National Marine
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Fishery Bulletin
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Abundance and distribution of Atlantic cod (*Gadus morhua*) in a warming southern New England

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Abstract—Atlantic cod (*Gadus morhua*) in southern New England (SNE) and along the mid-Atlantic coast have been described as the world's southernmost population of this species, but little is known of their population dynamics. Despite the expectation that SNE Atlantic cod are or will be negatively influenced by increasing water temperatures due to climate change, fisheries that target Atlantic cod in this region have reported increased landings during the past 2 decades. The work described here used ichthyoplankton and trawl survey data to investigate spatial and temporal patterns of abundance of Atlantic cod, and their potential links to environmental factors, across multiple life stages in Rhode Island. The results identify waters of the state of Rhode Island as a settlement and nursery area for early stages of Atlantic cod until water temperatures approach 15°C in late spring. Atlantic cod that were age 1 or older used coastal habitats when water temperatures were within their documented thermal preferences. The data indicate that abundance of Atlantic cod in SNE has increased since 2000, but continued warming of winter water temperatures may limit future recruitment. The improved understanding of the life history and population dynamics of Atlantic cod in SNE provides insights into stock structure and productivity in a poorly understood and vulnerable portion of their geographic distribution.

Manuscript submitted 26 October 2019.
Manuscript accepted 13 May 2020.
Fish. Bull. 118:145–156 (2020).
Online publication date: 29 May 2020.
doi: 10.7755/FB.118.2.4

Atlantic cod (*Gadus morhua*) in the northwest Atlantic Ocean have historically ranged as far south as Cape Hatteras, North Carolina (Schroeder, 1930; Bigelow and Schroeder, 1953). However, because aggregations documented during the winter months off New York, New Jersey, and Rhode Island represent the southern limit of known spawning activity for this species (Smith, 1902; Wise, 1963) and no significant quantity of eggs or larvae have been found south of Long Island in recent decades (Serchuk and Wood[1]; Berrien and Sibunka, 1999), the geographic region of southern New England (SNE) is thought to have the world's southernmost indigenous population of Atlantic cod (Wise, 1958). Atlantic cod within U.S. waters are assessed and managed as 2 stocks: Georges Bank and the Gulf of Maine, with Atlantic cod in SNE included in the Georges Bank management unit (Zemeckis et al., 2014a). Both stocks are currently in a critically depleted state (NEFSC[2,3]), but the status of Atlantic cod in SNE is poorly understood because Atlantic cod have been infrequently observed in fishery-independent trawl surveys. Consequently, survey sampling areas, or strata, in SNE are not incorporated

[1] Serchuk, F. M, and P. W. Wood. 1979. Review and status of the southern New England–Middle Atlantic cod, *Gadus morhua*, populations. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent., Woods Hole Lab. Ref. Doc. 79-37, 77 p. [Available from Woods Hole Lab., Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., 166 Water St., Woods Hole, MA 02543.]

[2] NEFSC (Northeast Fisheries Science Center). 2017. Georges Bank Atlantic cod. *In* Operational assessment of 19 Northeast groundfish stocks, updated through 2016. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 17-17, p. 38–46. [Available from website.]

[3] NEFSC (Northeast Fisheries Science Center). 2017. Gulf of Maine Atlantic cod. *In* Operational assessment of 19 Northeast groundfish stocks, updated through 2016. NOAA, Natl. Mar. Fish. Serv., Northeast Fish. Sci. Cent. Ref. Doc. 17-17, p. 26–37. [Available from website.]

in the stock assessment for the Georges Bank management unit of Atlantic cod (NEFSC, 2013). Although the region has not sustained biomass levels as high as other waters of the United States, Atlantic cod in SNE have historically supported significant recreational and commercial fisheries that have made important economic contributions to coastal communities (Serchuk and Wood[1]; Oviatt et al., 2003).

Results of past research provide some insights into population dynamics of Atlantic cod in SNE. Findings from tagging experiments indicate that SNE Atlantic cod may represent a separate spawning group that significantly mixes with cod inhabiting the Nantucket Shoals region but that exhibits very limited movements to the stock area in the Gulf of Maine (Schroeder, 1930; Wise, 1958; Tallack, 2011). The results of these efforts indicate that Atlantic cod south of Cape Cod, Massachusetts, may represent 2 distinct spawning groups: 1 group south of Massachusetts and Rhode Island in SNE and 1 group off the coast of New Jersey (Smith, 1902). These groups are thought to use similar habitats around the Great South Channel and Nantucket Shoals during the summer months (Wise, 1963; Serchuk and Wigley, 1992). Peak spawning of Atlantic cod in the SNE region has historically occurred during the winter, on the basis of collections of fish in spawning condition (Wise, 1958; Serchuck and Wood[1]) and eggs or larvae of Atlantic cod in ichthyoplankton tows (Berrien and Sibunka, 1999), and the peak in spawning has overlapped with a peak in commercial fishing effort (Serchuk and Wood[1]). More contemporary winter–spring observations of spawning Atlantic cod collected from waters south of Rhode Island indicate that this spawning seasonality has remained stable (Loehrke, 2013).

Although spawning in SNE is well-documented, the connectivity among Atlantic cod in SNE and in other regions is uncertain. Results from larval modeling studies indicate that Atlantic cod eggs or larvae spawned within the western Gulf of Maine (i.e., near Ipswich Bay, Massachusetts, or in Cape Cod Bay) may reach SNE prior to settlement (Huret et al., 2007; Churchill et al., 2011). Meanwhile, findings from other dispersal studies indicate that larvae spawned on the northeastern peak of Georges Bank largely remained near their spawning sites with little transport to SNE (Lough et al., 2006). In agreement with these results, findings from genetic analyses indicate that Atlantic cod in SNE are more closely related to winter-spawning Atlantic cod from the Gulf of Maine than to Atlantic cod spawning on eastern Georges Bank (Wirgin et al., 2007; Kovach et al., 2010). Although genetic results indicate that some connectivity exists, it is likely that the larval transport contribution of the Gulf of Maine to SNE may be minor or negligible. Furthermore, the role of physical transport (i.e., wind) in spawner–recruit dynamics of Atlantic cod has been shown to be less robust than previously proposed, indicating that physical oceanography may be less of a factor in recruitment and stock abundance of this species (Hare et al., 2015). Given documentation of local spawning in SNE, these lines of evidence have been used to theorize whether or not Atlantic cod in this region should be considered self-sustaining (Zemeckis et al., 2014a).

The SNE region is relatively shallow and warm when compared with other areas inhabited by Atlantic cod (ICES, 2005). As a result, productivity of Atlantic cod in this region has been expected to decline because of anticipated adverse effects of climate change on their life history, including decreased recruitment, increased competition, reduced available thermal habitat, and increased metabolic costs (Drinkwater, 2005; Fogarty et al., 2008). Atlantic cod on Georges Bank are thought to have a high climate exposure and high potential for distributional change (Hare et al., 2016) and are therefore expected to shift their distribution and center of biomass northward (Drinkwater, 2005; Kleisner et al., 2017; Selden et al., 2018), potentially resulting in the extirpation of Atlantic cod from SNE. Nye et al. (2009) found that the center of biomass of the Georges Bank stock of Atlantic cod had already shifted poleward by an average of 1.48 km/year and that the area it occupied had decreased by an average of 454.5 km^2/year between 1968 and 2007. In contrast to these expectations, however, accounts from recreational anglers indicate that abundance of Atlantic cod in waters south of Rhode Island has significantly increased during the past 15 years (Sheriff, 2018). If true, such an increase would indicate that the adverse effects of climate change on Atlantic cod in SNE, and perhaps elsewhere, may be less severe or more complex than has been previously hypothesized.

The aim of the work described here was to analyze existing data sets to provide a better understanding of the distribution and habitat utilization of Atlantic cod in the most southern portion of their geographic range. Several fishery-independent surveys and fishery-dependent data sources capturing multiple life stages (i.e., larva, young of the year [YOY], juvenile, and adult) of Atlantic cod from Rhode Island, which is at the center of the SNE region, were investigated to address 3 objectives: 1) provide a contemporary description of the distribution of Atlantic cod in SNE waters, 2) evaluate trends in relative abundance, and 3) determine if recent trends in abundance in SNE appear to have any significant relationship with habitat characteristics or environmental conditions (e.g., temperature).

Materials and methods

Larval surveys

Data on the abundance of larval Atlantic cod were available from ichthyoplankton surveys conducted by the Rhode Island Department of Environmental Management (RIDEM) during 2001–2008 and later renewed by RIDEM and the University of Rhode Island Graduate School of Oceanography (URIGSO) during 2016–2017. For the RIDEM survey in 2001–2008, tows of 335-μm plankton nets for 6 min at 15 stations within Narragansett Bay (Fig. 1, A and B) were performed biweekly throughout each year. The collected samples were identified to the species level, and their densities were reported as number per 100 cubic meters. For the RIDEM and URIGSO survey in 2016–2017, the methods of the earlier study were followed closely, and 6-min tows of 335-µm plankton nets were performed weekly at 15 stations within Narragansett Bay between February and April.

In both surveys, the nets were towed for 2 min each near the bottom, at half the bottom depth, and at the surface for stations located at depths ≥11 m and were towed for 3 min each near the bottom and at the surface for stations located at depths <11 m. During tows, date, location, depth, and water temperatures at the surface and bottom were recorded. Fourteen of the stations sampled during the survey in 2016–2017 matched those sampled in 2001–2008, with 1 station relocated from the

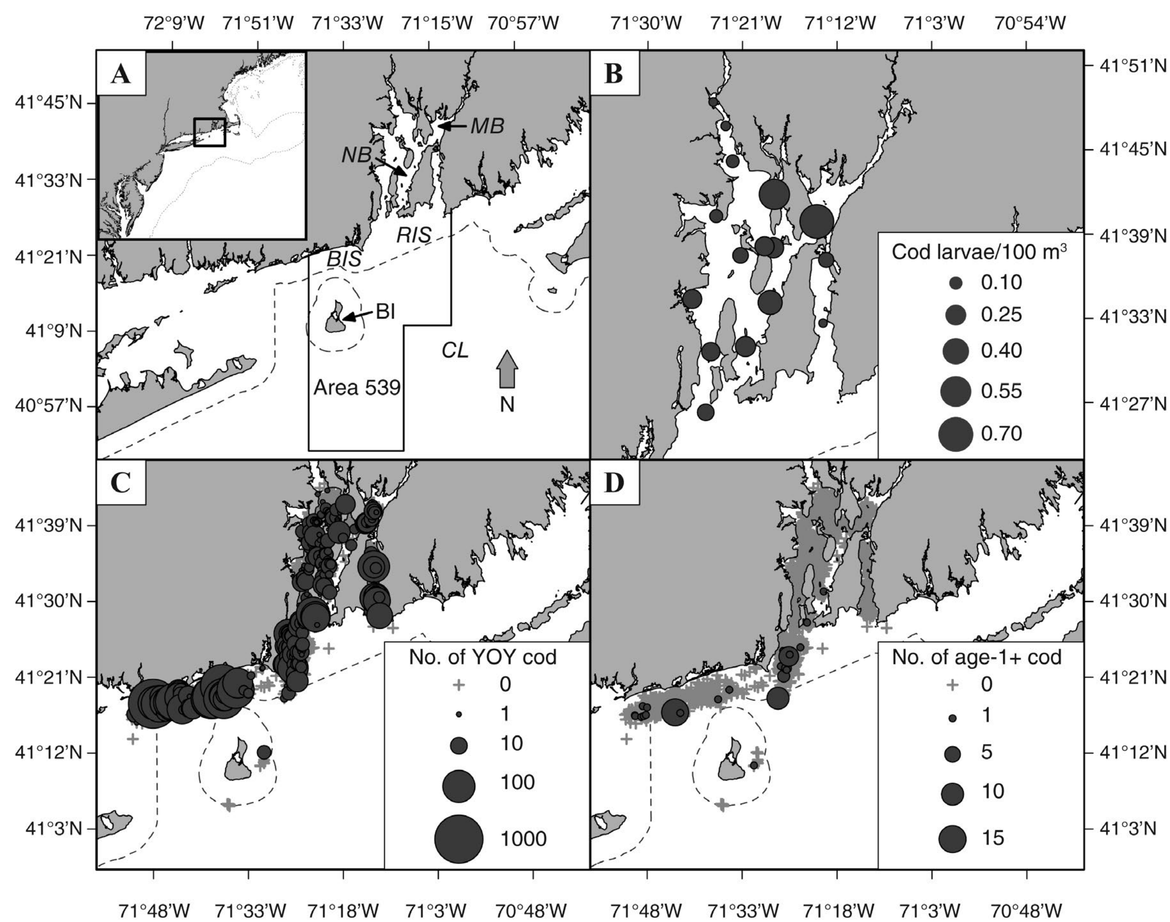

Figure 1

(**A**) A map of nearshore waters in Rhode Island where Atlantic cod (*Gadus morhua*) were sampled, and maps showing abundance of (**B**) larval and (**C**) young-of-the-year (YOY) Atlantic cod and (**D**) those age 1 or older (age 1+). The dashed black lines depict the limit of state waters for Rhode Island and neighboring states, and the black line in panel A indicates the boundaries of NOAA statistical area 539. In panel B, abundance from ichthyoplankton surveys conducted in 2001–2008 and 2016–2017 is presented as the mean measured density (number of larvae/100 m^3) for the time series by location, with circle size depicting differences in density between locations. In panels C and D, values of abundance for YOY and age-1+ Atlantic cod are from trawl surveys conducted in 1979–2018 by the Rhode Island Department of Environmental Management. Abundance of YOY Atlantic cod is presented as total counts for the time series by location, with circle size proportional to log-abundance and plus signs representing tows in which no Atlantic cod were caught. Abundance of age-1+ cod is presented as total counts for the time series by location, with circle size proportional to abundance and plus signs representing trawls in which no Atlantic cod were caught. The following locations are designated: Narragansett Bay (NB), Mount Hope Bay (MB), Rhode Island Sound (RIS), Block Island Sound (BIS), Block Island (BI), and Cox Ledge (CL).

mouth of Narragansett Bay to Mount Hope Bay in the northeastern portion of the estuary (Fig. 1A). The samples collected as part of this survey were then preserved in 5% buffered formalin and returned to the lab where larval cod were identified, counted, and measured. Data were collected on the volume sampled during each tow by using Sea-Gear Mechanical Flowmeters (Sea-Gear Corp., Melbourne, FL), and larval densities were calculated for comparisons among years. Differences in the size distributions and temperature conditions in 2016 and 2017 were evaluated with Wilcoxon rank-sum tests because of non-normality. Additionally, ages were approximated by using the average linear and exponential growth curves reported by Green et al. (2004) and by assuming a mean egg stage duration of 18 d (Fahay et al., 1999) in order to estimate the spawning season. A 2-sample Kolmogorov–Smirnov test was used to test for agreement in the distributions of estimated spawning dates between years. All statistical analyses were conducted in R, vers. 3.5.1 (R Core Team, 2018).

Trawl surveys and landings data

Data on abundance of Atlantic cod were analyzed from the URIGSO weekly trawl survey and the RIDEM trawl survey. The URIGSO trawl survey has been (1959–present) conducted at 2 stations in Narragansett Bay: a mid-bay habitat with a mean depth of ~7 m and an outer-bay habitat with a mean depth of ~23 m (Collie et al., 2008). For this survey, an otter trawl net with 7.6-cm mesh shrinking to 5.1 cm in the codend and an effective opening of 6.5 m is towed at a speed of 1.03 m/s (2 kt) for 30 min. Counts and, beginning in 1994, aggregate weights have been recorded for each species upon retrieval of every tow. The RIDEM survey has been conducted as 3 distinct components varying spatiotemporally. The monthly survey (1990–present) is conducted at 13 fixed stations in Narragansett Bay, with each station being sampled once a month throughout the year. The spring and fall (seasonal) surveys (1979–present) include the same fixed stations of the monthly survey and additional fixed and randomly chosen stations in Narragansett Bay, Rhode Island Sound, and Block Island Sound (Fig. 1, A, C, and D). The spring survey traditionally operates between mid-April and mid-May, and the fall survey is conducted from mid-September through early October. For these trawl surveys, an otter trawl net with a 6.7-m effective opening and a 0.6-cm mesh liner in the codend is towed at a speed of 1.29 m/s (2.5 kt) for 20 min. The total catch is weighed, and all fish are measured for total length (TL).

Atlantic cod captured in the RIDEM trawl survey were separated into approximate age classes based on TL for the purpose of analysis. Size thresholds of 20 and 37 cm TL were used to differentiate YOY Atlantic cod from juveniles (NEFSC, 2013) and juveniles from adults (Serchuk and Wood[1]; NEFSC, 2013), respectively, on the basis of the average size at age of 1- and 2-year-old Atlantic cod reported in the stock assessment for the Georges Bank management unit. Because YOY Atlantic cod were observed in many months, descriptive statistics for observations of this life stage were calculated by using only the RIDEM monthly survey component to avoid bias from the temporal constraints of the seasonal trawl surveys. Juvenile and adult Atlantic cod were observed infrequently in the RIDEM trawl survey and were most often caught in areas sampled only during the seasonal surveys. Therefore, all available observations of these age classes were considered in descriptive analyses. Because of the limitations of data from the URIGSO survey, only data on Atlantic cod from the RIDEM survey could be analyzed by size class. It was assumed that Atlantic cod captured in the URIGSO trawl survey were juveniles or adults on the basis of the mesh size of the net. During tows, date, location, depth, and bottom water temperature were recorded as part of the URIGSO and RIDEM surveys. Comparisons of the depth and temperature of capture by age class were made with Wilcoxon rank-sum tests.

To assess prospective responses to observed changes in abundance by using fishery catch data, landings of Atlantic cod were obtained from the Marine Recreational Information Program (MRIP) (recreational fisheries statistics, available from website) and the vessel trip report (VTR) program of the NOAA Northeast Fisheries Science Center (NEFSC) (Ares[4]). Specifically, recreational landings of Atlantic cod by Rhode Island anglers for all waves and modes of fishing were analyzed for the period 1981–2018. The VTR data were gathered for commercial fisheries and party and charter (recreational) vessels operating in NOAA statistical area 539 (i.e., the closest spatial representation to the state waters of Rhode Island) between 2004 and 2018 (Fig. 1A). Although VTRs are not mandated for the state-permitted party and charter fleets, most of these Rhode Island businesses report their activity by using VTRs (Lake[5]). Landings data were compared with abundances of Atlantic cod in surveys of Rhode Island waters by using Pearson's product-moment correlation coefficient (r).

To gain insight into the potential causes of modern trends in observed abundance of Atlantic cod in Rhode Island state waters, the relationship between water temperature and the annual mean catch per unit of effort (CPUE) in the URIGSO and RIDEM trawl surveys was explored during the period of reported increase (2000–2018) with generalized linear models (GLMs) by using the R package mgcv, vers. 1.8-24 (Wood, 2011). Because the CPUE values are positively skewed and contain many zeros, Tweedie distributions were used to describe the errors of the regression fits. For comparison with abundance of YOY Atlantic cod and those that were age 1 or older (age 1+), monthly bottom water temperatures were obtained from the URIGSO trawl survey for the outer-bay habitat at the mouth of Narragansett Bay during 1959–2018.

[4] Ares, N. 2020. Personal commun. Rhode Island Div. Mar. Fish., 3 Fort Wetherill Rd., Jamestown, RI 02835.

[5] Lake, J. 2019. Personal commun. Rhode Island Div. Mar. Fish., 3 Fort Wetherill Rd., Jamestown, RI 02835.

Additionally, other factors that could influence the dispersal and survival of cod larvae were tested in the GLMs for YOY Atlantic cod. Monthly mean wind speed and direction and monthly precipitation accumulation (a proxy for estuarine salinity) data were accessed from the NOAA National Climatic Data Center (available from website) for the monitoring station at the Theodore Francis Green Memorial State Airport in Warwick, Rhode Island. Here, each daily vector for the direction of the fastest 2-min wind was assumed to have unit length and have decomposed into northerly and easterly components before being averaged by month. The winter index (mean for December–March) of the North Atlantic Oscillation was also obtained, from the National Weather Service Climate Prediction Center (available from website), because of the documented effect of this climate phenomenon on the winter wind field and circulation south of Rhode Island (Luo et al., 2013). Forward variable selection was performed for all GLMs with an inclusion threshold of a 2-point reduction in the Bayesian information criterion (BIC).

Results

Distribution in waters of Rhode Island

During the ichthyoplankton surveys conducted in 2001–2008 and 2016–2017, larvae and postlarvae of Atlantic cod were observed throughout Narragansett Bay between January and May, with the highest densities observed in the northeastern and southern portions of the estuary (Fig. 1B). Specimens captured in the survey in 2016–2017 (number of samples [n]=510) ranged in size between 4 and 34 mm TL (Fig. 2A). The median dates of capture were 2 April in 2016 and 23 March in 2017. Further, the median length of larvae captured in 2016 (13.2 mm TL) was significantly larger than that of larvae caught in 2017 (8.7 mm TL; Wilcoxon rank-sum test: P<0.001). The median surface water temperature at which larval Atlantic cod were collected was significantly warmer in 2016 (7.6°C) than in 2017 (3.9°C; Wilcoxon rank sum test: P<0.001). Estimated spawning dates for the collected larval Atlantic cod were between late December and mid-February (linear growth: 26 December–18 February; exponential growth: 1 January–15 February; Fig. 2B). Despite differences in larval size, time of capture, and temperature at capture, the frequency distributions of estimated spawning dates were not significantly different between collection years (Kolmogorov–Smirnov test: P>0.05).

Young-of-the-year Atlantic cod (n=8259) were observed throughout all of Rhode Island state waters in the RIDEM trawl survey between 1979 and 2018 (Fig. 1C). These Atlantic cod were caught across a wide depth range, with collections occurring between 2.7 and 46.0 m (95% highest density interval in the RIDEM monthly survey component: 4.6–20.4 m). The YOY Atlantic cod were captured primarily between March and June, with the vast majority being observed in April and May (Fig. 3A) and at temperatures ranging from 0.0°C to 22.3°C. The 95% highest density interval of collections in the RIDEM monthly survey component occurred between 0.0°C and 14.0°C (Fig. 3B). Although some YOY Atlantic cod were observed during the fall months in the RIDEM fall survey component (August–December: n=15), this age class

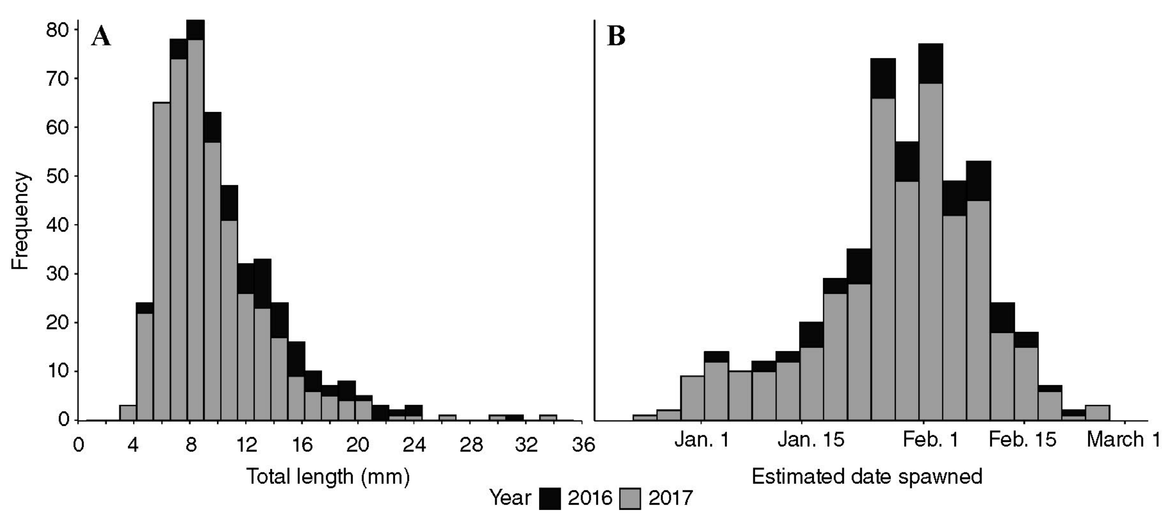

Figure 2

Frequency distributions of (**A**) total length and (**B**) estimated spawning dates of larval Atlantic cod (*Gadus morhua*) captured during ichthyoplankton surveys conducted in 2016 and 2017 by the Rhode Island Department of Environmental Management and the University of Rhode Island Graduate School of Oceanography in Narragansett Bay, Rhode Island.

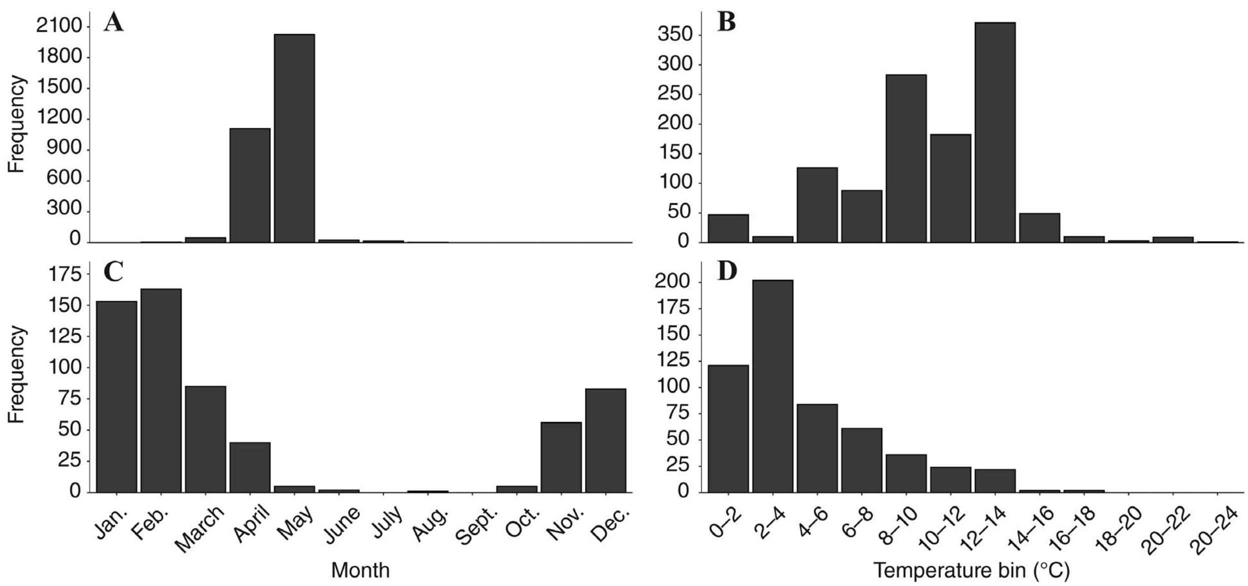

Figure 3

Frequency distributions of the months during and bottom water temperatures at which (**A** and **B**) young-of-the-year (YOY) Atlantic cod (*Gadus morhua*) and (**C** and **D**) those age 1 or older (age 1+) were captured in Rhode Island. The YOY Atlantic cod were sampled during a monthly trawl survey conducted by the Rhode Island Department of Environmental Management in 1979–2018, and age-1+ Atlantic cod were sampled during the trawl surveys conducted by the Graduate School of Oceanography, University of Rhode Island, in 1959–2018.

primarily utilizes Narragansett Bay and the Rhode Island coastal zone during the spring when water temperatures are colder.

In the URIGSO and RIDEM (Fig. 1D) trawl surveys, age-1+ (juvenile and adult life stages combined) individuals were caught primarily in waters of Rhode Island and Block Island Sound, but observations of juveniles and adults at the mouth of Narragansett Bay were frequent in the URIGSO trawl survey prior to 1975. In the URIGSO trawl survey, Atlantic cod (n=589) were almost exclusively captured between October and June (99.8%) and at the mouth of Narragansett Bay (97.5%), corresponding to temperatures below 15.0°C (95% highest density interval: 0.9–13.6°C) (Fig. 3, C and D). In the RIDEM survey, age-1+ Atlantic cod (n=63) were captured at depths between 19.5 and 39.9 m (95% highest density interval: 19.5–38.1 m) and at bottom water temperatures between 0.0°C and 19.2°C (95% highest density interval: 4.0–15.0°C). Juvenile (n=40) and adult (n=23) Atlantic cod captured in the RIDEM survey did not appear to have different temperature or depth preferences (Wilcoxon rank-sum test: P>0.05). Although few Atlantic cod were captured in the URIGSO or RIDEM trawl surveys between June and October, landings data from MRIP document catches of Atlantic cod in Rhode Island during all sampling waves, primarily outside of state waters (Fig. 4A). These landings data, therefore, indicate continued presence of age-1+ Atlantic cod farther offshore during the summer months.

Evaluation of a recent population trend

Landings in both the MRIP and VTR data sets increased from the early to late 2000s and fluctuated near the increased level thereafter (Fig. 4), an increase that is consistent with anecdotal reports from recreational anglers in Rhode Island. However, MRIP sampling does not occur during the winter months, when effort in the recreational fishery for Atlantic cod peaks in Rhode Island, making it more difficult to detect and interpret trends. Both the URIGSO and RIDEM trawl survey data sets indicate increases in catches of age-1+ Atlantic cod during the late 2000s after a period of low catches beginning in the 1990s (Fig. 5). After 2000, levels of total catch of Atlantic cod in the RIDEM survey are similar to those observed during the 1980s, but contemporary catches in the URIGSO trawl survey were only a fraction of those recorded around 1970. However, the limited catch of age-1+ Atlantic cod in both surveys makes it difficult to draw definitive conclusions.

The only life stage consistently observed in high abundance through time was YOY Atlantic cod in the RIDEM trawl survey (Fig. 5B), in which a pronounced increase in annual CPUE began in 2002. When compared with the VTR landings data, YOY mean annual CPUE in the RIDEM trawl survey was significantly correlated at a lag of 2 years both to future landings by the party and charter fleets (r=0.688, P=0.005) and to future landings by commercial vessels (r=0.586, P=0.022). Although the

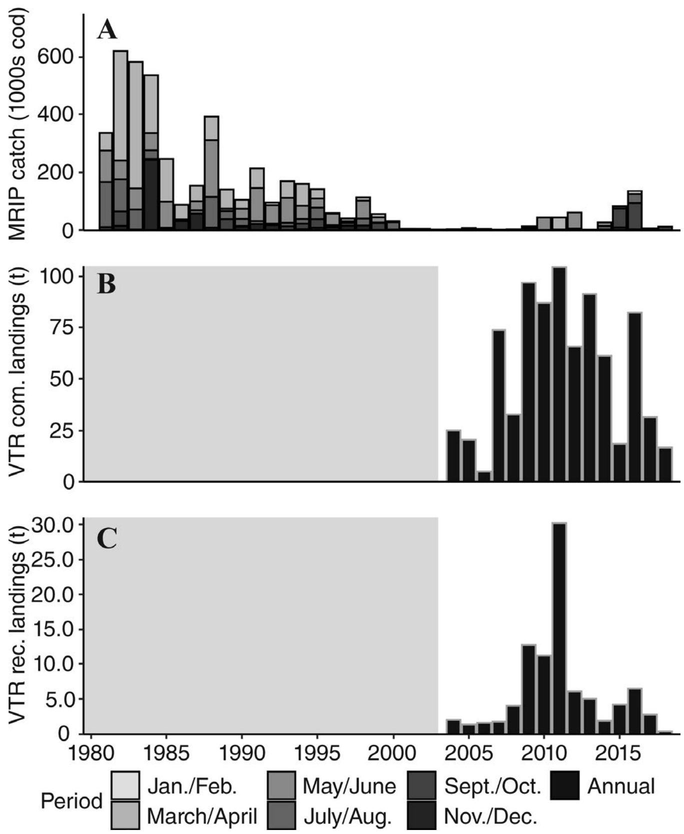

Figure 4

Abundance of Atlantic cod (*Gadus morhua*) in waters of Rhode Island from fishery-dependent sources of landings data, separated into bimonthly bins unless data were annual. Abundances shown include the following data: (**A**) landings of Atlantic cod recorded by the Marine Recreational Information Program (MRIP) during 1981–2018 and landings from the NOAA Northeast Fisheries Science Center vessel trip report (VTR) program for (**B**) commercial and (**C**) party and charter (recreational) fishing activities conducted in NOAA statistical area 539 during 2004–2018. Bimonthly bins match the sampling waves of the MRIP. Gray shaded areas indicate the periods for which no data are available.

correspondence of abundance of YOY Atlantic cod in Rhode Island state waters to overall abundance of Atlantic cod in SNE is unknown, this trend indicates that an increase in abundance of Atlantic cod has occurred in this region during the last 2 decades and has contributed to this fishery.

Investigation of links between abundance and environmental processes

Significant environmental covariates were found only for the GLM fit to CPUE of YOY Atlantic cod. No statistically significant correlations were found between abundance of YOY Atlantic cod and monthly mean wind speed, monthly mean wind direction, the North Atlantic Oscillation winter index, or monthly rain and snow accumulations. However, a strong negative relationship was identified with bottom water temperature in February (P=0.002, deviance explained=27.2%; Fig. 6). The inclusion of any other months did not provide a significant improvement in the BIC of the GLM fit, indicating that the mean bottom water temperature in February, the coldest month of the year in Narragansett Bay, is the primary tested environmental condition driving variability in abundance of YOY Atlantic cod.

Discussion

The results of this study reveal that early life stages of Atlantic cod were frequently observed in Rhode Island state waters. Larval Atlantic cod were collected throughout Narragansett Bay in 2001–2008 and 2016–2017 between the months of February and May at sizes indicating the presence of newly hatched larvae and late-stage larvae preparing for settlement or in the process of settling (Fahay et al., 1999). The observed pattern of peak abundance for larval Atlantic cod in the southern and northeastern portions of Narragansett Bay may be due to larval transport from ocean intrusion of water through the eastern portions of Narragansett Bay and the estuary's mean counter-clockwise circulation (Pfeiffer-Herbert et al., 2015). The estimated ages of the larval Atlantic cod caught in 2016 and 2017 indicate that they were spawned between mid-December and mid-February. However, there is significant uncertainty in this estimate due to 3 factors: the variability of larval growth, the use of growth curves fit with data from surveys conducted on Georges Bank (Green et al., 2004) to estimate age, and the role of temperature in larval growth and mortality rates of Atlantic cod (Buckley et al., 2004). It is noteworthy that the difference in distribution of estimated spawning dates was statistically insignificant between 2016 and 2017 despite shifts in the temporal, thermal, and size distributions of collections. The estimated spawning window matches those of previous research (Kovach et al., 2010; Loehrke, 2013; Zemeckis et al., 2014a) and the historical peak of commercial fishing activity in SNE (Serchuk and Wood[1]), all of which appear to be temporally aligned (Zemeckis et al., 2014b).

The spawning location from which Atlantic cod larvae collected in Narragansett Bay originate is unclear. Although spawning activities have been observed in the SNE region (Wise, 1958; Loehrke, 2013), results of past investigations also indicate that larval Atlantic cod spawned in the western Gulf of Maine could reach SNE prior to settlement (Huret et al., 2007; Churchill et al., 2011). Such a link has been corroborated by genetic evidence, indicating reproductive connectivity among Atlantic cod in SNE and winter spawning groups north of Cape Cod

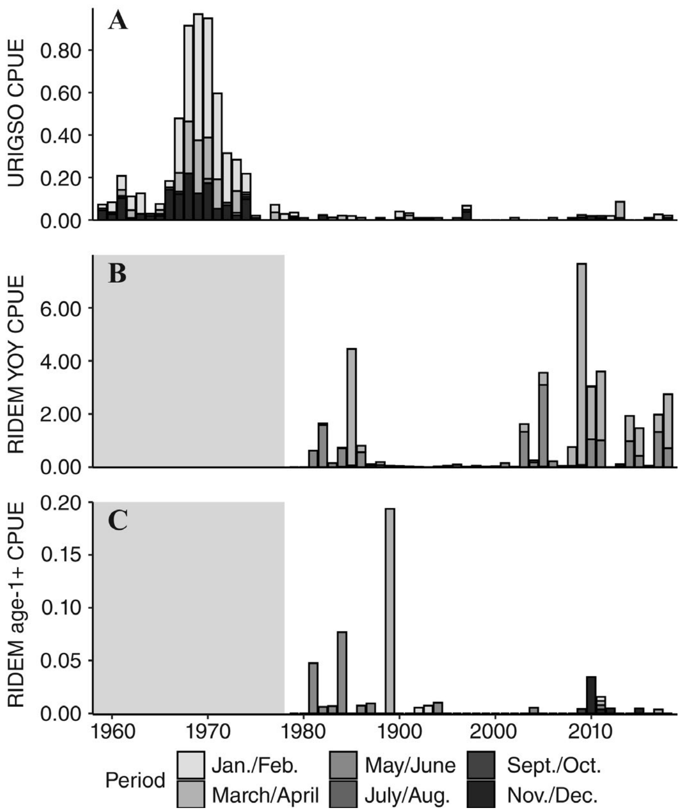

Figure 5

Abundance of Atlantic cod (*Gadus morhua*) in waters of Rhode Island from fishery-independent sources of catch-per-unit-of-effort (CPUE) data, separated into bimonthly bins. Abundances shown include the following data: (**A**) annual CPUE of Atlantic cod in the trawl survey conducted by the University of Rhode Island Graduate School of Oceanography (URIGSO) in 1959–2018, (**B**) CPUE of young-of-the-year Atlantic cod in the seasonal and monthly trawl surveys conducted by the Rhode Island Department of Environmental Management (RIDEM) in 1979–2018, and (**C**) CPUE of Atlantic cod that were age 1 or older (age 1+) in the RIDEM seasonal and monthly trawl surveys conducted in 1979–2018. Gray shaded areas indicate the periods for which no data are available.

and at the Great South Channel and Nantucket Shoals (Wirgin et al., 2007; Kovach et al., 2010). However, 42 larvae of the size at first hatch (3.3–5.7 mm TL; Fahay et al., 1999) were captured between 2016 and 2017. Although the egg stage can last up to 60 d (Fahay et al., 1999), the approximate amount of time it would take for eggs spawned in the western Gulf of Maine to reach SNE (Huret et al., 2007; Churchill et al., 2011), these observations indicate that at least some of the captured larvae came from local spawning. On the basis of studies of circulation south of Rhode Island, it is plausible that eggs and larvae spawned in the vicinity of Block Island or Cox Ledge (Fig. 1A) during winter, as documented by Loehrke (2013), would reach Narragansett Bay prior to settlement (Kincaid et al., 2003; Luo et al., 2013; Liu et al., 2016a, 2016b). The results of this work therefore provide preliminary insight into the relationship of Atlantic cod in SNE to spawning groups throughout U.S. waters and motivate further investigation to inform ongoing research into Atlantic cod stock structure (Annala[6]).

Young-of-the-year Atlantic cod were also observed throughout Rhode Island state waters. The presence of these Atlantic cod along the southern coast of Rhode Island, concurrent with observations in Narragansett Bay, indicates that larvae likely also settle in this area. In waters of Rhode Island, YOY Atlantic cod appear to have a wide temperature tolerance, a finding that is consistent with those of previous studies (Fahay et al., 1999). However, the facts that almost all of these fish were observed at bottom water temperatures <12.0°C and that fall observations occurred at a mean depth of 24.9 m indicate that YOY Atlantic cod may seek thermal refuge in deeper waters outside of Narragansett Bay as temperatures rise in the spring, and this result is consistent with research conducted in the Gulf of Maine (Grabowski et al., 2018). Although Fahay et al. (1999) noted that the rare presence of juvenile Atlantic cod inside Narragansett Bay during the 1990s made it difficult to determine their temperature and depth preferences, the reported ranges of 5–22°C and 3–34 m were close to the ranges observed for YOY Atlantic cod in this study. Young-of-the-year Atlantic cod have been found to associate with cobble substrates or areas of structural complexity after settlement (Fahay et al., 1999; Grabowski et al., 2018), but Narragansett Bay is known to be dominated by fine-grain sediments (McMaster, 1960). This sediment composition indicates that Narragansett Bay and coastal Rhode Island may be used as a settlement and early nursery habitat because of available vertical relief (e.g., macroalgae and boulders) for predator avoidance and feeding.

Although not many juvenile Atlantic cod were caught, their temperature and depth preferences, coupled with the seasonality of YOY Atlantic cod in Narragansett Bay, indicate that Atlantic cod move to deeper waters during their first summer. Given that approximately twice as many juvenile Atlantic cod as adults were observed in the RIDEM survey, these juvenile Atlantic cod may be more inclined to occupy nearshore habitats. Their depth and temperature preferences were similar, but data on recreational catches of Atlantic cod throughout the summer indicate that it is possible that adults make greater use of offshore banks in SNE, as suggested by Fahay et al. (1999) and Loehrke (2013). Specifically, recapture of Atlantic cod

[6] Annala, J. H. 2012. Report of the workshop on stock structure of Atlantic cod in the Gulf of Maine region; Portsmouth, NH, 12–14 June, 25 p. Gulf Maine Res. Inst., Portland, ME. [Available from website.]

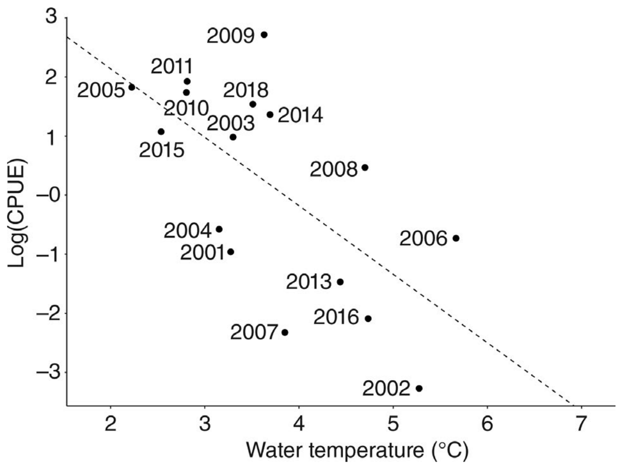

Figure 6

The approximately log-linear relationship between mean bottom water temperature in February and log-transformed mean catch per unit of effort (CPUE) of young-of-the-year (YOY) Atlantic cod (*Gadus morhua*) in March–July, during the period of observed increase in CPUE in Rhode Island state waters in 2001–2018. Water temperatures in February were recorded during trawl surveys conducted by the University of Rhode Island Graduate School of Oceanography and are used to represent values for each year, and CPUE data are from trawl surveys conducted by the Rhode Island Department of Environmental Management. The diagonal dashed line depicts a linear regression fit to the data (P<0.001, coefficient of multiple determination=0.413). Data from the surveys conducted in 2017 were omitted because of missing temperature measurements. Data from surveys conducted in 2012 were omitted because no YOY Atlantic cod were captured.

tagged in SNE by Loehrke (2013) occurred in the New York Bight, near the Nantucket Shoals and Great South Channel, and close to their point of release south of Rhode Island. Although more research is needed to develop a better understanding of offshore habitat utilization by Atlantic cod in this region, our results and those of previous studies indicate that, counter to the hypothesis of Serchuk and Wood[1], Atlantic cod may complete their life cycle in SNE. As suggested by Zemeckis et al. (2014a), we hypothesize that Atlantic cod in SNE are largely self-sustaining with some contribution of larvae from other spawning groups in the western Gulf of Maine, Great South Channel, or Nantucket Shoals.

It is difficult to assess population trends in SNE Atlantic cod with the limited data available; however, MRIP and VTR landings in nearshore federal waters support anecdotal accounts from anglers in Rhode Island of a population increase since the early 2000s. Although few juvenile and adult Atlantic cod have been caught in trawl surveys in Rhode Island state waters since the mid-1970s, catches increased slightly during the late 2000s and early 2010s. The life stage most consistently observed in these surveys was YOY Atlantic cod, for which a noteworthy increase in observed abundance began in the early 2000s. Eight of the 10 highest mean annual CPUE values in the RIDEM survey were observed between 2003 and 2018, with 6 of those occurring since 2009. However, it is unclear what proportion of settlement habitat exists within the state waters sampled as part of the RIDEM survey or how representative these areas are of regional abundance. Landings data from VTRs for NOAA statistical area 539, which encompasses Rhode Island state waters and portions of the spawning areas documented by Loehrke (2013), peaked in 2011, 2 years after the largest collection of YOY Atlantic cod observed in the RIDEM trawl survey. The identified correlation patterns, although circumstantial, do indicate that the trends in abundance of coastal YOY Atlantic cod may manifest in abundance of adults offshore.

If abundance of Atlantic cod in SNE has increased, it runs counter to expected declines in productivity of Atlantic cod as waters warm as a result of climate change. Drinkwater (2005) suggested that Atlantic cod would be outcompeted by warm-water species at mean annual water temperatures above 12°C and that the stock on Georges Bank could be expected to decline in abundance with continued warming. Although it was not possible in our study to determine the mean temperature of the habitats occupied by Atlantic cod throughout the year, data from the NEFSC fall bottom-trawl survey (available from website) indicate that late-September bottom water temperatures averaged across the approximate area in which Atlantic cod were tagged and recaptured by Loehrke (2013) (40°30′–41°15′N, 70°30′–72°0′W) can reach 16°C and have increased by ~2°C since 2000. Additionally, the temperatures at which Atlantic cod have been captured in surveys of Rhode Island state waters provide no evidence of tolerance of temperatures higher than those that have been reported in other regions. It appears, therefore, that Atlantic cod in SNE may be exposed to temperatures outside of their preferred range (Righton et al., 2010) during the summer months and have been confronted with a rapid increase in temperature in late summer during the last 2 decades. It remains possible that Atlantic cod are able to seek thermal refuge in features like the cold pool off the mid-Atlantic states during this period (Chen et al., 2018); however, these results indicate that their thermal habitat is already limited during portions of the summer and may only become more limited in the future (Drinkwater, 2005; Kleisner et al., 2017; Selden et al., 2018).

Furthermore, regression analysis of trends in CPUE of YOY Atlantic cod in Rhode Island state waters since 2000 revealed a strong negative relationship with February bottom water temperature recorded at the mouth of Narragansett Bay. This relationship agrees with work by Drinkwater (2005) and Fogarty et al. (2008), who suggested that productivity and recruitment of southern stocks of Atlantic cod would decline with increasing temperature. Yet, it is unclear if the link to winter water temperature reflects relative abundance of YOY Atlantic cod in state waters only or absolute abundance throughout the region.

Data from the URIGSO trawl survey indicate that February is the coldest month of the year in Narragansett Bay. It is possible that this annual minimum influences the prey distribution for larval and YOY Atlantic cod and that their distribution in turn affects their survival, as has been observed on Georges Bank (Lough et al., 2017). Additionally, the estimate of the spawning period produced in our study, coupled with observed Atlantic cod egg and larval development rates (Fahay et al., 1999; Drinkwater, 2005), indicates that most Atlantic cod larvae would be in the pelagic larval stage during February and that survival could be influenced by water temperature or mixing of the water column. If water temperature in February does indeed have a strong negative influence on recruitment of Atlantic cod in SNE, it raises yet more questions about how the regional population has increased in abundance. Six of the 10 warmest Februarys observed in the URIGSO trawl survey have occurred since 2002, the period of apparent increase in abundance of Atlantic cod. Because wind direction and speed were found to have no significant relationship with abundance of YOY Atlantic cod, and given the finding of Hare et al. (2015) that wind dynamics may play less of a role in successful settlement of Atlantic cod than previously thought, the abundance patterns observed in our study appear not to be due to differences in transport. However, a more thorough study is needed to conclusively rule out such dynamics in SNE.

A recent increase in abundance of Atlantic cod in SNE would also be anomalous relative to other documented changes in the regional ecosystem. Atlantic cod were most abundant in the URIGSO trawl survey prior to 1975, when data from the NEFSC spring and fall bottom-trawl surveys indicate water temperatures across the continental shelf of the northeastern United States were ≥2°C colder than they have been in recent years. As waters warmed, abundance of Atlantic cod and other cold-water species declined sharply in Narragansett Bay as the ecosystem underwent a significant regime shift during the 1980s (Collie et al., 2008) toward a warm-water, pelagic-dominated community that also has been detected in the rest of Rhode Island state waters by the RIDEM trawl survey. Given the increase of bottom water temperature and abundance of warm-water species in the last 2 decades, it is unclear what conditions have allowed an increase in abundance of Atlantic cod in the region, what time scale at which warming has affected their productivity, or how their role in the ecosystem has evolved. However, their apparent temperature preferences and the negative influence of winter temperatures on YOY abundance indicate that regional abundance will likely decline in the future.

The results of this analysis indicate that Atlantic cod in SNE may complete their life cycle within SNE waters and that the population is likely to be at least partially self-sustaining. Atlantic cod in this region appear to have increased in abundance despite evidence of limitations to available thermal habitat and recruitment due to climate change. However, several knowledge gaps remain that will be critical to effective management of Atlantic cod in SNE. First, additional work needs to evaluate the reproductive connectivity among Atlantic cod in SNE and other regions, including the New Jersey coast, as a part of ongoing investigations into Atlantic cod stock structure (Annala[6]), and to determine the degree to which the increased abundance described here is due to local spawning and to contributions from other spawning groups. Tagging efforts will also allow greater characterization of habitat utilization by juvenile and adult Atlantic cod in the region. Expanded survey efforts and a complete understanding of regional settlement, sources of early-life-stage mortality, feeding, and spawning habitats will aid in both monitoring abundance and assessing the vulnerability of this population to continued warming. Understanding how this southernmost group of indigenous Atlantic cod is interacting with temperatures at the upper end of their tolerance will be key both to successfully managing this species in SNE and to developing a better picture of how Atlantic cod will respond to future climate change throughout their global range.

Acknowledgments

We gratefully acknowledge the contributions of G. Klein-MacPhee, who conducted the RIDEM ichthyoplankton survey in 2001–2008, and A. Frey and R. Krulee, who identified, counted, and measured larval Atlantic cod from the survey in 2016–2017. The survey conducted during 2016–2017 was funded by Rhode Island Sea Grant (award no. NA14OAR4170082). The RIDEM trawl survey is supported by a U.S. Fish and Wildlife Sportfish Restoration Grant. The URIGSO trawl survey is funded by RIDEM and URI. This work is a contribution of the Rhode Island Marine Fisheries Institute.

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