generating a means of post-survey data collection, and they have been successfully deployed alongside traditional fisheries survey gear (Starr *et al.,* 2016; Williams *et al.,* 2016; Stokesbury *et al.,* 2017; Miller *et al.,* 2019; Lee *et al.,* 2022; Nelson *et al.,* 2024). The crossover applications between survey and industry-based operations include exploration of technological limits, validation of new applications, and compilation of annotated video or photographic data for advanced machine learning and automated video processing.

The Gulf of Maine Bottom Longline Survey (BLLS) is a twice yearly, cooperative groundfish survey conducted on contracted commercial fishing vessels by the U.S. Northeast Fisheries Science Center (NEFSC). Beginning in 2020, camera systems were deployed on the vessels to test their potential utility in survey research activities (Nelson *et al.,* 2024). The present study seeks to validate the use of EM as a method for collecting fish lengths that are comparable to lengths collected via more traditional methods used on fisheries-independent surveys. Similar validation studies have been conducted in the Taiwanese longline albacore tuna fishery (Chang *et al.,* 2010), Welsh lobster and brown crab fisheries (Hold *et al.,* 2015), the Pacific halibut longline fishery (Wallace *et al.,* 2015), and Solomon Islands longline fisheries (Hosken *et al.,* 2016). Here, lengths were recorded twice from individuals of six anatomically variable groundfish species according to their specified measuring methods: the first measurement using at-sea data collection protocols and the second using EM protocols. The resulting measurement distributions were compared and the calculated differences between each measurement method were further examined.

Materials and Methods

Fish Measurement Data Collection

Field surveys were conducted in accordance with survey protocols (McElroy *et al.,* 2019) on the contracted partner vessel F/V *Mary Elizabeth*. The vessel crew members were responsible for setting and retrieving the longline gear and the NEFSC survey staff collected catch and biological information. The AI Hub and SnapIT camera system were provided and installed by the electronic monitoring service provider Teem Fish Monitoring[1] of Prince Rupert, British Columbia, Canada. A camera with 720p high definition resolution (1920x1080) and a frame rate of 30 frames per second was mounted underneath the deck overhang and aimed directly down and over the processing table. Video of catch processing was continuously recorded onto a hard drive throughout each trip. Following completion of the survey, video was processed, uploaded to cloud storage, and viewed using the proprietary software provided by Teem Fish Monitoring.

Fish length data collected during the survey, hereby referred to as L_S, were recorded to the nearest millimetre with the Ichthystick II Electronic Fish Measuring Board (Price *et al.,* 2015). The board consists of an electronic measuring stick with visible tick marks housed in a rectangular plastic case and backstop at the 0 centimetre mark (Fig. 1). When calibrated properly, the accuracy of the Ichthystick II is ±0.1 centimetres with a slight negative bias. Fish were laid on the measuring board as flat as possible with the snout against the backstop. Measurements were taken by tapping a magnetic wand onto the plastic housing at the desired measurement location. Measurements were automatically saved into a tablet-based data collection application. Lengths collected using EM protocols, hereby referred to as L_E, were collected using a color-coded EM measuring strip overlaid on the electronic measuring board, also provided by Teem Fish Monitoring. Post-survey video review and collection of L_E was conducted by a NEFSC staff member. When a candidate fish was held steady on the measuring board, the video was paused and fish lengths were visually determined by the reviewer using the EM measuring strip markings, consistent with the NEFSC Northeast Fisheries Monitoring Operations Branch guidance (Pers. Comm. Corinne Endres). To reduce bias, the moment in the video when L_E was collected may not have been the exact moment when L_S was collected. The design of this length strip consisted of colored markings in 1-centimetre increments (Fig. 1). The length of 0.01–1.00 centimetres

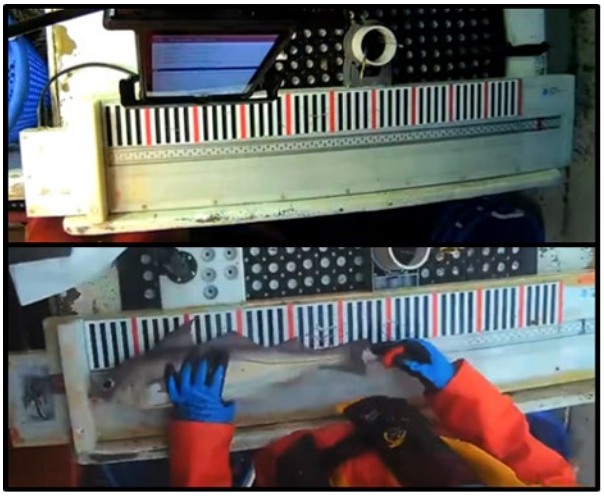

Fig. 1. Top: Electronic monitoring camera view of the catch processing area, including electronic measuring board with backstop, tablet, and the electronic monitoring length strip. Bottom: a haddock laid on the measuring board prior to recording the length using the magnetic wand. The EM reviewer would record this individual's fork length as 54 centimetres (note: this individual is not part of the dataset).

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[1] Reference to any specific commercial product, process, or service, or the use of any trade, firm or corporation name is for descriptive purposes only, and does not constitute endorsement, recommendation, or favoring by NOAA Fisheries.

was recorded as 1 centimetre, 1.01–2.00 centimetres was recorded as 2 centimetres, etc.; therefore, fish lengths were recorded as whole centimetres. Marking color aided in quick assessment of length: white markings were odd values, black markings were even values, and red markings were every 10 centimetres. Records of L_S and L_E as well as station data were merged into one dataset in R Studio version 1.4.1106 (R Core Team 2021, RStudio Team 2021). L_E were converted from centimetres to millimetres for direct comparison to L_S and reduced by 5 mm. This reduction shifts L_E records around the center of each 1 cm marking and conforms to traditional rounding convention. For example, a fish that fell on a black bar between 41.01 and 42.00 cm was initially recorded as 42 cm, then converted to 420 mm and reduced to 415 mm. L_S are the reference measurements and were not adjusted in any way.

We also examined whether morphology and length type impacted the accuracy between L_S and L_E. To do this, we selected the following six fish species with diverse tail morphologies that are also well represented in the BLLS: Atlantic cod (*Gadus morhua*), cusk (*Brosme brosme*), spiny dogfish (*Squalus acanthias*), haddock (*Melanogrammus aeglefinus*), white hake (*Urophycis tenuis*), and thorny skate (*Amblyraja radiata*). The length type used for each species is based on the NEFSC bottom trawl survey's protocols. Total length, recorded as the measurement from tip of the snout to the tip of the tail, was recorded for species with rounded tails (Atlantic cod, cusk, and white hake) or pointed tails (thorny skates). Fork length, recorded as the measurement from tip of the snout to the deepest part of the tail fork, was recorded for the only species with a slightly concave tail (haddock). Finally, stretched total length, recorded as the measurement from tip of the snout to tip of the upper tail lobe when the tail was stretched down and in line with the body midline, was recorded for the only species with a forked tail with asymmetric lobes (spiny dogfish).

Identifying subset of stations and individuals

The dataset included individuals from three sampling periods: spring (April–May) 2021 and 2022, and autumn (October–November) 2021. L_S was recorded for all catch encountered on the survey, but recording a census L_E from all individuals of the chosen species would have been very time consuming. Therefore, for the purposes of this study and for each species, a representative subsample of individuals from the BLLS population was identified. We estimated the target subsample size for each species using two methods. First, the R package "samplingbook" version 1.2.4 (Manitz *et al.,* 2021) was used to estimate subsample sizes with the same mean length ±5%, standard deviation, and a 95% confidence interval as the BLLS population. Second, Kolmogorov-Smirnov (K-S) tests determined the minimum subsample size needed to produce a similar distribution to the BLLS population (Marsaglia *et al.,* 2003). To determine the appropriate sample size, a simulation of fish length resampling without replacement from the BLLS population was conducted for subsample sizes from 10 to 100 by intervals of 10 and a K-S test was conducted on each subsample by calling the *ks.test* command from the package "stats" version 4.2.2. This process was repeated for 1,000 iterations and the resulting plots of K-S test p-values were used to visually determine a target subsample size (Supplementary Material S1). The smallest subsample size per species in which the p-values of all 1,000 iterations was above 0.05 was selected as the minimum subsample size. The plots for the three most abundant species (cusk, spiny dogfish, and haddock) did not indicate any differentiation among subsample sizes, so sample sizes of 50 were arbitrarily selected for the K-S method. The greater of the two subsample estimation methods was selected as a minimum subsample size target for each species (Atlantic cod = 72, cusk = 50, haddock = 50, spiny dogfish = 50, thorny skate = 87, and white hake = 50; Supplementary Material S2).

Next, we identified a subset of candidate stations from which to measure all available individuals of the interest species. From the initial 69 stations across the three survey cruises, only 64 of those had length data available at the time of the data pull. We eliminated four stations where the video was available (*i.e.* not missing due to power failure or system malfunction), 4 stations where the length strip was missing from the measuring board, and one station where the length strip was improperly placed. For each distinct species, the remaining 55 candidate stations were further reduced according to species specific length thresholds in order to avoid cluster sampling of the most common lengths. Each available station must have at least one representative below the lower length threshold or above the higher length threshold (Supplementary Material S2, S3). The thresholds for Atlantic cod, cusk, spiny dogfish, and white hake were the median length ±50%, while the threshold for thorny skate was the median length ±20%, due to its non-normal length distribution. The stations were finally narrowed according to a minimum and/or maximum number of individuals measured at that station. These limits were different for each species and dependent on whether the species was typically caught as schools or as incidental individuals. Prioritizing stations with the greatest number of individuals increased our data collection efficiency. The resulting candidate stations were visually assessed and selected such that the full length-range of each species was represented and the minimum subsample size was achieved.

Analysis

Analyses comparing the L_S and L_E distributions were conducted for all species combined and each species separately. The first comparison was the Wilcoxon signed rank test, a non-parametric test of equal means between paired samples which does not assume equal variance, by calling the *wilcox.test* command and specifying *paired* = *T* from the R package "stats" version 4.2.2 (Wilcoxon, 1945; Bauer, 1972). The second comparison were K-S tests as described previously. Mathematical differences between the survey and EM data collection methods, hereby referred to as L_D, were calculated for each individual where $L_D = L_E - L_S$. This value evaluates whether the EM method over- or under-estimated length measurements (positive or negative L_D values, respectively). Records with L_D >±10 millimetres were reevaluated in video review, taking care

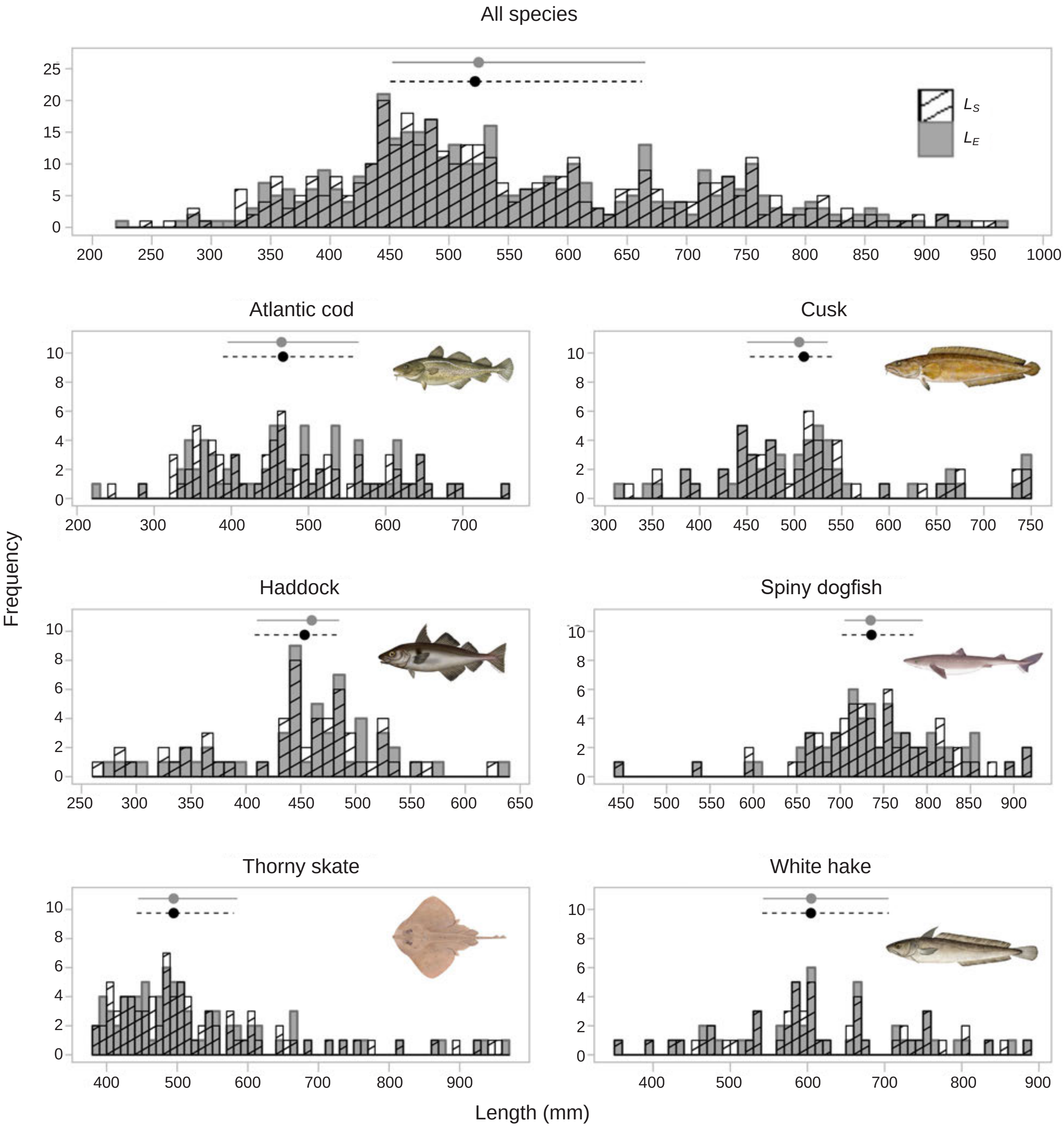

Fig. 2. Frequency distribution of length measurements, binned at 10 mm for clarity, collected from the survey Ichthystick II fish boards (L_S: black striped fill) or from electronic monitoring video review (L_E: solid gray). Above the histograms, the filled circle and line segments represent the median length and inter-quartile ranges of each distribution (L_S: black dashed line, L_E: solid gray line). Frequencies are displayed for all species combined (top) and for each species individually. Fish images downloaded from the ©NOAA fisheries website (fisheries.noaa.gov/species), thorny skate illustration by Lindsay Gutteridge, downloaded from the Florida Museum (floridamuseum.ufl.edu/science/thorny-skates/).

to note circumstances surrounding their measurement and possible sources of error such as measuring incorrect individuals, fish handling, fish condition, EM measuring strip position, and view obstructions. From these records, there were two instances where the EM measuring strip had shifted away from the measuring board backstop, creating offsets of 10 and 40 millimetres. The L_E for these records were corrected by adding the number of millimetres associated with the specific offset. An additional test to determine whether absolute L_D values correlated with fish length or whether any species was prone to increased L_D was conducted by calling the *lm* command from the R package "stats" version 4.2.2, where absolute L_D was predicted as a function of L_S. Finally, comparisons of mean L_D among length types (fork, total, stretched total) were made using t-tests.

Results

A total of 388 fish were included in the dataset. For each species, the number of individuals (*n*), the length range, and mean length (μ) were as follows: Atlantic cod (n = 74, 246–759 mm, μ = 480.28 mm), cusk (n = 55, 321–746 mm, μ = 514.26 mm), haddock (n = 56, 269–628 mm, μ = 444.04 mm), spiny dogfish (n = 65, 443–919 mm, μ = 739.75 mm), thorny skate (n = 84, 382–959 mm, μ = 537.39 mm), and white hake (n = 54, 356 –888 mm, μ = 618.50 mm). For all species collectively, differences between the L_S and L_E distributions were detected by the paired Wilcoxon test (μ = 554.94 mm and 560.82 mm, respectively; $p < 0.001$) but not the K-S test (Fig. 2, Table 1). When comparing L_S and L_E for each species, the paired Wilcoxon test detected differences for Atlantic cod, cusk, haddock, and spiny dogfish ($p < 0.001$) but again, the K-S tests did not detect any statistical differences between the distributions.

The mean L_D values provided evidence for length over-estimation by the EM measurement method for Atlantic cod, haddock, and spiny dogfish, and evidence for under-estimation for cusk, thorny skate, and white hake (Fig. 3, Table 1). Regardless of the direction, these values

Table 1. Summary of statistical tests between length measurement distributions collected from the survey (L_S) and electronic monitoring video review (L_E). Rows indicate all species combined and individually; n = number of measured individuals; Wilcoxon signed rank test statistics where V = test value, bold if $p \leq 0.05$; Kolmogorov-Smirnov (K-S) test statistics, where D = test statistic; Summary of the mathematical differences between L_S and L_E (L_D), where min = minimum, μ = mean, max = maximum, and SD = standard deviation; Linear Reg. = Linear regression testing absolute value of L_D as a response to L_S, where β = slope coefficient, bold if $p \leq 0.05$).

Species	***n***	**Wilcoxon-test**	**K-S test**	**L_D (mm)**				**Linear Reg.**
				min	μ	max	SD	
All Species	388	**$V = 39063$** **$p < 0.001$**	$D = 0.039$ $p = 0.934$	-24	0.89	25	5.90	β = 0.0003 $p = 0.814$
Atlantic cod	74	**$V = 1995$** **$p < 0.001$**	$D = 0.068$ $p = 0.993$	-21	2.28	20	5.79	**β = -0.013** **$p = 0.003$**
Cusk	55	**$V = 259$** **$p < 0.001$**	$D = 0.073$ $p = 0.997$	-10	-1.98	13	4.37	β = 0.004 $p = 0.297$
Haddock	56	**$V = 1159$** **$p < 0.001$**	$D = 0.125$ $p = 0.736$	-19	2.39	12	4.91	β = 0.005 $p = 0.442$
Spiny dogfish	65	**$V = 1656$** **$p < 0.001$**	$D = 0.077$ $p = 0.987$	-17	3.09	20	5.69	β = 0.011 $p = 0.113$
Thorny skate	84	$V = 1391$ $p = 0.356$	$D = 0.060$ $p = 0.999$	-24	-0.49	25	7.48	β = 0.004 $p = 0.371$
White hake	54	$V = 492$ $p = 0.776$	$D = 0.056$ $p = 1.000$	-8	-0.17	8	3.55	β = 0.003 $p = 0.276$

were very small (-1.98–3.09 mm, overall $\mu = 0.89$ mm). White hake had the lowest L_D range and standard deviation (-8–8 mm, 3.55 mm, respectively) and thorny skate had the greatest L_D range and standard deviation (-24–25 mm, 7.48 mm, respectively), the latter indicated both a greater frequency and magnitude of non-zero L_D. Linear regression did not detect a significant relationship between L_S and absolute value of L_D for all fish collectively, meaning that in general, individuals of extreme small or large lengths are not prone to increased absolute value of L_D. Of the individual species, only Atlantic cod exhibited a significant trend, where absolute value L_D was highest at small lengths and decreases with increasing fish length ($\beta = -0.013$, $p = 0.003$).

Among the three length types, total length had near-zero mean L_D and the highest standard deviation (Fig. 4, Table 2). Fork length and stretched total length had comparatively

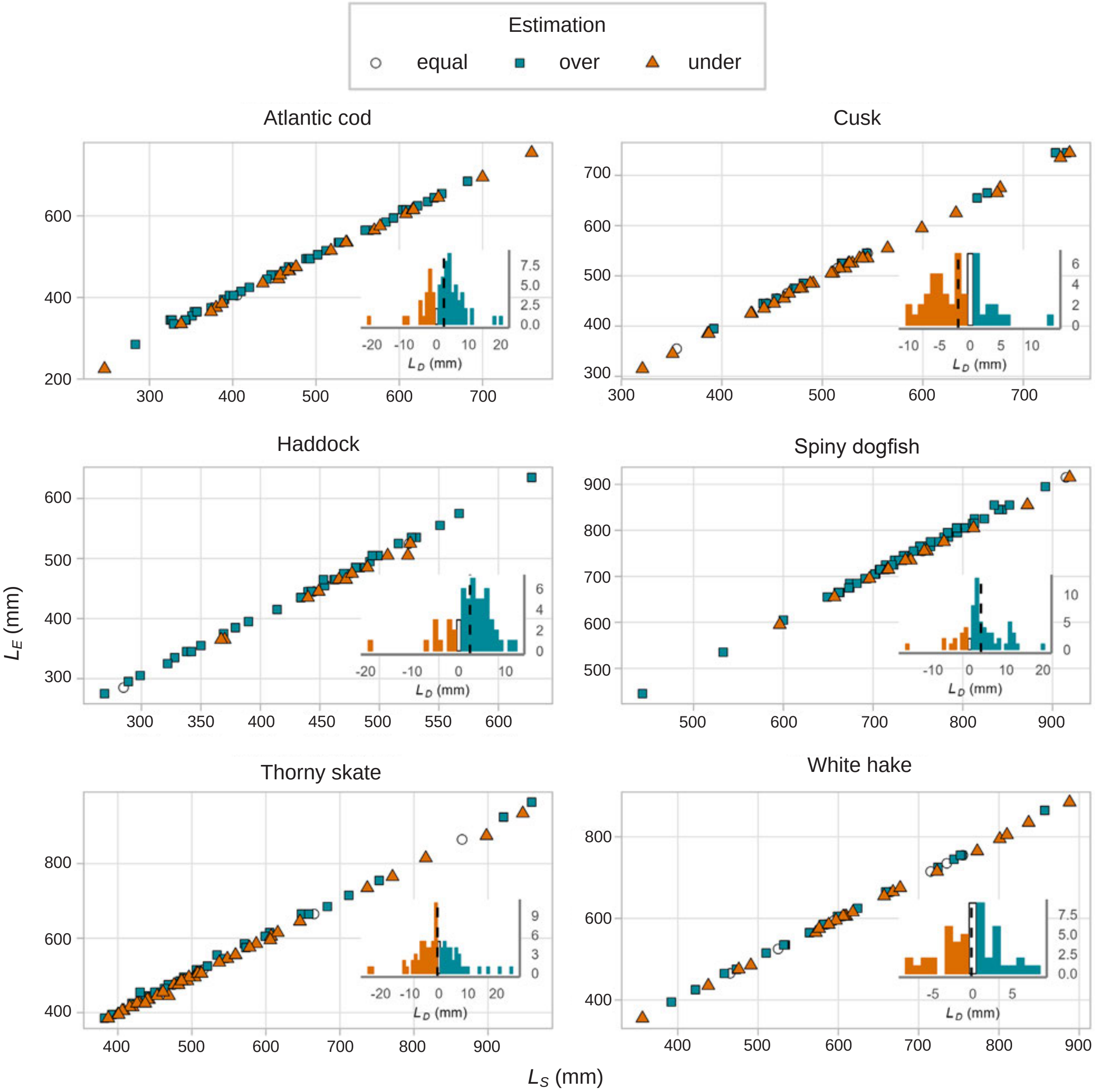

Fig. 3. Dot plot of the length measurements collected from the survey Ichthystick II fish boards (L_S) versus the electronic monitoring video review (L_E) for each individual. Colours and shapes indicate when L_E was over estimated (teal squares), under estimated (orange triangles), or equally estimated (white circles) relative to L_S. Inset plots illustrate frequency of L_D values with corresponding over, under, and equally estimated colors, and mean L_D value (dashed line).

Table 2. Summary statistics of the differences between length measurements collected from the survey and electronic monitoring video review (L_D) among the three length types: n = number of individuals; min = minimum, μ = mean, max = maximum, SD = standard deviation. The pairwise t-test t-statistics are below the diagonal, p-values are above diagonal, bold if $p \leq 0.05$.

Length Type	***n***	**L_D (mm)**				**Pairwise T-test**		
		min	μ	max	SD	Fork	Stretched Total	Total
Fork	56	-19	2.39	12	4.91	-	0.469	**0.002**
Stretched Total	65	-17	3.09	20	5.69	-0.726	-	**< 0.001**
Total	267	-24	0.04	25	5.95	**3.139**	**3.846**	-

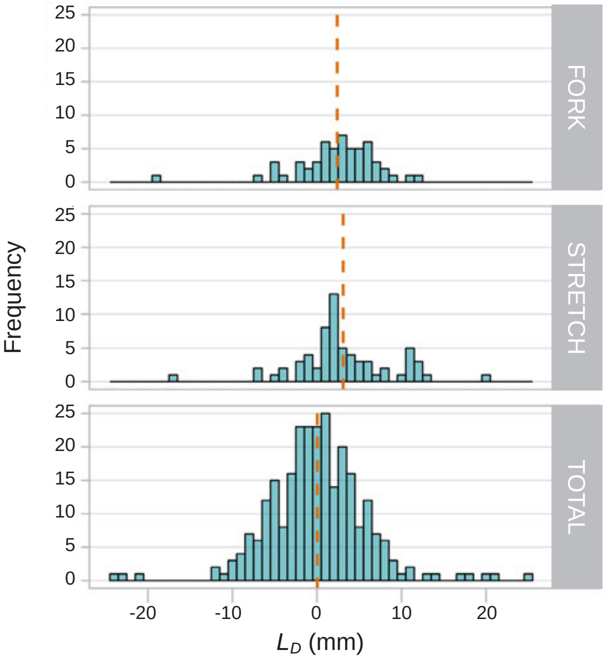

Fig. 4. Frequency plot and mean (orange dashed line) of the differences (L_D) between length measurements collected from the survey and electronic monitoring video review among the three length types.

higher mean L_D, and lower standard deviations. Pairwise comparisons indicated that the differences in mean L_D were significantly different between total and both fork and stretched total length ($p = 0.002$, $p < 0.001$, respectively) and that there was no difference between the mean L_D of the latter two ($p = 0.469$). Because both fork and stretched total length were comprised of a single species and total length was comprised of four species the resulting uneven sample sizes among the measurement methods may have introduced bias in the calculations.

Discussion

This study successfully demonstrated that EM systems and associated video analysis can be used as a tool to collect fish lengths at an accuracy comparable to the lengths collected by fishery-independent longline survey staff. Depending on the test used, the distributions of L_S and L_E may be statistically different from each other. Disparities were most evident when examining L_D, the mathematical differences between L_S and L_{E}. The EM method over-estimated lengths for half of our species and under-estimated for the other half. Although some of these distributions were statistically different, the effect on downstream BLLS data end users would be minimal in practice. However, this may not be the case for other data collectors and users, and the precision of the data should be considered in the context of individual programs.

The primary source of non-zero L_D stems from the study design itself. Comparing measurements from two units of measure (centimetres vs millimetres) inherently loses precision and the chances that the reading of one 1-cm mark matches the reading from the 1-mm unit board is not common. A second source of non-zero L_D stemmed from fish handling and positioning on the EM measuring strip. Despite best efforts to lay fish flat, lively individuals defensively and evasively curled or twisted themselves. A change in the position or configuration of an individual between the times when lengths were recorded on the BLLS and recorded from the video could have affected measurement accuracy. For example, second review of the video for the greatest L_D record for Atlantic cod (-21 mm) revealed that the fish curled its tail upward, towards the camera, though at first glance, it appeared to be resting flat. To mitigate this source of increased L_D, the EM reviewer must not rush data collection and ensure the fish is truly laid flat. A third source of non-zero L_D was the improper alignment of the EM measuring strip on top of the electronic measuring board and against the backstop. This occurred for two records of thorny skate, as noted prior. In the event the EM measuring strip becomes offset for an entire haul or basket of fish, a batch of consistently negative L_D would be evident and should be regularly checked for in data quality procedures. To mediate improper alignment between the EM measuring strip and the backstop we recommend using a fixed or permanently integrated EM measuring strip.

It is important that studies using EM should consider two potential sources of non-zero L_D that were not directly observed here. The first is the distortion of the measuring strip at the edges of the camera view. In the current study, the camera was centered over the measuring board backstop and the lower range of measurement values. As the EM measuring strip extended away from the center of the camera view, the 1-centimetre wide markings narrowed, and this distortion presents an opportunity to introduce uncertainty. To minimize this, efforts should be made to center the camera over the EM measuring strip and install the camera at a distance from the EM measuring strip that would reduce image distortion. A second source of potential L_D may be in the accuracy of the measurement tools. The level of error for the Ichthystick II boards is low (±0.1 cm) and well within the nearest whole or half centimetre data standards required by most of the U.S. Northeast region stock assessments (Grosslein, 1969;Wigley *et al.*, 2003; Price *et al.,* 2015). The standard deviations of L_D reported here also fall within the whole centimetre data standard, which support the idea that lengths collected by EM systems could be a valid component of stock assessments. The design of the particular EM measuring strip is also important to note. Providers of EM systems supply their own independently designed measuring strips for regulatory compliance. The measuring strip and subsequent initial measuring method in this study did not conform to traditional rounding standards, thus necessitated shifting L_E by 5 mm. Proper rounding is a critical component to estimating abundance of year classes or when dealing with harvest size limits. The accuracy of EM-collected lengths using alternative EM measuring strip designs should be tested for by conducting studies in a similar manner to the present one.

We detected differences in measurement accuracy among fish length types. Morphological diversity prevents a single length type from being used for all species, but standardized measures based on shared morphology are commonly used (Francis, 2006). These standardized measures can be of varying reproducibility success and therefore potentially introduce variability into L_D. For example, a study of three freshwater species found lower mean and standard deviation for fork length and total length compared to “standard length”, a length type that has a history of inconsistent definition, for three freshwater fish species (Carlander and Smith Jr., 1945). Furthermore, fork length may be more easily reproducible than standard length or total length, though the difference in accuracy is marginal (Kahn *et al.*, 2004). Although the handling of fish while collecting fork length and total length in the BLLS are similar (*i.e.* no manipulation of tail placement), the distributions of L_D were statistically different between them. The greater variance seen in total length in this study may be driven by the data from thorny skates, which have the highest variance of all examined species. It was expected that stretched total length would have the highest variance because the extent to which the anterior tail lobe is stretched by the handler to the center of the measuring board may not be consistent. In addition, spiny dogfish are notoriously lively and their bending and flexing could create measurement inconsistencies that are independent of the stretched length methodology. The results among length types may have been further influenced by unequal sample sizes, which could be clarified by conducting the study again with equal number of fish per length type or with the inclusion of other species with slight morphological differences.

This study was performed by collecting one L_E per fish by a single video reviewer. Although between-reviewer variability is routinely assessed when estimating fish ages (Campana *et al.,* 1995; Buckmeier, 2002), few such comparisons exist for morphological measurements (Petrtýl *et al.*, 2014). Additional investigation of between-reviewer variability would provide insight into the feasibility and caveats of collecting length data using EM, expansion towards team-oriented data collection, development of data collection protocols, and conducting routine between-reader tests. Further, it is important to note that EM video reviewers should follow fish measuring protocols according to guidelines set by data users, thereby minimizing measurement variation among datasets and the time spent creating protocols or adjustment factors.

The current study demonstrated how camera system utilization can increase the volume of scientific data and expand survey operations. The camera system and length strip equipment simplify fish length measurement collection process such that proper placement and handling of the fish in front of the camera can be performed by a single person with minimal training. In addition, a durable length strip and post-survey data collection eliminates the onus of collecting or transcribing data by hand, maintaining water sensitive cables and costly tablets, and troubleshooting Bluetooth connectivity issues, as are encountered on the BLLS. These benefits are particularly applicable to small or industry vessels, where installation of EM systems or recruitment of those with existing systems can open doors for collaborative projects with government agencies and academic institutions (Sigler and Lunsford, 2009; McElroy *et al.*, 2019). Such collaborative efforts have gained support in recent years. For example, offshore wind development in the United States Northeast region will impact existing federally based surveys (Methratta *et al.*, 2023), and smaller industry based surveys are being looked to as alternatives. Similarly, the Gulf of Maine shrimp fishery participants are responding to federal funding cuts to the current sampling program by mobilizing self-funded and operated sampling efforts, part of which involves EM camera equipment (Molyneaux, 2024). The benefits of using EM to collect fish lengths is less applicable to mature, large scale fishery-independent surveys. In these survey operations, collection of fish lengths is a regular task that can account for a large proportion of catch processing (Link *et al.,* 2008) and replacing well-established, systematic methods with video-based and post-survey methods is unlikely to improve efficiency. However, EM could be a viable backup option in the event of scientific staffing shortages or increased reliance on vessel crew to collect data. There is also application of this work in the fishery-dependent sector. EM review could serve as an oversight tool where catch is sorted into market categories or product types based on fish length, such as at processing plants or on catcher-processor vessels. It could also be an effective way to collect lengths at any size range, expanding its use from discards to retained catch lengths. This last point is particularly useful as funding for port samplers or on-board observers is reduced or not keeping pace with the required cost.

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Aspects of the Population Dynamics and Biology of the Daubed Shanny (*Leptoclinus maculatus*) from the Gulf of Maine

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Abstract

The daubed shanny (*Leptoclinus maculatus*) is an Arctic-boreal fish species with a circumpolar distribution and whose southernmost extent of its range in the northwest Atlantic is the Gulf of Maine. Because life history characteristics of fishes often vary along latitudinal gradients, the daubed shanny population in the Gulf of Maine may exhibit different biological characteristics and population dynamics than the Arctic populations from which most information about the species comes. To improve our knowledge, this study was undertaken to document trends in temporal abundance, spatial abundance, and depth and temperature ranges based on historical trawl surveys, and to evaluate sex-specific differences in size, weight and age of individuals captured in the Gulf of Maine. The species was distributed throughout the western Gulf of Maine, primarily at depths from 30 to 120 m in spring and in waters ≥82 m in fall and was associated with the near-lowest temperatures available in the survey regions. Most daubed shanny were ≥8–9 cm total length in spring, but small fish (7–11 cm total length) dominated catches in fall, possibly representing pelagic post-larvae settling to the benthos. The population abundance of daubed shanny fluctuated widely since 1963 but appeared to collapse after 2009 in concert with warming temperatures and declines in *Calanus* copepod abundance in the Gulf of Maine. Female daubed shanny were larger and heavier than males, and both sexes reached a maximum age of six years. Compared to published data, daubed shanny in the Gulf of Maine has a shorter life span, grows faster and likely experiences higher natural mortality than the Svalbard, Norway, population above the Arctic circle.

Keywords: Abundance, Gulf of Maine, *Leptoclinus maculatus*, population biology

Introduction

The daubed shanny (*Leptoclinus maculatus*) is an Arctic-boreal benthic species of the family Stichaeidae that has a circum-polar Arctic distribution between latitudes 43°N and 79°N (Mecklenburg *et al*., 2011; Meyer Ottesen *et al*., 2011). In the North Atlantic, this species ranges from the Arctic south to Norway and Sweden on the eastern side, and to southern Gulf of Maine, USA, on the western side (Scott and Scott, 1988; Collette, 2002; Meyer Ottesen *et al*., 2011). Throughout its range, daubed shanny is a prey species for marine fishes (Bowman *et al*., 2000; Hovde *et al*., 2002), sea birds (Bryant *et al*., 1999; Jones *et al*., 2002; Elliot *et al*., 2008) and marine mammals (Labansen *et al*., 2007; Lesage *et al*., 2020). Species of the Stichaeidae family are considered intermediate links between zooplankton and higher trophic levels (Murzina *et al*., 2012).

Most knowledge of the life history of daubed shanny comes from studies in the Barents Sea and around Svalbard, Norway in waters north of 75°N. In those areas, the species is typically found at depths between 2 and 475 m with temperatures between -1.6 and 2.0°C (Andriyashev, 1954; Byrkjedal and Høines, 2007). Daubed shanny reaches a maximum of about 200 mm total length (TL), but most individuals are <170 mm or so (Andriyashev, 1954). Females and males mature between 125- and 130-mm standard length at about 7 and 6 years, respectively, and males grow faster and tend to be larger than females (Meyer Ottesen *et al*., 2014). Adults spawn in the winter, probably in shallow water, and females produce few (<1000), large (0.7–1.7 mm) eggs (Murzina *et al*., 2012; Meyer Ottesen *et al*., 2014, 2018). Daubed shanny likely exhibits parental care where females guard eggs and males defend territories in soft bottom areas like other Stichaeidae (Meyer Ottesen *et al*., 2011), and has been observed residing in burrows (Meyer Ottesen *et al*., 2011). It is unknown if daubed shanny larvae have a yolk-sac stage, but the post-larvae remain in the pelagic environs feeding on *Calanus* copepods and storing lipids in a specialized sac (as a winter food source) for 2–3 years and then settle to the benthic habitat when they reach about 80 mm caudal length (Meyer Ottesen *et al*., 2011; Pekkoeva *et al*., 2023).

In the Gulf of Maine, the southernmost extent of its range, almost nothing is known about daubed shanny. Information on biology cited in Bigelow and Schoeder's *Fishes of the Gulf of Maine* (Collette, 2002) comes from studies conducted in its northern range with the exceptions of Tyler (1971) who caught daubed shanny during a community structure study in a Maine estuary, and Bowman *et al*. (2000) who listed the species as a diet item of other Gulf of Maine fishes. Given that life history characteristics of fishes with wide latitudinal ranges often vary along latitudinal gradients (Legget and Carscadden, 1978; Shepherd and Grimes, 1983; Trip *et al*., 2014; Riesch *et al*., 2018), the daubed shanny population in the Gulf of Maine may exhibit different biological characteristics and population dynamics than the northern populations. Therefore, to improve our knowledge, this study was undertaken to document trends in temporal and spatial abundance, depth and temperature ranges, and size structure of daubed shanny based on historical trawl survey data, and to evaluate sex-specific differences in size, weight and age of individuals captured in the Gulf of Maine.

Materials and Methods

Historical Data

Data used to analyze trends in historical abundance, spatial distribution, depth and temperature, and size composition came from the Northeast Fisheries Science Center (NEFSC), Maine Department of Marine Resources (MEDMR) and Massachusetts Division of Marine Fisheries (MADMF) spring and fall bottom trawl surveys in the Gulf of Maine (GoM; Fig. 1). The details of each survey are described below.

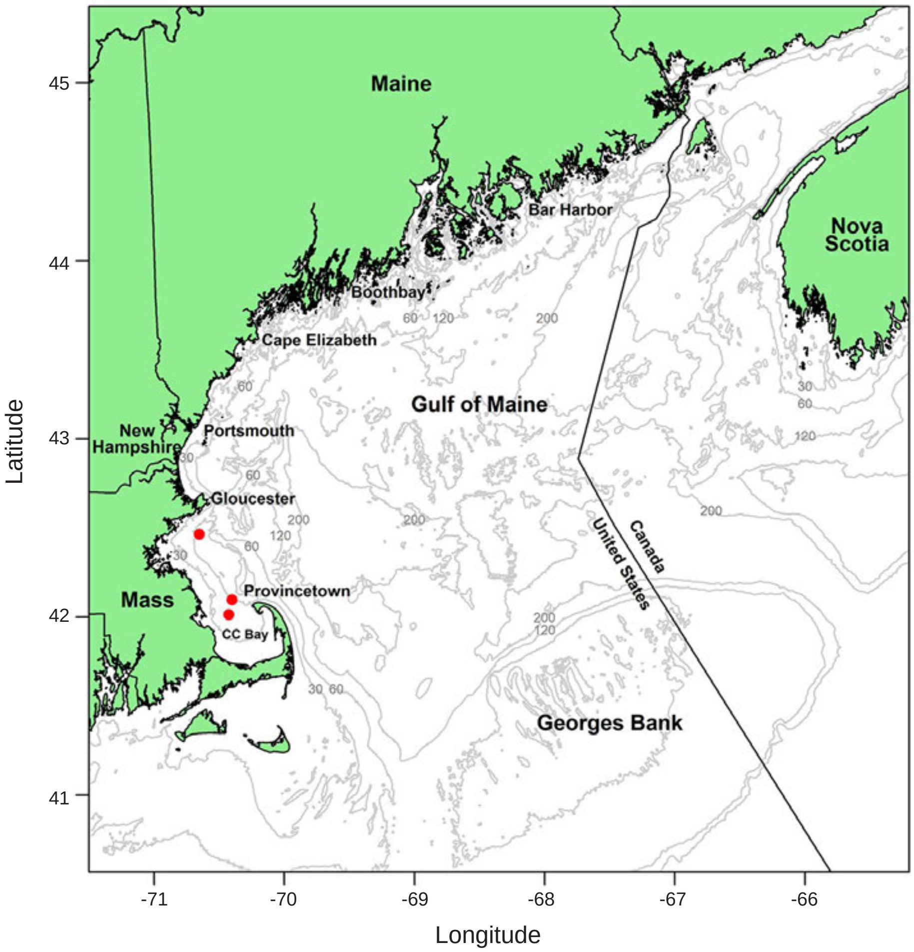

Fig. 1. Map of the Gulf of Maine and adjacent areas (Georges Bank and southern Nova Scotia) showing locations mentioned in the text. Mass = Massachusetts; CC Bay = Cape Cod Bay. Red circles indicate locations where biological samples were collected in 1990. Bathymetric lines are shown for depths 30 m, 60 m, 120 m, and 200 m.

The NEFSC survey was initially based on a stratified random sampling design for continental shelf water >27 m in depth, partitioned into strata of unequal area based on depth and geographic location (Azarovitz, 1981). In the Gulf of Maine, the survey occurs in both US and Canada territorial seas. From 1963 to 1967, sampling was conducted in fall (September–November). A spring (March–May) survey was added in 1968. Sampling effort was expanded in 1972 to include the inshore waters, but effort did not begin in the Gulf of Maine until 1979. Sampling stations were randomly selected within each stratum and allocated among strata in proportion to stratum area. From 1963–2008, a standard #36 or #41 Yankee bottom trawl with a 1.25 cm stretched mesh cod-end liner was towed by primarily the R/V *Albatross IV* (the R/V *Delaware* was used on occasion to supplement sampling) at each station at approximately 3.5 knots for 30 minutes; depth (at the start and end of each tow) and temperature (after arriving on station) were also recorded (Azarovitz, 1981). In 2009, a new, much larger modern vessel, R/V *Henry B. Bigelow*, replaced the R/V *Albatross IV*. Major changes to the fishing methods and survey design were also made. A four-seam bottom trawl replaced the #36 Yankee trawl and tow duration was reduced to 20 minutes and, due to the vessel size, some inshore strata were eliminated. Relative catch efficiency studies of the R/V *Henry B. Bigelow* and R/V *Albatross IV* for many fish species have been conducted (Miller *et al*., MS 2010; Miller, 2013), but conversion factors are not available for the daubed shanny; therefore, no adjustments to catch after 2008 were made. Data from the inshore (strata: 57–90) and offshore (strata: 24, 26–40) regions of the Gulf of Maine (see Supplemental Document Appendix SA for spatial maps of strata) from 1963–2022 were used in the analyses. Spring and fall surveys were not conducted in 2020 due to COVID restrictions.

The MADMF survey began in 1978 in Massachusetts territorial waters and was conducted in spring (May) and fall (September)(Howe *et al*., MS 2002). The survey used a stratified random sampling design with strata defined by region and depth. Regions were stratified into depth strata: ≤9 m, 10–18 m, 19–27 m, 28–36 m, 37–55 m, and >55 m. Sampling sites were proportionally allocated to each stratum based on stratum area. A 20-minute tow (vessel speed is 2.5 knots) was made at each station with a two-seam 3/4 Whiting trawl that contains a 6.3 mm-mesh cod-end liner. At each station, starting depth and ending depth were recorded for a tow (only starting depth was recorded from 1978–1980), and a marine hydrographic instrument was used to record bottom water temperature at the end of each tow. The survey was initially conducted with the R/V *Wilbur* in 1978 and 1979, but later switched to the NEFSC vessel R/V *Gloria Michelle* in 1980. Only data from strata defined as occurring in the Gulf of Maine (strata: 25–36) were used in analyses (see Supplemental Document Appendix SB for a spatial map of strata). The spring and fall surveys were not conducted in 2020 due to COVID restrictions.

The MEDMR inshore trawl survey began in 2000 and mainly covered New Hampshire and Maine waters shallower than 120 meters. In 2003, strata were expanded to deeper waters. The MEDMR survey used a stratified random design. The areas sampled included four depth strata: 9–36 m, 37–64 m, 65–100 m, and >100 m out to approximately the 12-mile limit, and five longitudinal regions based on oceanographic, geologic, and biological features (Sherman *et al*., MS 2005). Number of tows was proportionally allocated to each stratum based on area. Two virtually identical commercial fishing vessels, the F/V *Tara Lynn* and F/V *Robert Michael*, were used for this survey. Both vessels were Down East 54's constructed of a combination of solid and sandwich fiberglass. Until spring of 2004, the two vessels alternated between spring and fall surveys. Since spring of 2004, the survey has been conducted solely by the F/V *Robert Michael*. The net used was a modified version of a shrimp net design for Maine waters (see Sherman *et al*., MS 2005 for specifications) constructed of 5 cm polyethylene mesh and a 2.54 cm cod-end mesh liner and was towed for 20 minutes at each station. Depth was recorded at the start and end of each tow, and temperature was recorded at the end of each tow. We used data from all strata but restricted our analyses to years 2003–2023 to maintain design consistency across years (see Supplemental Document Appendix SC for a spatial map of strata). The spring survey was not conducted in 2020 due to COVID restrictions.

During all surveys, fish captured in the otter trawls were brought onboard, sorted to species, counted, weighed collectively to the nearest 0.1 kg and measured individually to the nearest cm (daubed shanny TL was measured). If tow catch of a fish species was deemed large, a random subsample was taken for length measurements and expanded to the total catch during data processing. Errors in tow data were identified mainly via different statistical summaries and plots; if found, data were eliminated from analyses.

Abundance

Relative abundance indices for spring and fall were computed as the stratified mean number of daubed shanny per standardized tow (Fogarty, 1985; Thompson, 2002):

$$\overline{Y}_{str} = \frac{\sum_k A_k \overline{Y}_k}{\sum_k A_k}$$

where A_k is the area of stratum k and $\overline{Y}_k$ is the mean number per haul in stratum k. The standard error was calculated as

$$SE(\overline{Y}_{str}) = \sqrt{\frac{\sum_k A_k^2 var(\overline{Y}_k)}{(\sum_k A_k)^2}}$$

where $var(\overline{Y}_k)$ is the variance of the mean number per haul in stratum k defined as

$$var(\overline{Y}_k) = \frac{s_k^2}{n_k}$$

where s_k^2 is the sample variance and n_k is the number of tows in stratum *k*. Standardized tow data deemed acceptable were extracted by using gear/tow condition codes for each survey (Supplemental Document Table S**A**). Catch data (numbers) were transformed using $\log_e(y+1)$ prior to calculation to stabilize variance and reduce the influence of sampling variability between tows (Fogarty, 1985; Sokal and Rohlf, 1995). The R package *survey* (Lumley, 2023) was used for all computations. Function *svydesign* was used to define the survey design (*fpc* = stratum area) and then function *svymean* was used to calculate means and standard errors. For the NEFSC survey, indices were calculated separately for the inshore and offshore strata regions.

To determine if trends in seasonal relative abundances were similar within and among surveys, the Spearman rank correlation test (Sokal and Rohlf, 1995) was applied to pairings of indices that were truncated to match the span of the shortest time series in the comparison.

Depth, Temperature and Size Distributions

Abundance-weighted mean depth (m) and temperature (°C) were calculated by season to examine patterns in spatial and temporal distributions of catches. Data from all years were combined for these analyses to increase sample sizes of positive tows and individuals for analyses. The abundance-weighted mean for depth or temperature was calculated as

$$\overline{X} = \frac{\sum_i w_i \cdot x_i}{\sum_i w_i}$$

and its standard deviation

$$SD = \sqrt{\frac{\sum_{i=1}^{P'} w_i \left(x_i - \overline{X}\right)^2}{\left(\left(P' - 1\right) \cdot \sum_{i=1}^{P'} \mathrm{w}_\mathrm{i}\right)/P'}}$$

where w_i is the number of fish in non-zero tow *i*, P' is the number of non-zero weights, and x_i is either depth or temperature at tow *i*. For all analyses, the mean depth of a tow was used. All calculations were performed by using functions *svymean, svyvar and svyquantile*.

To determine if the depth and temperature patterns observed reflected strong affinities of daubed shanny for specific ranges of depth and temperature, the method of Perry and Smith (1994) was used to test if the depth and temperature associated with fish abundance was significantly different from the ranges of environmental conditions measured by each survey. Briefly, empirical cumulative distribution functions (CDF) of a habitat variable for the survey and for fish were constructed and the Kolmogorov-Smirnov maximum absolute vertical distance (D_s) statistic (Siegel, 1956) between CDFs was calculated and then compared to a null distribution of the test statistic created via randomization. The empirical cumulative distribution function for a habitat variable of the complete survey was constructed by

$$f(t) = \sum_k \sum_i \frac{A_k}{n_k} I(x_{k,i})$$

where the $\mathrm{I}(x_{ki})$ is an indicator function of the form

$$I(x_{k,i}) = \begin{cases} 1, \ if\ x_{k,i} \leq t \\ 0, \ otherwise \end{cases}$$

and *t* represents an index, ranging from the lowest to the highest value at a step size appropriate for the desired resolution (Perry and Smith, 1994). The habitat CDF for a species was constructed by

$$g(t) = \sum_k \sum_i \frac{A_k}{n_k} \frac{y_{k,i}}{\overline{Y}_{str}} I(x_{k,i})$$

where $y_{k,i}$ is the *i*th tow in stratum *k*. The Ds test statistic was calculated as

$$D_s = max\left|g(t) - f(t)\right|$$

The null distribution of the test statistic was constructed by randomizing pairings of

$\left(\mathrm{W}_k/\mathrm{n}_k\right)\left[\left(y_{k,i} - \overline{Y}_{str}\right)/\overline{Y}_{str}\right]$ and $x_{k,\mathrm{i}}$ over all *k* and *i* and then calculating the test statistic (D) for the new pairs. The $x_{k,i}$ for the pairings was obtained by sampling with replacement the observed $x_{k,i}$ with probability $W_k n_k$. This procedure was repeated 2000 times and the significance level determined by dividing the number of times D≥ Ds by 2000. The method was applied to catch data grouped into seasons and regions.

Regional and seasonal changes in size structure were investigated by comparing summary statistics and seasonal length frequencies (computed as proportions in 1-cm length intervals) among surveys. Due to the variable nature of catches, data from all years were combined for most analyses. All summary statistics and proportions were calculated assuming a random cluster design (Nelson, 2014). Bootstrapping was used to estimate standard errors of proportions-at-length.

Biology

Daubed shanny were collected opportunistically for biology and ageing information and subsampled non-proportionally from three (stations 24, 26 and 27) out of eight positive tows located in Cape Cod Bay and off Gloucester, Massachusetts in spring of 1990 during the MADMF trawl survey (Fig. 1). Subsampled fish ($n = 101$) were frozen at sea. In the laboratory, individuals were thawed, and total length (TL ±1 mm) and total weight (TW ±0.001 g, measured after each fish was blotted dry) were recorded for all individuals. Sex determination was accomplished by macroscopically and microscopically inspecting gonads.

Because fish were not proportionally subsampled from hauls, data were weighted before analyses. A weighted correction applied to individual data from each haul in subsequent analyses was based on the inverse sampling fraction:

$$w_h = \frac{N_h}{n_h}$$

where w_h is the weight for haul h, n_h is the number of fish subsampled and N_h is the total number caught in haul h. The haul weights derived for stations 24, 26, and 27 were 2.2667 (34/15), 2.0888(94/45) and 1.7073 (70/41), respectively.

Sex-specific differences in length and weight were explored via summary statistics calculated by using function *svymean*, and by using the design-based two-sample Kruskall-Wallis test (function *svyranktest*; Lumley and Scott, 2013) to test for significant differences in median values. Differences in total weight versus total length relationships were also explored. One-way analysis of covariance (Sokal and Rohlf, 1995), conducted by using function *svyglm*, was used to test for differences in intercepts and regression slope parameters between sexes. Total length and total weight were log10 transformed prior to estimation. The full model fitted was

$$log_{10}TW = \beta_0 + \beta 1 \cdot log_{10} TL + \beta_2 \cdot sex + \beta_3 \cdot log_{10} TL \cdot sex$$

where $\log_{10}$ *TL* was treated as a continuous predictor, *sex* as a factor, and an interaction term between the two predictors was included. The *anova.svyglm* function was used to test whether the sequential addition of a predictor significantly contributed to a reduction in overall variance by using the Rao-Scott Likelihood Ratio Test (Lumley and Scott, 2014), and diagnostic plots (standardized residuals-fitted values, qq-residuals and residuals-leverage) were examined for potential violations of model assumptions.

Sagittal otoliths were used for ageing. Sagittae were removed, cleaned of soft tissue and stored dry in coin envelopes, which after 34 years, were free of any decomposition. One otolith was randomly picked from an individual and cut in half close to the core by using an Isomet saw. Both halves were mounted core-side up on slides with Flo-Texx and viewed in mineral oil under reflected light on a computer monitor using Image Pro 10 connected to an Infinity Lumenera 3 camera and Optem Zoom 125 lens tube. Annuli were identified following standard protocols developed for other northwest Atlantic fishes (Elzey *et al*., MS 2015). Age determinations were made by the latter two authors who are experienced age readers. If age readings disagreed, a final age was reached via consensus. Daubed shanny spawn in winter (Pekkoeva, *et al*., 2018); therefore, a January 1 birthdate was assumed. Although not processed until 2024, there was no apparent degradation of the otoliths that may have comprised the accuracy of age determination.

Sex-specific differences in age composition were explored as described above for length and weight. Due to the limited sample sizes, growth curves were not fitted to length and age data; rather, data were summarized to compare mean size- and weight-at-age between sexes and to compare results to previously published growth information for the Svalbard population of daubed shanny (Meyer-Ottesen *et al*., 2014). The caudal-length (Meyer Ottesen *et al*., 2011) sizes from Meyer-Ottesen *et al*. (2014) were converted to total length by using a ratio of 1.08 derived from photographs of individuals in Pekkoeva *et al*. (2018) and Meyer Ottesen *et al*. (2018).

Results

Abundance

Number-per-tow indices for daubed shanny fluctuated markedly from 1963–2023 in NEFSC regions. In the inshore region prior to 2009, spring and fall indices showed little trend as means varied widely over time due to low number of tows made annually and low positive tows (Fig. 2; see Supplemental Document Tables SB

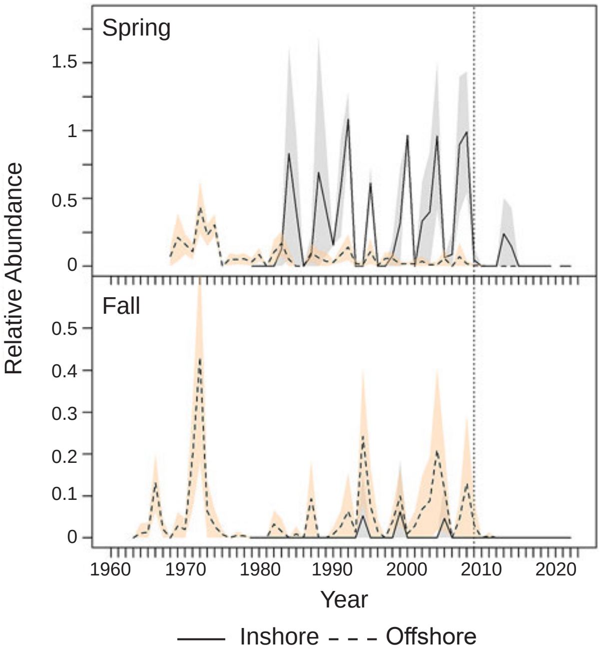

Fig. 2. Spring and fall indices of relative abundance for *L. maculatus* from the inshore and offshore regions of the Northeast Fisheries Science Center (NEFSC) survey, 1963–2022. Shaded regions represent the 95% confidence intervals for survey indices. The vertical dotted line represents the year when the R/V *Bigelow* was instated.

and SC for statistics). Although daubed shanny were sporadically caught in the offshore region, some weak trends in relative abundance were observed. Stratified means were highest in the late 1960s to early 1970s in spring and fall, but then declined to lower levels in the mid-1970s (Fig. 2). Starting in the mid-1990s, spring indices declined further and remained low through 2008, but fall indices increased during the same period. After the switch to the R/V *Bigelow* in 2009, daubed shanny were rarely caught in any region or season (Fig. 2). Correlations among inshore and offshore indices were only significant in fall (ρ = 0.47, p = 0.008, n = 30); however, this result should be viewed with caution given that inshore means were greater than zero in only 3 out of 30 years (Fig. 2).

In Massachusetts waters, mean numbers-per-tow were high in the 1980s in spring and fall but declined in the 1990s (Fig. 3; see Supplemental Document Table SD for statistics). Spring relative abundance peaked again in 2004, gradually declined through 2013, increased slightly in 2014, but then declined to near zero starting in 2017. No fish were caught in 2023. There was little trend in the fall index except daubed shanny were not captured after 2014. Daubed shanny were typically caught in higher numbers in spring than in fall (Fig. 3). The spring and fall indices were significantly correlated (ρ = 0.62, p = 0.000, n = 45).

Similar temporal trends and seasonal patterns in relative abundance were observed in the MEDMR survey compared to the MADMF survey (Fig. 3; see Supplemental Document Table SE for statistics). Mean numbers-per-tow were highest in spring. Spring indices peaked in 2005 and 2009, but then steadily declined to zero or near zero levels in 2016. No fish were captured after 2020 (Fig. 3). Trends in the spring and fall indices were not significantly correlated (ρ = 0.01, p = 0.973, n =2 0).

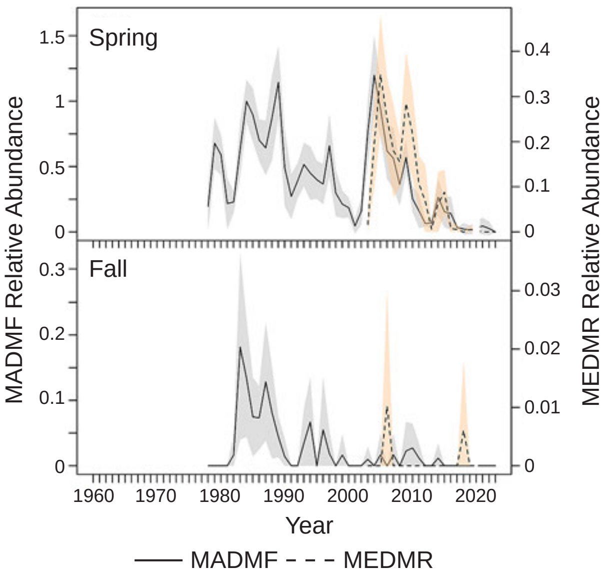

Fig. 3. Spring and fall indices of relative abundance for *L. maculatus* from the Massachusetts Division of Marine Fisheries (MADMF) survey and the Maine Department of Marine Resources (MEDMR) survey in the Gulf of Maine, 1978–2023. Shaded regions represent the 95% confidence intervals for survey indices.

Results of the Spearman rank correlation tests indicated that, among all survey indices, the only significant pairings were between the MEDMR spring index and the MADMF spring and fall indices (MEDMR spring versus MADMF spring: ρ = 0.85, p = 0.000, n = 20; MEDMR spring versus MADMF fall: ρ = 0.60, p = 0.005, n = 20).

Depth, Temperature and Size Distributions

Changes in depth, temperature and size distributions were evident across seasons.

Spring. Catches of daubed shanny were primarily distributed in the western Gulf of Maine from Massachusetts to just north of Bar Harbour, Maine (Fig. 4). Fish catches occurred in waters between 11 and 79 m ($\overline{D}$: 49.0 m; SD: 13.63 m) with bottom temperatures between 3.0 and 8.9°C ($\overline{T}$: 4.0°C; SD: 0.60°C) in the NEFSC inshore region, and at depths between 33 and 233 m ($\overline{D}$: 84.6 m; SD: 22.91 m) with bottom temperatures between 2.2 and 8.3°C ($\overline{T}$: 4.4°C; SD range: 0.86°C) in the NEFSC offshore region (Table 1). Most daubed shanny (95%) were captured in depths ≥31 m and ≤130 m in the inshore and offshore regions, respectively (Table 1). Comparisons between the NEFSC fish and survey CDFs indicated that fish catches were significantly associated with the deeper waters and lower temperatures of the inshore region, and shallower depths and lower temperatures of the offshore region (Fig. 5). The sizes of fish ranged between 5 and 22 cm TL, but most (97.5%) individuals were ≥8–9 cm TL, and few fish >16 cm TL were captured (Fig. 6). Mean lengths for all years combined were similar between the inshore and offshore regions, but the largest individuals (>16 cm TL) were captured in the offshore region (Fig. 6).

In the MADMF survey, daubed shanny catches were concentrated in Cape Cod Bay and areas surrounding Gloucester, Massachusetts (Fig. 4) at depths between 7 and 85 m ($\overline{D}$: 59.0 m; SD: 11.96 m) with bottom temperatures between 1.3 and 11.5°C ($\overline{T}$: 4.3°C; SD: 1.21°C). Most catches (97.5%) occurred in waters ≥30 m (Table 1). Catches were significantly associated with the deeper waters and lower temperatures of the sampled survey area (Fig. 5). The sizes of captured fish ranged between 4 and 22 cm TL, but most individuals (97.5%) were ≥8 cm TL, and few fish were >17 cm TL (Fig. 7). Fish were slightly larger than those caught in the NEFSC survey (Figs. 6 and 7).

Daubed shanny captured in the MEDMR survey were distributed and concentrated in similar areas as the NEFSC

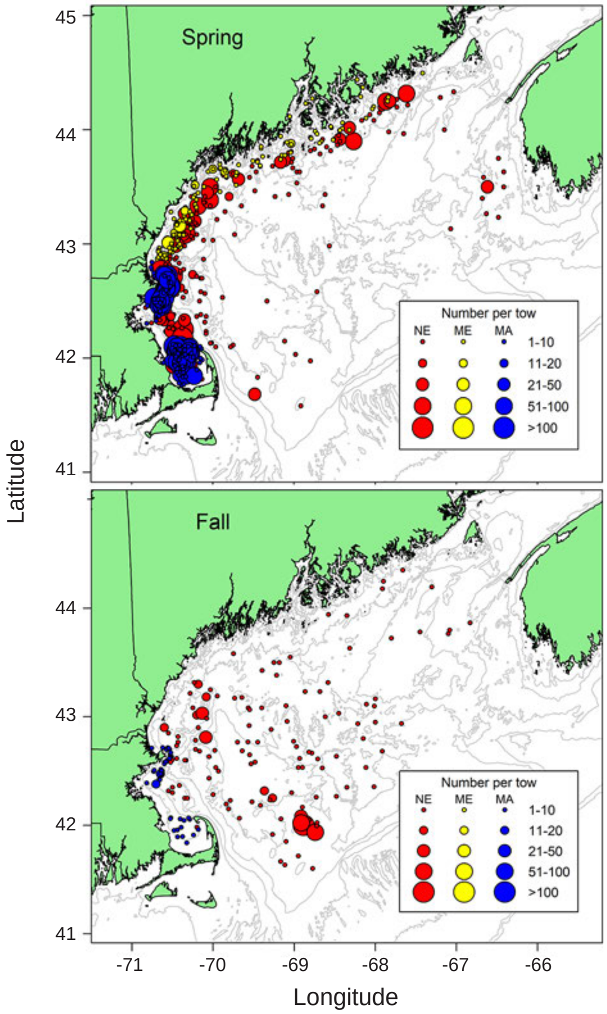

Fig. 4. Spatial distribution of daubed shanny captured in the Gulf of Maine during the Northeast Fisheries Science Center (NE), the Maine Department of Marine Resources (ME), and Massachusetts Division of Marine Fisheries (MA) spring and fall surveys, 1963–2023.

survey (Fig. 4). Catches occurred in waters between 27 and 142 m ($\bar{D}$: 68.1 m; SD: 18.75 m) with bottom temperatures between 2.9 and 8.7°C ($\bar{T}$: 4.4°C ; SD: 1.0°C). Most catches were taken at depths ≥35 m and were significantly associated with the deeper waters and lower temperatures of the survey area (Fig. 5). Sizes of daubed shanny ranged between 8 and 22 cm TL, but most individuals (97.5%) were ≥9 cm TL, and few fish >16 cm TL were captured (Fig. 7). Fish were similar in size compared to individuals captured in the MADMF survey (Fig. 7).

Among-survey comparisons revealed that daubed shanny were caught in relatively consistent temperatures in spring regardless of fish depth (Table 1), suggesting the species either experienced a well-mixed thermal environment or it preferred specific temperature ranges. Comparison of fish abundance-weighted mean temperatures and survey mean temperatures (with associated standard deviations), calculated for 10-m depth intervals, indicated that daubed shanny likely selected specific temperatures because fish mean temperatures for the shallower, warmer nearshore surveys (NEFSC inshore region, MADMF and MEDMR) were in the lower range of temperatures measured by the surveys and were generally consistent across depths (Fig. 8)(see Supplemental Document Tables SF and SG for statistics).

Fall. Catches of daubed shanny were low compared to spring and were primarily distributed throughout Gulf of Maine away from nearshore areas (Fig. 4). In the offshore region of the NEFSC survey, catches occurred in deeper waters between 52 and 282 m ($\bar{D}$: 136.1 m; SD: 32.23 m) with bottom temperatures between 3.6 and 10.8°C ($\bar{T}$: 6.1°C; SD: 1.15°C), but mostly in depths ≥82 m (Table 1). Although the distribution shifted to deeper waters, daubed shanny catches were still significantly associated with the shallower waters and lower temperatures of the survey area (Fig. 5), and fish selected the lower range of temperatures across depths as in spring (Fig. 8; see Supplemental Document Table SH for statistics). Compared to spring, fall catches were dominated by small individuals 7–11 cm TL ($\bar{L}$: 8.2 cm TL, mode: 8 cm TL), and few fish >11 cm TL were caught (Fig. 6).

In the MADMF survey, low catches were distributed similarly as in spring (Fig. 4) and were significantly associated with the deeper waters and lower temperatures of the sampled survey area (Fig. 5). The size composition of the MADMF survey in fall was similar to the size composition in spring (Fig. 7). Few positive tows and very low numbers of daubed shanny caught in the NEFSC inshore region and MEDMR survey precluded analyses of depth and temperature data.

Biology

The 101 fish subsample (out of 297 fish caught in the entire 1990 survey) consisted of 56 females, 41 males and 4 unsexed individuals ranging in size from 100 to 167 mm TL and were similar to the range of sizes (~92–167 mm TL) captured by Meyer Ottensen *et al*. (2014). Sex composition of the subsamples was consistent across tows: female proportions ranged from 54 to 60%. The final weighted sex composition was 58% female and 42% male. Gulf of Maine females were significantly larger ($\bar{L} = 144.3$ mm, SD = 14.92 mm, range: 103–167 mm, n = 56) and heavier ($\bar{W} = 9.8$ g, SD = 3.22 g, range: 3.2–17.2 g, n = 56) than males ($\bar{L} = 132.6$ mm, SD = 9.75 mm, range:113–152 mm, n = 41; $\bar{W} = 7.7$ g, SD = 2.15 g, range: 3.3–12.0 g, n = 40) (Fig. 9).

Table 1. Abundance–weighted mean depth ($\overline{D}$, m) and temperature ($\overline{T}$, °C), standard deviation (SD), range, 2.5th percentile, 97.5th percentile, and number of positive tows with variable measurements (n) by season for the Northeast Fisheries Science Center, Maine Department of Marine Resources and Massachusetts Division of Marine Fisheries bottom trawl surveys.

Survey	**Season**	$\overline{D}$	**SD**	**Range**	**2.5%**	**97.5%**	**n**
			Depth				
NEFSC Inshore	Spring	49.0	13.63	11–79	31	70	56
	Fall	63.7	23.11	37–78			3
NEFSC Offshore	Spring	84.6	22.91	33–233	59	130	204
	Fall	136.1	32.23	52–282	82	214	139
MADMF	Spring	59.0	11.96	7–85	30	79	380
	Fall	61.2	15.37	10–86	32	80	53
MEDMR	Spring	68.1	18.75	27–142	35	106	132
	Fall	34.5	10.15	27–42			2

Survey	**Season**	$\overline{T}$	**SD**	**Range**	**2.5%**	**97.5%**	**n**
			Temperature				
NEFSC Inshore	Spring	4.0	0.60	3.0–8.9	3.1	5.1	49
	Fall	10.2	3.15	8.0–12.4			2
NEFSC Offshore	Spring	4.4	0.86	2.2–8.3	3.1	7.4	176
	Fall	6.1	1.15	3.6–10.8	4.5	9.3	125
MADMF	Spring	4.3	1.21	1.3–11.5	1.6	6.7	374
	Fall	7.5	1.98	4.0–15.7	4.7	11.0	49
MEDMR	Spring	4.4	1.00	2.9–8.7	3.1	6.5	132
	Fall	11.3	0.64	10.9–11.8			2

Significant intercept, slope, sex factor and interaction term indicated the total-length on total-weight relationships were different between sexes (Table 2). The regression slope for males was steeper (3.89), but less precise, than the slope (3.34) for females, indicating the former gained more weight per unit increase in length than the latter. Although diagnostics plots showed that the model described the length-weight relationships well, the smaller sample size for males may not have captured the relationship adequately. Therefore, a combined sex model was fitted to provide an overall weight-length relationship for the species that may be impacted less by sample size (Table 2).

Ages of daubed shanny ranged from 1 to 6 years. The majority (female: 95%; male: 92%) were ≥3 years; there was no difference in age distributions between sexes (Fig. 9). Comparison of mean length- and mean weight-at-age for ages 3 and 4 (ages with largest sample size) indicated that females were larger and heavier than males of the same age (Table 3), implying females grow faster than males in the Gulf of Maine. Additionally, mean length-at-age for ages 3 and 4 are much larger than growth curve predictions of mean lengths at ages 3 and 4 for females (~71 and ~104.9 mm TL, respectively) and males (~100 and ~112 mm TL, respectively) in Meyer Ottesen *et al*. (2014), suggesting Gulf of Maine fish grow faster than the Svalbard population as well.

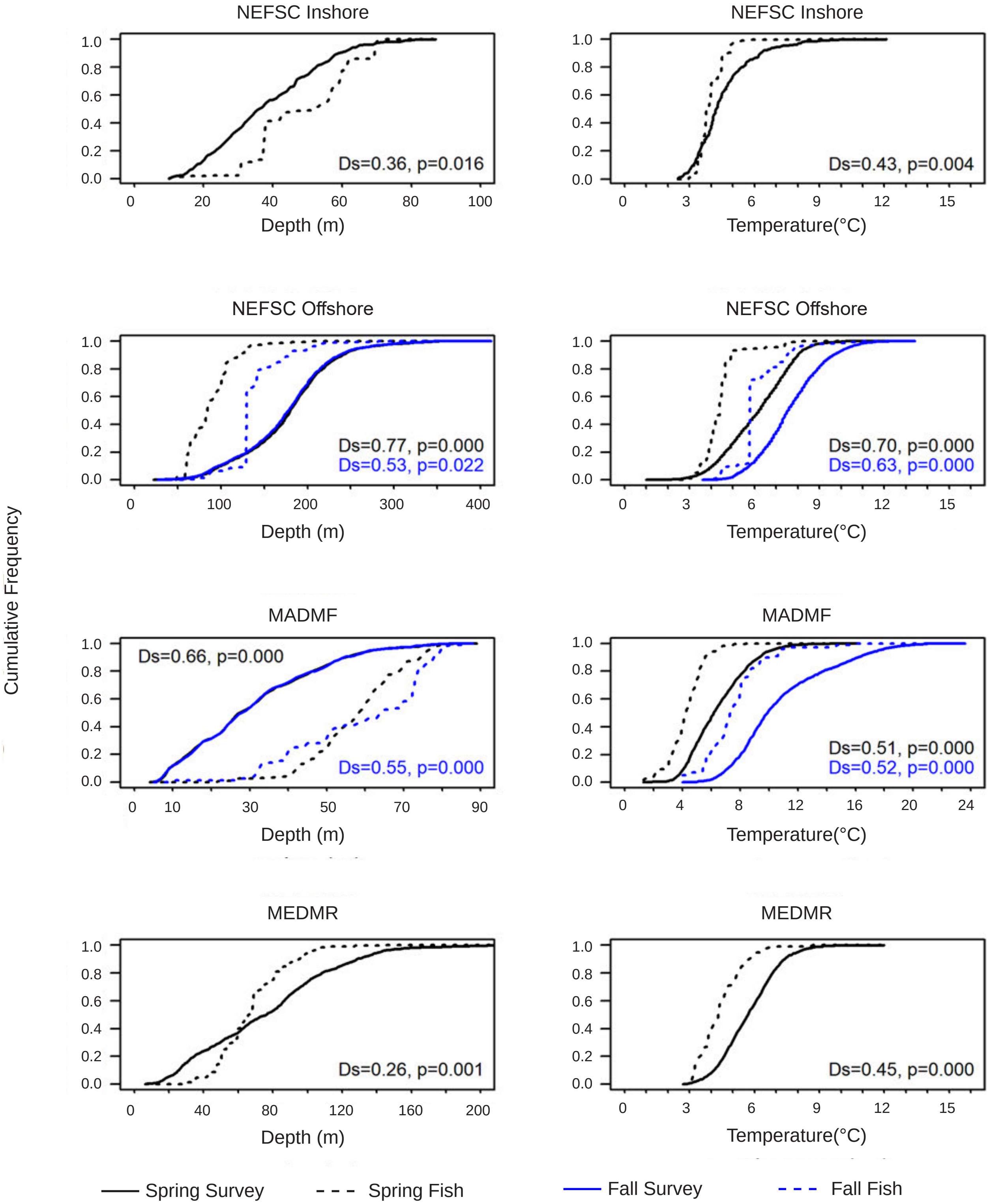

Fig. 5. Daubed shanny and survey depth (left) and temperature (right) cumulative frequency distributions from the inshore and offshore regions of the Northeast Fisheries Science Center (NEFSC) bottom trawl survey, the Maine Department of Marine Resources (MEDMR) survey, and Massachusetts Division of Marine Fisheries (MADMF) survey in the Gulf of Maine during spring (black) and fall (blue), all years combined. *Ds* is the Kolmogorov-Smirnov maximum absolute vertical distance and *p* is the significance probability.

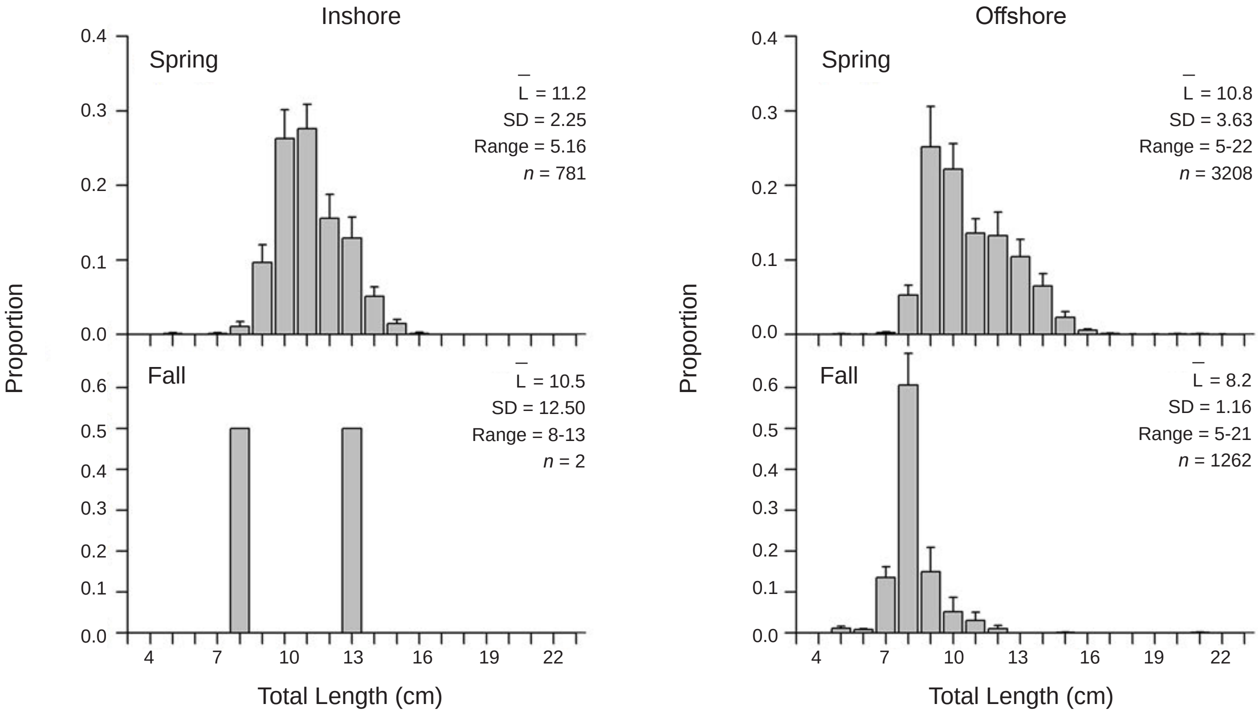

Fig. 6. Spring and fall proportions-at-length and length summary statistics for daubed shanny captured in the inshore and offshore regions of the Northeast Fisheries Science Center surveys. *L* is mean length, *SD* is the standard deviation and *n* is total number of fish caught. Whiskers are +1 standard errors.

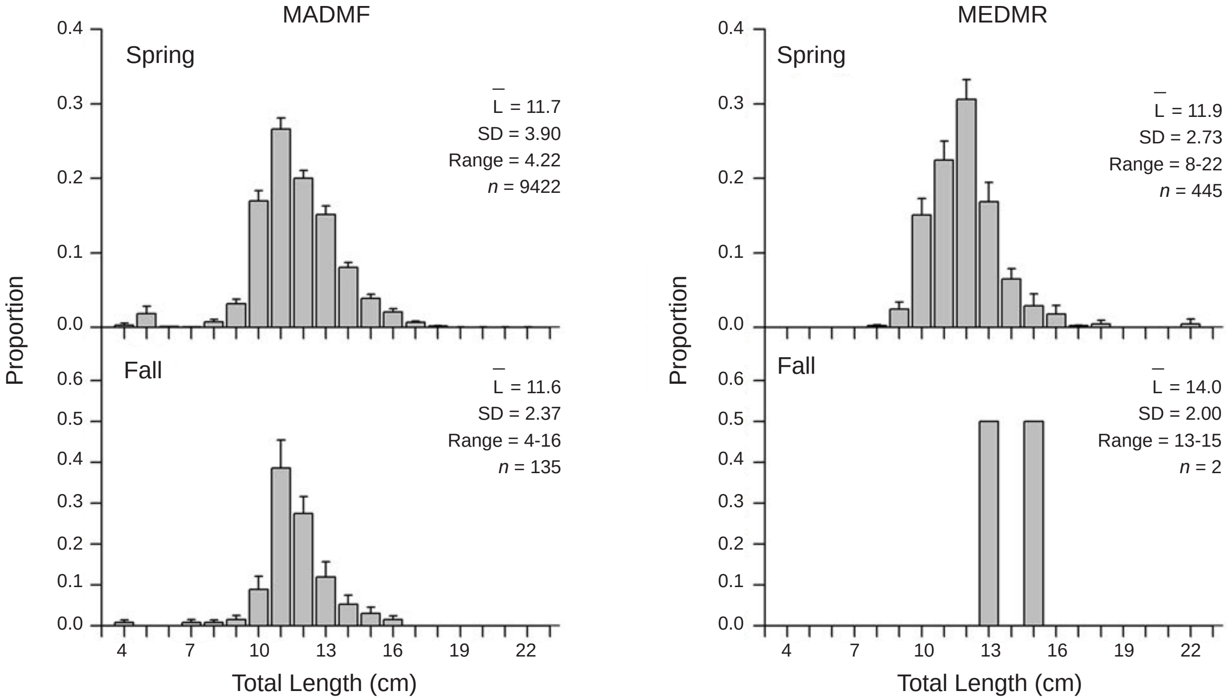

Fig. 7. Spring and fall proportions-at-length and length summary statistics for daubed shanny captured in the Massachusetts Division of Marine Fisheries (MADMF) and Maine Department of Marine Resources (MEDMR) bottom trawl surveys, all years combined. *L* is mean length, *SD* is the standard deviation and *n* is total number of fish caught. Whiskers are +1 standard errors.

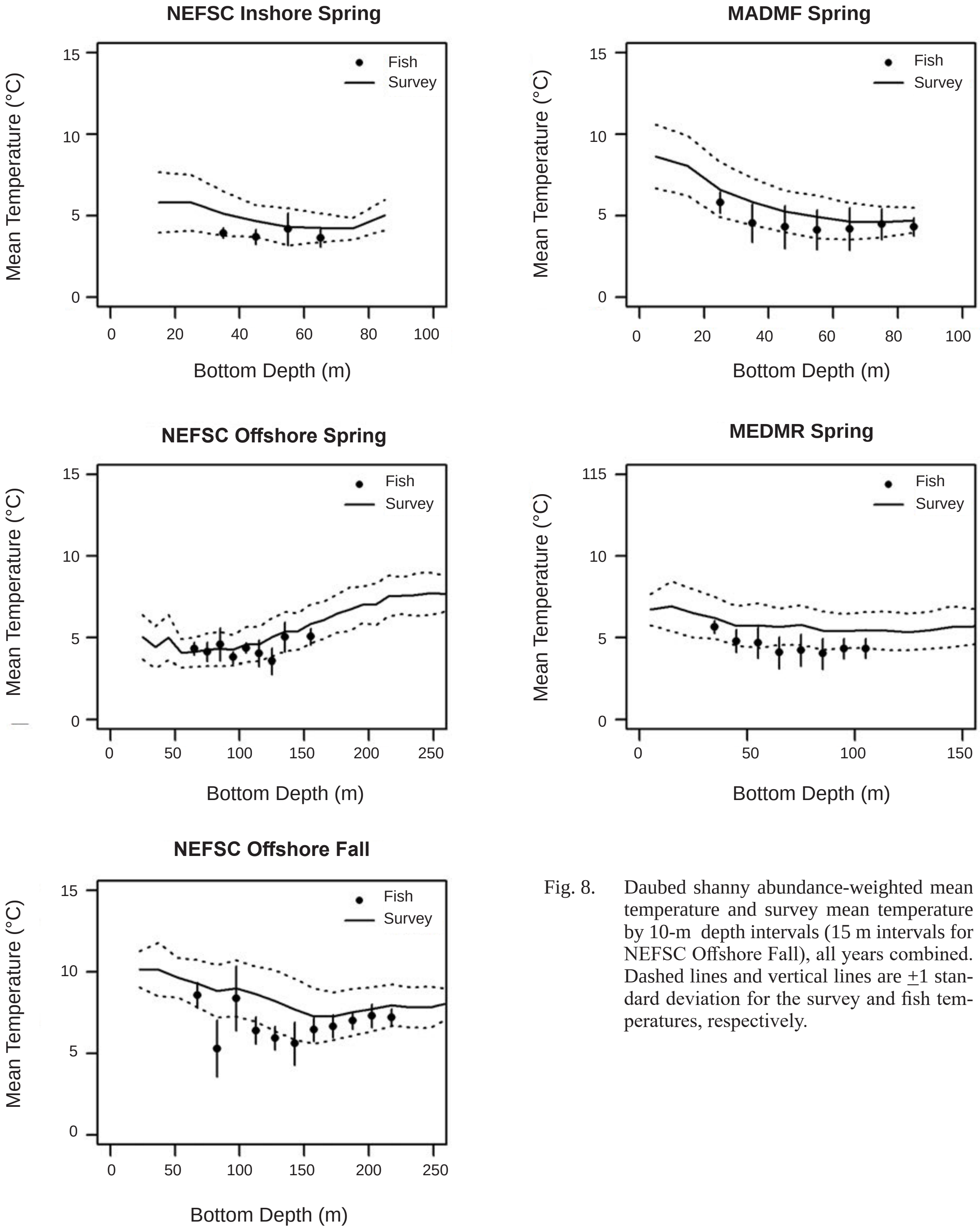

Fig. 8. Daubed shanny abundance-weighted mean temperature and survey mean temperature by 10-m depth intervals (15 m intervals for NEFSC Offshore Fall), all years combined. Dashed lines and vertical lines are ±1 standard deviation for the survey and fish temperatures, respectively.

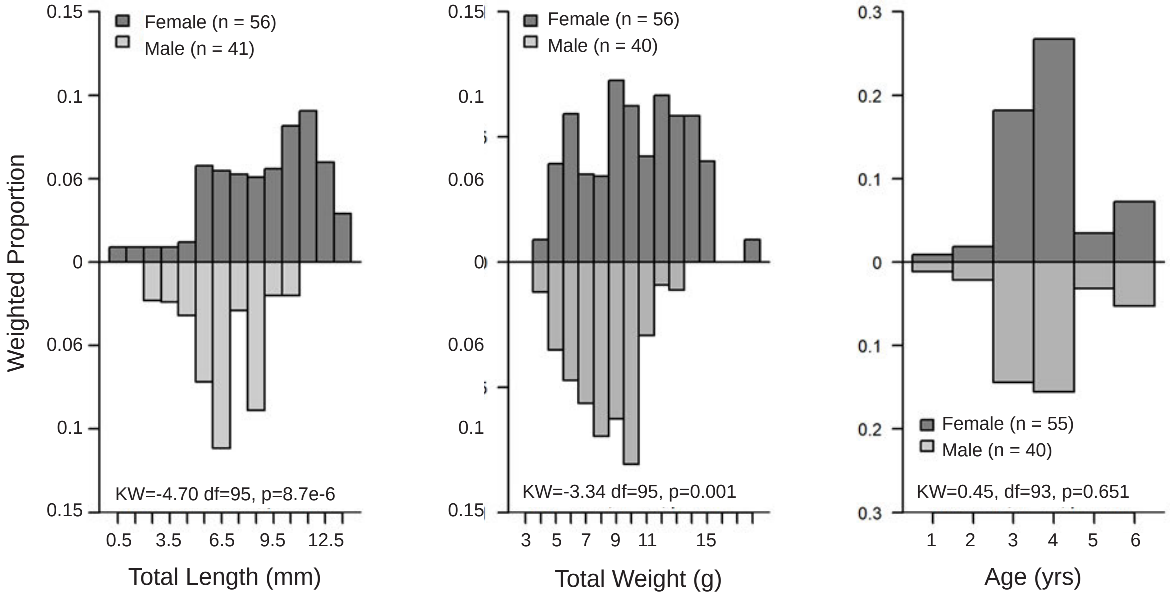

Fig. 9. Length, weight and age distributions for daubed shanny captured in spring of 1990 during the Massachusetts Division of Marine Fisheries bottom trawl survey. Results of Kruskal-Wallis tests comparing the medians of the sex-specific distributions are shown at the bottom of each graph.

Table 2. Estimates of regression coefficients and corresponding statistics from the $\log_{10}$ total weight -$\log_{10}$ total length regression models. SE is the standard error, CV is the coefficient of variation (SE/β), *ts* is t test statistic determining if β>0, P(>|t|) is significance probability of test, df is degrees of freedom, r^2 is the coefficient of determination, Rao-Scott statistics from the sequential Anova table, and Pr is the probability that the added component provides a significant reduction in variance. Equation parameters for each sex were derived from the full model; Female: $log_{10} TW = \beta_0 + \beta_1 \cdot log_{10} TL$; Male: $log_{10} TW = (\beta_0+\beta_2) + (\beta_1+\beta_3) \cdot log_{10} TL$. The combined sexes (includes unsexed) model is $log_{10} TW = \beta_0 + \beta_1 \cdot log_{10} TL$.

Parameter	Estimate	SE	CV	t_s (β=0)	P(>|t|)	df	r^2	Rao-Scott	Pr
Full Model									
β_0	-6.24	0.246	0.04	-25.39	<2e-16	92	0.925		
β_1	3.34	0.113	0.03	29.55	<2e-16			2.163	<2e-16
β_2	-1.14	0.570	0.50	-1.99	0.049			0.014	0.017
β_3	0.55	0.267	0.49	2.04	0.044			0.009	0.045
Female									
β_{0F}	-6.24	0.246	0.04						
β_{1F}	3.34	0.113	0.03						
Male									
β_{0M}	-7.38	0.514[1]	0.07						
β_{1M}	3.89	0.242[2]	0.06						
Combined									
β_0	-6.31	0.200	0.03	-31.56	<2e-16	97	0.921		
β_1	3.37	0.093	0.03	36.45	<2e-16			1328.8[3]	<2e-16

[1] $SE(\beta_0+\beta_2)=\sqrt{var(\beta_0) + var(\beta_2) + 2 \cdot cov(\beta_0,\beta_2)} = \sqrt{0.0605 + 0.3249 - 2 * 0.0605}$

[2] $SE(\beta_1+\beta_3)=\sqrt{var(\beta_1) + var(\beta_3) + 2 \cdot cov(\beta_1,\beta_3)} = \sqrt{0.0128 + 0.0713 - 2 * 0.0128}$

[3] Wald Test from function *regTermTest*

Table 3. Length- and weight-at-age statistics for female and male Daubed Shanny collected in spring of 1990. *n* is the observed sample size, $\overline{L}$ is the mean length-at-age (TL mm), $\overline{W}$ is the mean weight-at-age (g), *SD* is the standard deviation, *Min* is minimum observed length and *Max* is the maximum observed length.

Age	**Female**					**Male**				
	n	$\overline{L}$	**SD**	**Min**	**Max**	**n**	$\overline{L}$	**SD**	**Min**	**Max**
1	1	103.0		103	103	1	113.0		113	113
2	2	115.0	2.82	113	117	2	118.6	9.10	113	126
3	17	135.3	8.05	124	153	14	129.0	5.69	118	140
4	25	149.4	10.41	128	164	15	133.4	9.16	116	152
5	3	157.0	10.92	145	165	3	142.8	2.08	141	145
6	7	158.2	7.79	145	167	5	141.6	9.49	127	150

Age	**Female**					**Male**				
	n	$\overline{W}$	**SD**	**Min**	**Max**	**n**	$\overline{W}$	**SD**	**Min**	**Max**
1	1	3.2		3.2	3.2	1	4.1		4.1	4.1
2	2	4.6	0.25	4.4	4.8	2	4.6	2.10	3.3	6.3
3	17	7.8	2.06	4.8	12.4	13	7.0	1.44	4.0	9.5
4	25	10.7	2.56	5.8	14.5	15	8.0	1.99	4.3	11.6
5	3	12.0	3.62	8.0	14.7	3	9.7	2.49	6.9	12.0
6	7	12.7	2.58	8.9	17.2	5	9.1	2.34	5.4	10.9

Discussion

Abundance

The historical status of daubed shanny population abundance, as measured by three bottom trawl surveys, was difficult to determine because of disparate patterns in relative abundance indices among surveys and seasons. The highest catches and encounters (positive tows) occurred in spring in all surveys, suggesting spring indices may reflect population trends best. However, the spring regional indices from the NEFSC survey are likely unreliable measures of abundance because of the sporadic encounters of daubed shanny that created quite variable fluctuations in relative abundance and little correlation among regions. The variable nature of encounters in this survey may be due to the species possible preference for mud/silt habitats (Meyer Ottesen *et al*., 2014), the nets used during the surveys, and changes in net design, vessel usage and door design over time (Sissenwine and Bowman, 1978; Azarovitz, 1981; NEFSC, MS 1997). With the instatement of the R/V *Bigelow* in 2009, it appears the NEFSC survey will have little ability to monitor daubed shanny in the Gulf of Maine in the future.

The best information for determining trends in relative abundance of daubed shanny may come from the MEDMR and MADMF spring surveys. Those surveys had higher encounter rates (Supplemental Document Table SD and SE), no gear changes over time, vessel changes occurred once at the beginning of the time series examined, and survey trends were very similar and highly correlated. Based on those surveys, it appears that daubed shanny may be disappearing from the nearshore areas of Gulf of Maine given that relative abundance has been near zero or zero since 2016–2017 (no fish were caught in the MEDMR survey since 2021 and in the MADMF survey in 2023). The reasons why abundance has declined are unclear. One potential cause may be that rising water temperatures in the nearshore region (LaFreniere *et al*., 2023) and remaining Gulf of Maine (Townsend *et al*., 2023) are making areas less hospitable for a species adapted to living in cold waters. In fact, the rapid decline in daubed shanny abundance may be related to effects of a new baseline of warmer temperatures established in the Gulf of Maine in 2010 (Townsend *et al*., 2023). Being in the southern extent of its range, the species was likely already physiologically limited at historical temperatures (Sexton *et al*., 2009; Ern *et al*., 2023), and with the recent increases, its physiological thermal tolerances may have been pushed over upper thermal limits, affecting the species ability to survive. Declines in areal abundances of daubed shanny and other Arctic-boreal species are expected as warming waters push species northward (Fossheim *et al*., 2015).

An indirect effect of warming temperatures may also be causing the decline in daubed shanny. Post-larvae feed primarily on *Calanus* copepods and store lipids from this high-energy prey in a specialized lipid sac for winter survival (Meyer Ottesen *et al*., 2011). In the Gulf of Maine, *Calanus finmarchicus* was historically a dominant copepod (Pershing *et al*., 2005). After the establishment of the new thermal regime in 2010, *C. finmarchicus* abundance declined (Meyer-Gutbrod *et al*., 2021). Survival of daubed shanny post-larvae may have been greatly reduced because lower availability of *Calanus* translates to fewer encounters with this species, and lower encounters can affect a fish's ability to capture enough prey to build energy reserves for overwintering (*e.g.*, Letcher *et al*., 1996; Geissinger *et al*., 2021). Comparison of the MADMF and MEDMR survey indices with *Calanus* abundance index from Meyer-Gutbrod *et al*. (2021) (Fig. 10), suggests that a plausible link between *Calanus* and daubed shanny abundances exists.

Another indirect effect of warming temperatures is the potential for increased predation as distributions of marine predators change in response to warming waters. The biomasses of three hake species (Gulf of Maine red hake, *Urophycis chuss*, white hake, *Urophycis tenuis*, and northern silver hake, *Merluccius bilinearis*), identified as predators of daubed shanny through NEFSC stomach content analyses (Supplemental Document Table SI), have increased over time in the Gulf of Maine (Supplemental Document Fig. SA), likely related to distributional shifts in response to changing climate (Ney *et al*., 2011; LaFreniere *et al*., 2023). The decline of daubed shanny coincided with increases in hake biomass starting around 2006–2007 (Supplemental Document Fig. SA), suggesting potential interactions between daubed shanny and the predators. However, the very low occurrences of daubed shanny in stomachs of those and other fish predators (<0.15%; Supplemental Document Table SI) indicates that interactions may not be strong, and the observed inverse trends could be purely coincidental. Interestingly, warming waters and predation by longfin squid (*Doryteuthis pealeii*) appear responsible for the population collapse of the Gulf of Maine northern shrimp (*Pandulus borealis*), another boreal species with the southernmost extent of its range being the Gulf of Maine (Richards and Hunter, 2021). As suggested by one reviewer, there could be a potential predatory impact of marine mammals like the gray (*Halichoerus grypus atlantica*) and harbour (*Phoca vitulina vitulina*) seals that have also increased in abundance throughout the Gulf of Maine (Wood *et al*., 2019; Hayes *et al*., MS 2023), but a review of food habits showed that daubed shanny has not been found in the diet of those species in US waters (Waring *et al*., 2010; Lyssikatos and Wenzel, 2024; McCosker *et al*., 2024), suggesting a relationship may not exist.

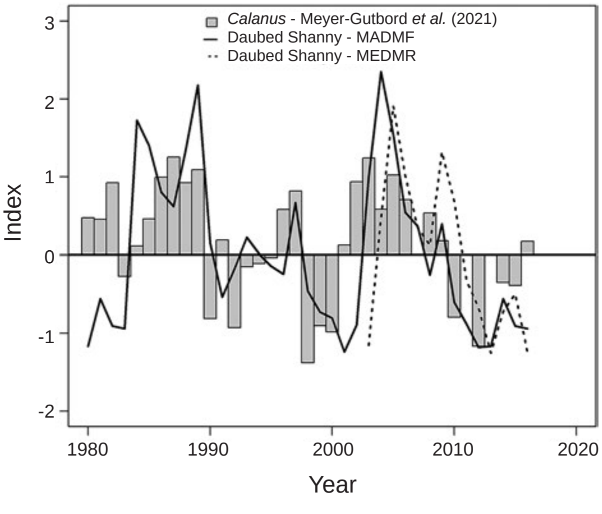

Fig. 10. Comparison of the *Calanus* abundance index from Meyer-Gutbord *et al*. (2021) and the MADMF and MEDMR daubed shanny standardized ((x-mean)/sd) indices, 1980–2016. The original *Calanus* data were provided by Dr. Erin Meyer-Gutbord.

Finally, commercial fishing in the Gulf of Maine could have a direct impact on daubed shanny abundance. The Gulf of Maine is an important fishing area for groundfishes such as Atlantic cod (*Gadus morhua*) and Atlantic haddock (*Melanogrammus aeglefinus*), and many gear types from bottom trawls to gillnets are used to target those species (Pol and Carr, 2000). Bycatch of non-targeted fish species in fisheries has been an issue for decades (Beutel *et al*., 2008) and it is possible to impact fish populations through bycatch mortality (Lawson *et al*., 2017). To determine if bycatch mortality could be an impactful cause, the NEFSC observer and at-sea monitoring database (https://www.fisheries.noaa.gov/inport/item/24111) was queried for any records of "shanny" collected between 2000 and 2024 from all areas, gear types and target fisheries. Only two records of catch (0.045 kg each) out of over 600 000 records were found, one for an unknown shanny and another for radiated shanny (*Ulvaria subbifurcata*), suggesting that bycatch impacts were unlikely a significant cause of the population decline of daubed shanny.

Depth, Temperature and Size Distributions

Andriyashev (1954) reported that daubed shanny were most abundant at depths from 50 to 240 m with temperatures between -1.6 and 2.0°C in the Barents Sea and as deep as 400 m off Greenland. In this study, the species was found in Gulf of Maine waters between 7 and 282 m within a wide range of much higher temperatures (1.3–15.7°C). Tyler (1971) also captured daubed shanny within a similar temperature range (1.2–10.7°C) in a Maine estuary. The average temperatures experienced in spring (all surveys: 4.0–4.4°C) and fall (NEFSC offshore and MADMF: 6.1–7.5°C) were close to the range of summer bottom temperatures (4–7°C) for daubed shanny captured in the White Sea (Andriyashev, 1954).

A seasonal change in depth distribution was noted as fish were caught mostly in shallow waters between 30 and 130 m in spring and in deeper waters ≥82 m in fall. In addition, daubed shanny were caught in the near-lowest temperatures available within most survey areas regardless of depth and season, suggesting the species has a thermal preference. The seasonal change in depth distribution could be the result of daubed shanny seeking specific temperatures, as has been observed in many fish species (Murawski, 1993; Henderson *et al*., 2017; Brazo *et al*., 2021), but this is unlikely because there was no concomitant shift of individuals of the same sizes found in spring to deeper waters in fall. However, the change in depth distribution was related to the appearance of small individuals (mean: 8 cm TL cm) not typically captured in spring. Daubed shanny post-larvae settle to the benthic habitat at sizes 70–100 mm CL (~76–108 mm TL) and mostly in waters >100 m (Meyer Ottesen *et al*., 2011; Murzina *et al*., 2012; Pekkoeva *et al*., 2018). Based on the observed size frequencies and depths-at-capture, the individuals captured in fall were likely benthic-settling post-larvae recruiting to offshore waters of the Gulf of Maine.

Fall catches and encounters of daubed shanny were greatly reduced in the nearshore (NEFSC inshore, MADMF, and MEDMR) surveys compared to spring. The catch of fish is dependent on gear selectivity (related to gear characteristics such as mesh size, net type, door design, etc.) and fish availability (related to the spatial distribution of fish relative to the distribution of the survey) (Maunder *et al*., 2014; McElroy *et al*., 2021). A change in gear selectivity was unlikely a cause of the seasonal change in daubed shanny abundance because gears used were relatively consistent across seasons in most surveys. A change in fish availability may be a more plausible cause of the seasonal differences in abundance; however, because little is known about daubed shanny habitat use and behavior, it is difficult to surmise likely hypotheses. Nevertheless, the disappearance of large (>11 cm TL) individuals in fall and their reappearance in spring, particularly in the offshore region of the NEFSC survey (see Supplemental Document Tables SJ-SM), suggests daubed shanny may be avoiding the gear by possibly moving to untowable habitats like rocky bottoms in fall. The fact that fish captured in the MADMF survey in fall had a similar size range as fish captured in spring and were still present, albeit in lower abundance, may be evidence to support that hypothesis.

Biology

In this study, we captured similar-sized individuals as the Meyer Ottesen *et al*. (2014) study but found that female daubed shanny comprised a higher percentage (weighted) of catches than males (58% versus 42%). The disparity in sex composition between the studies is likely due to differences in how fish were collected. In the Meyer Ottesen study, individual fish were collected over three years during April–October and were only sampled in deep water (150–400 m). As suggested by the authors, they may have missed females that could have been more abundant in shallower waters. Our sampling occurred within depths 48–60 m in Massachusetts waters where daubed shanny were concentrated in spring (May). Biases could have been produced by our limited sampling because fish were collected from only three tows, and we did not sample outside of Massachusetts waters. However, the consistency of higher female proportions across tows (0.54–0.6) suggests the pattern was real. Regardless, our results are closer in agreement with patterns of female dominance in other Stichaeidae species (Antonenko *et al*., 2004; Kolpakov and Klimkin, 2004; Kalchugin *et al*., 2006).

Meyer Ottesen *et al*. (2014) reported that daubed shanny males caught in Svalbard waters were larger and heavier than females, which agreed with the general pattern of larger and heavier males in other Stichaeidae species (Kalpakov and Klimkin, 2004; Kalchugin *et al*., 2006). In this study, we found the opposite for Gulf of Maine daubed shanny - females were significantly larger and heavier than males. We believe the difference is real and not created by our limited sampling. If the scope of spatial sampling in this study created bias, catches in surveys outside Massachusetts waters would be comprised of larger individuals, presumably males, than were captured in the MADMF survey. However, this was not the case. The MADMF survey tended to catch larger individuals compared to the other surveys (Figs. 6 and 7), and there was no evidence of higher fractions of larger individuals being caught or a trend of increasing size with increasing depth in the NEFSC inshore, MEDMR, or NEFSC offshore surveys (Supplemental Documents Table SN). Additionally, if bias was introduced by limited sampling of tows (3 out of 8 tows) and small sample size (101 out of 297 individuals) in this study, the estimated size composition from sampling might differ from the size composition of the entire survey, or sex-specific size compositions may vary among tows. Actually, there was little difference in estimated size compositions from the sampled tows and the entire survey (see Supplemental Document Fig. SB), and the pattern of smaller male size was consistent across tows (see Supplemental Document Fig. SC). Therefore, the reverse dimorphic patterns observed for Gulf of Maine daubed shanny were unlikely created by bias in our sampling.

Meyer Ottesen *et al*. (2014) found no difference in the gutted-weight versus caudal-length equation estimates between male and female daubed shanny from Svalbard waters. In this study, total weight versus total length equations for males and females were significantly different from each other, possibly due, in part, to the smaller sample size for males. The different measures of weight and length between the two studies make comparing and interpreting differences in equation estimates difficult. However, the equation slopes for female daubed shanny and for individuals pooled in the Gulf of Maine (3.34 for both) were close in magnitude to the slopes (3.43–3.46) estimated for both sexes and pooled individuals of the Svalbard population, which indicates both populations exhibit positive allometric growth and become disproportionately heavier with increasing length.

This study is the first to report age and growth estimates for daubed shanny in the Gulf of Maine. We aged both females and males to a maximum of 6 years, and females appear to grow faster and become larger than males. In comparison, Meyer Ottesen *et al* (2014) found females and males in Svalbard waters live a maximum of 10 and 12 years, respectively, and males tend to grow faster (after maturation) and larger than females. In addition, based on size frequencies and mean length-at-age comparisons, Gulf of Maine daubed shanny appear to grow faster and attain the same sizes earlier than fish from Svalbard waters.

The shorter life span and inter- and intra-population differences in body sizes and growth rates of females and males indicate that fish from the Gulf of Maine exhibit different life history characteristics than fish from the Svalbard population. These differences are likely adaptations of the species to living in much higher temperatures (1.3–15.7°C) at the southern extent of its range compared to the northern populations (-1.6–2.0°C; Andriyashev, 1954; Byrkjedal and Høines, 2007). Shorter lifespans and faster growth rates in lower latitude populations is a pattern observed in fishes with wide latitudinal distributions often attributed to increasing temperature and duration of the growing season as latitude decreases (Curtis and Shima, 2005; Heibo *et al*., 2005; Trip *et al*., 2014; Estlander *et al*., 2016; Riesch *et al*., 2018; Andrade *et al*., 2023). A within-species pattern of larger body sizes and faster growth rates of females in low latitude populations with a reversal to smaller sizes and slower growth rates in higher latitude populations has also been documented in several fish species, possibly the result of temperature influencing the relative costs of reproduction (Curtis and Shima, 2005; Estlander *et al*., 2016). Although not measured, daubed shanny in the Gulf of Maine likely experience higher natural mortality rates and mature earlier than northern populations because these life history characteristics covary with body size and growth rates, and increase and decrease, respectively, as latitude declines (Trip *et al*., 2014; Alvarez-Noriega *et al*., 2023). Our results demonstrate the importance of evaluating the life history of a species across its whole distributional range to understand the complex factors that may influence its survival and the species' ability to respond to natural- and anthropogenic-induced environmental changes.

The prognosis for the continued presence of daubed shanny in the Gulf of Maine is not promising. The species is no longer captured in nearshore areas where it was historically abundant, and its disappearance may be linked to direct and indirect factors associated with increasing water temperatures. As temperatures continue to rise in the Gulf of Maine, as is projected (Brickman *et al*., 2021), the region will continue to become a very inhospitable environment for Arctic-boreal species like the daubed shanny. Our results give support to the conclusions of other studies (*e.g.*, Richards and Hunter, 2021; LaFreniere *et al*., 2023) that major changes are occurring in the Gulf of Maine ecosystem due to climate change.

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Seasonal succession of the larval fish community from coastal areas of eastern Newfoundland, Canada

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Abstract

We present a synthesis of all sampling programs aimed at collection of ichthyoplankton conducted in coastal waters of eastern Newfoundland during the period 1982–2016, describing seasonal patterns in the succession of 22 taxa in terms of diversity, probability of occurrence, and overall abundance. Additionally, we assess whether changes in these patterns occurred prior to and after the collapse of major commercial fish stocks and accompanying shifts in ecosystem structure. Despite differences in relative species composition and community structure among bays, we identified clear and repeatable patterns in the seasonal cycle of species succession from Placentia Bay, on the south coast, to White Bay on the northeastern coast of the island. Some of the differences among bays reflected latitudinal patterns in the timing of the seasonal environmental cycle, with increasing delays toward northerly bays. Relatively few species generally dominated the larval fish community, although dominance varied seasonally, particularly once emergence of capelin commenced in July and August. Abundance of larval fish reflected the changes in abundance of adult stocks of commercial species, with strong declines in density following stock collapses, but larval decreases extended to non-commercial coastal taxa potentially removed as bycatch or through impacts of changes in ocean conditions that contributed to the decline of major ecosystem stocks (*e.g.*, Atlantic cod, capelin, American plaice). Although differences in timing and extent of ichthyoplankton collections confounded our data, the general consistency of our observations with other sources of information (*e.g.*, research vessel trawl surveys) highlights the value of such collections to monitoring of areas poorly represented by other types of surveys. Knowledge of changes in larval fish community structure in coastal areas can set a foundation to understand better the potential interaction between anthropogenic and climate impacts on the ecosystem state in coastal areas.

Keywords: biodiversity, community structure, ecosystem state, ichthyoplankton, reproduction, spawning cycle

Introduction

Atlantic cod (*Gadus morhua*) populations on the Newfoundland and Labrador continental shelves collapsed in the late 1980s and early 1990s as a result of overfishing and changes in ocean conditions (Lilly *et al*., 2013) concurrent with major changes in the broader marine ecosystem (Gomes *et al*., 1995; Pedersen *et al*., 2017). The precipitous decline in the northern cod stock (*e.g.*, Myers *et al*., 1997), paralleled the abrupt decline in abundance of capelin (*Mallotus villosus*), a keystone forage species (Buren *et al*., 2014; Buren *et al*., 2019), along with dramatic changes in other commercial and non-commercial species (Pedersen *et al*., 2017). Other studies provide evidence of changes in life history characteristics and production potential of several stocks (Stares *et al*., 2007; Morgan *et al*., 2018; Murphy *et al*., 2021; Tripp *et al*., 2024). Despite evidence of a partial return of regional ecosystems to their historical structure in the mid-2010s, most stocks remain depleted (Koen-Alonso and Cuff, 2018) and substantial changes in community structure persist (Aune *et al*., 2024). Although many factors contributed to this regional crisis, Harris (1990) noted that achieving a basic understanding of the Newfoundland shelf ecosystem, beyond data on adult fish of commercial stocks, represented an important source of information that could reduce future risks in the provision of management advice.

Ichthyoplankton surveys provide a means to understand the biology and ecology of fish populations, an essential component to forecasting the effects of changes in climate and ecosystem state on regional productivity and resilience (Koslow and Wright, 2016). Extensive programs studying early life stages of fish have focussed on understanding the drivers of change in stock productivity. However, multidisciplinary population level research programs are often limited in duration (*e.g.*, GLOBEC – a study of Global Ocean Ecosystem Dynamics (Lehodey *et al*., 2006; Batchelder and Kim, 2008; Voss *et al*., 2012; Fogarty *et al*., 2013)) and thus base their inferences and conclusions on only a few cohorts of a given taxon. Such programs also seldom consider aspects of ichthyoplankton community structure. There are relatively few long-term observation programs focus on larval fish dynamics (*e.g.*, North Sea (Simmonds, 2009), California Current (Gallo *et al*., 2019), Japan (Oozeki, 2018), Bering Sea (Goldstein *et al*., 2019)). Nevertheless, collections of fish eggs and larvae have provided fishery-independent estimators of spawning stock abundance (*e.g.*, Fissel *et al*., 2011; Dickey-Collas *et al*., 2012; Somarakis *et al*., 2012), predictors of year-class strength (*e.g.*, Auth and Brodeur, 2013; Islam *et al*., 2015), and changes in climate driven community composition (*e.g.*, Boeing and Duffy-Anderson, 2008; Morson *et al*., 2019; Nielsen *et al*., 2021). Seasonal sampling programs can also provide insights into the timing of reproductive activity, filling a particularly useful niche where scientific research surveys do not effectively collect data on all relevant species. Ichthyoplankton surveys can also identify ecosystem elements or factors that influence early life survival, a critical aspect of recruitment variability (Houde, 2008; Pepin, 2016), as well as provide insights into shifts in community composition or the introduction of new taxa to a region (*e.g.*, Peterson *et al*., 2022). Tracking of larval fish cohorts through time has informed studies on patterns of variation in growth rates (Hare and Cowen, 1997; Robert *et al*., 2007; May *et al*., 2020) and the potential impact of predators (Robert *et al*., 2010; Takasuka *et al*., 2017; de Queiroz *et al*., 2024). Because of high vulnerability of fish larvae to changes in feeding conditions and sources of loss (Houde, 1987; Beyer, 1989), ichthyoplankton studies provide a strong foundation to investigate how changes in ecosystem conditions and productivity can affect natural resource management (*e.g.*, Möllmann *et al*., 2008; Siddon *et al*., 2011; Marshall *et al*., 2019). In short, basic knowledge on the occurrence, abundance, and distribution of early life history stages across a broad range of taxa offers critical information to understand how underlying processes may affect the stability of food webs and fish populations.

Coastal environments represent areas of high biodiversity and productivity (DFO, 2019) but the focus on management of commercially important and broadly distributed fish and invertebrate stocks in nations with highly developed industrial fisheries often limits knowledge of ecosystem features and dynamics. These regions of high productivity are typically vulnerable to changes in atmospheric and climate forcing (*e.g.*, Evans and Pepin, 1989; Tian *et al*., 2003). Complex habitat structure and diversity characterize coastal regions (*e.g.*, Proudfoot *et al*., 2020; Amani *et al*., 2022), often enhancing reproductive opportunities (*e.g.*, nesting sites, algal cover, complex geomorphology) and providing diverse nursery sites for a broad range of taxa (*e.g.*, Ings *et al*., 2008; Renkawitz *et al*., 2011; Dalley *et al*., 2017). Wind-driven changes in circulation and water mass distributions in coastal environments can affect the dynamics of ichthyoplankton by altering retention of eggs and larvae in suitable habitats, or shifting their overlap with potential prey and predators (Leggett *et al*., 1984; Grant and Brown, 1998; Snelgrove *et al*., 2008; Stanley *et al*., 2013).

The more than 17 500 km of coastlines in Newfoundland and Labrador encompass many physically dynamic bays and fjords, for which numerous studies have investigated the response of ichthyoplankton species to fluctuations in ocean currents and productivity (Laprise and Pepin, 1995; Pepin *et al*., 1995; Bradbury *et al*., 2003; Snelgrove *et al*., 2008; Stanley *et al*., 2013). A subarctic Atlantic plankton community characterizes the Labrador Northeast-Newfoundland shelf ecosystem (Davis, 1982; Davis, 1986; Pepin *et al*., 2011); however, most reports of seasonal variation in the occurrence, abundance, diversity and dynamics of early life stages of fish have focused on single species from a single bay (*e.g.*, Leggett *et al*., 1984; Bradbury *et al*., 2003; Pepin *et al*., 2003; Bradbury *et al*., 2008; Murphy *et al*., 2018; Wilson *et al*., 2018). Effective use of information from coastal areas to inform and supplement other approaches aimed at monitoring of ecosystem state remains a challenge. Our study aims to synthesize data from multiple ichthyoplankton surveys conducted in coastal Newfoundland bays in recent decades to:

- Compare community structure among bays and evaluate changes prior to and after the major change in the ecosystem to assess the potential consequences of the loss of dominant groundfish and forage fish in coastal environments;
- Evaluate variations in species richness and beta diversity (variation in species composition of assemblages) among bays, with the objective of disentangling the contribution of spatial species turnover and nestedness resulting from antithetic processes of species replacement and species loss, in order to assess patterns of variation in the underlying biodiversity among surveys;
- Provide a general description of seasonal occurrences and abundance cycle of as many dominant taxa as possible to evaluate spawning patterns and contrast our observations with knowledge of stocks located on the adjacent continental shelf.

We predict similarities in species composition among bays but also a seasonal progression in community structure that follows a latitudinal progression reflective of differences in the local environmental cycle. Differences in species ranges of adult fish may also affect overlap in taxonomic composition among sites. We base this synthesis on the amalgamation of multiple ichthyoplankton collections aimed at providing advice concerning the management of fish stocks and cycles of abundance, investigations into processes affecting the growth and mortality of larval fish, and studies into the dispersal and retention of commercially important species. We collected data from sampling throughout eastern Newfoundland, from April through October, between 1982 and 2016, acknowledging that variation in year, month, and bay confounded sampling activities throughout this period. Collections ranged from White Bay on the northeast coast of Newfoundland to Placentia Bay on the south coast (Fig. 1). Although suboptimal, a synthesis based on multiple sources of data generated for a wide range of purposes nonetheless provides a critical first step to understanding variation in the dynamics of coastal ichthyoplankton in the absence of comprehensive knowledge of the general patterns of larval fish occurrence in a broad geographic region. Such an approach provides a foundation to develop more comprehensive assessments of the reproductive cycles of fishes in the region and to identify critical information gaps.

Oceanographic setting

The flow of the inner branch of the Labrador current strongly influences coastal areas of the Newfoundland continental shelf and Grand Banks (Loder *et al.*, 1998). White, Notre-Dame, Bonavista, Trinity, and Conception Bays face in a northeastern direction, in contrast to southwestern facing Placentia Bay (Fig. 1), resulting in differential effects of wind forcing. In the Newfoundland region, southwesterly winds prevail and induce upwelling in northeast facing bays, whereas northeasterly winds likely suppress upwelling and intensify surface heating (Yao, 1986; deYoung *et al.*, 1993a; deYoung *et al.*, 1993b; deYoung and Sanderson, 1995; Davidson *et al.*, 2001; Ma *et al.*, 2012). Average currents are generally weak and highly variable, with largely meagre tides (~2–3 $\text{cm}\cdot\text{s}^{-1}$). Local winds drive surface circulation on short time scales (hours to days) but density-driven exchanges with shelf waters and the inshore branch of the Labrador current drive circulation on longer time scales (weeks to months). Storms can generate Kelvin waves trapped within about 5 km of either coast with associated jet-like currents (deYoung *et al.*, 1993a; deYoung *et al.*,

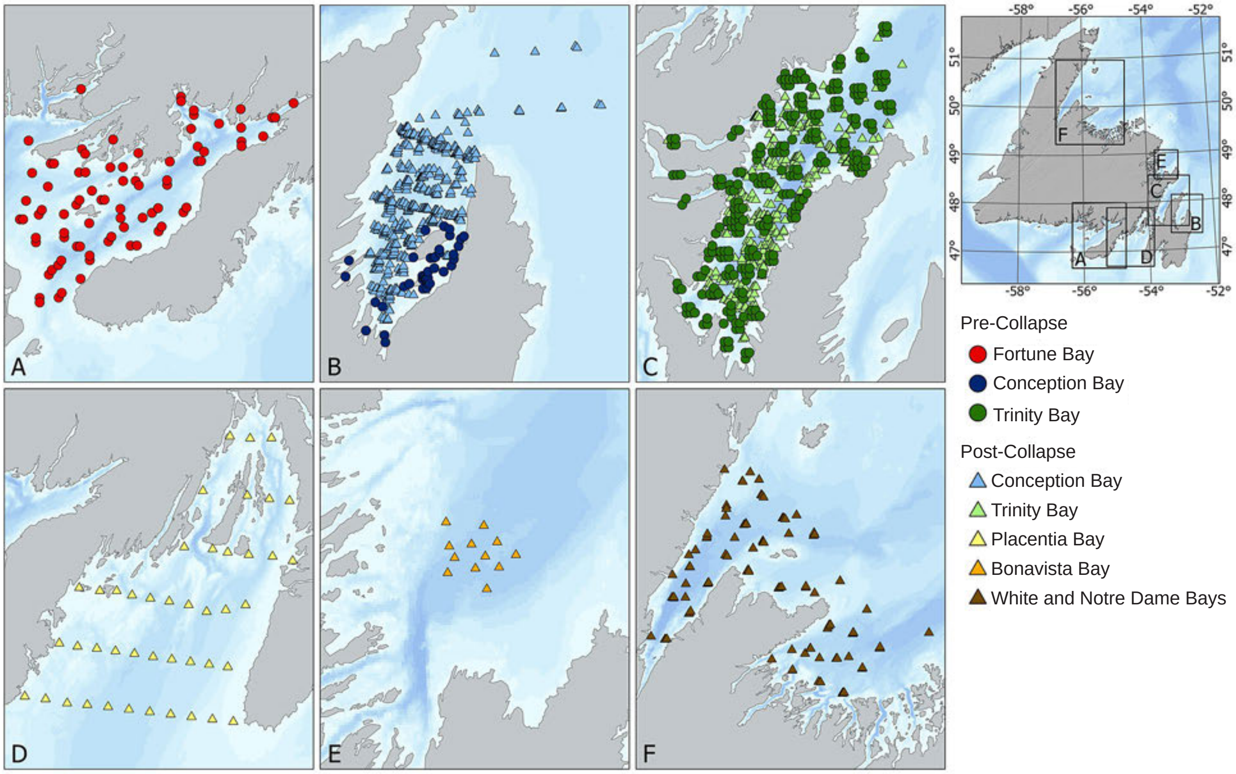

Fig.1. Map of region, bays and station locations of the data for this study. The inset map of Newfoundland highlights the location of bays around the island of Newfoundland appearing in panels a-f. Circles represent sampling locations during the pre-collapse period, triangles represent sampling locations during the post-collapse period.

1993b). Salinity strongly influences stratification, and summer mixed layer depth ranges from 10–40 m, with an internal Rossby radius of ~5–8 km. Sub-zero temperatures in the cold intermediate layer form locally in winter on the Newfoundland and Labrador shelf, typically below 50 m and extending to depths exceeding 150 m near the coast (Petrie *et al*., 1988). Considerable large-scale coherence characterizes seasonal and interannual variation in oceanographic conditions and their response to fluctuations in atmospheric forcing (DFO, 2023).

The seasonal temperature and salinity cycles, at a high frequency sampling site (Station 27– 47.55°N, 52.59°W) on the east coast of Newfoundland (Petrie *et al*., 1991; Petrie *et al*., 1992), demonstrate notable fluctuations in surface waters and more limited variation with increasing depth (Supplementary Fig. 1). Stratification starts in March/April through a combination of changes in temperature and salinity. Surface temperature reaches a maximum in August/September, and minimum in January/February. Notable freshening of the surface layer occurs in May and reaches a maximum in September. Mesozooplankton abundance at Station 27 is lowest in May and increases progressively until September (Supplementary Fig. S2). There are no reliable monitoring data concerning the seasonal cycle of copepod nauplii, the principle prey of fish larvae, other than that reported by Pepin (2023). Copepods dominated non-copepod taxa throughout the year, with highest proportional abundance of non-copepods between May and October, and lowest in winter. Copepod taxa most important in the diet of larval fish (*Oithona* spp., *Pseudocalanus* spp., *Calanus finmarchicus*, and *Temora longicornis*) generally comprise more than 80% of the abundance of copepodite stages. Strong seasonal variability characterized taxonomic composition of non-copepods.

Environmental conditions

Numerous studies have documented the environmental history of the Newfoundland Shelf ecosystem. Most recently, the Newfoundland and Labrador Climate Index (NLCI – Cyr and Galbraith (2021)), composed of 10 variables that quantify atmospheric, ice, and oceanographic variables summarizes broad-scale regional conditions and demonstrates cyclic patterns of variation over time (Fig. 2). In general, the patterns of change in the NLCI demonstrate that increased variability, quantified by the 11-year running average of the standard deviation in NLCI, occurs every 7–9 years, with the exception of the most recent period (2005–present) when overall variability has remained high. From 1951 to 1970 physical conditions fluctuated around an average state, with some elements (*e.g*., air temperature, salinity) generally below the 1991–2020 average, in contrast to other elements of the index that were generally above normal. From 1970 to 1980, the NLCI abruptly declined to below normal levels, but most elements of the index gradually increased to above normal by 1981. After this improvement, environmental conditions declined rapidly to below normal for an extensive period (1982–1996), although with pronounced fluctuations during this period in some index elements. Since 1998, the NLCI has generally remained above normal, although with considerable short-term variability (~5 year periodicity) that likely results from climate change.

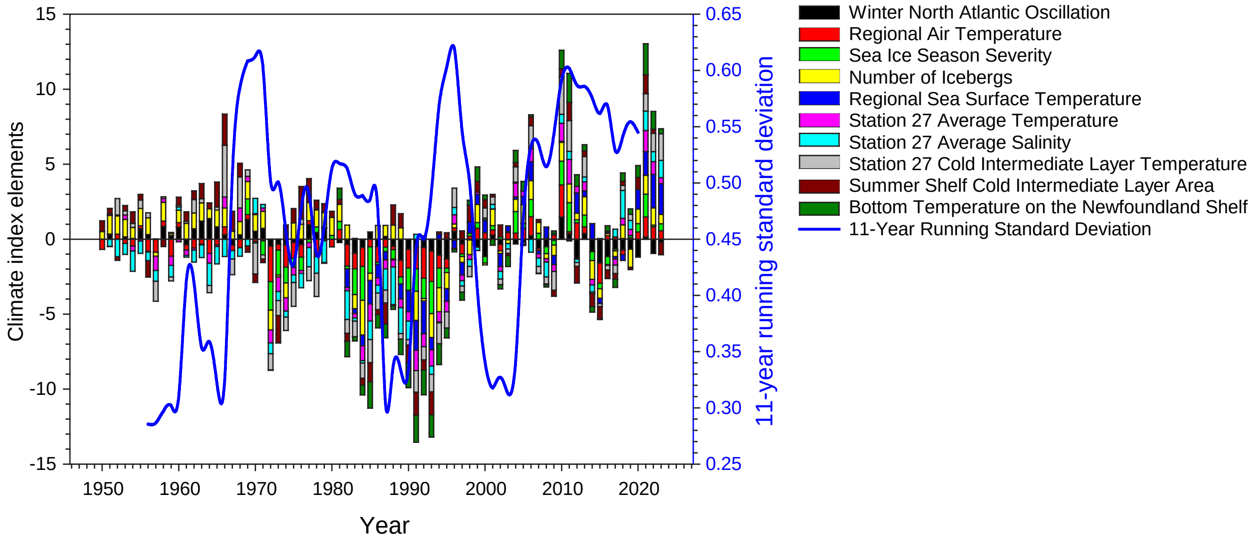

Fig. 2. The Newfoundland and Labrador Climate Index (NLCI) time series for the period 1951–2023. Stacked bars represent the standardized contribution of various atmospheric, ice and oceanographic variables (see legend) used to derive the index based on the climatological averaging period 1991–2020 as described by Cyr and Galbraith (2021). The blue line represents the 11-year running average standard deviation of the NLCI, centered on ± 5 years on either side of the estimate.

Extensive analyses document the collapse of the northern cod stock in the late 1980s and early 1990s (*e.g.*, Myers *et al*., 1997), but the combined effects of over-exploitation and environmental change also resulted in a decline and major shift in the structure and distribution of the remainder of the groundfish community (Gomes *et al*., 1995; Pedersen *et al*., 2017). Capelin, a keystone forage species of the Newfoundland ecosystem, also collapsed in the early 1990s, coincident with the decline in demersal fish biomass (Buren *et al*., 2019). These changes were associated with a shift in overall community structure that resulted in increased overall biomass of shellfish in the 1990s, mainly in the form of snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*), which peaked in the mid-2000s and have since declined (Aune *et al*., 2024). Similar shifts from groundfish to shellfish have been reported in other geographic regions (Worm and Myers, 2003). Coincident with the decline in invertebrate stocks, a modest recovery of groundfish stocks occurred, but which has yet to reach pre-collapse levels of biomass, on either the Newfoundland Shelf or the Grand Banks (NAFO, 2023).

Ichthyoplankton surveys

The ichthyoplankton data encompass surveys of Trinity and Fortune Bay (1982–1986) aimed at monitoring herring populations, process studies conducted in Conception, Trinity, or Bonavista Bays (1985–1986, 1990–2013), seasonal surveys of Placentia Bay (1997–1999), and monitoring surveys of capelin in Trinity Bay (2002–2016). Monitoring surveys used 60-cm bongo nets with 333-µm mesh towed obliquely from the surface to 200 m. Most process studies used a 4 m^2 Tucker trawl with variable mesh sizes (Pepin and Shears, 1997), towed obliquely from the surface to 50 m, and occasional use of 60 cm bongo nets, as did the surveys of Placentia Bay. One process study in Conception Bay 1985–1986 used a 0.75 m ring net towed horizontally at a depth of 7 m. Vessel speed varied between 1.5 and 2.5 $m \cdot s^{-1}$. All nets were equipped with flowmeters to estimate the distance towed. Abundance of each species at each station was calculated as $N = CD/AL$ where N is the number of larvae$\cdot m^{-2}$, C is the number of larvae collected (n), D is the maximum sample depth (m), L is the distance towed (m), and A is the area of the net opening (m^2). Tow depth differences among surveys required application of area-based estimates of density.

The combined surveys collected a total of 5 022 samples throughout eastern Newfoundland, from April through October, between 1982 and 2016, and encompassed 98 separate research missions. Some process-oriented missions involved up to 3 surveys of the bay under study, and our analyses considered each survey separately. Surveys of Placentia Bay (April to August), Conception Bay (April to September) and Trinity Bay (May to October) provided relatively complete coverage of the seasonal cycle of larval fish occurrence, in contrast to limited seasonal coverage of Notre Dame and White Bays (July, August, and September), and Fortune and Bonavista Bays (July only). Because of limited temporal collections, we grouped data from Fortune and Bonavista Bays with information from the adjacent Placentia and Trinity Bays, respectively. Only data from Conception and Trinity Bays provided community structure prior to (1980s) and after (1990–2016) the major shift in the Newfoundland coastal ecosystem. The number of samples per mission ranged from 5 to 205, with a median of 34. We note the unbalanced sample collection across years and months, with sample collections heavily weighted toward the 1980s (56% of samples collected between 1982–1986), and an emphasis on warmer/summer months when we anticipated highest larval abundances (74% of samples collected in June, July, and August (Fig. 3)). We acknowledge large gaps in sample collection, both in time and geography, with very few collections occurring in early spring and fall (Fig. 3). This bias primarily reflects the opportunistic nature of sample collections, vessel availability, and project objectives. Sample collection also heavily favoured two locations, with 55% of samples collected in Trinity Bay and 30% collected in Conception Bay (Fig. 3).

All samples were preserved in 4–5% buffered formaldehyde, with the exception of projects aimed at otolith-based estimation of growth rates that used 95% ethanol. Ichthyoplankton were sorted from samples and identified to the lowest taxonomic level possible (Fahay, 1983; Fahay, 1992a; Fahay, 1992b, and references therein). For this analysis we identified 22 taxa (Table 1), representing 15 families, and with 16 taxa reliably identified to species level. We combined six taxa to genus level because of variations in technical and taxonomic expertise among the different surveys and studies that resulted in inconsistent levels of identification. *Ammodytes* sp. and *Pholis* sp. likely each consisted of a single species (*Ammodytes dubius* and *Pholis gunnellus*, respectively), based on Scott and Scott (1988). Specimens of *Lumpenus* spp. identified to species consisted principally of *Leptoclinus macculatus* (formerly accepted as *Lumpenus macculatus*) with a few specimens of *Lumpenus lampretaeformis*. *Liparis atlanticus* likely dominated *Liparis* spp. (Pepin, unpublished data), with *Liparis gibbus* as the second most frequently identified species, along with a few specimens identified as *Liparis inquilinus* and *Liparis liparis*. Larvae of *Myoxocephalus* spp. that could be identified to species included *Myoxocephalus scorpius*, *Myoxocephalus scorpioides*, *Myoxocephalus octodecemspinosus* and *Myoxocephalus aenaeus*, but the majority of specimens were not identified to species level. *Sebastes* spp. could not be identified to species level but likely consisted of *Sebastes norvegicus* (formerly *Sebastes marinus*) and/or *Sebastes fasciatus* on the east coast, although *Sebastes mentella* also occurs on the south coast of Newfoundland, in proximity to Placentia

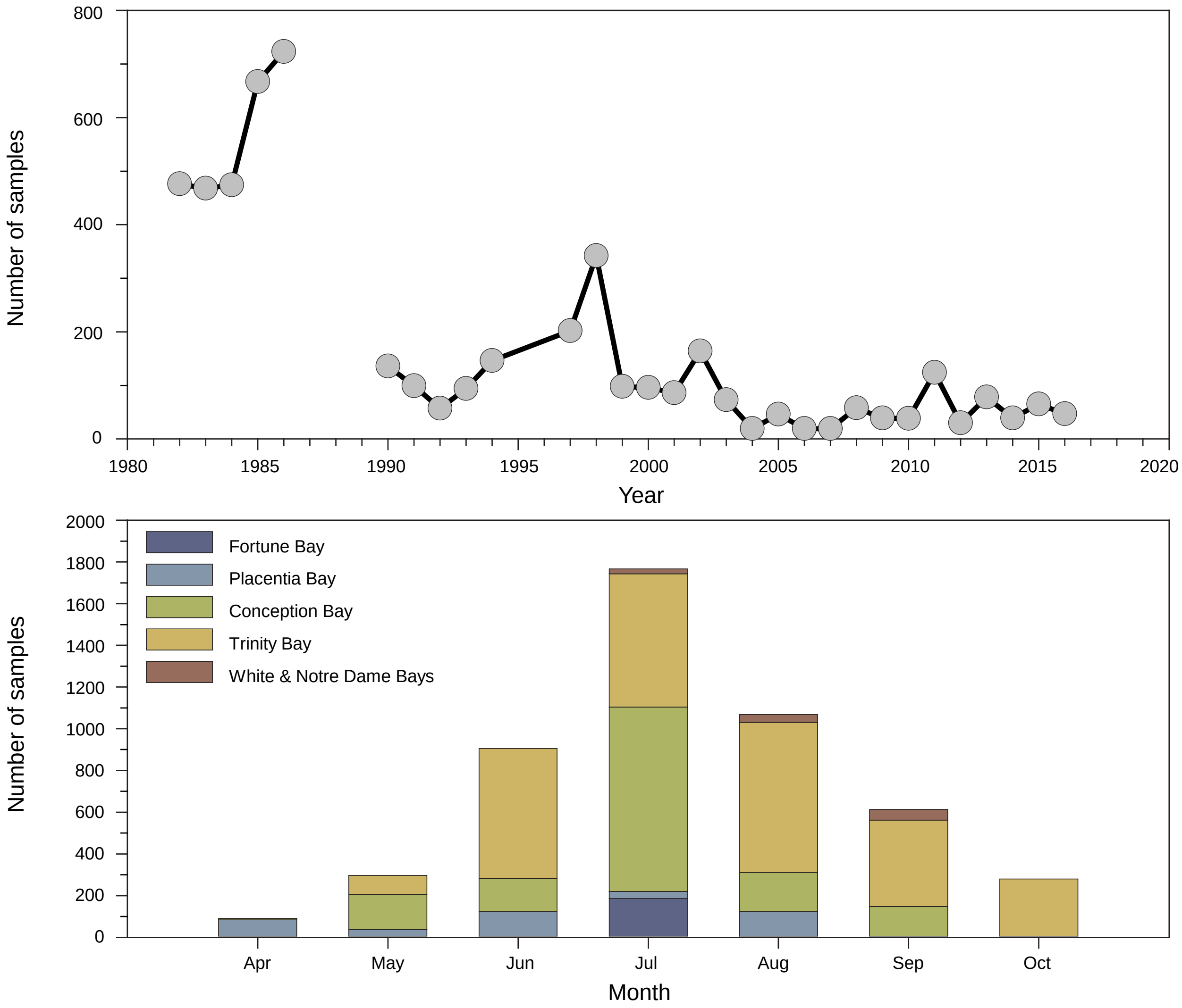

Fig. 3. Yearly total number of ichthyoplankton samples (top panel) and seasonal distribution of sample numbers for each bay (bottom panel). There were too few samples from Bonavista Bay to include in the graph.

Bay. Infrequent taxa, identified in fewer than 90 samples included: *Liopsetta putnami* (Pleuronectidae), *Pollachius virens* (Gadidae), *Anarhichas lupus* (Anarhichadidae), *Gymnocanthus tricuspis* (Cottidae), *Icelus* sp. (Cottidae), *Triglops* sp. (Cottidae), *Hemitripterus americanus* (Hemitripteridae), *Urophycis* sp. (Phycidae), *Hippoglossus hippoglossus* (Pleuronectidae), and *Gaidropsarus* sp. (Gaidropsaridae), in descending order of relative occurrence. When frequent and infrequent taxa from our collections are considered, Pleuronectidae was the most specious family (6), followed by Cottidae (4), Stichaeidae (3), Gadidae (3), Agonidae (2), with all other families represented with only one consistently identified species. However, Cottidae, Stichaeidae, Liparidae and Sebastidae likely consisted of 7, 4, 4, and 3 species, respectively, but identification to species were inconsistent or not possible. Egg type and diameter were collated from Scott and Scott (1988), Fahay (1992a) and Fahay (1992b). Taxonomic names were verified from the World Register of Marine Species (https://www.marinespecies.org/).

Analyses

The first part of the analytical approach of this study involved the use of multivariate methods aimed at synthesizing and describing general seasonal community structure, and evaluating patterns of change in diversity among the different geographic areas around Newfoundland. These analyses address the first two objectives described in the introduction. The second part of the analyses aimed to describe the seasonal cycle of individual species, the variation in length of larvae (minimum and maximum), and contrast the overall abundance prior and after the collapse of major fish stocks, and the substantial changes in ecosystem state that occurred at the same time.

Table 1. Scientific name, common name, family and egg type (demersal, pelagic, viviparous) and diameter (mm) of the taxa used in the analysis of ichthyoplankton community structure. Egg type and diameter based on Scott and Scott (1988), Fahay (1992a) Fahay (1992b) and Froese and Pauly (2024). The taxonomic order is based on the phylogenetic classification of Betancur-R *et al.* (2017) and the NIH National Library of Medicine National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/).

Scientific name	**Common name**	**Family**	**Egg type & diameter**
Lumpenus spp.	Blenny	Stichaeidae	Demersal – 1.5 mm[1]
Stichaeus punctatus	Arctic shanny	Stichaeidae	Demersal – 1.7 mm
Ulvaria subbifurcata	Radiated shanny	Stichaeidae	Demersal – 1.55 mm
Liparis spp.	Snailfish	Liparidae	Demersal – 0.8–1.4 mm
Pholis sp.	Gunnel	Pholidae	Demersal – 1.7–2.2 mm
Sebastes spp.	Redfish	Sebastidae	Ovoviviparous – 6.0–8.9 mm[2]
Myoxocephalus spp.	Sculpin	Cottidae	Demersal – 1.5–2.5 mm[3]
Leptagonus decagonus	Atlantic poacher	Agonidae	Demersal – unknown
Aspidophoroides monopterygius	Alligatorfish	Agonidae	Demersal – unknown[4]
Cyclopterus lumpus	Lumpfish	Cyclopteridae	Demersal – 2 mm
Ammodytes sp.	Sand lance	Ammonytidae	Demersal – 0.9–1.0 mm
Tautogolabrus adspersus	Cunner	Labridae	Pelagic – 0.84–0.92 mm
Mallotus villosus	Capelin	Osmeridae	Demersal – 0.90–1.16 mm
Scomber scombrus	Atlantic mackerel	Scombridae	Pelagic – 1.1–1.3 mm
Glyptocephalus cynoglossus	Witch flounder	Pleuronectidae	Pelagic – 1.10–1.45 mm
Hippoglossoides platessoides	American plaice	Pleuronectidae	Pelagic – 1.5–2.8 mm[5]
Pseudopleuronectes americanus	Winter flounder	Pleuronectidae	Demersal – 0.71–0.96 mm
Myzopsetta ferruginea	Yellowtail flounder	Pleuronectidae	Pelagic – 0.8–0.9 mm
Enchelyopus cimbrius	Fourbeard rockling	Lotidae	Pelagic – 0.65–0.75 mm
Gadus morhua	Atlantic cod	Gadidae	Pelagic – 1.2–1.6 mm
Boreogadus saida	Arctic cod	Gadidae	Pelagic – 1.5–1.9 mm
Clupea harengus	Atlantic herring	Clupeidae	Demersal – 1.0–1.4 mm

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1 Assuming that *Lumpenus* spp. is principally representative of *Leptoclinus maculatus*

2 Length at extrusion (“hatch”) is species dependent: *Sebastes fasciatus* (7.0 mm), *Sebastes mentella* (6.0–8.9 mm), *Sebastes norvegicus* (6.7–7.2 mm).

3 Egg diameter is species dependent: *Myoxocephalus scorpius* (2.0-2.5mm), *Myoxocephalus scorpioides* (unknown), *Myoxocephalus octodecemspinosus* (1.9–2.3 mm) and *Myoxocephalus aenaeus* (1.5–1.7 mm).

4 Egg diameter 0.8–1.2 mm observed in females of related species *Aspidophoroides olrikii*. Based on Frost, K. J., and Lowry, L. F. 1983. Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort seas, 1976–77. *NOAA Technical Report* NMFS SSRF-764: 22p.

5 *Hippoglossoides platessoides* eggs have a large perivitelline space. Embryo length at hatch is 4–6 mm, similar to Atlantic cod (*Gadus morhua*) at 3.3–5.7 mm.

Ichthyoplankton community

Analytical design of this study was developed from explorations of observations from the various collections and data series. To describe overall seasonal patterns of larval production, the first steps focussed on overall abundance and diversity, along with comparison of species richness and Shannon’s diversity index among bays. We followed this analysis with a description of the average seasonal succession of fish taxa in Placentia, Conception, Trinity, and the combined data from Notre Dame and White Bays (hereafter referenced as the northern bays). This description of the seasonal abundance and probability of occurrence of each taxon synthesizes patterns of reproduction of dominant fish in coastal Newfoundland. Finally, a multivariate comparison of community structure among all bays and prior to and following the major change in the Newfoundland coastal ecosystem provided a means to quantify and contrast species composition.

Abundance, richness and diversity

We provide a general description of the seasonal cycle in overall ichthyoplankton abundance, and variation in density within surveys and among sampling stations, based on the sum of all fish larvae within each sample.

We estimated alpha diversity for each sample as species richness ($N_0 = q$, where q is the number of taxa) based solely on taxa presence, giving rare and abundant taxa equal importance. For each sample we estimated Shannon's entropy ($H_1 = -\sum_{i=1}^{j} p_i \ln p_i$, where p_i is the proportion of each species present in each sample), with the maximum value dependent on overall species richness of the sample ($\ln q$). Shannon's entropy diminishes the relative weight of rare species.

To assess our ability to evaluate beta diversity, we estimated the pattern of variation in species composition among sites in the geographic area of separate surveys within research missions, when applicable, based on the approach developed by Baselga (2012). This approach separates the elements of nestedness, when the biotas of sites with smaller numbers of species represent subsets of the biotas at richer sites, from spatial turnover, which involves the replacement of some species by others from site to site. Jaccard dissimilarity (β_{JAC}) is the sum of the turnover component of Jaccard dissimilarity (β_{JTU}) and nestedness-resultant component of Jaccard dissimilarity (β_{JNE}). Estimates of dissimilarity components were obtained using R package `betapart` (Baselga *et al.*, 2023) using R 4.3.1 (R Core Team, 2023). Baselga (2010) noted high sensitivity to sample size in comparison of beta diversity components among sites, a real concern for our study because of substantial variation in numbers of sites sampled among the various surveys collated for this synthesis. Baselga (2010) used randomization to contrast sites with different numbers of observations, but such an approach would place severe limitations on the inferences we could draw in comparing surveys with fewer sites relative to more comprehensive collection programs. Instead, we used all of our surveys and estimated the dependency in the three dissimilarity metrics on the number of samples contributing to each survey. Based on *a priori* data exploration, we fitted estimates of both β_{JAC} and β_{JTU} to a three parameter exponential rise to a maximum ($\beta_i = \beta_{i,0} + a_i(1 - e^{-b_i N})$), where β_i is either β_{JAC} or β_{JTU}, N is sample size, and a_i and b_i are estimated parameters, which we report as average ± standard error), whereas we fit a three parameter exponential decay to estimates of β_{JNE} ($\beta_i = \beta_{i,0} + a_i e^{-b_i N}$). Understanding the sample size dependency in estimates of dissimilarity provides insight into survey requirements to evaluate effectively how to quantify beta diversity in coastal regions, and assess potential factors and processes driving the larval fish community. An analysis of variance evaluated whether the residuals from these relationships differed significantly among bays and ecosystem states.

Seasonal occurrence cycle

We based our description of the seasonal cycle in the occurrence and production of larval fish across all bays on the presence of each fish taxon in all the samples from all research missions over 10-day time intervals. We then estimated the probability of occurrence as the sum of samples in which each taxon was present relative to the total number of samples collected during each time interval. Assessment of patterns in the seasonal production of larval fish, a metric of reproductive activity, used group-average clustering based on square-root transformation of the probability of occurrence among all samples from all bays. These comparisons used PRIMER's CLUSTER algorithm combined with an evaluation of the similarity profile test (SIMPROF) (Clarke and Gorley, 2006).

Species composition and community structure

We developed a general description of the species composition among bays from the relative species composition based on the arithmetic average density of fish larvae from all samples, including zero values, in each month for each bay with seasonal coverage. We defined the relative contribution of each taxon qualitatively as minor for species with a maximum relative contribution to species composition of <3%, moderate for species with maximum relative contribution of 3–10%, major for species with maximum relative contribution of 10–30%, and dominant for those with a maximum contribution >30%.

To evaluate the seasonal cycle in larval fish composition, we used a principal coordinate analysis (PCoA) of community structure, which provides a relative comparison of different bays and ecosystem states in multivariate space. A PERMANOVA (permutational multivariate analysis of variance) comparison based on location (bay), month, their interaction, and period of ecosystem state (pre-collapse [1982–1986] and post-collapse [1990–2016]), evaluated whether either of these factors had a statistically significant influence on similarity and dissimilarity in species composition by testing for pairwise differences among groups. An analysis of similarity (ANOSIM) evaluated the findings of the PERMANOVA, but based on a non-parametric assessment of the distances among samples within groups relative to distances among groups. This approach thus provided a sense of scale of the findings of the parametric analysis. A two-way analysis of similarity/dissimilarity percentages (SIMPER) identified which species had greater influence in differentiating among bays and months using pairwise comparisons. The PCoA, PERMANOVA, and ANOSIM used a resemblance matrix of community composition abundance data of all the samples based on the Hellinger distance (Legendre and Gallager, 2001). SIMPER two-way (bay, month) analyses used both Euclidean distance of log-transformed abundance data and a Bray-Curtis similarity matrix based on presence/absence transformation. These multivariate analyses explored the composition of patterns of variation in the larval fish community in coastal Newfoundland. All multivariate analyses were conducted using PRIMER v 6.1.13 (Clarke and Gorley, 2006) and PERMANOVA+ v 1.0.3 (Anderson *et al.*, 2008).

Species specific cycles

For each taxon, we report the data and narrative describing seasonal cycles in probability of occurrence, average density, and minimum and maximum length in relation to day of year in the supplementary material. Separation of the data from Conception and Trinity Bays into pre- and post-collapse periods provided a comparison between ecosystem states. We based the seasonal cycle in the occurrence and production of each taxon of larval fish on the presence of each fish taxon in all the samples over 10 day time intervals for each research mission and bay. To estimate the probability of occurrence, we summed the number of samples in which each taxon was present relative to the total number of samples collected during each interval, bay and research mission, and reported it in relation to the average day of year of each of those sample collections. We reported patterns in the seasonal production of larval fish for each species, bay and research mission, a metric of reproductive activity, as the arithmetic average density (larvae·m^{-2}) based on all non-zero observations from the aggregation of data subsets. We established a cutoff of ~ 1 larva·100 m^{-2} for most reporting to provide scope in the graphics presented in the supplementary material. Because data on larval length were reported unevenly among the various data sources, we used only the data from Conception Bay to estimate the minimum and maximum length of larvae present, estimated for each day of the year across all research missions in that Bay. Length observations provided an indicator of spawning or reproduction when small individuals were present, as well as a metric of larval development, in relation to day of year.

To contextualize our new knowledge of temporal shifts in timing of reproduction or spawning activity achieved from our analyses, we contrasted our observations with information from syntheses for the northwest Atlantic (Scott and Scott, 1988; Fahay, 1992a; Fahay, 1992b). To ensure that we included the latest information available, we conducted a search of the Web of Science using the search terms TS = *taxon name* AND PY = 1986–2024 AND (TS = larva* OR TS = egg*).

We based the order of presentation of taxa on the outcome of the cluster analysis of the seasonal cycle in the occurrence of larval fish, and estimated the average day of occurrence as the weighted probability of occurrence on the midpoint for each 10 day interval (i), starting from day 90, across all bays ($\bar{D}_{taxa} = \left[\sum_{i=95}^{i=325} p_i \cdot i\right] / \sum_{i=95}^{i=325} i$, for $p_i > 0$).

Results

Ichthyoplankton community

Abundance, richness and diversity

Seasonal change in total average larval fish density in all coastal bays varied by 3.2, 2.8 and 1.5 orders of magnitude in Placentia, Conception, and Trinity Bays, respectively (Fig. 4). Average within-survey total density varied by 1.78 orders of magnitude (range: 0.4 – 4.0), demonstrating a high degree of spatial heterogeneity in the abundance of fish larvae within bays.

Low species richness in May, June, and September contrasted with highest values in July and August (Fig. 5), and richness was generally greater in Conception and Placentia Bays relative to Trinity and northern Bays. A

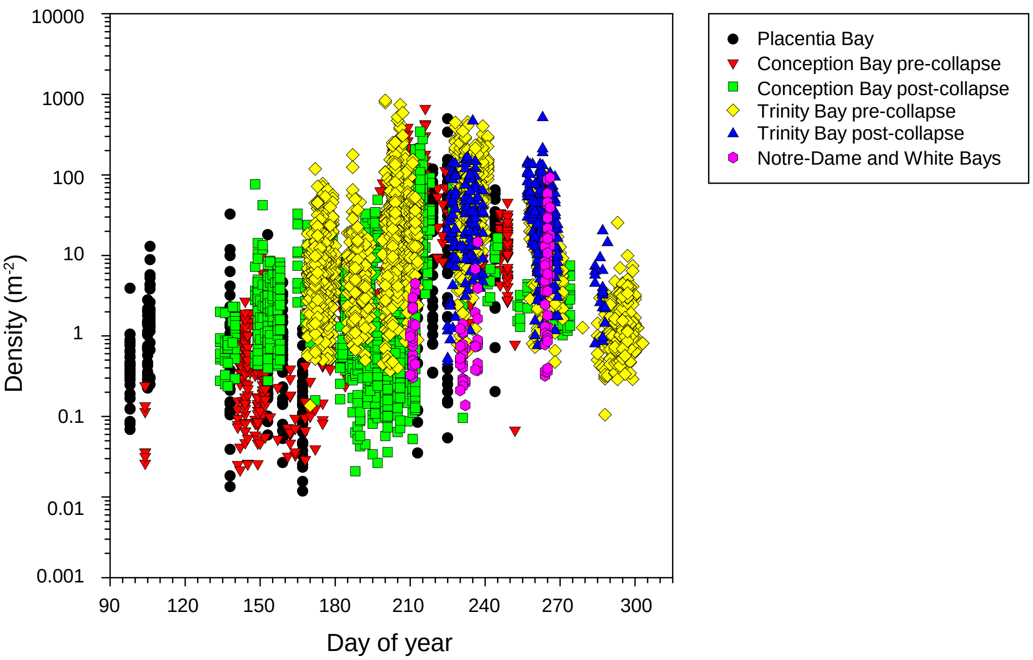

Fig. 4. Seasonal cycle in total larval fish density (m^{-2}) in relation to day of year for each bay in the study. Each symbol represents a single sample.

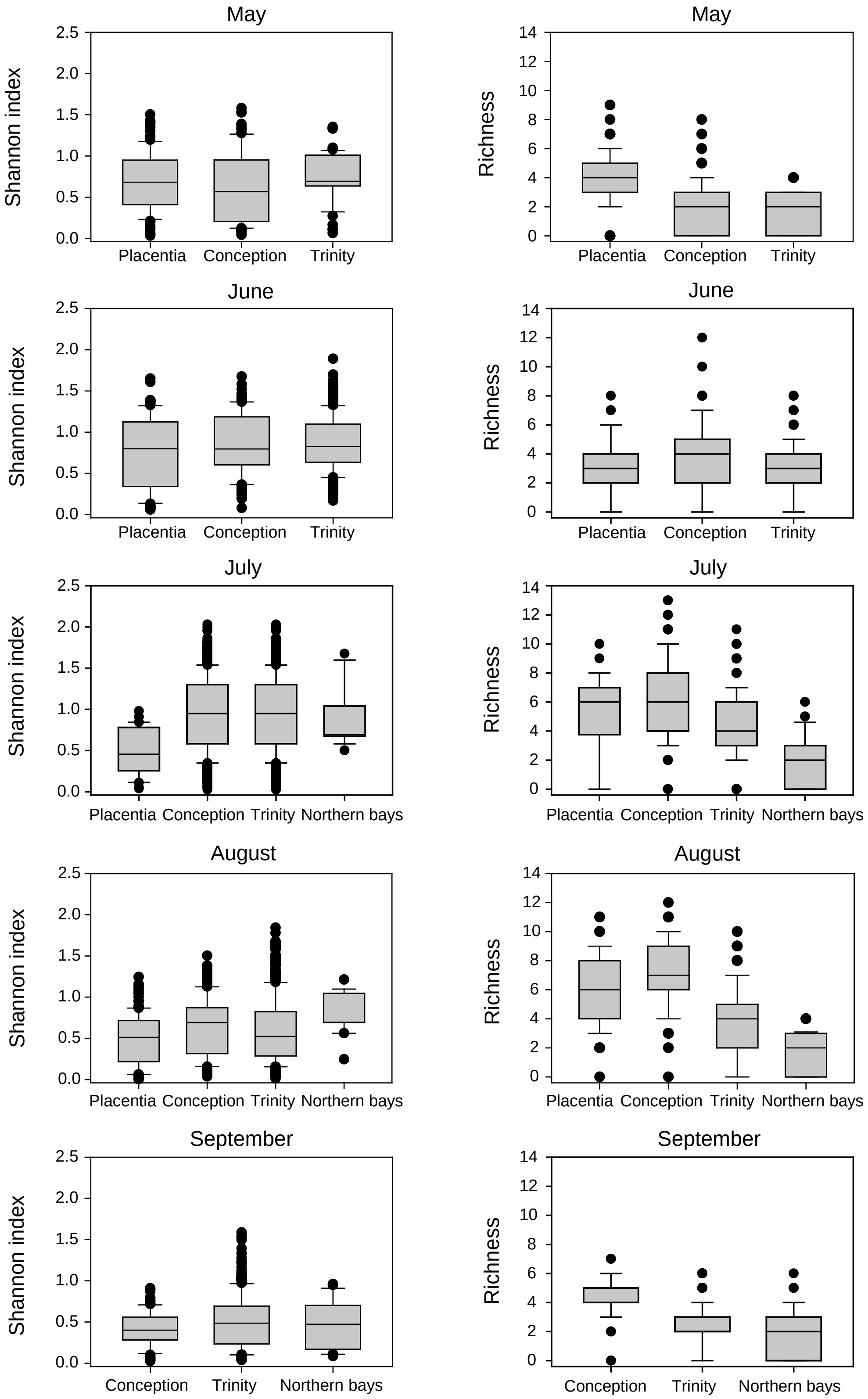

Fig. 5. Monthly distribution of Shannon's index of entropy (left-hand panels) and species richness (right-hand panels) for each bay. Distributions are based on all samples collected during each month. Boxes represent upper and lower quartiles and median, error bars represent 10th and 90th percentiles and circles represent outliers. Data for Notre Dame and White Bays are combined as Northern Bays.

maximum of 13 taxa occurred in a given sample from single surveys, although total richness among samples from that location was generally greater. There were 766 samples with only one taxon present. Despite generally similar Shannon's entropy among bays, a greater range of values characterized Conception and Trinity Bays relative to other locations, indicative of a more even distribution in relative abundance within samples. The limited number of research missions from Notre Dame and White Bays limited our capacity to derive inferences in the comparison with other bays. The distribution of Shannon's entropy only achieved near maximum values for richness levels of 5 species or fewer (Supplementary Fig. S3). Median entropy increased from 0.48 at richness of 2 to 0.98 at richness of 8 taxa, after which it declined to a value of ~ 0.5 at the highest richness levels. Median entropy was 69% of the expected maximum at a richness of 2 and progressively declined to ~20% of the expected maximum at the highest richness levels, indicative of increasing relative dominance of one or a few taxa in each sample as overall richness increased.

Variation in Jaccard dissimilarity (β_{JAC}), as well as elements of nestedness and spatial turnover, depended strongly on the number of sampling sites among surveys (Fig. 6). All non-linear relationships were statistically highly significant ($p < 0.001$). Both β_{JAC} and β_{JTU} reached an asymptote (0.97 and 0.94, respectively) but their intercepts ($\beta_{0,JAC} = 0.37$ (± 0.054), $\beta_{0,JTU} = 0.21$ (± 0.082), respectively) and rates of increase ($b_{JAC} = 0.093$ (± 0.0093), $b_{JTU} = 0.058$ (± 0.0098)) differed significantly. The exponential decline in nestedness (β_{JNE}) to a low of 0.03 at a large sample size was highly significant ($p < 0.001$). The inflexion point in Jaccard dissimilarity (β_{JAC}) occurred at a sample size of ~25. However, the contribution of nestedness and spatial turnover varied greatly until sample size reached ~50 stations, with particularly high variability at a sample size of 25 stations or fewer. These patterns indicate that the processes of larval production (*e.g.*, hatching, emergence from demersal sites), physical mixing, and transport reach an equilibrium in their contribution to beta diversity patterns only once the entire bay has been sampled comprehensively. The residuals of Jaccard dissimilarity ($p < 0.05$) and nestedness ($p < 0.05$) differed significantly among bays, but spatial turnover did not ($p > 0.1$). However, only one bay contributed to the significant results, pre-collapse Conception Bay for Jaccard dissimilarity, and post-collapse Trinity Bay for nestedness, with extreme outliers contributing heavily to these outcomes, suggesting only moderate differences among coastal areas.

Seasonal occurrence cycle

Cluster analysis of the seasonal cycle in larval fish occurrence across all bays revealed groupings reflective

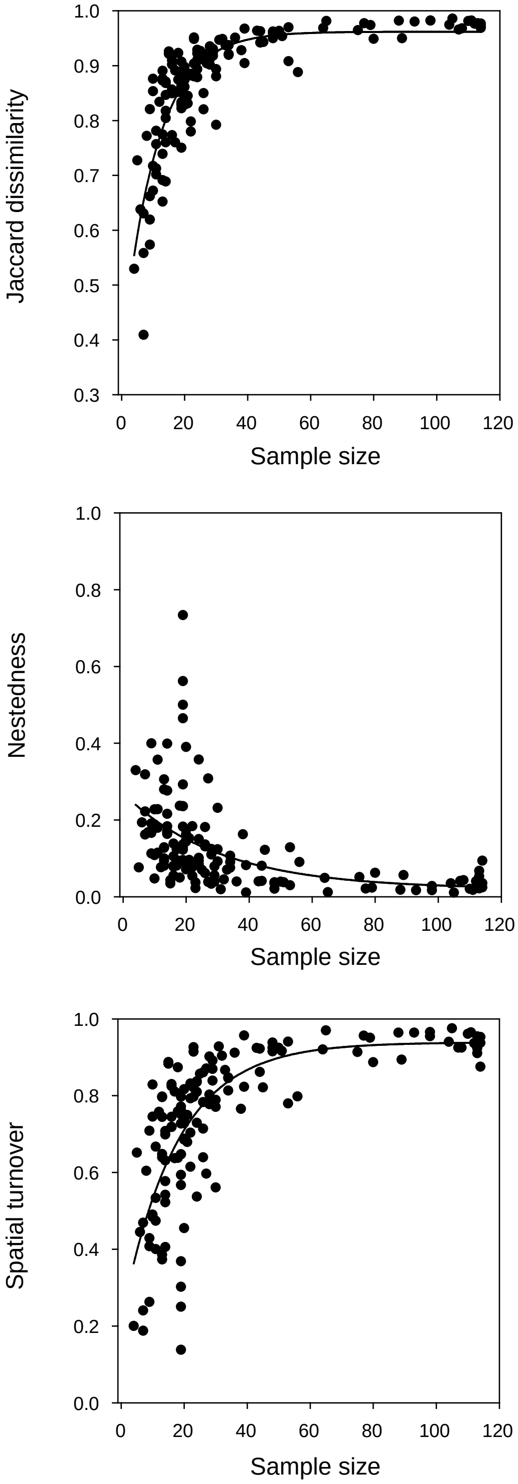

Fig. 6. Sample size (N) dependent patterns of variation in Jaccard dissimilarity (top panel) [$\beta_{JAC} = 0.37 + 0.59 (1 - e^{-0.093N})$, $r = 0.85$], nestedness (center panel) [$\beta_{JNE} = 0.02 + 0.25 e^{-0.033N}$, $r = 0.49$], and spatial turnover (bottom panel) [$\beta_{JTU} = 0.21 + 0.73(1 - e^{-0.058N})$, $r = 0.74$].

of the timing of larval production and period during which larvae of each taxon occurred in the plankton. Gunnel (*Pholis* sp.), alligatorfish (*Aspidophoroides monopterygius*), sculpin (*Myoxocephalus* spp.), sand lance (*Ammodytes* sp.), and blenny (*Lumpenus* spp.) (cluster ***b*** – Fig. 7, Supplementary Figure S4) larvae appeared first in the spring, with peak occurrence in late March/early April, likely indicative of winter spawning (Supplementary Figs. S5–S9). Sand lance and blenny were seasonally dominant taxa in Placentia and Conception Bays, respectively, whereas sculpin and gunnel were moderate contributors to species composition, and alligatorfish were minor contributors to the larval community (Fig. 8). Clustering linked the occurrence of Arctic shanny (*Stichaeus punctatus*) (cluster ***a***) (Supplementary Fig. S10) with that of the previous group (cluster ***b***) with a similarity of 62.5%, but Arctic shanny first appeared in April and peaked in late May, at which times they were dominant contributors to community structure (Fig. 8). The next group (cluster ***c***), with 45% similarity with the previous two clusters, consisted of Arctic cod (*Boreogadus saida*) and Atlantic poacher (*Leptagonus decagonus*), which were present during the earliest surveys but peaked in relative occurrence in late June and disappeared from the plankton shortly thereafter (Supplementary Figs. S11–S12). Both species were minor contributions to larval fish community structure. The next grouping consisted of several clusters (***f***, ***g***, ***h***, ***i***) in which numerous species of fish larvae appeared over an extended period that varied among clusters, ranging from April to October (cluster ***h*** – American plaice (*Hippoglossoides platessoides*) and Atlantic cod (*Gadus morhua*)), April to August (cluster ***i*** – snailfish (*Liparis* spp.) and radiated shanny (*Ulvaria subbifurcata*)) (Supplementary Figs. S13–S16). These taxa grouped with less frequent taxa with long periods of occurrence from April to August (cluster ***g*** – redfish (*Sebastes* spp.) and winter flounder (*Pseudopleuronectes americanus*)) and June to October (cluster ***f*** – yellowtail founder (*Myzopsetta ferruginea*)) (Supplementary Figs. S17–S19). American plaice dominated at times whereas cod, snailfish, and radiated shanny were major contributors to the ichthyoplankton community (Fig. 8). Members of cluster ***g*** were moderate contributors to the larval community whereas yellowtail flounder was a minor taxon in the community (Fig. 8). Clusters ***f***, ***g***, ***h***, ***i*** likely occurred across seasons from spring to

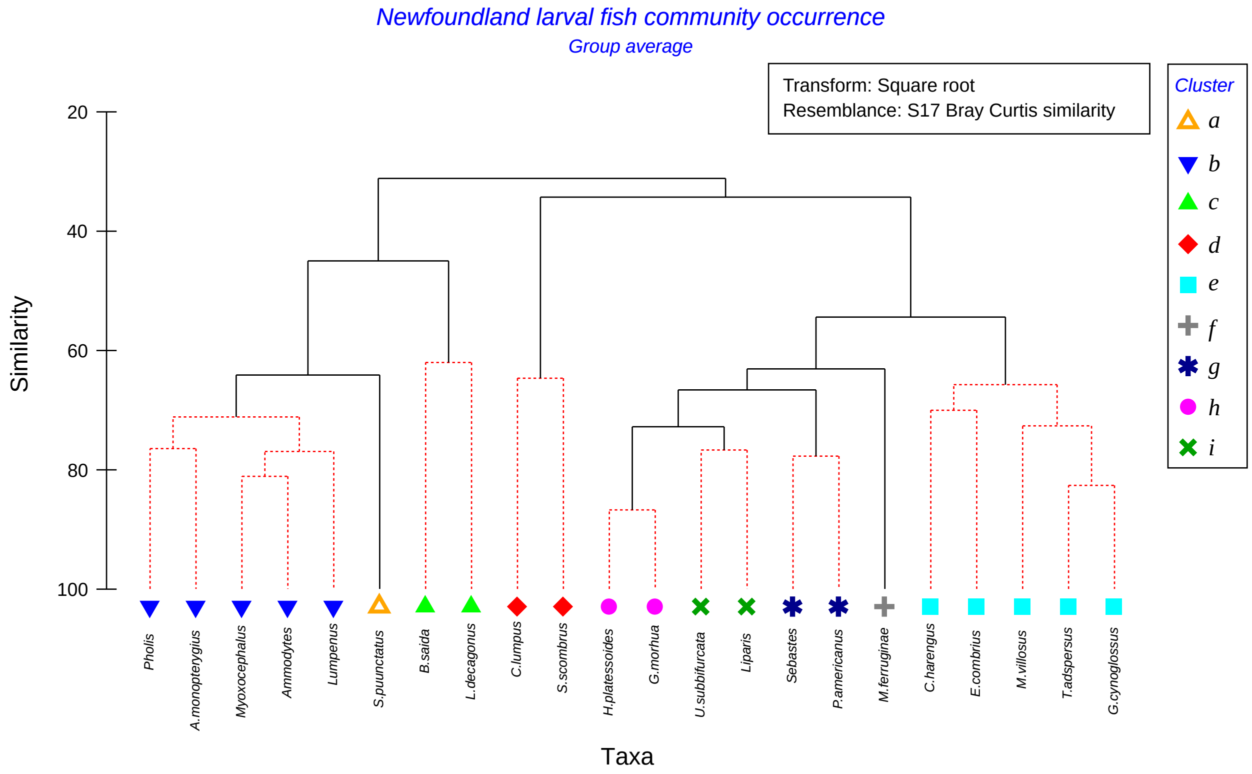

Fig. 7. Dendrogram of species aggregation based on cluster analysis of relative occurrence across all bays and sampling dates. Joined solid black lines represent statistically significant groupings. Taxa names are either represented as genus or abbreviated genus and species name. Colored symbols represent individual clusters, and are matched with histograms in Supplemental Figure S4. Position of taxa on the x-axis of the dendrogram reflect general timing of occurrence, from early occurrence on the left (cluster ***b***) to later occurrence on the right (cluster ***e***). Note that taxa in cluster ***d*** start to occur later than taxa in clusters ***f***, ***g***, ***h***, and ***i*** but the occurrence of taxa from cluster ***d*** ends earlier than that of the taxa in clusters ***f***, ***g***, ***h***, and ***i***.

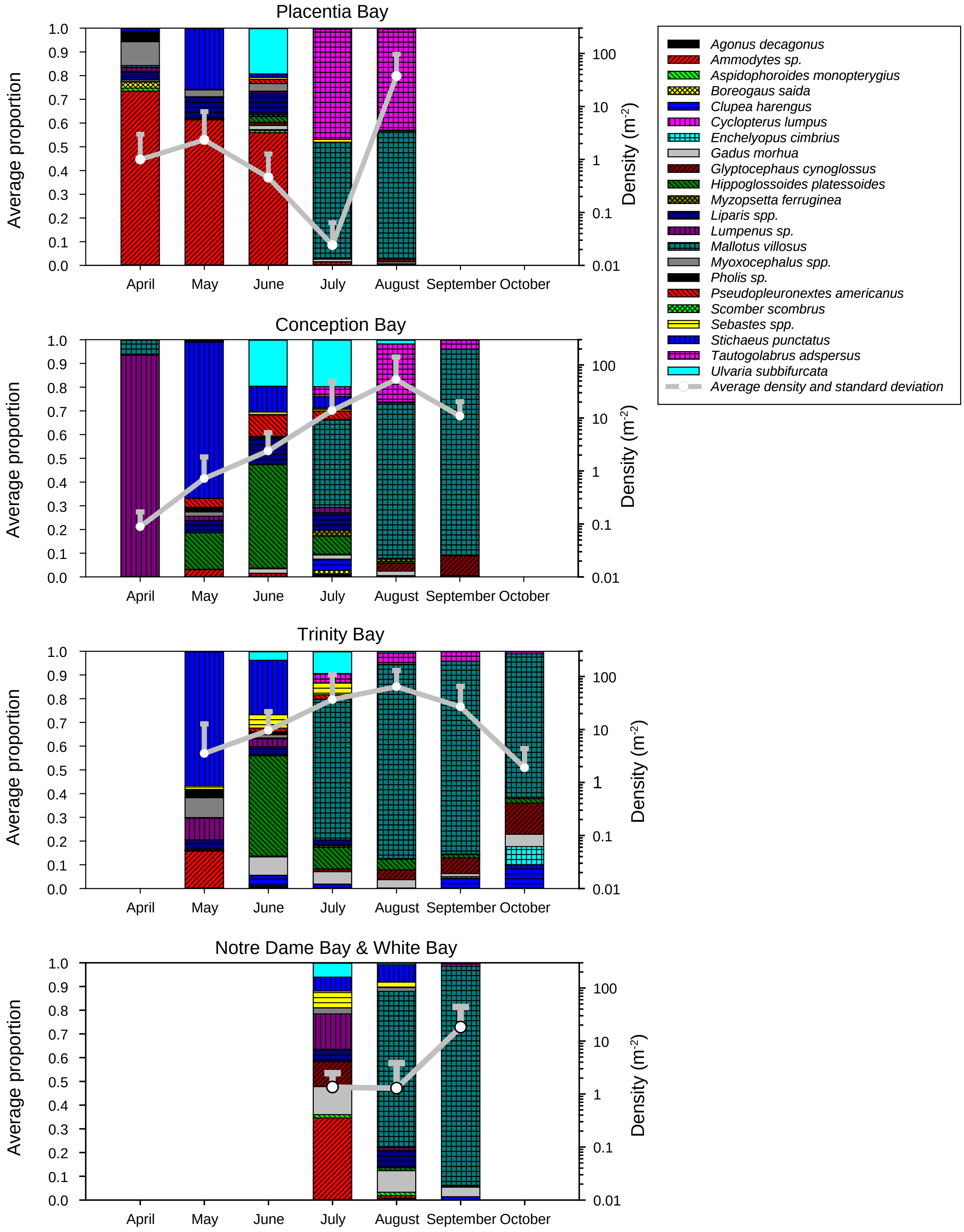

Fig. 8. Average monthly species composition proportionally and total ichthyoplankton density (larvae·m^{-2}, light grey line – error bar represents + 1 standard deviation) of larval fishes from Placentia, Conception, Trinity, and Notre Dame and White Bays.

fall and link with 72.8% (***h***, ***i***), 66.6% (***g***) and 63.1% (***f***) similarity. The next group consisted of five taxa that occurred mostly from late June until September or October (cluster ***e*** – Atlantic herring (*Clupea harengus*), fourbeard rockling (*Enchelyopus cimbrius*), capelin (*M. villosus*), cunner (*Tautogolabrus adspersus*), and witch flounder (*Glyptocephalus cynoglossus*)), for which spawning likely takes place from June through August (Supplementary Figs. S20–S24). Clusters ***f***, ***g***, ***h***, and ***i*** join with cluster ***e*** at 54.4% similarity. Herring and rockling were moderate components of the larval community, witch flounder was a major element, and capelin and cunner were dominant species (Fig. 8). The final group (cluster ***d*** – lumpfish (*Cyclopterus lumpus*) and Atlantic mackerel (*Scomber scombrus*)) occurred in very low overall relative numbers during restricted periods from late June to late August (Supplementary Figs. S25–S26). The period of occurrence for lumpfish may represent a dispersal window following emergence of the larvae from the nests, normally guarded by the males, whereas the occurrence of Atlantic mackerel aligns with the seasonal migration of adults along with limited spawning activity in coastal Newfoundland. Both lumpfish and mackerel were minor contributors to the ichthyoplankton community. Cluster ***d*** linked with other summer occurring taxa with 34.3% similarity. All cluster linkages reported above were statistically significant ($p < 0.05$ or less), based on 999 permutations. The seasonal succession of taxa also revealed a negative, significant correlation between the average day of maximum occurrence and egg diameter ($r = -0.51$, $p < 0.05$, $n = 19$), whereby species with larger eggs spawned earlier in the year.

Species composition and community structure

Average species composition strongly varied seasonally and differed greatly among bays (Fig. 8). In all bays, larval fish density appeared at low levels in the spring and peaked in August, although low densities were present during July in Placentia Bay. One of two species of larval fish generally dominated Placentia Bay, with the greatest complexity in June when the larval assemblage shifted from sand lance domination to a community shared primarily by capelin and cunner. One or two species dominated the ichthyoplankton community in Conception Bay in April/May (blenny and Arctic shanny, respectively) and August/September (capelin, cunner, and witch flounder), but greater complexity and changes in species occurred in June and July, during which 19 and 22 taxa occurred, respectively. High densities of American plaice, Atlantic herring, winter flounder, and radiated shanny occurred in Conception Bay in June, followed by increasing importance of capelin larvae in July. Larval fish species composition in Trinity Bay distinctly differed from that of Placentia and Conception Bays in that Arctic shanny, blenny, sculpin, and sand lance dominated in May, followed by the continued presence of Arctic shanny and growing importance of American plaice and Atlantic cod in June. However, in July, capelin became the dominant taxon and remained so well into October, when the relative importance of witch flounder, Atlantic herring, fourbeard rockling, and Atlantic cod increased, albeit at a time of lowest overall density of larvae. Larval fish species composition in Notre Dame and White Bays highlights a later production cycle of ichthyoplankton species relative to other bays, with very low densities throughout the summer but with a substantial increase in September, largely driven by capelin larval production. A complex mix of taxa in July suggests a combination of local spawning by coastal species and possibly larval import from offshore spawners. Sand lances, blenny, Atlantic cod and witch flounder dominated July samples, although redfish, Arctic and radiated shanny, and snailfish also contributed notably to the larval fish assemblage. Capelin only appeared in August, when they became the dominant taxon, although Atlantic cod, snailfish, and Arctic shanny remained important elements of the ichthyoplankton community. In September, capelin dominated the larval fish assemblages, with Atlantic cod as the next most abundant species. All the bays shared the common feature of relative dominance and high densities of capelin starting in July and persisting throughout the remainder of the summer and fall. Most taxa occurred in all the bays, with the exception of lumpfish in Placentia Bay and the northern bays, as well as winter flounder, gunnel, and Atlantic mackerel in the northern bays. Arctic cod only occurred in Conception and Placentia Bays. The limited seasonal coverage of Notre Dame and White Bays constrained our capacity to comment extensively on "missing" taxa but we note that 17 of the 22 taxa considered in this synthesis occurred in at least one sample.

Principal coordinate analysis revealed striking similarities among bays in the progression of the seasonal cycle in the larval fish assemblage with positive loadings on PCoA 1 at the start of the larval production cycle and negative loadings in August, September, and October (Fig. 9). Notre Dame and White Bays assemblages in June resembled those in April and May in the more southerly bays, with average loadings in August very distant from those of other bays on PCoA 1 but similar to those of Placentia Bay on PCoA 2. The greatest differences among the bays appear on PCoA 2 and PCoA 3. Similar cycles on PCoA 1 and PCoA 2 characterize pre- and post-collapse Conception Bay and pre-collapse Trinity Bay from May to September with the greatest differentiation in July. However, major changes in the seasonal larval production cycle during the post-collapse period in Trinity Bay, with community loading on PCoA 1 and PCoA 2 in June similar to that of the pre-collapse system in May, in contrast to a similar pre- and post-collapse July assemblage. The Placentia Bay larval production cycle on the first two principal coordinates distinctly differs from that of Conception and Trinity Bays, except in April and May, which likely reflects the strong influence of the continued presence in all bays of sand lance in June and the high contributions of

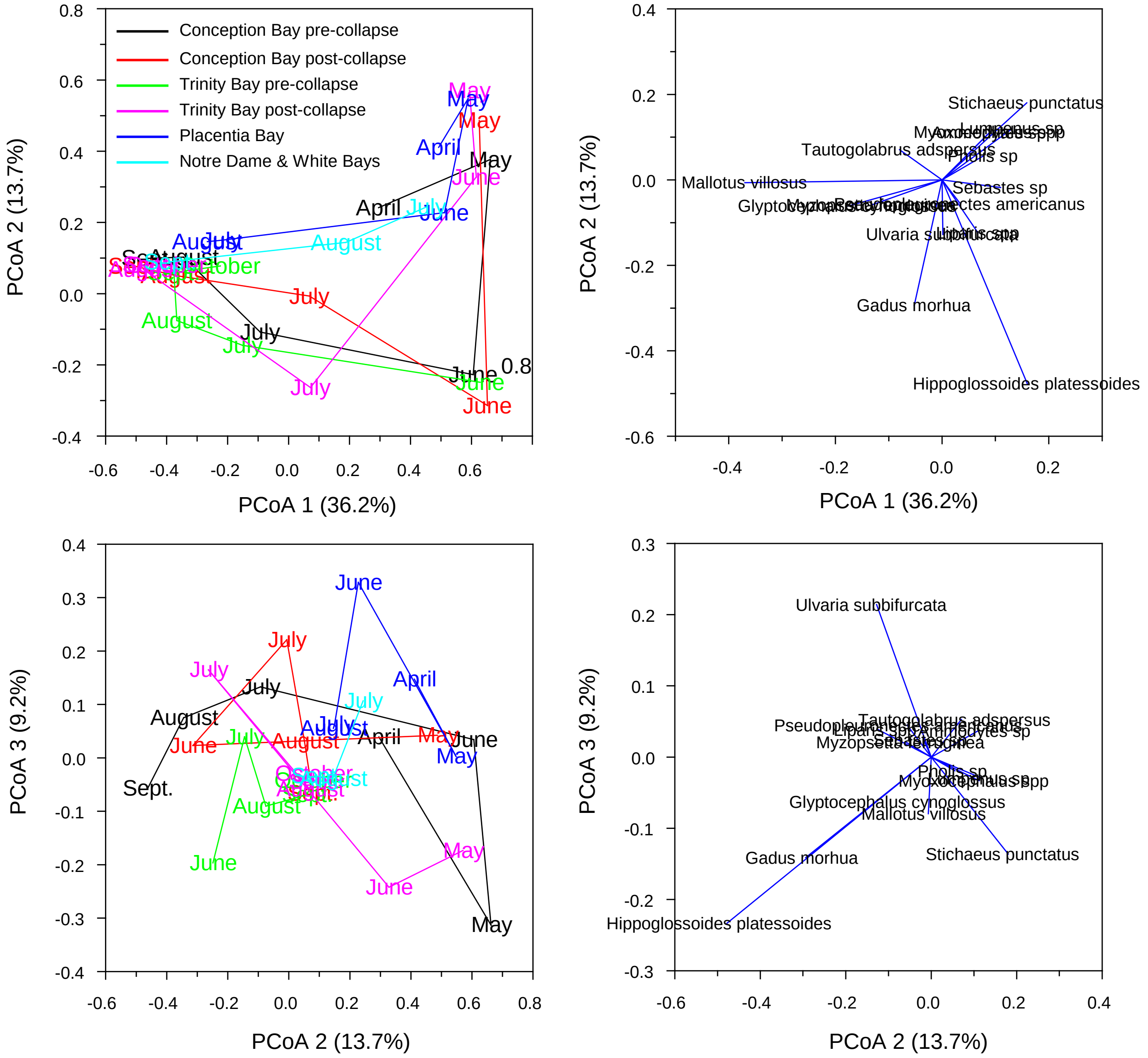

Fig. 9. Plot of average monthly principal coordinate loading for each bay and ecosystem state for the first three principal coordinates (left-hand panels) and average loadings for each taxon across all bays on each principal coordinate (right-hand panels).

cunner and capelin in July and August. Placentia Bay also differed from the other bays as a result of the lower overall abundance of commercial groundfish species, likely a reflection of the post-collapse state of the ecosystem on the south coast of Newfoundland. PCoA 3 likely characterizes differences in the occurrence of relatively less abundant species among the bays that we cannot synthesize succinctly (see species-specific cycles). The species loadings on the first two principal coordinates demonstrate the general seasonal succession of species. Winter/spring spawners (*e.g.*, Arctic shanny, sculpin) load positively on PCoA 1 and PCoA 2, spring/summer spawners (*e.g.*, Atlantic cod, American plaice, radiated shanny) load positively on PCoA 1 and negatively on PCoA 2, and late summer/fall spawners (*e.g.*, cunner, witch flounder, capelin) load negatively on PCoA 1 with low loadings on PCoA 2. The strongest influence on PCoA 3 reflects differences in the relative abundance of Arctic shanny, Atlantic cod, American plaice, and radiated shanny among the bays, with relatively minor differences among other taxa.

PERMANOVA analysis of fixed effects of bay and month, which partitions the variance among factors based on Euclidean distances to assess multivariate dispersion among groups, revealed highly significant ($p < 0.001$)

effects of bay, month and month·bay interactions, explaining 30.7% of the total variance in larval fish assemblages, based on 999 permutations and Type III sums of squares. Month accounted for 19.7% of the variance, whereas month·bay interactions accounted for 7.2%, and differences among bays accounted for 3.8%. These results confirm the patterns noted in the principal coordinates analyses that revealed strong similarity in seasonal cycles in larval production, but which differed slightly among bays in terms of timing of occurrence of different taxa. All pairwise comparisons among bay, including pre- and post-collapse comparisons within Conception and Trinity Bays, were highly significantly different ($p < 0.001$), as were comparisons among months. Two-way analysis of similarities (ANOSIM) did not fully confirm this result in that it detected no significant differences among pre- and post collapse larval fish communities in Conception Bay ($p > 0.3$), and no significant difference between larval fish communities in Trinity and Conception Bays during the post-collapse period ($p > 0.6$). All other pairwise comparisons indicated highly significant differences. The ANOSIM global R value for the comparisons among bays was 0.213 ($p < 0.001$) and the global R value for the comparisons among months was 0.315 ($p < 0.001$), based on 999 permutations. The differences in the outcomes may reflect that PERMANOVA tests for differences between groups whereas ANOSIM tests whether distances between groups are greater than within groups. The high variability in larval community structure at any given time may have resulted in the lack of differentiation in Conception Bay between ecosystem states.

SIMPER analyses based on Euclidian distances of log-transformed abundance data revealed that capelin always drove differences among bays (average 54.1% contribution to the comparisons, range 34.7–78.9) (Table 2). The next most important taxa contributed an average of 19.1% of the dissimilarity (range 7.52–31.76) but species varied among comparisons. American plaice was the second most important contributor to comparisons of Trinity Bay pre-collapse with other areas. Cunner was important in most of the other comparisons among bays, with the exception of the comparison between Trinity Bay and the northern bays, where Atlantic herring was more important. Witch flounder and Atlantic cod contributed to differences among most systems. Similar average capelin densities characterized pre- and post collapse periods in Conception and Trinity Bays but their occurrence was delayed temporally during the post-collapse period. Witch flounder was less abundant following the collapse whereas radiated shanny and cunner were more abundant. Atlantic cod, American plaice, and witch flounder were important contributors to dissimilarities between pre- and post-collapse larval fish communities of Trinity Bay, with all abundances substantially lower post-collapse. Capelin abundances were nonetheless similar in Trinity Bay, although with a delayed seasonal cycle, as seen in Conception Bay.

SIMPER analyses based on Bray-Curtis similarity of presence/absence substantially reduced the influence of capelin on comparisons, and no single taxon had a highly dominant effect on dissimilarity in comparisons between bays. Average dissimilarity ranged from 48.9 (Conception Bay pre- and post-collapse) to 82.3 (Conception Bay post-collapse with Notre Dame and White Bays) (Table 3). Four to six species were required to account for at least 50% of the dissimilarity between bays. Occurrences of sand lance, cunner, American plaice, radiated shanny, and snailfish were the more important taxa in differentiating the Placentia Bay community from other bays. Higher densities and occurrence of American plaice, radiated shanny, along with yellowtail, witch, and winter flounders tended to characterize pre-collapse larval fish assemblages in Conception Bay relative to other bays. Conception Bay post-collapse generally differed from other bays, with greater average densities of American plaice, radiated shanny, snailfish, and lower densities of cod. Trinity Bay during the pre-collapse period generally differed from other bays with higher densities and occurrence of Atlantic cod, American plaice, capelin and lower densities of winter and yellowtail flounders. Several species of larval fish were depleted in post-collapse Trinity Bay with the exception of capelin, which appeared in greater abundance and frequency than in other bays. Atlantic cod and capelin densities and occurrence in Notre Dame

Table 2. Average squared distance for bays and ecosystem state (pre- and post-collapse) periods based on a two-way analysis of similarity/dissimilarity percentages (SIMPER) based on Euclidean distances of the log-transformed abundance of larval fish.

BAY	Placentia	CB pre-	CB post-	TB pre-	TB post-	NDBWB
Plaentia	1.80					
CB pre-	4.95	2.97				
CB post-	5.71	8.36	2.68			
TB pre-	10.6	9.60	9.92	4.19		
TB post-	5.82	5.26	4.71	8.25	1.92	
NDBWB	9.33	8.52	6.25	13.6	7.35	1.63

Table 3. Average similarity (in **bold**) and dissimilarity (in *italics*) for bays and ecosystem state (pre- and post-collapse) periods based on a two-way analysis of similarity/dissimilarity percentages (SIMPER) using a Bray-Curtis similarity matrix of a presence/absence transformation of the larval abundance data.

BAY	Placentia	CB pre-	CB post-	TB pre-	TB post-	NDBWB
Placentia	**53.6**					
CB pre-	*62.3*	**61.9**				
CB post-	*59.7*	*48.9*	**45.8**			
TB pre-	*66.5*	*51.9*	*58.6*	**50.4**		
TB post-	*68.2*	*58.4*	*58.1*	*56.6*	**57.6**	
NDBWB	*81.1*	*73.8*	*82.3*	*74.6*	*58.4*	**42.6**

and White Bays were comparable to other systems but the relative absence or infrequency of several species contributed substantially to differentiating these systems from other bays. Comparison of Conception Bay between the periods of differing ecosystem state indicates a decline in the occurrence of winter and witch flounders, and Atlantic cod, and increases in snail fish, capelin, radiated shanny, redfish, and blennies (Fig. 10). Comparison of Trinity between pre- and post-collapse periods revealed substantial declines in American plaice, Atlantic cod, witch and winter flounders, radiated shanny, snailfish, and redfish, along with modest increases in Arctic shanny and Atlantic herring, but similar levels of occurrence of capelin and cunner (Fig. 10). Changes in average abundance in Trinity Bay were generally more pronounced than those in Conception Bay.

Species specific cycles

The presence of larvae close to the size at hatch later in the year than previously noted by Scott and Scott (1988) were noted for gunnel, sand lance, blenny, snailfish, winter flounder, radiated shanny, American plaice, yellowtail flounder, Atlantic cod, and capelin, possibly indicative of protracted spawning activity relative to previous knowledge (Table 4, Supplementary Material). The notable presence in April and May of large larvae of blenny, gunnel, sculpin, snailfish and Arctic shanny may indicate spawning in winter or early spring (Table 4, Supplementary Material). The presence in April and May of large larvae of Atlantic herring and capelin is likely indicative that fish spawned in the previous year overwintered in coastal waters.

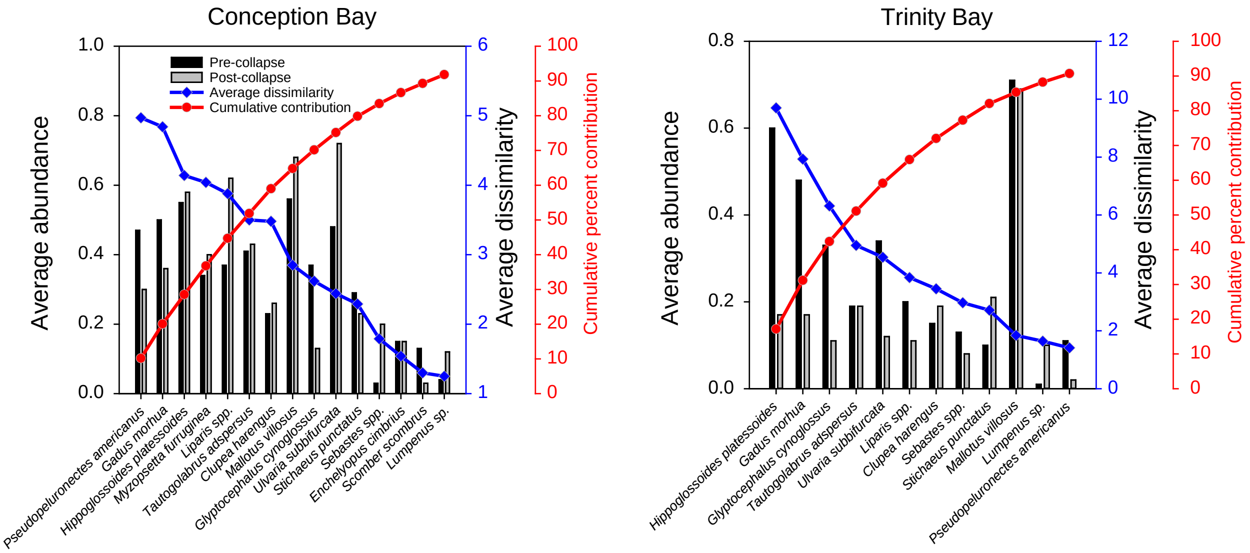

Fig. 10. Results of the Bray-Curtis analysis of similarity for Conception (left-hand panel) and Trinity (right-hand panel) Bays based on presence/absence transformation of abundances contrasting pre- (black bars) and post-collapse (grey bars) periods. Species names contributing to the first 90% of the dissimilarity between the periods appear on the x-axis. Average abundance based on presence/absence appear on the left axis. The right blue axis and lines represent the average dissimilarity of each taxon, and the right offset red axis and lines represent the cumulative proportion of the variance explained by the taxa. Note differences in species composition between bays.

Overall occurrence patterns across all bays did not change consistently during the post-collapse period among fish taxa (Table 4, Supplementary Material), with increases in six taxa, declines in five, and no change in the remaining eleven taxa, although some patterns of change were location dependent (Supplementary Material and Figs. S5–S26). Post-collapse densities declined in 13 taxa, with important declines in commercially exploited species (Atlantic cod, American plaice, yellowtail flounder, winter flounder and lumpfish), but notable declines occurred in other demersal species not subjected to directed fisheries (radiated shanny, snailfish, blenny and fourbeard rockling) as well as one commercially targeted species (witch flounder) (Table 4). All forage species (capelin, Atlantic herring, and Atlantic mackerel) declined after the collapse of the Newfoundland commercial groundfish fisheries, but the extent of the declines varied spatially (Table 4, Supplementary Material). There were no changes in the abundance of eight non-commercial taxa (Table 4, Supplementary Material), although we note that adults of many of these taxa occur principally in habitats close to the coast and in relatively shallow waters (< 50 m), where fishery impacts caused by trawls may have been limited. A χ^2 test revealed no significant difference in the distribution of egg types between taxa that declined in abundance versus those that did not change in abundance ($p > 0.5$), and a two-tailed t-test found no significant difference in average egg diameter between the two groups ($p > 0.3$).

Discussion

Our analyses demonstrate the value of long-term ichthyoplankton monitoring in quantifying changes in community structure from coastal Newfoundland, particularly those associated with the shifts in adult fish communities that resulted from either overexploitation, or changes in environmental conditions (Koslow and Wright, 2016; Gallo *et al*., 2019). Clear seasonal succession in species occurrence and composition were apparent in nearly all the bays included in our study, but this pattern reflected the relative mixture of taxa representing local differences in demersal and pelagic species community

Table 4. Timing of occurrence, direction of change in the occurrence and density of larval fish taxa from Conception and Trinity Bays during the post-collapse period relative to the pre-collapse period, and noteworthy aspects of the seasonal presence of larval fish species in eastern bays of coastal Newfoundland. ↑ indicates a general increase, ↓ indicates a general decline, ↑↓ indicates location dependent change, and NC indicates no notable change. * adjacent to timing of occurrence indicates evidence of protracted spawning relative to previous knowledge.

Scientific name	Timing	Occurrence	Density	Notes
Lumpenus spp.	April–July *	NC	NC	Winter spawner
Stichaeus punctatus	April–July *	NC	NC	May spawn in April
Ulvaria subbifurcata	May–August *	NC	↓	
Liparis spp.	June–August *	NC	↓	May spawn in spring
Pholis sp.	April–June	NC	NC	Winter spawner
Sebastes spp.	May–September	↑	↓	
Myoxocephalus spp.	April–July *	NC	NC	Winter spawner
Leptagonus decagonus	May–August	↑	↓	
Aspidophoroides monopterygius	April–September	NC	NC	
Cyclopterus lumpus	July–September	NC	↓	
Ammodytes sp.	April–August *	↑	NC	
Tautogolabrus adspersus	July–September	NC	NC	
Mallotus villosus	July–October *	NC	↑↓	0+ group overwintering
Scomber scombrus	July–August	↓	↓	
Glyptocephalus cynoglossus	July–October	↑↓	NC	
Hippoglossoides platessoides	May–October *	NC	↓	
Pseudopleuronectes americanus	May–August *	↓	↓	
Myzopsetta ferruginea	June–September *	NC	↓	
Enchelyopus cimbrius	July–October	NC	↓	
Gadus morhua	April–October *	↓	↓	
Boreogadus saida	May–July	NC	NC	
Clupea harengus	April–October *	↑↓	↓	0+ group overwintering

structure from adjacent continental shelves, and the latitudinal differences in the seasonal progression in environmental conditions. Furthermore, the data revealed longer spawning activity in many taxa than had previously been inferred from observations of gonadal development and condition in adult fish. Overall, these data provide a foundation from which to investigate possible changes in spawning activity and timing within each bay, identify expansion of species distributions in response to climate change, and monitor changes in the occurrence and abundance of taxa that standard scientific research trawl surveys may not effectively sample.

Precise timing of the collections during the year, spatiotemporal frequency of surveys, and differences in gear types confounded the various data sets in this synthesis, contributing to uncertainty in inferences derived from our analyses and assessments. However, comparable seasonal coverage prior to and following the collapse of several stocks should provide accurate representation of seasonal patterns in species occurrence and abundance. Overall, differences in community structure in ichthyoplankton composition were consistent with patterns reported in adult fish communities (Gomes *et al*., 1995; Pedersen *et al*., 2017), particularly the specific nature and magnitude of changes in ecosystem state. As for differences in gear types, Pepin and Shears (1997) demonstrated comparable catchabilities between the Tucker trawls used predominantly in Conception and Placentia Bays during the post-collapse period, and that of bongo nets, particularly for smaller and more abundant fish larvae. This inter-comparability would not have resulted in substantial errors in describing community structure because larger larvae would contribute less to overall catches for both gear types. Furthermore, Pepin and Shears (1997) found that Tucker trawl catches achieved greater precision in estimating the average abundance of fish eggs and larvae, although the abundance of very small larvae (1–3 mm) were sometimes less accurate for the Tucker trawl relative to bongo nets. In terms of occurrence, however, the patterns of change pre- and post-collapse indicated limited and variable changes for different taxa between periods. Furthermore, consistent declines in overall larval abundance of both commercial and non-commercial fish taxa were coherent with changes in adult fish community structure, suggesting that any potential bias in larval fish catchability resulting from differences in gear types did not affect the overall outcome of our synthesis. Consequently, the general patterns of occurrence and abundance described in our analyses are likely robust to potential uncertainty resulting from the differences in data sources.

Marked seasonality in environmental conditions and production of lower trophic levels characterize temperate, subarctic, and Arctic environments. Fish reproduction has adapted to release young to match availability of appropriate prey and thus meet larval metabolic requirements, known as the match-mismatch hypothesis (Cushing, 1969). Our analyses reveal that larval fish occur over a broad time period, starting in March–April, likely under the ice in some parts of coastal Newfoundland, until September–October. Relatively low densities at the start of the larval production cycle in April-May (~ 1 larva·m^{-2}, range 0.01–10) quickly increase to ~100 larvae·m^{-2} (range 0.01–1 000) by late July, when larval capelin dominate the ichthyoplankton community. Larger egg diameters tend to characterize species that spawn early in the year, a pattern consistent with patterns of variation in egg diameter within and among species from the Gulf of St. Lawrence and the Scotian Shelf (Ware, 1977; Markle and Frost, 1985; Miller *et al*., 1995). This larger egg size has important implications for embryonic development rates (Pauly and Pullin, 1988; Pepin, 1991) and larval size (Bradbury *et al*., 2001), metabolic requirements (Moyano *et al*., 2018; Peck *et al*., 2021), ecological match between prey size and larval feeding capacity (Pepin and Penney, 1997; Pepin, 2023), and change in length required to reach metamorphosis (Chambers and Leggett, 1987; Benoit *et al*., 2000), which all relate to the seasonal environmental temperature cycle. Although absolute density and timing of peak abundance differed among bays, we observed relatively similar overall seasonal patterns in abundance and species composition over the limited latitudinal range covered by our synthesis. Lowest richness in the spring increased progressively to peak in July-August, declining thereafter to levels comparable to the spring. Higher species diversity in Conception and Trinity Bays relative to Placentia and the northern bays likely reflects the complexity of adult fish communities adjacent to Conception and Trinity Bays, and which transition into one another at the northern edge of the Grand Banks relative to areas further north or south of these systems (Mahon *et al*., 1998; Pepin *et al*., 2010; Pedersen *et al*., 2017). Median values of Shannon's index of entropy, generally below 1 in most samples, coincides with uneven species composition across bays, and index values were highest in June and July when reproductive activity increases in many fish species. This pattern suggests more varied and richer larval communities during early summer months, when the copepod community, the principal prey of larval fish in the region (Pepin, 2023), increases most rapidly in diversity and composition (Maillet *et al*., 2022). Increased prey diversity may limit overlap in diet composition among species of larval fish, and thereby competition among larval fish species, although evidence from Conception Bay downplays the importance of food limitation in feeding and survival given high densities of small mesozooplankton in the coastal areas (Pepin and Penney, 2000; Tian *et al*., 2003). However, reproductive cycles in adult fish represent adaptations to conditions encountered at broader spatial scales representative of the stock's or the species distribution rather than reflecting general features of local habitats that are not primary spawning locations (Lowerre-Barbieri *et al*., 2017). Instead, covariation in zooplankton diversity and ichthyoplankton species evenness in coastal Newfoundland likely reflects the transition from spring to early summer production of both communities that may result in favourable conditions for overall larval survival. Some differences in larval production cycles among bays likely also reflect latitudinal differences in the seasonal progression in oceanographic conditions and the reproductive cycles of local and adjacent adult fish populations.

Evaluating patterns of variation in beta diversity proved difficult because our analyses demonstrated strong dependency in metrics of local dissimilarity to the number of samples from the surveys included in this synthesis. Many of our process studies provided limited spatial coverage of each bay that resulted in large variability in turnover and nestedness of species composition among samples, which describe patterns of variation in replacement and inclusion of different taxa, particularly for surveys with fewer than 25 observations. The high variability in turnover and nestedness reflects the balance between larval sources within each bay (*e.g.*, spawning beds, nest, habitat driven aggregations) and physical dispersal and mixing from currents, eddies, and areas of convergence and divergence in coastal Newfoundland (Pepin *et al*., 1995; Helbig and Pepin, 2002; Bradbury *et al*., 2003; Bradbury *et al*., 2008; Snelgrove *et al*., 2008; Pepin and Helbig, 2012). The asymptotic patterns in dissimilarity indicate limited (~3%) overall contribution of nestedness to beta diversity among samples, in which sites with smaller numbers of species represent subsets of the biotas at richer sites. This limited nestedness indicates horizontal mixing can substantially alter species composition among samples through species turnover, which involves the replacement of some species by others from site to site (Helbig and Pepin, 2002; Snelgrove *et al*., 2008). Dispersal and horizontal mixing play important roles in reproductive success of fish (Lowerre-Barbieri *et al*., 2017) and in connectivity among habitats and environments (Cowen *et al*., 2006). Previous studies in coastal Newfoundland emphasized the importance of transport and retention of larvae as drivers of ichthyoplankton distributions in relation to spawning locations to settlement or aggregation sites (Laprise and Pepin, 1995; Helbig and Pepin, 2002; Bradbury *et al*., 2003; Bradbury *et al*., 2008; Stanley *et al*., 2013; Murphy *et al*., 2018). The dynamic nature of currents in coastal bays of Newfoundland, and their vulnerability to short-term changes in atmospheric forcing (*e.g.*, deYoung *et al*., 1993a; deYoung *et al*., 1993b), results in high variability in ichthyoplankton distributions in these systems, an issue highlighted by the large sample size required to accurately quantify variations in species composition of assemblages (*i.e.*, beta diversity). Consequently, accurate monitoring of ichthyoplankton community structure and distribution in such ecosystems requires a significant investment in comprehensive sampling programs. Comprehensive sampling can avoid obscuring the response of fish populations or communities to changes in ecosystem state as a result of uncertainty in abundance estimates caused by vagaries in ocean circulation, and compounded by limited sample size (Pepin and Helbig, 2012). The limited differentiation in alpha and beta diversity of ichthyoplankton communities among coastal bays of Newfoundland indicates that similar underlying processes drive these embayments, both in terms of sources of larval fish and the physical dynamics of nearshore areas. These confounding processes often limit use of simple metrics of biodiversity to identify changes in coastal fish communities, and to infer changes in ecosystem functionality (Mori *et al*., 2018). Quantifying the drivers of biodiversity change in these complex systems will require in-depth evaluation of changes in the balance of occurrence and abundance of individual taxa to determine their role in overall community structure, and the influence of interactions among fish species.

Our synthesis revealed important similarities and differences among bays in the seasonal progression of the larval fish community structure, which indicates that no one location can serve as indicator of ecosystem state. Differences in adult species distributions along with vulnerabilities to environmental change and fishing activity have potentially important consequences to the survival potential of young fish from different parts of the coast. Our surveys revealed that major ecosystem change resulted in declines in larval abundance of commercially exploited species, and also declines in many non-commercial groundfish and pelagic species. We suggest limited likelihood that these changes resulted from by-catch in regional commercial fisheries, although we cannot discount the potential impact to small fish species resulting from increased shrimp trawling on the Newfoundland Shelf from the early 1990s onward (EJF, 2003). The magnitude and direction of change in abundance varied considerably among fish taxa following major regional changes in the ecosystem. For example, changes in abundance of capelin varied between pre and post collapse periods, whereas other taxa either increased in abundance (sand lance, redfish) or maintained similar densities (gunnel, sculpin, Arctic shanny, witch flounder, herring in Trinity Bay, and cunner). This variability suggests that, because of differences in life histories, not all taxa responded to ecosystem change in the same way. In the case of capelin, low stock biomass characterized the post-collapse period, along with delayed spawning and production of weaker year-classes despite a relatively high spawning extent (and larval densities) in some core areas (Trinity and Conception Bays) (Lewis *et al*., 2019; Murphy *et al*., 2021; Tripp *et al*., 2024). However, the limited basic research into the life history characteristics of other fish species in the region (*e.g.*, Stares *et al*., 2007; Morgan *et al*., 2014; Morgan *et al*., 2018) constrains any inferences on how life history characteristics affected the varied response to changes in ecosystem state. Clearly, the densities of 13 of 22 fish taxa declined between pre- and post-collapse periods, reflecting important changes in the productivity of fish populations from the Newfoundland shelf and northern Grand Banks. Note, however, that the majority of taxa that demonstrated no change in abundance between pre- and post-collapse periods were principally those with habitats closely associated to the coast in relatively shallow waters, potentially limiting fishery impacts. Scientific trawl surveys also report important shifts in communities (Pedersen *et al*., 2017; Koen-Alonso and Cuff, 2018; Aune *et al*., 2024), and many coastal species not readily sampled by these surveys also decreased in abundance. However, assessing whether these declines resulted from unmonitored fishery impacts or from changes in lower trophic level productivity remains challenging. Chan *et al*. (2017) inferred long-term changes in primary productivity on the Labrador shelf from barium-to-calcium ratios and carbon isotopes from long-lived coralline algae, which they linked to the Atlantic Multidecadal Oscillation (AMO). They inferred that the AMO has been increasing since the late 1990s, as part of a prolonged Atlantic warming phase. Despite the continued positive phase in the AMO, our synthesis, and that of the broader fish and invertebrate community (Pedersen *et al*., 2017; Koen-Alonso and Cuff, 2018; Aune *et al*., 2024), indicates that the overall production potential has not resulted in a complete recovery to a pre-collapse state by the fish community on the Newfoundland shelf and northern Grand Banks. This recovery failure may indicate that ecosystem capacity and functionality may have changed between pre- and post-collapse periods, which could affect the sustainability of fisheries into the future.

A limited number of species often dominate the ichthyoplankton community in an area of interest (Auth and Brodeur, 2006; Campfield and Houde, 2011; Guan *et al*., 2017; Siddon *et al*., 2018). Our synthesis documented similar patterns, whether considered from a seasonal perspective or through differences in the seasonal succession among the four major coastal Newfoundland bays. The general dominance of capelin larvae from July until October in each of these bays was unusual relative to ichthyoplankton from other ecosystems. Capelin represent a keystone species on the Newfoundland shelf and Grand Banks (Buren *et al*., 2014; Buren *et al*., 2019). Like many other forage species (*e.g*., anchovy, herring, sardines, sprat), capelin larvae have an elongated body form, anguilliform swimming mode, and a relatively small mouth; they are vulnerable to starvation resulting partly from limited foraging capability (Peck *et al*., 2021; Moyano *et al*., 2023). Although previous studies cast significant doubt on food limitation for larval fish in coastal Newfoundland, even considering the high densities of capelin larvae (Pepin and Penney, 2000), the persistence of larger capelin larvae throughout the fall and winter months may result in local depletion of zooplankton during periods of low secondary productivity, although we were unable to find estimates of their potential impact. Randall *et al*. (2022) studied feeding patterns in Atlantic herring in Trinity Bay and concluded that they showed an adaptive feeding strategy, and O'Driscoll *et al*. (2001) found similar adaptive capacity in their analysis of adult and juvenile capelin diets. However, neither study evaluated the potential consumption rates of juvenile fish on their prey. Thus, the consequences of high capelin density, combined with that of other zooplanktivorous species that were once abundant, on coastal ecosystems and how this may impact survival and recruitment is unclear.

We detected no pre-/post-collapse differences in the occurrence or densities of capelin larvae in Trinity and Conception Bays despite important changes in larval survival potential (Penton and Davoren, 2013b; Murphy *et al*., 2018), and spawning characteristics (Penton and Davoren, 2013a; Murphy *et al*., 2021; Tripp *et al*., 2023), as well as much lower overall abundance of the stock (Buren *et al*., 2019; DFO, 2024) relative to that found during the pre-collapse period. The seasonal occurrence of capelin spawning starts on the south coast of Newfoundland and progressively moves later in the year as adult fish move in a northerly direction as the summer progresses (Nakashima, 1992; Murphy, 2022). Persistence of relatively high levels of larval abundance in Conception and Trinity Bays suggest that these two areas may represent core spawning locations. Any changes related to the recovery of the stock, despite current low levels of recruitment (Murphy *et al*., 2018; Murphy *et al*., 2021), could influence reproductive activities in other areas along the coast, or resulted in lengthened spawning periods across the range of the stock (Murphy, 2022). Alternatively, the high frequency of occurrence and dominance of capelin larvae in ichthyoplankton surveys, combined with the reduction in the number of samples collected and spatial coverage between pre- and post-collapse periods, could suggest bias in our findings about current states of the stock based on our opportunistic synthesis of survey information. Properly contrasting larval capelin abundance and its relationship with the adult population will require comprehensive sampling to characterize the reproductive potential of the Newfoundland capelin stock.

Combining multiple ichthyoplankton surveys provided a finer-resolution perspective of spawning activity in coastal Newfoundland that extended the periods of reproduction of half of the taxa included in our analyses relative to previous syntheses of information (Scott and Scott, 1988; Fahay, 1992a; Fahay, 1992b). This extended spawning season may, however, have minimal consequences for recruitment variability and population dynamics given that individuals spawned later in the season may lack sufficient energy reserves to survive periods with reduced productivity of lower trophic levels (Post and Parkinson, 2001; Laurel *et al*., 2003; Geissinger *et al*., 2023). This limitation may be a particularly important aspect of early life dynamics for capelin in which delayed beach spawning since the stock’s collapse has generally yielded weak year classes (Murphy *et al*. 2021). The consequences of protracted spawning activity to population dynamics and productivity will depend entirely on overall energetic demands on adults and the relative magnitude of egg and larval production later in the season, which are currently unknown for most species in the study region. However, spawning activity may provide an opportunity for certain taxa to benefit from the impacts of climate change, which will likely increase temperatures later in the season and thereby lengthen the period of enhanced plankton productivity (Han *et al*., 2015).

Conclusions

Combining data from multiple ichthyoplankton surveys conducted in coastal Newfoundland has provided important new knowledge about the seasonal larval production cycle across a broad range of species. Clearly, the consequences of major changes in commercial fish stocks resulting from overfishing and abrupt changes in environmental conditions also affected several non-commercial species found in coastal ecosystems. We achieved this finding despite imperfect overlap in the timing and occurrence of ichthyoplankton surveys. Our findings highlight the importance of basic biological knowledge of life history cycles of fish which is enabled by better observations of lower trophic levels in the form of pre-recruits. Determining whether such knowledge can serve to inform scientists about the underlying processes affecting multispecies dynamics from the Newfoundland shelf and Grand Banks will require further analysis.

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Author contributions

PP conceptualized the study, carried out the analyses, and prepared the initial draft of the manuscript. All authors contributed data (collection, curation, quality control, and verification) for the synthesis, and participated in the writing, critical review, editing and revision of the manuscript.

Data availability

The data from this synthesis are available as an independent dataset from the corresponding author's ResearchGate profile https://www.researchgate.net/profile/Pierre-Pepin/research

Conflict of interest

The authors have no conflict of interest to declare.

Ethics statement

The current study was based on existing data, therefore no ethical approval was needed.

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Spatiotemporal changes in the Atlantic cod (*Gadus morhua*) stock at Flemish Cap (1993–2019) and their relationships with demersal communities

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Abstract

Changes in Atlantic cod (*Gadus morhua*) abundance at Flemish Cap, likely due to exploitation and perhaps also to changing environmental conditions, have been well documented since 1980s. While the ecological implications of cod fluctuations have been explored in relation to dominant and commercially important species including redfish (*Sebastes* spp.), northern shrimp (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*), the broader ecological impacts, *e.g.* on less abundant species, remain less well explored. This study aimed to analyse spatiotemporal variation in the distribution and abundance of cod, and identify associated changes in distribution and abundance of other species with various trophic relationships to cod. This analysis used a delta Generalized Additive Model (GAM) approach, incorporating binomial and quasi-Poisson GAMs fitted to EU bottom trawl survey data from 1993 to 2019. Trophic species and guilds were defined based on the sizes and feeding habits of each species, as established in previous studies. Atlantic cod is considered to comprise of two trophic species: cod under 46 cm and larger cod. Model predictions were used to construct distribution maps and estimate distribution range and annual total abundance. Bottom temperature was a more important predictor in abundance (quasi-Poisson) models than in presence (binomial) models. The observed decline in cod abundance was associated with contraction in the distribution range. Significant negative correlations were identified between cod trophic species and all but one of the other trophic species in the same trophic guilds, for both distribution range and abundance. Species in other trophic guilds that rely on northern shrimp as prey also exhibited negative correlations with cod. The abundances of the main prey of cod, namely juvenile redfish and northern shrimp, showed negative correlations with cod abundance but no relationship was seen for distribution range. The abundance of large Acadian redfish (*S. fasciatus*) and large beaked redfish (*S. mentella*), which are major prey species of cod, was positively correlated with that of large cod, suggesting that the abundance of these prey species depends more on external variables, such as intense exploitation, than on their predator-prey relationships. These findings highlight the importance, for fishery management, of considering both the direct effects of fishing mortality and the indirect effects via trophic relationships.

Keywords: demersal fish, deep-sea, ecology, trophic relationship, Northwest Atlantic

Introduction

The collapse of Atlantic cod (*Gadus morhua*) abundance in the Northwest Atlantic in the late 20th Century has been well documented (Boudreau *et al.*, 2017) but less attention has been given to associated changes in the spatial dimension (Pérez-Rodríguez *et al.*, 2012, 2017; Garrido *et al.*, 2023a) or to wider ecosystem effects (Dawe *et al.*, 2012).

As the abundance of a population declines, ultimately its distribution range will also decline (Rose *et al.*, 2000; Thorson *et al.*, 2016). Identifying a fished population's spatial response to external stress can provide valuable information for spatial management measures, such as protected areas, which could ensure preservation of the stock when depleted. Fishery closures, even if temporary, can be employed as precautionary measures to maintain a healthy stock condition (Gell and Roberts, 2003). The Northwest Atlantic Fisheries Organization (NAFO) has implemented seasonal area closure for cod fisheries in Division 3M during the spawning period, *i.e.* in the first quarter of the year (NAFO, 2021). Permanent closure has also been employed in parts of NAFO Division 3M to conserve the biodiversity of vulnerable ecosystems (NAFO, 2022). Better understanding of the relationships between fish abundance and distribution and their changes under various circumstances could help improve spatial management.

In a complex ecosystem, fluctuations of key species such as cod, whether caused by human activities or varying environmental conditions can, in turn, influence their competitors and prey (Pérez-Rodríguez *et al.*, 2017). Areas that have experienced overfishing of high trophic level species often show regime shifts and trophic cascades that are challenging to reverse and may even be irreversible (Fisher *et al.*, 2015). The nature of such changes is, however, not necessarily obvious. Thus, the decline of cod, a higher trophic level species, would lead to both reduced pressure on its prey and reduced competition for other carnivores, effects that would ultimately be antagonistic.

Flemish Cap is an underwater mountain with a summit at a depth of 125 m, located near the Canadian Exclusive Economic Zone (EEZ) to the east of Grand Bank. It is one of the historically most significant fishing grounds for cod. The area is regulated by NAFO as part of management area Division 3M. It is semi-isolated from the continental shelf by a 1 100 m deep channel known as Flemish Pass, which limits migration between the seamount and the continental shelf (Stein, 2005; Vázquez *et al.*, 2014). Records of cod exploitation and biomass in the area clearly showed signs of overfishing and stock collapse in the late 1990s (González-Troncoso *et al.*, 2022). A fishery moratorium was implemented in 1999 but the overall abundance of cod continued to decline and did not show clear signs of recovery until the late 2000s, suggesting the involvement of unfavourable environmental conditions in delaying the recovery (Ruiz-Díaz *et al.*, 2022). The population subsequently recovered sufficiently to reopen the fishery in 2010 and has since been closely monitored to maintain spawning stock biomass (SSB) above the reference limit set by NAFO Scientific Council (NAFO, 2019).

There is evidence that the wide fluctuations in cod abundance over the years have had significant impacts on the ecosystem. Flemish Cap hosts a diverse range of over one hundred identified fish species, most being demersal (Vázquez *et al.*, 2013). Since 1988, the EU has conducted fisheries-independent surveys in the area, providing data that have been used to investigate the impact of fishing and the environment on fish stocks and community structure (Pérez-Rodríguez *et al.*, 2012). The complex trophic interactions in the area have been studied for common fish species, revealing shared feeding habits such that demersal fish can be grouped into four trophic guilds (Pérez-Rodríguez *et al.*, 2011). Guild I members predominantly prey on small invertebrates, mainly northern shrimp (*Pandalus borealis*) and hyperiids. Guild II exhibits the most diverse invertebrate diet and some of the members rely largely on northern shrimp but still have greater dietary variation than Guild I members. Guild III consists exclusively of redfish with diets strongly based on pelagic invertebrates and northern shrimp. Guild IV is predominantly piscivorous, with one of the main prey items being redfish. Recent studies modelling the dominant system of cod-redfish-shrimp, considering their biomass and energy flows in the area, have shown an intensely intertwined relationship among them, and the change in one species due to fishing or natural mortality could profoundly affect the others (Pérez-Rodríguez *et al.*, 2022). In the period of cod depletion, a major assemblage shift was detected, with other normally less abundant species in the area such as Greenland halibut (*Reinhardtius hippoglossoides*) and wolffishes (*Anarhichus* spp.) becoming more dominant (Pérez-Rodríguez *et al.*, 2017).

While changes in the demersal fish community have been observed in recent decades, the spatial aspects of these changes have been less well explored (Pérez-Rodríguez *et al.*, 2012; Pham *et al.*, 2019). A previous study exploring changes in fish distribution through spatial modelling approaches identified contraction in the distributions of cod and another commonly co-occurring species in the area, American plaice (*Hippoglossoides platessoides*), when their biomass is low, and a significant increase in the dominance of Greenland halibut (Hendrickson and Vázquez, 2005). It is expected that the spatial structure of the demersal community as a whole, including species that are less abundant and/or of lesser commercial interest, will also have been influenced by the fluctuations in cod abundance, and these wider ecological impacts of cod fluctuations still need to be investigated. Understanding the effects on the demersal community of fluctuations in key species can help inform ecosystem-based fisheries management (Hilborn, 2011).

This study aims to explore the ecological impacts of cod stock fluctuations by investigating the correlations in distribution and abundance between cod and other trophic species. Specifically, we (i) investigate changes in the spatial distribution and abundance of cod in Flemish Cap over periods of differing fishing intensity during 1993 to 2019 and compare abundance estimates based on the modelling approach with those from traditional calculations, (ii) explore the influence of environmental variables on changes in abundance and distribution, and (iii) examine changes in distribution and abundance of other species with varying trophic associations to cod.

Material and methods

Survey sample collection

Flemish Cap bottom trawl surveys have been conducted by the EU since 1988, following the protocol described by NAFO and led by four collaborating institutes from Spain and Portugal: the Institute of Marine Research (IIM-CSIC), the Spanish Institute of Oceanography (IEO), AZTI-Tecnalia Foundation and the Institute of Fisheries and the Sea (IPMA) (Vázquez *et al.*, 2014). Sampling was conducted using two vessels, RV *Cornide de Saavedra* from 1988 to 2002, reaching a maximum depth of 730 m, and RV *Vizconde de Eza* since 2003. The depth limit was extended to 1460 m in 2004 to cover a larger area where species preferring deeper water resided. Due to the vessel replacement, the catch data of the focal species including

Atlantic cod, redfish, American plaice, Greenland halibut and roughhead grenadier (*Macrourus berglax*) prior to 2004 were transformed using calibration factors calculated by González-Troncoso and Casas (2005) to standardize the fishing effort to that of the current vessel. The study area was divided into 34 strata for stratified random sampling (Fig. 1). The initial 19 strata are limited to a depth of 730 m and are consistently present each year. The additional strata were sampled from 2004 onward, except strata 26 and 27, which were irregularly sampled due to a dense sponge ground and were only present from 2004 to 2007. The sampling effort was approximately one haul per 100 square miles per year for every stratum except for stratum 33, the smallest stratum, which received a sampling effort close to two hauls per 100 square miles per year.

A Lofoten trawl was used for sampling due to its durability and similarity to the gear used by commercial fisheries in the area. The cod-end mesh size was 35 mm, which is considered to be appropriate for retaining juveniles of commercial species. The trawl opening was 0.0075 mile wide, and the boat maintained a speed of 3.5 knots for 30 minutes after the net made contact with the bottom. Trawling was conducted between 6:00 and 22:00 h daily.

The captured fish were initially identified to species before individual measurements were taken, with the exception of juvenile redfish (<15 cm fork length) due to practical challenges associated with species identification for this genus. Fish size was generally recorded as total length (TL) in centimetres (to the nearest 1 cm), except for redfish, for which fork length (FL) was recorded, and Macrourid fishes (roughhead grenadier and marlin-spike grenadier (*Nezumia bairdii*)), for which anal length (AL) to the nearest 0.5 cm was recorded. The size of northern shrimp was measured by carapace length in millimetre. In cases where a particular species was highly abundant in the catch and it was impractical to measure all individuals, subsamples were selected for measurement based on a stratified random procedure. The target subsample size

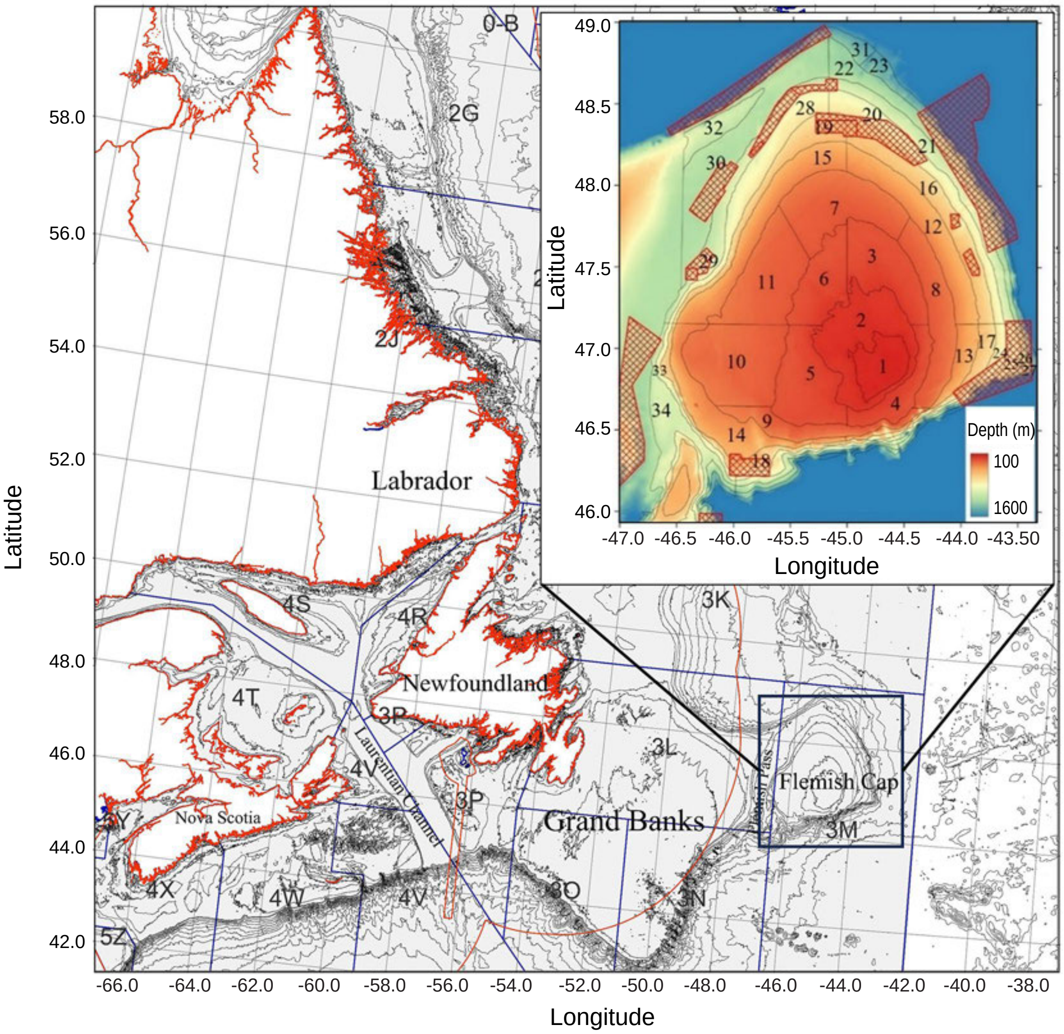

Fig. 1. Flemish Cap depth and sampling strata and NAFO vulnerable marine ecosystem closure areas (red mesh). The Canadian Exclusive Economic Zone is represented by the red border. NAFO Division boundaries are represented by blue borders.

was 50 individuals (25 fish for each identified sex) for each species in each haul, except for juvenile redfish for which the target was 20 individuals. The overarching goal was to collect 10 samples for each class by the conclusion of each survey.

Trophic species

To investigate the ecological impact of fluctuations in Atlantic cod abundance, 14 other fish species and northern shrimp were chosen for the study. All fish species and juveniles of redfish were classified into trophic species based on their size and feeding habits, following a previous study on the main fish species in the area (Pérez-Rodríguez *et al.*, 2011) (Table 1). These authors classified the trophic species into four trophic guilds (I to IV) based on observed dietary similarity between 1993 to 2008. In the present study, we include an additional guild (V) for northern shrimp as it is one of the key prey species in Flemish Cap ecosystem that should be modelled for its distribution and abundance.

Table 1. Trophic species and guilds of main fishes found in Flemish Cap as classified by Pérez-Rodríguez *et al*. (2011) with the addition of northern shrimp (*Pandalus borealis*).

Guild	Biological species	Size(cm)	Trophic species
I	*Gadus morhua*	≤46	*Gadus morhu*a 1(GM1)
	Amblyraja radiata	All	*Amblyraja radiat*a (AR)
	Macrourus berglax	≤15.5**	*Macrourus berglax* 1 (MB1)
	Macrourus berglax	>15.5**	*Macrourus berglax* 2 (MB2)
	Nezumia bairdii	≤6**	*Nezumia bairdii* 1 (NB1)
	Nezumia bairdii	>6**	*Nezumia bairdii* 2 (NB2)
	Phycis chesteri	All	*Phycis chesteri* (PC)
	Reinhardtius hippoglossoides	≤31	*Reinhardtius hippoglossoides* 1(RH1)
II	*Anarhichas lupus*	≤41	*Anarhichas lupus* 1(AL1)
	Anarhichas minor	≤46	*Anarhichas minor* 1(AM1)
	Glyptocephalus cynoglossus	All	*Glyptocephalus cynoglossus* (GC)
	Hippoglossoides platessoides	All	*Hippoglossoides platessoides* (HP)
	Lycodes reticulatus	All	*Lycodes reticulatus* (LR)
III	Juvenile *Sebastes* spp.	All*	Juvenile *Sebastes* spp. (SJ)
	Sebastes fasciatus	≤21.5*	*Sebastes fasciatus* 1 (SF1)
	Sebastes fasciatus	>21.5*	*Sebastes fasciatus* 2 (SF2)
	Sebastes mentella	≤27.5*	*Sebastes mentella* 1(SM1)
	Sebastes mentella	>27.5*	*Sebastes mentella* 2 (SM2)
	Sebastes norvegicus	≤27.5*	*Sebastes norvegicus* 1 (SN1)
	Sebastes norvegicus	>27.5*	*Sebastes norvegicus* 2 (SN2)
IV	*Gadus morhua*	>46	*Gadus morhua* 2 (GM2)
	Anarhichas denticulatus	All	*Anarhichas denticulatus* (AD)
	Anarhichas lupus	>41	*Anarhichas lupus* 2 (AL2)
	Anarhichas minor	>46	*Anarhichas minor* 2 (AM2)
	Reinhardtius hippoglossoides	>31	*Reinhardtius hippoglossoides* 2 (RH2)
V	*Pandalus borealis*	All***	*Pandalus borealis* (PB)

Note: size measurements differed among species: "*" indicates fork length, "**" indicates annal length, "***" indicates carapace length. For all other species, total length is used.

Bottom temperature

July monthly average bottom temperatures (BT) spanning from 1993 to 2019 were obtained from Copernicus Marine Service (CMEMS). The monthly average temperature was used instead of the in-situ data to minimise the contribution of daily BT variation within each survey. The consistency of bottom temperature mapping by CMEMS is also advantageous for predictive spatial models. The BT data were based on reanalyses from the CMEMS Global Ocean Reanalysis Products, which incorporate real-time global forecasting (Drévillon *et al.*, 2021). The standard grids used had a spatial resolution of 1/12°. Temperature values were attributed to trawls based on the specific grids corresponding to the sampling locations.

Data analysis

Density calculation

Density, expressed as number of individuals per square mile (n/mile^2) was calculated for each sampling location by dividing the total number of individuals caught in the haul by the trawled area (*i.e.*, trawling distance × trawl opening width).

Spatiotemporal GAM

The delta GAM approach, as described by Grüss *et al.* (2014), was utilized to analyse the spatial structure of abundance for each trophic species over time. This approach combines a binomial GAM that describes the probability of presence and a quasi-Poisson GAM that describes the density when a trophic species is present. The models were fitted using the "mgcv" package (Wood, 2023) in R version 4.1.1 following the equations:

$$g(\eta)=s(\text{latitude})+s(\text{longitude})+s(\text{depth})+s(\text{year})+s(\text{BT}) \tag{1}$$

$$g(\eta)=s(\text{latitude, longitude})+s(\text{depth})+s(\text{year})+s(\text{BT}) \tag{2}$$

$$g(\eta)=s(\text{latitude, longitude, year})+s(\text{depth, year})+s(\text{BT}) \tag{3}$$

where η is the binary response of presence/absence data for the binomial GAM, and the density response when non-zero data are present for quasi-Poisson GAM, g represents the model link function, and *s* is a regression spline. The spline used for the modelling is the "thin-plate regression spline", chosen for its flexibility and data driven suitable for when there is no prior knowledge of the form of relationships among the variables. The Restricted Maximum Likelihood (REML) method was used to estimate the smoothness parameters of the smooth functions in GAMs. To determine the best-fitting model for each trophic species, interactions among certain variables were explored by comparing models (1), (2) and (3). A logit link function was used for binomial GAMs, and a log link was used for quasi-Poisson GAMs. Note that coordinates were transformed from the recorded decimal degrees to Universal Transverse Mercator (UTM) coordinate system before being fitted to the models.

The best-fit binomial GAMs were selected for each trophic species using the Akaike Information Criterion (AIC) (Akaike, 2011). Deviance explained was used to identify best-fit quasi-Poisson GAMs since the quasi-Poisson family does not provide the necessary likelihood information to compute the AIC. The adequacy of the basis dimension (k) was checked for all best-fit GAMs using the gam.check function. Delta GAM predictions were generated by multiplying the probability of presence estimated by the best-fit binomial models with the density estimated by the best-fit quasi-Poisson models at the same coordinates. Thus, the delta predicted density (y, n/mile^2) was calculated using the equation:

$$y=p*a \tag{4}$$

where p represents probability of presence, and a represents density if present.

Model prediction and validation

Best-fit delta GAMs were validated by performing non-parametric Spearman's correlation analysis to compare observed and predicted densities. A test with 1 000 bootstraps sampling with replacement was used to estimate the Spearman´s correlation coefficient (ρ) and conclude whether ρ was significantly different from zero. In addition, the magnitude of differences between the observed density and that predicted by delta GAM is observed through value ranges and distributions.

The best-fit delta GAMs were used to predict density by year, coordinates, depth and temperature across the 1/20° gridded maps. The resolution was chosen based on the efficiency in computational effort while providing a fine spatial scale for observing spatial variation in presence probability and density. The depth inputs for the prediction were extracted from the seamless gridded topographic and bathymetric bare-earth evaluation data set ETOPO 2022 (NOAA, 2023). The temperature inputs for the model prediction are from the previously extracted CMEMS data. Following the sampling depth fitted to the model, the predictions from 1993 to 2003 were made for depths up to 730 m while the prediction since 2004 are for depths up to 1 460 m.

The annual total abundances of the focal species, Atlantic cod, as predicted by best-fit delta GAMs, were compared to the conventional calculations based on the same survey data as published by NAFO (González-Troncoso *et al.*, 2022). The predicted total abundance was calculated as followed:

$$\text{Total abundance} = \sum_{i=0}^{n} y_i * GA_i \tag{5}$$

where y_i is density at grid i and GA_i is the area of grid square i.

As the published abundance values are provided by age class, the predicted total abundance of GM1 was compared to summed abundances of fish aged 1 to 3 years old, while the abundance of GM2 was compared to the summed abundance of older age classes. The comparison was performed using Wilcoxon signed rank test.

Mapping and distribution area calculation

Chronological (annual) maps were constructed for all trophic species for 1993–2019, following the available temperature map data. Mapping was carried out using QGIS version 3.20. The distribution area of each trophic species was defined as the area with a density of at least 10 individuals per square mile. The centroids of polygons weighted by density were then calculated.

Correlation of cod to other trophic species

Although the delta GAMs are constructed using all available data and the predictions for mapping since 2004 were made at all depths, only the annual distribution area and total abundance at depths of less than 730 m (*i.e.*, the depth ranged sampled prior to 2004) were used for correlation analyses between cod and other trophic species. This is due to the fact that cod does not generally occur at greater depths and its correlations to other species can be expected to be much more discernible if the analysis is confined to depths 730 m or less than if we were to include deeper areas.

The correlations between annual distribution area of cod (≤730 m depth) and those of other species throughout the study period were estimated using Spearman's correlation test with 1000 bootstraps. The correlations between annual total abundances for ≤730 m depth were also tested using the same method. Due to the potential lagged effects of cod population abundance on other species, the correlations paired cod total abundance or distribution area of a given year to the abundance or distribution area of other species from the following year. The one-year lag was chosen as it is the most immediate possible time to assess the direct impact of cod on other trophic species with the least interference from recruitment.

Results

Best-fit Delta GAMs

A total of 3 941 hauls was included in the binomial GAM fitting. For most trophic species, the best-fit binomial GAMs revealed significant interactions between coordinates and year, as well as between depth and year (p-value <0.05) (Table 2). The only exceptions were MB1, MB2 and HP, as their best-fit binomial GAMs lacked interaction terms. There are 12 trophic species for which the temperature term has a significant effect in the best-fit binomial GAMs.

Table 2. Best-fit binomial and quasi-Poisson GAM deviance explained (DE) of trophic species.

Guild	Trophic species	Average predicted density (n/mile^2)	Binomial GAM		Quasi-Poisson GAM		
			Best-fit model (equation)	DE (%)	Hauls (n)	Best-fit model (equation)	DE (%)
I	*Gadus morhua* 1	4 856.19	3	74.3	1 243	3*	78.2
	Amblyraja radiata	90.02	3*	29.1	1 609	3*	35.5
	Macrourus berglax 1	141.37	2	70.3	1 506	3*	62.2
	Macrourus berglax 2	149.63	2	72.9	1 532	3	52.0
	Nezumia bairdii 1	561.91	3*	50.3	1 959	3	61.6
	Nezumia bairdii 2	579.71	3*	57.1	2 080	3*	66.6
	Phycis chesteri	355.86	3*	59.3	1 376	3*	52.5
	Reinhardtius hippoglossoides 1	215.14	3	48.8	1 179	3	69.6
II	*Anarhichas lupus* 1	642.53	3	63.4	1 704	3*	66.4
	Anarhichas minor 1	110.55	3	50.7	876	3	45.8
	Glyptocephalus cynoglossus	226.12	3	40.2	1 674	3*	63.9
	Hippoglossoides platessoides	511.99	2	60.7	1 643	3*	62.5
	Lycodes reticulatus	882.30	3	66.5	1 341	3*	57.8
III	Juvenile *Sebastes* spp.	43 738.66	3*	68.8	1 779	3*	62.6
	Sebastes fasciatus 1	29 125.04	3*	55.0	2 326	3*	70.5
	Sebastes fasciatus 2	9 840.54	3*	57.4	1 994	3*	56.8
	Sebastes mentella 1	33 665.70	3*	58.7	1 914	3*	44.8
	Sebastes mentella 2	3 514.75	3	51.1	1 234	3	50.2
	Sebastes norvegicus 1	16 761.30	3*	60.2	1 866	3*	76.6
	Sebastes norvegicus 2	3 386.46	3	46.5	1 610	3*	57.2
IV	*Gadus morhua* 2	1 334.08	3*	66.6	1 587	3*	50.0
	Anarhichas denticulatus	53.76	3	15.6	1 418	2*	17.3
	Anarhichas lupus 2	110.55	3	46.0	1 406	3*	49.9
	Anarhichas minor 2	81.47	3	39.7	1 368	3*	45.0
	Reinhardtius hippoglossoides 2	1 113.02	3*	65.7	2 649	3	65.2
V	*Pandalus borealis*	160 750.79	3*	48.7	2 027	3	62.2

Note: "*" indicates significant bottom temperature variable in the model (p<0.05).

The number of hauls with non-zero density varied among species, ranging from 876 to 2 649 hauls (Table 2). The best-fit quasi-Poisson model for all trophic species except AD featured significant interaction terms between spatial variables and year ($p<0.05$). In contrast to binomial models, most of the best-fit quasi-Poisson GAMs included a significant temperature term.

Both binomial and quasi-Poisson models explained over 50% of the deviance for most species, irrespective of their trophic guild. However, trophic species such as AR, AD, AL2 and AM2 were less effectively described by both GAMs. Despite belonging to different guilds, these species share the characteristic of lower abundance (<120 n/mile^2) compared to the others while still commonly occurring, as can be seen through the high number of non-zero haul (>1 300 presences) (Table 2). GC is another species that is less well described by the binomial GAM but its density is well-fitted by quasi-Poisson GAM.

Spearman's correlation tests indicate significant ($p<0.01$) and positive correlations between all observed and predicted values (Table 3). The majority of the Spearman's *p* exceed 0.7 for both presence-absence and density tests. Strong positive correlations were found between observed non-zero density and predicted values even for trophic species for which the best-fit quasi-Poisson GAMs had low values of deviance explained, which suggests that the models were reasonably reliable for prediction. Only observed density and quasi-Poisson GAM predictions of SM1, SM2 and AD show *p* below 0.5. The correlation test also revealed strong and significant ($p<0.01$) positive correlations ($p>0.7$) between the observed density (0 included) and delta GAM prediction for most species.

Due to the large number of absences (0 density) in sampling, which could significantly skew the value distribution to the median of 0, the predicted density was compared to observed density only for hauls with presence (non-zero density). The values of observed non-zero density and the predictions by delta GAM are similar in range and distribution in all trophic species. The detailed comparisons between the observations and predictions can be found in the supplementary materials

Table 3. Spearman's correlation coefficients (ρ) between observed and predicted values by binomial and quasi-Poisson GAMs for all trophic species. Spearman's ρ is significant at p-value <0.01 for all GAMs.

		Spearman's ρ		
Guild	Trophic species	Binomial GAM	Quasi-Poisson GAM	Delta GAM
I	*Gadus morhua* 1	0.80	0.76	0.81
	Amblyraja radiata	0.57	0.53	0.59
	Macrourus berglax 1	0.80	0.75	0.81
	Macrourus berglax 2	0.81	0.62	0.82
	Nezumia bairdii 1	0.73	0.70	0.79
	Nezumia bairdii 2	0.77	0.79	0.83
	Phycis chesteri	0.75	0.61	0.74
	Reinhardtius hippoglossoides 1	0.50	0.71	0.68
II	*Anarhichasl upus* 1	0.79	0.77	0.83
	Anarhichas minor 1	0.61	0.50	0.60
	Glyptocephalus cynoglossus	0.58	0.58	0.69
	Hippoglossoides platessoides	0.73	0.73	0.83
	Lycodes reticulatus	0.69	0.72	0.76
III	Juvenile *Sebastes* spp.	0.81	0.71	0.80
	Sebastes fasciatus 1	0.75	0.74	0.77
	Sebastes fasciatus 2	0.77	0.68	0.78
	Sebastes mentella 1	0.78	0.38	0.58
	Sebastes mentella 2	0.71	0.32	0.49
	Sebastes norvegicus 1	0.78	0.69	0.78
	*Sebastes norvegicus*2	0.64	0.52	0.65
IV	*Gadus morhua* 2	0.80	0.64	0.81
	Anarhichas denticulatus	0.43	0.36	0.46
	Anarhichas lupus 2	0.69	0.58	0.73
	Anarhichas minor 2	0.61	0.53	0.64
	Reinhardtius hippoglossoides 2	0.74	0.75	0.87
V	*Pandalus borealis*	0.72	0.69	0.71

(Fig. S1). The median of observed values falls within the predicted interquartile range for all trophic species except AD, which also show the lowest *p* between observations and predictions. The observed and predicted density distribution and range are more similar in species that show stronger correlations between them.

Bottom temperature effects

The bottom temperature at sampling locations during the study period typically fell within a narrow interquartile range of 1.5ºC, between 3 and 4.5ºC (Fig. 2). However, the minimum-maximum range in within the entire period is approximately 3.3ºC, ranging from 1.9–5.2ºC. The range within one year can be as large as 2.2ºC, as seen in 2005. The spatial variation in bottom temperature displayed a distinct pattern of warmer southwest waters and colder northeast waters in most years (Fig. 3). Nevertheless, there are exceptional years showing a clear departure from this pattern such as seen in 1994, 2000 and 2018.

Trophic species for which there were significant relationships between occurrence and temperature share a common pattern whereby occurrence increases with

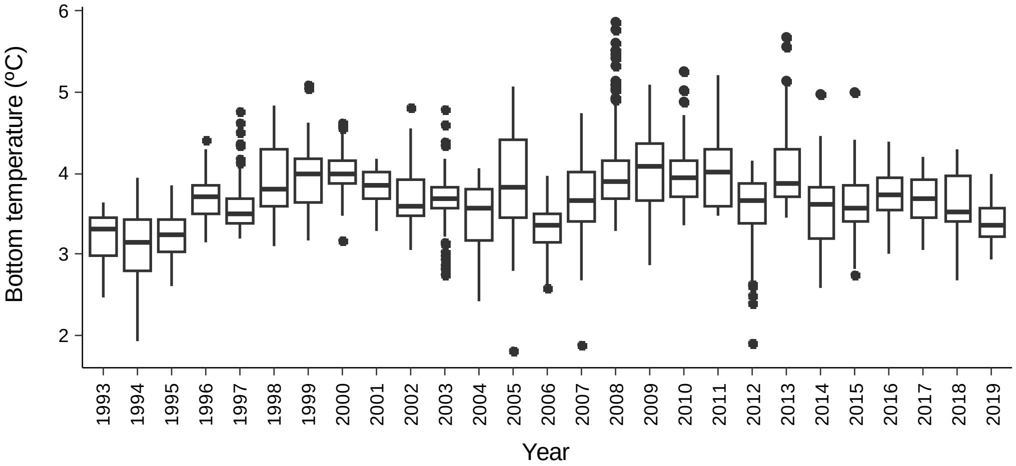

Fig. 2. Boxplot depicting the monthly average bottom temperature in July at sampling locations from 1993–2019, extracted from Copernicus Marine Service. The plot includes the minimum, first quartile, median, third quartile, and maximum values. Black dots represent outliers outside the minimum and maximum bars.

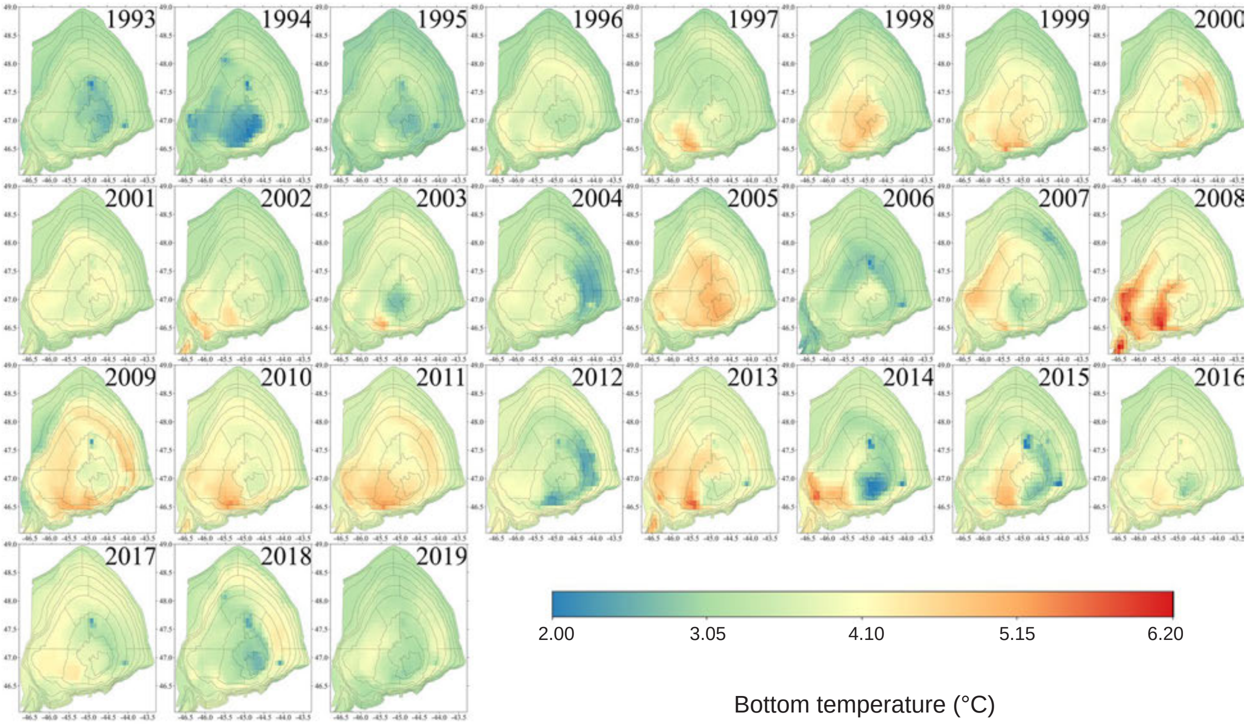

Fig. 3. Monthly average July Flemish Cap bottom temperature maps in 1993–2019 extracted from Copernicus Marine Service.

temperature up to 3ºC (Fig. 4a). Trajectories at warmer temperatures diverge and can be categorized into three types. The first type shows a continuous increase with low deceleration, exemplified by PC, SF2 and PB. The second type reveals a trajectory that plateaus, as demonstrated by NB1, NB2, SM1 and RH2. The third type features a trajectory that re-accelerates from a plateau when the temperature surpasses a certain threshold (around 5ºC), as seen in AR, SJ, SF1, SN1 and GM2. It is important to note that the models were fitted to data with higher numbers in moderate temperatures and fewer instances for extreme highs and lows. This may impact the fitting accuracy as can be seen in wide 95% confidence intervals.

Fig. 4. (a) Smoothers for the partial effect of bottom temperature on occurrence (binomial GAMs), and (b) smoothers for the partial effect of bottom temperature on density (quasi-Poisson GAMs). Shaded areas represent 95% confidence intervals, with each mark along the inside of the x-axis corresponding to a single observation (the "rugplot"). Note that the scale of the x and y-axes varies among plots for display purposes.

Significant effects of BT on density revealed by quasi-Poisson GAMs exhibited more diverse trends than binomial GAM fits. Only AL1 and GM2 show a continuous increase in density with temperatures warmer than 3ºC (Fig. 4b). In contrast to binomial GAM fits, multiple trophic species show a clear negative effect of warming temperature on density. These include MB1, NB2, HP, AD and AM2. In some trophic species, a distinct peak in density can be identified within commonly observed temperature ranges. These distinct peaks appear in SJ between 4–5ºC, and SN1 along with SN2 between 3–4ºC.

Distribution and abundance prediction

Densities for all trophic species were estimated on 1/20° grids using the corresponding best-fit delta GAMs. Density maps of every second year were generated for GM1 (Fig. 5a) and GM2 (Fig. 5b), illustrating spatiotemporal variations in density. The mapping results for all trophic species in all years can be accessed in the supplementary materials (Fig. S2–S27).

The mapping results for GM1 reveal a declining trend from the initial period (Fig. 5a). The density and distribution area reached their lowest levels in 1999 when the fishing moratorium was implemented. The stock remained stagnant until the mid-2000s when signs of

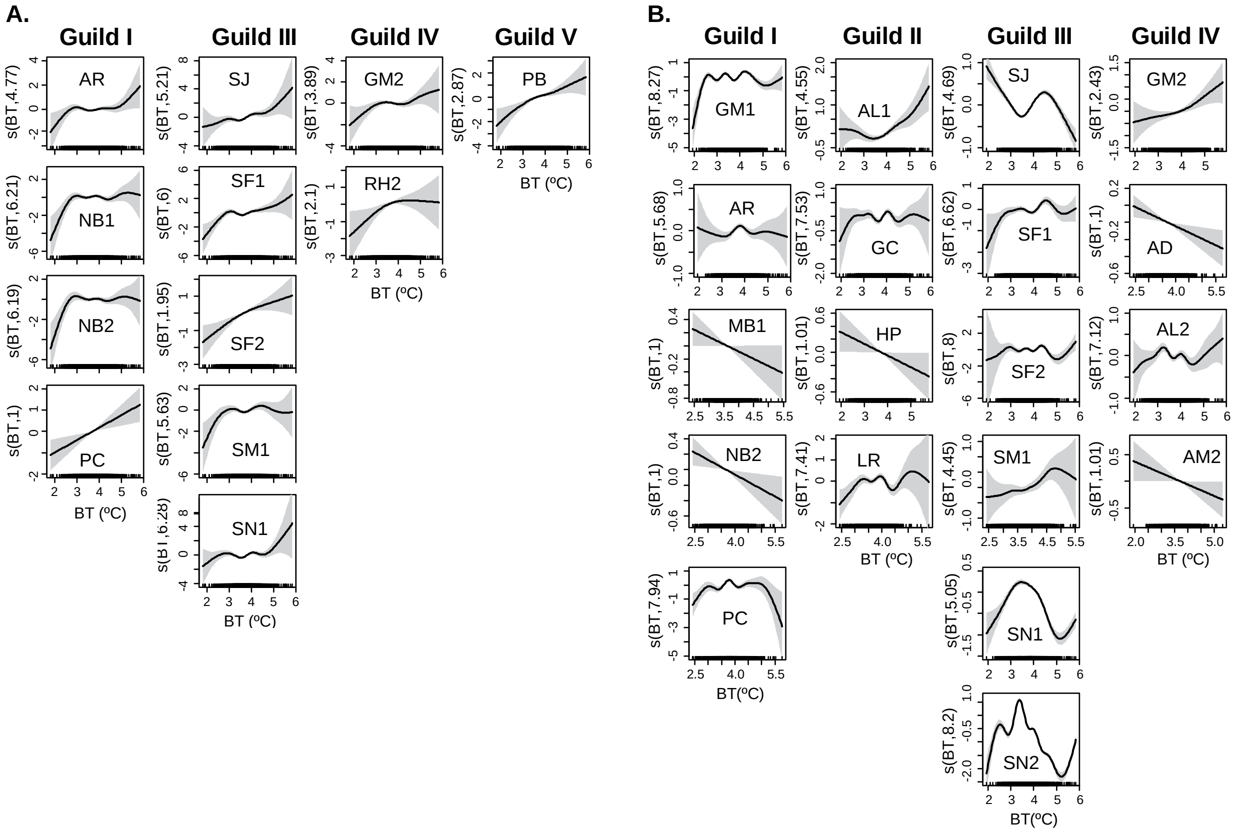

Fig. 4. (**A**) Smoothers for the partial effect of bottom temperature on occurrence (binomial GAMs), and (**B**) smoothers for the partial effect of bottom temperature on density (quasi-Poisson GAMs). Shaded areas represent 95% confidence intervals, with each mark along the inside of the x-axis corresponding to a single observation (the "rugplot"). Note that the scale of the x and y-axes varies among plots for display purposes.

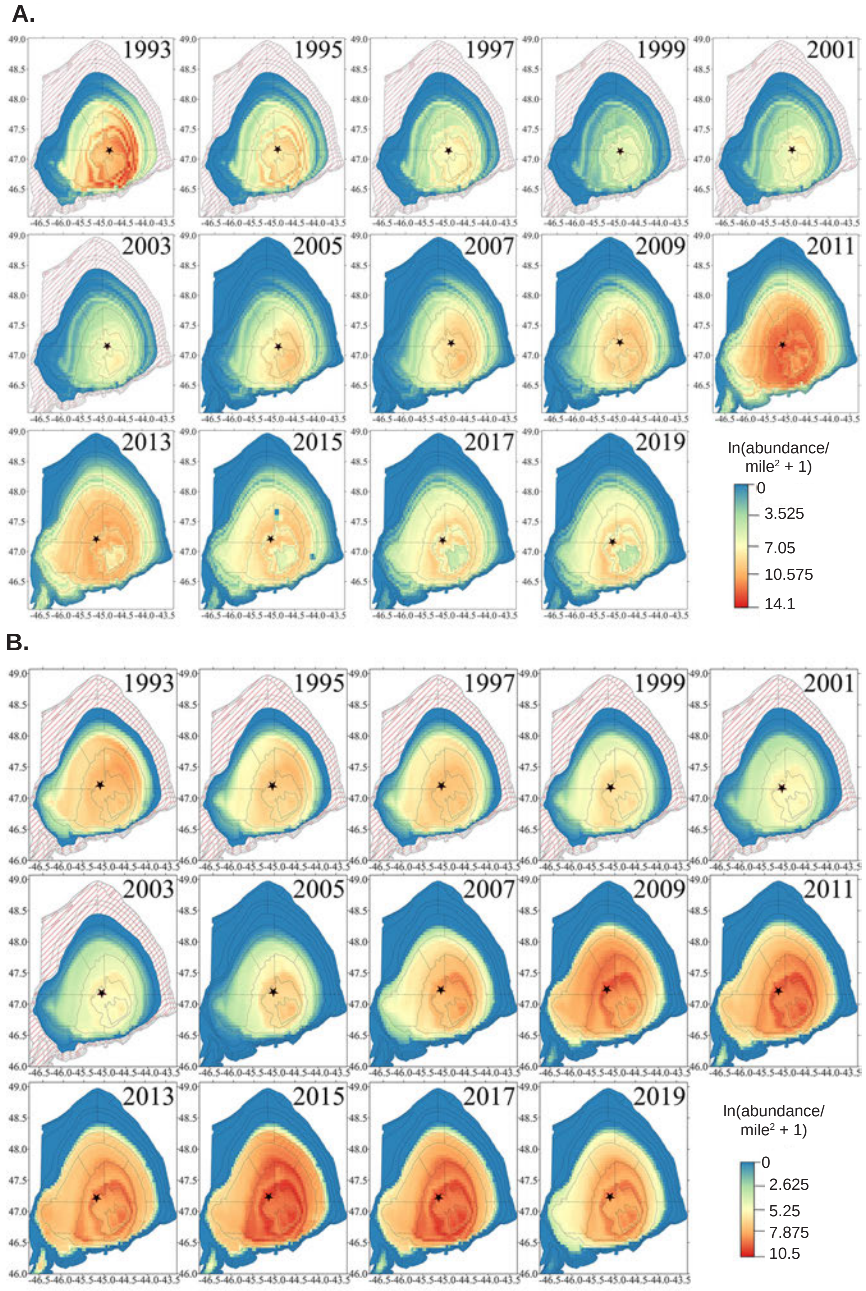

Fig. 5. Delta GAM predicted small Atlantic cod (≤46 cm) (**A**) and large Atlantic cod (>46 cm) (**B**) density distribution over Flemish Cap in every second year between 1993 to 2019. Stars represent weighted centroids of polygons by density.

recovery started to appear. Both density and distribution area increased until the moratorium was lifted in 2010. However, the recovered high abundance experienced a subsequent decline after 2012. Notably, during periods of relatively low abundance, there was a contraction in the distribution area with small cod remaining mainly at the top part of the cap. The weight centroids of polygons slightly shifted away from near the top of Flemish Cap towards the deeper parts in the northeast direction when the density was high.

The density and distribution of GM2 generally followed a similar trend to GM1, experiencing the decline in the early years (Fig. 5b). GM2 abundance bottomed in 2001, two years after GM1 reached its lowest level (Fig. 6). The distribution area continued to contract until it reached its smallest coverage in 2004. The stock then recovered and reached its highest abundance in 2014, three years after GM1 achieved its highest level. Signs of decline can again be seen in the later years. Although the trend is similar to GM1, the area coverage is more stable for GM2 with

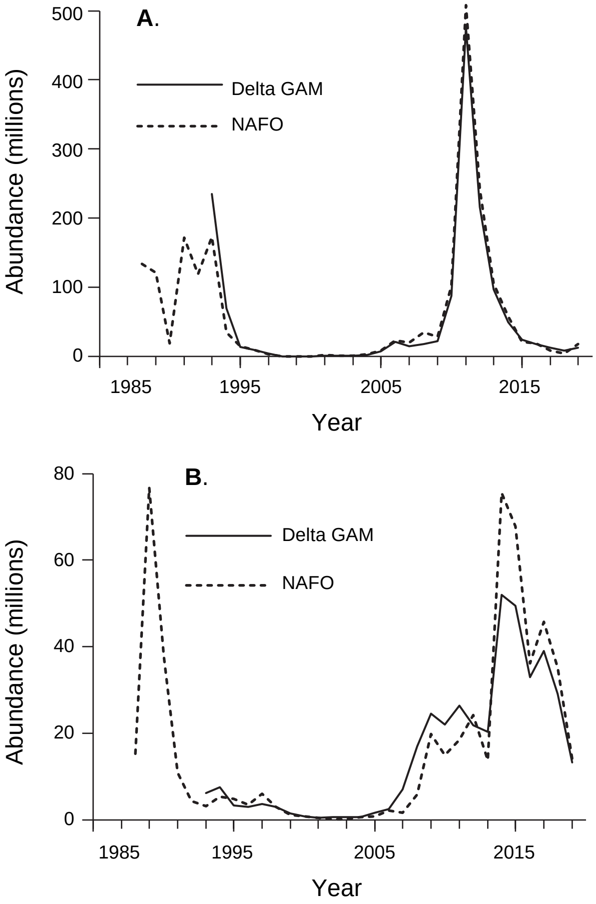

Fig. 6 The swept-area total abundance estimates (numbers in millions) of Atlantic cod used to assess the Division 3M cod stock by NAFO and total abundance predicted by delta GAMs: (**A**) total abundance estimated at age 1–3 years alongside the GM1 delta GAM prediction; (**B**) total abundance estimated for ages over 3 years alongside the GM2 delta GAM prediction

less contraction when overall abundance decline. The changes in the weight centroids of polygons are much less perceivable than in GM1.

The annual total abundances of Atlantic cod in Flemish Cap estimated by delta GAMs were validated by comparing them to results from NAFO Division 3M cod abundance estimation. The GAM predictions closely resemble the reported abundances (Fig. 6). Wilcoxon signed-rank tests showed no significant differences in total abundance between NAFO estimated Atlantic cod aged 1–3 years and delta GAM prediction of GM1 (*p*-value = 0.09) or between NAFO estimated Atlantic cod older than 3 years and delta GAM prediction of GM2 (*p*-value = 0.79). Although the sign-rank tests indicate that there is no significant difference in the medians between the two estimation methods, the magnitude of differences is notable in GM2. Compared to the NAFO estimation, the result from delta GAM of GM2 is discernibly higher than the NAFO swept-area estimation when the reported abundance is low (late-2000s) while being lower when the reported number is high (mid-2010s).

Cod correlations to other trophic species

Total area of Flemish Cap (≤730 m depth) was estimated to be 10 862.10 miles$^{2.}$ The occupied portion of this area by each trophic species was estimated for each year (Fig. 7a). The area occupied by cod fluctuated greatly. For GM1, its smallest occupied area was 69% smaller than the maximum coverage. For GM2, the smallest occupied was 42% smaller than the maximum coverage. The occupied areas of most members of Guild III (SJ, SF1, SF2, SM1 and SM2) and Guild V were more stable than others over time.

Spearman's correlation analysis revealed significant strong positive correlations between the GM1 and GM2 distribution area. The correlation between GM2 and a later year's GM1 is stronger than the correlation between GM1 and a later year's GM2 (Table 4). Both size classes displayed significant negative correlations with most of the other trophic species in a following year, regarding both abundance and distribution area (Table 4). Both GM1 and GM2 were significantly negatively correlated to most trophic species within their respective guilds. The only exception is NB2 not being significantly correlated to GM1. Most members of Guild II are also significantly negatively correlated to GM1 and GM2, except for shallow water flatfishes GC and HP, which showed strong positive correlations. Most of Guild III members were not significantly correlated to cod, except for positive correlations between SF2 to both GM1 and GM2; negative correlations of SM1 to both GM1 and GM2; and negative correlation between SN1 and GM2. Guild V was not significantly correlated with either GM1 nor GM2.

The annual total abundance (≤730 m depth) for all species was estimated, and fluctuations over time are illustrated in Fig. 7b. The changes in total abundance for most species mirrored the expansions and contractions of their distribution area, with the exception of redfish in Guild III and northern shrimp in Guild V, for which total abundance fluctuations were much more pronounced than distribution area changes. Spearman's correlation analysis results for abundance were similar to those for distribution area in most cases (Table 4). A strong, significant positive correlation was found between GM1 and GM2, both of which were consistently negatively correlated with members of Guilds I and IV, except for AD. The cod abundance correlations to Guild II were similar to distribution area correlation but weaker. In contrast to the results for distribution area, both GM1 and GM2 showed a strong, significant negative correlation with PB abundance. A significant negative correlation between SJ

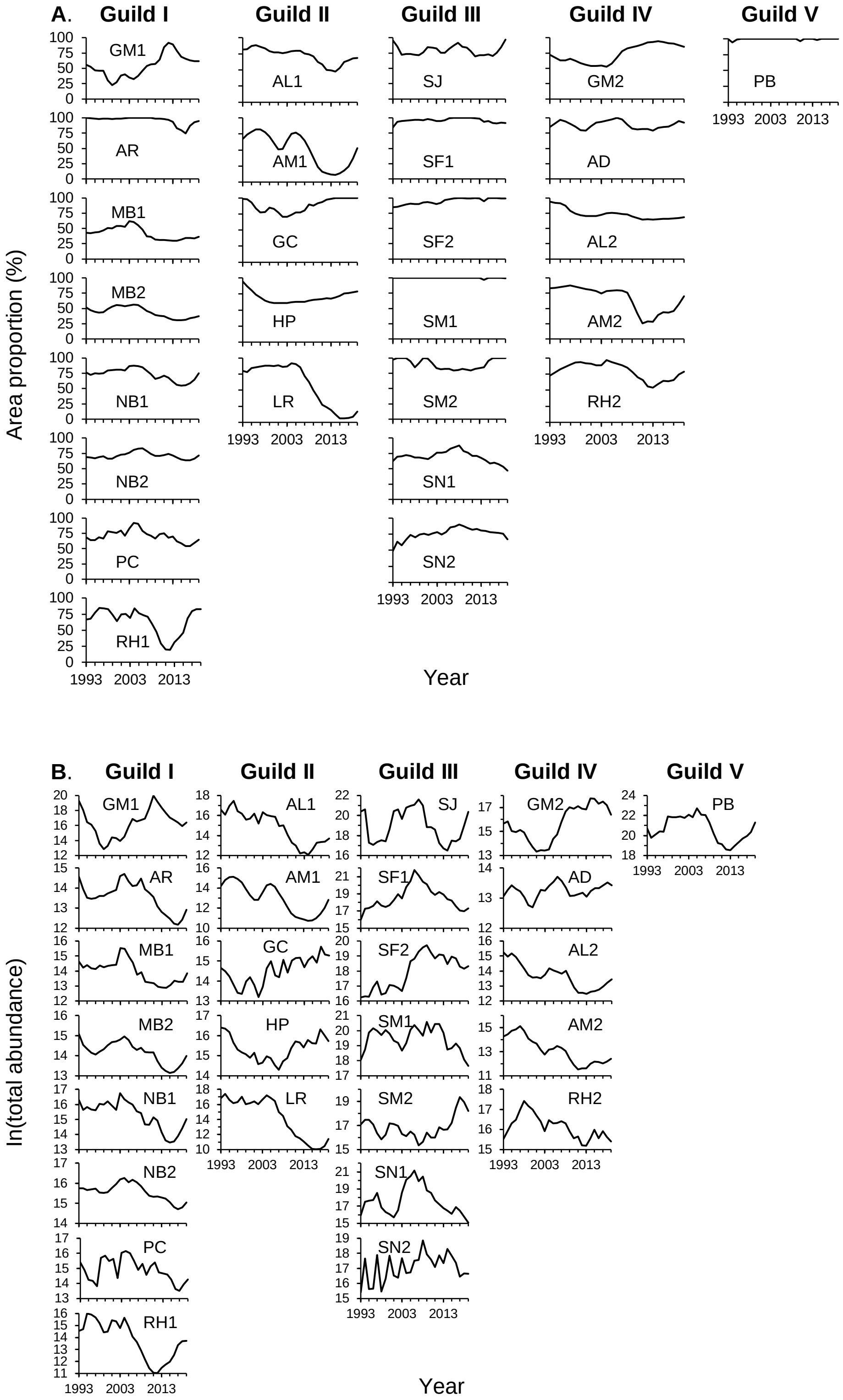

Fig. 7. (**A**) Predicted area of distribution as proportion of total area (≤730 m depth), and (**B**) log transformed annual total abundance of trophic species (≤730 m depth), from 1993 to 2019. Note that scales of y-axis vary between plots for display purposes.

Table 4. Spearman´s correlations for annual distribution areas and total abundances (≤730 m depth) between the two trophic species of Atlantic cod and other trophic species in a following year, based on data from 1993 to 2019. Significant correlations are indicated by * (p<0.05) and ** (p<0.01)

Guild	Trophic species	Spearman's ρ Distribution area GM1	Distribution area GM2	Total abundance GM1	Total abundance GM2
I	*Gadus morhua* 1	-	0.94**	-	0.77**
	Amblyraja radiata	-0.70**	-0.81**	-0.43*	-0.78**
	Macrourus berglax 1	-0.91**	-0.90**	-0.75**	-0.82**
	Macrourus berglax 2	-0.95**	-0.96**	-0.60**	-0.88**
	Nezumia bairdii 1	-0.91**	-0.94**	-0.71**	-0.87**
	Nezumia bairdii 2	-0.36	-0.55**	-0.44*	-0.88**
	Phycis chesteri	-0.74**	-0.79**	-0.47*	-0.64**
	Reinhardtius hippoglossoides 1	-0.48*	-0.44*	-0.61**	-0.67**
II	*Anarhichas lupus* 1	-0.75**	-0.74**	-0.55**	-0.68**
	Anarhichas minor 1	-0.71**	-0.71**	-0.44*	-0.64**
	Glyptocephalus cynoglossus	0.85**	0.94**	0.50**	0.76**
	Hippoglossoides platessoides	0.69**	0.71**	0.56**	0.68**
	Lycodes reticulatus	-0.91**	-0.93**	-0.46*	-0.80**
III	Juvenile *Sebastes* spp.	-0.25	-0.23	-0.42*	-0.46*
	Sebastes fasciatus 1	-0.18	-0.24	-0.03	-0.40*
	Sebastes fasciatus 2	0.59**	0.65**	0.42*	0.42*
	Sebastes mentella 1	-0.41*	-0.45*	0.09	-0.18
	Sebastes mentella 2	0.03	0.17	0.14	0.42*
	Sebastes norvegicus 1	-0.36	-0.50*	0.33	-0.37
	Sebastes norvegicus 2	0.28	0.21	0.23	0.15
IV	*Gadus morhua* 2	0.87**	-	0.68**	-
	Anarhichas denticulatus	-0.33	-0.42*	0.10	0.09
	Anarhichas lupus 2	-0.68**	-0.69**	-0.39	-0.60**
	Anarhichas minor 2	-0.74**	-0.66**	-0.50*	-0.60**
	Reinhardtius hippoglossoides 2	-0.96**	-0.89**	-0.66**	-0.68**
V	*Pandalus borealis*	-0.23	-0.20	-0.83**	-0.75**

and both cod classes was found. Other notable differences in correlation analysis results are the non-significance of SM1 and SN1, while a significant positive correlation was shown between SM2 and GM2. Notably, the correlations for abundance were generally weaker than those for distribution area. Overall, the correlations were all stronger for GM2 than GM1, except the correlation to PB.

Discussion

The present study employed a variety of statistical tools to investigate the spatiotemporal dynamics of Atlantic cod and other demersal species in Flemish Cap. Our findings shed light on the changes in the cod abundance and distribution over time due to fishing pressure and environmental variation, and reveal how the fluctuation of this top predator impacted the entire demersal community. Moreover, the study highlights the heterogeneity of these impacts among different trophic groups.

Delta GAM for spatiotemporal modelling

The estimation of cod abundance using the delta GAM approach in this study yielded results that aligned with observations and traditional methods (González-Troncoso *et al.*, 2022). Nevertheless, it is important not to disregard the noticeable differences in estimations between the two methods, especially evident in large cod. The swept-area method estimates abundance by multiplying the density by the stratum area for each stratum, before combining the abundance from all strata (Vázquez *et al.*, 2014). On the other hand, the GAMs estimate the number of individuals in fine grids. Then the numbers of individuals in all fine grids are combined to derive the total abundance. The use of fine grids by the modelling approach could pick up finer scale changes that the swept-area extrapolation did not. Moreover, the modelling approach derived the estimates from the use of covariates, unlike the relatively simple multiplication by the swept-area method which did not consider spatiotemporal factors. Although the delta GAM approach can offer valuable spatial information on a finer scale, further exploration is required to assess its accuracy and precision when determining abundance, compared to the traditional estimation method, before considering its use for stock assessment. We consider sampling effort bias among strata to be negligible, but spatial treatment or post-stratification schemes that could help reduce model uncertainty in the future are worth exploring. Integrating fishery data in addition to the survey data for more input and validation could also improve the modelling, as estimations by NAFO also use commercial fishery data (Garrido *et al.*, 2023a).

To gain further insights into the drivers of overall abundance and distribution changes, it is essential to integrate environmental factors into the modelling and mapping approach. Previous studies have explored depth-related demersal assemblages in Flemish Cap (Nogueira *et al.*, 2017). However, our best-fit models indicate that other environmental variables could also affect the distribution. Sea bottom temperature was clearly shown to be a significant factor affecting density and distribution. All models also included significant terms for spatial coordinates which suggested the presence of unexplained spatial variation due to spatial variation in other environmental variables that were not included in modelling. Environmental variables such as sediment types and benthic faunas, including deep-sea corals and sponges, which vary spatially, could play a role in habitat preference (Murillo *et al.*, 2011, 2016, 2020b, 2020a). Future analyses that incorporate these factors could further explain the assemblage variation found in this study. In this study we used year as a fixed factor to arbitrarily represent possible temporally dynamic factors such as fishing mortality, currents, salinity, primary productivity and zooplankton. In the future investigation when these factors are explicitly included in the model, a modification of GAMs to generalized additive mixed models (GAMMs) to treat year as a random effect might be needed (Lin and Zhang, 1999).

While the spatiotemporal variation in bottom temperature is typically low, as expected in deep-sea environments (Yasuhara and Danovaro, 2016), incorporating this variable into the models has proven important for predicting occurrence and abundance of several species. This supports the hypothesis that changes in the distribution patterns of Flemish Cap are associated with oceanographic conditions (Cerviño *et al.*, 2005). Other investigation also found abiotic factors such as the North Atlantic Oscillation, which is linked to local oceanographic variables including temperature, salinity and currents, to be associated with changes and trends in Flemish Cap demersal community (Pérez-Rodríguez *et al.*, 2012). Binomial GAMs with a significant temperature term unanimously show bottom temperature below 3ºC to be less favourable for fish occurrence but varying effects of temperature can be seen on density. In most of the trophic species for which there appeared to be a negative relationship between temperature and density (when the species was present), including small roughhead grenadier, American plaice, northern wolffish (*A. denticulatus*) and large spotted wolffish (*A. minor*), temperature apparently did not affect occurrence. The lack of significant temperature term in binomial GAMs of several species could be because the temperature effects are relatively weak and/or because such effects are partially confounded with depth or spatial variables.

Cod abundance and distribution fluctuation

The findings of this study reinforced the notion that a significant decline in the overall population of a species could come with a contraction of its distribution range, which had previously been shown in multiple taxa across multiple areas (Thorson *et al.*, 2016; Orio *et al.*, 2019). In the case of Flemish Cap cod, abundance and distribution can be observed across three distinct periods: the pre-moratorium, the moratorium and the post-moratorium. In the pre-moratorium period, the abundance and distribution area of cod markedly declined, evidently due to high fishing mortality pressure on low SSB until 1999 when the moratorium was enforced (González-Troncoso *et al.*, 2022).

Throughout the moratorium, both abundance and distribution area further declined until the mid-2000s, marking the species' lowest recorded abundance despite the cessation of fishing pressure. Unfavourable environmental conditions and limited food availability likely hampered recruitment and delayed recovery (Ruiz-Díaz *et al.*, 2022). Notably, bottom temperatures also declined from 1999 to their lowest point in 2006. This potentially affected recovery as the models indicated that cod generally thrives in warmer temperatures. During this low abundance period, the distribution area was predominantly confined to the top of the cap at depths shallower than 270 m. This aligns with a previous spatial modelling study describing cod distribution changes from 1988 to 2002 (Hendrickson and Vázquez, 2005). A noticeable distribution expansion occurred only in the late-2000s when species' density showed signs of recovery, coinciding with the increase of temperature since 2006.

The recovery from the mid to late-2000s prompted the lifting of the moratorium in 2010 and fishing mortality was reintroduced (Garrido *et al.*, 2023a). In the post-moratorium period, both the abundance and distribution area began to decline once more but remained within the "safe" zone, maintaining a biomass above the reference point and fishing mortality below the target (NAFO, 2023b). After the abundance peaked in 2011 for small cod and 2014 for large cod, the distribution contracted again, following the decline in stock status. This pattern suggests that the most preferred habitat for cod is in the shallowest part of the mount, and they only occupy deeper space when the area becomes sufficiently congested, likely reflecting intraspecific competition (Planque *et al.*, 2011; Thorson *et al.*, 2016).

Observing changes in spatial distribution by size classes is advantageous, as different size classes do not play the same ecological role and are subject to different fishing pressure (Kindsvater and Palkovacs, 2017). This study reveals a clear decline in larger cod density that started several years prior to the decline of small cod. This is likely due to the higher catchability of older and larger fish, which were intensively exploited and depleted before the impact escalated to cause recruitment overfishing (Walters and Maguire, 1996; González-Troncoso *et al.*, 2022). Conversely, the signs of recovery appeared earlier in small cod, as expected, preceding the recovery of the larger size class in subsequent years.

Cod fluctuation effects on the community

The spatiotemporal changes observed in other species, many of which are less threatened by fisheries, could be caused by changes in the trophic structure rather than direct fishing impacts (Nogueira *et al.*, 2016). The severe depletion of cod, particularly the larger size class that predominantly preys on fish, notably juvenile redfish, between the mid-1990s and mid-2000s, might have opened up more access to resources for other piscivores of Guild IV (Pérez-Rodríguez *et al.*, 2017). A prominent shift in distribution was evident in large Greenland halibut, which typically resides in deeper areas (Nogueira *et al.*, 2017). Its presence and density drastically increased in shallower regions when large cod populations collapsed, causing significant changes in the assemblage structure. This finding aligns with a previous spatial modelling study, which clearly illustrated the contraction of the distributions of cod and American plaice from 1988 to 2002, and their replacement by Greenland halibut (Hendrickson and Vázquez, 2005). A multispecies model also describes Flemish Cap ecological shifts from a system in which the dominant species by biomass were cod and redfish to a system characterised by the predominance of other fish species by the late-1990s, before the subsequent recovery (Pérez-Rodríguez *et al.*, 2017). This study's wider scope sheds light on other species that share trophic niches with cod, large and small, which showed increases in abundance and expansion in their distribution range in the absence of Atlantic cod. These species include thorny skate (*A. radiata*), roughhead grenadier, marlin-spike grenadier, longfin hake (*P. chesteri*), Arctic eelpout (*L. reticulatus*), Greenland halibut and wolffishes.

While small cod primarily feed on northern shrimp and hyperiids, their increased presence can still have adverse effects on other fish species due to competition. The spatial distribution of northern shrimp remained relatively stable over shallow areas, yet its overall abundance fluctuated greatly, showing a strong negative correlation to small cod. As the cod population recovered to the point of lifting the moratorium, the shrimp fishery had to enter its own moratorium in 2011 due to the species being unable to sustain both the fishery and increased predation mortality (Casas Sánchez, 2023). Other trophic species in Guild I, which largely consume northern shrimp, exhibited strong negative correlations with small cod in terms of both distribution area and abundance (Pérez-Rodríguez *et al.*, 2011). Multiple species in Guild II, known for having the most diverse diets, also demonstrated negative correlations with small cod due to northern shrimp being a significant part of their diet. In contrast, benthic fishes in Guild II that rely less on northern shrimp, namely American plaice which primarily preys on ophiuroids and witch flounder (*G. cynoglossus*), which mainly feeds on polychaetes (Link *et al.*, 2002; González *et al.*, 2005), appeared to benefit from the increase in the cod population. These species could be less threatened by cod competition and predation but more susceptible to other predators, such as the large Greenland halibut, a benthic flatfish known to prey on other flatfish (Hovde *et al.*, 2002). It should also be noted that some of the correlation results might arise from the species reacting to the changes in bottom temperature or other unaccounted variables. The densities of some species that show strong negative correlations to cod such as small roughhead grenadier, large marlin-spike grenadier and large spotted wolffish also show an opposite relationship with temperature compared to that seen in cod.

While the total abundance of northern shrimp and juvenile redfish is negatively correlated with cod, reflecting their established prey-predator relationship (Pérez-Rodríguez and Saborido-Rey, 2012; Pérez-Rodríguez *et al.*, 2017), their distribution areas do not exhibit a clear correlation. The distribution area of northern shrimp and redfish, including juveniles, remained consistently high throughout the study period, irrespective of the abundance situation. This suggests a lesser density-dependent impact on their distribution, at least within the depth range of ≤730 m. A study investigating density-dependent effects across multiple taxa in areas including Northwest Atlantic also found the area occupied by scorpaeniform fishes to be less positively correlated to abundance than was seen in gadiform and pleuronectiform fishes (Thorson *et al.*, 2016).

Apart from juvenile redfish and small Acadian redfish, most members of Guild III display no significant negative abundance correlations to cod. This could be primarily explained by the size of the fish, as larger redfish are less susceptible to predation. Redfish larger than 27 cm were not found in the stomach contents of cod, as indicated by a previous study in Flemish Cap (Iglesias *et al.*, 2012). This size effect is evident in the significant negative correlation between large cod and small Acadian redfish, which has a smaller upper limit of 21.5 cm. Small beaked redfish and Golden redfish (*S. norvegicus*), having larger upper size limits of 27.5 cm, show a negative but non-significant correlation to large cod.

The weak but significant positive correlations found between large cod and large redfish might appear unexpected at first glance, as the higher abundance of cod would be expected result in high consumption of juvenile redfish and subsequently lower recruitment in the later years. However, these positive correlations could be influenced by external variables rather than reflecting their trophic relationship, especially the effect of overexploitation which occurred over the same period (Ávila de Melo *et al.*, 2019). Since the surveys began in 1988, redfish SSB underwent a drastic decline up until the mid-1990s, largely due to a sharp increase in fishing mortality (Ávila de Melo *et al.*, 1998). A significant portion of juveniles was also removed as bycatch by shrimp fisheries between 1993 and 1995, contributing to the low recruitment of large redfish in subsequent years (Pérez-Rodríguez *et al.*, 2017). The SSB then rebounded swiftly due to strong recruitment from the early to late-2000s and remained at a high level while fishing mortality was suppressed (Gonçalves *et al.*, 2023). The coincidental collapse of cod and redfish due to the overexploitation, followed by a similar period of recovery, could overshadow the negative impact of cod predation on young redfish. It should be noted that the lag used in the analysis was only one year for assessing the immediate direct impact of cod on other species. The results may not demonstrate the longer-term effect that could be associated to cod such as reduced recruitment that may take more than one year to realise. A further investigation with different lags, depending on life history, to discern cod effects on other species through recruitment should be conducted.

Although unfavourable abiotic conditions were suspected to be the main cause of impaired recruitment, the shift in assemblage and trophic structure after the collapse could also have contribute significantly to the recovery delay (Borovkov *et al.*, 2005; Kuparinen *et al.*, 2014; González-Troncoso *et al.*, 2022). Cod abundance fluctuations may not have a one-way effect on other species, as recent studies showed that food availability can also impact cod recovery (Sguotti *et al.*, 2018; Ruiz-Díaz *et al.*, 2022). The decline of the spawning stock due to the lower food availability could lead to recruitment reduction and delayed recovery (Pérez-Rodríguez *et al.*, 2010). High fishing mortality on their prey could lead to a decrease in cod biomass, making it practically impossible to have high yields and maintain healthy populations of cod, redfish and shrimp concurrently (Pérez-Rodríguez *et al.*, 2022). The replacement of cod by other predators, such as Greenland halibut and wolffishes, which are strongly negatively correlated to cod, might hinder the remaining cod's ability to compete for food and habitat, impeding their immediate reoccupation of the area after the moratorium. Such phenomena are known as trophic cascades, where the trophic structure experiences a fundamental change and is difficult to restore the original system state due to the removal of key species (Fisher *et al.*, 2015; Ripple *et al.*, 2016). Only after the recovery of shrimp, then redfish, to a high abundance level, did the cod population begin to recover (Pérez-Rodríguez *et al.*, 2017).

Management implications

The cod fisheries management in NAFO Division 3M predominantly relies on catch quotas derived from single-species stock assessment (NAFO, 2023a). Since the fishery reopened in 2010, the cod population has been closely monitored to ensure sustainably low fishing mortality (González-Troncoso *et al.*, 2022). While precautionary approaches are considered in management, the reliance on single-species assessments may overlook the ecosystem's complexity, as illustrated by several studies in the area (Pérez-Rodríguez *et al.*, 2011, 2017; Pérez-Rodríguez and Saborido-Rey, 2012; Nogueira *et al.*, 2018). Tests on multiple harvest control rules have emphasized the necessity for target fishing mortalities for cod, redfish and shrimp to be jointly designed (Pérez-Rodríguez *et al.*, 2022). Although the spatial modelling results of this study at this stage do not offer a mechanism to replace the current stock assessment, they do expand the evidence about ecological interactions of cod to include a broader range of species, beyond those commercially targeted. The pressure exerted by cod, whether through competition or direct predation, can significantly impact non-commercially targeted species, including thorny skate, roughhead grenadier, marlin-spike grenadier, longfin hake, wolffishes, Arctic eelpout and presumably some other less abundant species that are not included in this study due to the lack of samples. Although maintaining cod SSB at a safe level should remain a key management priority, the unavoidable impact of cod on other species highlights the necessity of ensuring low fishing pressure on redfish and shrimp to maintain their ecological status (Gonçalves *et al.*, 2023). The ongoing moratorium on shrimp is likely to be crucial for maintaining the structure of the ecosystem - and future reopening should carefully consider the impacts on shrimp biomass as well as their predators (Casas Sánchez, 2023).

Variations in the spatial distribution and abundance of species can offer valuable insights for spatial management (Stelzenmüller *et al.*, 2013). For example, the cod population typically resides at the top of the mount, and only spills over into deeper waters when density is high. Protecting the shallowest part could help ensure cod survival, particularly small individuals, and allow catches to only remove the excess fish that spill over from the protected area (Di Lorenzo *et al.*, 2016). The NAFO Scientific Council reports until 2020 showed that the long line fishery consistently operates mainly around the top of Flemish Cap while bottom trawl fisheries were already operating less intensely in the same area, especially those not directly targeting cod (NAFO, 2015, 2020). Therefore, limiting fisheries access to the shallow area may benefit the cod population. Investigation should be carried out into the impacts of closure on the fisheries.

Recent management measures, aiming specifically to protect cod, were implemented in 2021 (NAFO, 2021). First, the closure of the cod fishery during the first quarter of the year, which aligns with the cod spawning period in the area. Second, the employment of sorting grids or grates with a maximum bar spacing of 55 mm for trawls directly targeting cods to reduce small cod bycatch. Since the new measures were put in place, the proportion of the cod catch that is smaller than 45 cm has decreased. However, longlines fishing patterns shifted to concentrate even more in the central part, although the spatial change might be attributed to the lower abundance and TAC rather than solely in response to the measures (Garrido *et al.*, 2023c). This observation suggests that non-spatial measures could reduce juvenile catches but when the stock is in a poor state and concentrated at the top of the cap, the fishing activity would still put more pressure on their refuge area. An explicit special management measure aiming to protect cod, especially when vulnerable, should be considered to ensure their survival and promote recovery.

Fisheries targeting other commercial species, such as the redfish trawl fishery, which catches the highest percentage of cod bycatch, should avoid operating over the shallow areas of less than 270 m depth to reduce small cod bycatch (Garrido *et al.*, 2023c). The shallow area is already not typically densely populated by all redfish species as modelled in this study and observed in other investigations (Nogueira *et al.*, 2017). Therefore, protecting the shallow area from redfish trawls, even partially or temporally, should be considered to help protecting cod. It could follow an example of temporal area closure for shrimp fishery within the 200 m depth contour from 1st June to 31st December, which has already been established independently from the overall shrimp moratorium (NAFO, 2023a). However, the socio-economic impact of closure, even temporary, compared to the ecological benefits should be studied for each fishery before decision making.

Protecting marine biodiversity is an important management objective to maintain ecosystem functioning and services, and spatial management is a tool that can help achieve this (Mangano *et al.*, 2015). Some trophic species with inherently lower numbers, including wolffishes, thorny skate, longfin hake, Arctic eelpout and small Greenland halibut, were typically found at the bottom edge of their distribution range when their abundance drastically declined, forming a ring around 400 to 600 m. Accounting for these spatial patterns can be valuable in spatial management efforts to reduce bycatch risk and preserve biodiversity (Komoroske and Lewison, 2015; Hazen *et al.*, 2018). In efforts to conserve biodiversity, NAFO has already instituted numerous closure areas to protect vulnerable marine ecosystems around Flemish Cap, which have been recently reassessed and extended (NAFO, 2022). Most of these closures are situated at depths exceeding 500 m and primarily focus on benthic invertebrate diversity. Integrating the insights from this study could add another layer to future closure assessments, specifically emphasising rare fish species. This inclusion, beyond protecting biodiversity, could also aid vessels in avoiding bycatch that exceeds quotas, potentially reducing the need for time-consuming and costly measures such as exiting the division or conducting tow trials (NAFO, 2023a).

Conclusion

This study utilized a statistical modelling approach to reveal spatiotemporal changes in cod and other demersal species, indicating that fishing and environmental variations affect not only cod abundance but also their distribution range. Cod distribution range greatly contracted when the abundance was low. The results also highlight the secondary effects of cod stock fluctuation on trophic structure and show potential ecosystem-wide impacts from exploiting key species. Nevertheless, not all trophic groups responded uniformly to changes in cod population. The distribution changes for juvenile redfish and northern shrimp $\leq$730 m depth were small, yet their abundance significantly benefitted from the reduction in cod populations. Cod competitors, including Greenland halibut, thorny skate, roughhead grenadier, marlin-spike grenadier, longfin hake, Atlantic wolffish (*A. lupus*), spotted wolffish and Arctic eelpout also benefitted from cod depletion. Large redfish do not show a sign of benefiting from cod depletion despite their young being a main cod prey. This could be due to external variables including fishing and environmental pressure having stronger effects. Other species with minimal trophic relationships with cod but residing at a similar depth, such as American plaice and witch flounder, could benefit from cod recovery because their predators could be supressed by cod. These ecological ties should be considered for future wider multispecies interaction modelling and management decision-making.

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