

PATTERNS OF FISH AND MACRO-INVERTEBRATE DISTRIBUTION IN THE
UPPER LAGUNA MADRE: BAG SEINES 1985-2004

A Thesis

by

AMY BETH LARIMER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

August 2008

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Co-Chairs of Committee,	Fran Gelwick,
	William Neill
Committee Member,	Michael Speed
Head of Department,	Thomas Lacher

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ABSTRACT

Patterns of Fish and Macro-invertebrate Distribution in the Upper

Laguna Madre: Bag Seines 1985-2004. (August 2008).

Amy Beth Larimer, B.S., Troy State University

Co-Chairs of Advisory Committee: Dr. Fran Gelwick
Dr. William Neill

The Laguna Madre is a hypersaline lagoon. Despite harsh conditions, the upper Laguna Madre (ULM) is a highly productive ecosystem and a popular sportfishing area, especially for spotted seatrout and red drum. It is also the most important Texas bay for commercial fishing of black drum. TPWD's Coastal Fisheries division began conducting routine monitoring of coastal fishery resources in 1977 to guide management. The goal of the present study was to improve understanding of spatio-temporal trends in relative abundance of selected fish and macro-invertebrate species in the upper Laguna Madre. I used TPWD's bag-seine and water-quality data from the years 1985-2004 to examine variation in species' relative abundances and relationships to several environmental factors. I hypothesized that one or more of these variables, alone or in combination, were related to spatial and temporal trends in community composition. I used detrended correspondence analysis (DCA) to measure species turnover (beta diversity) and to determine which model (linear or unimodal) of species response along a gradient to apply. I used canonical correspondence analysis to relate species abundances directly to explanatory variables. The explanatory variables were

tested for significance and the variance partitioned among three groupings: temporal, spatial and environmental.

DCA indicated complete species turnover along two dimensions: seasonal and spatial. It also indicated that a unimodal method such as CCA was appropriate for further analysis. The CCA model included 39 variables. The included variables explained 14% of the variation in species abundance in the data set. Since the first four axes explained 67% of the variation contained in the first two DCA axes, the chosen explanatory variables were sufficient to explain the majority of the tractable variation in species abundance. The variance partitioning procedure indicated that temporal effects were the most important in explaining species variation in the Upper Laguna, followed by the spatial component. The pure environmental component explained the least amount of variation.

In this study, much of the variability in species abundance was due to the spawning patterns of estuary-dependent species, most of which spawn in the spring and summer months, leading to higher abundances from spring through fall.

DEDICATION

To Nana

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NOMENCLATURE

CCA	Canonical Correspondence Analysis
CFRMP	Coastal Fisheries Resource Monitoring Program
CPUE	Catch Per Unit Effort
DCA	Detrended Correspondence Analysis
TPWD	Texas Parks and Wildlife Department
ULM	Upper Laguna Madre

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1. INTRODUCTION

Some of the most productive habitats for fishery species are the shallow areas of coastal bays and estuaries. These areas include seagrass beds, shallow marshes, tidal flats, mangroves and oyster reefs (Rozas and Minello 1997). Communities of these areas are highly variable in time, with short-term fluctuations in the numbers of individuals, although the number of species tends to remain constant in the long-term (Livingston et al. 1976). Because numbers-density (the total number of individuals of a given species per unit habitat) is the result of recruitment, mortality and emigration, numbers-density estimated for juveniles can be an indicator of the relative values of estuarine habitats as nursery areas (Rozas and Minello 1997). Biomass-density (biomass of all individuals per unit habitat) reflects weight or size of individuals as well as total numbers. The amount of production (numbers or biomass) reaching adult stages is dependent upon successful recruitment to juvenile habitats, and subsequent growth and survival (Minello et al. 2003). Fishes are typically more abundant in vegetated areas than over bare substrate (Tolan et al. 1997; Rozas and Minello 1998). Possible explanations for this pattern include increased prey abundance and protection from predators for early life history stages. Studies on a variety of aquatic prey have documented that structural habitat complexity reduced predation rates by reducing predator effectiveness (Heck and Thoman 1981, Orth et al.1984).

This thesis follows the style of Transactions of the American Fisheries Society.

Structural complexity also affects abundance of food resources (Rozas and Odum 1988). Differential mortality rates may lead to variation in abundance of organisms in different habitats, with lower predation rates in areas of high structural complexity (Stunz et al. 2001; Stunz and Minello 2001), but this also depends on the type of predator (Shervette and Gelwick 2008).

Bell and Westoby (1986) found that when they excluded predators from vegetated plots and then decreased the amount of seagrass cover, prey densities decreased. This suggested that the prey species chose other, more densely vegetated habitat. They concluded from this that predation was not the direct cause of low prey abundance in habitats with sparse vegetation cover but rather the driving force in the selection of the superior (more densely vegetated) habitat.

In non-vegetated areas, fish may segregate by size, with smaller fish being found in shallower water (Ruiz et al. 1993). Smaller fish are able to take advantage of the shallows where larger predators are more vulnerable to avian predators (Power 1987). Other unidentified factors are likely to be important because fish densities were highest in natural marshes as compared to created marshes, even for created habitats in existence for many years (Minello and Webb 1997).

Estuarine species can be categorized as transient or resident. Transient species are mostly larvae or juveniles of species that occur primarily in marine habitats as adults, but enter or approach closer to estuaries during the spawning season (e.g., the red drum, *Sciaenops ocellatus*). Weinstein et al. (1980) observed that 70% of community dominants in coastal marshes of the Cape Fear River estuary were juveniles of such

species. In contrast, resident species, like spotted seatrout (*Cynoscion nebulosus*), spend most of their lives within the estuary. In some estuarine habitats, resident species may dominate collections, but large seasonal pulses can occur due to transient larvae or juveniles recruited from spawning areas elsewhere (Sogard et. al. 1987, Rozas 1995). Many of these transient species are commercially important, such as the penaeid shrimps (*Litopenaeus setiferus*, *Farfantepenaeus duorarum* and *F. aztecus*) and Gulf menhaden (*Brevoortia patronus*) (Gunter 1967).

Many factors are responsible for structuring fish communities in estuarine environments. Physiological tolerances, morphological adaptations, habitat preferences as well as biological interactions such as predation and competition are factors that determine the presence, abundance, or absence of a species in a given habitat (Orth et al. 1984). The distribution of species along an environmental gradient often follows Shelford's Law of Tolerance. The species survives best across an optimum range of values for multiple environmental variables, and survival declines at more extreme values. The occurrence of a species is thus constrained to habitats with a restricted range of environmental values within its fundamental niche as determined by its physiological requirements (Hutchinson 1959). However, since species normally exist within communities, the actual or realized niche is also determined by biotic interactions such as predation or competition (Ter Braak and Verdonschot 1995). Species are replaced by others along an environmental gradient according to the preferences and tolerances of each species. Whether abiotic or biotic factors are more important in shaping

communities may depend on the harshness of environmental conditions (Chesson and Huntly 1995).

High or low salinity, high or low temperature and low dissolved oxygen may cause stress in marine organisms. Salinity is a loading or masking factor on the metabolism of fishes (Fry 1971; Brett 1979) and can be especially important in hypersaline systems like the Laguna Madre. Some energy is constantly required to maintain internal osmotic balance. Salinities beyond the optimal range for an organism require greater expenditures of energy, limiting the energy available for growth (Brett 1979). Many estuarine organisms can tolerate a wider range of salinity than either freshwater or marine forms (Gunter 1961).

Temperature also affects fish abundance through mortality, as well as local re-distribution due to movement (Weinstein 1982). Temperature may be more important at high latitudes where extreme values are more divergent. Some species may have general temperature and salinity preferences, but others show a wide tolerance for short-term changes in these parameters (Livingston et al. 1976). Fish are usually able to escape intolerable conditions. However, acute and extreme cold weather has caused massive fish kills in the Laguna Madre of Texas. Three major freezes occurred on the Texas coast during the 1980's, affecting 159 species of fish and invertebrates. The most severe recent freeze, in 1983, is estimated to have killed 14 million fish (McEachron et. al. 1994). Such periodic freezes may be followed by a decline in recreational and commercial catches in subsequent years (Gunter 1945). A freeze in 1989 (less extreme than the one in 1983) was followed in the next year by a 21% reduction in recreational

fish-catch rates on the Texas coast (Weixelman et al. 1992; Green and Campbell 2005). Such mortalities may result in the loss of spawning adults and lower recruitment (McEachron et al. 1994) and enactment of regulations to reduce fishing pressure and allow the species to recover.

2. OBJECTIVES

The goal of this study was improved understanding of spatio-temporal trends in the relative abundances of fish and invertebrates in the upper Laguna Madre of Texas. My specific objective was to evaluate the variation in catches of selected organisms from the seine-sampling program operated by Texas Parks and Wildlife Department (TPWD) over the period 1985-2004, and their relationships to spatial and temporal variation in values of environmental factors (salinity, temperature, dissolved oxygen, season, day-length, and distance from the Laguna's juncture with Corpus Christi Bay) concurrently recorded for each sample. I hypothesized that one or several of these variables, either alone or in combination, would influence the spatial and temporal trends in community composition. Given the hypersaline conditions that generally exist in the Laguna Madre, I expected high-salinity-tolerant species (such as *Cyprinodon variegatus*) to be relatively more abundant during times of higher salinity or at sites further from the mouth of the Laguna (and away from the salinity-moderating influence of Corpus Christi Bay). Seasonal changes in community composition were expected to reflect the different spawning seasons of these organisms. I also expected to identify combinations of factors among these relationships that can be used to alert biologists to important trends that indicate need for intervention and evaluation of alternative management actions.

3. STUDY AREA

Lacking freshwater inflows, the Laguna Madre (Figure 1) is not a true estuary but is actually a hypersaline lagoon, one of only a few worldwide. Salinities can be much higher than oceanic salinities but can also vary considerably depending on the amount of rainfall in the watershed. The Laguna Madre extends southward from Corpus Christi Bay, Texas, into Mexico. In Texas, it is divided into upper and lower sections by an area of sand dunes and mudflats known as the Land Cut, about 80 km southwest of the Laguna's juncture with Corpus Christi Bay. The Intracoastal Waterway links the two sections. The area for this study includes the upper Laguna Madre and the Baffin Bay complex, which includes Baffin Bay and three inlets—Cayo del Grulla, Alazan Bay and Laguna Salada. Depths in Baffin Bay are up to 4 m but most of the Laguna is much shallower. The total surface area is 1554 square kilometers (600 square miles) (Hedgpeth 1967).

Freshwater inflows into the upper Laguna Madre are meager. There are no major streams flowing into it, and only a few small streams enter the Baffin Bay complex. Evaporation is also quite high, especially in warmer months. These factors lead to mean annual salinities of 25.3-48.6 ppt, which are higher than in other bay systems on the Texas coast (Martinez-Andrade et al. 2005).

Human activities have moderated upper Laguna salinities somewhat. In the 1940s, salinities exceeding 100 ppt were recorded regularly (Quammen and Onuf 1993).

After the dredging of the Gulf Intracoastal Waterway in 1949, salinities moderated, declining into the range of 30-60 ppt. (Pulich 1980). The channel allows water to circulate between the Gulf and the lower Laguna Madre, through the upper Laguna Madre, and out through Aransas Pass. Tides in the Laguna Madre have diel amplitudes less than 3 cm. Although wind tides account for most of the water level rise and fall, there is a dominant semi-annual rise and fall, leading to extreme high tides in the spring and fall and extreme low tides in the summer and winter (Smith 1978). With recent re-opening of Packery Channel, between the southwestern end of Corpus Christi Bay and the Gulf, there is now the possibility of increased flux of water through the Laguna Madre, and further moderation of salinity in the upper Laguna Madre.

Despite the harsh and fluctuating conditions, the upper Laguna Madre is a highly productive system. Of the commercial finfish landings from 1997 to 2001 across the Texas coast, 43% came from the upper Laguna Madre, black drum (*Pogonias cromis*) accounted for the majority of these landings. In 2001, just over 1.4 million pounds of black drum were landed, 55% of the statewide total (Culbertson et al. 2004). The latest gill net data for black drum (spring 2006) show some of the highest catch rates on record since gill net sampling began (K. Spiller, per. comm.). The Upper Laguna Madre is also a popular sportfishing area, with Baffin Bay as a persistent “hot spot” for trophy-size spotted seatrout.

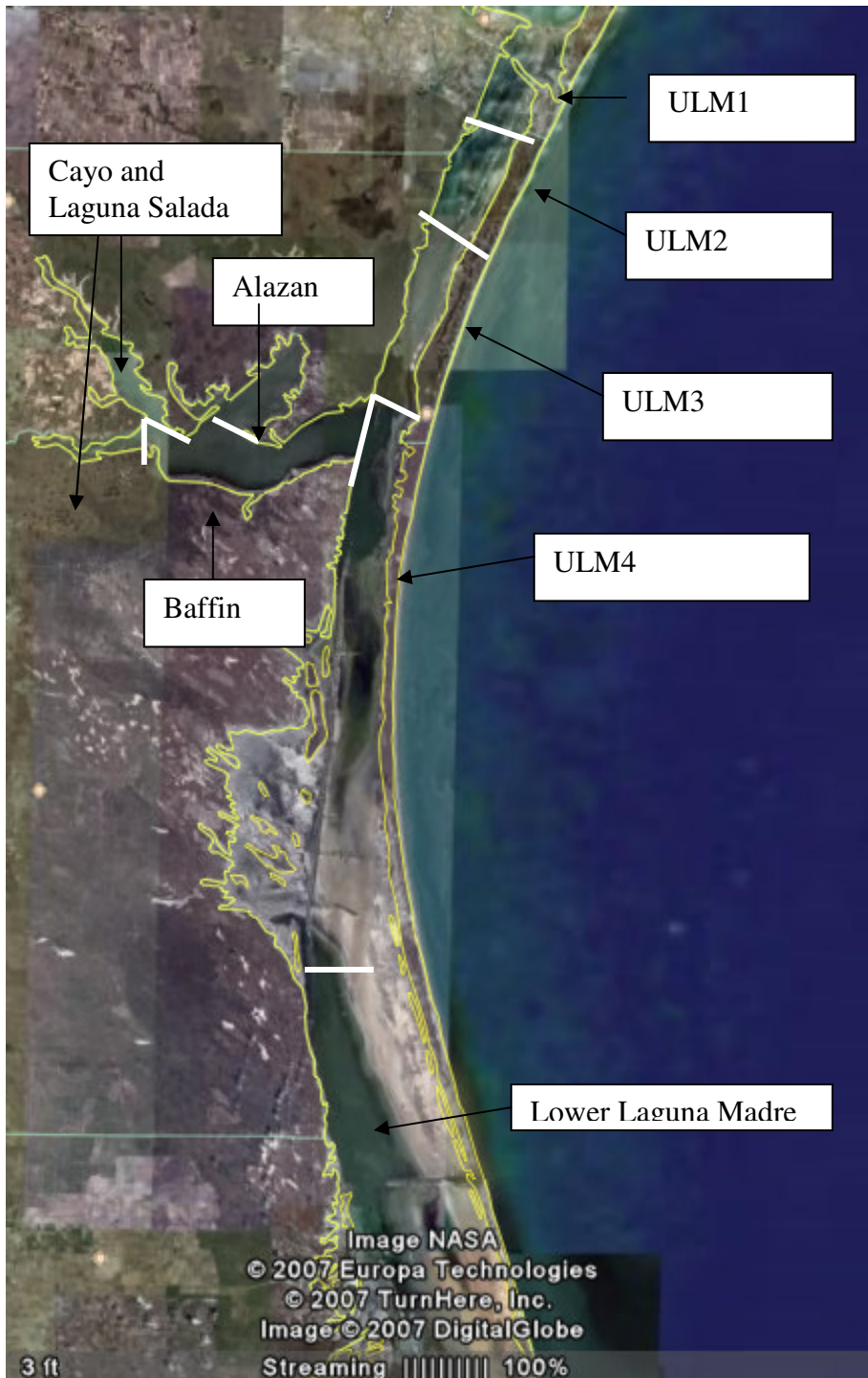


Figure 1.—The upper Laguna Madre bay system. Samples were subdivided into seven locations; each location contained approximately an equal amount of potential sampling area. Image obtained from Google Earth™.

4. DATA SOURCE

The data for this study come from the TPWD's Coastal Fisheries Resource Monitoring Program (CFRMP). This program was established in 1977 to aid the Department in managing the fisheries. Long-term monitoring programs such as this are needed to differentiate seasonal or local changes from population-level changes (Paperno et al. 2001). These long-term programs also provide a baseline to study changes in the habitat or in species diversity. CFRMP data have been used to set bag and size limits for a variety of commercial and recreational species.

Three types of gear are used in CFRMP—bag seines, trawls and gill nets. My study focused on the bag seine data from 1985-2004. The CPUE (catch per unit effort) in bag seines were used as an index of relative abundance for small species and as an index of recruitment for young of larger species such as red drum, black drum and spotted seatrout.

For purposes of the CFRMP component involving bag-seine sampling, the upper Laguna Madre is divided into 345 grid-units (1 minute latitude by 1 minute longitude). Twenty of those grid-units containing shoreline are randomly chosen every month. The bag seine is 18.3 m long and 1.9 m deep, with 13-mm stretched nylon mesh in the bag and 19-mm stretched mesh in the wings. The poles to which the seine is attached are marked in tenths of meters, to facilitate measuring water depth. Two people pull the seine along the shoreline for 15.5 meters and then bring it up on shore. Organisms are identified and counted. Up to 19 individuals of each species of fish and

macroinvertebrates are measured. The catch data can be converted to an estimate of spatial density of fish and invertebrate numbers by dividing the number of individuals of each species caught by the area sampled, which is 0.03 hectares per seine haul.

Along with data on species abundance and individual total-length, data on water quality also are collected for each seine haul. A YSI dissolved oxygen meter is used to measure water temperature, salinity and dissolved-oxygen concentration (DO). Water depth is measured at each end of the seine as it is being pulled parallel to shore. Water samples are also collected for turbidity analysis.

5. METHODS

The data for this study consisted of 4,146 bag-seine samples from 1985-2004; these samples included a total of 89 species of fish and 49 species of invertebrates. The data had zero-catches for some species and involved a high degree of variability among catches, traditional parametric statistical tests were deemed inappropriate. It also was likely that many of the environmental variables were correlated with each other, which can create inflated significance tests (e.g., high Variance Inflation Factors). Instead, I utilized a method called canonical correspondence analysis. This is a form of direct gradient analysis (in which the species occurrences are directly related to the environmental variables) and is a special case of multivariate regression extending to multiple dependent variables, but the tests of significance do not rely on parametric statistical tests but rather Monte Carlo permutations to determine probability distributions of the actual data for testing hypotheses (Palmer 1993). To prevent sporadic occurrence of high abundance values from unduly influencing the ordination and to better model correlations between species and explanatory (environmental) data, species catch-data were square-root transformed. Because rare species may have a disproportionate influence on such analyses (Ter Braak and Šmilauer 2002), I omitted data for species that occurred in less than 1% of all samples. This left 31 fish species and 10 invertebrate species, but eliminated only 0.3% of all individuals. Explanatory data were standardized and centered.

To determine which model of species response (linear or unimodal) along an environmental gradient to apply, I used detrended correspondence analysis (DCA) to measure species turnover (beta diversity), using the software package CANOCO (Ter Braak and Šmilauer 2002). DCA is an indirect gradient analysis that orders species data and samples along the same axis, scaled in units of standard deviations (SD) of species compositional change across samples. The gradient length in SD measures the extent of species turnover in community composition along the ordination axes (Lepš and Šmilauer 2003). If the largest value is greater than 4.0 SD, it declares complete species turnover across the gradient. It also indicates that a unimodal model is appropriate for further analysis, because the species data will deviate from assumptions of such linear response models as Principal Components Analysis (Lepš and Šmilauer 2003). Unimodal methods include DCA, correspondence analysis (CA) and canonical correspondence analysis (CCA).

I used CCA in the software package CANOCO, version 4.5, to quantify species-environment relationships and because that methodology directly relate species' abundances to explanatory variables. It models a unimodal (Gaussian) relationship between species abundances and the explanatory variables. CCA is also an effective method for analysis of community data with many zero values. In CCA, the modeled relationship of actual data is tested against the null hypothesis of no relationship between the species data and the environmental variables. Because the distribution of the test statistic is unknown (i.e., cannot be assumed a priori as for parametric statistics) and often depends on the number of environmental variables included in the model, a Monte

Carlo permutation test is used to test the significance of the first axis (i.e., one major explanatory gradient) as well as a complex of gradients for all canonical axes combined (N=499 permutations, $P < 0.05$).

The environmental or explanatory variables I used were water temperature, dissolved oxygen, salinity, turbidity, day length, delta day length (the signed difference in day length from one sampling day to the next), four seasons (as categorical variables), calendar year (also a categorical variable), seven locations within the bay system (categorical), distance (as measured from the Corpus Christi Bay-Upper Laguna Madre confluence), algae (not identified to species or genus), and seagrasses. The amount and type of seagrasses and the amount of algae collected in the sample were recorded as an estimated density code (1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%) as an estimated percentage of the volume in the seine. In practice, most were 0-1, so it was, in effect, a presence-absence code. Each of the categorical variables was composed of a number of classes. A sample was given a “1” if it occurred in that class, a “0” if it did not. Each class centroid can be interpreted as representing a “supersample” of all the samples in that class. I applied stepwise forward-selection from the pool of variables, using Monte Carlo randomization to calculate significance (N = 499 permutations, $P < 0.05$) for each additional explanatory variable added to the model until no remaining variables explained a significant additional amount of the species variation.

Across the group of significant variables, I partitioned the explained variance among three types of sources: spatial, temporal and environmental (following the method of Anderson and Gribble 1998). The spatial source was the qualitative variable

location. The temporal source included season, year, day-length and delta day-length. The environmental source included temperature, salinity, dissolved oxygen, turbidity, *Halophila* and algae. The other types of seagrasses were not significant in the stepwise forward selection. Following Anderson and Gribble (1998), I used eight components of variation: pure environmental, pure spatial, pure temporal, shared variation between environmental and spatial, shared variation between environmental and temporal, shared variation between spatial and temporal, variation shared among all three, and the amount of variation unexplained by the significant group of environmental variables. I used CCA and CCA with covariables (partial CCA) to determine the eigenvalues for each model run. The eigenvalue obtained in a partial CCA run was equivalent to a portion of the sum of all eigenvalues obtained for the full model (all significant variables). That proportion was converted to a percentage for each combination of variables and covariables. I also tested each combination for significance ($P < 0.05$) using Monte Carlo permutation tests, with 499 permutations.

6. RESULTS

A total of 346,016 fish were collected in bag seine samples (Table 1). These included representatives from 38 families and 89 species. The most common species was the sheepshead minnow, *Cyprinodon variegatus*, with 142,325 individuals (41% of the total), followed by *Menidia* sp. (mostly likely *M. peninsulae*) (14.41% of the total) and pinfish, *Lagodon rhomboides* (9.54% of the total). At the level of family, the drums, Sciaenidae, were most prominent, with nine species and over 39,000 individuals in the catch data. Names for fishes were verified with the latest American Fisheries Society guide (Nelson et al. 2004).

Invertebrates included 154,636 individuals from 49 species (Table 2). The most abundant was grass shrimp (61.49%, *Palaemonetes* sp.), followed by brown shrimp *Farfantepenaeus aztecus* (26.59%) and blue crab *Callinectes sapidus* (4.21%). Scientific names for invertebrates were verified using the most recent American Fisheries Society guides to names for crustaceans and mollusks (Turgeon et al. 1998; McLaughlin et al. 2005).

The mean salinity for the entire bay system was 36.4 ppt but fluctuated greatly from year to year (Figure 2). Temperatures were much higher in summer (mean 30.9 C) than in winter (17C) but fall and spring temperatures were more similar (Figure 3).

Table 1.—Fish from the Upper Laguna Madre, in bag-seine samples from 1985 to 2004. Total number is the number of individuals caught, Percentage of Total is the percentage for each species of the total number of fish caught, Count of Samples is the number of samples containing the species, Percentage of Samples is the percentage of the samples containing the species and CPUE is catch-per-unit-effort in number per hectare (No./ha). Species in bold occurred in > 1% of samples and were included in analyses.

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
Achiridae					
<i>Trinectes maculatus</i>	159	0.046	63	1.52	1.28
<i>Achirus lineatus</i>	158	0.046	85	2.05	1.27
Ariidae					
<i>Ariopsis felis</i>	402	0.116	85	2.05	3.23
<i>Bagre marinus</i>	2	0.001	1	0.02	0.02
Atherinopsidae					
<i>Menidia sp.</i>	49873	14.413	2378	57.36	400.97
<i>Membras martinica</i>	22	0.006	12	0.29	0.18
Batrachoididae					
<i>Opsanus beta</i>	99	0.029	71	1.71	0.80
Belonidae					
<i>Strongylura marina</i>	242	0.070	164	3.96	1.95
<i>Strongylura notata</i>	1	0.000	1	0.02	0.01
Blenniidae					
<i>Chasmodes bosquianus</i>	8	0.002	7	0.17	0.06
<i>Hypoleurochilus geminatus</i>	3	0.001	1	0.02	0.02
<i>Hypsoblennius hentz</i>	2	0.001	2	0.05	0.02
<i>Scartella cristata</i>	2	0.001	1	0.02	0.02
Carangidae					
<i>Oligoplites saurus</i>	70	0.020	43	1.04	0.56
<i>Caranx hippos</i>	6	0.002	5	0.12	0.05
<i>Trachinotus carolinus</i>	6	0.002	2	0.05	0.05
<i>Chloroscombrus chrysurus</i>	1	0.000	1	0.02	0.01
<i>Trachinotus falcatus</i>	1	0.000	1	0.02	0.01
Centrarchidae					
<i>Lepomis cyanellus</i>	4	0.001	2	0.05	0.03
Centropomidae					
<i>Centropomus undecimalis</i>	1	0.000	1	0.02	0.01
Clupeidae					
<i>Brevoortia patronus</i>	8592	2.483	205	4.94	69.08
<i>Opisthonema oglinum</i>	24	0.007	1	0.02	0.19
<i>Harengula jaguana</i>	8	0.002	5	0.12	0.06
<i>Dorosoma cepedianum</i>	2	0.001	2	0.05	0.02
<i>Jenkinsia lamprotaenia</i>	1	0.000	1	0.02	0.01
Cynoglossidae					
<i>Symphurus parvus</i>	1	0.000	1	0.02	0.01
<i>Symphurus plagiusa</i>	28	0.008	15	0.36	0.23

Table 1.—Continued

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
Cyprinodontidae					
<i>Cyprinodon variegatus</i>	142325	41.132	2795	67.41	1144.28
Dasyatidae					
<i>Dasyatis sabina</i>	27	0.008	21	0.51	0.22
Diodontidae					
<i>Chilomycterus schoepfi</i>	1	0.000	1	0.02	0.01
Eleotridae					
<i>Dormitator maculatus</i>	4	0.001	4	0.10	0.03
<i>Eleotris amblyopsis</i>	1	0.000	1	0.02	0.01
Elopidae					
<i>Elops saurus</i>	501	0.145	185	4.46	4.03
Engraulidae					
<i>Anchoa mitchilli</i>	14770	4.269	838	20.21	118.75
<i>Anchoa hepsetus</i>	27	0.008	12	0.29	0.22
<i>Anchoa lyolepis</i>	10	0.003	5	0.12	0.08
Fundulidae					
<i>Fundulus similis</i>	15590	4.506	1514	36.52	125.34
<i>Fundulus grandis</i>	9527	2.753	1395	33.65	76.60
<i>Lucania parva</i>	8494	2.455	837	20.19	68.29
<i>Adinia xenica</i>	12	0.003	5	0.12	0.10
<i>Fundulus chrysotus</i>	1	0.000	1	0.02	0.01
Gerreidae					
<i>Eucinostomus argenteus</i>	774	0.224	165	3.98	6.22
<i>Eucinostomus melanopterus</i>	169	0.049	50	1.21	1.36
<i>Eucinostomus gula</i>	137	0.040	47	1.13	1.10
<i>Diapterus auratus</i>	1	0.000	1	0.02	0.01
Gobiesocidae					
<i>Gobiesox strumosus</i>	11	0.003	8	0.19	0.09
<i>Gobiesox punctulatus</i>	2	0.001	1	0.02	0.02
Gobiidae					
<i>Gobiosoma bosc</i>	954	0.276	260	6.27	7.67
<i>Gobiosoma robustum</i>	451	0.130	210	5.07	3.63
<i>Ctenogobius boleosoma</i>	89	0.026	27	0.65	0.72
<i>Microgobius gulosus</i>	61	0.018	28	0.68	0.49
<i>Microgobius thalassinus</i>	46	0.013	25	0.60	0.37
<i>Evorthodus lyricus</i>	31	0.009	4	0.10	0.25
<i>Gobionellus oceanicus</i>	9	0.003	8	0.19	0.07
<i>Bathygobius soporator</i>	1	0.000	1	0.02	0.01
Haemulidae					
<i>Orthopristis chrysoptera</i>	115	0.033	36	0.87	0.92
Hemiramphidae					
<i>Hyporhamphus unifasciatus</i>	8	0.002	5	0.12	0.06
<i>Hemiramphus brasiliensis</i>	2	0.001	2	0.05	0.02

Table 1.—Continued

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
Lutjanidae					
<i>Lutjanus griseus</i>	2	0.001	2	0.05	0.02
Megalopidae					
<i>Megalops atlanticus</i>	1	0.000	1	0.02	0.01
Mugilidae					
<i>Mugil cephalus</i>	10636	3.074	1181	28.49	85.51
<i>Mugil curema</i>	6420	1.855	559	13.48	51.62
Paralychthidae					
<i>Paralichthys lethostigma</i>	101	0.029	74	1.78	0.81
<i>Citharichthys spilopterus</i>	84	0.024	46	1.11	0.68
<i>Paralichthys albigutta</i>	19	0.005	15	0.36	0.15
<i>Etropus crossotus</i>	4	0.001	2	0.05	0.03
Genus <i>Paralichthys</i>	1	0.000	1	0.02	0.01
Poeciliidae					
<i>Poecilia latipinna</i>	15	0.004	6	0.14	0.12
<i>Poecilia formosa</i>	1	0.000	1	0.02	0.01
Polynemidae					
<i>Polydactylus octonemus</i>	17	0.005	5	0.12	0.14
Sciaenidae					
<i>Leiostomus xanthurus</i>	26679	7.710	1147	27.67	214.50
<i>Pogonias cromis</i>	9750	2.818	515	12.42	78.39
<i>Cynoscion nebulosus</i>	1446	0.418	549	13.24	11.63
<i>Sciaenops ocellatus</i>	892	0.258	343	8.27	7.17
<i>Micropogonias undulatus</i>	757	0.219	107	2.58	6.09
<i>Bairdiella chrysoura</i>	379	0.110	73	1.76	3.05
<i>Menticirrhus americanus</i>	11	0.003	9	0.22	0.09
<i>Cynoscion arenarius</i>	8	0.002	5	0.12	0.06
<i>Menticirrhus littoralis</i>	3	0.001	2	0.05	0.02
Serranidae					
<i>Centropristis ocyurus</i>	5	0.001	2	0.05	0.04
Sparidae					
<i>Lagodon rhomboides</i>	33000	9.537	1378	33.24	265.32
<i>Archosargus probatocephalus</i>	15	0.004	10	0.24	0.12
Stromateidae					
<i>Peprilus burti</i>	1	0.000	1	0.02	0.01
Syngnathidae					
<i>Syngnathus scovelli</i>	1768	0.511	595	14.35	14.21
<i>Syngnathus louisianae</i>	14	0.004	13	0.31	0.11
<i>Hippocampus zosterae</i>	6	0.002	6	0.14	0.05
Synodontidae					
<i>Synodus foetens</i>	16	0.005	12	0.29	0.13
Tetraodontidae					
<i>Sphoeroides parvus</i>	91	0.026	37	0.89	0.73

Table 1.—Continued

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
Triglidae					
<i>Prionotus tribulus</i>	4	0.001	4	0.10	0.03
Uranoscopidae					
<i>Astroscopus y-graecum</i>	1	0.000	1	0.02	0.01

Table 2.—Invertebrates from the Upper Laguna Madre, in bag-seine samples from 1985 to 2004. Total number is the number of individuals caught, Percentage of Total is the percentage of the total number of individuals caught for each species, Count of Samples is the number of samples containing the species, Percentage of Samples is the percentage containing the species and CPUE is catch-per-unit-effort in number per hectare (No./ha). Species in bold occurred in > 1% of samples and were included in analyses.

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
<i>Palaemonetes sp.</i>	95092	61.49	1509	36.40	764.53
<i>Farfantepenaeus aztecus</i>	41110	26.59	913	22.02	330.52
<i>Callinectes sapidus</i>	6511	4.21	1481	35.72	52.35
<i>Litopenaeus setiferus</i>	4285	2.77	325	7.84	34.45
<i>Mulinia lateralis</i>	3203	2.07	31	0.75	25.75
<i>Farfantepenaeus duorarum</i>	1976	1.28	241	5.81	15.89
<i>Dyspanopeus texanus</i>	526	0.34	199	4.80	4.23
<i>Cerithium lutosum</i>	513	0.33	46	1.11	4.12
<i>Callinectes similis</i>	494	0.32	122	2.94	3.97
<i>Tozeuma carolinense</i>	301	0.19	48	1.16	2.42
<i>Bulla striata</i>	115	0.07	10	0.24	0.92
<i>Cerithidea pliculosa</i>	75	0.05	21	0.51	0.60
<i>Alpheus estuariensis</i>	65	0.04	41	0.99	0.52
<i>Pagurus longicarpus</i>	64	0.04	48	1.16	0.51
<i>Bursatella leachii pleii</i>	50	0.03	8	0.19	0.40
<i>Chione cancellata</i>	50	0.03	15	0.36	0.40
<i>Clibanarius vittatus</i>	40	0.03	31	0.75	0.32
<i>Petrolisthes armatus</i>	19	0.01	7	0.17	0.15
<i>Libinia dubia</i>	18	0.01	14	0.34	0.14
<i>Argopecten irradians</i>	17	0.01	13	0.31	0.14
<i>Lolliguncula brevis</i>	11	0.01	7	0.17	0.09
<i>Laevicardium mortoni</i>	9	0.01	5	0.12	0.07
<i>Haminoea antillarum</i>	8	0.01	2	0.05	0.06
<i>Hippolyte zostericola</i>	8	0.01	4	0.10	0.06
<i>Puberella intapurpurea</i>	6	0.00	2	0.05	0.05
<i>Cantharus cancellarius</i>	6	0.00	3	0.07	0.05
<i>Menippe adina</i>	6	0.00	6	0.14	0.05
<i>Tectonatica pusilla</i>	5	0.00	1	0.02	0.04
<i>Speocarcinus lobatus</i>	5	0.00	1	0.02	0.04
<i>Cancellaria reticulata</i>	5	0.00	1	0.02	0.04
<i>Sicyonia stimpsoni</i>	5	0.00	1	0.02	0.04
<i>Crassostrea virginica</i>	5	0.00	3	0.07	0.04
<i>Unidentified Holothuroidea</i>	5	0.00	4	0.10	0.04
<i>Stomolophus meleagris</i>	5	0.00	5	0.12	0.04
<i>Libinia emarginata</i>	4	0.00	4	0.10	0.03
<i>Tellina alternata</i>	3	0.00	3	0.07	0.02

Table 2.—Continued

Species	Total Number	Percentage of total	Count of Samples	Percentage of samples	CPUE
<i>Nassarius vibex</i>	2	0.00	1	0.02	0.02
<i>Amygdalum papyrium</i>	2	0.00	2	0.05	0.02
<i>Brachidontes exustus</i>	2	0.00	2	0.05	0.02
<i>Anomalocardia auberiana</i>	1	0.00	1	0.02	0.01
<i>Cerithiopsis emersonii</i>	1	0.00	1	0.02	0.01
<i>Littorina irrorata</i>	1	0.00	1	0.02	0.01
<i>Uca sp.</i>	1	0.00	1	0.02	0.01
<i>Tellina tampaensis</i>	1	0.00	1	0.02	0.01
<i>Crepidula convexa</i>	1	0.00	1	0.02	0.01
<i>Acetes americanus</i>	1	0.00	1	0.02	0.01
<i>Mercenaria campechiensis</i>	1	0.00	1	0.02	0.01
<i>Neverita duplicata</i>	1	0.00	1	0.02	0.01
<i>Pagurus pollicaris</i>	1	0.00	1	0.02	0.01

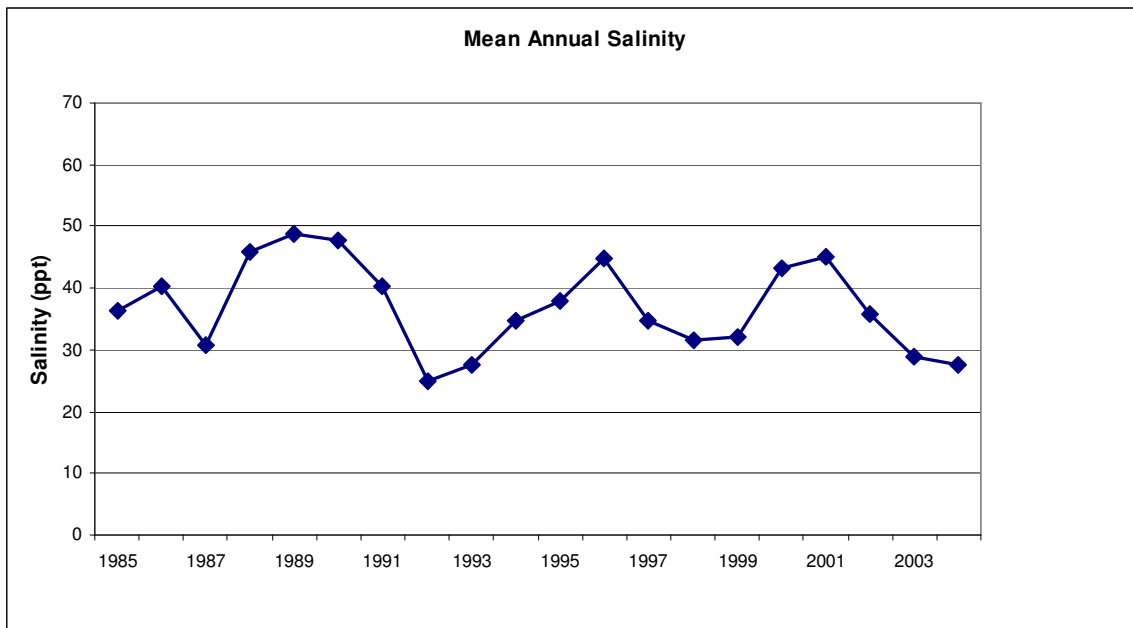


Figure 2.—Mean annual salinity for the Upper Laguna Madre, 1985-2004.

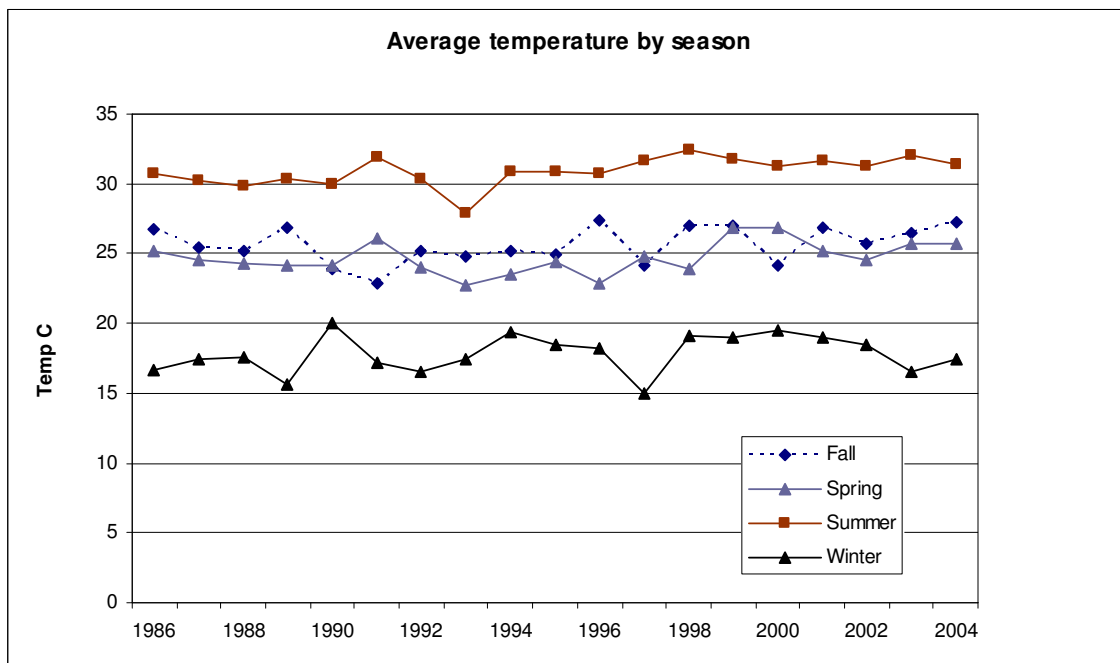


Figure 3.—Mean annual temperature (C) by season for the upper Laguna Madre, 1985-2004.

6.1 DCA

For the Laguna Madre seine-samples, the length of the longest DCA axis was 5.9 SD (Table 3, Axis 2) and also indicated that a unimodal method like CCA was appropriate for further analysis. The second axis explained 6% of the total species variability. The first axis was slightly shorter (4.9 SD) but explained slightly more of the total species variability (8%) among samples. This seemed to indicate that there was no single dominant gradient. In the DCA species plot (Figure 4), axis 1 was interpreted as a temporal gradient representing seasonal and associated temperature changes in species composition among samples. Temperature and day-length were interpreted as increasing from left to right, with species occurring mainly at higher temperature (i.e. *Litopenaeus setiferus*, mainly a late-summer species), further from the origin to the right. Axis 2 was interpreted as an east-west location gradient, with species occurring in samples from the western areas of the Laguna (Cayo, Baffin, and Alazan) at the top of the plot.

Resident species and estuary-dependent species differed in their temporal occurrence in the samples. Catches in cooler water (late fall and winter samples - Figure 4) consisted mainly of resident species.

Table 3.—Results of DCA for 4146 samples and 41 species of fish and invertebrates in the Upper Laguna Madre. The eigenvalue is a measure of the importance of the axis. The lengths of the Axes 1 and 2 are standard deviations for scores, and respectively indicate how much species turnover occurs along each axis. A length greater than 4 S.D. indicates complete species turnover along the axis.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.423	0.328	0.265	0.207	5.269
Lengths of gradient	4.488	5.925	4.423	3.916	
Cumulative percentage variance of species data	8	14.2	19.3	23.2	
Sum of all eigenvalues					5.269

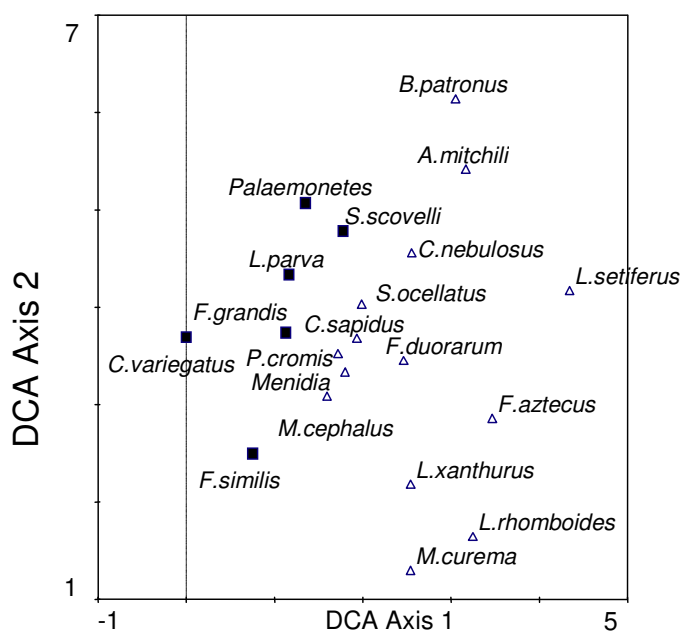


Figure 4.—Species plot of DCA. Black squares represent resident species, and blue triangles represent estuary-dependent species. Axis 1 is interpreted as representing a temperature-season axis. Axis 2 is interpreted as representing a location-distance axis, specifically an East-West axis.

6.2 CCA

The final model included 39 variables, comprising three groups of categorical variables, temperature, salinity, dissolved oxygen, day length, delta day-length, turbidity, *Halophila* and algae. The variable “distance” (a measure of the distance of the sample from the Laguna Madre-Corpus Christi Bay confluence) was strongly collinear with other variables (high VIF, value > 10) and was removed from the final group of explanatory variables. The Monte Carlo permutation tests indicated statistically significant relationships between species and explanatory variables for each of the first thirteen axes and for all axes together. Only the most important axes are displayed in Tables 4 and 5.

The eigenvalues for the individual axes, although significant, were each small proportions of the total inertia (Table 5), indicating that these were not strong gradients. The percentage of variance in species data among samples that was explained by each axis was estimated by dividing the eigenvalue by the total inertia. The first axis explained 4.2% of the variance in the species, and the first four axes together explained 9.7% of the variance in species. For abundance data, these percentages are usually low because such data typically contain many zero values. The total variance for all the fitted values was the sum of all canonical eigenvalues. In this study, that sum was small, 0.737, or approximately 14% of the total inertia. Each successive axis explained a part of this variance, which is listed cumulatively (Table 5).

Table 4.—Results of Monte Carlo permutation tests for each of the first four CCA axes and all axes together. All axes were significant ($P < 0.05$), indicating a relationship between species abundances and explanatory variables.

Axis	Eigenvalue	F-ratio	P-value
1	0.219	170.554	0.002
2	0.116	92.44	0.002
3	0.091	73.142	0.002
4	0.084	69.018	0.002
All (trace)	0.737	17.789	0.002

Table 5.—Results of CCA analysis for 4146 samples with 41 species and 39 explanatory variables. The eigenvalue is a measure of the importance of the axis.

Axis	1	2	3	4	Total Inertia
Eigenvalues	0.219	0.116	0.09	0.084	5.269
Species-environment correlations	0.77	0.643	0.54	0.60	
Cumulative percentage variance					
of species data	4.2	6.4	8.1	9.7	
of species-environment relation	29.7	45.4	57.7	69.1	
Sum of all eigenvalues					5.269
Sum of all canonical eigenvalues					0.737

Table 6.—Correlation coefficients and coefficients of determination for the first two DCA axes and the first four CCA axes.

	<i>Correlation coefficients (r)</i>		<i>Coefficients of determination (r^2)</i>	
	DCA axis 1	DCA axis 2	DCA axis 1	DCA axis 2
CCA axis 1	-0.670	0.814	0.450	0.660
CCA axis 2	0.218	0.369	0.050	0.150
CCA axis 3	-0.718	-0.207	0.510	0.040
CCA axis 4	0.047	0.199	0.002	0.040

The eigenvalues for the first two CCA axes were smaller (Table 5) than those for the first two DCA axes (Table 3). The first three CCA axes explained as much of the variance (8%) among species as the first DCA axis. The first thirteen CCA axes were significant, but each explained a small proportion of the overall species-environment relation. The first four axes together accounted for 69% of the species-environment relationship (Table 6) and 67% of the variation contained in the first two DCA axes. Correlations for CCA axes 1 and 2 were strongest with DCA axis 2, and CCA axis 3 has its strongest correlation with DCA axis 1 (Table 6).

The CCA diagram (Figures 5 and 6) consists of points for species and categorical explanatory variables. Arrows indicate vectors for quantitative environmental variables. The distance between species points in the CCA diagram (Fig. 5) approximates the dissimilarity in relative abundance of those species in samples related to the complex gradient described by the environmental variables, and conversely, points in proximity to each other correspond to species that often occur together in samples. For example, *Cyprinodon variegatus* (CV) and *Fundulus grandis* (FG) often occurred in samples together, along with the rainwater killifish, *Lucania parva* (LP). *Lagodon rhomboides* was infrequent in samples containing *Trinectes maculatus*. Species plotted in the center of the axes may actually be associated with conditions in the middle of the environmental gradient represented by those axes, but it is also possible that the distribution of those species was not related to the variables chosen for this study and hence their location at the center represented weak to no correlation with those axes.

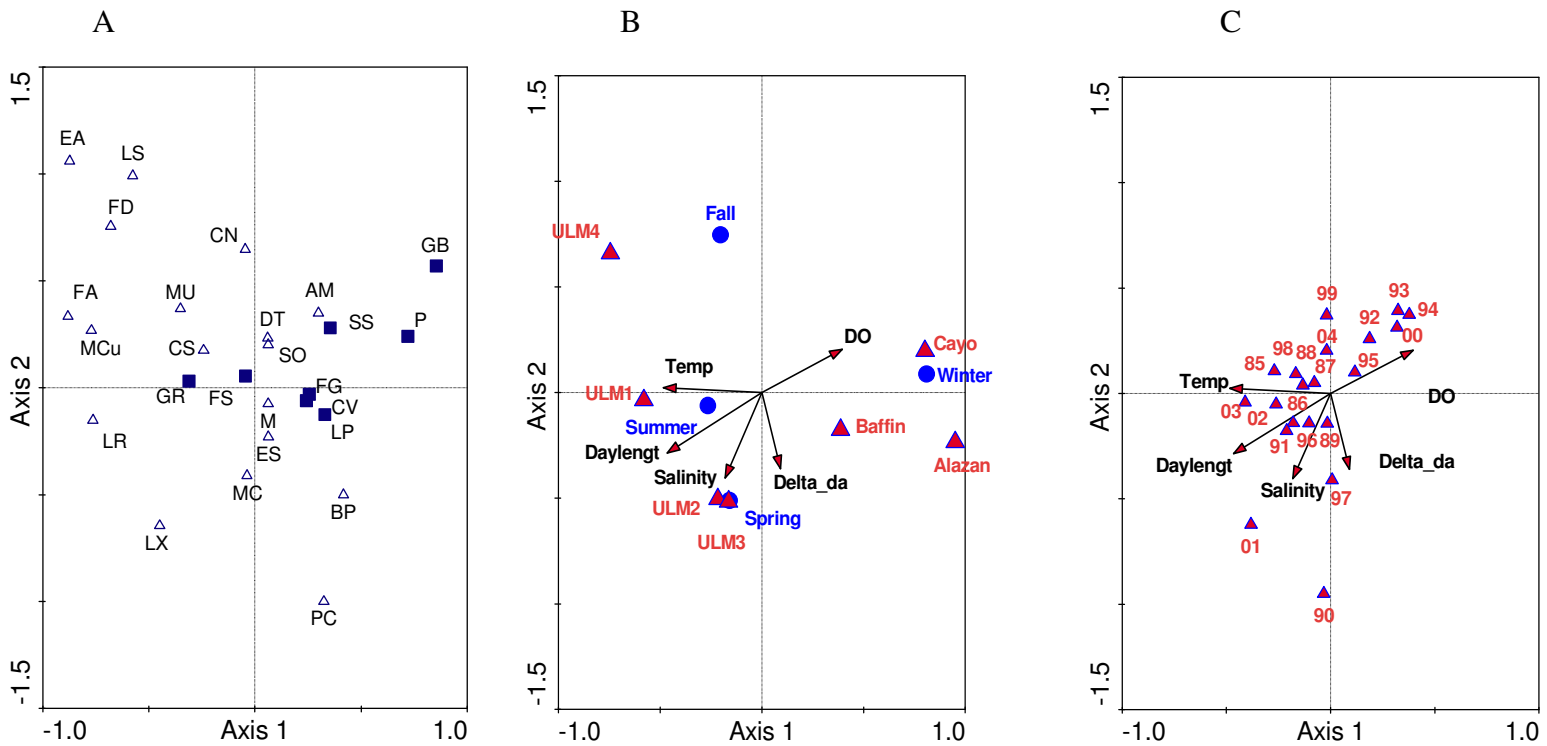


Figure 5.—Plot of species data and environmental variables on the first two CCA axes. Species abbreviations are as follows: AM-*Anchoa mitchilli*; BP- *Brevoortia patronus*; CN- *Cynoscion nebulosus*; CV- *Cyprinodon variegatus*; CS- *Callinectes sapidus*; DT- *Dyspanopeus texana*; EA- *Eucinostomus argenteus*; ES- *Elops saurus*; FG- *Fundulus grandis*; FS- *Fundulus similis*; FA- *Farfantepenaeus aztecus*; FD- *Farfantepenaeus duorarum*; GB- *Gobiosoma bosc*; GR- *Gobiosoma robustum*; LR- *Lagodon rhomboides*; LX- *Leiostomus xanthurus*; LP- *Lucania parva*; LS- *Litopenaeus setiferus*; M- *Menidia*; MC- *Mugil cephalus*; MCu- *Mugil curema*; MU- *Micropogonias undulatus*; PC- *Pogonias cromis*; P- *Palaemonetes*; SO- *Sciaenops ocellatus*; SS- *Sygnathus scovelli*. Plot A shows resident species (solid squares) and estuary-dependent species (open triangles). Plot B shows quantitative environmental variables (arrows) and qualitative variables Season (blue) and location (red). Plot C shows quantitative environmental variables and qualitative variable year (red).

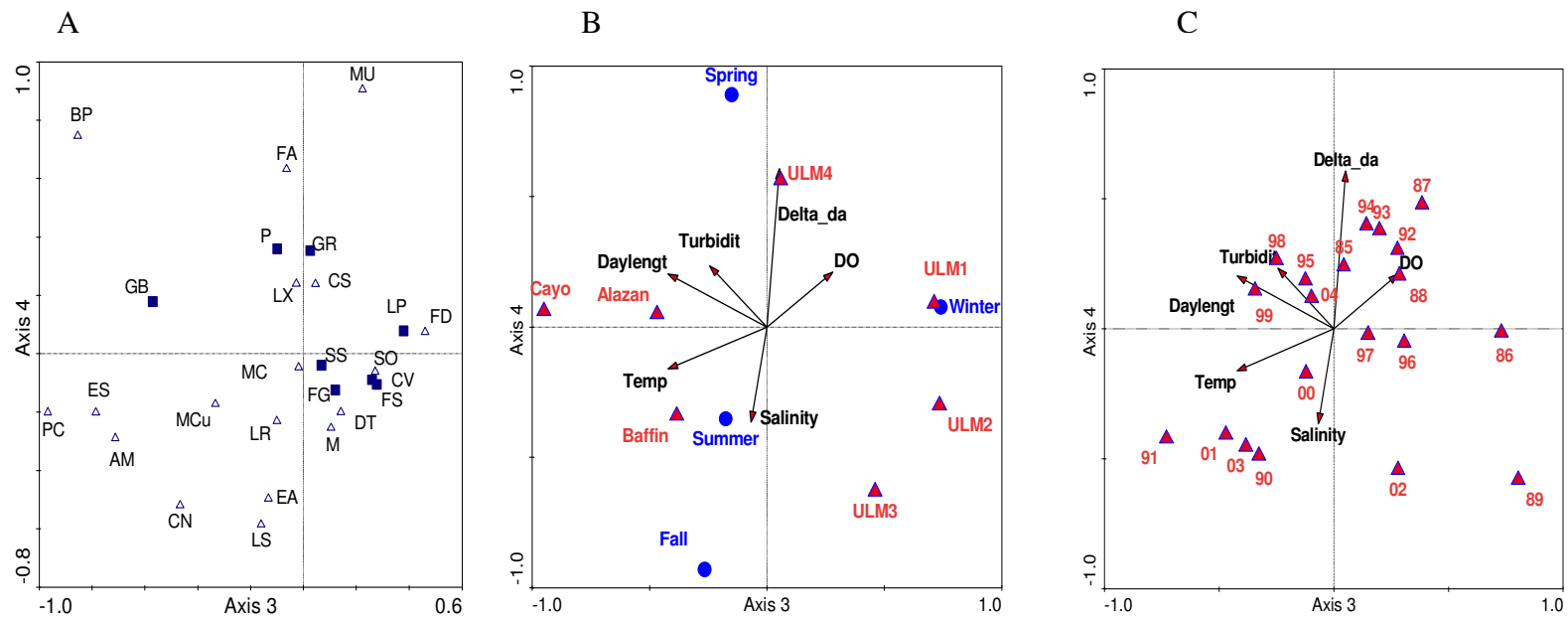


Figure 6.— Plot of species data and environmental variables for CCA axes three and four. Plot A shows resident species (solid squares) and estuary-dependent species (open triangles). Plot B shows quantitative environmental variables (arrows) and qualitative variables Season (blue) and location (red). Plot C shows quantitative environmental variables and qualitative variable year (red).

Comparisons of species abundance with actual environmental data and examination of the cumulative variance explained for each species on each axis provides information to answer this question. *Cyprinodon variegatus* (CV) had only a weakly positive relationship with winter and a weakly negative relationship with day length. *Sciaenops ocellatus* (SO) occurred in the middle because it had a strongly negative relationship with day length but a slightly positive relationship with both fall and winter. *Cynoscion nebulosus* had a strongly positive relationship with fall and strongly negative relationship with spring. *Pogonias cromis* (PC) had a strongly positive relationship with salinity, Alazan and the year 1990. Species at the edges of the diagram often carry low weights and may have little influence on the analysis, whereas species with larger weights and larger variances have a greater influence on the diagram (Ter Braak and Smilauer 2002). Species with high variance, despite having relatively low weights, can have disproportionate influence on the analysis. For example, fishes in the genus *Eucinostomus* had relatively low weights but high variances. For clarity, species with low weights were removed from the diagram (but not from the analysis).

For the environmental variables, each arrow points in the direction of increasing value of that variable. The length of the arrow indicates the importance of that variable, with longer arrows having a stronger relationship with the axes and more acute angles between the variable and the axis indicates stronger correlation between the variable and that axis. Implicit (but not drawn) is an arrow of equal length in the opposite direction indicating species whose optima are negatively correlated with increasing values (or positively correlated with decreasing values) of that variable. Axis 1 scores for species

were negatively correlated with temperature and day length and positively with DO (Figure 5). Axis 2 scores for species were negatively correlated with salinity and delta-day-length and positively correlated with DO. Axes 3 and 4 were also linear combinations of environmental variables that maximize the dispersion of species scores, with the only constraint being that these axes were uncorrelated with the previous axes (Ter Braak 1987). On Axes 3-4 (Figure 6B) DO was positively correlated with delta day-length, whereas it was negatively correlated with delta day-length on Axis 1-2. Axis 4 was positively associated with delta-day-length and turbidity but negatively associated with salinity (Figure 6). Turbidity had a much weaker relationship with Axes 1 and 2 and was not displayed in the plot for clarity but it had a much stronger correlation with axes 3 and 4.

Each classification centroid can be interpreted as representing a “supersample” of all the samples in that class. On a CCA diagram, centroids for classes of categorical variables are represented by points. The distance between the points indicates the similarity of samples and species composition among classes with respect to the values for variables represented by those axes. Classes that are closer together share more species. There was no strong annual trend on the first four axes, but the years 1992, 1993, 1994 and 1995 (Figure 5C) were located closely together on the right side of the diagram, indicating that assemblages were very similar in these years and negatively associated with salinity. These were also years of fairly moderate salinity (Figure 2). The year 1990 was plotted on the extreme bottom center of the diagram, and was a year of very high catches for black drum (PC in Figure 5A). Figure 7 shows the mean annual

CPUE (mean number of individuals per sample) for fish and invertebrates. The highest peaks were for the years 1990-1997.

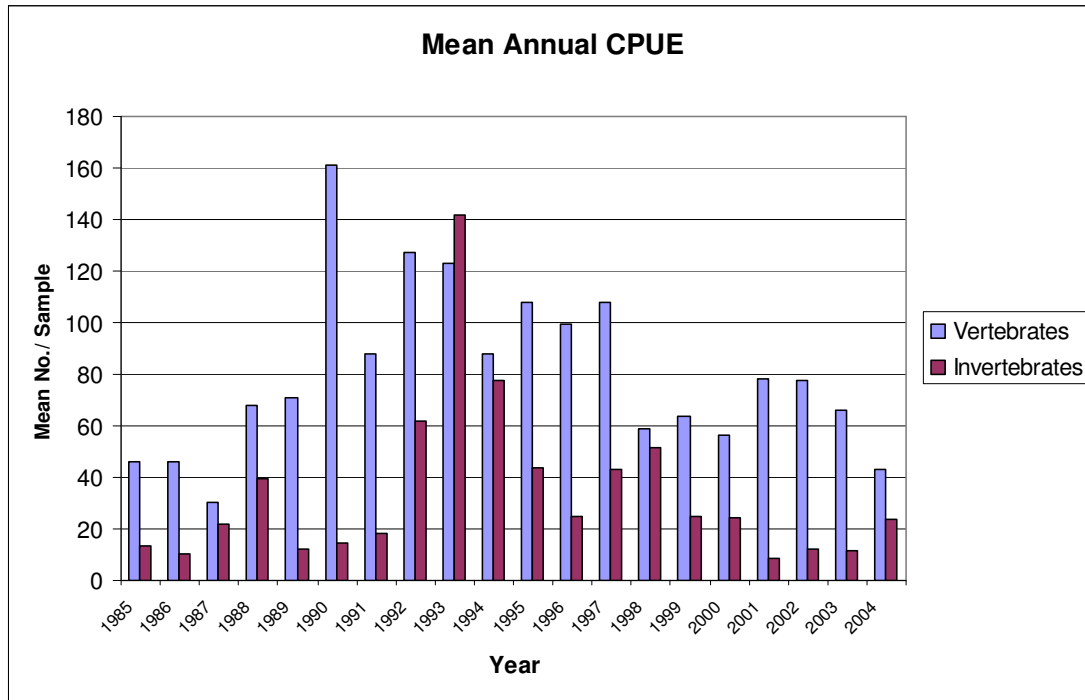


Figure 7.—Mean annual catch per unit effort for fish and invertebrates in bag seine samples for the Upper Laguna Madre, 1985-2004.

The plot on axis 1 (Figure 5B) of class centroids for “location” within the bay (Figure 1), indicated that assemblages in Baffin, Alazan and Cayo were on the opposite side of the environmental gradient from centroids for ULM1, ULM2, ULM3 and ULM4. This indicated that with regard to species-environment relationships on these axes these areas had almost completely different species compositions, whereas assemblages for ULM2 and ULM3 were almost identical. Figure 8 shows the mean abundance by location, with the highest peak for ULM 4. Figure 9 is a plot of N2 species diversity for the first two CCA axes. Species diversity increased from right to left. ULM4 had higher species diversity than the other locations.

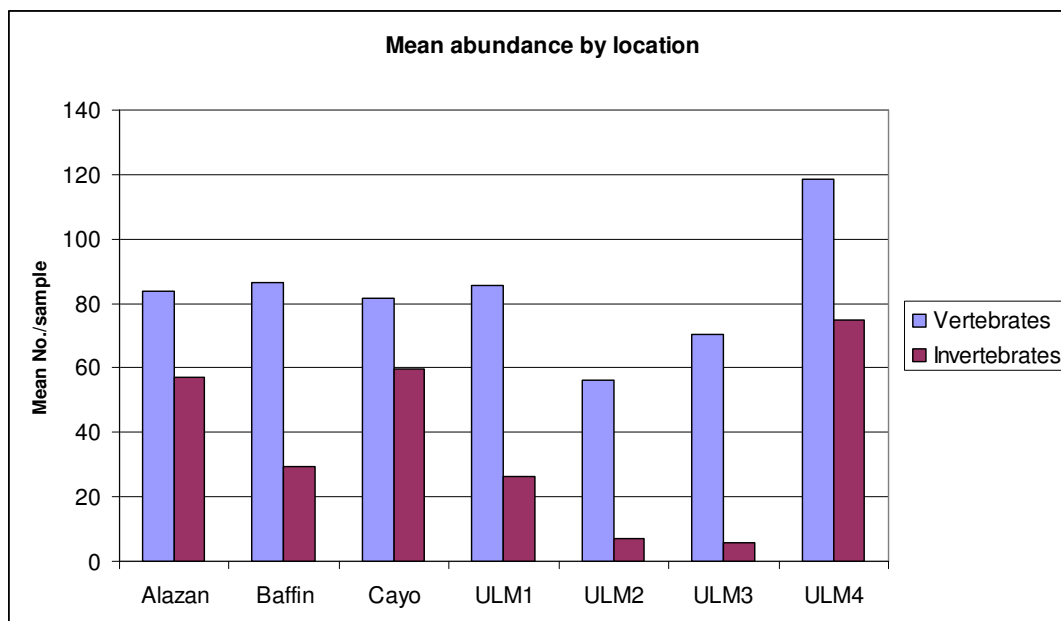


Figure 8.—Mean annual catch per unit effort (mean number per sample) in bag seine samples for each location in the Upper Laguna Madre, 1985-2004.

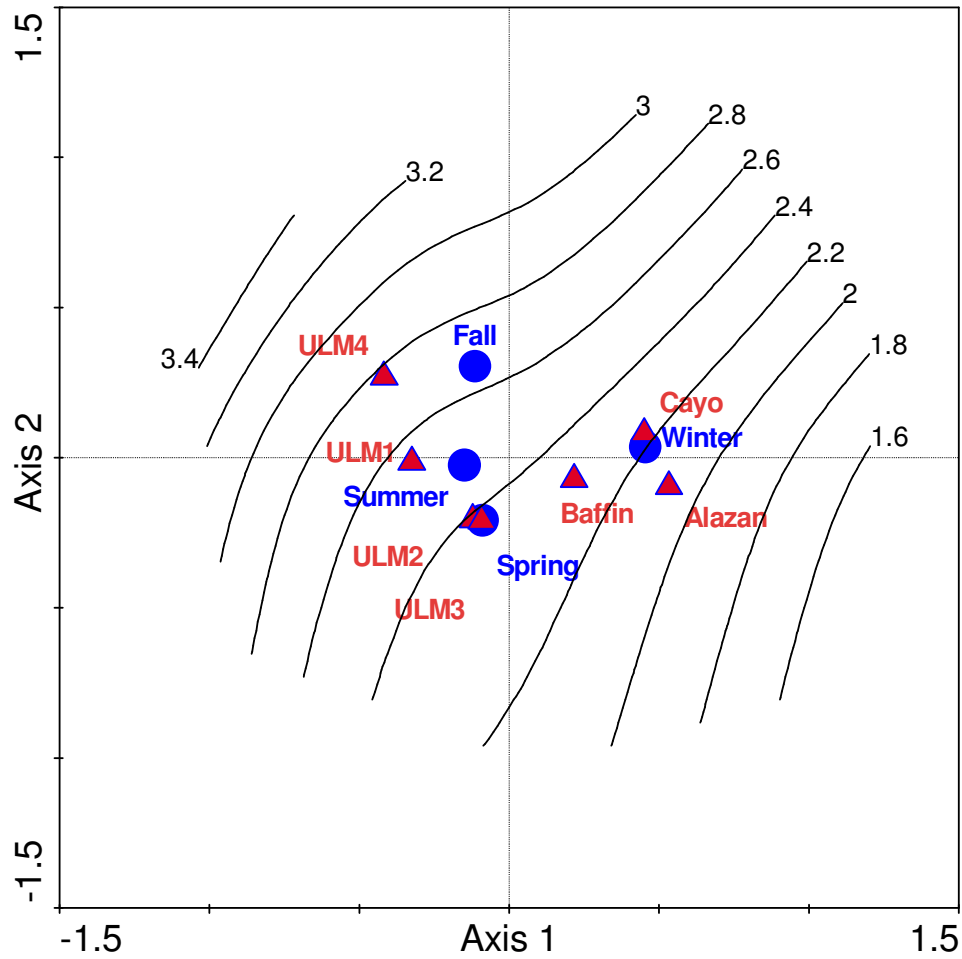


Figure 9.—Contour plot for N2 species diversity and nominal variables location (red triangles) and season (blue circles) for the first two CCA axes. The contour lines represent levels of species diversity as calculated by regression (Generalized additive model).

For the categorical variable “season” on axes 1 and 2, winter samples differed almost completely in species composition from the other seasons. Spring and fall were likewise very different, while each shared some species in common with summer. As shown in the DCA plot, most of the species collected in winter were resident species such as *Cyprinodon variegatus* (CV- Figure 5A), *Lucania parva* (LP), and the other two killifish, *Fundulus grandis* (FG) and *Fundulus similis* (FS). Figure 10 shows mean seasonal abundances. Species diversity for spring, summer and fall was similar (Figure 9), while winter had the lowest species diversity.

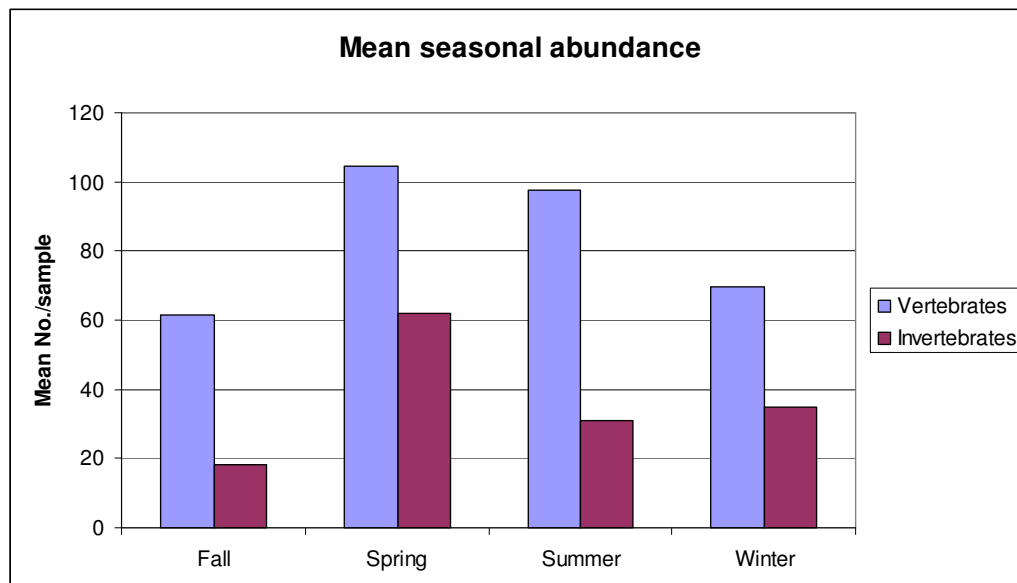


Figure 10.—Mean CPUE (mean number of individuals per sample) in bag seine samples by seasons for the Upper Laguna Madre, 1985-2004.

6.3 VARIANCE PARTITIONING

Table 7 lists the environmental variables in the order of their inclusion in the model, the additional variation explained by its inclusion (λ -A), the P-value of the Monte Carlo permutation test and the test statistic (F-value). A variable contributed significant additional variance to the model if its P-value was less than 0.05. From the table, all of the variables were significant except for the variable *Halodule*. All except *Halodule* were tested for the amount of variability explained, using a partial CCA.

The amount of variability in species abundance explained by all the environmental variables included in the model was 14%. Most of the variability (86%) was unexplained. The temporal component explained the greatest amount of variation (Table 8), followed by the spatial component. The environmental component explained the least amount of variation in the data set. The greatest amount of overlap was between the temporal component and the environmental component (1.5%). This was actually larger than the pure environmental component.

Table 7.—The explanatory variables in order of their inclusion in the final CCA model of species relative abundances among samples from Upper Laguna Madre, 1985-2004. The other columns are the percentage of additional variation explained by each (Lambda-A), the P-value of the Monte Carlo test (significance level < 0.05) and the F-statistic.

<i>Conditional Effects</i>				
Variable	Var.N	LambdaA	P	F
ULM4	15	0.090	0.002	71.42
Distance	7	0.090	0.002	68.46
Daylengt	2	0.090	0.002	66.73
Fall	5	0.070	0.002	63.17
Spring	3	0.050	0.002	40.1
Salinity	10	0.050	0.002	36.46
Alazan	17	0.030	0.002	24.41
Cayo	18	0.020	0.002	20.9
2003	40	0.020	0.002	16
1990	27	0.020	0.002	15.48
DO	9	0.010	0.002	12.85
2001	38	0.020	0.002	12.29
Baffin	16	0.010	0.002	11.42
ULM1	12	0.020	0.002	10.81
1991	28	0.010	0.002	10.11
2000	37	0.010	0.002	9.24
Temp	8	0.010	0.002	8.55
Halophil	20	0.010	0.002	7.98
1988	25	0.010	0.002	7.51
1993	30	0.010	0.002	7.77
1994	31	0.010	0.002	9.52
1999	36	0.010	0.002	6.79
Summer	4	0.000	0.002	6.09
Algae	19	0.010	0.002	5.84
1985	22	0.010	0.002	6.24
1989	26	0.000	0.002	5.75
1997	34	0.010	0.002	5.72
2002	39	0.010	0.002	5.48
ULM2	13	0.000	0.002	4.13
1996	33	0.010	0.002	3.92
1995	32	0.000	0.002	4.06
1992	29	0.000	0.002	3.96
Turbidit	11	0.010	0.006	3.56
1987	24	0.000	0.002	3.05
Delta_da	1	0.000	0.024	2.24
1986	23	0.010	0.002	2.95
1998	35	0.000	0.002	2.67
Halodule	21	0.000	0.13	1.54

Table 8.—Summary of the variation in species abundance among bag seine samples from Upper Laguna Madre, 1985-2004, partitioned into three main components (spatial, temporal and environmental) and all possible shared components. The eigenvalue measures the strength of the species-environment relationship and is the sum of all canonical eigenvalues for each CCA run. The explained variation is calculated as a percentage of the total eigenvalue for all canonical axes in the complete CCA (5.269).

Component	Eigenvalue	Explained Variation (%)
Temporal	.301	5.70
Spatial	.222	4.20
Environmental	.055	1.00
Shared Temporal-spatial	.014	0.26
Shared Temporal-environmental	.114	1.50
Shared Spatial-environmental	.028	0.53
Shared Spatial-temporal-environmental	.004	0.07
Total Explained Variation	.738	14.00

7. DISCUSSION

The DCA results demonstrated the high beta diversity in the data set. Whittaker (1972) defined beta diversity as the change in communities along a habitat or environmental gradient. Since both of the first two axes in the DCA exceeded 4 SD, the results showed complete species turnover along two dimensions: seasonally and by location within the bay system. This was further confirmed by the variance partitioning procedure of CCA in which temporal and spatial variables accounted for most of the total explainable variation in the data set. Temporal variables were correlated somewhat with the environmental variables; particularly salinity and temperature (Figure 5B and Table 8- TE). Some collinearity between variables is expected because the highest temperatures, for example, usually occur in summer or fall and the coolest temperatures occur in winter. Often, highest salinities in the Laguna Madre occur in the summer, when evaporation is highest.

The peak spawning season for many estuary-dependent species along the Gulf coast is from early spring through early fall. After a period of growth, ranging from a few days to a few weeks, juveniles of those species then become vulnerable to bag seines. For example, the peak spawning season for spotted seatrout is from May through October and they will generally begin appearing as small juveniles in bag seines in June. Catches in bag seines are therefore driven mainly by seasonal availability of these species. The presence of penaeid shrimps in bag seines is driven by the seasonal availability of juveniles. For example, *Farfantepenaeus aztecus* (brown shrimp) is much

more common in spring than at other times of the year; whereas, *F. duorarum* (pink shrimp) and *Litopenaeus setiferus* (white shrimp) are more common in fall. Brown shrimp spawn in the spring; whereas, the other species spawn in summer and fall. Other studies have found similar seasonal trends for abundance (Rakocinski et al. 1996; Akin et al. 2003). Resident species are constantly available to be captured but may be more susceptible to capture in cooler months. *Cyprinodon variegatus*, the sheepshead minnow, was the most commonly caught organism in the bag seines (present in 67% of samples). This species is highly tolerant of cooler and more saline conditions. It was often found in samples with low occurrences of other species. Its ubiquity probably explains why it has had no apparent strong relationship with any of the explanatory variables. The next most abundant species, *Menidia* spp. occurred in 57% of the samples and showed a similar lack of a relationship with any of the explanatory variables. The other resident species are also more tolerant of harsh conditions and their relative abundances are expected to be greater compared to other species during those seasons, years and locations when conditions are harsher. They tolerate both higher and lower temperatures than many of the estuary-dependent species such as spotted seatrout or red drum. As was expected, spotted seatrout showed a stronger relationship with fall than with any other season, with peaks from May to October (Pattillo et al. 1997), reflecting their growth (therefore increased catchability in nets with standard mesh sizes) after spawning throughout the warmer months.

There was no strong overall annual trend. The years 1990-1997 had higher catch rates than the other years in the data set (Figure 7), especially for the finfish. Some of

these years coincided with periods of low-salinity, in particular 1992-1995. Because the environmental component of the variation was relatively small (1%), salinity is unlikely to be a singular factor explaining the high catch rates for those years. It is possible that the average catch rate may have been driven by one or a few species in those years. The year 1990 in particular was driven by catch rates for black drum, which were the highest on record. Black drum are the most abundant large sciaenid and a very important part of the commercial fishery on the Texas coast (Culbertson et al. 2004). The overall catch rate for fish in 1990 was the highest of all the years (Figure 7). The increase in juvenile fish in bag seines may be due to a reduction in the number of predatory finfish during the freezes of 1989. The freezes (one in February and one in December) killed many adult predators such as spotted seatrout (Weixelman et al. 1992; McEachron et al. 1994) resulting in lower catch rates and landings in the recreational fishery in 1990. Recreational catch rates for spotted seatrout, a major predator on other fish, declined by more than 50% coastwide from 1989 to 1990 (Weixelman et al. 1992). Catch rates for red drum and black drum also declined during the same period (Green and Campbell 2005). Although black drum juvenile catch rates were the highest on record, catches for red drum and spotted seatrout in bag seines were much lower in 1990 (Figure 5). The decline in juveniles for those species may be due to the death of mature adults during the freezes. Red drum and black drum killed in December of 1989 were larger than those killed during the February 1989 freeze (McEachron et al. 1994). It is possible that the reduction in predators may have allowed juveniles of many other species to survive in higher numbers in 1990.

Location was the second most important factor in explaining the variability in the species assemblage data. ULM4 (the southern-most portion of the upper Laguna Madre) had higher mean abundance (Figure 9) and slightly higher mean species diversity (Figure 10) than the other areas. Many sample sites in ULM4 are along the edges of the Intracoastal Waterway (ICWW). They are somewhat deeper than other areas in the Laguna Madre and tend to be the center of high penaeid shrimp abundance for the Upper Laguna Madre (Fig 5A). Water circulates between the upper and lower Laguna through the ICWW (Simmons, 1957) and circulation patterns may allow larval fish and invertebrates to enter the Land Cut area, where they settle onto the substrate. Baffin and Alazan Bays have different species assemblages than does the upper Laguna Madre. Black drum in particular are much more numerous in these areas than in the rest of the bay system, and accounted for much of the structural differences in assemblages among those areas (Fig 5A and B). The middle areas (ULM2 and ULM3) of the Laguna had the lowest abundances for most species. Many of the sites in this area are on the Padre Island shoreline. These sites are very shallow (< 0.3 m) and are mostly bare sand habitats, which tend to have lower fish abundances than vegetated areas (Rozas and Minello 1998).

CCA analyses typically account for only a small fraction of total variation. This may be due in part to the highly variable nature of these the data analyzed (Lepš and Šmilauer 2003). Some of this unexplained variation may be due to biotic interactions such as competition or predation (Martino and Able 2003). The variability in species abundances that was explained by measured environmental variables in this study

appears rather small (14%), but actually accounted for a majority (67%) of the variation identified in the two dominant (spatial and temporal) trends in the indirect (CCA) gradient analysis that is driven by species abundances alone. Abundance data are highly variable, often contain many zero values, and are subject to 'noisy' or stochastic fluctuations that may not be readily explained by the kind of information collected in typical sampling programs. Noisy environmental data may also influence CCA and give a misleadingly high correlation, especially with regards to the species-environment correlation (McCune 1997). Polynomial distortion caused by the transformation used to make the axes orthogonal to each other may also inflate the eigenvalues for axes other than the first one, increasing the value of the "total inertia" used in the variance partitioning procedure. Thus, much of the "unexplained" variation (86% in this study) may simply be due to a lack of statistical fit to the model (Økland 1999). Other factors such as tides or water level were not included in this study. Although diurnal tides generally have low amplitude, there are semi-annual tides that account for greater fluctuations in water level (Smith 1978) and these may have an influence on species distributions.

In addition to noise in both the species and environmental data, there may be a time lag between environmental factors and species abundances. Low temperatures may kill fish outright but also affect the number of adults left to spawn in subsequent years, resulting in fewer juveniles available to be captured in years following freeze events (McEachron et al. 1994; Martinez-Andrade et al. 2005). Changes in fishing regulations

or increases in fishing pressure on adults may also affect the availability of juveniles for those species that are part of a recreational or commercial fishery.

Because the TPWD sampling program is designed to examine relative species abundances among whole bay systems and coast wide, differences within a system such as the upper Laguna Madre are more difficult to detect. Samples are not equally distributed among locations, seasons and years. A great deal also depends on which variables were included in the analysis. For example, the only information recorded about vegetation was the density code for the type of vegetation found in the bag seine, which may or may not bear a relationship to what type of vegetation was found on the substrate. The most common type of seagrass in the Laguna Madre is *Halodule beaudettei* (shoal grass) which was not a significant environmental factor in this study (Table 7), despite its ubiquity in the Laguna. Much of the seagrass collected in the bag seines is dead seagrass floating on the water. Because of the prevailing southeast winds, much of the dead seagrass is pushed into areas which may not contain any living shoal grass. Thus, the density code may not reflect the actual amount of seagrass at a given station. For future sampling programs, a more quantitative assessment of the substrate, including the amount and type of seagrasses would be preferable.

8. CONCLUSIONS

Despite the harsh and fluctuating conditions, the Upper Laguna Madre is a highly productive ecosystem. Although it is not considered a typical estuary due to its hypersaline conditions and lack of freshwater inflows, salinity is not the primary influence on species abundance and diversity. In this study, much of the variability in species abundance was due to the spawning patterns of estuary-dependent species, most of which spawn in the spring and summer months, leading to higher abundances from spring through fall.

Secondarily, location within the bay system also influenced patterns of species abundances. Some species such as black drum are primarily found in the western portions of the Upper Laguna Madre (Baffin and Alazan Bays). Areas closest to sources of larvae for those species that spawn in the offshore Gulf (i.e. penaeid shrimps) had higher abundances of those species.

Since 1977, Texas Parks and Wildlife has been conducting a variety of fishery-independent resource monitoring studies designed to detect trends in species abundance and determine the effectiveness of fishery regulations. The results from this study of a portion of those resource monitoring efforts may help to guide fishery managers into further refining those efforts.

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VITA

Name: Amy Beth Larimer

Address: Texas Parks and Wildlife Department
6300 Ocean Drive, Suite 2500
Corpus Christi, TX 78412

Email Address amy.larimer2@gmail.com

Education: B.S., Marine Biology, Troy State University, 1990.