



Abstract—The black sea bass (*Centropristis striata*) is extending its range northward, into a warming Gulf of Maine. Here, we plot the geographic distribution of specific life stages to examine whether spawning and settlement, and therefore productivity, are extending northward. In order to align these life stages with the correct sampling season, we first resolve confusion about the spawning seasonality of this species, by collecting age-0 individuals from coastal waters of southeastern Massachusetts (Buzzards Bay and Nantucket Sound) and aging them by using daily otolith microincrements. Wild-caught age-0 fish ($n=381$), ranged in size from 32 to 88 mm total length (mean: 53 mm [standard deviation (SD) 11]), and in age from 50 to 129 d old (84 d [SD 16]). They hatched from May 2 to July 21 (June 6 [SD 14 d]), and grew at linear rates from 0.32 to 1.22 mm/d (0.65 mm/d [SD 0.15]). The literature and two 40-year trawl surveys confirm that black sea bass have spawned in Buzzards Bay and Nantucket Sound since the 1880s. Farther north, in the southern Gulf of Maine, spawning has likely occurred in the last 15 years. Settlement has increased about 1°N latitude over the recent 4 decades in association with warming sea temperatures in the southern Gulf of Maine.

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Reproduction, first-year growth, and expansion of spawning and nursery grounds of black sea bass (*Centropristis striata*) into a warming Gulf of Maine

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The black sea bass (*Centropristis striata*) is an important fishery species in temperate and subtropical latitudes of the western North Atlantic Ocean (Musick and Mercer, 1977; Hood et al., 1994; NEFSC¹) and is the only serranid that spawns north of Cape Hatteras, North Carolina (Kendall, 1972). The northernmost stock, subject of this study, has been historically distributed in temperate waters from Cape Hatteras to Cape Cod, Massachusetts (Roy et al., 2012; McCartney et al., 2013; McBride, 2014), but in recent years its range has been extending northward into the colder Gulf of Maine (Klein-MacPhee, 2002; Miller et al., 2016). Coastal warming along the U.S. northeast coast is accompanied by the shifting distributions for many marine species (Nye et al., 2009; Per-

¹ NEFSC (Northeast Fisheries Science Center). 2017. 62nd Northeast Regional Stock Assessment Workshop (62nd SAW) assessment summary report. Northeast Fish. Sci. Cent. Ref. Doc. 17-01, 37 p. [Available from [web-site](http://www.nmfs.gov).]

shing et al., 2015; Henderson et al., 2017), and has led to predictions of “winning and losing” species as climate changes (Graham and Harrod, 2009; Hare et al., 2016). Unlike some New England species that appear to be losing ground in the region, the warm-temperate black sea bass may be a winner; however, our ability to predict the effects of climate on fish remains difficult (Brander, 2015; Kleisner et al., 2017; Frank et al., 2018). For example, it is unclear whether random individuals or a specific subset of adults are simply moving farther north on a seasonal basis, or whether spawning or settlement is increasing in previously unoccupied or sparsely populated habitats of the Gulf of Maine.

Fish movements may be a cause for distributional shifts. This northern stock is composed of subregional ‘contingents’ that provide evidence of phenotypic, particularly meristic, variation along a latitudinal cline (Shepherd, 1991). A potential mechanism underlying this phenotypic cline is contingent-specific seasonal

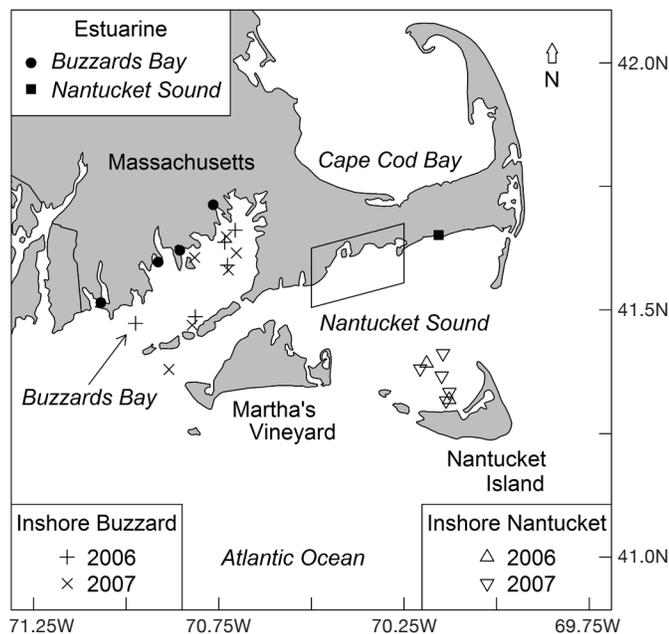


Figure 1

Map of estuarine and inshore sites where black sea bass (*Centropomus striata*) were collected off southeastern Massachusetts during 2006–2007. Collections were used for otolith microincrement analyses. The rhombus indicates the spawning area identified by Kolek (1990), from Succunneset Shoal to Point Gammon in Nantucket Sound.

migrations, because individuals move offshore and south in autumn and back inshore and north in spring and show a substantial degree of site-fidelity evident from tag-recapture data (Moser and Shepherd, 2009; Fabrizio et al., 2013). One or more contingents may be leading the way in expanding northward.

Climate change may also be affecting reproduction by shifting spawning seasons or grounds in a manner that could affect productivity rates (Pankhurst and Munday, 2011), which is our focus here. Testing this hypothesis is challenging given that the first year of life of black sea bass at the northern extent of its historical range is poorly understood. Kendall (1972; p. 1254) advanced the idea: “Seasonally, there seems to be some northerly progression of spawning” but added “Details of the suggested northward progression of spawning need clarification” (p. 1257). Differences in modal peaks in spawning seasonality north versus south of Cape Hatteras are not in dispute here (Table 1). To the south, black sea bass spawn in a protracted manner, beginning as early as January, peaking in March, and ending with a smaller peak in September (Mercer, 1978; Wenner et al., 1986). Juveniles, 3–17 cm standard length, are reported year-round off South Carolina, within a coastal, subtropical range of practical salinities (11–35) and temperatures (10–32°C) (Lehnert and Allen, 2002). Farther north, in Maryland and Virginia, Musick and Mercer (1977) concluded that spawning peaked in June. Klein-MacPhee (2002) stated

that spawning between Chesapeake Bay and Long Island peaked in August. Age-0 black sea bass, 3–11 cm total length (TL), have occurred in New Jersey coastal habitats during summer–autumn, but they cannot survive winter temperatures, and instead migrate offshore (Able and Hales, 1997; Hales and Able, 2001; Fabrizio et al., 2013).

Although sparse, such data fit Kendall’s (1972) initial proposal that spawning progresses seasonally from south to north. However, Caruso’s (1995) and Wuenschel et al.’s² sampling of black sea bass off Massachusetts, at the northernmost range limit of this species, provide evidence of peak spawning activity early, in late May or mid-June, not later in the season. They examined gonads macroscopically for evidence of spawning, whereas much of the other research was based on ichthyoplankton collections (Table 1). Ichthyoplankton surveys in waters off Massachusetts are not representative of black sea bass spawning, because such surveys did not sample in Nantucket or neighboring sounds (Table 1), where black sea bass have been observed in spawning condition during May–June and juveniles are present in autumn (Fig. 1; Wilson, 1889; Lux and Nichy, 1971; Kolek, 1990; Able et al., 1995; Caruso, 1995; Drohan et al., 2007). We conclude that spawning seasonality and the first year of life have not been adequately described for this species at the northern extent of its range.

To resolve the issue of spawning seasonality, age-0 black sea bass were collected with multiple gears in Buzzards Bay and Nantucket Sound during summer and autumn of 2006 and 2007 to determine age, by day, within that annual age class. Herein and elsewhere (Hales and Able, 1995), this otolith microincrement method has been validated as both accurate and precise with respect to daily increment formation. In addition to defining spawning seasonality based on backcalculated hatch dates, we examined growth rates and resulting size of age-0 fish entering their first over-wintering period.

To check for shifting spawning and nursery grounds, we examined geographic distributions of spawning adults and age-0 black sea bass from 2 time series of fishery-independent groundfish (otter trawl) surveys since at least the 1980s. We plot the distributions of these fish roughly by decade and correlate the annual distributions of settled, age-0 fish by both latitude and temperature.

² Wuenschel, M. J., G. R. Shepherd, R. S. McBride, R. Jorgensen, K. Oliveira, E. Robillard, and J. Dayton. 2011. Sex and maturity of black sea bass collected in Massachusetts and Rhode Island waters; preliminary results based on macroscopic staging of gonads with a comparison to survey data. A working paper for SARC 53- Black Sea Bass Data Meeting. In 53rd Northeast Regional Stock Assessment Workshop (53rd SAW) assessment report. Northeast Fish. Sci. Cent. Ref. Doc. 12-05, p. 529–559. [Available from [website](#).]

Materials and methods

Daily age validation and precision

Age-0 black sea bass were collected from the Swan River (Dennis, Massachusetts) on August 10, 2008, with minnow traps (42 cm×20 cm in size, with 7-mm mesh, and a 2.5-cm opening) baited with surf clams. Fifty-nine individuals were transferred to a 90-L aquarium and immersed in a 500 µg/L solution of oxytetracycline (OTC) for 5 h at a salinity of 15 and temperatures of 21–22°C on August 13 (McBride, 2002). These fish were then held in a 970-L tank with a supply of flow-through sea water at 30–32 salinity and 21–22°C and fed to satiation a daily diet of squid and clams. After 24 h (day 2), 5 fish were sacrificed to verify that an OTC mark was present (these fish were not aged later). On day 7, 1 fish was sacrificed to check again the formation of an OTC mark. On day 16, 10 fish were sacrificed for daily ring counts along the distal edge of the OTC mark. Also on day 16, 15 fish were re-marked by immersing them in OTC, in a similar manner as before. On day 30, all remaining fish, some with double OTC marks, were sacrificed for additional counts. There was no other evidence of mortality during the experiment. After fish were sacrificed, sagittal otoliths were removed, cleaned, and stored dry.

Of the 54 marked fish, 17 were selected from each date in a simple random fashion: 1 fish at day 7, 8 fish at day 16, 8 fish at day 30 (including 1 fish with a double mark). One otolith per fish was embedded in epoxy resin, and a 300-µm transverse section was cut with a double-bladed IsoMet Low Speed Saw³ (Buehler, Lake Bluff, IL). These sections were mounted on microscope slides with a clear, thermoplastic adhesive (Crystalbond 509, Electron Microscopy Sciences, Hatfield, PA) and polished with 3-µm and 5-µm metallurgical lapping film. OTC marks were identified with an ultraviolet light, and microincrements were counted with a light microscope (200×) and imaging software (Image-Pro Plus, vers. 7.0, Media Cybernetics, Inc., Rockville, MD). Standard tests for accuracy, bias, and precision of these daily ages included plotting the data, using Chang's coefficient of variation (CV; Chang, 1982), and using Evans and Hoenig's test of symmetry (Evans and Hoenig, 1998). Age-bias plots follow the bubble format advocated by McBride (2015), and the statistic tests were produced by the FSA package, vers. 0.8.20 (Ogle, 2018) in R software, vers. 3.5.0 (R Core Team, 2018) (Ogle, 2016).

Precision (i.e., repeatability) of daily age estimates from wild-caught fish was checked for 37 otoliths (10% of the 372 fish examined). These otoliths—from 5 randomly selected fish over 10-d intervals (range: 51–129 d)—were aged a second time, independently but by the

same reader. Bias and precision tests were performed as described above.

Hatching dates and growth rates

In the estuary, age-0 black sea bass were collected during August–September, 2006 and 2007, off southeastern Massachusetts, by using minnow traps as described in the previous section (Fig. 1). Four sites were sampled in Buzzards Bay (Westport River; Clarks Cove; Nantucket Bay; Sippican River) and 1 site was sampled in Nantucket Sound (Swan River). Estuarine surface salinity ranged from 17 to 23 and surface temperature ranged from 14° to 23°C during the sampling period.

Inshore, off southeastern Massachusetts, age-0 black sea bass were also collected during the Massachusetts Division of Marine Fisheries (MA-DMF) autumn survey in September 2006 and 2007 by trawl (with 7-mm codend liner). Trawl sites were selected following a stratified-random design (King et al.⁴), and these sites were then stratified into two areas (Buzzards Bay and Nantucket Sound [Fig. 1]) in analyses. Inshore bottom salinity ranged from 31 to 33 and bottom temperature ranged from 6° to 20°C in September.

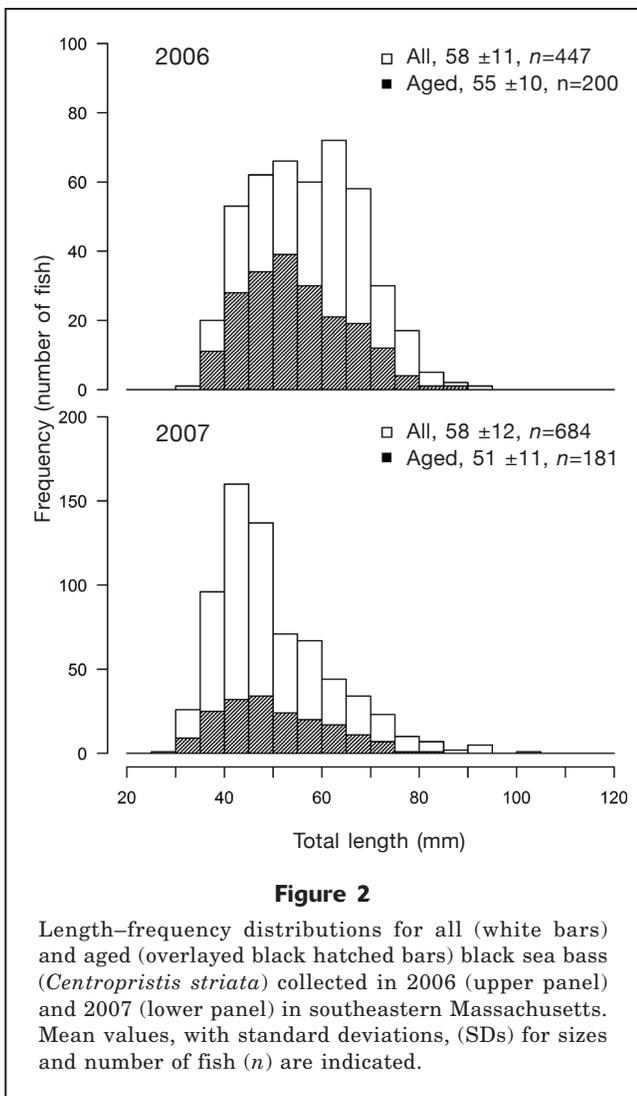
The TL of each fish was measured to the nearest mm from the snout to the posterior of the medial caudal fin ray. Sagittal otoliths were removed, cleaned, and stored dry. Otoliths were embedded, sectioned, and mounted as described above; however, 400-µm sections were initially produced, and these became thinner (150–200 µm) after subsequent wet sanding with 1200-grit wet or dry sandpaper. These otoliths were also soaked for 24–96 h in a 2% trypsin solution to enhance the visibility of the rings (Roemer and Oliveira, 2007), and were then polished with metallurgical lapping film, to finish.

Prepared otoliths were dabbed with immersion oil and viewed under a light microscope (100×), aided by imaging software (Image-Pro Plus). Counts began with the first visible ring near the nucleus and continued to the edge of the otolith. Variation in clarity of different areas of the otolith section meant that no single axis was used to count microincrements ('images' in Tweedie, 2014).

A total of 1131 black sea bass were collected in 2006 and 2007 from 5 estuarine sites and 18 different inner shelf sites. Fish were selected for age determination by simple, random subsampling when more than 20 fish were collected within a month-year-area (estuarine, inshore, Buzzards Bay, or Nantucket Sound) aggregate, which resulted in 34% ($n=381$) of these fish being aged (Fig. 2). Selected fish were statistically smaller than all fish collected in 2006 (Student's $t=2.7$, $df=636$, $P=0.006$), but by <3 mm; therefore this difference was

³ Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

⁴ King, J. R., M. J. Camisa, and V. M. Manfredi. 2010. Massachusetts Division of Marine Fisheries trawl survey effort, lists of species recorded, and bottom temperature trends, 1978–2007. Mass. Div. Mar. Fish. Tech. Rep TR-38, 151 p. [Available from [website](#).]



of limited biological significance; there was no difference in aged and all fish collected in 2007 (Student's $t = -0.27$, $df = 863$, $P = 0.78$) (Fig. 2).

Hatching dates were calculated by subtracting the total count of microincrements for each fish from the date of capture, assuming that the first ring observed corresponded to the hatching date and that there was negligible time difference between spawning and hatching (unknown but considered in the discussion). Capture dates were similar between years (mean: August 28 or 29 [standard deviation (SD) 18–19 d], in 2006 and 2007) and areas (August 28–31 [SD 18–20 d], Buzzards Bay and Nantucket Sound); however, capture dates were 1 month earlier for estuarine than for inshore collections (August 18 [SD 13 d] vs. September 19 [SD 3 d]). Therefore, capture date was a confounding variable, which precluded a comparison of a full 3-way analysis of variance (ANOVA) of hatching dates between years, and between estuarine and inner shelf sites in both Buzzards Bay and Nantucket Sound. Also,

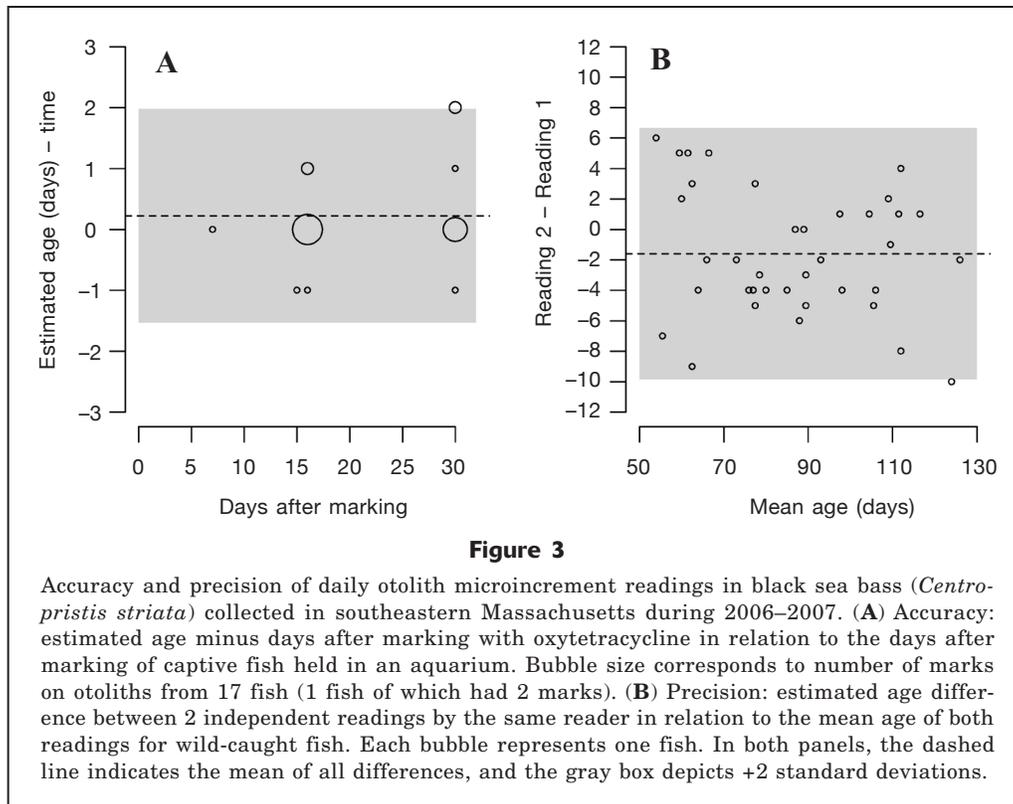
because different sampling gears (traps, trawls), were used in estuarine and inshore habitats, there may also have been a gear effect, although this effect would not arise from mesh selectivity, which was the same for both gears (7-mm mesh). Because of these potential confounding variables, hatching dates are described and plotted separately by year and location.

Daily increments and TL at capture were also used to calculate mean growth (in millimeters per day). As reported above for hatching dates, capture date had a significant effect when included in a full multifactorial ANOVA comparison of growth rates between years, and between estuarine and inner shelf sites in both Buzzards Bay and Nantucket Sound. Consequently, size at age and growth rates are also described separately by year and sampling location.

A time series of fish distributions

Annual time series, from 2 otter trawl surveys conducted since the late 1970s and early 1980s, were examined to map the distribution of adult female and age-0 black sea bass collected in coastal waters and on the continental shelf. Plots of different maturity classes depict distributions of adult females and spawning grounds. Maturity classification, completed at sea, followed Burnett et al. (1989). For graphical clarity, 3 classes were plotted: 1) developing fish (prespawning females but also likely to include spawning fish between batch spawning events [Klibansky and Scharf, 2015]); 2) spawning fish (females with hydrated oocytes), and 3) postspawning fish (spent females). Immature and resting fish were not plotted because these were reproductively inactive at time of capture. Distributions of age-0 fish depict nursery grounds. Identification of age-0 fish followed the methods of Penttila and Dery (1988) for examinations of prepared otoliths. Subsequently, it was determined that age-0 fish were readily identified by size (Suppl. Material), and a proxy size (<12 cm TL) was used to select age-0 fish in order to include individuals that were age-0 but that had not been specifically examined for age.

Site selection for these 2 otter trawl surveys followed a stratified-random sampling design. The first survey (MA-DMF), in coastal waters off Massachusetts, was the inshore bottom trawl survey described in the previous section; sampling occurred during spring (May) and autumn (September). The second survey was performed by the National Marine Fisheries Service's Northeast Fisheries Science Center (NMFS-NEFSC) in the spring (March–May) and autumn (September–November). It was conducted in federal waters primarily, covering offshore waters across the continental shelf to the shelf break, from North Carolina to the northern Gulf of Maine, including adjacent territorial seas of Canada. For both surveys, the time series of age-0 fish started in 1978, the time series of mature adults started in 1983, and the terminal year of all data was 2016. Further details are summarized in Reid et al. (1999).



For later examination in relation to age-0 fish distributions, local sea-surface temperature data were measured from NOAA Buoy Station 44013, 30 km (or 16 nautical miles) east of Boston, Massachusetts (42°21'N, 70°39'W, National Data Buoy Center, [web-site](#)), 1984–2016.

Results

Microincrement analyses

Otolith microincrements were validated as daily in marked fish held captive for up to 30 d (Fig. 3A). The mean bias, 0.22 d, was not significant (test of symmetry: $\chi^2=2.0$, $df=2$, $P=0.37$) and there was agreement between known-age and estimated ring count along the distal edge of the OTC mark (Chang's $CV=1.8$). Microincrement counts made from wild-caught individuals were also repeatable (Fig. 3B). The mean bias, -1.6, was not significant (test of symmetry: $\chi^2=11.0$, $df=10$, $P=0.36$) and there was high precision between the first and second paired readings (Chang's $CV=3.3$). Wild-caught age-0 fish ranged in size from 32 to 88 mm TL (mean: 53 mm TL [SD 11]), and in age from 50 to 129 days old (84 d [SD 16]) (n [no. of fish sampled]=381).

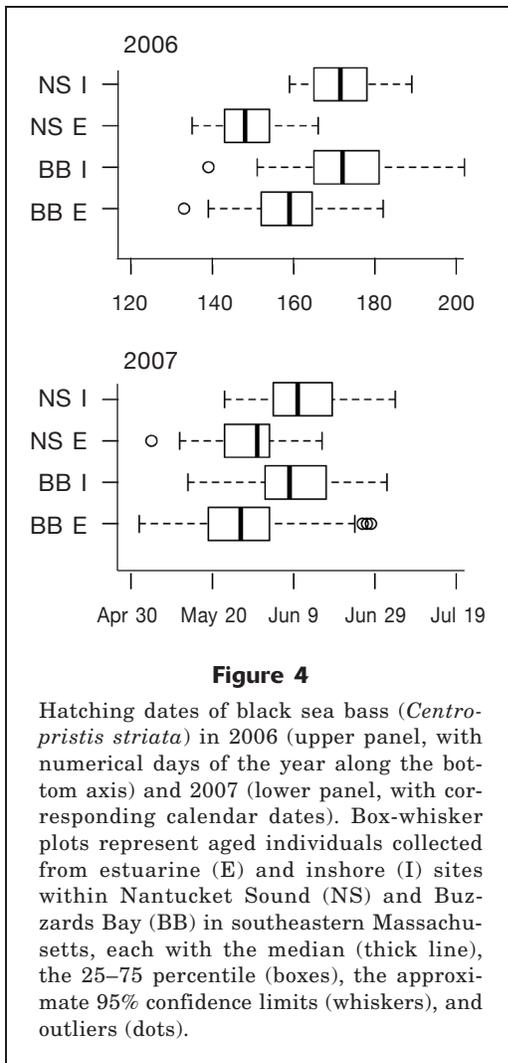
Results based on daily age counts showed that black sea bass spawn from early May to mid-July off southern New England. Individual hatching dates for all aged black sea bass ranged from May 2 to July 21

(mean: June 6 [SD 14 d], $n=381$) (Fig. 4). Mean hatching dates, pooled by year, were at least a week later in 2006 (June 11 [SD 13 d], $n=200$) than in 2007 (June 1 [SD 13 d], $n=181$). They were only 1 d apart between Buzzards Bay and Nantucket Sound (June 6 [SD 14 d], $n=273$ and June 7 [SD 14 d], $n=108$, respectively), and they were 2 weeks earlier in fish collected in estuaries (June 1 [SD 11 d], $n=257$) than at inshore sites (June 16 [SD 12 d], $n=124$).

Age-0 black sea bass had variable growth rates ranging from 0.32 to 1.22 (mean: 0.65 mm/d [SD 0.15]) (Fig. 5). Mean growth rates, pooled by year, were faster in 2006 (0.70 [SD 0.14]) than in 2007 (0.58 [SD 0.12]); pooled by locations, they were less variable between Buzzards Bay and Nantucket Sound regions (0.66 [SD 0.15] and 0.61 [SD 0.12], respectively), than between estuaries (0.68 [SD 0.14]) and inshore sites (0.57 [SD 0.13]).

Trawl survey analyses

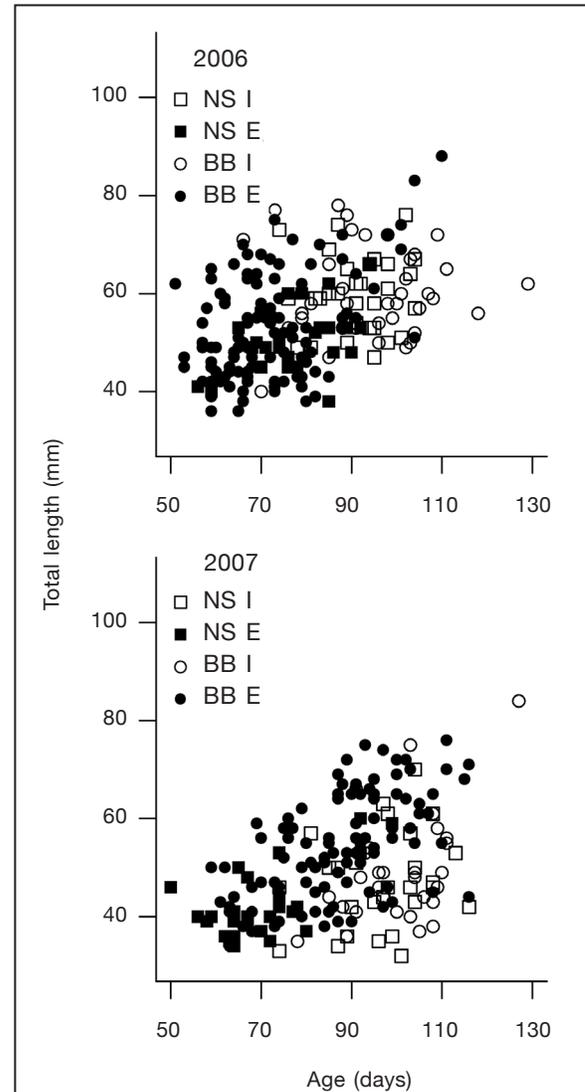
Black sea bass have been spawning farther north for the last 40 years (Fig. 6). Before 2000, spawning was focused in Buzzards Bay and Nantucket Sound, and there were no indications of spawning in the Gulf of Maine. In the 2000s, developing females appeared in Cape Cod Bay. Since 2010, developing females have been caught as far north as Cape Ann off northeastern Massachusetts (42°39'N, 70°36'W). Few spawning females were observed in the Gulf of Maine—a finding



that would provide the most direct evidence of spawning. Few spent females were found.

Black sea bass nursery grounds have also been moving northward over the last 40 years (Fig. 7). Overall, age-0 black sea bass were found distributed from the southern Gulf of Maine, specifically Cape Cod and Massachusetts Bay, to North Carolina (Suppl. Material). In the Gulf of Maine, they have been most frequently collected during the last decade, but they have been present in the southern Gulf of Maine since both surveys operated together in the late 1970s. Although the NMFS-NEFSC trawled well into Canadian waters (> 45°N), the maximum latitude of age-0 black sea bass occurrence during 1978–2016 ranged from 41°35'N in 1993 to 42°56'N in 2014.

The maximum latitude of age-0 black sea bass has steadily increased 0.021 degrees annually, on average, since 1978, for a total of about 1°N during the last 40 years (Fig. 8). Most relevant for future monitoring is the association between autumn sea temperature and the maximum latitude of age-0 fish. This association



is modeled in Figure 8 as a linear relationship, but also suggests a break point pattern, with a break value around 16–17°C, below which this species is found much farther south and above which it is found much farther north.

Discussion

Black sea bass is already a winner under conditions of warming temperatures. Earlier spring warming has led to earlier and more extensive spring migrations,

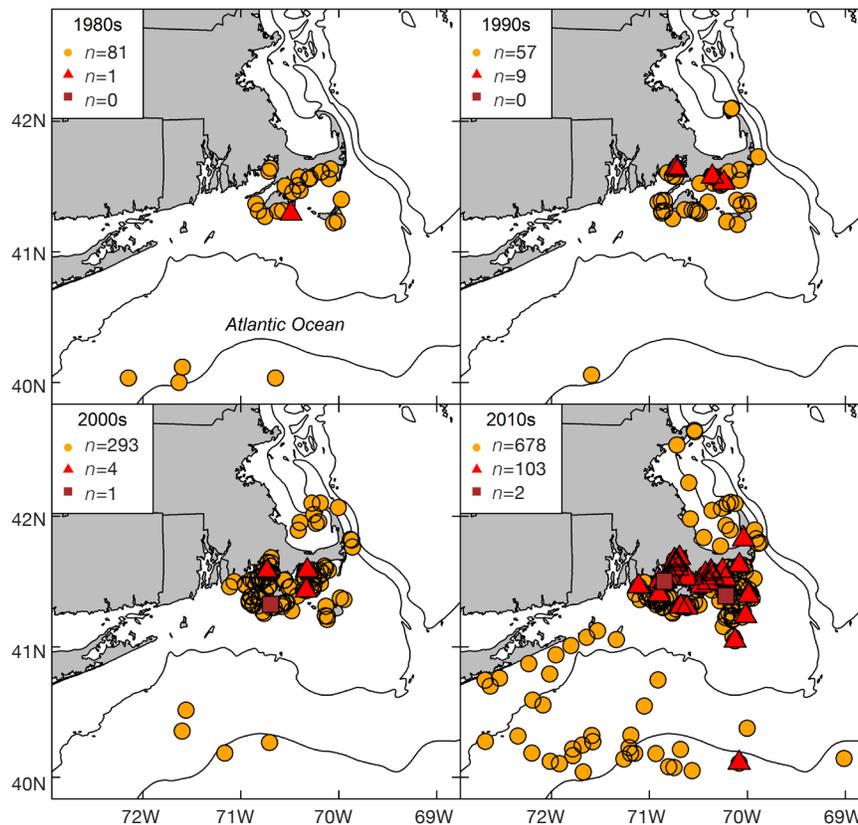


Figure 6

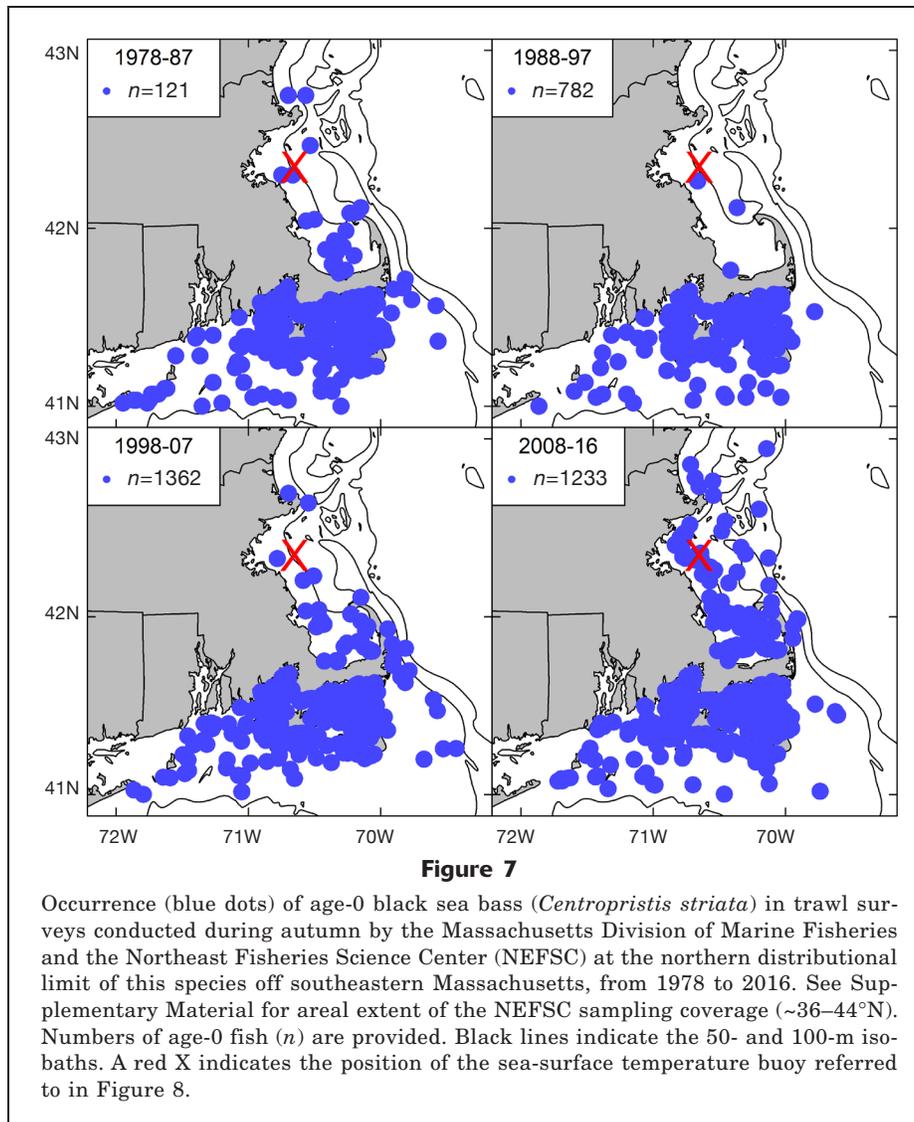
Occurrence of mature female black sea bass (*Centropristis striata*) in trawl surveys conducted during spring by the Massachusetts Division of Marine Fisheries (MA-DMF) and the Northeast Fisheries Science Center (NEFSC) at the northern distributional limit of this species off southeastern Massachusetts, from 1983 to 2016. Most fish are from the MA-DMF survey (Suppl. Material), but we examined fish from both surveys because the NEFSC survey shows broader spawning across the continental shelf. Mature fish are depicted in 3 spawning conditions: developing (orange circles), spawning (red triangles), and postspawning (brown squares). Numbers of fish in each spawning condition (n) are provided. Black lines indicate the 50- and 100-m isobaths.

and longer summer durations appear to favor growth, which increases their biomass (Henderson et al., 2017). Our new analyses support a hypothesis that increasing reproductive productivity by the northernmost spawning contingents is driving the broader increasing abundance of this northern stock. As evidence, we define black sea bass spawning seasonality at the northern extent of its range, comment on juvenile growth rates, and examine geographic shifts in spawning females and settled juveniles. Trends in the northward expansion of settled age-0 fish are also correlated with a warming trend in the southern Gulf of Maine.

Spawning seasonality

Using an otolith microincrement method, we found that black sea bass spawning seasonality does not conform to Kendall's (1972) preliminary proposal that spawning

for this species occurs progressively later with latitude. True, peak spawning is much earlier in the year south versus north of Cape Hatteras, North Carolina, but black sea bass also have the potential for a very prolonged spawning period in some regions but not others. In the south, in offshore waters of South Carolina and Georgia, Wenner et al. (1986) documented an early and prolonged spawning peak, from January to April, and a smaller peak in September. Farther north, in offshore waters of the middle Atlantic seaboard, from North Carolina to New York, spawning appears protracted from as early as April to as late as November (Table 1). At the northernmost extent of black sea bass distribution, as shown herein, spawning begins later but appears less prolonged: from May to July, peaking in June. Earlier spawning is not likely, because adults return to Massachusetts waters in spring, from an overwintering migration. We postulate that later

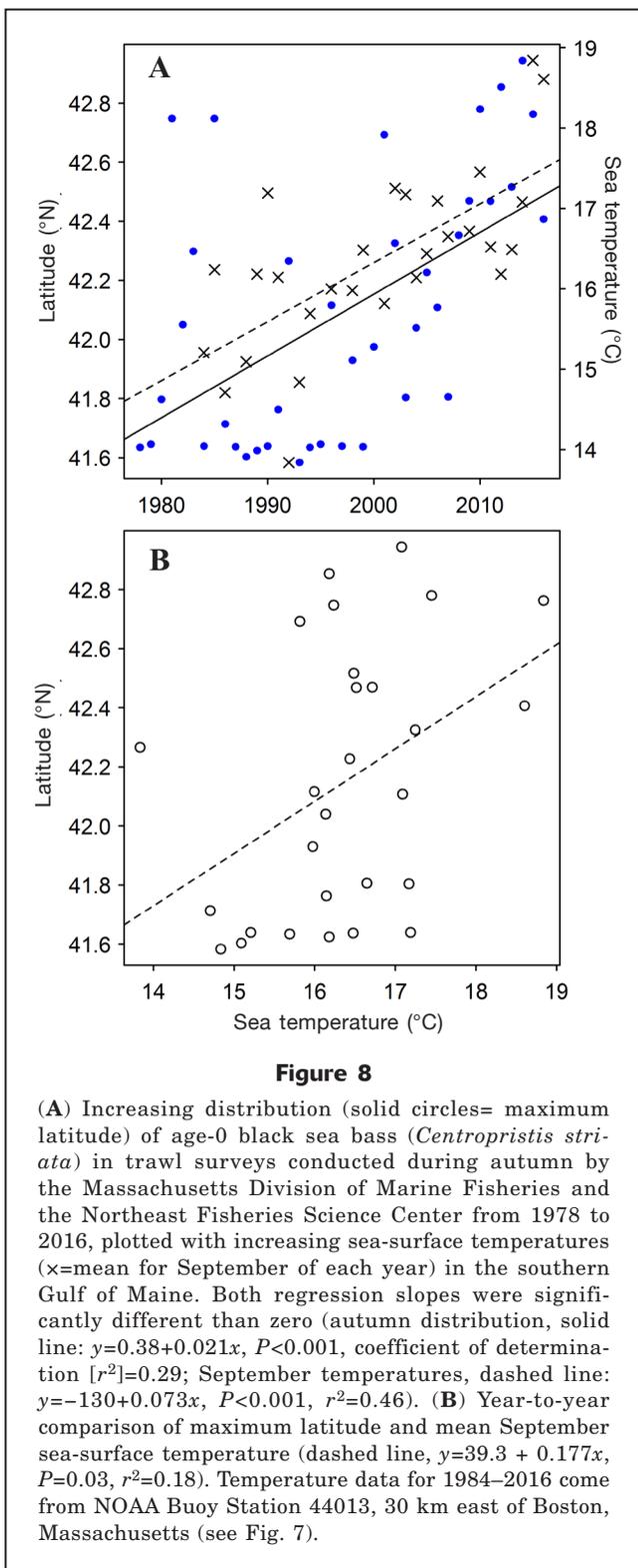


spawning is not favored in southern New England waters because the resulting age-0 fish would not grow to a sufficient size or store sufficient energy to avoid overwintering mortality (Munch et al., 2003; Bell, 2012). The timing and length of the spawning season may itself be subject to change, if warming continues, as suggested by supplemental data in Walsh et al. (2015); therefore further monitoring is warranted.

Our estimates of hatching dates are both accurate and precise. Daily microincrement formation in black sea bass otoliths has been validated by Hales and Able (1995) using OTC marked fish released and recaptured in the wild. Our effort confirms the age validation step of Hales and Able (1995) and shows the level of precision in our specific estimates. Nonetheless, we have assumed that the first microincrement corresponds with hatching specifically, but it could be laid down earlier during embryogenesis. In general, we assume a negligible difference between the times of deposition of the

first growth ring, hatching, and spawning. A review of the literature suggests that our estimates of hatching dates may differ from spawning dates by as much as a week. Egg incubation is reported to range from 38 h at 23°C to 75–120 h at 15–16°C (Wilson, 1889; Hoff⁵; Kendall, 1972). The difference between spawning, hatching, and the first microincrement may be more than 5 d in Buzzards Bay and Nantucket Sound with May bottom temperatures of 10–12°C (King et al.²), but would be shorter later, June or July, as temperature increases and survival of eggs would improve (optimized at 22–25°C; Watanabe et al., 2003). These potential adjustments would push the calculation of spawning seasonality earlier, especially when sea temperatures are

⁵ Hoff, F. H. 1970. Artificial spawning of the black sea bass *Centropristis striata melanus* (Ginsberg), aided by chorionic gonadotrophic hormones. Fla. Dept. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 25, 17 p.



cooler, but such adjustments would not push spawning or hatching outside a May–July period.

We note few differences in hatching dates among our sampling years or locations. There was no difference between years, and although temperature may drive spawning seasonality, June temperatures at the buoy in offshore waters of Boston varied by less than 0.5°C between 2006 and 2007 (14.2°C vs 14.5°C), leaving little contrast between our years of sampling. It may be that—with the longer-term pattern of warming temperatures—black sea bass spawning seasonality is undergoing a directional selection so that spawning begins earlier in the year (Pankhurst and Munday, 2011), which would justify replicating our study design to test such a hypothesis in Massachusetts waters. We were curious whether there was a spatial difference in hatching dates between neighboring Buzzards Bay and Nantucket Sound but found no difference. Finally, earlier hatching dates for fish that settle in estuarine sites, as opposed to inshore sites, may arise from early warming in estuarine waters, if warmer water initiates earlier seasonal spawning. However, our sampling design was confounded in two specific ways. First, different gears were used in estuarine and inshore sites, which may lead to gear selectivity, although this seems unlikely because the smallest mesh was a similar size in both gears. Second, sampling at estuarine sites began earlier than at inshore sites: if all fish originated across the same hypothetical hatching date distribution, then fish sampled earlier (versus later) would experience less cumulative mortality, resulting in different back-calculated hatching dates between early and late samples. Or they may have experienced different dispersal patterns with respect to age and habitat. These may be interesting considerations to pursue in the future, but their resolutions are not likely to reveal a radically different perception of spring–summer spawning by black sea bass in coastal waters off southeastern Massachusetts.

It is unlikely that spawning occurs later, such as in August, but our study design may not have captured late spawning. For example, larvae from a hypothetical August spawning may have been too small to be retained by traps or they may have had a high mortality rate. However, spawning after July by local fish is not consistent with the predominance of immature or spent individuals observed by Kolek (1990), Caruso (1995) and Wuenschel et al.² in late summer. Late summer spawning is occurring farther south. For example, a check of the NMFS-NEFSC data base from 35°N to 41°N shows an average of 8.9% (range: 3–19% by 1° latitude) of mature females are in spawning condition (ripe or ripe and running) during autumn, whereas the percentage of spawning females drops to 0.3% north of 41°N. Thus, if black sea bass spawn into autumn in Massachusetts waters, it is rare.

The dynamics and overlap between spawning and targeted fishing seasons is relevant for managing the reproductive potential of a fish population (Peer and Miller, 2014). For example, the (Massachusetts and

Table 1

Evidence from literature of black sea bass (*Centropristis striata*) spawning seasons by locations, ordered from north to south: Gulf of Maine (GOM, >42°N), southern New England (SNE, ~42–41°N), Long Island Sound (LIS, 41.5–41°N), New York Bight (NYB, 41–39°N), Chesapeake Bight (CB, 39–35°N), and South Carolina and Georgia (SC/GA, 33.5–31.5°N). Sampling habitats are identified as estuarine (E) or offshore (O). Months indicate the period during which eggs or larvae were present or when ripe or ripe and running gonads were observed by ichthyoplankton sampling (I) or by macroscopic or histological examination of gonads (G). Years of sampling are indicated, as are the citations for the sources of evidence.

Location	Habitat	Months present	Method	Year	Citation
GOM	O	–	I (larvae)	1977–87	Able et al., 1995
GOM	O	–	I (eggs)	1977–87	Berrien and Sibunka, 1999
GOM	O	–	I (larvae)	1969–70	Chenoweth, 1973
SNE	–	Jun ^a	–	1898	Bumpus, 1898
SNE	–	May–Jun	–	–	Bigelow and Schroeder, 1953
SNE	E	Jul	I (larvae) ^b	1957–8	Herman, 1963
SNE	E	–	I (eggs and larvae)	1972–3	Bourne and Govoni, 1988
SNE	O ^c	–	I (larvae)	1966	Kendall, 1972
SNE	O ^c	–	I (eggs)	1977–87	Berrien and Sibunka, 1999
SNE	O ^c	–	I (larvae)	1977–87	Able et al., 1995
SNE	O	May–July	G (macro)	1993	Caruso, 1995
SNE	O	May–Jun ^d	G (macro)	2010	Wuenschel et al. (fn. 2 in main text)
LIS	E	–	I (eggs and larvae)	1950s	Richards, 1959
NYB	–	May–Jun	–	–	Bigelow and Schroeder, 1953
NYB	O	Aug–Oct	I (larvae)	1966	Kendall, 1972
NYB	O	Jun–Oct	I (eggs)	1977–87	Berrien and Sibunka, 1999
NYB	O	Jul–Nov	I (larvae)	1977–87	Able et al., 1995
NYB	O	May–Jul	G (macro)	1974–5	Wilk et al., 1990
CB	E ^e	Jun–Jul	I (larvae)	1929–30	Pearson, 1941
CB	–	May	–	–	Bigelow and Schroeder, 1953
CB	O	Jun, Aug, Oct–Nov	I (larvae)	1966	Kendall, 1972
CB	O	Apr–Oct, Jan	I (eggs)	1977–87	Berrien and Sibunka 1999
CB	O	Apr–Nov	I (larvae)	1977–87	Able et al., 1995
CB	O	Jul–Aug	G (macro)	1987	Eklund and Targett, 1990
SC/GA	O	Jan–Apr (Sep)	G (histology)	1978–81	Wenner et al., 1986

^aSpawns in June (sampling locations and method not explicit).

^b $n=2$ at mouth of Narragansett Bay, probably a product of offshore spawning.

^cNo sampling in Nantucket Sound.

^dSampling May–Oct but not July.

^eMost taken in July at the mouth of the Chesapeake Bay.

federal) fishing season begins in mid-May and extends until at least August, completely overlapping the spawning season. Migrants that may arrive or start spawning after fishing starts are more vulnerable than earlier migrants to mortality and the potential disruption of spawning behavior, and their vulnerabilities may vary on a yearly basis or could be reduced over time if the spawning season is pushed earlier.

First year growth

Farther south, off New Jersey (39.5°N; Able and Hales, 1997) and Maryland (38.0–38.4°N; Peters and Chigbu,

2017), autumn age-0 fish size distributions overlap (range: 50–110 mm TL, mode: 70 mm TL) with what we observed off southern New England. If anything, age-0 growth was slower to the south (mean: 0.43 mm/d, Able and Hales, 1997; 0.58 mm/d, Peters and Chigbu, 2017), but a counter gradient pattern of juvenile growth has not been described for this species (Conover, 1992) and more data across its range appear necessary before speculating further on growth patterns. Growth is likely affected by temperature and by salinity as well: Berlinsky et al. (2000) reported higher growth at a salinity of 20 in relation to salinities of 10 and 32. Able and Hales (1997) observed high site

fidelity of age-0 black sea bass, at least until they migrate offshore as winter approaches; therefore local conditions are relevant to juvenile growth and survival (Miller et al., 2016). Although more experimental work would be useful to define a full response to temperature and salinity combinations, first-year growth conditions off southern New England do not appear to be suboptimal in relation to the central portions of the middle Atlantic seaboard.

Spawning and nursery habitats

Black sea bass spawning during June was historically documented in Nantucket Sound by Wilson (1889), and later, Kolek (1990) identified spawning black sea bass in shallow waters, <6 m, along the south shore of Cape Cod during May–July. In our analysis of spawning fish from trawl samples, ripe females were deeper and more variable in deeper water (mean: 18.7 m [SD 21.1], range: 6–146 m, $n=341$) than that reported for running ripe females (mean: 12.2 m [SD 5.3], range: 5–35 m, $n=83$; MADMF and NEFSC spring surveys, 1984–2017). These characterizations of spawning depth are similar to, or even shallower than, Drohan et al.'s (2007) characterization of black sea bass spawning: at 20–50 m depth. Recaptures of spawning fish in subsequent years, on the spawning grounds where they were tagged, indicate homing behavior to Nantucket Sound (Kolek, 1990).

We assume limited movements by spawning fish between locations of capture and spawning, which appears reasonable on the basis of field observations of tagged fish (Fabrizio et al., 2013). Our conclusion that spawning is expanding into the Gulf of Maine is dependent on whether the developing females observed there since 2000 do spawn there. Our prediction is that actively spawning females (i.e., ovulating) will eventually be documented in the Gulf of Maine, or that with gonad histological methods, partially spent females (i.e., with fresh postovulatory follicles) between batch spawning events will be identified there.

The NMFS-NEFSC trawling data may reflect a bias caused by a switch to a larger trawl and research vessel in 2008, which increased catches (NEFSC¹). However, expansion of mature adults into the southern Gulf of Maine was also evident in the MA-DMF survey, which has not switched gear or ships during this period (Suppl. Material). Another concern is to explain why some age-0 fish were present in the southern Gulf of Maine in the 1980s, before spawning adults were documented. Some researchers have suggested early life stages of bass are transported through the Cape Cod Canal, but no ichthyoplankton data exist to confirm such transport.

These first approximations of areal extent and dynamics of spawning suggest additional avenues for research. Tagging returns from previous years by Kolek (1990) and Moser and Shepherd (2009) indicate that a combined use of acoustic tags may not only be successful for documenting philopatry, but may also be

successful for contrasting spawning activity in different habitats and elucidating details of black sea bass mating systems, as has occurred recently for Atlantic cod (*Gadus morhua*) (e.g., Dean et al., 2014; Zemeckis et al., 2014).

Further focus on age-0 fish appears warranted. For example, the success of newly settled fish in habitats in the Gulf of Maine depends on the prey base there. Are there aspects of habitat at time of settlement that are being preconditioned by warming or is there already suitable habitat there now, but the area lacked competent larvae (i.e., larvae capable of undergoing metamorphosis) previously. Black sea bass do not use estuarine habitats extensively as nurseries, but age-0 juveniles do use polyhaline, subtidal habitats in estuaries (this study; Able and Hales, 1997; Peters and Chigbu, 2017), and larvae and juveniles are tolerant of a wide range of salinities (10–32; Berlinsky et al., 2000). The expansion of early life stages, those of both larvae and settled juveniles, on Georges Bank off the coast of New England (Suppl. Material) is quite recent and warrants continued scrutiny, as well. Given this breath of possible settlement habitats, examining the microchemistry and isotopic signatures of otolith cores may be fruitful to test the hypothesis that fish settling at more northern latitudes have been responsible for the recent trend in increasing biomass of the northern stock.

This study details black sea bass spawning and nursery habitats in a poorly studied region, noting that habitat use has been dynamic over the last 4 decades. Spawning adults and juveniles have extended northward as coastal waters warm, and possibly to the east, on Georges Bank (Suppl. Material). Nye et al. (2009) did not include black sea bass in their review of changing fish distributions in continental shelf waters of the U.S. Northeast, but more recent examinations of the same data set show that the distribution range of this species is moving northward (Bell et al., 2015; Kleisner et al., 2016; Miller et al., 2016). Such analyses have been conducted at a coarse level, i.e., by examining changes in geographic centroids, without consideration of life stage. The most recent stock assessment (NEFSC¹) showed that the northern (north of Hudson Canyon off the New Jersey coast) but not the southern contingents of black sea bass have been increasing in abundance, which could give the impression that the fish are moving north, when what is changing is the productivity rates of each set of contingents. Also, the geographic distribution of this species may appear to be moving 'north' in spring because warmer temperatures initiate an earlier migration to inshore waters off Long Island, New York, as well as north of Cape Cod (Suppl. Material). Warm-temperate species, like black sea bass, are preconditioned to wide seasonal fluctuations in temperature, and thus may be better able to expand into new habitats caused by warming seas at high latitudes. Still, just because this stock migrates seasonally, we should not assume that aggregate changes in the distribution of this population are solely the result of individuals per se moving farther north.

Details, such as described here, will help form predictions about the ways in which population abundance and geographic distribution may change (Cheung et al., 2016). In this regard, black sea bass is an informative stock to watch in the future.

Looking farther north, there is scant but growing evidence of black sea bass reaching the northern Gulf of Maine. Bigelow and Schroeder (1953) regarded black sea bass as ‘a rare stray from the south,’ mostly captured in offshore waters off Massachusetts, and not known north of Maine’s Matinicus Island (43°51’N). Even today, evidence that black sea bass are moving seasonally into the northern Gulf of Maine is the result more of anecdotal accounts than survey records. Recent state records have been reported in New Hampshire (Xu⁶), there have been accounts of increased bycatch of black sea bass in lobster pots (Rudalevige, 2015), and rare catches (3 fish from 2012 to 2016) have been reported in an inshore trawl survey along coastal New Hampshire and Maine (Sherman et al.⁷). During the NMFS-NEFSC trawl survey, few black sea bass were captured in offshore waters of Maine, either in the spring (Suppl. Material) or in the autumn (data not depicted but only 2 adults north of 43°N). Still, the northward expansion of this species led to the implementation of fishing regulations in 2014.⁸

Will this expansion of spawning and nursery grounds contribute to greater population productivity or resiliency? Maybe, but another phase of the first year needs to be recognized. Miller et al. (2016) report that cohort strength is limited by overwintering survival, a juvenile phase later than that examined here. Therefore warming near the shelf break may be more important to recruitment variability than warming in the Gulf of Maine. However, these relationships often break down when new data are added. If expansion of spawning and nursery grounds continues northward, then the corresponding effect on increasing local productivity could interact, perhaps nonlinearly, with Miller et al.’s (2016) predictive model of year-class strength. The information reported in this study provides additional context regarding the dynamics of the early life history of black sea bass, because year class strength may be set at multiple stages of ontogeny.

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