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ARTICLE

Influence of Size, Age, and Spawning Season on Sex Change in Black Sea Bass

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Abstract
A tagging study was conducted off the New Jersey coast to study sex change in Black Sea Bass *Centropristis striata* as a function of size, age, and spawning season. Throughout 2011–2013, 3,670 fish were measured and 1,498 were tagged from research, charter, and commercial fishing vessels. Of the tagged fish, 437 were recaptured. Size at 50% probability of sex change was 355 mm TL; the proportion of female fish in sexual transition increased with body size from 0.5% at 175–225 mm to 15.7% at 375–425 mm and increased with age from 0.6% at 3 years old to 18.2% at 6 years old. Relatively few females (8 of 107) changed sex during the spawning season, but a larger proportion (8 of 22 females) transitioned between spawning seasons. The proportion of females with transitional gonads was lowest at the start of the spawning season in June (0.2%), slowly increased over the summer, and sharply peaked just after the spawning season in October (9.5%). In addition, a high proportion of young mature fish were male (40% at age 2), which may indicate the presence of primary males. This is the first tagging study to estimate sex change as a function of size, age, and season in a protogynous hermaphroditic fish species. Use of tagging avoids potential problems that are associated with inferring sex change rates from sex ratios based on catch data.

Sex change in hermaphroditic fishes can have important implications for fishery management (Alonzo and Mangel 2004; Heppell et al. 2006; Hamilton et al. 2007). The relationship between sex change and size, age, and season is of interest with regard to hermaphroditic species from multiple geographic regions, including tropical (Warner and Swearer 1991; Blaber et al. 1999; DeMartini et al. 2011) and temperate (Benton and Berlinsky 2006; Villegas-Rios et al. 2013) areas. Evidence suggests that harvest may bring about changes in the size at sex change (Warner and Swearer 1991; Hamilton et al. 2007; Götz et al. 2008) and in population sex ratios (Beets and Friedlander 1998; McGovern et al. 1998) and may influence the seasonality of sexual transition (Loke-Smith et al. 2010). These types of shifts in population structure and life history

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can have profound effects on population dynamics (Alonzo et al. 2008); as a consequence, the effects of fishing on hermaphroditic species present unique challenges for fishery managers. In most fish species, the timing of reproductive events (e.g., differentiation, sex change, and age at maturity) plays an essential role in reproductive success, and these parameters should be considered across a variety of temporal scales (Lowerre-Barbieri et al. 2011). For example, is sex change restricted to specific months or seasons? Do fish transition within the spawning season? The paucity of knowledge on the timing of reproductive events in hermaphroditic fish species is a large hurdle for scientists and managers seeking to anticipate how fish stocks will respond to fishing pressure given their complicated life histories.

The Black Sea Bass *Centropristis striata* is an economically important, protogynous hermaphroditic fish species found along the entire East Coast of the United States. The present study focuses on the northern stock of Black Sea Bass, which is located north of Cape Hatteras, North Carolina. Fishing mortality rates for the northern stock are thought to have been well above sustainable benchmarks from the late 1970s to the early 2000s, at which point they apparently declined to levels associated with maximum sustainable yield (Shepherd 2012). However, this understanding of fishing mortality rates and population dynamics is based on a stock assessment that was rejected as the basis for management by a peer review panel. One of the concerns raised by the review panel was the limited consideration of the protogynous life history of Black Sea Bass within the assessment model (Miller et al. 2011). The panel recommended "…research on rate, timing and occurrence of sex-change in this species" (Miller et al. 2011:17). The call for further research into sex change in Black Sea Bass adds to the growing concern over the manner in which stock assessments currently address sex change in hermaphroditic species within U.S. waters (Provost and Jensen 2015).

Commercial and recreational fishing seasons overlap with the spawning season (late spring, summer, and early fall), during which Black Sea Bass populate reefs and artificial wrecks near shore. An acoustic tagging study conducted in the Mid-Atlantic Bight during May–September suggested that mature male Black Sea Bass that arrived early to spawning sites maintained larger home ranges than males arriving later in summer (Fabrizio et al. 2014). After the peak spawning season (May–August), when water temperatures drop in late October, adults migrate off the coastline and move southeast toward the continental shelf, where they remain throughout winter until the following spring (Musick and Mercer 1977; Moser and Shepherd 2009). Conditions during the winter period are likely the primary factor determining year-class strength of new Black Sea Bass recruits, as the presence of a strong age-0 year-class during the fall is not always indicative of whether that year-class will be strong during the following spring (i.e., at age 1; Miller et al. 2016).

The mating system of Black Sea Bass is not completely known. Most male Black Sea Bass tend to be larger than females, but small males are also observed (Wenner et al. 1986; Wuenschel et al. 2011), possibly suggesting that some individuals develop as "primary" males instead of maturing first as females and then changing sex. Previous studies of Black Sea Bass have used experiments in controlled laboratory settings to understand the social and hormonal controls of sex change. Benton and Berlinsky (2006) manipulated sex ratios in Black Sea Bass held in tanks and found that the presence of large males discouraged females from changing sex in captivity, whereas the removal of males led the largest female in the group to undergo sexual transition within six weeks.

For other sequential hermaphrodite species that are located in relatively accessible shallow-water reefs, the social dynamics that facilitate sex change have been observed directly in the species' natural habitat (e.g., Bluehead *Thalassoma bifasciatum*: Warner and Swearer 1991; Halfmoon Grouper *Epinephelus rivulatus*: Mackie 2003). However, for many temperate hermaphroditic fishes, such as seabasses (Serranidae), groupers (Epinephelidae), and some wrasse species (Labridae), populations range over large geographic areas and inhabit deep water, which makes it difficult to perform direct observations and manipulative experiments in the field. Previous studies of these temperate species have estimated transition rates by examining fluctuations in the sex ratio based on catch data by size, age, or season (e.g., Erisman et al. 2010; Mariani et al. 2013). Other studies have used catch data to measure the percentage of transitional fish as a way to approximate the prevalence of sex change in the population (e.g., Wenner et al. 1986; Brule et al. 2003; Burgos et al. 2007).

Unfortunately, the use of catch data to estimate the population sex ratio and size at sex change can be biased for three specific reasons. First, catch data cannot distinguish between two phenomena in protogynous species: (1) fish in sexual transition may be rare in the catch if the process of sex change is rapid (i.e., it is difficult to capture fish "in the act" of transitioning); or (2) sex change may occur in a very small percentage of the population. Either phenomenon would result in low observed rates of transitional individuals unless sampling was conducted frequently throughout the year. Without knowledge of the duration of sexual transition, it is difficult to interpret such observations. Second, catch data can only estimate the size and age of transition if captured individuals are observed in the act of changing sex. It would be nearly impossible to know how many males in the catch had transitioned from females unless histology was used on every captured male to look for the remnants of female tissue that are present in male gonads after transitioning (Lavenda 1949). Catch data provide only a small subset of the data used to estimate the size and age at transition and the seasonality of sex change because the males that have already transitioned cannot be identified. Third, the size and age at transition have been inferred from shifts in the sex ratio at length or age from catch data, but changes in these ratios may result in part from sex-specific mortality rates—a phenomenon that has been observed in other fish species (e.g., Maunder and Wong 2011; Bunnell et al. 2012).

An alternative that reduces challenges associated with interpretation of catch data is to track the sex change in individual fish. We conducted a tagging study to assess the size, age, and seasonality of sex change in Black Sea Bass inhabiting the Mid-Atlantic Bight. Tagging allowed us to observe the sex of individual fish at two points in time: once at tagging and again upon recapture (and, rarely, a third time for individuals that were recaptured twice). These data thus provide a direct estimate of the sex change rate through observation of individual sex change events rather than via interpretation of changes in sex ratio. Our objective was to use a tagging study as a new method for assessing the influences of size, age, and season on the sex change rate, with the goal of providing important life history information to improve stock assessment of Black Sea Bass.

METHODS

Field sampling.—This study was conducted along the coast of south-central New Jersey (between 39.527°N, 74.0815°W and 39.1439°N, 74.4941°W) from research, charter, party, and commercial fishing vessels (Figure 1). Tagging was conducted from May to October in 2011 and 2012. Fish were sampled 6–20 km from shore in water depths of 15–30 m. Fishing sites were a combination of natural hard bottom, wrecks, and artificial reefs, chosen based on fish availability and accessibility from the ports of departure. Tagging and sampling efforts were focused during early spring through autumn, when Black Sea Bass are located in nearshore waters. In addition, this period overlaps with the recreational and commercial fishing seasons, increasing the likelihood of receiving tagged fish from fishers. Tagging and sex determination during the winter months would have been logistically difficult due to the fish's offshore migration and gonadal recrudescence (Wenner et al. 1986).

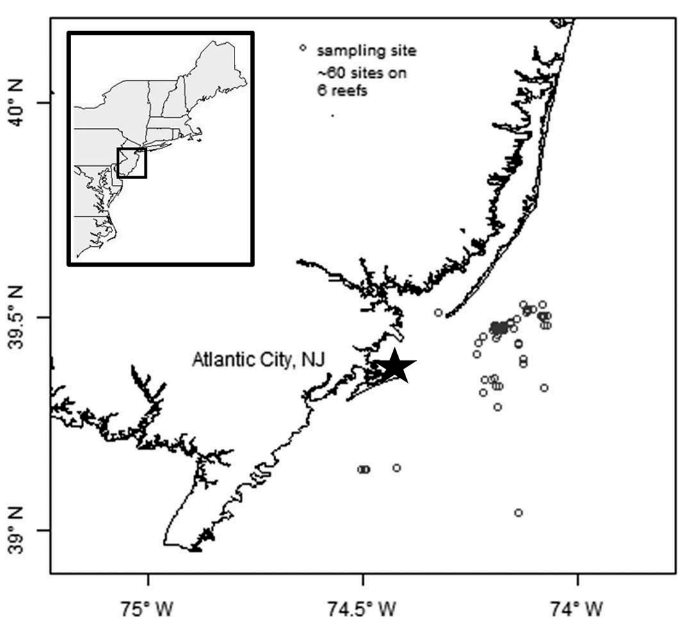

FIGURE 1. Map showing the sampling sites where Black Sea Bass were collected along the southern New Jersey coast. Multiple sampling sites were distributed across six reefs located approximately 8–24 km offshore.

Fish were captured using two different gears: (1) standard recreational hook-and-line fishing gear comprising a single or double hook that was baited with clam or fish (generally Atlantic Mackerel *Scomber scombrus*), leading off a dropper loop connected to a 56.7–226.8-g (2–8-oz) lead sinker; and (2) standard commercial fish traps that were 110.5 cm long, 53.3 cm wide, and 34.3 cm tall and were not baited, as is customary in the New Jersey fishery for Black Sea Bass. The trap entrance was 11 cm in diameter, and each trap had a 6.7-cm-diameter escape vent, which is a mandatory feature in the commercial trap fishery. Traps were deployed for 5–14 d at a time between retrievals. The hook-and-line and trapping efforts were carried out in overlapping locations. All Black Sea Bass that were captured by both gear types were measured and sexed. Fish that were over 280 mm TL and clearly identifiable as either male or female (see *Sex and age determination* section below) were tagged and released. Black Sea Bass smaller than 280 mm TL were below the fishery length limits and therefore were not tagged so that fishers returning tagged fish could comply with fishery regulations. Representative subsamples of Black Sea Bass were collected monthly for dissection and histology.

Tagging and recapture.—Black Sea Bass of both sexes (724 males, 759 females) were tagged with Floy internal anchor tags (Model FM-84). An additional 15 individuals larger than 280 mm were captured but were not tagged because their sex could not be determined conclusively. Male Black Sea Bass are not thought to change sex, but they were tagged to verify that sex change is from female to male only. Floy internal anchor tags were chosen because they had high long-term retention during a previous study in which tagged Black Sea Bass were recaptured after 4 years and tagged fish held in captivity showed no evidence of tag-induced mortalities (Moser and Shepherd 2009). The tagging procedure followed the methods of Moser and Shepherd (2009), and postrelease survival was predicted to be high based on the methods used to capture, tag, and release the fish (Bugley and Shepherd 1991). A 5-mm incision was made in the abdominal cavity approximately 2 cm posterior of the pectoral fin on the left side of the fish, and the base of the tag was inserted into this incision. The tag was tugged gently to verify that it was securely anchored; each fish was handled no longer than approximately 2 min in total. Fish were kept in live wells to monitor their recovery for 2–5 min, and those in good condition were released immediately. Fish that were swimming abnormally were not released. Fish that were captured at depths from 25 to 30 m often showed signs of barotrauma, such as a bloated abdomen. Pressure was usually released when the incision for tag insertion was made in the abdominal cavity. In the rare instance that a fish died from tagging, that individual was kept for dissection in the laboratory to permit histological verification of the sex determination made in the field (see *Sex and age determination* section). All tagging was performed by trained researchers, and the failure of fish to recover from tagging was rare (<4% of tagged fish).

All tags were printed with a unique identification number, a telephone contact number, and the phrase “Rutgers Reward.” Tags were color coded by recapture reward value (orange [reward = baseball cap], n = 1,297; red [reward = $100], n = 201). This system of high- and low-value tags made it possible to estimate the number of low-value tags that were likely captured but not returned (Pollock et al. 2001). The tag return program was publicized through posters that were posted at bait-and-tackle shops, marinas, and commercial fishing docks in four New Jersey counties. Posters were also reprinted in local fishing periodicals and on angler websites throughout the project’s duration. Poster text encouraged fishermen to retain whole fish or filleted carcasses with organs intact so that the gonads could be examined. Fish that were recaptured by local fishers were reported via telephone and e-mail; when possible, the capture date and location were recorded. For cases in which the fish carcass was saved by the fisher, the recaptured fish (either still fresh or frozen) and its tag were retrieved from the fisher. If the gonads were intact, sex was determined by use of the methods described below.

Sex and age determination.—Gametes of Black Sea Bass in the advanced stages of development (e.g., hydration, ovulation, and spermiation) can easily be expressed by applying slight pressure to the fish’s ventral surface (DeGraaf et al. 2004), and this method was initially employed for determining the sex of living fish. If gametes (milt or eggs) could not be expressed, fish were identified as females by performing an ovarian biopsy (oocyte extraction) with a polypropylene tube (1.49-mm outer diameter, 1.19-mm internal diameter; Pentair Aquatic Eco-Systems, Apopka, Florida) via the methods of Shehadeh et al. (1973) and Benton and Berlinsky (2006). Biopsies can only definitively identify female fish (Howell et al. 2003; Benton and Berlinsky 2006), and only those from which oocytes could be extracted were tagged and released. If sex could not be determined by gamete expression or ovarian biopsy, the fish was retained and its sex (generally male or transitioning) was verified by gonadal histology. In rare instances, when a fish did not survive tagging, its sex was also identified by use of histology. To verify the accuracy of in situ sex identification procedures, Black Sea Bass were randomly sampled monthly for dissection and histology (May–October 2011–2013). Both sexes and all sizes were represented in these monthly collections, and they did not include any tagged individuals. Even though visual examination of Black Sea Bass gonads is a sufficient method to identify sex most of the time (Klibansky and Scharf 2015), sex was verified via histology in all dissected fish, and the number of individuals undergoing sexual transition was noted.

For histological analysis, gonads were extracted and fixed in 10% formalin for 24 h and then transferred to 70% ethanol for preservation before histological processing. One entire gonad per fish was processed and examined; when necessary, gonads were cut in half (cross-sectioned), and each half was processed separately. Gonads were embedded in paraffin, sectioned longitudinally at 5 μm, stained with hematoxylin and eosin, and examined under a light microscope (Zeiss AxioCam MRm, Carl Zeiss, Inc., Thornwood, New York). Gamete stages were classified by using the characteristics described by Lavenda (1949), Nakamura et al. (1998), and Benton and Berlinsky (2006). Gonadal photomicrographs of both male, female, and transitioning Black Sea Bass have been published (Howell et al. 2003; Benton and Berlinsky 2006; Colburn et al. 2009). Fish with any proportion of both testicular and ovarian tissue in the gonad were classified as transitional. For tagged fish, sex was determined by expressing gametes in 70% of fish at first capture and via biopsy in 30% of fish at first capture.

To determine age, scales were removed from behind the pectoral fin on the left side of the fish and were pressed into acetate slides. Scales were collected from all captured fish. Concentric annuli were counted on an Eyecom 3000 Com Fiche Reader. On Black Sea Bass scales, the first annulus is often poorly developed and corresponds to a zone of compacted circuli near the focus (Dery and Mayo 1988). Annuli were identified as “cutting-over” marks that follow the edge of the scale (Dery and Mayo 1988). Seventy percent of scales were aged by two readers and were validated by experts at the National Oceanic and Atmospheric Administration (NOAA) Aging Laboratory in Woods Hole, Massachusetts; the remainder were aged by a reader who was trained by Black Sea Bass aging experts at the NOAA Aging Laboratory (coefficient of variation = 0.96; 95.3% agreement between aging experts and the trainee).

Data analysis.—Analyses in this study used different data subsets involving both tagged and untagged fish. First, both tagged and untagged fish were included to calculate the sex ratio at length and at age and the proportion of females in transition by size, age, and month. Second, different parts of the tag–recapture data set were used to estimate the transition rate and the size at 50% probability of sex change.

The ratio of male to female fish was calculated at different body lengths and ages by using tagged and untagged fish. Transitional individuals were not included. Total sample sizes for the sex ratio at length and the sex ratio at age were not the same because 45% of the scales that were used to determine age were not readable.

The proportion of females in transition was plotted by body length (50-mm length-bins), by fish age (years), and by month in three separate analyses. The data used in all three analyses included all females and transitional fish captured in this study (tagged or untagged); any fish identified as male was not included. Sex was determined by either ovarian biopsy or expressing eggs to identify females and by histological examination of the gonads to identify transitional fish. For the proportion of transitional fish by month, only the months May–October (combining observations from 2011, 2012, and 2013) were included. Limited sampling was performed in November–April because Black Sea Bass are offshore during those months.

Two transition rates were estimated from the tag–recapture data: (1) the probability of a female changing sex during the spawning season (May–October) and (2) the probability of a female changing sex between annual spawning seasons (from 2011 to 2012; or from 2012 to 2013). The spawning season for mid-Atlantic Black Sea Bass is characterized by the presence of late vitellogenic oocytes and hydrated oocytes and by the presence of secondary spermatocytes and spermatozoa in the testes (Wenner et al. 1986). The probability density function of the rate of sex change was estimated by using a beta distribution. The beta distribution—continuous and bounded from 0 to 1—has two shape parameters ($\alpha + 1$ and $\beta + 1$) and is well suited for modeling the probability density of a rate based on binomial data. Here, α represents the number of females that changed sex (successes), and β represents the number of females that remained female (failures; Bolker 2007). To estimate the rate of sex change during the spawning season, the analysis was restricted to the set of female fish that were tagged and recaptured within a single spawning season. A second beta distribution was used to estimate the rate of sex change between spawning seasons; this analysis was restricted to the set of females that were tagged and then recaptured 6–17 months later during the subsequent spawning season. The beta probability density function was implemented using the "dbeta" function in R version 3.2.3 (R Core Team 2015).

To estimate the size at 50% probability of sex change, the probability of sex change was modeled by using a generalized linear model with a logit-link function and a binomial error distribution (commonly referred to as logistic regression) and implemented with the "glm" function in R version 3.2.3 (R Core Team 2015). The response variable was given a value of 0 for individuals that did not change sex and a value of 1 for individuals that did change sex; length was the midpoint between the length at tagging and the length at recapture. The analysis used only tag–recapture data and was restricted to individuals that were female at the time of tagging (male-to-female sex change has not been reported in Black Sea Bass and was not observed in this study). Recaptures were also limited to individuals that were recaptured more than 30 d after initial capture (86% of recaptures were at large for >30 d).

RESULTS

Overall, 3,670 Black Sea Bass were captured in 2011 and 2012: 1,744 males, 1,896 females, and 30 fish in transition at first capture (Table 1). Of the 3,670 fish that were captured, we tagged and released a total of 1,498 individuals: 972 fish in 2011 and 526 fish in 2012. Among the tagged Black Sea Bass, the female : male ratio was 1.04:1 at first capture, and 437 fish (29.2%) were recaptured. Sex was determined for 269 (117 females, 142 males, 10 in transition) of the 437 recaptures; these fish were recaptured by the study team, or their carcasses (with gonads intact) were returned by fishers for purposes of sex identification. Of the 269 recaptures for which sex was determined, 93 individuals (47 males and 46 females) were released again by the study team, and 13 individuals (7 females, 5 males, and 1 in transition) were later recaptured a second time. In summary, 41 transitional individuals were found: 30 individuals in transition at the time of first capture, 10 tagged fish in transition at the time of recapture, and 1 tagged fish in transition at the time of the second recapture. The tag return rate was 36.8% (74 of 201) for red tags and 28.0% (363 of

TABLE 1. Summary of sample sizes for tagged and untagged Black Sea Bass, including males, females, and transitional fish, collected along the southern New Jersey coast.

Sample size	Description
3,670	Total number of tagged and untagged fish that were captured (1,744 males, 1,896 females, and 30 in transition at first capture)
1,498	Tagged fish (724 males, 759 females, and 15 individuals in which sex could not be identified and therefore were not released); 972 tags were released in 2011 and 526 tags were released in 2012
269	Recaptured fish (142 males, 117 females, and 10 in transition at recapture); 126 of these recaptures occurred within the same spawning season (May–October), and 22 recaptures occurred in the next year
41	Fish that were identified as being in transition (30 fish at first capture, 10 fish at recapture, 1 fish at second recapture)
126	Tagged females that were recaptured and for which length was measured at the time of recapture (108 were still female at recapture; 18 had changed sex or were in transition at recapture)
107	Tagged females that were recaptured within the same spawning season (99 were still female when recaptured; 8 had changed sex or were in transition at recapture)
22	Tagged females that were recaptured during the next spawning season (14 were still female when recaptured; 8 had changed sex or were in transition at recapture)

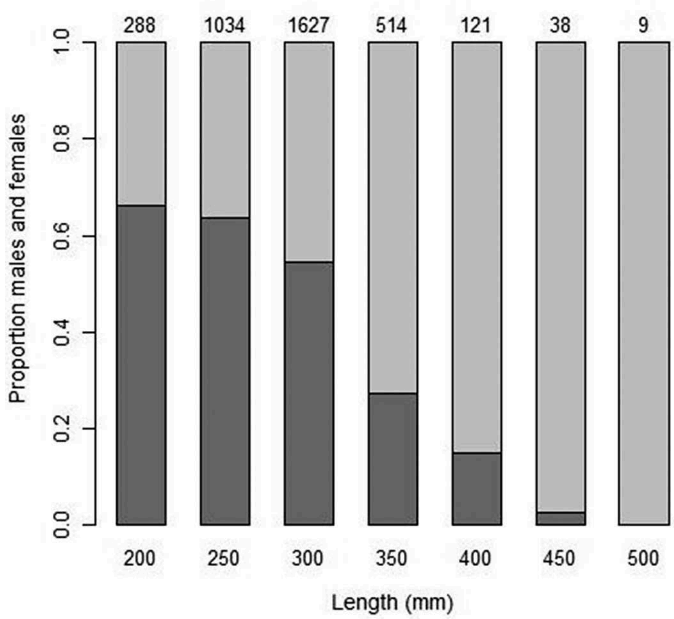

FIGURE 2. Proportions of male (light gray) and female (dark gray) Black Sea Bass at length (TL, mm). The *x*-axis values are midpoints for 50-mm length-bins. Overall, 3,631 fish were identified as either male (*n* = 1,738) or female (*n* = 1,893). The number above each column is the sample size for the corresponding length-bin.

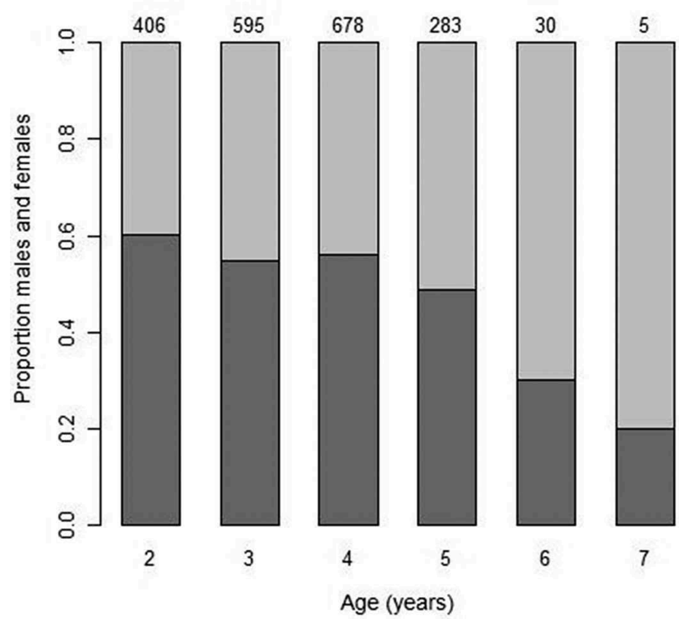

FIGURE 3. Proportions of male (light gray) and female (dark gray) Black Sea Bass at each age. Age was determined for a total of 1,997 fish, which were identified as either male (*n* = 901) or female (*n* = 1,096). Ages were estimated from annulus counts on scales. The number above each column is the sample size for the corresponding age.

1,297) for orange tags; the overall return rate was 29.2% (437 of 1,498).

Sex Ratio at Age and at Size

The proportion of Black Sea Bass that were male increased with body size such that 33.7% of individuals in the 175–225-mm size-class were male and 100% of fish larger than 475 mm were male (Figure 2). Males were present in all size-classes, and the smallest male observed was 172 mm TL. A similar pattern was observed with age; the proportion male was 40% at age 2 and increased to 80% by age 7, and the oldest fish sampled in this study was age 8 (Figure 3).

Proportion of Transitional Fish by Size, Age, and Month

As body size increased, the proportion of females undergoing sexual transition also increased (Figure 4): 0.5% of female fish (1 of 191) within the 175–225-mm size-class were in transition, whereas 15.7% of females (3 of 19) within the 375–425-mm size-class were in transition. This analysis included females and transitional fish identified at first capture and at recapture. Sex was determined via biopsy or expressing gametes in females, and transitional fish were identified by histology.

Among the 41 transitional fish, age was determined for 32 individuals. Fish in transition were identified by histology at first capture (if sex could not be determined by gamete expression or biopsy; or if fish were part of the representative samples that were collected monthly) or at recapture. Age could not be determined for nine fish because their scales were not readable. The proportion of females in transition increased with age (Figure 5): none of the age-2 fish were transitioning; approximately 0.6% of age-3 females were in transition; about 5% of age-4 and age-5 females were transitioning; and 18.2% (the peak percentage) of age-6 females were in transition.

During 2011 and 2012, the proportion of female fish in sexual transition increased from May through October, peaking at 10% at the end of the spawning season in October (Figure 6). Because sampling was not carried out year-round, the proportion of fish in transition was not available during December–April.

Length at 50% Probability of Sex Change

Length was measured and sex was determined for 126 recaptured individuals that were female at first capture. At recapture, 108 of those individuals remained female, 9 had completely transitioned to male, and 9 were in the midst of transitioning. The 126 recaptured individuals were at large for 30–431 d. We limited this analysis to only those fish that were at large for over 30 d because transition can occur within a time period as short as 6 weeks (Benton and Berlinsky 2006). After 30 d, tagged females had enough time to initiate sexual transition but not necessarily to complete the transition.

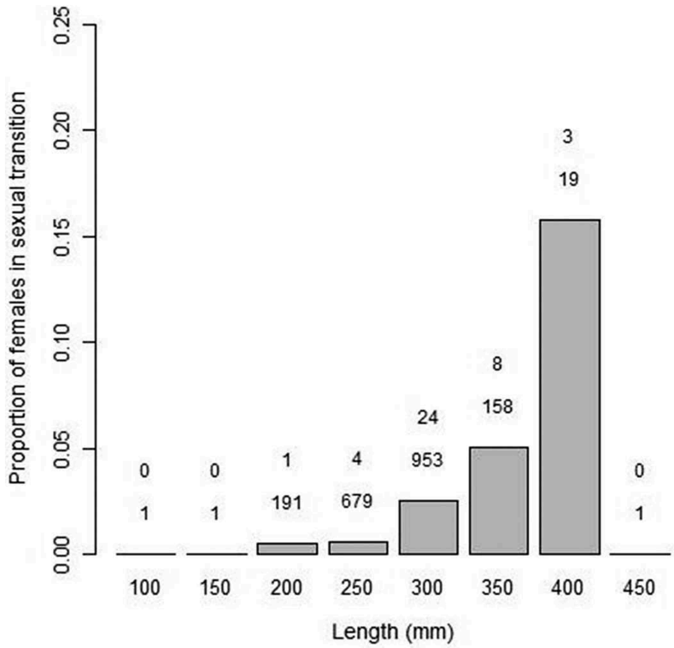

FIGURE 4. Proportion of female Black Sea Bass in sexual transition at different size-classes (TL, mm). The *x*-axis values are midpoints for 50-mm length-bins. Overall, 2,003 individuals were identified as female based on ovarian biopsy or gamete expression, and 40 individuals were found to possess transitional gonads as identified by histology (41 transitional fish were captured, but length measurements were reliable for 40 of those fish). Above each column, the upper number represents the number of females in transition, and the lower number represents the sample size.

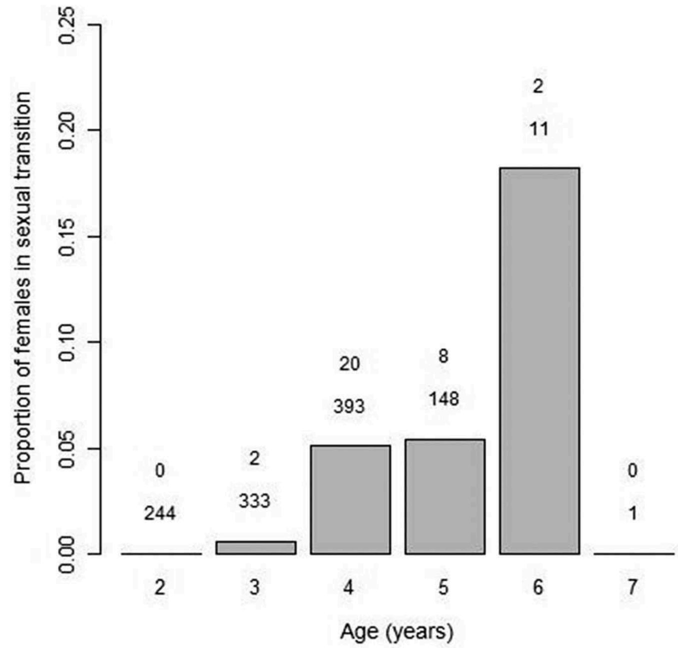

FIGURE 5. Proportion of female Black Sea Bass in sexual transition at different ages. Overall, 1,130 individuals were identified as female based on ovarian biopsy and gamete expression, and 32 individuals were found to have transitional gonads as determined by histology. Ages were estimated from annulus counts on scales. Above each column, the upper number represents the number of females in transition, and the lower number represents the sample size.

Using logistic regression, we estimated the length at 50% probability of sex change as 355 mm TL (Figure 7). All nine of the complete sex change events occurred in females ranging in size from 290 to 370 mm at first capture; at the time of recapture, these newly developed male fish ranged from 326 to 480 mm. The additional nine Black Sea Bass that were in transition at the time of recapture were slightly smaller than the nine fish that had completed sex change; the transitional fish ranged in size from 280 to 385 mm. Size at maturity in Black Sea Bass is 200–250 mm (Wenner et al. 1986); therefore, females that transitioned to male most likely had matured and spawned as females at least once before changing sex.

Seasonality of Sex Change

Analysis of transition rates showed that female Black Sea Bass were more likely to change sex at the very end of the spawning season and before the next spawning season than during the breeding months (May–October). Overall, sex was determined for a total of 107 females that were tagged and recaptured within the same spawning season (May–October in either 2011 or 2012); of those 107 females, 8 fish changed sex during the spawning season, and 99 fish remained female (Table 2). In comparison, among the 22 females that were at large over the winter and then recaptured during the subsequent year, 8 individuals had changed sex and 14 remained female. Based on the proportion of females that changed sex during the spawning season (8 of 107) and annually (8 of 22), the rate of sex change during the spawning season was estimated at 0.07 (95% confidence interval [CI] = 0.03–0.13), and the rate of sex change during the nonbreeding season was estimated at 0.36 (95% CI = 0.18–0.57; Figure 8).

DISCUSSION

Sex change in Black Sea Bass does not occur uniformly throughout the year; rather, it is concentrated in October after the peak spawning season, during nonbreeding months and possibly through the winter months. The 50% probability of transition occurs at 355 mm TL, and sex change was observed in fish of ages 4–6. Since Black Sea Bass mature at age 2 and at approximately 200–250 mm, observations from this study suggest that transitioning fish first develop and reproduce as females before changing sex. Male Black Sea Bass tended to be larger than females, as would be expected in a protogynous hermaphrodite species. However, because males were found across all size-classes, it is likely that some individuals developed first as males (i.e., primary

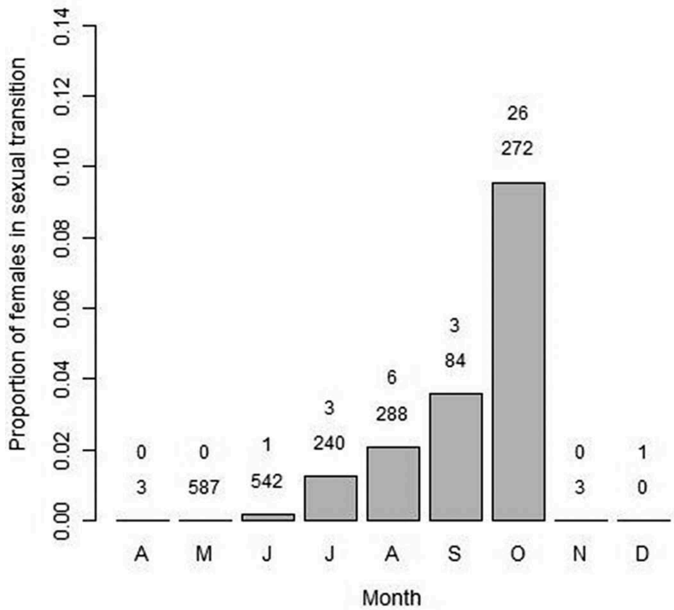

FIGURE 6. Proportion of female Black Sea Bass that were in sexual transition throughout the spawning season (May–October) in 2011 and 2012. In total, 2,019 females and 40 transitional fish were sampled; no fish were sampled during January–March, and very limited sampling was conducted in April, November, and December because Black Sea Bass are offshore during those months. Above each column, the upper number represents the number of females in transition, and the lower number represents the sample size.

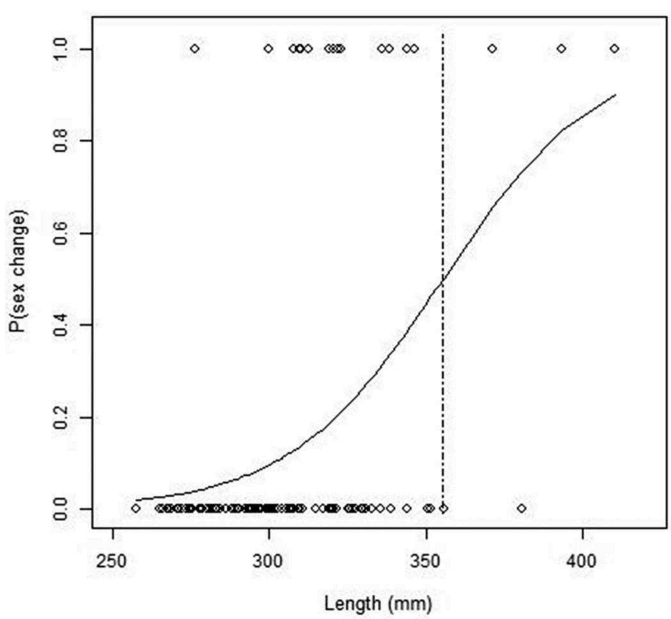

FIGURE 7. Probability (P) of sexual transition in female Black Sea Bass, plotted in relation to fish length (TL, mm). Sex was determined for 126 recaptured individuals that were identified as females at the time of tagging. Among those 126 recaptures, 9 had changed sex, 9 were in the process of transition, and 108 remained female. Length here is the average of the length at tagging and the length measured at recapture. The vertical line indicates the size at 50% probability of sex change (i.e., 355 mm TL).

TABLE 2. Number of tagged female Black Sea Bass that had changed sex or were in transition when recaptured and the number of tagged females that were still female when recaptured either (1) within the spawning season (May–October) in 2011 and 2012 or (2) between spawning seasons (2011 and 2012; or 2012 and 2013).

	Status at recapture	
Time period	Females that had changed sex	Females that stayed female
2011 spawning season	3	35
2012 spawning season	5	64
Total	8	99
Between the 2011 and 2012 spawning seasons	7	9
Between the 2012 and 2013 spawning seasons	1	5
Total	8	14

males). This finding aligns with earlier observations of small male Black Sea Bass (Wenner et al. 1986; Wuenschel et al. 2011).

Size at Sex Change and Size-Selective Fishing

Black Sea Bass are vulnerable to fishing before they undergo sex change, as both the federal commercial minimum length limit (280 mm [11 in]) and the New Jersey recreational length limit (318 mm [12.5 in]) are below the size at 50% probability of sex change (i.e., 355 mm TL). Earlier studies have not estimated the size at 50% probability of sex change, but the size of transitioning fish has been below legal catch limits and varies among geographic regions. Wenner et al. (1986) found that the highest percentage of transitional Black Sea Bass occurred at 160–259 mm in the South Atlantic Bight; Wuenschel et al. (2011) observed transitional fish ranging between 290 and 410 mm in Massachusetts and Rhode Island; and Hood et al. (1994) observed transitional individuals at 160–230 mm in the Gulf of Mexico. Compared to these size ranges, the transitioning Black Sea Bass we observed in the mid-Atlantic (280–480 mm) were similar in size to those from Massachusetts and Rhode Island and were much larger than those from the South Atlantic Bight and the Gulf of Mexico. Simulations by Alonzo and Mangel (2004, 2005) suggested that the population dynamics of a protogynous fish species may be particularly sensitive to fishing mortality when harvest targets individuals smaller than the mean size at sex change, as appears to be the case for mid-Atlantic Black Sea Bass. Alonzo and Mangel (2004, 2005) further pointed out that even at moderate levels of fishing, protogynous populations are more vulnerable to overfishing if all male size-classes are fully exploited and if the size at sex change in females is invariant. Under these

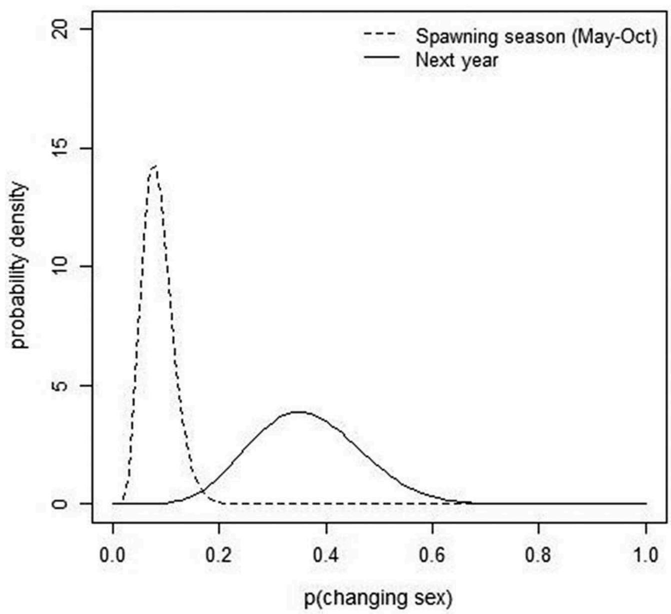

FIGURE 8. Probability density function for the rate (*p*) of sex change in Black Sea Bass during the spawning season (May–October; dashed line) and between breeding seasons (i.e., between the 2011 and 2012 seasons and between the 2012 and 2013 seasons; solid line). Of the 107 tagged females that were recaptured within the same spawning season, 8 had changed sex or were in transition and 99 remained female; the rate of sex change during spawning months was estimated as 0.07 (95% confidence interval [CI] = 0.03–0.13). Of the 22 tagged females that were recaptured during the next year's spawning season, 8 had changed sex or were in transition and 14 remained female, suggesting that the rate of sex change between spawning seasons was 0.36 (95% CI = 0.18–0.57).

conditions, many females will not survive long enough to replace males, and it is expected that the sex ratio will become increasingly skewed in favor of females, thereby leading to a greater risk of sperm limitation.

Despite these conditions, two factors suggest that Black Sea Bass may not be unusually sensitive to fishing. First, sex change in this species appears to be plastic given that in captivity, sexual transition in females is hindered by the presence of males (Benton and Berlinsky 2006). This life history characteristic implies that if male fish become increasingly scarce through size-selective fishing, the expected size and age at transition among females would decrease. Protogynous species that have the capacity to compensate for disproportionately high male mortality (i.e., females that are able to change sex at smaller sizes or to accelerate their growth to attain the size at transition) may be less vulnerable to fishing because they are predicted to produce more fertilized eggs than protogynous species that cannot compensate for high male mortality (Huntsman and Schaaf 1994). Second, we found males that were well below the minimum commercial size limit of 280 mm. Individuals smaller than 280 mm likely experience very low fishing mortality; thus, a portion of the male population is relatively invulnerable to fishing. Based on population dynamic models, if some male size-classes are invulnerable to capture, then the risks of sperm limitation and associated potential reproductive failure in the population can be substantially decreased (Huntsman and Schaaf 1994; Alonzo and Mangel 2005; Heppell et al. 2006). Since a high proportion of small Black Sea Bass are males, this may provide added resiliency to exploitation in comparison with the typical protogynous species in which all small fish are females, whereas males arise only as a result of sex change by females (Blaylock and Shepherd 2016).

If population size structure is dominated by small males, then other factors could negatively impact Black Sea Bass reproduction. Will small males be just as successful at establishing mating opportunities with females and defending territories compared to larger and more dominant males? Does parental size affect recruitment such that the large spawning males and females produce more offspring than the smaller individuals? Multiple studies suggest that large females contribute disproportionately more to the production of offspring and toward recruitment (see references reviewed by Hixon et al. 2014), and the same may also be true for large males (Green and McCormick 2005). Easter and White (2016) demonstrated that the shape of the mating function (i.e., the relationship between the sex ratio and fertilization success) has a strong influence on the dynamics of exploited protogynous populations. Even though the mating function for Black Sea Bass is unknown, the relative degree of polygyny could inform predictions for what constitutes a dangerously low sex ratio.

The presence of small, young male Black Sea Bass in the mid-Atlantic adds one additional point of interest. Males were present in all size-classes sampled during this study, and a substantial portion (40%) of age-2 fish were males. The presence of small males is consistent with observations by Wenner et al. (1986), who reported that small male Black Sea Bass made up less than 5% of fish smaller than 120 mm captured in coastal waters between North Carolina and Florida. Wuenschel et al. (2011) similarly observed small Black Sea Bass males as young as age 2 in Massachusetts and Rhode Island waters. The observations from our study and from earlier studies point to a diandric pattern of sex allocation in Black Sea Bass. Diandry refers to the existence of multiple paths to reach the terminal sex (in this case, male): terminal males may result from the transition of mature females or may arise directly from immature fish (primary males). This pattern of sex allocation is relatively common and has been found in other protogynous hermaphrodites, such as the Daisy Parrotfish *Chlorurus sordidus* (Munday et al. 2004), Chocolate Hind *Cephalopholis boenak* (Liu and Sadovy 2004), Orange-spotted Grouper *Epinephelus coioides* (Liu and Sadovy De Mitcheson 2011), and Bluehead (Munday et al. 2006). Among the 244 age-2 individuals whose gonads were histologically examined, none were transitional, further indicating that these young males did not previously mature as females. There are considerable management implications if the harvested species is diandric because the abundance of males is presumably less vulnerable to changes in total mortality rate than it would be for a monandric species, such as the California Sheephead *Semicossyphus pulcher* (Adreani et al. 2004), in which all males come from sex-changing females.

Seasonality of Sex Change

Mid-Atlantic Black Sea Bass were more likely to change sex between spawning seasons than during the spawning season, which corresponds with similar evidence from other Black Sea Bass populations and from other protogynous species. For Black Sea Bass in the south Atlantic, there are two spawning seasons, and the percentage of females in transition based on catch data increased from an average of 6% during the spawning seasons to 23% during the nonbreeding seasons (Wenner et al. 1986). A similar pattern was found in Gulf of Mexico Black Sea Bass (Cochran and Grier 1991). Wuenschel et al. (2011) observed transitional fish in August and September (i.e., after the peak spawning season) in Massachusetts and Rhode Island. The Hogfish *Lachnolaimus maximus*, a protogynous wrasse, almost exclusively initiates sex change immediately after a 6-month spawning season and completes the transition process over the 6 months preceding the next spawning season (McBride and Johnson 2007).

Changing sex during nonbreeding periods is not surprising, as this strategy is predicted to maximize seasonal reproductive output in individual fish. For example, the gonads of transitioning California Sheephead lack vitellogenic oocytes and fully developed sperm crypts, indicating that there is a period of reproductive dormancy during sexual transition (Sundberg et al. 2009). Female Black Sea Bass are probably similar in that they are unable to produce eggs and spawn while transitioning. Avoidance of a reduction in reproductive output during the peak mating season in May–August (Musick and Mercer 1977) may explain why most of the transitional fish in this study were observed just after peak spawning in October. Our histological analysis showed gonad tissue patterns similar to those reported by previous investigations (Wenner et al. 1986; Cochran and Grier 1991) in that testicular tissue was found first in the posterior section of the gonad and occurred in fish at different states of maturity. However, the findings from this study and previous studies were unable to determine conclusively whether Black Sea Bass also experience a period of reproductive dormancy during sexual transition.

The observed seasonality of sex change has implications for estimating the sex ratio from survey data in stock assessments. If females change sex during the nonbreeding months, the abundance of male fish could increase during this time period, assuming that males and females have equal mortality rates or that mortality in both sexes is negligible between the pre-sex-change period and the post-sex-change period. Seasonal shifts in sex ratio have been observed in other hermaphroditic species and have been attributed to seasonal variation in sex change rates. For example, the sex ratio (female : male) of Gags *Mycteroperca microlepis* is approximately 25:1 during January and February but decreases to 3:1 by June and July (McGovern et al. 1998). In *Diplodus* spp., a genus of protogynous hermaphrodite fishes in the Mediterranean, relatively more females were observed during nonbreeding months (March–September) than during the spawning season (October–February; Mouine et al. 2012). Stock assessments often estimate male and female biomass based on surveys conducted at specific times of the year. If surveys are performed just prior to when fish change sex, the survey data may fail to account for the influx of newly formed male biomass as well as the corresponding loss of female biomass, especially if the rate of sex change in the population is unknown. In this study, the female : male sex ratio in Black Sea Bass remained nearly unchanged during the spawning season: the ratio was 1.31:1 in May and 1.16:1 in October. Additional research could be dedicated to understanding the link between seasonal variation in the rate of sex change and the population sex ratio—specifically, whether the population sex ratio shifts throughout the nonbreeding months in October–April, since such knowledge could inform the scheduling of stock assessment surveys while accounting for seasonal fluctuations in sex-specific biomass.

Two observations from this study seem to contradict one another: sex ratios were fairly similar between the end of one spawning season and the beginning of the next, yet the estimated transition rate suggested that 36% of female Black Sea Bass undergo the sex transition each year. There are two possible reasons why the sex ratio remained constant: first, male Black Sea Bass may have higher mortality than females. Disproportionately high male mortality may balance the addition of new males from sex-changing females. Second, a subset of male Black Sea Bass may be difficult to sample, thereby obscuring the true sex ratio of Black Sea Bass in this study.

Quantifying the rate of sex change in addition to the seasonality of sex change may substantially improve population dynamic models because changes in the transitioning rate could significantly alter a cohort's contribution to female spawning biomass. Shepherd and Idoine (1993) showed that a doubling in the transition rate could decrease the amount of female spawning stock biomass yielded from recruits by as much as 39%. If such alterations in the rate of sex change can greatly impact stock productivity, future research will need to identify the variables that affect transition rates in regional Black Sea Bass populations. Stock assessment models designed for gonochoristic species can result in considerably different interpretations of stock status relative to models that allow for a female-to-male transition (Shepherd and Idoine 1993; Alonzo et al. 2008). For these reasons, direct estimates of the sex change rate may be an important population characteristic to consider for inclusion in stock assessments.

Our results are applicable to mid-Atlantic Black Sea Bass, but their applicability to populations in the south Atlantic and Gulf of Mexico is unknown due to differences in life histories and potential for geographic variation in gonad development. Genetic analyses have shown that Gulf of Mexico Black Sea Bass represent a separate subspecies, *C. striata melana*, and there is sufficient genetic variability between the northern (mid-Atlantic) and southern (south Atlantic) stocks along the East Coast to support the occurrence of distinct Black Sea Bass populations in the three regions (Roy et al. 2012). Studies of sex change in each population indicate that gonad development may vary geographically. Histological analysis of gonads from Black Sea Bass in the Gulf of Mexico (Cochran and Grier 1991) and off the coast of South Carolina (Wenner et al. 1986) demonstrated that all females exhibit some amount of testicular tissue but only in transitional individuals is there a proliferation of testicular tissue throughout the gonad. This is in contrast to Black Sea Bass in the mid-Atlantic, where only a small fraction of females in the population contain testicular tissue and these individuals are considered transitional (Howell et al. 2003; Benton and Berlinsky 2006; Klibansky and Scharf 2016; and present study). However, to definitively conclude that gonad development varies geographically, a systematic study would have to directly compare the gonads of males, females, and transitional individuals from all three populations. To date, no such investigation has been conducted, but it would be of value if completed in the future.

In conclusion, this is the first study to use tagging to estimate sex change as a function of size, age, and season in a protogynous hermaphrodite fish species. This method avoids potentially serious challenges associated with using catch data to estimate the seasonality and frequency of sexual transition, which have not been addressed in previous studies of sex change in hermaphroditic fish. The size at 50% probability of sex change was approximately 355 mm TL, indicating that sex-changing females are vulnerable to fishing because minimum length limits are currently set well below the size at which females are expected to transition. Sex change was more likely to occur during the period between spawning seasons than during the summer breeding months: approximately 36% of females were expected to change sex between the 2011 and 2012 seasons and between the 2012 and 2013 seasons, whereas approximately 7% were expected to change sex during the spawning seasons in 2011 and 2012. Although this study included observations from thousands of captured Black Sea Bass, sample sizes for the analysis of sex change rates were smaller and should be considered when planning future tagging studies. The present observations have important implications for stock assessment of mid-Atlantic Black Sea Bass, but these specific life history findings could vary geographically because the maximum size of Black Sea Bass varies with latitude (Wuenschel et al. 2011) and because regional populations vary in life history and morphology (Roy et al. 2012). Future studies should focus on evaluating the size at sex change and the transition rates in Black Sea Bass occurring in regions outside of the mid-Atlantic.

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