ABUNDANCE AND DIVERSITY OF SUB-ADULT FISHES IN IMPOUNDED SOUTH CAROLINA MARSHES: THE EFFECTS OF TIDAL EXCHANGE

by

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(Under the direction of Cecil A. Jennings)

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. I sampled two impoundments of each management type monthly in 2008 and 2009. I 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); C.I.=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.

INDEX WORDS: Impoundment, Marsh, Estuary, Fragmentation, Diversity, Hierarchical linear model, South Carolina coastal wetland, Early life stages of fishes, Nemours Wildlife Foundation

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B.A., University of Virginia, 2002

A Thesis Submitted to the Graduate Faculty of the University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GA

2012

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August 2012

DEDICATION

This work is dedicated to my grandfather, John Lamar Carswell, Sr. who supported my education and set an example of scholarship, creativity, and curiosity about that natural world that will be with me always.

ACKNOWLEDGMENTS

Thank you to my major professor and mentor, Dr. Cecil Jennings, for his patient guidance and encouragement, and for sharing his wisdom gained from years of experience in science and other realms. I am also fortunate to have such distinguished committee members, Dr. Meryll Alber and Dr. Mary Freeman; thank you both for your time and for setting an example of professionalism that I hope to emulate.

The Georgia Cooperative Fish and Wildlife Research Unit is a team I am proud to have been part of. Special thanks to Dianne Pritchett, Cynthia and Don Dennerline, Jim and Rebecca Peterson, John Ruiz, Colin Shea, Kelly Robinson, Justin Dycus, Mike Homer, Patrick Ely, and Brittany Trushel. Thanks also to Robert Bringolf, Andrea Fritz, Daniel Farrae, Pete Hazleton, Mike Bednarski, and the staff of Georgia Sea Grant. This work would not have been possible without The Nemours Wildlife Foundation and the local expertise and technical assistance of Dr. Ernie Wiggers and Eddie Mills.

Words cannot express my appreciation to my family for helping me reach this point and for believing that I could. Finally, I want to thank my best friend and loving companion Rachel Marie Garrison for inspiring me and cheering me on.

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CHAPTER 1:

INTRODUCTION

About 16% (28,593 ha) of South Carolina’s 179,455 hectares of estuarine wetlands are restricted by impoundments (Tiner 1977, Tompkins 1987, Dahl 1999). Most of these impoundments are relics of rice agriculture that flourished in many areas of the coastal Southeast circa 1760 – 1860 (Milgarese and Sandifer 1982, Chaplin 1992). As such, they represent cultural as well as natural resources. After the civil war and the demise of the rice industry, much of the former rice plantation land and impoundments came to be owned by wealthy sportsmen. They discovered that the impoundments, if maintained and carefully managed, attracted an abundance of waterfowl to support recreational hunting (Milgarese and Sandifer 1982, Gordon et al. 1989).

South Carolina’s coastal wetland impoundments have been the subject of public and scientific interest since the 1970’s (Devoe et al. 1988, Tufford 2005). Milgarese and Sandifer (1982) identified two opposing concerns on the issue of marsh impoundment. In one camp are those who advocate tidally restrictive management of impoundments because it provides extensive resting, feeding, and nesting habitat for waterfowl, wading birds, and shore birds. In the other camp are those who oppose impoundments and would like to have them breached to restore the 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).

Marsh impoundment can affect aquatic habitat in a variety of ways, depending upon the management strategy in use. In general, lower dissolved oxygen concentration, decreased turbidity, increased sedimentation rate, increased salinity range, and altered habitat availability are associated with marsh impoundments (Wenner et al.1986, Montague et al. 1987). The net effect is that managed impoundments may exhibit a marked departure from the ecological characteristics of unrestricted tidal salt marsh. The potential for impoundments to interrupt the export of biomass from the salt marsh to the open estuary is of particular concern. Kneib (2000) proposed a conceptual model that describes biomass flow across the salt marsh ecoscape. In this model, biomass is transferred, via trophic interactions among the nektonic community, from the salt marsh to the open estuary and coastal ocean. The dikes and water control structures associated with marsh impoundments can act as major impediments to such a relay.

Research concerning fish in impoundments has characterized fish assemblages based upon 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 peer-reviewed work focusing specifically on larval and juvenile fishes in salt marsh impoundments was conducted by McGovern and Wenner (1990) at Cat Island in Georgetown County, South Carolina. The approach of that study was to simultaneously quantify the ichthyoplankton assemblage in the unrestricted tidal creek flowing into their study impoundments, along with the flux of ichthyoplankton into and out of the impoundments. Sixty species of larval and juvenile fishes were documented; this diversity was more than was found by any other estuarine larval fish study for this part of the coast. The seasonality of the catch was similar to catches reported by other studies of larval fish carried out in the open estuary in nearby Winyah Bay, SC (Shenker and Dean 1979, Bozeman and Dean 1980, Allen and Barker 1990).

The research reported here was conducted at Nemours Wildlife Foundation (NWF) on the Combahee River, SC. NWF has addressed the sometimes conflicting impoundment management needs of ichthyofauna and avifauna by spatially separating the two priorities. Tidal circulation is restricted in some impoundments to a few short periods each year to promote forage and habitat for birds. Elsewhere at Nemours other impoundments are managed to allow daily tidal circulation to support recreational fisheries. Few studies have investigated fish assemblages in impoundments like those at Nemours that are situated along the oligohaline and mesohaline reaches of riverine estuaries. Yet, these salinities zones are where most coastal wetland impoundments are located (Montague 1987, Chaplin 1992). Previous work in South Carolina took place at impoundments much closer to the ocean adjacent to a polyhaline, lagunal estuary (Mcgovern and Wenner 1990).

This study had two primary objectives: the first was to characterize the composition of the larval and juvenile fish assemblage in impoundments at NWF over the course of one year, and the second was to compare the diversity and abundance of fishes between impoundments managed for waterfowl and those managed for fishes. This assessment of recruiting ichthyofauna at the Nemours site provides managers information upon which to base decisions regarding the degree of tidal circulation in impoundments.

CHAPTER 2:

LITERATURE REVIEW

Coastal wetlands and estuaries

Estuarine wetlands have been widely recognized for their remarkable ecological value. High rates of productivity and a high degree of structural complexity are typical of shallow, protected, coastal habitats around the globe. These and other biotic and abiotic characteristics collectively function to support rich populations of commercially and recreationally targeted fish and macro-invertebrates (Weinstein et al. 1980, Montague et al. 1987, Beck et al. 2001, Able 2005). Tidal marshes in particular play an integral role in the life histories of a broad array of fishes and are hypothesized to provide sites for reproduction, enhanced feeding opportunities, optimal conditions for physiological processes and refuge from predation (Rountree and Able 2007). Taken together these conditions are conducive to the survival and growth of early life stages of a variety of nektonic organisms.

The concept of nursery habitat is well established among biologists, but Beck et al. (2001) offered a concise definition that illustrates the concept well. Specifically, "A habitat is a nursery for juveniles of a particular species if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur" (Beck et al. 2001). Indeed, numerous studies document dense aggregations of post-larval marine fishes in shallow, upper-estuarine tributaries (Weinstein et al 1980, Bozeman and Dean 1980, Rogers et al. 1984, Allen and Barker 1990). A frequently cited estimate claims that 65-70% of commercially and recreationally valuable nekton from the Gulf of Mexico and southeastern Atlantic depend on coastal wetlands during some phase of life (McHugh 1966, Peterson 2003) The nursery role concept is now widely recognized and accepted by ecologists, resource managers, conservation groups, policy makers, and the public (Beck et al. 2001). Though the concept is well established, robust data demonstrating direct linkages between inshore and offshore waters are surprisingly rare (Boesch and Turner 1984, Deegan et al. 2002, Able 2005, Rountree and Able 2007).

Many researchers have postulated the importance of the estuarine zone in providing for the transfer of nutrients and biota. Early works focused on carbon exports, in the form of detritus and phytoplankton, from marshes and mangroves (Odum and De La Cruz 1967, Odum 1970, Montague et al. 1987). Weinstein et al. (1980) described a functional continuum connecting salt marsh with estuarine basins via community dynamics and energy cycling. Kneib (2000) introduced the trophic relay concept, whereby energy derived from primary production in salt marshes is transferred among various nektonic species and life stages, ultimately transporting it seaward. Rountree and Able (2007) extended these concepts to incorporate ecological habitat gradients that influence spatial and temporal patterns of marsh use by nekton. In support of these theories, stable isotope signatures indicative of salt marsh plants were ubiquitous in samples of bay anchovy collected offshore in Delaware Bay (Weinstein et al. 2000). These concepts all advance the theory that estuaries function as a continuum that provides both habitat for organisms and pathways for the transport of energy and nutrients to the coastal marine environment.

Anthropogenic physical alteration of estuarine wetlands is widespread and has been well documented (Odum 1970, Kennish 2001, Peterson 2003). Such alteration is the product of diverse activities such as filling of wetlands, excavation of canals and ditches, shoreline stabilization, road construction, aquaculture, freshwater diversion, and tidal restriction. In many cases, the net result has been loss or degradation of habitat. In the United States, less than half of pre-colonial tidal salt marsh habitat remains (Kennish 2001). San Francisco Bay on the west coast of the United States presents an extreme example; since 1850, it has been subjected to wetland losses in excess of 90%, diversion of more than 50% of inflowing freshwater, widespread introduction of exotic species, and declines in commercial fisheries (Nichols et al. 1986). Other large estuaries such as Chesapeake Bay and the Everglades have been officially recognized as degraded and are the target of considerable public attention and funding (Alber 2002, Kemp et al. 2005).

Fragmentation

Anthropogenic fragmentation of estuarine and coastal habitats is a phenomenon with deep historic roots. As early as the 1500's, native Hawaiian islanders constructed "fishponds" by taking advantage of natural shoreline geomorphology or by building extensive sea walls of coral rock (Kikuchi 1976). Some of the ponds combined agriculture and aquaculture by allowing fish access to fields already flooded for taro farming. A wooden sluice gate was constructed across a narrow entrance to the fishpond, thereby allowing small fish to come and go freely with the tidal cycle, while larger fish were trapped inside (Kikuchi 1976).

Coastal fragmentation occurs on spatial scales from less than 1 hectare to over 100^2 kilometers. The following account of Lake Grevelingen in the Netherlands from Nienhuis (1992) is exemplary of the upper end of this range. In 1971, the mouth of the Grevelingen estuary was closed off, thus creating a 108 km^2, tideless, marine lake. The resulting changes in the physical and chemical properties of the Grevelingen, for better or worse, provided a large scale experiment in the effects of impoundment on estuarine biota. The immediate effects were dramatic and catastrophic for intertidal invertebrates. Wading birds that fed on the invertebrate communities likewise disappeared from the area. Eelgrass, *Zostera marina,* expanded and colonized the formerly subtidal sandflats. Three species of marine flatfish that were transient to the estuary were cut off by installation of the dam, which caused a gradual decline and eventual extirpation of the flatfish populations. Smaller resident fish species, particularly gobiids, capable of carrying out their life cycles within the new lake were released from predation by the flatfish and began to increase in number. In response to the increases in aquatic vegetation and small fish, populations of herbivorous and piscivorous birds expanded (Nienhuis 1992).

Fragmentation may occur to varying degrees, all with implications for faunal assemblages. Layman et al. (2004) used underwater visual census to assess the response of fish assemblages in Andros Island, Bahamas, estuaries to four categories of fragmentation that differed in the degree of disassociation from tidal influence. They found that fish species density was significantly greater in unfragmented and minimally-fragmented (less fragmentation) estuaries than in partially or totally-fragmented estuaries (more fragmentation). Similarly, at Elkhorn Slough on the central California coast, communities of algae, fish, crabs, birds, and mammals did not differ between sites with full tidal exchange and muted tidal exchange; however, sites classified as minimal exchange differed significantly in community composition from both full and muted exchange sites (Ritter et al. 2008). In addition to creating a physical barrier to movement, fragmentation and the resultant altered environmental conditions upstream of the barrier may render the affected habitat inhospitable to many marine species (Layman et al. (2004).

Impoundment

Impoundments are a common cause of fragmentation in coastal and estuarine systems. In the United States, coastal wetland impoundments are common along the southeastern Atlantic coast from North Carolina to Florida (Montague 1987) and in coastal Louisiana (Rogers et al. 1994). They can also be found along the Mid-Atlantic (Nemerson and Able 2005), New England (Raposa and Roman 2001), and California (Ambrose and Meffert 1999) coasts. There is a unique history and body of research concerning impoundments in each of these areas.

The Carolinas and Georgia: Former Rice Fields

Beginning in the mid-1700s in the coastal region of the Southeastern United States, impoundments were constructed in tidal areas for the large scale production of rice (Chaplin 1992). This process required the use of earthen dikes to enclose large sections of tidal swamp or salt marsh, depending on the prevailing salinity of the waters. Planters were able to control water levels in the impoundments by means of a wooden conduit called a “trunk”, which had adjustable flap-gates on either end (Chaplin 1992). This practice led to the conversion of vast areas of natural wetland to impounded agricultural land. In South Carolina alone, nearly 60,000 hectares were converted (Tufford 2005).

Tidal rice agriculture was labor intensive, and required constant maintenance of ditches, dikes, and water control structures, in addition to planting, weeding, and harvesting. All of this labor was performed by slaves (House 1954, Chaplin 1992, Jackson 2008). Southern agriculture, including the rice industry, was a driving force behind the importation of African slaves to the United States. Slaves from coastal West Africa were particularly in demand, as rice had been in cultivation there for thousands of years (Chaplin 1992). West African slaves brought with them knowledge and experience of rice growing techniques and may have supplied some of the cultivars (Chaplin 1992). Over 100 slaves were required to work an average-sized plantation of 400 acres (House 1954). The profits from rice cultivation supported a wealthy, elite class and contributed largely to the booming economies of cities like Charleston, SC and Savannah, GA, where the extravagance of that era is still in evidence today (Chaplin 1992).

The outcome of the civil war freed the rice industry's enslaved labor force (Carney 1996). Some plantations attempted to continue rice cultivation with paid labor, but the industry was never again truly successful (Stewart 1991). A series of damaging tropical storms and hurricanes that swept through the low country of Georgia and South Carolina in the 1890's breached dikes and washed out water control structures, essentially ending the era of rice culture in the coastal Southeast by the early 20th century (Gordon et al. 1989).

The physical alteration of tidal wetland habitat is still visible in coastal South Carolina. Aerial and satellite imagery reveals the immense scale of hydrologic modification that has taken place here. The marshes are etched with rectilinear patterns that mark the boundaries, plots, and rows of rice fields where slaves once toiled. The sinuous paths of former channels are visible on the landscape where water no longer flows freely. Although the physical evidence is still apparent, about half (~33,000 ha) of South Carolina's former rice fields are breached and open to the daily tidal cycles. The remainder, over 28,000 ha, 14% of the state's marshland, remains impounded (Tompkins 1987, Devoe et al. 1988).

Gordon et al. (1989) presents a thorough account of the post-war history of south Atlantic coastal impoundments, from which the following paragraph derives. From the turn of the century through the 1930's, many of the derelict plantations were purchased by wealthy, primarily northern, recreational sportsman. The new proprietors discovered that the impoundments provided habitat and forage for waterfowl migrating along the Atlantic coast and attracted a great abundance and diversity of wintering ducks. They proceeded to repair and rebuild the deteriorating infrastructure of the impoundments and developed management techniques that were gradually improved upon throughout the 1900's. Today, managers actively manipulate water levels with the goal of creating optimal salinity and depth conditions for the growth of plants such as widgeon grass (*Ruppia maritima*), saltmarsh bulrush (*Scirpus robustus*), and dwarf spikerush (*Eleocharis parvula*), which are preferred forage for a number of duck species. The depth of the water is adjusted during the winter waterfowl season to provide the optimal foraging depth for dabbling ducks. In the fall, the impoundments are drained to facilitate controlled burning of emergent vegetation.

The same management practices that attract waterfowl provide habitat for and attract large numbers of 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 (Miglarese and Sandifer 1982, Nareff 2009). In response to this success in providing habitat for avifauna, a number of organizations and agencies have endorsed waterfowl-oriented management practices in established tidal wetland impoundments. Ducks Unlimited, The Audubon Society, the US Fish and Wildlife Service, and the Department of Natural Resources in both Georgia and South Carolina have partnered to continue to improve management practices (Gordon et al. 1989, Tufford 2005).

In the 1970's and 1980's, a growing number of applications for permits to re-impound South Carolina marshes sparked controversy. Impoundment owners and supporters of waterfowl management advocated for their legal rights to maintain or re-establish impounded marshes, ostensibly because the ability to manage water levels produces extensive habitat for a variety of birds, reptiles, and mammals. Others were opposed to permitting new or restored impoundments because of a belief that breached dikes re-established natural tidal cycles that are linked to production of estuarine nekton. Also at issue was whether impounded and formerly impounded tidal wetlands should be considered a common pool resource or private property (Miglarese and Sandifer 1982, Devoe et al. 1988). As of 1987, an estimated 68% of impounded and formerly impounded tidal wetlands in South Carolina were in private ownership (Tufford 2005).

McGovern and Wenner (1990), investigating the seasonal recruitment of larval and juvenile fishes into impounded and non-impounded wetlands in coastal South Carolina, concluded that waterfowl-oriented management practices negatively affected marine transient fish species for two main reasons. First, because management strategies close off impoundments to tidal circulation for periods of several months during the year, fish that recruit during those months are denied access to the otherwise valuable nursery habitat within. Secondly, the fish that do recruit to the impoundment are not likely to emigrate out of the impoundment. In these instances, immigration significantly exceeded emigration for larval and juvenile stages of a number of important marine transients (McGovern and Wenner 1990). In other studies from the same site, planktonic and benthic communities differed inside impoundments compared to an adjacent free flowing tidal creek (Devoe and Baughman 1987, Wenner and Beatty 1988). These studies highlight the distinct ecology of impounded marshes and draw attention to the possibility of negative consequences for certain groups of organisms.

Florida: Mosquito Control

In Florida, many of the lagoons along the central Atlantic coast were impounded between 1950 and 1970 in an effort to control mosquito and sand fly populations (Rey and Rutledge 2001). These nuisance insects require exposed, moist soil to reproduce. Impoundments allowed managers to hold standing waters on large areas of marsh and mangrove wetland that would otherwise have been exposed in periods of low water (Rey and Rutledge, 2001). This strategy was effective at controlling insect numbers, but total isolation of impoundments from the estuary resulted in a number of negative effects, including reduced fish diversity and loss of mangroves (Harrington and Harrington 1982, Taylor et al. 2008).

In response to these negative effects, a new technique termed rotational impoundment management (RIM) was developed. This system uses flap gated culverts that are set to allow water exchange from October through May and then closed for the remainder of the year during the mosquito breeding season (Brockmeyer et al. 1997). Sixty percent of the impoundments in the Indian River Lagoon system were converted to RIM by 1998 (Brockmeyer et al. 1997). This conversion presented an opportunity for scientists to study the effects of partially reestablished connectivity on aquatic fauna. One study found that within the first 15 weeks of reconnection, fish species diversity increased from 9 to 40 species (Poulakis et al. 2002). This impoundment had been isolated for over 39 years. In another case, fish began to move through culverts in both directions immediately following impoundment reconnection (Taylor et al 2008). Diversity of transient species increased in this case, while abundance of resident species decreased because of predation by the transients. Yet another study demonstrated a net export in fish biomass from a reconnected study impoundment (Stevens et al. 2006). These studies suggest that impoundments with sufficient water circulation may be able to support management objectives and minimize negative effects on aquatic biota.

Louisiana: Structural Marsh Management

In Louisiana, more than 200,000 ha of coastal marshlands, which comprise about 16% of total wetland area in the coastal zone, are affected by weirs and other water control structures

(Herke et al. 1992). These works are collectively referred to by the term, structural marsh management (SMM). SMM, traditionally employed to enhance habitat for waterfowl and furbearing mammals, has become a tool in large scale efforts to control marsh erosion and limit saltwater intrusion (Rogers et al. 1992). Impoundment research in Louisiana has focused on differences in nekton movement in relation to multiple approaches to water level management and has revealed additional evidence that impoundments present distinct challenges and opportunities for different life history strategies.

Like other forms of fragmentation, SMM varies by degrees. In Louisiana, weirs instead of trunks or culverts are typically employed to manage water levels. Weirs allow water to circulate in and out of impoundments when the tide rises above the crest of the weir, which may be fixed or adjustable. Weired impoundments have been referred to by researchers as semi-impounded (Rogers et al. 1992, Hoese and Konikoff 1995); there have been documented instances of reduced immigration to and emigration from even semi-impounded marshes. For example, one study found an 80% decrease in the biomass of marine transient fishes and crustacean species emigrating from semi-impounded marsh compared to natural marsh (Herke et al., 1992). Another found reduced immigration rates and standing stock biomass of obligate migratory species even when water control structures were set to allow maximal exchange (Rozas and Minello, 1999). These studies demonstrate that the fragmentation effects of SMM can have negative implications for migratory marine species despite efforts to maintain limited connectivity. However, one species' loss may be another's gain.

The compensatory adjustment hypothesis, as described by Hoese and Konikoff (1995), postulates that impoundments may alter community composition, but that overall productivity is preserved. For instance, biomass of marine transients may be reduced, but biomass of residents could expand because of release from predation or competition. This hypothesis finds support in many of the same studies that report negative effects on marine transients. A review of 20 studies comparing managed impoundments to reference, unmanaged areas, revealed that in 17 of those comparisons there was a positive effect of more restrictive water control on standing stock of resident nekton (Rogers et al. 1994). Likewise, significantly more studies detected negative (14) than positive (3) effects on marine transient standing stock.

New England, Mid-Atlantic and California: Restoration

Discussions about impoundment management on the southeast Altantic and Gulf of Mexico coasts have focused on the degree and timing of water control. Similar discussions in New England (Warren et al. 2002), Delaware (Nemerson and Able 2005), and California (Madon 2008) have been about efforts to fully reestablish tidal connectivity to former impoundments. These efforts have created opportunities to study the effects of marsh restoration.

In Connecticut, a publicly funded tidal marsh restoration program has restored tides to 57 formerly impounded sites along the coast. Warren et al. (2002) studied nine of these sites within six separate marsh systems on Long Island Sound with restoration times of 5 - 21 years. They found that fish assemblages in restoration site creeks were equivalent to those of natural reference marshes within five years. Some macroinvertebrates took much longer to colonize the new marsh, up to 20 years in the case of the salt marsh snail, *Melampus bidentatus* (Warren et al. 2002). The slow recovery of invertebrates could help explain the persistence of diet composition differences observed for mummichog in some restoration marshes. However, a study of a marsh restoration site in coastal New Jersey on Delaware Bay found that juvenile Sciaenid feeding patterns in a restored marsh did not differ from those seen in reference marshes after only three years (Nemerson and Able, 2005). These and similar studies provide support for continued application of marsh restoration where it is conducive to management objectives. Even areas of marsh that have been filled and developed may be successfully restored and recolonized by a representative native fish assemblage, as has been demonstrated at Malibu Lagoon in southern California (Ambrose and Meffert 1999).

Water Control Structures and Fish Passage

A variety of structures have been used to conduct water and fish through estuarine barriers. The tide gate is one such structure that is simple yet elegant in design and has been widely employed for centuries (Rozsa 1995, Knottnerus 2005). In its most basic form, a tide gate is composed of a culvert or wooden trunk passing through a road, dike or other barrier; the trunk has a hinged gate on one or both ends. Differences in water pressure caused by tidal fluctuations determine whether the gate is open or closed (Giannico and Souder, 2004).

A fish attempting passage at a tide gate may be blocked either by the gate itself or by conditions within the culvert. In theory, because tidal cycles are evenly split between ebb and flood conditions, a tide gate can be expected to be closed at least 50% of the time. In practice, the open/closed condition can be greatly affected by the position of the gate in relation to mean tide height, the influence of wind on tide heights, the configuration and weight of the gate door, and its state of repair (Giannico and Souder, 2004). A wooden gate may be rotten and leaky, and wrack or epifaunal growth may prevent its complete closure. If the gate is open, the width of the opening places an upper limit on the size of fish that may pass through. Heavy gate doors or insufficient differential in head pressure can result in narrow openings and reduced passage (Rulifson and Wall 2006). Narrow openings can also cause turbulence barriers, and a fish that successfully navigates the gate itself must be capable of dealing with the current speed and turbulence conditions within the culvert (Giannico and Souder, 2004).

Different types of water control structures may affect connectivity differently. An investigation at a tidal bay lake in North Carolina found that a change from large, wooden tide gates to small, steel gates resulted in reduced passage of fish and blue crabs, *Callinectes sapidus* (Rulifson and Wall 2006). These differences were hypothesized to be related to higher water velocity and turbulence associated with the heavy, steel gates. Additionally, this study found that more fish and blue crabs passed through wooden weirs than through steel tide gates (Rulifson and Wall 2006). Similarly, vertically slotted weirs allowed for more egress of commercially valuable shrimp from impoundments in Louisiana than did weirs without slots (Rogers et al. 1992). In Australia, addition of vertical slots to a fishway at a dam in the tidal zone of a coastal river increased species diversity above the dam. However, fishes shorter than 25 mm did not ascend the fishway, an outcome that highlighted the importance of evaluating connectivity for all life stages (Stuart and Mallen-Cooper, 1999).

How water control structures affect larval and early juvenile fishes is largely unknown, but there are a few studies that touch on this issue. For example, critical swimming speed, the speed at which a fish cannot maintain position in a current, for four species of marine perciform ranged from 0.1 to 0.2 m s^{-1} for fish near settlement stage (Clark et al. 2005). In Oregon, the Department of Fish and Wildlife recommends a maximum velocity of 0.6 m s^{-1} to allow for passage of juvenile Salmonids through tide gates (Giannico and Souder, 2004). In Louisiana, water velocities through vertical slots in a salt marsh water control structure were typically less than 0.2 m s^{-1}, low enough to allow passage by juvenile Atlantic menhaden, *Brevortia tyrannus*

(6 cm total length), and striped mullet, *Mugil cephalus* (3 cm total length), with critical swimming speeds of 1 m s^{-1} and 0.47 m s^{-1}, respectively (Kimball et al. 2010).

Community Structure and Recruitment

Estuarine researchers have long sought to describe fish assemblages in terms of community structure, ecological function, and spatial and temporal distribution. Whereas these attributes may exhibit a high degree of variability, estuarine fishes can be assigned to functional groups or guilds according to their use of habitat and movements along a continuum from fresh to salt water. Broadly, fishes found in estuarine waters are classified according to whether their life cycle can be completed within the estuary (i.e., resident fishes) or requires use of habitat outside the estuary for reproduction or migration (i.e., transient or marine transient fishes). Numerous classification schemes have been proposed that further break down this basic dichotomy to define regional (Nordlie 2003) or global (Elliot et al. 2007) commonalities governing spatial partitioning of estuarine habitat among guilds of fishes.

The coastal southeastern U.S. is exemplary of tidal sub-tropical estuaries and has been well studied. The states of Georgia and South Carolina together contain 288,535 ha of salt marsh habitat (GADNR 2012, SCDNR 2012), about 42% of the total for the Atlantic coast of the United States (Stedman and Dahl 2008). This region also is a prime target for studies of estuarine nursery function because it contains some of least developed coastline on the Atlantic seaboard.

Recruitment of fishes to the estuarine zone in the coastal southeast occurs in two pulses. The first pulse begins in winter and carries on through the spring months. Recruitment during this period consists primarily of marine transient species such as spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonius undulates*), Atlantic menhaden and pinfish (*Lagodon rhomboides*). The second pulse occurs during the summer months and is dominated by estuarine and amphidromous genera including *Gobiidae*, anchovies (*Anchoa spp.*), and silversides (*Menidia spp.*) (Allen and Barker 1990, Unchurch and Wenner 2008). Relative abundance and size distribution exhibit marked daily and annual variation (Shenker and Dean 1979, Varnell et al. 1995); however, seasonal timing of recruitment may be highly predictable (Allen and Barker, 1990). Despite variation, catches are nearly always dominated by a small number of highly abundant species (Dahlberg and Odum 1970, Shenker and Dean 1979, Bozeman and Dean 1980, Rogers et al. 1984, Allen and Barker 1990, Warlen and Burke 1990).

Investigators have employed a variety of gear types, including small-mesh channel nets (Bozeman and Dean 1980), lift nets (Rooker et al.1996), seines (Strydom 2003) and towed gear (Hickford and Shiel 1999) to sample the early life stages of fishes in estuarine habitats. Plankton nets may also be pushed ahead of a boat (Tolan et al. 1997). Pushed nets have advantages over towed nets in that they can be fished at a fixed depth and are not subjected to water disturbance associated with the action of the boat's propeller and the tow bridle.

The positive phototaxis exhibited by many fishes during early development (Doherty 1987) provides a means of attracting fishes into traps for sampling. The quatrefoil light trap (Floyd et. al., 1984) is a commonly employed light-trap design. This gear has been successfully applied in a variety of environments, including freshwater, saltwater, shallow, and vegetated habitats (Dewey and Jennings 1992, Lindquist and Shaw 2005). Quatrefoil light traps have been useful in comprehensively assessing ichthyoplankton assemblages especially when used in concert with methods such as plankton nets that allow for estimation of density (Dewey and Jennings, 1992; Hickford and Schiel, 1999; Hernandez and Shaw, 2003). Prior to this study, light traps had not yet been used to sample larval and juvenile fishes in coastal wetland impoundments.

Many studies have sought to identify environmental factors associated with the assemblage structure, abundance, and distribution of fishes in estuarine habitats. Measures of temperature, salinity, dissolved oxygen, substratum characteristics, and vegetative cover typically explain a large degree of the variability in catches. For example, in the Lake Pontchartrain estuary, Louisiana, common fishes were significantly more abundant in vegetated habitats compared to non-vegetated ones. Temperature, salinity and substratum type accounted for 41.54% of the environmental variance in this system (Duffy and Baltz 1998).

Another factor that can affect habitat quality for fishes is dissolved oxygen concentration. High rates of productivity and microbial decomposition in marshes may result in episodic hypoxia, particularly during summer months. The resulting decline in prey availability may compromise the energy budgets of juvenile fishes. Intermittent hypoxia decreased habitat quality for juvenile Atlantic croaker by reducing prey abundance and limiting access to prey, which resulted in >50% declines in growth rate (Eby et al. 2005). Similarly, juvenile anchovy (*Anchoa spp*.) increased swimming speeds in response to hypoxic conditions and sustained swimming and foraging at night. This increased activity, resulted in 20% greater energy expenditures than before the onset of hypoxia (Taylor et al. 2007).

Populations of marine transient fish frequently exhibit greater abundance in association with low salinity waters that accompany increased freshwater inflows. For example, newly recruited Atlantic menhaden, southern flounder (*Paralichthys lethiostigma*) and silver perch (*Bairdiella chrysoura*) concentrated in the lowest salinity portions of their range in the Ogeechee River, GA (Rogers et al. 1984). Furthermore, peak recruitment of these species coincided with prolonged periods of increased river discharge into the estuary, which highlights the importance of oligohaline estuarine headwaters for marine transients. Similarly, Atlantic croaker occurred in greatest abundance and exhibited lower mortality rates in oligohaline reaches of Cape Fear River, NC, tidal tributaries compared to other habitats (Ross 2003). In coastal Maryland lagoons, variation in stream discharge was positively correlated with inter-annual variation in fish assemblages (Love et al. 2009); recruiting marine transient fishes were more frequent in habitats where salinity was less variable. These results suggest that although marine transients may be actively recruiting to salinity optima associated with increased freshwater inflow, frequent variability in salinity may reduce habitat value, probably because of physiological stress.

Interactions between estuarine organisms, physical habitat, and water chemistry contribute to recruitment success, yet these interactions are exceeding complex and inherently unpredictable. This complex system can be described in terms of dynamic (water chemistry) and stationary (structural habitat) components; where the two components overlap spatially on the estuarine ecoscape, recruitment is maximized (Sklar and Browder 1998, Peterson 2003). This model explains how impoundments and other forms of estuarine barriers can limit the spatial and temporal overlap of recruitment optima.

Diversity

Measures of ecological diversity are used to quantify differences in species assemblages among habitat types and may be viewed as indicators of ecosystem health or stability (Magurran 2004). Numerous formulas have been derived to calculate “indices” that express both the number and proportional abundance of species; the result is contention over which measures are most accurate for a given study (Magurran 2004). Despite the complexity, diversity measures can be broadly classified according to how influenced they are by rare vs. dominants species (Hill 1973). The following narrative derives from Jost, *The New Synthesis of Diversity and Similarity Measures* (Jost 2012), an online resource that synthesizes peer-reviewed material from Jost (2006), Jost (2007), and Chao and Jost (in press).

Species richness is the simplest of diversity measures, nothing more than a count of the number of species present in a sample. A count gives equal weight to all species regardless of abundance. This is problematic for comparisons of species richness among communities because the species richness of a community with 10 equally-abundant species would have the same diversity measure as one with two highly-abundant species and eight rare ones. There is broad agreement among ecologists that the second community, although it supports the same number of species, is less diverse in terms of the ecological interactions it supports.

To address this problem, indices have been developed to measure diversity in terms of proportional abundance. Among these, the Shannon-Weiner index has been widely used in ecological research in general (Magurran 2004) and in studies of fish assemblages in particular (Dahlberg and Odum 1970, Wenner et al. 1986, Upchurch and Wenner 2008).

The Shannon index,

$$\mathrm{H}' = -\sum_{i=1}^{S} p_i \ln p_i$$

where p_i = the proportion of individuals in the i^{th} species, has broad appeal because it weighs each species according to its frequency. In this sense, it is the most equitable of the diversity measures.

Although the Shannon index has been commonly employed to measure and compare the diversity of ecological communities, it is subject to a shortcoming that can result in misleading interpretations of data. The problem arises from the non-linear nature of the relationship between the Shannon index and diversity. For example, a community with 10 equally-common species has a Shannon index of 2.3, while a community with 20 equally-common species has a Shannon index of 3.0. Clearly, the latter community can be considered twice as diverse as the former, but this is not reflected in the Shannon index.

This non-linear relationship between indices and their equivalent number of species occurs because indices are actually measures of uncertainty, or entropy, rather than diversity. Fortunately, there is a simple, algebraic approach that allows us to convert diversity indices to an equivalent number of species. For any community with diversity index Y, there is a community made up of equally-common species that also produces the same diversity index Y. For example, a community made up of 5 species, each with 10 individuals, has a Shannon index of 1.61. Suppose another community supports 6 species. One of these species is dominant, with 11 individuals, while the other 5 all have just 3 individuals. This community also has a Shannon index of 1.61. These two communities are equivalent in terms of the Shannon index, and the latter community can be thought of as supporting ecological diversity equivalent to that of the former after accounting for proportional abundance via Shannon. To determine the number of equally common species (D, each species having a proportion abundance of 1/D) equivalent to a particular diversity index, simply set the expression for the index in question equal to its actual value (x), and solve the equation for D.

For the Shannon index,

$$x = - D\,(1/D)\,(\ln 1/D) \quad \text{so,} \quad D = \exp(x)$$

Calculation of D allows us to interpret diversity indices in terms of the number of equally common species (MacArthur 1965) that would result in an index value equal to that of any given real community. D can be thought of as the Effective Number of Species or ENS. Conversion of diversity indices to ENS simplifies comparisons of diversity among communities or assemblages (Jost 2012).

Hierarchical Linear Models

Hierarchical Linear Modeling (HLM), also commonly referred to as Multilevel Modeling (MLM), was originally developed and applied to sociological studies (Roberts 2004). The technique has since proven to be an effective tool for analyzing data from ecological studies (McMahon and Diez 2007, McCargo and Peterson 2010, Craven et al. 2010). The term "hierarchical" refers to a nested data structure. For example, ecological data are often based on samples, or measurements, nested within sampling sites, which are nested within study locations. In a longitudinal study, sampling events may be considered to be nested within months, seasons, or years. Alternatively, when considering the abundance of different species, the individual species may be thought of as nested within, or dependent upon, another descriptor such as age class or habitat preference. Particularly relevant to this study, HLM allows us to evaluate species-specific effects of environmental variables by including one or more random effects in the model that allow for a unique variance and regression slope for each species. The unique combination of randomly varying parameters is referred to as the variance structure. HLM is a powerful technique because it can account for spatial, temporal, and biological dependencies simultaneously within a single model (Roberts 2004, McMahon and Diez 2007).

HLM can be seen as an extension of the General Linear Model (GLM), which includes familiar methods such as t-tests, ANOVA, and regression (Roberts, 2004). HLM is based upon the simple linear-regression equation [all notation follows Raudenbush and Bryk (2002)]:

$$Y_{ij} = \beta_{0j} + \beta_{1j}X_{ij} + r_{ij} \qquad \text{Equation 1.}$$

where, Yij is a response variable i that is measured in a group j, β_{0j} is the intercept of group j, β_{1j} is the slope of predictor variable X_{1ij}, and r_{ij} is the residual error associated with the individual i within group j. Simple linear regression aggregates individual observations (i) within groups (j) to model the response; the residuals are thus correlated and cannot be assumed to be independent. The false assumption of independence in such a case is what Hurlbert (1984) refers to as pseudo-replication and has plagued ecological research.

As a component of HLM, the simple linear-regression model is usually referred to as the level-1 model. HLM accounts for dependence by combining the level-1 model with independent, level-2 regressions for each j group, based on the following equations.

$$\beta_{0j} = \gamma_{00} + \gamma_{01}W_j + u_{0j} \qquad \text{Equation 2.}$$

$$B_{1j} = \gamma_{10} + \gamma_{11}W_j + u_{1j} \qquad \text{Equation 3.}$$

Here, γ_{00} and γ_{10} are intercepts and γ_{01} and γ_{11} are slopes predicting β_{0j} and β_{1j}, the intercept and slope from the level-1 model based on the level-2 predictor variable, W_j. The group level variances of the mean, $u_{0j,}$ and slope, u_{1j}, can differ between groups in HLM. Thus, group variances need not be assumed equal as in the simple linear model.

Substitution of equations 2 and 3 into equation 1 yields the 2-level hierarchical linear model describing the relationships between all predictor and response variables and their associated error terms from both level-1 and level-2.

$$Y_{ij} = \gamma_{00} + \gamma_{01}W_j + \gamma_{10}X_{ij} + \gamma_{11}W_jX_{ij} + u_{0j} + u_{1j}X_{ij} + r_{ij} \qquad \text{Equation 4.}$$

Fundamentally, HLM gives researchers the ability to interpret hierarchically-structured data while accounting for dependencies among variables. It accomplishes this by including random error terms at both the individual and group level to reflect the complex and unique variance structure of a particular dataset (Roberts, 2004).

Summary

Coastal and estuarine wetlands are widely recognized as essential nursery habitat for a broad array of commercially and recreationally valuable species of fishes and invertebrates. Furthermore, these areas function as continuous pathways for the transfer of nutrients and biota from inshore to offshore areas. Anthropogenic activities can cause structural and chemical alterations of the estuarine ecoscape and fragment habitat available to estuarine organisms. Impoundment of coastal wetlands is a common form of fragmentation affecting a substantial portion of the coastal United States. Research into the effects of impoundments reveals a complex array of positive and negative effects. However, the ecology of coastal wetlands and their connectivity with surrounding habitat clearly is altered to some degree by impoundment. Often, transient marine fishes are negatively affected by exclusion from habitat and barriers to essential mobility. The consequences for resident fishes can be positive or negative. Their ability to reproduce *in situ*, along with physiological adaptation to stressful environments such as intertidal marsh pools and rivulets, can give some species an ecological advantage in impoundments. Recruitment to impoundments and the composition of larval and juvenile fish assemblages within impoundments has received relatively little attention. Successful recruitment depends on a spatial and temporal convergence of dynamic environmental variables and stationary habitat components. The degree to which impoundments disassociate these vital elements is unknown. By assessing seasonal abundance and diversity of early-life stages of fishes in marsh impoundments, predictable patterns of response to management of tidal circulation may be identified, presenting opportunities to maximize recruitment by adjusting management techniques.

CHAPTER 3:

METHODS

Study Area

The current research was conducted in impoundments owned by Nemours Wildlife Foundation (NWF), which operates the 3,966-ha Nemours Plantation on the Combahee River in Beaufort County, South Carolina. Established by the late Eugene du Pont III and his family in 1995, NWF sets an example of responsible stewardship in South Carolina's coastal zone by fostering scientific research, education, and sustainable management.

NWF is a key partner in the ACE Basin Project, a public/private partnership with the stated mission of maintaining the natural character of the basin by promoting sustainable resource management. Other partners include the Nature Conservancy, Ducks Unlimited, the U.S. Fish and Wildlife Service, the National Oceanic and Atmospheric Administration, and the South Carolina Department of Natural Resources.

The ACE Basin, defined by its constituent rivers the Ashepoo, Combahee, and Edisto is recognized as one of the least-developed, large estuaries on the east coast of the United States (NOAA 2006). The estuary provides habitat used by a broad array of native flora and fauna including nine federally-endangered and six federally-threatened species (NOAA 2006). The ACE Basin is also unique for the cultural heritage represented by the former rice impoundments and plantation sites, physical reminders of the enslaved west-African people who shaped the landscape we see today (Chaplin 1992, Jackson 2008).

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 originates at the confluence of the Big and Little Salkehatchie rivers; it flows southeastwardly to St. Helena Sound (Upchurch and Wenner 2008). The estuarine system extends 61-km upstream from the mouth of the river. Impounded marshes and formerly impounded marshes are prevalent along the river's banks from 24-53 km upriver (Upchurch and Wenner 2008). Near the middle of this reach, the Nemours impoundments lie on either side of the bridge on U.S. Route 17, which marks the legally-designated freshwater/saltwater boundary. The bridge is about 39 km upriver from the mouth, where the Combahee joins St. Helena Sound, and about 53 km from the confluence of the sound with the open ocean (Figure 1). The inland boundary of the ACE Basin National Estuarine Research Reserve is 14.5 km down river from the Route-17 bridge.

NWF manages the majority of its 809-ha of impounded marshes and wetlands with the primary goal of maximizing waterfowl habitat. This goal requires that impoundments be closed to tidal flow for much of the year. 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 opportunities. The water-control structures for these two areas are maintained such that some tidal exchange occurs daily throughout the year. In effect, "waterfowl" impoundments restrict tidal exchange to a much greater degree than do "fish" impoundments.

Study Sites

To allow for comparison between "waterfowl" impoundments and "fish" impoundments at Nemours, I selected two study sites representing each management type. The two "waterfowl" impoundments are known as Nieuport (119 ha) and Big Rice Field (48 ha) (Figure 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 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) (Figure 1). Boss’ pond is similar in design to the waterfowl impoundments. However, its canals have been widened and deepened, expanding the area of open water uninterrupted by emergent vegetation. The remaining bed area in Boss’ pond generally remains submerged throughout the year. Branford differs from the other study sites in that it lacks canals, does not have a bed area, and is bounded by dikes on only two of its sides. These dikes create upstream and downstream barriers on a reach of a former tidal-creek tributary of the Combahee. By contrast, the other three impoundments were established by encircling areas of fringing marsh with dikes along the main-stem Combahee River. The fish impoundments are managed to allow daily inundation by tidal water throughout the year.

Fish Sampling and Water Quality Measurements

I used quatrefoil light traps and a pushed plankton net ("push net") to collect larval and juvenile 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. My 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^{TM} 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. In "waterfowl" impoundments, the stations were in the perimeter canal. In Boss' Pond, two stations were in perimeter canals, while the third bisected an area of open water. In Branford, the three stations were each positioned along a transect through the open-water interior from one bank to the other. 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/hr. 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. Samples were collected after 255 m of distance traveled with the net in the water 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. Developmental stages of larval, juvenile, and adult were assigned to each species 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.

Two researchers extracted the fishes from samples. Extraction efficiency was assessed by randomly selecting and reprocessing 10% of samples and was calculated for each researcher as the mean % of fishes missed during initial processing. Reprocessing of samples was carried out by the researcher who did not process the sample initially.

Diversity Indices

I 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 derived from the exponential of the Shannon Index (Jost 2006).

Effective number of species (ENS) 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, and because push-net samples rarely contained species undetected in light-trap samples.

Statistical Analysis

To examine differences in diversity measures between “waterfowl” and “fish” impoundments and between seasons, I calculated management-type and season-specific means and 90% confidence intervals, based on a t-statistic with n-1 degrees of freedom. I used hierarchical linear regression (Raudenbush and Bryk 2002, Roberts 2004) to model sub-adult catch per unit effort (CPUE) for light-trap data and sub-adult density for push-net data; separate models were fitted for each method. CPUE was defined as the average catch per trap for an impoundment in one trap-night. Models of density were based on the average number of fish sampled per 50-m^3 push-net tow. Natural-log transformations were used on both CPUE and density data to meet the assumption of normality; zero-values were accounted for by adding 0.0001 to all 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.

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, relative to the mean and standard deviation for each impoundment throughout the study period.

Akaike’s Information Criteria (AIC; Akaike 1973) with a small sample size adjustment (AIC_c; Hurvich and Tsai 1989) was calculated to evaluate the relative fit of each candidate model. AIC is an entropy-based measure 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 detected when two or more random effects were included in a candidate model (Burnham and Anderson 2002). A confidence set of models was constructed based on Akaike importance weights (Burnham and Anderson 2002), which range from zero to one. The most plausible model has the greatest weight. Candidate models were excluded from the confidence set if their Akaike weights were less than 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 (1994).

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%-confidence intervals 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).

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 AIC_c was considered the best approximating variance structure and was then used during the evaluation of the relative plausibility of the candidate models. All random effects were assumed to be normally distributed with a mean of zero and variance specific to the random effect.

Each candidate model represented a unique hypothesis regarding the variables that predict CPUE or density. Only those species for which five or more sub-adult individuals were captured during the study were included in calculations of CPUE and density. Parameter slopes and intercepts were allowed to vary by species according to the best-fitting random effects structure. All models were run with the MIXED procedure in SAS statistical software (Littell et al. 1996).

CHAPTER 4:

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 (Figure 2). Salinity in fish impoundments ranged from 0.5 ppt 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 (Figure 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 (Figure 4).

Catch Composition

Light trap samples contained 61,527 sub-adult fish, representing 21 species and 16 families. Of these, 7,634 fish (12.4%), representing 9 species and 8 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).

Push net samples contained 12,670 sub-adult fish representing 13 species and 11 families. Larval fish accounted for of 10.5% of the catch (1,325 sub-adult fish), 7 species and 6 families. Inland silverside and bay anchovy made up 92% of the catch (Table 2). Over the course of the study, all the species collected with push-nets were also caugh t by light-traps. Mean extraction efficiency, regardless of collection method, was 97% (S.E. = 3%).

Species Richness

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 (Figure 5). The mean of monthly species richness was 5.5 (±1.49) species. For the entire study period, a mean of 15.5 (±0.82) species were detected in “fish” impoundments.

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 (Figure 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 effective number of species (ENS) between the two types of impoundments depended on which developmental stages were 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 significant (Figure 6).

For the larval component of the catch, the mean effective number of species for “fish” impoundments exceeded the effective number of species for “waterfowl” impoundments in both winter and summer. “Fish” impoundments averaged 2.52 effective species in summer months, (±0.20) and 2.02 effective species (±0.66) in winter. “Waterfowl” impoundments averaged 1.27 effective species (±0.14) 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 (Figure 7).

Abundance Models

Light-trap CPUE

Fourteen species were represented by more than 5 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 (resident or transient). 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 3). 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 for both resident and transient species sub-adult CPUE was greater in summer than in winter. The relationship between dissolved oxygen concentration and sub-adult CPUE was negative for resident species and positive for transient species (Table 4). The relationship between salinity and CPUE was positive for resident species and negative for transient species (Table 4). Parameter estimates for “management”, “transience”, and “salinity” had 90% confidence intervals that overlapped zero.

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*) (Figure 8). Estimates for transient fishes revealed little difference between management types; only spot were predicted to have lower CPUE in association with waterfowl management (Figure 9).

Density

Eleven species were represented by more than five individuals in push-net samples and were used to calculate density. Predictor variables for these models included salinity, season (winter or summer), management type (fish or waterfowl), and species life history in relation to estuarine wetlands (resident or transient). The best approximating variance structure for the global model predicting sub-adult density consisted of four normally distributed random effects. The random effects allowed to vary by species included the intercept, a management type (waterfowl) slope, and a slope accounting for covariance between the intercept and the management effect. An additional random effect for sampling location (impoundment) that did not vary by species was also included.

Three of the candidate models had sufficient support based on Akaike weights to be included in the confidence set (Table 5). The most plausible model included management type, transience, salinity, season, and interactions between transience and salinity and between transience and season as predictor variables. This model was 3.63 times more likely than the next most plausible model, which lacked the interaction between transience and season but was otherwise the same. The 3rd most plausible model was the global model that, in addition to the predictor variables in the best model, included interactions between management type and season and between management type and transience. This model's Akaike weight was 13% of the weight of the best model. All three confidence models had R^2 values of 0.51.

Parameter estimates from the best model indicated that for resident species sub-adult density would be greater in summer than in winter and greater at higher salinities. For transient species, the model predicted little difference in density between seasons, and a negative relationship between density and salinity. Parameter estimates for “management” and “transience” had 90% confidence intervals that overlapped zero (Table 6).

Empirical Bayes estimates of resident fish density were lower in association with waterfowl management for bay anchovy and naked goby, but waterfowl management was predictive of higher density for rainwater killifish, sailfin molly, and mosquitofish (Figure 10). White mullet (*Mugil curema*) were estimated to occur at greater density in “waterfowl” impoundments; mullet was the only transient species for which predictions were conclusive (Figure 11).

CHAPTER 5:

DISCUSSION

Water Quality

Water quality conditions are important determinants of habitat quality, and highly variable or extreme conditions can be stressful to aquatic organisms (EPA 2008). Water temperature (Figure 2) at the Nemours impoundments followed the expected seasonal pattern with the lowest values recorded during November ‘08 and January ‘09 sampling trips when the temperature dropped below 10 °C at some stations and the highest measurements recorded during July and August of ‘08 and June ‘09 when temperatures climbed 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. Considerable spatial and temporal variation is therefore to be expected. Salinity in the Nemours impoundments (Figure 3) did not follow a seasonal pattern and showed more influence of climate variability. Mean salinity recorded during the first two 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. I did not detect increasing salinity during the summer of 2009, as would be expected in this typically dryer season. 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 I 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 (Figure 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). 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 – 5 mg/l as "fair"; lower values are considered "poor" (EPA 2008). On average, 44% 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 my measurements, physiologically challenging for fishes not adapted to hypoxic conditions.

The temperature and salinity data collected during this study had a much greater range than was recorded in the main stem of the Combahee River downstream from my study site (Upchurch and Wenner 2008). Rather, the range of these variables resembles the data recorded at the Cat-Island impoundments (Wenner et al. 1986). Cat Island, being much closer to the Atlantic Ocean, had somewhat higher salinities at the upper end of the range. Dissolved oxygen concentration also ranged widely in my study, as it did at Cat Island (Wenner et. al. 1986). My 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 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 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, white mullet, 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 in association with winter/spring recruitment pulses and low salinity that has been reported by other researchers (Rogers 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 my samples of larval and juvenile fishes.

Robinson (2011) 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. However, all of the comparison study sites were far closer (approx. 20-50 km) to the ocean-estuary interface than the Nemours impoundments, a caveat necessitated by the paucity of research from mid and upper-estuary impoundments. Published data with analogous methodology and geography to which the Nemours fish assemblage can be compared are not available.

The Gulf pipefish is a notable resident of the Nemours impoundments. Gulf pipefish are classified in the family *Syngnathidae*, which includes pipefishes, seahorses, and sticklebacks (Helfman et al. 2009). The species occurs in coastal habitats along the southern-Atlantic coast of the U.S., throughout the Gulf of Mexico, and along the coasts of Central and South America to the Southern-Atlantic coast of Brazil; the Northern extent of the range has been unclear.

Recently published papers (Gasparini and Teixeira 1999, Bolland and Boettcher 2005, Storer 2009) and online references (Smithsonian 2012) cite, as the northern extent of the species' range, a breeding population recorded in the Ogeechee River estuary in Georgia (Targett 1984). Before this population was discovered, the mouth of the St. Johns River in Florida was considered the northern limit of the species (Targett 1984). The occurrence of Gulf Pipefish in South Carolina has been documented (Wenner et al. 1986, Upchurch and Wenner 2008), but these papers have not subsequently been cited when describing the range of the species. Whether the specimens collected by these researchers were indicative of a breeding population is unknown. The specimens collected during my study clearly were from a breeding population, with sexually mature females, mature males, gravid males, and newly-hatched juveniles collected on multiple sampling occasions. Targett (1984) noted that, unlike the SAV habitat common to the Gulf pipefish in the rest of its range, the Ogeechee River specimens were collected from salt marsh creeks with soft bottom sediments without grass beds and speculated that the species may not be as closely associated with SAV as previously thought. However, with the exception of a single individual, my specimens were collected in impoundments that contained extensive widgeon-grass beds. Widgeon grass is one of the preferred forage plants that managers seek to encourage in coastal wetland impoundments throughout South Carolina and Georgia (Gordon et al. 1989) and has been shown to be predictive of pipefish presence (Kanouse et al. 2006, La Peyre et al. 2007). My observation of Gulf pipefish in the Nemours impoundments thus raises an interesting question; could the SAV habitat supported by the low-energy, high-productivity environment prevalent in managed marsh impoundments be a factor contributing to range expansion of Gulf pipefish or other species that are closely associated with SAV?

Diversity

Both management types supported similar numbers of species, but “waterfowl” impoundments supported greater proportional abundance of dominant species. A lower effective number of species (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 (Figure 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 my 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 2011).

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 – 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 my measurements at Nemours, but the high end exceeds them by a wide margin. Care should be taken when comparing my 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 I 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 I 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 less species than “fish” impoundments. Although my study was not designed to compare the diversity of fishes between impounded and un-impounded waters, my finding that the ENS of the larval component of my 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 2003, 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 (5 - 18 ppt). 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. Bulger et al. (1993) used principal-component analysis to derive a series of overlapping salinity zones based on a large data set of salinity ranges for fishes that use the estuarine environment. This analysis revealed the presence of a mid-estuarine zone, occurring at salinities between 11 ppt and 18 ppt that is associated with freshwater transient and marine transient fishes with very high or very low salinity tolerances, respectively. This zone constitutes a physiological barrier for other marine or freshwater fishes beyond which osmoregulatory stress ensues (Bulger 1993). Wagner (1999) hypothesized that the ESM will be most evident in riverine estuaries with long salinity gradients, an attribute common to shallow gradient southeastern U.S. drainages with high tidal amplitude such as the Combahee River.

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 km, 5 km, 13 km, 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 and density from my best approximating models predict that some taxonomic groups will occur in greater numbers in impoundments 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 (Figure 8). Cyprinodontiforms could be more abundant in "waterfowl" impoundments because they are intertidal specialists capable of surviving in the extreme conditions found in small pools, puddles, and rivulets left behind in the marsh surface between tides (Able and Fahay 2010). Whereas non-Cyprnodontiform resident fishes utilize the shallow marsh edge where conditions are less extreme than on the marsh surface. This idea is supported by the findings of researchers that used an array of flume nets and seine-net sampling to identify four general patterns of salt marsh utilization by fishes and macro-invertebrates in a Louisiana tidal marsh (Peterson and Turner 1994).

"Interior Marsh Residents" are species that are capable of surviving the extremes of temperature, salinity, and dissolved oxygen likely to occur in intertidal habitats including puddles, burrows, rivulets, and trails that remain available to fishes at low tide (Peterson and Turner 1994). "Interior Marsh Users" also use the marsh surface but may require slightly deeper water and tend to retreat to creek margins at low tide rather than seek refuge on the marsh surface. In a Louisiana study, all the fishes classified in the “Interior Marsh Resident” and “Interior Marsh User” groups, which included sheepshead minnow, sailfin molly, and rainwater killifish, were in the family Cyprinodontiformes (Peterson and Turner 1994). In my study, fishes that were predicted to be more abundant in “waterfowl” impoundments included these same cyprinodontiform species as well as mosquitofish, a livebearer that is ecologically similar to sailfin molly and probably an “Interior Marsh Resident” (Harrington and Harrington 1982, McIvor and Odum 1988).

“Edge Marsh Users” are common along tidal-creek margins but typically do not access the marsh surface beyond 3 meters from the margin (Peterson and Turner 2011). “Subtidal Marsh Users” utilize open-water estuarine habitats including creek margins but rarely, if ever, access the marsh surface. Fishes assigned to these two groups by Peterson and Turner (2011) that also occurred in the Nemours impoundments included inland silverside, gobies, mullet, bay anchovy, and menhaden. Likewise at Nemours, several of these species, including inland silverside, gobies, and bay anchovy were predicted to be more abundant in “fish” impoundments. Gulf pipefish and spot, two species that were not present in the Louisiana study, were also predicted to be more abundant in “fish” impoundments compared to “waterfowl” impoundments at Nemours. Based on the ecology of these fishes, they would be classified as Edge Marsh Users (Hettler 1989, Kanouse et al. 2006, La Peyre et al. 2007). The fact that non-cyprinodontiform resident fishes were more common in marsh-edge and subtidal estuarine habitats compared to marsh interior habitats suggests that this habitat association may also be an important factor influencing their greater abundance in “fish” impoundments compared to “waterfowl” impoundments at Nemours.

My model results shed 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. Potential benefits include greater availability of food resources and decreased predation risk (Hoese and Konikoff 1995, Rozas and Minello 1999). Most studies that assessed standing stock of resident fishes in impoundments documented positive effects on these taxa (Rogers et al. 1994). My work reveals that differences in tidal circulation related to impoundment management can have opposing effects on the relative abundance of different species of estuarine-resident fishes. These findings suggest that studies that draw conclusions about resident fishes as a group (Rogers et al. 1994, Rozas and Minello 1999) may not sufficiently capture variability among individual resident taxa. For instance, my results show that cyprinodontiform fishes are likely to be more abundant in tide-restricted “waterfowl” impoundments compared to “fish” impoundments. Conversely, non-cyprinodotiform 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.

Management Implications

My results indicate that restrictive management of tidal circulation in “waterfowl” impoundments affects the assemblage composition of sub-adult fishes by reducing diversity of early life stages and increasing the abundance of cyprinodontiform resident fishes relative to non-cyprinodontiform resident fishes. This information adds evidence to the existing body of literature that suggests infrequent tidal circulation can reduce the habitat quality of impounded coastal wetlands for many fishes (Wenner et al. 1986, Herke et al. 1992, Rozas and Minello 1999, Poulakis et al 2002, Taylor et al. 2008). Taxa such as Cyprinodontiformes that are adapted to stressful habitats are equipped to exploit these conditions, but the population stability of even these species may be compromised (Robinson 2011).

Robinson (2011) suggested that restructuring of the dominance hierarchy amongst resident fishes may be a common inter-annual occurrence in coastal wetland impoundments that receive little tidal circulation. Within impoundments, the resident assemblage can be structured differently in different years, with dominance by inland silversides occurring sporadically but not persisting (Robinson 2011). Further study is required to determine if the stability of the resident-fish assemblage can be reliably affected by management decisions about tidal circulation and if increased stability has desirable management outcomes. Research investigating the trophic consequences of an unstable resident-fish assemblage on other important elements of the impoundment ecological community, including fish, birds, and reptiles, would help inform impoundment management decisions.

Currently, the trophic linkages between the fish assemblage in impoundments and other secondary consumers are poorly understood. Stevens et al. (2006) estimated the fate of fish production in a Florida salt marsh impoundment that had been tidally reconnected to the estuary by culverts. They estimated that 20% of fish production in impoundments is consumed and exported by large piscivorous fishes, whereas 13% is consumed and exported by piscivorous birds. This relationship may be similar at the Nemours "fish" impoundments, but may differ from "waterfowl" impoundments because of the reduced ability for transient piscivorous fishes to emigrate (Robinson 2011). Furthermore, piscivorous birds could be more important vectors relative to other taxa in "waterfowl" impoundments because they occur in greater abundance in these areas (Nareff 2009). American alligators (*Alligator mississippiensis*) present another unmeasured, but likely substantial vector for redistribution of biomass to or from the Nemours impoundments. Alligators are abundant at Nemours and are apex predators that are known to move between estuarine and marine systems (Rosenblatt and Heithaus, 2011).

My research was intended to inform management decisions regarding impounded wetlands at Nemours and similar sites, not to critique any particular management strategy. Whereas "waterfowl" impoundments may provide sub-optimal habitat for some species of common estuarine fishes, benefits for avian communities are well documented at Nemours (Nareff 2009). Despite the increasing body of evidence that tidally-restrictive management of marsh impoundments has negative consequences for fish diversity, production, and mobility, the Compensatory Adjustment Hypothesis (Hoese and Konikoff 1995) has not been challenged. Therefore, to what degree reduced fisheries productivity in "waterfowl" impoundments (Robinson 2011) may be offset by gains in productivity of other consumers including birds, reptiles, mammals, and insects is still unknown; all of these components are capable of mobilizing biomass within the coastal ecosystem. Thus, I suggest a refinement of Kneib's "trophic relay" concept (Kneib 2000) that is expanded beyond aquatic species to include all taxa that use the marsh for feeding and then move to other habitats.

Management of the abundant natural resources at Nemours Plantation requires a careful balance between attention to the details of site-specific ecology and consideration of the local system's role in the regional landscape. My results indicate that the marine-transient fish, spot, is more likely to occur in greater abundance in "fish" impoundments than in "waterfowl" impoundments at Nemours. Robinson (2011) used a Bayesian Belief Network to model the likelihoods of different factors affecting the export of young-of-year (YOY) spot from impoundments to the estuary. The results indicated that spot export was most sensitive to rates of juvenile settlement and natural mortality and insensitive to impoundment water-control decisions. Together, these results indicate that, for spot, decisions about water control can have a within-impoundment affect on the local population but are not among the most important factors structuring the population outside of the impoundments.

The assumption that the wooden tide gates (i.e., "rice trunk") used to control water levels in many coastal wetland impoundments in the Southeast effectively disallow immigration and emigration by fishes when flap gates are thought to be closed also calls for additional focused investigation. Wooden structures rot and require repair and replacement every 15 - 30 years (Ernie Wiggers, NWF, personal communication), and older rice trunks may be degraded to the point that fish passage could occur even when the structures are technically closed to tidal movements. Robinson (2011) frequently captured adult longnose gar (*Lepisosteus osseus*) and American eel (*Anguilla rostrata)* in "waterfowl" impoundments. Both of these fishes are capable of surviving in hypoxic conditions (Tesch 2003, Helfman et al. 2009) and appear to be the primary large piscivorous fishes that persist from year to year in "waterfowl" impoundments at Nemours (Robinson 2011). Because of their catadromous life cycle, American eel are highly adapted to navigating through or around barriers (Tesch 2003). Neither species was captured as larvae or early juveniles in my study. Therefore, they may be immigrating to impoundments as large juveniles or adults during controlled-flooding events or through permeable, “closed” tide gates. If the latter is true, these fishes may be able to emigrate from impoundments through “closed” gates. Estimates of the effect of gate permeability on passage rates for different fishes through water-control structures would be helpful in formulating effective management plans for coastal wetland impoundments. Dual-frequency identification sonar (DIDSON) has been used to assess fish movement through vertically-slotted water control structures in Louisiana (Kimball et al. 2010) and has been successfully tested on wooden “rice trunk” flap gates (Matthew E. Kimball, personal communication).

The information presented here about the composition of the fish assemblage in the two types of impoundments at Nemours helps complete the ecological understanding of impoundment communities and the tradeoffs that can result from “waterfowl” impoundment management. However, I caution that species diversity should not be considered alone as an indicator of ecosystem integrity by which to set conservation and management priorities (Fleishman et al. 2006). The possibility that the Nemours impoundments exist within an ESM highlights the difficulty that arises in attempts to partition anthropogenic stress from natural stress in highly variable estuarine systems (Elliot and Quintino 2007). For these reasons, some researchers have suggested that measures of ecosystem function, such as trophic relationships, supplement measures of diversity when assessing the effects of stress on system integrity (Fleishman et al. 2006, Elliot and Quintino 2007). The composition of the fish assemblage at Nemours is an important piece of the local system that must be considered alongside other conservation objectives such as providing habitat for avifauna and opportunities for recreation and education. Managers should establish clearly-defined goals for impoundment services and evaluate those goals with an adaptive approach to assess the effects of incremental changes in tidal circulation on desired conditions.

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TABLES AND FIGURES

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

		Waterfowl		Fish	
Scientific Name (family)	Common Name	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)	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	23974	11420	9092	9840
Microgobius sp. (Gobiidae)	unidentified goby	0	0	1	8
Micropogonius undulates (Sciaenidae)	Atlantic croaker	0	4	1	1
Mugil curema (Mugilidae)	white mullet	0	9	1	1

Table 1. Continued.

Scientific Name (family)	Common Name	Waterfowl Nieuport	 Big Rice Field	Fish Boss' Pond	 Branford
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

Table 2. Sub-adult fishes sampled with push nets 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	1	3	237	219
Brevortia tyrannus (Clupeidae)	Atlantic menhaden	0	1	75	4
Cyprinodon variegates (Cyprinodontidae)	sheepshead minnow	1	0	0	0
Elops saurus (Elopidae)	ladyfish	1	5	6	0
Gambusia holbrooki (Poeciliidae)	mosquitofish	483	32	25	0
Gobiosoma bosc (Gobiidae)	naked goby	1	0	13	6
Leiostomus xanthurus (Sciaenidae)	spot	0	0	31	2
Lucania parva (Fundulidae)	rainwater killifish	21	4	0	4
Menida beryllina (Atherinidae)	inland silverside	8918	424	688	1293
Micropogonius undulates (Sciaenidae)	Atlantic croaker	0	1	0	0
Mugil curema (Mugilidae)	white mullet	1	53	0	1
Poecilia latipinna (Poeciliidae)	sailfin molly	74	25	9	0
Syngnathus scovelli (Syngnathidae)	gulf pipefish	1	2	3	2
unknown (damaged)		0	0	0	1

Table 3. 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. 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.

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

Table 4. Parameter estimates, standard errors, and 90% confidence intervals (C.I.) in the confidence set of hierarchical models 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). An “*” indicates an interaction effect. Models are based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009 and are listed in order of plausibility. Random effects parameter estimates are variance components.

Parameter	Estimate	Standard Error	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

Table 4. (continued; 2nd best model)

Parameter	Estimate	Standard Error	Lower C.I	Upper C.I.
Fixed Effects				
Intercept	-6.266	1.449	-8.757	-3.775
Management	-0.662	1.011	-2.420	1.096
Transience	-2.077	1.700	-5.065	0.911
Season	2.377	0.878	0.861	3.893
Transience * Season	-4.636	1.026	-6.441	-2.831
Salinity	0.060	0.401	-0.631	0.751
DO	-0.389	0.300	-0.887	0.109
Random Effects				
Intercept	17.626	7.102	10.122	39.934
Management	11.171	4.877	6.174	27.577
Salinity	1.182	0.617	0.596	3.681
Season	1.881	1.362	0.781	11.254
Month	0.576	0.407	0.243	3.239
Residual	15.549	1.036	13.982	17.414

Table 5. Predictor variables, number of parameters (K), AIC$_c$, ΔAIC$_c$, and Akaike weights (*w*), for candidate models relating density of sub-adult fishes from push-net samples to impoundment management (fish or waterfowl), transience (resident or transient), season (summer or winter), mean dissolved oxygen concentration (DO), and mean salinity. 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.

Candidate Model	K	AIC$_c$	ΔAIC$_c$	w_i	percent of maximum w_i	R^2
management, transience|season, transience|mean salinity	12	2256.81	0.00	0.71	100%	0.51
management, season, transience|mean salinity	11	2259.39	2.58	0.20	28%	0.51
management|transience, management|season, transience|season, transience|mean salinity	14	2260.96	4.15	0.09	13%	0.51
management, transience|mean salinity	10	2272.50	15.69	0.00	0%	N/A
management, transience|season, mean salinity	11	2280.17	23.36	0.00	0%	N/A
management, transience, season, mean salinity	10	2288.43	31.62	0.00	0%	N/A
management|season, transience, mean salinity	11	2290.42	33.61	0.00	0%	N/A
management|transience, mean salinity, season	11	2290.44	33.63	0.00	0%	N/A
transience|season, transience|mean salinity	9	2295.36	38.54	0.00	0%	N/A
season, transience|mean salinity	8	2297.27	40.46	0.00	0%	N/A
management, transience|season	10	2410.71	153.89	0.00	0%	N/A
management	7	2438.56	181.75	0.00	0%	N/A

Table 6. Parameter estimates, standard errors, and 90% confidence intervals (C.I.) in the confidence set of hierarchical models relating density of sub-adult fishes from push-net samples to impoundment management (baseline: “fish” impoundment), transience (baseline: resident species), season (baseline: winter), and salinity (centered on the mean). An “*” indicates an interaction effect. Models are based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009 and are listed in order of plausibility. Random effects parameter estimates are variance components.

Parameter	Estimate	Standard Error	Lower C.I.	Upper C.I.
Fixed Effects				
Intercept	-8.453	1.233	-10.612	-6.293
Management	0.280	1.224	-1.932	2.491
Transience	-2.183	1.638	-5.095	0.729
Season	2.186	0.488	1.381	2.991
Transience * Season	-1.760	0.809	-3.093	-0.426
Salinity	1.111	0.249	0.700	1.522
Transience * Salinity	-2.114	0.412	-2.793	-1.435
Random Effects				
Intercept	9.499	4.378	5.111	24.998
Management	10.686	5.256	5.561	30.585
Impoundment (location)	0.373	0.434	0.112	17.612
Residual	14.249	1.045	12.681	16.147

Table 6. (Continued; 2nd best model)

Parameter	Estimate	Standard Error	Lower C.I.	Upper C.I.
Fixed Effects				
Intercept	-8.138	1.224	-10.287	-5.989
Management	0.280	1.223	-1.931	2.491
Transience	-3.048	1.589	-5.902	-0.193
Season	1.546	0.392	0.900	2.192
Salinity	1.181	0.249	0.771	1.591
Transience * Salinity	-2.306	0.405	-2.974	-1.639
Random Effects				
Intercept	9.492	4.380	5.104	25.016
Management	10.676	5.260	5.550	30.627
Impoundment (location)	0.371	0.434	0.111	18.166
Residual	14.430	1.059	12.842	16.352

Table 6. (Continued; 3rd best model)

Parameter	Estimate	Standard Error	Lower C.I	Upper C.I.
Fixed Effects				
Intercept	-8.373	1.328	-10.714	-6.033
Management	0.122	1.513	-2.552	2.797
Transience	-2.206	2.057	-5.869	1.457
Management * Transience	0.040	2.204	-3.915	3.996
Season	2.051	0.606	1.052	3.050
Management * Season	0.287	0.762	-0.970	1.543
Salinity	1.110	0.249	0.699	1.522
Transience * Salinity	-2.115	0.413	-2.796	-1.434
Transience * Season	-1.759	0.809	-3.093	-0.425
Random Effects				
Intercept	9.501	4.379	5.112	25.004
Management	10.690	5.258	5.563	30.594
Impoundment (location)	0.379	0.439	0.114	17.272
Residual	14.242	1.045	12.675	16.139

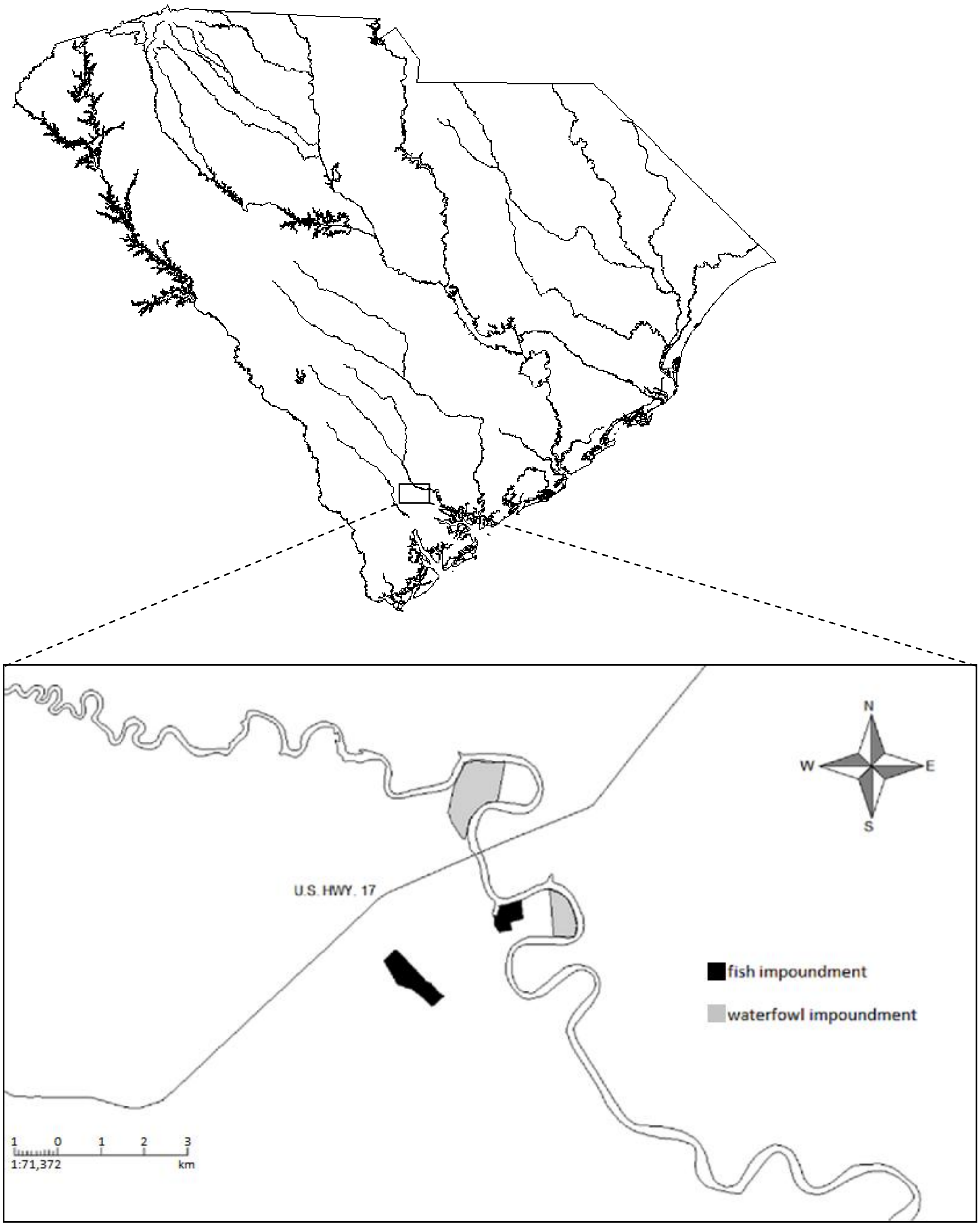

Figure 1. The location of the four study sites during 2008 and 2009 at Nemours Plantation on the Combahee River above St. Helena Sound in coastal South Carolina. From West to East, the "fish" impoundments are Branford and Boss' Pond, the "waterfowl" impoundments are Nieuport and Big Rice Field.

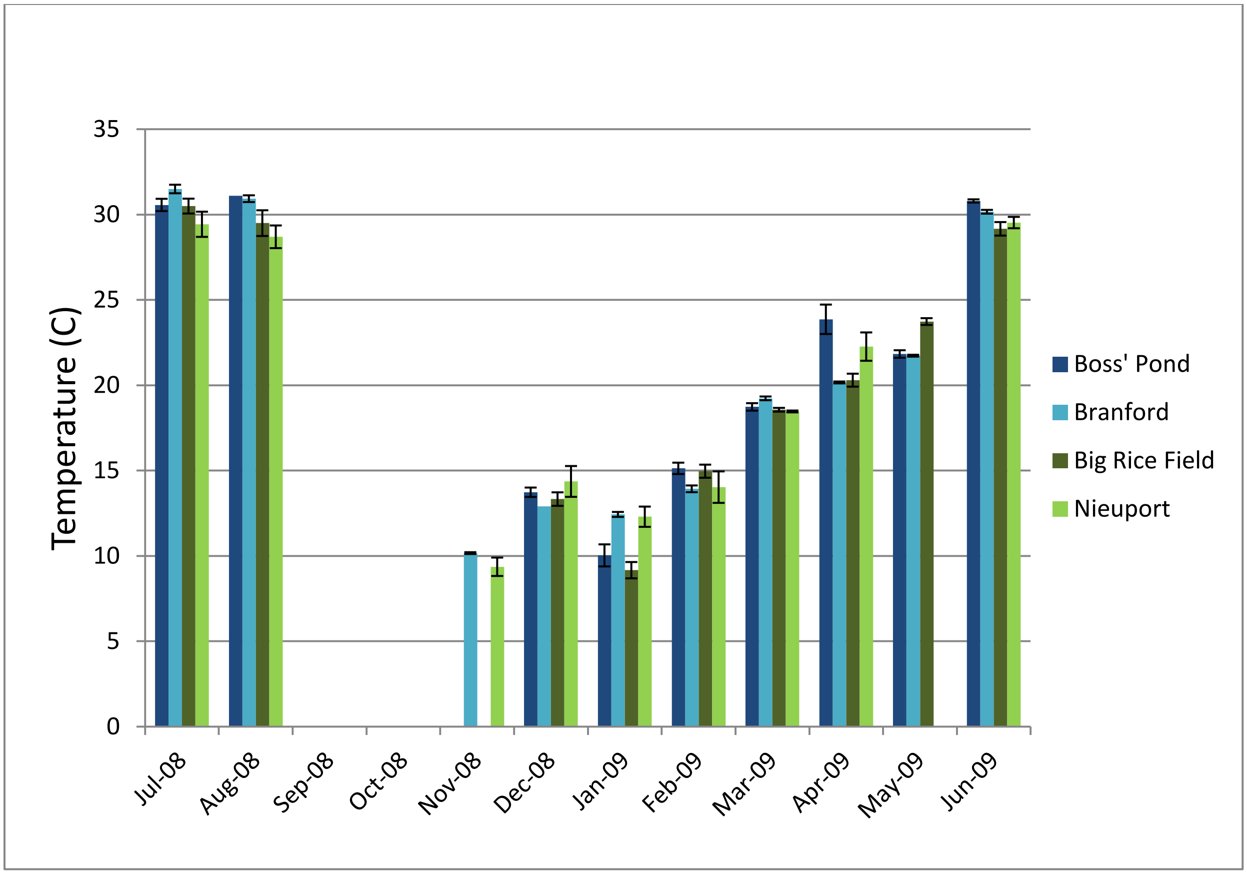

Figure 2. Mean water temperature and 90% confidence intervals in “fish” impoundments (Boss’ Pond and Branford) and in “waterfowl” impoundments (Big Rice Field and Nieuport) during the study period (n=3). Confidence intervals are not given for Boss’ Pond in August or for Branford in December because only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

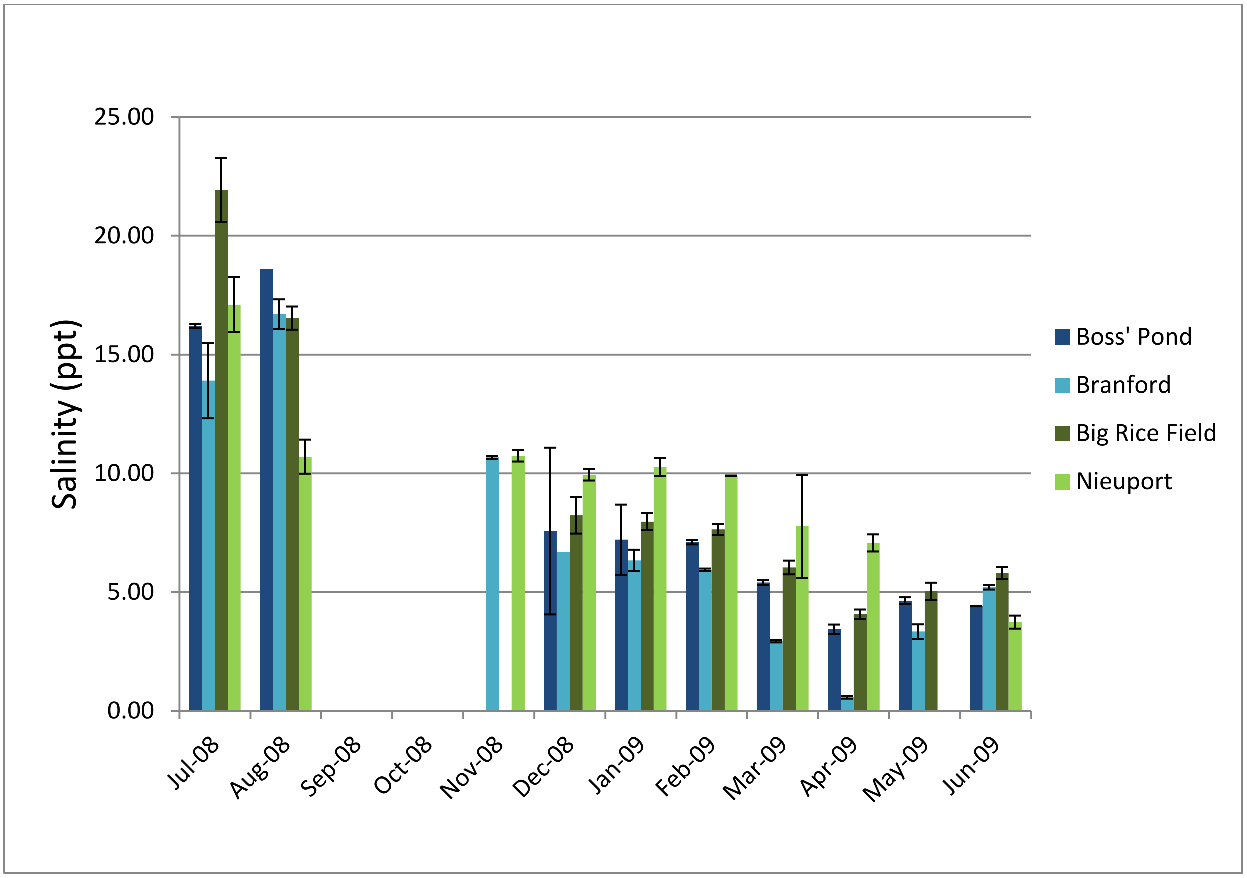

Figure 3. Mean salinity and 90% confidence intervals in "fish" impoundments (Boss' Pond and Branford) and in "waterfowl" impoundments (Big Rice Field and Nieuport) during the study period (n=3). Confidence intervals are given not for Boss' Pond in August or for Branford in December because only one measurement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

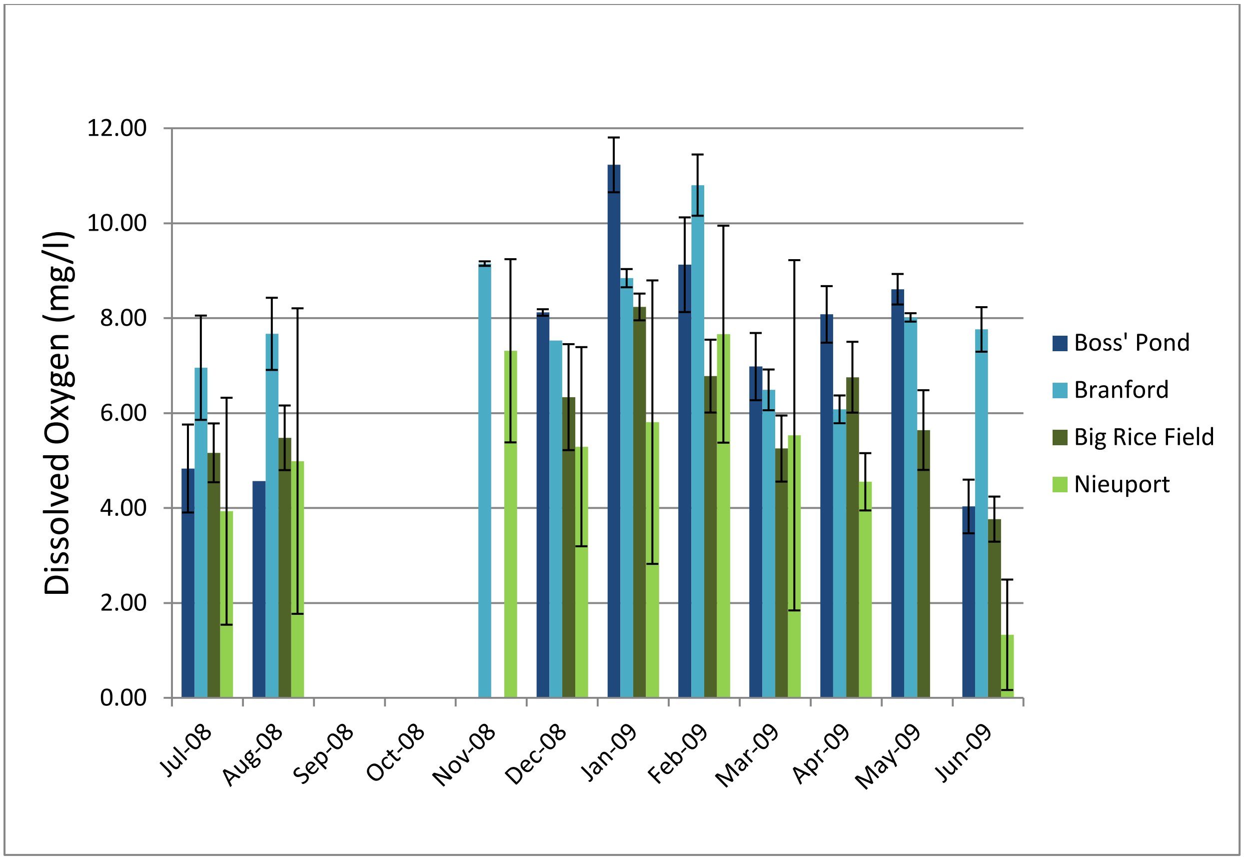

Figure 4. Mean dissolved-oxygen concentration and 90% confidence intervals in "fish" impoundments (Boss' Pond and Branford) and in "waterfowl" impoundments (Big Rice Field and Nieuport) during the study period (n=3). Confidence intervals are not given for Boss' Pond in August or for Branford in December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

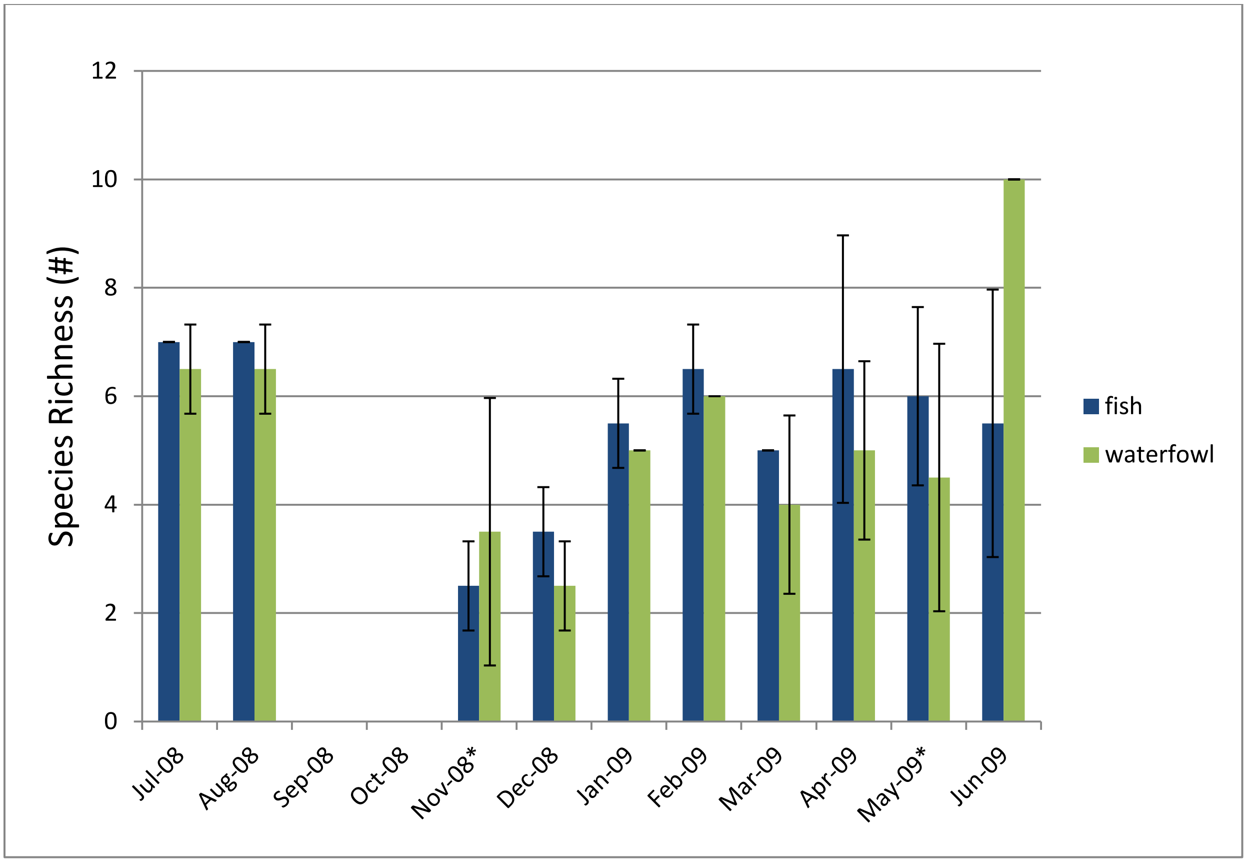

Figure 5. Mean species richness of sub-adult fishes in light-trap and push-net gear for "fish" and "waterfowl" impoundments during the study period (n=2). Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009.

* 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.

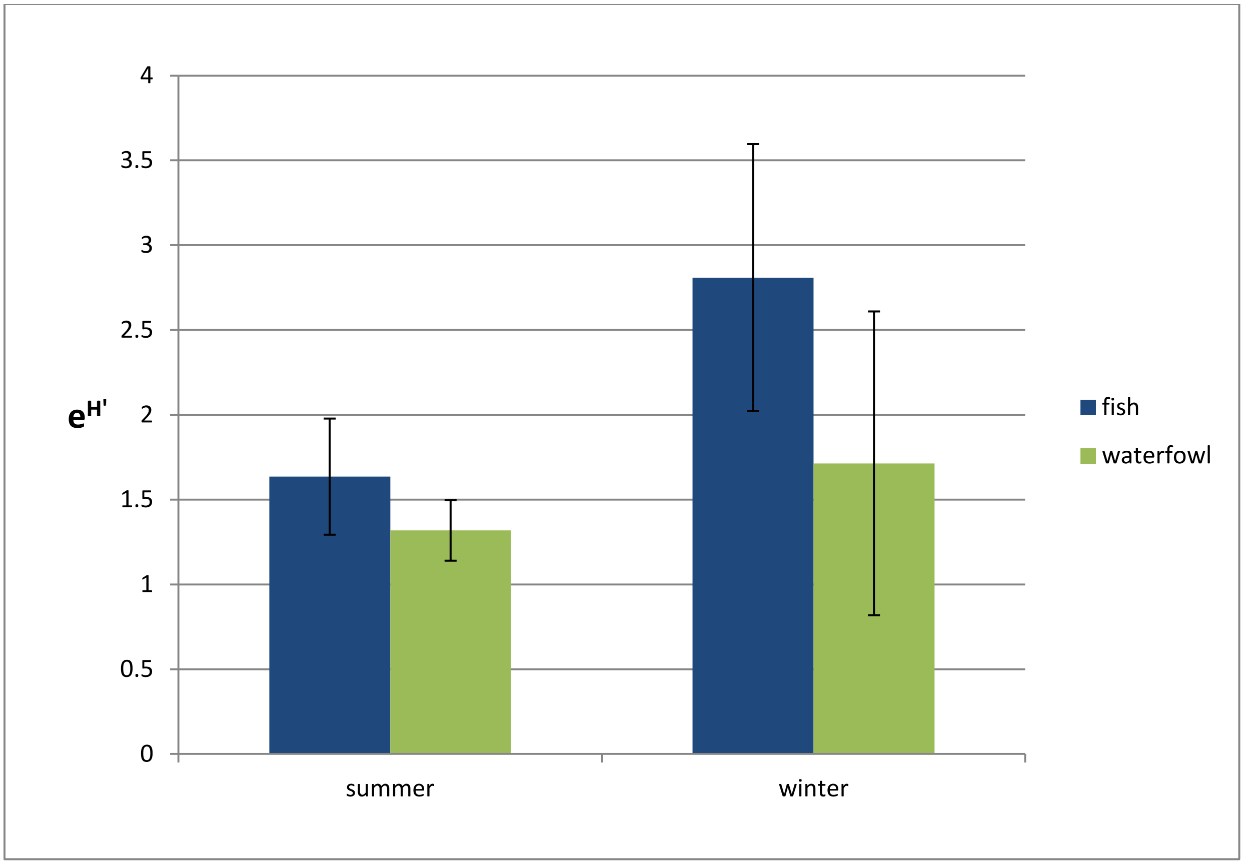

Figure 6. Mean effective number of species ($e^{H'}$) calculated from the sub-adult component of light-trap catch in fish impoundments and in waterfowl impoundments during summer (April - August) and winter (November - March)(n=2). Data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008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

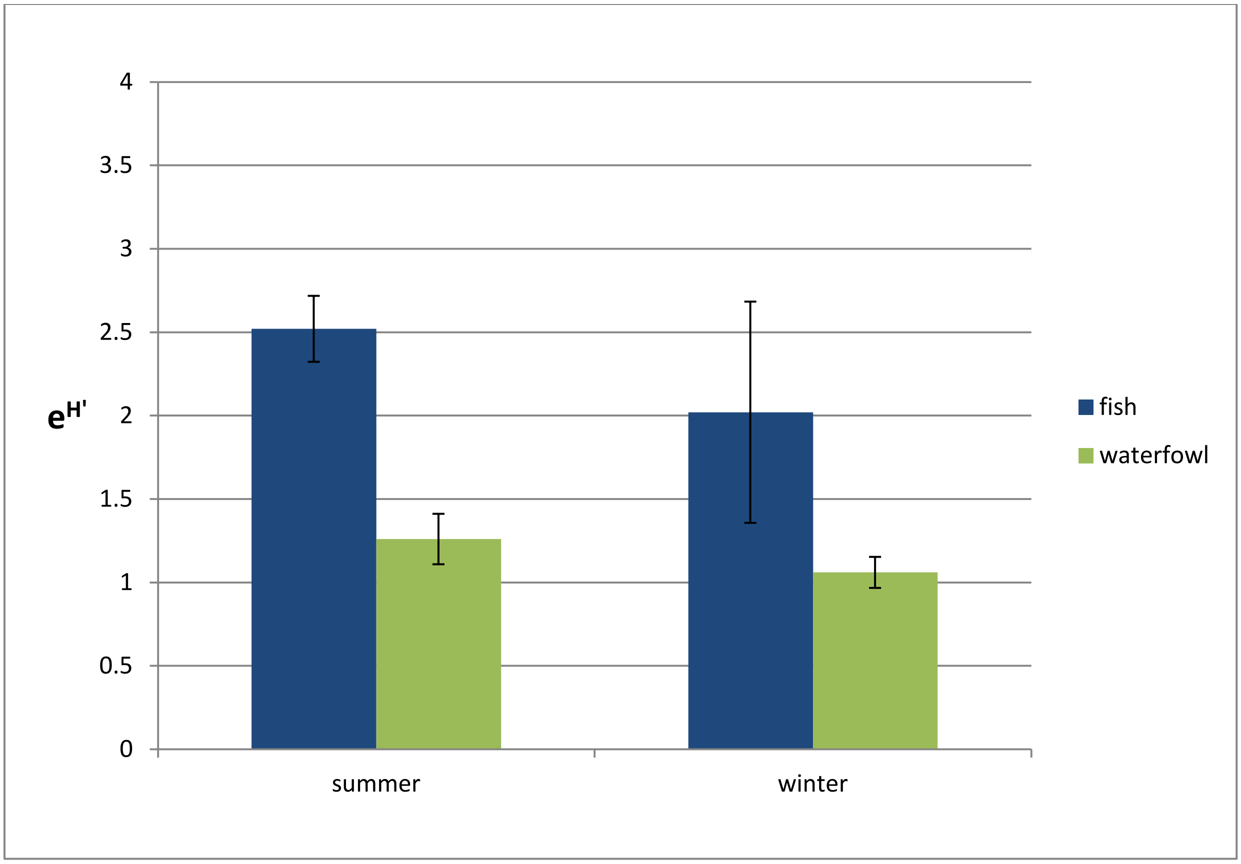

Figure 7. Mean effective number of species ($e^{H'}$) and 90% confidence intervals calculated from the larval component of light-trap catch in "fish" impoundments and in "waterfowl" impoundments during summer (April - August) and winter (November - March)(n=2). Data collected at Nemours Wildlife Foundation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

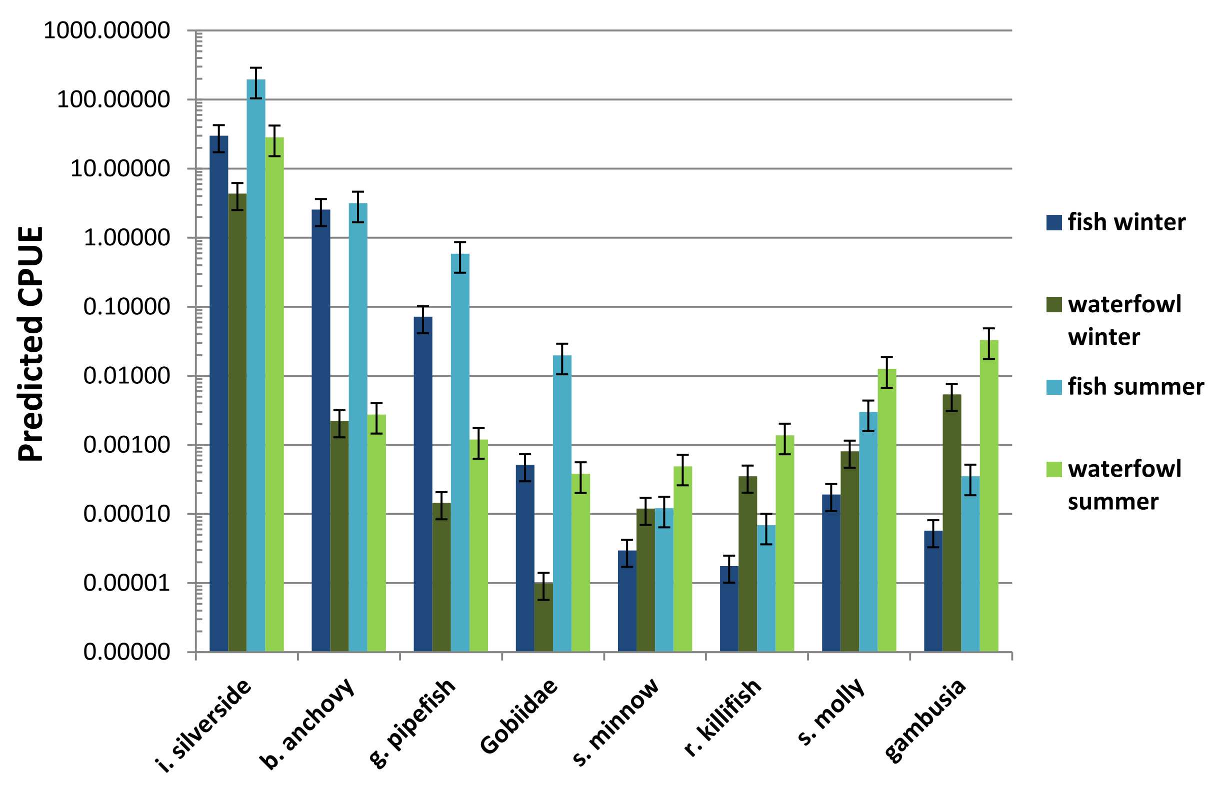

Figure 8. Empirical Bayes estimates of light-trap CPUE and 90% confidence intervals for sub-adult, resident fishes during winter (November – March) and summer (April – August) from the best-fitting hierarchical linear model (n=5). Predictions assume mean salinity and dissolved oxygen concentration. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009.

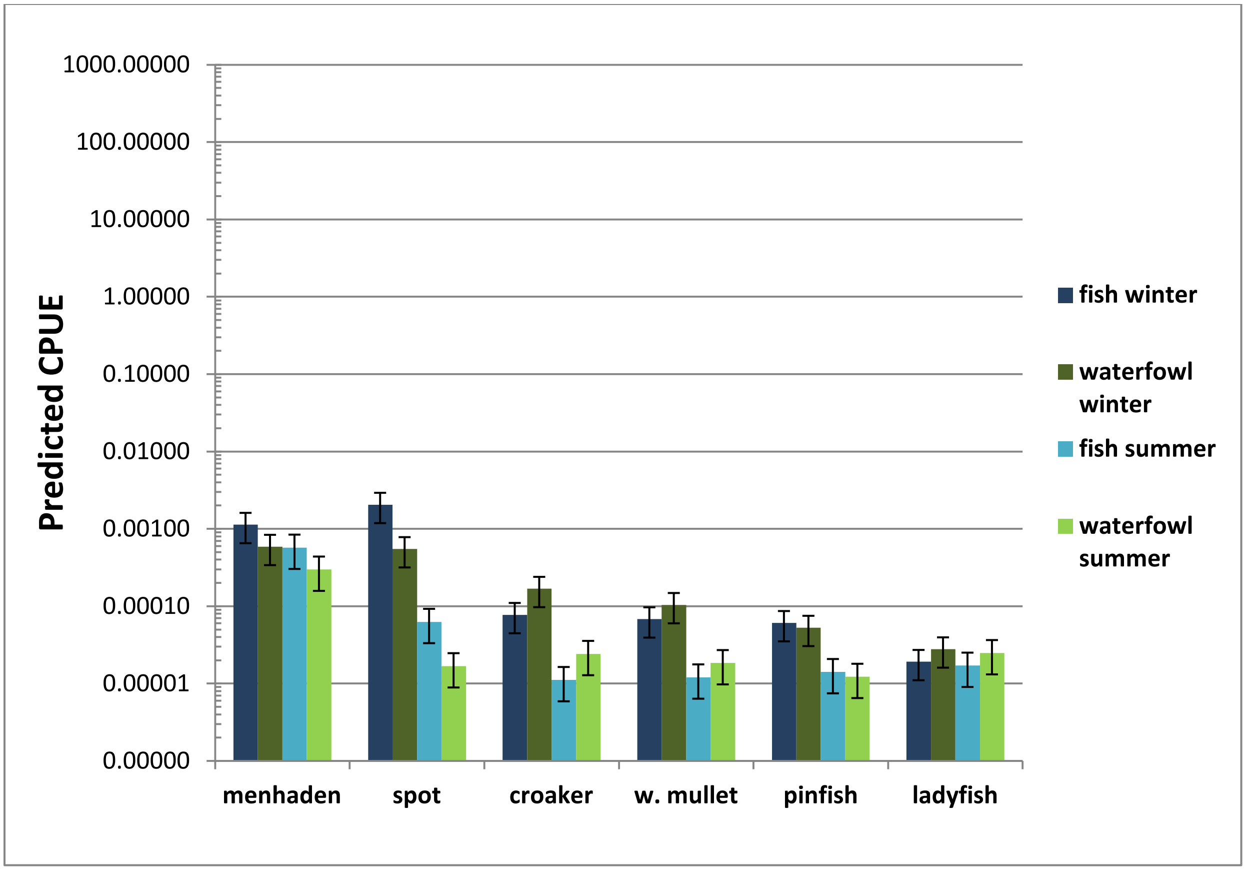

Figure 9. Empirical Bayes estimates of light-trap CPUE and 90% confidence intervals for sub-adult, transient fishes during winter (November – March) and summer (April – August) from the best-fitting hierarchical linear model (n=5). Predictions assume mean salinity and dissolved oxygen concentration.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

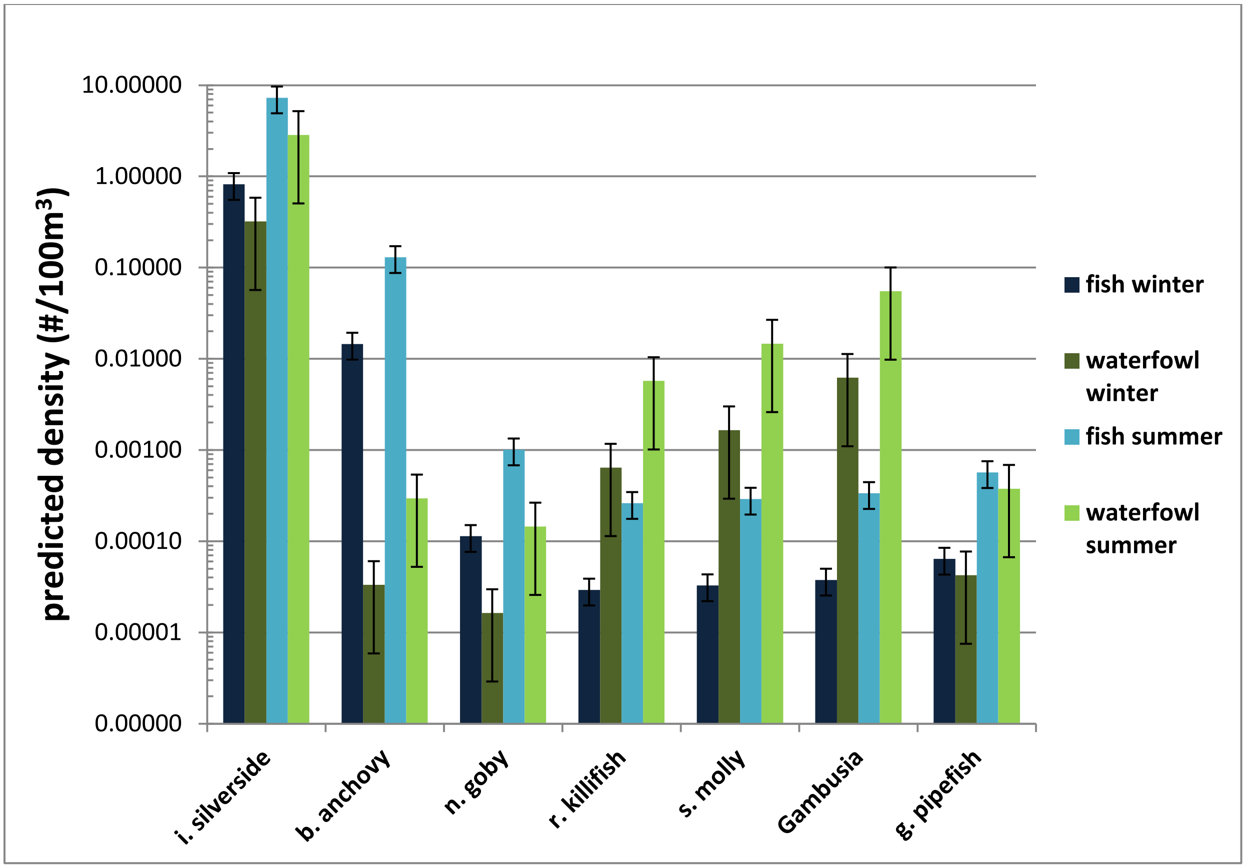

Figure 10. Empirical Bayes estimates of density in push-net samples and 90% confidence intervals for sub-adult, resident fishes during winter (November – March) and summer (April – August) from the best-fitting hierarchical linear model (n=2). Model output predicted the number of fish per 50 m^3 of water. These values were multiplied by 2 to report the standard, fish/100 m^3, here. Predictions assume mean salinity. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009.

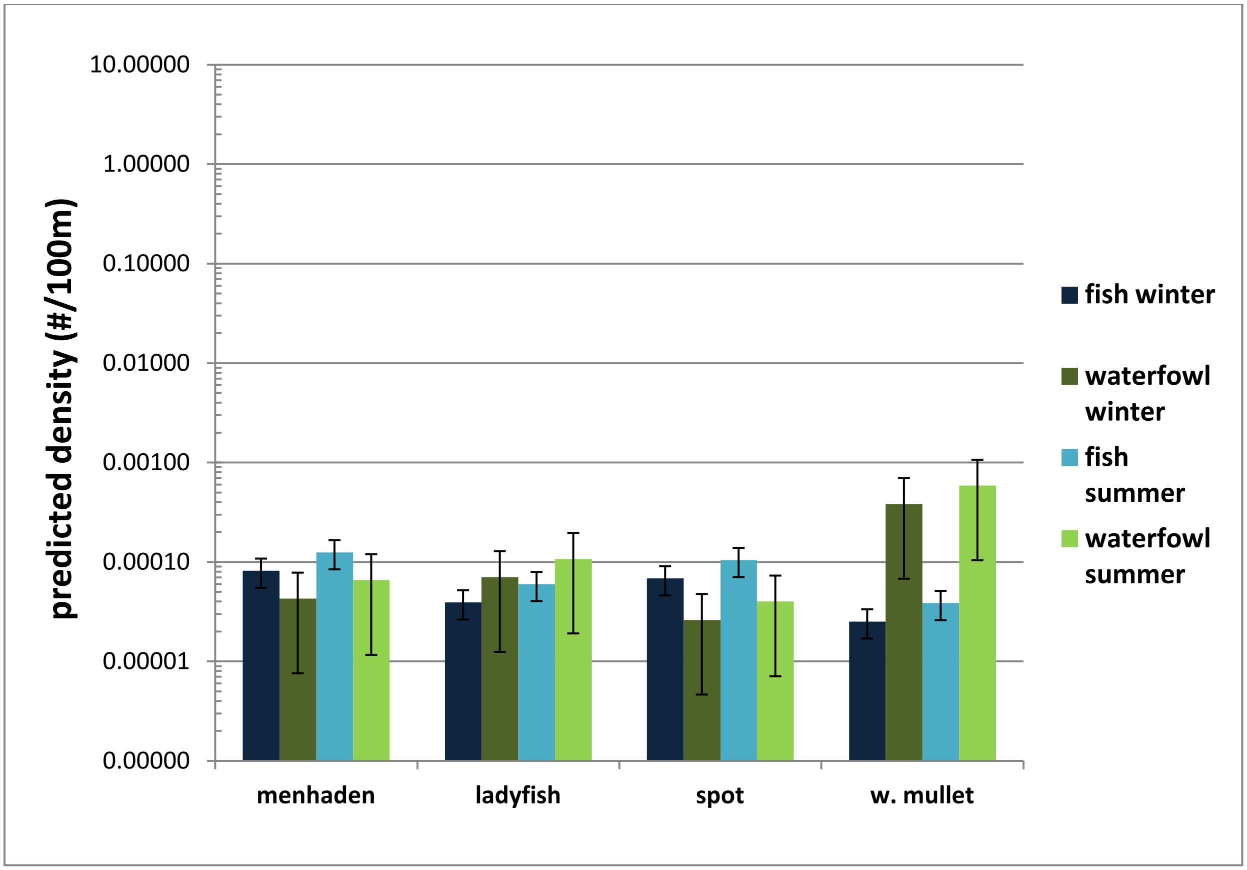

Figure 11. Empirical Bayes estimates of density in push-net samples and 90% confidence intervals for sub-adult, transient fishes during winter (November – March) and summer (April – August) from the best-fitting hierarchical linear model (n=2). Model output predicted the number of fish per 50 m^3 of water. These values were multiplied by 2 to report the standard, fish/100 m^3, here. Predictions assume mean salinity. Models based on data collected at Nemours Wildlife Foundation (Yemassee, SC) during 2008 and 2009.

APPENDICES

Appendix A. Geographic coordinates demarcating the ends of push net transects at each of the three sampling stations in the study impoundments at Nemours Wildlife Foundation (Yemassee, SC). Light traps samples were also collected within these transects.

Impoundment	Station	Latitude 1	Longitude 1	Latitude 2	Longitude 2
Nieuport	1	N 32 39.851	W 80 40.888	N 32 39.797	W 80 40.990
Nieuport	2	N 32 40.327	W 80 40.746	N 32 40.320	W 80 40.591
Nieuport	3	N 32 40.091	W 80 41.268	N 32 40.222	W 80 41.197
Big Rice Field	1	N 32 38.546	W 80 39.881	N 32 38.675	W 80 39.904
Big Rice Field	2	N 32 38.548	W 80 39.663	N 32 38.427	W 80 39.589
Big Rice Field	3	N 32 38.193	W 80 39.573	N 32 38.112	W 80 39.684
Boss' Pond	1	N 32 38.536	W 80 40.314	N 32 38.407	W 80 40.290
Boss' Pond	2	N 32 38.425	W 80 40.694	N 32 38.524	W 80 40.544
Boss' Pond	3	N 32 38.229	W 80 40.584	N 32 38.271	W 80 40.729
Branford	1	N 32 37.293	W 80 41.621	N 32 37.358	W 80 41.508
Branford	2	N 32 37.478	W 80 42.082	N 32 37.583	W 80 41.794
Branford	3	N 32 37.651	W 80 42.207	N 32 37.756	W 80 42.023

Appendix B. Mean water quality measurements with 90% confidence intervals for study impoundments at Nemours Wildlife Foundation in 2008 and 2009. “X” indicates that data were not collected.

Impoundment	Jul-08	Aug-08	Nov-08	Dec-08	Jan-09	Feb-09	Mar-09	Apr-09	May-09	Jun-09
Temperature (C)										
Boss' Pond	30.57 (±0.36)	31.10 (N/A)	X	13.73 (±0.27)	10.03 (±0.65)	15.13 (±0.33)	18.73 (±0.22)	23.87 (±0.86)	21.83 (±0.22)	30.80 (±0.09)
Branford	31.50 (±0.25)	30.93 (±0.20)	10.17 (±0.05)	12.90 (N/A)	12.43 (±0.15)	13.93 (±0.20)	19.23 (±0.11)	20.17 (±0.05)	21.73 (±0.05)	30.17 (±0.11)
Big Rice Field	30.50 (±0.44)	29.50 (±0.75)	X	13.33 (±0.40)	9.17 (±0.48)	14.97 (±0.38)	18.57 (±0.11)	20.30 (±0.38)	23.73 (±0.20)	29.17 (±0.40)
Nieuport	29.43 (±0.74)	28.70 (±0.66)	9.37 (±0.54)	14.37 (±0.90)	12.30 (±0.59)	14.03 (±0.92)	18.47 (±0.05)	22.27 (±0.83)	X	29.53 (±0.33)
Salinity (ppt)										
Boss' Pond	16.20 (±.0.09)	18.60 (N/A)	X	7.57 (±3.51)	7.20 (±1.48)	7.10 (±0.09)	5.40 (±0.09)	3.43 (±0.20)	4.63 (±0.15)	4.40 (±0.00)
Branford	13.90 (±1.59)	16.70 (±0.62)	10.67 (±0.05)	6.70 (N/A)	6.33 (±0.45)	5.93 (±0.05)	2.93 (±0.05)	0.57 (±0.05)	3.33 (±0.31)	5.20 (±0.09)
Big Rice Field	21.93 (±1.34)	16.53 (±0.49)	X	8.23 (±0.77)	7.97 (±0.36)	7.63 (±0.24)	6.03 (±0.29)	4.07 (±0.20)	5.03 (±0.36)	5.80 (±0.25)
Nieuport	17.10 (±1.16)	10.70 (±0.72)	10.73 (±0.24)	9.93 (±0.24)	10.27 (±0.38)	9.90 (±0.00)	7.77 (±2.17)	7.07 (±0.36)	X	3.73 (±0.27)
Dissolved Oxygen Concentration (mg/L)										
Boss' Pond	4.83 (±0.93)	4.57 (N/A)	X	8.12 (±0.07)	11.23 (±0.58)	9.13 (±1.00)	6.98 (±0.71)	8.08 (±0.60)	8.61 (±0.32)	4.03 (±0.57)
Branford	6.96 (±1.10)	7.67 (±0.76)	9.15 (±0.05)	7.53 (N/A)	8.84 (±0.19)	10.80 (±0.65)	6.49 (±0.43)	6.08 (±0.29)	8.02 (±0.09)	7.76 (±0.47)
Big Rice Field	5.16 (±0.62)	5.48 (±0.68)	X	6.34 (±1.12)	8.24 (±0.28)	6.78 (±0.77)	5.25 (±0.70)	6.76 (±0.75)	5.64 (±0.84)	3.77 (±0.47)
Nieuport	3.93 (±2.39)	4.99 (±3.22)	7.31 (±1.93)	5.29 (±2.10)	5.81 (±2.99)	7.66 (±2.29)	5.53 (±3.69)	4.55 (±0.60)	X	1.33 (±1.16)