



FEATURE ARTICLE

Sciaenid courtship sounds correlate with juvenile appearance and abundance in the May River, South Carolina, USA

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ABSTRACT: Black drum *Pogonias cromis*, red drum *Sciaenops ocellatus*, silver perch *Bairdiella chrysoura*, and spotted seatrout *Cynoscion nebulosus* belong to the family Sciaenidae and are commonly found in South Carolina (USA) estuaries. Fish within this family produce sounds that are associated with courtship behavior and spawning. By listening to estuarine soundscapes, we can identify spawning aggregations. In this study, our objectives were to investigate long-term patterns of black drum, silver perch, spotted seatrout, and red drum calling and chorusing (i.e. indicative of spawning) over a 6 yr time span; identify any shifts in seasonal sound production from one year to the next; and examine the relationship between chorusing and young-of-the-year (YOY) abundance collected through haul seines. We found that in years with warmer springs, black drum, silver perch, and spotted seatrout began chorusing earlier and had longer chorusing seasons than in the years with cooler temperatures. Inversely, cooler temperatures during late summer led to earlier and longer spawning seasons for red drum. We detected the appearance of YOY in the estuary approximately 1 mo after initiation of the chorusing season. Silver perch were the most abundant in the spring, spotted seatrout during the summer, and red drum during the fall. Additionally, we found positive correlations between chorusing and YOY abundance. In years with longer chorusing seasons, we detected higher abundance of silver perch, spotted seatrout, and red drum YOY than in the years with shorter chorusing periods. These patterns provide supporting evidence that passive acoustics can aid in monitoring reproductive output of an estuary.



Passive acoustic recorders and seining were used to investigate long-term patterns of fish courtship sounds and their relationship to young-of-the-year appearance and abundance

Illustration: Claire Mueller

KEY WORDS: Passive acoustics · Soundscapes · Sciaenids · Spawning · Seining · Estuary

1. INTRODUCTION

Over recent years, there has been an increasing interest in studying sound-producing fish that belong to the family Sciaenidae, such as black drum *Pogonias cromis*, silver perch *Bairdiella chrysoura*, spotted seatrout *Cynoscion nebulosus*, and red drum *Sciaenops ocellatus* (e.g. Mok & Gilmore 1983, Con-

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naughton & Taylor 1996, Locascio & Mann 2011, Montie et al. 2015, Rice et al. 2016, Monczak et al. 2017). These fish produce characteristic sounds when contractions of sonic muscles vibrate the swim bladder by pulling an aponeurosis that sits lateral and ventral to the swim bladder (Tavolga 1960). Differences in muscle activation patterns are most likely responsible for different acoustic signatures produced by various fish species (Tavolga 1960, Connaughton et al. 2000). Hence, acoustic signals can encode crucial information about species identity and behavior (e.g. Saucier & Baltz 1993, Mann & Lobel 1995, Luczkovich et al. 2008a). The main role of these sounds in sciaenids is associated with courtship and spawning (e.g. Connaughton & Taylor 1996). These species aggregate during spawning, and vocalizations may serve to signal the readiness of males to spawn, attract females to a spawning location, aid to aggregate individuals, or serve as a cue for the release of gametes (Gray & Winn 1961, Lobel 1992, Erisman & Rowell 2017, Biggs & Erisman 2021). In fact, sound pressure levels of acoustic signaling can correlate with reproductive potential, fish density, and population abundance (Vasconcelos et al. 2012, Rowell et al. 2017).

Despite the immense literature on sciaenid sound production, we know relatively little about its biological significance and correlations with reproductive output within an ecosystem (Ramcharitar et al. 2006). In spotted seatrout and red drum, captive studies have shown a positive correlation between the number of calls and the quantity of eggs released by females (Montie et al. 2016, 2017). However, it is more challenging to establish similar correlations in the wild without investing in time consuming, traditional sampling methods (e.g. plankton tows, haul seines, trawl surveys) (e.g. Locascio et al. 2012). Passive acoustic data can provide timelines of calling activity with high temporal resolution (e.g. Monczak et al. 2017, 2020); however, we have little knowledge of how yearly courtship calls correlate with year-class strength. Spawning success and egg, larval, and juvenile survival depend on many abiotic (e.g. salinity, temperature, pH, dissolved oxygen) and biotic (e.g. food availability, disease, competition, predation) factors (e.g. Holliday 1969, Nieceza & Metcalfe 1997, Song et al. 2013, Anweiler et al. 2014). Yet, monitoring courtship calls at the chorusing level may provide a basic understanding of spawning potential as well as how environmental, biological, and anthropogenic factors may affect spawning success.

Chorusing-level sounds of black drum, silver perch, spotted seatrout, and red drum are associated with

the spawning season, and this behavior often peaks during late afternoon or nocturnal hours when fish form large, conspecific spawning aggregations (e.g. Mok & Gilmore 1983, Connaughton & Taylor 1996). In the southeastern USA, during the spring, as the water temperature and daylight hours increase, black drum, silver perch, and spotted seatrout begin chorusing (Locascio & Mann 2011, Montie et al. 2015, Rice et al. 2016, Monczak et al. 2017, 2019, Mueller et al. 2020). As summer approaches and water temperatures rise and daylight lengthens, black drum and silver perch chorusing fades, and spotted seatrout become the dominant sound producer (e.g. Luczkovich et al. 2008b, Montie et al. 2015, Monczak et al. 2017, 2019, Mueller et al. 2020). As fall approaches, and the water temperature declines and daylight hours shorten, spotted seatrout chorusing begins to wane, and red drum chorusing begins (Lowerre-Barbieri et al. 2008, Montie et al. 2015, Monczak et al. 2017, 2019, Mueller et al. 2020).

Spatially, spawning and chorusing of these species occur in specific habitats. For example, in the May River, South Carolina, USA, a subtidal river estuary, chorusing of black drum, silver perch, spotted seatrout, and red drum was not detected at stations closest to the headwaters (Montie et al. 2015). This region of the May River is shallower and narrower with a lower and broader salinity range (18.6–33.7 ppt) than locations further towards the mouth (Montie et al. 2015, Monczak et al. 2017). The lower salinity and lower dissolved oxygen levels near the headwaters may impede reproduction. Conditions beyond the environmental thresholds of tolerance may cause deformities, lower hatching rates, reduced growth, and decreased larval survival in spotted seatrout, silver perch, and red drum (Alshuth & Gilmore 1995, Kucera et al. 2002). For example, spotted seatrout inhabit waters with salinities ranging from 0.2 to 35 ppt, but spawning is thought to occur in a more restricted range from 20 to 31 ppt (Simmons 1957, Helser et al. 1993). There is evidence that spotted seatrout egg diameter correlates with salinity; smaller eggs are produced in higher salinities, while larger eggs are produced in lower salinities (Holt & Holt 2002, Kucera et al. 2002). This adaptation is important because eggs that are not neutrally buoyant will sink and could be buried in the sediment and experience anoxic conditions. Similar findings have been reported for silver perch, where egg diameter varies inversely with salinity (Alshuth & Gilmore 1995). Red drum eggs hatch within a wide range of salinities, with the most successful hatches occurring between 33 and 43 ppt (Kesaulya & Vega

2019). In the May River, chorusing aggregations of spotted seatrout and silver perch were frequently detected near steep banks near the shore opening to a deep hole, while red drum chorusing occurred only at the mouth (~21 m deep) (Montie et al. 2015).

Advances in long-term passive acoustic monitoring have allowed scientists to better understand spatial and temporal patterns of fish sound production and its relationship to environmental parameters (Mann et al. 2008, Lillis et al. 2018, Mueller et al. 2020). Temperature and photoperiod are the principal, natural cues triggering seasonal maturation and mating activity in many fish species (e.g. Locascio & Mann 2011, Tellechea et al. 2011). Evidence now exists that some sound-producing fish have temperature-dependent spawning seasons, and rapid rises and declines in temperature can increase or decrease acoustic activity, respectively (e.g. Ricci et al. 2016, Monczak et al. 2017, Van Wert & Mensinger 2019). However, most studies have been short-term, which limits the possibility of understanding whether courtship patterns could change gradually in response to environmental changes but also human impacts (e.g. Lobel 2002, Rice et al. 2016, Mueller et al. 2020).

In this study, we deployed 3 passive acoustic recorders over a 6 yr period (February 2013 to December 2018) in the May River to investigate calling timelines of black drum, silver perch, spotted seatrout, and red drum (Monczak et al. 2020). Additionally, we performed haul seines once per month overlapping a 3 yr period (May 2016 to December 2018) of acoustic data to assess the abundance of young-of-the-year (YOY) caught in intertidal pools and creeks located near deployed passive acoustic recorders. Our specific objectives were to: (1) determine the temporal patterns of fish calling over the 6 yr time span; (2) examine how environmental factors influence fish acoustic behavior; (3) investigate the phenology of acoustic activity with relationship to water temperature; and (4) investigate the relationship between yearly fish acoustic activity (i.e. chorusing) and yearly YOY appearance and abundance.

2. MATERIALS AND METHODS

2.1. Study site

We deployed passive acoustic recorders in the May River (32° 12' 49" N, 80° 52' 23" W), at Stns 9M, 14M, and 37M between 2013 and 2018 (Fig. 1). We selected these stations for long-term monitoring based upon the prevalence of fish sound production

previously reported in a larger spatial study completed in 2012 (Montie et al. 2015). The May River is a ~22 km long subtidal river estuary with no true freshwater input beyond groundwater intrusion; the estuary contains various microhabitats including oyster reefs, salt marshes, mudflats, and sand bars with first- and second-order creeks branching off the main river channel. Stns 9M, 14M, and 37M are located at the main river channel close to riverbanks, which are covered with smooth cordgrass *Spartina alterniflora* and/or oyster rubble. Stn 9M is located close to the headwaters, Stn 14M near the middle part of the river, and Stn 37M at the mouth. The depth ranges are 3–7 m at the headwaters, 5–10 m mid-river, and 4–18 m at the mouth. Salinity varies seasonally, with the highest values recorded during the fall compared to the other 3 seasons (Soueidan et al. 2021). Additionally, salinity is dramatically lower on the ebb tide and higher on the flood tide (Soueidan et al. 2021). Ocean water floods the estuary during the rising tide, which increases the salinity, while on the low tide, a combination of receding oceanic water and fresh, groundwater intrusion decreases the salinity (Soueidan et al. 2021). Generally, the highest salinity values (mean \pm SD ppt) occur at the mouth of the river (Stn 37M: 29.23 \pm 2.56), lower near the mid-river (Stn 14M: 26.86 \pm 2.30), and the lowest near the headwaters (Stn 9M: 24.92 \pm 5.30).

2.2. Passive acoustic data collection and analysis

We deployed DSG-Ocean recorders (Loggerhead Instruments) in the May River at Stns 9M, 14M, and 37M from 23 February 2013 to 31 December 2018 over 22 deployments (Fig. 1). From 2013 to 2015, we did not deploy passive acoustic recorders during the winter; in addition, data gaps occurred due to maintenance and servicing instruments during those years. DSG-Ocean recorders malfunctioned or were scheduled improperly on 2 occasions, once in the spring of 2017 at Stn 37M and once in the fall/winter of 2018 at Stn 9M. Acoustic recorders were equipped with HTI-96-Min hydrophones (i.e. sensitivity of -185 dB re: 1V/mPa) with a flat frequency response between 2 Hz to 30 kHz. This system is calibrated by the manufacturer with a 0.1 V (peak) frequency sweep from 2 to 100 kHz. Recorders were mounted in custom-built frames (Mooring Systems), painted with antifouling paint (Trilux 33, West Marine), and deployed on the bottom ~10 m from the shore following methods previously described (Monczak et al. 2017, 2019, 2020, Mueller et al. 2020, Marian et al.

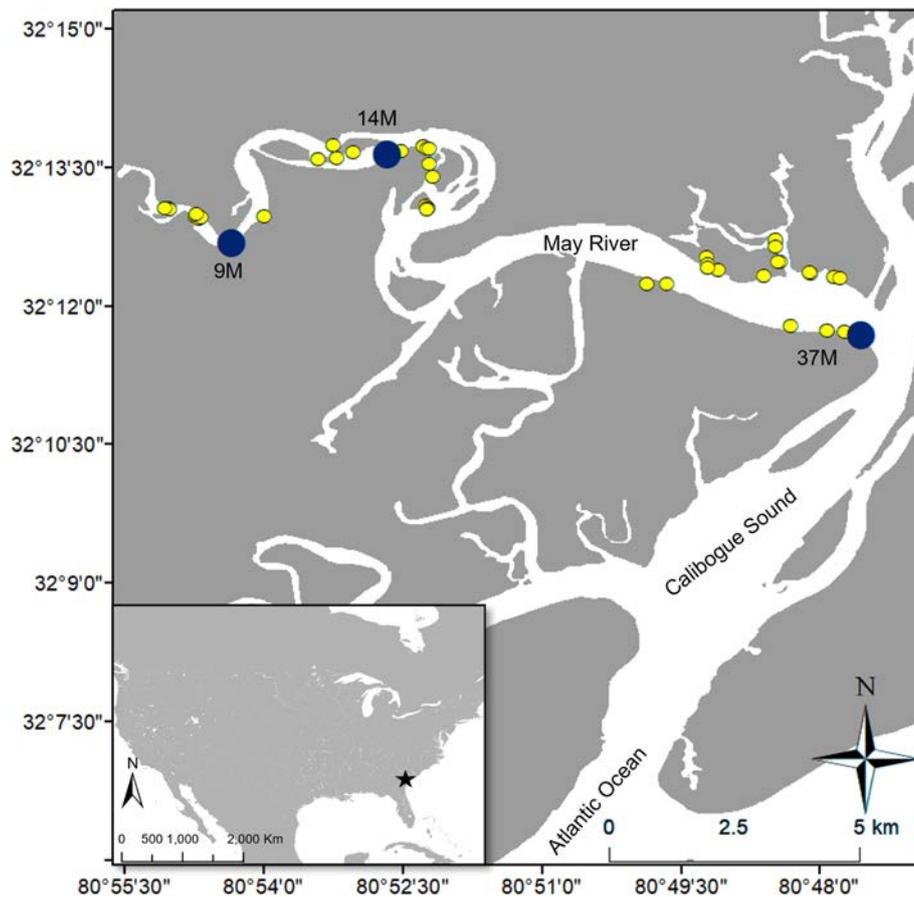


Fig. 1. May River estuary, South Carolina, USA, showing locations of Stns 9M, 14M, and 37M that were acoustically monitored from February 2013 to December 2018 (blue) and seining locations monitored from May 2016 to December 2018 (yellow). Inset shows the location of the May River (black star) in reference to the US east coast

2021). To allow easy deployment and retrieval, we attached a 7 m galvanized chain to the frame, which attached to a line and auger along the side of the river. DSG-Ocean units recorded sound for 2 min every 20 min at a sampling rate of 80 kHz in Eastern Standard Time (EST) (UTC $-5:00$ h), and no adjustment to Eastern Daylight Time was made for spring/summer months. At the end of each deployment, DSG files were downloaded and batch converted into wav files using DSG2wav© software (Loggerhead Instruments). Water level and temperature loggers (HOBO 100-Foot Depth Water Level Data Logger U20-001-02-Ti and HOBO Water Temperature Pro v2 U22-001, Onset Computer) were deployed on passive acoustic platforms following methods previously described (Monczak et al. 2017, 2019, 2020, Mueller et al. 2020, Marian et al. 2021). Water depth and temperature loggers recorded data every hour at each passive acoustic station.

We subsampled the passive acoustic dataset and manually reviewed wav files on the hour from each

acoustic recorder. In total, we analyzed 130 702 files (i.e. from recorders deployed at Stns 9M, 14M, and 37M) by visualizing wav files using Adobe Audition CS5.5 software (Adobe Systems). During analysis, we identified calls of black drum, silver perch, spotted seatrout, and red drum by comparing spectrograms to previous studies (e.g. Luczkovich et al. 1999, Montie et al. 2015, 2016, 2017, Monczak et al. 2017). For each 2 min wav file, the intensity score of fish calling was determined based on 4 categories (i.e. 0 = no calls; 1 = one call; 2 = multiple calls; 3 = overlapping calls or chorusing) following methods described previously (Luczkovich et al. 2008b, Monczak et al. 2017). Chorusing-level sounds (category = 3) of black drum, silver perch, spotted seatrout, and red drum equate to spawning in wild and captive studies (e.g. Mok & Gilmore 1983, Connaughton & Taylor 1996, Montie et al. 2016, 2017). We entered these data into Microsoft Excel 2010 worksheets.

From the analyzed acoustic files, we determined the seasonal start and end dates of calling (i.e. cate-

gory 1 and 2 detections combined) and chorusing (i.e. category 3 detection only) as well as corresponding temperatures and daylight hours for chorusing of each fish species for each year between 2013 and 2018. Since these fish species exhibit nightly calling patterns, we summed fish calling intensity scores (i.e. categories 0, 1, 2, and 3) centered on the night (i.e. from 12:00 to 12:00 h the next day), and we plotted these sums with corresponding water temperature and hours of daylight versus the date. To examine shifts in calling seasons, we created heat maps in MATLAB R2017b (MathWorks) by plotting the sum of fish calling intensity scores (i.e. categories 0, 1, 2, and 3) for each year versus day of year. We calculated the percentage of hours calling (i.e. categories 1 and 2 combined) and chorusing (i.e. category 3 only) for each year by summing the intensity scores of the 2 min files for calling and chorusing events, dividing these values by the total number of hours monitored for each year, and multiplying by 100% across the stations. We focused the analysis on the calendar year, since spawning seasons of these fish species did not occur between January and December.

2.3. Seining data collection and analysis

Between 2016 and 2018, we performed haul seines once per month (i.e. 2 seine samples per passive acoustic station per month) (Fig. 1). Seining sites were located near (i.e. generally within 0.1–1 km) the passive acoustic recorders and were selected at the beginning of the study based on accessibility during the low tide (Fig. 1). We identified a total of 13, 16, and 21 seining sites near passive acoustic recorder Stns 9M, 14M, and 37M, respectively. Seining sites included tidal pools (i.e. shallow pools of water created during low tide), intertidal creeks (i.e. small secondary or tertiary creeks branching off from the main river), and sides of the river (i.e. stations located along the bank of the primary river). In order to increase statistical power, we sampled 6 sites (i.e. 2 sites per passive acoustic station) per month selected randomly from the total accessible sites. With this approach, the dimensions of the tidal pools and creeks differed, but we measured this area and corrected for effort by dividing species abundance by area, following the methodology published in other studies (e.g. Allen et al. 1992). During sampling, we used haul seines (seine width = 9.1 m, height = 1.2 m, and mesh diameter = 3.2 mm) and block nets (additional stationary seine nets to stop animals from

escaping). We transferred the catch into a live well, quantified the total abundance, and then randomly selected and measured the standard length of 50 individuals of each species and released the live organisms at the sampling site. Environmental parameters (water temperature, salinity, pH, and dissolved oxygen) were recorded with a YSI 556 Handheld Multiparameter Instrument (YSI/Xylem) before each seine.

For the species that were caught during haul seines, including silver perch, spotted seatrout, and red drum, we reported the date on which YOY appeared for the first time during the 2016, 2017, and 2018 spawning seasons. We only caught 4 black drum during sampling, so we did not perform any additional analysis for this fish species. We calculated the mean abundance standardized by seine area per month and plotted these values with corresponding temperature, as well as chorusing scores (i.e. category 3) summed per evening. We calculated the yearly mean abundance standardized by the seine area and plotted these values with corresponding average water temperature and the total percentage of hours chorusing (i.e. category 3). We calculated the frequency distribution of fish lengths measured in 2016, 2017, and 2018 to illustrate that seining mostly targeted YOY. In addition, we plotted the total length versus the date combining all stations, and calculated growth rates for each species using linear regression. From regression equations, we calculated the estimated time of hatching by assuming the birth length was 3.6 mm for silver perch, 1.3 mm for spotted seatrout, and 6.0 mm for red drum (Froese & Pauly 2000). Seining was conducted under South Carolina Department of Natural Resources permit numbers 5135 and 5136 as well as IACUC protocol 2233-101181-022217.

2.4. Statistical analyses

For all statistical analyses, we used R version 4.0.2. To assess the significance of specific factors in explaining variations in acoustic activity in each fish species, we used the R package 'Boruta', a wrapper algorithm based on the random forest algorithm in R (Kursa & Rudnicki 2010, Kursa 2014, Wright & Ziegler 2017, Degenhardt et al. 2019). Since acoustic activity of fish was scored with 4 categories (i.e. 0, 1, 2, and 3), we used random forest classification. We tested the influence of location, year, lunar phase, tidal cycle, day/night, and temperature on calling intensity scores of black drum, silver perch, spotted

seatrout, and red drum within their specific calling seasons (i.e. based on our acoustic data). We used 4 categories to differentiate the lunar cycle: new moon (lunar days 27–4), first quarter (lunar days 5–11), full moon (lunar days 12–19), and third quarter (lunar days 20–26) (Monczak et al. 2017, 2019). We used 4 categories (rising, high, falling, low) to distinguish tidal cycles following methods previously described (Monczak et al. 2017, 2019). In the final models, we used default values for each setting, and we set the seed to 42 (Breiman 2001, Díaz-Uriarte & Alvarez de Andres 2006, Li et al. 2013). We then investigated the accuracy of each model, and report the mean importance score (Z-score) for each factor. To determine which groups were significantly different from each other, we used the package 'DTK' in R and applied Dunnett-Tukey-Kramer pairwise multiple comparison tests, adjusted for unequal variances and unequal sample sizes, and used a 95 % confidence level (Lau 2013).

3. RESULTS

3.1. Year to year patterns of fish calling

We investigated 6 yr of acoustic data, and we detected calls of black drum, and calls and choruses of silver perch, spotted seatrout, and red drum (Fig. 2; Audio S1–S8 at www.int-res.com/articles/suppl/m693p001_supp/). Spatially, the highest species diversity (i.e. all 4 sciaenids detected) occurred at Stn 37M and the lowest at Stn 14M (Fig. 3). We detected patterns of calling (i.e. summed calling intensity scores of 0, 1, 2, and 3 categories) that were consistent from one year to the next (Fig. 3). Silver perch initiated their calling season in the late winter (February/March) and finished in the late spring (June) (Fig. 3). Black drum had the shortest calling season that lasted from March to early May (Fig. 3). Spotted seatrout had the longest spawning season, with acoustic activity present between March and September (Fig. 3). Red drum started to call in August, increased acoustic activity in September and October, and decreased in November (Fig. 3).

3.2. Factors that influenced calling intensity scores

Temperature, day/night, location, year, lunar phase, and tidal phase were factors that significantly influenced calling intensity scores (i.e. categories 0, 1, 2, or 3) of black drum, silver perch, spotted seatrout, and red drum (Fig. 4; Table S1 in the Supplement

at www.int-res.com/articles/suppl/m693p001_supp/). Temperature had the most significant effect on the calling of fish species that were acoustically active in the spring (i.e. black drum, silver perch, and spotted seatrout) (Fig. 4A–C; Table S1, $p < 0.01$). Within the respective fish-spawning season, we detected an increase in calling intensity scores of black drum, silver perch, and spotted seatrout when the water temperature increased. Interestingly, for red drum, a fish species that started spawning in late summer and continued into early fall, temperature had a lower importance (Fig. 4D; Table S1, $p < 0.01$). In addition to temperature, day/night factor had a high importance for silver perch and spotted seatrout calling and chorusing (Fig. 4B & C; Table S1, $p < 0.01$). These fish species exhibited very distinct calling and chorusing patterns with increasing activity shortly before sunset and high activity during the night. Day and night had a lower importance for black drum and red drum, which tended to call and chorus in the late afternoon into the night (Fig. 4A & D; Table S1, $p < 0.01$). We also tested the importance of location, which influenced calling patterns of black drum, and calling and chorusing patterns of silver perch and red drum but not spotted seatrout (Fig. 4; Table S1, $p < 0.01$). Spotted seatrout calls and choruses were detected at all 3 stations in the May River (i.e. 9M, 14M, and 37M); calls of black drum, calls and choruses of silver perch, and calls and choruses of red drum were predominant at Stn 37M (i.e. closest to the mouth of the May River; Fig. 3).

We investigated the calling patterns within this 6 yr span and discovered that the total number of hours calling and chorusing (i.e. intensity scores of 1, 2, and 3 combined) for silver perch was highest in 2017 and lowest in 2014 and 2018 (Fig. S1). Calls of black drum only occurred at Stn 37M, and choruses did not occur. There was an indication that calling of black drum decreased as the study progressed. We recorded the most calling of black drum in 2013 and 2014 and the least in 2016 and 2018 (Fig. S1). Spotted seatrout calling and chorusing was the longest in 2016 and the shortest in 2014 (Fig. S1). Chorusing of red drum only occurred at Stn 37M. Red drum calling and chorusing occurred for the longest period in 2018 and the shortest in 2013 and 2014 (Fig. S1).

Tidal and lunar phases influenced calling intensity scores of all fish species (Fig. 4; Table S1, $p < 0.01$). We observed an increase in calling and chorusing during the first and third quarters of the lunar cycle as compared to the new and full moons. We reported an increase in calling and chorusing of silver perch, spotted seatrout, and red drum on the flood tide, followed by

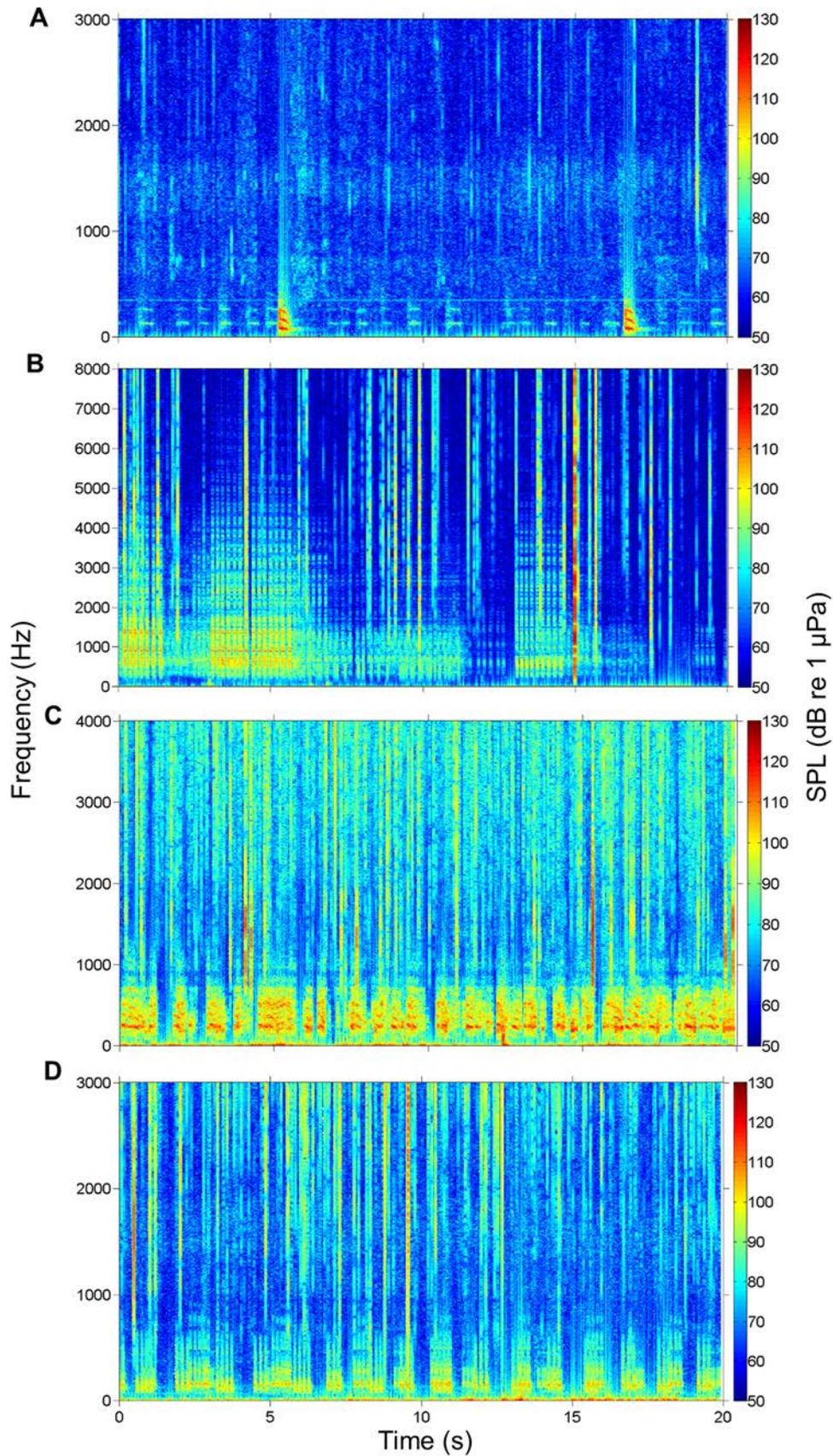


Fig. 2. Spectrograms of identified fish calls detected in the May River estuary and discussed in this study: (A) black drum *Pogonias cromis*, (B) silver perch *Bairdiella chrysoura*, (C) spotted seatrout *Cynoscion nebulosus*, and (D) red drum *Sciaenops ocellatus*. Spectrograms were created in Matlab with a sample rate of 80 kHz and 256-point FFT, using a rectangular window with length of 0.1 s and overlap of 90% from original 2 min wav files

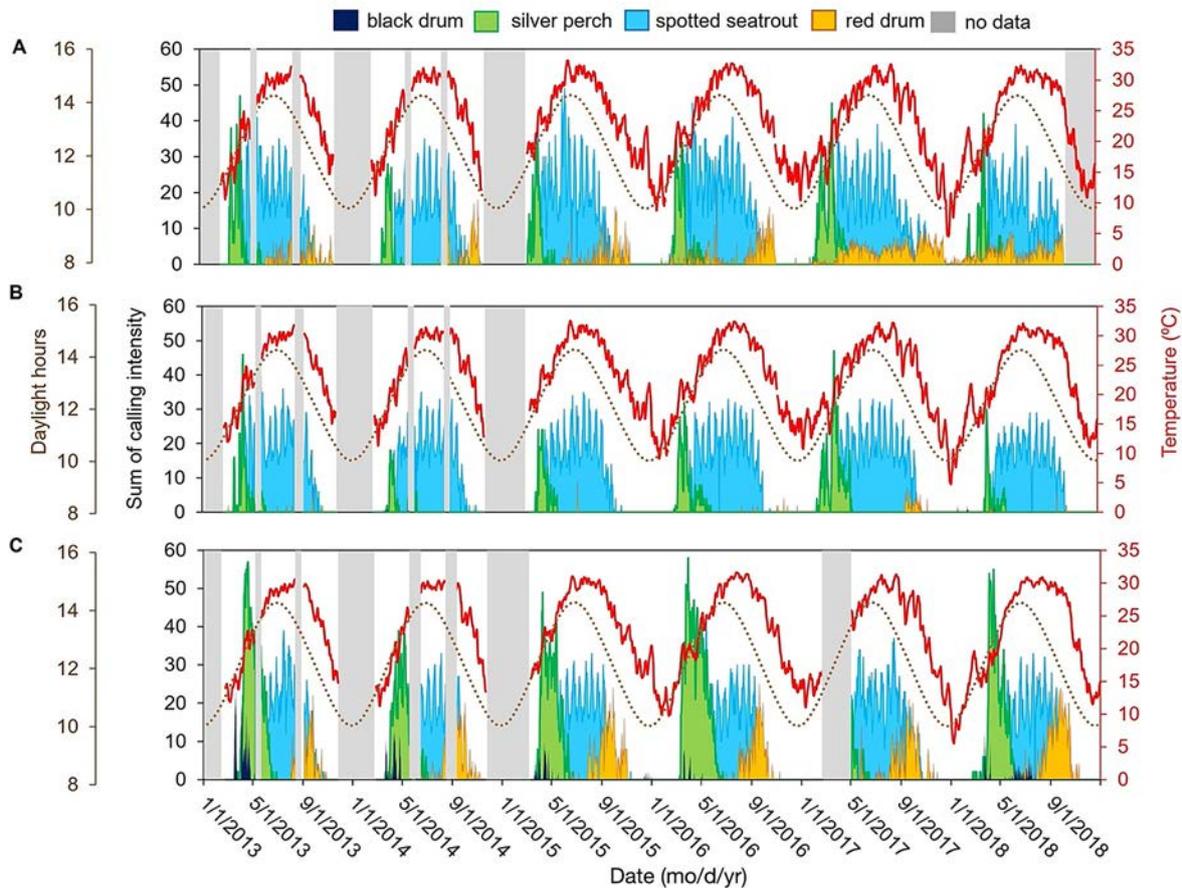


Fig. 3. Time series of fish sound production in the May River estuary. Sum of calling intensity scores (i.e. categories 0, 1, 2, and 3) from noon to noon of the next day at Stns (A) 9M, (B) 14M, and (C) 37M. Also shown are water temperature (red line) and hours of daylight (brown dotted line). Gaps in data (gray boxes) correspond to breaks between deployments due to maintenance of equipment or equipment malfunction. From 2013 to 2015, we did not deploy passive acoustic recorders during the winter. DSG-Ocean recorders malfunctioned or were scheduled improperly on 2 occasions, once in the spring of 2017 at Stn 37M and once in the fall/winter of 2018 at Stn 9M

the rising and falling tides, and the least on the ebb tide (Table S1, $p < 0.01$). We observed similar tidal patterns for black drum calling (Table S1, $p < 0.01$).

3.3. Shifts in calling timelines

We detected shifts in the start and end dates of acoustic activity (i.e. calling and chorusing combined) among the 6 sampling years for silver perch, spotted seatrout, and red drum (see Figs. 3 & 5). The calling season of silver perch shifted 32 d earlier in 2017 (10 February) compared to 2013 (14 March) at Stn 9M (Fig. 5A). Interestingly, in 2017 at Stn 9M, we detected the longest calling season for silver perch. In 2018, the start of the calling season for silver perch was detected much later (2 April) at Stns 9M and 14M than in other years due to cooler winter and spring temperatures (Fig. 5A–C,H). Chorusing sea-

sons followed the same patterns, and during each year, we detected the first and last chorusing events of silver perch when water temperature reached ~ 19 and $\sim 25^{\circ}\text{C}$, respectively. Spotted seatrout started calling the earliest in 2016 at Stns 9M and 14M, when we also recorded the longest calling seasons (Fig. 5E–G). For spotted seatrout, the start of the calling season in 2016 was detected 21 d earlier (28 March) than in 2013 (10 April) at Stn 9M. Calling in 2018 started on 15 April (similar to 2013), and the total calling activity was shorter than in other years due to cooler spring water temperatures (Fig. 5E–H). Chorusing seasons followed the same patterns, and between 2013 and 2018, we detected the first and last chorusing events of spotted seatrout when the water temperature reached ~ 22 and $\sim 28^{\circ}\text{C}$, respectively (6 yr average at all 3 stations). The calling and chorusing seasons for red drum started later in 2013 and 2017 and earlier in 2014 and 2018 (Fig. 5D). We detected the first chorus-

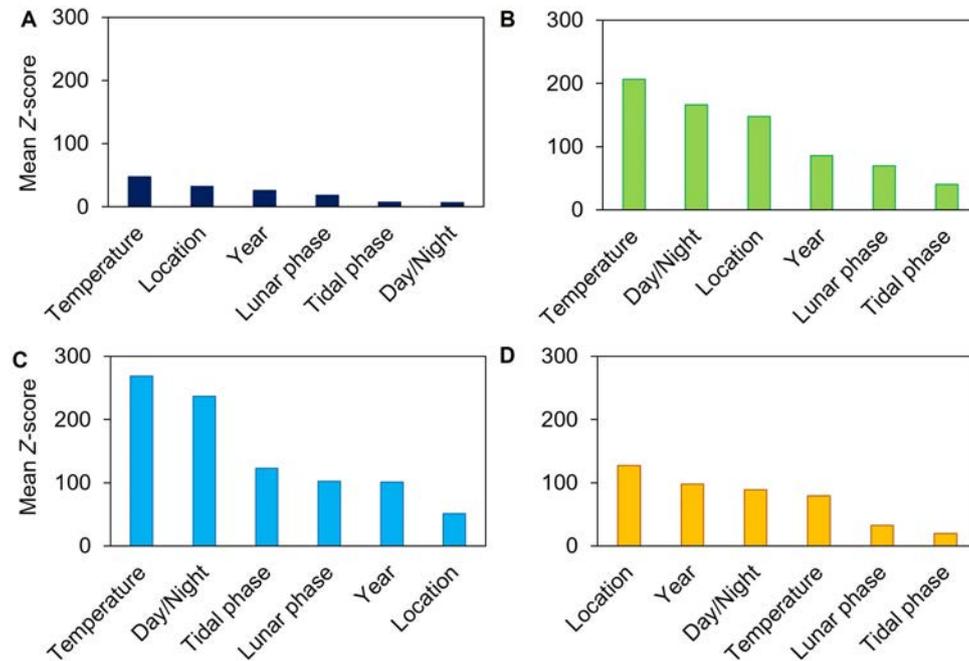


Fig. 4. Influence of environmental variables on fish calling intensity scores (i.e. 0, 1, 2, or 3). Results of the Boruta wrapper algorithm based on a random forest model that tested the significance (mean Z-score) of specific variables on acoustic activity of (A) black drum, (B) silver perch, (C) spotted seatrout, and (D) red drum within their specific calling season. All factors were significant at $p < 0.01$

ing event of red drum when the water temperature cooled to $\sim 29^{\circ}\text{C}$ (after high summer temperatures) and the last chorusing event when the water temperature reached $\sim 26^{\circ}\text{C}$ in the late fall (6 yr average at Stn 37M). In addition, calling (i.e. intensity scores of 1 and 2) of black drum occurred earlier in 2013 and 2016 and later in 2014 and 2018. We did not detect any black drum choruses during acoustic analysis.

3.4. Correlations between fish calling and YOY

Over the entire seining period between 2016 and 2018, we caught a total of 4 black drum, 18 126 silver perch, 281 spotted seatrout, and 215 red drum YOY (Fig. 6). During 3 yr of sampling, we caught silver perch with lengths of 5–185 mm, spotted seatrout 7–145 mm, and red drum 9–70 mm (Fig. 6; Figs. S2–S4). In 2016, 2017, and 2018, the average lengths of silver perch were 25.12, 50.25, and 54.82 mm; spotted seatrout 42.81, 42.06, and 46.01 mm; and red drum 21.25, 30.90, and 25.69 mm, respectively (Figs. S2–S4). These average lengths represent age 0 fish and predominately YOY as the frequency distributions highlight (Figs. S2–S4). The growth rates of YOY silver perch, spotted seatrout, and red drum were highest in 2017 and lowest in 2016, indicating that biotic/abiotic factors could have influenced growth (Figs. S5–S7).

The appearance of YOY in our haul seines occurred approximately 1 mo after we detected the first chorusing events of silver perch, spotted seatrout, and red drum. Silver perch started chorusing in March/April and were caught between April/May and September/October with the highest abundance in May, April, and June in 2016, 2017, and 2018, respectively (Fig. 7A). Spotted seatrout started chorusing in April, and YOY were caught between May and December, with the highest abundance in August and September in all years (Fig. 7B). Red drum started chorusing at the end of August/beginning of September, and YOY were caught between October and December, with the highest abundance in October and November in all years (Fig. 7C).

We investigated length data and growth curves, and calculated the estimated times of larval hatching (Figs. S5–S7). Hatching occurs approximately 36, 18, and 24 h after fertilization of the egg for silver perch, spotted seatrout, and red drum, respectively (Holt et al. 1985). In general, the estimated time of larval hatching in the May River corresponded closely to the date when chorusing was first detected for silver perch, spotted seatrout, and red drum. However, errors in these estimates are possible based on additional factors such as individuals hatching at different times during the spawning season, several spawning events during one season,

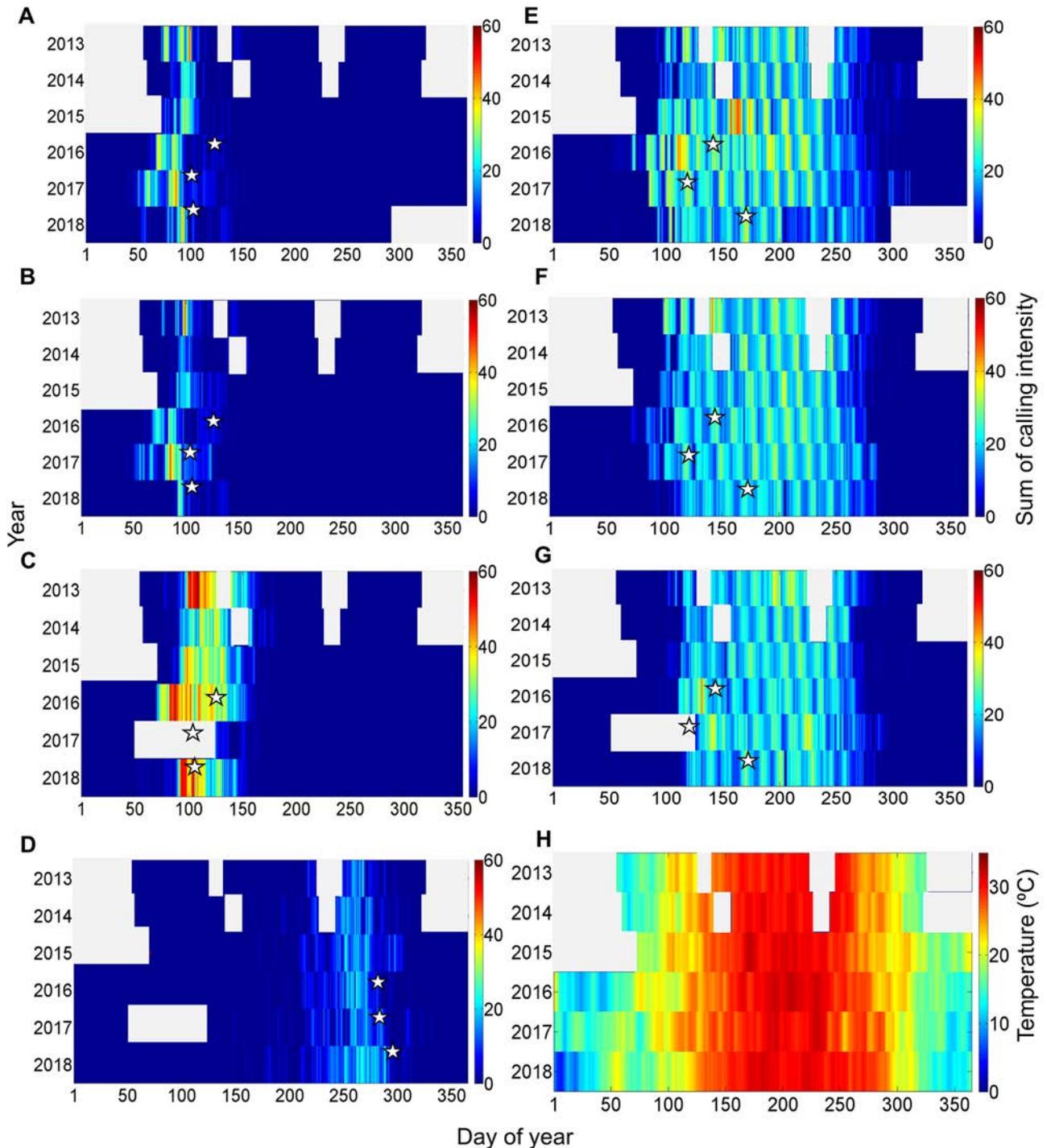


Fig. 5. Heat maps representing the sum of calling intensity scores (i.e. categories 0, 1, 2, and 3) and water temperature between 2013 and 2018. Sum of intensity scores between 2013 and 2018 versus day of the year for silver perch at Stns (A) 9M, (B) 14M, and (C) 37M; for red drum at Stn (D) 37M; and spotted seatrout at Stns (E) 9M, (F) 14M, and (G) 37M. Stars indicate the first appearance of young-of-the-year observed in haul seines in 2016, 2017, and 2018. (H) Water temperature versus day of the year between 2013 and 2018 at Stn 14M. Gaps in data (white boxes) correspond to breaks between deployments due to maintenance of equipment or equipment malfunction as described in Fig. 3

and different growth rates during the spawning season (i.e. due to environmental parameters and food availability).

We detected shifts in the seasonal appearance of YOY for silver perch, spotted seatrout, and red drum. Silver perch were first caught in our seine nets on



Fig. 6. Young-of-the-year caught in the May River estuary. (A) Black drum, (B) silver perch, (C) spotted seatrout, and (D) red drum collected in haul seines between 2016 and 2018

5 May, 25 April, and 24 April; spotted seatrout on 25 May, 11 May, and 17 June; and red drum on 3 October, 3 October, and 18 October in 2016, 2017, and 2018, respectively (Fig. 5A–G; Fig. S8). Generally, the seasonal shifts in YOY appearance correlated with the seasonal shifts in calling and chorusing for silver perch, spotted seatrout, and red drum and followed the temperature patterns of the estuary (Figs. 5 & 7; Fig. S8).

We found positive relationships between the total percentages of hours chorusing per year and corresponding mean YOY abundance of silver perch and spotted seatrout caught in seines at Stns 9M and 14M (Fig. 8). During the spring of 2017, silver perch chorused for the longest period over the 3 yr, and we collected the highest abundance of YOY during this year (Fig. 8A). We observed similar patterns in the spring and summer of 2016 for spotted seatrout (Fig. 8B) and in the fall of 2018 for red drum (Fig. 8C). Of the 3 years monitored, we recorded the highest mean water temperature in 2017, then in 2016, and the lowest in 2018 across all 3 stations (Fig. 8). During 2016 and 2017, fish species that began spawning in the spring (i.e. silver perch and spotted seatrout) called earlier and exhibited longer chorusing seasons, and the abundance of YOY was higher than in

2018, which exhibited cooler spring temperatures (Fig. 8A,B). However, lower temperatures in 2018 led to a higher percentage of hours chorusing and a higher abundance of red drum YOY as compared to the patterns observed in 2016 and 2017 (Fig. 8C).

4. DISCUSSION

One of the main goals of this study was to determine how varying water temperature patterns from one year to the next affected spawning potential, which was measured through chorusing hours and related to YOY abundance. We demonstrated that chorusing of silver perch, spotted seatrout, and red drum correlated with seasonal abundance of YOY. Spatially, we detected the most sound-producing fish species at Stn 37M (i.e. the mouth of the May River). The fish soundscape exhibited distinct temporal patterns that followed day/night, tidal, lunar, and seasonal time scales. We showed that, for spring-spawning fishes (i.e. silver perch and spotted seatrout), temperature was the major factor initiating the onset of chorusing, with warmer temperatures leading to an earlier and more protracted spawning

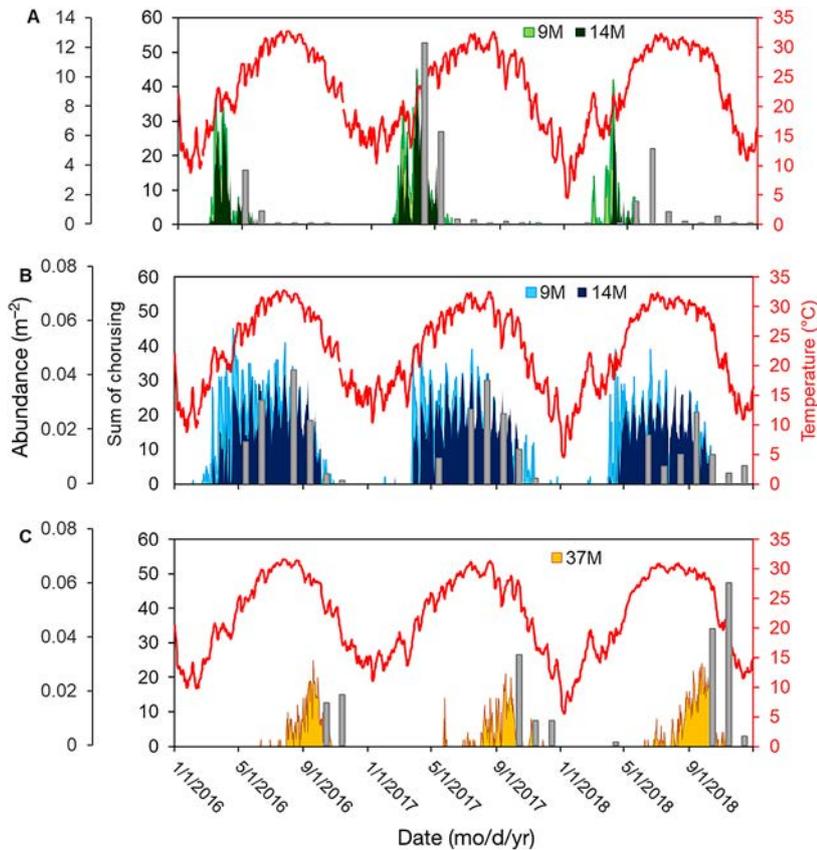


Fig. 7. Seasonal patterns of fish chorusing and young-of-the-year abundance in the May River estuary. Sum of calling intensity scores (i.e. category 3 that represents chorusing) from noon to noon of the next day with mean monthly abundance m^{-2} (gray bars) for (A) silver perch and (B) spotted seatrout at Stns 9M and 14M, and for (C) red drum and at Stn 37M. Red line = water temperature. Note that scales of abundance are species specific

season. Inversely, cooler temperatures during late summer/fall led to earlier and longer spawning seasons for red drum, a fall spawning species. In addition, we found positive relationships between the duration of the chorusing season and YOY abundance. Longer seasonal episodes of chorusing correlated with higher YOY abundance of silver perch, spotted seatrout, and red drum.

4.1. Year-to-year patterns of fish calling

Tracking fish sounds can help in predicting long-term presence/absence of species, and more importantly, monitoring soundscapes can track fish spawning activity (e.g. Montie et al. 2015, Parsons et al. 2016, Monczak et al. 2017). In our study, we documented the acoustic patterns of 4 fish species during 6 continuous years; we observed that their calling patterns were persistent from one year to the next,

and that environmental variables influenced calling and chorusing. Similar to other studies, we observed that location, temperature, day/night, year, and lunar and tidal cycles significantly influenced calling and chorusing (Ricci et al. 2016, Caiger et al. 2020, Wirth & Warren 2020). We concluded that locations within larger bodies of water that were deeper and exhibited fewer fluctuations in environmental parameters (e.g. salinity and temperature) had higher species diversity (i.e. Stn 37M). In agreement with other studies, we found that the sounds of soniferous fish species like black drum and red drum occurred in deeper locations with higher salinity (e.g. Saucier & Baltz 1993, Lowerre-Barbieri et al. 2008). In addition, increasing temperatures cued calling and chorusing events in spring-spawning species (i.e. black drum, silver perch, spotted seatrout), and falling temperatures stimulated production of acoustic signals in autumn-spawning fish (i.e. red drum) (Pankhurst & Munday 2011, Rice et al. 2016, Monczak et al. 2020). Moreover, circadian, tidal, and lunar cycles played an important role in duration and frequency of calling and chorusing of all fish species (Monczak et al. 2017).

4.2. Phenology of fish calling and water temperature

Monitoring biological processes using sound can provide information on the timing of recurring phenomena (e.g. migration, spawning, and/or appearance), and long-term monitoring of this timing can be used to help determine any shifts in these biological processes (Lieth 1974). Over the past few decades, studies have reported shifts in the cyclic nature of biological events like migration, breeding, and spawning (Brown et al. 1999, Walther et al. 2002, Root et al. 2003). Those changes were first detected using traditional methods (e.g. visual surveys); however, with advances in passive acoustics, some of these processes can now be monitored more efficiently (Buxton et al. 2016). During our baseline studies conducted in 2013, we reported the exact days of the onset of the calling and chorusing seasons for silver perch, spotted seatrout, and red drum (Monczak

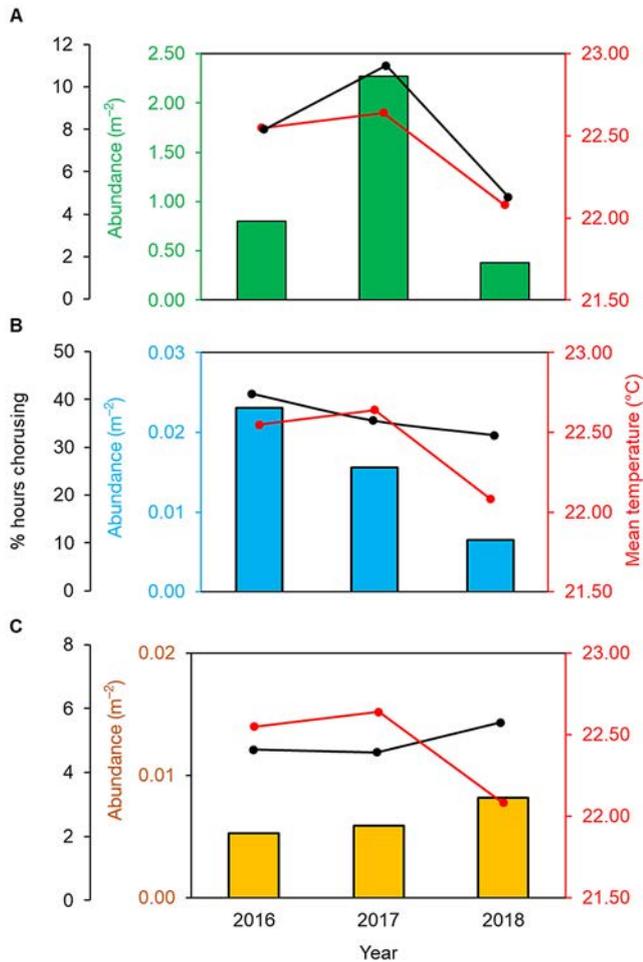


Fig. 8. Comparison between the percentage (%) of hours chorusing, young-of-the-year (YOY) abundance, and temperature in the May River estuary. Mean yearly YOY abundance m^{-2} of (A) silver perch and (B) spotted seatrout in the May River with corresponding total % hours chorusing (black line), and mean water temperature (red line) at Stns 9M and 14M. Mean yearly YOY abundance m^{-2} of (C) red drum with corresponding total % hours chorusing (black line), and mean water temperature (red line) at Stn 37M. Note that scales of abundance and % hours chorusing are species specific

et al. 2017). In the current study, we compared the baseline 2013 study to our multi-year 2013–2018 data set. The most impactful finding was that the start date of the acoustic seasons (i.e. first calling and chorusing events) for silver perch and spotted seatrout (i.e. spring spawners) shifted to an earlier timeframe, while the start date for red drum (i.e. fall spawner) shifted to a later date. Our findings show that these shifts correlated with elevated water temperatures during spring/fall, respectively.

Studies have shown that temperature plays an important role in initiating the spawning seasons of certain species by stimulating gonadal maturation, which leads to an increase in courtship calls (e.g.

McQueen & Marshall 2017). In fish, birds, and amphibians, the earlier detection of spring breeding occurs during warmer winters and springs (e.g. Brown et al. 1999, Fincham et al. 2013, Benard 2015). This earlier occurrence of biological processes linked to warmer winter/spring temperatures can have multiple consequences for individuals and populations (Benard 2015). Shifts in spawning events could lead to a trophic mismatch, which could affect the reproductive output of spawning (e.g. egg quality, larval survival, size and abundance of YOY, and year-class strength) (Asch et al. 2019).

4.3. Fish chorusing correlates with YOY appearance and abundance

During our study, we detected the appearance of YOY in the estuary approximately 1 mo after we detected chorusing of silver perch, spotted seatrout, and red drum. We detected several calls of black drum, but we did not detect chorusing during acoustic analysis, which could explain why we only caught 4 YOY of this species (Locascio & Mann 2011). The approximate timelines of larval hatching corresponded closely to the timelines of when chorusing first occurred for silver perch, spotted seatrout, and red drum. This correlation between the initiation of the chorusing season and YOY appearance in the estuary suggested that sound production was closely associated with spawning events. These findings correspond to the results reported in other studies that demonstrated an association between sound production and spawning through the simultaneous collection of passive acoustic data and eggs (e.g. Mok & Gilmore 1983, Saucier & Baltz 1993, Luczkovich et al. 1999). For example, Luczkovich et al. (1999) reported that the abundance of early-stage sciaenid-type eggs was highly correlated with maximum sound pressure levels in weakfish *Cynoscion regalis*. In addition, captive studies with red drum and spotted seatrout observed positive relationships between the amount of calling, call duration, and the number of pulses in a call, and the number of eggs detected in tanks of spawning fish (Montie et al. 2016, 2017). Substantiating these types of relationships is necessary to assess the utility of passive acoustics in monitoring fish reproduction in the wild. However, these data are challenging to obtain because it is difficult to ensure that the eggs and/or larvae collected are from the same population of fish that are producing sound (Locascio et al. 2012). In addition, the number of eggs/larvae collected in the field can

be influenced by external factors including efficiency of sampling, predator activity, water movements (currents and tides), and disease that could all affect estimates of spawning activity (Locascio et al. 2012).

In our studies, we showed a positive relationship between the seasonal duration of courtship sounds (i.e. chorusing) and YOY abundance of silver perch, spotted seatrout, and red drum. In the years that we recorded earlier and more protracted chorusing seasons, we collected higher abundances of YOY. It is possible that longer courtship seasons could result in larger yields of egg biomass and lead to higher reproductive output and YOY abundance (Guest & Lasswell 1978, Mok & Gilmore 1983). However, YOY abundance is a tertiary, indirect measure of reproductive output that follows egg and larval stages. Limitations in connecting chorusing durations to YOY abundance as a proxy of reproductive output include the drifting of eggs/larvae from the original spawning sites, predation, natural mortality, and disease (Locascio et al. 2012).

Nonetheless, evidence does exist that these fish exhibit behaviors to enhance retention of early life stages in nursery habitats such as tidal river estuaries. Silver perch, spotted seatrout, and red drum spawn in estuaries and/or near the mouth; fertilized eggs float, and eggs of these species quickly hatch 18–30 h after fertilization (Powles 1980, Holt et al. 1981, McMichael & Peters 1989, Saucier et al. 1992, Grammar et al. 2009). Based upon observing the behavior of red drum, newly hatched larvae are negatively buoyant and drift downward headfirst (Holt et al. 1981). Three days after hatching, red drum swim in a horizontal position and spend more time swimming (Holt et al. 1981). By Day 4, the swim bladder develops and red drum actively search for and attack prey (Holt et al. 1981). It is obvious that eggs and newly hatched larvae are passive and drift from the original spawning location due to currents and tidal movements (Holt et al. 1981, McMichael & Peters 1989, Grammar et al. 2009). However, we discovered that fish chorused more frequently on the high and rising tide, providing some evidence that this type of spawning behavior may retain eggs within the May River estuary.

It takes about 30 d for silver perch, spotted seatrout, and red drum to reach lengths of 15–20 mm, which is the approximate size when we started catching this cohort in our seines (Powles 1980, Holt et al. 1981, McMichael & Peters 1989, Saucier et al. 1992, Grammar et al. 2009). Many behavioral mechanisms of active, larval fishes can facilitate retention in nursery habitats rather than advection seaward

(e.g. Kimmerer et al. 1998). A classic and well-studied behavior is vertical migration, where in estuaries with semidiurnal or diurnal tidal cycles, larval fish migrate upward on nightly flood tides and downward into lower velocity flow during daytime ebbs (Weinstein et al. 1980, Jenkins et al. 1998, Kimmerer et al. 1998, Bennett et al. 2002). To limit the complications associated with dispersal from a spawning location, we did follow a conservative approach and treated the May River (which is 22 km long) as 1 nursery habitat. We compared YOY abundance to the total number of hours chorusing of the entire tidal river (i.e. Stns 9M, 14M, and 37M combined) rather than performing correlations at each station. Regardless, limitations associated with egg/larval dispersal, predation, natural mortality, and disease may affect the relationship between chorusing durations and YOY abundance.

We found that spring water temperature influenced initiation and duration of the calling and chorusing seasons. In 2016 and 2017, we recorded the highest winter/spring water temperatures, an earlier start, and longer calling and chorusing seasons of silver perch and spotted seatrout, and a higher YOY abundance. Conversely, during the winter and spring of 2018, we recorded the lowest water temperature and delayed start and shorter acoustic seasons of silver perch and spotted seatrout, and the lowest abundance of YOY. Studies have shown that temperatures below 5°C can cause higher mortality of spotted seatrout (175–220 mm), which could explain why we had the lowest YOY abundance in 2018 (Anweiler et al. 2014).

Climate variability and change may affect fish acoustic activity and cause shifts in spawning seasons and reproductive output, which may lead to ecosystem imbalance by limiting food sources, creating trophic mismatch, and affecting fish abundance and distribution (Edwards & Richardson 2004, Carter et al. 2018, VanCompernelle et al. 2019). Tracking inter-annual variability in courtship sounds may be helpful in fishery management and understanding how climate variability affects populations of soniferous fish species. Shifts in initiation and termination of calling seasons and changes in their duration could lead to changes in seasonal egg yields and may result in a stronger or weaker year class. In the future, this type of acoustic data could be compared to long-term abundance samples collected by the South Carolina Department of Natural Resources (e.g. electrofishing, trammel net, estuarine trawl, and longline surveys). Other factors influence juvenile fish abundance (e.g. mortality, competition, and anthropogenic

stressors); however, monitoring estuarine soundscapes at a high temporal resolution and measuring fish acoustic activity could be, in the future, a reliable indicator of spawning potential. This approach allows the ability to eavesdrop on fish courtships sounds, which may change rapidly or gradually in response to environmental changes and human impacts, thus providing a measure of resilience or shifting baselines in a globally changing environment (e.g. Clark et al. 2009, Mann et al. 2010, Slabbekoorn et al. 2010).

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