



## Comparison of fish assemblages associated with native and exotic submerged macrophytes in the Lake Pontchartrain estuary, USA

Kenneth C. Duffy\*, Donald M. Baltz

Coastal Fisheries Institute and Department of Oceanography and Coastal Sciences, CCEER, Louisiana State University, Baton Rouge, Louisiana 70803-7503, USA

Received 25 January 1996; received in revised form 5 June 1997; accepted 23 June 1997

### Abstract

Since the exotic Eurasian milfoil *Myriophyllum spicatum* (L.) was first reported in the Lake Pontchartrain estuary in 1978, it has become established as a dominant species of submerged macrophyte, but its distribution and abundance have varied considerably. We compared fish assemblages among two native macrophytes, *Vallisneria americana* (Michx) and *Ruppia maritima* (L.), the exotic *M. spicatum*, and unvegetated substratum to determine if milfoil influenced assemblage structure and microhabitat use by common littoral fishes. We used a modified Wegener ring to quantitatively assess fish densities. In monthly sampling from March 1991 to January 1993, we collected 3564 fishes of 29 species, but four dominant species, rainwater killifish *Lucania parva* (Baird), naked goby *Gobiosoma bosc* (Lacepede), gulf pipefish *Syngnathus scovelli* (Evermann and Kendall), and clown goby *Microgobius gulosus* (Girard) accounted for over 87% of the fishes. Community diversity was highest in *V. americana*, intermediate in unvegetated areas, and lowest in *R. maritima* and *M. spicatum*. The patterns for evenness and richness differed from that of diversity among the four habitat types. Analyses of percent similarity and rank correlation of community structure showed no significant differences between *M. spicatum* and native macrophytes. The common fishes were significantly more abundant in vegetated areas than on adjacent unvegetated substratum, and total abundances were higher in *M. spicatum* and *R. maritima* than in *V. americana*. Only three fishes showed significant differences among macrophyte species: rainwater killifish and clown goby were more abundant in *M. spicatum* and *R. maritima*, and bay anchovy *Anchoa mitchilli* (Valenciennes) was more abundant in *M. spicatum* than in *V. americana*. Additionally, fish abundances were related to environmental variables in a factor analysis that resolved nine variables into four axes, characterized in order of importance as: a large-scale spatial (salinity) axis, a seasonal axis, a turbidity axis, and a plant surface area axis. The different patterns of fish species in environmental space revealed spatial and temporal

\*Corresponding author. Tel.: +1 504 3886512 or +1 504 2934473; fax: +1 504 3886513; e-mail: kduffy@worldnet.att.net

differences in resource utilization. The exotic macrophyte *M. spicatum* may not have had a detectable influence on fish assemblages or abundances relative to the native macrophytes because high wave energy in the open system may prevent it from growing densely enough to strongly alter microhabitat characteristics. © 1998 Elsevier Science B.V.

*Keywords:* Community structure; Estuarine fishes; Exotic species; Microhabitat; *Myriophyllum*

---

## 1. Introduction

The introduction of exotic species is one of the primary factors threatening biodiversity (Ehrenfeld, 1970; Diamond and Case, 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). *Myriophyllum spicatum* was first reported in the Lake Pontchartrain estuary in 1978 (Thompson and Verret, 1980). It is now established as a dominant aquatic macrophyte and has been partially replacing native macrophytes, primarily widgeongrass *Ruppia maritima* (Mayer, 1986). Because of the importance of submerged 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. 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 *M. spicatum* significantly affects biologically important variables (e.g., dissolved oxygen concentration and substratum characteristics) relative to many native plants, reducing habitat suitability for some fishes and macroinvertebrates (Keast, 1984). If *M. spicatum* reduces habitat quality for fishes, the populations of native fishes may be adversely affected by reduced growth rates or survival.

In marine and estuarine systems, structural complexity of submerged aquatic vegetation provides important refuge and foraging sites for many organisms (Orth and van Montfrans, 1987; Rozas and Odum, 1988; Heck and Crowder, 1991; Carr, 1994). Submerged macrophytes in the littoral zones in the Lake Pontchartrain estuary serve important nursery functions and contrast 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, especially for recruiting fishes (Carr, 1994), 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). Different aspects of the architecture of the submerged macrophytes may also influence the recruitment of fishes to these sites (Carr,

1994). 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 the ensuing increase in 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 substratum allows more organisms to occupy a given area of substratum. The PSA index includes both the amount (number and height of stems) and complexity (morphology of stems and leaves) of macrophytes. 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 (Keast, 1984).

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 individual is ultimately defined as the place where that individual 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 distribution pattern (i.e., means, variances, ranges) along environmental and temporal gradients occupied by individuals collected in the study area (Hurlbert, 1981). To address the question of habitat quality, we used a comparative descriptive approach (Crowder, 1990) at three stations to infer the underlying patterns of fish assemblage structure and to describe population responses of common fish species to environmental variables, including three submerged macrophytes and unvegetated substratum. The objectives of this study were: (1) to compare fish assemblages associated with submerged macrophytes to determine if the pattern of usage in *M. spicatum* differed from those of the native macrophytes and bare substratum, and (2) to compare spatial and temporal resource utilization by common fishes in these assemblages.

### 1.1. Study area

Lake Pontchartrain is a large, shallow bay located just north of New Orleans in southeast Louisiana (Fig. 1). It covers an area of 1,630 km<sup>2</sup>, 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. The fish assemblages and several environmental variables, including macrophyte species and abundance, 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 mouths of Cane Bayou and Bayou Lacombe in Lake Pontchartrain and in Grand Coin Bay at the north end of Lake St. Catherine.

Historically, submerged vegetation was abundant on all shores of Lake Pontchartrain, but between the late 1950s and 1985 the total area covered by submerged macrophytes

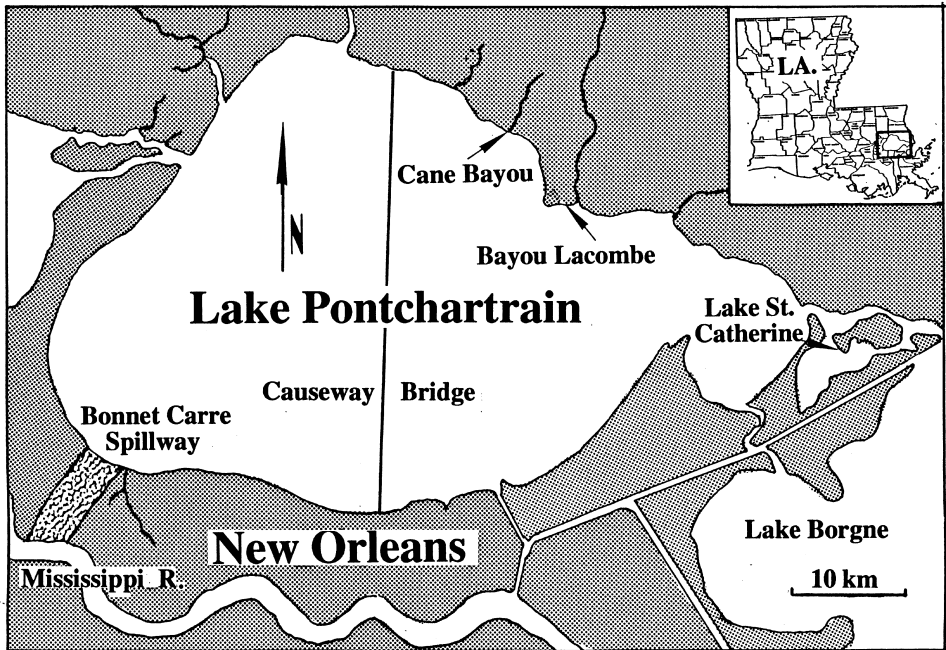


Fig. 1. The Lake Pontchartrain estuary in southeast Louisiana showing the three stations sampled in this study (after Mayer, 1986).

decreased by over 90% (Darnell, 1961; Montz, 1978; Mayer, 1986). High turbidity apparently contributed substantially to limiting the 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 vegetation beds to the northeastern shore of Lake Pontchartrain and the adjacent coastal bays (Mayer, 1986). Shell dredging was also implicated as a cause of higher turbidity, but has not been permitted since 1990. Native macrophytes in the estuary include wild celery *Vallisneria americana*, wigeongrass *Ruppia maritima*, southern naiad *Najas quadalupensis*, and slender pondweed *Potamogeton pusillus*. *Vallisneria americana* grows in clusters of ribbon-like blades, and *R. maritima* has slender, branching stems with slim, flat leaves (Chabreck and Condrey, 1979). The exotic Eurasian milfoil *Myriophyllum spicatum* generally has whorls of four feathery leaves along a cylindrical stem (Chabreck and Condrey, 1979). While the native macrophytes were declining, the area covered by *M. spicatum* was increasing (Mayer, 1986). Nevertheless, the trend of increasing coverage by *M. spicatum* now seems to have been arrested or reversed (pers. comm., M. Poirrier, University of New Orleans, Louisiana).

## 2. Methods

A modified Wegener ring (Weinstein and Brooks, 1983) was used to quantitatively

estimate fish abundances on a monthly basis from March 1991 to January 1993. 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 high  $\times$  1.23 m diameter, 1.18 m<sup>2</sup>). When deployed, the fabric walls were supported by a float ring at the top. This ring design was adequate for sampling adults of small fishes, juveniles of larger species, and most macroinvertebrates (Chick et al., 1992). A boom extending 3 m beyond the bow of a 5.2 m boat was used to deploy the sampler. The sampler was held 0.5 m 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 substratum to permit a quantitative estimate of species abundances.

Each month, 12 samples at each station were stratified among the three common submerged macrophytes and unvegetated substrata. When all of the macrophytes were not present, the samples were equally divided among the existing plant species and unvegetated substrata to maximize the information gained per trip. Within strata, each sampling site was randomly selected to represent the range of submerged vegetation densities present and the range of depths up to a maximum of 1 m. Samples, and associated environmental data, were collected during daylight hours and were considered to be unique and independent for statistical purposes.

In conjunction with each sample, we collected microhabitat data, including dissolved oxygen concentration, water temperature, salinity, water surface velocity, minimum and maximum water depth, distance from shore, turbidity, and substratum 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 10 s. Turbidity was measured in NTU with a Monitek model 21 PE portable nephelometer. Substratum type was tactually estimated on a particle size scale: 1 = clay, 2 = mud (clay and silt), 3 = silt, 4 = sand, 5 = organic detritus, 6 = shell or shell fragments. Additionally, macrophyte species present were identified and the number and median length of stems for each species was assessed directly by counting and measuring subsamples of stems within the Wegener ring.

Five submerged macrophytes were found in the study area, including *Vallisneria americana*, *Muriophyllum spicatum*, *Ruppia maritima*, the southern naiad *Najas quadalupensis*, and the slender pondweed *Potamogeton pusillus*. Names for macrophyte species follow Chabreck and Condrey (1979). The most abundant submerged macrophyte in Lake Pontchartrain, especially at the Bayou Lacombe station, was *V. americana*; *M. spicatum* and *R. maritima* were also common. *Najas quadalupensis* and *P. pusillus* were infrequently encountered, and 26 samples (4.8%) in which they dominated were omitted from further analyses.

Plant surface area (PSA) was calculated from estimates of stem density and length for each species. We photometrically measured the surface area of multiple samples of individual submerged macrophyte stems and leaves using a Li-Cor LI-3000 portable leaf area meter. After pressing and drying, each leaf from the stem samples was fed into the meter individually, and the surface areas of all the leaves on a stem and the surface area of the stem were combined and regressed on stem length to generate species-specific relationships:

*Vallisneria americana*:  $PSA = 1.258 * L * C / 10\ 000$  ( $n = 20$ ,  $r^2 = 0.99$ ),  
*Myriophyllum spicatum*:  $PSA = 1.058 * L * C / 10\ 000$  ( $n = 20$ ,  $r^2 = 0.80$ ),  
*Ruppia maritima*:  $PSA = 0.232 * L * C / 10\ 000$  ( $n = 19$ ,  $r^2 = 1.00$ ),

where  $L$  is the stem length (cm) and  $C$  is the number of stems of that species in the sample. Total PSA (in  $m^2$  plant surface  $\cdot m^{-2}$  substratum) for a sample is reported, and samples were assigned to macrophyte species (*Vallisneria*, *Ruppia*, and *Myriophyllum*) by dominance. If a sample had less than  $0.0118 m^2 \cdot m^{-2}$  total surface area ( $< 1\%$ ) it was treated as an unvegetated site.

Following the environmental characterization of each sample site, 25 g of dry rotenone cube (SureCo, Inc., SureGuard powdered cube, 5% rotenone) was uniformly suspended in the sampler to facilitate recovery of organisms (Davies and Shelton, 1983). For a water depth of 0.5 m this was equivalent to a concentration of 2.1 ppm (concentrations ranged from 1.0 to 7.1 ppm depending on water depth). 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 ( $39 \times 30$  cm, 5 mm diamond mesh) to capture a high percentage of the remaining organisms that were then preserved with a 10% buffered formalin solution for 24 h, then transferred to 95% ethanol. All fishes were identified, counted, and measured to the nearest millimeter standard length (SL). Densities of fishes are reported as individuals  $\cdot m^{-2}$ , and common and scientific names of fishes (Table 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 7.6 mm carapace length), was used to identify an adequate level of hand netting effort. A log-linear relationship was used to regress cumulative catch against effort. The regression analysis of two independent trials 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  $12$ ,  $P < 0.0001$ ;  $r^2 = 0.97$ ).

We 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 common fish species. Environmental variables that accounted for significant variation in the abundance of each species were identified, as were overall effects of variables on assemblage structure patterns. Abundances were transformed ( $\log_e$  [abundance + 1]) to normalize the data (Sokal and Rohlf, 1981). Uncommon fishes (i.e., species with  $< 10$  total individuals caught or with 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.

Table 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 (3564 fish) 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 of total numbers	Number of samples present	Percent frequency of occurrence
Rainwater killifish	<i>Lucania parva</i>	1128	31.65	147	28.4
Naked goby	<i>Gobiosoma bosc</i>	824	23.12	187	36.2
Gulf pipefish	<i>Syngnathus scovelli</i>	789	22.14	270	52.2
Clown goby	<i>Microgobius gulosus</i>	381	10.69	121	23.4
Bay anchovy	<i>Anchoa mitchilli</i>	65	1.82	16	3.1
Inland silverside	<i>Menidia beryllina</i>	55	1.54	33	6.4
Speckled worm eel	<i>Myrophis punctatus</i>	54	1.52	35	6.8
Bluegill	<i>Lepomis macrochirus</i>	39	1.09	21	4.1
Skilletfish	<i>Gobiesox strumosus</i>	37	1.04	21	4.1
Pinfish	<i>Lagodon rhomboides</i>	33	0.93	21	4.1
Freshwater goby	<i>Gobionellus shufeldti</i>	27	0.76	14	2.7
Sailfin molly	<i>Poecilia latipinna</i>	23	0.65	2	0.4
Hogchoker	<i>Trinectes maculatus</i>	20	0.56	16	3.1
Least killifish	<i>Heterandria formosa</i>	18	0.51	2	0.4
Spotted seatrout	<i>Cynoscion nebulosus</i>	15	0.42	10	1.9
Spot	<i>Leiostomus xanthurus</i>	14	0.39	7	1.4
Atlantic croaker	<i>Micropogonias undulatus</i>	9	0.25	7	1.4
Atlantic needlefish	<i>Strongylura marina</i>	9	0.25	9	1.7
Blackcheek tonguefish	<i>Symphurus plagiusa</i>	8	0.22	7	1.4
Warmouth bass	<i>Lepomis gulosus</i>	5	0.14	1	0.2
Yellow bass	<i>Morone mississippiensis</i>	3	0.08	3	0.6
Atlantic stingray	<i>Dasyatis sabina</i>	1	0.03	1	0.2
Blue catfish	<i>Ictalurus furcatus</i>	1	0.03	1	0.2
Diamond killifish	<i>Adinia xenica</i>	1	0.03	1	0.2
Sheepshead minnow	<i>Cyprinodon variegatus</i>	1	0.03	1	0.2
Silver perch	<i>Bairdiella chrysoura</i>	1	0.03	1	0.2
Southern flounder	<i>Paralichthys lethostigma</i>	1	0.03	1	0.2
Spotted gar	<i>Lepisosteus oculatus</i>	1	0.03	1	0.2
Largemouth bass	<i>Micropterus salmoides</i>	1	0.03	1	0.2

A factor analysis was employed to identify highly 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 yielded four axes with eigenvalues greater than one (SAS Institute, 1989). 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 substratum) 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 was used to test for differences among the groups of environmental variables (SAS Institute, 1989). In addition to the groupings of season and station, differences among the three macrophytes were also analyzed. Differences in the mean abundance of fishes for statistically significant groups of environmental variables were tested a posteriori with the Least Squares Means test (LSMeans) (SAS Institute, 1989). 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 relative seasonal sampling effort (weight = total # samples / # samples by season). 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). Spearman's rank correlations (SAS Institute 1989) and Schoener's index of similarity (Schoener, 1970) were also used to compare fish assemblage structures between macrophytes and unvegetated sites.

For each vegetation type, the average diversity of fish species (Shannon–Weiner  $H'$ ) was calculated (Pielou, 1966) using the cumulative 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.

### 3. Results

From 517 samples obtained between March 1991 and January 1993, we collected 29 fish species totaling 3564 individuals (Table 1). The fishes were dominated by rainwater killifish (31.65%). Other abundant fishes were naked goby (23.12%), gulf pipefish (22.14%), and clown goby (10.69%). Together these four species constituted 87.6% of all the fishes collected and occurred in one-fourth to one-half of all samples. Ten resident species and four transient species in the fish assemblage were abundant enough for analysis. Other common resident species included in the analyses (Table 1) were inland silverside, speckled worm eel, bluegill, skilletfish, freshwater goby, and hog-choker. 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.

Environmental conditions changed seasonally during the study period (Table 2). All variables, except water velocity, showed at least one significant difference among seasons for all sites combined (LSMeans,  $P \leq 0.0083$  for all significant comparisons). Temperature means were 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



Table 2

Seasonal means ( $\pm 1$  SEM) of environmental variables observed in the Lake Pontchartrain estuary between March, 1991 and January, 1993

	Winter <i>n</i> = 94	Spring <i>n</i> = 97	Summer <i>n</i> = 217	Autumn <i>n</i> = 109
Plant surface area ( $\text{m}^2 \cdot \text{m}^{-2}$ )	0.26 (0.03) A	0.44 (0.06) AB	0.55 (0.04) B	0.57 (0.07) B
Temperature ( $^{\circ}\text{C}$ )	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
Substratum code	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 ( $\text{mg} \cdot \text{l}^{-1}$ )	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 ( $\text{cm} \cdot \text{s}^{-1}$ )	3.23 (0.23)	3.74 (0.25)	3.48 (0.13)	3.15 (0.24)

Significant differences among seasonal means ( $P < 0.0083$ , LSMeans) are indicated by different letters reading horizontally.

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, 6 of 9 measured environmental variables including PSA, temperature, salinity, substratum, median depth, and distance from shore significantly ( $n = 517$ ,  $df = 17$  and  $488$ ,  $P \leq 0.0057$ ) affected overall fish abundances (Table 3). Each of these environmental variables also significantly ( $P \leq 0.0057$ ) contributed to the prediction of the abundance pattern for at least one fish species, based on type III sums of squares; moreover, for most fishes, more than one environmental variable significantly influenced abundance. For example, the density of naked goby was significantly influenced by PSA, salinity, substratum, depth, and distance from shore. 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).

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 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 substratum 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 which 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 substratum) showed relationships with environmental gradients in the factor analysis that were also reflected in the similarity of their fish assemblages. *Myriophyllum spicatum* and *Ruppia maritima* were closely associated along all four axes (Fig. 2a) and separated from *Vallisneria americana* and unvegetated substratum along the spatial and PSA axes. *Vallisneria americana* and unvegetated substrata were generally found in less saline water and on

Table 3  
Means of environmental variables utilized by common fishes ( $\pm 1$  SEM), adjusted for seasonal differences in sampling effort

	Plant surface area ( $\text{m}^2 \cdot \text{m}^{-2}$ )	Temperature ( $^{\circ}\text{C}$ )	Salinity (‰)	Substratum code	Depth (cm)	Distance from Shore (m)	Dissolved Oxygen ( $\text{mg} \cdot \text{l}^{-1}$ )	Turbidity (NTU)	Water Velocity ( $\text{cm} \cdot \text{s}^{-1}$ )
<i>Resident species</i>									
Rain water 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 worm eel	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)
<i>Transient species</i>									
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)
<i>F</i> value of overall MANOVA effect	13.16	10.24	10.12	8.24	3.32	3.17	2.20	2.12	1.72
Pr > <i>F</i>	0.0009	0.0009	0.0009	0.0009	0.0009	0.0009	0.0604	0.0857	0.3571

Significance levels of the influence of environmental variables on the fish abundances after adjusting for multiple comparisons are indicated with asterisks: \* < 0.05; \*\* < 0.01; \*\*\* < 0.001 (MANOVA, Type III SS:  $n = 517$ ,  $df = 1$  and 509).

*F* values from the overall effect of the environmental variable from the MANOVA analysis are given, as are the associated adjusted significance levels ( $df = 14, 494$ ).

Table 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
Substratum	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

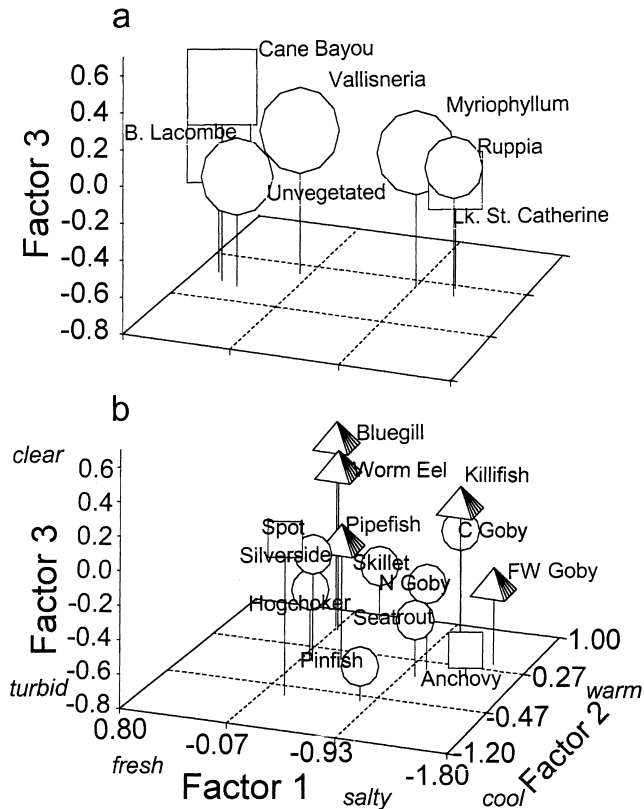


Fig. 2. a) Station and plant species centroids of the three stations (squares) and four submerged vegetation types (circles) in three-dimensional factor space. The radii of shapes estimate one standard deviation about the centroids. b) Species plot of centroids for 14 common near-shore fishes in three-dimensional 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.

coarser substrata than *M. spicatum* and *R. maritima*. Along the PSA gradient, *V. americana* had the highest value (0.452), unvegetated substrata had the lowest value (−0.771), and *M. spicatum* and *R. maritima* were intermediate (0.029 and −0.186, respectively). Rainwater killifish, naked goby, gulf pipefish, clown goby, speckled worm eel, bluegill, and skilletfish were significantly more abundant in vegetated areas than in adjacent unvegetated areas (LSMeans,  $P \leq 0.05$ ). Nevertheless, with three exceptions we were generally unable to detect significant differences in the abundances of the 14 common fishes among the macrophyte species (Table 5). Rainwater killifish and clown goby were less abundant 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,  $P \leq 0.0002$ ) in *R. maritima* and *M. spicatum* than in *V. americana*, and densities were significantly (LSMeans,  $P \leq 0.0001$ ) higher in vegetated areas ( $7.51 \pm 0.50$  fish  $\cdot$  m<sup>−2</sup>) than in adjacent unvegetated areas ( $0.33 \pm 1.07$  fish  $\cdot$  m<sup>−2</sup>).

Compared to the similarities of the fish assemblages among three common submerged macrophytes, the percent similarities (Schoener 1970) of the unvegetated assemblage with those found in the macrophyte species were low (40.5%, 41.3%, and 33.1% for *Vallisneria americana*, *Myriophyllum spicatum*, and *Ruppia maritima*, respectively). Nevertheless, an analysis of rank correlation of fishes between combined vegetated and

Table 5

Selected fish species densities among three macrophytes and unvegetated areas in the Lake Pontchartrain estuary between March, 1991 and January, 1993

	<i>Vallisneria</i> <i>n</i> = 283	<i>Myriophyllum</i> <i>n</i> = 102	<i>Ruppia</i> <i>n</i> = 40	Unvegetated <i>n</i> = 92
<i>Resident species</i>				
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)
<i>Transient species</i>				
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) *

Mean abundances are expressed as individuals  $\cdot$  m<sup>−2</sup> ( $\pm$  1 SEM), and are adjusted for differences in seasonal sampling effort.

*n* = number of independent samples.

Significant differences among the three macrophytes at  $P < 0.017$  (Least Squares Means Test) are indicated with different letters reading horizontally. Significant differences between total vegetated and unvegetated areas for each species ( $P < 0.0002$ , Least Squares Means Test) are indicated by asterisks in the 'Unvegetated' column.

unvegetated areas did not indicate significant differences (Spearman's  $r = 0.15$ ,  $df = 13$ ,  $P \leq 0.60$ ). The structure of fish assemblages was most similar between *M. spicatum* and *R. maritima* (86.1%), and the rank order of species was highly correlated (Spearman's  $r = 0.71$ ,  $df = 13$ ,  $P \leq 0.005$ ). The structure of the fish assemblage associated with *V. americana* was more similar to that of *M. spicatum* (72.4%, Spearman's  $r = 0.62$ ,  $df = 13$ ,  $P \leq 0.017$ ) than to *R. maritima* (63.8%, Spearman's  $r = 0.62$ ,  $df = 13$ ,  $P \leq 0.021$ ). Assemblages in the native macrophytes (*V. americana* and *R. maritima* combined) were significantly correlated with the exotic *M. spicatum* (Spearman's  $r = 0.57$ ,  $df = 13$ ,  $P \leq 0.033$ ).

When combined across sampling dates, the means ( $\pm$  SEM) for species diversities, evenness, and richness of fishes differed significantly among habitat types. The mean diversity in *Vallisneria americana* ( $1.83 \pm 0.006$ ) was significantly higher (LSMeans,  $P \leq 0.0001$ ) than in the other macrophytes and unvegetated substrata, and mean diversities in *Ruppia maritima* ( $1.60 \pm 0.021$ ) and *Myriophyllum spicatum* ( $1.59 \pm 0.012$ ) were significantly lower (LSMeans,  $P \leq 0.0001$ ) than in unvegetated areas ( $1.76 \pm 0.014$ ). Species evenness was significantly different among all vegetation types, with the highest evenness in unvegetated samples ( $0.87 \pm 0.005$ ) followed by *R. maritima* ( $0.65 \pm 0.007$ ), *V. americana* ( $0.62 \pm 0.002$ ), and *M. spicatum* ( $0.54 \pm 0.004$ ). Species richness also differed significantly among all vegetation types, and was highest in *V. americana* ( $20.18 \pm 0.212$ ), followed by *M. spicatum* ( $18.79 \pm 0.398$ ), *R. maritima* ( $12.04 \pm 0.693$ ), and unvegetated areas ( $7.90 \pm 0.476$ ).

Several common fishes were well separated along the Factor One axis (Fig. 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 vegetation 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 substrata, whereas fish species most abundant in the Lake Pontchartrain stations were associated with lower salinities and coarser substrata. 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 present at all stations, were also more abundant in Lake St. Catherine (Table 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 reflected primarily 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 (Fig. 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 7). Rainwater killifish, naked goby, clown goby, and gulf pipefish were present all year, but were slightly more abundant in warmer months and were placed toward the

Table 6

Densities of selected fishes at the three stations sampled in the Lake Pontchartrain estuary between March, 1991 and January, 1993

	Cane Bayou <i>n</i> = 170	Bayou Lacombe <i>n</i> = 185	Lake St. Catherine <i>n</i> = 162
<i>Resident species</i>			
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 worm eel	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)
<i>Transient species</i>			
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

Means are expressed as individuals  $\cdot$  m<sup>-2</sup> ( $\pm$  1 SEM), and are adjusted for seasonal differences in sampling effort. *n* = number of independent samples.

Significant differences among the three stations at *P* < 0.0167 (Least Squares Means Test) are indicated with different letters reading horizontally.

Table 7

Seasonal densities of selected fishes in the Lake Pontchartrain estuary between March, 1991 and January, 1993

	Winter <i>n</i> = 94	Spring <i>n</i> = 97	Summer <i>N</i> = 217	Autumn <i>N</i> = 109
<i>Resident species</i>				
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 worm eel	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)
<i>Transient species</i>				
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

Means are expressed as individuals  $\cdot$  m<sup>-2</sup> ( $\pm$  1 SEM) and *n* = number of independent samples.

Significant differences adjusted for sampling effort among seasons (*P* < 0.0083, Least Squares Means Test) are indicated by different letters reading horizontally.

positive end of the seasonal axis. Spot and pinfish were more abundant in winter and separated strongly from the other species.

The common fishes did not segregate strongly (Fig. 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 this axis explained 14.3% of the environmental variance. Bluegill were found at the highest mean turbidity (Table 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,  $P \leq 0.0025$ ).

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, and bluegill was found at the highest (Table 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,  $P \leq 0.0111$ ).

The structure of fish assemblages in littoral habitat types was seasonally dynamic. Abundances of the 14 common fish species varied greatly among seasons (Table 7), and 9 of 14 species showed significant seasonal differences in density (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 7). Transient fishes showed peaks in abundance, due primarily to the presence of juveniles, that we interpreted as recruitment events. Small juvenile pinfish were first observed in December ( $12.0 \pm 0.76$  mm SL,  $n = 10$ ), and their numbers declined through July ( $64.0 \pm 9.0$  mm SL,  $n = 2$ ), but their size increased significantly (linear slope =  $6.71$  mm SL  $\cdot$  month<sup>-1</sup>,  $df = 27$ ,  $P < 0.0001$ ). Spot were also first observed in December ( $10.0 \pm 0.0$  mm SL,  $n = 1$ ), were collected through May ( $31.7 \pm 4.5$  mm SL,  $n = 3$ ), and their growth was also significant (slope =  $4.98$  mm SL  $\cdot$  month<sup>-1</sup>,  $P > 0.0021$ ).

Fish abundances differed significantly among stations (Table 6). The combined abundance of the common fishes was significantly higher at the Lake St. Catherine station than at 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 skilfish 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 density was significantly greater at the Cane Bayou station than at the Bayou Lacombe station, and intermediate at the Lake St. Catherine station.

#### 4. Discussion

This study was designed to detect differing patterns, if any, of fish usage among

exotic and native submerged macrophytes, and to define the important environmental variables that influence the structure of the fish assemblage in the littoral areas. It is the first survey of the potential effects of the introduction and spread of an exotic macrophyte in a brackish estuarine system. We were unable to detect any significant differences in the patterns of assemblage structure of common fishes among the exotic Eurasian milfoil and the native macrophytes in Lakes Pontchartrain and St. Catherine. Nevertheless, in the analysis of individual abundances of common species some significant differences were detected. Three common fishes (rainwater killifish, clown goby, and bay anchovy) were significantly denser in *Myriophyllum spicatum* compared to *Vallisneria americana*, the most common native species. Also, the most common fishes were generally more abundant and similar in the exotic *M. spicatum* and the native *R. maritima* than in *V. americana*. Spearman's rank correlations and Schoener's index of similarity supported these observations. The rank correlations also showed that the pattern of fish abundances in the exotic *M. spicatum* was not detectably different from native macrophytes. As expected, assemblage structures in all vegetation types were dissimilar and uncorrelated to that in unvegetated areas.

While the community diversities differed significantly among some vegetation types, more information was gained from the measurements of evenness and richness. Species richness was highest in *Vallisneria americana* and lowest in unvegetated samples, whereas species evenness was highest in unvegetated samples. Evenness was lower in submerged vegetation because of the dominance of four species (rainwater killifish, naked goby, gulf pipefish, and clown goby) that were significantly less abundant in unvegetated areas. This illustrates the shortcoming of using only the diversity index to characterize habitats. Based on only the diversity index, unvegetated areas provided a 'better' habitat than two of the submerged macrophyte species. A closer examination of species richness reveals that these macrophytes were inhabited by significantly more species, although species evenness was lower.

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. The findings of Keast (1984) contrast with the Lake Pontchartrain estuary, where *M. spicatum* was utilized by fishes as much as, and even more than, the native macrophytes. This contrast may reflect differences in hydrology between open estuarine systems and closed freshwater lake systems (Wetzel, 1975; Day et al., 1991; 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 macrophyte density (Wetzel, 1975; Day et al., 1991; 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, although at night dissolved oxygen levels may drop substantially.

Wave energy also may have had an effect on the relative abundance of the three



macrophyte species. *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, allowing fragile submerged vegetation 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., 1991; 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 can influence fish community structure as well (Heck and Orth, 1980).

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 Lipcus, 1991, Orth, 1992). Dionne and Folt (1991) found that plant morphology is more important than plant density in determining the abundance of inhabiting organisms. Nevertheless, only three of the common fishes showed significant differences among submerged macrophytes, whereas PSA was a significant predictor of abundance for five fishes (Table 3). With the exceptions of rainwater killifish, clown goby, and bay anchovy, the amount of vegetation (PSA) was more related to fish abundances than was macrophyte species. While this appears to contradict the findings of Dionne and Folt (1991), our results may be related to the significantly higher mean PSA for *V. americana* ( $0.715 \pm 0.04 \text{ m}^2 \cdot \text{m}^{-2}$ ) than for *R. maritima* ( $0.210 \pm 0.06 \text{ m}^2 \cdot \text{m}^{-2}$ ) and *M. spicatum* ( $0.362 \pm 0.03 \text{ m}^2 \cdot \text{m}^{-2}$ ). Although greater fish densities were expected in the more complex macrophytes, the greater PSA of the simpler *V. americana* may have overshadowed the effect of macrophyte morphology.

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 substratum, 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 environmental 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 substrata (Table 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., 1991; 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 was only modestly related to the structure

of littoral fish assemblages. Turbidity 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 our 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 a turbidity gradient (Fig. 2b). In contrast, 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 (Fig. 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 (Rakocinski et al., 1992), and gain little protection from submerged vegetation. This may have led to their greater use of turbid water in this study.

Aquatic vegetation has complex interactions with substratum and turbidity (Ward et al., 1984, Orth, 1992). Probably because plant structure has a dampening effect on water velocity (Machata-Wenninger and Janauer, 1991), PSA was negatively correlated with water velocity (Table 4), although macrophytes may grow better in more protected sites. Most of the 14 common fishes collected in our study showed some association with submerged vegetation (Tables 3 and 5), but 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 vegetation (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 substrata (Smith and Coull, 1987). Spot < 30 mm SL are seldom found in samples with emergent vegetation (Baltz et al., 1993). In contrast, spotted seatrout generally associate with submerged (Chester and Thayer, 1990) and emergent (Rakocinski et al., 1992) vegetation. 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 vegetation. In this study pinfish were not significantly more abundant in submerged vegetation. Additionally, we 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 our objectives.

In aquatic environments, submerged vegetation, 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, 1986; Rozas and Odum, 1988; Ryer, 1988; Lubbers et al., 1990). In the study area, the three common submerged macrophytes provided most of the underwater structure, and fishes were significantly more

abundant in the macrophytes than on adjacent unvegetated substrata. 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 three common fishes among macrophytes. At the community level, the fish assemblage in *M. spicatum* was more similar to that in *Ruppia maritima* than *V. americana*, but a rank correlation test did not detect significant differences in assemblages among macrophytes. Nevertheless, it is obvious that the community associated with the submerged vegetation 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 coverage of 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 macrophyte beds. Based on the morphologies of the three macrophytes and observations made by Mayer (1986), though, we feel that *Myriophyllum spicatum* has been replacing *Ruppia maritima*, and not *Vallisneria americana*, because *V. americana* is much more resistant to the high wave energy in areas where it dominates (Mayer, 1986). In Lake St. Catherine, *M. spicatum* constituted 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.

The presence of *Myriophyllum spicatum* in the Lake Pontchartrain estuary has been a somewhat mixed blessing. During the period when the total area covered by submerged macrophytes was declining, the spread of the exotic macrophyte provided better habitat than unvegetated substratum. Nevertheless, we found that the diversity of the fish assemblages in the most common native macrophyte was significantly higher than in the exotic. Although some fishes were more abundant in *M. spicatum* than in *Vallisneria americana*, the differences in diversity raise concerns for management interested in maintaining biodiversity. Given the historical coverage of submerged vegetation in Lake Pontchartrain, changes in the total coverage and species composition of submerged vegetation need to be observed carefully, and management practices that enhance the coverage of native submerged macrophytes should be implemented.

## Acknowledgements

Many people contributed to the collection, analysis, and synthesis of the data. We appreciate the help of Bill Hayden, Tom Reinert, Alejandro Arrivillaga, Michael Saucier, Drew McNaughton, Monica McGee, and the other graduate students in collecting samples, and Becky Grouchy, Sean Keenan, Tommy Benton, Courtney Baggert, Jeanne Cawston, and Bryon Justice in sorting the samples. We also thank Jim Chambers for the use of the leaf area meter. James Geaghan's assistance was invaluable

with the design and interpretation of the statistical analysis. John Fleeger, Irv Mendelsohn, Steve Murray, and Chuck Wilson all made numerous helpful suggestions during the course of the study. This research was funded by a Louisiana Board of Regents Fellowship, the Coastal Fisheries Institute at LSU, and a grant from the Louisiana Sea Grant College Program, which is a part of the National Sea Grant College Program maintained by NOAA, U.S. Department of Commerce.

## References

- Baltz, D.M., 1990. Autecology. In: Schreck, C.B., Moyle, P.B. (Eds.), *Methods for Fish Biology*. American Fisheries Society, Bethesda, pp. 585–607.
- Baltz, D.M., Moyle, P.B., 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecol. Appl.* 3, 246–255.
- Baltz, D.M., Rakocinski, C., Fleeger, J.W., 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* 36, 109–126.
- Bell, J.D., Westoby, M., 1986. Abundance of macrofauna in dense seagrass is due to habitat preference, not predation. *Oecologia* 68, 205–209.
- Blackburn, R.D., Weldon, L.W., 1967. Eurasian watermilfoil, Florida's newest underwater menace. *Hyacinth Control J.* 6, 15–18.
- Boesch, D.F., Turner, R.E., 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7, 460–468.
- Carr, M.H., 1994. Predicting recruitment of temperate reef fishes in response to changes in macrophyte density caused by disturbance. In: Stouder, D.J., Fresh, K.L., Feller, R.J. (Eds.), *Theory and Application in Fish Feeding Ecology*. University of South Carolina Press, Columbia, pp. 255–269.
- Chabreck, R.H., Condrey, R.E., 1979. *Common Vascular Plants of the Louisiana Marsh*. Center for Wetland Research, Louisiana State University, Baton Rouge.
- Chester, A.J., Thayer, G.W., 1990. Distribution of spotted seatrout (*Cynoscion nebulosus*) and gray snapper (*Lutjanus griseus*) juveniles in seagrass habitats of western Florida Bay. *Bull. Mar. Sci.* 46, 345–357.
- Chick, J.H., Jordan, F., Smith, J.P., McIvor, C.C., 1992. A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. *J. Freshwater Ecol.* 7, 353–361.
- Christenson, B., Persson, L., 1993. Species-specific antipredatory behaviors: effects on prey choice in different habitats. *Behav. Ecol. Sociobiol.* 32, 1–9.
- Crowder, L.B., 1990. Community ecology. In: Schreck, C.B., Moyle, P.B. (Eds.), *Methods for Fish Biology*. American Fisheries Society, Bethesda, pp. 609–632.
- Cyrus, D.P., Blaber, S.J.M., 1987. The influence of turbidity on juvenile marine fishes in estuaries. Part 2: Laboratory studies, comparisons with field data and conclusions. *J. Exp. Mar. Biol. Ecol.* 109, 71–91.
- Cyrus, D.P., Blaber, S.J.M., 1992. Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuar. Coast. Shelf Sci.* 35, 545–563.
- Darnell, R.M., 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain. *Louisiana Ecol.* 42, 553–568.
- Davies, W.D., Shelton, W.L., 1983. Sampling with toxicants. In: Nielson, L.A., Johnson, D.L. (Eds.), *Fisheries Techniques*. American Fisheries Society, Bethesda, pp. 199–213.
- Davis, G.J., Jones, M.N., Linney, C.Z., Clark, G.M., 1974. Inhibition of sodium chloride toxicity in seedlings of *Myriophyllum spicatum* L. with calcium. *Plant Cell Physiol.* 15, 577–581.
- Day, J.W., Jr., Hall, C.A.S., Kemp, W.M., Yanez-Arancibia, A., 1991. *Estuarine Ecology*. Wiley, New York, 558 pp.
- DeLury, D.B., 1947. On the estimation of biological populations. *Biometrics* 3, 158–162.
- Diamond, J., Case, T.J., 1986. Overview: Introductions, extinctions, exterminations, and invasions. In: Diamond, J., Case, T.J. (Eds.), *Community Ecology*. Harper and Row, New York.
- Dionne, M., Folt, C.L., 1991. An experimental analysis of macrophyte growth forms as fish foraging habitat. *Can. J. Fish. Aquat. Sci.* 48, 123–131.

- Ehrenfeld, D.W., 1970. Biological Conservation. Holt, Rinehart and Winston, New York.
- Everett, R.A., Ruiz, G.M., 1993. Coarse woody debris as refuge from predation in aquatic communities: an experimental test. *Oecologia* 93, 475–486.
- Feller, R.J., Coull, B.C., Hentschel, B.T., 1990. Meiobenthic copepods: tracers of where juvenile *Leiostomus xanthurus* (Pisces) feed?. *Can. J. Fish. Aquat. Sci.* 47, 1913–1919.
- Grace, J.B., Wetzel, R.G., 1978. The productive biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.): a review. *J. Aquat. Plant Manage.* 16, 1–11.
- Grossman, G.D., Nickerson, D.M., Freeman, M.C., 1991. Principal component analyses of assemblage structure data: utility of tests based on eigenvalues. *Ecology* 72, 341–347.
- Harlan, S.M., Davis, G.T., Pesacreta, G.J., 1985. *Hydrilla* in three North Carolina lakes. *J. Aquat. Plant Manage.* 23, 68–71.
- Heck, K.L., Jr., Crowder, L.B., 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman and Hall, New York, pp. 281–299.
- Heck, K.L., Jr., Orth, R.J., 1980. Seagrass habitats: the roles of habitat complexity, competition, and predation in structuring associated fish and motile macroinvertebrate assemblages. In: Kennedy, V.S. (Ed.), *Estuarine Perspectives*. Academic Press, New York, pp. 449–464.
- Heck, Jr. K.L., Thoman, T.A., 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. *J. Exp. Mar. Biol. Ecol.* 53, 125–134.
- Heck, Jr. K.L., Thoman, T.A., 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7, 70–92.
- Hettler, Jr. W.F., 1989. Nekton use of regularly-flooded saltmarsh cordgrass habitat in North Carolina, USA. *Mar. Ecol. Prog. Ser.* 56, 111–118.
- Hoese, H.K., Moore, R.H., 1977. *Fishes of the Gulf of Mexico, Texas, Louisiana and adjacent waters*. Texas A and M Univ. Press, College Station, 327 pp.
- Horne, J.K., Campana, S.E., 1989. Environmental factors influencing the distribution of juvenile groundfish in nearshore habitats of southwest Nova Scotia. *Can. J. Fish. Aquat. Sci.* 46, 1277–1286.
- Hurlbert, S.H., 1981. A gentle depilation of the niche: Dicean resource sets in a resource hyperspace. *Evol. Theor.* 5, 177–184.
- Hurtubia, J., 1973. Trophic diversity measurement in sympatric predatory species. *Ecology* 54, 885–890.
- Johnson, R.A., Wichern, D.W., 1988. *Applied Multivariate Statistical Analysis*. Prentice Hall, Englewood Cliffs, second edition, 607 pp.
- Keast, A., 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. *Can. J. Zool.* 62, 1289–1303.
- Lubbers, L., Boynton, W., Kemp, W., 1990. Variations in structure of estuarine fish communities in relation to abundance of submersed vascular plants. *Mar. Ecol. Prog. Ser.* 65, 1–14.
- Machata-Wenninger, C., Janauer, G.A., 1991. The measurement of current velocities in macrophyte beds. *Aquat. Bot.* 39, 221–230.
- May, R.M., 1975. Some notes on estimating the competition matrix,  $\alpha$ . *Ecology* 56, 737–741.
- Mayer, M.S., 1986. The submerged aquatic vegetation of the Lake Pontchartrain estuary system, Louisiana. Masters Thesis, Univ. of New Orleans, 100 pp.
- Minello, T.J., 1993. Chronographic tethering: a technique for measuring prey survival time and testing predation pressure in aquatic habitats. *Mar. Ecol. Prog. Ser.* 101, 99–104.
- Montz, G.N., 1978. The submerged vegetation of Lake Pontchartrain, La. *Castanea* 43, 115–128.
- Mooney, H.A., Drake, J.A., 1986. *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York.
- Muncy, R.J., 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico): pinfish. U.S. Fish. Wildl. Serv., FWS/OBS-82/11.26, U.S. Army Corps of Engineers, TR EL-82-4, 18 pp.
- Olm, III E.J., Lipcius, R.N., 1991. Predation on postlarvae of the blue crab *Callinectes sapidus* Rathbun by sand shrimp *Canon septemspinosa* Say and grass shrimp *Palaemonetes pugio* Holthuis. *J. Exp. Mar. Biol. Ecol.* 151, 169–183.
- Olney, J.E., Boehlert, G.W., 1988. Nearshore ichthyoplankton associated with seagrass beds in the lower Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 45, 33–43.

- Orth, R.J., 1992. A perspective on plant-animal interactions in seagrasses: physical and biological determinants influencing plant and animal abundance. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), *Plant-Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford, pp. 147–164.
- Orth, R.J., Heck, Jr. K.L., van Montfrans, J., 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7, 339–350.
- Orth, R.J., van Montfrans, J., 1987. Utilization of a seagrass meadow and tidal marsh creek by blue crabs (*Callinectes sapidus*): I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Mar. Ecol. Prog. Ser.* 41, 283–294.
- Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 10, 131–144.
- Rakocinski, C.F., Baltz, D.M., Fleeger, J.W., 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Mar. Ecol. Prog. Ser.* 80, 135–148.
- Robins, C.R., Bailey, R.M., Bond, C.E., Booker, J.R., Lachner, E.A., Lea, R.N., Scott, W.B., 1991. *Common and Scientific Names of Fishes from the United States and Canada* (5th ed). Amer. Fish. Soc. Spec. Pub. no. 20, 183 pp.
- Room, P.M., Fernando, I.V.S., 1992. Weed invasions countered by biological control: *Salvinia molesta* and *Eichhornia crassipes* in Sri Lanka. *Aquat. Bot.* 42, 99–107.
- Rozas, L.P., Odum, W.E., 1987. Fish and macrocrustacean use of submerged plant beds in tidal freshwater marsh creeks. *Mar. Ecol. Prog. Ser.* 38, 101–108.
- Rozas, L.P., Odum, W.E., 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* 77, 101–106.
- Ryer, C.H., 1988. Pipefish foraging: effects of fish size, prey size and altered habitat complexity. *Mar. Ecol. Prog. Ser.* 48, 37–45.
- SAS Institute, 1989. *SAS Language and Procedures*. SAS Institute, Inc., Cary, version 6.
- Savino, J.F., Stein, R.A., 1989. Behavior of fish predators and their prey: Habitat choice between open water and dense vegetation. *Environ. Biol. Fish.* 24, 287–293.
- Schoener, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51, 408–418.
- Scott, J.S., 1982. Selection of bottom type by groundfishes of the Scotian shelf. *Can. J. Fish. Aquat. Sci.* 39, 943–947.
- Sedberry, G.R., Carter, J., 1993. The fish community of a shallow tropical lagoon in Belize, Central America. *Estuaries* 16, 198–215.
- Sikora, W.B., Kjerfve, B., 1985. Factors influencing the salinity regime of Lake Pontchartrain, Louisiana, a shallow coastal lagoon: analysis of a long-term data set. *Estuaries* 8, 170–180.
- Smith, L.D., Coull, B.C., 1987. Juvenile spot (*Pisces*) and grass shrimp predation on meiobenthos in muddy and sandy substrata. *J. Exp. Mar. Biol. Ecol.* 105, 123–136.
- Sokal, R.R., Rohlf, F.J., 1981. *Biometry*. W.H. Freeman and Company, San Francisco. 2nd edition.
- Stoner, A., 1982. The influence of benthic macrophytes on the foraging behavior of the pinfish, *Lagodon rhomboides* (Linnaeus). *J. Exp. Mar. Biol. Ecol.* 58, 271–284.
- Subrahmanyam, C.B., Drake, S.H., 1975. Studies on the animal communities in two north Florida salt marshes. *Bull. Mar. Sci.* 25, 445–465.
- Sutton, D.L., 1986. Growth of *Hydrilla* in established stands of spikerush and slender arrowhead. *J. Aquat. Plant. Manage.* 24, 16–20.
- Tanner, C.C., Clayton, J.S., Coffey, B.T., 1990. Submerged-vegetation changes in Lake Rotoroa (Hamilton, New Zealand) related to herbicide treatment and invasion by *Egeria densa*. *New Zeal. J. Mar. Freshwater Res.* 24, 45–57.
- Thompson, B.A., Verret, J.S., 1980. Nekton of Lake Pontchartrain, Louisiana, and its surrounding wetlands. In: Stone, J.H. (Ed.), *Environmental Analysis of Lake Pontchartrain, Louisiana, Its Surrounding Wetlands and Selected Land Uses*. CEL, CWR, LSU, BR, LA 70803. Prepared for U.S. Army Engineer District, New Orleans. Contract No. DACW29-77-C-0253. pp 711–863.
- Thompson, B.A., Fitzhugh, G.R., 1985. Synthesis and analysis of Lake Pontchartrain environments, influencing factors and trends. CFI, CWR, LSU, BR, LA 70803-7503. Prepared for Louisiana Department of Environmental Quality, Office of Water Resources. 238 pp.

- Turner, R.E., Darnell, R.M., Bond, J.R., 1980. Changes in the submerged macrophytes of Lake Pontchartrain (Louisiana): 1954–1973. In: Stone, J.H. (Ed.), *Environmental Analysis of Lake Pontchartrain, Louisiana, Its Surrounding Wetlands, and Selected Land Uses*. CEL, CWR, LSU, BR, LA 70803. Prepared for U.S. Army Engineer District, New Orleans. Contract No. DACW29-77-C-0253. pp. 647–657.
- Turner, A.M., Mittlebach, G.G., 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71, 2241–2254.
- Valiela, I., 1984. *Marine Ecological Processes*. Springer-Verlag, New York, 546 pp.
- Ward, L.G., Kemp, W.M., Boynton, W.R., 1984. The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar. Geol.* 59, 85–103.
- Weinstein, M.P., Brooks, H.A., 1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadows: community composition and structure. *Mar. Ecol. Prog. Ser.* 12, 15–27.
- Wetzel, R.G., 1975. *Limnology*. W.B. Saunders, Philadelphia.