Fish Assemblage Structure in Shallow Water Habitats on the Eastern Shore of Virginia Barrier Islands

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Introduction

The barrier islands along the Atlantic and Gulf Coasts of the United States are considered to be among the most dynamic of ecosystems (Hayden *et al.,* 1991). The rate of landscape change of the Virginia islands is especially rapid; in fact, within North America the rate of change is exceeded only by that of the Chandeleur Islands off the Mississippi coast (Dolan *et al.*, 1983). The complex landscape and ecosystem patterns that result from the dynamic island geomorphology are hypothesized to be determined, in large part, by the relative positions of the sediment surface, sea-level, and fresh-water table. Examining the interaction of these three "free surfaces" is one of the central goals of the Virginia Coast Reserve Long-Term Ecological Research Project (VCR LTER). A natural extension of this objective is to examine the impact that the relative positions these "free surfaces" has on the ecology of barrier island plant and animal assemblages. This thesis describes efforts to provide a link between one aspect of the "free surface" conceptual model (the land-sea interaction) and assemblage ecology by investigating assemblages and ecological processes that occur in shallow aquatic habitats on the Virginia barrier islands. There were three distinct components of this research:

(1) The effectiveness of minnow traps, one of the most commonly used aquatic sampling techniques, was evaluated in various shallow water habitats of the VCR. I demonstrate a distinct sampling bias toward collection of resident marsh fish species (primarily *Fundulus heteroclitus*) and a bias against collection of juvenile estuarine species. This bias underscores the difficulty of adequately sampling fish assemblages of coastal shallow water habitats, and thus the difficulty elucidating assemblage structure patterns.

(2) Assemblage structuring mechanisms in island ponds were evaluated using a series of laboratory and field experiments. Specifically, I examined why surf-zone fishes, which are introduced into the island ponds during periodic wash-over events, are unable to survive for extended periods of time. I demonstrate that the relative importance of biological and physical factors in controlling fish assemblage structure varies predictably in response to a temporal gradient of environmental stress.

(3) The fish assemblages of the shallow surf-zone (the extremity of the surf-zone less than 40 cm in depth) were comprehensively examined. Distinct seasonal trends in abundance, as well as less important diel and tidal trends, were identified. Additionally, I suggest that a distinct movement of fishes parallel to the beach occurs, as fishes seek sheltered runnel habitats.

Together these components represent a multi-faceted analysis of the ecology of the shallow water habitats on the Virginia barrier islands, and especially how ecological processes relate to the dynamic geomorphology of the islands.

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Chapter One

Sampling Methodology: The Sampling Bias of Minnow Traps in Shallow Aquatic Habitats on the Eastern Shore of Virginia

1.1 Abstract

This study demonstrates the specific sampling biases of minnow traps in semi-permanent barrier island ponds, permanent brackish mainland marsh ponds, tidal pools, and tidal creeks on the Eastern Shore of Virginia. We exhaustively seined six shallow-water habitats and compared these collection data to those obtained with baited and unbaited minnow traps. Data were arranged in a separate contingency table for each of the six habitats, and then each table was analyzed with the Chi-square statistic. The relative frequencies of fish species were significantly different between the two methods in each of the six habitats (p=.001 or less). Further comparison of the two techniques at ten additional sites representing a wide variety of habitat types and sizes suggested similar biases inherent to the minnow trap collection method. Specifically, minnow traps exhibit a distinct bias toward collection of the mummichog, Fundulus heteroclitus, and a bias against collection of juvenile estuarine fishes and other non-resident marsh fish species. Minnow traps can be an effective collection technique for certain nekton species, however, the specific biases inherent to the technique preclude its use as a method to accurately describe the fish assemblages in shallow-water habitats.

1.2 Introduction

Shallow estuarine habitats typically support large populations of resident and transient nekton species. However, accurately describing these assemblages with traditional sampling techniques remains problematic. Rozas and Minello (1997) describe the techniques used to sample shallow, estuarine habitats and suggest that passive sampling devices are ineffective. The authors accurately contend that passive sampling traps are highly size and species selective, but they do not include quantitative data to illustrate the selectivity of the passive traps. The present study provides a detailed account of the biases associated with the minnow trap sampling technique, one of the most commonly used passive sampling methodologies.

Passive sampling techniques require little labor, are simple, inexpensive, and easily replicable (Sargent and Carlson, 1987; Rozas and Minello, 1997), and are often utilized despite their drawbacks. For example, in shallow coastal habitats passive sampling techniques have been used to examine patterns of habitat usage in Fundulus heteroclitus (Halpin, 1997), describe nekton utilization of a restored marsh (Lasalle *et al.*, 1991), and to collect killifish for diet analysis from tidal salt-marsh rivulets (Rozas and LaSalle, 1990). Minnow traps also have been used frequently in freshwater systems; for example, they have been used to examine fish species assemblages and habitat choice in lakes (Tonn and Magnuson, 1982; Magnuson, et al., 1985; Tonn, 1985; Tonn and Paskowski, 1986; He and Lodge, 1990; Chisnall, 1996) and to investigate activity patterns of fishes in freshwater wetlands (Suthers and Gee, 1986; Langston and Kent, 1997) and temperate streams (Reebs, 1995). In addition, minnow traps have been used extensively in rice fields to sample and monitor mosquitofish populations (Norland and Bowman, 1976; Takahashi et al., 1982; Schooley and Page, 1984; Stewart and Miura, 1985; Botsford et al., 1987; Blaustein, 1989).

Although it is often assumed that minnow traps are highly species-selective (Rozas and Minello, 1997), the nature and extent of this bias has received little attention, especially in estuarine habitats. Pot et al. (1984) demonstrated a distinct species bias in a small freshwater pond by comparing minnow trap samples to fish collected following rotenone poisoning. Only five of fifteen species ultimately recovered from the pond were initially collected with minnow traps. Brazner (1995) found that both fyke nets and seines provided a more accurate representation of the fish assemblages in Great Lakes coastal wetlands than did minnow traps. Blaustein (1989) details the size bias associated with using minnow traps to describe mosquitofish populations, but the author does not address any species biases associated with the technique.

Sargent and Carlson (1987) found that there was a behavioral bias associated with another common passive sampling technique, Breder traps (Breder, 1960), in shallow mangrove habitats of Florida, but the authors are not clear as to whether the observed biases actually were attributable to the traps. Their results include not only the biases associated with the Breder traps, but also biases associated with the other two sampling methods, throw nets and modified seine nets. To identify the exact biases associated with passive sampling traps, other potential sampling biases must be excluded. The present study compares minnow trap collection data to that obtained by exhaustive habitat seining, allowing the efficiency of the minnow traps to be determined directly.

1.3 Methods

1.3.1 Site Description

This study was conducted at the Virginia Coast Reserve Long-Term Ecological Research Site (VCR-LTER) which includes a 100 km stretch of barrier islands, mainland marsh, and the associated lagoons along the Virginia portion of the Delmarva Peninsula (Fig. 1.1). Within this region, there are numerous shallow-water habitats including tidal creeks, permanent brackish marsh ponds, semi-permanent barrier island ponds, and tidal pools, each of which was sampled in this study. Table 1.1 provides a summary of the general characteristics of habitats sampled. Pond area was estimated by taking widths at 1 m intervals along a transect bisecting the pond. The approximate area of the ponds was then calculated by determining areas for each of the 1 m sections, then summing the sections. Salinity and temperature were measured with a YSI model 30 SCT meter and dissolved oxygen with a YSI model 57 DO meter taken at five random mid-depth locations. Sampling was conducted from June to August 1998.

1.3.2 Field Protocol

Relatively small pond and creek sites were chosen because these areas could be exhaustively sampled with traditional seining techniques. By sampling the entire fish assemblage within each habitat, the fish collected with the minnow traps could be compared to the fish that were actually present in that habitat. This enabled us to assess the effectiveness of the minnow traps directly, not just compare two different sampling techniques. All minnow traps were made of galvanized wire and measured 42 cm in length and 23 cm wide at their largest diameter, with a 1.9 cm-hole and 0.64 cm square mesh. Six traps were placed in each pond, three baited with canned sausage and three unbaited. All traps were completely submerged and placed on the habitat bottom. After approximately six hours, the traps were then removed from the ponds and the fishes captured were identified, enumerated and released back into the ponds.

Twenty-four hours later the ponds were exhaustively seined. The seine measured 4 m long and 1.5 m deep with a 1 m square bag and 1 mm square mesh throughout. All fishes were identified, enumerated and placed in a holding tank until the sampling was complete. Vegetation was carefully sorted to ensure no fishes were overlooked. The process was repeated so that ultimately each pond was seined ten times. It is feasible that some of the more evasive fishes escaped all ten seines, perhaps by burrowing into the mud or swimming under the net lead line, but these fishes likely make up a very small percentage of the

Figure 1.1

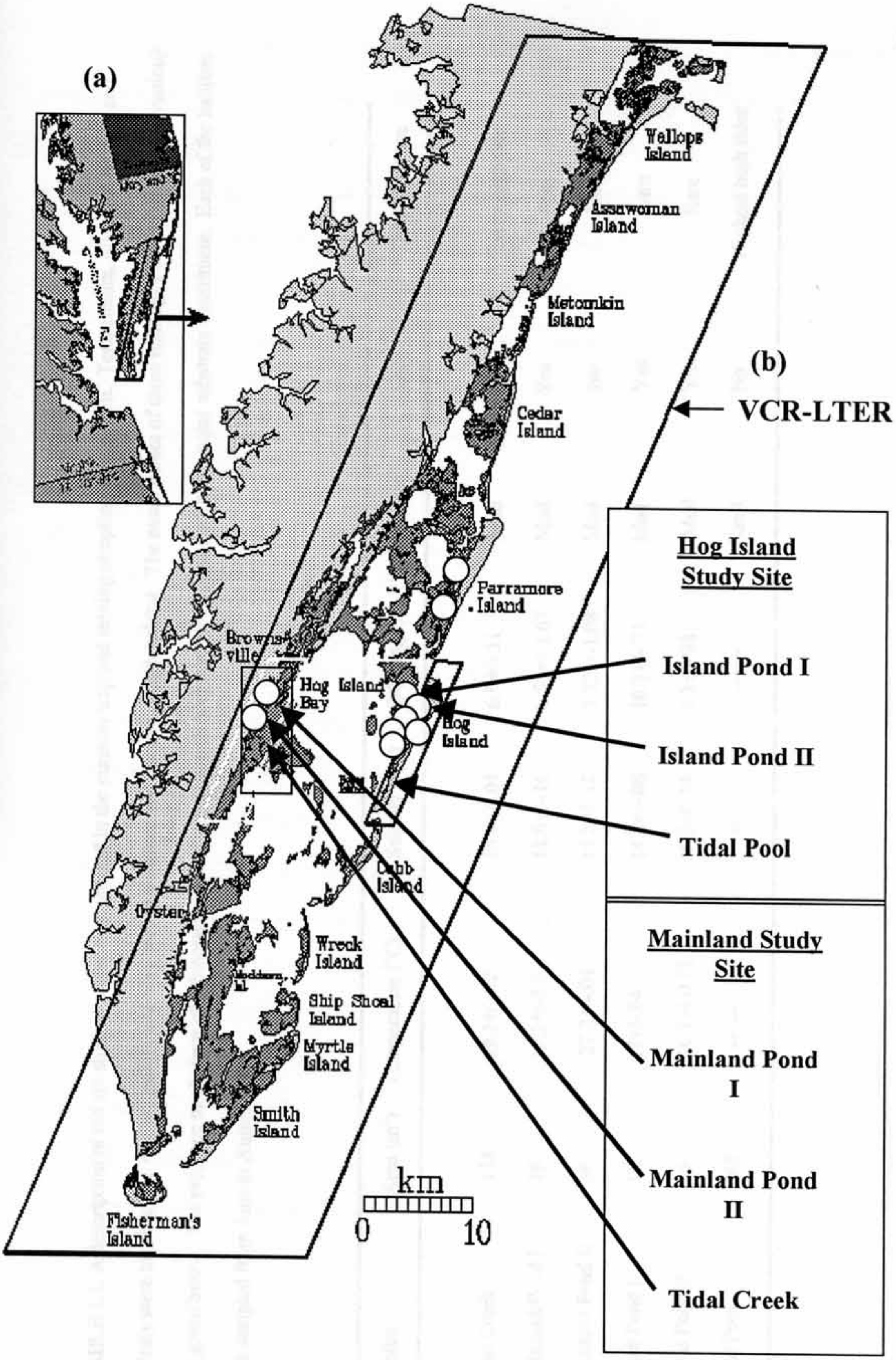
(a)
(b)
VCR-LTER
Wallops Island
Assawoman Island
Metomkin Island
Cedar Island
Parramore Island
Browns-ville
Hog Island Bay
Hog Island
Cobb Island
Oyster
Wreck Island
Mockhorn Isl
Ship Shoal Island
Myrtle Island
Smith Island
Fisherman's Island
km
0
10
Hog Island Study Site
Island Pond I
Island Pond II
Tidal Pool
Mainland Study Site
Mainland Pond I
Mainland Pond II
Tidal Creek

TABLE 1.1. A description of the six shallow water sites utilized in the minnow trap and seining sampling comparison. Temperature, dissolved oxygen and salinity were taken at five random points mid-way between surface and bottom in each habitat. The mean values of these readings (+/- one standard deviation) are given below. The presence or absence of submerged aquatic vegetation (SAV) is reported, along with the major substrate constituent. Each of the habitats was sampled from June to August 1998.

Habitat	Area (m^2)	Temperature (°C)	Salinity (ppt)	DO (mg/l)	Substrate	SAV	Tidal Influence
Tidal Creek	174	29.1+/-.02	15.8+/-.01	6.9+/-.31	Mud	No	Every high tide
Mainland Pond I	18	25.2+/-0.0	11.0+/-.16	6.52+/-1.67	Mud	Yes	Rare
Mainland Pond II	36	27.2+/-.04	11.2+/-.12	3.22+/-1.08	Mud	No	Rare
Island Pond I	19	27+/-.04	14.2+/-.08	10.7+/-.73	Mud	Yes	Rare
Island Pond II	26	26.1+/-0.12	19.2+/-.14	8.3+/-.98	Mud	Yes	Rare
Tidal Pool	760	------	------	------	Sand	No	Highest high tides

total fish populations. Sampling data support this assumption. In each of the five ponds less than 0.8% of the fishes were collected in the last three seine passes combined. Allen et al. (1992) found that mummichogs (Fundulus heteroclitus), a fish commonly collected in this study, were the most evasive fish species in a South Carolina tidal pool and that, in general, seining is not an efficient method of estimating the abundance of this and similar species. Unlike their study, we employed a seine that was large enough to sample 100% of each habitat with each seine pass. We collected more of every species, including more of the extremely evasive mummichogs, with the seining technique than with minnow traps in each pond. Due to our methods and the size of the habitats examined, the seining trials accurately reflect the fish assemblage of each pond.

The tidal creek was sampled in a slightly different manner. A larger seine, 8 m long and 1.5 m deep, with a 1 m square bag, and 0.48 cm mesh throughout, was placed across the mouth of a small tidal rivulet at high tide. The lead line of the net was pushed into the mud along the entire creek bottom. The top of the net was suspended above the water using wooden stakes to prevent fish from jumping over the net. This method allowed us to entirely block the rivulet at high tide. Immediately after setting up this net, three traps baited with canned sausage and three unbaited traps were placed on the bottom of the creek. After two hours of falling tide the traps were removed and the fish captured were identified, enumerated, and released back into the blocked tidal creek. By mid-tide, the creek had almost completely drained leaving only a 1-2 cm pool of water directly in front of the net mouth. The smaller seine described above was then pulled through the shallow pool up to the front of the larger block seine. The large seine was then immediately removed and all fish identified and enumerated.

To further validate our findings we sampled ten additional shallow-water habitats, each of which was too large to be exhaustively seined (see Fig. 1.1). Six minnow traps, three unbaited and three baited with canned sausage, were completely submerged and placed on the habitat bottom. After approximately six hours, the traps were removed and the fish identified and enumerated. The large bag seine described above was then pulled at random locations in each of the habitats. Seining trials were conducted until a trial yielded no additional fish species. A standard seining strategy could not be employed because of the variety of sizes, shapes, depths, and types of habitats examined. For each of the seine trials, the species captured were recorded, but no effort was made to enumerate the fish. Each of these ponds was sampled between June 1997 and August 1998. All fish collected in the field sampling were identified using Fishes of the Chesapeake Bay (Murdy, *et al.*, 1997).

1.3.3 Statistical Analysis

Our data suggest that there was no difference in the number of species or the total number individuals caught in baited and unbaited traps, so the minnow trap collection data was pooled for the six traps. Likewise, the number of fish captured in the ten seines was pooled. The data from each of the six exhaustively seined habitats were then arranged in separate contingency tables and analyses were carried out independently for each of the sites. Since multiple comparisons were made (six separate contingency tables were analyzed), the alpha level of 0.05 was adjusted downward according to the Bonferroni procedure (Howell, 1987). Furthermore, in order to avoid statistical bias in calculating the chi-squared statistic, Zar (1997) suggests that the average expected frequency in a contingency table exceed 6.0. We met this criterion for each of the six contingency tables used in this analysis.

Adjusted standardized residuals were calculated and reported for each of the contingency tables. Since the seining technique approximated the entire fish population in each habitat, only the residuals associated with the minnow traps are reported. Positive adjusted residual scores indicate that the fish species of interest make up a larger percentage of the total individuals in the minnow trap counts than would be expected based on the expected values in the contingency table. Negative scores indicate that the species is underrepresented in the minnow trap counts. Larger values indicate a stronger departure from expected values and thus a stronger sampling bias for or against a species.

Data from the additional ten habitats were analyzed differently since the habitats were not exhaustively seined. The number of species captured in the minnow traps were compared to the number of species captured with the seining technique using a paired t-test. Significance was evaluated at the .05 significance level. All statistical tests were carried out using SPSS for Windows software package (Norusis, 1993).

1.4 Results

A total of 3,544 total fish representing 16 different species in 8 families were captured in the habitats that were exhaustively seined. Only 5 species from 2 families, a total of 654 total individuals, were collected with the minnow traps in these six habitats. In a single habitat the most fish were collected from the tidal creek (1808). Within the pond habitats, the total number of individuals ranged from 58 to 1073. Nine species were collected in the five ponds, while eleven were found in the tidal creek. Fundulus heteroclitus was the only fish species that was captured in each of the six habitats with both of the sampling techniques.

F. heteroclitus was the species most commonly captured species in minnow traps within each of the six habitats (Table 1.2). This species accounted for as much as 99.5% of the total number of individuals captured in minnow traps. The relative numerical proportion of F. heteroclitus was always less in the seining technique than in the minnow traps (Fig. 1.2). The largest discrepancy in the proportion of F. heteroclitus between the two techniques was recorded in the second mainland pond, where 93.8% of the minnow trap fish were mummichogs, compared to only 14.9% of the seine-collected fish.

The results of the X^2 analysis of the six contingency tables were highly significant (p=.001 or less) for each habitat (Table 1.3). Consequently, the minnow trap collections characterize a fish assemblage that is significantly different from the actual assemblage found in each of the six habitats. Two particular biases are apparent when examining the adjusted standardized residual scores in Table 1.4. First, mummichogs are strongly selected for when using the minnow trap technique. In each of the habitats, the residual scores for F. heteroclitus are relatively large positive values, ranging from 3.0 to 19.4. In contrast, juveniles of common estuarine species, Leiostomus xanthurus, Bairdiella chrysoura, Paralichthys dentatus, Pogonias cromis and Anguilla rostrata are selected against by the traps. Minnow traps also bias against other non-resident marsh fish species, including Menidia menidia, Fundulus majalis, and Symphurus plagiusa. The minnow trap technique was found to be biased against Lucania parva, Gambusia affinis, Gasterosteus aculeatus, and Gobiosoma bosc, all of which are common resident marsh species. Both Cyprinodon vareigatus and Fundulus luciae, also common marsh residents, were selected for in some habitats and selected against in others. Factors accounting for these biases are suggested in the discussion below.

TABLE 1.2. The number of fish captured using minnow traps (MT) and exhaustive seining (S) in the six habitats sampled. The minnow trap totals are based on six total traps, three unbaited and three baited, and the seine values are based on a total of ten separate seine trials. The overall estimated fish density in each pond is given based on the seining trials. A series of dashes (----) indicates the species was not captured in the habitat with that particular sampling technique.

Habitat	Tidal Creek		Mainland Pond I		Mainland Pond II		Island Pond I		Island Pond II		Tidal Pool	
Fish density (fish/ m^2)	10.4		3.2		2.8		56.5		8.9		0.4	
Species	MT	S	MT	S	MT	S	MT	S	MT	S	MT	S
Mummichog (*Fundulus heteroclitus*)	423	858	37	37	15	15	49	311	18	25	60	61
Sheepshead minnow (*Cyprinodon variegatus*)	----	21	----	3	----	----	39	159	4	29	---[a]	---[a]
Striped killifish (*Fundulus majalis*)	----	----	----	----	----	----	----	----	----	----	1	164
Atlantic silverside (*Menidia menidia*)	----	871	----	----	----	----	----	----	----	----	----	----
Mosquitofish (*Gambusia affinis*)	----	----	----	17	----	7	----	----	----	----	----	----
Spotfin killifish (*Fundulus luciae*)	2	10	1	1	1	1	----	208	1	22	----	----
American eel (*Anguilla rostrata)*	----	----	----	----	----	76	----	8	----	9	----	----
Rainwater killifish (*Lucania parva*)	----	22	----	----	----	2	----	16	----	26	1	10
Black drum (*Pognias cromis*)	----	5	----	----	----	----	----	----	----	----	----	----
Spot (*Leiostomus xanthurus*)	----	7	----	----	----	----	----	----	----	----	----	----
Siver perch (*Bairdiella chrysoura*)	----	4	----	----	----	----	----	----	----	----	----	----
Summer flounder (*Paralichthys dentatus*)	----	3	----	----	----	----	----	----	----	----	----	----
Blackcheek tonguefish (*Symphurus plagiusa*)	----	1	----	----	----	----	----	----	----	----	----	----
Naked goby (*Gobiosoma bosc*)	----	6	----	----	----	----	----	----	----	----	----	----

Threespine stickleback (*Gasterosteus aculeatus*)	----	----	----	----	----	----	----	371	1	120	----	----
Rough silverside (*Membras martinica*)	----	----	----	----	----	----	----	----	----	----	----	38

Figure 2: The relative abundances of fish species in the two sampling techniques.

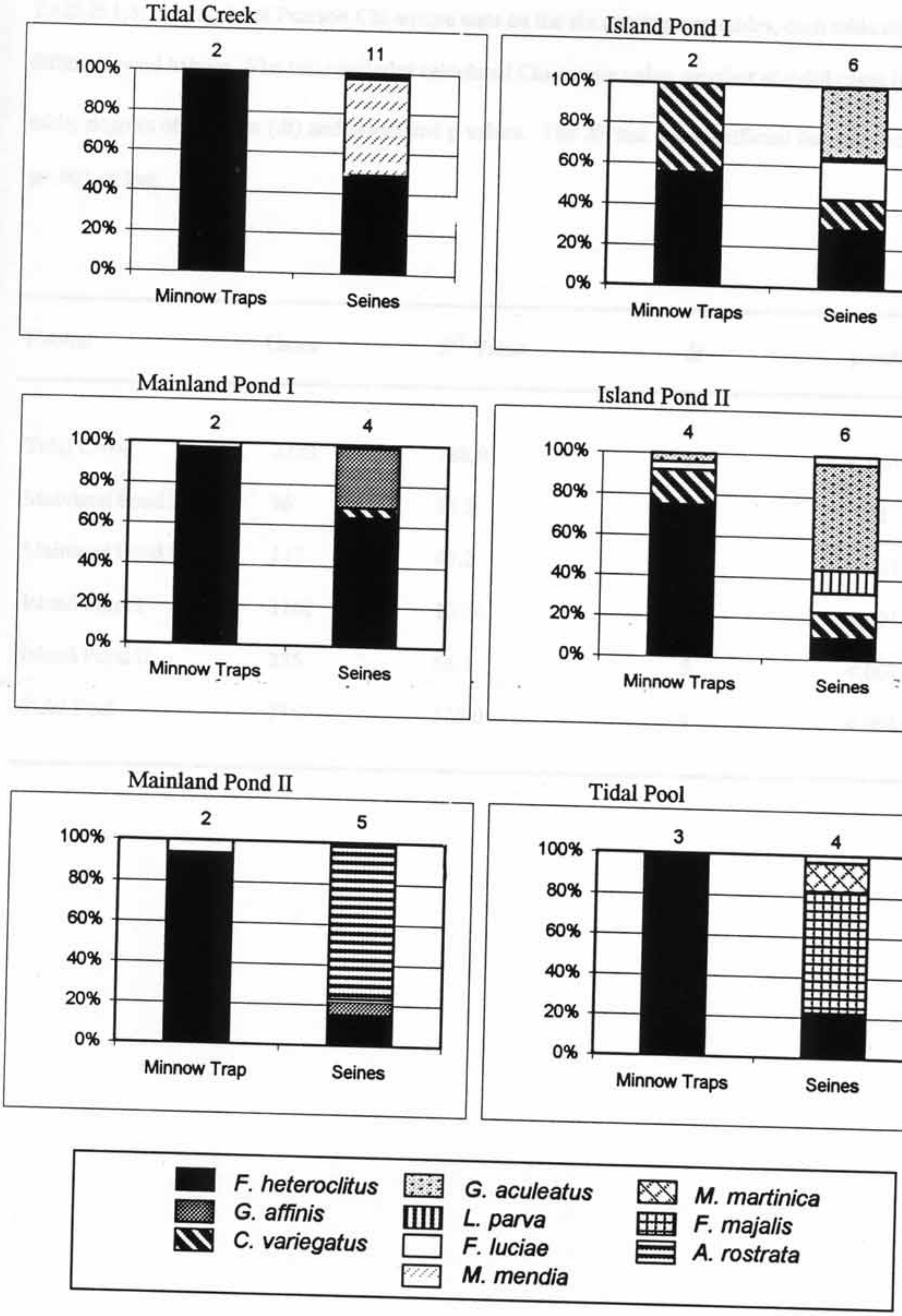

TABLE 1.3.The results of Pearson Chi-square tests on the six contingency tables, each table representing a different pond habitat. The table includes calculated Chi-square value, number of valid cases (fish) in each table, degrees of freedom (df) and associated p-values. The X^2 test was significant for each habitat at p=.001 or less.

Habitat	Cases	X^2 Value	df	p-value
Tidal Creek	2223	388.9	10	<.001
Mainland Pond I	96	16.5	3	.001
Mainland Pond II	117	49.2	4	<.001
Island Pond I	1161	109.6	5	<.001
Island Pond II	255	68.1	5	<.001
Tidal Pool	336	125.0	4	<.001

TABLE 1.4. The adjusted residual scores for each of the six contingency tables (Abbreviations: TC=Tidal Creek, MP=Mainland Pond, IP=Island Pond, TP=Tidal Pool). Positive adjusted residual scores indicate that the fish species of interest makes up a larger percentage of the total individuals in the minnow trap counts than would be expected based on the actual population of the fish in the pond. Negative scores indicate that the species is underrepresented in the minnow trap counts. Larger values indicate a stronger departure from expected values in the contingency tables. A series of dashes (----) indicates the species was not captured in the habitat with that particular sampling technique.

Species	TC	MPI	MP II	IP I	IP II	TP
Mummichog (*Fundulus heteroclitus*)	19.5	3.0	6.7	5.2	8.0	11.0
Sheepshead minnow (*Cyprinodon variegatus*)	-2.2	-1.4	-----	7.1	-----	-----
Striped killifish (*Fundulus majalis*)	-----	-----	-----	-----	-----	-8.3
Atlantic silverside (*Menidia menidia*)	-18.3	-----	-----	-----	-----	-----
Mosquitofish (*Gambusia affinis*)	-----	-3.7	-1.1	-----	-----	-----
Spotfin killifish (*Fundulus luciae*)	-.2	.3	1.5	-4.6	-.9	-----
American eel (*Anguilla rostrata*)	-----	-----	-5.9	-.8	-1.0	-----
Rainwater killifish (*Lucania parva*)	-2.3	-----	-.6	-1.2	-1.7	-.8
Black drum (*Pognias cromis*)	-1.1	-----	-----	-----	-----	-----
Spot (*Leiostomus xanthurus*)	-1.3	-----	-----	-----	-----	-----
Siver perch (*Bairdiella chrysoura*)	-1.0	-----	-----	-----	-----	-----
Summer flounder (*Paralichthys dentatus*)	-.8	-----	-----	-----	-----	-----
Blackcheek tonguefish (*Symphurus plagiusa*)	-.5	-----	-----	-----	-----	-----
Naked goby (*Gobiosoma bosc*)	-1.2	-----	-----	-----	-----	-----
Threespine stickleback (*Gasterosteus aculeatus*)	-----	-----	-----	-6.7	-4.5	-----
Roughsilverside (*Membras martinica*)	-----	-----	-----	-----	-----	-3.1

Results from the ten additional ponds support the results of the above statistical analyses (see Table 1.5). Significantly more species were captured (df=9; p <.001) in the seine trials than were collected with the six minnow traps. Mummichogs were collected from minnow traps in each habitat where they were found using the seining technique. There was only a single habitat, a tidal pool adjacent to the surf-zone, where there were no mummichogs collected using either sampling technique. Only two non-resident marsh fish species were collected in minnow traps, Mugil curema and Fundulus majalis. Marsh resident species were usually captured with both techniques, but were sometimes absent from the minnow trap collections. In all sixteen ponds sampled, there were no instances where a fish was captured in the minnow traps, but not collected in the seine trials.

TABLE 1.5. The number of species captured using the minnow trap and seining techniques in ten different pond habitats. Six minnow traps were used at each site, three baited with canned sausage and three unbaited. Seines were conducted until no additional species were collected on a given seine. A star (*) designates the species was collected in that particular habitat with the sampling technique.

Site	Hog Island											
Habitat Type	Marsh Pond A		Marsh Pond B		Marsh Pond C		Marsh Pond D		Marsh Pond E		Tidal Pool	
Species	MT	S	MT	S	MT	S	MT	S	MT	S	MT	S
Mummichog (*Fundulus heteroclitus*)	*	*	*	*	*	*	*	*	*	*		
Sheepshead minnow (*Cyprinodon variegatus*)	*	*	*	*		*		*		*		
Striped killifish (*Fundulus majalis*)		*		*	*	*						*
Atlantic silverside (*Menidia menidia*)												
Mosquitofish (*Gambusia affinis*)												
Spotfin killifish (*Fundulus luciae*)								*				
American eel (*Anguilla rostrata*)								*				
Rainwater killifish (*Lucania parva*)		*	*	*		*	*			*		
Spot (*Leiostomus xanthurus*)		*		*								
Siver perch (*Bairdiella chrysoura*)												
Summer flounder (*Paralichthys dentatus*)												
Threespine stickleback (*Gasterosteus aculeatus*)		*		*				*				
White mullet (*Mugil curema*)				*								*
Menhaden (*Brevoortia tyrannus*)		*										
Blackcheek tonguefish (*Symphurus plagiusa*)		*				*						
Rough silverside (*Membras martinica*)		*		*		*						*

Site	Paramore Island				Mainland Marsh			
Habitat Type	Marsh Pond F		Marsh Pond G		Tidal Creek		Marsh Pond H	
Species	MT	S	MT	S	MT	S	MT	S
Mummichog (*Fundulus heteroclitus*)	*	*	*	*	*	*	*	*
Sheepshead minnow (*Cyprinodon variegatus*)	*	*		*		*		
Striped killifish (*Fundulus majalis*)								
Atlantic silverside (*Menidia menidia*)		*				*		
Mosquitofish (*Gambusia affinis*)							*	*
Spotfin killifish (*Fundulus luciae*)		*	*	*				
American eel (*Anguilla rostrata*)								
Rainwater killifish (*Lucania parva*)	*	*		*		*	*	*
Spot (*Leiostomus xanthurus*)								
Siver perch (*Bairdiella chrysoura*)						*		
Summer flounder (*Paralichthys dentatus*)		*				*		
Threespine stickleback (*Gasterosteus aculeatus*)		*						
White mullet (*Mugil curema*)								
Menhaden (*Brevoortia tyrannus*)								
Blackcheek tonguefish (*Symphurus plagiusa*)		*				*		
Rough silverside (*Membras martinica*)								

1.5 Discussion

Since the exhaustive seining provided an excellent representation of the fish assemblage present in each habitat, any differences between the two sampling techniques can be attributed to biases inherent to minnow traps. We believe three primary factors account for the biases detailed:

(1) Attraction to Traps. Fish may be attracted to traps by either bait or by the trap structure. In fourteen of the sixteen ponds sampled in this study, every species captured in a baited trap was also found in an unbaited trap. In three of the ponds, a species captured in an unbaited trap was not found in a baited trap. Furthermore, in a related study, we found no significance differences in the number of species or total number of individuals that were collected in traps with a variety of different bait types (unpublished data). This suggests some fish species are attracted to the structure provided by the traps, not just by the bait. It has been well established that fishes utilize structurally complex habitats for various reasons. For example, structurally complex habitats serve to reduce predator encounter rates of their prey and the overall prey capture efficiency of predators (Crowder and Cooper, 1982; Anderson, 1984; Savino and Stein, 1989a,b; Christensen, and Persson, 1993; Persson and Eklöv, 1995). The most commonly collected fish in this study, Fundulus heteroclitus, often aggregate around structurally complex objects such as dead logs and docks (pers. obs). Therefore, mummichogs initially may be attracted to minnow traps due to the structure provided by the traps, perhaps as a behavioral adaptation to minimize predation risk. The affinity of mummichogs for the traps would thus result in a relatively high collection of the mummichogs relative to other species.

Laboratory observations support this hypothesis. Mummichogs, and other fishes commonly found in the habitats of this study, were placed in a large aquarium with a single minnow trap. Mummichogs were the most likely species to enter the traps, whether or not the traps were baited. In contrast, non-resident marsh fish species, Menidia menidia for example, would often take many hours to move into the traps, if they entered the traps at all. Further, many of the mummichogs could easily find their way back out of a trap and, when startled, the individuals that had already been inside the minnow trap would swim into the confines of the trap. This behavioral response suggests that mummichogs may have evolved an affinity for structure as a means to minimize the risk of predation in their natural habitats.

(2) Fish size and/or morphology. Many juvenile and larval fish species can move freely through the mesh of the traps. For example, no Anguilla rostrata were caught in minnow traps despite being collected in a number of individual seines. Minnow traps are an effective method of capturing adult eels (Chisnall, 1996), but these traps are not an effective method for collecting the elvers that are commonly found in shallow water ponds of the mid-Atlantic coast (Rowe and Dunson, 1995; Layman and Smith, *unpublished data). Juvenile and larval individuals of other species, including* Fundulus heteroclitus, Cyprinodon variegatus, Lucania parva, Gasterosteus aculeatus, and Fundulus luciae, also can move easily in and out of minnow traps. Therefore, in habitats where the majority of the individuals of a given species are small juveniles, this species is likely to be underrepresented by the minnow trap sampling technique. Similarly, most Leiostomus xanthurus and Bairdiella chrysoura individuals were too large to enter the traps and were thus underrepresented in the minnow trap collections. The flatfishes, Paralichthys dentatus and Symphurus plagiusa, are unable to move into the traps because of their body morphology. Therefore, the size and morphology of the juvenile estuarine fishes precludes their collection with minnow traps.

(3) Frequency of Encounter. The location of the traps within a habitat may change the frequency at which fish species encounter the traps and thus affect the composition of the minnow trap collection. For example, non-resident marsh fish species that are adapted to an open water lifestyle are less likely to encounter a minnow trap placed directly on the substrate. Additionally, some of the fish that are biased against by the minnow trap sampling technique are primarily zooplanktivorous water column feeders, Menidia menidia for instance (Bengston, 1984; Morgan, 1990; Allen *et al.*, 1995). Because of their feeding preferences, these fish species may not be attracted to the bait and are less likely to encounter the traps at all.

The results of other recent studies support the bias described here. Sargent and Carlson (1987) compared another passive sampling technique, Breder traps, to throw and pull net sampling techniques in

Florida mangroves. Their data demonstrate a clear bias against juvenile estuarine species including, Pogonias cromis, Sciaenops ocellatus, Leiostomus xanthurus, and Lagodon rhomboides, as well as a bias against the non-resident species, Anchoa mitchelli and Diapterus sp. A similar bias is apparent in the study by LaSalle *et al.* (1991). The authors captured five non-resident marsh fish species, Cynoscion regalis, Mugil cephalus, Anchoa mitchilli, Menidia menidia, and Brevoortia tyrannus, in block net sampling, none of which were captured in Breder traps placed in the same tidal creeks. Their trap captures were instead dominated by Fundulus sp., a result not surprising based on the findings of our study. Likewise, Halpin (1997) reports that 91,436 of 93,560 fish captured in Rhode Island tidal creeks were mummichogs. This result likely reflects the minnow trap sampling bias as much as the actual numerical dominance of mummichogs in these creeks.

Two important issues arise regarding the bias demonstrated in a variety of Eastern Shore habitats. First, very similar biases are likely to exist in other estuarine and coastal habitats, but the *nature* of the bias is likely to be quite different from region to region. Each region has its own distinct fish assemblage and, therefore, the bias will vary from location to location. For example, in this study there was a clear bias toward capturing F. heteroclitus in each of the habitats sampled, but in Gulf Coast habitats Fundulus grandis are more commonly captured with minnow traps (Rozas and Lasalle, 1990). Second, the nature and magnitude of the minnow trap selectivity is likely to change seasonally. In tidal creeks, the composition of fish assemblages changes from season to season and thus the relative bias of the traps will vary based on what fish are present during any particular time of the year. Furthermore, the extent of the bias may depend on a host of other factors including tidal cycle and specific location of trap placement.

The use of minnow traps should be dictated by the aim of the hypotheses being tested. If the overall objective is to collect a specific fish species, then the technique may be rather useful. If, on the other hand, the primary objective of a study is to sample and accurately describe the nekton utilizing a particular habitat, then minnow traps are not an effective technique. As Rozas and Minello (1997) suggested, passive sampling traps should be considered "collecting" rather than "sampling" devices because of the biases associated with these techniques. Our study documents that minnow traps are biased sampling techniques and shows why this method should not be used as a means to quantitatively assess the nekton utilizing shallow water habitats.

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Chapter Two

Island Pond Study: A Seasonal Cycle of Abiotic and Biotic Structuring Mechanisms in Marsh Pond Fish Assemblages

2.1 Abstract

A series of field and laboratory experiments elucidated the mechanisms that contribute to fish assemblage structure in barrier islands ponds on the Eastern Shore of Virginia. We investigated why surf-zone fishes, which are introduced to the island ponds during periodic wash-over events, are unable to persist for extended periods. We simulated wash-over events by collecting fishes from the shallow surf-zone and introducing them into large (0.56 m^2) field enclosures. During summer months, surf-zone fishes typically died within 24 hours. Levels of dissolved oxygen and salinity frequently exceeded the tolerance limits of the surf-zone fishes (examined in a series of laboratory of experiments), suggesting that these variables were responsible for fish mortality. In non-summer months, when temperature and dissolved oxygen stresses were ameliorated, surf-zone fishes could survive for months, or even longer, in the ponds. We conducted field-enclosure experiments at three fish densities in order to evaluate the survival and condition of a common surf-zone fish, *Membras martinica* (the rough silverside), in the ponds: (1) 8 *Membras* (14 fish/ m^2), (2) 16 *Membras* (28 fish/ m^2), and (3) 8 *Membras* + 8 *Fundulus heteroclitus* (28 fish/ m^2). After approximately one month during the spring, fall and winter, survival and condition of fishes in treatments 2 and 3 were significantly reduced, suggesting that biological interactions were an important cause of surf-zone fish mortality. These results suggest that competition for food is the primary mechanism underlying the reduced survival and condition of the surf-zone fish in the non-summer months. A temporal environmental harshness gradient can be used to predict the relative importance of physical and biological factors in structuring the marsh pond fish assemblages. Based on these findings, we propose a conceptual model that predicts the relative importance of abiotic and biotic factors in response to a seasonal cycle of varying environmental harshness.

2.2 Introduction

The relative importance of abiotic and biotic factors in structuring natural faunal assemblages has received much attention in recent years. One approach for evaluating assemblage structure has been to assess the relative importance of abiotic factors, competition, and predation based on a gradient of environmental stress (Connell, 1975; Menge, 1976; Peckarsky, 1983; Menge and Sutherland, 1987; Huston, 1994; Leonard *et al.*, 1998). Menge and Sutherland (1987) propose a conceptual framework in which the relative importance of biotic factors increases as environmental stress decreases. Empirical evidence of assemblages organized in this fashion has been provided in rocky intertidal assemblages (Dayton, 1971; Menge, 1976; 1978a,b, 1983; Connell, 1985; Menge and Farrell, 1989; Menge *et al.*, 1993) and stream benthic invertebrate associations (Lancaster 1990, 1996; Peckarsky *et al.*, 1990; Hansen *et al.*, 1991).

With regard to fish assemblages, either biological factors (Grossman, 1982; Schlosser, 1982; Moyle and Vondracek, 1985; Ross *et al.*, 1985; Matthews, 1998), or physical factors (Kushlan, 1976a; Thompson and Lehner, 1976; Gorman and Karr, 1978; Horowitz, 1978; Harrell 1978; Matthews and Styron, 1981; Tonn and Magnuson, 1982; Poulin and Fitzgerald, 1989; Capone and Kushlan, 1991; Poff and Allan, 1995; Grossman *et al.*, 1998; Matthews, 1998), can be the primary determinants of fish assemblage structure. However, there have been few attempts to integrate both abiotic and biotic mechanisms into a single model. One study that has integrated these approaches concerns Midwestern United States stream fish assemblages (Schlosser, 1987). Their conceptual model predicts that upstream habitats are characterized by a high level of environmental stress and thus the fish assemblages are primarily shaped by physical forces. As environmental stress decreases downstream, competition and predation are hypothesized to be more important structuring mechanisms. Schlosser and Ebel (1989) provided empirical support for this model, although evidence to the contrary has since been presented (Capone and Kushlan, 1991; Fausch and Bramlett, 1991; Grossman, *et al.*, 1990; Poff and Allen, 1995; Grossman *et al.*, 1998).

The relative importance of assemblage structuring mechanisms is often defined using spatial variation in environmental stress. For example, this spatial gradient is based on degree of wave exposure in rocky intertidal systems (Menge and Farrell, 1989) or on environmental variability (the frequency of floods and/or droughts) in temperate streams (Schlosser, 1987). In this study we present evidence that a temporally defined gradient of environmental stress, instead of the more common spatial gradient, may be useful in evaluating the predictions made by Menge and Sutherland (1987). Using this temporal context, we evaluated the importance of abiotic and biotic factors in structuring fish assemblages of barrier island marsh ponds on the Eastern Shore of Virginia.

In such marsh ponds, Dunson *et al.* (1993) and Poulin and Fitzgerald (1989) have found that abiotic factors play the predominant role in structuring fish assemblages. In contrast, Dunson and Rowe (1996) and Weisberg (1986) suggest that biological interactions may be relatively more important. Combining these approaches, Rowe and Dunson (1995) found that both abiotic (salinity) and biotic (competition) factors influence the growth and survival of three common salt marsh pool residents: *Cyprinodon variegatus* (sheepshead minnow), *Lucania parva* (rainwater killifish), and *Menidia beryllina* (inland silverside). These studies suggest that a variety of factors are likely to contribute to patterns of assemblage structure in marsh ponds, although none specifically define the circumstances in which abiotic or biotic factors are more important in determining the structure of the fish assemblages.

Previous studies of barrier island ponds are primarily descriptive and do not elucidate the mechanisms that shape fish assemblages. Studies on Horn Island, Mississippi (Franks, 1970; Ross and Doherty, 1994) and the Outer Banks, North Carolina (Schwartz, 1988; Schwartz *et al.*, 1990a,b), have found that the assemblages are dominated by relatively few species, primarily poeciliids, cyprinodontids, fundulids, and atherinids. Ross and Doherty (1994) found that no combination of physiochemical variables could be used to explain these fish assemblage patterns, although they were able to discern trends in assemblage composition. They identify two groups of fishes based on source of colonization, “marsh” fishes and “surf-zone” fishes, and they found that ponds dominated by surf-zone species shifted over time to a marsh-fish dominated assemblage. The surf-zone species were assumed to be unable to tolerate the physiological demands in the ponds, although the specific reasons for the mortality were not directly examined.

The present study was directly towards the mechanisms that underly fish assemblage structure in near-shore marsh ponds on the Virginia barrier islands. These ponds are typically dominated by resident marsh species, primarily *Fundulus heteroclitus* (common mummichog) and *C. variegatus,* despite wash-over events from sub-tidal surf-zone habitats that bring influxes of other species. As was observed by Ross and Doherty (1994), surf-zone fishes are unable to persist in the ponds for extended periods of time. This study describes why these surf fishes are unable to persist in the ponds and provides empirical evidence for the regulatory mechanisms operating within these ponds. The following hypotheses were tested: (1) abiotic factors are the primary cause of surf-zone fish mortality during the summer, and (2) competitive interactions contribute to surf-zone mortality in other seasons of the year when the environmental stress of the ponds is ameliorated. These results are used to propose a conceptual model in which a temporal gradient of environmental stress is used to predict the relative importance of abiotic and biotic factors in structuring these fish assemblages.

2.3 Methods

2.3.1 Site Description

The Virginia Coast Reserve Long-Term Ecological Research Site (VCR-LTER) includes a 100 km stretch of barrier islands, mainland marsh, and associated lagoons, along the Virginia portion of the Delmarva Peninsula (Figure 2.1). The experiments were conducted on Hog Island, an island that is approximately 11 km in length and up to 3 km wide. There are numerous shallow (usually <1 m) ponds on the island that range in area from less than 1 m^2 to more than 150,000 m^2. The ponds investigated in this study were primarily located on the ocean-side (North, South, Y, West and Back Ponds) or middle (Low, Shallow and Middle Island Pond) of Hog Island (see Figure 2.1). All ponds included in this study were located in typical high marsh terrain in which the primary vegetation was salt marsh hay, *Spartina patens*. Salinities in the ponds commonly vary from 10 to 40 ppt, although more extreme levels have been observed. The ponds are characterized by abundant submerged aquatic vegetation including numerous filamentous algae species, as well as other species of both micro- and macro-algae. Widgeon grass, *Ruppia maritima*, is common in some of the ponds. Substrates range from thick, organically rich mud to fine sand. Some ponds on the island are permanent, but others dry up during the summer. In general, ponds contain much more water during the wet winter and spring months, and they dry throughout the summer. During high tides, ponds are periodically over-washed by the ocean or by adjacent back bays, trapping intertidal fishes in the ponds (Layman, *pers. obs.*).

2.3.2 Pond Surveys

The experimental fish densities were based on estimated densities of fishes in ponds on the Virginia barrier islands. Table 2.1 gives fish densities for all species and densities of the rough silverside, *Membras martinica* (the most common shallow surf-zone fish and the species that was used in the experiments described below), in the two most extensively sampled ponds, North and South Ponds. Densities were estimated by sampling conducted with two nets: (1) a 8 m long seine 1.5 m deep, with a 1 m square bag and 0.48 cm mesh and (2) 4 m long seine 1.5 m deep with a 1 m square bag and 1 mm square mesh throughout. Fish densities fluctuated substantially among months, as well as within months, due to precipitation, overwash, dynamic island geomorphology, and the immigration, emigration, birth and death

Figure 1. The (a) Delmarva Peninsula, (b) Virginia Coast Reserve Long-Term Ecological Research Site, and (c) pond study sites on the north end of Hog Island.

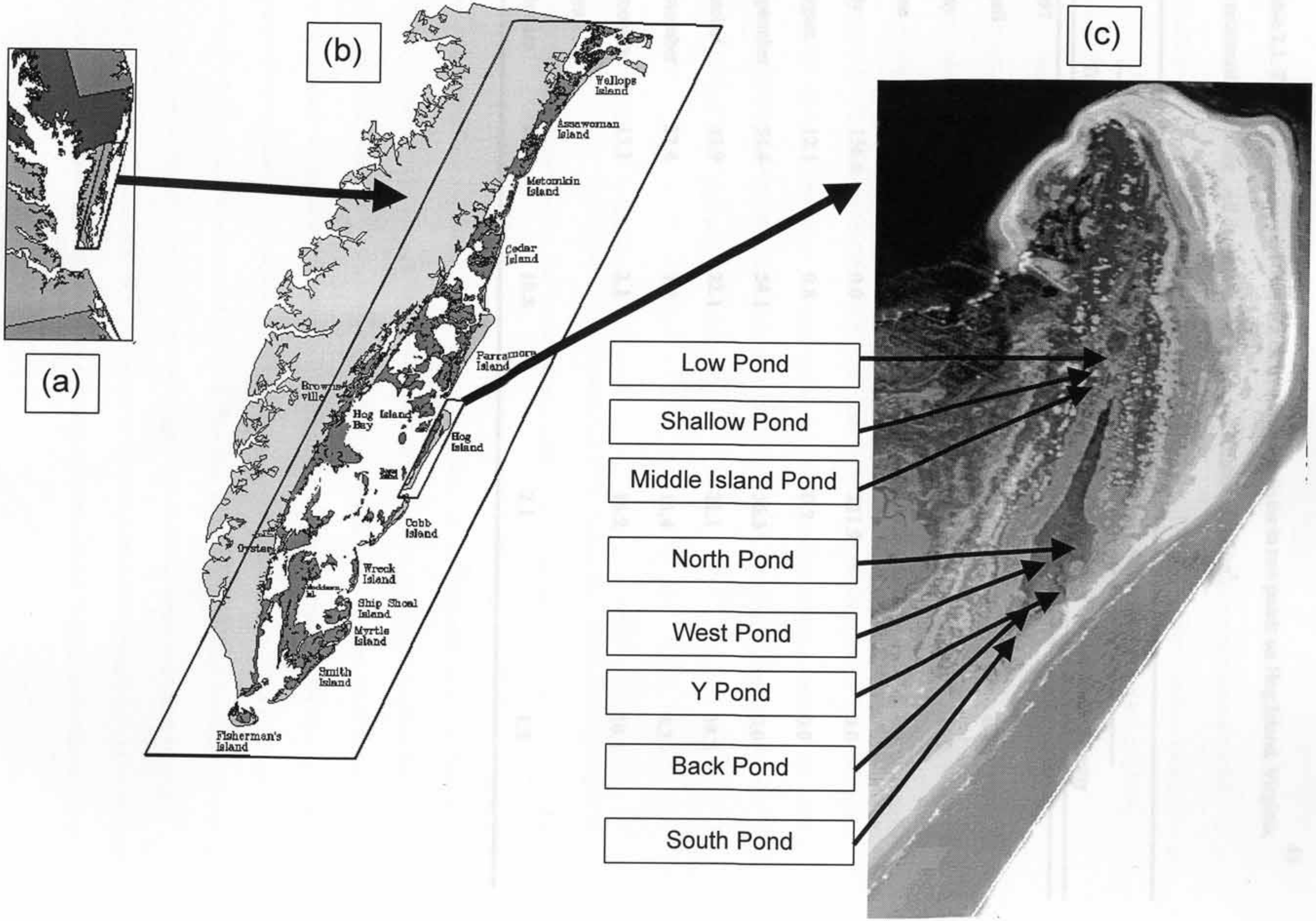


Table 2.1. Total fish densities and densities of *Membras martinica* in two ponds on Hog Island, Virginia, as estimated by seining. All densities are expressed as number of fish/m^2.

	North Pond		South Pond	
	Total Density	*Membras* Density	Total Density	*Membras* Density
1997				
April	3.2	1.2	5.6	1.2
May	32.1	26.7	57.4	38.9
June	112.3	0.7	156.2	0.0
July	156.8	0.0	211.9	0.0
August	12.1	0.8	0.7	0.0
September	54.4	54.1	56.3	0.0
October	43.9	22.1	21.1	38.2
November	32.4	7.7	11.4	4.2
December	13.1	2.1	16.2	10.1
1998				
February	12.5	10.8	2.1	1.9

of the fishes. Densities of fish also varied substantially among pond microhabitats. Furthermore, collection efficiency likely varied due to pond shape and size, as well as the composition of the fish assemblage (Allen *et al.,* 1995). Despite these confounding variables, the reported densities were similar to those reported for marsh ponds elsewhere (Whoriskey and Fitzgerald, 1987; Loftus and Eklund, 1994; Rowe and Dunson, 1995).

Based on these extensive pond surveys and sampling of the surf-zone (see Chapter 3), all fish species are classified as resident "marsh" species or "surf-zone" species. The classification corresponds to that of Ross and Doherty (1994) except both *M. martinca* and *Fundulus majalis* are considered to be surf-zone species, while Ross and Doherty (1994) grouped all of the atherinids and fundulids into the "marsh" fish category. *M. martinica* was the most common shallow surf-zone fish (see Chapter 3) and *F. majalis* were rarely collected in the ponds. Table 2 provides a complete list of all species collected in the ponds from 1996 to 1999, whether juveniles, adults, or both were collected, as well as the classification as "marsh" or "surf-zone" species.

2.3.3 General Experimental Protocol

Experiments were designed to simulate an actual wash-over event in which *Membras* would be introduced into the island ponds. This particular species was selected because it is the most common fish of the shallow surf-zone of the Virginia Eastern Shore barrier islands (see Chapter 3). During an actual wash-over event, *Membras* are presumably subjected to varying levels of environmental stress and biological interactions once they are trapped within the discrete ponds. In order to evaluate these effects on the survival and condition of *Membras*, a series of enclosure experiments were conducted over several seasons. Three treatments were utilized in the experimental designs: (1) *Control* - 8 *Membras* (14 fish/ m^2), (2) *Intraspecific interactions* - 16 *Membras* (28 fish/ m^2), and (3) *Interspecific interactions* - 8 *Membras martinica* + 8 *Fundulus heteroclitus* (28 fish/ m^2). *Fundulus* was used in Treatment 3 because it is one of the most common fishes (along with *Cyprinodon variegatus*) in the island ponds, and thus one of the species most likely to influence the success of *Membras*. These experimental densities were based on those estimated by seining and were well within actual pond fish densities on the Virginia barrier islands (Table

Table 2.2. A list of all fish species collected in ponds on Hog Island from 1996-1998. The classification is based on the primary habitat on the Virginia barrier islands (M, resident marsh species; S, surf-zone resident).

		Adult	Juvenile	Classification
American eel	*Anguilla rostrata*		*	M
Atlantic menhaden	*Brevoortia tyrannus*		*	S
Atlantic needlefish	*Strongylura marina*	*		S
Atlantic silverside	*Menidia menidia*	*	*	S
Blackcheek tonguefish	*Symphurus plagiusa*		*	S
Florida Pompano	*Trachinotus carolinus*		*	S
Gulf kingfish	*Menticirrhus littoralis*		*	S
Halfbeak	*Hyporhamphus unifasciatus*		*	S
Mojarra species	*Eucinostomus* sp.	*	*	S
Mummichog	*Fundulus heteroclitus*	*	*	M
Northern kingfish	*Menticirrhus americanus*		*	S
Northern pipefish	*Syngnathus fuscus*	*	*	S
Rainwater killifish	*Lucania parva*	*	*	M
Rough silverside	*Membras martinica*	*	*	S
Sheepshead	*Archosargus probatocephalus*		*	S
Sheepshead minnow	*Cyprinodon variegatus*	*	*	M
Siver perch	*Bairdiella chrysoura*		*	S
Spot	*Leiostomus xanthurus*		*	S
Spotfin killifish	*Fundulus luciae*	*	*	M
Striped killifish	*Fundulus majalis*	*	*	S
Summer flounder	*Paralichthys dentatus*		*	S
Threespine stickleback	*Gasterosteus aculeatus*	*	*	M
White mullet	*Mugil curema*	*	*	S

2.1). Although there are inherent difficulties in interpreting the results of competition experiments (see Connell, 1983), choosing densities that are representative of naturally occurring assemblages helps minimize those confounding effects.

All experiments were conducted in enclosures constructed with a square, welded rebar frame (0.95 diameter rebar) covered with 0.48 cm nylon mesh. Each side of the frame enclosure measured 0.75 m resulting in an enclosed surface area of 0.56 m^2. The depth of water (although variable during the course of the experiment) was initially 60 cm in each enclosure. The mesh was attached to the frame with plastic cable ties at 1 cm increments and was pulled extremely taut to ensure that it would remain tight once placed in the water. Both the sides and the bottoms of the enclosures were covered with this nylon mesh, allowing water, small organisms, or sediment to pass freely. The enclosures were secured in the ponds by 10 cm extensions on each enclosure leg pressed into the substrate. All enclosures in each pond were separated by 1 m. The top of each enclosure was covered with a 1.3 cm wire mesh top with numerous perpendicular wire extensions to deter birds.

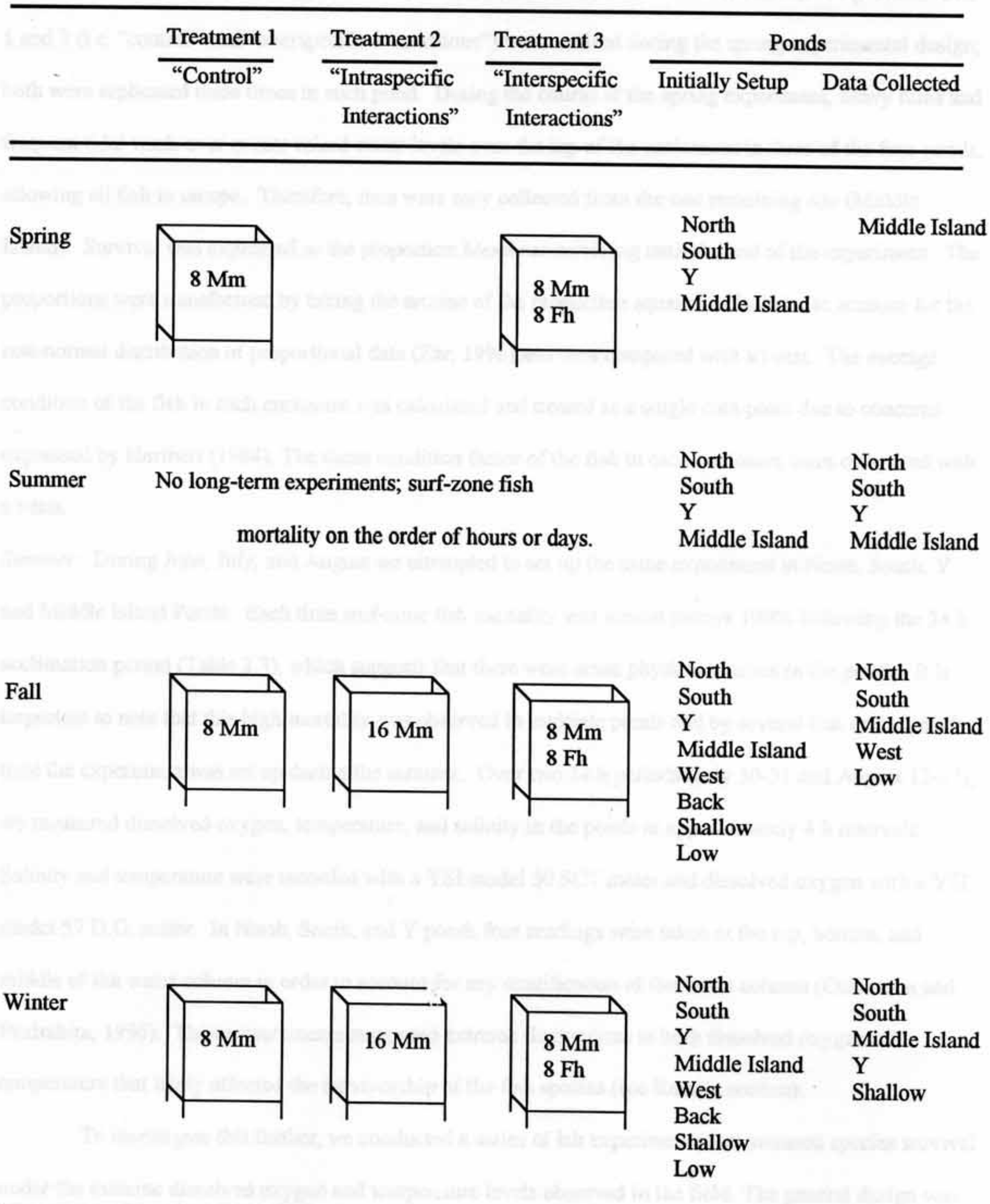
The *Membras* used in the experiments were collected by pulling a seine parallel to the shore in the shallow water (< 0.4 m) adjacent to the beach. The fish were placed in buckets filled with seawater and the buckets were immediately covered with lids to prevent over-heating. Battery-powered air pumps were used to oxygenate the water continuously. Once the bucket water temperature had adjusted to within 1°C of the water temperature in the ponds, the fish were introduced into the field enclosures. *Fundulus* were collected using minnow traps in the pond where the experiment was to take place. *Fundulus* were placed in a separate enclosure from the silversides and both species were allowed to acclimate for 24 h. After this period, the experiment was initiated by distributing the fish among the enclosures according to the experimental design specific to each season (see Seasonal Experimental Design section and summary in Figure 2.2).

Two indices were used to compare fish from the experimental treatments: survivability and condition. The condition of the fish was analyzed using the K condition factor (see Weatherly, 1972; Everhart and Youngs, 1981 for further discussion):

$$K = W / L^3$$

where: K represents the condition index, W the fish weight (grams) x 100, and L the fish length (cm). For

Figure 2.2. A summary of the experimental sampling design. Also included are the ponds in which the experiments were initially set up and the ones from which data were collected. Data were not collected from a given pond if fish escaped during the experiment due to high water levels, overturned enclosures, or damage to mesh. Abbreviations are as follows: Mm, *Membras martinica*; Fh, *Fundulus heteroclitus*.



	Treatment 1	Treatment 2	Treatment 3	Ponds	
	"Control"	"Intraspecific Interactions"	"Interspecific Interactions"	Initially Setup	Data Collected
Spring	8 Mm		8 Mm 8 Fh	North South Y Middle Island	Middle Island
Summer	No long-term experiments; surf-zone fish mortality on the order of hours or days.			North South Y Middle Island	North South Y Middle Island
Fall	8 Mm	16 Mm	8 Mm 8 Fh	North South Y Middle Island West Back Shallow Low	North South Middle Island West Low
Winter	8 Mm	16 Mm	8 Mm 8 Fh	North South Y Middle Island West Back Shallow Low	North South Middle Island Y Shallow

fishes of a given length, a higher K generally indicates a more "fit" fish.

2.3.4 Seasonal Experimental Designs

Spring. The spring experiment was conducted from April 28 until June 10. A total of twenty-four enclosures were utilized, six in each of four ponds (North, South, Middle Island, and Y). Only Treatments 1 and 3 (i.e. "control" and "interspecific interactions") were utilized during the spring experimental design; both were replicated three times in each pond. During the course of the spring experiment, heavy rains and frequent tidal wash-over events raised water levels over the top of the enclosures in three of the four ponds, allowing all fish to escape. Therefore, data were only collected from the one remaining site (Middle Island). Survival was expressed as the proportion *Membras* surviving until the end of the experiment. The proportions were transformed by taking the arcsine of the proportion squareroot in order to account for the non-normal distribution of proportional data (Zar, 1996) and then compared with a t-test. The average condition of the fish in each enclosure was calculated and treated as a single data point due to concerns expressed by Hurlbert (1984). The mean condition factor of the fish in each enclosure were compared with a t-test.

Summer. During June, July, and August we attempted to set up the same experiment in North, South, Y and Middle Island Ponds. Each time surf-zone fish mortality was almost always 100% following the 24 h acclimation period (Table 2.3), which suggests that there were acute physical stresses in the ponds. It is important to note that this high mortality was observed in multiple ponds and by several fish species each time the experiment was set up during the summer. Over two 24 h periods (July 30-31 and August 12-13), we measured dissolved oxygen, temperature, and salinity in the ponds at approximately 4 h intervals. Salinity and temperature were recorded with a YSI model 30 SCT meter and dissolved oxygen with a YSI model 57 D.O. meter. In North, South, and Y ponds four readings were taken at the top, bottom, and middle of the water column in order to account for any stratification of the water column (Culberson and Piedrahita, 1996). The measurements suggested extreme fluctuations in both dissolved oxygen and temperature that likely affected the survivorship of the fish species (see Results section).

To investigate this further, we conducted a series of lab experiments that assessed species survival under the extreme dissolved oxygen and temperature levels observed in the field. The general design was

Table 2.3. Attempts to introduce the four most common surf-zone residents to four ponds during the summer of 1998. All fish were placed in one of the field enclosures and then checked on the next trip to the study site. Survivorship proportions are averaged across all species. Fish species abbreviations are as follows: *Membras martinica,* Mm; *Trachinotus carolinus,* Tc; *Menticirrhus littoralis,* Ml; *Fundulus majalis,* Fm.

Date	Pond	Number of Fish Introduced				Total Survival	Time Since Introduction
		Mm	Tc	Ml	Fm		(Days)
6/8	South	50	-	-	-	0 %	3
7/1	North	50	-	-	-	0%	1
7/1	Middle	50	-	-	-	4%	2
7/1	Y	50	-	-	-	4%	2
7/9	North	8	8	8	-	0%	3
7/17	North	8	8	8	3	0%	1
7/17	South	8	8	8	0	0%	1
7/17	Y	8	8	8	0	0%	1
7/24	Y	5	6	5	6	0%	1
7/30	Y	5	5	5	5	0%	1
7/30	North	5	5	5	0	0%	1
8/10	South	3	8	4	0	0%	1
8/10	North	4	5	4	0	0%	1
8/10	Y	3	1	11	0	0%	1
8/12	South	5	5	5	1	0%	1
8/12	Y	4	5	14	1	29%**	1

** Survivorship higher due to over-wash event on 8/12 (see Results section).

based on acute tolerance tests conducted by Dunson *et al.* (1993). All laboratory tests were conducted at the Virginia Coast Reserve Laboratory in one of four 30 gallon aquariums. The aquaria were filled with locally collected estuarine water. Five fish species (*Fundulus heteroclitus, Cyprinodon variegatus, Membras martinica, Trachinotus carolinus,* and *Menticirrhus americanus*) were collected from the surf-zone or ponds on Hog Island and were immediately transported back to the lab in aerated containers. The fish were acclimated to laboratory aquaria for a minimum of 24 hours and fed brine shrimp (*Artemia sp.*) to satiation an hour before each experiment. At the start of each test, four randomly picked specimens of each of the five species were placed in a plastic aerated holding tank. Experiment timing began when the fish were transferred from the holding tank to the experimental aquarium with a dip net. Tank salinity, temperature, and dissolved oxygen were monitored throughout the test.

Two separate groups of experiments were conducted, one for dissolved oxygen extremes and one for temperature extremes. Dissolved oxygen was adjusted by bubbling nitrogen gas into the aquarium prior to the initiation of the experiment. Acrylic tops covered the tanks to help reduce diffusion of oxygen into the water. Temperature adjustments were made using 3 Penn Plex 15" 200watt Thermaflow PC Plus heaters. In both sets of experiments, all other physical conditions were kept constant at standard levels to which the fish were initially acclimated. The time to fish mortality was recorded as the last observed movement of the opercle (Dunson *et al.*, 1993). Fish were collected at the end of the experiments, weighed, and measured. For all experiments (four dissolved oxygen and two temperature trials) the time until death for each species was calculated as an average of the individuals from that trial. The dissolved-oxygen data were analyzed using an analysis of variance (ANOVA) followed by the Tukey multiple comparison procedure. Data from the two temperature trials did not meet homogeneity of variance assumptions and were analyzed with a Kruskal-Wallis non-parametric ANOVA.

Fall and Winter. The experimental approach was modified from the initial spring design in order to increase the number of ponds included. A randomized block design (each of the eight ponds designated in Figure 1 served as a block) was employed in which the three treatments were established in each pond. The experiment was conducted for three weeks during the fall of 1998 (October 18 – November 8) and four weeks in the winter of 1999 (February 15 – March 13). Three sites were excluded from analyses in the fall, and again in the winter, because certain enclosures were over-turned by the wind or the enclosure mesh was damaged by blue crabs, *Callinectes sapidus*, either of which allowed the experimental fishes to escape. Proportional survival data were arcsine transformed as described above and then analyzed with a two-way ANOVA with pond serving as a blocking variable. The mean condition of fish within each enclosure was calculated and values compared with the same ANOVA design. All statistical analyses were conducted with Sigma Stat statistical software (1997). The seasonal design of the experiments throughout the course of the study is summarized in Figure 2.2.

2.4 Results

Spring. In Treatment 1, *Membras* survival averaged 92% (Figure 2.3), significantly higher than the 42% observed in Treatment 3 (t-test, df = 4, t = 4.6, p = 0.01). Likewise, the mean condition of *Membras* in Treatment 1 was significantly higher than in Treatment 3 (t-test, df = 4, t = 2.9, p = 0.04). The higher survival in the lower density treatment suggests that physical conditions in the ponds, although potentially providing a long-term chronic stress on the fishes, did not preclude their prolonged survival over the five-week study period. In Treatment 3, survival and condition of the surf-zone fishes was significantly reduced, suggesting that a biological interaction between the species. None of the *Fundulus* died during the course of the experiment.

Summer. The same experiment was set-up in four ponds throughout the summer using the four most common shallow surf-zone fish species, but mortality was almost always 100% after 24 hours (Table 2.3). Only minutes after their introduction into the ponds, the behavior of the fish was noticeably affected. Some fish died during the afternoon hours when temperatures reached a maximum, but most died soon after sunset; almost all fish were dead by the following morning in every case. In contrast, resident marsh species, *Fundulus* and *Cyprinodon*, would typically survive for weeks or much longer in the same enclosures. One exception to this pattern was observed on August 12 in Y-pond when some of the surf-zone fishes were able to survive for 24 h. This increased survival coincided with a wash-over event that served to ameliorate temporarily the physical conditions in the pond. Even so, all of the surf-zone fish were dead within four days as physical conditions again deteriorated.

The 24 h pond profiles of dissolved oxygen and temperature during the same time period suggest extremely stressful physical conditions (Figure 2.4). Dissolved oxygen levels were clearly not limiting during the daylight hours, reaching levels higher than 20 mg/l in one of the ponds on July 30. Immediately following sunset, however, the dissolved oxygen levels fell dramatically. In all three ponds on July 30, and two of the three ponds on August 12, the dissolved oxygen level was 0.1 mg/l before midnight. Dissolved oxygen levels remained extremely low until sunrise when photosynthesis began to re-oxygenate the water. Temperature readings during the afternoon reached 38 °C on July 30, but readings as high as 41°C have been observed in shallow ponds on Hog Island (Layman, *pers.obs.*). Figure 2.4 depicts mid-water

Figure 2.3. The percentage of *M. martinica* surviving during each seasonal experiment and the average condition (K) of the fish that survived. Error bars represent +/- 1 S.E..

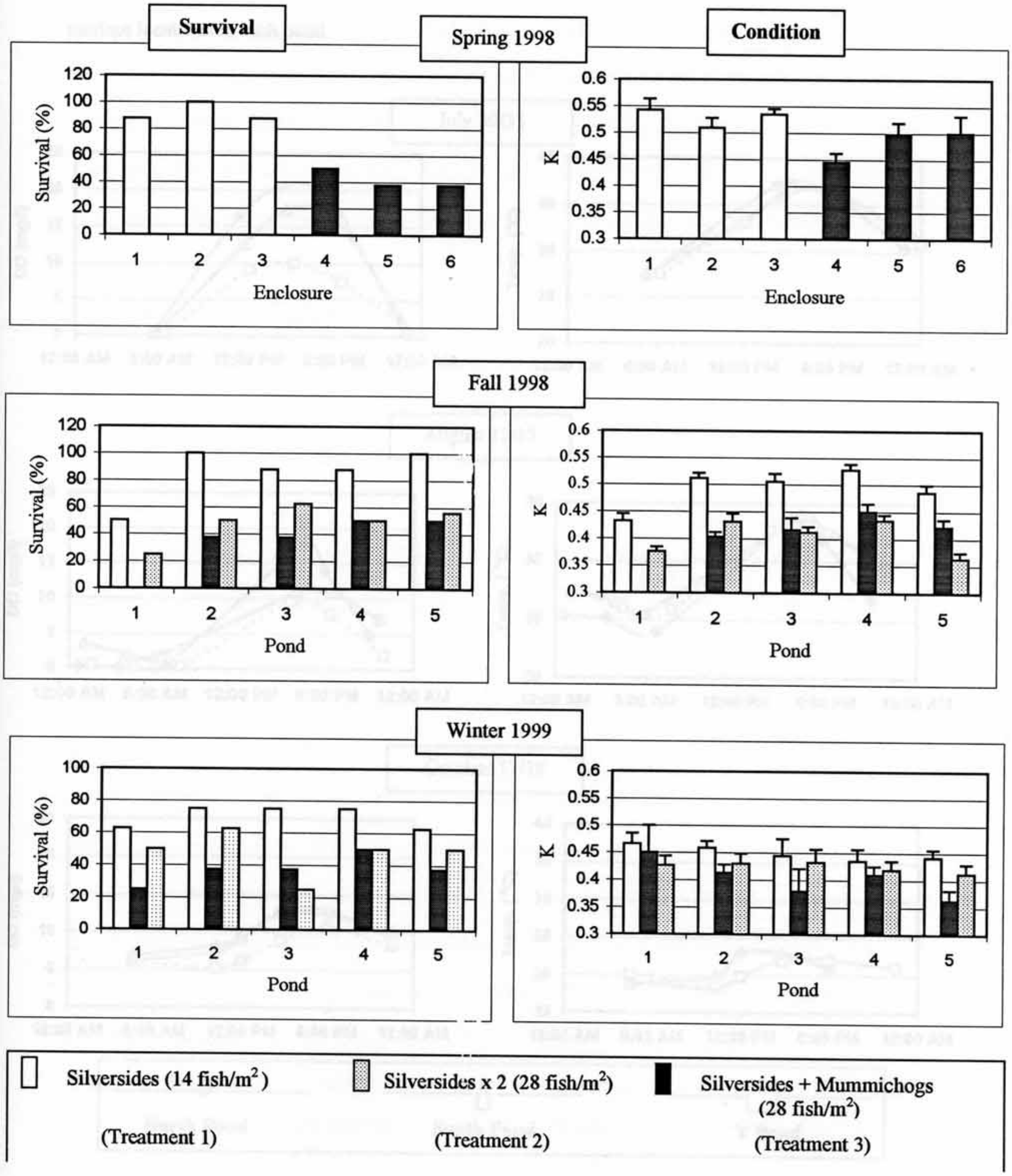
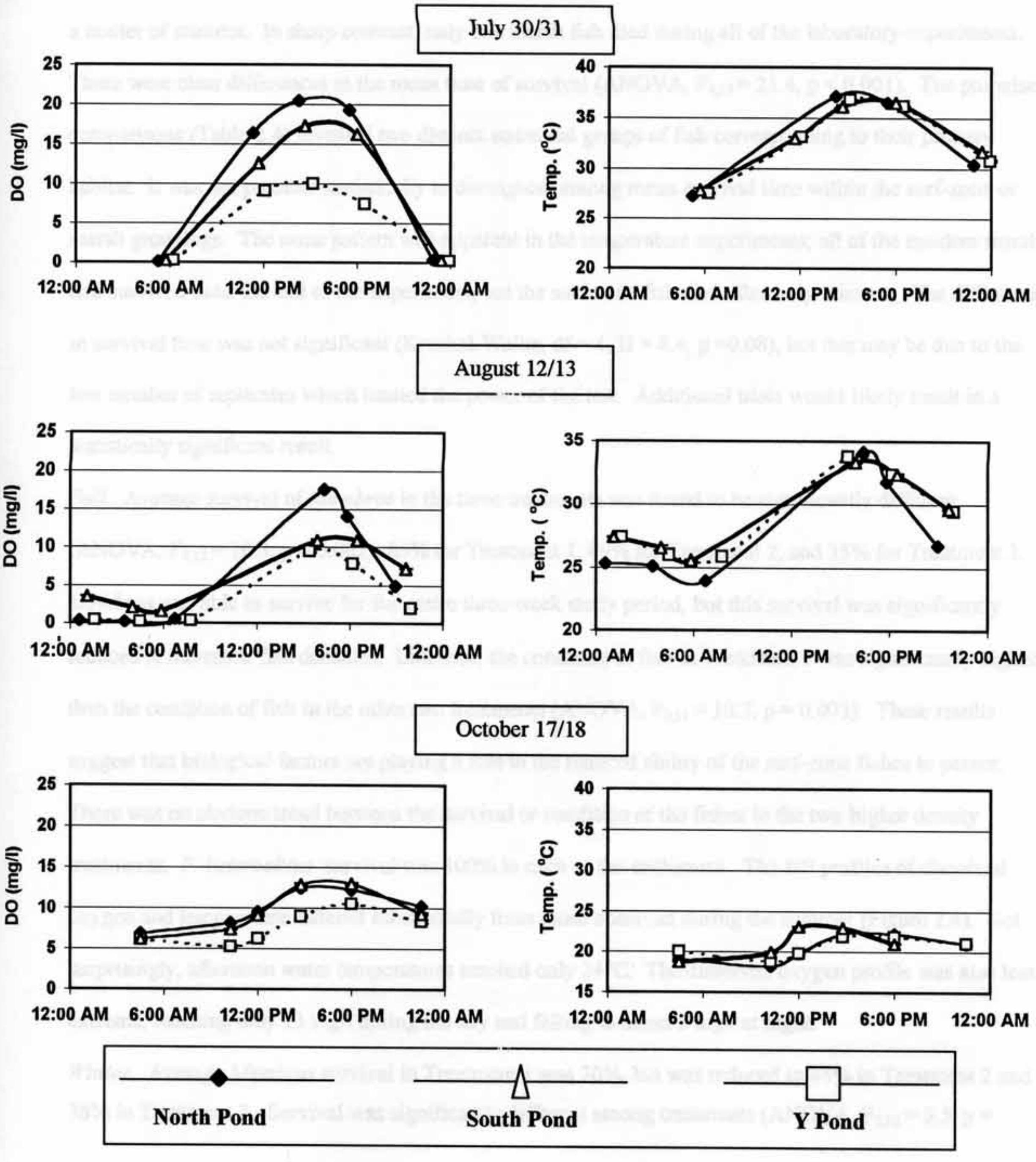


Figure 2.4. The dissolved oxygen and temperature profiles over 24 hour periods on July 30/31, August 12/13, and October 17/18 in North, South and Y Ponds. The July and August cycles are representative of the summer (dry) season and the October profiles of the corresponding cycles in a non-summer (wet) season. The readings given in these graphs are based on an average value of four measurements taken at random locations in each pond.



measurements, but the trends and extremes of dissolved oxygen and temperature were very similar throughout the water column. Salinities varied less than 1.0 ppt during the 24 h measurement periods and remained at levels that were not likely to cause short-term fish mortality (20 to 40 ppt).

Laboratory experiments supported the above findings (Figure 2.5). At each oxygen level (all of which were less severe than those observed in the ponds) the surf-zone fishes were able to survive for only a matter of minutes. In sharp contrast, only one marsh fish died during all of the laboratory experiments. There were clear differences in the mean time of survival (ANOVA, $F_{4,15} = 21.4$, $p < 0.001$). The pairwise comparisons (Table 2.4) revealed two distinct statistical groups of fish corresponding to their primary habitat. It was not possible statistically to distinguish among mean survival time within the surf-zone or marsh groupings. The same pattern was apparent in the temperature experiments; all of the resident marsh fish survived until the end of the experiment, but the surf-zone fish died after only minutes. The difference in survival time was not significant (Kruskal-Wallis, df = 4, H = 8.4, p =0.08), but this may be due to the low number of replicates which limited the power of the test. Additional trials would likely result in a statistically significant result.

Fall. Average survival of *Membras* in the three treatments was found to be significantly different (ANOVA, $F_{2,12} = 10.3$, $p = 0.002$): 85% for Treatment 1, 49% for Treatment 2, and 35% for Treatment 3. *Membras* was able to survive for the entire three-week study period, but this survival was significantly reduced at increased fish densities. Likewise, the condition of fish in Treatment 1 was significantly higher than the condition of fish in the other two treatments (ANOVA, $F_{2,11} = 10.7$, $p = 0.003$). These results suggest that biological factors are playing a role in the reduced ability of the surf-zone fishes to persist. There was no obvious trend between the survival or condition of the fishes in the two higher density treatments. *F. heteroclitus* survival was 100% in each of the enclosures. The fall profiles of dissolved oxygen and temperature differed substantially from those observed during the summer (Figure 2.4). Not surprisingly, afternoon water temperatures reached only 24°C. The dissolved oxygen profile was also less extreme, reaching only 13 mg/l during the day and falling to about 5 mg/l at night.

Winter. Average *Membras* survival in Treatment 1 was 70%, but was reduced to 48% in Treatment 2 and 38% in Treatment 3. Survival was significantly different among treatments (ANOVA, $F_{2,12} = 5.5$, p =

Figure 2.5. The results of the two sets of laboratory tests examining the acute tolerances of fishes to extreme dissolved oxygen and temperature levels. All other physio-chemical variables were held at non-stressful levels during the tests. Each bar represents the mean (+/- 1 S.E.) of 4 individual (n=4) fish of each species. Each experiment was terminated after 130 minutes.

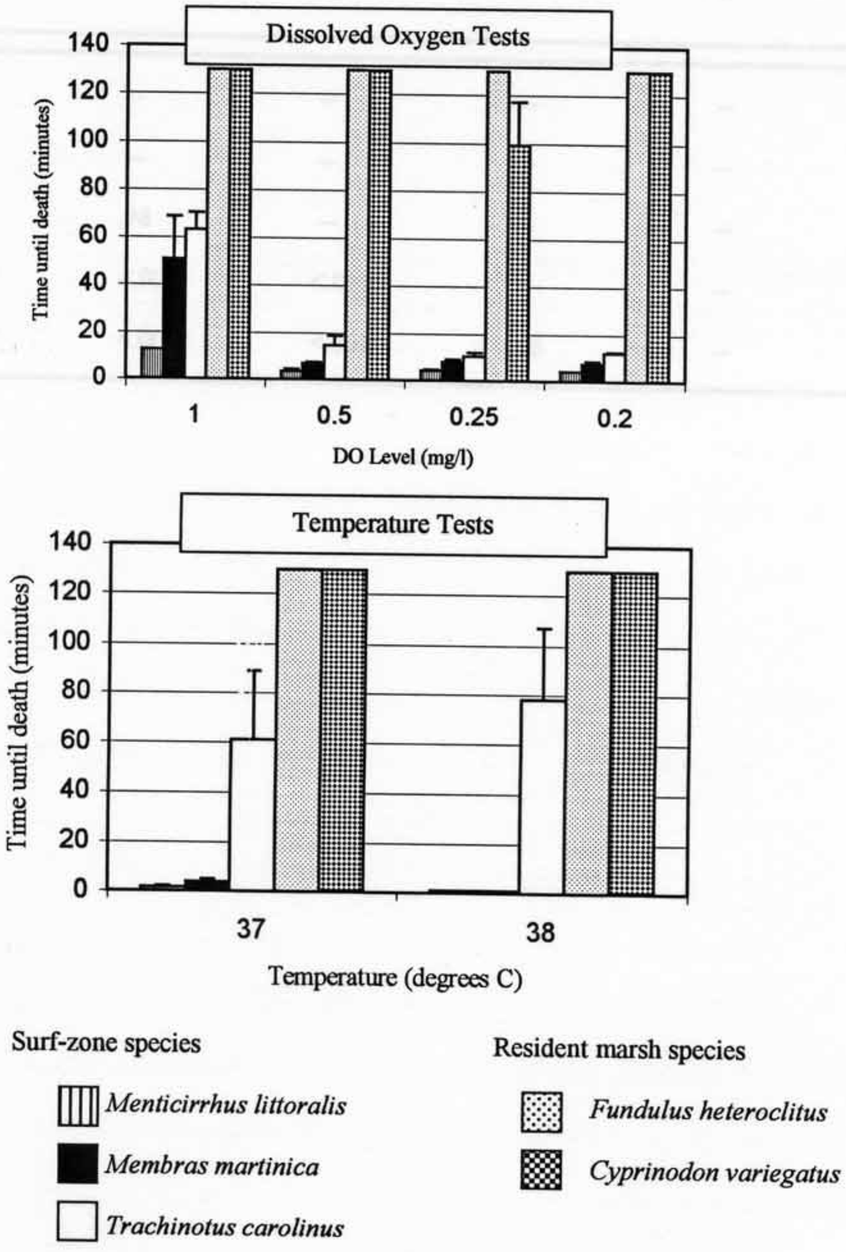


Table 2.4. P-values generated from Tukey pairwise comparisons following a significant one way ANOVA on the mean time until death of fish. Significant p-values are designated using *. Fish are abbreviated as follows: *Menticirrhus littoralis*, Ml; *Membras martinica*, Mm; *Trachinotus carolinus*, Tc; *Fundulus heteroclitus*, Fh; *Cyprinodon variegatus*, Cv.

	Ml	Mm	Tc	Fh	Cv
Ml	--	--	--	--	--
Mm	.83	--	--	--	--
Tc	.51	.98	--	--	--
Fh	<.001*	<.001*	<.001*	--	--
Cv	<.001*	<.001*	<.001*	.96	--

0.02), because of a higher rate of survival in Treatment 1 compared to the higher density treatments. There was no consistent difference in survival between Treatments 2 and 3. The mean condition of fishes also was significantly different (ANOVA, $F_{2,12} = 5.8$, $p = 0.001$). The condition of fish in the low density enclosures was higher than that of the other two treatments in each of the five ponds. Only a single *F. heteroclitus* died in all five ponds during the course of the winter experiments.

2.5 Discussion

The research shows that local extinctions of surf-zone fishes in marsh ponds is caused both by susceptibility to dissolved oxygen and temperature extremes (abiotic factors) and competition (biotic factors). Previous models (i.e. Menge and Sutherland, 1987) concerning the importance of abiotic and biotic structuring mechanisms are based on a spatial gradient of environmental stress. Here, we identify a temporal environmental stress gradient. During summer, dissolved oxygen and temperature reach extreme levels, resulting in surf-zone fish mortality. During non-summer months, dissolved oxygen and temperature levels are moderated, allowing biological interactions to become relatively more important. The structuring mechanisms in summer and non-summer periods are considered separately below.

2.5.1 Summer Structuring Mechanisms

During summer months, pond temperatures exceeded 41 °C, well above the short-term tolerance limits of the surf-zone fishes. The combination of warm water temperatures and benthic decomposition, as well as respiration by fishes, invertebrates, and algae in the ponds, resulted in near anoxic conditions at night. A pattern of high afternoon temperatures and low nighttime dissolved oxygen levels has been reported in similar pond habitats (Kushlan, 1979; Krom *et al.* 1985a,b; Whoriskey and Fitzgerald, 1987; Culberson and Piedrahita, 1996). Other physiochemical variables, including low pH (Haines, 1981; Horne and Dunson, 1995), high ammonia levels (Krom *et al.*, 1985b), and extreme salinities may also contributed to the death of the surf-zone fishes; however, either dissolved oxygen or temperature alone can account for the rapid surf-zone fish mortality during summer.

The most abundant fishes in the Virginia island marsh ponds, *F. heteroclitus* and *C. variegatus*, are extremely tolerant of such harsh conditions. *C. variagatus* has been found in waters with salinities ranging from 0 - 142 ppt (Simpson and Gunter, 1956; Nordlie, 1985; Dunson *et al.*, 1998) and *F. heteroclitus* from 0 – 120 ppt (Griffith, 1974). *C. variegatus* is considered the most eurythermic of all fishes with critical thermal minima and maxima ranging from 0.6 to 45.1 °C (Bennet and Beitinger, 1996). *F. heteroclitus* has been shown to survive for extended periods in temperatures ranging from –1.5°C (Umminger, 1972) to 36 °C (Garside and Chin-Yuen-Kee, 1972). Both of these species are also extremely well-adapted to low dissolved oxygen due to morphological (Lewis, 1970) and behavioral adaptations

(Kramer, 1987). For example, *F. heteroclitus* increase aquatic surface respiration under low dissolved oxygen conditions, as has been documented for other fishes (Lewis, 1970; Gee *et al.*, 1978; Congleton, 1980; Kramer and Mehegan, 1981; Kramer and McClure, 1982).

In addition to causing surf-zone fish mortality, the extreme environmental stress of the ponds likely affects the relative abundance of resident marsh fishes. For example, large mummichogs were more likely to perish under hypoxic conditions than were juvenile conspecifics or smaller *C. variegatus* (Layman, *per.obs.*). Kushlan (1974) similarly found that large fishes were more susceptible to stresses during dry periods in the Everglades, perhaps because larger fishes have a higher oxygen demand (Jobling, 1994; Moyle and Cech, 1996). Dunson *et al.* (1993) described the tolerances exhibited by marsh fishes to physio-chemical extremes and suggested that these may have important implications for assemblage structure. Dunson and Travis (1994) further discuss the importance of abiotic variables on estuarine assemblages. The present study emphasizes the role that physical conditions have on marsh pond fish assemblage structure during the environmentally harsh summer months.

Biotic interactions may play some assemblage structuring role in the summer. In fact, as ponds shrink during dryer months, fishes are forced into smaller areas, thereby increasing competition for limiting resources (Zaret and Rand, 1971; Lowe-McConnell, 1987). Shrinking ponds are also excellent feeding areas for various species of wading and shore birds (Kushlan, 1976b; Kushlan, 1986; Master, 1992). Therefore, dominant abiotic structuring parameters do not eliminate intense biological interactions that occur among species that can tolerate the environmental stress of the ponds. As Matthews (1998) suggests, physical harshness may provide a filter that precludes existence of some species (see Smith and Powell, 1971), but this does not necessarily reduce the importance of biological interactions on the individuals that are able to persist.

Finally, it is important to note that a biotic, as well as an abiotic, process may be the mechanism by which physical parameters become limiting in the ponds. Whereas temperature stress is the result of solar radiation, biological processes (i.e. oxygen consumption, decomposition) are actually the underlying mechanisms that result in low dissolved oxygen levels. Identifying the mechanism underlying an observed phenomena is essential to understanding what processes actually control assemblage structure (see Tilman, 1987). The control of abiotic parameters by biological mechanisms is often overlooked in ecological studies and deserves further examination.

2.5.2 Non-Summer Structuring Mechanisms

Membras exhibited high survival in Treatment 1 (i.e. "control") during all three seasons, but survival, as well as the condition of the survivors, was significantly reduced in the other two treatments. These experiments, using an *in situ* approach which has yet been attempted in such a system, provide evidence that biological interactions may affect the relative abundance of marsh fishes. Although the biological interaction was not directly observed strong inferences can be made based from our results. Predation by fundulids on atherinids of similar size is very unlikely. Furthermore, the non-significant differences in survival and condition between Treatments 2 and 3 (with and without mummichogs) suggests that direct *Fundulus* agnostic behavior was not a mechanism underlying surf-zone fish mortality. There may be some competition for space within the enclosures, but this is unlikely due to the demersal nature of *Fundulus* and schooling, and pelagic habitat of *M. martinica*. The most likely explanation is that competition for food (both intra- and interspecific) ultimately affects the survival and/or growth *Membras*. In the terminology used by Schoener (1983), this interaction between species can be described as "consumptive competition", in which a quantity of a given resource is consumed by an individual, thus depriving others of the opportunity to utilize it. Alternatively, *Fundulus* survival was almost always 100% in the experimental treatments, suggesting asymmetric competition (see Connell, 1983). Mummichogs can consume a wide range of food items (Fritz, 1974; Baker-Dittus 1978; Kneib and Stiven, 1978; Kneib *et al.*, 1980; Kneib, 1986), whereas silversides are primarily zooplanktivorous (Bengston, 1984; Morgan, 1990; Allen *et al.*, 1995). Therefore, insufficient zooplankton biomass likely has a greater impact on the less facultative species. The numerical dominance by *F. heteroclitus* in the marsh ponds may partially be due to the fact that marsh fish species are competitive dominants over other colonizers of the ponds.

Competition has been found to be an important structuring mechanism for fish assemblages in rocky intertidal habitats (Grossman, 1982) and in freshwater streams (Ross *et al.*, 1985; Matthews, 1998). Other studies suggest that intra-specific (Rubenstein, 1981; Persson, 1983; Wooton 1985) and inter-specific competition (Echelle and Schnell, 1972; Page and Schemske, 1978; Edlund and Magnhagen, 1981;

Fitzgerald and Whoriskey, 1985; Moyle and Vondracek, 1985; Fausch and White, 1986; Winemiller, 1989; Bergman, 1990; Persson and Greenberg, 1990) can have detrimental effects on the growth, reproductive success, or resource utilization of fishes. We conclude that it is not yet clear whether competition contributes to patterns in marsh pond fish assemblage structure (Poulin and Fitzgerald, 1989; Rowe and Dunson, 1995; Dunson and Rowe, 1996), but the results of the present study suggest that during periods of reduced environmental stress, competition may indeed be a key assemblage structuring element.

Physical factors likely do play a prominent role in structuring the fish assemblages during the non-summer months. For example, cold winter temperatures are more likely to be detrimental to the surf-zone fishes (Snelson and Bradley, 1978; Hall *et al,* 1982) than to the tolerant resident marsh fishes. Other studies have shown that abiotic conditions may have important moderating effects on biotic interactions of shallow estuarine fish assemblages, even if this effect is indirect (Poulin and Fitzgerald, 1989; Rowe and Dunson, 1995; Dunson and Rowe, 1996). The harshness of the environment may lower the threshold at which competition becomes detrimental to a particular species, making competitive exclusion more likely (Holt, 1985; Chesson and Huntly, 1997). *Membras* kept under conditions of low dissolved oxygen in laboratory aquaria became sluggish and were slower to feed. When *Membras* were held in the same tank as *F. heteroclitus*, the *Fundulus* (seemingly unaffected by the chronically low dissolved oxygen conditions) would quickly consume the food before the silversides would even begin to feed (Layman, *pers. obs.*). Such a reduced inclination to feed in low oxygen conditions has been observed for a variety of fish species (Petit, 1973; Carlson *et al.*, 1980; Weber and Kramer, 1983; Whoriskey *et al.*, 1985). Furthermore, low oxygen conditions may have indirect effects on reproduction, as well as predator avoidance capabilities, of fishes (Kramer, 1987 and sources therein).

2.5.3 Study Limitations

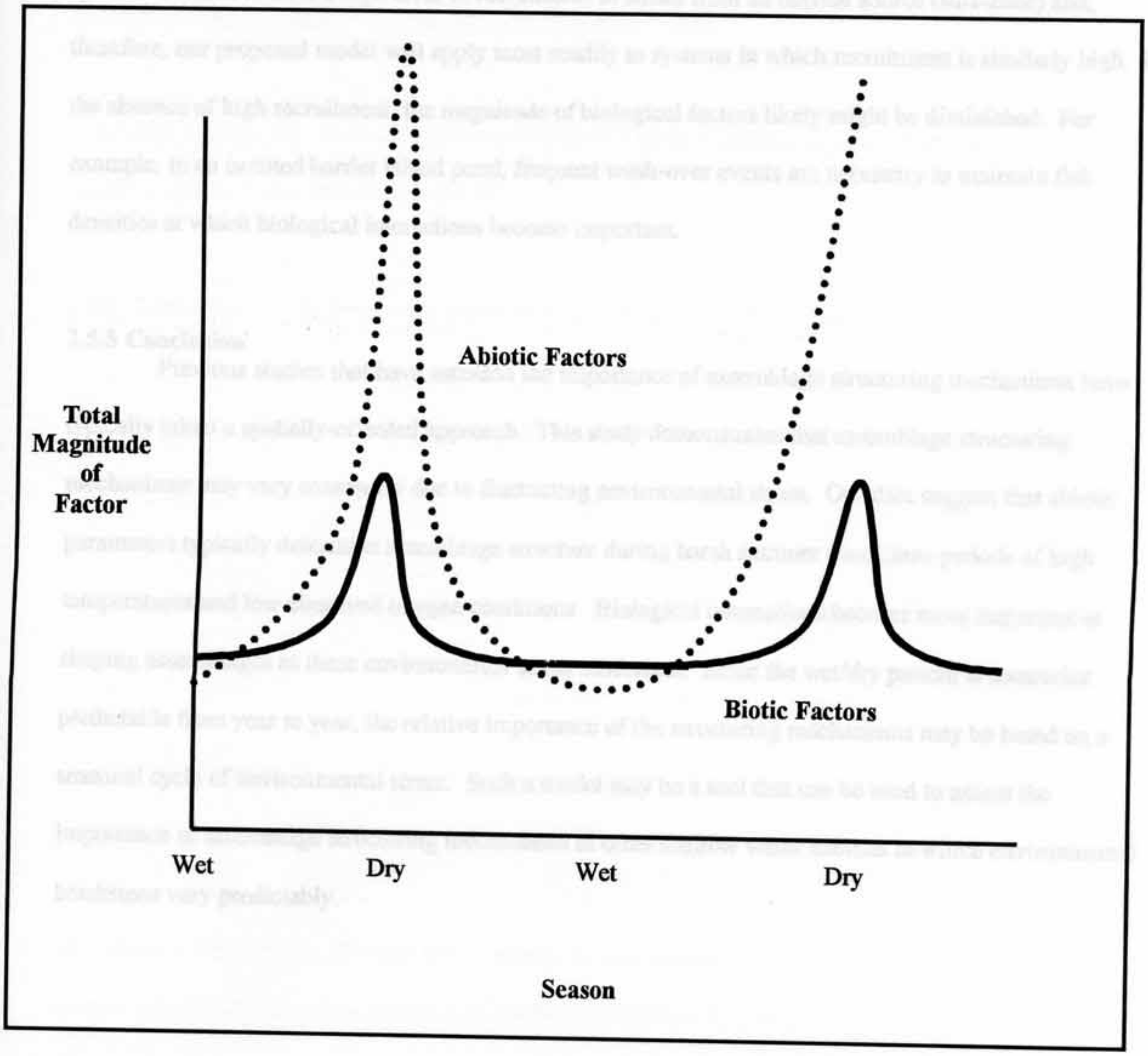
Our study have two major limitations: (1) the inherent difficulties of demonstrating competition using enclosure experiments and (2) a relatively short experimental study period. First, confining mobile organisms may alter behavior and make it problematic to deduce natural assemblage properties (Connell, 1983). Additionally, indirect interactions, such as food availability, may confuse the mechanisms behind observed responses (Connell, 1983; Bender *et al.*, 1984; Tilman 1987). Finally, the structure of the enclosures themselves may alter physical conditions and disrupt the natural relationship between organisms (Rothschild and Osborn, 1988; MacKenzie and Leggett, 1991). In spite of these limitations, other fish assemblage studies have utilized enclosures (Rubenstein, 1981; O'Neill and Hyatt, 1987; Bergman, 1990; Persson and Greenberg, 1990; Dieter *et al.*, 1991; Abrahams, 1996; Duffy *et al.*, 1996), largely because this approach provides the best possible representation of the natural physical and chemical environment. We have minimized experimental artifacts by using large, permeable enclosures, replicating the experiment in several ponds, and by having our experimental densities at naturally occurring levels. These considerations make "scaling-up" from the experimentals to entire pond fish assemblages seem reasonable.

Second, our experiments were conducted over the course of a single year. Despite this drawback, we have studied ponds on the Virginia barrier islands since 1995 and the same general wet/dry pattern and associated pond dynamics have been observed each year; additionally, these patterns are very similar to those described for the Florida Everglades (Kushlan, 1976, 1980, 1986). Thus, the results presented in this study should provide a basis for future studies of similar systems. Such studies might consider how spatial variability (i.e. the food availability, depth, or substrate of ponds), the inclusion of different fish species, or differing regional study sites might affect assemblage structuring mechanisms.

2.5.4 Conceptual Model

Figure 2.6 is a proposed model of fish assemblage regulation for shallow aquatic habitats characterized by a seasonal gradient of environmental stress. In this model, we emphasize the role of temporal change, not spatial differences, on assemblage structuring mechanisms. Our approach also differs from similar models (i.e. Menge and Sutherland, 1987) in that we depict the total, not relative, magnitude of the structuring factors. This ensures that the importance of one mechanism is not completely masked in the presence of another. For example, during the summer in marsh ponds of Virginia, physical conditions are the dominant structuring factors, even though intense biological interactions may also be occurring. The importance of these biological factors is greatly diminished because of the extreme physical conditions, but the biological pressures may be intense nonetheless. That is, if environmental stress were to become less

Figure 2.6. A conceptual model of the importance of abiotic and biotic factors in structuring marsh pond fish assemblages. The horizontal axis depicts a time scale in which dry and wet seasons alternate and vertical the total magnitude of abiotic or biotic influences. In east coast shallow water habitats, the dry season corresponds to the summer months.



severe during a particular summer, in a particularly cool year, for example, the biological interactions would become relatively more important in structuring the fish assemblages.

An important component of the Menge and Sutherland (1987) model is the impact of recruitment on the relative contribution of abiotic and biotic factors. Our experiments were conducted in an open system in which there is a high level of recruitment of fishes from an outside source (surf-zone) and, therefore, our proposed model will apply most readily to systems in which recruitment is similarly high. In the absence of high recruitment, the magnitude of biological factors likely might be diminished. For example, in an isolated barrier island pond, frequent wash-over events are necessary to maintain fish densities at which biological interactions become important.

2.5.5 Conclusion

Previous studies that have assessed the importance of assemblage structuring mechanisms have typically taken a spatially-oriented approach. This study demonstrates that assemblage structuring mechanisms may vary seasonally due to fluctuating environmental stress. Our data suggest that abiotic parameters typically determine assemblage structure during harsh summer conditions periods of high temperatures and low dissolved oxygen conditions. Biological interactions become more important in shaping assemblages as these environmental stress moderates. Since the wet/dry pattern is somewhat predictable from year to year, the relative importance of the structuring mechanisms may be based on a seasonal cycle of environmental stress. Such a model may be a tool that can be used to assess the importance of assemblage structuring mechanisms in other shallow water habitats in which environmental conditions vary predictably.

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Chapter Three

Fish Assemblage Structure and Dynamics of the Shallow Ocean Surf-Zone on the Eastern Shore of Virginia Barrier Islands

3.1 Abstract

This study provides an in-depth description of the fish assemblage structure in the shallow surf-zone (< 0.4 m), a little-studied micro-habitat of the ocean surf. Fish assemblage patterns were examined with respect to three temporal cycles, seasonal, diel, and tidal, and at both large and small spatial scales. Sampling was conducted at the Virginia barrier islands using an 8 m bag seine dragged parallel to the beach. One person set the net at a depth of 0.4 m and the second person extended the net to the shoreline; therefore, samples were taken in water with an average depth of approximately 0.2 m. The fish assemblage was found to be relatively species poor; in fact, there were only two year-round residents, the rough silverside (*Membras martinica*) and white mullet (*Mugil curema*). Three species, *Membras martinica,* Florida pompano (*Trachinotus carolinus*), and gulf kingfish (*Menticirrhus littoralis*), comprised 95 % of all species captured. Fish species richness and total abundance peaked in the late summer and were lowest in the winter. Based on multidimensional scaling analysis, no distinct nighttime fish assemblage was identified. However, univariate analyses revealed that there was a significant increase in species richness at night, due to an influx of predatory adult fishes. There were also significantly more species collected at high than low tide. The most noteworthy trends were higher species richness and total abundance of fishes in the shallow water (< 0.4 m) of runnels (low wave energy habitats on the backside of small sand bars). The increased richness and abundance suggests a small-scale movement of fishes parallel to the beach face as fishes seek sheltered runnel habitats. This study suggests that some fishes are able to utilize the shallow surf-zone, perhaps to minimize predator encounters and/or take advantage of an under-utilized intertidal food source.

3.2 Introduction

Many of the fishes and macro-crustaceans that comprise ocean surf-zone faunal assemblages are larval and juvenile individuals that use the shallow water as a nursery habitat (Warfel and Merriman, 1944; Gibson, 1973; Guillen and Landry, 1980; Modde, 1980; Modde and Ross, 1980; Lasiak, 1981, 1983, 1986; Robertson and Lenanton, 1984; Ruple, 1984; Senta and Kinoshita, 1985; Ross *et al.,* 1987; Wright, 1988; Gibson *et al.,* 1993; Santos and Nash, 1995; Clark *et al.*, 1996b). Such near-shore shallow water habitats are beneficial to juvenile fishes as refugia from aquatic predators or they may provide potential foraging areas. For example, in east coast salt marshes, fishes [e.g. mummichogs (*Fundulus heteroclitus*) and spotfin killifish (*Fundulus luciae*)] and invertebrates [grass shrimp (*Palaemonetes pugio*)] have been shown to utilize the shallow water on the marsh surface in order to minimize encounters with aquatic predators or to take advantage of an under-utilized food resource (Weisberg and Lotrich, 1982; Kneib, 1984; Talbot and Able, 1984; Kneib, 1986; Smith and Able, 1994; Yozzo, *et al.*, 1994; Kneib, 1997). If the distribution of fishes in the surf-zone likewise is determined by these factors, it is a logical hypothesis that these organisms should move into the shallowest water possible, given their species-specific size and/or morphological adaptations.

Despite the potential importance of the shallow surf-zone as a habitat for fishes, previous surf ichthyofaunal studies have usually examined fish assemblages in water 0.4 m and deeper; very few have focused on the fishes that utilize water less than 0.4 m. Harvey (1998) specifically examined the shallowest waters on a sandy beach of Sapelo Island, Georgia, and was able to demonstrate that the striped killifish, *Fundulus majalis,* exhibits a clear preference for runnel habitats (isolated troughs of water behind small sand bars). However, his sampling was both temporally (i.e. one week) and spatially (i.e. one site on one beach) constrained. Santos and Nash (1995), Abou-Seedo (1990), and Peters and Nelson (1987) included water less than 0.4 m deep in their analyses, but in each study the authors seined perpendicularly to the shoreline, thereby integrating fish collections over a broad range of depths. The focus of this study was exclusively on the waters shallower than 0.4 m in order to elucidate fish assemblage structure and dynamics of the fishes that utilize the shallow surf-zone on the Virginia barrier islands.

Previous authors have extensively described the invertebrate assemblages of United States east coast beaches (Anderson, 1977; Leber, 1982; McDermott, 1983), but similar comprehensive ichthyofaunal analyses have not been conducted. McDermott (1983), in New Jersey, and DeLancey (1989), in South Carolina, focused primarily on the food web relationships of shallow surf-zone fishes. The most common fish species were found to be either planktivores [Atlantic silverside (*Menidia menidia*), Anchovies (*Anchoa* sp.)], benthic invertivores (Gulf kingfish (*Menticirrhus littoralis*), Florida pompano (*Trachinotus carolinus*)] or benthic omnivores/detritivores [White mullet (*Mugil curema*)]. Peters and Nelson (1987) and Peters (1984) have reported that a similar low diversity fish assemblage is found in the surf-zone on the east coast of Florida.

The objective of this study was to conduct an in-depth analysis of the Virginia barrier island surf, focusing on fish assemblage structure and dynamics in water shallower than 0.4 m. The dynamics of the fish assemblages are described with respect to three temporal scales: (1) seasonal, (2) diel, and (3) tidal. In addition, spatial assemblage structure variation was examined on two scales: (1) small scale spatial differences between exposed sites and adjacent runnel habitats, and (2) large scale variations among island sites.

3.3 Materials and Methods

3.3.1 Study Site

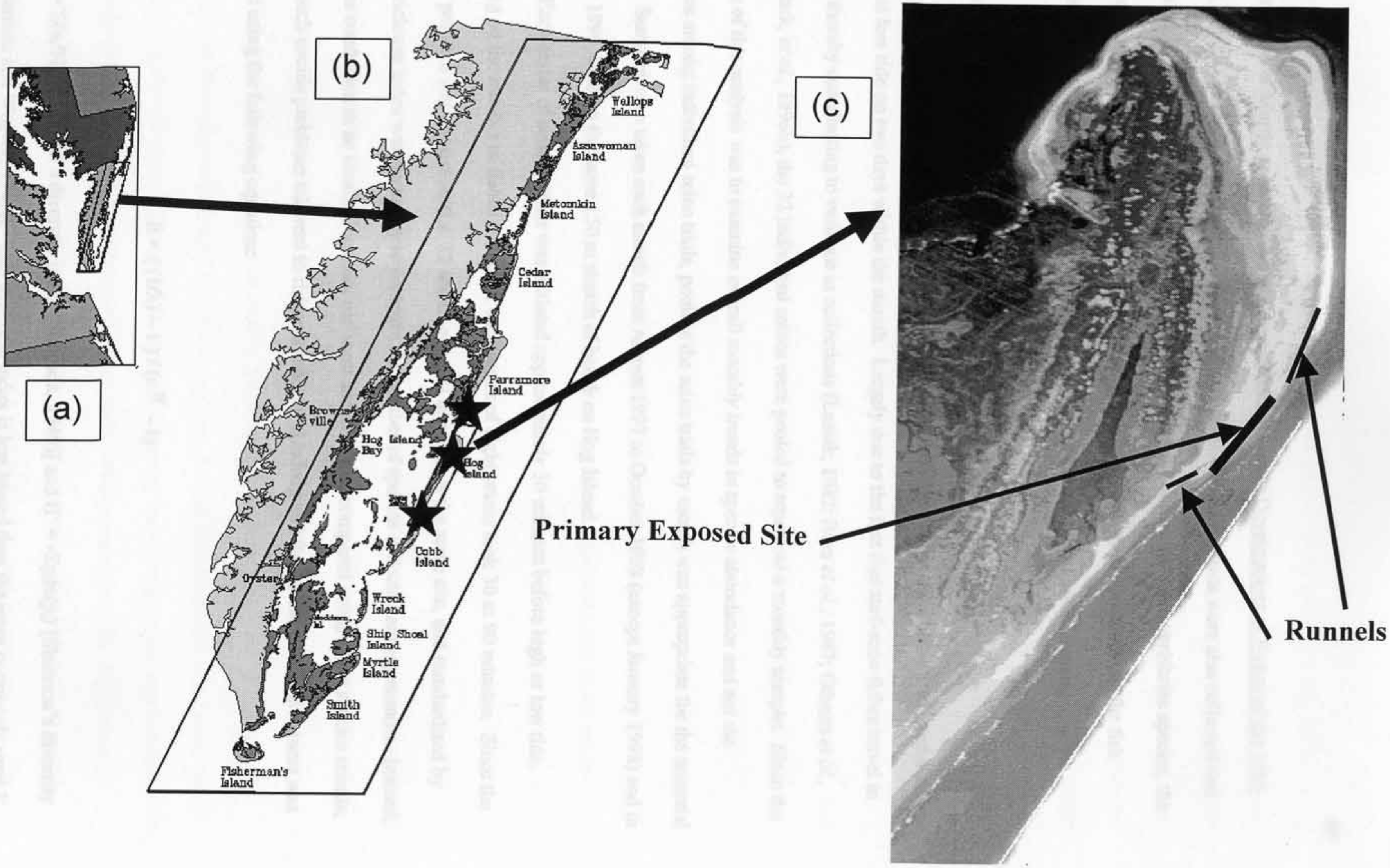
The study took place at the Virginia barrier islands, part of the Virginia Coast Reserve Long-Term Ecological Research Site (Figure 3.1). The main North Hog sampling location was an exposed beach site with no offshore sandbars. This site was characterized by moderate to heavy wave action (waves typically exceed 1 m in height), no permanent macrofaunal burrows within the intertidal zone, a rather wide surf-zone, presence of relatively deep reduced sediment layers, and intermediate beach particle size. Based on the classification system of McLachlan (1980), the North Hog Island Site is rated 12 [assessed from data collected by Harris (1988) and Layman (*unpubl. data*)] and falls within the range of beaches described as "moderately exposed". Salinity in the Hog Island surf-zone ranged from 32 to 36 ppt during the study period.

3.3.2 General Shallow Surf-Zone Sampling Protocol

The portion of the surf-zone examined here will be referred to as the "shallow surf-zone", the area of the surf immediately adjacent to the beach that is less than 0.4 m deep. All collections were made with a seine 8 m long and 1.5 m deep, with a 1 m square bag and 0.48 cm mesh throughout. For each individual seine trial, the net was pulled by two persons through the shallow swash area parallel to the beach face. The person farthest from the beach face dragged the seine at a depth of approximately 0.4 m (estimated at the troughs of passing waves). The second person pulled the net along the beach face at the edge of the shoreline. This protocol resulted in an average seining depth of approximately 0.2 m. This depth varied as waves passed, but multiple (up to 32) individual seine trials were taken on each sampling date in an attempt to minimize overall variations in depth across sampling dates or locations.

For each seine trial the net was pulled 15 m along the beach into the prevailing longshore current. The next seine trial within each series was conducted 5 m further up the beach, so that each individual seine sampled a different section of the shallow surf. Each individual seine was estimated to have swept an approximate area of 120 m^2. All fishes were identified and enumerated in the field and then held in an aerated holding bucket until all seines at a sampling site or time were completed; this ensured that no individuals were captured more than once in a set of seines. Adult fishes were identified based on

Figure 3.1. The (a) Delmarva Peninsula, (b) Virginia Coast Reserve Long-Term Ecological Research Site, and (c) the north end of Hog Island. The three sampling locations are designated by a ★ on map (b). At our main sampling site on the north end of Hog Island, the exposed sampling location and adjacent runnel sites are indicated.



the descriptions of Murdy *et al.* (1997) and juveniles using the text Development of Fishes of the Mid-Atlantic Bight. (Chesapeake Biological Laboratory, 1978). Macro-crustaceans were also collected and enumerated, but since the seining technique was effective sampling only certain invertebrate species, the number of crustaceans collected was rather low. Therefore, analyses focused primarily on the fish collections. Temperature was recorded with each sample using a YSI model 30 SCT meter.

3.3.3 Seasonal Analysis

Each monthly sample consisted of a series of eight individual seine trials at high tide and a series of eight at low tide on two days within the month. Largely due to the fact that surf-zone fishes travel in schools, thereby contributing to variance in collections (Lasiak, 1982; Ross *et al.*, 1987; Gibson *et al.*, 1993; Clark, *et al.*, 1996b), the 32 individual seines were pooled to represent a monthly sample. Since the objective of this analysis was to examine overall monthly trends in species abundance and not the differences among individual seine trials, pooling the seine trials by month was appropriate for the seasonal analysis. Samples were taken each month from August 1997 to October 1998 (except January 1998) and in February 1999, each on the same 150 m stretch of beach on Hog Island.

Each series of seining trials was initiated approximately 30 minutes before high or low tide. Depending on the number of fishes collected, each series of eight seines took 30 to 90 minutes. Since the sampling protocol was consistent (i.e. 32 seines of equal distance, at the same site, and standardized by tide), no richness index was necessary to compare the number of species collected among months. Instead, collections conducted in an identical manner can most accurately be compared using direct species counts; this approach avoids problems inherent to richness indexes (Ludwig and Reynolds, 1988). Evenness was calculated using the following equation:

$$E = ((1/\lambda) - 1) / (e^{H'} - 1)$$

where $\lambda = \Sigma(n_i/N)^2$ [Simpson's diversity index (Simpson, 1949)] and $H' = -\Sigma p_i \ln(p_i)$ [Shannon's diversity index (Shannon and Weaver, 1949)]. This evenness index is less biased than the more commonly used J' of Pielou (1975, 1977) because it is independent of sample richness (Ludwig and Reynolds, 1988). Clark *et al.* (1996b) suggest that seasonal fluctuations in surf faunal abundance is especially important on beaches in which temperature change exceeds 20 °C annually, a criterion that is met in our study. In order to elucidate this potential relationship between temperature and fish abundance in the shallow surf, species richness, total number of individuals, and eveness were regressed against the average monthly temperature. Additionally, in June, July and August, the three most common fish species were measured for total length.

3.3.4 Day/Night Analysis

For day/night comparisons, sampling was conducted on three nights: July 7/8, July 30/31, and August 12/13. Over the three nights, eight series of samples were collected. Each series of samples consisted of eight consecutive seine trials, as is described in the monthly sampling protocol. Each series of seines was compared to a set of daytime seines conducted at the identical tide on the previous day.

3.3.5 Tidal Analysis

Comparisons between high and low tide fish collections were made using the seasonal data. Within a month, the sixteen high and sixteen low tide seines were pooled and compared in a pairwise fashion.

3.3.6 Runnel Analysis

Small-scale spatial variations in fish assemblage structure were analyzed by comparing collections at the north Hog Island site to those in shielded "runnel" habitats (Komar, 1998). The width and depth of the runnels, as well as the height of the shielding sand bar, varied considerably due to tidal conditions, recent sediment transport, and various other factors. Unlike the study of Harvey (1998), we sampled runnels that were not completely isolated from wave exposure, for example at high tide when small waves moved across the bar and through the runnel. Even so, during every runnel sample there was a clear bar that dissipated wave energy and the runnel itself was always a well-formed depression. Eight seine collections at the main North Hog site were compared with eight seine collections in one of two runnel habitats immediately adjacent to the exposed site (runnels were within 100 m of the exposed site). Each series of seines were taken at random times within the tidal cycle, but the eight paired runnel seines and exposed site seines were always taken consecutively. The seine was deployed in the same manner at the runnels and at the exposed site.

3.3.7 Inter-Island Analysis

In order to evaluate the structure of fish assemblages at different locations on the Virginia barrier islands, two additional sites were sampled (the southern end of Hog Island and Parramore Island) in July and August, 1999 (See Figure 3.1). All three locations were exposed beach sites with similar wave energy, surf-zone width, beach slope and particle size. Thirty-two seines were taken each month at these sites, following the collection protocol used in the monthly sampling.

3.3.8 Sampling Efficiency

Earlier studies have discussed the effect that net efficiency can have on beach seine collections (Gulland, 1983; Lasiak, 1984a; Lyons, 1986; Nash, 1986; Parsley *et al.,* 1989; Pierce *et al.*, 1990; Romer, 1990; Monteiro-Neto and Musick, 1994; Nash *et al.*, 1994; Lamberth *et al.*, 1995). In this study, net collection efficiency may have been slightly lower in the turbulent water of the exposed beach site than in the calm runnel water, despite a focused effort to minimize among site sampling variations. Conversely, fishes may be more likely to detect and avoid the net in the calm water. Similarly, earlier studies have debated the validity of making direct day and night collection comparisons (e.g. Horn, 1980; Nash 1986; Wright, 1989; Gibson, *et al.,* 1996). In an attempt to minimize these sampling problems, numerous individual samples were taken at a given site or sampling time (a minimum of 16 individual seines for any particular comparison).

3.3.9 Statistical Analyses

All data sets used in univariate tests (comparing species richness, total number of individuals, or fish lengths among months, site, day/night or high/low tide samples) which met assumptions of normality and homegeneity of variance were compared using analysis of variance (ANOVA), or with paired t-tests when data were collected in paired fashion. Comparisons which did not meet variance or distributional assumptions were carried out with the Kruskal-Wallis (multiple comparisons) or Wilcoxon Signed Rank (paired comparisons) non-parametric tests. There is much concern over the "experimentwise" error rate when multiple comparisons are made within a given study; however, the objective of this study was to make a series of individual comparisons. For example, day/night and runnel/exposed site analyses are considered separately. Therefore, significance of each experiment was evaluated at the 0.05 level following the precedent set by Carmen and Walker (1982) and Soto and Hurlbert (1991). All univariate statistical analyses were conducted with Sigma Stat statistical software (1997).

For analyses in which sufficient samples were available (seasonal, day/night, and exposed/runnel comparisons), the multidimensional scaling (MDS) technique proposed by Field *et al.* (1982), Clarke (1993), and Clarke and Ainsworth (1993) also was used to compare fish assemblage structure. Such a multivariate technique is useful in determining if distinct fish assemblages are identifiable at a given site or time. The benefit of this technique relative to other multivariate approaches (e.g. principal co-ordinates or correspondence analysis) is that dissimilarity matrices, not eigenvalues, are used to construct ordination plots (Field *et al.*, 1985).

In all multivariate analyses in this study, fish abundances were first root-root transformed in order to decrease the influence of the most abundant species (Clarke and Green, 1988). Similarity matrices were calculated using the Bray-Curtis similarity index (Bray and Curtis, 1957). Ordination plots based on these pairwise similarities were constructed by the MDS technique using the SPSS statistical software package. Stress values, a measure of the distortion caused by compressing the sample distances into a 2-dimensional "map", are reported for each of the plots. Low values indicate the "map" well represents the actual distances among points. The stress values of the MDS plots presented here (0.11 and 0.14) are relatively low, and the plots are good representations of the actual similarity among points on the graph. Since the scale of the axes in the ordination plots are arbitrary, they are not labeled.

3.4 Results

3.4.1 Seasonal Analysis

A low diversity fish assemblage utilizes the shallow surf-zone on the Virginia barrier islands. At the main North Hog sampling site, three species rough silverside (*M. martinica*), gulf kingfish (*M. littoralis*), and Florida pompano (*T. carolinus*) accounted for 94 % of all individuals collected. The seven most common species accounted for 99.9% of all individuals collected (Table 3.1). *M. martinica* was the most commonly collected fish species (51% of all individuals). There was a distinct seasonal trend in species richness and abundance (Figure 3.2). The majority of fishes were collected June through October, with the largest collection in August 1998 (1378 total fish; estimated density = 0.36 fish/m^2). Fish species richness was highest in the summer and early fall. The lowest species richness and overall fish abundance occurred during the winter and spring. Species eveness was also at a minimum during winter months. Seasonal abundance trends were further supported by distinct positive correlations of species richness, total number of individuals and eveness with temperature (Figure 3.3). Both richness ($R^2 = 0.54$; $p = 0.002$) and total number of individuals ($R^2 = 0.51$; $p = 0.003$) were found to be significantly correlated with temperature.

A MDS ordination plot (Figure 3.4) revealed distinct groupings of the monthly fish samples. All of the winter and spring samples fall within a well-defined group; each of these months is characterized by low species richness and low overall fish abundance. A second major grouping corresponds to the late summer and early fall samples (August through October) in which fish species richness and abundance are high. The June sample is differentiated by the fact that overall abundance was rather low, but species richness was characteristic of the summer months. The July and November samples are differentiated in ordination space because of the presence of species that were not captured in other months.

The length distribution plots highlight that the majority of fishes were relatively small individuals, almost all of which were less than 100 mm in total length (Figure 3.5). There was a clear trend of increasing size from the early to late summer. This trend was most pronounced for *T. carolinus,* which had an average size of 22.7 mm in June and 90.1 mm in August. The average length of *M. littoralis* decreased slightly from July to August, but both months had a significantly higher mean length than June. In fact, for

Table 3.1. The total number of individuals captured in 32 seines conducted each month at the main exposed beach site on Hog Island, Virginia from August 1997 to February 1999. Density is expressed as number of fish/m^2. Species abbreviations are as follows: *Membras martinica* = Mm; *Menticirrhus littoralis* = Ml; *Trachinotus carolinus* = Tc; *Fundulus majalis* = Fm; *Mugil curema* = Mc; *Menticirrhus saxatilis* = Ms; *Cyprinodon variegatus* = Cv; *Fundulus heteroclitus* = Fh; *Sphyraena* sp. = Ssp.; *Sciaenops ocellatus* = So; *Paralichthys dentatus* = Pd; *Syngnathus fuscus* = Sf.

Month	Mm	Ml	Tc	Fm	Mc	Ms	Cv	Fh	Ssp.	So	Pd	Sf	Total	Average Density
Aug-97	419	372	31	34	-	9	3	-	-	-	-	1	869	0.226
Sep-97	14	528	2	6	4	16	-	-	-	-	-	-	570	0.148
Oct-97	145	260	4	7	-	7	-	-	-	-	-	-	424	0.110
Nov-97	40	15	-	4	2	2	20	-	-	2	-	-	83	0.022
Dec-97	12	-	-	-	-	-	-	-	-	-	-	-	12	0.003
Feb-98	18	-	-	-	-	-	-	-	-	-	-	-	18	0.005
Mar-98	104	-	-	-	3	-	-	-	-	2	-	-	107	0.028
Apr-98	141	-	-	-	17	-	-	-	-	-	-	-	158	0.041
May-98	46	-	-	-	2	-	-	-	-	-	-	-	48	0.013
Jun-98	17	-	5	1	12	-	2	-	-	-	-	-	37	0.010
Jul-98	340	17	249	1	30	2	1	3	1	-	1	3	643	0.167
Aug-98	1027	221	81	30	3	14	2	-	-	-	-	-	1378	0.359
Sep-98	2	118	14	3	-	2	-	-	-	-	-	-	139	0.036
Oct-98	10	84	5	1	-	-	-	-	-	-	-	-	100	0.026
Feb-99	19	-	-	-	2	-	-	-	-	-	-	-	21	0.006
Total	2354	1615	391	87	75	52	29	3	3	2	1	1	4607	
(%)	51	35	8	2	2	1	1	<1	<1	<1	<1	<1		

Figure 3.2. Fish and macro-crustacean species richness, number of fishes and macro-crustaceans, and fish assemblage evenness at the main sampling site on Hog Island over the 15 month study period. Richness is expressed as total number of species. Evenness was calculated using the index given in the methods section (Ludwig and Reynolds, 1988).

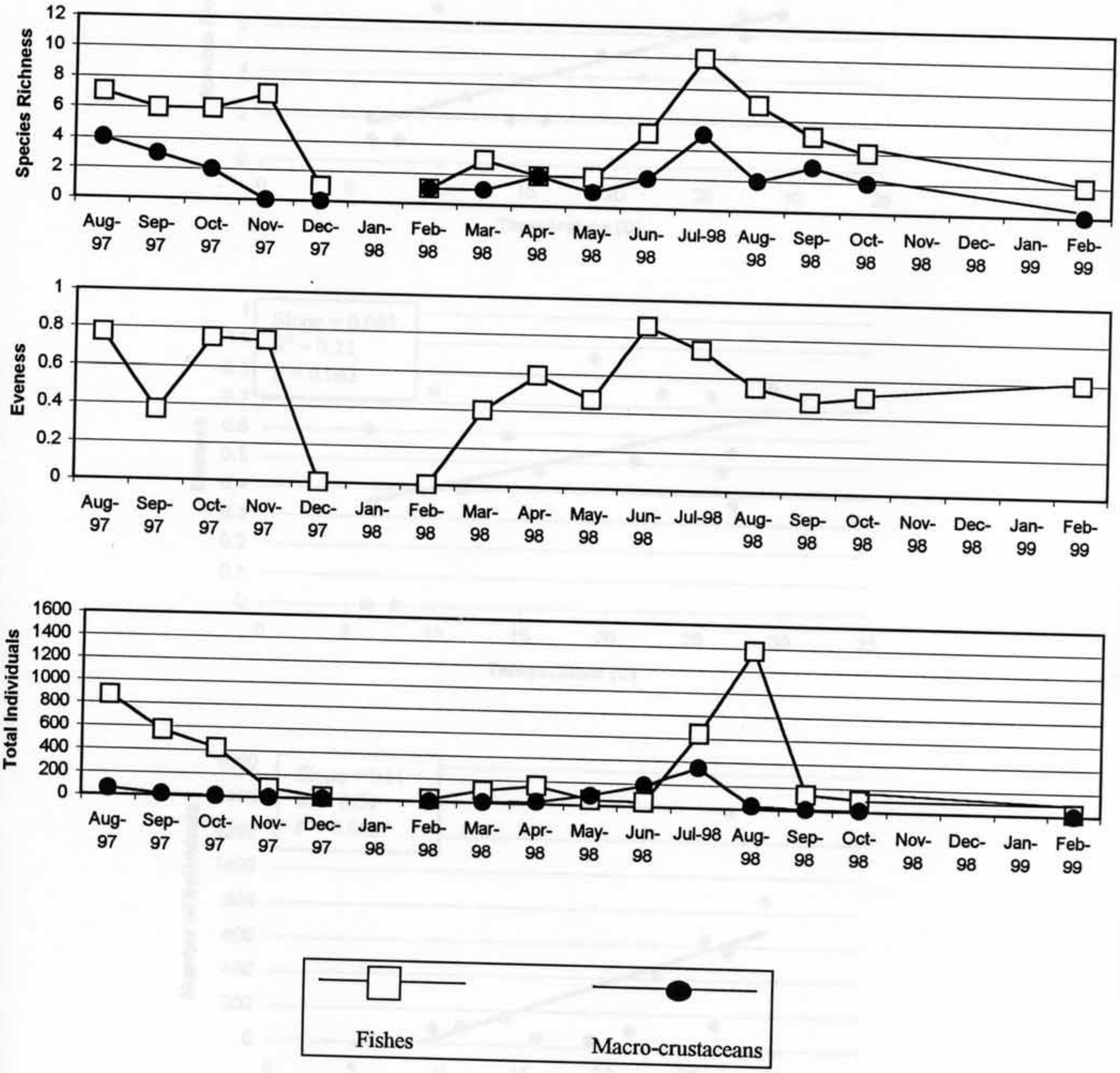


Figure 3.3. Fish species richness, evenness, and number of individuals regressed against temperature of the shallow surf-zone on the monthly sampling dates. Slopes of the lines, R-squared values and p-values are indicated on the plots. Significant regressions are indicated with a *.

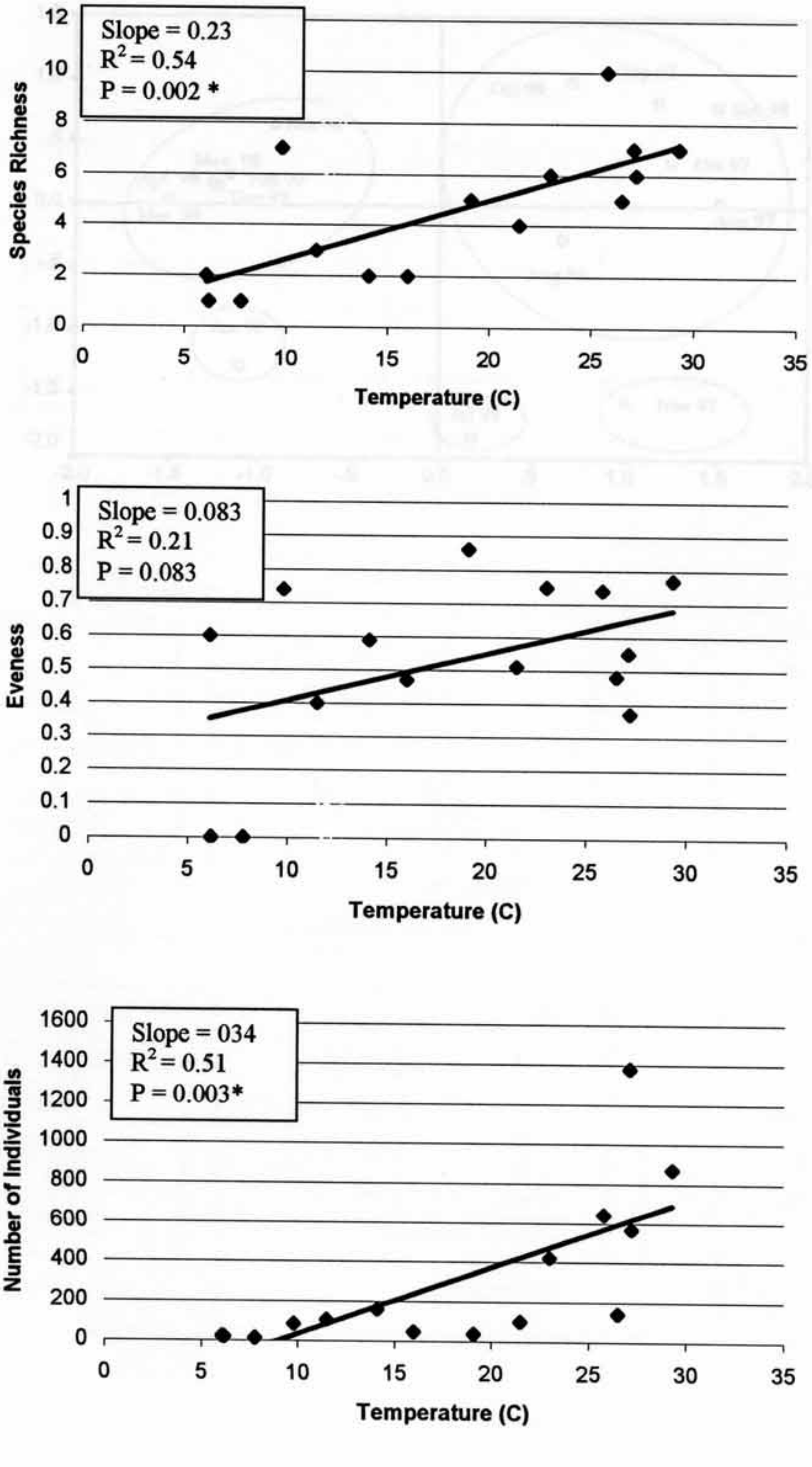


Figure 3.4. Multidimensional scaling ordination plot of the monthly fish collections at the main exposed Hog Island sampling location. Groups of samples are delineated at the 60% level of similarity. Stress of the plot = 0.11 (see description in results section).

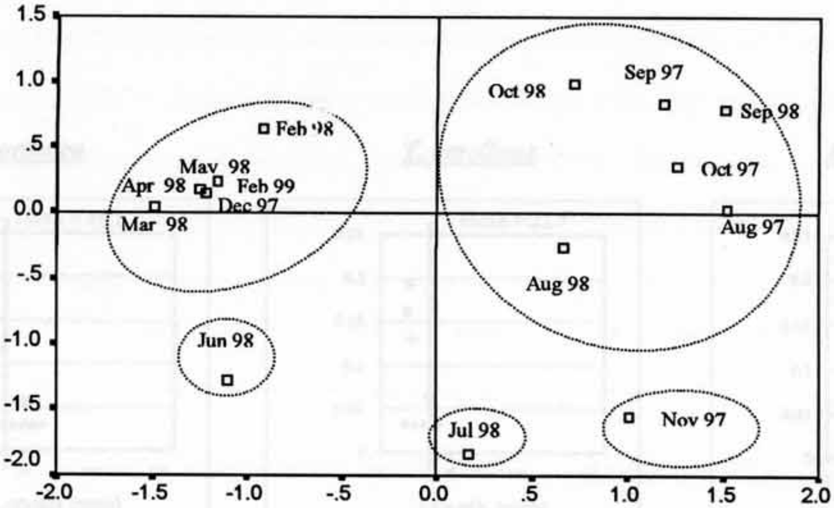
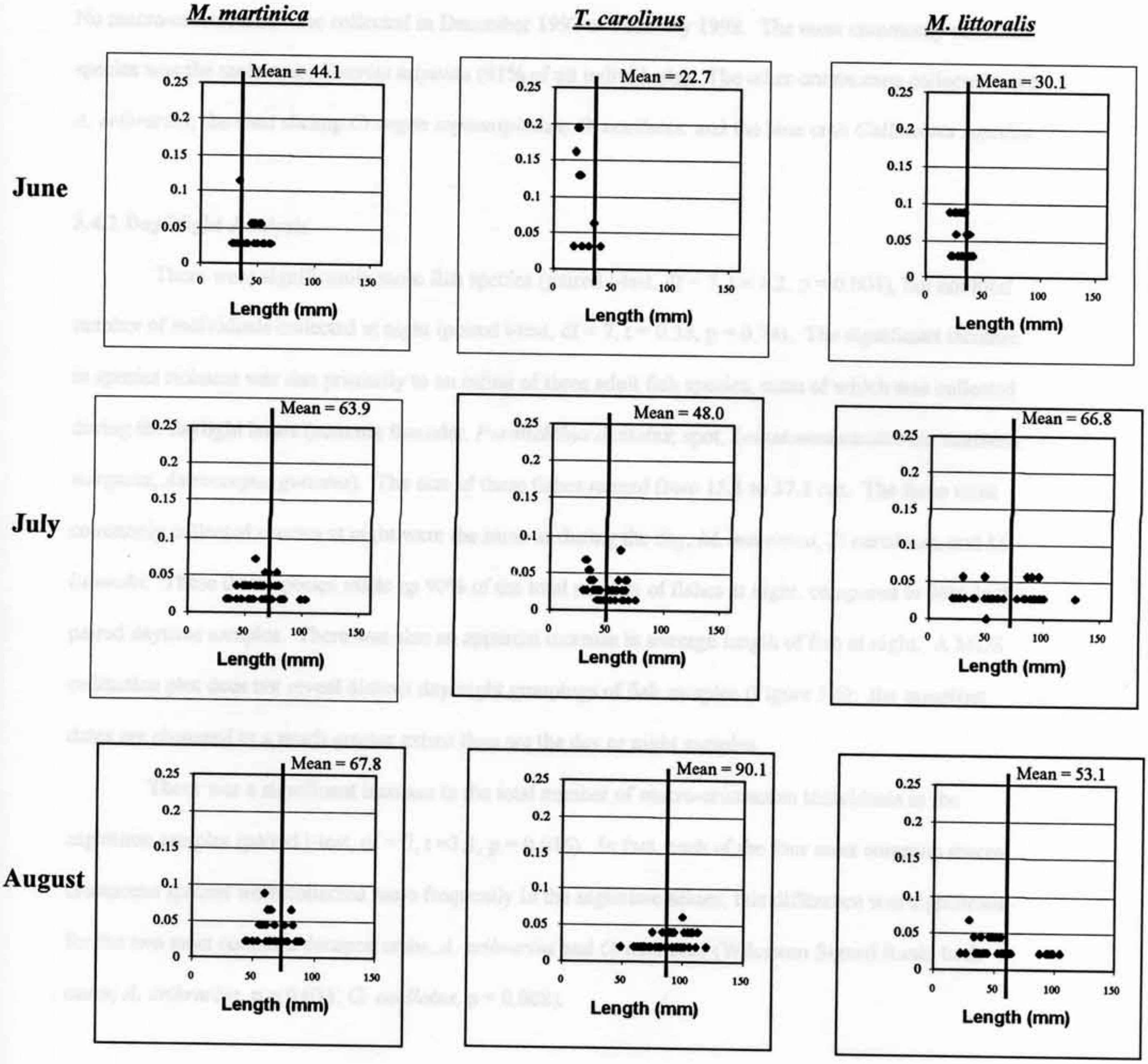


Figure 3.5. Length frequency histograms of the three most common fish species in June, July, and August. The y-axis in each graph represents the relative proportion of individuals of the given length. The vertical bars represent the mean fish length of that species for the indicated month (mm).



the three most commonly collected species, there was a significant difference in the mean length among months (*M. martinica*, ANOVA, $F_{2,134} = 38.8$; *T. carolinus*, Kruskal-Wallis, df = 2, H = 119.2; *M. littoralis*, Kruskal-Wallis, df = 2, H = 45.2; $p < 0.001$ for all cases). The same pattern of increasing average size over the summer was apparent for the two most common decapod crab species, the speckled crab, *Arenaeus cribrarius*, and lady crab, *Ovalipes ocellatus*.

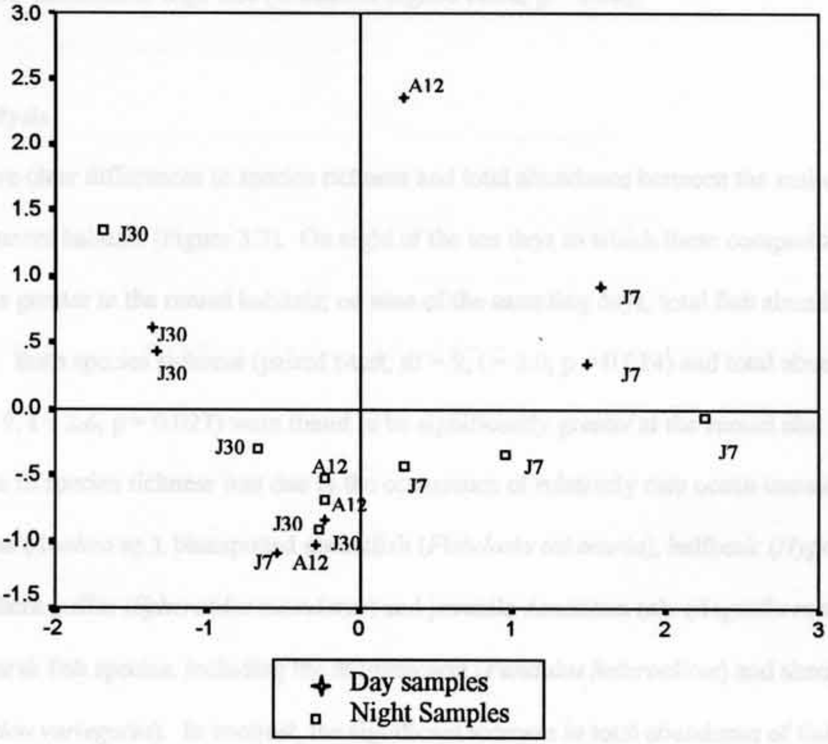
The overall abundance and richness of macro-crustaceans followed seasonal patterns very similar to that of the fishes (Figure 3.2). Abundance and richness peaked in July 1998 (350 individuals; 5 species). No macro-crustaceans were collected in December 1997 or February 1998. The most commonly collected species was the mole crab, *Emerita talpoida* (91% of all individuals). The other crustaceans collected were *A. cribrarius*, the sand shrimp *Crangon septemspinosa*, *O. ocellatus*, and the blue crab *Callinectes sapidus*.

3.4.2 Day/Night Analysis

There were significantly more fish species (paired t-test, df = 7, t = 4.2, p = 0.004), but not total number of individuals collected at night (paired t-test, df = 7, t = 0.35, p = 0.74). The significant increase in species richness was due primarily to an influx of three adult fish species, none of which was collected during the daylight hours (summer flounder, *Paralichthys dentatus*; spot, *Leiostomus xanthurus;* northern stargazer, *Astroscopus guttatus*). The size of these fishes ranged from 15.1 to 37.1 cm. The three most commonly collected species at night were the same as during the day, *M. martinica*, *T. carolinus*, and *M. littoralis*. These three species made up 90% of the total number of fishes at night, compared to 98% in the paired daytime samples. There was also an apparent increase in average length of fish at night. A MDS ordination plot does not reveal distinct day/night groupings of fish samples (Figure 3.6); the sampling dates are clustered to a much greater extent than are the day or night samples.

There was a significant increase in the total number of macro-crustacean individuals in the nighttime samples (paired t-test, df = 7, t =3.1, p = 0.016). In fact, each of the four most common macro-crustacean species were collected more frequently in the nighttime seines; this difference was significant for the two most common decapod crabs, *A. cribrarius* and *O. ocellatus* (Wilcoxon Signed Rank, both cases; *A. cribrarius*, p = 0.031; *O. ocellatus*, p = 0.008).

Figure 3.6. The multidimensional scaling ordination plot of the sixteen day/night sampling data sets. The dates of sampling are abbreviated as follows: July7/8 = J7, July 30/31 = J30, and August 12/13 = A12. Stress of the plot = 0.14 (see description in results section)..



3.4.3 Tidal Analysis

For both high and low tide samples, richness peaked in the summer or early fall and declined to a single species in the winter (Table 3.2). Species richness was significantly greater at high tide (paired t-test, df = 14, t = 3.86, p = 0.002), although there was no significant difference between the total number of individuals collected (paired t-test, df = 14, t = 1.24, p = 0.23). Regarding specific species, *T. carolinus* was more commonly collected at high tide (Wilcoxon Signed Rank, p = 0.02).

3.4.4 Runnel Analysis

There were clear differences in species richness and total abundance between the main North Hog site and adjacent runnel habitats (Figure 3.7). On eight of the ten days in which these comparisons were made, richness was greater in the runnel habitats; on nine of the sampling days, total fish abundance in the runnel was higher. Both species richness (paired t-test, df = 9, t = 3.0, p = 0.014) and total abundance (paired t-test, df = 9, t = 2.6, p = 0.027) were found to be significantly greater at the runnel site. The significant increase in species richness was due to the occurrence of relatively rare ocean transient species including anchovies (*Anchoa* sp.), bluespotted cornetfish (*Fistularia tabacaria*), halfbeak (*Hyporhamphus unifasciatus*), northern puffer (*Spheroides maculatus*) and juvenile American eels (*Anguilla rostrata*), as well as resident marsh fish species, including the mummichog (*Fundulus heteroclitus*) and sheepshead minnow (*Cyprinodon variegatus*). In contrast, the significant increase in total abundance of fishes was due to extremely large collections of the three most common shallow surf residents, *M. martinica, M. littoralis,* and *T. carolinus*. Despite the clear trends in univariate statistical analyses, there were no distinct groupings of the exposed and runnel sites in MDS space (Figure 3.8). This suggests that although the richness and abundance of fishes on a given day will typically be higher in the runnel than at an adjacent exposed beach site, the assemblage of species is not predictable from day to day.

Table 3.2. Fish species richness, total number of individuals, and number of the three most common species at high and low tide. These data are compiled from the monthly seining samples in which 8 seines were conducted at high tide and 8 at low tide on two days during the month of interest. The high and low tide data were compared with a paired t-test and resulting p-values are given at the bottom of the table. Significant results are designated with an asterisk. Abbreviations are as follows: *Membras martinica*, Mm; *Menticirrhus littoralis*, Ml; *Trachinotus carolinus*, Tc.

Month	Richness		Total Individuals		Mm		Ml		Tc	
Tide	H	L	H	L	H	L	H	L	H	L
Aug- 97	7	3	351	518	39	380	238	134	31	0
Sep-97	6	3	262	308	14	0	229	299	2	0
Oct-97	6	4	247	177	23	122	121	48	4	0
Nov-97	7	5	34	51	7	33	2	13	0	0
Dec-97	0	1	0	12	0	12	0	0	0	0
Feb-98	1	1	6	12	6	12	0	0	0	0
Mar-98	3	1	67	42	62	42	0	0	0	0
Apr-98	2	2	49	109	41	100	0	0	0	0
May-98	2	1	26	22	24	22	0	0	0	0
Jun-98	5	3	13	0	6	11	0	0	2	3
Jul-98	8	6	320	325	30	310	8	9	248	1
Aug-98	7	4	452	926	185	842	161	60	64	17
Sep-98	4	4	114	25	0	2	98	20	12	2
Oct-98	4	3	23	77	7	3	12	72	3	2
Feb-99	2	2	10	11	9	10	0	0	0	0
P-values	.0002 *		.67		.06		.25		.03*	

Figure 3.7. Fish species richness and number of individuals collected in paired runnel and exposed site analyses. Each comparison was made on a different date in July at various times within the tidal cycle. Series of runnel and exposed seine trials were taken consecutively.

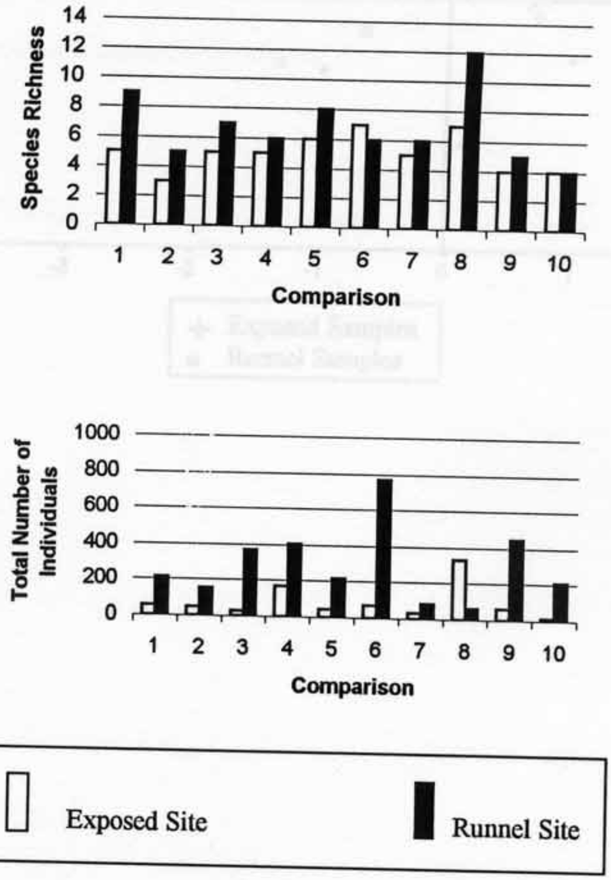
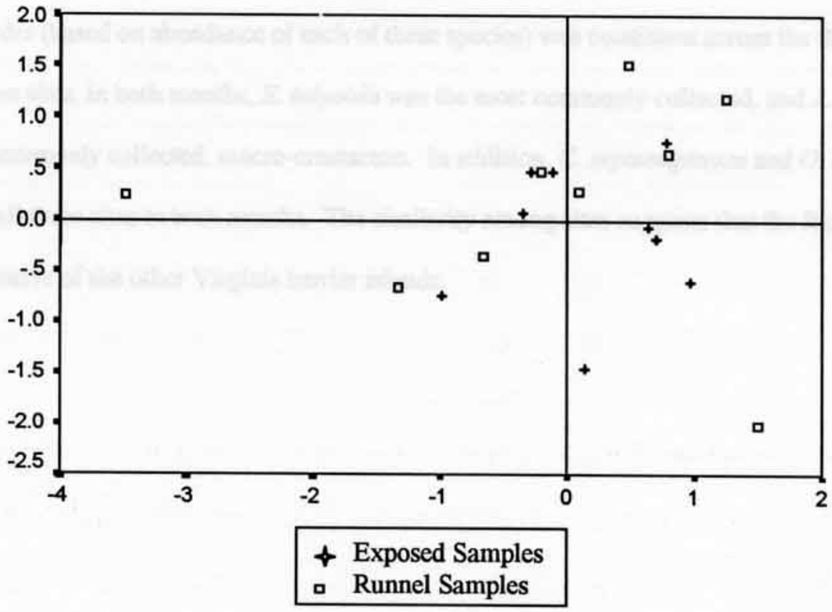


Figure 3.8. The multidimensional scaling ordination plot of samples taken at exposed sites and adjacent runnel habitats during July. Stress of the plot = 0.14 (see description in results section)..



3.4.5 Inter-Island Analysis

M. martinica, T. carolinus and *M. littoralis* were the three most commonly collected fish species at the North Hog, South Hog, and Parramore sites during both July and August (Table 3.3). During each month the rank order (based on abundance of each of these species) was consistent across the three sites. At each of the three sites, in both months, *E. talpoida* was the most commonly collected, and *A. cribrarius* the second most commonly collected, macro-crustacean. In addition, *C. septemspinosa* and *O. ocellatus* were collected at all three sites in both months. The similarity among sites suggests that the fauna of Hog Island is representative of the other Virginia barrier islands.

Table 3.3. Percent composition of fishes collected at the sites on the north end of Hog Island, south end of Hog Island, and on Parramore Island in July and August 1998.

	July			August		
	North	South	Parramore	North	South	Parramore
M. martinica	51	44	80	75	51	51
T. carolinus	37	27	13	6	10	6
M. littoralis	6	24	6	15	36	42
M. curema	4	-	-	<1	-	-
F. majalis	<1	-	-	-	2	2
C. varieagtus	<1	<1	-	<1	-	-
M. saxatilis	<1	<1	<1	<1	<1	<1
Sphyraena sp.	<1	-	-	-	-	-
F. heteroclitus	<1	<1	-	-	-	-
P. dentatus	<1	-	-	-	-	-

3.6 Discussion

The most common species of the shallow surf-zone on Hog Island are very similar to those reported in other studies of U.S. east coast beaches. In the surf of Sapelo Island, Georgia (Harvey, 1998), and on Folly Beach, South Carolina (DeLancey, 1989), the fish assemblages are dominated by *M. menidia, T. carolinus, M. littoralis, F. majalis,* and *Anchoa* sp. On an Avalon, New Jersey beach, *M. menidia* alone accounted for over 85% of all fishes collected (McDermott, 1983). Here, *M. martinica* was found to be much more common than *M. menidia.* This discrepancy is likely due to the difficulties in identifying the two species, and not due to a distinct difference in species composition among sites. Likewise, the macro-crustaceans were similar to those reported on a North Carolina beach (Leber, 1982) and a New Jersey beach (McDermott, 1983). *E. talpoida* was found to be the most common macro-crustacean at each of these locations (Leber, 1982; McDermott, 1983). These same studies reported the decapods *A. cribrarius* and *O. ocellatus,* the two most commonly collected crab species in this study, to be prevalent as well.

The number of fish species collected in the shallow surf-zone on Hog Island (25) is below the range (26 to 71) reported in previous surf-zone ichthyofaunal studies (Brown and McLachlan, 1990). Importantly, only seven species accounted for 99% of all fishes collected. Although surf-zone habitats are typically dominated by relatively few species (Lasiak, 1984; Ross *et al.*, 1987; Brown and MacLachlan, 1990; Romer 1990), the shallow surf-zone was even more species poor. Very few species are able to utilize the turbulent, shallow water. The species that were found in the shallow surf-zone can be classified into one of five life-history categories (Table 3.4): seasonal nursery juveniles, adult transients, year-round residents, seasonal or nocturnal migrants, and marsh pond residents. The majority of the species collected in this study were either seasonal juveniles that utilize the shallow waters as a nursery area or transient residents that are more much common in other marine habitats. These fishes are typically invertivores or planktivores, and are common in the shallow surf-zone during the warmer months of the year. Only two species, *M. martinica* and *M. curema,* were year-round residents. Other adult marine

Table 3.4. List of species captured in the shallow swash zone of Hog Island during sampling conducted from August 1997 until February 1999. Each species is classified according to site (s) of capture, time of capture, life history, and trophic level. Trophic level classifications (for the age class of fish which we specifically collected) are based on the descriptions of Murdy *et al.* (1997). *Site*: E = exposed; R = runnel; B = Both. *Time:* D = Day; N = Night; B = Both. *Life history*: R = year-round resident; J = seasonal nursery juvenile; S = seasonal adults; M = island marsh pond resident; T = adult transient common in other marine habitats. *Trophic level*: P = planktivore; W = water column macroinvertebrates; I = benthic invertivore; F = piscivore; A = algavore; D = detritivore.

Scientific Name	Common Name	Site	Time	Life History	Trophic Level
Fish species					
Anchoa sp.	Anchovy species	R	B	J	P
Anguilla rostrata	American eel	R	D	J	P/I
Astroscopus guttatus	Northern stargazer	E	N	T	F
Brevoortia tyrannus	Atlantic menhaden	R	D	J	P
Caranx hippos	Crevalle Jack	R	D	J	I/W
Cyprinodon varieagtus	Sheepshead minnow	B	B	M	A
Fistularia tabacaria	Bluespotted cornetfish	R	D	T	W/F
Fundulus heteroclitus	Common mummichog	B	B	M	I/W/D
Fundulus majalis	Striped killifish	B	B	T	I/W
Hyporhamphus unifasciatus	Halfbeak	R	D	T	W/F
Leiostomus xanthurus	Spot	B	N	T	I/F
Membras martinica	Rough silverside	B	B	Y	Z
Menidia menidia	Atlantic silverside	B	B	Y	Z

Menticirrhus saxatilis	Northern kingfish	B	B	J	I
Menticirrhus littoralis	Gulf kingfish	B	B	J	I
Mugil curema	White mullet	B	B	Y	A/D
Paralichthys dentatus	Summer flounder	B	B	J/T	W/F
Peprilus sp.	Butterfish	B	B	J	P/W
Psenes sp.	Driftfish	B	D	J	P/W
Sciaenops ocellatus	Red drum	E	D	T	F/I
Spheroides maculatus	Northern puffer	R	D	T	I
Sphyraena sp.	Barracuda species	B	B	J	W/F
Stongylura marina	Atlantic needlefish	B	D	T	W/F
Sygnathus fuscus	Northern pipefish	B	B	T	P/I
Trachinotus carolinus	Florida pompano	B	B	J	I/W
Other vertebrate					
Malaclemys terrapin	Diamondback terrapin	R	D	T	I/F
Macro-crustaceans					
Arenaeus cribrarius	Speckled crab	B	B	J	I/F/W/A
Callinectes sapidus	Blue crab	B	B	S/J	I/F/W/A
Crangon septemspinosa	Sand shrimp	B	B	S/J	D/P/I
Emerita talpoida	Mole crab	B	B	S	Z
Ovalipes ocellatus	Lady crab	B	B	S/J	I/F/W/A
Pagurus sp.	Hermit crabs	B	B	Y	I/D/A
Palaemonetes pugio	Common grass shrimp	B	B	M	D/P/I
Panopeus hebstii	Black-clawed mud crab	B	D	T	I/A

species occasionally moved into the shallows either at night (*L. xanthurus* and *P. dentatus*) or during a particular season (*S. ocellatus*). Finally, some of the fish species were residents of marsh ponds on the Virginia barrier islands. These fishes are swept into the ocean as the ponds periodically drain (Layman *et al.*, unpubl. data).

The majority of species utilize the shallow surf during the summer and early fall and then migrate to deeper waters during cooler months, as has been reported previously (Gunter, 1945; McFarland, 1963; Modde and Ross, 1981; Guillen and Landry, 1982; Leber, 1982; Lasiak, 1984b; Peters, 1984; Peters and Nelson, 1987;Ross *et al.*, 1987; Santos and Nash, 1995; Clark, *et al.*, 1996b). This seasonal migration is supported by the strong relationship between species abundance and average monthly temperature. Although not directly demonstrated here, it seems likely that temperature either directly, or indirectly (i.e. by influencing the timing of spawning), is the underlying mechanism of seasonal shallow surf-zone abundance patterns.

MDS revealed no distinct grouping that would suggest distinct day and night fish assemblages. However, the univariate statistics clearly showed a significant increase in species richness at night. This agrees with other studies which have shown that the abundance of relatively rare species may increase at night, but the main changes in fish assemblage structure are due to variability of the most common fish species (Romer, 1990; Gibson *et al.*, 1996). Additionally, I was able to identify a significant trend of increased richness, as well as a significant trend in increased abundance of *T. carolinus,* in high tide samples. Gibson *et al.* (1998) identified three main reasons for such diel, tidal, or similar fish migrations: (1) foraging considerations, (2) predator avoidance, and (3) selection of suitable environmental conditions. The former two explanations are most likely in the shallow surf-zone. Nocturnal increases in species richness are related to the shoreward movements of piscivorous fishes at night, forcing prey fishes into shallower water (Girsa and Zhuravel, 1983; Brown and McLachlan, 1990; Ansell and Gibson, 1990; Gibson *et al.,* 1996). In contrast, tidal migrations within the shallow surf are likely related to the availability of food (Brown and McLachlan, 1990; Gibson *et al.,* 1996). High tides allow some fishes to move into the uppermost "zones" of intertidal invertebrate distributions, an area inaccessible to other fishes (Brown and McLachlan, 1990). This foraging explanation may explain the increased abundance of *T. carolinus*, a benthic invertivore (Armitage and Alevizon, 1980), at high tide. In contrast, fishes that do not migrate with tidal cycles may be utilizing food items that are available at various intertidal depths (e.g. the zooplanktivorous *M. martinica*), and their presence in the shallow surf-zone is primarily due to predator avoidance. Movements based on selection of optimal environmental conditions is unlikely, as the shallow surf-zone actually necessitates increased energy expense in order to maintain position and move freely in such a dynamic, turbulent area (Clark *et al,* 1996b).

Previous studies have made surf-zone wave exposure comparisons among sites separated by many hundreds of meters (Reynolds and Thompson, 1974; Hillman, 1977; Berghahn, 1986; Brown and McLachlan, 1990; Romer 1990; Pihl and van der Veer, 1992; Gibson, 1994; Clark *et al.*, 1994; Clark *et al.*, 1996a; Clark, 1997). One drawback of such large-scale comparisons is that many factors, including substrate type, sediment size, distance from potential sources of colonization, temperature, and presence of structure, likely vary among the sites. The present study minimized these spatial differences by examining the effects of wave exposure on a much smaller scale; fish assemblages were compared in runnel and exposed sites immediately adjacent to one another.

Due to variable collections of common species and the sporadic occurrence of relatively rare fish species, there was no distinct runnel fish assemblage identifiable in MDS space. However, the univariate statistical approaches reveal a very important trend in the data; both fish species richness and overall fish abundance were significantly higher in the runnels. This statistical result further substantiates the observations of Harvey (1998), who documented the preference of *F. majalis* for runnels. Overall the data suggest that even though there were not distinct runnel and non-runnel fish assemblages (i.e. assemblages varied more among days than between runnel and exposed sites on a single day), there were typically more species and a higher number of species in the runnels on any given day. This concentration of fishes in the runnels may be in direct response to decreased physical wave energy (Romer, 1990; Clark, *et al.*, 1996a), or an indirect effect resulting from turbidity preferences (Warfel and Merriman, 1944; Lasiak, 1984b; Clark, *et al.,* 1996a), avoidance of predation (Robertson and Lenanton, 1984; Gibson *et al.*, 1998; Harvey, 1998), increased food availability (DeLancey, 1989; Gibson *et al.*, 1998; Harvey, 1998), or the benefits of macrophyte/debris accumulation (Lenanton, 1982; Robertson and Lenanton, 1984; Peters and Nelson, 1987; Lenanton and Caputi, 1989).

A possible convergence of shallow surf-zone fishes into runnels emphasizes a much debated question in surf-zone assemblage ecology; what factors actually cause differences in fish assemblage structure among sites with varying levels of wave exposure? The shallow surf-zone may provide the ideal habitat in which this question can be evaluated. The abundance of runnel systems on many beaches (Komar, 1998) provides a natural experiment in which there is significant wave exposure variation among sites (i.e. runnel and exposed locations) in close proximity. Such close sampling locations helps minimize the influence of confounding variables inherent to spatial comparisons. Furthermore, the shallow surf-zone is more easily sampled (i.e. doesn't require use of a boat or extensive trawl system) and multiple samples can be taken in a short time period.

Earlier studies have documented the movement of fishes in and out of the surf-zone on seasonal, diel, or tidal cycles (Lasiak, 1984a,b; Peters, 1984; Senta and Kinoshita, 1985; Ross *et al.*, 1987; Wright, 1988, 1989; Abou-Seedo, 1990; Brown and McLachlan, 1990; Gibson *et al.*, 1993; Burrows *et al.*, 1994; Lamberth *et al.*, 1995; Santos and Nash, 1995; Clark *e tal.* 1996a,b; Gibson *et al,* 1996; Gibson *et al.*, 1998). These patterns can be considered *perpendicular* movements, toward or away from the beach. The present study has provided evidence that the same perpendicular movements occur in the shallow surf-zone. For example, this study clearly demonstrates the importance of seasonal movements in and out of the shallow water, due primarily to the influx of nursery juveniles during the summer months. Also important are perpendicular movements on diel and tidal cycles, as fish species richness increases at night and during high tide.

The results of this study also suggests that an additional movement might occur *parallel* to the beach face, as fishes move into or among preferred runnel habitats. The dynamic nature of the runnels themselves (due to tidal influences, shifting sediment, etc.) suggests that fish may undertake frequent small-scale movements seeking runnels that provide maximum benefit. A related observation was made by McLachlan and Hesp (1984) who suggested that fishes prefer lower energy bay habitats over high energy horn areas on beaches with distinct cusp morphology. Fishes may migrate parallel to the beach seeking bay habitats, much as they move into runnels in the shallow surf-zone. The result is a convergence of surf-zone residents and a distinct concentration of food web interactions (McLachlan and Hesp, 1984).

In conclusion, the shallow surf-zone is characterized by low species diversity, but may be a nursery area (or, in certain cases, a year-round habitat) for those species which are able to effectively utilize the shallow water. Some characteristics of the shallow surf reflect those reported for the overall surf-zone, including seasonal, tidal, and diel trends in richness and abundance. Of these temporal scales, seasonal movements seem to be the most important component of the shallow surf-zone fish dynamics. Additionally, fishes of the shallow surf demonstrate a preference for low energy runnel habitats. The mechanism underlying this phenomena remains unclear, but it may be the end result of small-scale movements parallel to the beach face.

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Chapter Four

Conclusions

The previous chapters provide a detailed analysis of the fish ecology of the Virginia barrier islands. Three important themes can be drawn from the results: (1) shallow-water, near-shore habitats are extremely difficult habitats in which to assess nekton assemblage structure and dynamics, (2) ecological change on the barrier islands occurs on short time scales, and (3) fish assemblage structure is determined by a complex series of mechanisms that act at a variety of scales, of which only small scale processes were directly examined in this thesis. Each of these themes will be considered separately below.

4.1 Sampling Difficulties

The sampling bias of minnow traps underscores the problems associated with elucidating trends in assemblage structure in coastal shallow water habitats. Such biases have been well documented in previous studies, most recently in Rozas and Minello (1997). These sampling biases are especially problematic in barrier island ponds because the size, shape, and characteristics of the ponds are changing due to geomorphological processes, rainfall, or many other factors. With each set of pond characteristics, there is an optimal technique that would minimize sampling bias. Thus, as the ponds change, the ideal sampling method often changes concomittantly. It is essential that an integrative sampling approach be used in such a system. Only by using a combination of sampling techniques, each of which is especially effective at elucidating specific trends in assemblage structure, can assemblage structure and associated community dynamics be adequately assessed in coastal shallow water habitats.

4.2 Rapid Rates of Ecological Change

It was apparent throughout the course of the study that changes in fish assemblage structure occur on extremely rapid time scales. For example, the effects of abiotic factors (i.e. dissolved oxygen and temperature) can act within minutes to deplete species richness in any given pond. Therefore, sampling a pond immediately following a wash-over event may result in a description of a pond assemblage much different from a description based on sampling conducted 24 hours earlier. The exact time frame at which various factors affect assemblage composition varies significantly (i.e. competition acts to reduce fish fitness on longer time scales than would a dramatic decrease in dissolved oxygen), but the sum of these assemblage structuring mechanisms results in a rapidly changing aquatic assemblage. In general, fish assemblages were both extremely unstable (frequently changing species abundances) and non-persistent (few species were able to survive in ponds for extended periods of time). Such characteristics make these habitats extremely distinct from similar in-shore pond assemblages.

The rapid rate of change has important implications for the way in which these habitats are studied. Yearly, seasonal, or even weekly samples are usually insufficient to accurately assess fish assemblage dynamics. In the most comprehensive study of barrier island ponds prior to this thesis (Ross and Doherty, 1994), the authors sampled at three month intervals in an attempt to assess the stability and persistence of fish species. This sampling interval is clearly too infrequent to accurately describe the dynamics that are occurring in such ponds. Less frequent sampling suggests a assemblage that is more stable and/or persistent than it actually is. Such less frequent sampling may elucidate long-term patterns in assemblage composition, but this sampling is insufficient to describe the assemblage dynamics at a level comparable to the actual rate of change.

4.3 Scale of Assemblage Structuring Mechanisms

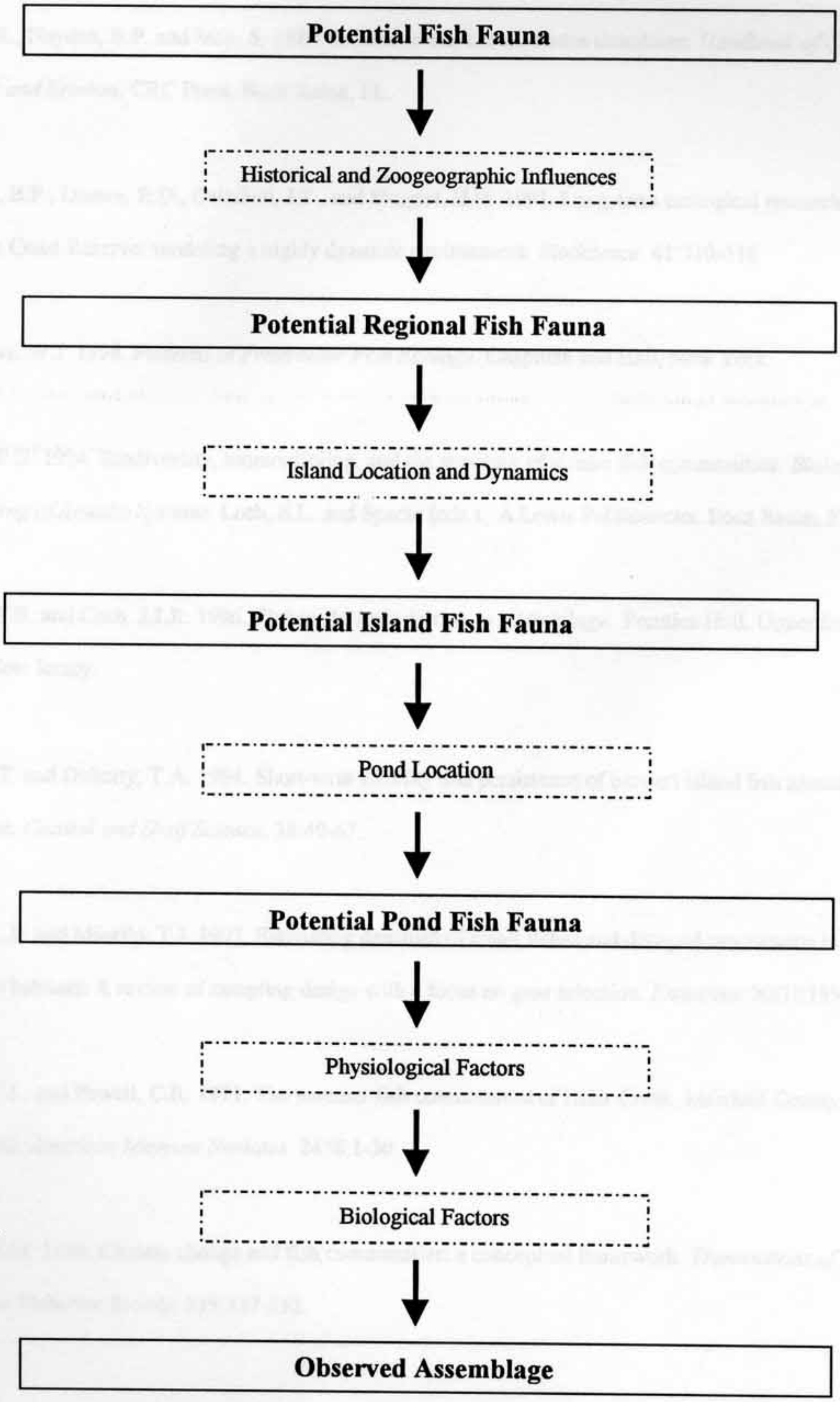
The fish assemblage structure in any given pond on the Virginia barrier islands can be attributed to a series of mechanisms that act at multiple spatial and temporal scales; therefore, these mechanisms may be thought of as a series of "filters" operating at different scales. This approach has been previously used to describe a variety of fish assemblages (Smith and Powell, 1971; Tonn, 1990; Moyle, 1994; Moyle and Cech, 1996; Matthews, 1998). Figure 4.1, largely based on the framework provided by Moyle and Cech (1996), suggests the system of filters that ultimately determine fish assemblage structure on the Virginia barrier islands.

The first filter is a set of large-scale processes, including two distinct components: historical and zoogeographical barriers. The zoogeographical filter establishes groups of fish fauna in specific regions due to biogeographical processes affecting the distribution of fish families. Also influencing these zoogeographical faunal realms are historical factors which have further altered the distribution of the fishes within or among zoogeographic realms. For example, historical filters include the effects of lowered sea level due to glacial coverage during the most recent ice age. Based on these large-scale processes, there exists a potential fauna in any given area, and thus a specific potential fish fauna for the Atlantic coast of the United States.

The location of a particular barrier island on the east coast of the United States further narrows the potential fauna. New England islands have a different potential group of species than Virginia islands because of species ranges within the coastal zoogeographic region. The local position of an island will further define the potential island fauna. Islands partially isolated within an estuary will likely have a different fish fauna than those exposed to the ocean. On any particular island, the specific location of a pond is another level of mechanisms affecting potential fauna. A pond on the lagoonal side of an island is primarily influenced by estuarine or marsh fish species. In contrast, a pond on the ocean side of the island is likely to be influenced primarily by oceanic fish species. It is at this scale that the dynamic nature of the barrier islands is especially important. Ponds located on the seaward side of eroding islands are subjected to increased rates of change which has profound implications for the fauna of these habitats.

The work of this thesis focused on the final two filters that act on a localized scale and ultimately shape potential fish fauna into observed assemblages. Physiological factors, including dissolved oxygen, temperature, salinity, and pH, among many others, act to determine what fish can inhabit a pond. Only those fishes which can effectively utilize a particular pond will then be subjected to biological interactions. Finally, competition for resources, predation, disease, and many other biological factors, determine the relative abundance of fish species. Therefore, the specific abiotic and biotic processes investigated in this study "fine-tune" potential fish assemblages. The importance of these small-scale abiotic and biotic processes vary considerably on diel, seasonal, and annual time scales, as well as from one pond to another. The spatial variation among ponds is greatly impacted by the rapid rates of geomorphological change that is prevalent on the barrier islands. Therefore, there is an essential link between the rapid landscape change and the small-scale structuring parameters that ultimately determine individual species abundances.

Figure 4.1. The series of filters (the dotted boxes) which contribute to fish assemblage structure in barrier island ponds.



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