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ORIGINAL PAPER

Tidal management affects sub-adult fish assemblages in impounded South Carolina marshes

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Abstract In coastal South Carolina, most impounded marshes are managed for waterfowl; fewer are managed for fishes. Tidal control is central to each strategy but raises concerns that nursery function could be impaired. This research examined the assemblage composition of fishes during early-life stages. We sampled two impoundments of each management type monthly in 2008 and 2009. We used light traps to collect 61,527 sub-adult fish representing 21 species and 16 families and push nets to collect 12,670 sub-adult fish representing 13 species and 11 families. The effective number of species detected at larval stage in "fish" impoundments (summer mean = 2.52 ± 0.20, winter mean = 2.02 ± 0.66) was greater than in "waterfowl" impoundments (summer mean = 1.27 ± 0.14, winter mean = 1.06 ± 0.09); CI = 90 %. Species richness did not differ between management types, but hierarchical linear models predicted differences in assemblage composition. These findings underscore the importance of frequent water exchange for maintaining diverse assemblages of early-life-stage fishes in marsh impoundments.

Keywords Diversity · Early-life stages · Fragmentation · Impoundment · Light trap · Salt marsh

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Introduction

South Carolina's coastal wetland impoundments are valued as natural and cultural resources and have been the subject of public and scientific interest since the 1970s (Devoe et al. 1988; Tufford 2005). Milgarese and Sandifer (1982) identified two opposing concerns on the issue of marsh impoundment. On one side of this discussion are those who support the tidally restrictive management practices currently in favor because such management provides extensive resting, feeding, and nesting habitat for waterfowl, wading birds, and shore birds. On the other side are those who oppose the status quo because they believe that managed impoundments interrupt natural tidal cycles that are intimately linked with production of estuarine nekton (Milgarese and Sandifer 1982). Although multi-species management is increasingly *en vogue* in the conservation community, avifauna still trumps ichthyofauna in most marsh impoundment management plans in the Carolinas and Georgia (Devoe et al. 1988; Tufford 2005). This may be because the impoundment management techniques that enhance waterfowl habitat are well established and have been adopted by federal land management agencies, such as the U.S. Fish and Wildlife Service and private conservation organizations, such as Ducks Unlimited. Furthermore, researchers have demonstrated that the same techniques that promote waterfowl use are also attractive to other bird species. Wading birds, raptors, migrating shorebirds, and diving piscivores, such as cormorants and grebes all use the impoundments for food, refuge or both during some part of the year (Milgarese and Sandifer 1982; Nareff 2009). The effects of these management practices on fishes are less clear.

Marsh impoundment can have a variety of effects on aquatic habitat depending upon the management strategy in use. Marsh impoundments have been associated with lower dissolved oxygen concentration, decreased turbidity, increased sedimentation rate, increased salinity range, and barriers to movement (Wenner et al.1986; Montague et al. 1987). The net effect is a marked departure from the ecological characteristics of unrestricted tidal salt marsh. The effects of impoundments on different species of fishes may depend on whether their life cycle can be completed within estuarine wetlands (i.e., resident fishes) or requires use of habitat outside the estuary for reproduction or migration (i.e., transient or marine-transient fishes) (Robinson and Jennings 2014). The potential for impoundments to interrupt the export of biomass from the salt marsh to the open estuary is of particular concern (Kneib 2000).

Research concerning fishes in impoundments has characterized assemblages based on standing stock or flux (ingress and egress) of juveniles and adults, but relatively few investigations have targeted early life stages (Rogers et al. 1994). The only published work focusing specifically on larval fish in salt-marsh impoundments was conducted by McGovern and Wenner (1990) at Cat Island in Georgetown County, South Carolina. Our work differs in that it was carried out in impoundments alongside the mesohaline reaches of a riverine estuary 68 km from the ocean rather than a lagunal estuary near to the Atlantic confluence. In this spatial respect, our study impoundments are more representative of the majority of tidal wetland impoundments in South Carolina and Georgia.

The primary objective of this research was to compare the diversity and abundance of larval and juvenile fishes, hereafter "sub-adult", between impoundments managed for waterfowl and those managed for fishes. This knowledge is valuable given the history of conflict over the impoundment of tidal wetlands, increasing interest in ecosystem-based, multi-species management, and the relative paucity of information regarding early life stages of fishes within impoundments.

Materials and methods

Study area and sites

Our research was conducted in impoundments owned by Nemours Wildlife Foundation (NWF), which operates the 3966-ha Nemours Plantation in Beaufort County, South Carolina. Nemours Plantation is situated along the Combahee River and its impoundments are influenced by this waterway. The Combahee River drains an area of 414,203 ha and flows southeastwardly to St. Helena Sound (Upchurch and Wenner 2008) about 39 km downriver from Nemours (Fig. 1).

Nemours Wildlife Foundation manages the majority of its 809-ha of impounded marshes and wetlands with the primary goal of maximizing waterfowl habitat. Only two of the impoundments, accounting for about 11 % of the plantation's total impounded acreage, are managed with the primary objective of maximizing recreational fishing for red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and southern flounder (*Paralichthys lethostigma*). To allow for comparison between "waterfowl" impoundments and "fish" impoundments at Nemours, we selected two study sites representing each management type.

The two "waterfowl" impoundments are known as Nieuport (119 ha) and Big Rice Field (48 ha; Fig. 1). The perimeter of each of these areas is defined by an earthen dike and canal. Smaller canals penetrate the interior or "bed" of each impoundment. The bed

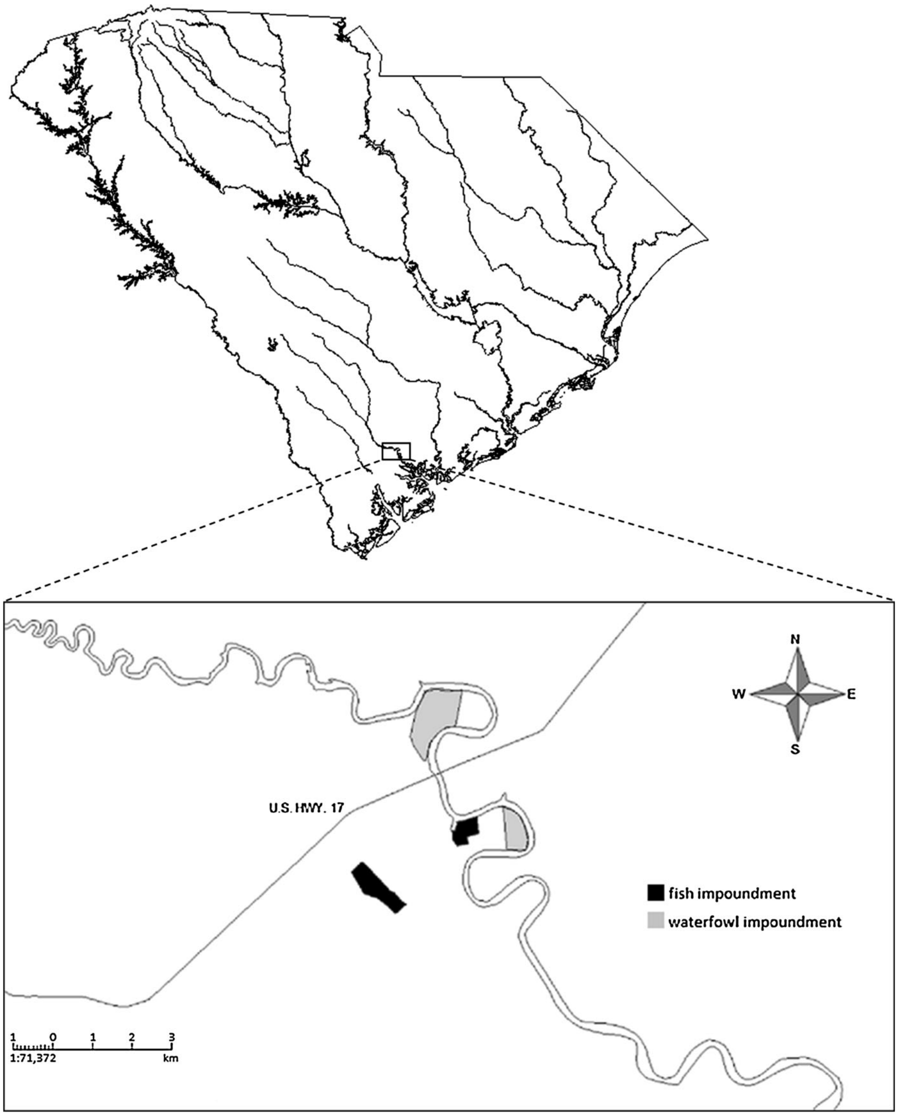

Fig. 1 The location of the four study sites during 2008 and 2009 at Nemours Plantation on the Combahee River above St. Helena Sound in coastal South Carolina, from West to East, the "fish" impoundments are Branford and Boss' Pond, the "waterfowl" impoundments are Nieuport and Big Rice Field

makes up most of the impounded area and is dominated by emergent vegetation. The bed may be exposed or submerged depending on the phase of the waterfowl-management cycle. These impoundments are drained partially in spring to reduce the water level to just above the surface of the bed. Another drawdown occurs in late summer to expose the bed, and emergent vegetation may be burned off at this time. Rapid flooding occurs in fall to prepare for the arrival of migrating waterfowl. These periods of draining and flooding to manipulate water levels are typically the only substantial exchange of water that occurs over the course of a year.

The two "fish" impoundments are Boss' Pond (30 ha) and Branford (61 ha; Fig. 1). The fish impoundments are managed to allow daily inundation by tidal water throughout the year. In effect, "waterfowl" impoundments restrict tidal exchange to a much greater degree than do "fish" impoundments.

Fish sampling and water quality measurements

We used quatrefoil light traps and a pushed plankton net ("push net") to collect sub-adult fishes from all four study sites once a month during July, August, November and December of 2008 and January through

June of 2009. The quatrefoil light trap (Floyd et al. 1984) is fished passively and takes advantage of the positive phototaxis of many early stage fishes to attract and contain them. Our traps were constructed of clear polycarbonate polymer and were designed to float on the surface while tethered to a small anchor. Trap entrance funnels were 4-mm wide and allowed larvae, juveniles, and adults of some species to enter the traps, which were powered by 6-V batteries connected to white Ever LED™ light-emitting-diode lamps.

Monthly sampling events were conducted when the moon was less than ¼ full and as close to the new moon as possible to minimize ambient light interference with the traps. Three traps were set at each of three stations in each impoundment, for a total of nine traps per impoundment. Stations were chosen that evenly dispersed sampling effort throughout the study impoundments to account for environmental gradients. Spacing between traps at each station was greater than 100 m; this reduced the probability of interaction between the traps. Traps were set in the evening hours as close to sunset as possible and picked up the next morning shortly after sunrise. Measurements of temperature, dissolved oxygen concentration, and salinity were collected with a YSI® model 85 multimeter at each station after the light traps were retrieved.

Push net samples were collected with a 750-µm mesh plankton net with a circular mouth, 0.5 m^2 in diameter, pushed in front of a jon boat at 8 km/h. Three push-net samples were collected during daylight hours at the same stations where the light traps were set, likewise producing nine samples per impoundment. Each push net haul was 255 m as measured by a Garmin® GPS unit. Samples from traps and net hauls were preserved in 70 % ethanol in the field before being transported to the lab for processing.

Sample processing and fish identification

All samples were processed at the Warnell Fisheries Laboratory (University of Georgia, D.B. Warnell School of Forestry and Natural Resources). The processing protocol specified draining and rinsing ethanol from samples, extracting fishes from debris, identifying all individuals to species, and enumerating them by developmental stage. Sub-adult fishes were separated from adults according to lengths at transformation and maturity as recorded in the literature (Lippson and Moran 1974; Able and Fahay 1998; Richards 2006) and by observations of fin and scale development. Extraction efficiency of the two researchers who processed the samples was assessed by randomly selecting and reprocessing 10 % of samples and calculated for each researcher as the mean percentage of fishes missed during initial processing. Reprocessing of samples was carried out by the researcher who did not process the sample initially.

Diversity indices

We calculated species richness and effective number of species (ENS) as measures of assemblage diversity. The former is simply a count of the total number of species detected in a study impoundment during monthly sampling periods, including fishes sampled with both gear types. The latter is a measure of diversity calculated by taking the exponential of the Shannon index, $e^{H'}$ (Jost 2006). To compute species richness, the number of species detected in light traps was combined with any additional species detected in push nets for each station within each study impoundment. Push net data were not included in any further analyses presented here because push-net samples rarely contained species undetected in light-trap samples.

Effective number of species was calculated based on the proportional abundances of species by season. November through March were designated as winter months and April through August were considered summer. These seasons were defined around a threshold water temperature of 20 °C and encompass the winter and summer peaks in recruitment of estuarine fishes documented for the region (Shenker and Dean 1979; Bozeman and Dean 1980; Allen and Barker 1990). Data from push-net samples were not used to calculate ENS because the capture efficiency of the two gear types could not be assumed to be the same for all species.

Statistical analysis

To examine differences in diversity measures between "waterfowl" and "fish" impoundments and between seasons, we calculated management-type and season-specific means and 90 % CIs, based on a *t* statistic with $n - 1$ degrees of freedom. We used hierarchical linear regression (Raudenbush and Bryk 2002; Roberts 2004) to evaluate the relationships between sub-adult light-trap catch per unit effort (CPUE) and impoundment management, species life history in relation to estuarine wetlands (transient or resident), season, and water quality characteristics. Hierarchical linear models differ from traditional linear regression models in that they contain fixed and random effects. The fixed effects represent the average effect of a factor (e.g., management type) on the response (e.g., CPUE) and random effects represent the variability of the effect from group to group, here species.

There were no a priori expectations that the effect of specific impoundment management, season, and water quality characteristics would vary predictably among fish species. Therefore, the relative fit of random-effects variance structures for the hierarchical models was evaluated by fitting the global model (all predictors) with all possible combinations of randomly varying parameters. The combination that produced the lowest Akaike's Information Criteria was considered the best approximating variance structure and was then used during model selection. All random effects were assumed to be normally distributed with a mean of zero and variance specific to the random effect. All models were run with the MIXED procedure in SAS statistical software (Littell et al. 1996).

CPUE was defined as the average number of individuals caught per trap for an impoundment in one trap-night. The CPUE data were natural-log transformed to meet the linear model assumption of normality and homogeneous variance. A small constant (0.0001) was added to CPUE before transformation to account for zero-values. Examination of the residual plots confirmed that the transformations achieved the desired distribution. Larval and juvenile developmental stages were combined into a "sub-adult" stage for model analysis. Only those species for which five or more sub-adult individuals were captured during the study were included in calculations of CPUE.

Prior to modeling, Pearson's correlation analysis was conducted on all pairs of predictor variables, and only uncorrelated variables ($|r| < 0.7$) were used to construct the candidate models. Categorical predictors were binary coded with summer months coded "1" and winter months coded "0", waterfowl-managed impoundments coded "1" and fish-managed impoundments coded "0", and transient species coded "1" and resident species coded "0". Zero-coded predictors served as baselines. To compare continuous predictor variables (mean water temperature, mean DO, and mean salinity) on a common scale, the data were standardized with a mean of zero and a standard deviation of one.

An information theoretic approach was used to identify the factors that were most strongly related to sub-adult CPUE. Candidate models were created to represent a unique hypothesis regarding the effect of impoundment management, species characteristics, season, and water quality characteristics on CPUE. Akaike's information criteria (AIC; Akaike 1973) with a small sample size adjustment (AIC_c; Hurvich and Tsai 1989) was then used to evaluate the relative fit of each candidate model. AIC is an entropy-based measure that is used to compare candidate models (Burnham and Anderson 2002), with the best-fitting model having the lowest AIC_c. The number of parameters used to estimate AIC_c included all fixed effects, random effects, and any covariance when two or more random effects were included in a candidate model (Burnham and Anderson 2002). To account for model selection uncertainty, a confidence model set was created by using Akaike importance weights (Burnham and Anderson 2002) that range from zero to one with the most plausible model having the greatest weight. Candidate models were included in the confidence set if their Akaike weights were within 10 % of the largest weight (Royall 1997). For the models in the confidence set, R^2 values were calculated following the methodology of Snijders and Bosker (1999).

The relative magnitude of fixed and random effects were interpreted by plotting empirical Bayes estimates (Snijders and Bosker 1999) of back-transformed CPUE for each species included in the models for both "waterfowl" and "fish" impoundments and for winter and summer seasons. The precision of each fixed and random effect was determined by computing 90 %-CIs based on a t statistic with $n - 1$ degrees of freedom (Littell et al. 1996). Degrees of freedom were calculated using the Satterthwaite approximation (Satterthwaite 1941). Goodness-of-fit for the confidence-set models was evaluated by examining residual plots (Raudenbush and Bryk 2002).

Results

Water quality

Water quality measurements varied within and among the Nemours impoundments during the study period.

In fish impoundments Boss' Pond and Branford, the minimum water temperature was 9.5 °C and the maximum water temperature was 31.8 °C. Mean water temperature for the study period was 20.9 °C. In waterfowl impoundments, Big Rice Field and Nieuport, the minimum water temperature was 8.7 °C, the maximum was 30.9 °C, and the mean was 20.4 °C (Fig. 2). Salinity in fish impoundments ranged from 0.5 to 18.6 ppt, and averaged 7.4 ppt over the course of the study. In waterfowl impoundments, the minimum salinity was 3.4 ppt, the maximum was 22.8 ppt, and the mean was 9.5 ppt (Fig. 3). The minimum dissolved oxygen concentration in fish impoundments was 3.66 mg/l. The maximum was 11.91 mg/l and the mean for the study was 7.74 mg/l. The minimum for waterfowl impoundments was 0.37 mg/l, the maximum was 10.00 mg/l, and the mean was 5.55 mg/l (Fig. 4).

Catch composition and species richness

Light trap samples contained 61,527 sub-adult fishes, representing 21 species and 16 families. Of these, 7634 fishes (12.4 %), representing nine species and eight families, were larvae. Inland silverside (*Menidia beryllina*) and bay anchovy (*Anchoa mitchilli*) were the two most abundant species and together accounted for 95 % of the sub-adult catch (Table 1). Mean extraction efficiency, regardless of collection method, was 97 % (SE = 3 %).

Push net samples contained 12,670 sub-adult fish representing 13 species and 11 families. Larval fishes representing seven species and six families accounted for of 10.5 % of the catch (1325 sub-adult fish). Inland silverside and bay anchovy made up 92 % of the catch (Table 1). Over the course of the study, all the species collected with push-nets were also caught by light-traps. Mean extraction efficiency, regardless of collection method, was 97 % (SE = 3 %).

The number of species detected was similar between "waterfowl" and "fish" impoundments. Mean sub-adult species richness varied in "fish" impoundments from a minimum of 2.5 (±0.82) in November of 2008 to a maximum of 7 (±0.00) in July and August of 2008 (Fig. 5). For the entire study period, a mean of 15.5 (±0.82) species were detected in "fish" impoundments. This is the total number of species detected among all stations in each impoundment over the course of the entire study averaged to produce a single value for each management type.

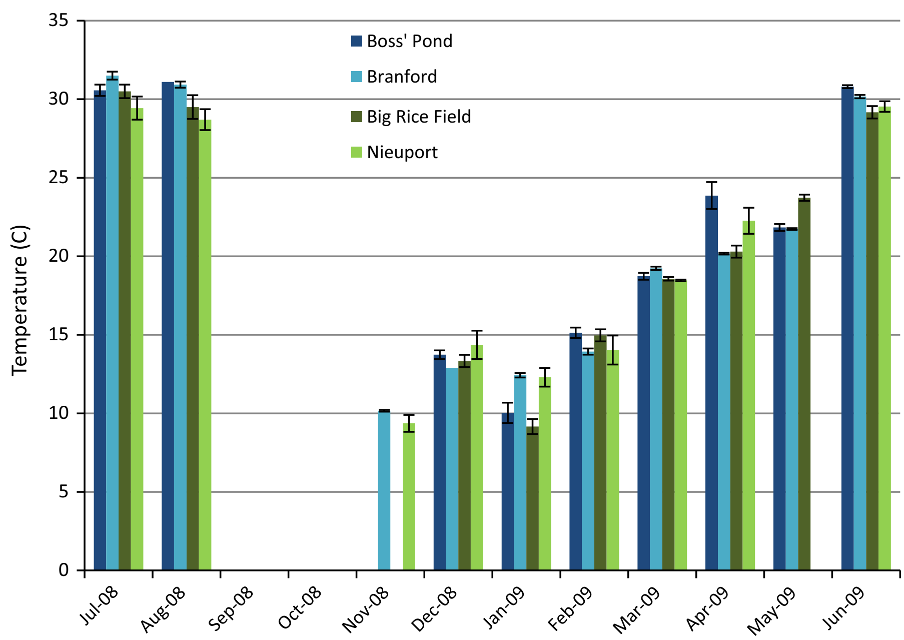

Fig. 2 Mean water temperature and 90 % CIs in "fish" impoundments (Boss' Pond and Branford) and in "waterfowl" impoundments (Big Rice Field and Nieuport) during the study period ($n = 3$). Confidence intervals are not given for Boss' Pond in August or for Branford in December because only one measurement was taken on these occasions. Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

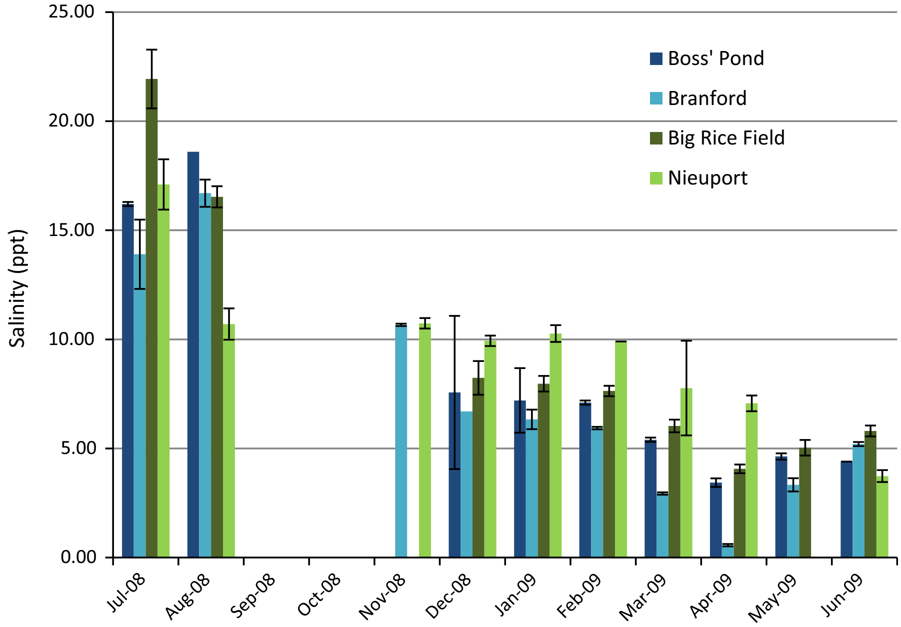

Fig. 3 Mean salinity and 90 % CIs in "fish" impoundments (Boss' Pond and Branford) and in "waterfowl" impoundments (Big Rice Field and Nieuport) during the study period ($n = 3$). CIs are given not for Boss' Pond in August or for Branford in December because only one measurement was taken on these occasions. Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

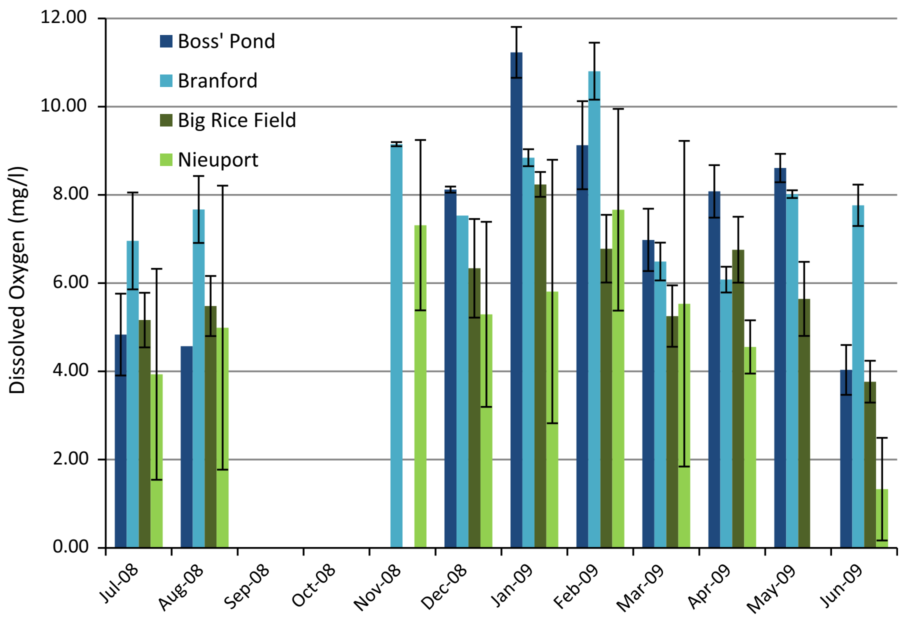

Fig. 4 Mean dissolved-oxygen concentration and 90 % confidence intervals in "fish" impoundments (Boss' Pond and Branford) and in "waterfowl" impoundments (Big Rice Field and Nieuport) during the study period ($n = 3$). CIs are not given for Boss' Pond in August or for Branford in December because only one measurement was taken on these occasions. Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

Table 1 Sub-adult fishes sampled with light traps from impoundments at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

Scientific name (family)	Common name	Waterfowl		Fish	
		Nieuport	Big rice field	Boss' Pond	Branford
Anchoa mitchilli (*Engraulidae*)	Bay anchovy	51	783	1105	2066
Brevortia tyrannus (*Clupeidae*)	Atlantic menhaden	2	306	664	670
Cynoscion regalis (*Sciaenidae*)	Weakfish	0	2	0	0
Cyprinodon variegates (*Cyprinodontidae*)	Sheepshead minnow	29	2	1	1
Cyprinus carpio (*Cyprinidae*)	Common carp	0	0	0	2
Elops saurus (*Elopidae*)	Ladyfish	0	4	1	0
Fundulus heteroclitus (*Fudulidae*)	Mummichug	0	1	0	0
Gambusia holbrooki (*Poeciliidae*)	Gambusia or mosquitofish	543	74	10	1
Gobiosoma bosc (*Gobiidae*)	Naked goby	1	11	22	24
Lagodon rhomboides (*Sparidae*)	Pinfish	0	1	4	1
Leiostomus xanthurus (*Sciaenidae*)	Spot	0	37	81	79
Lucania parva (*Fundulidae*)	Rainwater killifish	39	4	0	2
Menida beryllina (*Atherinidae*)	Inland silverside	23,974	11,420	9092	9840
Microgobius sp. (*Gobiidae*)	Unidentified goby	0	0	1	8
Micropogonius undulates (*Sciaenidae*)	Atlantic croaker	0	4	1	1
Myrophis punctatus (*Ophichthidae*)	Speckled worm eel	0	0	1	0
Paralichthys lethiostigma (*Paralichthyidae*)	Southern flounder	0	0	0	2
Poecilia latipinna (*Poeciliidae*)	Sailfin molly	130	35	17	10
Syngnathus scovelli (*Syngnathidae*)	Gulf pipefish	3	52	240	58
Trinectes maculates (*Achiridae*)	Hogchoker	1	0	0	0
Unknown (damaged)	–	0	2	0	0

In "waterfowl" impoundments, sub-adult species richness varied from a minimum of 2.5 (±0.82) in December of 2008 to a maximum of 10 (±0.00) in June of 2009 (Fig. 5). The mean of monthly species richness was 5.35 (±1.08) species. For the entire study period, a mean of 14 (±3.29) species were detected in "waterfowl" impoundments.

Effective number of species

Differences in the ENS detected in light traps between the two types of impoundments depended on the developmental stage considered. For sub-adult fishes, the mean ENS ($e^{H'}$) in "Fish" impoundments averaged 1.64 (±0.34) in summer months, and 2.81 (±0.79) in winter months. In "Waterfowl" impoundments, ENS averaged 1.32 (±0.18) in summer and 1.71 (±0.90) in winter. The "fish" means exceeded the "waterfowl" means, but the overlapping confidence intervals indicate the differences between these groups were not statistically significant (Fig. 6).

For the larval component of the catch, the mean ENS for "fish" impoundments exceeded the ENS for "waterfowl" impoundments in both winter and summer. "Fish" impoundments averaged 2.52 (±0.20) effective species in summer months, and 2.02 (±0.66) effective species in winter. "Waterfowl" impoundments averaged 1.27 (±0.14) effective species in summer months and 1.06 effective species in winter (±0.09). For the larval component, the confidence intervals did not overlap between "fish" and "waterfowl" impoundments (Fig. 7).

CPUE models

Fourteen species were represented by five or more individuals in light trap samples and were used to calculate CPUE. Predictor variables for the CPUE models included water-quality measures (salinity and dissolved oxygen concentration) season (winter or summer), management type (fish or waterfowl), and species life history in relation to estuarine wetlands

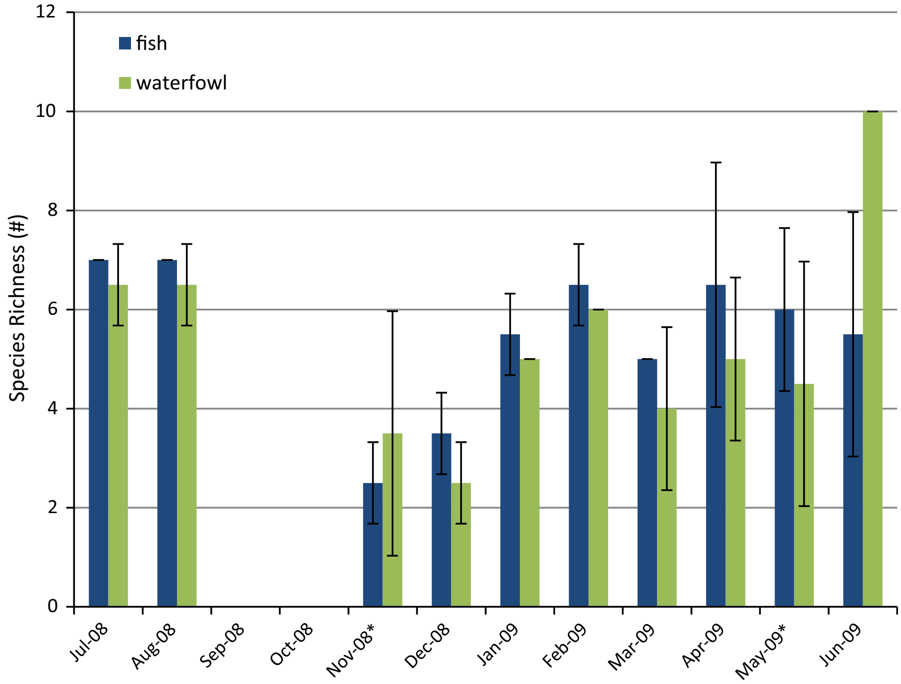

Fig. 5 Mean species richness and 90 % CIs of sub-adult fishes captured in light-trap and push-net gear for "fish" and "waterfowl" impoundments during the study period ($n = 2$). Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009. *In November, one impoundment of each type (Big Rice Field and Boss' Pond) was sampled with push net only. In May, both waterfowl impoundments (Nieuport and Big Rice Field) were sampled with light traps only

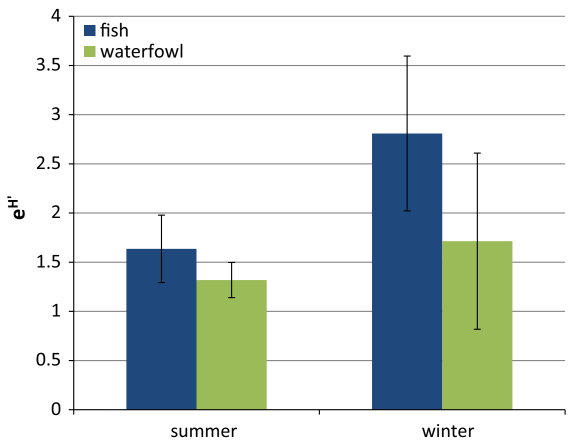

Fig. 6 Mean effective number of species ($e^{H'}$) and 90 % CIs calculated from the sub-adult component of light-trap catch in fish impoundments and in waterfowl impoundments during summer (April–August) and winter (November–March) ($n = 2$). Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

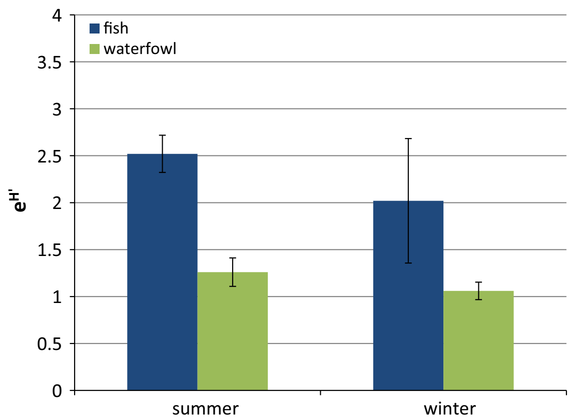

Fig. 7 Mean effective number of species ($e^{H'}$) and 90 % CIs calculated from the larval component of light-trap catch in "fish" impoundments and in "waterfowl" impoundments during summer (April–August) and winter (November–March)($n = 2$). Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

(transient or resident). The variance structure for the global model predicting sub-adult, light-trap CPUE consisted of six normally-distributed random effects. The random effects allowed to vary by species included the intercept, a management type (fish or waterfowl) slope, a slope accounting for covariance between the intercept and the management effect, a season (summer or winter) slope, and a salinity slope. An additional random effect for sampling month was also included, but this did not vary by species.

Two of the candidate models had sufficient support based on Akaike weight to be included in the confidence set (Table 2). The global model, including all predictor variables and interactions had the lowest $AIC_{c,}$ which makes it the most plausible model. The global model was 3.48 times more likely than the next most plausible model, which included management type, dissolved oxygen, salinity, transience, season, and a transience-season interaction. The first and second most plausible models had R^2 values of 0.62 and 0.61, respectively.

Parameter estimates from the best model indicated that sub-adult CPUE for resident species was greater in summer than in winter, whereas CPUE was smallest for transient species in the summer. Similarly, dissolved oxygen concentration was negatively related to sub-adult CPUE for resident species but was positively related to transient species CPUE (Table 3). The relationship between salinity and CPUE also varied between resident and transient species and was weakly and positively related to resident CPUE and negatively related to transient CPUE (Table 3). Parameter estimates for "management", "transience", and "salinity" had 90 % CIs that overlapped zero. However, the random effect for management was relatively large, which suggests that the effect of management varied substantially among species.

Empirical Bayes estimates of CPUE for resident fishes were lower in association with waterfowl management for inland silverside, bay anchovy, gulf pipefish (*Syngnathus scovelli*), and the two Gobiidae species. Waterfowl management was predictive of higher CPUE for sheepshead minnow (*Cyprinodon variegates*), rainwater killifish (*Lucania parva*), sailfin molly (*Poecilia latipinna*), and mosquitofish (*Gambusia holbrooki*) (Fig. 8). Estimates for transient fishes revealed little difference between management types; only spot (*Leiostomus xanthurus*) were predicted to have lower CPUE in association with waterfowl management (Fig. 9).

Discussion

Water quality

Water quality conditions are important determinants of habitat quality, and highly variable or extreme

Table 2 Predictor variables, number of parameters (K), AIC_c, ΔAIC_c, and Akaike weights (w), for candidate models relating light-trap CPUE of sub-adult fishes to impoundment management (fish or waterfowl), transience (resident or transient), season (summer or winter), mean dissolved oxygen concentration (DO), and mean salinity

Candidate model	K	AIC_c	ΔAIC_c	w_i	Percent of maximum w_i (%)	R^2
Management|transience, transience|season transience|mean salinity, transience|mean DO	17	3027.60	0.00	0.75	100	0.62
Management, mean DO, mean salinity transience|season	14	3030.10	2.50	0.21	29	0.61
Management, season, mean salinity transience|mean DO	14	3033.69	6.09	0.04	5	N/A
Management, season, mean DO, transience|mean salinity	14	3038.10	10.50	0.00	1	N/A
Management, transience, season, mean salinity, mean DO	13	3040.59	12.99	0.00	0	N/A
Mean salinity, season, mean DO, management|transience	14	3042.69	15.09	0.00	0	N/A
Mean salinity, mean DO, transience|season	14	3085.49	57.89	0.00	0	N/A
Season, mean salinity, transience|mean DO	14	3088.35	60.76	0.00	0	N/A
Season, mean DO, transience|mean salinity	14	3091.76	64.17	0.00	0	N/A
Transience, season, mean salinity, mean DO	13	3091.84	64.24	0.00	0	N/A
Management, transience|season	11	3118.23	90.63	0.00	0	N/A
Management	7	3165.89	138.29	0.00	0	N/A

Vertical lines (|) indicate that main effects and interactions between predictors were included in the candidate model. Akaike weights are interpreted as relative plausibility of candidate models. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009. For models in the confidence set, R^2 values are given

Table 3 Parameter estimates, standard errors, and 90 % CIs for the best approximating model relating light-trap CPUE of sub-adult fishes to impoundment management (*baseline* "fish impoundment"), transience (*baseline* resident species), season (*baseline* winter), dissolved oxygen concentration (DO, centered on the mean) and salinity (centered on the mean)

Parameter	Estimate	SE	Lower	Upper
Fixed effects				
Intercept	−5.840	1.620	−8.655	−3.025
Management	−1.092	1.322	−3.394	1.210
Transience	−3.071	2.402	−7.271	1.129
Management * transience	1.003	2.000	−2.488	4.493
Season	1.877	0.901	0.328	3.425
Transience * season	−3.468	1.134	−5.419	−1.517
Salinity	0.608	0.443	−0.157	1.372
Transience * salinity	−1.279	0.596	−2.328	−0.229
DO	−0.853	0.366	−1.459	−0.248
Transience * DO	1.083	0.494	0.268	1.897
Random effects				
Intercept	17.604	7.086	10.113	39.845
Management	11.063	4.830	6.115	27.306
Season	1.912	1.365	0.801	11.034
Salinity	0.773	0.460	0.362	3.000
Month	0.572	0.403	0.242	3.189
Residual	15.389	1.026	13.837	17.234

An "*" indicates an interaction effect. Models are based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009. Random effects parameter estimates are variance components that represent the variability from species to species

conditions can be stressful to aquatic organisms (EPA 2008). Water temperature (Fig. 2) at the Nemours impoundments followed the expected seasonal pattern. The lowest temperatures were recorded during November 2008 and January 2009 sampling when the temperature dropped below 10 °C at some stations. The highest measurements were recorded during July and August of 2008 and June 2009 when temperatures were above 30 °C at some stations. Throughout the study, mean temperatures exhibited little difference among impoundments and little variation among stations within impoundments. Consistent temperature patterns differentiating "waterfowl" impoundments from "fish" impoundments did not emerge.

Salinity patterns in impoundments are influenced by climate conditions, impoundment management decisions, and site-specific hydrology. Salinity in the Nemours impoundments (Fig. 3) did not follow a seasonal pattern and instead exhibited the influence of climate variability. Mean salinity recorded during the first 2 months of the study (July and August, 2008) was high because of drought conditions that reduced freshwater inputs to the impoundments (SCDNR 2012). Through the winter of 2008 and the spring of 2009 as the drought broke, mean salinity trended downward, with the lowest measurements recorded in April. Mean salinity measured in "waterfowl" impoundments was nominally higher than in "fish" impoundments in July, through the winter months (December–March), and in April. This difference is likely because of tidal circulation flushing and mixing "fish" impoundment waters, which mitigates the salt-concentrating effects of evaporation. The salinity extremes we observed in both types of impoundments at Nemours, ranging from oligohaline to polyhaline over the course of a year, would make growth and survival physiologically difficult for non-euryhaline fishes (Bulger et al. 1993).

Dissolved oxygen (DO) concentration (Fig. 4) followed the expected seasonal pattern with lower DO measured during the summer months and higher DO measured during winter, a cycle that is the result of the inverse relationship between temperature and the solubility of gases (Evans and Claiborne 2006).

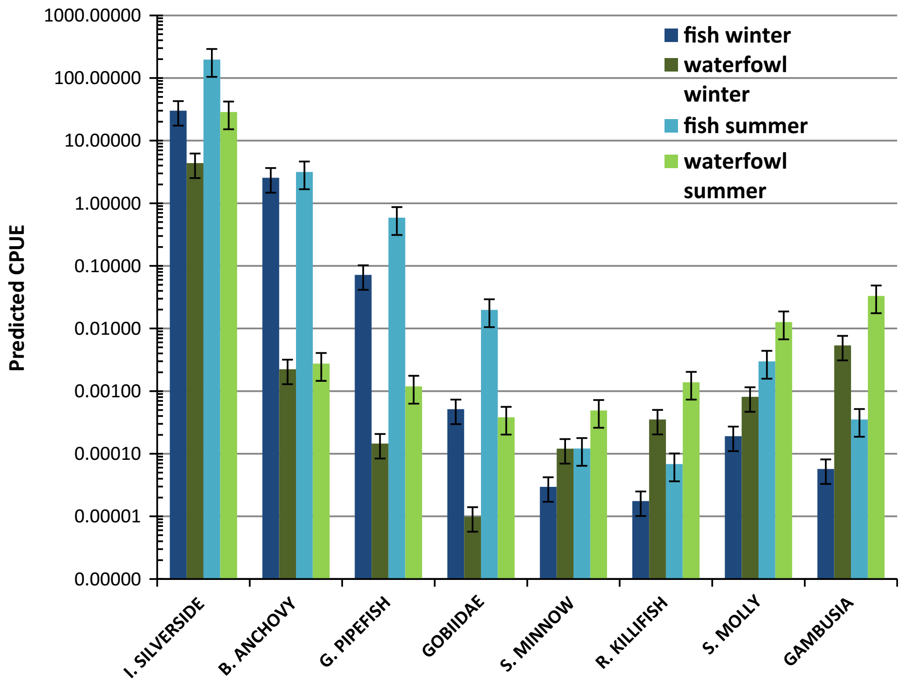

Fig. 8 Empirical Bayes estimates of light-trap CPUE and 90 % CIs for sub-adult, resident fishes during winter (November–March) and summer (April–August) from the best-fitting hierarchical linear model ($n = 5$). Predictions assume mean salinity and dissolved oxygen concentration. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009. Refer to Table 1 for complete names of species abbreviated here. "Gobiidae" includes both *Microgobius* and *Gobiosoma* species

Although DO varied considerably in all impoundments, the overall mean was nominally lower in "waterfowl" impoundments. This observation was expected because of decreased tidal circulation and increased production and decomposition known to be common in tidally-restricted impoundments (Montague et al. 1987). The U.S. EPA assesses coastal water quality and rates DO values from 2 to 5 mg/l as "fair"; lower values are considered "poor" (EPA 2008). On average, 44 % of measurements from "waterfowl" impoundments would be assessed as "poor" or "fair", compared to 12 % for "fish" impoundments. Of particular importance are the very low means and minimum DO concentrations measured in "waterfowl" impoundments during the summer months. DO below 5 mg/l is considered hypoxic and has sub-lethal effects for many fishes, whereas DO below 2 mg/l is considered anoxic and lethal to many fishes (EPA 2008; Evans and Claiborne 2006). The conditions that occurred in the Nemours waterfowl impoundments in the summers of 2008 and 2009 were, at the time of our measurements, physiologically challenging for fishes not adapted to hypoxic conditions.

The water quality data collected during this study had a much greater range than was recorded in the main stem of the Combahee River downstream from our study site (Upchurch and Wenner 2008). Our results are consistent with prevalent conclusions in the literature suggesting that salinity and DO can be highly variable in impoundments and can create stressful conditions for fishes (Wenner et al. 1986; Montague et al. 1987; Rogers et al. 1994; Stevens et al. 2006).

Catch composition

The sub-adult ichthyofaunal assemblage of the Nemours impoundments was composed of fishes that are commonly observed in association with estuaries of the southern-Atlantic coast of the U.S. Eleven orders were represented in the catch, which was numerically dominated by *Atheriniformes* (inland silversides), *Clupeiformes* (bay anchovy and Atlantic

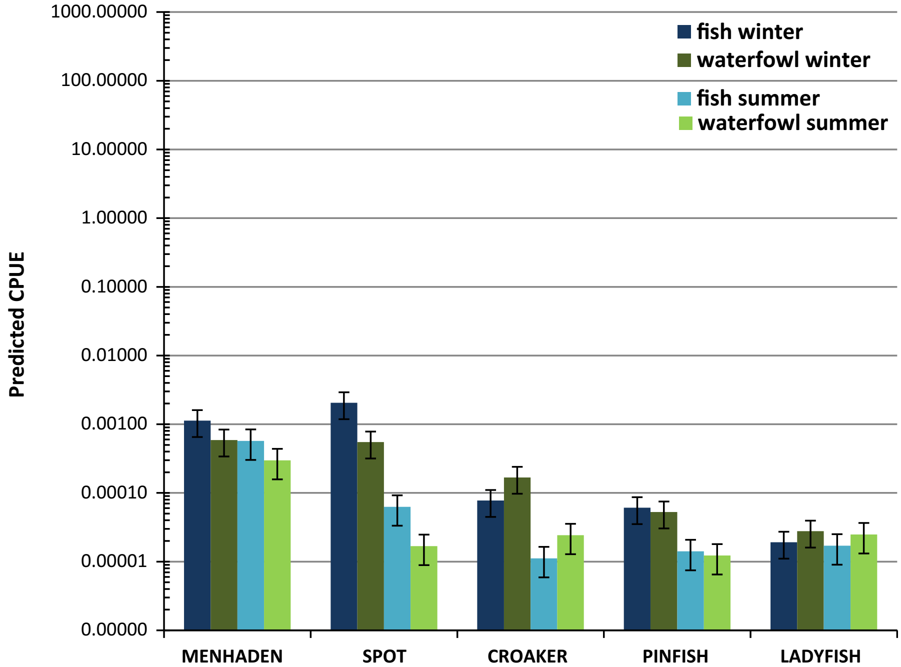

Fig. 9 Empirical Bayes estimates of light-trap CPUE and 90 % CIs for sub-adult, transient fishes during winter (November–March) and summer (April–August) from the best-fitting hierarchical linear model ($n = 5$). Predictions assume mean salinity and dissolved oxygen concentration. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009

menhaden), and *Cyprinodontiformes* (mosquitofish, rainwater killifish, sailfin molly, and sheepshead minnow). These species, with the exception of Atlantic menhaden, are estuarine-resident fishes. The simultaneous presence of adults, juvenile, and larvae of these resident fishes suggests that they may be capable of carrying out their life cycles within the impoundments. Conversely, Atlantic menhaden have a marine-transient life history that requires offshore spawning followed by transport of eggs and larvae inshore. Juvenile menhaden use oligohaline estuarine marshes, such as those along the Combahee River in the vicinity of Nemours, as nursery habitat before migrating offshore to complete their life cycle (Rogers et al. 1984). Other marine-transient fishes sampled, such as spot, croaker, pinfish, and ladyfish have similar life cycles (Rogers et al. 1984) that could be disrupted by reduced connectivity imposed by impoundments.

The numerical dominance of marine-transient fishes and the associated winter/spring recruitment pulses and low salinity that have been reported by other researchers (Rogers et al. 1984; Ross 2003; Love et al. 2009) was conspicuously muted at Nemours. Many marine-transient fishes reported as common in other studies of recruiting estuarine fishes in the southeastern U.S. were rare (e.g. southern flounder and Atlantic croaker) or absent (e.g. silver perch) in our samples of larval and juvenile fishes. Robinson and Jennings (2014) used Morisita's Index of Similarity to demonstrate that the community of fishes present in the Nemours "waterfowl" impoundments was consistently dissimilar from communities of fishes sampled for other studies in tidal creeks in South Carolina and North Carolina.

Diversity

Both management types supported similar numbers of species, but "waterfowl" impoundments supported greater proportional abundance of dominant species. A lower ENS in "waterfowl" impoundments reflects the increased dominance of abundant species along with less-frequent occurrence of rare species relative to "fish" impoundments. This effect is more pronounced for larval stages (Fig. 7). These findings suggest that tidal regulation as determined by impoundment-management objectives is an important factor determining the diversity of fishes in impoundments. Prolonged periods without tidal exchange in "waterfowl" impoundments probably limit access and reduce habitat value for the early stages of some species while increasing the dominance of others. This inference is supported by our model results and is consistent with numerous studies that document differences in nektonic assemblage structure in response to differing degrees of tidal restriction (Rogers et al. 1994; Lin and Beal 1995; Layman et al. 2004; Robinson and Jennings 2014).

Compared to other assessments of sub-adult fish diversity in South Carolina, this study documented relatively low diversity. In the Combahee River, ENS ranged from 2.56 to 8.85 at a site about 15.5 km down river from Nemours (Upchurch and Wenner 2008). Nearer to the ocean, ENS ranged from 1.49 to 13.46 at Cat Island (Wenner et al. 1986). The low end of these ranges overlaps our measurements at Nemours, but the high end exceeds them by a wide margin. Care should be taken when comparing our results with those from other studies because of differences in temporal and geographic scope and methodology. However, multiple hypotheses can be put forward to explain the low diversity we observed at the Nemours impoundments and inform future research and management efforts.

The hypothesis that increased fragmentation, such as that imposed by impoundment, leads to reductions in diversity is one potential explanation for the relatively lower diversity we observed. Island biogeography theory predicts that species richness depends in part on the rate of immigration, as fewer species colonize remote islands (MacArthur and Wilson 1967). If reduced immigration results in reduced species richness, then the less accessible "waterfowl" impoundments would be expected to support fewer species than "fish" impoundments. Although our study was not designed to compare the diversity of fishes between impounded and un-impounded waters, our finding that the ENS of the larval component of our samples was approximately doubled in "fish" impoundments compared to "waterfowl" impoundments suggests that decreased water exchange results in decreased functional diversity. The degree to which this relationship extends to un-impounded waters adjacent to the Nemours impoundments is uncertain. Other researchers who have investigated the effects of varying degrees of fragmentation have observed that negative effects on species richness sometimes occur only in the most hydrologically disconnected sites; whereas partially disconnected sites (e.g., the Nemours "fish" impoundments) may maintain species richness equivalent to unfragmented sites (Raposa and Roman 2001; Layman et al. 2004).

Alternatively, the supply of fish species available to colonize the Nemours impoundments from the adjacent Combahee River could be low relative to other study areas. This would result in low impoundment diversity regardless of the effects of fragmentation. The estuarine species minimum (ESM) concept provides a plausible explanation of why this could be true. The ESM, a concept first described by Remane (1934), proffers that a common feature of estuarine systems is a species minimum occurring in association with the mesohaline salinity zone. This phenomenon has been demonstrated along the U.S. Atlantic coast for fish assemblages in the Cape Fear River estuary in North Carolina (Weinstein et al. 1980), three tributaries of lower Chesapeake Bay (Wagner 1999), The Great Bay/Mullica River Estuary in New Jersey (Martino and Able 2003), and the St. Sebastian River Estuary in Florida (Paperno and Brodie 2004). In all of these cases, a minimum occurred in measurements of fish diversity in the estuarine zones of rivers when salinity averaged between 8 and 18 ppt.

Data suggesting the presence of an ESM for fishes in the Combahee River comes from Upchurch and Wenner (2008). This 6-year record of samples was collected with a 0.64-cm, stretch-mesh, otter-trawl net at four stations along the Combahee River at 1.6, 5, 13, and 21 km above its confluence with St. Helena Sound. The number of species detected over the course of the study was negatively correlated with distance upstream. The lowest species richness was detected at the most upstream station where salinity varied between 4.3 and 13.2 ppt (Upchurch and Wenner 2008), which overlaps with the hypothesized ESM range for estuarine fishes. Additional sampling farther upstream, towards Nemours, could determine the upstream point at which species richness begins to rise and thus the location of the ESM in the Combahee and its proximity to the Nemours impoundments.

Abundance

The empirical Bayes estimates of CPUE from our best approximating models predict that in impoundments some taxonomic groups will occur in greater numbers depending upon management type. Among the resident fishes, the cyprinodontiforms, including mosquitofish, sailfin molly, rainwater killifish, and sheepshead minnow have higher predicted CPUE in “waterfowl” impoundments. Conversely, non-cyprinodontiform residents, including inland silverside, bay anchovy, gulf pipefish and the two species of Gobiidae have higher predicted CPUE in “fish” impoundments (Fig. 8). Cyprinodontiforms could be more abundant in “waterfowl” impoundments because, unlike non-cyprinodontiforms, they are intertidal, marsh-surface specialists capable of surviving in the extreme conditions found in small pools, puddles, and rivulets left behind in the marsh surface between tides (Peterson and Turner 1994; Able and Fahay 2010).

Our model results reveal that differences in tidal circulation related to impoundment management can have opposing effects on the relative abundance of different taxonomic groups of estuarine-resident fishes. This finding sheds light on questions that arise from the literature regarding the quality of impounded marsh habitat for resident fishes. Several researchers have speculated that populations of resident fishes may benefit from the environmental conditions within marsh impoundments. Hypothesized benefits include greater availability of food resources and decreased predation risk (Hoese and Konikoff 1995; Rozas and Minello 1999). Most studies that have assessed standing stock of resident fishes in impoundments conclude that the effects of impoundment are likely to be positive for taxa classified as resident (Rogers et al. 1994). On the contrary, our findings suggest that studies that draw generalized conclusions about all resident fishes (Rogers et al. 1994; Rozas and Minello 1999) may not sufficiently capture variability among individual resident taxa. For instance, our results show that cyprinodontiform fishes are likely to be more abundant in tide-restricted “waterfowl” impoundments compared to “fish” impoundments. Conversely, non-cyprinodontiform estuarine residents are likely to be more abundant in “fish” impoundments where management allows daily tidal circulation. By eliminating frequent tidal circulation, “waterfowl” impoundments appear to create an environment that ecologically mimics the marsh interior, which allows marsh-interior specialists (cyprinodontiforms) to expand their populations. In “fish” impoundments, daily tidal circulation supports the habitat requirements of marsh-edge and marsh-subtidal specialists (non-cyprinodotiforms), which leads to the abundance of species in these groups. Thus, taxon-specific ecology and fine-scale marsh use patterns are important determinants of the abundance of resident estuarine fishes in marsh impoundments.

Peterson (2003) describes the estuarine system in terms of dynamic (water chemistry) and stationary (structural habitat) components. Where the two components overlap spatially, recruitment is maximized. Impoundments and other forms of estuarine fragmentation impose barriers that limit the spatial and temporal overlap of recruitment optima. Our results indicate that increasing tidal exchange above what is currently present in “waterfowl” impoundments will improve estuarine connectivity and enhance ecological diversity of recruiting estuarine fishes. Impoundment managers aiming to achieve a parsimonious balance between waterfowl-habitat goals and fish-habitat goals could consider adaptive-management strategies that manipulate and enhance tidal exchange.

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