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ARTICLE

Effects of Cold Winters on the Genetic Diversity of an Estuarine Fish, the Spotted Seatrout

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Abstract

Spotted Seatrout *Cynoscion nebulosus* are recreationally important fish that have been harvested in South Carolina for centuries. The Spotted Seatrout in South Carolina suffered substantial declines in estuarine abundance during the cold winters of 2000, 2009, and 2010, when water temperatures dropped below their tolerance threshold. As these population declines may result in genetic bottlenecks and their repetitive occurrence over a short timescale could reduce the population's adaptive potential, we estimated the genetic diversity and effective population size (N_e) of the Charleston Harbor Spotted Seatrout population at six time points related to recent cold winters using a suite of 13 microsatellite markers. Grouping individuals by year-class (fish spawned in the same year) was the most appropriate and effective method for measuring interannual fluctuations in observed and expected heterozygosity and allelic richness, superior to partitioning fish by collection year. The genetic diversity of Spotted Seatrout was significantly influenced by catch per unit effort, although only minor changes were observed and N_e remained high. Short overlapping generations appear to allow Spotted Seatrout to genetically recover during population growth and maintain moderate levels of genetic diversity.

Fish have long been harvested from the world's oceans as a food resource, and in recent years the overexploitation of certain fish stocks has led to severe population declines or fishery collapses (Myers et al. 1995; Hutchings 2000). Although overfishing is a leading cause of declines in many fish populations, climatic variation can also exert a strong influence on fish population dynamics and have effects that are independent of or synergistic with overexploitation (Clark et al. 2003; Harley and Rogers-Bennett 2004; Tolimieri and Levin 2005; Eero et al. 2011). Therefore, fisheries managers need to consider the effects of climate in their regulatory strategies (Perry et al. 2010; Planque et al. 2010). With complex anthropogenic and environmental interactions driving fish population dynamics, informed, science-based management is essential to the recovery of depleted fish stocks (Botsford et al. 1997; Beddington et al. 2007). Thus, it is critical to understand not only the population dynamics of fish stocks but also how significant declines in abundance affect the health and resilience of the remaining individuals within a population.

Spotted Seatrout *Cynoscion nebulosus* is an estuarine resident that ranges from Cape Cod, Massachusetts, in the western Atlantic Ocean to Campeche, Mexico, in the southern Gulf of Mexico (Welsh and Breder 1923; Tabb 1966). The Spotted Seatrout is an important recreational species throughout its

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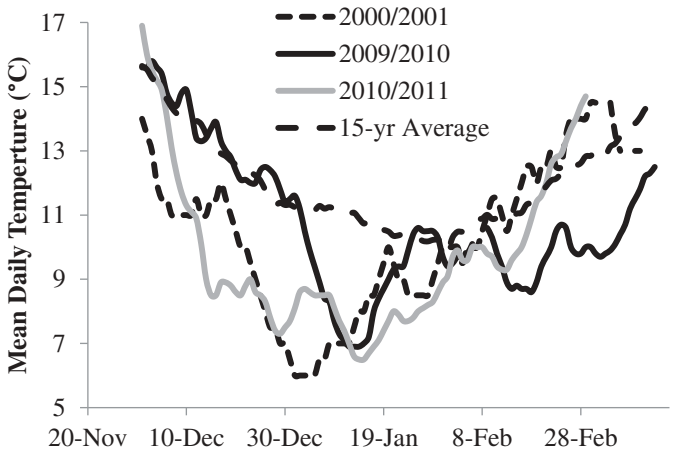


FIGURE 1. Mean daily water temperatures at the Customs House in Charleston Harbor during extremely cold winters and the 15-year average daily water temperatures calculated as the means of all daily water temperatures for those dates from 1996 to 2011.

range, and in South Carolina an estimated mean of 212,000 fish (120 metric tons) have been harvested annually from 1981 to 2010 (National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, Maryland, personal communication). In recent years, below-average estuarine water temperatures during cold winters in South Carolina have caused population declines among Spotted Seatrout (Figures 1, 2); however, Spotted Seatrout have continued to support a strong recreational fishery due to intermittent mild winters and regulatory changes including a decrease in the bag limit in 1998 and an increase in the minimum size limit in 2007. Without prudent management, the repetitive occurrence of cold winters in the past decade may have made it difficult for Spotted Seatrout populations to sustain high numbers in the face of fishing pressure.

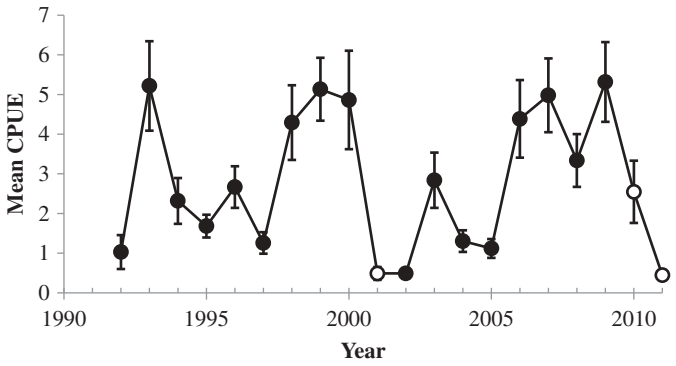


FIGURE 2. Mean CPUE (number per trammel net haul) of Spotted Seatrout in SCDNR's trammel net surveys in the Charleston Harbor system during the first quarter of each year. Open circles indicate sampling years immediately following cold winters; error bars = SEs.

Spotted Seatrout routinely experience large fluctuations in physical water characteristics, including temperature, salinity, dissolved oxygen, and pH (Hubertz and Cahoon 1999). For the majority of these parameters, Spotted Seatrout show a wide range of physiological tolerances and are likely capable of moving to areas within estuaries that are within their tolerable ranges (Tabb 1966). When severe winter cold fronts move along the southeastern U.S. coast, strong winds and falling air temperatures promote the mixing of estuarine waters, which can cause a rapid drop in water temperature in the shallow estuarine habitats where Spotted Seatrout are commonly found, including oyster reefs, marsh grass, and tidal creeks. While climate change does predict an overall trend of warming temperatures, models also predict greater temperature variability and extremes as well as an increase in extreme precipitation events (Kharin et al. 2013), which will promote rapid cooling of shallow estuarine waters during the winter months. Low, falling temperatures immobilize Spotted Seatrout, making it difficult for them to escape these shallow-water habitats to find warmwater refugia in deeper areas of the estuary (Tabb 1958). Based on historical environmental data, Spotted Seatrout populations in Florida experience substantial mortality when water temperatures fall below 7.2°C for longer than 24 h (Tabb 1958). Current evaluation of the cold temperature tolerance of Spotted Seatrout in South Carolina indicates that the threshold is actually much lower than 7.2°C; Spotted Seatrout experienced mortality at ~3°C, depending on the length of exposure (Anweiler 2014). While temperature drops of this magnitude are uncommon in deep channels, temperatures in the shallow tidal creeks that Spotted Seatrout commonly inhabit regularly drop below 5°C during extremely cold winters.

A relationship between cold winter events and decreased abundance of Spotted Seatrout in South Carolina has been documented over the past decade. For example, water temperatures in Charleston Harbor were 5.2°C below their average in the winter of 2000–2001 (U.S. Geological Survey 2012; Figure 1), with subsequent first quarter 2001 catch rates of Spotted Seatrout decreasing to ~10% of the level recorded the previous year in the South Carolina Department of Natural Resources' (SCDNR) trammel net survey of estuarine fish populations (Figure 2). Surface water temperatures dropped below the apparent tolerance of Spotted Seatrout again in January 2010, when they were 4.2°C below the average for a 3-week period, with a resulting decrease in catch. A cold event similar to that of 2000–2001 occurred during 2010–2011, when the water temperature fell to 4.7°C below average, resulting in decreased catch rates during the first quarter of 2011 and representing the second consecutive cold winter experienced by Spotted Seatrout, perhaps confounding the mortality effects of a single cold-water event.

A substantial reduction in population size can result in genetic bottlenecks, or a loss of genetic diversity (Nei et al. 1975). High genetic diversity in populations is desirable, as it provides a population greater adaptive potential and therefore a better

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chance of survival in a dynamic environment (Frankham 2005). Additionally, the occurrence of short repetitive population bottlenecks (similar to those that have occurred in Spotted Seatrout) often results in a lower probability of retaining alleles than is the case with long-term bottlenecks (England et al. 2003). Therefore, the recent reductions in the abundance of Charleston Harbor Spotted Seatrout could be detrimental to the population's genetic diversity and genetic effective population size (N_e).

To understand how the recent population declines have affected the genetic health of Spotted Seatrout, the genetic diversity of Charleston Harbor Spotted Seatrout was evaluated temporally with specific attention to years surrounding substantial cold winter events. Assessing the genetic diversity of Spotted Seatrout in response to the recent cold winters will allow evaluation of their genetic response and potential recovery from large population declines that they might encounter in the future. Finally, the influence of cold winters on N_e was evaluated to improve our understanding of Spotted Seatrout population dynamics. We hypothesized that the genetic diversity and N_e of Spotted Seatrout would decrease immediately following a reduction in their abundance associated with cold water temperatures. An increase in genetic diversity over a relatively short time following a population reduction, or a constant genetic diversity throughout the entire time period, would indicate that Spotted Seatrout are capable of withstanding periodic population declines while maintaining high levels of genetic variation.

METHODS

Sample collection and study design.—Spotted Seatrout tissue samples were provided by the SCDNR's trammel net survey (n = 756) and recreational anglers using hook-and-line sampling (n = 146). The samples used in the present study were collected from the Charleston Harbor system (Charleston Harbor and the Ashley, Cooper, and Wando rivers) which exhibits high gene flow between the rivers and the harbor, resulting in no significant differences in genetic composition; therefore, the Charleston Harbor system represents a single population (O'Donnell et al. 2014). Although gene flow is apparent between the Charleston Harbor system and neighboring estuaries (O'Donnell et al. 2014), adult migration rates are low, with 95% of tagged Spotted Seatrout being recaptured within 31 km of their release location (J. Archambault, SCDNR, personal communication). While the Charleston Harbor system is not a closed population, adult migrants from neighboring estuaries (located ~55 km from Charleston Harbor) are believed to be rare. Additionally, O'Donnell et al. (2014) found that there were no significant differences in allele frequencies in Spotted Seatrout from five major estuaries in South Carolina and Georgia, suggesting that the limited migration from neighboring estuaries would have minimal influence on estimates of genetic diversity. Only samples acquired during the spawning season (April to September) were utilized in order to represent the reproductive pool of each year. Fin clips preserved in sarcosyl urea (1% sarcosyl, 8 M urea, 20 mM sodium phosphate, 1 mL EDTA of pH 6.8) were available from all fish collected in 2010 and later, while genetic tissues of fish collected prior to 2010 were recovered from the extracellular matrix of archived otoliths.

To assess genetic diversity and N_e temporally, specific collection years over the past decade were sampled (Table 1). The periods 2000–2001 and 2008–2010 were examined to determine the effect of a rapid reduction in abundance on the genetic diversity and N_e of Spotted Seatrout in Charleston Harbor. The years 2000 and 2008 were collection years immediately prior to a cold winter that induced mortality in Spotted Seatrout, while 2001 and 2010 were years in which samples were available immediately following a severe population decline. Selecting years that bookended population declines was intended to aid us in determining the effects of a decrease in population size on genetic diversity and N_e in Spotted Seatrout. Genetic diversity was assessed in 2011 to quantify the effects of two consecutive cold winters on the genetic diversity and N_e in Charleston Harbor. Samples from 2005 were also included in this study despite their not being directly associated with a population bottleneck. Spotted Seatrout population numbers showed a stable increase in the years following the population decrease from the cold winter of 2000–2001 winter; 2005 thus served as an intermediate time point between 2001 and 2008 from which the pattern and rate of change in diversity could be assessed.

In addition to assessing genetic diversity based on collection years, fish were assigned to a year-class (i.e., year of spawning) based on their ages as determined from their otoliths. Year-class assignments provided the opportunity to evaluate the reproductive output of each spawning year, which could capture greater interannual variability in genetic diversity. After initial data analyses showed support for the utility of samples grouped by year-class, additional genotyped individuals were incorporated into the temporal diversity evaluations to provide more time points in the later years (2011 and 2012 year-classes). Year-classes with <25 samples were

TABLE 1. Number of Spotted Seatrout samples from the Charleston Harbor system genotyped from each collection year.

Collection year	Number of samples
2000	160
2001	128
2005	98
2008	142
2010	82
2011	116

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TABLE 2. Number of Spotted Seatrout samples from the Charleston Harbor system genotyped from each year-class.

Year-class	Number of samples
1997	41
1998	52
1999	126
2000	59
2003	27
2004	73
2005	26
2006	62
2007	55
2009	72
2010	83
2011	53
2012	123

removed from further analyses, resulting in 13 year-classes ranging from 1997 to 2012 (Table 2).

DNA isolation.—DNA was isolated from fin clips preserved in sarcosyl urea using a metal beads isolation protocol. Magnetic metal beads (10 µL; Sera-mag) were mixed with 80 µL of 100% isopropanol and 50 µL of fin clip sample. After being incubated on a magnetic plate for 5 min, the solution was drained and the DNA-coated metal beads were washed five times with 100 µL of cold 70% ethanol. The samples were dried on the magnetic plate, DNA was eluted with 50 µL of 1× TE (10 mM tris, 1 mM EDTA), and the isolated DNA was transferred to a clean microfuge tube for long-term storage (−20°C).

DNA was isolated from otoliths according to a modified Wizard SV Genomic DNA Purification System protocol (Promega Corporation, Fitchburg, Wisconsin). Each otolith was placed in 200 µL of digestive solution comprised of nuclei lysis solution, 0.5 M EDTA, 20 mg/mL proteinase *K*, and RNase. After incubation for 15 h, the otolith was rinsed with 180 µL of lysis buffer and removed from the solution, allowing the lysis buffer to drain into the digestive solution. Manufacturer's instructions were followed until the final step, when DNA was eluted with 100 µL of 55°C nuclease-free water and transferred to a −20°C freezer for long-term storage.

Microsatellite genotyping.—For all samples, 13 microsatellites, multiplexed into three groups, were amplified using polymerase chain reaction (PCR). Multiplexed primers (M. Tringali, Florida Fish and Wildlife Commission, personal communication) were designed and optimized to amplify under identical reagent and cycling conditions based on Tringali's singleplex reactions. The forward primers in each pair were labeled with a WellRed fluorescent dye (Table 3). All amplifications occurred in 11-µL reaction volumes containing 1× HotMaster Buffer, 0.2 mM dNTPs (Fisher), 2.5 mM $MgCl_2$ (Fisher), 0.3 µM forward and reverse primers (Sigma), 0.03 U HotMaster *Taq* DNA polymerase, and ~5 ng DNA. All samples were amplified with two negative controls for each multiplex group to detect any contamination, and PCRs were performed using I-Cycler thermocyclers (Bio-Rad Laboratories, Hercules, California) using the following reaction profile: initial denaturing at 94°C for 2 min followed by 30 cycles of denaturing at 94°C for 30 s, annealing at 58°C for 1 min, and extension at 65°C for 1 min and final extension at 65°C for 1 h.

After DNA amplification, the PCR products were analyzed and genotyped using capillary gel electrophoresis. The DNA was denatured with formamide and supplemented with a size standard (400 bp; Beckman Coulter, Inc., Fullerton, California) for accurate fragment length analysis. Fragments were identified by their WellRed dye and separated by size on a CEQ 8000 (Beckman Coulter). The chromatograms were analyzed using the frag3/PA version 1 analysis algorithm to determine the size of the alleles at each locus. Two people independently scored the chromatograms using the CEQ 8000 Fragment Analysis Software; their scores were compared using Compare Spreadsheets software (Office Assistance LLC) to determine the degree of agreement. All samples genotyped at <11 loci were removed from any further analyses.

Marker validation.—Samples were independently evaluated by year-class for marker validation. All of the loci from each year-class were tested for deviations from Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using GenePop version 4.1 (Raymond and Rousset 1995) with the input parameters set to 100 batches of 5,000 iterations per batch with a 10,000 step burn-in. The probability of null alleles was calculated for all loci using Cervus 3.0.3 (Kalinowski et al. 2007). A sequential Bonferroni correction for simultaneous tests was used for all multiple comparisons (Rice 1989).

Genetic parameters.—The Microsoft Excel add-in Microsatellite Toolkit (Park 2001) was used in conjunction with Arlequin 3.11 (Excoffier et al. 2005) to produce summary statistics from the genotype data. A number of different indices were used to genetically characterize the Spotted Seatrout populations. The genetic diversity of each locus was characterized by calculating heterozygosity, the number of alleles, and the presence or absence of rare alleles. Arlequin and GenePop were used to calculate the number of alleles per locus (N_a), allelic size range, observed heterozygosity (H_O), expected heterozygosity (H_E; Nei 1987), and inbreeding coefficients (F_{IS}). FSTAT 2.9.3 (Goudet 1995) was used to calculate the allelic richness (A) for individual loci, and the R package (R Core Team 2012) program standArich (Alberto 2006) was used to calculate the allelic richness across all loci. In standArich, 75 individuals were randomly sampled without replacement 1,000 times from each collection year (when the data were partitioned by collection year), and 25 were randomly sampled without replacement 1,000 times from each year-class (when the data were partitioned by year-class). The mean number of alleles per locus and the variance were

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TABLE 3. Multiplexed microsatellite markers for Spotted Seatrout. The number of alleles per locus and the allelic size range are based on all project samples from the Charleston Harbor system. The forward primers in each primer pair were labeled with a fluorescent WellRed dye.

Multiplex group	Locus	Size range (bp)	CEQ dye	Motif	Primer concentration (nM)	Number of alleles
1	*Cneb31*	90–112	D3	$(CA)_8$	20.3	9
	Cneb07	116–132	D4	$(GT)_{12}$	50.7	8
	Cneb39	132–160	D3	$(CA)_{12}$	30.4	10
	Cneb37	159–197	D2	$(GA)_7$	162.2	12
	Cneb01	160–178	D4	$(CG)_3(CA)_{10}$	36.5	10
2	*Cneb22*	110–136	D2	$(TG)_{10}$	22.6	14
	Cneb33	119–161	D3	$(AC)_{16}$	34.0	17
	Cneb41	155–171	D2	$(TC)_4(CT)_3C(CT)_7$	226.4	7
	Cneb09	178–210	D4	$(CA)_{15}$	17.0	11
3	*Cneb35*	92–126	D2	$(CA)_{13}$	71.4	15
	Cneb24	110–144	D4	$(GA)_{10}$	42.9	16
	Cneb12	137–173	D2	$(TC)_{10}$	114.3	9
	Cneb04	164–190	D4	$(TG)_{18}(GA)_5$	71.4	13

calculated around those 1,000 replicated subsamples in standArich. The measure of variance around the replicated subsamples for each time point was more appropriate than the variance around the different loci (calculated in FSTAT), which is influenced by the level of polymorphism at each microsatellite marker. Therefore, standard errors (Figure 3) were calculated using the variance parameter calculated in standArich.

The N_e of Spotted Seatrout in Charleston Harbor was estimated at each of the collection years in relation to cold winters (Table 1). The software LDNe (Waples 2006) was used to calculate N_e at each time point; allele frequencies were set at default values (0.01, 0.02, and 0.05) and a random mating model was assumed. The program LDNe uses an LD-based model (Hill 1981) to calculate N_e at a single time point. The model was based on determining the level of LD between pairs of loci because nonrandom associations among unlinked loci are caused by genetic drift events. As biases in LD-based N_e estimates are minimized in populations with overlapping generations by randomly sampling the population's entire age structure, N_e estimates were calculated with data partitioned by collection year (Robinson and Moyer 2013). However, LDNe was also used to estimate the effective number of breeders (N_b) in each year-class of Spotted Seatrout (Table 2).

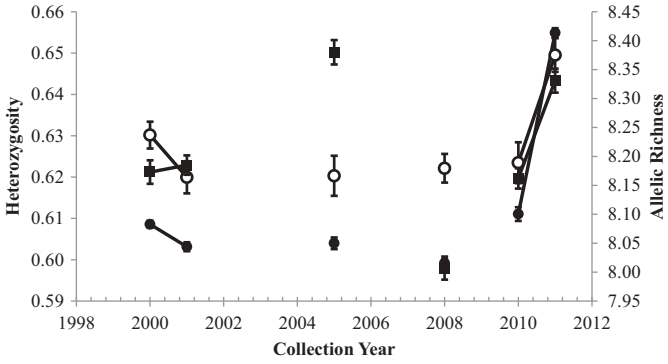


FIGURE 3. Observed heterozygosity (filled circles), expected heterozygosity (open circles), and allelic richness (squares) for Spotted Seatrout in the Charleston Harbor system for each collection year. Lines connect points in consecutive years; error bars = SEs.

The N_e of Spotted Seatrout in Charleston Harbor was also estimated using a two–time point temporal method that estimates the genetic drift between sequential year-classes; N_e was estimated at 10 time points between all sequential year-classes when genetic data were available (Table 2). Temporal estimates of N_e are often biased for organisms exhibiting overlapping generations, such as Spotted Seatrout. Therefore, the program GONe (Coombs et al. 2012) was used to estimate N_e because it incorporates a correction factor for overlapping generations (Jorde and Ryman 1995) based on age-specific survival and fecundity estimates. Estimates of N_e were calculated using 100 iterations of the correction factor, a calculated generation time, and equal male and female birth and survival rates. Age-specific survival was calculated from the SCDNR trammel net survey catch-at-age data in the Charleston Harbor system from 1992 to 2009, and age-specific fecundity values from Roumillat and Brouwer (2004) were used.

Potential influences of cold winters on genetic diversity.—Observed heterozygosity, expected heterozygosity, and allelic richness were used to describe the genetic diversity for each collection year and year-class in the Charleston Harbor system. The variance for observed heterozygosity was calculated according to Weir (1990 [equation 4.4]) and the variance for expected heterozygosity was calculated according to Nei (1987 [equation 8.8]), which were used to calculate the standard error values plotted (Figures 4, 5). Student's *t*-tests were used to test

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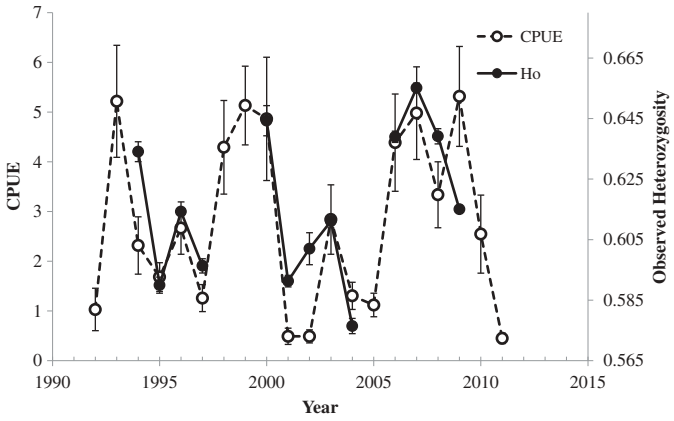


FIGURE 4. Mean CPUE of Spotted Seatrout in the Charleston Harbor system in the first quarter of every year and the observed heterozygosity of year-classes (adjusted) 3 years earlier (lag based on cross correlation analysis); error bars = SEs.

for significant differences in genetic diversity between consecutively sampled collection years and year-classes. Pairwise comparisons of R_{ST} (Arlequin) and exact tests for allelic frequency distributions performed with a Markov chain randomization method (1,000 dememorizations, 100 batches, and 5,000 iterations per batch; GenePop) were used to evaluate changes in genetic composition through time.

An index of the abundance of the Spotted Seatrout population in the Charleston Harbor system was derived using the arithmetic mean CPUE for Spotted Seatrout in the SCDNR trammel net survey during the first quarter of each year. The CPUE of each year was calculated as the total number of Spotted Seatrout captured in the Ashley River, Wando River, and Charleston Harbor from January to March divided by the number of trammel net sets in those strata during the same time period. Fish were sampled using a stratified random design from 1991 to 2011, with between 34 and 98 trammel sets being made per year during January–March (see Arnott et al. 2010 for more details).

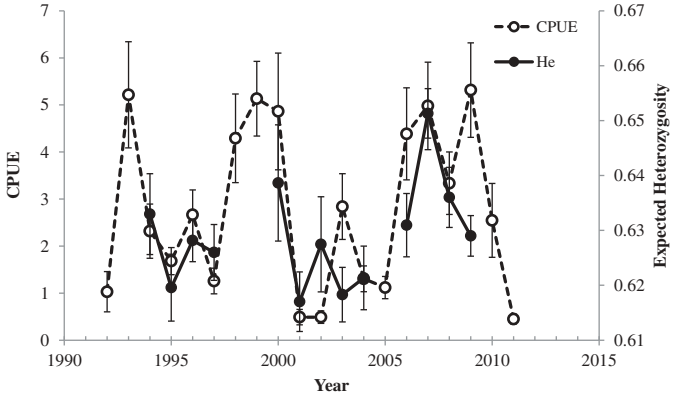


FIGURE 5. Mean CPUE of Spotted Seatrout in the Charleston Harbor system in the first quarter of each year and expected heterozygosity of year-classes (adjusted) 3 years earlier; error bars = SEs.

Cross correlation analyses between Spotted Seatrout CPUE and the different genetic diversity parameters (observed heterozygosity, expected heterozygosity, and allelic richness) were run in R (R Core Team 2012) using the ccf() function (Gilbert and Plummer), with lag times of 0 to 9 years for both collection year and year-class partitioned genetic data. Cross correlation analyses were performed to determine whether there was a lag between changes in CPUE and genetic diversity and whether those changes could be detected in the genetic diversity parameters. Lag times were considered significant when the cross correlation coefficient exceeded the 95% confidence interval of two uncorrelated time series. The lag time that produced the strongest correlation coefficient was interpreted to be the appropriate one, and linear regression was used to verify the relationship between CPUE in the first quarter of each year and the appropriately lagged genetic diversity metric.

RESULTS

Marker Validation and Characterization

A total of 902 Spotted Seatrout samples were successfully genotyped for analysis. The number of alleles per locus varied, ranging from 2 to 15 with an overall mean of 7.6 (Table 4). Allelic richness also varied by locus, ranging from 2.0 to 8.9 with a mean of 6.0. Most loci showed moderate values for expected heterozygosity (~0.4–0.8), with *Cneb41* exhibiting much lower levels of expected heterozygosity (ranging from 0.05 to 0.29), which lowered the overall mean to 0.63 (compared with 0.66 without *Cneb41*). *Cneb41* had a similar effect on the estimates for observed heterozygosity, which had an overall mean of 0.62 and a range of 0.05–0.93. Inbreeding coefficients also varied by locus but showed low overall levels (mean = 0.02; range = −0.24 to +0.36).

There were four instances in which loci within a single year-class deviated from HWE after Bonferroni correction: *Cneb31* in the 1999 year-class (chi-square test: df = 22, $P < 0.001$), *Cneb07* in the 2005 year-class (df = 22, $P = 0.001$), *Cneb22* in the 1998 year-class (df = 22, $P = 0.001$), and *Cneb12* in the 2009 year-class (df = 22, $P = 0.001$). These departures from HWE represent isolated instances, however, and no loci exhibited multiple departures from HWE across year-classes. None of the loci were significantly linked after Bonferroni correction ($\chi^2 \leq 37.8$, df = 22, $P \geq 0.020$). The low probability of null alleles (≤0.07) provides additional support for the strength and functionality of the locus suite.

N_e Estimates

Across all of the time points, LDNe produced negative N_e and N_b estimates for at least one of the allele frequency settings, and infinity was included in the upper bound for all of the estimates (see Supplementary Tables S.1 and S.2 available separately online). The inability to produce estimates as well as the large variation and uncertainty around the estimates indicate that N_e and N_b were high (likely >1,000) in the Charleston Harbor population. As no relationship is apparent between the ability to calculate

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TABLE 4. Summary statistics for the 13 microsatellite loci in 13 year-classes of Spotted Seatrout from the Charleston Harbor system. Abbreviations are as follows: n = sample size, N_a = number of alleles, A = allelic richness, H_E = expected heterozygosity, H_O = observed heterozygosity, P_{HW} = probability of conformity to Hardy–Weinberg genotypic expectations, and F_{IS} = the inbreeding coefficient. Asterisks indicate significant departures from Hardy–Weinberg expectations after Bonferroni correction.

	Year-class												
Locus and metric	1997	1998	1999	2000	2003	2004	2005	2006	2007	2009	2010	2011	2012
Cneb31													
n	39	52	121	56	26	72	26	61	54	70	83	53	121
N_a	7	6	9	7	6	7	5	7	8	8	8	6	9
A	6.28	5.22	6.69	6.27	5.93	5.95	4.81	5.64	6.17	5.77	6.55	5.68	5.80
H_E	0.687	0.629	0.694	0.692	0.76	0.651	0.683	0.686	0.694	0.678	0.732	0.711	0.669
H_O	0.667	0.481	0.579	0.554	0.808	0.514	0.615	0.59	0.611	0.571	0.627	0.725	0.724
P_{HW}	0.358	0.090	***0.000****	0.154	0.260	0.024	0.178	0.243	0.121	0.524	0.290	0.197	0.291
F_{IS}	0.03	0.238	0.167	0.202	−0.064	0.211	0.101	0.14	0.121	0.158	0.145	–0.021	–0.082
Cneb07													
n	41	52	126	59	27	68	26	62	54	72	82	53	123
N_a	5	6	5	4	5	5	5	6	6	4	6	4	5
A	4.76	4.8	4.3	4	4.78	4.66	4.81	4.66	5.02	4	4.51	3.97	4.31
H_E	0.691	0.646	0.668	0.666	0.646	0.631	0.6	0.601	0.698	0.698	0.659	0.634	0.648
H_O	0.537	0.692	0.587	0.678	0.778	0.603	0.385	0.597	0.593	0.694	0.683	0.717	0.593
P_{HW}	0.123	0.857	0.168	0.540	0.519	0.693	***0.001****	0.453	0.071	0.730	0.180	0.609	0.406
F_{IS}	0.226	−0.072	0.122	−0.018	−0.208	0.045	0.364	0.008	0.152	0.006	−0.036	−0.133	0.084
Cneb39													
n	41	52	125	59	27	73	26	62	55	72	83	53	123
N_a	4	5	5	5	4	8	3	5	4	5	6	5	5
A	3.51	3.81	3.59	3.71	3.78	4.64	3	3.68	3.62	3.58	4.47	4.03	3.99
H_E	0.466	0.483	0.536	0.468	0.562	0.471	0.41	0.538	0.5	0.504	0.52	0.509	0.493
H_O	0.463	0.481	0.544	0.39	0.407	0.493	0.423	0.565	0.418	0.514	0.53	0.528	0.463
P_{HW}	0.627	0.751	0.777	0.391	0.008	0.689	1.000	0.679	0.055	0.699	0.070	0.654	0.518
F_{IS}	0.005	0.006	−0.015	0.169	0.279	−0.047	−0.034	−0.049	0.165	−0.019	−0.02	−0.037	0.060
Cneb37													
n	41	52	126	59	27	72	26	62	55	71	83	53	123
N_a	7	7	9	7	5	6	4	6	7	6	9	7	7
A	5.94	5.18	5.23	5.36	4.56	4.8	3.99	4.86	5.54	4.44	5.62	5.34	4.75
H_E	0.647	0.494	0.51	0.493	0.601	0.529	0.597	0.535	0.601	0.477	0.579	0.537	0.517
H_O	0.61	0.558	0.452	0.458	0.741	0.5	0.577	0.516	0.618	0.535	0.602	0.472	0.463
P_{HW}	0.157	0.401	0.186	0.528	0.716	0.237	0.675	0.870	0.455	0.954	0.393	0.062	0.322
F_{IS}	0.058	−0.13	0.114	0.072	−0.238	0.055	0.034	0.036	−0.029	−0.123	−0.04	0.123	0.104
Cneb01													
n	39	46	119	53	27	73	26	61	55	72	83	53	122
N_a	5	6	7	7	7	9	8	8	7	8	8	7	8

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TABLE 4. Continued.

Locus and metric	Year-class												
	1997	1998	1999	2000	2003	2004	2005	2006	2007	2009	2010	2011	2012
A	4.58	5.29	5.27	6.41	6.89	6.32	7.38	5.8	5.73	6.42	5.51	5.95	5.65
H_E	0.594	0.667	0.632	0.637	0.714	0.659	0.645	0.64	0.608	0.676	0.628	0.661	0.643
H_O	0.513	0.674	0.613	0.66	0.667	0.63	0.615	0.557	0.491	0.653	0.639	0.654	0.626
P_{HW}	0.452	0.722	0.645	0.873	0.345	0.381	0.587	0.123	0.006	0.047	0.963	0.106	0.877
F_{IS}	0.139	−0.01	0.03	−0.036	0.068	0.044	0.047	0.13	0.193	0.035	−0.016	0.010	0.027
Cneb22													
n	38	47	112	54	24	52	23	50	45	67	82	53	119
N_a	10	10	13	10	9	10	8	9	10	10	10	10	14
A	8.23	8.67	7.94	8.09	8.6	8.79	7.81	7.55	8.18	8.8	7.72	8.11	8.66
H_E	0.783	0.802	0.797	0.816	0.768	0.842	0.781	0.794	0.773	0.807	0.796	0.813	0.788
H_O	0.816	0.596	0.759	0.759	0.75	0.808	0.739	0.88	0.778	0.806	0.805	0.776	0.780
P_{HW}	0.346	***0.001****	0.590	0.289	0.079	0.228	0.198	0.006	0.437	0.304	0.558	0.088	0.956
F_{IS}	−0.043	0.26	0.048	0.07	0.024	0.041	0.054	−0.11	−0.007	0.002	−0.011	0.047	0.009
Cneb33													
n	41	52	126	59	27	72	26	62	55	72	83	53	123
N_a	11	10	12	11	8	12	9	10	9	13	12	10	15
A	8.41	7.09	7.09	7.45	7.02	7.19	7.97	6.78	7.11	8.3	7.43	7.18	7.91
H_E	0.643	0.62	0.59	0.598	0.508	0.547	0.548	0.556	0.566	0.62	0.646	0.612	0.610
H_O	0.707	0.615	0.627	0.593	0.481	0.542	0.577	0.5	0.527	0.639	0.699	0.623	0.610
P_{HW}	0.801	0.375	0.896	0.046	0.083	0.628	0.739	0.040	0.655	0.323	0.596	0.954	0.966
F_{IS}	−0.102	0.008	−0.064	0.008	0.053	0.01	−0.053	0.102	0.07	−0.031	−0.083	-0.017	0.000
Cneb41													
n	40	50	120	50	21	58	24	62	55	72	83	53	122
N_a	3	3	7	5	2	4	5	6	4	4	5	5	7
A	2.5	2.86	3.53	3.97	2	3.16	4.72	4.3	3.12	2.97	3.58	3.91	3.88
H_E	0.142	0.187	0.188	0.287	0.048	0.178	0.235	0.252	0.187	0.133	0.242	0.247	0.232
H_O	0.15	0.2	0.183	0.32	0.048	0.138	0.25	0.258	0.164	0.111	0.253	0.250	0.236
P_{HW}	1.000	1.000	0.256	1.000		0.054	1.000	0.545	0.425	0.199	0.798	0.642	0.205
F_{IS}	−0.056	−0.072	0.022	−0.116	0	0.228	−0.066	−0.024	0.125	0.167	−0.045	-0.012	-0.017
Cneb09													
n	41	52	124	58	27	73	26	62	55	72	83	53	123
N_a	7	6	8	6	4	6	5	5	7	9	6	6	10
A	5.68	4.6	4.95	4.55	4	4.87	4.8	4.31	4.91	5.66	4.61	4.91	5.60
H_E	0.684	0.665	0.697	0.681	0.718	0.713	0.706	0.659	0.622	0.711	0.681	0.679	0.718
H_O	0.78	0.654	0.718	0.621	0.63	0.74	0.808	0.71	0.545	0.708	0.663	0.679	0.707
P_{HW}	0.854	0.077	0.586	0.092	0.678	0.955	0.618	0.599	0.214	0.236	0.777	0.600	0.449
F_{IS}	−0.144	0.017	−0.031	0.089	0.126	−0.038	−0.148	−0.077	0.125	0.003	0.028	−0.001	0.014
Cneb35													

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TABLE 4. Continued.

Locus and metric	Year-class												
	1997	1998	1999	2000	2003	2004	2005	2006	2007	2009	2010	2011	2012
n	41	52	126	59	27	73	26	62	54	72	83	53	123
N_a	8	10	13	9	9	10	7	11	10	12	10	11	12
A	7.58	7.91	7.96	7.36	7.84	7.72	6.61	7.72	7.07	8.7	8.33	8.41	7.62
H_E	0.736	0.712	0.689	0.632	0.698	0.688	0.652	0.727	0.625	0.698	0.754	0.712	0.690
H_O	0.732	0.75	0.675	0.627	0.741	0.74	0.692	0.71	0.593	0.764	0.687	0.717	0.699
P_{HW}	0.364	0.979	0.740	0.582	0.702	0.410	0.632	0.854	0.393	0.606	0.666	0.877	0.015
F_{IS}	0.006	−0.054	0.021	0.009	−0.062	−0.076	−0.063	0.024	0.053	−0.096	0.09	−0.007	−0.014
Cneb24													
n	41	49	125	57	26	73	25	61	53	72	83	52	123
N_a	9	9	11	10	9	11	9	8	8	9	12	9	13
A	7.77	7.63	7.76	8.31	8.73	8.94	8.65	7.16	7.36	7.28	8.14	7.52	8.34
H_E	0.796	0.749	0.763	0.782	0.829	0.775	0.807	0.762	0.805	0.775	0.801	0.770	0.782
H_O	0.927	0.714	0.808	0.737	0.808	0.699	0.76	0.852	0.792	0.778	0.831	0.811	0.779
P_{HW}	0.114	0.569	0.864	0.197	0.526	0.071	0.564	0.703	0.161	0.417	0.211	0.907	0.167
F_{IS}	−0.167	0.047	−0.059	0.059	0.026	0.1	0.06	−0.12	0.016	−0.004	−0.038	−0.054	0.004
Cneb12													
n	41	51	125	59	27	73	26	62	55	72	83	53	123
N_a	7	7	7	7	5	7	6	7	7	8	6	7	7
A	5.8	5.7	5.69	5.28	4.78	5.74	5.77	5.57	5.14	5.67	5.67	5.89	5.40
H_E	0.725	0.737	0.739	0.722	0.739	0.741	0.736	0.734	0.732	0.731	0.749	0.710	0.729
H_O	0.659	0.667	0.744	0.729	0.741	0.767	0.692	0.645	0.691	0.847	0.795	0.717	0.650
P_{HW}	0.425	0.146	0.951	0.272	0.309	0.033	0.201	0.306	0.591	***0.001****	0.570	0.637	0.061
F_{IS}	0.093	0.097	−0.007	−0.01	−0.002	−0.035	0.061	0.122	0.057	−0.16	−0.062	−0.011	0.108
Cneb04													
n	41	51	125	59	27	72	26	62	55	70	81	52	120
N_a	6	8	9	9	8	9	7	7	9	9	12	9	11
A	5.71	6.93	6.94	7.14	7.5	6.82	6.77	5.52	7.1	7.47	7.94	7.18	7.14
H_E	0.635	0.662	0.663	0.662	0.711	0.596	0.757	0.554	0.667	0.694	0.679	0.673	0.660
H_O	0.683	0.588	0.696	0.627	0.778	0.514	0.692	0.565	0.673	0.686	0.704	0.640	0.664
P_{HW}	0.9417	0.2999	0.632	0.5475	0.4473	0.038	0.2977	0.9712	0.4253	0.247	0.6797	0.400	0.719
F_{IS}	−0.077	0.112	−0.05	0.053	−0.096	0.138	0.087	−0.019	−0.009	0.012	−0.037	0.050	−0.006

estimates and sample sizes, the study sample sizes appear to have been sufficient.

The GONe calculations resulted in a population correction factor of 6.51, with a generation time of 2.53 years. GONe produced results similar to those of LDNe, with almost all estimates of N_e between consecutive year-classes being negative, again indicating that N_e was in the thousands for these time points (Table S.3). However, GONe did produce bounded N_e estimates between the 2003 and 2004 and 2011 and 2012 year-classes.

Temporal Genetic Variation: Collection Year

None of the pairwise comparisons of R_{ST} between collection years were significantly different from zero after Bonferroni correction (permutation test: df = 1, $P \geq 0.054$). Similarly, pairwise comparisons of the allele frequency distributions between collection years showed no significant differences after Bonferroni correction (exact *G*-test: df = 26, $P \geq 0.049$).

Observed heterozygosity showed little variation among collection years 2000–2010, remaining between ~0.60 and 0.61 before increasing to 0.65 in 2011 (Figure 3). Despite the small differences between most of the annual values, significant changes in diversity were detected (*t*-tests: df = 1, $P \leq 0.006$) between most of the consecutively sampled time points due to the narrow confidence intervals. The only exception was the 2001–2005 comparison, which was not significant (*t*df = 1, $P = 0.655$). A significant cross correlation occurred between the CPUE of Spotted Seatrout and observed heterozygosity after the latter was lagged 4 years ($r = 0.446$), suggesting that that was the most likely lag time. A 4-year lag for observed heterozygosity would result in CPUE pairing with the heterozygosity of Spotted Seatrout collected 4 years later. However, when regressed against each other, observed heterozygosity lagged 4 years and CPUE did not show a significant relationship ($r^2 = 0.594$, $P = 0.073$).

Expected heterozygosity showed a trend similar to that for observed heterozygosity, with estimates between ~0.62 and 0.63 for collection years 2000–2010 and an increase to 0.65 in 2011 (Figure 3). A significant difference occurred between collection years 2010 and 2011 (*t*-test: df = 1, $P < 0.001$), but no other differences were detected after Bonferroni correction (df = 1, $P \geq 0.043$). No significant cross correlation occurred between CPUE and expected heterozygosity, regardless of how many years expected heterozygosity was lagged, although a lag time of 4 years was the most likely one, showing the strongest cross correlation ($r = 0.432$). The selected 4-year lag time for expected heterozygosity did not show a significant relationship with CPUE when regressed on it ($r^2 = 0.558$, $P = 0.088$).

Allelic richness showed more interannual variability than the heterozygosity estimates, but the magnitude of change was nevertheless small over the entire sampling period, ranging from ~8.0 to 8.3 (Figure 3). No significant difference occurred in allelic richness between collection years 2000 and 2001 (*t*-test: df = 1, $P = 0.649$), but significant differences occurred between all other consecutively sampled collection years after Bonferroni correction (df = 1, $P < 0.001$). No significant cross correlation between CPUE and allelic richness occurred regardless of how many years allelic richness was lagged, with the strongest correlation at a lag time of 6 years ($r = 0.301$), showing that 6 years was the most likely lag time of those tested. Lagging allelic richness 6 years did not produce a significant relationship with CPUE ($r^2 = 0.4820$, $P = 0.126$).

Temporal Genetic Variation: Year-Class

Similar to the collection year results, those for year-class did not differ significantly (R_{ST}: permutation test; df = 1, $P \geq 0.009$; allelic frequency distributions: exact *G*-test; df = 26, $P \geq 0.002$). Observed heterozygosity showed greater interannual variation by year-class than by collection year, fluctuating up and down throughout the time period (1997–2012) and ranging from ~0.58 to 0.66 (Figure 4). Observed heterozygosity was not significantly different between year-classes 2004 and 2005 (*t*-test: df = 1, $P = 0.066$) and 2005 and 2006 (df = 1, $P = 0.121$); however, it differed significantly between all other consecutively sampled year-classes after Bonferroni correction (df = 1, $P < 0.001$). A significant cross correlation occurred between the CPUE and observed heterozygosity of year-classes lagged 3 years ($r = 0.597$; Figure 6), providing support for that as an appropriate lag time. In this case, a 3-year lag time for observed heterozygosity results in CPUE pairing with the heterozygosity of Spotted Seatrout spawned 3 years later. Applying a lag time of 3 years to observed heterozygosity did produce a strong, significant relationship with CPUE ($r^2 = 0.605$, $P = 0.002$).

Expected heterozygosity showed a trend similar to that for observed heterozygosity, fluctuating between ~0.62 and 0.65

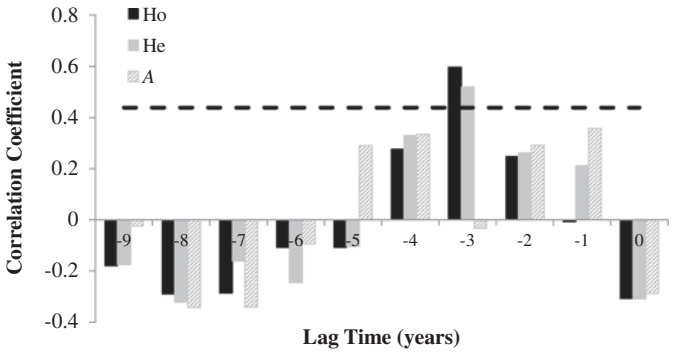


FIGURE 6. Summary of cross correlation analysis for Spotted Seatrout CPUE in the Charleston Harbor system in the first quarter of each year and year-class observed heterozygosity, expected heterozygosity, and allelic richness with various lags. The dashed line at 0.438 is the 95% confidence interval of two uncorrelated time series.

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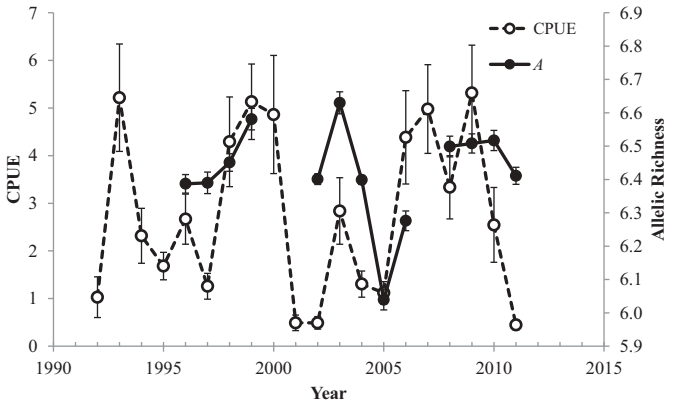


FIGURE 7. Mean CPUE of Spotted Seatrout in the Charleston Harbor system in the first quarter of each year and allelic richness of year-classes (adjusted) 1 year earlier; error bars = SEs.

(Figure 5). No significant differences in expected heterozygosity occurred between any of the consecutively sampled year-classes after Bonferroni correction (*t*-tests: df = 1, $P \geq 0.006$). A significant cross correlation occurred between CPUE and expected heterozygosity with a lag of 3 years ($r = 0.533$; Figure 6), providing support for that as the most likely lag time. Applying the 3-year lag to expected heterozygosity produced a significant relationship with CPUE ($r^2 = 0.456$, $P = 0.011$).

Allelic richness in Spotted Seatrout showed greater interannual variation when the data were partitioned by year-class than when they were partitioned by collection year, with a range of ~6.0 to 6.6 (Figure 7). No differences in allelic richness occurred between any consecutively sampled year-classes after Bonferroni correction from 1997 to 1999 (*t*-test: df = 1, $P \geq 0.145$) and from 2010 to 2012 (df = 1, $P \geq 0.008$). All consecutively sampled year-classes from 2000 to 2009 showed significant differences in allelic richness after Bonferroni correction (df = 1, $P < 0.002$). No significant cross correlations occurred between CPUE and allelic richness; however, the strongest correlation occurred when allelic richness was lagged 1 year ($r = 0.357$; Figure 6), showing that to be the most likely lag of those tested. However, applying a 1-year lag to allelic richness did not produce a significant relationship with CPUE ($r^2 = 0.164$, $P = 0.170$).

DISCUSSION

In analyzing the temporal variation in the genetic diversity of Spotted Seatrout, partitioning individuals by year-class (i.e., fish spawned in the same year but collected at various times) rather than by collection year (fish collected at the same time but having various ages) was more informative and provided better support for a relationship with population abundance. The greater interannual variation observed in the year-class genetic diversity estimates captured minor changes in the diversity of the reproductive output of each year that were masked when several year-classes were pooled in a single collection year. The greater number of time points and stronger statistical support for the relationship between genetic diversity and CPUE provide more confidence in the genetic diversity estimates based on year-class than in those based on collection year. Additionally, the lag times calculated via the cross correlation analyses for the year-class data were more biologically relevant, as alleles are lost at a faster rate relative to decreases in heterozygosity after a bottleneck (Nei et al. 1975; Allendorf 1986), while the estimated lag times for the collection year data were likely due to stochastic variation. Therefore, analyses of Spotted Seatrout genetic diversity by year-class are the most biologically relevant ones for interpretation.

While separating samples by year-class provides a greater number of time points and is the most biologically relevant approach, it reduces the sample size at each time point relative to separating samples by collection year. With relatively small sample sizes and the detection of only minor changes in genetic diversity, one might assume that the observed trends in genetic diversity in Spotted Seatrout over the study period were due to sampling variance rather than a genuine signal in the population. There are, however, several trends in the data that support the contention that the sample sizes are sufficient. The standard errors calculated for each year-class with respect to observed heterozygosity and allelic richness (which is rarefied) are narrow (~0.42% of the mean for both metrics), resulting in significant differences between several time points. If sampling variance were responsible for the trends in these metrics, the error bars would show overlap among almost all time points, which is not the case. Secondly, if the sample sizes used in the present study were insufficient to capture the diversity of the population, a relationship between sample size and heterozygosity would occur. However, no relationship was detected between either metric of genetic diversity (observed or expected heterozygosity) and sample size using linear regression ($r^2 < 0.001$, $P > 0.965$). Therefore, we believe that the sample sizes used in the year-class analyses were sufficient to capture the population-level genetic diversity of Spotted Seatrout in the Charleston Harbor system.

The abundance of Spotted Seatrout in the Charleston Harbor system significantly influenced the genetic diversity of the population, depending on which diversity metric was used (heterozygosity or allelic richness). Effective population size remained high despite changes in CPUE, and allelic richness showed no significant relationship with CPUE at any of the lag times tested. The allelic diversity of Spotted Seatrout in Charleston Harbor may not be strongly affected by fish abundance, but a 1-year lag had the most statistical support despite not being significant. After applying a 1-year lag, we found that in most cases in which allelic richness correlated poorly with CPUE this represented differences in magnitude rather than a deviation in the trend of the two metrics, which suggests that the abundance of Spotted Seatrout has an

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effect on allelic richness. A lag time of 1 year for allelic richness in Spotted Seatrout would be expected, however, because alleles are rapidly lost in a population following a bottleneck (Fuerst and Maruyama 1986) and cold winters would reduce the abundance of Spotted Seatrout and their allelic richness prior to spawning in the spring and summer months. Spotted Seatrout offspring take approximately 1 year to grow to a size for capture by SCDNR's 2.5-in (5.5-cm) stretched-mesh trammel net, which would coincide with the 1-year lag for detecting changes in allelic richness.

Alternatively, the observed 3-year lag in observed and expected heterozygosity occurred due to a delay in genetic recombination (i.e., a spawning event), which must take place prior to detecting any changes in a measure of genotypic diversity. When individuals are removed from a population, there is the potential to immediately lose rare alleles; however, heterozygosity will remain unchanged until alleles are reshuffled during a reproductive event. Two-year-old Spotted Seatrout contribute the majority of the reproductive effort during each spawning season in South Carolina (Roumillat and Brouwer 2004); therefore, it should take an average of 2 years for alleles to be recombined during reproduction. After reproduction, Spotted Seatrout offspring must grow for approximately 1 year before they recruit to the trammel net gear, making a 3-year lag time appropriate. Another potential explanation for a 3-year lag between changes in CPUE and heterozygosity is size-dependent mortality during winter-kill events. McDonald et al. (2010) found that two adult size-classes of Spotted Seatrout were more tolerant of low temperatures than juvenile Spotted Seatrout. The abundance of the juvenile size-class that McDonald et al. (2010) found to be more vulnerable to mortality at low temperatures cannot be adequately monitored in South Carolina by the trammel net gear due to size selectivity. However, the SCDNR trammel net catch data support size truncation of Spotted Seatrout during cold winter events, providing possible evidence that the largest individuals are more susceptible to winter mortality. If the extreme size-classes of Spotted Seatrout show a higher rate of mortality during cold winters and young-of-year Spotted Seatrout are removed from the population at a higher rate, there will be a delay before new individuals enter the breeding population and thus a delay in the response of heterozygosity. Theoretical studies support a longer lag time for heterozygosity than for allelic richness because there is a delay between a population's experiencing a bottleneck and the subsequent decrease in heterozygosity (Nei et al. 1975) while changes in allelic richness are detected more quickly after a bottleneck (Allendorf 1986). While the genetic metrics of Spotted Seatrout are responsive to changes in population abundance following cold winter events, we note that the fluctuations (i.e., the differences between the largest and smallest values over the entire sampling period) that we detected in observed heterozygosity (0.079), expected heterozygosity (0.034), and allelic richness (0.59) are relatively minor. Therefore, functional genetic diversity remained fairly stable at moderate levels over time despite there being large fluctuations in population abundance associated with cold winter events.

The resiliency of Spotted Seatrout genetic diversity to substantial fluctuation in population abundance is likely the result of the species' biology and life history. As batch spawners, Spotted Seatrout reproduce throughout the spawning season (April to September) each year (Roumillat and Brouwer 2004). In South Carolina, Spotted Seatrout may live for up to 10 years, but few survive beyond 3 years (unpublished SCDNR data on >15,000 otolith-aged fish). The variability of the different age-classes present during each spawning season and the temporal variation in individuals present during each spawning event enable a high diversity of genes to be available for recombination both within and between years. The mixed pool of potential spawning adults promotes spawning between different year-classes to maintain stable genetic diversity levels despite large fluctuations in overall population abundance. The lack of change in observed and expected heterozygosity when analyzed by collection year indicates that sampling a population's entire age structure at a single time point can mask the fine-scale changes in genetic diversity that may be present at an annual timescale. Therefore, the Spotted Seatrout's overlapping generations and reproductive strategy allows for the maintenance of a moderate level of genetic diversity and a high N_e.

The effect of changes in population abundance on the genetic diversity of marine fishes has been examined in several species (i.e., European Sardine [also known as the European Pilchard] *Sardina pilchardus*, Ruggeri et al. 2012; Atlantic Cod *Gadus morhua*, Hutchinson et al. 2003; New Zealand Snapper *Pagrus auratus*, Hauser et al. 2002) using microsatellites. However, these studies estimated genetic diversity over much longer time periods (~30–50 years) and under the scenario of a single population bottleneck caused by overfishing. Larger decreases in allelic richness were found than in the present study, with the declines in expected heterozygosity being similar. The longer timescales of the previous studies did not allow for the exploration of interannual changes in diversity associated with small changes in abundance or the detection of a relationship between abundance and genetic diversity, which our study documents for the first time in a marine fish.

Previous studies of the genetic diversity of imperiled nonmarine species that have experienced severe population bottlenecks (Copper Redhorse *Moxostoma hubbsi*, Lippe et al. 2006; geometric tortoise *Psammobates geometricus*, Cunningham et al. 2002; ornate box turtle *Terrapene ornata*, Kuo and Janzen 2004) failed to detect a reduction in genetic diversity despite substantial declines in population size. These studies focused on species that exhibit long, overlapping generation times, which the authors hypothesized to mask any potential effects of a decline in census size on genetic diversity. It is possible that these long-lived species show a lag in diversity responses, as found in our study, but the long

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generation times may create a lag that is longer than the time between the population bottleneck and census sampling, making any changes in genetic diversity undetectable. By contrast, the relatively short generation time of Spotted Seatrout allowed changes in genetic diversity associated with population abundance to be detected on a shorter timescale.

A more appropriate comparison for Spotted Seatrout may be with rodent populations that exhibit cyclical population dynamics and short generation times. A compilation of data from five lemming species (subfamily Arvicolinae) with high-amplitude population cycles demonstrated that all five species maintained high levels of mitochondrial genetic diversity despite a history of repetitive population declines; the high genetic diversity was attributed to a patchy spatial distribution and high rates of gene flow (Ehrich and Jorde 2005). It is possible that during periods of population growth, as the number of Spotted Seatrout increased statewide, density-dependent factors altered their movement behaviors to increase the likelihood of migrants between neighboring estuaries. Such increased movement would heighten the gene flow in the isolation-by-distance pattern observed in the southeastern United States (O'Donnell et al. 2014), potentially increasing heterozygosity. A similar scenario was observed in a study of a cyclic population of meadow voles *Microtus pennsylvanicus* (Plante et al. 1989), which found that high-density conditions were associated with higher mitochondrial genetic diversity and higher rates of gene flow while lower-density conditions were associated with decreases in both diversity and gene flow. The results from Plante et al. (1989) support the notion that populations at higher density are more likely to experience higher gene flow through migration and that changes in genetic diversity similar to that seen in Spotted Seatrout can occur after 1 year amidst a fluctuation in population abundance. Genetic diversity has also been evaluated in a cyclic fossorial water vole *Arvicola terrestris* using microsatellites at four time points over a 2-year period while the population transitioned from low to high density. During this transition, a steady increase was found in both allelic richness and expected heterozygosity (Berthier et al. 2006). While the results of genetic studies on cyclical rodent populations show similarities to the findings of our study, these studies lacked sampling throughout several population cycles and thus were unable to provide strong support for a correlation between abundance and genetic diversity; by contrast, the longer sampling period of our study on Spotted Seatrout was able to detect a relationship.

Although we found that the genetic diversity of Spotted Seatrout in the Charleston Harbor system was responsive to fluctuations in population abundance, the magnitudes of change in genetic diversity were minor and genetic recovery was rapid during periods of population growth. Therefore, Spotted Seatrout populations appear to be genetically resilient to cold winter mortality events at the magnitude of those that occurred during our study period. Short overlapping generations allow Spotted Seatrout to maintain fairly constant moderate levels of genetic diversity and a high N_e despite substantial fluctuations in abundance. The intermittent times of population growth associated with mild winters are also instrumental in the maintenance of stable genetic diversity in Spotted Seatrout. In 2011, during the most recent population decline, South Carolina fishery managers requested a voluntary catch-and-release practice for Spotted Seatrout to allow populations to recover from two consecutive cold winters, which may have contributed to a quicker population rebound. However, if Spotted Seatrout populations suffer a considerable population decline and remain at low abundance for several years, the impacts on genetic diversity would likely be larger and genetic recovery slower. Our findings imply that future studies of temporal changes in the genetic characterization of species that exhibit overlapping generations would benefit from analyzing age-structured data in order to capture the fine-scale variability that may be masked by overlapping generations.

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