



# Intertidal Creek Pool Nekton Assemblages: Long-term Patterns in Diversity and Abundance in a Warm-Temperate Estuary

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## Abstract

Estuarine nekton (fishes, crabs, and shrimps) play key ecological roles and support valuable commercial and recreational fisheries. Long-term research programs focused on nekton can provide insight into community and population-level changes over time, but are uncommon due to funding and logistical constraints. We describe patterns and changes in a nekton assemblage from an intertidal creek in the North Inlet estuary, South Carolina, USA based on 19 years of observations. From 1984 to 2002, biweekly seine collections (approximately every 2 weeks,  $n = 469$ ) were made in a pool isolated within an intertidal creek at low tide. The assemblage was composed of juvenile and small adult (mostly  $< 100$  mm) fishes, shrimps, and crabs. The 10 most abundant species made up  $> 97\%$  of the catch; these species included (in descending order): *Leiostomus xanthurus*, *Litopenaeus setiferus*, *Fundulus heteroclitus*, *Mugil cephalus*, *Farfantepenaeus aztecus*, *Eucinostomus* spp., *Mugil curema*, *Fundulus majalis*, *Menidia menidia*, and *Brevoortia tyrannus*. The assemblage exhibited a distinct seasonality across years, with peak total abundance in mid-spring, peak total biomass in late spring, and highest species richness in late summer and early fall. Total abundance and species richness showed evidence of significant increases across years, total biomass and the Shannon diversity index remained unchanged, and evenness significantly declined. The composition of the assemblage shifted during the sampling period, with the abundance of key year-round residents (*F. heteroclitus*, *M. cephalus*) decreasing and warm-season species (*L. xanthurus*) increasing. Most of the five metrics of the nekton assemblage and the abundances of the five top species were positively correlated with both water temperature and salinity. Direct and indirect effects of hurricanes and storm events on the hydrogeomorphology of the creek and pool were also recognized as influences on the long-term patterns and trends. Long-term (decadal) sampling programs like this can provide important baseline information, and thus insight into the influence of significant weather events and global climate change on nekton populations and their roles in ecosystem dynamics, as well as inform the management of estuaries and fisheries in the southeastern US.

**Keywords** Salt marsh · Fishes · Shrimp · Spot · Seine · Juvenile · Long-term patterns

## Introduction

Salt marsh-dominated estuaries are composed of mosaics of multiple, interconnected habitat types (e.g., the vegetated marsh surface, pools and ponds, intertidal and subtidal creeks, open water) that can serve as critical nursery areas for numerous fish and natant invertebrate species (nekton)

(Rountree and Able 2007; Sheaves 2009). Nekton use of salt marsh habitats varies temporally and spatially relative to physical and biological factors such as tidal cycle and species-specific migration patterns (Rozas 1995; Kneib 1997; Bretsch and Allen 2006). In general, estuarine nekton migrate or follow the tide as it rises (i.e., floods), thereby gaining access to highly productive intertidal areas including the marsh surface, then follow the ebbing tide as waters recede into subtidal habitats. Intertidal creeks are particularly important as they serve as primary corridors, both biologically and physically, linking marsh surface and subtidal habitats. However, intertidal creeks, unless very small, rarely drain completely during low tide and often have one or a series of permanently flooded pools along the axis of the creek, especially closer to the creek mouth (Kneib 1997).

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While most tidal migrants return to adjacent subtidal areas during low tide, some remain in intertidal creek pools, which may serve as staging areas and provide refuge for nekton that will move into higher intertidal areas when they are flooded again (Allen et al. 2007, 2017).

Intertidal creek pools are features in many salt marsh-dominated estuaries along the southeastern US Atlantic coast and their likely importance to nekton at low tide has been suggested (Hettler 1989; Kneib and Wagner 1994; Allen et al. 2007); however, efforts to assess nekton use of intertidal creek pools have been scarce (but see Crabtree and Dean 1982; Allen et al. 2013; Rieucou et al. 2015). Since large piscivorous nekton are largely absent from intertidal creek pools at low tide, nekton may use pools to evade predation in adjacent open subtidal waters until water levels rise again; however, individuals must then endure other risks such as overcapacity, which may lead to degraded environmental conditions (e.g., low dissolved oxygen) (Crabtree and Dean 1982; Rieucou et al. 2015). In addition, nekton retreating from food-rich, flooded marsh, and other intertidal areas and remaining in pools during low tide were shown to enrich these isolated water bodies with ammonium and orthophosphate through excretion (Allen et al. 2013). Nekton dwelling in intertidal creek pools provide an important ecosystem service when their concentrated nutrients are flushed from the pool by the flooding tide into higher intertidal areas, thereby stimulating primary production. However, beyond these few studies little is known regarding nekton seasonal, annual, and long-term use of intertidal creek pools. The relative paucity of information about nekton use of pools in intertidal salt marsh creeks contrasts starkly with an abundance of information on nekton use of pools on the marsh platform (see Mace et al. 2019).

Nekton use of intertidal creeks varies spatially, but in a comparison of eight intertidal creeks over 2 years, the levels of use (ranks based on abundance and biomass) remained largely unchanged through the seasons and years (Allen et al. 2007). All creeks appeared to respond similarly to broad-scale changes in larval supply and environmental conditions. That study supported an effort to better understand how nekton use of intertidal creeks changes in response to environmental conditions over years and decades. Long-term studies of nekton assemblages are crucial to better understanding the life history of ecologically and economically important nekton species, as well as the changing nature of nekton assemblages over time in response to shifting environmental conditions. Therefore, the primary objective of the present study is to characterize nekton use of an intertidal creek pool on multiple temporal scales. Specifically, this study examines intra- and inter-annual patterns in nekton assemblage composition, abundance, and biomass as well as the richness, evenness, and diversity of the assemblage and relationships between the fauna and environmental

conditions, especially water temperature and salinity, over a 19-year study period (1984–2002). In addition, species-level trends in occurrence and abundance were evaluated for the most abundant (top 5) nekton species. The results of this study provide baseline information regarding nekton use of intertidal creek pools, an understudied habitat within the estuarine salt marsh habitat mosaic, in a warm-temperate estuarine system along the southeastern US Atlantic coast.

## Methods

### Study Area

The study was conducted in the Oyster Landing Creek basin within the North Inlet estuary in Georgetown County, South Carolina, USA. The North Inlet estuary is a well-mixed, high salinity, system in which *Spartina alterniflora* is the dominant emergent vegetation (Allen et al. 2014). Oyster Landing Creek, the main intertidal tributary servicing the 5.1-ha marsh basin, is located near the forest border, about 3 km from the inlet, and is subject to periodic influence from rainwater runoff from a 55-ha undeveloped and forested watershed. Tides are semidiurnal with a mean range of 1.4 m.

### Field Collections

Fishes, crabs, squids, and shrimps (i.e., nekton) were collected at slack low tide using a nylon bag seine (15.2 m long  $\times$  1.2 m high, 6-mm mesh) to make a single sweep of an intertidal creek pool (33° 21' 06.44 N, 79° 11' 29.92 W) for each sampling event (Fig. S1). All seine collections took place during the day, approximately biweekly (almost every 2 weeks) from January through December 1984–2002. The area of the roughly circular (approximately 17 m diameter) creek pool was approximately 308 m<sup>2</sup> at mean low tide. Most of the pool was 50–100 cm deep with steep edges. The pool was a depression in the intertidal creek bed, and generally was disconnected from the creek on either side at low tide. Occasionally, however, a small trickle (< 10 cm) of water remained present at the time of sampling on either side; in this case, nets (6-mm mesh) were strung upstream and downstream of the pool to ensure isolation. On the pool bottom, a thin layer of soft mud covered a firm base of sand. About one third of the intertidal area bordering the permanently flooded portion of the pool was marsh edge, and the remainder was mostly composed of firm muddy sand and low profile oyster reef.

All collected nekton species were identified and enumerated, and up to the first 100 individuals of each species (haphazardly selected) were measured to the nearest millimeter; standard length (SL) for fish, cephalothorax length (length from tip of rostrum to posterior dorsal edge of carapace; CL)

for shrimp (Ditty 2011), carapace width (CW) for crabs, and mantle length (ML) for squids. The wet weight (g) of each species (all individuals together) was also determined. Water temperature and salinity were measured in the pool prior to seine collections using a thermometer and refractometer in the early years of the study period and, starting in 1993, with a handheld multiparameter meter.

Some closely related species were difficult to confidently distinguish from one another morphologically and were listed as Genus followed by spp. For the following Genus spp. categories, the likely species included are in parentheses: *Alosa* spp. (*A. aestivalis*, *A. pseudoharengus*, *A. sapidissima*), *Alpheus* spp. (*A. heterochaelis*, *A. normanni*), *Astroscopus* spp. (*A. guttatus*, *A. y-graecum*), *Callinectes* spp. (*C. sapidus*, *C. similis*, *C. ornatus*), *Eucinostomus* spp. (*E. argenteus*, *E. gula* and unidentified *Eucinostomus*), *Menticirrhus* spp. (*M. americanus*, *M. saxatilis*), *Paralichthys* spp., (*P. lethostigma*, *P. dentatus*, *P. albigutta*), *Prionotus* spp. (*P. carolinus*, *P. tribulus*), *Sygnathus* spp. (*S. fuscus*, *S. louisianae*, *S. floridae*), and *Urophycis* spp. (*U. floridana*, *U. regia*). These Genus spp. groupings are treated as though they were single species in all analyses and discussion. *Palaeomonetes* spp. (mostly *P. pugio*) were usually very abundant in the pool, but, because only the largest individuals were retained by the 6 mm mesh, grass shrimp were not quantified in the collections.

## Data Analyses

### Nekton Species Composition, Abundance, and Size

Species-level catch data (number of individuals per haul and length measurements) were aggregated across all 469 sampling dates to determine the total number of individuals collected, the median length, and the length range for each species across the 19-year time series. We calculated the percent of total catch as the species-level total catch divided by the total number of individuals collected (all species combined). Overall occurrence was the number of individual seine hauls in which a species was collected and percent occurrence was calculated as the occurrence divided by the total number of seine hauls. Annual summaries were compiled using the total number of individuals collected each year (for a given species and all species combined). Monthly length frequencies (all measurements within a month, aggregated across years) were plotted for the 10 most abundant species.

For each biweekly seine sample, we calculated abundance, biomass, and three metrics of diversity. Total catch was calculated as the total number of individuals of all species collected in a given seine haul. Total biomass was calculated as the sum of the species-specific wet weights in a given seine haul. Species richness was determined as the total number

of species collected per seine haul. The Shannon diversity index was determined as  $H' = -\sum_i p_i \times \log_e p_i$  where the index  $i$  indicates individual species, and  $p_i$  the individual species catch per seine haul, divided by total catch of all species per seine haul. Species evenness, a measure of the relative abundance of all species within an assemblage, was calculated as the Shannon diversity index ( $H'$ ) divided by the natural logarithm of species richness per seine haul. In this formulation, species evenness values range from 0 (uneven) to 1 (completely even).

Generalized additive mixed effect models (GAMMs) were used to explore intra- and inter-annual changes in the abundance, biomass, and diversity metrics. GAMMs are statistical models that extend the generalized linear model (GLM) by allowing for substitution of smooth functions in place of some (or all) parametric terms in a traditional GLM, and have proven useful in estimating non-linear trends over time for irregular time series (Wood 2017). They can accommodate a range of statistical distributions, as well as incorporate random effects and various correlation structures. For each metric (total catch, total biomass, richness, Shannon diversity index, and evenness), we fit a GAMM incorporating the additive effects of two fixed continuous predictor variables, day of year (intra-annual time scale) and year (inter-annual time scale), where day of year was the Julian date within a given year the sample was taken. All metrics except biomass included years 1984–2002; biomass data were unavailable from 1984, and therefore modeled from 1985 to 2002. Day of year was modeled using a cyclic cubic regression spline with knots at day 1 and day 366, and year as a thin-plate regression spline. Different probability distributions and link functions were used for each metric, depending on the distribution of the response variable (Table S1). Specifically, total catch was modeled as a negative binomial distribution with the log link, biomass as a Tweedie distribution with a log link, richness as a Poisson distribution with the log link, Shannon diversity index as a Gaussian distribution with the identity link, and evenness as a beta regression distribution (where the response is assumed to be bounded within 0 to 1). Each of the five models showed evidence of temporal autocorrelation when initially fit without any error structure specified; this was addressed by fitting models to each response metric using two different error structures (autoregressive order one and autoregressive moving average of order two), and selecting the model with the lowest Akaike information criterion (AIC) value. No random effects were incorporated, but specification of error structure dictated our use of a GAMM (specifically the gamm function within R package mgcv; Wood 2011, 2017).

A similar approach using GAMMs was employed to evaluate intra- and inter-annual trends in the catch of the top 5 most abundant species. For each species, we fit a GAMM incorporating the additive effects of day of year and year. For the five

species, catch was modeled as either a negative binomial or Tweedie distribution, all using the log link (Table S2). Temporal autocorrelation was addressed by including error structures in the same manner as the assemblage GAMM models. Due to the seasonal nature of estuarine use by nekton, plots of raw data suggested potential for significant overdispersion and zero inflation of catches. To cope, catch data were truncated to include the seasons of greatest abundance. Seasons were defined by month of year: January–March (winter), April–June (spring), July–September (summer), October–December (fall). Because we did not model over the full range of the day of year variable, both day of year and year were modeled as thin-plate regression splines. All GAMM modeling was performed using the packages *mgcv* and *gratia* in R (Wood 2011, 2017; Simpson 2021).

### Nekton Assemblages

We used non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) to evaluate multivariate patterns in the intertidal creek pool nekton assemblages seasonally and among years (Kruskal and Wish 1978; Anderson 2001). NMDS and PERMANOVA analyses were implemented with the *vegan*: community ecology package (Oksanen et al. 2020). To examine the seasonality of the nekton pool assemblages, we aggregated biweekly catch data for all species by season and year, and calculated mean catch values for each species. Seasons were defined as above. The resulting seasonal catch estimates ( $n = 76$ ) were square root transformed (to reduce the influence of highly abundant taxa) and converted into Bray–Curtis dissimilarities prior to NMDS ordination (Clarke and Warwick 2001). Inter-annual shifts in assemblage composition were explored using NMDS ordination in a similar manner, except that the biweekly catch data for all species were aggregated solely by year ( $n = 19$ ). Next, mixed-model PERMANOVA was performed to test for statistically significant ( $\alpha = 0.05$ ) differences in assemblage composition among seasons, followed by subsequent pairwise comparisons between seasons if  $P < 0.05$  was indicated (accompanied by the Bonferroni adjustment to account for multiple comparisons). Specifically, both the overall seasonal PERMANOVA and the post hoc pairwise PERMANOVAs tested the significance of season (winter, spring, summer, fall) as a fixed effect, and incorporated year (1984–2002) as a randomized factor. Both overall and pairwise PERMANOVAs used the original catch matrix, square root transformed (again, to reduce the influence of highly abundant taxa), and converted into Bray–Curtis dissimilarities, as the dependent variable ( $n = 468$ ; one seine haul removed due to zero catch). The randomized factor was included in an effort to account for possible autocorrelation among seine hauls on assemblage composition. Finally, a test of inter-annual assemblage change over time was conducted by grouping the 19-year dataset into three time periods (1984–1990, 1991–1996,

1997–2002), and performing a mixed-model PERMANOVA on the original catch matrix (converted into a Bray–Curtis distance matrix, as above) to test for statistically significant differences among periods ( $n = 468$ ). In this PERMANOVA, time period was incorporated as a fixed effect and year as a randomized factor, nested within time period, again to account for autocorrelation among seine hauls. These three time periods are arbitrary distinctions that allow an examination of potential temporal trends (Curran and Wilber 2019). Subsequent pairwise comparisons between periods were performed if a significant difference ( $P < 0.05$ ) was indicated.

### Nekton Correlations with Environmental Conditions

To assist in interpreting intra- and inter-annual patterns in assemblage metrics and species-level catches, we conducted two examinations of the association of these responses with environmental conditions at the time of sampling. First, Spearman rank order correlation tests were conducted to evaluate the correlation between each of the assemblage metrics (abundance, biomass, richness, Shannon, and evenness) and the catches of the top 5 species with water temperature and salinity across all sampling dates ( $n = 469$ ). Second, a separate set of Spearman rank order correlation tests were run to evaluate the correlation between the annual averages of water temperature and salinity and the annual averages of all 10 responses ( $n = 19$  for each set, excluding biomass [ $n = 18$ ], for which data was unavailable in 1984). Annual averages included data from all 12 months of sampling within each year. Results were considered significant at  $P < 0.05$ .

## Results

### Nekton Species Composition, Abundance, and Size

A total of 88 species and 2,497,207 individuals were collected over the 19-year study period (Table 1). A small number of species dominated the total catch in the intertidal creek pool; specifically, the 10 most abundant species made up 97.34% of all individuals collected (in order from 1 to 10): *Leiostomus xanthurus*, *Litopenaeus setiferus*, *Fundulus heteroclitus*, *Mugil cephalus*, *Farfantepenaeus aztecus*, *Eucinostomus* spp., *Mugil curema*, *Fundulus majalis*, *Menidia menidia*, and *Brevoortia tyrannus* (Table 1; Fig. 1). Out of these 10 most abundant species, 6 species (making up 84% of the total catch) were economically important species: *L. xanthurus*, *L. setiferus*, *F. aztecus*, *M. cephalus*, *M. curema*, and *B. tyrannus*. The 30 most abundant species made up essentially the entirety of all individuals collected (99.94%) (Table 1; Fig. S2). *Leiostomus xanthurus* was the most abundant species captured, accounting for 62% of all individuals collected during the 19-year sampling period (Table 1). It was ranked the most abundant species in 18 out of the 19 years (Table 2). *Litopenaeus setiferus* was

**Table 1** Overall occurrence, abundance, and length for all species collected in an intertidal creek pool biweekly with a seine in Oyster Landing Creek in the North Inlet estuary, SC 1984–2002

Species	Occurrence		Abundance			Length (mm)	
	#	%	Total	% of Total	Mean (SE)	Median	Range
<i>Alosa aestivalis</i>	23	4.9	110	< 0.01	0.23 (0.09)	85.5	47–212
<i>Alosa pseudoharengus</i>	4	0.85	20	< 0.01	0.04 (0.03)	72	62–81
<i>Alosa sapidissima</i>	2	0.43	4	< 0.01	0.01 (0.01)	98	84–102
<i>Alosa</i> spp.	9	1.92	65	< 0.01	0.14 (0.11)	97	26–132
<i>Alpheus</i> spp.	3	0.64	7	< 0.01	0.01 (0.01)	14	13–16
<i>Anchoa hepsetus</i>	11	2.35	25	< 0.01	0.05 (0.02)	68	19–94
<i>Anchoa mitchilli</i> (20)	75	15.99	1,378	0.06	2.94 (0.81)	43	18–62
<i>Anchoa</i> spp.	1	0.21	1	< 0.01	0 (0)	42	42–42
<i>Anguilla rostrata</i>	12	2.56	13	< 0.01	0.03 (0.01)	335	194–550
<i>Archosargus probatocephalus</i>	1	0.21	2	< 0.01	0 (0)	18	18–18
<i>Astroscopus</i> spp.	1	0.21	1	< 0.01	0 (0)	26	23–29
<i>Bairdiella chrysoura</i> (12)	64	13.65	8,899	0.36	18.97 (5.1)	51	11–131
<i>Brevoortia tyrannus</i> (10)	197	42.00	35,680	1.43	76.08 (17.91)	46	19–155
<i>Callinectes</i> spp. (16)	406	86.57	3,707	0.15	7.9 (0.52)	29	2–171
<i>Caranx hippos</i> (18)	122	26.01	2,195	0.09	4.68 (0.9)	49	17–129
<i>Caranx latus</i>	3	0.64	5	< 0.01	0.01 (0.01)	56	45–74
<i>Centrarchus macropterus</i>	1	0.21	1	< 0.01	0 (0)	43	43–43
<i>Centropomus undecimalis</i>	9	1.92	18	< 0.01	0.04 (0.02)	76	48–97
<i>Chaetodipterus faber</i>	3	0.64	3	< 0.01	0.01 (0)	29	16–42
<i>Chasmodes bosquianus</i>	2	0.43	2	< 0.01	0 (0)	61	57–65
<i>Chloroscombrus chrysurus</i>	2	0.43	2	< 0.01	0 (0)	34.5	9–60
<i>Citharichthys spilopterus</i> (28)	92	19.62	319	0.01	0.68 (0.1)	40	11–122
<i>Cynoscion nebulosus</i>	47	10.02	1,31	0.01	0.28 (0.06)	76	30–139
<i>Cynoscion regalis</i>	5	1.07	5	< 0.01	0.01 (0)	56	24–65
<i>Cyprinodon variegatus</i> (13)	254	54.16	5,039	0.2	10.74 (1.74)	30	14–53
<i>Diapterus auratus</i> (23)	126	26.87	978	0.04	2.09 (0.33)	32	11–71
<i>Dormitator maculatus</i>	4	0.85	4	< 0.01	0.01 (0)	47	42–60
<i>Dorosoma cepedianum</i> (22)	92	19.62	1,041	0.04	2.22 (0.56)	71	41–205
<i>Dorosoma petenense</i> (14)	117	24.95	4,528	0.18	9.65 (2.84)	58	13–139
<i>Elops saurus</i> (17)	158	33.69	3,446	0.14	7.35 (0.95)	126	42–275
<i>Etropus crossotus</i>	18	3.84	32	< 0.01	0.07 (0.02)	30	17–70
<i>Eucinostomus</i> spp. (6)	223	47.55	65,852	2.64	140.41 (16.03)	45	11–95
<i>Evorthodus lyricus</i>	2	0.43	3	< 0.01	0.01 (0)	49	46–72
<i>Farfantepenaeus aztecus</i> (5)	221	47.12	81,180	3.25	173.09 (28.63)	21	2–71
<i>Farfantepenaeus duorarum</i> (19)	160	34.12	1,845	0.07	3.93 (0.61)	15	5–69
<i>Fundulus heteroclitus</i> (3)	420	89.55	193,762	7.76	413.14 (42.76)	41	8–94
<i>Fundulus luciae</i>	6	1.28	10	< 0.01	0.02 (0.01)	30	24–36
<i>Fundulus majalis</i> (8)	393	83.8	41,737	1.67	88.99 (8.64)	46	17–153
<i>Gambusia affinis</i> (29)	30	6.40	299	0.01	0.64 (0.25)	32	19–43
<i>Gobionellus boleosoma</i>	15	3.20	24	< 0.01	0.05 (0.02)	29.5	21–55
<i>Gobionellus oceanicus</i>	44	9.38	79	< 0.01	0.17 (0.03)	47	20–120
<i>Gobionellus shufeldti</i>	41	8.74	106	< 0.01	0.23 (0.05)	43.5	17–60
<i>Gobiosoma bosc</i>	27	5.76	40	< 0.01	0.09 (0.02)	35	17–81
<i>Hypsoblennius henz</i>	1	0.21	1	< 0.01	0 (0)	27	27–27
<i>Lagodon rhomboides</i> (11)	266	56.72	23,947	0.96	51.06 (7.36)	57	13–148
<i>Leiostomus xanthurus</i> (1)	393	83.8	1,542,059	61.75	3,287.97 (308.9)	48	8–173
<i>Litopenaeus setiferus</i> (2)	211	44.99	243,110	9.74	518.36 (83.32)	23	3–79

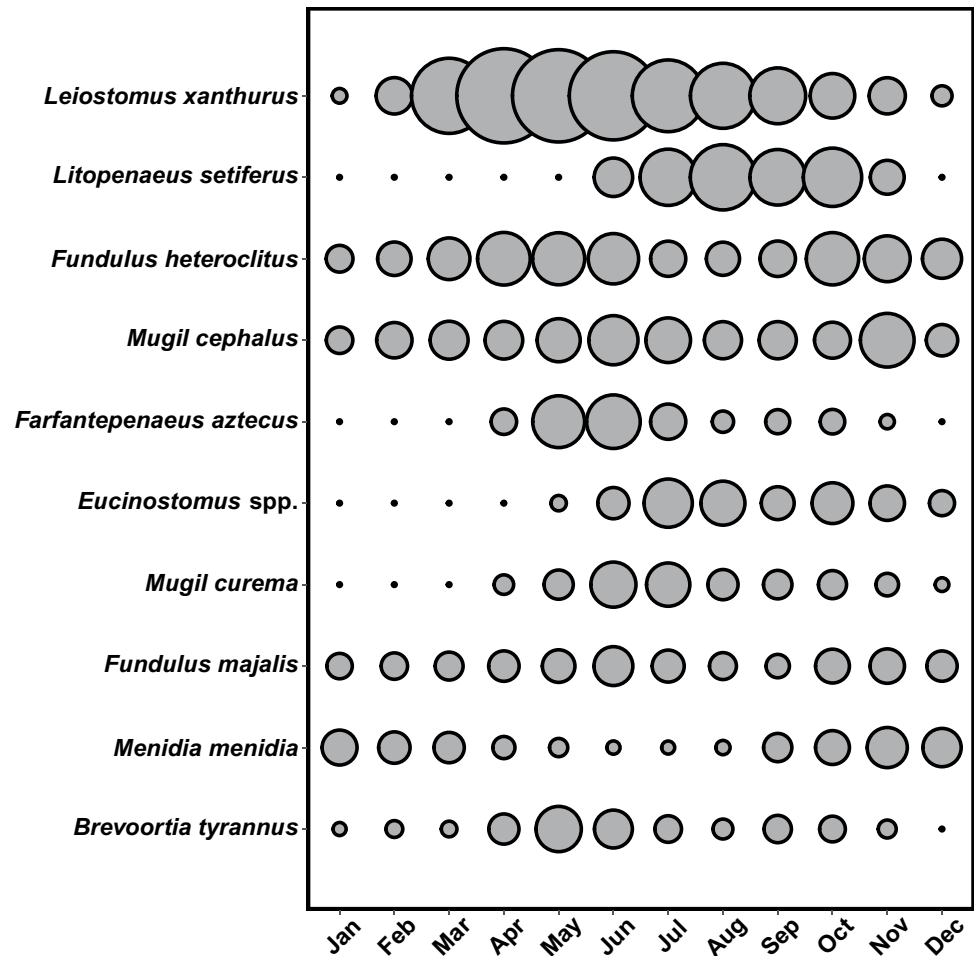
**Table 1** (continued)

Species	Occurrence		Abundance			Length (mm)	
	#	%	Total	% of Total	Mean (SE)	Median	Range
<i>Lolliguncula brevis</i>	11	2.35	20	< 0.01	0.04 (0.02)	28	15–59
<i>Lutjanus griseus</i>	21	4.48	31	< 0.01	0.07 (0.02)	30.5	14–75
<i>Megalops atlanticus</i>	19	4.05	56	< 0.01	0.12 (0.05)	195	116–258
<i>Membras martinica</i>	1	0.21	1	< 0.01	0 (0)	59	59–59
<i>Menidia beryllina</i> (15)	200	42.64	3,934	0.16	8.39 (1.26)	45	22–80
<i>Menidia menidia</i> (9)	277	59.06	39,796	1.59	84.85 (12.21)	59	17–97
<i>Menticirrhus</i> spp.	1	0.21	1	< 0.01	0 (0)	36	36–36
<i>Microgobius thalassinus</i>	9	1.92	11	< 0.01	0.02 (0.01)	33	23–39
<i>Micropogonias undulatus</i> (24)	80	17.06	820	0.03	1.75 (0.37)	52	12–158
<i>Morone americana</i> (26)	43	9.17	424	0.02	0.9 (0.28)	100	60–155
<i>Mugil cephalus</i> (4)	447	95.31	143,529	5.75	306.03 (70.8)	74	15–532
<i>Mugil curema</i> (7)	259	55.22	43,993	1.76	93.8 (17.91)	66	18–225
<i>Mycteroperca microlepis</i>	9	1.92	18	< 0.01	0.04 (0.01)	96	22–155
<i>Myrophis punctatus</i>	3	0.64	4	< 0.01	0.01 (0.01)	NA	NA
<i>Opisthonema oglinum</i>	2	0.43	10	< 0.01	0.02 (0.02)	52	50–73
<i>Orthopristis chrysoptera</i>	4	0.85	10	< 0.01	0.02 (0.01)	50	30–56
<i>Pagrus pagrus</i>	1	0.21	1	< 0.01	0 (0)	109.5	59–160
<i>Paralichthys dentatus</i> (30)	73	15.57	204	0.01	0.43 (0.08)	49.5	13–195
<i>Paralichthys lethostigma</i> (25)	113	24.09	461	0.02	0.98 (0.13)	77	14–320
<i>Paralichthys</i> spp.	41	8.74	193	0.01	0.41 (0.12)	19	10–65
<i>Poecilia latipinna</i>	18	3.84	32	< 0.01	0.07 (0.02)	40	22–56
<i>Pogonias cromis</i>	14	2.99	17	< 0.01	0.04 (0.01)	69	48–127
<i>Pomatomus saltatrix</i>	4	0.85	9	< 0.01	0.02 (0.01)	44	27–200
<i>Prionotus carolinus</i>	1	0.21	1	< 0.01	0 (0)	24	24–24
<i>Prionotus</i> spp.	12	2.56	14	< 0.01	0.03 (0.01)	22	14–40
<i>Prionotus tribulus</i>	1	0.21	1	< 0.01	0 (0)	23	23–23
<i>Sardinella aurita</i>	1	0.21	1	< 0.01	0 (0)	NA	NA
<i>Sciaenops ocellatus</i> (27)	94	20.04	408	0.02	0.87 (0.19)	47	18–355
<i>Selene vomer</i>	4	0.85	6	< 0.01	0.01 (0.01)	39	34–43
<i>Sphoeroides maculatus</i>	1	0.21	1	< 0.01	0 (0)	NA	NA
<i>Sphyraena borealis</i>	1	0.21	2	< 0.01	0 (0)	88	88–88
<i>Squilla empusa</i>	5	1.07	6	< 0.01	0.01 (0.01)	14	8–64
<i>Stephanolepis hispidus</i>	4	0.85	5	< 0.01	0.01 (0.01)	18	13–20
<i>Strongylura marina</i>	1	0.21	1	< 0.01	0 (0)	NA	NA
<i>Symphurus plagiusa</i> (21)	214	45.63	1,340	0.05	2.86 (0.27)	46	9–110
<i>Syngnathus fuscus</i>	2	0.43	2	< 0.01	0 (0)	NA	NA
<i>Syngnathus</i> spp.	1	0.21	1	< 0.01	0 (0)	NA	NA
<i>Synodus foetens</i>	11	2.35	19	< 0.01	0.04 (0.01)	70	34–90
<i>Trachinotus falcatus</i>	47	10.02	106	< 0.01	0.23 (0.05)	30	10–104
<i>Trinectes maculatus</i>	1	0.21	1	< 0.01	0 (0)	40	40–41
<i>Urophycis</i> spp.	2	0.43	2	< 0.01	0 (0)	40.5	39–42
All species combined	–	–	2,497,207	–	5394.40 (357.85)	47	2–550

Species are listed in alphabetical order and the 30 most abundant species are indicated with a number (rank 1–30) in parentheses after the scientific name. Occurrence # refers to the number of seine hauls in which a species was collected over the 19-year sampling period (total  $n = 469$ ), and occurrence % is the percentage of all hauls in which a species was collected. Total abundance (total) is the number of individuals collected across all seine hauls. The percent of total abundance (% of total) was calculated as number of individuals collected for a given species, divided by the total number of individuals collected, multiplied by 100. Mean abundance (with one standard error) is the mean number of individuals collected per seine haul for a species. Median length (mm) is standard length for fishes, cephalothorax length for shrimps, carapace width for crabs, and mantle length for squids. Length range is the minimum and maximum length collected for a given species



**Fig. 1** Mean monthly catch (number of individuals per seine haul) of the top 10 most abundant intertidal creek pool nekton species collected in Oyster Landing Creek in the North Inlet estuary, SC. The size of each circle is proportional to the monthly catch of each species, averaged across all 19 years of the study (1984–2002). Each circle represents between 37 and 42 samples. The top 10 species comprised 97.3% of the total number of individuals collected. Species are listed in descending order of abundance. The smallest dots indicate a species was absent (or nearly absent) during that month



the next most abundant species, accounting for 10% of the catch (Table 1). A greater than threefold difference in total catch was observed between the year of maximum (2000; 231,314) and minimum (1984; 71,065) abundances (Table 2). The number of species collected within a year ranged from a low of 38 in 1992 to a high of 50 in 1998 (Table 2).

Among the top 10 species collected overall, *F. heteroclitus*, *F. majalis*, and *M. cephalus* occurred in intertidal creek pool seine catches in considerable abundances throughout the year (Fig. 1). *Mugil cephalus* occurred in 95% of the year-round collections, and *F. heteroclitus* was present in 90%; they accounted for about 6% and 8% of the total catch, respectively (Table 1). In contrast, *Callinectes* spp. occurred in 87% of the collections but only made up < 0.2% of the total catch (Table 1). *Leiostomus xanthurus* occurred in the intertidal creek pool throughout the year, but exhibited the highest mean catches in April, May, and June (Fig. 1). *Fundulus heteroclitus* and *M. cephalus* had peaks in the spring and fall. *Mugil curema* occurred in greatest abundance in summer. *Fundulus majalis* had the most even pattern of abundance through the year. *Farfantepenaeus aztecus* used the pool mostly in May and June, then *L. setiferus* reached peak use from July to September; both

shrimps rarely occurred in intertidal creek pool catches during winter (Fig. 1). *Eucinostomus* spp. occurred in the intertidal creek pool from summer through fall (Fig. 1). *Menidia menidia* was the only top 10 species that was most abundant in the fall/winter. *Brevoortia tyrannus* occurred mostly in late spring and early fall, but occurred in every month (Fig. 1).

With a maximum length < 100 mm for most species and a median length of 47 mm for all species combined, the intertidal creek pool was used primarily by small nekton (Table 1). Overall length ranges were 8–550 mm for fishes, and 2–171 mm for invertebrates. Considering the ten most abundant nekton species, median lengths and length-frequency histograms indicated that most individuals collected were young-of-the-year, with the exception of some larger individuals representing other year classes of *L. xanthurus*, *M. cephalus*, and *B. tyrannus* (Table 1; Figs. S3–S12). Successive increases in length distributions over periods of months indicated apparent growth during the different periods of intertidal creek pool use (Figs. S3–S12). Two cohorts of *L. xanthurus* and *M. cephalus* occurred from January through June (Figs. S3 and S6).

GAMM predictions provided strong evidence of seasonality in all five of the assemblage metrics calculated (Fig. 2,

Table S1). In addition, model predictions generally aligned with observed values (raw means of the calculated metrics aggregated at the monthly or annual level). Specifically, day of year was a statistically significant predictor of all five metrics, and predicted values varied non-linearly within a given year (all five metrics  $P < 0.001$ , and effective degrees of freedom  $> 1$ ). For total catch, the low abundance (small catches) in winter was followed by a peak in mid to late spring, before decreasing steadily from summer into fall and winter. Biomass showed a similarly dome-shaped response over the year, with a peak somewhat later, in late spring to early summer. Species richness was lowest in winter, increased in spring, and remained high until early fall. The Shannon index was lowest in early spring, and gradually rose to a peak in early fall. Evenness remained at roughly the same level for much of the year, though a noticeable decrease was observed from winter to spring (Fig. 2).

Similarly, though our modeling approach prevented full statistical examination of seasonal trends, fitted GAMMs did provide substantial evidence in support of seasonal variation in the catch of the top 5 most abundant species (Fig. 3, Table S2). Day of year was a statistically significant and non-linear predictor of catch for all five species examined. For *L. xanthurus*, *M. cephalus*, *F. aztecus*, and *F. heteroclitus*

Fig. 2 Seasonal (left column) and annual (right column) trends for the study period (1984–2002) in total catch (number of individuals per haul), biomass (total wet weight per haul; only 1985–2002), species richness (number of species per haul), Shannon index, and evenness from intertidal creek pool nekton collections in Oyster Landing Creek in the North Inlet estuary, SC. Lines are predicted trends estimated from fitted generalized additive mixed models (GAMMS), and gray bands show simultaneous 95% confidence intervals. Points are means per seine haul for each response, aggregated by month (left column) or year (right column). Seasons delineated with vertical dashed lines and text labels in upper region of each plot to assist with interpretation. Seasons were defined as: January–March (Winter), April–June (spring), July–September (summer), October–December (fall). The approximate significance of smooth term estimated by GAMM ( $P$ -value) and the effective degrees of freedom (e.d.f.) are reported for each model

during their seasons of greatest abundance (i.e., spring and summer; April–September), larger predicted catches in spring were followed by declines leading into summer. For *L. setiferus*, examined during its seasons of greatest abundance (i.e., summer and fall; July–December), predicted catches in summer exceeded those of the fall.

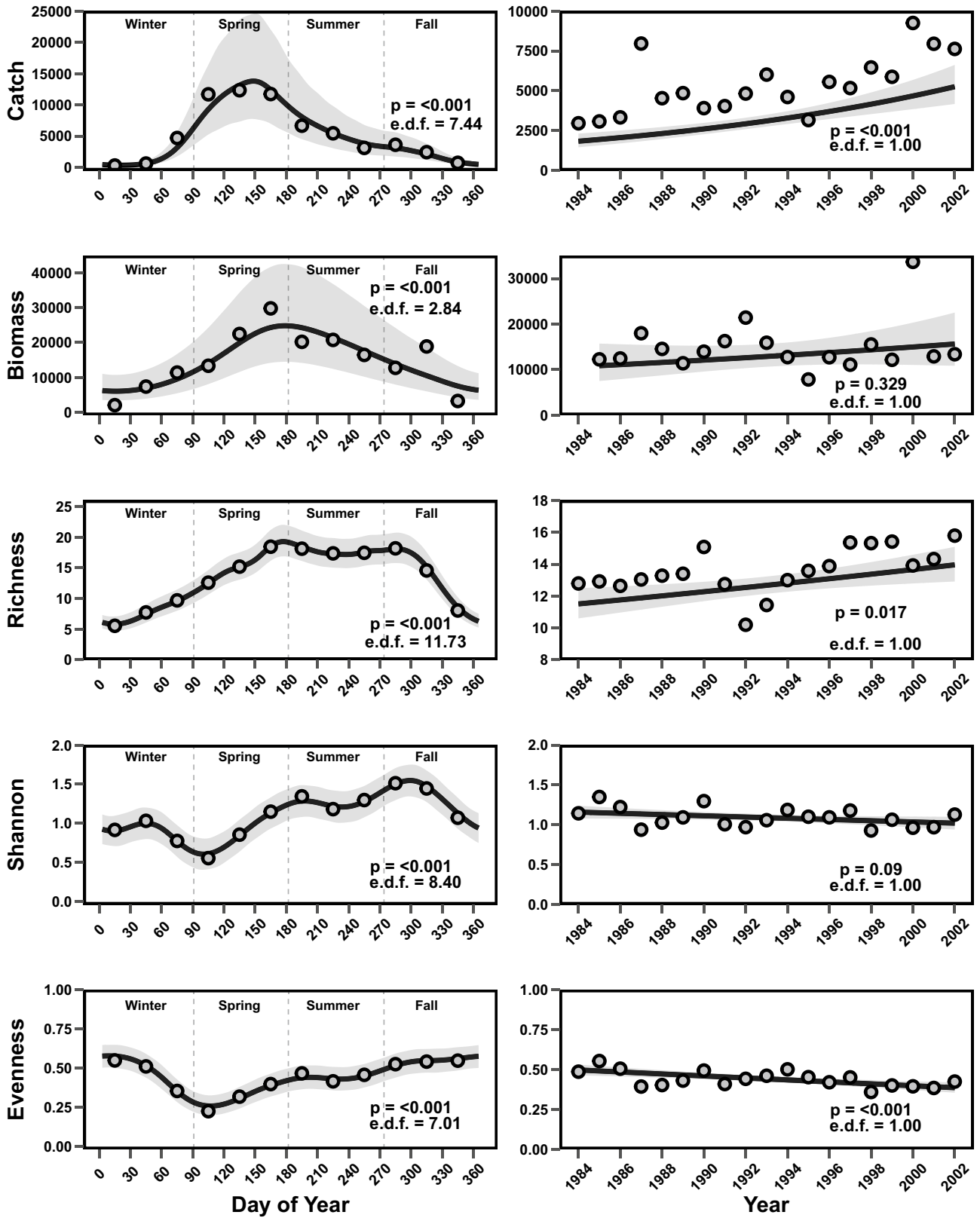
The fitted GAMMs also provided evidence of inter-annual trends (Fig. 2). Year was a statistically significant ( $P < 0.05$ ) and linear predictor in the fitted total catch, richness, and evenness GAMMs (Fig. 2, Table S1). Annual catch increased significantly

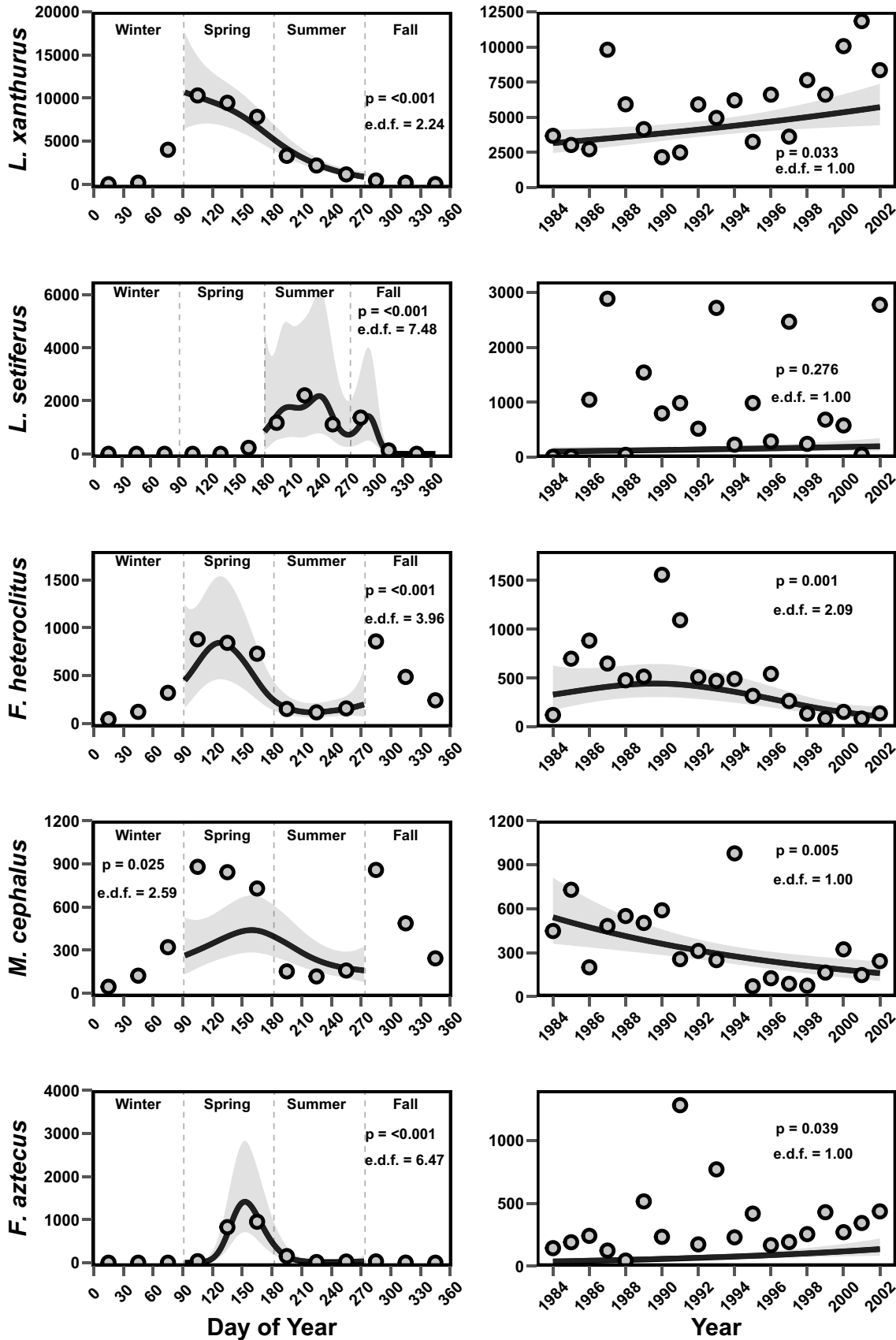
**Table 2** Summary of annual sampling effort and nekton collections in an intertidal creek pool in Oyster Landing Creek in the North Inlet estuary, SC, for the 19-year study period (1984–2002)

Year	Seines	Species	Total catch	% of Total catch	Top 5 species				
					1	2	3	4	5
1984	24	44	71,065	89	<i>L. xanthurus</i>	<i>M. cephalus</i>	<i>F. heteroclitus</i>	<i>F. majalis</i>	<i>B. chrysoira</i>
1985	25	41	76,918	87.5	<i>L. xanthurus</i>	<i>M. cephalus</i>	<i>F. heteroclitus</i>	<i>F. majalis</i>	<i>B. tyrannus</i>
1986	25	45	83,267	87.3	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>L. setiferus</i>	<i>B. chrysoira</i>	<i>M. cephalus</i>
1987	24	39	191,036	96	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>F. heteroclitus</i>	<i>M. cephalus</i>	<i>Eucinostomus</i> spp.
1988	25	42	113,331	91.2	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>M. cephalus</i>	<i>B. tyrannus</i>	<i>Eucinostomus</i> spp.
1989	25	45	121,274	86	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>B. tyrannus</i>	<i>F. heteroclitus</i>	<i>M. cephalus</i>
1990	25	46	97,769	86.9	<i>F. heteroclitus</i>	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>M. cephalus</i>	<i>M. curema</i>
1991	24	48	96,873	90.4	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>F. aztecus</i>	<i>L. setiferus</i>	<i>M. cephalus</i>
1992	25	38	120,608	88.6	<i>L. xanthurus</i>	<i>M. curema</i>	<i>F. heteroclitus</i>	<i>L. setiferus</i>	<i>M. cephalus</i>
1993	25	39	150,357	87.3	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>F. heteroclitus</i>	<i>F. aztecus</i>	<i>Eucinostomus</i> spp.
1994	25	39	115,187	92.2	<i>L. xanthurus</i>	<i>M. cephalus</i>	<i>F. heteroclitus</i>	<i>L. setiferus</i>	<i>Eucinostomus</i> spp.
1995	24	44	75,880	90.4	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>F. heteroclitus</i>	<i>F. aztecus</i>	<i>Eucinostomus</i> spp.
1996	25	42	138,872	87.9	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>M. menidia</i>	<i>L. rhomboides</i>	<i>L. setiferus</i>
1997	25	48	129,228	91.7	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>F. heteroclitus</i>	<i>Eucinostomus</i> spp.	<i>L. rhomboides</i>
1998	25	50	161,558	89.5	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>B. tyrannus</i>	<i>M. menidia</i>	<i>L. rhomboides</i>
1999	24	46	141,005	91.6	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>M. menidia</i>	<i>F. aztecus</i>	<i>Eucinostomus</i> spp.
2000	25	41	231,314	94.2	<i>L. xanthurus</i>	<i>M. cephalus</i>	<i>F. heteroclitus</i>	<i>L. setiferus</i>	<i>Eucinostomus</i> spp.
2001	25	44	198,676	94.4	<i>L. xanthurus</i>	<i>F. heteroclitus</i>	<i>Eucinostomus</i> spp.	<i>F. aztecus</i>	<i>M. cephalus</i>
2002	24	40	182,989	92.2	<i>L. xanthurus</i>	<i>L. setiferus</i>	<i>F. aztecus</i>	<i>M. cephalus</i>	<i>Eucinostomus</i> spp.

Seines are the number of seine hauls within a year (January–December). Species is the number of species collected and total catch is the total number of individuals collected within a year. Percent (%) of total catch is the percentage of the catch made up by the top 5 most abundant species that year. The top 5 most abundant species are listed in rank order for each year







**Fig. 3** Seasonal (left column) and annual (right column) trends in catch of the top 5 most abundant species for the study period (1984–2002) from intertidal creek pool nekton collections in Oyster Landing Creek in the North Inlet estuary, SC. Lines are predicted trends estimated from fitted generalized additive mixed models (GAMMS), and gray bands show simultaneous 95% confidence intervals. Points are means for each response, aggregated by month (left column) or year (right column). Seasons delineated with vertical dashed lines and text labels in upper region of each plot to assist with interpretation. Seasons were defined as: January–March (winter), April–June (spring), July–September (summer), October–December (fall). The approximate significance of smooth term estimated by GAMM ( $P$ -value) and the effective degrees of freedom (e.d.f.) are reported for each model. To improve model precision, catches for all species but *L. setiferus* were modeled in spring and summer only; *L. setiferus* catches were modeled in summer and fall

from 1984 to 2002, though the uncertainty associated with these estimates (and with the variance in the raw data) increased over time and the fitted GAMM consistently yield conservative predictions of total catch, relative to observed values (Fig. 2). Predicted total biomass displayed an increasing trend, but this term was not significant in the fitted GAMM. Richness exhibited a significant increasing trend across years, whereas evenness exhibited a significant decrease. The predicted Shannon index declined across years, though year was not a statistically significant term in the fitted GAMM ( $P = 0.09$ ).

The relationship between year and catch was statistically significant for 4 of the top 5 species, though the correspondence of model predictions with observed values (raw means of the calculated metrics aggregated at the annual level) varied considerably by species (Fig. 3). *Farfantepenaeus aztecus* and *L. xanthurus* catches displayed an increasing, linear trend over time. Predicted catches of *M. cephalus* decreased in a linear fashion across years, whereas *F. heteroclitus* catches demonstrated a non-linear, declining trend in the predicted catch. Specifically, model predictions for *F. heteroclitus* showed a dome-shaped relationship over the 19-year period, with lowest values in the late 1990s and early 2000s. A statistically significant long-term trend was not observed in predicted *L. setiferus* catches. In addition, the scale of model predictions for *L. setiferus* differed considerably from that of the observed values, which showed signs of substantial year-to-year variation across the time series (Fig. 3).

### Nekton Assemblages

The structure of intertidal creek pool nekton assemblages also exhibited strong seasonality across years, indicated by clustering of points in the NMDS ordination by season (Fig. 4). Season was a significant factor in explaining dissimilarity among overall assemblage composition (PERMANOVA,  $R^2 = 0.296$ , pseudo- $F = 77.073$ ,  $P < 0.001$ , Table S3), and all pairwise tests ( $n = 6$  total) indicated significant differences between

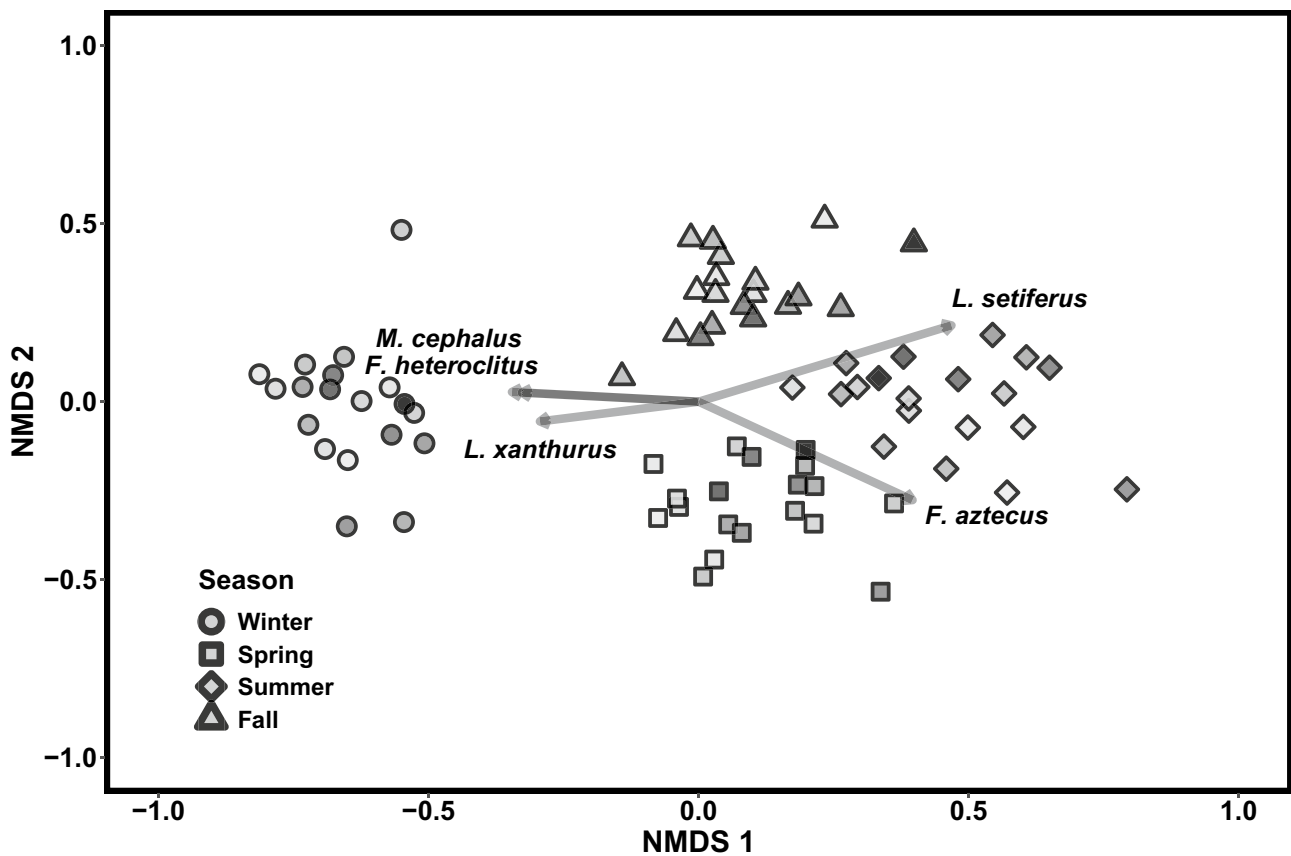
seasons (all  $P < 0.01$ , Table S4). When overlaid on the NMDS ordination, species scores for *L. xanthurus*, *F. aztecus*, and *L. setiferus* aligned with winter/spring, spring/summer, and summer/fall, respectively, while *M. cephalus* and *F. heteroclitus* were associated primarily with winter. NMDS ordination also provided evidence of inter-annual changes in the structure of nekton assemblages (Fig. 5). Earlier years (e.g., 1984, 1985) were separated from later years (e.g., 1997, 2002) along the first ordination axis. Intervening years were arrayed in between, with some deviation from this general pattern. *Leiostomus xanthurus* and *L. setiferus* species scores also showed some alignment with the later years of the time series. *Farfantepenaeus aztecus* species scores showed some alignment with the mid-to-late 1990s. Time period was not a significant factor in explaining the dissimilarity of the overall assemblage composition among years, however (PERMANOVA,  $R^2 = 0.025$ , pseudo- $F = 6.01$  0.875,  $P = 0.483$ , Table S5).

### Environmental Conditions

Mean observed water temperatures were typical of warm-temperate estuaries in the southeastern US, rising in spring, peaking around  $\geq 30$  °C in early summer, and declining through fall to annual lows of 10–15 °C in winter (Fig. 6). No long-term patterns were apparent for either water temperature or salinity via visual examination. Average salinity fluctuated through the year, with the lowest salinities occurring in winter and then hovering around 20 for much of the spring, summer, and fall, with notable drops in salinity in late summer and again in late fall. Annual means for water temperature were largely consistent over the 19-year study period, while annual mean salinities varied considerably from a low of 10.9 in 1992 and a high of 25.9 in 2001, although no clear pattern emerged (Fig. 6).

### Nekton Correlations with Environmental Conditions

In the overall analyses using all sampling dates ( $n = 445$  for biomass,  $n = 469$  for all other metrics), abundance, biomass, richness, and the Shannon index were positively correlated (Spearman's  $\rho$  estimates) with both water temperature and salinity measured at the time of sampling, though the value of  $\rho$  varied considerably among metrics (Table 3). In general, correlations with water temperature were more strongly positive than with salinity. Evenness was negatively correlated with water temperature, and there was no evidence of a significant relationship with salinity. Positive significant correlations were demonstrated for each of the five most abundant species with both water temperature and salinity. The estimated  $\rho$  values for water temperature exceeded that of salinity for all species except *F. heteroclitus* where the estimated value for salinity was greater than that for water temperature (Table 3).



**Fig. 4** Non-metric multidimensional scaling of the intertidal creek pool nekton assemblages from Oyster Landing Creek in the North Inlet estuary, SC, by season and year for the study period (1984–2002). Different symbol shapes represent season, and darker symbols indicate later years. Arrows represent the species scores for the five most abundant nekton

species overall. Ordination performed using a matrix consisting of mean catch values of all 88 nekton species, aggregated by season and year. Seasons defined as follows: January–March (winter), April–June (spring), July–September (summer), October–December (fall). Two-dimensional stress = 0.13

In Spearman rank tests between the annual values of the five assemblage metrics and average annual water temperature and salinity, no statistically significant relationships were revealed (Table 4). Correlation tests between the annual averages of the top five species and corresponding annual averages for water temperature and salinity indicated one statistically significant relationship, between *F. aztecus* and water temperature (Table 4). While not significant at  $\alpha = 0.05$ , there was some suggestion of a positive correlation between mean annual water temperature and the annual average abundance of *L. setiferus* and the average annual richness estimate (both  $P < 0.1$  but greater than  $P > 0.05$ ).

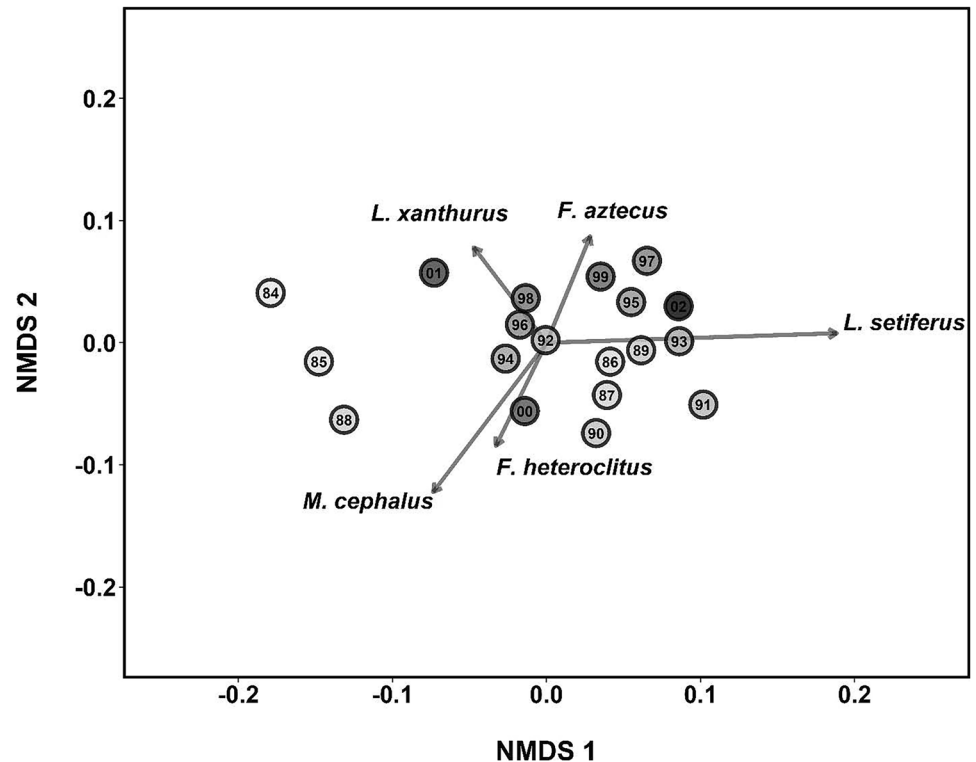
## Discussion

Year-round sampling of an intertidal creek pool over a period of 19 years demonstrated use of the pool by a diverse group of species, primarily small year-round residents (e.g., *F. heteroclitus*) and similarly sized young-of-the-year transient fishes and shrimps (e.g., *L. xanthurus*, *L. setiferus*). We are aware of no

other contemporary studies of intertidal creek habitats in southeastern US Atlantic estuaries to make comparisons of long-term seasonal and annual trends in nekton habitat use. However, the species composition was similar to those reported for other shallow salt marsh habitats in estuaries along the southeastern US Atlantic (Dahlberg 1972; Cain and Dean 1976; Shenker and Dean 1979; Bozeman and Dean 1980; Reis and Dean 1981; Crabtree and Dean 1982; Allen et al. 2007, 2017) and Gulf coasts (Turner and Johnson 1972; Swingle and Bland 1974; Subrahmanyam and Drake 1975; Subrahmanyam and Coultas 1980). Thus, the consistent and sustained use of intertidal creek pools by numerous ecologically and economically important species indicates that these habitats should be considered a valuable component of the estuarine mosaic for nekton.

Nekton using the intertidal creek pool exhibited predictable seasonal peak patterns of occurrence and a sequence of succession as various species arrived, grew, and left the intertidal basin during the year. Strong positive relationships observed between most assemblage metrics, and water temperature and salinity at the time of sampling, reflect the distinct seasonality

**Fig. 5** Non-metric multidimensional scaling of the intertidal creek pool nekton assemblages from Oyster Landing Creek in the North Inlet estuary, SC, by year for the study period (1984–2002). Point labels and shading indicate years; darker circles indicate later years. Arrows represent the species scores for the five most abundant nekton species overall. Ordination performed using a matrix consisting of annual mean values of all 88 nekton species. Two-dimensional stress = 0.14

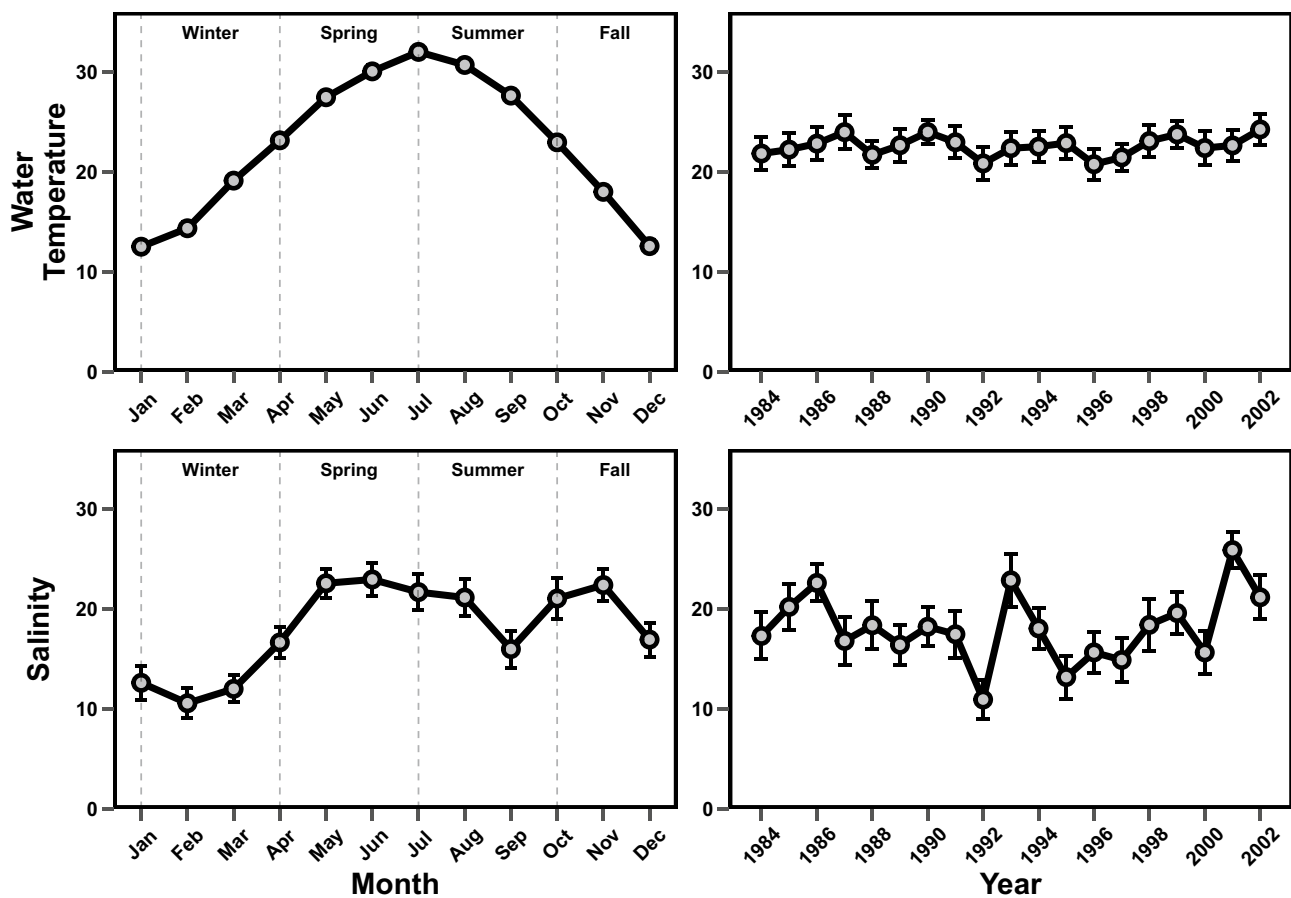


of this warm-temperate intertidal creek habitat. Coupled with the numerical dominance of the assemblage by a small number of resident and juvenile transient species, the patterns of salt marsh intertidal creek pool use by nekton in the North Inlet estuary generally aligns with observations of intertidal creek nekton assemblages over various temporal scales in other estuaries in North America (e.g., Desmond et al. 2000; Kimball and Able 2007a, b) and worldwide: Africa (Paterson and Whitfield 1996, 2000, 2003; LeQuesne 2000; Wanjiru et al. 2021; Asare and Javier 2022), Asia (Jin et al. 2007, 2010, 2014; Quan et al. 2009; Krumme et al. 2015), South America (Barletta et al. 2003; Giarrizzo and Krumme 2007), and Europe (Cattrijsse et al. 1994; Salgado et al. 2004; Koutsogiannopoulou and Wilson 2007; Friese et al. 2021). The stability of the nekton assemblage composition and dominant species over the duration of our 19-year study matches observations of assemblages from other long-term studies of intertidal creek nekton that we are aware of. Over seven and nine-year periods (1999–2005 and 1996–2004) of seasonal (May–November) observations of salt marsh intertidal creek nekton in multiple northeastern US Atlantic estuaries, assemblages were annually consistent and dominated by a small number of many of the same species observed in the North Inlet estuary intertidal creek pool (e.g., *F. heteroclitus*, *M. menidia*, *L. xanthurus*, *B. tyrannus*; Able et al. 2008; Kimball et al. 2010). Mangrove intertidal creek nekton displayed a similarly stable pattern of assemblage composition when compared at the beginning (1999) and end (2012) of a

14-year period in a north Brazil estuary, where the assemblage was dominated by small number ( $n = 7$ ) of abundant species during each year (Castellanos-Galindo and Krumme 2014). Considered together, despite major differences in physical settings and environmental conditions, these studies indicate that intertidal creeks provide important roles for nekton throughout the estuaries of the world (Krumme et al. 2014).

While some characteristics of the assemblage composition remained steady over the study period, our analyses also revealed both considerable inter-annual variation and significant longer-term changes in numerous aspects of the assemblage. Many of these trends were likely linked to changes in the abundance of dominant species over the study period. Given the numerical dominance of *L. xanthurus* in the overall assemblage, increases in annual catches of this species likely drove some of the corresponding increase in overall catches. Similarly, declining catch size of *F. heteroclitus* and *M. cephalus*, together with the increase in *L. xanthurus* catches likely contributed as well to the decline in estimated evenness across years. The significant increase in richness coincided with the increase in total catch over the period. Biomass per haul was one of the few metrics that did not exhibit significant directional change during the 19-year study period, despite the increase in total catch (overall) and the total catch of *L. xanthurus*. This counter-intuitive result (one might expect more individuals to amount to more biomass) requires further exploration. One





**Fig. 6** Monthly (left column) and annual (right column) means ( $\pm 1$  standard error) in intertidal creek pool water temperature ( $^{\circ}\text{C}$ ) and salinity for the study period (1984–2002) in Oyster Landing Creek in the North Inlet estuary, SC. Points are means of each variable measured at the time of sampling, aggregated by month (left column) or year (right column). Seasons delineated with vertical dashed lines and text labels

in upper region of each plot to assist with interpretation. Seasons were defined as follows: January–March (winter), April–June (spring), July–September (summer), October–December (fall). Sample size for each point is between 37 and 42 for the monthly (left column) figures, and 24–25 for the annual (right column) figures

explanation could be related to year-to-year variations in year class strength, which could result in density-dependent differences in individual growth. In years with high numbers of young, slower growth could result in less biomass per individual than in years when fewer individuals occupied the habitat. Also, it is possible that a carrying capacity existed for the pool at low tide, and a self-regulating system existed among nekton choosing to remain in the pool so that the space and perhaps dissolved oxygen availability was not exceeded during the pool's isolation for one to several hours. If biomass was a stronger determinant of capacity than numbers, variations in biomass within the pool could be less than those for numbers of individuals. Support for this idea comes from many years of observations that never included a mass mortality (or even obvious stress) among nekton isolated in the pool even on hot summer days.

Results of this study also point to the influence of short-term disturbances, such as hurricanes and severe local storms, on the

intertidal creek pool nekton assemblage. The passage of hurricanes can affect salt marsh nekton communities via numerous mechanisms, including rapid changes in water temperature, salinity, and dissolved oxygen, as well physical alteration to habitat (Allen et al. 2017, Oakley and Guillen 2019). The single biggest perturbation to the study area occurred in September 1989, when the wave action and storm surge from Hurricane Hugo scoured most of the mud off of the marsh surface and from the intertidal creek bed (Gardner et al. 1992, DMA, pers. comm.). Although the main structural configuration of the intertidal creek pool did not change greatly, the loss of fine sediment (i.e., pluff mud) and associated high densities of infauna persisted through the following spring and summer (DMA, pers. comm.). While 1990 did not stand out as an unusual year for total nekton abundance or biomass, it was the lowest abundance year for *L. xanthurus* and the only year during which *L. xanthurus* did not rank first among all species. The highest abundance for *F. heteroclitus* was in 1990, and it ranked first

**Table 3** Results (test statistics and *P*-values) of Spearman rank order correlation tests between environmental variables at the time of sampling, assemblage metrics, and species-specific catch totals from an intertidal creek pool in Oyster Landing Creek in the North Inlet estuary, SC, for the 19-year study period (1984–2002)

	Water temperature		Salinity	
	Spearman's $\rho$	<i>P</i>	Spearman's $\rho$	<i>P</i>
Assemblage metrics				
Total catch	0.688	< 0.001	0.383	< 0.001
Total biomass	0.687	< 0.001	0.346	< 0.001
Richness	0.740	< 0.001	0.374	< 0.001
Shannon	0.114	<b>0.013</b>	0.161	< 0.001
Evenness	−0.229	< 0.001	0.007	0.876
Species catch				
<i>Leiostomus xanthurus</i>	0.681	< 0.001	0.230	< 0.001
<i>Litopenaeus setiferus</i>	0.563	< 0.001	0.186	< 0.001
<i>Fundulus heteroclitus</i>	0.282	< 0.001	0.386	< 0.001
<i>Mugil cephalus</i>	0.423	< 0.001	0.314	< 0.001
<i>Farfantapenaeus aztecus</i>	0.689	< 0.001	0.332	< 0.001

All samples ( $n = 469$ ) were used for all tests except total biomass ( $n = 445$ ). Bolded values indicated statistical significance ( $p < 0.05$ )

among all species collected. Although many factors determine the abundance of species in the estuary, differences in the feeding ecology of these two species could be responsible for the opposite responses to the change in habitat. Juvenile *L. xanthurus* sieve out meiofauna in mouthfuls of soft sediment (Stickney et al. 1975; Archambault and Feller 1991), whereas *F. heteroclitus*

**Table 4** Results (test statistics and *P*-values) of Spearman rank order correlation tests between the annual average of environmental variables measured at the time of sampling and annual averages of the assemblage metrics and species-specific catches from an intertidal creek pool in Oyster Landing Creek the North Inlet estuary, SC, for the 19-year study period (1984–2002)

	Water temperature		Salinity	
	Spearman's $\rho$	<i>P</i>	Spearman's $\rho$	<i>P</i>
Assemblage metrics				
Total catch	0.200	0.410	0.106	0.665
Total biomass	0.038	0.882	0.002	0.993
Richness	0.391	0.099	0.050	0.839
Shannon	−0.070	0.776	0.105	0.668
Evenness	−0.211	0.385	0.030	0.903
Species catch				
<i>Leiostomus xanthurus</i>	0.063	0.798	0.110	0.655
<i>Litopenaeus setiferus</i>	0.454	0.052	−0.077	0.753
<i>Fundulus heteroclitus</i>	0.019	0.940	−0.140	0.576
<i>Mugil cephalus</i>	−0.042	0.866	0.051	0.836
<i>Farfantapenaeus aztecus</i>	<b>0.481</b>	<b>0.039</b>	0.295	0.220

All years ( $n = 19$ ) were used for all tests except total biomass ( $n = 18$ ). Bolded values indicated statistical significance ( $P < 0.05$ )

can consume epibenthic invertebrates and insects when infauna resources are scarce (Thompson 2015).

Longer-term changes in the intertidal creek pool assemblage during the 19-year study period may have been driven, at least in part, by changes in geomorphology and hydrology of the creek pool itself. Following Hurricane Hugo (> 1989), an intertidal oyster reef at the downstream edge of the pool increased in height (DMA, pers. comm.). That resulted in a slower and less directed water flow through the pool with the ebbing tide, and the accumulation of more fine sediment in the pool (e.g., Colden et al. 2016; Southwell et al. 2017). This likely resulted in an increase in benthos and suitable foraging area for *L. xanthurus*, *L. setiferus*, *F. aztecus*, and other consumers of small infauna when more elevated intertidal areas were no longer accessible. The higher oyster reef also appeared to favor retention of tidal migratory nekton in the pool by discouraging movement down the creek at an earlier stage of the ebbing tide. These and other local changes could be largely responsible for the overall increase in total abundance of nekton in the study area over the years. Similarly, these local changes may have influenced catchability of nekton within the pool, contributing to the observed increase in species richness over the study period as well. This possibility speaks to the challenges of long-term studies that use a single or few sites; while somewhat easier to sustain from a logistical perspective, changes in the collected assemblage data can be driven largely (or in part) by changes at the sampling site itself. In future studies, efforts to quantify changes in hydrogeomorphological features that appear most likely to affect nekton species and assemblages are likely to provide a better understanding of factors influencing the use of habitat by nekton (e.g., Allen et al. 2007).

Though the results of a single-site study like ours must be interpreted with some caution, several characteristics of the

sampling program and field site itself serve to mitigate some of the drawbacks of single-site sampling, and also lend significance to the work. One is the lengthy temporal nature (nearly two decades) of the study and its remarkable consistency of sampling effort over the study period (three of the five coauthors participated in over 95% of the 469 sampling events). The lack of studies in which salt marsh nekton have been sampled at even one site, let alone multiple sites, frequently over many consecutive years is a reflection of the considerable funding costs and logistical challenges of such efforts, and makes the existence of a long-term dataset such as ours unique. Second is the dynamic nature of intertidal creek habitats themselves. Specifically, the North Inlet estuary experiences two high tides and two low tides each day with a range of 1.4 m; thus, intertidal creeks experience near constantly changing conditions except for short periods around slack high tide and slack low tide. Between each sampling event, the intertidal creek pool experienced ~28 tidal cycles without human disturbances, and factors such as water temperature, salinity, flow, and depth fluctuated at smaller time scales (e.g., hours) during the ebb and flood portions of each tide. Nekton in intertidal creeks moved into, out of, and around the creeks in response to these dynamic conditions as well. In many ways, the aquatic environment and nekton assemblage at the site were effectively “reset” during the approximate two weeks between each sampling event, thus increasing the relative independence of each consecutive sample. Third, our study builds on a previous study in the North Inlet estuary in which eight intertidal creeks were sampled synoptically for 2 years (Allen et al. 2007). Their observation that patterns of seasonal and inter-annual use by nekton were similar among creeks provides additional justification for our focus on a single creek in order to better understand variations in nekton use and relationships with changing environmental conditions at a finer temporal scale over many years.

Though our results indicated a relatively predictable assemblage over the 19-year study period (likely reflecting the generally consistent environmental conditions across most years), nekton assemblages could become less stable when experiencing more variable environmental conditions. As a result of observed significant increases in atmospheric temperature and changes in precipitation (salinity) in the southeastern US region in recent decades (e.g., Kimball et al. 2020), the use of intertidal creek pools by nekton could be expected to change. Moreover, given the influence of the major disturbance event (Hurricane Hugo) on dominant taxa use of the pool during the study period, the increase in frequency and severity of storms in recent decades could be expected to have significant effects on intertidal creek pool nekton assemblages. The strength of future analyses will be enhanced by ongoing studies underway in this intertidal creek system; work in another nearby pool in this creek will extend the time series in an effort to also investigate longer-term (e.g., 40 years) changes in the phenology

(timing of migrations and reproduction) and growth of species during their occupancy of this estuarine habitat. Conducting these studies over long time periods (decades) in an estuary that is minimally impacted by local human activities should provide more insights into nekton assemblages and community dynamics in relation to regional and global natural phenomena related to climate change, such as sea-level rise, warming winter water temperatures, and increased frequency of extreme weather (e.g., Allen et al. 2008).

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