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Macrofaunal Community Structure in the Introduced and Native Submerged Macrophyte Beds of the Lake Pontchartrain Estuary.

Kenneth Charles Duffy
Louisiana State University and Agricultural & Mechanical College

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**MACROFAUNAL COMMUNITY STRUCTURE IN THE
INTRODUCED AND NATIVE SUBMERGED
MACROPHYTE BEDS OF THE
LAKE PONTCHARTRAIN ESTUARY**

A Dissertation

**Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy**

in

The Department of Oceanography and Coastal Sciences

**by
Kenneth Charles Duffy
B.S., The University of Miami, 1989
May 1997**

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ABSTRACT

Introductions of exotic aquatic plants raise concerns for the health of assemblages of native species. The possible influence of the establishment of the exotic Eurasian watermilfoil Myriophyllum spicatum on fish and invertebrate assemblages in the Lake Pontchartrain estuary was examined with a microhabitat approach. Fish and invertebrate assemblage structure and population responses were compared among macrophyte species and unvegetated areas. Native macrophytes included wild celery Vallisneria americana and wigeongrass Ruppia maritima. Additionally, the relationships of the common submerged macrophytes to environmental and temporal variables were analyzed. A total of 517 samples, collected with a modified Wegener ring, included 3,564 fishes of 29 species and 53,006 macroinvertebrates of 13 taxa. The distribution and abundance of M. spicatum were positively related to turbidity and depth, whereas for V. americana they were positively related to sandy substrates. Along the northeast shore of Lake Pontchartrain, high wave energy probably limited the distribution of M. spicatum and R. maritima and favored the dominance of V. americana. In the Lake Pontchartrain estuary, R. maritima was probably replaced, in part, by M. spicatum. Most fishes and invertebrates were denser in submerged vegetation, although no significant differences in assemblage structure of fishes and macroinvertebrates were detected among submerged macrophyte species. Three of the common fishes and all of the common invertebrates differed significantly in density among macrophyte species, but overall patterns were not clearly different. Juvenile blue crab Callinectes sapidus, which were analyzed in three size classes, were more abundant in vegetated areas than in unvegetated areas, and all size classes were significantly denser in at least one native macrophyte species than in M. spicatum. Resident fishes were more abundant in spring and summer, whereas transient fishes were more abundant during recruitment events, usually in late winter and early spring. Amphipods and other small invertebrates were

generally more common in winter. The use of M. spicatum by blue crab declined with increasing crab size, whereas the use of V. americana increased. Although the apparently benign exotic macrophyte M. spicatum did not measurably affect assemblage structure, it did significantly influence distributions of several littoral fishes and macroinvertebrates.

CHAPTER 1: INTRODUCTION

Submerged aquatic vegetation can have a dramatic influence on the community structure and species diversity of littoral communities. It serves as a substrate, energy source, and habitat for nekton and sessile organisms, and it can influence the community structure of benthic organisms (Virnstein 1987, Heck and Crowder 1991).

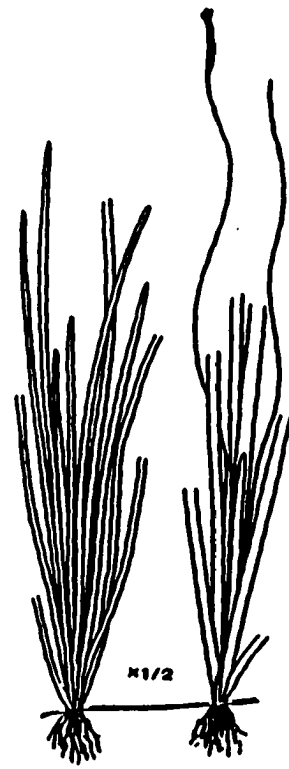
Nevertheless, the establishment of exotic macrophytes can decrease the quality of this littoral habitat by replacing more suitable native species and altering biologically important variables, such as dissolved oxygen (Blackburn and Weldon 1967, Grace and Wetzel 1978, Keast 1984). Although abundances of fishes and invertebrates are much higher in submerged vegetation than on adjacent unvegetated substrates (Lewis and Stoner 1983, Heck and Thoman 1984, Rozas and Odum 1988, Lubbers et al. 1990, Heck and Crowder 1991), the proliferation of exotic macrophytes can result in reductions of densities of associated organisms relative to native macrophytes (Blackburn and Weldon 1967, Keast 1984). The exotic Eurasian milfoil Myriophyllum spicatum was first reported in the Lake Pontchartrain estuary in 1978 (Thompson and Verret 1980), and has displaced native macrophyte species to become one of the dominant macrophytes in the estuary (Mayer 1986).

The establishment of exotic species is a primary concern in many ecosystems, and may be second only to rainforest destruction in the reduction of biodiversity (Ehrenfeld 1970, Diamond and Chase 1986, Mooney and Drake 1986). Although most invasions are unsuccessful, some exotic plants can displace native macrophyte species, and if they have no effective herbivores they can alter biologically important gradients, rendering habitats less suitable for some fishes and invertebrates (Blackburn and Weldon 1967, Grace and Wetzel 1978, Keast 1984, Harlan et al. 1985, Mooney and Drake 1986, Sutton 1986, Tanner et al. 1990, Room and Fernando 1992). This study is an inquiry into how the distributions of fishes and invertebrates inhabiting submerged

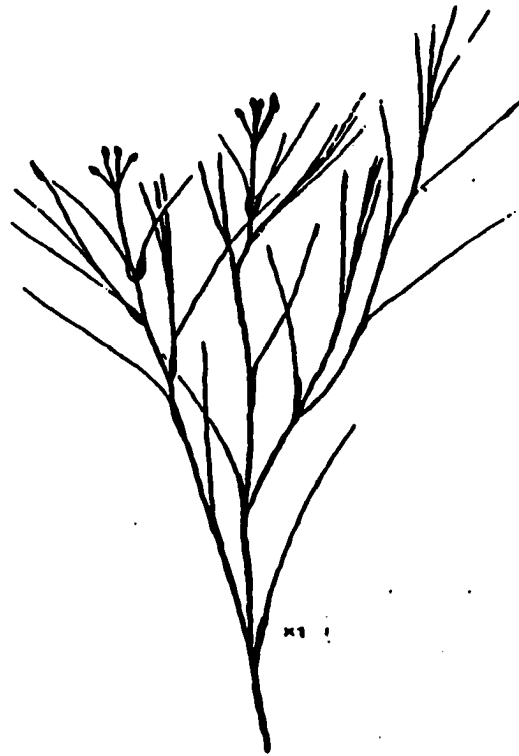
inquiry into how the distributions of fishes and invertebrates inhabiting submerged vegetation in the Lake Pontchartrain estuary have been affected by the presence of Myriophyllum spicatum.

Abundances of fishes and invertebrates are generally higher in submerged vegetation because the plant structure provides protection from predation and increases food resources. Many studies have demonstrated the negative relationship between submerged vegetation density and predation pressure (Virnstein 1987, Rozas and Odum 1988, Lubbers et al. 1990, Heck and Crowder 1991, Christenson and Persson 1993). Increased protection makes submerged vegetation vital in the survival of many juvenile fishes and invertebrates (Heck and Thoman 1984, Orth and van Montfrans 1987, Chester and Thayer 1990). In addition to providing protection, submerged macrophytes are richer in food resources than unvegetated areas (Stoner 1982, Boesch and Turner 1984, Rozas and Odum 1988). While submerged macrophytes are directly consumed by a few fishes and invertebrates, the epiphytes that grow on them from the base of extremely productive ecosystems (Heck and Thoman 1984, Virnstein 1987, Heck and Crowder 1991). Small invertebrates that graze on epiphytes are in turn preyed upon by fishes and larger invertebrates (Heck and Orth 1980b, Butler 1989). Although foraging success of predators is generally reduced in more complex vegetated habitats (Rozas and Odum 1988, Ryer 1988), the enhanced survival provided by refugia may be offset by the attraction of predators to sites of high prey density and the resulting increase in predator-prey encounters (Ryer 1988, Hettler 1989, Feller et al. 1990). Some researchers view increased invertebrate prey abundances as the result of selection for increased food resources (Bell and Westoby 1986a and 1986b, Edgar 1990), whereas others hypothesize that predation primarily influences invertebrate abundances (Heck and Orth 1980a, Rozas and Odum 1988, Ryer 1988, Dionne and Folt 1991, Heck and Crowder 1991). This study supports the theory that invertebrate prey abundances respond more to predation pressure than food availability (see Chapter 5).

The structure of macrophytes makes littoral habitats more complex, increasing the number and types of available habitats for demersal fishes and invertebrates (Virnstein 1987, Holmund et al. 1990, Dionne and Folt 1991, Heck and Crowder 1991, Olmi and Lipcus 1991, Orth 1992). This complexity is also increased by the presence of epiphytes, which use the surface of submerged macrophytes as substrate. Predation rates are generally expected to decline with increasing macrophyte complexity (Heck and Orth 1980, Virnstein 1987, Dionne and Folt 1991, Heck and Crowder 1991), but other studies have cast doubt on the generality of this relationship (Stoner 1982, Bell and Westoby 1986a, Edgar 1990, Holmund et al. 1990). The risk of predation by pinfish Lagodon rhomboides to amphipods increases with habitat complexity across seven species of macroalgae (Holmund et al. 1990). Obviously other factors, such as predator and prey sizes (Stoner 1982, Ryer 1988, Heck and Crowder 1991), predatory strategies (Stoner 1982, Ryer 1988, Dionne and Folt 1991, Heck and Crowder 1991), and behavioral responses of prey (Heck and Crowder 1991) also influence predation rates and prey abundances (Bell and Westoby 1986a, Holmund et al. 1990). In the Lake Pontchartrain estuary, the three dominant submerged macrophyte species (Figure 1.1) differ widely in morphology (Chabreck and Condrey 1979). Wild celery Vallisneria americana grows in rosettes of ribbon-like blades that can reach a length of 160 cm (Titus and Adams 1979), and have a width of about 13 mm (Chabreck and Condrey 1979). The other dominant native, the widgeongrass Ruppia maritima, has thin branching stems with fine, threadlike leaves. The exotic Eurasian milfoil Myriophyllum spicatum has long stems (up to 4 m) that branch near the terminal end, with groups of four finely pinnate leaves arranged in whorls about each stem, becoming more concentrated near the terminus (Grace and Wetzel 1978), concentrating biomass at the surface. Each macrophyte species offers inhabiting organisms different levels of complexity.



Vallisneria americana
Michx.



***Ruppia maritima* L.**



***Myriophyllum spicatum* L.**

Figure 1.1: The three submerged macrophyte species sampled in the Lake Pontchartrain estuary (from Chabreck and Condrey 1979).

Plant surface area (PSA) provides a good measure of macrophyte complexity (Heck and Orth 1980a, Heck and Crowder 1991). Submerged vegetation beds may provide many square meters of surface area per square meter of bottom substrate (Burkholder and Wetzel 1989). This increased surface area allows more organisms to occupy a given area of substrate. Increased PSA generally increases the diversity and abundance of the inhabiting organisms (Heck and Crowder 1991). Thus, submerged vegetation offers increased living area, but plant growth form and plant density may influence habitat quality with consequent changes in faunal assemblage structure. Some growth forms can negatively influence biologically important variables, such as dissolved oxygen levels, through litter production (Grace and Wetzel 1978). Also, water flow decreases in dense macrophytes, which may lead to hypoxia (Grace and Wetzel 1978, Keast 1984). For example, in Lake Opinicon, Canada, dissolved oxygen levels at the sediment-water interface in beds of Myriophyllum spicatum are significantly lower than in beds of native macrophytes, which were structurally simpler (Keast 1984).

In the Lake Pontchartrain estuary (Figure 1.2), submerged vegetation is currently restricted to the northeast shore of Lake Pontchartrain and the smaller lakes associated with it to the east (Mayer 1986), including Lakes Borgne and St. Catherine. Historically, Lake Pontchartrain supported extensive macrophyte beds, covering 8,097 ha along the north shore (Montz 1978, Mayer 1986). In 1973, these areas supported only 810 ha of submerged macrophytes (Montz 1978). By 1985, the north shore littoral zone only supported 397 ha of submerged macrophytes, and 60 ha were contributed by M. spicatum (Mayer 1986). In Lake St. Catherine in 1986, 861 ha of submerged macrophytes were reported, of which 95 % was M. spicatum (Mayer 1986). V. americana was not reported from Lake St. Catherine in 1985 (Mayer 1986).

Several factors may help control the establishment and spread of exotics, and also affect the distributions of native species. The Lake Pontchartrain estuary is a stressed system, and factors such as shell dredging, poorly treated agricultural and

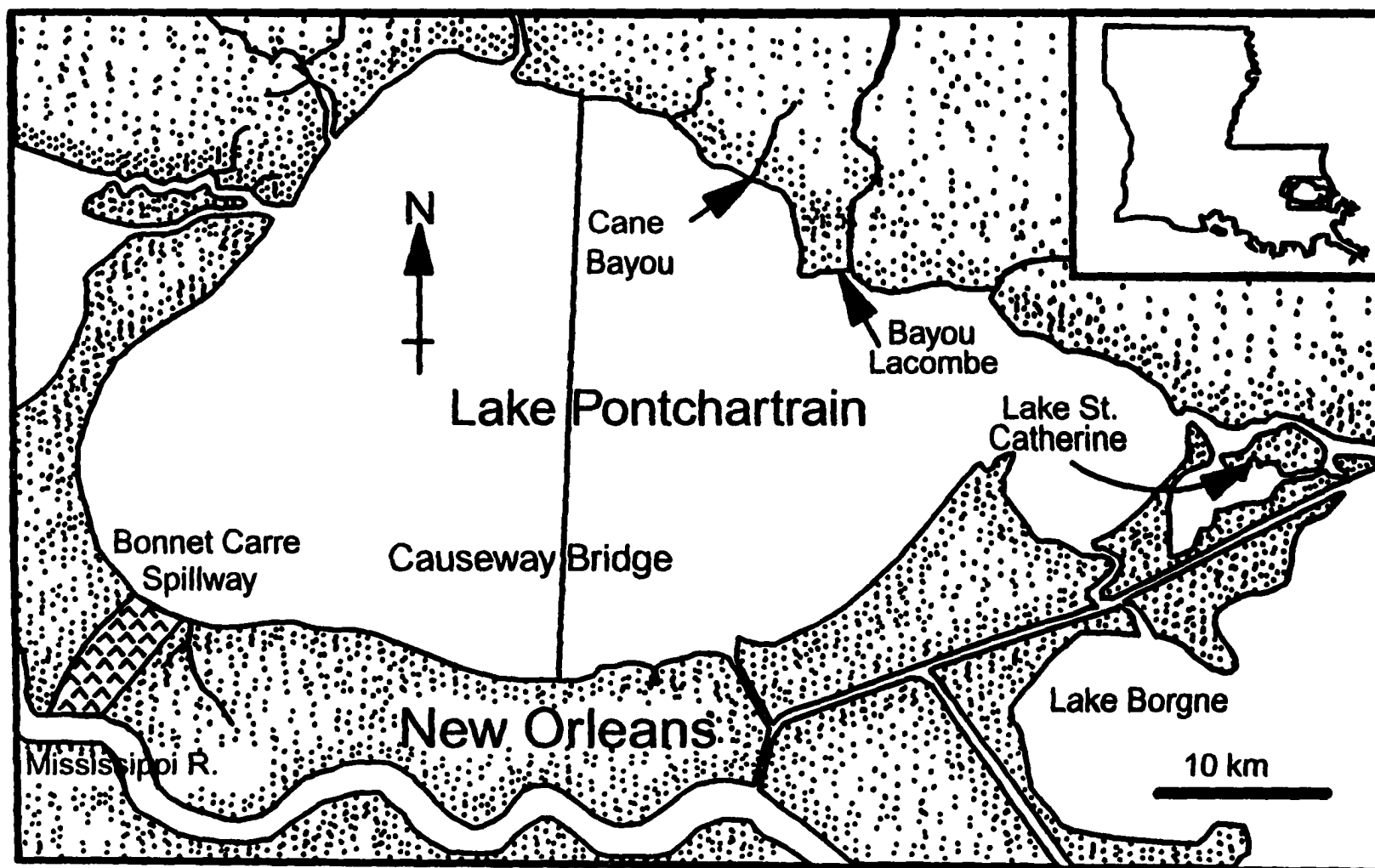


Figure 1.2: The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer 1986).

municipal runoff result in increased turbidity through both biotic and abiotic means (Stone et al. 1980). Nutrient availability may affect distributions directly or indirectly. In nutrient-poor waters, some uptake of sediment nutrients by the roots is possible, but growth rates may be lower than in more eutrophic situations. In nutrient-rich waters, phytoplankton and epiphyte blooms may cause light limitation by shading macrophytes (Dennison et al. 1993). Turbidity levels increased in Lake Pontchartrain by about 50 % from 1955 to 1980 due to shell dredging and increased nutrient loading (Stone et al. 1980). Some macrophytes, especially Myriophyllum spicatum, respond to low light levels by increasing stem length and concentrating more biomass nearer the surface (Grace and Wetzel 1978). Carbohydrate storage patterns may indicate that Vallisneria americana is more dependent on water clarity than M. spicatum, but higher productivity in the summer may allow coexistence when other factors are equal (Titus and Adams 1979).

Salinity can also affect distributions of submerged macrophytes. Those found in the Lake Pontchartrain estuary are primarily freshwater species, but V. americana and M. spicatum can tolerate salinities of at least 12 ‰ (Mayer 1986, Twilley and Barko 1990). Both species typically have limited osmoregulatory capabilities, and may leak nutrients at higher salinities encouraging epiphyte growth (Twilley and Barko 1990). Epiphyte growth can reduce the light available to macrophytes by up to 50 % (Twilley and Barko 1990). Additionally, in estuarine systems, where frontal passages and storm surges can cause isohalines to move great distances in short periods, the rate of salinity change and duration of exposure may be more important than the maximum salinity (Twilley and Barko 1990). High wave energy may also limit distributions of more delicate macrophyte species (Wetzel 1975, Titus and Adams 1979, Mayer 1986, Day et al. 1989, Heck and Crowder 1991).

Lake Pontchartrain is a large semi-enclosed bay covering 1,630 km², and historically has supported extensive fisheries (Thompson and Stone 1980, Guillory et al.

1996). Nevertheless, while little work has been done on the distributions of fishes and invertebrates in littoral areas of Lake Pontchartrain, no studies have adequately explored the factors influencing distributions of individual submerged macrophyte species. While several studies documented abundances of fishes and invertebrates (Darnell 1958, Darnell 1961, Bahr et al. 1980, Fannaly 1980, Thompson and Stone 1980, Thompson and Verret 1980), trophic interactions (Darnell 1961, Levine 1980) and submerged vegetation (Suttkus et al. 1954, Turner et al. 1980), none explored in detail the relationship of organisms with the environmental gradients that influence their distributions.

Ecological change generally happens slowly over time, but no adequate baseline for the Lake Pontchartrain ecosystem was established long enough ago against which to gauge changes. Newer studies have to base comparisons on relatively recent reference points, resulting in the use of a "shifting baseline" (Pauly 1995, Sheppard 1995). For example, the relative abundances of individual submerged macrophytes were not reported for the Lake Pontchartrain estuary until Mayer (1986), when only 397 ha of submerged vegetation was reported for Lake Pontchartrain. Although previous studies reported much greater distributions (8,097 ha) of submerged vegetation (Montz 1978, Mayer 1986), species relative abundances were not reported, so inferences are limited to addressing submerged vegetation changes and influences, whereas more complete data would allow more specific comparisons and conclusions. The distributions of submerged macrophyte species at the turn of the century are largely unknown. Likewise, the distributions of fishes and invertebrates in submerged macrophytes and factors that influence them were largely unknown. Some species were known to associate with the submerged macrophytes (Darnell 1961, Thompson and Verret 1980), but responses to individual macrophyte species and environmental variables were unknown.

The objectives of this study were: 1) to assess the influence of the exotic Myriophyllum spicatum on the assemblage structures of fishes and macroinvertebrates in the Lake Pontchartrain estuary, 2) to measure the differences in the abundances of individual fish and invertebrate species among submerged macrophytes and unvegetated substrates and identify other influencing factors controlling the distributions of fishes and invertebrates, and 3) to identify the factors controlling the distribution and abundance of the submerged macrophytes. In Chapter 2, the PSA and relative dominance of the three most common submerged macrophytes are examined to determine the influence of temporal and environmental gradients. In Chapter 3, the fish assemblages of the three macrophytes and unvegetated substrates are examined. Because of the importance of blue crabs to the ecology and economy of the estuary, they are examined in detail in Chapter 4. In Chapter 5, the natant macroinvertebrate assemblages are examined. Chapter 6 provides a summary of the results and conclusions.

CHAPTER 2: RESPONSES OF SUBMERGED AQUATIC MACROPHYTES ALONG ENVIRONMENTAL AND TEMPORAL GRADIENTS IN THE LAKE PONTCHARTRAIN ESTUARY, USA

Introduction:

Changes in the distributions of submerged macrophytes can strongly influence populations of associated fishes and invertebrates (Orth and van Montfrans 1987, Rozas and Odum 1988, Lubbers et al. 1990, Heck and Crowder 1991). Altered macrophyte species composition or reductions in coverage by submerged macrophytes can lead to reductions in abundances of many fishes and invertebrates (Keast 1984, Orth and van Montfrans 1990, Thomas et al. 1990, Edgar 1990). In the Lake Pontchartrain estuary, the total area covered by submerged aquatic vegetation has declined dramatically over the past few decades (Montz 1978, Mayer 1986). Additionally, the exotic Myriophyllum spicatum became established as one of the dominant macrophytes in the estuary (Thompson and Verret 1980, Mayer 1986).

Submerged macrophytes are an integral part of the ecology of most coastal estuarine and shelf systems (Day et al. 1991, Heck and Crowder 1991), as well as in lakes and streams (Keast 1984, Heck and Crowder 1991). Submerged vegetation provides habitat, refuge and food resources for associated fishes and invertebrates (Kitting 1984, Orth and van Montfrans 1984, van Montfrans et al. 1984, Orth and van Montfrans 1987, Rozas and Odum 1988, Heck and Crowder 1991) as well as substrate for epiphytic algae (Orth and van Montfrans 1984, Edgar 1990). Although few organisms graze directly on the macrophytes, submerged vegetation is an extremely productive habitat in both primary production of vascular plants and macroalgae and secondary production of fishes and invertebrates (Kitting 1984, Orth and van Montfrans 1984, Virnstein 1987, Day et al. 1989).

For the last four decades, extensive beds of submerged macrophytes in the Lake Pontchartrain estuary have declined, and are now restricted to the northeast shore of

Lake Pontchartrain and the lakes associated with it to the east, including Lakes Borgne and St. Catherine. This relatively recent decline in macrophyte abundances was largely due to a degradation in water quality from agricultural runoff, urban runoff, inadequate sewerage treatment, and clam shell dredging (Montz 1978, Mayer 1986). The exotic Myriophyllum spicatum was first observed in Lake Pontchartrain in 1978 (Thompson and Verret 1980), and its distribution increased concurrently with the decline in the area covered by native submerged macrophytes. In the late 1960's, the native macrophytes Vallisneria americana and Ruppia maritima covered 8,097 ha along the north shore of Lake Pontchartrain (Montz 1978). In 1973 the littoral areas supported only 810 ha of submerged macrophytes (Montz 1978). By 1985, V. americana had decreased in coverage to 258 ha in Lake Pontchartrain, and it was not detected in Lake St. Catherine, while the area covered by R. maritima had decreased to 60 ha in Lake Pontchartrain and 43 ha in Lake St. Catherine (Mayer 1986). While native species were declining, M. spicatum was expanding. By 1985, the area covered by M. spicatum had increased to 60 ha in Lake Pontchartrain and 818 ha in Lake St. Catherine (Mayer 1986).

At some level, the invasion and establishment of exotic species almost always has a deleterious effect (Grace and Wetzel 1978, Mooney and Drake 1986), as even benign exotics modify native communities and deprive us of knowledge of natural community structure and function. Whether or not the invasion of Myriophyllum spicatum in coastal Louisiana is benign, it is probably not reversible, and insights into its influences on native species are required to assess overall ecosystem health and to plan for ecosystem management. M. spicatum has become a nuisance in many lakes and waterways across the North American continent (Blackburn and Weldon 1967, Grace and Wetzel 1978, Keast 1984), but problems arise from its abundance rather than its presence (Grace and Wetzel 1978). As part of a larger study examining the influence of M. spicatum on fishes and invertebrates in littoral habitats of the Lake Pontchartrain estuary, the relationships of the macrophyte species to temporal and environmental variables were

analyzed, and substantial differences were found in environmental variables associated with the common submerged macrophyte species.

Study Area:

Lake Pontchartrain is a large, shallow bay located just north of New Orleans in southeast Louisiana (Figure 2.1). It covers an area of 1,630 km², has a mean depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). Salinity in the estuary ranges from fresh water in the western end and near riverine input to 10 ‰ in the eastern reaches (Sikora and Kjerfve 1985). Lake Pontchartrain is connected to several smaller lakes to the east and to the Gulf of Mexico by two main passes. Myriophyllum spicatum is also established in these lakes, which include Lakes Borgne and St. Catherine. Three stations were chosen to characterize the salinity gradient, and included littoral areas near the mouths of Cane Bayou and Bayou Lacombe in Lake Pontchartrain and the north end of Lake St. Catherine (Figure 2.1).

Methods:

The submerged aquatic vegetation of the nearshore habitats in Lake Pontchartrain and Lake St. Catherine was characterized by 517 observations made between March 1991 and January 1993. A modified Wegener ring (Weinstein and Brooks 1983) consisting of a vertical cylinder of heavy fabric extending 110 cm in height with a circular stainless steel base ring (10 cm wide x 1.23 m diameter, 1.18 m²) was used to collect microhabitat and submerged macrophyte species density data, as well as allow for the quantitative characterization of fish and invertebrate abundances. When deployed the walls were supported by a float ring at the top. A boom extending three meters beyond the bow of a 5.2 m boat was used to deploy the sampler. The Wegener ring was held one-half meter above the water's surface until it was released with a pull-pin. Twelve samples were collected from each station monthly. The available macrophyte species present were sampled using a stratified approach, since not every

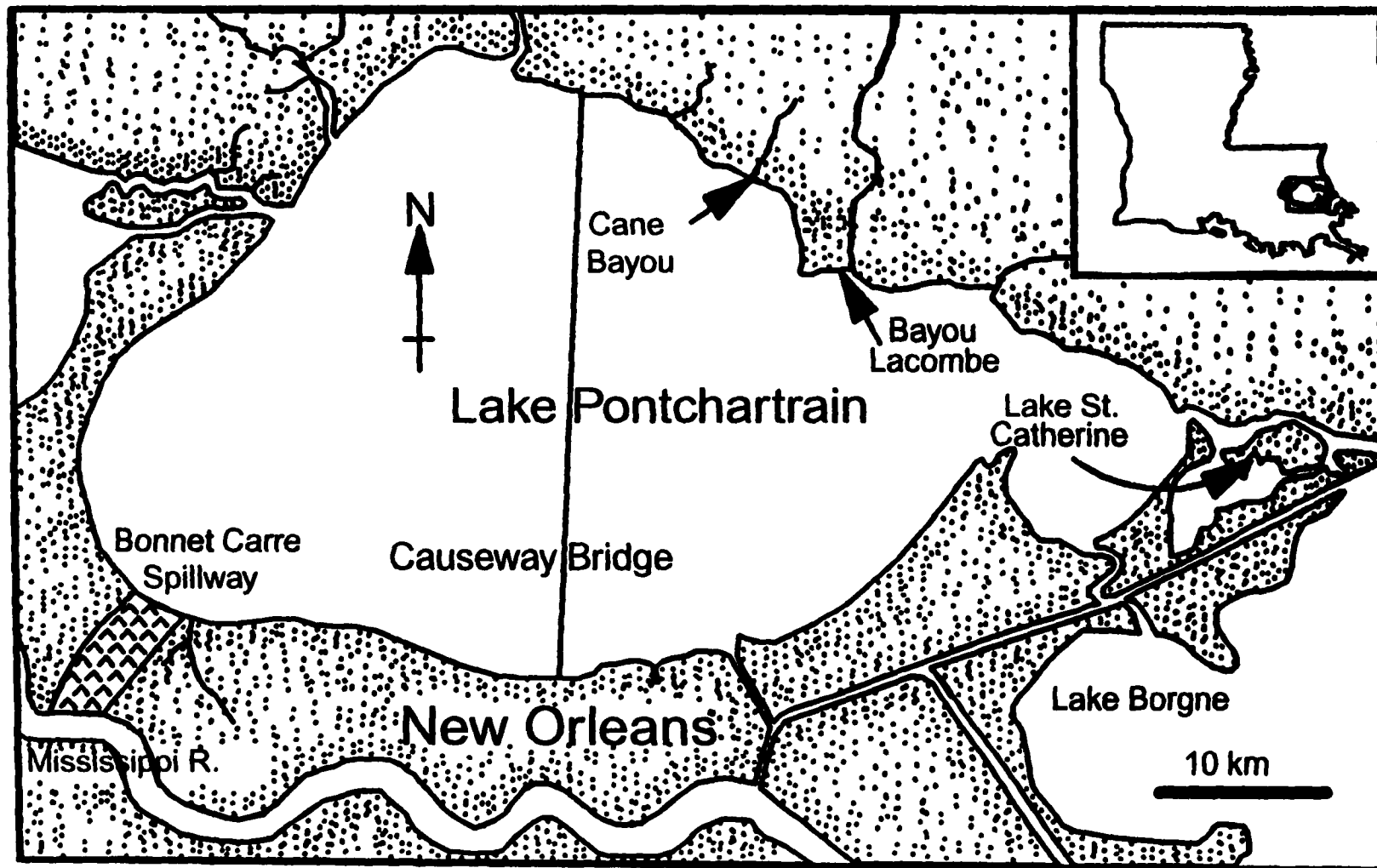


Figure 2.1: The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer 1986).

vegetation type was present at every location on every trip. Unvegetated areas and sparsely vegetated areas were also sampled.

For each observation the species present were recorded, and the number of stems and the average height of the stems were estimated for each species by subsampling. Measurements were also made of temperature, salinity, dissolved oxygen, median depth (cm), water velocity, turbidity, distance from shore (m), and substrate type. Temperature (°C), salinity (‰), and dissolved oxygen (mg / l) were measured with a Hydrolab model SRV2-SU datasonde, and turbidity was measured in nephelometer turbidity units (NTU) using a Monitek model 21PE portable nephelometer. Surface water velocity (cm / s) was estimated by timing a neutrally buoyant object in the water for ten seconds and measuring mean displacement per second. Substrate type was estimated by touch on a particle size scale: 1 = clay; 2 = mud; 3 = silt; 4 = sand; 5 = organic detritus; and 6 = shell fragments. Both the dominant and sub-dominant sediment types were recorded.

Plant surface area (PSA) was calculated from the estimates of the stem density and mean stem length in each sample using species-specific formulas. The formulas were derived from surface area measurements of samples of each submerged macrophyte species. A Li-Cor LI-3000 portable leaf area index meter was employed to measure the surface area of a subset of leaves for each macrophyte species. We then regressed plant surface area (m² plant area per m² substrate) on stem length to describe species-specific relationships (SAS Institute 1989):

Vallisneria americana: $PSA = 1.258 * L * C / 10000$ (N = 20, R² = 0.991),

Myriophyllum spicatum: $PSA = 1.058 * L * C / 10000$ (N = 20, R² = 0.797),

Ruppia maritima: $PSA = 0.232 * L * C / 10000$ (N = 19, R² = 0.998),

where L = mean stem length and C = stem count per sample. Additionally, relative dominance was calculated as the percentage of the total PSA in a sample contributed by each species (Mueller-Doubois and Ellenberg 1974).

Three approaches were used to examine relevant patterns of the common submerged macrophyte species. First, the relationships of temporal and environmental variables to PSA and relative dominance were examined to identify possible influences of these variables on macrophyte species. PSA and relative dominance of each macrophyte species were then examined across stations and seasons. Finally, environmental variables were examined across samples where individual submerged macrophyte species dominated to identify possible influences of environmental variables on macrophytes and to compare the availability of environmental variables to the macrophyte species.

In a general linear models (GLM) approach, temporal and environmental variables were used to predict the surface area of the three most common submerged macrophyte species. First, a stepwise regression tested the eight environmental variables for inclusion in each macrophyte species model that was constrained to include four temporal variables (first to fourth order terms for month). Terms that were included at the 15 % significance level were entered into a GLM analysis to test the temporal variables. The Type I sums of squares, with the temporal variables adjusted for all included environmental variables, identified which temporal variables had a significance level of less than 15 %. These were excluded from the subsequent analyses (Johnson and Wichern 1988), but if a higher order temporal term was significant, all of the lower order terms were retained for theoretical reasons (Johnson and Wichern 1988). The appropriate temporal variables were included in another stepwise regression to verify the significance of the environmental variables, and a final model was selected. The final models were entered into a GLM analysis, and the results of this final GLM are reported. This approach was also used to identify significant relationships between the relative dominance of each species and temporal and environmental variables. Significance levels

were adjusted to an overall level of 0.05 using the Dunn-Šidák formula: $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α' = adjusted significance level, α = desired overall significance level, and k = number of comparisons (Sokal and Rohlf 1981).

A second GLM approach was used to examine PSA patterns for the three most common submerged macrophyte species among stations and seasons (SAS Institute 1989). Significance levels were also adjusted for multiple comparisons (Sokal and Rohlf 1981). A least squares means (LSMeans) test was used to identify significant differences in PSA values. PSA values were plotted by month using a three month moving average.

Finally, means for environmental variables were compared among the three submerged macrophytes and to the overall mean for each variable. The overall means constituted an estimate of the availability of the environmental characteristics of sites. Samples were assigned to a macrophyte species if the relative dominance of the species exceeded 70 %. The overall means for environmental variables were calculated from the combined set of all stratified random samples, including samples in which no macrophyte species was dominant, to give an estimate of the availability of the environmental characteristics that defined microhabitats. The means for environmental variables where each macrophyte species was dominant were compared using a GLM approach, and differences significant at a probability level of 0.0064 (to control for multiple comparisons at an α of 0.05) were further analyzed using LSMeans (SAS Institute 1989).

Results:

A total of 517 samples collected from March 1991 to January 1993 included abundance data for submerged macrophyte species. PSA values were calculated for the common macrophytes. Vallisneria americana occurred in 63 % of the samples and was dominant in 51 %. Myriophyllum spicatum occurred in 42 % of the samples and was dominant in 15 %. Ruppia maritima occurred in 27 % samples and was dominant in 7 %.

The regression of PSA values for each macrophyte on temporal and environmental variables only explained between 6.7 and 16.4 % of the total variances. For V. americana, two of the three temporal variables included in the model were significant, and explained 4.8 % of the variance, while substrate type only explained 1.6 % (Table 2.1), and the total model only explained 12.0 % of the variance. For M. spicatum three temporal variables included in the final regression model were not significant. Substrate type, salinity, water velocity, and depth were significant, and explained 14.0 % of the variance, and the total model only explained 16.4 % of the variance. For R. maritima, only substrate type was significantly related to PSA, but only explained 1.6 % of the variance (Table 2.1). The total model only explained 6.7 % of the variance in R. maritima PSA patterns.

In the regression of relative dominance of macrophyte species on independent temporal and environmental variables, environmental variables were generally more important than temporal variables (Table 2.2) in models that explained between 12.1 and 28.4 % of the total variance. For Vallisneria americana, substrate type and depth were significant and explained 6.5 % of the variance, but no temporal variables were included in the final model. The V. americana model explained 12.1 % of the variance. For Myriophyllum spicatum, substrate type, depth, distance from shore, water velocity, salinity, and turbidity were significant, and explained 20.0 % of the variance, and one significant temporal variable explained 1.8 % of the variance. The M. spicatum model explained 28.4 % of the variance. For Ruppia maritima, salinity, substrate type, distance from shore, and depth were significant, and explained 6.5 % of the variance, and one temporal variable was significant, explaining 1.8 % of the variance (Table 2.2). The R. maritima model explained 15.8 % of the variance.

In the GLM analyses comparing macrophyte PSA and relative dominance among stations, both variables showed significant differences for all macrophyte species (Table 2.3). For Vallisneria americana, mean PSA in Lake St. Catherine was significantly lower

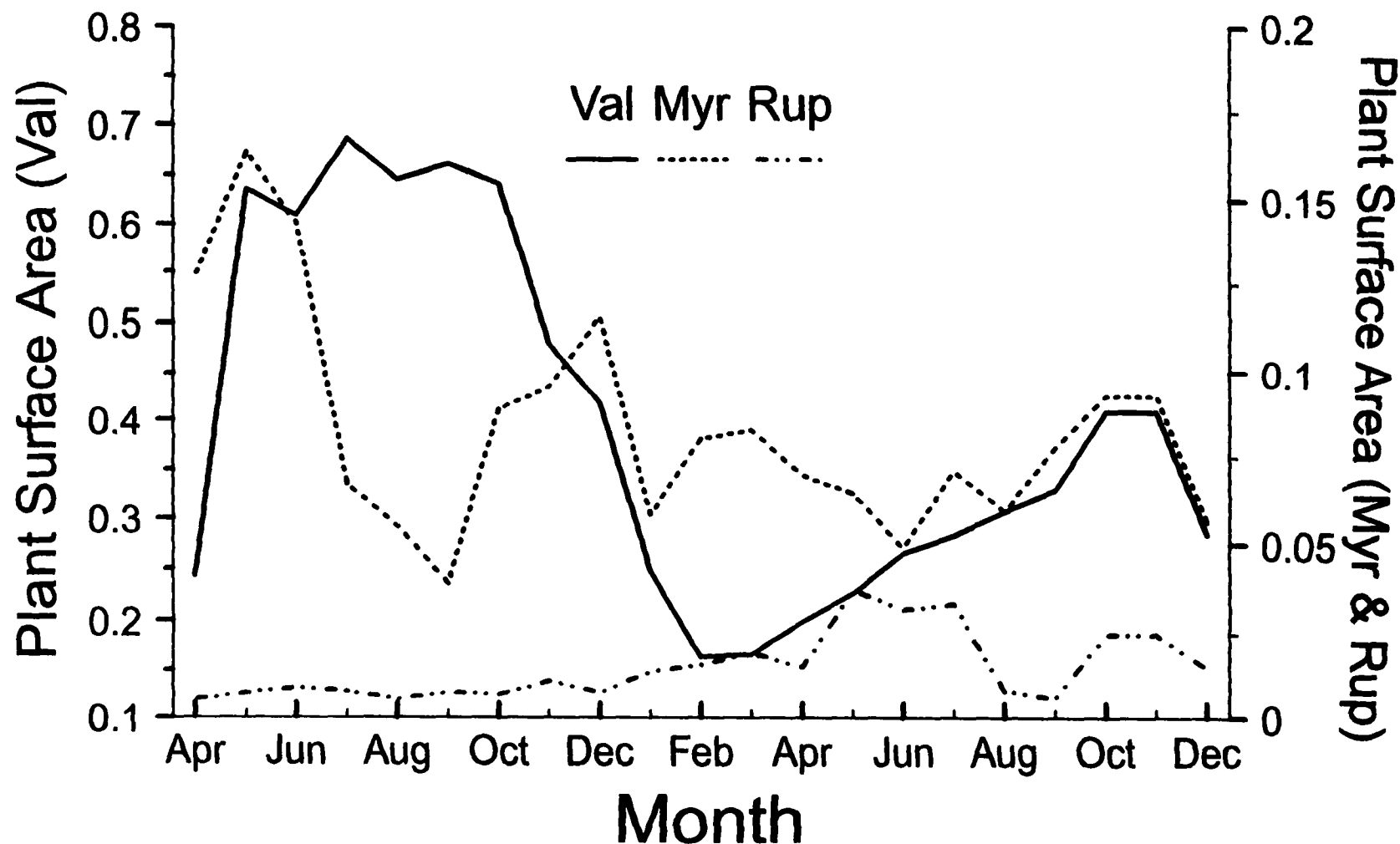


Figure 2.2: Mean plant surface area measured for the three submerged macrophytes in the Lake Pontchartrain estuary from March 1991 to January 1993. The plotted mean PSA for each month includes the previous and following months, for a three month moving average.

Table 2.1: Results of the final model from a model building approach (see text for explanation) of the relationship of submerged macrophyte PSA with temporal and environmental variables in the Lake Pontchartrain estuary. Asterisks denote effects that are significant at $p \leq 0.05$ after adjusting for multiple comparisons.

Macrophyte species and variable	Coefficient	Partial r^2	P > F
<u>V. americana</u>			
Intercept	-0.7907		0.0001 *
Month	0.0010	0.0318	0.0001 *
Month ²	0.0171	0.0169	0.0019 *
Substrate	0.0906	0.0161	0.0024 *
Depth	0.0043	0.0098	0.0179
Dissolved Oxygen	0.0346	0.0082	0.0296
Water Velocity	-0.0232	0.0078	0.0344
Distance	0.0024	0.0053	0.0822
Month ³	-0.0013	0.0040	0.1304
Model		0.1200	0.0001 *
<u>M. spicatum</u>			
Intercept	0.2206		0.0008 *
Substrate	-0.0488	0.0483	0.0001 *
Salinity	-0.0209	0.0376	0.0001 *
Water Velocity	-0.0148	0.0366	0.0001 *
Depth	0.0016	0.0172	0.0013 *
Month ³	0.0006	0.0094	0.0171
Month	0.0549	0.0066	0.0461
Turbidity	0.0018	0.0061	0.0555
Distance	-0.0006	0.0035	0.1473
Month ²	-0.0104	0.0020	0.2666
Model		0.1644	0.0001 *
<u>R. maritima</u>			
Intercept	0.0307		0.6598
Substrate	-0.0182	0.0159	0.0034 *
Dissolved Oxygen	0.0080	0.0098	0.0211
Month ²	0.0286	0.0094	0.0243
Month ⁴	0.0001	0.0085	0.0324
Turbidity	0.0014	0.0074	0.0456
Salinity	0.0058	0.0056	0.0822
Month	-0.0776	0.0003	0.6684
Month ³	-0.0035	0.0000	0.9228
Model		0.0667	0.0001 *

Table 2.2: Results of the final model from a model building approach (see text for explanation) of the relationship of percent dominance of submerged macrophyte species with temporal and environmental variables in the Lake Pontchartrain estuary. Asterisks denote effects that are significant at $p \leq 0.05$ after adjusting for multiple comparisons.

Macrophyte species and variable	Coefficient	Partial r^2	P > F
<u>V. americana</u>			
Intercept	-0.1979		0.0648
Substrate	0.1272	0.0525	0.0001 *
Depth	0.0033	0.0121	0.0081 *
Distance	0.0022	0.0076	0.0362
Turbidity	0.0042	0.0056	0.0705
Model		0.1210	0.0001 *
<u>M. spicatum</u>			
Intercept	0.7746		0.0001 *
Substrate	-0.1099	0.0585	0.0001 *
Depth	0.0050	0.0421	0.0001 *
Distance	-0.0038	0.0373	0.0001 *
Water Velocity	-0.0263	0.0278	0.0001 *
Salinity	-0.0314	0.0205	0.0001 *
Month ²	0.0048	0.0177	0.0004 *
Turbidity	0.0054	0.0141	0.0017 *
Month	-0.0568	0.0048	0.0661
Model		0.2841	0.0001 *
<u>R. maritima</u>			
Intercept	0.3979		0.0001 *
Salinity	0.0235	0.0216	0.0003 *
Month	-0.0110	0.0183	0.0009 *
Substrate	-0.0425	0.0152	0.0026 *
Distance	-0.0018	0.0142	0.0035 *
Depth	-0.0020	0.0135	0.0045 *
Water Velocity	0.0100	0.0070	0.0407
Turbidity	-0.0025	0.0050	0.0839
Model		0.1579	0.0001 *

than at the two Lake Pontchartrain stations, whereas for Ruppia maritima, mean PSA was significantly higher in Lake St. Catherine. For Myriophyllum spicatum, mean PSA at the Bayou Lacombe station was significantly lower than at the other two stations. PSA values also showed monthly variation, as well as seasonal cycles (Figure 2.2). In

winter, V. americana had a significantly lower mean PSA than in summer and autumn, and M. spicatum had a significantly lower mean PSA than in spring (Table 2.4). No significant differences among seasons were detected for R. maritima.

For samples dominated ($\geq 70\%$) by a single macrophyte species, significant differences in environmental variables were noted for five of the eight means (Table 2.5). For samples dominated by Vallisneria americana, the substrate was significantly sandier and farther from shore than for samples dominated by the other two macrophytes, and the overall mean substrate type was intermediate. Myriophyllum spicatum dominated samples were collected from significantly greater depths and lower mean water velocities than the two native macrophytes and the overall mean depth. Mean salinity was

Table 2.3: Differences in mean plant surface areas (± 1 SE) and mean relative dominance (± 1 SE) for individual macrophyte species among stations sampled in the Lake Pontchartrain estuary. Means are adjusted for seasonal sampling effort, and significant differences (LSMeans, $p \leq 0.0085$) among stations are indicated by different letters, reading horizontally.

	Cane Bayou	Bayou Lacombe	Lake St. Catherine
PSA (m^2 / m^2)			
<u>V. americana</u>	0.408 (0.044) A	0.407 (0.043) A	0.221 (0.044) B
<u>M. spicatum</u>	0.111 (0.012) A	0.007 (0.012) B	0.113 (0.012) A
<u>R. maritima</u>	0.006 (0.009) A	0.005 (0.009) A	0.053 (0.009) B
Relative dominance (%)			
<u>V. americana</u>	57.7 (3.3) A	70.6 (3.2) B	29.1 (3.3) C
<u>M. spicatum</u>	24.1 (2.3) A	0.4 (2.3) B	40.4 (2.3) C
<u>R. maritima</u>	1.1 (1.8) A	3.5 (1.8) A	26.9 (1.8) B

significantly higher for samples dominated by Ruppia maritima than by V. americana and the mean salinity estimate.

Discussion:

Although the distribution and abundance of submerged aquatic vegetation has been studied in Lake Pontchartrain (see Montz 1978, Mayer 1986) and other systems (see Orth and Moore 1984 for a review of Chesapeake Bay, Adair et al. 1994), few studies have examined the relationships between submerged macrophytes and environmental gradients (but see Dennison et al. 1993). In the Lake Pontchartrain estuary, the changing species composition of the submerged macrophytes and the reduction of the area covered are also concerns (Montz 1978, Mayer 1986). Vallisneria

Table 2.4: Differences in mean plant surface areas (\pm 1SE) and mean relative dominance (\pm 1SE) for individual macrophyte species among seasons in the Lake Pontchartrain estuary. Significant differences (LSMeans, $p \leq 0.0085$) among seasons are indicated by different letters reading horizontally.

	Winter	Spring	Summer	Autumn
PSA (m^2 / m^2)				
<u>V. americana</u>	0.200 (0.050) A	0.280 (0.050) AB	0.442 (0.050) B	0.460 (0.050) B
<u>M. spicatum</u>	0.049 (0.014) A	0.115 (0.014) B	0.070 (0.014) AB	0.075 (0.014) AB
<u>R. maritima</u>	0.013 (0.011)	0.040 (0.011)	0.016 (0.011)	0.015 (0.011)
Relative dominance (%)				
<u>V. americana</u>	55.8 (4.0)	46.4 (4.0)	58.8 (4.0)	50.3 (4.0)
<u>M. spicatum</u>	16.3 (3.0) A	28.5 (3.0) B	17.1 (3.0) A	22.7 (3.0) AB
<u>R. maritima</u>	12.9 (2.3)	13.4 (2.3)	6.3 (2.3)	8.8 (2.3)

americana habitat was characterized by exposed sandy areas and low salinities (Table 2.5). Myriophyllum spicatum habitat was characterized by relatively greater depths, finer substrates, lower salinities, and slower currents. Ruppia maritima habitat was characterized by nearshore shallow areas with relatively higher salinity and fine substrates.

The relationships of abundance and relative dominance (Mueller-Doubois and Ellenberg 1974) of particular macrophyte species with environmental variables allow a more accurate prediction of future changes in the distribution and species composition of submerged macrophytes. The high significance of substrate type with PSA and relative dominance support the theory that wave and current energy strongly influence the distributions and abundances of the macrophytes in the Lake Pontchartrain estuary, especially Myriophyllum spicatum. Salinity also influenced macrophyte dominance (Table 2.2), abundance (Table 2.1), and distribution (Table 2.5). Nevertheless,

Table 2.5: Environmental means for measured variables among samples with a relative dominance of over 70 % and the overall means. Significant differences (LSMeans, $p \leq 0.0085$) among macrophyte species and overall means are indicated by different letters, reading horizontally.

	<u>V. americana</u>	<u>M. spicatum</u>	<u>R. maritima</u>	Overall Mean
Substrate	4.0 (0.06) A	3.0 (0.11) B	3.2 (0.15) B	3.7 (0.04) C
Distance (m)	38.7 (1.30) A	22.3 (2.29) B	19.4 (3.20) B	33.4 (0.91) C
Depth (cm)	44.7 (1.01) A	50.8 (1.78) B	38.6 (2.48) A	43.7 (0.71) A
Salinity (‰)	2.8 (0.13) A	3.3 (0.23) AB	4.2 (0.32) B	3.0 (0.09) A
Velocity (cm / s)	3.5 (0.14) A	2.6 (0.25) B	3.9 (0.35) A	3.3 (0.10) A
Temperature (°C)	21.8 (0.49)	21.5 (0.86)	19.3 (1.20)	21.7 (0.34)
Dissolved Oxygen (mg /	9.2 (0.12)	9.1 (0.20)	9.7 (0.29)	9.2 (0.08)

l)

variables such as water velocity can both influence and be influenced by the presence of macrophytes (Titus and Adams 1979), so any inferences must be made with caution.

Substrate type can both influence and be influenced by the presence of submerged macrophytes (Grace and Wetzel 1978, Keast 1984), although in some instances other factors can influence both. Submerged macrophytes grow faster when rooted in fine, organic-rich sediments (Grace and Wetzel 1978). Nevertheless, submerged macrophytes can increase the organic content of the sediments through production of leaf litter (Grace and Wetzel 1978, Keast 1984). By dampening waves and currents (Machata-Wenninger and Janauer 1991), submerged macrophytes also facilitate the deposition of fine sediments (Keast 1984, and see Chapter 5). Other factors, such as wave energy, can influence both substrate characteristics and macrophyte abundances. V. americana is more resistant to damage from wave energy than Myriophyllum spicatum and Ruppia maritima (Titus and Adams 1979, Mayer 1986), which resulted in dominance by V. americana at the more exposed Bayou Lacombe and Cane Bayou stations (Table 2.3). Wave energy at the Lake Pontchartrain stations are higher due to greater wind fetches (> 25 km, versus < 1 km in Lake St. Catherine) in a relatively uniform wind field (Pond and Pickard 1983). The higher wave energy at this station results in a coarser substrate through size-selective resuspension of finer sediments (Kennett 1982). Therefore, the relationships of the distribution and relative dominance of V. americana to coarser substrates were probably due to the influence of high wave energy on all of these variables. The protected nature of the Lake St. Catherine station allowed factors other than wave energy to influence macrophyte distributions, and the relative dominance of M. spicatum and R. maritima was higher under these conditions (Table 2.3).

The distributions of many macrophytes, especially freshwater species, are also strongly affected by salinity (Orth and Moore 1984, Mayer 1986, Twilley and Barko

1990). Nutrient loss from freshwater macrophytes increases with salinity (Twilley and Barko 1990), and encourages epiphytic growth, which can reduce available light by up to 50 %. Additionally, freshwater macrophytes such as Vallisneria americana and Myriophyllum spicatum have limited osmoregulatory capabilities (Twilley and Barko 1990). Although V. americana and M. spicatum can withstand salinities as high as 12 and 15 ‰, respectively (Grace and Wetzel 1978, Mayer 1986, Twilley and Barko 1990), the rate of change of salinity may strongly influence survival within their tolerance ranges (Twilley and Barko 1990). Whereas Ruppia maritima can grow in fresh water, it is a halophyte with a salinity tolerance of up to 40 ‰ (Mayer 1986), and was observed at salinities significantly higher than both V. americana and the overall mean salinity (Table 2.5).

Because submerged macrophytes require light for photosynthesis, their distributions can also be limited by depth and turbidity. Myriophyllum spicatum can grow at depths of up to 4 m in clear water (Grace and Wetzel 1978). A high spring growth rate utilizing stored carbohydrates (Titus and Adams 1979) and a longer growing season (Grace and Wetzel 1978) establishes M. spicatum earlier in the growing season than Vallisneria americana. V. americana has a dormancy period at higher latitudes (Grace and Wetzel 1978, Titus and Adams 1979) and declined in winter months in the Lake Pontchartrain estuary (Table 2.4 and Figure 2.2), but did not become dormant. Whereas the light compensation point for M. spicatum is about 1 to 2 % of the surface light (Grace and Wetzel 1978), for Ruppia maritima it is 8.2 % (Dennison et al. 1993). In addition to the low light compensation point, M. spicatum responds more strongly to shading by stem elongation than does V. americana (Twilley and Barko 1990). The morphology of M. spicatum also concentrates photosynthetic biomass near the surface (Grace and Wetzel 1978), allowing growth in turbid water. This surface growth shades slower growing macrophytes, possibly limiting their growth (Grace and Wetzel 1978). Turbidity in Lake Pontchartrain increased by 50 % between the mid 1950's and 1980

(Stone et al. 1980), resulting in a reduction of the maximum depth of native macrophyte beds from 1.8 m to 1.2 m (Mayer 1986). Although M. spicatum is most commonly found in depths of 1.5 to 4 m (Grace and Wetzel 1978), in the Lake Pontchartrain estuary high turbidity limits the exotic macrophyte to depths of 1.8 m (Mayer 1986). Because of its adaptations to low light intensities, M. spicatum can grow in deeper water than the native macrophytes. Nevertheless, the relatively shallow depths that support M. spicatum may inhibit the full development of its canopy (Grace and Wetzel 1978).

In the last 40 years, the area covered by submerged macrophytes in Lake Pontchartrain estuary has declined dramatically, and the species composition has changed as well. The vegetated areas of Lake Pontchartrain have declined from over 8,000 ha in the 1960's to less than 400 ha in 1985 (Montz 1978, Mayer 1986). Concurrent with this decline, the exotic Myriophyllum spicatum increased its distribution, and is currently one of the three dominant macrophyte species in the estuary (Mayer 1986, personal observation). M. spicatum partially replaced Vallisneria americana in a Wisconsin lake (Titus and Adams 1979) and displaces other macrophytes through strong competition (Grace and Wetzel 1978). In the Lake Pontchartrain estuary it has partially replaced Ruppia maritima and V. americana (Mayer 1986). Although high wave energy restricts the distribution of M. spicatum along the north shore of Lake Pontchartrain more than V. americana, which is more resistant to mechanical damage (Titus and Adams 1978, Mayer 1986), in the lower energy waters of Lake St. Catherine M. spicatum has apparently partially displaced R. maritima. In a 1985 survey of macrophytes in Lake St. Catherine, M. spicatum accounted for 95 % of the submerged vegetation, whereas R. maritima only accounted for 5 % (Mayer 1986). No rooted specimens of V. americana were observed in 1985, but V. americana was present there during this study. Since no historical records exist on the distribution of submerged macrophyte species in Lake St. Catherine prior to 1985, it is unclear whether M. spicatum invaded bare substrate or displaced R. maritima. The results of other studies, however, suggest that the highly

competitive M. spicatum partially replaced R. maritima (Blackburn and Weldon 1967, Grace and Wetzel 1978, Keast 1984).

The establishment and persistence of Myriophyllum spicatum in the Lake Pontchartrain estuary results from a combination of factors. The estuary is a stressed system (Stone et al. 1980, Mayer 1986), and therefore susceptible to invasion by exotics (Mooney and Drake 1986, and references within). Historically, a variety of influences, such as urban and agricultural runoff, improper sewerage treatment, shell and channel dredging, and shoreline modification have resulted in more than a 50 % increase in the turbidity of the estuary (Stone et al. 1980). This increase in turbidity has apparently lead to a long-term decline in the distribution of native macrophytes (Montz 1978, Mayer 1986). High turbidity limits the depth distribution of macrophytes, but adaptations of M. spicatum to low light levels (Grace and Wetzel 1978, Titus and Adams 1979, Twilley and Barko 1990) allows growth over a greater depth range than the native macrophytes. High wave energy limits the density and distribution of M. spicatum more than the native macrophytes, but in protected lakes and embayments M. spicatum can partially replace native macrophytes (Titus and Adams 1979, Mayer 1986). In the Lake Pontchartrain estuary, conditions favor the persistence of M. spicatum, but management strategies to continue a declining trend in turbidity will probably prevent the exotic from dominating the system.

CHAPTER 3: FISH ASSEMBLAGE DIFFERENCES AMONG NATIVE AND EXOTIC SUBMERGED AQUATIC MACROPHYTES IN THE LAKE PONTCHARTRAIN ESTUARY, USA

Introduction:

The introduction of exotic species is one of the primary factors threatening biodiversity (Ehrenfeld 1970, Diamond and Chase 1986, Mooney and Drake 1986) and is probably second only to the destruction of tropical rain forests as a general threat to the diversity of natural systems. Exotic aquatic plant species can cause a reduction in habitat quality available to the assemblages of associated plants and animals (Grace and Wetzel 1978, Keast 1984, Harlan et al. 1985, Sutton 1986, Tanner et al. 1990, Room and Fernando 1992). Eurasian milfoil Myriophyllum spicatum was first observed in the North American continent in the late 19th century (Blackburn and Weldon 1967). It spread rapidly throughout the eastern United States and Canada, and has been found in salinities ranging from 0 to 14 ‰ (Davis et al. 1974). M. spicatum was first observed in the Lake Pontchartrain estuary in 1978 (Mayer 1986) and is now established as a dominant aquatic macrophyte. Because of the importance of submerged aquatic vegetation to fishes and macroinvertebrates, the continued replacement of native macrophyte species could strongly influence the recruitment and population dynamics of the fishes inhabiting the macrophyte beds. If M. spicatum reduces habitat quality for fishes, the populations of native fishes may be adversely affected by reduced growth rates or survival. In contrast to the dominant native macrophytes in the system, the leaves of M. spicatum are finely branched and concentrate near the water's surface (Grace and Wetzel 1978). At high densities in lakes M. spicatum has a significant effect on biologically important variables compared to many native plants, reducing habitat suitability for some fishes and macroinvertebrates (Keast 1984).

In marine and estuarine systems, structural complexity of submerged macrophytes provides important refuge and foraging sites for many organisms (Orth and

van Montfrans 1987, Rozas and Odum 1988, Heck and Crowder 1991). Submerged vegetation in the littoral zones in the Lake Pontchartrain estuary serves important nursery functions and contrasts sharply with the simple soft bottoms that dominate much of the littoral and deeper portions of the system. The structural complexity of submerged aquatic macrophytes offers protection from predation and in some cases provides an increased availability of food resources, especially for smaller organisms (Stoner 1982, Boesch and Turner 1984, Rozas and Odum 1988); moreover, the complexity contributes to the relatively high secondary productivity and high abundance of fishes and invertebrates in submerged vegetation (Wetzel 1975, Heck and Thoman 1984, Lubbers et al. 1990). Nevertheless, the enhanced survival provided by refugia may be offset by the attraction of predators to sites of high prey density and more predator-prey encounters (Ryer 1988, Hettler 1989, Feller et al. 1990). Plant surface area (PSA) is a good index of structural complexity (Heck and Orth 1980, Heck and Crowder 1991), because the increased surface area per square meter of substrate allows more organisms to occupy a given area of substrate. Increased PSA probably increases the diversity and abundance of the inhabiting organisms. Thus, submerged vegetation offers increased living area, but plant growth forms and densities may influence fish habitat quality with consequent changes in assemblage structure.

At the microhabitat level, fishes presumably select sites in response to environmental variables, balancing net energy gain with predator avoidance and competition (Baltz 1990, Baltz et al. 1993). The microhabitat of an organism is ultimately defined as the place where that organism is located at a point in time (Baltz 1990). For the purposes of this study, the pattern of microhabitat use for a species is the statistical picture of the population's response (i.e., means, variances, ranges) to environmental and temporal gradients occupied by individuals collected in the study area (Hurlbert 1981). To address the question of habitat quality, I used a comparative descriptive approach (Crowder 1990) across several locations to infer the underlying

patterns of fish assemblage structure and to describe population responses of common fish species to environmental variables, including three submerged macrophyte species and unvegetated substrate. The objectives of this study were: (1) to compare fish assemblages associated with submerged macrophytes to determine usage patterns and determine if the patterns of usage in M. spicatum differed from those of the native macrophytes, and (2) to compare spatial and temporal resource utilization by common fishes in these assemblages.

Study Area:

Lake Pontchartrain is a large, shallow bay located just north of New Orleans in southeast Louisiana (Figure 3.1). It covers an area of 1,630 km², has a mean depth of 3.7 m, and has a maximum depth of 5 m (Sikora and Kjerfve 1985). Myriophyllum spicatum is established in Lake Pontchartrain and several smaller lakes to the southeast, including Lakes Borne and St. Catherine, which are connected to the lake and to the Gulf of Mexico by two main passes, the Rigolets and Chef Pass. Submerged macrophytes were sampled at two stations along the northeastern shore of Lake Pontchartrain and at one station in Lake St. Catherine. The three stations, chosen to characterize the salinity gradient, were near the mouth of Cane Bayou and the mouth of Bayou Lacombe in Lake Pontchartrain, and in Grand Coin Bay at the north end of Lake St. Catherine.

Historically, submerged macrophytes were abundant on all shores of Lake Pontchartrain, but between 1963 and 1985 the total area covered by submerged macrophytes decreased by 50 % (Darnell 1961, Montz 1978, Mayer 1986). High turbidity limited submerged macrophytes to depths in the littoral zone of two meters or less, and reductions in water quality due to municipal and agricultural run-off restricted the major submerged macrophyte beds to the northeastern shore of Lake Pontchartrain and the adjacent coastal bays (Mayer 1986). Shell dredging has also been implicated as a cause of higher turbidity, but has not been permitted since 1990. While the native

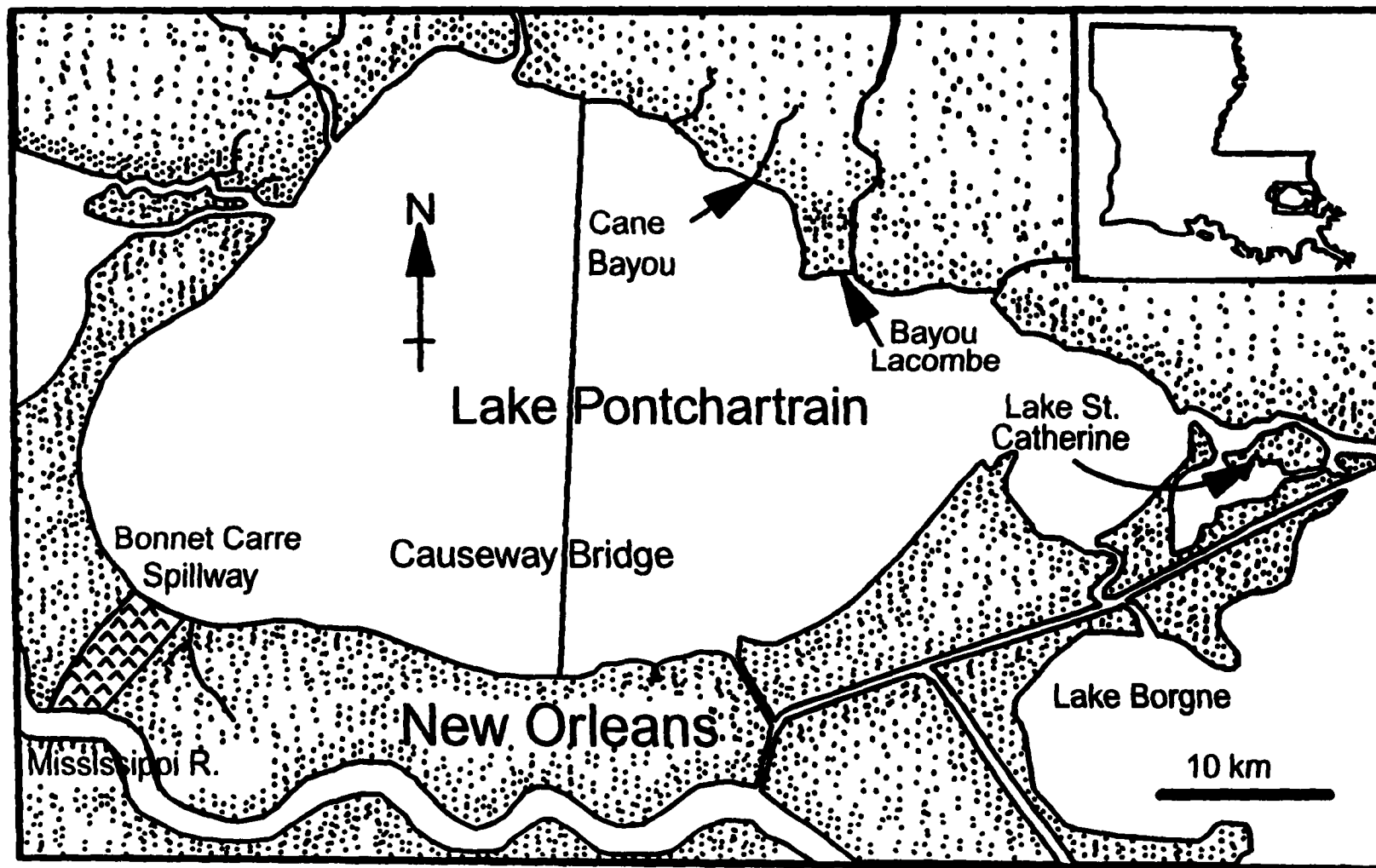


Figure 3.1: The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer 1986).

submerged macrophytes, primarily the wigeongrass Ruppia maritima, and wild celery Vallisneria americana, were declining between 1973 and 1986, the area covered by the southern naiad Najas quadalupensis and the exotic milfoil Myriophyllum spicatum was increasing (Mayer 1986). Nevertheless, the trend of increased area covered by M. spicatum now seems to have been arrested or reversed (personal communication, Michael Poirrier, University of New Orleans, Louisiana).

Methods:

A modified Wegener ring (Weinstein and Brooks 1983) was used to estimate fish abundances on a monthly basis from March 1991 to January 1993, except January 1992. The Wegener ring consisted of a vertical cylinder of heavy fabric that extended 110 cm in height above a circular stainless steel base ring (10 cm wide x 1.23 m diameter, 1.18 m²). When deployed, the fabric walls were supported by a float ring at the top. This ring design was adequate for sampling small adult fishes, juveniles of the larger fish species, and most macroinvertebrates (Chick et al. 1992). A boom extending three meters off the bow of a 5.2 m boat was used to deploy the sampler. The Wegener ring was held one-half meter above the water's surface until it was dropped with a pull-pin release. Upon deployment, the base ring was checked to ensure that it had adequately penetrated the substrate to permit a quantitative estimate of species abundances.

Each month, twelve samples at each station were stratified among the common submerged macrophyte species and unvegetated substrate. When all of the submerged macrophytes were not present, 12 samples were stratified among the existing plant species and unvegetated substrate to maximize the information gained per trip. Within strata each sampling site was randomly selected to represent the range of submerged macrophyte densities present and the range of depths up to a maximum of one meter. Each sample was unique and considered to be independent for statistical purposes.

In conjunction with each sample, I collected microhabitat data, including dissolved oxygen concentration, water temperature, salinity, water surface velocity,

minimum and maximum water depth, distance from shore, turbidity, and substrate type. Median water depth was calculated as the mean of minimum and maximum depths. Temperature, salinity, and dissolved oxygen were measured with a Hydrolab model SRV2-SU. Surface water velocity was estimated by measuring the horizontal displacement of a neutrally buoyant object for ten seconds. Turbidity was measured in NTU with a Monitek model 21 PE portable nephelometer. Substrate type was estimated on a particle size scale: 1 = clay, 2 = mud (sand and silt), 3 = silt, 4 = sand, 5 = organic detritus, 6 = shell or shell fragments. Additionally, submerged macrophytes present were identified and the number and median length of stems for each species was assessed directly by counting stems and measuring subsamples of lengths within the drop ring.

Five submerged macrophyte species were found in the study area, including Vallisneria americana, Myriophyllum spicatum, Ruppia maritima, Najas quadalupensis, and the slender pondweed Potamogeton pusillus. Names for submerged macrophytes follow Chabreck and Condrey (1979). The most abundant submerged macrophyte in Lake Pontchartrain, especially at the Bayou Lacombe station, was V. americana, which grows as clusters of ribbon-like blades. M. spicatum and R. maritima were also abundant. M. spicatum generally has whorls of four feathery leaves along a cylindrical stem, and R. maritima has slender, branching stems with slim, flat leaves. N. quadalupensis and P. pusillus were infrequently encountered, and 26 samples (4.8 %) in which they dominated were omitted from the initial data set and further analyses.

The plant surface area was calculated from estimates of stem density and length for each species. I measured the surface area of multiple samples of individual submerged macrophyte stems and leaves using a Li-Cor LI-3000 portable leaf area meter. I then regressed plant surface area (PSA, in m² plant area per m² substrate) on stem length to provide species-specific relationships:

<u>Vallisneria americana</u> :	$PSA = 1.258 * L * C / 10000$ (N = 20, $R^2 = 0.99$),
<u>Myriophyllum spicatum</u> :	$PSA = 1.058 * L * C / 10000$ (N = 20, $R^2 = 0.80$),
<u>Ruppia maritima</u> :	$PSA = 0.232 * L * C / 10000$ (N = 19, $R^2 = 1.00$),

where L is the stem length (cm) and C is the number of stems of that species in the sample. Total PSA for a sample is reported, and samples were assigned to vegetation types by dominance. If a sample had less than $0.0118 \text{ m}^2 / \text{m}^2$ total surface area it was treated as an unvegetated site.

Following the environmental characterization of each sample site, a 100 cc solution of 5 % dry rotenone cube' was uniformly suspended in the sampler to facilitate recovery of organisms (Davies and Shelton 1983). All fishes affected by the rotenone were collected with a small dip net and preserved in 95 % ethanol. The enclosed area was then systematically swept six times with a large rectangular hand net (39 x 30 cm, 5 mm diamond mesh) to capture a high percentage of the remaining organisms that were preserved with a 10 % buffered formalin solution for 24 hrs, then transferred to 95 % ethanol. All fishes were identified, counted, and measured to the nearest millimeter standard length (SL). Common and scientific names of fishes (Table 3.1) follow Robins et al. (1991).

The DeLury (1947) depletion method was used during a preliminary study to estimate the capture efficiency by systematic hand netting for organisms that were not easily captured following the application of rotenone. A common organism in the study area, the grass shrimp (Palaemonetes pugio, mean size 7.55 mm carapace length), was used to identify an adequate level of hand netting effort. The results indicated that six systematic sweeps, each of which covered the entire basal area of the Wegener ring, were sufficient to remove 96.5 % of the individuals present ($F = 179.9$, $df = 1$ and 12 , $p \leq 0.0001$; $R^2 = 0.97$).

I used a multiple analysis of variance (MANOVA) to examine the responses of fish populations along environmental gradients. The MANOVA simultaneously compared all environmental variables measured with the abundances of multiple fish species. Environmental variables that accounted for significant variation in the abundance for each fish species were identified, as were overall effects of variables on assemblage structure patterns. Abundances were log transformed ($\log_e[\text{abundance} + 1]$) to normalize the data. Rare fishes (i.e., < 10 total individuals caught or a frequency of occurrence in < 1 % of the samples) were excluded from this and subsequent analyses. Fishes that complete their life cycle in the Lake Pontchartrain estuary were classified as resident species, and those that migrate into or out of the estuary for some stage of their life cycle were classified as transients. Speckled worm eel and skilletfish were classified as residents after Baltz et al. (1993) and Hoese and Moore (1977). Transient species abundances and sizes were also regressed against months to identify recruitment periods.

A factor analysis was employed to identify groupings of correlated environmental variables and to identify species responses to these groupings (Grossman et al. 1991). The varimax rotation option (Johnson and Wichern 1988) in the factor analysis of environmental data from 517 samples (SAS Institute 1989) yielded four axes with eigenvalues greater than one. Weighted means of the factor scores were calculated for each fish species, and were plotted on four axes to identify the major responses of fish abundances to environmental variables. The centroids, or three-dimensional means (May 1975, Baltz and Moyle 1993), of the four submerged vegetation types (including unvegetated substrate) and the three stations along these axes were plotted to visualize the relationships of class variables to the fish abundances.

The factor analysis identified groups of environmental variables. Two were interpreted as seasonality and station differences. A general linear models approach (SAS Institute 1989) was used to test the groups of environmental variables for

significance. In addition to the groupings of season and station, differences among the three submerged macrophytes were also analyzed. Differences in the mean abundance of fishes for statistically significant groups of environmental variables (SAS Institute 1989) were tested a posteriorily with the least squares means test (LSMeans). Because unequal numbers of samples were collected in each season (defined by solstices and equinoctial dates), sampling bias was avoided by using weights based on seasonal sampling effort. To yield a conservative Type I error rate of 0.05 (Johnson and Wichern 1988), the alpha level was adjusted using the Dunn-Šidák correction (Sokal and Rohlf 1981). The appropriate critical values were computed using the expression: $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α' is the experimentwise adjusted error rate, k is the number of comparisons, and α is the critical value. Spearman's rank correlations (SAS Institute 1989) and Schoener's index of similarity (Schoener 1970) were also used to compare fish assemblage structures between vegetation species and unvegetated sites.

For each vegetation type, average fish species diversities (Shannon-Weiner H') were calculated (Pielou 1966) using an approach described by Hurtubia (1973). Samples within each vegetation type were randomly ordered and progressively accumulated to calculate and plot H' at each step. Plots of cumulative diversity were examined to identify asymptotic values, and subsequent points were used to estimate the mean and variance (Hurtubia 1973). Species evenness and richness were also compared using this method.

Results:

From 517 samples obtained between March 1991 and January 1993, I collected 29 fish species totaling 3,564 individuals (Table 3.1). The fishes were dominated by rainwater killifish (31.65 %). Other abundant fishes were gulf pipefish (22.14 %), naked goby (22.14 %), and clown goby (10.69 %). Together these four species comprised 87.6 % of all the fishes collected and occurred in one-fourth to

Table 3.1: List of fish species collected from the Lake Pontchartrain estuary by drop sampling (March, 1991 to January, 1993), with the total number of each species collected, the percentage of the total (3,564 fishes) caught, the number of samples in which the species was observed, and the percent frequency of the samples in which the species was observed (517 samples total).

Common Name	Scientific Name	Total Number Caught	Percent Total Numbers	Number of Samples Present	Percent Frequency of Occurrence
rainwater killifish	<u>Lucania parva</u>	1,128	31.65	147	28.4
naked goby	<u>Gobiosoma bosc</u>	824	23.12	187	36.2
gulf pipefish	<u>Syngnathus scovelli</u>	789	22.14	270	52.2
clown goby	<u>Microgobius gulosus</u>	381	10.69	121	23.4
bay anchovy	<u>Anchoa mitchilli</u>	65	1.82	16	3.1
inland silverside	<u>Menidia beryllina</u>	55	1.54	33	6.4
speckled wormeel	<u>Myrophis punctatus</u>	54	1.52	35	6.8
bluegill	<u>Lepomis macrochirus</u>	39	1.09	21	4.1
skilletfish	<u>Gobiesox strumosus</u>	37	1.04	21	4.1
pinfish	<u>Lagodon rhomboides</u>	33	0.93	21	4.1
freshwater goby	<u>Gobionellus shufeldti</u>	27	0.76	14	2.7
sailfin molly	<u>Poecilia latipinna</u>	23	0.65	2	0.4
hogchoker	<u>Trinectes maculatus</u>	20	0.56	16	3.1
least killifish	<u>Heterandria formosa</u>	18	0.51	2	0.4
spotted seatrout	<u>Cynoscion nebulosus</u>	15	0.42	10	1.9
spot	<u>Leiostomus xanthurus</u>	14	0.39	7	1.4
Atlantic croaker	<u>Micropogonias undulatus</u>	9	0.25	7	1.4
Atlantic needlefish	<u>Strongylura marina</u>	9	0.25	9	1.7
blackcheek tonguefish	<u>Symphurus plagiusa</u>	8	0.22	7	1.4
warmouth bass	<u>Lepomis gulosus</u>	5	0.14	1	0.2
yellow bass	<u>Morone mississippiensis</u>	3	0.08	3	0.6
Atlantic stingray	<u>Dasyatis sabina</u>	1	0.03	1	0.2
blue catfish	<u>Ictalurus furcatus</u>	1	0.03	1	0.2
diamond killifish	<u>Adinia xenica</u>	1	0.03	1	0.2
sheepshead minnow	<u>Cyprinodon variegatus</u>	1	0.03	1	0.2
silver perch	<u>Bairdiella chrysoura</u>	1	0.03	1	0.2
southern flounder	<u>Paralichthys lethostigma</u>	1	0.03	1	0.2
spotted gar	<u>Lepisosteus oculatus</u>	1	0.03	1	0.2
largemouth bass	<u>Micropterus salmoides</u>	1	0.03	1	0.2

one-half of all samples. I selected ten resident species and four transient species in the fish assemblage, based on abundance ($> 0.3\%$ total numbers) and occurrence (present in > 10 samples). Other common resident species included in the analyses (Table 3.1) were speckled worm eel, bluegill, skilfish, and freshwater goby. Transient fishes included bay anchovy, pinfish, spotted seatrout, spot, and Atlantic croaker. Of the transient species, only bay anchovy, pinfish, spotted seatrout, and spot were collected in numbers adequate for detailed analyses. Differential sampling effort across season (Table 3.2) led to a slightly skewed rank order (Table 3.1). After adjusting for sampling effort, the first six species retained the same rank order; however, the adjusted ranks for the seventh through tenth species were speckled worm eel, bluegill, skilfish, and pinfish, respectively. Freshwater goby was still eleventh after adjustment, and the remaining fishes were not collected in sufficient numbers for further analysis.

Environmental conditions changed seasonally during the study period (Table 3.2). All variables, except water velocity, showed at least one significant difference among seasons (LSMeans, $p \leq 0.0083$ for all significant comparisons). Temperature means were significantly different in each season, highest in summer and lowest in winter. Salinity means were generally higher in autumn and winter and lower in spring and summer. Mean turbidity was highest in spring and also high in winter. Mean dissolved oxygen levels were significantly lower in spring and summer than in autumn and winter. Mean depth sampled was highest in summer months, and mean distance from shore was highest in winter. Mean PSA was significantly higher in the summer and autumn than in winter, with spring having an intermediate value. Vallisneria americana had peak PSA means in summer and autumn, whereas Ruppia maritima and Myriophyllum spicatum had peak PSA means in spring.

Environmental conditions influenced the distribution and abundance of most of the common fishes. In the MANOVA, 8 of 9 measured environmental variables including PSA, temperature, salinity, substrate, median depth, distance

Table 3.2: Seasonal means (\pm 1SE) of environmental variables observed in Lake Pontchartrain between March, 1991 and January, 1993. Significant differences among seasonal means ($p \leq 0.0083$, Least Squares Means Tests) are indicated by different letters reading horizontally.

	Winter	Spring	Summer	Autumn
	N = 94	N = 97	N = 217	N = 109
Plant Surface Area (m ² / m ²)	0.26 (0.03) A	0.44 (0.06) AB	0.55 (0.04) B	0.57 (0.07) B
Temperature (°Celsius)	13.10 (0.16) A	25.84 (0.50) B	30.41 (0.19) C	17.41 (0.47) D
Salinity (‰)	3.26 (0.18) A	2.70 (0.21) B	2.25 (0.15) B	3.88 (0.20) C
Substrate	3.92 (0.09) A	3.46 (0.12) B	3.78 (0.07) AB	3.76 (0.09) AB
Median Depth (cm)	39.15 (1.53) A	45.70 (1.76) B	50.71 (1.14) B	39.35 (1.25) A
Distance from Shore (m)	38.80 (2.45) A	28.16 (1.87) B	36.39 (1.56) AC	30.20 (1.76) BC
Dissolved Oxygen (mg / l)	10.46 (0.09) A	8.31 (0.23) B	8.29 (0.11) B	9.91 (0.13) A
Turbidity (NTU)	8.31 (1.06) A	9.30 (1.12) A	6.06 (0.32) B	5.18 (0.47) B
Water Velocity (cm / s)	3.23 (0.23)	3.74 (0.25)	3.48 (0.13)	3.15 (0.24)

from shore, dissolved oxygen, and turbidity had significant ($N = 517$, $df = 17$ and 488 , $p \leq 0.01$) effects on overall fish abundances (Table 3.3). Each environmental variable also significantly ($p \leq 0.05$) contributed to the prediction of the abundance pattern for at least one fish species; moreover, for most fishes, more than one environmental variable significantly influenced abundance. The density of naked goby was significantly influenced by every environmental variable measured except water velocity. Three species, inland silverside, hogchoker, and spot, did not qualify for a posteriori testing (MANOVA, $p > 0.61$, $p > 0.73$, and $p > 0.08$, respectively).

Table 3.3: Means of environmental variables utilized by common fishes (\pm 1SE), adjusted for seasonal differences in sampling effort. Significance levels of the influence of environmental variables on the fish abundances are indicated with asterisks: * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001 (MANOVA: $n = 517$, $df = 1$ and 509). F values from the overall effect of the environmental variable given by MANOVA analysis are given, as are the associated significance levels ($df = 14$ and 494).

	Plant Surface Area (m^2 / m^2)	Temperature (Celsius)	Salinity (‰)	Substrate	Depth (cm)	Distance from Shore (m)	Diss. Oxygen (mg / l)	Turbidity (NTU)	Water Velocity (cm / s)
Resident species:									
rainwater killifish	0.68 (0.05)***	27.31 (0.52)***	3.42 (0.22)**	3.26 (0.10)***	46.94 (1.20)	22.99 (1.18)	9.01 (0.18)*	7.19 (0.51)	3.14 (0.14)
naked goby	0.55 (0.04)***	24.56 (0.52)*	4.18 (0.18)***	3.00 (0.09)***	52.20 (1.13)***	24.90 (1.54)***	9.03 (0.11)**	7.46 (0.56)**	3.28 (0.14)
gulf pipefish	0.68 (0.04)***	24.21 (0.46)*	3.29 (0.15)*	3.55 (0.07)	47.66 (0.94)	30.31 (1.15)*	9.12 (0.11)**	6.47 (0.41)	3.03 (0.12)
clown goby	0.50 (0.05)	26.76 (0.57)***	4.50 (0.23)***	2.85 (0.10)***	52.69 (1.38)**	19.33 (1.00)*	8.77 (0.15)**	7.22 (0.56)**	2.94 (0.15)
inland silverside	0.51 (0.08)	25.51 (1.25)	2.95 (0.34)	3.59 (0.19)	44.38 (2.78)	31.36 (3.13)	9.20 (0.33)	6.06 (0.84)	3.21 (0.35)
speckled wormeel	0.68 (0.09)	29.99 (0.39)***	2.95 (0.43)	3.78 (0.16)	51.18 (2.22)	28.03 (2.69)	8.56 (0.25)	6.89 (0.82)	3.53 (0.31)
bluegill	1.13 (0.20)***	27.60 (1.33)	2.51 (0.56)	3.71 (0.20)	49.19 (3.47)	24.57 (2.52)*	8.45 (0.56)*	7.89 (1.42)	3.48 (0.47)
skilletfish	0.76 (0.12)	29.13 (0.72)*	3.87 (0.48)*	3.13 (0.30)**	58.81 (2.61)	37.14 (5.28)*	8.05 (0.26)	2.91 (0.25)	3.19 (0.39)
freshwater goby	0.80 (0.19)**	24.37 (2.18)	4.94 (0.34)	1.88 (0.23)***	50.96 (3.49)	20.50 (2.76)	8.11 (0.56)	6.89 (0.82)	2.21 (0.38)
hogchoker	0.49 (0.12)	23.97 (2.12)	3.20 (0.47)	3.63 (0.26)	52.66 (3.75)	33.44 (3.95)	9.35 (0.27)	3.86 (0.76)	2.94 (0.49)
Transient species:									
bay anchovy	0.18 (0.05)	26.98 (1.67)	5.38 (0.69)***	2.94 (0.26)*	60.97 (4.12)**	18.06 (3.13)	8.33 (0.36)	7.51 (1.12)	3.31 (0.42)
pinfish	0.40 (0.05)	17.54 (0.40)***	4.67 (0.44)	3.01 (0.25)	47.52 (2.69)	26.90 (3.94)	9.37 (0.32)	4.89 (0.59)	2.95 (0.37)
spotted seatrout	0.91 (0.19)**	22.79 (2.26)	4.71 (0.59)	2.88 (0.43)*	54.35 (4.79)	28.50 (5.53)	9.03 (0.51)	3.00 (0.78)	4.10 (0.84)
spot	0.32 (0.10)	16.04 (1.84)	3.40 (0.70)	3.30 (0.46)	42.64 (4.61)	21.14 (3.07)	9.79 (0.38)	5.94 (1.38)	4.71 (0.84)
F Value of Overall MANOVA Effect	13.16	10.24	10.12	8.24	3.32	3.17	2.20	2.12	1.72
Pr > F	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0069	0.0099	0.0479

In the factor analysis used to examine associations among environmental variables and plant and fish species, each of nine environmental variables loaded heavily ($\geq |0.50|$) in one of four factors (Table 3.4). Four rotated factors had eigenvalues greater than one and together explained 68 % of the environmental variance measured. Factor One (21.0 % of the total variance) was interpreted as a large-scale spatial axis in which salinity was related negatively to substrate and distance from shore. Factor Two (19.9 %) was interpreted primarily as a seasonal axis and weighted positively for temperature and depth and negatively for dissolved oxygen. Factor Three (14.3 %) reflected a turbidity gradient that was also related positively with water velocity and negatively with salinity. Factor Four (12.3 %) was a PSA gradient that was also slightly negatively weighted for water velocity.

The major habitat types (i.e., macrophyte species and unvegetated substrate) showed relationships with environmental gradients in the factor analysis that were also reflected in the similarity of their fish assemblages. Myriophyllum spicatum and Ruppia

Table 3.4: Rotated factor loadings (VARIMAX rotation over four axes) for the environmental variables measured in 517 samples at three stations in the Lake Pontchartrain estuary between March, 1991 and January, 1993.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Substrate	0.86	-0.16	0.01	-0.01
Distance from Shore	0.80	0.01	-0.18	0.00
Salinity	-0.70	-0.16	-0.47	-0.15
Dissolved Oxygen	0.03	-0.80	0.10	0.13
Temperature	0.07	0.77	0.22	0.24
Median Depth	-0.11	0.69	-0.24	0.00
Turbidity	0.15	0.08	0.84	-0.04
Water Velocity	-0.11	-0.19	0.46	-0.52
Plant Surface Area	0.13	0.07	0.03	0.86
Variance	1.95	1.79	1.28	1.11
% Cum. Var.	21.6	41.5	55.8	68.1

maritima were closely associated along all four axes (Figure 3.2) and separated from Vallisneria americana and unvegetated substrate along the spatial and PSA axes. V. americana and unvegetated bottoms were generally found in less saline water and on coarser substrates than M. spicatum and R. maritima. Along the PSA gradient, V. americana had the highest value, unvegetated substrates had the lowest value, and the other two macrophyte species were intermediate. Rainwater killifish, naked goby, gulf pipefish, clown goby, speckled wormeel, bluegill, and skilletfish were significantly more abundant in vegetated areas than in adjacent unvegetated areas (LSMeans Test, $p \leq 0.05$). Nevertheless, with three exceptions I was generally unable to detect significant differences among the macrophyte species for the 14 common fishes (Table 3.5). Rainwater killifish and clown goby were less abundance in V. americana than in the other two macrophyte species, and bay anchovy was significantly more abundant in M. spicatum than in V. americana. Total densities of the common fishes were significantly higher (LSMeans Test, $p \leq 0.0002$) in R. maritima and M. spicatum than on V. americana, and densities were significantly (LSMeans Test, $p \leq 0.0001$) higher in vegetated areas (7.51 ± 0.50 fish / m^2) than in adjacent unvegetated areas (0.33 ± 1.07 fish / m^2).

Compared to the three common submerged macrophytes, the percent similarity (Schoener 1970) of the fish assemblage on unvegetated substrate was low (40.5 %, 41.3 %, and 33.1 %, for V. americana, M. spicatum, and R. maritima, respectively), and an analysis of rank correlation of assemblage structures between combined vegetated and unvegetated areas was not significant (Spearman's $r = 0.15$, $df = 13$, $p \leq 0.60$). The greatest similarity in fish assemblage structure was between M. spicatum and R. maritima (86.1 %), and the rank order of fishes was highly correlated (Spearman's $r = 0.71$, $df = 13$, $p \leq 0.005$). The fish assemblage structure associated with V. americana was more similar to that of M. spicatum (72.4 %, Spearman's $r = 0.62$, $df = 13$,

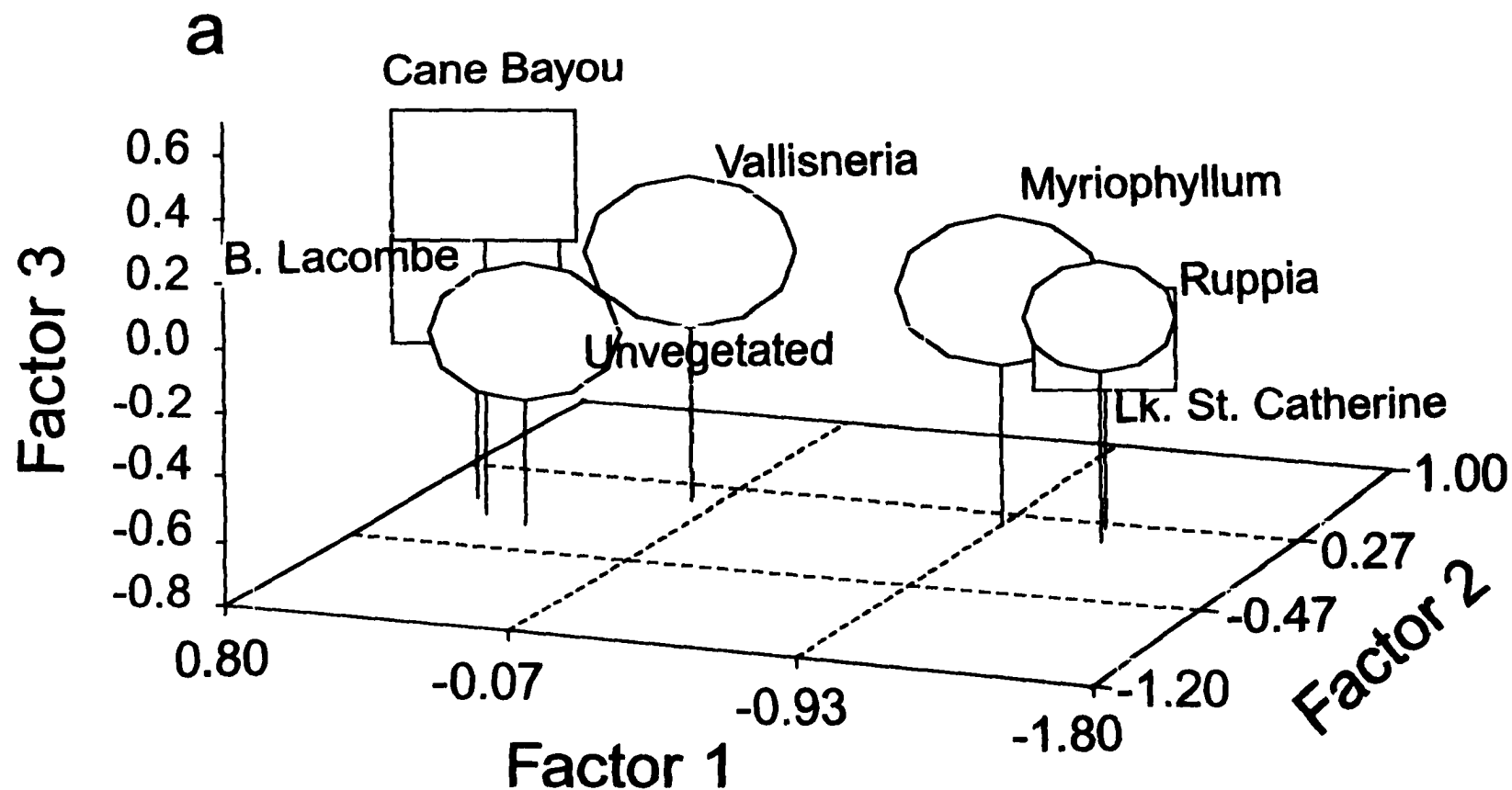


Figure 3.2: a) Station and plant species centroids of the three stations (squares) and four submerged vegetation types (circles) in three-dimensional factor space. The shapes encompass one standard deviation about the centroids. b) Species plot of centroids for 14 common near-shore fishes in three-dimensional factor space. Positions along the fourth factor axis are represented by the shapes: square = -1.5 to -0.5; circle = -0.5 to 0.5; pyramid = 0.5 to 1.5.

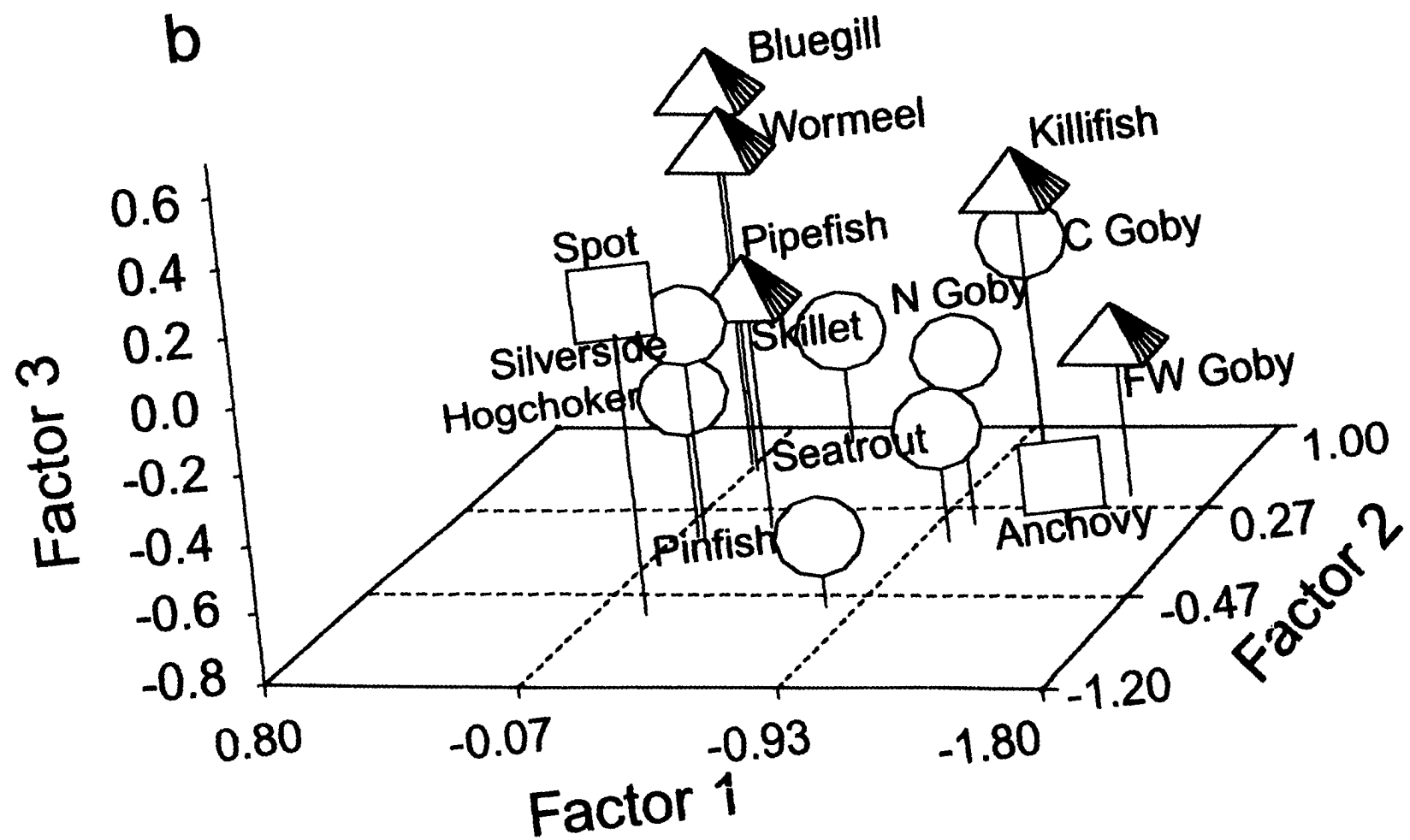


Table 3.5: Selected fish species densities among three submerged macrophytes and unvegetated areas in the Lake Pontchartrain estuary between March, 1991 and January, 1993. Mean abundances are expressed as individuals / m² (\pm 1SE), and are adjusted for differences in seasonal sampling effort. N = number of independent samples. Significant differences among the three macrophytes at $p \leq 0.017$ (Least Squares Means Test) are indicated with different letters reading horizontally. Significant differences between total vegetated and unvegetated areas for each species ($p \leq 0.0002$, Least Squares Means Test) are indicated by asterisks in the "unvegetated" column.

	<u>Vallisneria</u>	<u>Myriophyllum</u>	<u>Ruppia</u>	<u>Unvegetated</u>
	N = 283	N = 102	N = 40	N = 92
Resident species:				
rainwater killifish	0.985 (0.385) A	3.662 (2.097) B	4.885 (3.342) B	0.000 (0.000) *
naked goby	1.688 (0.435)	1.977 (0.728)	1.816 (0.800)	0.067 (0.100) *
gulf pipefish	1.499 (0.247)	2.076 (0.581)	1.921 (0.861)	0.006 (0.017) *
clown goby	0.305 (0.124) A	0.990 (0.367) B	1.562 (0.732) B	0.025 (0.047) *
inland silverside	0.100 (0.058)	0.145 (0.116)	0.058 (0.078)	0.050 (0.075)
speckled worm eel	0.084 (0.042)	0.041 (0.040)	0.031 (0.058)	0.000 (0.000) *
bluegill	0.091 (0.060)	0.052 (0.045)	0.000 (0.000)	0.000 (0.000) *
skilletfish	0.110 (0.065)	0.031 (0.035)	0.027 (0.078)	0.000 (0.000) *
freshwater goby	0.053 (0.041)	0.045 (0.093)	0.041 (0.086)	0.025 (0.047)
hogchoker	0.028 (0.019)	0.051 (0.049)	0.000 (0.000)	0.050 (0.095)
Transient species:				
bay anchovy	0.009 (0.014) A	0.502 (0.718) B	0.105 (0.163) AB	0.014 (0.025)
pinfish	0.087 (0.063)	0.083 (0.064)	0.219 (0.181)	0.014 (0.025)
spotted seatrout	0.043 (0.033)	0.037 (0.055)	0.014 (0.039)	0.000 (0.000)
spot	0.035 (0.042)	0.026 (0.032)	0.154 (0.204)	0.000 (0.000)
Total density:	5.456 (0.588) A	11.264 (0.980) B	12.450 (1.565) B	1.741 (0.732) *

$p \leq 0.017$) than to R. maritima (63.8 %, Spearman's $r = 0.62$, $df = 13$, $p \leq 0.021$).

Assemblages in the native macrophyte species (V. americana and R. maritima combined) were significantly correlated with the exotic M. spicatum (Spearman's $r = 0.57$, $df = 13$, $p \leq 0.033$).

I found significant differences in mean sample and cumulative measured of fish species diversities, evenness and richness across habitat types. The mean (\pm SE) cumulative diversity in V. americana (1.83 ± 0.006) was significantly higher (LSMeans, $p \leq 0.0001$) than all other vegetation types, and mean cumulative diversity in R. maritima (1.60 ± 0.021) and M. spicatum (1.59 ± 0.012) were significantly lower (LSMeans, $p \leq 0.0001$) than in unvegetated areas (1.76 ± 0.014). Mean cumulative species evenness was significantly different among all vegetation types, with the highest evenness in unvegetated samples (0.87 ± 0.005), followed by R. maritima (0.65 ± 0.007), V. americana (0.62 ± 0.002), and M. spicatum (0.54 ± 0.004). Mean cumulative species richness also differed significantly among all vegetation types, and was highest in V. americana (20.18 ± 0.212), followed by M. spicatum (18.79 ± 0.398), R. maritima (12.04 ± 0.693), and unvegetated areas (7.90 ± 0.476).

Several common fishes were well separated along the Factor One axis (Figure 3.2b), a large-scale spatial axis, which also separated the Lake Pontchartrain stations from the Lake St. Catherine station. Salinity significantly increased from west to east (LSMeans, $p \leq 0.0001$), and sand bars at the Bayou Lacombe station supported submerged macrophyte growth farther from shore than at the other stations. Fish species that were most abundant in Lake St. Catherine were usually associated with higher salinities and finer substrates, whereas fish species most abundant in the Lake Pontchartrain stations were associated with lower salinities and coarser substrates. The freshwater goby was found almost exclusively in Lake St. Catherine, and three of the most common resident fishes (naked goby, clown goby, and rainwater killifish), although

Table 3.6: Densities of selected fishes at the three stations sampled in the Lake Pontchartrain estuary between March, 1991 and January, 1993. Means are expressed as individuals / m² (\pm 1 SE), and are adjusted for seasonal differences in sampling effort. N = number of independent samples. Significant differences among the three stations at $p \leq 0.0167$ (Least Squares Means Test) are indicated with different letters reading horizontally.

	Cane Bayou	Bayou Lacombe	Lake St. Catherine
	N = 170	N = 185	N = 162
Resident species:			
rainwater killifish	0.795 (0.400) A	0.236 (0.139) A	4.074 (1.620) B
naked goby	0.162 (0.078) A	0.351 (0.142) A	3.920 (0.773) B
gulf pipefish	1.385 (0.288)	0.833 (0.243)	1.942 (0.467)
clown goby	0.191 (0.100) A	0.026 (0.026) A	1.304 (0.334) B
inland silverside	0.054 (0.039)	0.106 (0.080)	0.129 (0.088)
speckled wormeel	0.054 (0.043)	0.049 (0.036)	0.064 (0.051)
bluegill	0.125 (0.091) A	0.003 (0.008) B	0.053 (0.051) AB
skilletfish	0.003 (0.009) A	0.077 (0.063) AB	0.119 (0.092) B
freshwater goby	0.000 (0.000) A	0.008 (0.013) A	0.130 (0.096) B
hogchoker	0.054 (0.037)	0.015 (0.018)	0.035 (0.055)
Transient species:			
bay anchovy	0.011 (0.020)	0.007 (0.012)	0.343 (0.454)
pinfish	0.016 (0.019) A	0.018 (0.020) A	0.221 (0.121) B
spotted seatrout	0.000 (0.000) A	0.023 (0.021) AB	0.072 (0.063) B
spot	0.041 (0.069)	0.008 (0.013)	0.064 (0.056)
Total density:	1.702 (0.625) A	1.758 (0.674) A	9.884 (0.555) B

present at all stations, were also more abundant in Lake St. Catherine (Table 3.6). As a result, their locations along this axis were nearer to the Lake St. Catherine station than that of gulf pipefish, which was more evenly distributed among stations.

Seasonal variation was primarily reflected along the Factor Two axis by the negative relationship between the loadings of temperature (+0.77) and dissolved oxygen (-0.80). Median depth also weighted heavily (+0.69) in this factor, and was positively related to temperature, reflecting higher tide levels and a possible sampling bias in that deeper samples were taken in the warmer seasons than in the colder seasons (LSMeans, $p \leq 0.0011$). As expected, the three stations did not separate strongly along this gradient.

Resident and transient fishes separated widely along the seasonal axis (Figure 3.2b). Species were ordered from winter abundant species (negative factor scores) to summer abundant species (positive factor scores), with spring and autumn abundant species at intermediate scores. Skilletfish and bluegill were more abundant in the warmer months (Table 3.7). Rainwater killifish, naked goby, clown goby, and gulf pipefish were present all year, but were slightly more abundant in warmer months (Table 3.7), and were placed toward the positive end of the seasonal axis. Spot and pinfish were more abundant in winter (Table 3.7), and separated strongly from the other species.

The common fishes did not segregate strongly (Figure 3.2) along the turbidity gradient (Factor Three), which was positively correlated with water velocity. Limited separation along this axis indicated that turbidity and velocity did not explain much variation in microhabitat use among the common fishes, even though turbidity and velocity together explained 14.3 % of the environmental variance. Bluegill was found at the highest mean turbidity (Table 3.3). All of the common transient fishes except spot concentrated at the low end of the turbidity axis. The Cane Bayou station was more turbid than the other two stations (LSMeans, $p \leq 0.0025$).

Table 3.7: Seasonal densities of selected fishes in the Lake Pontchartrain estuary between March, 1991 and January, 1993. Means are expressed as individuals / m² (\pm 1 SE) and N = number of independent samples. Significant differences adjusted for sampling effort among seasons ($p \leq 0.0083$, Least Squares Means Test) are indicated by different letters reading horizontally.

	Winter	Spring	Summer	Autumn
	N = 94	N = 97	N = 217	N = 109
Resident species:				
rainwater killifish	0.117 (0.046) A	2.438 (0.606) B	2.519 (0.548) B	0.599 (0.227) A
naked goby	0.739 (0.234) A	1.145 (0.190) AB	1.082 (0.156) AB	1.975 (0.394) B
gulf pipefish	0.577 (0.099) A	1.311 (0.220) B	1.343 (0.151) B	1.431 (0.182) B
clown goby	0.063 (0.039) A	0.454 (0.119) AB	0.734 (0.109) B	0.435 (0.103) B
inland silverside	0.045 (0.027)	0.089 (0.036)	0.102 (0.036)	0.093 (0.040)
speckled wormeel	0.000 (0.000) A	0.044 (0.023) AB	0.121 (0.027) B	0.023 (0.013) A
bluegill	0.000 (0.000)	0.044 (0.029)	0.102 (0.035)	0.054 (0.028)
skilletfish	0.000 (0.000) A	0.149 (0.060) B	0.078 (0.026) AB	0.000 (0.000) A
freshwater goby	0.009 (0.009) A	0.000 (0.000) AB	0.059 (0.027) AB	0.086 (0.041) B
hogchoker	0.018 (0.013)	0.009 (0.009)	0.027 (0.012)	0.062 (0.034)
Transient species:				
bay anchovy	0.018 (0.018)	0.017 (0.013)	0.086 (0.041)	0.280 (0.257)
pinfish	0.189 (0.070) A	0.087 (0.032) AC	0.008 (0.006) B	0.000 (0.000) BC
spotted seatrout	0.045 (0.032)	0.000 (0.000)	0.016 (0.010)	0.047 (0.022)
spot	0.072 (0.047) A	0.052 (0.032) AB	0.000 (0.000) B	0.000 (0.000) AB
Total density:	2.349 (0.656) A	4.535 (0.647) AB	6.347 (0.669) B	4.561 (0.666) AB

Common fishes separated strongly along the PSA gradient (Factor Four). The range of fish placements along the PSA axis (2.0 factor units) was greater than along the turbidity axis (1.1 factor units). Spot and bay anchovy were found at the lowest mean PSA values (Table 3.3). Bluegill, freshwater goby, gulf pipefish, speckled worm eel, and rainwater killifish abundances were positively related to PSA. The remaining fishes were clustered in intermediate positions. PSA was significantly higher at Cane Bayou than at the other stations (LSMeans, $p \leq 0.0111$).

Fish assemblage structure in the littoral habitat was seasonally dynamic. The abundances of the 14 common fish species varied greatly among seasons (Table 3.7), and 9 of 14 species showed significant seasonal differences in densities (LSMeans, $p \leq 0.0083$). Combined densities of the common fishes were significantly higher in summer than winter ($p \leq 0.0001$), with other seasons having intermediate values. Seven resident species were significantly (LSMeans, $p \leq 0.0083$) less abundant, on the order of 2 to 10 fold, in winter than in at least one other season (Table 3.7). Transient fishes showed peaks in abundance, due primarily to the presence of juveniles, that were interpreted as recruitment events. Small juvenile pinfish were first observed in December (12.0 ± 0.76 mm SL, $N = 10$), and their numbers declined through July (64.0 ± 9.0 mm SL, $N = 2$), but their size increased significantly (linear slope = 6.71 mm SL / month, $df = 27$, $p \leq 0.0001$). Spot were also first observed in December (10.0 ± 0.0 mm SL, $N = 1$), were collected through May (31.7 ± 4.5 mm SL, $N = 3$), and their growth was also significant (slope = 4.98 mm SL / month, $p > 0.0021$).

Fish abundances differed among stations (Table 3.6). The combined abundance of the common fishes was significantly higher in Lake St. Catherine than in either Lake Pontchartrain station (LSMeans, $p \leq 0.0001$). Rainwater killifish, naked goby, clown goby, pinfish, and freshwater goby were significantly more abundant in Lake St. Catherine than in either Lake Pontchartrain station ($p \leq 0.0167$). Spotted seatrout and skilletfish were significantly more abundant at the Lake St. Catherine station than at the

Cane Bayou station, with the Bayou Lacombe station having an intermediate value.

Bluegill were significantly more abundant at the Cane Bayou station than at the Bayou Lacombe station, with Lake St. Catherine having an intermediate value.

Discussion:

This study was designed to detect differing patterns, if any, of fish usage among exotic and native submerged macrophyte species, and to define the important environmental variables that influence the occurrence of fishes in the littoral areas. I were generally unable to detect significant differences in the patterns of abundance of common fishes among the exotic Eurasian milfoil and the native submerged macrophytes in lakes Pontchartrain and St. Catherine. Nevertheless, I did find three significant differences in the abundance of the common fishes (rainwater killifish, clown goby, and bay anchovy) in Myriophyllum spicatum compared to Vallisneria americana, the most common native species. Also, the most common fishes were generally more abundant in the exotic M. spicatum and the native R. maritima than in the most abundant native, V. americana. Spearman's rank correlations and Schoener's index of similarity supported this observation. The rank correlations also showed that the pattern of fish abundances in the exotic M. spicatum was not detectably different from the most common native macrophyte (V. americana). As expected, assemblage structures in all vegetated areas were dissimilar to that in unvegetated areas.

While the average diversities differed among some vegetation types, more information was gained from the measurements of evenness and richness. The greatest difference in cumulative mean diversity among vegetation types was only 13 %, which probably was not biologically significant. Also, the cumulative mean diversity measurement for unvegetated areas was high, although species richness was low, due to high evenness. Vegetated areas were numerically dominated by four species: rainwater killifish, naked goby, gulf pipefish, and clown goby, that were significantly less abundant in unvegetated areas.

Although abundances of many fish species are positively correlated with plant biomass (Lubbers et al. 1990), the type of vegetation and the hydrology of the area are important as well. Keast (1984) found that the presence of Myriophyllum spicatum severely altered fish community structure in a Canadian lake. Dense stands of M. spicatum in deep waters resulted in near anoxic daytime dissolved oxygen levels near the sediment-water interface (Keast 1984), and significantly fewer fishes were associated with M. spicatum beds than with the native Potamogeton spp. and Vallisneria americana beds. Keast's (1984) findings contrast with the Lake Pontchartrain estuary, where M. spicatum was utilized by fishes as much as the native macrophytes, Ruppia maritima and V. americana. This contrast may reflect differences in hydrology between open estuarine systems and closed freshwater lake systems (Wetzel 1975, Day et al. 1989, Heck and Crowder 1991). Semi-protected littoral lake habitats may allow submerged macrophytes to grow more densely, whereas the higher energy of a large, open system may limit submerged macrophyte density (Wetzel 1975, Day et al. 1989, Heck and Crowder 1991). Thus the low daytime dissolved oxygen and sediment related changes found by Keast (1984) were not observed in the Lake Pontchartrain estuary.

Wave energy also may have had an effect on the relative abundance of the three macrophyte species (see Chapter 2). Myriophyllum spicatum and Ruppia maritima were more abundant in the more protected waters of Lake St. Catherine, and the Vallisneria americana beds were most extensive on the exposed sand flats near Bayou Lacombe. Lake St. Catherine has a shorter fetch than Lake Pontchartrain, resulting in less wave energy, and allowing fragile submerged macrophytes to grow more densely. In contrast, the higher energy of a large, open system may limit the density of fragile submerged macrophytes through wave scour and dewatering due to tidal and meteorological events (Wetzel 1975, Day et al. 1989, Heck and Crowder 1991). The morphologies of M. spicatum and R. maritima are more susceptible to damage by wave energy than is V. americana (Mayer 1986). Higher wave energy in Lake Pontchartrain compared to Lake

St. Catherine also maintains more unvegetated patches, which influences fish community structure (Heck and Orth 1980b).

The structural complexity of submerged vegetation can influence fish abundances by altering the distributions of both their predators and their prey (Heck and Crowder 1991, Olmi and Lipcius 1991, Orth 1992). Dionne and Folt (1991) found that plant morphology is more important than plant density in determining the abundance of inhabiting organisms. Although none of the common resident fishes showed significant differences among submerged vegetation species, PSA was a significant predictor of abundance for six fishes (Table 3.3). With the exceptions of rainwater killifish, clown goby, and bay anchovy, I found that the amount of vegetation (PSA) had more influence on fish abundances than the species of vegetation. While this appears to contradict Dionne and Folt's (1991) findings, these results may be related to the significantly higher mean PSA for *V. americana* ($0.715 \pm 0.04 \text{ m}^2 / \text{m}^2$) than for *R. maritima* ($0.210 \pm 0.06 \text{ m}^2 / \text{m}^2$) and *M. spicatum* ($0.362 \pm 0.03 \text{ m}^2 / \text{m}^2$). In the Lake Pontchartrain system, the two-fold increase in PSA could overshadow the morphological effect of plant complexity in the *R. maritima* and *M. spicatum* beds.

Few studies have adequately characterized responses of estuarine fishes to multiple environmental variables. Although many variables are related (e.g., seasonal patterns of temperature and dissolved oxygen), extended sampling of fish communities may be able to identify responses to individual variables, if they exist. Generally, estuarine fishes are influenced more by salinity and temperature, and to a lesser extent by substrate, than other physico-chemical variables (Subrahmanyam and Drake 1975, Scott 1982, Horne and Campana 1989, Cyrus and Blaber 1992). These three variables were major contributors to the first and second factors in this study, which explained 41.54 % of the environmental variance in this system. Many of the common fishes were associated more strongly with brackish waters and finer substrates (Table 3.3).

Abundances of most resident fishes are higher in the warmer months (Valiela 1984, Rozas and Odum 1987, Olney and Boehlert 1988, Day et al. 1989, Baltz et al. 1993), and transient fishes are most abundant during recruitment events. Pinfish and spot recruited into the Lake Pontchartrain estuary in December. This is consistent with recruitment patterns in Barataria Bay (Baltz et al. 1993), and Chesapeake Bay (Heck and Thoman 1984). Juvenile spotted seatrout were present in the Lake Pontchartrain estuary in moderate numbers from August through December, whereas Baltz et al. (1993) collected juveniles (< 30 mm) along the marsh edge in every season except winter.

In the Lake Pontchartrain estuary, turbidity only had a modest influence on assemblage structure. It was correlated positively to water velocity and negatively to salinity, reflecting the ability of moving water to suspend and maintain sediment loads (Ward et al. 1984) and either an increase of freshwater discharge or flocculation effects, which are important in the salinity range found in this study (Cyrus and Blaber 1992). Relatively high turbidity (5.8 to 9.3 NTU) is normal in this system (Sikora and Kjerfve 1985), but the common fishes did not segregate strongly along the gradient (Figure 3.2b); nevertheless, densities of common fishes in an Australian estuary are significantly related to turbidity (Cyrus and Blaber 1992). Although bay anchovy were more often found at high turbidities, they were generally associated with fishes found at low mean turbidities (Figure 3.2b) because the influence of salinity overshadowed that of turbidity. Some fishes may gain a refuge from visual predators in turbid water (Cyrus and Blaber 1987), but bay anchovy school in open water habitat (Rakocinski et al. 1992), and gain little protection from submerged vegetation. This may have lead to greater use of turbid water in this study.

Aquatic vegetation has a strong influence on fish abundances (Orth and van Montfrans 1987, Rozas and Odum 1988, Heck and Crowder 1991), and has complex interactions with substrate and turbidity (Ward et al. 1984, Orth 1992). Because the

plant structure has a dampening effect (Machata-Wenninger and Janauer 1991), water velocity was negatively correlated with PSA (Table 3.4). Most of the fourteen common fishes collected in this study showed some association with submerged macrophytes (Tables 3.3 and 3.5). Inland silverside, bay anchovy, hogchoker, pinfish, spotted seatrout, and spot did not significantly associate with submerged macrophytes. Bay anchovy dominate open-water habitats in Louisiana coastal waters, and do not associate strongly with submerged or emergent aquatic macrophytes (Rakocinski et al. 1992, Baltz et al. 1993). The spot collected were small juveniles (10 to 38 mm SL) recruiting into the near-shore environments. At this life stage, they forage in open water, and are found over fine substrates (Smith and Coull 1987). Spot < 30 mm SL are seldom found in samples with emergent macrophytes (Baltz et al. 1993). In contrast, spotted seatrout associate with submerged (Chester and Thayer 1990) and emergent (Rakocinski et al. 1992) macrophytes. Rainwater killifish (Lubbers et al. 1990), bluegill (Rozas and Odum 1987, Savino and Stein 1989, Turner and Mittlebach 1990), and pinfish (Muncy 1984) also associate strongly with submerged macrophytes. In this study pinfish were more abundant in submerged macrophytes, but the difference was not significant. Additionally, I found that gulf pipefish, freshwater goby, and naked goby associated strongly with submerged macrophytes. While naked goby in Virginia select marsh creek environments over Zostera marina and Ruppia maritima beds (Weinstein and Brooks 1983), in the Lake Pontchartrain estuary, tidal marsh creeks were rare, and sampling adjacent bayous was beyond the scope of the objectives.

In aquatic environments, submerged macrophytes, macroalgae, woody debris, and flooded riparian vegetation offer refuge from predation (Heck and Thoman 1981, Boesch and Turner 1984, Christenson and Persson 1993, Everett and Ruiz 1993, Minello 1993). Although complex underwater vegetation tends to accumulate food resources for predators, their feeding efficiency may be reduced by moderate to highly complex structure (Stoner 1982, Bell and Westoby 1986a, Rozas and Odum 1988, Ryer

1988, Lubbers et al. 1990). In the study area, the three common submerged macrophyte species provided most of the underwater structure, and fishes were significantly more abundant in the submerged macrophytes than on adjacent unvegetated substrates. In addition to providing more evidence for the importance of aquatic macrophytes to fish communities (Weinstein and Brooks 1983, Orth et al. 1984, Lubbers et al. 1990, Sedberry and Carter 1993), this study detected differences in the abundances of the common fishes among submerged macrophytes. The abundances of rainwater killifish and clown goby were least abundant in Vallisneria americana than in the other two macrophytes, and bay anchovy was more abundant in Myriophyllum spicatum than in V. americana. At a community level, the fish assemblage in M. spicatum was more similar to that in Ruppia maritima than V. americana, but no significant differences among macrophyte species were observed. Nevertheless, it is obvious that the community associated with submerged macrophytes differs from that of the adjacent unvegetated areas, and a continued decline in the total area covered by vegetation would be detrimental to the fish communities inhabiting them.

Because no historical data exist on the relative area coverage by individual submerged macrophyte species (Montz 1978, Turner et al. 1980, Thompson and Verret 1980, Thompson and Fitzhugh 1985) until Mayer (1986), no absolute predictions can be made about shifts in the overall community structure of the fishes in the submerged macrophytes beds. Considering the morphologies of the three submerged macrophytes, though, I feel that M. spicatum has been replacing R. maritima, and not V. americana, because V. americana is much more resistant to the high energy areas where it dominates (Mayer 1986). In Lake St. Catherine, M. spicatum comprised 95 % of the vegetation in 1983 (Mayer 1986), and this lake supported more total vegetation than Lake Pontchartrain (861 hectares versus 397 hectares total coverage, respectively). Thus, according to Mayer (1986), the total area covered by M. spicatum in the entire estuary was estimated at 963 ha, whereas V. americana only covered 329 ha, though it

accounted for 65 % of the total vegetation in Lake Pontchartrain. Given the historical coverage of submerged vegetation in Lake Pontchartrain, changes in the total coverage and species composition of submerged vegetation need to be monitored carefully, and management practices that enhance the coverage of submerged vegetation should be implemented.

CHAPTER 4: JUVENILE BLUE CRAB HABITAT USE IN SUBMERGED VEGETATION IN THE LAKE PONTCHARTRAIN ESTUARY

Introduction:

Introductions of exotic species have been characterized as primary threats to biodiversity, second only to rainforest destruction (Ehrenfeld 1970, Diamond and Chase 1986, Mooney and Drake 1986). Nevertheless, the effects of exotic plants in subtropical estuaries on important fisheries have not been evaluated. Although most invasions are unsuccessful, some exotic plants can displace native species and if they have no effective herbivores their abundance can cause a reduction in habitat quality for native fauna and flora (Blackburn and Weldon 1967, Grace and Wetzel 1978, Keast 1984, Harlan et al. 1985, Mooney and Drake 1986, Sutton 1986, Tanner et al. 1990, Room and Fernando 1992). Even apparently benign exotic plants can subtly, but significantly, affect important species. The exotic Eurasian milfoil Myriophyllum spicatum was first reported in the North American continent in the late 19th century (Blackburn and Weldon 1967). It was not documented in Lake Pontchartrain until 1978 (Thompson and Verret 1980), but has since increased its coverage to become one of the three major submerged macrophyte species (Mayer 1986).

This study addressed the potential ecological interactions of Myriophyllum spicatum and blue crab Callinectes sapidus populations in the Lake Pontchartrain estuary that may result from alterations to nursery habitat for juveniles, which associate strongly with emergent and submerged vegetation (Heck and Orth 1980, Heck and Thoman 1984, Orth and van Montfrans 1987, Thomas et al. 1990, Williams et al. 1990, Gibson 1991). Myriophyllum spicatum spread rapidly throughout the eastern United States and Canada and has been found in salinities up to 15 ‰ (Grace and Wetzel 1978). The leaves of M. spicatum are finely branched and concentrate near the water's surface (Grace and Wetzel 1978). At high densities in freshwater lakes, M. spicatum has a

significant detrimental effect on biologically important variables, reducing habitat suitability for some fishes and macroinvertebrates (Keast 1984). In Lake Pontchartrain M. spicatum accounted for 15 % of the submerged vegetation in 1985, and up to 95 % of the submerged vegetation in other parts of the estuary (Mayer 1986).

Juvenile blue crabs use estuarine littoral habitats as nurseries, are widely distributed and abundant in the Lake Pontchartrain estuary, and support large commercial and recreational fisheries (Fannaly 1980, Thompson and Stone 1980). The blue crab fishery in Lake Pontchartrain appears to be declining (Guillory et al. 1996). Although an estimated 16,645 metric tons of blue crabs were commercially harvested in Louisiana in 1994, the total catch and the catch per unit effort of adults have decreased significantly since 1978. These declines are believed to be due to habitat degradation and a four-fold increase in commercial fishing effort since 1980.

For early life history stages of blue crab, a strong association with aquatic vegetation (Heck and Orth 1980b, Orth and van Montfrans 1987, Williams et al. 1990) provides greater food resources (Heck and Wetstone 1977, Heck and Thoman 1984, Bell and Westoby 1986a, Virnstein 1987, Lubbers et al. 1990) and protection from predation (Heck and Orth 1980, Coen et al. 1981, Heck and Thoman 1981, Heck and Thoman 1984, Orth et al. 1984, Wilson et al. 1990a, Ryer et al. 1990). Because of the importance of submerged aquatic vegetation to blue crabs, the continued replacement of native macrophytes by Myriophyllum spicatum could strongly influence the recruitment and population dynamics of the juveniles inhabiting the macrophyte beds if M. spicatum reduces habitat quality. Concurrently with the spread of M. spicatum, the total area covered by submerged macrophytes in Lake Pontchartrain decreased by over 50 % from 1973 to 1985 (Mayer 1986). These changes are attributable primarily to a decline in water quality, due to eutrophication and pollution, and altered hydrology following the construction of bulkheads (Mayer 1986, Guillory et al. 1996).

Because juvenile blue crabs utilize submerged macrophytes for protection from predation and as profitable foraging sites (Heck and Thoman 1981, Bell and Westoby 1986b, Ryer et al. 1990, Thomas et al. 1990, Williams et al. 1990), the reduction of native submerged macrophytes and the presence of an exotic could have a detrimental effect on nursery quality and quantity, and ultimately on adult blue crabs (van Engel 1982, Orth and van Montfrans 1990, Thomas et al. 1990). This study was designed to test the null hypothesis of no differences in utilization by three juvenile crab size classes among habitat types (i.e., native and exotic macrophytes and unvegetated substrates) and to identify the most suitable environmental conditions used as blue crab nursery habitat in the Lake Pontchartrain estuary.

Study Site:

Lake Pontchartrain is a large, shallow bay located just north of New Orleans in southeast Louisiana (Figure 4.1). It covers an area of 1,630 km², has a mean depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). It is connected to several smaller lakes to the east and to the Gulf of Mexico by two main passes. Salinities in the study area range from fresh water at the westernmost station to over 10 ‰ at the easternmost station (Sikora and Kjerfve 1985). Myriophyllum spicatum is widely established along the northwest shore of Lake Pontchartrain and in Lakes Borgne and St. Catherine. The two most common native submerged macrophyte species in the estuary are Vallisneria americana and Ruppia maritima. Three stations were chosen to characterize the salinity gradient, including littoral areas near the mouths of Cane Bayou and Bayou Lacombe in Lake Pontchartrain and the north end of Lake St. Catherine (Figure 4.1).

Methods:

A modified Wegener ring sampler (Weinstein and Brooks 1983), consisting of a vertical cylinder of heavy fabric extending 110 cm in height with a circular stainless steel base ring (10 cm wide x 1.23 m diameter, 1.18 m²), was used to collect abundance data

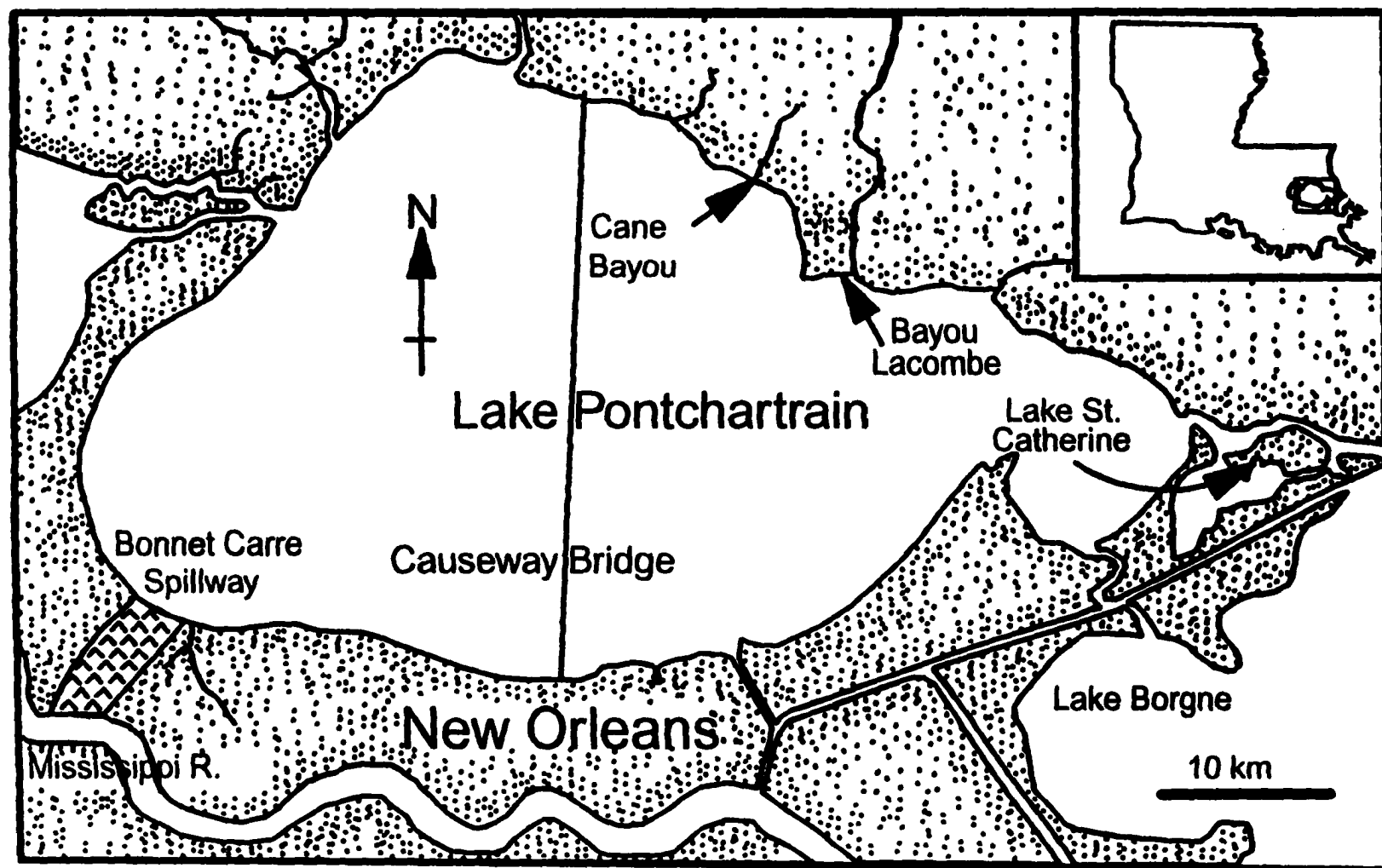


Figure 4.1: The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer 1986).

on a fine scale consistent with microhabitat characterizations. When deployed the walls were supported by a float ring at the top. The ring diameter was adequate for sampling the life history stages of interest (Chick et al. 1992). A boom extending three meters beyond the bow of a 5.2 m boat was used to suspend the sampler one-half meter above the water's surface until it was released with a pull-pin. Upon deployment, the ring was checked to ensure that it had adequately penetrated the substrate to permit a quantitative estimate of blue crab abundances.

Each month between March 1991 and January 1993, twelve samples collected at each station were stratified among the common submerged macrophyte species and unvegetated substrate. In months when all macrophytes were not present, samples were distributed among the existing species to maximize the amount of information collected. Sampling sites were selected to represent the range of submerged macrophyte densities present and the range of depths up to a maximum of one meter. Each sampling site was unique and considered to be independent for statistical purposes.

At the microhabitat level, organisms presumably select sites in response to environmental variables, balancing net energy gain with predator avoidance and competition (Baltz 1990, Baltz et al. 1993). The microhabitat of an organism is ultimately defined as the characteristics of the place where that organism is located at a point in time (Baltz 1990). From fine-scale measurements at multiple capture sites for juvenile crabs, the microhabitat characteristics and suitability (Bovee 1982) of nursery habitat can be inferred from the patterns of abundance along important environmental gradients (Hurlbert 1981). This approach also can be applied to determine ontogenetic shifts by comparing patterns among size classes. Environmental variables measured included dissolved oxygen concentration (mg / l), temperature (°C), salinity (‰), water surface velocity (cm / s), minimum and maximum water depth (cm), distance from shore (m), turbidity (NTU), and substrate type. Water depth was calculated as the median of minimum and maximum depths. Temperature, salinity, and dissolved oxygen were

measured with a Hydrolab model SRV2-SU. Surface water velocity was estimated by measuring the displacement of a neutrally buoyant object for ten seconds. Turbidity was measured in nephelometer turbidity units (NTU) with a Monitek model 21 PE portable nephelometer. Substrate was assigned a code based on particle size: 1 = clay; 2 = mud (i.e., clay and silt); 3 = silt; 4 = sand; 5 = organic detritus; 6 = shell or shell fragments. Additionally, any submerged macrophyte species present were identified (Chabreck and Condrey 1979), and the number and mean lengths of stems were estimated for each species.

Plant surface area (PSA) provides a better index of habitat complexity than stem density (Virnstein 1987). Submerged macrophyte species' surface areas were calculated using species-specific formulas derived from measurements of the surface area of stems and leaves. Surface areas, measured using a Li-Cor LI-3000 portable leaf area meter, were linearly regressed on stem length to provide species-specific formulas for estimating the total surface area (in m^2 / m^2 substrate) of common submerged macrophyte species (Chapter 2).

Following the environmental characterization of each sample site, the recovery of natant macrofauna was facilitated by the application of a suspension of 5 % rotenone to the contained water (Davies and Shelton 1983). Fishes and other organisms affected by the rotenone were collected with a small dip net and preserved in 95 % ethanol. The enclosed volume was then systematically swept six times with a large rectangular hand net (39 x 30 cm frame, 5 mm diamond mesh) and twice with a smaller dip net to capture a high percentage of remaining organisms which were preserved with a 10 % buffered formalin solution for 24 hrs, then transferred to 95 % ethanol. All blue crabs were identified, counted, measured to the nearest millimeter carapace width (CW), and assigned to a size class (Class I: < 12 mm; Class II: 12 to 25 mm; Class III: > 25 mm carapace width) according to Orth and van Montfrans (1987). Crabs > 100 mm CW were excluded from analyses because of possible avoidance of the sampling gear.

The DeLury (1947) depletion method was used during a preliminary study to estimate the capture efficiency of systematic hand netting for macroinvertebrates that were not affected by rotenone. A common organism, the grass shrimp Paleomonetes pugio, was used to identify an adequate level of netting effort. The results indicated that six systematic sweeps, each of which covered the entire basal area of the Wegener ring, were sufficient to remove at least 95 % of the individuals present ($F = 179.9$, $df = 1$ and 12 , $pr \leq 0.0001$, $r^2 = 0.97$).

The mean environmental availability of the variables along gradients was estimated from the stratified random sampling effort. Use of an environmental variable was estimated from the distribution of individuals of a size class along each variable measured. Blue crab density data were transformed ($\log_e(x + 1)$) to approximate more closely the normal distribution for analytical purposes (Sokal and Rohlf 1981). Analyses were weighted to adjust for differences in seasonal sampling effort and, where necessary, for blue crab size class density.

Habitat availability, use, and suitabilities were calculated for each size class at intervals along each environmental variable. Suitability (S) was defined as: $S = P(E|C) / P(E)$ = proportional use / proportional availability (Bovee 1982), where $P(E|C)$ was the probability of finding a particular value for an independent environmental (E) variable given the presence of juvenile blue crab (C), and $P(E)$ was the probability of finding that value whether any juvenile crabs were present or not. Suitabilities were standardized between 0 and 1. Because of the annual pattern of variation, temperature was analyzed seasonally to identify possible ontogenetic shifts in temperature utilization. Size class use and the distributions of environmental variables were plotted as relative frequency distributions to identify patterns and the most suitable intervals along each environmental variable.

Interrelationships among environmental variables and size classes were examined with Pearson's pairwise correlations after adjusting a for multiple comparisons using the

Dunn-Šidák correction (Sokal and Rohlf 1981). The appropriate critical values were computed using the expression: $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α' is the experimentwise adjusted error rate, k is the number of comparisons, and α is the critical value.

Univariate means for significant variables were compared for differences among blue crab size classes in their use of environmental gradients and the overall average availability of those gradients. Both the use and availability of environmental variables were analyzed with a multiple analysis of variance (MANOVA) model approach (SAS Institute 1989) in which temporal and environmental variables were predicted by size classes. Environmental gradients that were identified in the MANOVA (Johnson and Wichern 1988) as being significantly ($p \leq 0.005$) related to the size class distribution of the crabs were further analyzed using an a posteriori technique, the least squares means test (LSMeans), which adjusts for unbalanced comparisons. Separate general linear models (GLM) analyses (e.g., classI classII classIII = macrophyte species) were used similarly to identify differences in size class abundances among submerged macrophyte species, seasons, stations, and between total vegetated and unvegetated samples. Significant differences were also further analyzed with LSMeans.

A separate analytical approach was used to predict the densities of blue crab size classes from environmental variables and to identify ontogenetic shifts in gradient use. For each size class, a stepwise regression approach tested the nine environmental variables for inclusion in a model that was constrained to keep four temporal variables (first to fourth order terms for month). Terms that were included at the 15 % significance level were entered into a GLM analysis to test the temporal variables. Type I sums of squares with the temporal variables adjusted for the environmental variables identified which temporal variables could be excluded from the subsequent analyses. If a higher order temporal term was significant, all of the lower order terms were retained for theoretical reasons (Johnson and Wichern 1988). The appropriate temporal variables were included in another stepwise regression to recheck the significance of the

environmental variables, and a final model was selected. The final variables were entered into a GLM analysis, and the results of this final analysis are reported using model-order-independent sums of squares for environmental variables and model-order-dependent sums of squares for temporal variables.

Results:

A total of 1,386 blue crabs was recovered from 517 independent samples collected between March, 1991, and January, 1993 (Table 4.1). Juvenile blue crabs in

Table 4.1: Environmental means (± 1 SE) for all samples and three size classes of blue crabs collected in the Lake Pontchartrain estuary. Means are adjusted for differences in seasonal sampling effort. Significant differences (LSMeans, $p \leq 0.0085$) among columns are indicated by different letters, reading horizontally.

Size Class:				Overall Mean
	I	II	III	Availability
	≤ 11 mm	12 mm - 25 mm	> 25 mm	
PSA	0.37 (0.024)A	0.57 (0.021)B	0.87 (0.043)C	0.42 (0.026)A
Salinity	4.1 (0.09)AB	4.3 (0.08)A	3.9 (0.16)B	3.1 (0.10)C
Dist from Shore	22.3 (0.79)A	24.8 (0.67)AB	27.9 (1.39)B	32.7 (0.83)C
Substrate	3.2 (0.05)A	3.3 (0.04)A	3.4 (0.08)A	3.7 (0.05)B
Temperature	19.7 (0.30)A	22.1 (0.25)B	21.2 (0.52)AB	21.7 (0.31)B
Turbidity	8.4 (0.38)A	5.8 (0.32)B	7.1 (0.66)AB	7.6 (0.40)A
Dissolved Oxygen	9.6 (0.07)A	9.2 (0.06)B	9.4 (0.12)AB	9.2 (0.07)B
Water Velocity	3.3 (0.09)A	3.0 (0.08)AB	2.8 (0.16)B	3.3 (0.09)A
Median Depth	45.1 (0.62)	45.7 (0.53)	44.8 (1.10)	43.6 (0.66)
Total Numbers	480	728	178	

Table 4.2: Pearson's correlations (N = 517) among environmental variables and the densities of the three size classes (CI, CII, and CIII) of blue crabs collected in the Lake Pontchartrain estuary. All underlined correlation coefficients are significant at an overall level of $p \leq 0.05$ after adjusting for multiple comparisons.

	Vel	Subs	Turb	Dist	Depth	D Ox	Sal	Temp	PSA
CI Density	-0.01	<u>-0.33</u>	0.09	<u>-0.29</u>	0.05	0.10	<u>0.32</u>	-0.14	-0.07
CII Density	-0.04	<u>-0.32</u>	-0.08	<u>-0.26</u>	0.10	-0.03	<u>0.38</u>	0.03	0.13
CIII Density	-0.10	-0.13	-0.00	-0.10	0.02	0.03	0.14	-0.03	<u>0.28</u>
PSA	-0.14	0.05	-0.08	0.11	<u>0.16</u>	-0.01	-0.08	<u>0.15</u>	--
Temp	-0.01	-0.06	-0.09	-0.03	0.31	<u>-0.49</u>	<u>-0.22</u>	--	
Salinity	-0.12	<u>-0.49</u>	<u>-0.25</u>	<u>-0.32</u>	0.11	0.04	--		
D. Oxygen	0.11	0.08	<u>0.17</u>	0.08	<u>-0.40</u>	--			
Depth	-0.02	<u>-0.24</u>	<u>-0.18</u>	0.06	--				
Distance	0.06	<u>0.51</u>	-0.09	--					
Turbidity	<u>0.24</u>	0.02	--						
Substrate	0.07	--							

size classes I through III were present in 486 samples, for a frequency of occurrence of 94.0 %. Size Class I included 480 crabs ranging in size from 3 mm to 11 mm CW. Size Class II included 728 crabs ranging in size from 12 mm to 25 mm CW. Size Class III included 178 crabs ranging from 26 mm to 100 mm CW. Three crabs > 100 mm CW were excluded from analyses.

Several environmental variables were related to each other as well as to crab size class densities (Table 4.2). Of 66 pairwise comparisons, 26 were significant at $p \leq 0.001$. Densities of all size classes were positively related ($p \leq 0.0001$) to each other and salinity, and negatively related to substrate and distance from shore. The strongest of the environmental correlations were between temperature and dissolved oxygen (-),

salinity and substrate (-), depth and dissolved oxygen (-), and distance from shore and substrate (+). When PSA was resolved into its species components (i.e., areas of Vallisneria americana, Ruppia maritima, and Myriophyllum spicatum), three additional correlations were noted. V. americana leaf area was positively related to distance from shore ($r = 0.179$, $p \leq 0.0001$) and substrate ($r = 0.159$, $p \leq 0.0003$), M. spicatum leaf area was negatively related to distance from shore ($r = -0.157$, $p \leq 0.0003$), and both M. spicatum and R. maritima leaf areas were negatively related to substrate ($r = -0.267$ and -0.196 respectively, $p \leq 0.0001$ for both comparisons).

In the MANOVA of differences in environmental means among size classes, significant differences were observed for eight of the nine variables measured (Table 4.1). PSA, salinity, distance from shore, substrate, temperature, turbidity, dissolved oxygen, and water velocity significantly ($p \leq 0.0056$) predicted size class distributions. None of the size classes differed significantly in depth use or from depth availability. Trends in use were evident for PSA, distance from shore, substrate type, and water velocity. Blue crab size classes responded strongly to PSA, with increased use of denser vegetation with increasing size. Classes II and III were found at significantly higher mean PSA values than the overall mean PSA. Mean distance from shore increased with size, but all size classes were significantly closer to shore than the overall mean distance. Although a weak trend in substrate particle size was not significant among size classes, all size classes used significantly finer substrates than the overall mean substrate type. The largest size class used slower water velocities that differed significantly from Class I and the overall mean velocity, with Class II having an intermediate value. Class II was collected at a higher mean salinity than Class III, and all size classes were found at higher mean salinities than the overall mean salinity. Class II was found at significantly higher mean temperatures and lower mean turbidity and dissolved oxygen levels than Class I. The overall mean turbidity was higher than that for Class II, and the overall mean dissolved oxygen was lower than that for Class I.

In the GLM analyses comparing size class densities among submerged macrophyte species and unvegetated substrate, several significant differences in mean densities for blue crab size classes were observed (Table 4.3). Most notably, all three size classes were significantly more abundant in vegetated areas than in unvegetated areas. Additionally, macrophyte usage differed among size classes. Class I density was significantly higher in Ruppia maritima, and lower in Vallisneria americana, but density in Myriophyllum spicatum was intermediate. Class II density was significantly higher in R. maritima than in the other two macrophyte species. Class III was significantly higher in V. americana than in M. spicatum. Densities in at least one native macrophyte species were always significantly higher than in the exotic M. spicatum by a factor of two (Table 4.3).

In the stepwise GLM analyses within size classes, predicted densities were significantly related to environmental and temporal variables, as positive or negative factors (Table 4.4). For Class I, salinity and temperature were positively related ($p \leq 0.0057$), whereas distance from shore was negatively related, and together these three

Table 4.3: Mean (± 1 SE) densities of blue crabs in the submerged macrophyte species and unvegetated substrates sampled in the Lake Pontchartrain estuary. Means are adjusted for differences in seasonal sampling effort. Significant differences (LSMeans, $p \leq 0.017$) among the three submerged vegetation species are indicated by different letters reading horizontally. Asterisks in the 'Unvegetated' column indicate significant differences between vegetated and unvegetated areas (LSMeans, $p \leq 0.0001$ for all comparisons).

	<u>Vallisneria</u>	<u>Myriophyllum</u>	<u>Ruppia</u>	Unvegetated
Class I	0.7 (0.12)A	1.3 (0.19)B	2.9 (0.30)C	0.3 (0.19)*
Class II	1.4 (0.14)A	1.3 (0.23)A	2.9 (0.36)B	0.2 (0.22)*
Class III	0.4 (0.05)A	0.2 (0.08)B	0.4 (0.12)AB	0.1 (0.07)*

Table 4.4: Regression parameters and partial correlations from a model building approach (see text for explanation) of the relationship of the density of blue crab size classes with temporal and environmental variables in the Lake Pontchartrain estuary. Asterisks denote effects that are significant at $p \leq 0.05$ after adjusting for multiple comparisons. The variance explained by the model is the total R^2 for the final model.

Size Class and Variable	Coefficient	Partial r^2	P > F
Class I			
Intercept	-1.915		0.0001 *
Month ⁴	-0.003	0.085	0.0001 *
Month ³	0.078	0.047	0.0001 *
Salinity	0.080	0.038	0.0001 *
Temperature	0.046	0.038	0.0001 *
Month	2.113	0.023	0.0001 *
Distance	-0.004	0.010	0.0063 *
Depth	0.004	0.008	0.0154
Substrate	-0.066	0.006	0.0335
Month ²	-0.702	0.001	0.4012
Model		0.326	0.0001 *
Class II			
Intercept	-1.406		0.0001 *
Salinity	0.142	0.119	0.0001 *
PSA	0.237	0.036	0.0001 *
Month	1.341	0.026	0.0001 *
Month ⁴	-0.002	0.026	0.0001 *
Temperature	0.035	0.019	0.0003 *
Month ³	0.047	0.017	0.0007 *
Distance	-0.004	0.013	0.0033 *
Turbidity	-0.005	0.003	0.1298
Month ²	-0.430	0.000	0.9043
Model		0.269	0.0001 *
Class III			
Intercept	0.075		0.4670
PSA	0.209	0.105	0.0001 *
Salinity	0.026	0.016	0.0020 *
Month	0.056	0.009	0.0224
Distance	-0.001	0.006	0.0514
Month ²	-0.016	0.006	0.0572
Month ³	0.001	0.006	0.0598
Model		0.133	0.0001 *

environmental variables explained 8.6 % of the total variance. Three of the four temporal variables were also significant, and explained an additional 15.6 % of the total variance. In combination the environmental and temporal variables explained 24.2 % of the total variance. For Class II, salinity, PSA, and temperature were positively related, and distance from shore was negatively related ($p \leq 0.0057$). The four significant environmental variables explained 18.7 % of the total variance for Class II, and the three significant temporal variables explained 6.9 % of the total variance. PSA and salinity were positively related to Class III densities ($p \leq 0.0083$), and explained 12.1 % of the total variance. No temporal variables were significantly related to Class III densities.

Patterns of habitat selection were evident from suitability analyses of four environmental variables that made significant contributions to the prediction of densities within size classes (Figures 4.2–4.6). Along the PSA gradient (Figure 4.2), Class I selected for lower plant surface areas than Classes II and III, although all sizes showed selection for vegetation. Suitabilities of salinities between 7.2 and 8.4 ‰ were high for all three size classes (Figure 4.3). Suitabilities for relatively great distances from shore were high for all size classes (Figure 4.4). Sand was the least suitable substrate (Figure 4.5). The suitabilities of temperature differed among seasons (Figure 4.6). In winter (Figure 4.6a) suitabilities of temperatures $< 16^{\circ}\text{C}$ were high for all size classes. In spring (Figure 4.6b), suitabilities of moderate temperatures were highest for all size classes. In summer (Figure 4.6c), the peak suitability for Class II was 6 to 9°C higher than the other two classes. In autumn (Figure 4.6d), suitabilities of temperatures between 16 and 19°C were high for all size classes.

In a GLM analysis, density patterns of blue crab size classes varied among seasons (Table 4.5), but did not respond strongly to gradients in temperature within seasons. No significant differences in mean temperatures among the size classes were detected within seasons (GLM, $p > 0.017$). Class I was significantly less dense in summer than the other seasons. Class II was significantly more dense in spring and

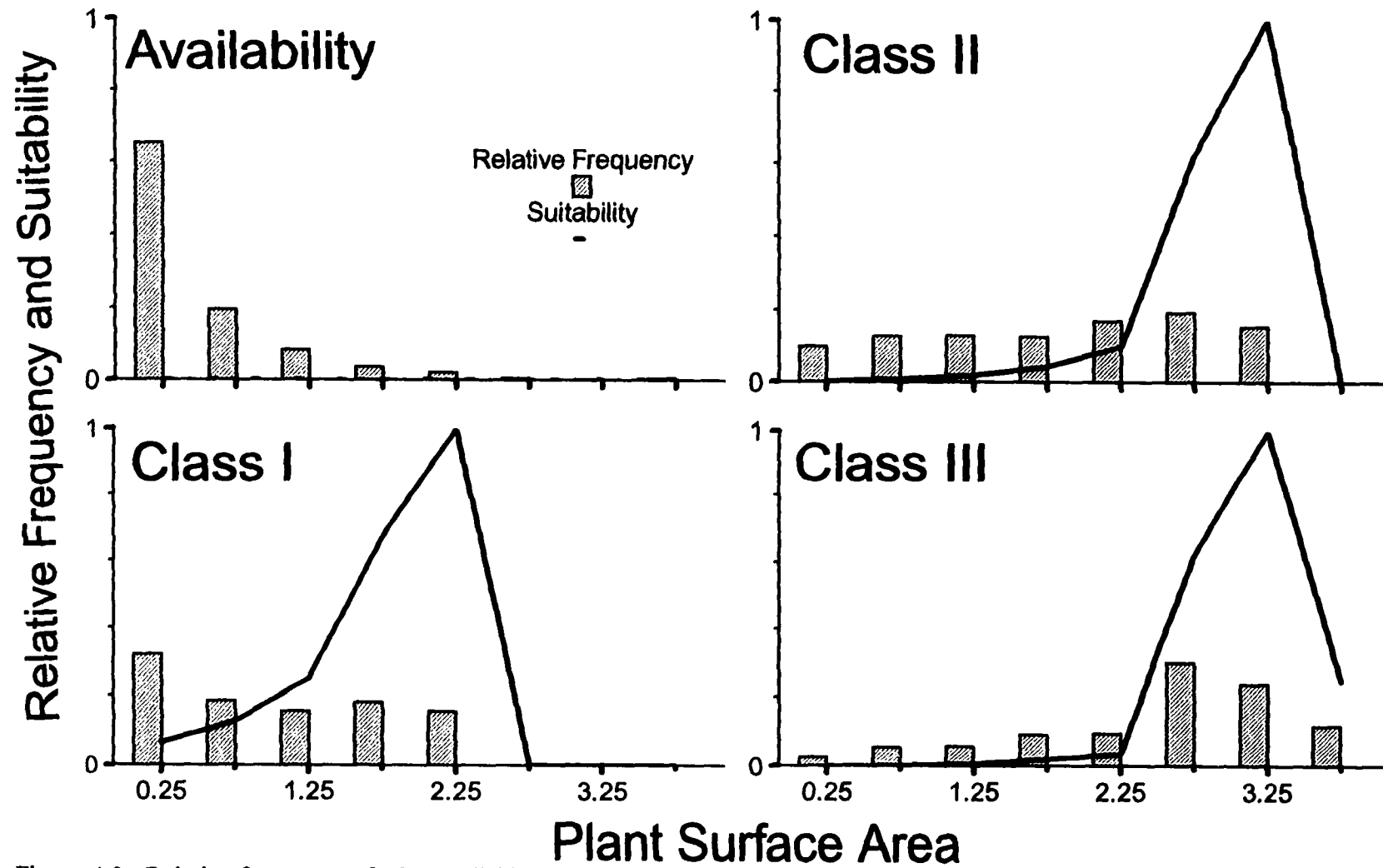


Figure 4.2: Relative frequency of PSA availability and blue crab size classes and relative suitabilities of plant surface area intervals (in m² plant surface per m² bottom, midpoints given) for the three size classes of blue crabs in the Lake Pontchartrain estuary, Louisiana.

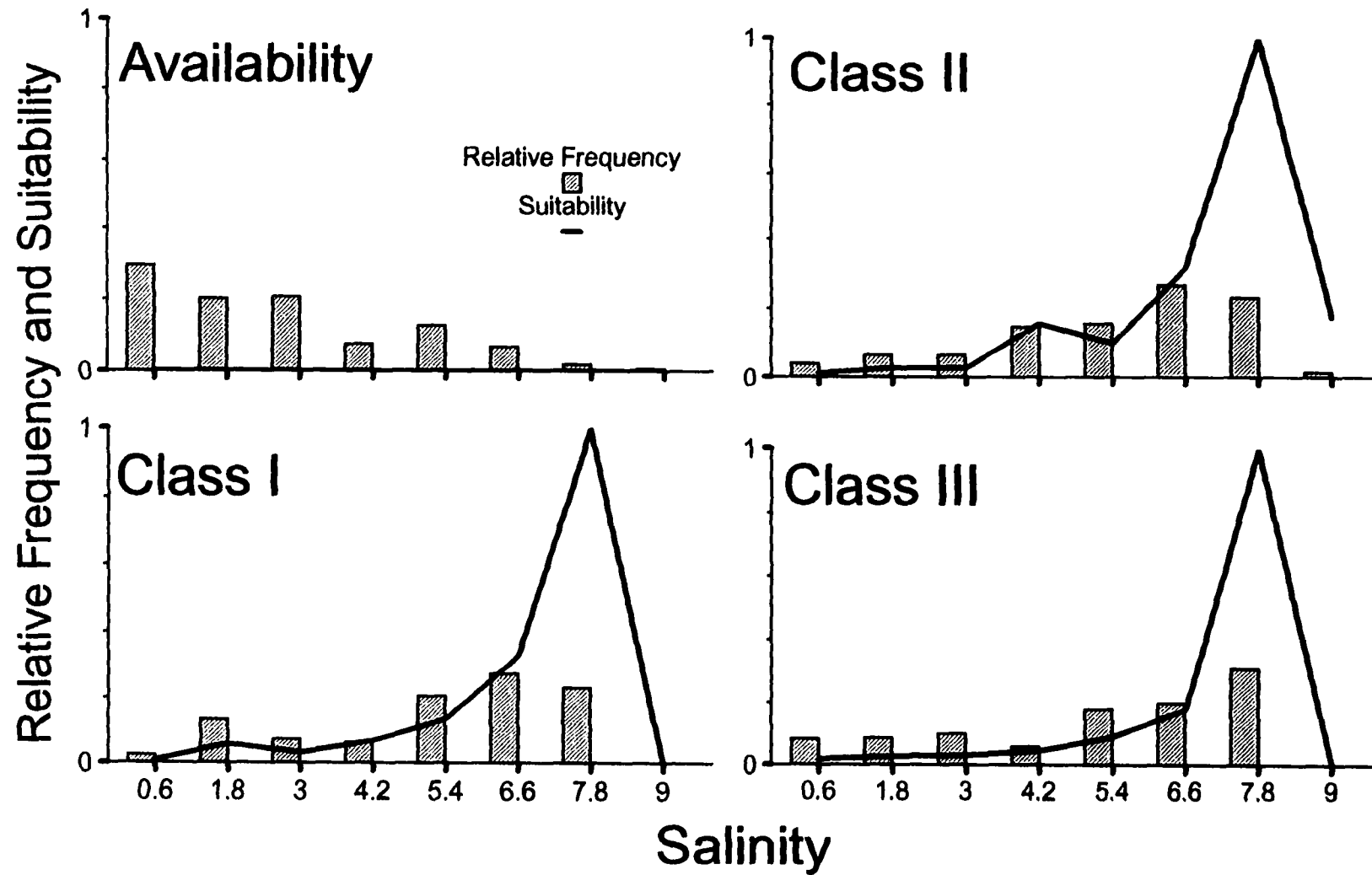


Figure 4.3: Relative frequency of salinity availability and blue crab size classes and relative suitabilities of salinity intervals (in ‰, midpoints given) for the three size classes of blue crabs in the Lake Pontchartrain estuary, Louisiana.

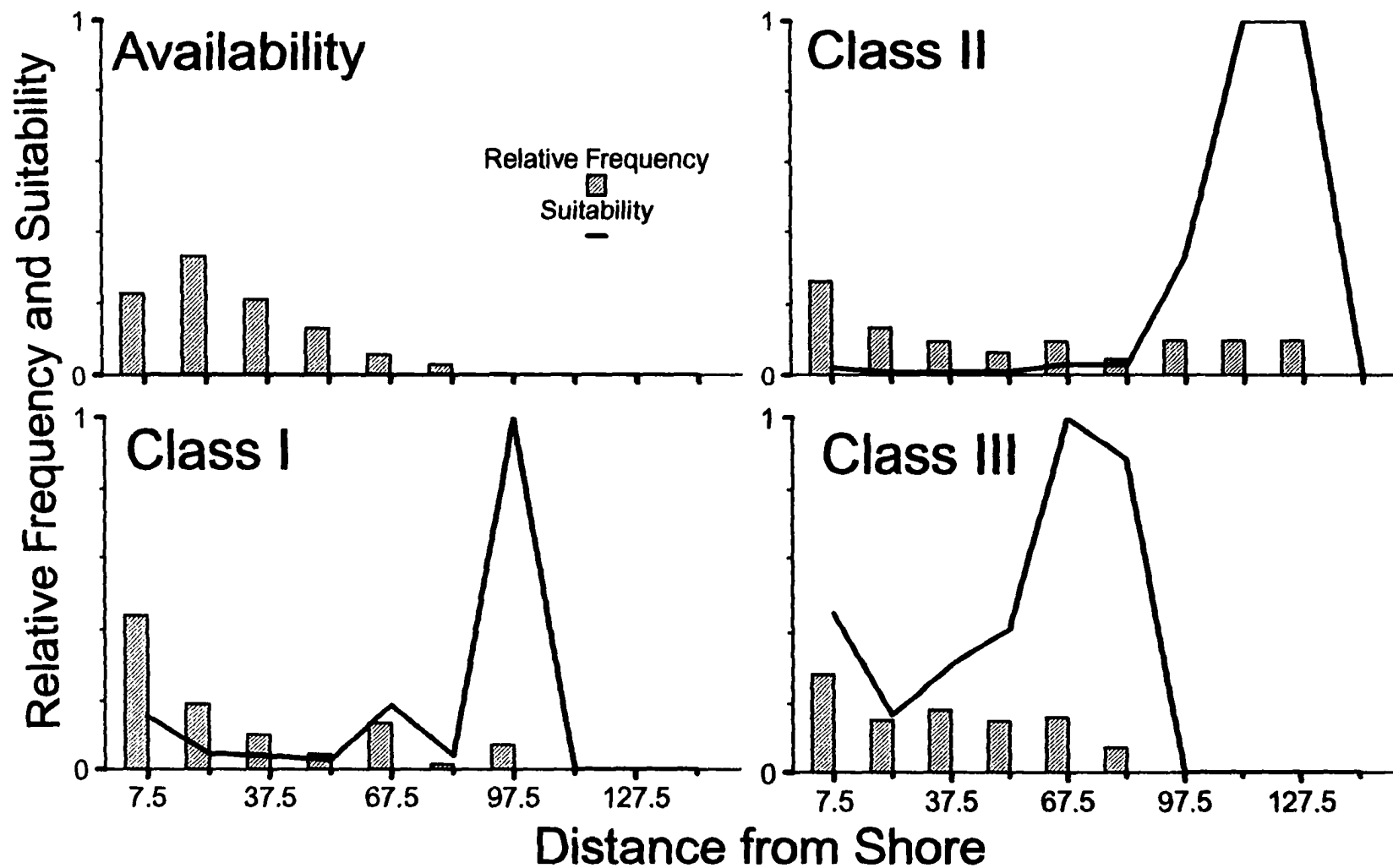


Figure 4.4: Relative frequency of distance availability and blue crab size classes and relative suitabilities of distance from shore intervals (in meters, midpoints given) for the three size classes of blue crabs in the Lake Pontchartrain estuary, Louisiana.

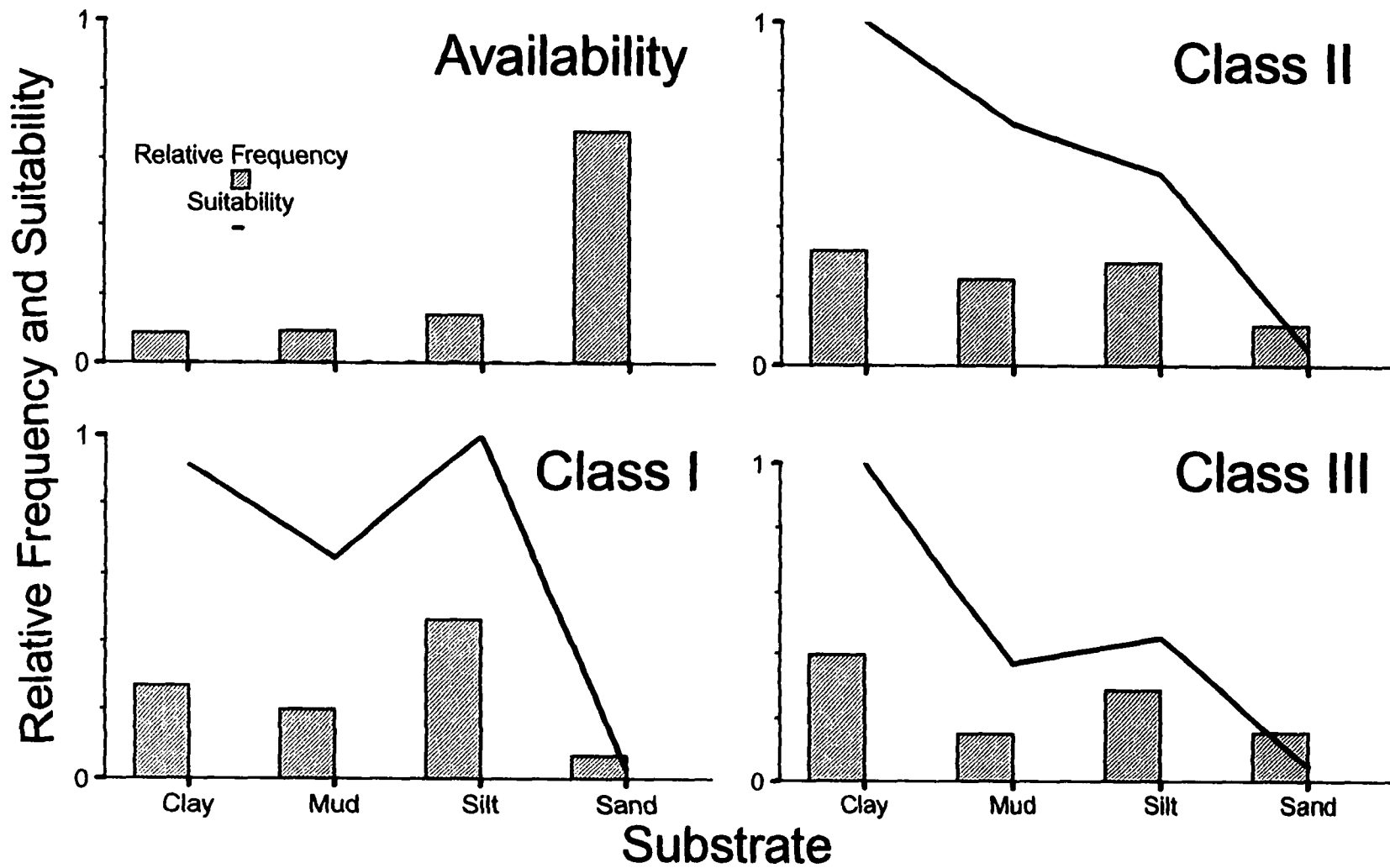


Figure 4.5: Relative frequency of substrate availability and blue crab size classes and relative suitabilities of substrate type for the three size classes of blue crabs in the Lake Pontchartrain estuary, Louisiana.

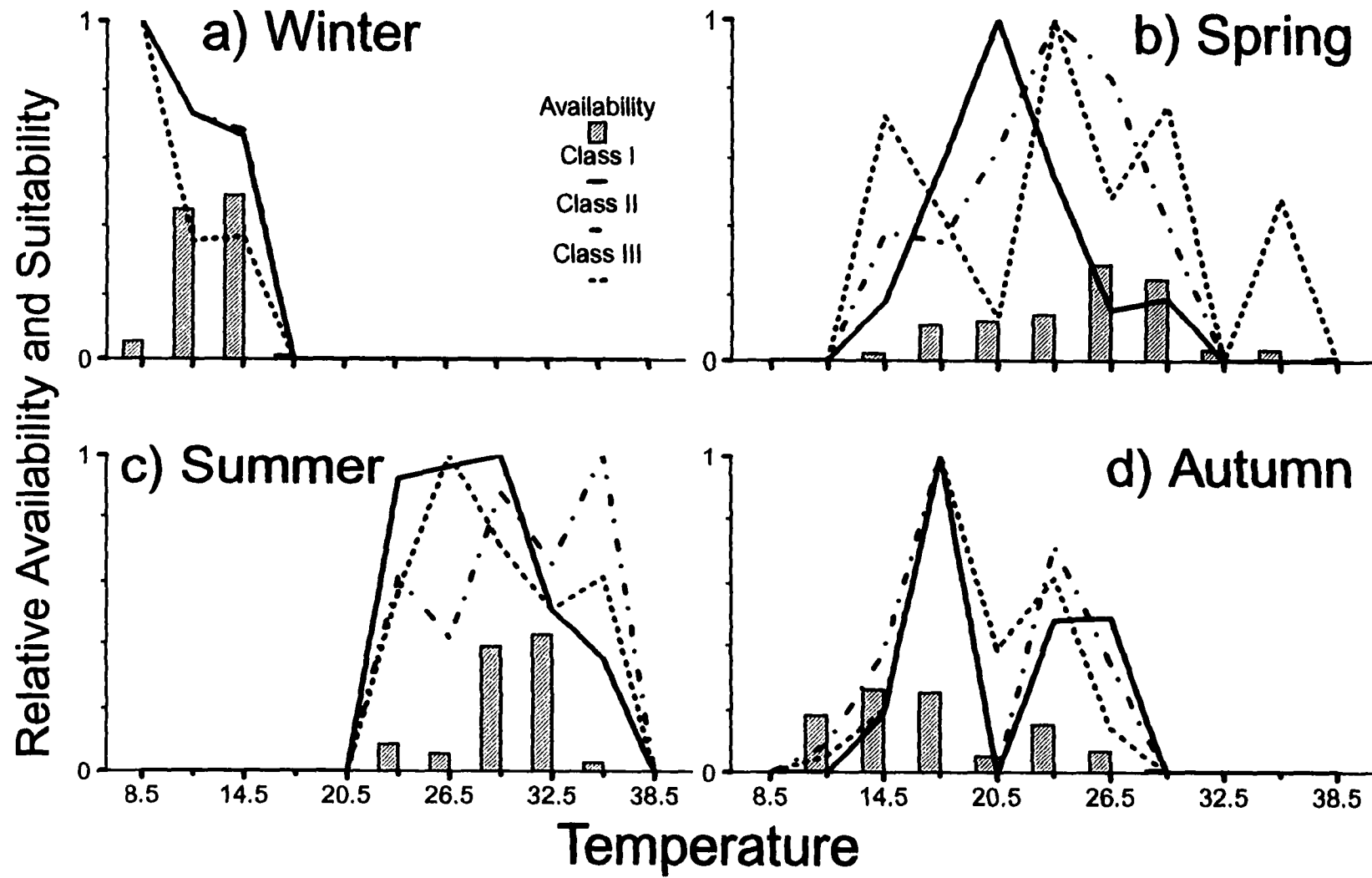


Figure 4.6: Relative availability and suitability of temperature intervals (in °C, midpoints given) for the three size classes of blue crabs for four seasons in the Lake Pontchartrain estuary.

autumn than in winter and summer. There were no significant differences in densities among seasons for Class III.

In a GLM analysis of size class densities among stations, several significant responses were noted (Table 4.6). Every size class had its highest density in Lake St. Catherine. Class I was significantly denser in Lake St. Catherine than at the Bayou Lacombe station. Class II was significantly denser in Lake St. Catherine than both of the Lake Pontchartrain stations. Class III was significantly denser in Lake St. Catherine than at the Cane Bayou station.

Table 4.5: Seasonal mean densities (± 1 SE) of blue crabs collected in the Lake Pontchartrain estuary. Means are adjusted for differences in seasonal sampling effort. Significant differences (LSMeans, $p \leq 0.0085$) among seasons are indicated by different letters, reading horizontally.

	Winter	Spring	Summer	Autumn
Class I	2.6 (0.40)A	3.4 (0.33)A	1.4 (0.54)B	3.5 (0.41)A
Class II	2.2 (0.36)A	3.3 (0.30)B	1.9 (0.35)A	3.8 (0.34)B
Class III	1.4 (0.18)	1.5 (0.20)	1.1 (0.19)	1.4 (0.19)

Table 4.6: Mean densities (± 1 SE) of blue crabs at the three stations sampled in the Lake Pontchartrain estuary. Means are adjusted for differences in seasonal sampling effort. Significant differences (LSMeans, $p \leq 0.017$) among stations are indicated by different letters, reading horizontally.

	Cane Bayou	Bayou Lacombe	Lake St. Catherine
Class I	2.3 (0.73)AB	2.2 (0.40)A	3.3 (0.25)B
Class II	2.0 (0.40)A	2.5 (0.31)A	3.4 (0.23)B
Class III	1.0 (0.16)A	1.2 (0.18)AB	1.7 (0.15)B

Discussion:

In the Lake Pontchartrain estuary, all juvenile blue crab size classes exhibited significant selection for vegetated areas over adjacent unvegetated areas, but the use of individual macrophyte species changed with increasing size (Table 4.3). Although Class I was significantly more abundant in Ruppia maritima and Myriophyllum spicatum than in Vallisneria americana, Class III was more abundant in V. americana than in M. spicatum. Class II was more abundant in Ruppia maritima than in V. americana or M. spicatum. The influence of seasonality became less evident with increasing blue crab size. Several ontogenetic shifts in gradient use were noted, but most could be attributed to the increased use of V. americana with increasing crab size. From the MANOVA, the most important environmental variable that predicted juvenile blue crab size class abundances was PSA, followed by salinity and distance from shore (Table 4.4).

In the littoral areas of the Lake Pontchartrain estuary, when compared to unvegetated substrates, all submerged macrophyte species harbored significantly higher densities and presumably provided superior nursery habitat for juvenile blue crabs (Table 4.3). Submerged vegetation offers enhanced forage (Heck and Wetstone 1977, Boesch and Turner 1984, Heck and Thoman 1984, Bell and Westoby 1986a, Virnstein 1987, Lubbers et al. 1990) and refuge opportunities (Heck and Orth 1980, Coen et al. 1981, Heck and Thoman 1981, Heck and Thoman 1984, Orth et al. 1984, Wilson et al. 1990a, Ryer et al. 1990). Nevertheless, little work has been done on the usage of different macrophyte species for blue crab, especially in estuarine systems. In New Jersey estuaries, Zostera americana appears to be superior habitat for epibenthic fishes, but Ulva lactuca is superior for blue crabs (Wilson et al. 1990b, Sogard and Able 1991). In two Texas bays, blue crab densities are highest in submerged vegetation, intermediate in salt marsh creeks, and lowest in unvegetated areas (Thomas et al. 1990), and juvenile blue crab abundances are not higher in salt marsh creeks when adjacent beds of submerged vegetation are absent. This pattern and the results of other studies suggest

that declines in submerged vegetation could eventually result in decreases in adult blue crab numbers (Heck and Thoman 1984, Orth and van Montfrans 1990, Thomas et al. 1990, Ruiz et al. 1993). In the Lake Pontchartrain estuary, the total area covered by submerged vegetation declined over 50 % from 1973 to 1985 (Mayer 1986). This decline coincided with the expansion of the exotic Myriophyllum spicatum (Mayer 1986) and a significant increase in fishing effort, resulting in a reduction in the catch per unit effort of adults (Guillory et al. 1996).

The composition and abundances of the submerged macrophyte species in the Lake Pontchartrain estuary have changed dramatically over the past few decades. In the 1960's, 8,097 ha of submerged vegetation were present in Lake Pontchartrain, but by 1973 only 810 ha of submerged vegetation were observed (Montz 1978). By 1985, only about 397 ha of submerged vegetation remained, of which 65 % was Vallisneria americana, while Ruppia maritima and Myriophyllum spicatum each comprised about 15 %. In 1985, an estimated 861 ha of submerged vegetation was reported for Lake St. Catherine, of which 95 % was M. spicatum (Mayer 1986). In protected lakes and embayments M. spicatum partially replaced native macrophytes (Mayer 1986). Nevertheless, no quantitative data exist on the relative abundance and total area covered by each submerged macrophyte species in Lake Pontchartrain prior to 1985 (Mayer 1986), so the extent of the replacement is unknown.

The changing composition and abundance of the submerged macrophyte species could strongly affect juvenile blue crab distributions. In this study, R. maritima harbored more than twice the densities of Classes I and II than the exotic M. spicatum and the dominant native, V. americana (Table 4.3). Additionally, Class III was significantly denser in V. americana than in M. spicatum. This shift in habitat use is evidence that the presence of M. spicatum is having a negative influence on juvenile blue crab populations, especially if it has been replacing R. maritima. M. spicatum and R. maritima are more sensitive to wave damage than V. americana, which limits their distributions to more

protected areas (Grace and Wetzel 1978, Mayer 1986, personal observation). Because M. spicatum and R. maritima grew in similar habitats, the increase in the abundance of M. spicatum in these areas probably resulted in the displacement of R. maritima.

The hydrological characteristics of the Lake Pontchartrain estuary appear to prevent Myriophyllum spicatum from growing at high densities. Exposure to wave energy during frontal passages, especially in spring, appears to be the primary factor that limits the distribution and abundance of the relatively fragile submerged macrophyte species M. spicatum and Ruppia maritima (Mayer 1986, personal communication, Michael Poirrier, University of New Orleans). The Lake Pontchartrain estuary is a large, open system that differs substantially from many other systems that M. spicatum has successfully invaded. Semi-protected lakes may allow submerged vegetation to grow more densely, whereas the higher energy of a large, open system may limit submerged vegetation density through wave scour and dewatering due to meteorological and tidal events (Wetzel 1975, Day et al. 1989, Heck and Crowder 1991). In closed systems, M. spicatum can form a thick canopy at the water's surface (Grace and Wetzel 1978, Keast 1984), negatively affecting biologically important variables. In a Canadian lake, dissolved oxygen levels are significantly lower, and substrates are significantly finer and contain more organic material in beds of M. spicatum than in the native vegetation (Keast 1984). Under these degraded conditions, most fishes and invertebrates associated with M. spicatum are significantly less abundant than with the native macrophytes. The morphology of M. spicatum is more susceptible to mechanical damage from waves and currents than V. americana (Grace and Wetzel 1978, Mayer 1986). Because its density in Lake Pontchartrain was lower than in Lake Opinicon, Ontario (Keast 1984, Mayer 1986, personal observation), the physico-chemical changes found by Keast (1984) have not developed to the same extent in more open systems like the Lake Pontchartrain estuary. These less than favorable conditions may have

prevented *M. spicatum* from having a stronger negative influence on juvenile blue crabs and other animal assemblages (Chapters 3 and 5).

Ontogenetic shifts were identified in gradient use along four of nine environmental axes. As crabs grew, their use of denser vegetation and coarser substrates increased significantly, as did their mean distance from shore (Table 4.1). Mean surface water velocity decreased significantly with increasing blue crab size. These observations concur with the increased use of *Vallisneria americana* with increasing size. *V. americana* had the highest PSA and was more common on sandy substrates, where high wave energy limited the growth of the other two macrophyte species (see Chapter 2). *V. americana* was also sampled farther from shore, in part because sand bars present near Bayou Lacombe supported only *V. americana* beds. Because of the high PSA associated with *V. americana* beds, the significant negative trend in water velocity could also be a result of greater usage of *V. americana* with increasing blue crab size. This size related difference in velocity use may reflect either an increased selection for *V. americana* or for increased PSA.

The PSA gradient was the most important environmental gradient for predicting the size distribution of juvenile blue crab in this study. PSA also helped to predict densities for Classes II and III (Table 4.4), which were found at significantly higher mean PSA values than the overall mean PSA (Table 4.1). This contrasts with the pattern of use in Cuban shoalgrass *Halodule wrightii* beds at Ono Island, Alabama (Williams et al. 1990), where crabs over 10 mm CW do not associate strongly with submerged macrophytes. At Ono Island, blue crabs between 5 and 10 mm CW associate with low density vegetation (Williams et al. 1990), and crabs < 5 mm CW are weakly associated with high density vegetation. Although the PSA values associated with Class I in this study were not significantly different from the overall mean PSA, the suitability index indicated selection for relatively high PSA values.

Submerged vegetation can increase food resources for juvenile blue crabs and at the same time decrease their ability to access those resources (Heck and Wetstone 1977, Heck and Thoman 1984, Bell and Westoby 1986a, Virnstein 1987, Lubbers et al. 1990). Increased plant density interferes with foraging on infaunal prey due to an increased presence of roots and rhizomes (Heck and Thoman 1984). In Lake Pontchartrain, clams, detritus, and meiofauna constituted most of the diet of juvenile and adult blue crabs (Darnell 1961). Because they depend on food resources of low accessibility, the positive relationship of crab and plant densities may reflect a response to refugia rather than to food resources (Heck and Thoman 1984). The structure provided by submerged vegetation confers protection to juvenile fishes and invertebrates (Boesch and Turner 1984, Heck and Orth 1984, Orth et al. 1984, Bell and Westoby 1986a, Virnstein 1987, Wilson et al. 1990a, Dionne and Folt 1991, Christenson and Persson 1993).

Juvenile blue crab size classes segregate along salinity gradients on the Gulf of Mexico and Atlantic coasts (Perry and van Engel 1982, Hill et al. 1989, Gibson 1991). In South Carolina, juveniles are more abundant at salinities less than 5 ‰ (Mense and Wenner 1989), but the analysis did not consider size classes. In the Lake Pontchartrain estuary, relatively high salinities (7.2 - 8.4 ‰) were highly suitable for all juvenile size classes (Figure 4.3), and regression models indicated positive relationships between salinity and densities for all sizes (Table 4.4). In Barataria Bay, juvenile blue crabs selected moderate (15 - 20 ‰) salinities (Gibson 1991), but the salinity range (6 - 22 ‰) was higher than that of Lake Pontchartrain (0 - 10 ‰). In Mississippi waters (Perry and Stuck 1982), the smallest size crabs (3 - 10 mm) are more common in more saline (15 - 20 ‰) waters than larger juveniles (10 to 40 mm), which are most common at salinities < 10 ‰. Salinity use by the 40 - 60 mm size class is related to temperature (Perry and Stuck 1982): at lower temperatures (15 - 20 °C), they are more common in fresher water (< 5 ‰), although at temperatures of 20 - 25 °C they are more common at higher salinities (15 - 20 ‰). This seasonal difference may reflect precipitation patterns rather

than differential habitat selection. The largest size class (> 60 mm) is most common at higher salinities (15 - 20 ‰). Comparisons with Mississippi data are difficult because absolute densities were not reported and the salinity range is dissimilar.

In the Lake Pontchartrain estuary, all size classes were abundant close to shore and regression models identified significant negative relationships between distance and densities of Classes I and II (Table 4.4). Nevertheless, suitabilities were always higher at greater distances from shore (Figure 4.4). This was independent of the relation of distance from shore with salinity, and distance from shore was independent from depth (Table 4.2). Juvenile crabs may be more susceptible to avian predation (e.g., egrets and herons), so habitat selection, especially along depth and distance gradients, is a trade-off between predation pressures from birds, fishes, and larger crabs. In Barataria Bay, blue crabs selected for distances closer to shore (Gibson 1991), but the emergent vegetation that provided refugia in that estuary is associated with the marsh edge. In the Lake Pontchartrain study area, refuge was provided primarily by submerged macrophytes that were not concentrated as closely to the marsh edge.

Juvenile blue crabs are more abundant on soft detritus, mud, or mud with shells (Hill et al. 1989). In the study area, all size classes were found on substrates that were significantly finer than the overall mean substrate type (Table 4.1 and Figure 4.5). In Barataria Bay, Louisiana, blue crabs selected primarily for organic detritus, and fine sediments were selected more strongly than sandy substrates (Gibson 1991). Substrate and salinity were negatively related in the Lake Pontchartrain estuary (Table 4.2), and the positive relationship of crab densities to fine substrates and relatively high salinities probably influenced densities among stations, with greater densities in Lake St. Catherine than in the Lake Pontchartrain stations.

Seasonality was a prevalent feature in the abundance patterns of juvenile blue crabs in this study and elsewhere (Orth and van Montfrans 1987, Thomas et al. 1990, Williams et al. 1990). It was more influential for smaller crabs in that temporal variables

accounted for 15.6 %, 6.9 % and about 2 % of the variances of Classes I, II, and III, respectively (Table 4.4). A strong temporal component is expected in species with seasonal recruitment patterns. A recruitment event with high densities was observed in the winter of 1991-1992, and densities were low for Class I during summer months. This pattern was similar to recruitment patterns in Texas and Alabama (Thomas et al. 1990, Williams et al. 1990), but lagged them by about a month. The lag was probably due to the greater migratory distance from high salinity spawning areas. A delay in the presence of suitable spawning temperatures at higher latitudes may account for a lag of several months in the Atlantic coast's peak abundance. In Chesapeake Bay, juveniles are more abundant in the summer months (Heck and Orth 1980b, Orth and van Montfrans 1987). Although the peak density (~ 18 crabs / m^2) in Barataria Bay was comparable to that in Lake Pontchartrain (9 crabs / m^2), the peak was in August (Gibson 1991). In the Lake Pontchartrain estuary, peak density for all juvenile blue crabs combined was in October, but Class I was densest in March.

Little work has been done on temperature selection for blue crabs, especially seasonally. High temperatures in cooler seasons and intermediate temperatures in warmer seasons are expected to be more suitable than extreme temperatures, because growth is proportional to temperature and mortality increases at temperatures above 30 °C (Hill et al. 1989). In Barataria Bay, however, suitabilities of low temperatures were higher for all seasons except summer (Gibson 1991). In summer, the maximum suitability was between 27 - 30 °C. In the Lake Pontchartrain estuary, low temperatures were highly suitable only in the winter (Figure 4.6). The observed suitabilities that varied from the expected could have been influenced by excursions into high temperature areas in response to other factors (e.g., food availability, refuge from predation) that affect overall fitness, which balances net energy gain with predation risks and other factors (Magnuson et al. 1979).

Although turbidity, dissolved oxygen, and water velocity contributed significantly to the prediction of blue crab size class distributions (Tables 4.1 and 4.4), they did not appear to be controlling factors. In coastal Mississippi, turbidity is a significant predictor for the abundances of many estuarine and marine fishes and decapods (Peterson and Ross 1991), and may generally confer some degree of protection from visual predators (Cyrus and Blaber 1992). Nevertheless, the difference in mean turbidity use among size classes was small (Table 4.1), and turbidity did not significantly predict the abundances of blue crabs within any size class. Dissolved oxygen levels are important for proper metabolism and molting (Van Engel 1982, Lowery and Tate 1986, Defur 1990, Defur et al. 1990, Ryer et al. 1990), but dissolved oxygen levels in this study did not appear to be controlling or limiting, nor did the range of water velocities observed. Although in Chesapeake Bay frontal passages can induce currents that can overpower blue crabs (van Engel 1982), such currents are unlikely in the submerged vegetation in the Lake Pontchartrain estuary, which dampens wave action and current velocity (Ward et al. 1984).

In the Lake Pontchartrain estuary, all three size classes of juvenile blue crabs showed a strong affinity with submerged vegetation (Table 4.1), but the use of individual macrophyte species varied with crab size. The long-term decline in the extent of submerged vegetation in Lake Pontchartrain (Montz 1978, Thompson and Verret 1980, Mayer 1986) is a serious concern because alternate nursery habitats of comparable quality are not widely available and the reduced habitat could result in a decline of the blue crab population (Heck and Thoman 1984, Lubbers et al. 1990, Orth and van Montfrans 1990). Changes in the total area covered by submerged vegetation and trends in the proliferation of the exotic Myriophyllum spicatum in the estuary are concerns because juvenile blue crab densities in M. spicatum are less than half of densities in Ruppia maritima, which has probably been partially replaced by the exotic. The reductions in the quality and quantity of nursery habitat could function as a

"demographic bottleneck" (Beck 1995) in the life history of blue crab. Given the continued decline in catch per unit effort for adult crabs, it may be appropriate to explore this effect more fully, as well as identify changes in blue crab nursery habitat, especially native macrophytes beds, for sustainable fishery management.

CHAPTER 5: INVERTEBRATE DIFFERENCES AMONG NATIVE AND EXOTIC SUBMERGED MACROPHYTES IN THE LAKE PONTCHARTRAIN ESTUARY, LOUISIANA

Introduction:

Introductions of exotic species have been characterized as primary threats to biodiversity, second only to rainforest destruction (Ehrenfeld 1970, Diamond and Chase 1986, Mooney and Drake 1986). Exotic submerged plant species can reduce habitat quality for fishes and invertebrates, leading to reductions in biodiversity and carrying capacity (Grace and Wetzel 1978, Keast 1984, Harlan et al. 1985, Sutton 1986, Tanner et al. 1990, Room and Fernando 1992). Some exotic aquatic macrophytes can displace native macrophyte species, and may have no effective herbivores (Grace and Wetzel 1978, Keast 1984, Harlan et al. 1985, Mooney and Drake 1986, Sutton 1986, Tanner et al. 1990, Room and Fernando 1992). The exotic Eurasian milfoil, Myriophyllum spicatum, was introduced to the North American continent in the late 19th century (Blackburn and Weldon 1967). It was first documented in Lake Pontchartrain in 1978 (Thompson and Verret 1980), and has since increased its distribution and abundance in the estuary to become one of the three major submerged macrophyte species (Mayer 1986).

Submerged macrophytes are highly productive habitats that are important to macroinvertebrate populations in littoral areas (Bell and Westoby 1986a, Virnstein 1987, Edgar 1990, Orth and van Montfrans 1990). Their epiphytes provide food resources for many macroinvertebrates (Kitting 1984, Orth and van Montfrans 1984, van Montfrans 1984, Heck and Crowder 1991), and their complex structure may confer some protection from predation (Orth and van Montfrans 1987, Rozas and Odum 1988, Heck and Crowder 1991). The increased surface area of macrophytes also provides more habitat complexity, which can increase the number, sizes, and diversity of inhabitable sites (Virnstein 1987, Holmund et al. 1990, Heck and Crowder 1991).

Many fishes and macroinvertebrates are more abundant in submerged vegetation than on unvegetated substrate (Bell and Westoby 1986a, Orth and van Montfrans 1987, Virnstein 1987, Rozas and Odum 1988, Edgar 1990, Heck and Crowder 1991). Macroinvertebrates are important to the overall ecology of estuaries because of the roles they play in nutrient cycling (Darnell 1958, Boesch and Turner 1984, Day et al. 1991), ecologically linking epiphytes and macrophytes with fishes and larger invertebrates (Heck and Orth 1980b, Boesch and Turner 1984). This parallels the role of zooplankton in nutrient cycling of pelagic systems (Darnell 1958, Day et al. 1991). Many fishes and crustaceans prey directly on the smaller macroinvertebrates (Kneib 1988, Gleason and Wellington 1988, Butler 1989), and some, such as spot, Leiostomus xanthurus (Nelson and Coull 1989), and grass shrimp, Palaemonetes pugio (Kneib 1988), feed on meiofauna and small macrofauna during critical stages of their ontogeny.

Because of the importance of submerged vegetation to macroinvertebrates, changes in the distribution and abundance of submerged macrophyte species can have a significant influence on macroinvertebrate populations (Bell and Westoby 1986a, Edgar 1990, Orth and van Montfrans 1990). From 1973 to 1985, the total area of submerged vegetation in Lake Pontchartrain declined by over 50 % (Montz 1978, Mayer 1986). Concurrent with this decline, the areal coverage of the exotic Myriophyllum spicatum increased. In a Canadian lake, the invasion of M. spicatum significantly affected distributions of the associated invertebrates and fishes (Keast 1984) by altering biologically important variables including the dissolved oxygen concentration at the sediment-water interface and the amount of organic matter in the sediments. Additionally, abundances of most fishes and macroinvertebrates were lower in M. spicatum than in the native beds of Vallisneria americana and Potamogeton spp. (Keast 1984). To determine if the presence of M. spicatum was having a similar effect on macroinvertebrate distributions in the Lake Pontchartrain estuary, this study was designed to: 1) compare natant macroinvertebrate communities among submerged

macrophyte species and adjacent unvegetated substrates, 2) identify the environmental variables important to the distribution of common invertebrate species in littoral areas, and 3) compare meiofaunal abundances and substrate characteristics among submerged macrophyte species and unvegetated substrates.

Study Area:

Lake Pontchartrain is a large, semi-enclosed estuary located just north of New Orleans in coastal Louisiana (Figure 5.1). It covers an area of 1,630 km², has a mean depth of 3.7 m, and a maximum depth of 5 m (Sikora and Kjerfve 1985). Salinity in the estuary ranges from 0 to 10 ‰ (Sikora and Kjerfve 1985). It is connected to two smaller lakes, Lakes Borgne and St. Catherine, to the east and to the Gulf of Mexico by two main passes. Myriophyllum spicatum is also established in these lakes, and is common in Lake St. Catherine. The two most common native submerged macrophytes in the estuary are Vallisneria americana and Ruppia maritima. Three stations were chosen to characterize the salinity gradient, including the littoral areas near the mouths of Cane Bayou and Bayou Lacombe in Lake Pontchartrain and the north end of Lake St. Catherine (Figure 5.1).

Methods:

macroinvertebrates:

A modified Wegener ring (Weinstein and Brooks 1983), consisting of a vertical cylinder of heavy fabric extending 110 cm in height and a circular stainless steel base ring (10 cm high x 1.23 m diameter, 1.18 m²), was used to collect microhabitat and abundance data. When deployed the walls were supported by a float ring at the top. The ring diameter was adequate for sampling the species of interest (Chick et al. 1992). A boom extending three meters beyond the bow of a 5.2 m boat was used to deploy the sampler. The sampler was held one-half meter above the water's surface until it was released with a pull-pin. Upon deployment, the basal ring was checked to ensure

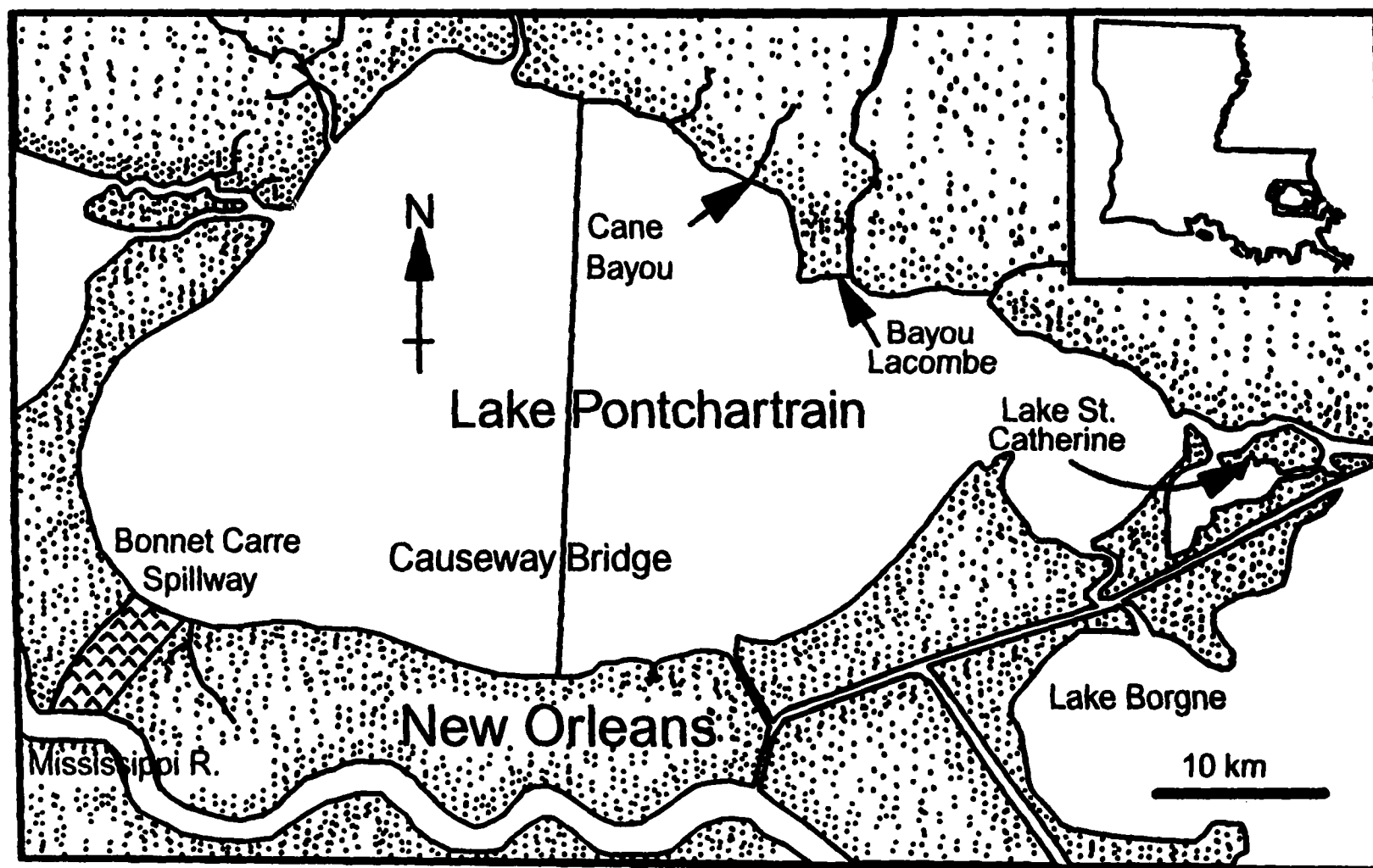


Figure 5.1: The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer 1986).

that it had adequately penetrated the substrate to permit a quantitative estimate of macroinvertebrate abundances.

Each month between March 1991 and January 1993, twelve samples collected at each station were stratified among the common submerged macrophyte species and unvegetated substrates. When all of the submerged macrophyte species were not present, samples were distributed among the existing species to maximize the amount of information collected each trip. Within strata, each sampling site was randomly selected to represent the range of submerged macrophyte densities present and the range of depths up to a maximum of one meter. Each sample was unique and considered to be independent for statistical purposes.

At the microhabitat level, organisms presumably select sites in response to environmental gradients, balancing net energy gain with predator avoidance and competition (Baltz 1990, Baltz et al. 1993). The microhabitat of an organism is ultimately defined as the characteristics of the place where that organism is located at a point in time (Baltz 1990). By measuring the environmental variables at multiple capture sites for individuals of a species, the microhabitat characteristics for that species can be inferred from the population's pattern of abundance along different environmental gradients (Hurlbert 1981). The environmental variables measured included dissolved oxygen concentration (mg / l), temperature (°C), salinity (‰), surface water velocity (cm / s), minimum and maximum water depth (cm), distance from shore (m), turbidity, substrate type, and the average height and number of stems for each macrophyte species present in the sampler. Water depth was calculated as the median of minimum and maximum depths. Temperature, salinity, and dissolved oxygen were measured with a Hydrolab model SRV2-SU. Surface water velocity was estimated by timing a neutrally buoyant object in the water for ten seconds and measuring the mean displacement per second. Turbidity was measured in nephelometer turbidity units (NTU) with a Monitek model 21 PE portable nephelometer. Substrate type was estimated by touch on a

particle size scale: 1 = clay; 2 = mud (i.e., clay and silt) ; 3 = silt; 4 = sand; 5 = organic detritus; 6 = shell and shell fragments. Additionally, the submerged macrophyte species present were identified (Chabreck and Condrey 1979), and the number of stems and mean stem lengths were estimated for each species by subsampling.

Plant surface area (PSA) provides a better index of habitat complexity than stem density (Virnstein 1987, Heck and Crowder 1991). For each submerged vegetation species, surface areas were calculated using species-specific formulas derived from measurements of the surface area of stems and leaves. Surface areas, measured using a Li-Cor LI-3000 portable leaf area meter, were linearly regressed on stem length to provide species-specific formulas for estimating the total surface area (in m² plant area per m² bottom area) of common submerged vegetation species:

<u>Vallisneria americana</u> :	$PSA = 1.258 * L * C / 10000$ (N = 20, R ² = 0.99),
<u>Myriophyllum spicatum</u> :	$PSA = 1.058 * L * C / 10000$ (N = 20, R ² = 0.80),
<u>Ruppia maritima</u> :	$PSA = 0.232 * L * C / 10000$ (N = 19, R ² = 1.00),

where L is the stem length (cm) and C is the number of stems of that species in the sample. Total PSA for a sample is reported, and samples were assigned to vegetation types by dominance. If a sample had less than 0.0118 m² / m² total surface area it was treated as an unvegetated site.

Following the environmental characterization of each sample site, the recovery of organisms was facilitated by the application of a suspension of 5 % rotenone to the enclosed water (Davies and Shelton 1983). Fishes and other organisms affected by the rotenone were collected with a small dip net and preserved in 95 % ethanol. The enclosed volume was then systematically swept six times with a large rectangular hand net (39 x 30 cm, 5 mm diamond mesh) and twice with a smaller dip net to capture a high percentage of remaining organisms which were preserved with a 10 % buffered formalin

solution for 24 hrs, then transferred to 95 % ethanol. All macroinvertebrates were identified and enumerated under a dissection microscope (Heard 1982).

The DeLury (1947) depletion method was used during a preliminary study to estimate the capture efficiency by systematic hand netting for macroinvertebrates that were not affected by rotenone. A common organism, the grass shrimp (Paleomonetes pugio), was used to identify an adequate level of netting effort. The results indicated that six systematic sweeps, each of which covered the entire basal area of the Wegener ring, were sufficient to remove at least 95 % of the individuals present ($r^2 = 0.97$, $F = 179.9$, $df = 1$ and 12 , $p \leq 0.0001$).

A multiple analysis of variance (MANOVA) was used to examine the relationship of macroinvertebrate populations to environmental gradients (SAS Institute 1989). Environmental variables that accounted for significant variation in the abundance for each macroinvertebrate taxon were identified, as were overall effects of variables on assemblage structure patterns. Abundances were log transformed ($\log_e(x + 1)$) to normalize the data (Sokal and Rohlf 1981). Rare macroinvertebrate taxa (i.e., < 0.5 % total individuals caught or a frequency of occurrence in < 2 % of the samples) were excluded from this and subsequent analyses.

A factor analysis was employed to identify highly correlated environmental variables and to identify responses of invertebrate taxa to these groupings (Grossman et al. 1991). The varimax rotation option (Johnson and Wichern 1988) in the factor analysis of environmental data from 517 samples (SAS Institute 1989) was used to identify major axes with eigenvectors ≥ 1 (For a more detailed description of the factor analysis, see Chapter 3). Weighted means of the factor scores were calculated for each taxa (May 1975, Baltz and Moyle 1993), and were plotted on the component axes to identify the major responses of macroinvertebrate abundances to groups of environmental variables. Pairwise overlap (Schoener 1970) between invertebrate taxa

was calculated from the distribution patterns of macroinvertebrate taxa across seven equally spaced intervals along each factor score (Baltz and Moyle 1993). Because the axes are orthogonal (May 1975, Johnson and Wichern 1988), total environmental overlaps were calculated as the product of overlaps for each factor. Additionally, assemblage structure patterns of common invertebrate taxa among macrophyte species and unvegetated substrates were tested using Kendall's W (Siegel 1956, Grossman 1982), and pairwise overlap of macroinvertebrate assemblage structure was calculated for submerged macrophyte species and unvegetated substrates from the relative abundances of the invertebrate taxa (Schoener 1970).

General linear models (GLM) approaches (SAS Institute 1989) were used to compare abundances of the common macroinvertebrates among stations, among seasons, and among the submerged macrophyte species. A separate GLM analysis compared abundances of common macroinvertebrates between vegetated and unvegetated samples to better distinguish patterns of use. Significant effects were tested with the a posteriori least squares means test (LSMeans). Because unequal numbers of samples were collected in each season (defined by solstices and equinoctial dates), sampling bias was avoided by using weights based on seasonal sampling effort. To yield a conservative Type I error rate of 0.05 (Johnson and Wichern 1988), the alpha level was adjusted using the Dunn-Šidák correction (Sokal and Rohlf 1981). The appropriate critical values were computed using the expression: $\alpha' = 1 - (1 - \alpha)^{1/k}$, where α is the experimentwise adjusted error rate, k is the number of comparisons, and α is the critical value.

meiofauna:

Meiofauna and small macrofauna were identified and enumerated from 15 drop samples to characterize infauna and identify possible differences in abundances among submerged vegetation types. Four samples with two replicates each for each vegetation type (three samples with replicates for unvegetated) were taken from the Lake St. Catherine station during spring of 1992. Cores 2 cm in diameter and 2 cm deep were

collected with a plunger corer and preserved in a 10 % formalin solution. After staining with a 10 % buffered formalin-Rose Bengal solution, the cores were washed through a 500 μm sieve onto a 63 μm sieve (Fleeger and Chandler 1983). The material retained on the 63 μm sieve was transferred to a centrifuge tube and excess water was removed by spinning at 1,300 rpm for 2 min. Ludox AM was added to the pellet and the material was centrifuged at 975 rpm for 3 min. The supernatant with the suspended organisms was rinsed through a 63 μm sieve and the collected material was preserved in a 10 % formalin solution (Fleeger and Chandler 1983). Pellets were preserved to measure the efficiency of the extraction. After sorting 5 pellets, efficiency averaged over 95 % for nematodes and copepods. Meiofauna were enumerated under a dissection microscope to major taxa.

The organic fraction and sand fraction were also determined for the same meiofaunal samples using two additional replicates. After drying at 70 °C for 48 hr, initial mass was determined. Organic matter was burned off (Krumbein and Pettijohn 1938) by adding increments of a 30 % hydrogen peroxide solution until bubbling stopped (several days). Sediments were dried again at 70 °C for 48 hr, after which a final mass was determined. The organic fraction was calculated as the difference divided by the initial mass. After the removal of the organic fraction, the samples were dispersed using a total of 200 ml of a 2 g / l sodium hexametaphosphate solution for 24 hr, then rinsed through a 63 μm sieve to remove the sand, which was dried and weighed (Krumbein and Pettijohn 1938). The sand fraction was calculated as the mass of sand retained divided by the initial mass of the sample.

A GLM approach was used to compare abundances of meiofaunal taxa among submerged macrophyte species and unvegetated substrates. Any significant differences were further tested using LSMeans. The relations of the organic and sand fractions to submerged macrophyte species and unvegetated substrates were also tested using a similar approach. Significance levels were again adjusted using the Dunn-Šidák

correction (Sokal and Rohlf 1981). Additionally, the correlations between the organic fraction and the sand fraction to common meiofaunal taxa were analyzed using Pearson's correlation coefficients (Johnson and Wichern 1980).

Results:

macroinvertebrates:

From 517 samples obtained between March 1991 and January 1993, we collected 53,006 individual macroinvertebrates from 13 major taxa, of which eight were identified to species (Table 5.1). The macroinvertebrates were numerically dominated by the amphipod Gammarus mucronatus (46.05 %). Other abundant macroinvertebrates were another amphipod Grandidierella bonnieroides (26.36 %), grass shrimp Palaemonetes pugio (9.78 %), and a third amphipod Gammarus tigrinus (9.14 %). Together these four macroinvertebrate species comprised 91.3 % of all the individuals collected and occurred

Table 5.1: List of invertebrate taxa collected from the Lake Pontchartrain estuary by drop sampling between March 1991 to January 1993. Total number of individuals collected, percentage of the total (51,620 invertebrates) caught, number of samples in which the species was observed, and percent frequency of the samples in which the species was observed (517 samples total) are reported, as are the Codes for selected taxa.

Taxa (Code)	Common Name	Number Collected	Percent of Total Number	Number of Samples	Percent Frequency
<u>Gammarus mucronatus</u> (Gm)	Amphipod	24,407	46.05	419	81.04
<u>Grandidierella bonnieroides</u> (Gb)	Amphipod	13,970	26.36	380	73.50
<u>Palaemonetes pugio</u> (Pp)	Grass shrimp	5,186	9.78	282	54.55
<u>Gammarus tigrinus</u> (Gt)	Amphipod	4,846	9.14	218	42.17
<u>Callinectes sapidus</u> (Cs)	Blue crab	1,386	2.61	486	94.00
Mysidacea (My)	Mysid	1,720	3.24	189	36.56
Odonata (Od)	Dragonfly larvae	631	1.19	160	30.95
Idoteidae (Id)	Idoteids	497	0.94	101	19.54
Polychaetae	Polychaetes	200	0.38	99	19.15
<u>Rithropanopeus harrissii</u>	Mud crab	92	0.17	21	4.06
Chironomiidae	Chironomids	59	0.11	6	1.16
Copepodae	Copepods	11	0.02	4	0.77
<u>Penaeus setiferus</u>	White shrimp	1	0.002	1	0.19
Totals		53,006		517	

in 42 % to 81 % of all samples. Eight invertebrate taxa were chosen for further analysis, based on abundance (> 0.5 % total numbers) and occurrence (present in > 2 % of samples), including blue crab Callinectes sapidus, mysids, Odonata, and Idoteidae. Five taxa, including polychaetes, mud crab Rithropanopeus harrisi, Chironomids, Copepods, and white shrimp Penaeus setiferus, did not qualify for inclusion in the analysis based on their abundances.

From the GLM comparing environmental variables among seasons (Table 5.2), all nine variables measured, except surface water velocity, showed at least one significant difference among seasons (LSMeans, $p \leq 0.0085$ for all significant comparisons). Mean PSA was significantly higher in the summer and autumn than in winter, with spring having an intermediate value. Vallisneria americana had high PSA values in summer and autumn, whereas Ruppia maritima and Myriophyllum spicatum had high PSA values in spring. Temperature and dissolved oxygen were negatively correlated (Pearson's $r = -0.49$, $p \leq 0.0001$), with temperature means high and dissolved oxygen means low in spring and summer. Salinity means were generally higher in autumn and winter and lower in spring and summer.

Environmental conditions influenced the distribution and abundance of most of the common invertebrates. In the MANOVA, 8 of 9 measured environmental variables, including distance from shore, PSA, temperature, turbidity, salinity, median depth, dissolved oxygen, and substrate, had significant ($N = 517$, $df = 8$ and 500 , $p \leq 0.0001$) effects on overall invertebrate abundances (Table 5.3). Each environmental variable except water velocity also significantly ($p \leq 0.0057$) contributed to the prediction of the abundance pattern for at least one invertebrate taxa; moreover, for most invertebrates, more than one environmental variable significantly influenced abundance.

In the factor analysis used to examine associations among environmental variables and invertebrate taxa, each of nine environmental variables loaded heavily ($\geq |0.50|$) in one of four factors (Table 5.4). Four rotated factors had eigenvalues greater

Table 5.2: Seasonal means (\pm 1SE) of environmental variables observed in Lake Pontchartrain between March 1991 and January 1993. Significant differences among seasonal means (LSMeans, $p \leq 0.0085$) are indicated by different letters, reading horizontally.

	Winter	Spring	Summer	Autumn
	N = 94	N = 97	N = 217	N = 109
Distance from Shore (m)	38.80 (2.45) A	28.16 (1.87) B	36.39 (1.56) AC	30.20 (1.76) BC
Plant Surface Area (m ² / m ²)	0.26 (0.03) A	0.44 (0.06) AB	0.55 (0.04) B	0.57 (0.07) B
Temperature (° Celsius)	13.10 (0.16) A	25.84 (0.50) B	30.41 (0.19) C	17.41 (0.47) D
Salinity (‰)	3.26 (0.18) A	2.70 (0.21) B	2.25 (0.15) B	3.88 (0.20) C
Turbidity (NTU)	8.31 (1.06) A	9.30 (1.12) A	6.06 (0.32) B	5.18 (0.47) B
Median Depth (cm)	39.15 (1.53) A	45.70 (1.76) B	50.71 (1.14) B	39.35 (1.25) A
Dissolved Oxygen (mg / l)	10.46 (0.09) A	8.31 (0.23) B	8.29 (0.11) B	9.91 (0.13) A
Substrate Code	3.9 (0.09) A	3.5 (0.12) B	3.8 (0.07) AB	3.8 (0.09) AB
Water Velocity (cm / s)	3.23 (0.23)	3.74 (0.25)	3.48 (0.13)	3.15 (0.24)

than one and together explained 68 % of the environmental variance measured. Factor One (21.0 % of the total variance) was interpreted as a large-scale spatial axis in which salinity was related negatively to substrate and distance from shore. Factor Two (19.9 %) was interpreted primarily as a seasonal axis and weighted positively for temperature and depth and negatively for dissolved oxygen; nevertheless, almost all variables showed some seasonal variation (Table 5.2). Factor Three (14.3 %) reflected a turbidity gradient which was also related positively with water velocity and negatively with salinity. Factor Four (12.3 %) reflected a PSA gradient that weighted slightly negatively for water velocity.

Table 5.3: Means of environmental variables utilized by selected invertebrates (\pm 1SE), adjusted for seasonal differences in sampling effort. Significance levels of the influence of environmental variables on the invertebrate abundances are indicated with asterisks: * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001 (MANOVA: N = 517, df = 1 and 509). F values from the overall effect of the environmental variable from the MANOVA analysis are given, as are the associated significance levels (df = 8, 500).

	Distance from Shore (m)	Plant Surface Area (m ² / m ²)	Salinity (‰)	Temperature (°C)	Turbidity (NTU)	Depth (cm)	Dissolved Oxygen (mg / l)	Substrate Code	Water Velocity (cm / s)
<i>G. mucronatus</i>	28.97 (4.63) ***	0.53 (0.15) ***	2.32 (0.52) ***	17.92 (1.96) ***	10.84 (4.01) *	39.71 (4.01) *	10.39 (0.51) ***	3.80 (0.27)	2.98 (0.70)
<i>G. bonnieroides</i>	24.32 (2.66) ***	0.25 (0.07) **	2.78 (0.36)	19.78 (1.60) **	20.36 (3.95) ***	42.36 (3.57) ***	9.80 (0.39) *	3.78 (0.21) **	3.88 (0.49)
<i>P. pugio</i>	23.83 (2.30) **	0.88 (0.09) ***	4.04 (0.33) ***	24.76 (1.07)	8.08 (1.26) ***	48.44 (2.06)	8.83 (0.25) **	2.93 (0.16) ***	2.90 (0.27)
<i>G. tigrinus</i>	35.76 (2.24)	0.57 (0.08) ***	2.07 (0.17) ***	15.51 (0.71) ***	11.82 (1.99) **	36.02 (1.49)	10.65 (0.18) ***	4.23 (0.06) **	3.16 (0.37)
<i>C. sapidus</i>	24.72 (1.14) **	0.55 (0.04) **	4.16 (0.14) ***	22.30 (0.45)	6.65 (0.53)	46.31 (0.92)	9.23 (0.10)	3.26 (0.07)	3.08 (0.13)
Mysidacea	31.91 (1.73) ***	0.34 (0.04)	2.95 (0.13)	24.09 (0.51) *	5.79 (0.53)	59.43 (1.53) ***	8.19 (0.16)	3.53 (0.08) *	4.23 (0.22)
Odonata	27.33 (0.65) ***	0.82 (0.03) ***	1.56 (0.09) ***	26.39 (0.37)	9.25 (0.40)	45.55 (0.71)	9.51 (0.10) ***	3.72 (0.05)	3.54 (0.09)
Idoteidae	40.13 (0.98) **	0.50 (0.02)	2.43 (0.06) ***	19.59 (0.29)	23.25 (0.85) ***	41.83 (0.56) **	10.20 (0.05) *	4.20 (0.03) **	3.94 (0.10)
F Value	25.21	21.02	18.68	17.22	14.05	6.869	6.31	5.83	1.04
p - F	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.4042

Table 5.4: Rotated factor loadings (VARIMAX rotation over four axes) for the environmental variables measured in 517 samples at three stations in the Lake Pontchartrain estuary between March 1991 and January 1993.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Substrate	0.86	-0.16	0.01	-0.01
Distance from Shore	0.80	0.01	-0.18	0.00
Salinity	-0.70	-0.16	-0.47	-0.15
Dissolved Oxygen	0.03	-0.80	0.10	0.13
Temperature	0.07	0.77	0.22	0.24
Median Depth	-0.11	0.69	-0.24	0.00
Turbidity	0.15	0.08	0.84	-0.04
Water Velocity	-0.11	-0.19	0.46	-0.52
Plant Surface Area	0.13	0.07	0.03	0.86
Variance	1.95	1.79	1.28	1.11
% Cum. Var.	21.6	41.5	55.8	68.1

Several common invertebrates were well separated along the Factor One axis (Figure 5.2), a large-scale spatial axis (see Chapter 3). Salinity significantly increased across stations (LSMeans, $p \leq 0.0001$); it was lowest at Cane Bayou, intermediate at Bayou Lacombe, and highest at Lake St. Catherine. Sand bars at the Bayou Lacombe station supported submerged vegetation growth farther from shore than at the other stations. Invertebrate taxa that were most abundant in Lake St. Catherine were usually associated with higher salinities and finer substrates, whereas those most abundant in the Lake Pontchartrain stations were associated with lower salinities and coarser substrates. Grass shrimp, blue crabs and mysids were most abundant in Lake St. Catherine (Table

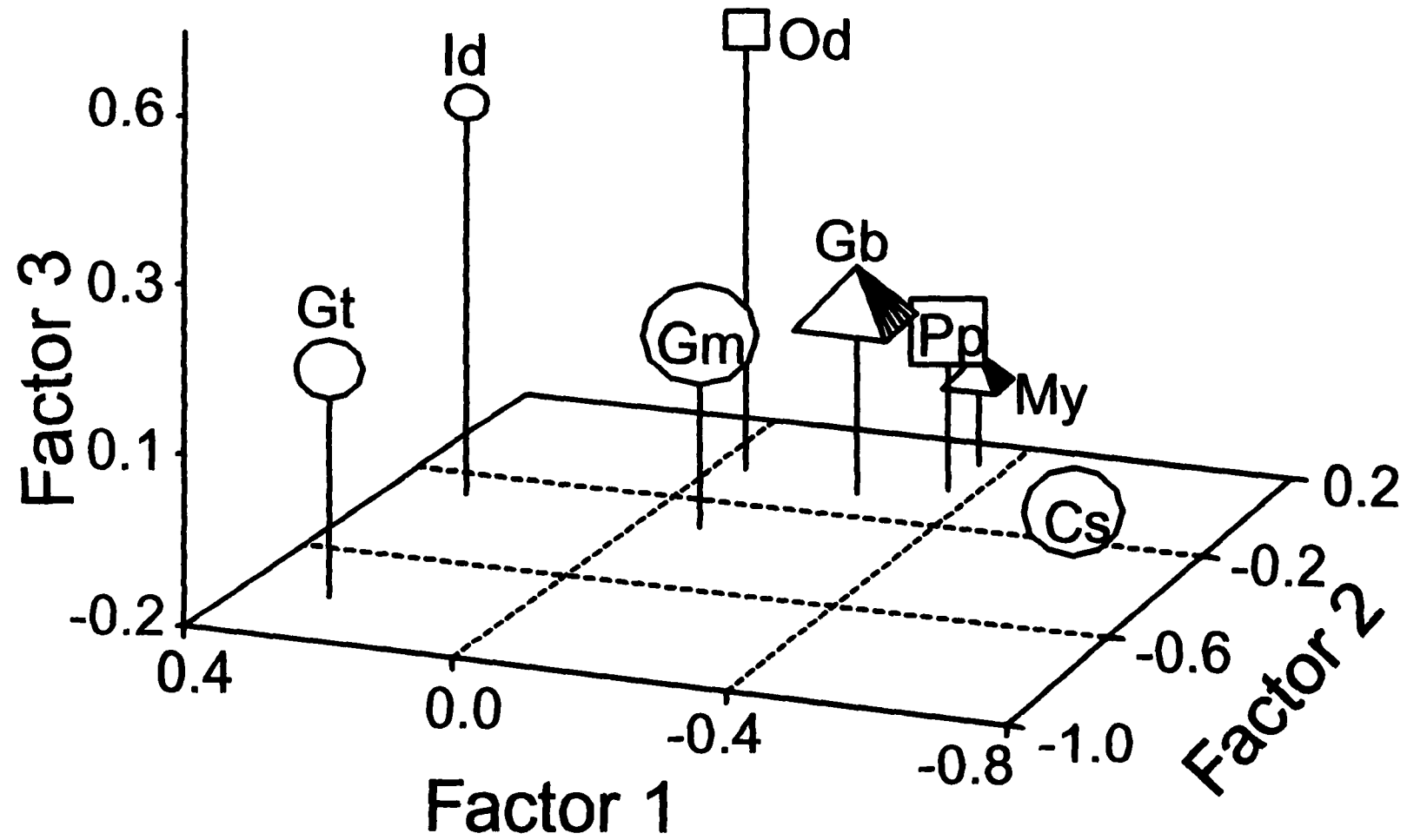


Figure 5.2: Three dimensional plot of centroids for eight macroinvertebrate taxa common in the submerged macrophytes of the Lake Pontchartrain estuary. Positions along the fourth factor axis are represented by the shapes: pyramid, < 0.0; circle, 0 to 0.45; square, > 0.45. Codes for taxa are defined in Table 5.1.

5.5), so their distribution patterns along this axis differed from the three amphipods, Odonata, and Idoteidae, which were more common in Lake Pontchartrain. Gammarus mucronatus was significantly (LSMeans, $p \leq 0.017$, $df = 2, 514$) less abundant at Bayou Lacombe than at Cane Bayou and Lake St. Catherine, whereas Grandidierella bonnieroides was most abundant at Bayou Lacombe (Table 5.6). Grass shrimp and mysids were most abundant and the amphipod Gammarus tigrinus was least abundant in Lake St. Catherine. Odonata was most abundant at Cane Bayou, whereas Idoteidae was most abundant at Bayou Lacombe.

Seasonal variation was primarily reflected along the Factor Two axis by opposite heavy loadings for temperature (+0.77) and dissolved oxygen (-0.80). Median depth also weighted heavily (+0.69) in this factor, and was positively related to temperature,

Table 5.5: Mean densities (individuals / $m^2 \pm 1SE$) of selected invertebrates collected from the three stations sampled in the Lake Pontchartrain estuary between March 1991 and January 1993. Means are adjusted for seasonal differences in sampling effort. Significant differences among the three stations (LSMeans, $p \leq 0.0170$) are indicated with different letters, reading horizontally.

Taxa	Cane Bayou	Bayou Lacombe	Lk. St. Catherine
<u>G. mucronatus</u>	101.67 (9.28) A	28.94 (8.95) B	47.18 (9.24) A
<u>G. bonnieroides</u>	8.57 (9.98) A	59.08 (9.62) A	25.90 (9.93) B
<u>P. pugio</u>	3.16 (1.74) A	5.57 (1.68) A	18.86 (1.73) B
<u>G. tigrinus</u>	23.32 (2.64) A	11.55 (2.54) B	1.31 (2.62) C
<u>C. sapidus</u>	0.90 (0.31) A	2.01 (0.34) B	4.68 (0.28) C
Mysids	1.65 (0.77) A	2.56 (0.74) A	4.26 (0.77) B
Odonata	1.69 (0.20) A	0.41 (0.19) B	1.07 (0.19) C
Idoteidae	0.27 (0.41) A	2.82 (0.39) B	0.30 (0.40) A
N	170	185	162

Table 5.6: Seasonal densities (individuals / m² ± 1 SE) of selected invertebrates in the Lake Pontchartrain estuary between March 1991 and January 1993. Significant differences (LSMeans, $p \leq 0.0085$) are indicated by different letters, reading horizontally.

Taxa	Winter	Spring	Summer	Autumn
<u>G. mucronatus</u>	121.06 (10.58) A	48.81 (10.41) A	12.20 (6.96) B	51.79 (9.83) A
<u>G. bonnieroides</u>	79.87 (11.43) A	16.23 (11.25) AB	13.69 (7.52) B	17.59 (10.61) A
<u>P. pugio</u>	7.64 (2.63)	5.18 (2.59)	12.76 (1.73)	10.98 (2.44)
<u>G. tigrinus</u>	30.21 (2.97) A	4.20 (2.93) B	1.03 (1.96) B	12.61 (2.76) A
<u>C. sapidus</u>	2.10 (0.33) AB	3.49 (0.32) C	1.39 (0.34) A	3.13 (0.33) BC
Mysids	1.97 (1.24)	1.75 (1.22)	5.00 (0.82)	2.58 (1.15)
Odonata	0.61 (0.31)	0.92 (0.31)	1.83 (0.21)	0.81 (0.29)
Idoteidae	3.43 (0.47) A	0.59 (0.46) B	0.43 (0.31) B	0.22 (0.43) B
N	94	97	217	109

reflecting higher tide levels and a possible sampling bias in that deeper samples were taken in the warmer seasons than in the colder seasons (LSMeans, $p \leq 0.0011$).

Macronvertebrate taxa were not separated widely along the Factor Two axis (Figure 5.2). Taxa were ordered from winter abundant species (negative factor scores) to summer abundant species (positive factor scores), with spring and autumn abundant species at intermediate scores. Gammarus tigrinus was rare in summer (Table 5.6), and separated from the remaining taxa, which, although generally less abundant in summer, were more common. All three amphipod species and Idoteidae were significantly (LSMeans, $p \leq 0.0085$, $df = 3, 513$) more abundant in winter. Gammarus mucronatus was significantly (LSMeans, $p \leq 0.0085$, $df = 3, 513$) less abundant in summer, with intermediate densities in spring and autumn. Grass shrimp, mysids, and Odonata were common in summer, and their placements along this axis reflected this pattern.

The common invertebrate taxa also separated along the turbidity gradient (Factor Three), which was positively correlated with surface water velocity (Figure 5.2).

Idoteidae was found at the highest mean turbidity (Table 5.3). All of the common invertebrate taxa except Idoteidae and Odonata concentrated at the low end of the turbidity axis.

The common invertebrate taxa were separated strongly along the PSA gradient (Factor Four). Grandidierella bonnieroides and mysids were found at the lowest mean PSA values (Table 5.3 and Figure 5.2). Grass shrimp and Odonata were found at the highest mean PSA values. The remaining invertebrates were clustered at intermediate PSA means.

In the GLM comparing abundances of common invertebrate taxa among submerged macrophyte species and unvegetated substrate, all eight of the invertebrate taxa were significantly ($p \leq 0.025$, $df = 1$, 515) more abundant in vegetated areas than on adjacent unvegetated substrate (Table 5.7), with the exception of mysids, which were relatively common on unvegetated areas. Among the amphipods, Gammarus mucronatus was significantly (LSMeans, $p \leq 0.017$, $df = 2$, 514) more abundant in Myriophyllum spicatum than in Vallisneria americana, whereas Grandidierella bonnieroides and Gammarus tigrinus were more abundant in V. americana than in M. spicatum and Ruppia maritima. Grass shrimp were more abundant in V. americana than in M. spicatum, whereas mysids were more abundant in R. maritima than in V. americana and M. spicatum. Odonata was most abundant in M. spicatum whereas Idoteidae was most abundant in V. americana.

Pairwise overlaps in environmental factor space between the eight common macroinvertebrate taxa were generally low (Table 5.8), the mean overlap was 0.24, and only exceeded 0.50 between Gammarus mucronatus and G. tigrinus (0.52), Grandidierella bonnieroides and Idoteidae (0.54), and grass shrimp and blue

Table 5.7: Densities (individuals / m² ± 1SE) of selected invertebrates collected in three submerged macrophytes and unvegetated areas in the Lake Pontchartrain estuary between March 1991 and January 1993. Mean abundances are adjusted for differences in seasonal sampling effort. N = number of independent samples. Significant differences among the three macrophyte species (LSMeans, $p \leq 0.017$) are indicated with different letters, reading horizontally. Comparisons were restricted to vegetated habitats to distinguish among macrophyte species. Significant differences between total vegetated and unvegetated areas for each species (LSMeans, $p \leq 0.025$) are indicated by asterisks in the "unvegetated" column. Total density was calculated from the sum of the common invertebrate taxa, and was not detectably different among macrophyte species.

Taxa	<u>Vallisneria</u>	<u>Myriophyllum</u>	<u>Ruppia</u>	Unvegetated
<u>G. mucronatus</u>	59.90 (7.27) A	107.55 (11.71) B	44.03 (18.27) AB	7.09 (12.27) *
<u>G. bonnieroides</u>	43.47 (7.89) A	21.45 (12.71) B	30.89 (19.83) B	10.61 (13.32) *
<u>P. pugio</u>	12.65 (1.40) A	7.89 (2.25) B	10.16 (3.51) AB	0.03 (2.36) *
<u>G. tigrinus</u>	18.46 (2.09) A	8.88 (3.37) B	1.88 (5.25) B	1.68 (3.53) *
<u>C. sapidus</u>	3.09 (0.22) A	2.01 (0.36) B	4.12 (0.58) A	0.89 (0.37) *
Mysids	1.98 (0.60) A	2.98 (0.97) A	4.52 (1.52) B	4.30 (1.02)
Odonata	1.09 (0.15) A	1.96 (0.25) B	0.71 (0.38) A	0.03 (0.26) *
Idoteidae	2.08 (0.32) A	0.28 (0.52) B	0.09 (0.81) B	0.03 (0.54) *
Total Density	142.19 (13.60)	153.81 (21.90)	98.43 (34.16)	24.31 (22.95) *
N	283	102	40	92

crab (0.53). The lowest pairwise overlaps were between grass shrimp and G. tigrinus (0.10), G. bonnieroides (0.12), and Idoteidae (0.12).

Macroinvertebrate assemblage structures of the submerged macrophyte species and unvegetated substrates, estimated from the rank order of abundance of the eight most common taxa, were significantly concordant (Kendall's $W = 0.88$, $p \leq 0.005$, $df = 7$). Nevertheless, pairwise comparisons of assemblage similarity among submerged macrophyte species and unvegetated substrates revealed that the assemblage structures

Table 5.8: Schoener's overlap among common invertebrate taxa of the Lake Pontchartrain estuary collected between March 1991 and January 1993. Overlap was calculated across seven equal intervals along each of four orthogonal axes from a factor analysis.

	<u>Idoteidae</u>	<u>Odonata</u>	<u>mysids</u>	<u>C. sapidus</u>	<u>G. tigrin.</u>	<u>P. pugio</u>	<u>G. bonn.</u>
<u>G. mucronatus</u>	0.29	0.23	0.21	0.30	<u>0.52</u>	0.22	0.27
<u>G. bonnieroides</u>	<u>0.54</u>	0.15	0.20	0.14	0.23	0.12	--
<u>P. pugio</u>	0.12	0.27	0.21	<u>0.53</u>	0.10	--	
<u>G. tigrinus</u>	0.30	0.14	0.15	0.15	--		
<u>C. sapidus</u>	0.16	0.25	0.28	--			
<u>mysids</u>	0.19	0.19	--				
<u>Odonata</u>	0.17	--					
<u>Idoteidae</u>	--						

in the native macrophytes were more similar to each other than to that of Myriophyllum spicatum (Table 5.9). The lowest similarity was between M. spicatum and unvegetated substrates. Pairwise similarities between native macrophytes and M. spicatum were comparable to the similarities between native macrophytes and unvegetated substrates.

meiofauna:

In a limited analysis of spring meiofauna abundances in 30 cores from Lake St. Catherine, thirteen taxa with 11,620 individuals were observed (Table 5.10). Meiofauna were numerically dominated by nematodes, which accounted for 77.7 % of all individuals counted. Other common taxa included in the analysis were foraminiferans, ostracods, harpacticoid copepods, kynorhynchs, acarina (water mites), and gastrotrichs.

Table 5.9: Schoener's overlap of the assemblage structure of common invertebrates among submerged macrophyte species and unvegetated substrates of the Lake Pontchartrain estuary.

	Unvegetated	<u>R. maritima</u>	<u>M. spicatum</u>
<u>V. americana</u>	0.70	0.88	0.71
<u>M. spicatum</u>	0.52	0.71	
<u>R. maritima</u>	0.71		

Table 5.10: Total numbers of meiofauna taxa collected in 30 sediment cores taken from three submerged macrophyte species and unvegetated substrates at the Lake St. Catherine station during spring of 1992.

Taxa	Number Collected	% Total Number	No. of Samples	% Freq.
Nematodes	9,026	77.68	30	100.00
Foraminifera	1,118	6.62	29	96.67
Ostracods	396	3.41	30	100.00
Kynorhyncha	333	2.87	25	83.33
Harpacticoidea	322	2.77	28	93.33
Acarina	272	2.34	19	63.33
Gastrotrichs	83	0.71	21	70.00
Amphipods	41	0.35	19	63.33
Chironomids	9	0.08	7	23.33
Bivalves	8	0.07	4	13.33
Annelids	6	0.05	3	10.00
Gastropods	3	0.03	3	10.00
Polychaetes	3	0.03	3	10.00
Totals	11,620		30	

A GLM analysis comparing the density of individual meiofauna taxa among submerged macrophytes and unvegetated substrates did not detect any significant differences (Table 5.11). A power analysis on the meiofauna data indicated that 30 to 60

samples with two replicates per sample would be necessary to ensure a beta error rate of 0.15 while maintaining an alpha rate of 0.05. From a similar GLM analysis, the mean organic fractions and sand fractions differed significantly (LSMeans, $p \leq 0.0085$) among macrophyte species and unvegetated substrates (Table 5.11). The organic fraction was highest in Vallisneria americana, intermediate in Myriophyllum spicatum, and lowest in Ruppia maritima and unvegetated samples. The sand fraction was highest in Ruppia maritima and unvegetated samples, intermediate in Myriophyllum spicatum, and lowest in Vallisneria americana. The organic and sand fractions were negatively related (Pearson's $r = -0.87$, $p \leq 0.0001$, $N = 23$). The abundance of acarina was positively related to the organic fraction ($r = 0.69$, $p \leq 0.0001$, $N = 23$), and marginally negatively related to sand fraction ($r = -0.48$, $p \leq 0.02$, $N = 23$).

Discussion:

Invertebrates are an integral part of the ecology of submerged macrophytes (Bell and Westoby 1986a, Virnstein 1987, Edgar 1990, Orth and van Montfrans 1990), linking epiphytes and detritus to higher predators (Heck and Orth 1980, Boesch and Turner 1984, Butler 1989). In the Lake Pontchartrain estuary, all of the common invertebrates except mysids were significantly more abundant in submerged macrophytes than on adjacent unvegetated substrate, but varied in their responses to macrophyte species. Patterns of invertebrate assemblage structure among submerged macrophyte species and unvegetated substrates were not detectably different. Abundances of invertebrate taxa varied among stations, and many of the analyzed taxa were most abundant in winter.

Leaves of submerged macrophytes provide the most physically complex habitat in estuaries (Bell and Westoby 1986b). As submerged macrophyte complexity increases, abundances of inhabiting invertebrates are expected to increase due to reductions in predation pressures (Bell and Westoby 1986a, Dionne and Folt 1991, Heck and Crowder 1991). Although foraging success of fish predators is reduced in more complex habitats (Rozas and Odum 1988, Ryer 1988), invertebrates may respond more to habitat

Table 5.11. Mean densities (individuals / core \pm 1 SE) of common meiofauna and substrate characteristics, including organic fraction and sand fraction (mean \pm 1 SE), for the three submerged macrophyte species and unvegetated substrates at the Lake St. Catherine station in spring of 1992. Total meiofauna was calculated as the sum of the common meiofauna taxa.

	<u>Vallisneria</u>	<u>Myriophyllum</u>	<u>Ruppia</u>	<u>Unvegetated</u>
Taxa				
Nematodes	204.0 (32.8)	304.1 (78.1)	334.1 (63.4)	381.3 (107.8)
Foraminifera	5.9 (2.5)	21.5 (8.4)	31.9 (12.4)	107.3 (51.9)
Ostracods	13.3 (2.6)	17.6 (2.9)	9.9 (2.0)	11.7 (1.8)
Kynorhyncha	9.6 (4.3)	10.6 (1.4)	8.8 (2.8)	16.8 (7.6)
Harpacticoidea	9.5 (2.4)	17.1 (2.8)	8.9 (1.7)	6.3 (2.4)
Acarina	11.1 (5.6)	20.4 (10.5)	0.5 (0.2)	2.7 (1.7)
Gastrotrichs	0.8 (0.3)	1.3 (0.4)	1.8 (0.7)	8.8 (4.0)
Total Density	254.13 (87.33)	392.63 (87.33)	39.75 (87.33)	535.00 (100.84)
Substrate				
Organic Fraction	0.071 (0.004) A	0.043 (0.002) B	0.017 (0.002) C	0.015 (0.003) C
Sand Fraction	0.134 (0.035) A	0.245 (0.025) A	0.617 (0.022) B	0.679 (0.025) B

preference than predation pressure (Bell and Westoby 1986a, Edgar 1990). In the Lake Pontchartrain estuary, the most common amphipod Gammarus mucronatus was denser in the complex exotic Myriophyllum spicatum than in the simpler native Vallisneria americana, whereas the other two amphipod species were denser in V. americana (Table 5.4). Grass shrimp and juvenile blue crabs were denser in the native macrophytes (V. americana and Ruppia maritima) than in M. spicatum. Whether or not these density differences are due to habitat preference, interspecific interactions, or other factors has

not been examined. Other studies have cast doubt on the generality that predation pressure is reduced by increased macrophyte complexity (Stoner 1982, Holmund et al. 1990). Amphipod predation risk by pinfish Lagodon rhomboides increased with complexity across seven species of macroalgae (Holmund et al. 1990). Other factors, such as predator and prey sizes (Stoner 1982, Ryer 1988, Heck and Crowder 1991), predatory strategies (Stoner 1982, Ryer 1988, Dionne and Folt 1991, Heck and Crowder 1991), and behavioral responses of prey (Heck and Crowder 1991) also influence predation rates and prey abundances (Bell and Westoby 1986a, Holmund et al. 1990).

In the Lake Pontchartrain estuary, the densities of all common macroinvertebrate taxa, except mysids, were higher in vegetation than on adjacent unvegetated substrates (Table 5.4). The relation of invertebrate abundances to vegetation is well documented (Stoner 1980, Lewis and Stoner 1983, Heck and Thoman 1984, Orth et al. 1984, Orth and van Montfrans 1990, Heck and Crowder 1991). Submerged vegetation provides protection from predation by fishes and larger invertebrates (Orth and van Montfrans 1987, Virnstein 1987, Rozas and Odum 1988, Heck and Crowder 1991, Minello 1993). The structure of the macrophytes provides increased substrate for the growth of epiphytic algae, which is the primary source of food for many invertebrates (Kitting 1984, Orth and van Montfrans 1984, Heck and Crowder 1991).

Macroinvertebrate abundances probably varied among seasons (Table 5.5) in response to fish abundances. The three amphipod species and Idoteidae were more abundant in winter than in summer. These invertebrates, which are prey for many fishes and larger macroinvertebrates (Heck and Orth 1980b, Boesch and Turner 1984), may have been more abundant in winter because of low predation pressure. Resident predatory fishes in the submerged vegetation of the Lake Pontchartrain estuary such as rainwater killifish Lucania parva, gulf pipefish Syngnathus scovelli, and clown goby Microgobius gulosus are significantly (LSMeans, $p \leq 0.0083$) less abundant in the winter than in the summer (Chapter 3). The greater densities of common macroinvertebrates in

winter correspond to low habitat availability (PSA), and low densities in summer correspond to high levels of epiphytic growth (personal observation). As a result, macroinvertebrate abundances in the Lake Pontchartrain estuary could possibly be more influenced by predation pressure than by habitat availability and food resources. The increase in epiphytes in warm months was probably due to reduced grazing intensity (Heck and Crowder 1991) resulting from a reduction in macroinvertebrate densities due to increased predation pressure. This study suggests different mechanisms than those proposed by Edgar (1990), who suggested that invertebrate abundances probably respond more to food availability than refuge, and that seasonal invertebrate abundance patterns are driven by fluctuations in epiphytes and macroalgae.

Invertebrate abundances among stations were independent from macrophyte distributions, and probably responded more to the salinity gradient. Decapod crustaceans were most common in Lake St. Catherine, and blue crabs and grass shrimp were strongly influenced by salinity (Table 5.3). Blue crab densities are also related to salinity along the coasts of the Atlantic and the Gulf of Mexico (Perry and van Engel 1982, Hill et al. 1989, Gibson 1991). The amphipods were collected at high mean substrates (Table 5.3), which corresponded to greater densities in Lake Pontchartrain than in Lake St. Catherine (Table 5.5).

In Lake St. Catherine, the organic matter and sand composition of substrates of R. maritima were more similar to the unvegetated substrate than to the other two submerged macrophyte species (Table 5.11), but no significant differences in meiofaunal abundances were detected among submerged macrophytes and unvegetated substrates. These results must be treated with caution, however, because the power of the analysis was low. In Lake St. Catherine, the organic fraction was significantly higher in Vallisneria americana, intermediate in Myriophyllum spicatum, and lower in Ruppia maritima and unvegetated substrates, but the sand fraction followed the opposite pattern.

In Lake Opinicon, Canada, the organic fraction is higher and the sediments are finer in M. spicatum than in the native V. americana and Potamogeton spp. (Keast 1984).

In contrast with macrofauna, most meiofauna are more abundant in unvegetated substrates than in vegetated areas (Decho et al. 1985) because meiofauna respond to different environmental pressures. Predators of meiofaunal organisms are more common in submerged vegetation (Kitting 1984, Decho et al. 1985, Orth and van Montfrans 1984, Orth and van Montfrans 1987, Rozas and Odum 1988, Heck and Crowder 1991) because they are more protected from higher trophic levels (Rozas and Odum 1988, Heck and Crowder 1991). This pattern was also evident in Lake St. Catherine, with higher meiofauna abundances in unvegetated substrates and significantly higher macroinvertebrate and fish abundances in vegetation. Abundances of nematodes and harpacticoid copepods were comparable to those in Florida seagrasses (Bell et al. 1984), and most of the taxa followed patterns similar to those reported in the Florida Keys (Decho et al. 1985).

The exotic Myriophyllum spicatum was first observed in the Lake Pontchartrain estuary in 1973 (Thompson and Verret 1980), and has since increased in abundance to become one of the three dominant macrophyte species. Its presence had a negative effect on habitat variables as well as fish and invertebrate populations in some systems (Blackburn and Weldon 1967, Elser 1969, Keast 1984), and has had a significant influence on the distribution and abundance of invertebrates in the Lake Pontchartrain estuary (Table 5.7). Blue crabs and mysids were significantly less abundant in M. spicatum than in the native Ruppia maritima, which has probably been partially replaced by M. spicatum (Mayer 1986, Chapter 2). Five of eight invertebrate taxa were significantly more abundant in Vallisneria americana than in M. spicatum, whereas only Gammarus mucronatus and Odonata were more abundant in M. spicatum than in native macrophytes. Although no differences in assemblage structure were detected, similarity was generally lower in comparisons of assemblages associated with M. spicatum to those

of native macrophytes than between the native macrophytes. Because the Lake Pontchartrain estuary is a relatively high energy system, waves and currents may prevent the exotic macrophyte from growing densely enough to strongly influence the assemblage structure of invertebrates inhabiting the submerged macrophytes. Nevertheless, M. spicatum has had a significant effect on abundances of many invertebrate species, and its presence combined with a decline in the total area covered by submerged macrophytes in the Lake Pontchartrain estuary may negatively influence invertebrate populations, and ultimately affect the populations of their predators and the overall structure of the littoral community.

CHAPTER 6: SUMMARY

Introductions of exotic macrophytes have significantly influenced populations of fishes and invertebrates in many aquatic systems. The exotic Eurasian watermilfoil Myriophyllum spicatum was first reported in the Lake Pontchartrain estuary in 1978, and has since increased its abundance to become one of the three dominant macrophyte species in the estuary. Its presence has negatively influenced fishes and invertebrates in enclosed lake systems, and this study was designed to measure the influence of the presence of this exotic in an estuarine system.

In addition to the spread of the exotic macrophyte, the native macrophytes of Lake Pontchartrain declined from over 8,000 ha in the 1950's to less than 400 ha in 1985. Some anecdotal evidence exists, however, supporting the reversal of this trend. Myriophyllum spicatum accounted for 15 % of the total submerged vegetation in Lake Pontchartrain, and up to 95 % of the submerged vegetation in other parts of the estuary, such as Lake St. Catherine. Since both the decline of total macrophyte coverage and the invasion of an exotic species can have detrimental effects on habitat quantity and quality for fishes and invertebrates, a detailed study of the abundances and community structure of fishes and invertebrates was necessary.

The primary objective of this study was to assess the influence of the presence of the exotic macrophyte Myriophyllum spicatum on fish and invertebrate community structure. This was accomplished by using Kendall's W to test differences in community structure among macrophyte species and unvegetated areas. The community structures of both fishes (Chapter 3) and invertebrates (Chapter 5) were significantly concordant among macrophyte species. Low densities of M. spicatum in the Lake Pontchartrain estuary probably prevented the exotic from having more noticeable effects on community structure. Conditions in the Lake Pontchartrain estuary, such as high wave energy, high

turbidity, and a salinity gradient, kept M. spicatum from fully developing its canopy (Chapter 2).

Whereas the community structures of fish species were similar among macrophyte species, diversity indices differed significantly among the macrophyte species and unvegetated areas (Chapter 3). Shannon-Weiner diversity (H') was highest in Vallisneria americana, intermediate in unvegetated areas, and lowest in Ruppia maritima and Myriophyllum spicatum. Species richness was highest in V. americana and lowest in unvegetated areas, but species evenness (J) was greatest in unvegetated areas, and lowest in Ruppia maritima and Myriophyllum spicatum.

This study was also designed to measure differences in the responses of individual fish and invertebrate populations to submerged macrophyte species and to identify other factors that influence their distributions. The greatest influence on fish and invertebrate abundances was the presence of vegetation. Because submerged macrophytes offer more protection from predation and greater food resources compared to unvegetated areas, most of the common invertebrates and resident fishes were significantly more abundant in vegetation than on adjacent unvegetated substrates.

The species of macrophyte can also influence the populations of natant macrofauna, although macrophyte species influenced densities of invertebrates (Chapter 5) more than densities of fishes (Chapter 3). Three fishes, rainwater killifish, clown gobies, and bay anchovies, were significantly more abundant in Myriophyllum spicatum than in Vallisneria americana, as was total fish density, but no fishes were more abundant in M. spicatum than in Ruppia maritima. Considering usage patterns and the diversity indices, M. spicatum offers habitat for fishes comparable to that of R. maritima. Invertebrates, however, differed significantly among submerged macrophyte species for every common taxa except mysids. Additionally, responses to macrophyte species varied among invertebrate taxa. For example, two amphipod species collected were significantly more

abundant in V. americana than in R. maritima and M. spicatum, whereas a third was more abundant in M. spicatum than in V. americana.

Because of the importance of blue crabs to the ecology and economy of the estuary, they were analyzed in more detail by comparing responses to macrophyte species and environmental variables for three juvenile size classes. All blue crab size classes were significantly more abundant in vegetation than on unvegetated substrates, and blue crabs increased the use of submerged macrophytes with increasing size. Additionally, responses to individual macrophyte species varied among size classes. The smallest class was most abundant in Ruppia maritima, intermediate in Myriophyllum spicatum, and least abundant in Vallisneria americana. The intermediate size class was more abundant in R. maritima than in the other two macrophytes, and the largest juvenile size class was more abundant in V. americana than in M. spicatum. All three size classes were at least twice as abundant in a native macrophyte than in the exotic M. spicatum. The most suitable macrophyte for blue crabs was R. maritima, which has been partially replaced by M. spicatum, although their use of V. americana increased with increasing crab size. The decline in native macrophyte coverage and the partial replacement of the most suitable native species by the exotic may negatively influence the blue crab population, creating a 'demographic bottleneck' in their ontogeny.

In addition to responses to macrophyte species, fish and invertebrate population responses to environmental variables were identified. Most fishes responded to gradients in plant surface area (PSA), salinity, and substrate type (Chapter 3). Invertebrates responded to gradients in distance from shore, PSA, and salinity (Chapter 5). The responses of blue crabs to temporal and environmental variables varied with size (Chapter 4). The smallest juvenile size class was strongly influenced by seasonality, but the importance of temporal variables in predicting juvenile crab abundance declined with increasing size. Whereas all three size classes were significantly influenced by salinity, PSA increased in importance with increasing size. A shift towards increased use of

Vallisneria americana by larger juvenile blue crabs was associated with observed changes in environmental variable usage, including the use of denser vegetation, greater distances from shore, and lower water velocities.

Most fishes and invertebrates were more abundant in Lake St. Catherine, but responses to season differed among taxa. Resident fishes were least abundant in winter, when transient fishes, including pinfish and spot, were most abundant following recruitment events (Chapter 3). Larger predatory invertebrates (grass shrimp and blue crabs) were more abundant in summer, whereas smaller grazing invertebrates (amphipods, etc.) were more abundant in winter (Chapter 5). Because food resources for the smaller invertebrates (i.e., epiphytic algae) were greater in the summer, I feel that these seasonal abundance patterns of fishes and invertebrates indicate that predation pressure influences the abundances of grazing invertebrates in the Lake Pontchartrain estuary more than food availability.

I also looked at differences in meiofaunal abundances among submerged macrophyte species and unvegetated substrates, using 15 replicated samples from Lake St. Catherine (Chapter 5). No significant differences were detected for meiofaunal taxa among treatments, but the power of the analysis was low. The results of the power analysis indicated that two to four times as many samples would be necessary for an adequate analysis. Additionally, if the meiofaunal taxa had been identified to species, differences may have been easier to detect, as in the case of the three amphipod species.

The third objective was to identify factors that may influence the distributions of the three macrophyte species in the Lake Pontchartrain estuary. This was accomplished by identifying the gradients that most significantly predicted PSA and relative dominance of the three macrophytes (Chapter 2). Relative dominance was calculated as the percentage of the total PSA of a sample that was contributed by each species, and allowed identification of gradients that influenced the relative distribution of the species, whereas the analysis of PSA identified gradients that influenced the density of each species.

The greatest influence on both the distribution and abundance of submerged macrophytes in the Lake Pontchartrain estuary was wave energy. The two Lake Pontchartrain stations were more exposed, with wind fetches of over 20 km, whereas the Lake St. Catherine station had an effective fetch of less than 1 km. The Lake Pontchartrain stations, Cane Bayou and Bayou Lacombe, were characterized by sandier sediments than the Lake St. Catherine station, probably due to size-selective suspension of sediment particles from the higher intensity of wave action. Since Vallisneria americana is more tolerant to mechanical damage than the other two macrophytes, it was more dominant at Cane Bayou and Bayou Lacombe. Myriophyllum spicatum and Ruppia maritima had significantly higher relative dominance in the more protected Lake St. Catherine than in the Lake Pontchartrain stations.

Salinity positively influenced both PSA and relative dominance of Ruppia maritima and negatively influenced both PSA and relative dominance of Myriophyllum spicatum. Although M. spicatum can tolerate salinities up to 15 ‰, it is a freshwater aquatic macrophyte. R. maritima is a halophyte, but can tolerate estuarine conditions, including fresh water. Salinity did not significantly influence Vallisneria americana.

Substrate type significantly influenced PSA and relative dominance for all three species. Vallisneria americana has significantly related to coarser substrates, whereas the other two macrophytes were related to finer substrates. This pattern also reflects the relative resistance of the macrophyte species to mechanical damage.

Myriophyllum spicatum was found at significantly greater depths than the other two macrophytes. This was probably due to its adaptations to low light levels. M. spicatum has a low light compensation point compared to most aquatic macrophytes, allowing it to grow in deeper, more turbid water. Also, the morphology of M. spicatum concentrates biomass near the surface, and it responds to shading with stem elongation, further concentrating its biomass at the surface.

The conditions of the Lake Pontchartrain estuary, while limiting Myriophyllum spicatum from becoming extremely dense, also favor its persistence. Nevertheless, the abundance, not merely the presence, of M. spicatum is the reason that it significantly influenced fish and invertebrate populations in smaller lakes. The densities of the exotic macrophyte found in the Lake Pontchartrain estuary do not significantly influence the community structure of the littoral fishes and invertebrates. Nevertheless, whereas the presence of M. spicatum offers habitat for fishes and most invertebrates comparable to Ruppia maritima, the presence of the exotic could have detrimental effects on the population of blue crabs in the estuary. By partially replacing the most suitable macrophyte species for juvenile blue crabs, M. spicatum may create an ecological bottleneck in the ontogeny of blue crabs.

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VITA

Kenneth C. Duffy was born in Key West, Florida, on April 11, 1967. He grew up in Baton Rouge, Louisiana, and developed a love for the oceans at an early age. He finished his SCUBA certification when he was 16, and graduated as valedictorian of McKinley High School in May 1985. Later that year he enrolled at the University of Miami in Coral Gables, Florida. He majored in Biology and Marine Sciences, and graduated Cum Laude with a Bachelor of Science degree in May 1989. In August 1989, he entered the Graduate School of Louisiana State University, majoring in Oceanography and Coastal Sciences, and minoring in Experimental Statistics.

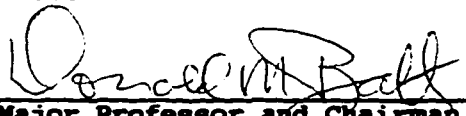
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Kenneth Charles Duffy

Major Field: Oceanography and Coastal Sciences


Title of Dissertation: Macrofaunal Community Structure in the Introduced and Native Submerged Macrophyte Beds of the Lake Pontchartrain Estuary

Approved:


Major Professor and Chairman

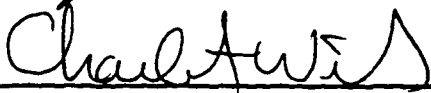

Dean of the Graduate School

EXAMINING COMMITTEE:

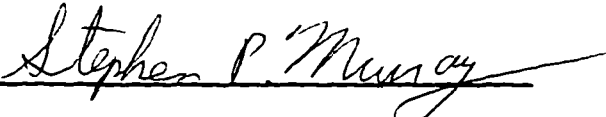












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