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## The effects of a freshwater diversion of nekton species biomass distributions, food web pathways, and community structure in a Louisiana estuary

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**THE EFFECTS OF A FRESHWATER DIVERSION ON NEKTON SPECIES BIOMASS  
DISTRIBUTIONS, FOOD WEB PATHWAYS, AND COMMUNITY STRUCTURE IN A  
LOUISIANA ESTUARY**

A Dissertation

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

in

The Department of Oceanography and Coastal Sciences

by  
Kim de Mutsert  
M.S., University of Amsterdam, 2003  
May 2010

## **DEDICATION**

To my parents, Gerrie and Charles de Mutsert, who have always encouraged me with their enthusiasm for the marine world.

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## ABSTRACT

A current method to restore Louisiana's estuaries includes reintroducing freshwater and sediments to wetlands that are hydrologically isolated from the Mississippi River due to the construction of levees. In this dissertation, I examined effects of the second largest freshwater diversion in Louisiana, the Caernarvon Freshwater Diversion (CFD), on estuarine nekton in Breton Sound. Before focusing on Breton Sound, I examined the status of nekton communities in the northern Gulf of Mexico (GOM), and Louisiana wetlands in particular, using the mean trophic level index (MTLI). I demonstrated that commercial targeting caused the previously reported low and declining MTLI from the GOM. Evaluation of Breton Sound alone showed an increasing MTLI, which is possibly a positive effect of hydrological restoration. With a Before-After-Control-Impact study, I demonstrated that nekton species biomass distributions (SBD) changed significantly after the opening of the CFD in 1991. The biomass of selected economically or ecologically important species showed an increase relative to the control (*Micropterus salmoides*, *Micropogonias undulatus*, *Brevoortia patronus*, *Farfantepenaeus aztecus* and *Litopenaeus setiferus*), one was not affected (*Cynoscion nebulosus*). In addition, nekton species richness, abundance and the proportion of smaller individuals increased, indicating increased nursery function. I identified salinity as the main environmental variable separating SBDs among study sites due to freshwater inflow, although seasonal variation had the greatest effect on SBD. The CFD did not change dissolved oxygen or turbidity to the extent that it had an effect on nekton in the areas examined. Applying stable isotope techniques, I identified a positive effect of freshwater inflow on trophic diversity and niche breadth of the consumer community, and on the relative contribution of particulate organic matter in the food web, resulting in energy density increases in nekton species. Finally, I created an ecosystem model of Breton Sound, which I used to simulate changes in SBD under different salinity scenarios. This

model can be used to evaluate future restoration projects. These various analyses, including the model predictions, revealed only neutral or positive effects of the CFD as currently operated on nekton communities in Breton Sound.



## GENERAL INTRODUCTION

Louisiana coastal wetlands are part of the Mississippi River deltaic ecosystem, which is one of the largest (~25,000 km<sup>2</sup>) coastal ecosystems in North America (Day et al. 2007; 2009). Over the last hundred years, a 25 % decrease in total coastal wetland area has been observed in Louisiana alone (Britsch and Dunbar 1993; Barras et al. 1994; Day et al. 2009). Because these wetlands serve as nursery grounds for an estimated 85-98 % of the commercially- and recreationally-important fisheries of the US Gulf of Mexico (McHugh 1984), loss of these wetland habitats could have detrimental effects on fishery production. While habitat degradation and wetland loss is ongoing, restoration projects to remit or reduce these losses are being developed and employed. The goal of these restoration efforts is to restore the ecosystem to a state that more closely resembles its unaltered condition (NRC 1992), and to reinstate natural ecosystem functions (Callaway 2005). Among the factors that contribute to wetland loss, hydrological isolation of coastal areas from the Mississippi River through the construction of levees is perhaps the most important, depriving wetlands of freshwater and sediment input.

Throughout the Holocene, the main stem of the Mississippi River has made six major channel switches that in each case formed delta lobes at the rivers terminus, creating what is now the Louisiana coastal area (Roberts 1997; Day et al. 2007). Learning from these historical processes, one practical and sustainable solution to wetland loss could be the implementation of river diversions to stimulate sediment deposition. Recently, river diversions have become a central focus in restoration plans for coastal Louisiana (Boesch et al. 2006; Costanza et al. 2006; Day et al. 2007; CPRA 2007). Benefits elucidated in previous studies of reintroducing Mississippi River water to hydrologically isolated estuaries include: 1) land gain through sediment deposition; 2) increased plant growth as a result of nutrient inputs; 3) reduced subsidence and plant mortality by counteracting saltwater intrusion; 4) increased precipitation of

toxic sulfide through increased iron concentrations; and 5) increased denitrification potential due to reduced salinities (McKee and Mendelssohn 1989; Rysgaard et al. 1999; Mendelssohn and Morris 2000; DeLaune and Pezeshki 2003; Day et al. 2007).

However, the linkage between wetlands, their restoration, and fisheries productivity and diversity is complex and remains unclear (Cowan et al. 2008). Although the use by nekton of wetland habitats are frequently given as justification for their protection and restoration, wetland restoration projects are seldom assessed for their fishery implications (Rozas et al. 2005a; Reed et al. 2007). In this dissertation I aim to examine the general status of nekton communities in the northern Gulf of Mexico (GOM) and in Louisiana estuaries, as well as the effects of a Mississippi River diversion on nekton communities in particular. The diversion central to this study is the Caernarvon Freshwater Diversion (CFD), currently the second largest diversion in the Mississippi Delta. It was originally constructed in 1991 to stimulate the oyster fishery in Breton Sound and the Biloxi Marshes (Chatry et al. 1983); more recently, the diversion is operated as a restoration tool to counteract salt-water intrusion and restore coastal wetlands by reintroducing freshwater, sediments, and nutrients into the Breton Sound estuary.

It is important to evaluate the effect of the CFD on nekton communities to ensure that it is beneficial, or at least satisfies the minimum biological criteria “to do no harm”. Changes in nekton communities can be expected, mainly because salinity will directly be affected by the input of freshwater, and salinity exerts among the strongest of the physical forces on the structure of aquatic nekton communities (Akin et al. 2003). Additionally, food sources such as particulate organic matter (POM) may become more available as the diversion transports inorganic nutrients and POM through the estuary. This can potentially change food web dynamics and species biomass distributions (SBD) of consumers (Wissel and Fry 2005). The increased nutrient load can have both positive and negative effects on estuarine consumers; a well-described positive

effect of increased nutrient inputs is a bottom-up increase in consumer biomass (Iverson 1990; Nixon and Buckley 2002). Controversy about diverting Mississippi River water includes predictions of eutrophication of the estuary (Turner and Rabalais 1991; but also read Lane et al. 1999), and the extirpation of recreationally and commercially important high salinity nekton species like spotted seatrout (*Cynoscion nebulosus*; Serafy et al. 1997; USACOE 2004) and brown shrimp (*Farfantepenaeus aztecus*; USACOE 2004; Rozas et al. 2005b).

In the first chapter I assess the state of nekton communities in the GOM and in Louisiana estuaries using the mean trophic level index (Pauly et al. 1998), and address problems with its application in previous studies (Pauly and Palomares 2005; De Mutsert et al. 2008). In the second chapter I direct my focus to the Breton Sound estuary and examine effects of the CFD on the Breton Sound nekton community through a Before-After-Control-Impact study. In the third chapter I describe the effects of environmental variables on nekton SBD in the Breton Sound and Fourleague Bay estuaries, and how freshwater input affects these relationships. Fourleague Bay is an estuary that receives freshwater input from the Atchafalaya River and serves as the reference area in this study. In the fourth chapter I investigate the changes in trophic structure, food web pathways, and energy densities in nekton communities as a result of freshwater inflow through the CFD by using stable isotope and caloric content analyses. In the fifth and final chapter I develop an ecosystem model of Breton Sound before the opening of the CFD, constructed with Ecopath with Ecosim (Christensen et al. 2004; 2009); introduce a new application of Ecosim that allows the simulation of nekton response to salinity changes; and simulate effects of three salinity scenarios on SBD as a result of freshwater inflow through the CFD.

Overall, I aim to increase knowledge of the current status of estuarine nekton communities in Louisiana, and the effects of freshwater diversions on these communities. This knowledge should serve as a resource or tool for implementing diversions in restoration projects.

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## **CHAPTER 1**

### **THE USE OF THE MEAN TROPHIC LEVEL INDEX TO ASSESS THE STATE OF NEKTON COMMUNITIES IN THE GULF OF MEXICO AND LOUISIANA ESTUARIES: ARE WE ‘FISHING UP THE FOOD WEB?’**

#### **INTRODUCTION**

In recent years, there has been a call for ecosystem-based management, which has become evident in the fields of fisheries management, as well as coastal sciences (Pikitch et al. 2005; Boesch 2006). The movement towards an ecosystem-based approach is stimulating the development and use of indices of ecosystem status (Chuenpagdee et al. 2003; Link 2005; NRC 2006; Piet et al. 2008; Salas et al. 2008; Thain et al. 2008; Rochet et al. 2008). Within fisheries science, a frequently used and oft-cited indicator of marine ecosystem status is the mean trophic level index (MTLI; Pauly et al. 1998).

The MTLI represents a biomass-weighted average of the trophic level of fisheries landings per year, calculated by using a trophic level assigned to each landed species based upon its position in a food web (Pauly et al. 1998). A food web can consist of species with trophic levels between 1 (primary producers) and 5, with 5 being assigned rarely to only the highest apex predators. To deal with mixed diets, Odum and Heald (1975) derived a method to calculate trophic levels with a decimal component based upon diet. Trophic levels based upon this method of calculation are used in this and all other studies employing the MTLI, and have been published for a large number of species on FishBase ([www.fishbase.org](http://www.fishbase.org)). The calculation of these fractional trophic levels is shown in the methods section. It is generally assumed that trends in the MTLI over time reflect changes in an ecosystem's food web structure (Pauly et al. 1998; Essington et al. 2006).

The use of the MTLI began with the pioneering work of Pauly and co-workers (1998), who demonstrated downward trends in the mean trophic level of fisheries landings from a variety

of marine ecosystems. They argued that this was an indication of serial overfishing and depletion of higher trophic levels in the ecosystem. Their initial findings have been repeated through subsequent and similar (Salas et al. 2008) analyses from many additional locations (Pauly et al. 2000; Pauly et al. 2001; Pauly and Palomares 2005). Most studies agreed with previous findings, while others found alternate explanations for the downward trend of the MTLI (Caddy et al. 1998; Essington et al. 2006). For example, Essington et al. (2006) showed that the downward trend in many of the 64 Large Marine Ecosystems (LMEs) could be explained by ‘serial addition’ of lower trophic level, but high biomass species, while higher trophic level species were still being caught. One obvious concern with all of these analyses is the use of landings data, complete with all of its inherent biases and gear selectivities (Essington et al. 2006; De Mutsert et al. 2008; Worm et al. 2009). While each study is meant to evaluate ecosystem status, landings data have frequently been shown to poorly reflect changes in nekton community structure in marine ecosystems (Lucena and O’Brien 2001; Gallaway et al. 2003; Beare et al. 2005; Dickey-Collas et al. 2007; Cowan et al. 2008; De Mutsert et al. 2008; Mesnil et al. 2009).

I use the Gulf of Mexico (GOM) as an example of an ecosystem that was deemed to have a much lower than typical MTLI (~2.3) of many of the LMEs to which this analysis has been applied (Pauly and Palomares 2005). Pauly and Palomares (2005) further argue that the low and declining MTLI for the GOM indicates a seriously degraded and altered food web, where top predators disappeared before the period of record (1950 – present) due to overfishing.

The analysis by Pauly and Palomares (2005) is based upon landings data from fisheries in a region (i.e., the GOM) that historically has been, and currently is, dominated by landings of menhaden and several shrimp species, which have low trophic levels (~2.2 and ~2.6 respectively). I hypothesize that the low GOM MTLI is driven by large landings of commercially targeted species of high-value, but low trophic level, instead of fishery induced changes in the



food web. The null hypothesis is that the GOM MTLI calculated with fisheries independent survey data does not differ in slope and intercept from the GOM MTLI calculated by Pauly and Palomares (2005).

In addition to the above hypothesis designed to compare my results with those of Pauly and Palomares (2005), I calculate the MTLI for two estuarine basins in the Louisiana deltaic ecosystem based upon biomass data of nekton species collected in a fisheries independent resource survey by state agency personnel. Breton Sound is a highly modified estuarine basin that has experienced rapid rates of subsidence and wetland loss, has suffered recent and significant disturbance by tropical storms, and is currently under the influence of the Caernarvon Freshwater Diversion (CFD; Day et al. 2000; 2007; 2009). The CFD is designed, in part, to mitigate wetland loss by locally redistributing Mississippi River water and sediment into the Breton Sound estuary (Lane et al. 1999; 2006). In contrast, Fourleague Bay is much less affected by human disturbance, has had less hurricane damage over the years, and experiences a natural freshwater flow regime from the Atchafalaya River (Van Heerden and Roberts 1980). My goal is to determine if the MTLI can detect differences when calculated for estuarine basins that are assumed to be near the end-points in the continuum of ecosystem health, or perhaps, at very different stages in the cycle of delta formation and decay (Roberts 1997). In these analyses, I compare trends in the MTLI over time, but also variability in the MTLI at the event scale, between basins to determine if temporal variation in the MTLI contains information about short-term changes in nekton community structure.

## **METHODS**

The commercial landings data used are published on the National Marine Fisheries Service (NMFS) website ([http://www.st.nmfs.gov/st1/commercial/landings/annual\\_landings.html](http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html)). Data are available

from 1950 to 2001. I excluded freshwater species that occur in the landings data that are not present in the areas of interest (e.g. carp, frogs), and landings not specified to genus. I calculated the MTLI with and without shrimp (*Farfantepenaeus aztecus*, *F. duorarum*, *Litopenaeus setiferus*, *Sicyonia brevirostris*, *Pleoticus robustus*, *Xiphopenaeus kroyeri*) and menhaden (*Brevoortia tyrannus*, *B. patronus*) for the US GOM and the Atlantic Ocean south of Chesapeake Bay, and the GOM alone. I chose to combine the commercial landings data from the GOM and the Atlantic south of Chesapeake Bay, in addition to calculating the MTLI for the GOM alone, making this analysis directly comparable to Pauly and Palomares (2005).

Longline data from the US GOM were collected by the NMFS Pascagoula laboratory (<http://www.nmfs.noaa.gov/>); data are available from 1995 till 2005. The estimates of shrimp bycatch in the GOM are derived from the SEAMAP (Southeast Area Monitoring and Assessment Program; <http://www.seamap.org/>) summer and fall groundfish resource surveys from 1987-2003, collected at stations on the shelf that are selected randomly from among a 10 km by 10 km statistical grid of the shelf. The SEAMAP surveys use fishing gears and tow durations that mimic standard practices by the shrimp industry. The SEAMAP data then are extrapolated based upon estimates of shrimp effort and location of fishing using Bayesian techniques to produce a spatially explicit annual bycatch estimate (Diamond 2003; Nichols 2004; Griffin and Paine 2010). The bycatch data from SEAMAP were reported in kg per trawling hour. I obtained the number of trawling hours per year, and calculated bycatch in kg per year (Griffin and Paine 2010).

Fisheries independent survey data have been collected by the Louisiana Department of Wildlife and Fisheries (<http://www.wlf.louisiana.gov/>) since 1966 in Louisiana estuaries (Figure 1.1) using a variety of gears (otter trawls, gill nets, beach seines and trammel nets). Surveys are ongoing, so I have used data over the period of record up to 2007. In the areas of interest in

Breton Sound and Fourleague Bay, for which I calculated the MTLI separately, surveys started in 1986.

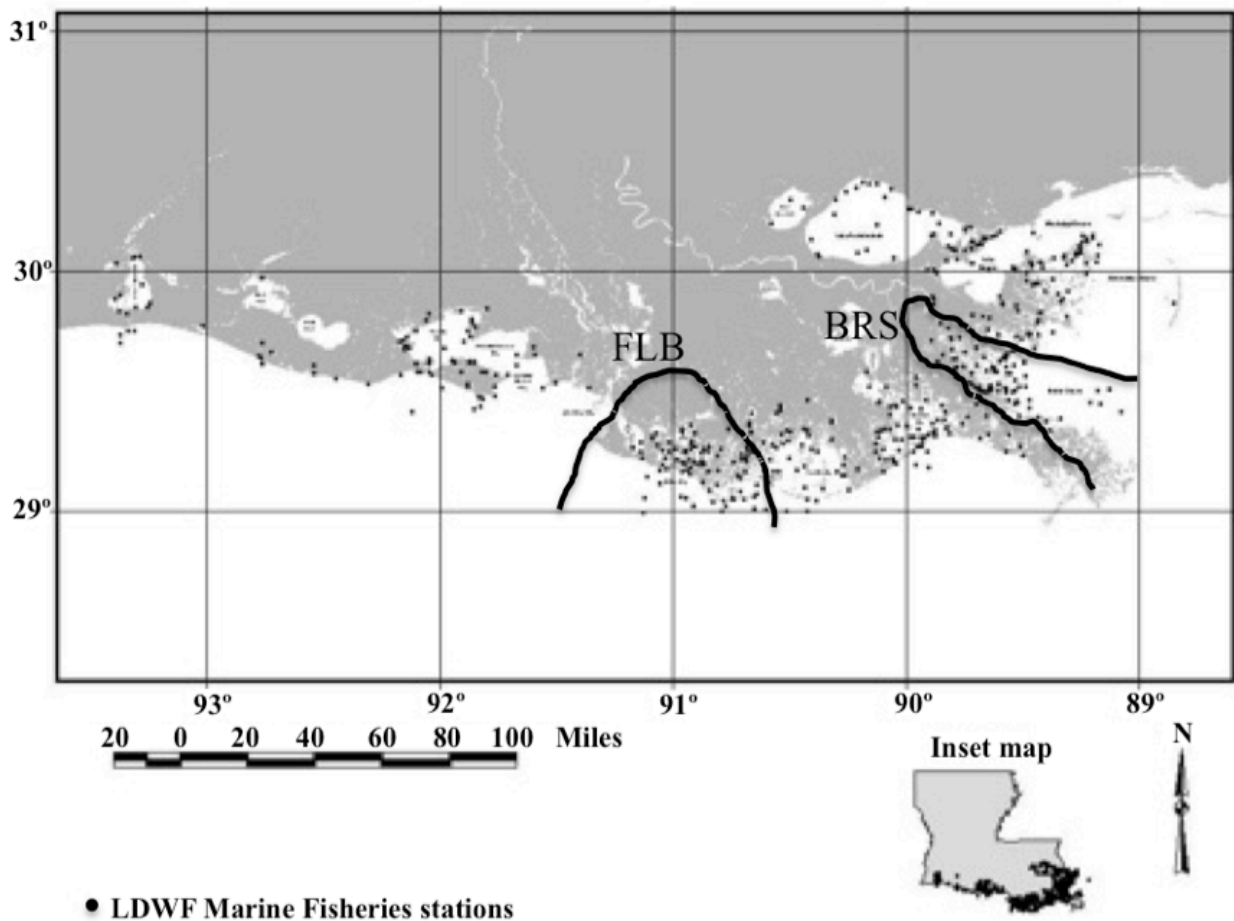


Figure 1.1. Coastal Louisiana. The sites where the Louisiana Department of Wildlife and Fisheries performs monthly surveys are indicated (•). All data collected at these sites are used to calculate the Louisiana survey MTLI, indicated in the graphs as ‘LA fisheries independent’. The Fourleague Bay (FLB) and Breton Sound (BRS) estuaries are indicated in the figure, sites within these boundaries are used to calculate the MTLI for each estuary respectively.

At each location, the surveys use replicated tows of 3.9 m otter trawls against the prevailing current (with 3 mm cod-end liner), replicated hauls of 15.2 m bag seines with 3 mm mesh, and replicated sets of 225 m long by 2.4 m high experimental gill nets with 5, 45 m panels consisting of mesh sizes (cm bar) of 2.5, 3.2, 3.8, 4.4 and 5.1 cm. Trammel nets used are 225 m long by 1.8 m tall, and have three walls. The inner wall is constructed of 4.1 cm bar mesh, and the

two outer walls are constructed of 15.2 cm bar. The trammel net is fished by setting it parallel to shore. It is fished as a strike net by running in concentric, ever tightening circles around it with a power-boat. Only otter trawls, gills nets and trammel nets are used at stations on the shallow shelf. If weather precludes use of any gear at any station, sampling is rescheduled. All fish and shellfish collected are identified, measured (nearest mm) and weighed (nearest 0.1 g).

The Louisiana survey methods have remained unchanged over the period of record because of their value as a relative measure of the abundance of species under state management. Data are used in stock assessments for recreationally and commercially important finfish species, and for determining the opening day of shrimp fishing seasons. Because each gear is designed to sample different members of the fish and shellfish community with respect to size and habitat affinity, I simply combined weights over all gears over all stations for each species to create the fishery-independent MTLI, calculating the index as described below. The fisheries independent survey data were collected monthly in Louisiana estuaries and on the shallow shelf at the sites indicated in Figure 1.1.

As in previous work (e.g., Pauly et al. 1998; Pauly and Palomares 2005; De Mutsert et al. 2008), FishBase ([www.fishbase.org](http://www.fishbase.org)) was used to obtain the trophic level of each species reported in the fisheries landings, bycatch data and fisheries independent survey data.

The equation to calculate a fractional trophic level is (Odum and Heald 1975):

$$TL_i = 1 + \sum_j (TL_j * DC_{ij}) \quad (\text{Eq. 1.1})$$

Where  $TL_i$  = the trophic level of species  $i$ ,  $TL_j$  = the fractional trophic level of prey  $j$  and  $DC_{ij}$  = the proportion of prey  $j$  in the diet of  $i$ .

To calculate the MTLI, I used the following equation (Pauly and Palomares 2005):

$$TL_y = \sum_i(TL_i * Y_{iy}) / Y_y \quad (\text{Eq. 1.2})$$

Where  $TL_y$  = the mean trophic level of an area in year  $y$ ,  $Y_{iy}$  = the landings (in weight) of species  $i$  in year  $y$  and  $Y_y$  = the total landings in year  $y$ . Trophic levels in all figures are shown on a scale from 1 to 5, with 1 representing primary producers and 5 the apex predators. To test the significance of MTLI slopes linear regressions were used, and for differences among slopes and intercepts DVRs (dummy variable regressions;  $\alpha = 0.05$ ) were used in SAS software (2005). The residuals of each regression model were normally distributed, so no transformations on data were necessary.

## **RESULTS AND DISCUSSION**

Total fisheries landings by weight in the GOM are dominated by shrimp and especially Gulf menhaden, with these two taxa contributing, on average, 72% of the total biomass. In addition, these two taxa generate 62% of the total value of all US GOM fisheries, thus explaining the high level of targeting of these taxa (Figure 1.2A-B).

The effects of targeting are evident in the MTLI for the GOM commercial landings data, with and without menhaden and shrimp, when considering both the initial estimate of the MTLI (Y-axis intercepts) and the time-dependency of the index (slope of the line).

### **Initial Estimates of the Gulf of Mexico MTLI (Y-Axis Intercepts)**

When menhaden and shrimp are included in the GOM calculations using commercial landings data, the Y-axis intercept (~2.4, Figure 1.3) is similar to results in Pauly and Palomares (2005). This is true whether or not I used combined landings from the US GOM and south Atlantic (defined as ‘USA only’), or from the US GOM alone (‘GOM’). The MTLI derived

from ‘USA only’ and from the ‘GOM’ are almost identical, differing by less than 3% in any year (Figure 1.3).

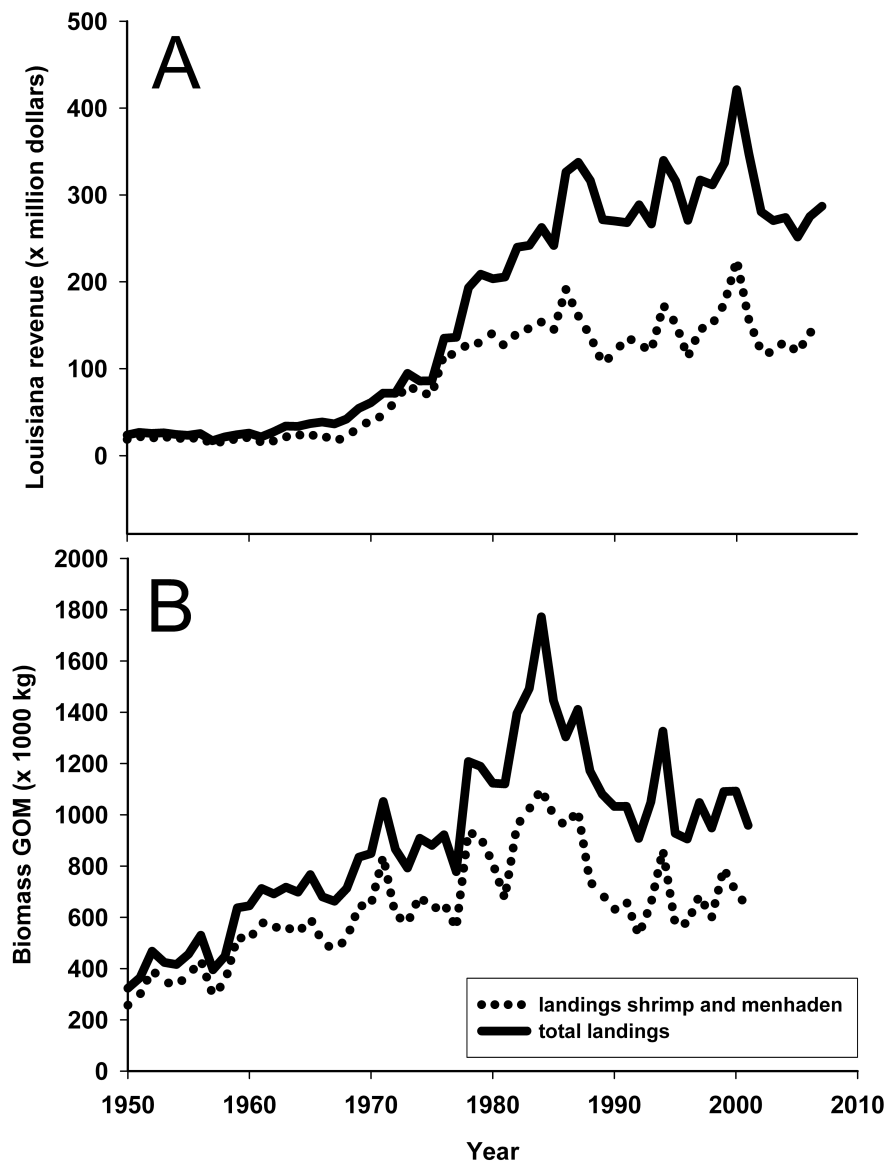


Figure 1.2. A comparison of A) Louisiana revenue (x million dollars), and B) landed biomass (x 1000 kg) of total fisheries landings (solid line), and shrimp and menhaden landings only (dotted line) in the Gulf of Mexico.

However, when I excluded menhaden and shrimp from the commercial landings data, the MTLI calculated for ‘GOM’ and ‘USA only’ have an initial MTLI (intercept) that is significantly

higher ( $p < 0.0001$ ) than when these taxa are included, and similar to other regions where the MTLI has been calculated ( $\sim 3.0$ ; Pauly et al. 2000; Pauly et al. 2001; Essington et al. 2006).

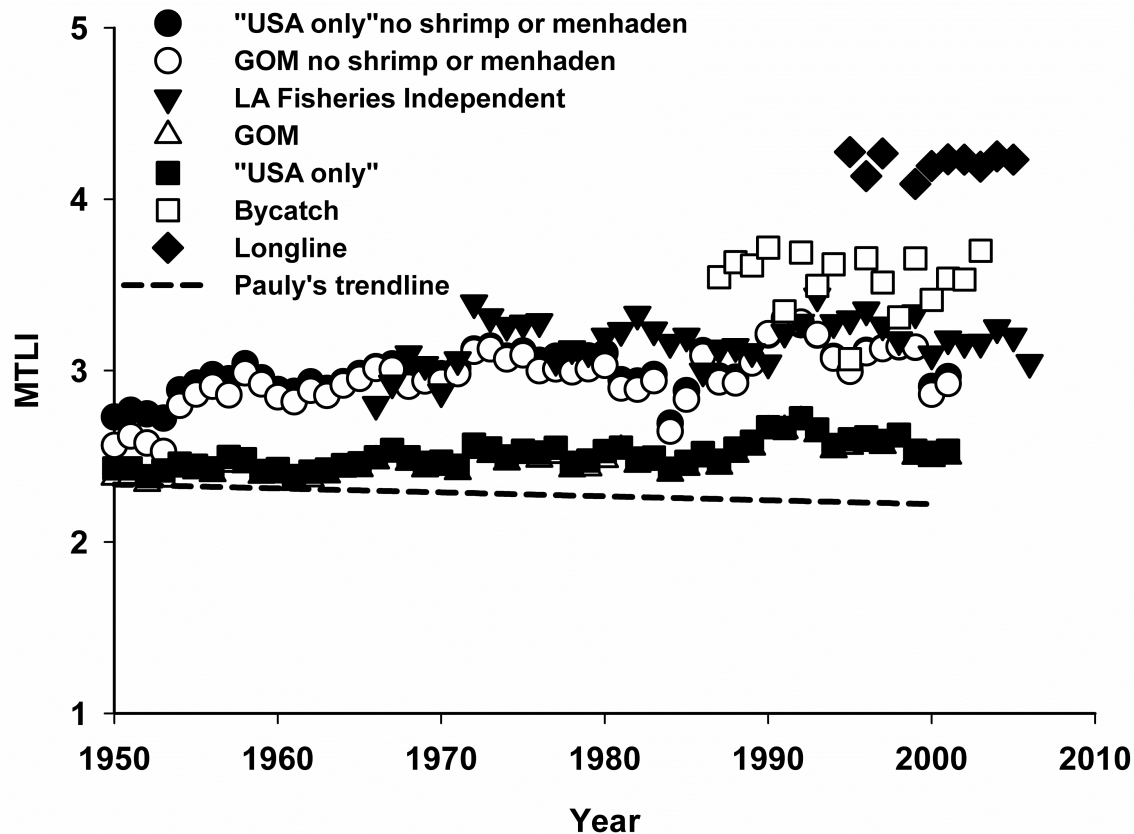


Figure 1.3. Annual mean trophic level indices in the Gulf of Mexico between 1950 to 2007. “USA only” is the northern Gulf of Mexico and the Atlantic south of Chesapeake Bay. GOM is the Gulf of Mexico alone. Both MTLI’s are calculated without shrimp and menhaden as well and included in the figure. The Louisiana Survey MTLI (LA Fisheries independent) overlaps with the ones without shrimp and menhaden. Bycatch and longline data are shown in the figure with the highest MTLI’s. The dashed line is the GOM MTLI as calculated by Pauly and Palomares (2005).

To further demonstrate the effects of targeting on MTLI intercepts, the longline data were similarly analyzed. Analyses of the GOM longline survey data produce a significantly higher MTLI than the GOM commercial landings, or any of the other GOM time series I evaluated ( $p < 0.0001$ , Figure 1.3). This clearly demonstrates that the MTLI is sensitive to targeting and gear selectivities, shown here because longline gear targets higher trophic level species (Bjorndal 1988;

Lokkeborg and Bjordal 1992). While I do not believe that the high MTLI derived from longline data alone is a true representation of the fisheries ecosystem, it serves to point out a significant flaw in the index as it normally applied.

The MTLI derived from the Louisiana survey data closely resembles (intercepts  $p > 0.05$ ) that derived from commercial landings data after shrimp and menhaden are excluded, while it is significantly higher than the MTLI's derived from total commercial landings ('USA only' and 'GOM';  $p < 0.0001$ ). Under the assumption that survey data provide more accurate information on species biomass distribution than landings data (Beare et al. 2005; Mesnil et al. 2009; Griffin and Paine 2010), this demonstrates not only that commercial targeting of these species lowers the MTLI, but also that the MTLI derived from the commercial landings as used in Pauly and Palomares (2005) does not accurately portray the status of the fishery ecosystem in the GOM.

I recognize that the Louisiana survey data used here are based upon a smaller area (Louisiana only; Figure 1.1) than the commercial landings data, but I believe this comparison to be useful because ~75% of US GOM landings occur in Louisiana (NMFS 2007). Moreover, more than 50% of all U.S. fishery yields have historically been derived from estuarine or estuarine-dependent species (Houde and Rutherford 1993); the fraction is higher in the GOM (Vidal-Hernandez and Pauly 2004). The Louisiana surveys are performed at least monthly at more than 250 locations in estuaries and on the shallow shelf in the northern GOM (~ 4,000 collections per year; Figure 1.1) where shrimp and menhaden are abundant, and many of the higher trophic level species that appear in the commercial landings occur in high numbers as juveniles and adults. Still, to evaluate whether the smaller spatial scale of the Louisiana survey is causing an elevated MTLI compared to commercial landings, I calculated the MTLI based on bycatch in the GOM shrimp trawl fishery, which is prosecuted at a scale similar to the overall commercial fisheries (see Methods).



The bycatch derived MTLI is also significantly higher than the landings derived MTLI ( $p < 0.0001$ ), and even higher than the Louisiana survey data. This is likely attributable to the large number of species present in the bycatch, the higher number of high trophic level species in the open GOM as compared to estuaries, and the enormous effort ( $\sim 2 \times 10^5$  hours per year) expended to catch shrimp. Clearly, targeting influences these results (Hall 1996), but the composition of the bycatch is very diverse, being comprised of hundreds of species of fishes and invertebrates.

### **Time-dependency of the Gulf of Mexico MTLI (Slopes)**

For each of the data time series discussed above, I show the trendlines (linear regressions) of the GOM MTLI over time (Figure 1.4). Only the last 20+ years are shown to facilitate comparisons with the shorter time series. The calculations of the trendline for each time series, however, are based upon all years available for that time series.

In contrast to the findings of Pauly and Palomares (2005), I did not find declines over time in the MTLI in any of GOM time series. The commercial landings without shrimp and menhaden, and the Louisiana survey data have small but positive slopes ( $p < 0.0001$ ), while the slopes of the bycatch and longline MTLI's are not significantly different from zero ( $p > 0.05$ ). The 'USA only' and the 'GOM' (including shrimp and menhaden) indices based upon commercial landings have intercepts and positive slopes ( $p < 0.001$ ) that do not differ from one another ( $p > 0.05$  [slopes and intercepts],  $b=0.004 \text{ yr}^{-1}$ ,  $R^2=0.54$  for 'USA only' and 'GOM'). These results were unexpected.

However, similar attempts to reproduce declines in MTLI have failed in other areas, e.g., compare the graph for the Mediterranean and Black Sea in Pauly (1999) with the one provided by the European Environment Agency (2005; <http://dataservice.eea.europa.eu/atlas/viewdata/viewpub.asp?id=1848>); the MTLI calculated twice in the same area is declining only in Pauly (1999).

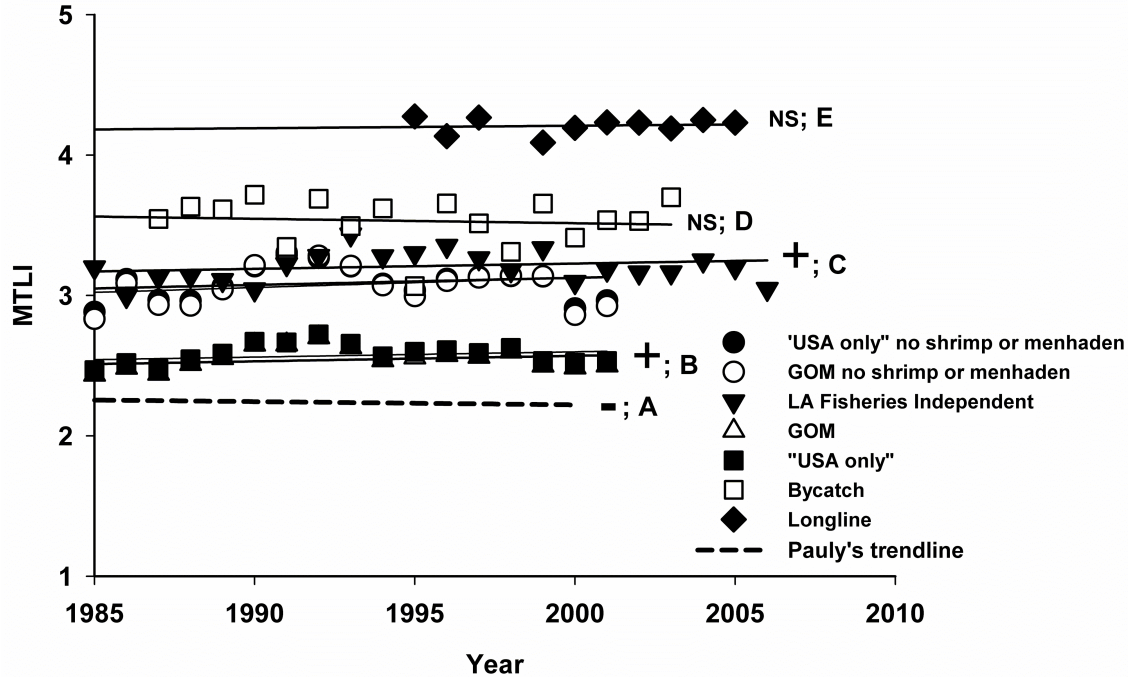


Figure 1.4. Detail of Figure 1.3 displaying the trend lines of each MTLI. All trend lines are based upon all data available for each index. Negative and positive slopes, or slopes not significantly different from zero are indicated with +, - or NS, respectively. The letters A-E indicate whether there is a significant difference between the slopes. Note that B is assigned to both the GOM and 'USA only' slopes, and C is assigned to the GOM and 'USA only' slopes without shrimp and menhaden, and the LA fisheries independent slope. Slopes with the same letter are not significantly different from one another.

Such discrepancies may be attributable to differences in landings data reported by different sources. Pauly and Palomares (2005) used data compiled by the Food and Agricultural Organization (FAO) that includes some landings from Mexico, whereas I used data reported by the NMFS. These data do not always agree. I chose to use the NMFS data because collection and management techniques are well described and based upon formal metadata guidelines (The Fisheries Information Network; <http://www.gsmfc.org/fin.html>) as recommend by the NRC

(2000), include data reported by state agencies for species not under federal jurisdiction, and are presumed to be the primary source of the FAO data.

Positive slopes in the trendlines are noteworthy, but may not imply that the health of the GOM fishery ecosystem is improving. When the commercial landings of shrimp and menhaden are removed from the GOM data, landings of other fishes show a clear and significant increase over time ( $p < 0.0001$ ; Figure 1.5): this may well explain the increasing MTLI. When the GOM landings data time series began in 1950, fisheries were being persecuted only on 27 species of fishes and invertebrates. Today, there are GOM fisheries for almost 3 times this number of species (72), and many of these newer fisheries are on higher trophic level species than menhaden or shrimp (NMFS 2007). In this case, fishers in the GOM may be ‘fishing up the food web’; originally having focused on highly abundant and valuable lower trophic level species, rather than “fishing through the food web” as described by Essington et al. (2006). This practice could still result in declines in large consumer species (Jackson et al. 2001), and declines in the MTLI for the GOM in the future. A recent study in Alaska also reported ‘fishing up’ the food web based on a 112-year time series (Litzow and Urban 2009); of note is that Louisiana and Alaska are among the states with the highest US fisheries landings (NMFS 2007).

I suggest caution when interpreting changes in the mean trophic level over time based upon commercial landings alone, especially when the slopes are very low and not significantly different than zero. Caution is especially important if information is not available regarding changes in fishing practices, markets, and data acquisition methods (Essington et al. 2006; De Mutsert et al. 2008). Where sufficient data exist, I see value in calculating the MTLI from survey data, because these may not be as susceptible to problems arising from selective targeting and changes in fishing practices. The value of indices derived from fisheries independent data have long been recognized by stock assessment scientists (NRC 1998).

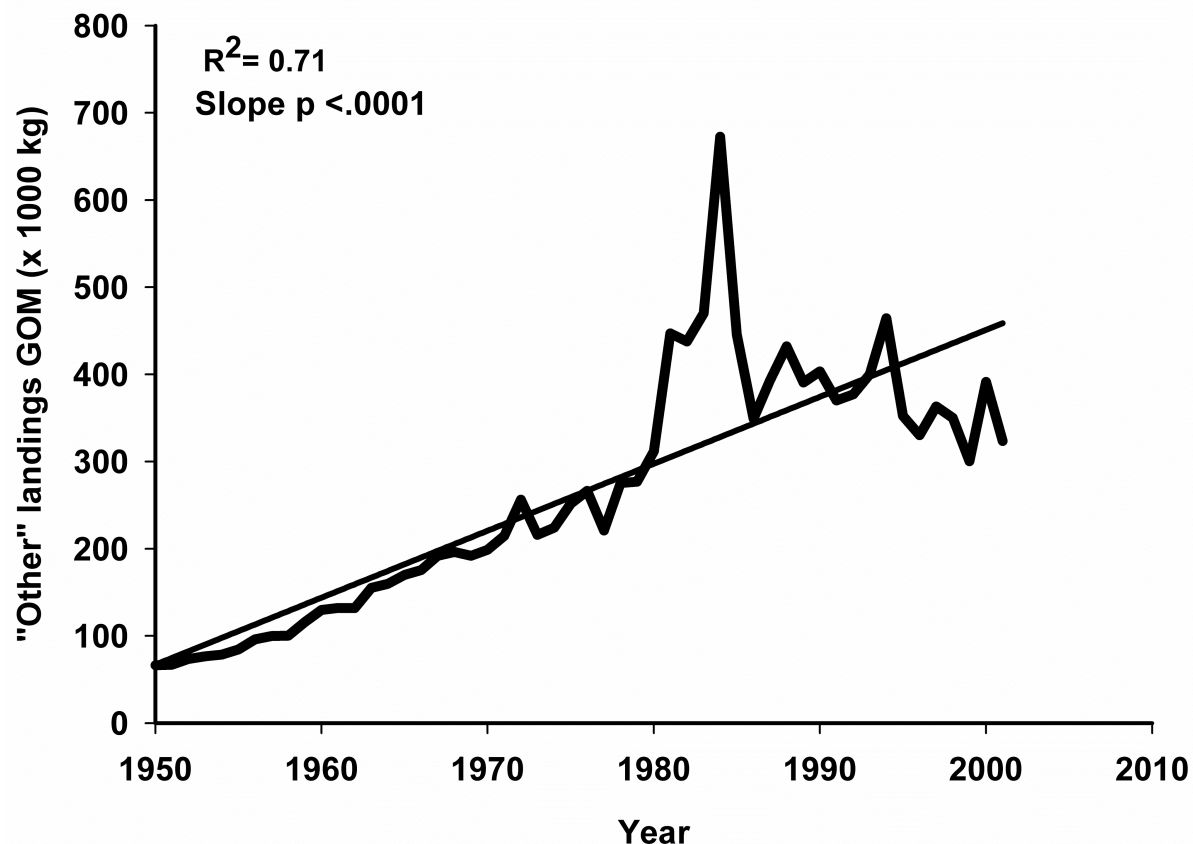


Figure 1.5. Fisheries landings from the GOM other than shrimp and menhaden (x 1000 kg). The trend line of the landings is indicated with  $R^2$  in the figure; there is a significant increase in landings since 1950 (p-value indicated in the figure).

### Does the MTLI Contain Information for Short-term Comparisons?

To evaluate the effect of environmental insults (both chronic and short-term) on the MTLI calculated using localized fisheries independent data, I compare the MTLI calculated for two Louisiana estuaries that are assumed to be near opposite end-points in the continuum of ecosystem health, or perhaps, at very different stages in the cycle of delta formation and decay (Van Heerden and Roberts 1980; Roberts 1997; Day et al. 2007). The 'healthy' reference area,

Fourleague Bay, has a significantly higher initial mean trophic level than Breton Sound ( $p = 0.0004$ ; Figure 1.6), which could be indicative of a more complex food web.

The slope of the MTLI for Fourleague Bay is not significantly different from zero ( $p = 0.7308$ ), while the Breton Sound slope is increasing ( $p = 0.0472$ ; Figure 1.6). Of note is that the Breton Sound index is approaching the level of the Fourleague Bay index (Figure 1.6). This may indicate that the restoration efforts in Breton Sound are improving the health of the Breton Sound food web. This is an encouraging result and the next chapters of this dissertation are devoted to investigating in detail what effects the restoration effort by means of the CFD is having on nekton populations in Breton Sound.

On shorter time scales, I examined variability in MTLI's of both estuarine basins in response to tropical storms that made landfall near each of the basins; no relationship was evident (Figure 1.6). This emphasizes the complexity of estuarine ecosystems. The MTLI time series of the two areas are also not correlated ( $p = 0.251$ ), so no coast-wide impact of tropical storms is indicated by the MTLI. Even though hurricane events and the opening of the diversion likely have an effect on foodwebs, these effects may be delayed or masked in the MTLI by other environmental factors that are operating at the same or on more rapid time scales. Conversely, the MTLI might not be a suitable indicator for environmental impacts on estuarine nekton, and more suitable for illuminating changes in fishing pressure and behavior, whether it is 'fishing down', 'fishing through' or 'fishing up' food webs (but see Litzow and Urban 2009).

In summary, while recognizing the threat of overfishing to the sustainability of fisheries and the ecosystems to which they belong, I question whether the low and declining slopes of the MTLI for the Gulf of Mexico (and elsewhere) found by (Pauly and Palomares 2005) is a "prevalent" and true reflection of the fisheries ecosystem, and suggestive of decreasing health and stability of marine food webs. In general I caution the use of commercial fish landings alone

to make statements concerning the state of fisheries and ecosystem health, as these data are driven by selective targeting, and other human decisions concerning fishing practices. I encourage the development and use of fisheries independent data, as indices like the MTLI can be useful tools if they truly represent community composition. Even though reliable, however, it should be recognized that fisheries independent data are highly variable since there are no landings limits or bioeconomics regulating the biomass per species captured. The MTLI seems most valuable when long-term data are available, and when conclusions are based upon long-term trends in the index.

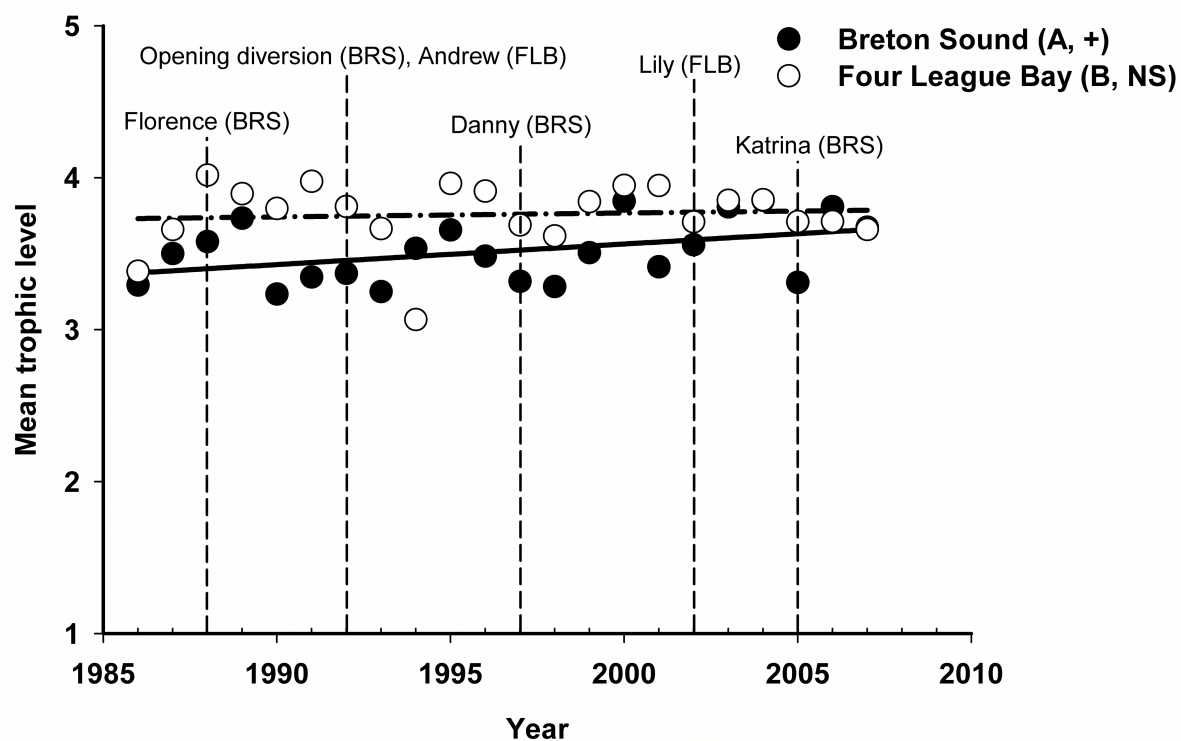


Figure 1.6. Comparison of the MTLI's of Breton Sound (BRS) and Fourleague Bay (FLB). Hurricane events and the opening of the diversion are indicated in the figure; which estuary was affected most by each hurricane is indicated in parentheses. There is no relation between these disturbance events and the MTLI, and the MTLI's are not correlated to each other. Overall, the MTLI of FLB is significantly higher than the MTLI in BRS (indicated with A and B in the figure) and the slope of the trend line is not significantly different from zero. The MTLI of BRS is significantly lower than FLB, and shows a significantly increasing slope (+).

Calculations of the MTLI for two Louisiana estuaries based upon fisheries independent data indicate that when environmental factors drive species biomass distributions, or when the index is used for small systems, the index is more variable. In the longer term, the result that the Breton Sound index is approaching the level of the index for Fourleague Bay is encouraging, given that restoration efforts to reduce wetland loss have been in place in Breton Sound since 1991. Demonstration of causality on the effects of restoration efforts, especially the largest effort (the CFD), on nekton populations, again is necessary to make informed decisions. Toward this end, I examined the Louisiana survey data introduced in this chapter in a comparative study, supplemented with nekton and environmental data in Breton Sound and Fourleague Bay that I collected from October 2006 - August 2008. To examine food web dynamics, I have performed isotope and caloric content analyses on the collected specimens, and have simulated the effect of the CFD on nekton populations and their species biomass distributions using an ecosystem model. These results are described in the remaining chapters of this dissertation.

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## CHAPTER 2

### A BEFORE-AFTER-CONTROL-IMPACT ANALYSIS OF THE EFFECTS OF A MISSISSIPPI RIVER FRESHWATER DIVERSION ON ESTUARINE NEKTON IN LOUISIANA, USA

#### INTRODUCTION

Louisiana accounts for 60-80% of the nation's total annual coastal wetland loss (Boesch et al. 1994; Day et al. 2000). That said, Louisiana wetlands are widely recognized for serving as nursery grounds for an estimated 85-98% of the state's commercially- and recreationally-important fisheries (McHugh 1984); moreover, Louisiana alone accounts for ~75% of all fisheries landings in the US Gulf of Mexico (GOM). While habitat degradation and wetland loss is still occurring, restoration projects are being designed and constructed to stop or reverse these losses. Restoration projects in Louisiana include the construction of river diversions developed to reintroduce fresh water and sediments into wetlands that are hydrologically isolated from the Mississippi River due to levees and flood control structures (Mossa 1996; Lane et al. 1999; Day et al. 2009). This study examines the effect of the Caernarvon Freshwater Diversion (CFD) on nekton biomass and abundance distributions in the Breton Sound estuary in southeastern Louisiana. The CFD is capable of diverting  $226 \text{ m}^3 \text{ s}^{-1}$  of Mississippi River water into the Breton Sound estuary; however, the diversion's mean discharge has been  $45 \text{ m}^3 \text{ s}^{-1}$  (SUNRIS-[www.dnr.state.la.us](http://www.dnr.state.la.us)). Discharge has mostly been pulsed, mimicking natural overbank flooding of the Mississippi River before the construction of levees. The pattern of moderate flooding with pulses generates high primary and secondary productivity (Day et al. 1995; Odum et al. 1995; Day et al. 2009).

The CFD was originally constructed in 1991 to stimulate the oyster fishery (Chatry et al. 1983) and reduce oyster predation by the parasitic oyster drill (*Stramonita haemastoma*) which is found in salinities  $>15$  psu (Butler 1954), and infections by the bacteria *Perkinsus marinus* which

is decreased by freshet events ( $< 5$  psu; La Peyre et al. 2009). More recently, the CFD is being used to redistribute Mississippi River water and sediment into the Breton Sound estuary in Louisiana as a measure to control salinity and restore coastal wetlands that have been degrading because of saltwater intrusion, subsidence, damage from tropical storms, and sea level rise (Rozas et al. 2005b; LCPRA 2007; USACOE 2008; Day et al. 2009). The need for coastal restoration was punctuated by damage caused by Hurricane Katrina in 2005 to New Orleans and the northern Gulf coast (Day et al. 2007). The fact that the eye of Hurricane Katrina passed directly over the study area also provides the opportunity to determine the effect of a direct impact of a hurricane on estuarine nekton in this area.

To date, marsh restoration projects are seldom assessed for fishery implications (Rozas et al. 2005a; Day et al. 2009), while the linkage between wetland loss and nekton production and diversity is complex (Zimmerman et al. 2000; Cowan et al. 2008). In some cases, the use of river diversions to restore an estuary is more obviously beneficial to nekton, e.g. when it is used to counteract hypersalinity or droughts (Ward et al. 2002; Palmer et al. 2002; Montagna et al. 2002). In Louisiana, concerns persist that river diversions will extirpate or harm nekton species that favor pre-diversion regimes by lowering salinities and increasing sediment and nutrient loads in the estuary (Turner and Rabalais 1991; Turner 2006; Reed 2007).

This study seeks to determine whether and how the addition of large amounts of freshwater has changed nekton community structure, abundance and biomass distributions. Data on estuarine nekton collected monthly in the Breton Sound estuary beginning in 1986 by the Louisiana Department of Wildlife and Fisheries were analyzed using a BACI (Before-After-Control-Impact) design (Downes et al. 2002).

The strength of a BACI design lies in the assumption that changes over time in the impact area, unrelated to the impact, are controlled for by changes over time in the control area, because

the time (before or after) x area (impact or control) interaction is analyzed (Downes et al. 2002). Both biomass and abundance data are analyzed to ensure that both impact of large and small species are made explicit, and changes in mean weight per individual through time can be investigated. For example, a decrease in total biomass through time of a species in a given area could mean an increase in small individuals, if the abundance of this species increases through time.

The following null hypotheses are evaluated: 1) nekton species biomass and abundance distributions (SBD and SAD respectively) do not change as a result of the opening of the CFD; 2) the opening of the CFD does not have an effect on the nursery function of Breton Sound; 3) there is no effect of the CFD on the biomass or abundance of selected ecologically, recreationally or commercially important species; and 4) there was no effect of Hurricane Katrina on both the control and impact area in the Breton Sound estuary.

Alternatively, I hypothesize that nekton species with a preference for higher salinities, many of which are marine transients, will be displaced by species with a preference for lower salinities, creating shifts in SBD and SAD. In addition to a direct salinity effect, shifts in SBD and/or SAD are expected to occur as a result of complex relationships between salinity and habitat changes, and food web interactions. For example, moderate freshwater flow can cause increases in euryhaline prey with a preference for higher salinities simply because of reductions in biomass of more stenohaline predators. In addition, increases in food availability in response to nutrients contained in Mississippi River water could increase biomass of euryhaline species (Nixon 1988; Nixon and Buckley 2002). I further hypothesize that the inflow of freshwater will increase the nursery function of the estuary by reducing predation pressure of marine transients on juvenile estuarine fishes, and that in 2005 an effect of Hurricane Katrina can be seen by a decrease in nekton abundance or biomass.

Within a nekton community consisting of 149 species, focus is placed upon six nekton species that are of particular ecological, recreational or commercial importance as emphasized in previous reports (USACOE 2004), and illustrative of the possible trade-offs attributable to the reintroduction of freshwater. The species are: *Litopenaeus setiferus*, *Farfantepenaeus aztecus*, *Brevoortia patronus*, *Cynoscion nebulosus*, *Micropogonias undulatus* and *Micropterus salmoides* (white shrimp, brown shrimp, gulf menhaden, spotted seatrout, Atlantic croaker, and largemouth bass, respectively). In addition, attention is given to species that contribute most to dissimilarities between the periods before and after the opening of the diversion, and between the control and impact areas.

## **MATERIALS AND METHODS**

### **Study Area**

The Breton Sound estuary is located south of New Orleans, Louisiana (Figure 2.1). It is bounded by the levee of the Mississippi River on the west side, and the levee of the Mississippi River Gulf Outlet (MRGO) on the east side. The CFD is a water control structure located in a bend in the Mississippi River at the north end of the estuary. From there, Mississippi River water flows directly into the estuary with a mean discharge of  $45 \text{ m}^3 \text{ s}^{-1}$  (Figure 2.2). Within the estuary, an elevated road divides the estuary roughly in half lengthwise, one half receiving CFD water while the other does not. This division extends down estuary as a boating channel with high banks, to the point of its terminus in Breton Sound. The area that is essentially isolated from freshwater inflow by the road is defined as the control area in this study, while the area receiving most of the freshwater flow is defined as the impact area. In both areas, the Louisiana Department of Wildlife and Fisheries (LDWF) has sampled nekton at fixed stations since 1986; data from 13 stations in the impact area, and 6 stations in the control area are the basis of the analyses in this study (Figure 2.1). The impact area is approximately twice the size of the control

area, therefore the number of stations in the two areas results in approximate equal representation of each area.



Figure 2.1. Aerial photograph of the study area. The study sites where all monthly nekton collections and salinity measurements were made are indicated in the Figure. The Caernarvon Freshwater Diversion discharge is indicated with an arrow. The sites in the impact area are indicated with circles, while the sites in the control area are indicated with squares. The elevated road separating the two areas is accentuated with a white line. The division extends down estuary as bayou Terre aux Boeufes, accentuated with the dashed white line.

## Field Methods

The Louisiana Department of Wildlife and Fisheries collected nekton monthly in each station during routine sampling trips in Breton Sound starting in 1986. They used 15.24-meter bag seines with 6 mm mesh deployed from a boat by setting and anchoring one end of the seine, and circling that point with the boat three times with the seine extended. One such net tow is treated as one unit of effort in catch per unit effort (CPUE) calculations. Fish and crustaceans were

identified, counted and weighed (to the nearest 0.1 g wet weight) and recorded along with salinity (ppt), water temperature ( $^{\circ}\text{C}$ ), date, time of day, and station location.

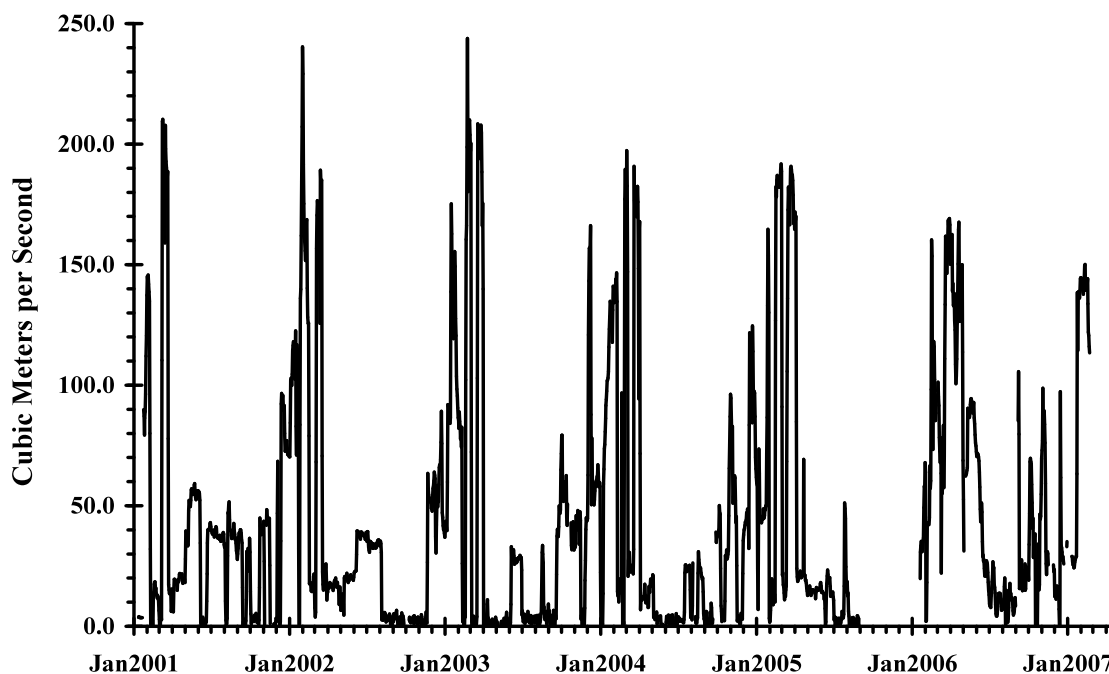


Figure 2.2. Daily mean discharge of the CFD since data became available in 2001.  
(Source DNR SUNRIS: [http://sonris-www.dnr.state.la.us/www\\_root/sonris\\_portal\\_1.htm](http://sonris-www.dnr.state.la.us/www_root/sonris_portal_1.htm))

I calculated mean CPUE (g) per species per year both in the impact area and control areas by dividing the total biomass (g) of each species caught in each year by the number of net tows in that area per year (i.e. one net tow is one unit effort). I also calculated abundance per unit effort by dividing the number of specimens per species caught per year in each area by the number of net tows in that area per year. This estimate of abundance per unit effort is referred to simply as ‘abundance’ throughout the paper, while the CPUE (g) is referred to as ‘biomass’. By dividing biomass by abundance I also calculated the mean weight per specimen per year to



determine if individual size changed through time, reflecting variability and/or improvement of nursery function of the estuary.

### **Data Analyses**

The data used covers the period from 1986 to 2007. The years 1986-1990 were used in the BACI analyses as the ‘before’ period, the years 1991 and 1992 were not included as these were considered to be transition years during the opening of the CFD, and the years 1993-2007 were used as the ‘after’ period. Because salinity is hypothesized to be a main driver of nekton community response in estuaries (Deegan et al. 1986; Evans 1993; Patillo et al. 1995; Moyle and Cech 2000), I first examined whether opening of the diversion changed salinities in the estuary. This was done to determine whether there was indeed a significant environmental change in the impact area that did not occur in the control area, which is a prerequisite for use of a BACI design (Downes et al. 2002). Following a BACIP design (Before-After-Control-Impact design with samples Paired in time) with one variable (Downes et al. 2002), I analyzed the difference between control and impact salinity values; I subtracted the monthly mean salinity in the impact area from the monthly mean salinity in the control area, and then analyzed if the mean control-impact difference in salinity in the ‘before’ period was significantly different from the mean difference in the ‘after’ period using a t-test in SAS v. 9.1.3 (2005).

I reduced the nekton data to four samples per year; the mean SBD, and the mean SAD per unit effort per year for the impact area, and for the control area. Each sample consisted of a community profile (the SBD or SAD), in which the variables were either the mean biomass or the mean abundance for each species in that year. All species collected in either of the study areas in any year between 1986 and 2007 were included in the profiles; if a species was not caught in area in a given year, the biomass or abundance was reported as zero for that year. Each

profile consisted of 161 species or groups (this is a higher number than the 149 species found, because it includes entries where individuals could only be identified to genus).

The profiles were analyzed using PRIMER 6 & PERMANOVA+, which is specifically designed for analyses of community composition, and species biomass and abundance distributions (Clarke and Warwick 2001; Clarke and Gorley 2006; Anderson et al. 2008). Both biomass and abundance data were square-root transformed, and all analyses were performed on resemblance matrices (using Bray-Curtis similarity) of the transformed biomass and abundance data. I used PERMANOVA, which is a semi-parametric equivalent of an ANOVA, to test the interaction between the factors Area ('control' or 'impact'), and Period ('before' or 'after') in a two-way analysis for both SBD and SAD; these were the nekton BACI analyses.

I also created a factor called Interaction, with the levels: 'before-impact', 'before-control', 'after-impact' and 'after-control' to test which of these specified combinations were significantly different from one another in a one-way pairwise ANOSIM procedure, which is a non-parametric equivalent of an ANOVA. For all PERMANOVA and ANOSIM procedures, I used 9999 permutations, and rejected the null hypotheses (of no difference) at a significance level of 1 in 1000 ( $p = 0.001$  in PERMANOVA and  $p = 0.1\%$  in ANOSIM). A high number of permutations allows for low  $\alpha$ -values, increasing both power and precision of the test (Hope 1968; Clarke and Warwick 2001; Anderson et al. 2008). Following this, I determined the species that contributed most to the dissimilarities between levels of the factor Interaction (ANOSIM main effect) using SIMPER (similarity percentages).

Further, I tested for individual species whether the biomass in the impact area after the opening of the diversion was significantly different from that in the control area with t-tests in SAS 9.1.3 (2005). I did this for six ecologically or economically important species mentioned in the introduction, for four species that contributed ~ 25% to dissimilarities between species

biomass distributions, and for four that contributed ~25% to dissimilarities between species abundance distributions of previously described ANOSIM main effect as indicated by SIMPER analyses. I used t-tests to compare total biomass, total abundance, total number of species, and mean weight per specimen of the complete catch per year in the control and in the impact area after opening of the diversion. For all parametric statistics an  $\alpha$ -level of 0.01 was used to reduce the chance of a type I error as multiple t-tests were performed. Bonferroni adjustments were not performed to avoid an increase in the chance of a type II error (Perneger 1998; Nakagawa 2004).

## **RESULTS**

While salinities decreased both in the control area and impact area after the opening of the diversion, there was a significantly larger decrease in salinity in the impact area after controlling for the changes that occurred in the control area ( $t = 4.68$ ,  $p < 0.0001$ ; Figure 2.3). The mean salinity in the impact area before and after the opening was  $10.6 \pm 3.2$  ppt and  $4.6 \pm 2.7$  ppt, respectively. Likewise, the mean salinity in the control area before and after the opening was  $14.8 \pm 3.8$  ppt and  $11 \pm 3.5$  ppt, respectively.

A total of 965,116 individuals of 149 species were captured in the combined study areas (control plus impact) between 1986 and 2007 (Table 2.1). The BACI approach revealed that the CFD caused significant changes in the relative biomass and abundance of nekton species in the impact area. This is evidenced by the results of the PERMANOVA analyses; SBD and SAD both showed a significant period x area interaction (pseudo- $F = 5.1738$ ,  $p = 0.0001$ ; and pseudo- $F = 6.2236$ ,  $p = 0.0001$  respectively).

Using ANOSIM, the pairwise comparisons of the period-area combinations revealed that SBD in the impact area were significantly different pre- and post-opening ( $R = 0.95$ ,  $p = 0.01\%$ ), as were distributions in the impact and control area after the opening ( $R = 0.775$ ,  $p = 0.01\%$ ). In contrast, distributions did not differ significantly between the two areas before the opening of the

CFD ( $R = 0.816$ ,  $p = 0.8\%$ ). Similar results were found in the analyses of SADs. There was a significant difference pre- and post-opening in the impact area ( $R = 0.602$ ,  $p = 0.06\%$ ), and between the impact and control area after the opening ( $R = 0.824$ ,  $p = 0.01\%$ ), while distributions in the two areas did not differ before the opening of the CFD ( $R = 0.78$ ,  $p = 0.8\%$ ). This again indicates significant changes in SBD and SAD in the impact area after opening of the CFD, even when controlling for the change that occurred in the control area.

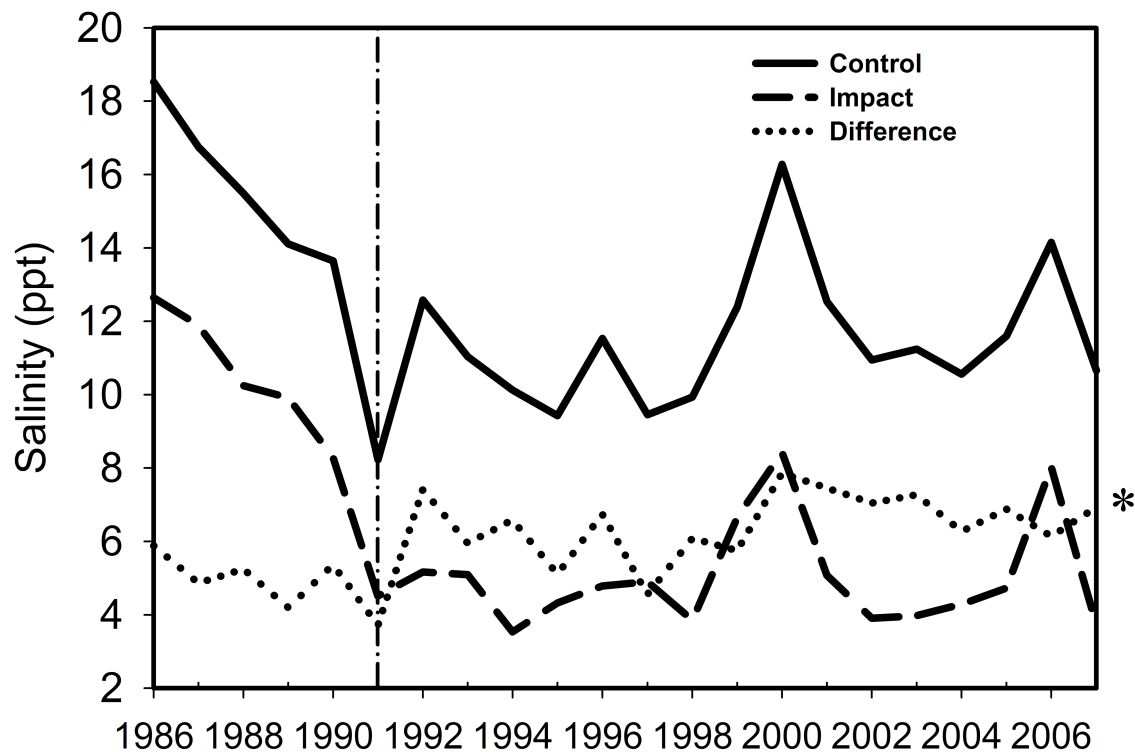


Figure 2.3. The yearly mean salinities in the study area from 1986 until 2007. For the BACIP analysis, paired monthly salinity data are used. The solid line represents the control area, the dashed line the impact area, and the dotted line the difference between the two. The vertical line indicates the opening of the CFD, and separates the ‘before’ and ‘after’ period. The asterisk indicates that the difference after the opening is significantly higher than the difference before the opening.

Table 2.1. List of all nekton species or groups (when individuals were only identified to genus) present in Breton Sound from 1986 to 2007. The mean abundance per seine tow is indicated for each species in each year in the table. The letters ‘c’ and ‘i’ stand for ‘control’ and ‘impact’ respectively. When the mean abundance per seine tow of a species was lower than 0.005 individuals, this is indicated with a ‘p’ of ‘present’; when a species was not found in a particular year this is indicated with ‘-’.

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Achirus</i>	c	-	-	-	0.04	0.02	0.02	0.01	-	0.01	-	-	0.01	-	-	-	-	-	-	-	-	-	-
<i>Lineatus</i>	i	-	0.01	0.08	0.01	-	-	-	-	-	p	-	0.03	-	0.01	p	-	-	-	-	-	-	-
<i>Adinia</i>	c	0.29	0.26	0.07	0.17	0.01	0.48	0.26	0.01	-	0.02	0.04	0.02	0.01	-	-	-	0.04	-	0.27	0.07	-	-
<i>Xenica</i>	i	3.89	1.23	0.65	0.94	1.91	0.77	0.02	0.03	0.01	0.37	0.01	0.01	0.01	0.12	0.16	p	0.02	0.01	-	0.38	-	-
<i>Alosa</i>	c	0.01	0.02	-	-	0.01	0.04	0.04	0.01	0.02	0.01	0.01	-	0.01	-	-	0.02	0.01	-	0.01	0.01	-	0.01
<i>chrysochloris</i>	i	0.01	0.01	p	0.02	0.03	0.02	0.02	0.01	0.02	0.01	0.01	0.01	0.02	0.02	0.02	p	0.05	0.02	0.04	0.05	-	-
<i>Alpheus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Florida-nus</i>	i	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Alpheus</i>	c	-	-	-	-	-	-	-	-	0.01	0.01	-	0.01	-	-	-	-	-	-	-	-	-	0.01
<i>hetero-chaelis</i>	i	-	-	0.01	p	-	-	-	-	-	-	-	-	-	-	p	-	-	-	p	-	-	-
<i>Anchoa</i>	c	0.06	0.14	0.04	0.09	0.02	-	0.04	0.01	0.03	-	0.06	0.01	0.23	0.04	0.06	0.01	0.19	0.18	-	0.01	0.06	0.01
<i>Hepsetus</i>	i	p	-	p	0.01	p	-	-	-	-	-	-	-	-	-	-	p	-	p	-	-	-	-
<i>Anchoa</i>	c	15.6	39.5	15.0	6.91	39.8	4.29	17.8	9.65	27.1	15.2	21.4	6.96	6.09	4.67	1.14	1.37	2.82	3.26	20.7	10.1	23.9	17.9
<i>Mitchilli</i>	i	2.92	22.6	6.18	3.88	21.1	7.08	7.79	7.47	4.86	20.5	40.7	38.7	29.6	30.6	107	39.6	24.6	53.8	22.0	12.9	7.97	6.89
<i>Anguilla</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rostrata</i>	i	-	-	p	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-
<i>Aplodino-tus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>grunniens</i>	i	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	p	p	0.02	0.01	-	-	-
<i>Archosar-gus</i>	c	0.68	0.36	0.08	0.42	0.11	0.06	0.07	0.16	0.19	0.09	0.14	0.01	0.03	-	0.05	0.11	0.02	0.18	0.06	0.10	0.11	0.02
<i>probato-cephalus</i>	i	0.39	0.18	0.24	0.13	0.11	0.13	0.22	0.25	0.16	0.15	0.08	0.04	0.07	0.04	0.04	0.05	0.02	0.03	0.05	0.09	0.05	0.06
<i>Arius</i>	c	3.70	2.26	4.02	3.89	1.91	2.55	1.27	3.44	4.41	1.74	0.77	0.96	0.47	0.72	2.04	2.09	2.62	3.35	1.78	2.27	0.90	1.71
<i>felis</i>	i	2.23	1.67	1.23	1.06	1.14	1.95	0.77	0.74	1.23	1.10	1.05	1.06	0.46	0.54	0.63	0.86	0.69	0.35	0.68	0.22	0.68	0.69
<i>Bagre</i>	c	0.10	0.05	0.10	0.03	0.04	0.12	0.01	0.08	0.23	0.07	0.02	0.02	-	-	0.01	-	-	0.01	-	-	-	0.01
<i>Marinus</i>	i	0.62	0.02	0.03	0.04	0.06	0.03	0.04	0.02	0.01	0.03	0.03	0.06	0.10	0.06	0.05	0.10	0.11	0.06	0.06	0.09	0.05	0.01
<i>Bairdiella</i>	c	0.67	1.19	1.25	0.34	0.69	0.06	0.20	0.19	0.09	0.64	0.16	0.69	0.23	0.01	0.20	0.25	0.48	0.18	0.14	0.04	0.66	0.06
<i>Chrysou-ra</i>	i	0.13	0.06	0.80	0.31	0.17	0.10	0.05	0.15	0.10	0.04	0.23	0.10	0.03	0.03	0.27	0.05	0.13	0.07	0.03	0.01	0.01	0.10

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Bathygobius soporator</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-
	i	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bellator Militaris</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>blenny sp.</i>	c	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brevoortia Patronus</i>	c	53.9	30.5	24.6	1.77	0.93	0.99	1.87	6.42	2.88	7.30	3.35	1.17	-	-	0.04	-	-	0.01	0.13	-	-	-
	i	2.21	10.1	4.40	4.84	3.22	0.98	9.67	14.6	37.5	0.83	6.75	4.62	2.84	8.43	1.51	5.96	13.7	2.46	13.6	7.71	16.3	0.42
<i>Callinectes sapidus</i>	c	1.30	0.96	0.25	0.36	0.21	0.62	0.35	0.38	0.57	0.12	1.50	0.26	0.05	0.12	0.01	-	-	-	-	-	-	-
	i	2.11	0.67	0.77	0.50	0.54	2.02	0.86	0.57	0.44	0.43	1.10	1.90	2.26	3.87	2.89	2.17	2.70	2.49	1.34	0.58	0.03	0.01
<i>Callinectes similis</i>	c	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Carangidae</i>	c	-	-	-	0.03	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Caranx Hippos</i>	c	0.02	0.17	0.01	0.04	0.03	0.14	0.01	0.02	0.02	0.01	-	0.01	0.01	0.01	0.02	0.02	0.02	0.04	0.10	0.01	0.01	0.01
	i	0.01	0.01	0.01	0.02	0.05	0.01	-	0.14	0.01	0.01	0.02	-	0.01	0.02	0.01	0.02	p	0.02	0.03	p	-	p
<i>Carcharhinus leucas</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.01	0.01	-
	i	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	p	p	-	-	-
<i>Carcharhinus limbatus</i>	c	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	p	-
<i>Chaetodipterus faber</i>	c	0.01	-	-	0.01	0.01	-	0.02	-	0.01	-	-	-	-	0.03	0.04	-	-	-	-	-	0.01	-
	i	-	-	-	-	p	-	-	-	-	-	-	-	-	-	p	-	p	-	-	-	-	-
<i>Chasmodes bosquianus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
	i	p	-	-	-	p	-	-	-	p	p	-	-	p	0.01	-	-	-	-	p	-	-	-
<i>Chloroscombrichthys mchrysurus</i>	c	-	0.02	-	-	-	-	-	-	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	0.01
	i	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-
<i>Citharichthys spilopterus</i>	c	0.87	0.37	0.04	0.08	0.03	0.02	-	0.02	-	0.01	-	0.01	0.15	0.01	-	-	-	-	-	-	0.01	0.02
	i	0.06	0.11	0.21	0.10	0.06	0.03	0.06	p	-	0.01	0.03	0.34	0.33	0.01	p	0.07	0.01	0.01	0.04	0.01	0.10	0.15
<i>Clupeidae</i>	c	-	-	-	-	-	0.04	-	-	0.57	0.01	-	-	-	-	-	-	0.01	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Cynoscion arenarius</i>	c	1.94	2.50	0.92	0.38	0.42	1.72	0.09	0.46	0.22	0.16	0.05	-	-	-	-	-	0.01	-	-	-	-	-
	i	0.18	0.53	0.27	0.32	0.25	0.42	0.41	0.29	0.25	0.28	0.66	0.68	0.19	0.23	0.16	0.42	0.58	0.71	0.10	0.06	0.10	0.09
<i>Cynoscion nebulosus</i>	c	1.24	2.29	3.88	2.54	1.17	1.23	0.97	1.07	1.57	0.85	1.20	0.55	0.61	0.53	0.78	0.63	1.26	2.09	0.76	1.32	1.02	1.54
	i	0.47	0.88	1.07	0.87	0.32	0.47	0.60	0.68	0.62	0.69	0.83	1.40	0.55	1.64	1.34	0.68	0.90	0.78	0.51	0.55	0.47	0.96
<i>Cyprinodon variegatus</i>	c	3.88	1.90	2.30	0.39	0.02	1.99	0.25	0.08	-	0.20	0.23	0.05	-	0.02	0.01	-	0.02	0.67	0.21	0.60	0.06	0.02
	i	6.44	26.3	14.3	2.07	18.4	9.40	1.30	2.65	0.49	0.24	0.33	2.15	0.57	1.90	2.75	0.63	0.43	0.07	0.14	p	-	0.74
<i>Cyprinus carpio</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	p	-	-	-	-	0.01	-	-	-	-	p	-	p	-	-	-	-
<i>Dasyatis Sabina</i>	c	0.39	0.26	0.23	0.15	0.06	0.06	0.02	0.01	0.03	0.03	0.02	0.04	0.07	0.04	-	0.01	0.01	0.01	-	0.01	-	-
	i	0.07	0.03	0.07	0.03	0.05	0.02	0.03	0.02	p	p	p	0.02	0.01	0.01	0.02	0.01	0.02	0.02	0.01	-	0.02	0.01
<i>Dormitator maculatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	p	0.21	-	-	-	p	0.03	-	-	p	0.01	0.01	-	-	p	-	-	-	-	-	-
<i>Dorosoma cepedianum</i>	c	0.01	0.08	-	0.02	0.03	0.88	0.07	0.06	0.14	0.09	0.09	0.23	0.40	0.18	-	0.01	0.08	0.08	0.05	0.04	-	0.03
	i	0.31	0.16	0.15	0.09	0.21	1.09	0.70	1.23	0.72	0.68	0.36	1.19	0.54	0.87	0.88	0.97	0.48	0.35	0.72	0.44	0.34	0.80
<i>Dorosoma petenense</i>	c	0.04	0.08	0.12	0.04	0.52	0.01	-	0.06	-	0.01	0.01	-	0.02	0.08	0.01	0.01	0.01	-	0.01	0.01	0.03	0.02
	i	0.63	p	0.12	0.01	0.08	0.01	0.02	0.25	0.01	0.03	p	0.09	0.05	0.01	0.16	p	0.02	0.04	0.09	-	-	-
<i>eel sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	p	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Elops saurus</i>	c	0.09	0.06	0.07	0.03	0.05	0.10	0.03	0.02	0.01	-	0.01	0.02	0.03	0.03	0.11	0.06	0.04	0.11	0.26	0.06	0.09	0.03
	i	0.03	0.14	0.08	0.04	0.04	0.07	0.01	0.03	0.01	0.06	0.08	0.08	0.05	0.08	0.04	0.06	0.15	0.16	0.17	0.17	0.04	0.04
<i>Etropus crossotus</i>	c	0.23	0.10	0.01	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	p	-	p	p	0.02	-	p	-	-	-	-	-	p	-	p	-	-	-	-	-
<i>Eucinostomus marginatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	0.01	0.01	0.04	0.12	0.01	0.03
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	0.01	-	-	-	-
<i>Eucinostomus sp.</i>	c	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	p	-	-	0.03	p	-	-	-	-	0.01	0.01	p	-	-	-	-	-	-	-	-
<i>Evorthodus lyricus</i>	c	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	p	-	-	-	-	-	p	-	p	-	p	-	-	-	-	-	-	-	-	-	-
<i>Fundulus grandis</i>	c	0.66	3.00	0.87	0.33	0.10	1.05	0.23	0.58	0.53	0.54	0.36	0.32	0.38	0.18	0.39	0.13	0.31	1.06	1.45	0.45	0.27	0.24
	i	2.69	3.91	9.85	2.64	3.10	4.94	1.00	1.07	0.29	0.63	0.23	0.27	0.49	0.67	0.90	0.28	0.32	0.11	0.10	0.09	0.10	0.41
<i>Fundulus jenkinsi</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	0.14	-	0.01	p	p	0.01	-	0.01	0.05	0.01	-	-	0.02	0.01	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Fundulus pulverous</i>	c	0.13	0.10	0.03	0.02	0.01	0.07	0.02	-	-	-	-	0.01	-	0.19	-	-	-	-	-	0.01	-	-
	i	0.09	1.95	0.39	0.74	0.98	0.87	0.10	0.12	0.01	0.03	0.03	0.01	0.05	0.02	0.13	0.02	0.05	0.02	0.02	-	-	0.01
<i>Fundulus similis</i>	c	0.04	0.02	0.07	0.15	0.03	0.05	0.02	0.05	0.15	0.07	0.44	0.29	0.07	0.05	0.39	0.06	0.04	0.10	0.13	0.10	0.04	0.34
	i	0.05	0.29	0.07	0.06	0.59	0.49	0.09	0.13	0.04	0.12	0.05	0.02	0.05	0.08	0.02	0.01	0.01	-	0.02	0.01	-	0.02
<i>Gambusia affinis</i>	c	0.03	0.01	-	-	-	-	-	-	-	0.72	-	-	-	-	-	-	0.01	0.01	1.06	0.59	0.03	0.21
	i	p	-	-	-	-	-	-	0.02	0.01	0.09	0.01	0.09	0.03	0.02	0.25	0.25	0.27	0.05	0.05	p	-	-
<i>Gobiesocidae</i>	c	-	-	-	-	-	-	-	-	0.01	-	-	0.01	-	-	-	-	-	-	-	-	-	0.01
	i	-	-	-	-	-	-	-	-	-	-	-	p	-	-	p	-	-	-	-	-	-	-
<i>Gobiesox strumosus</i>	c	0.01	0.02	-	0.01	-	-	-	-	-	-	-	0.01	-	-	-	0.01	0.01	-	0.01	0.01	0.02	-
	i	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gobiidae</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-
<i>Gobioides broussonetii</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	p	-	-	-	-	-	-	0.03	0.01	p	-	-	-	-	-
<i>Gobionellus boleosoma</i>	c	0.02	-	0.04	0.02	-	-	-	-	-	-	-	-	-	-	-	0.01	-	0.01	0.15	0.12	0.02	0.13
	i	0.03	0.04	0.06	0.09	-	p	0.07	0.03	0.03	-	0.07	0.04	0.03	0.03	0.22	0.01	p	0.76	0.05	0.02	-	-
<i>Gobionellus hastate</i>	c	0.01	0.01	-	-	-	0.01	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
	i	0.01	0.04	0.04	0.01	0.01	p	0.03	0.02	p	0.02	0.01	0.02	0.01	0.03	0.04	0.01	-	p	0.01	-	-	-
<i>Gobionellus shufeldti</i>	c	0.01	-	-	-	-	0.02	0.03	0.01	0.13	0.04	0.02	-	0.01	-	-	-	-	-	-	-	-	-
	i	-	0.03	0.11	-	0.03	0.12	0.01	0.05	0.06	0.13	0.14	0.22	0.87	0.34	0.37	0.23	0.06	0.65	0.18	-	-	-
<i>Gobiosoma bosc</i>	c	0.18	0.54	0.10	0.19	0.02	0.04	0.12	0.42	0.43	0.19	0.82	0.52	0.41	0.04	0.19	0.02	0.03	0.26	0.23	0.18	0.13	0.28
	i	0.10	0.24	0.15	0.27	0.32	0.29	0.20	0.46	0.14	0.98	0.83	1.49	1.59	2.74	3.62	1.71	1.46	2.58	1.52	0.93	0.23	0.39
<i>Harengula jaguana</i>	c	-	0.21	0.07	0.02	0.02	0.60	0.03	-	-	-	-	0.01	0.10	-	-	-	-	-	-	0.22	-	-
	i	0.01	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	p	-	p	-	-	-
<i>Hepatus epheliticus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-
<i>herring sp.</i>	c	-	-	-	-	3.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hexaparonopeus aulensis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-



(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Hyporhamphus unifasciatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	p	p	-	-	-	-	-	-	-	-
<i>Hypso-blennius hertz</i>	c	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hypso-blennius ionthas</i>	c	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ictalurus furcatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	0.01	-	-	-	-	0.01	-	-	-	-	-	-	-	p	0.01	0.02	0.01	0.05	0.05	p	0.05	0.02
<i>Ictalurus natalis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	p	-	-	-
<i>Ictalurus punctatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	0.02	p	p	-	0.01	-
<i>Ictalurus sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-
<i>Ictiobus bubalus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-
<i>Lagodon rhomboides</i>	c	0.07	0.17	0.74	0.27	0.31	0.39	0.19	0.63	0.38	0.32	0.13	0.35	0.18	0.54	0.57	0.26	0.11	0.07	0.19	0.07	0.03	0.08
	i	0.02	0.09	0.15	0.13	0.09	0.12	0.05	0.39	0.07	0.04	0.01	0.03	0.02	0.07	0.16	0.31	0.05	0.01	0.18	0.01	0.07	0.07
<i>Leiostomus xanthurus</i>	c	1.15	1.46	1.08	0.77	1.25	1.36	0.71	0.36	1.60	0.98	1.02	0.79	-	0.27	0.02	-	-	-	0.07	-	-	-
	i	0.43	2.22	2.12	1.54	1.35	2.25	1.83	1.40	1.56	0.51	3.53	1.77	0.36	1.25	3.02	1.98	1.11	0.23	1.13	0.78	0.26	0.63
<i>Lepisosteus oculatus</i>	c	0.01	0.23	0.01	0.01	-	-	0.01	0.01	-	-	-	0.01	-	-	-	-	0.03	-	0.05	0.04	0.02	0.01
	i	0.06	0.07	0.06	0.03	0.03	0.33	0.21	0.11	0.04	0.07	0.24	0.08	0.25	0.11	0.22	0.19	0.16	0.23	0.13	0.14	0.19	0.19
<i>Lepisosteus osseus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-
<i>Lepisosteus spatula</i>	c	0.04	-	0.06	-	0.02	0.02	0.02	0.04	0.01	-	-	-	-	-	0.01	0.01	-	-	0.01	0.05	-	0.03
	i	0.08	0.02	0.03	0.01	0.01	0.04	0.05	0.01	0.01	0.01	0.01	p	0.01	p	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01
<i>Lepisosteus sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	p	p	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-
<i>Lepomis cyanellus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-
<i>Lepomis humilis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Lepomis macrochirus</i>	c	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	-	-	-	-	p	-	-	p	0.86	0.25	0.20	0.19	0.14	0.22	1.33	0.71	0.52	0.75	0.31	0.04	0.07
<i>Lepomis megalotis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	p	-	-	-	p	-	-	-	-	p	-	-	-	-
<i>Lepomis microlophus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	0.01	-	-	0.02	0.01	-	-
	i	0.10	0.01	0.06	0.02	p	0.09	0.10	0.21	0.33	0.87	0.68	0.80	0.39	0.38	0.52	0.56	0.66	0.37	0.52	0.27	0.11	0.32
<i>Lepomis punctatus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	0.01	0.14	0.30	0.08	0.11	0.06	0.03	0.23	0.30	0.21	0.11	0.27	0.08	0.02	0.02
<i>Lepomis sp. (hybrid)</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	0.01	p	p	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lepomis sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	0.03	0.02	0.04	0.27	0.85	0.48	0.32	0.10	0.07	0.32	1.26	0.43	0.12	-	0.34	-	-
<i>Lobotes surinamensis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-
<i>Lolliguncula brevis</i>	c	0.11	0.19	0.03	-	-	-	0.01	-	0.01	-	0.03	-	-	-	0.01	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lucania parva</i>	c	0.36	2.14	2.19	1.20	0.01	-	0.08	0.08	0.14	0.07	0.16	0.79	-	-	0.18	-	-	-	0.01	-	-	-
	i	1.46	2.84	4.70	10.9	5.71	3.58	3.36	2.97	3.19	5.90	2.45	9.95	6.52	22.5	38.50	16.9	8.77	2.79	5.30	3.94	0.18	0.76
<i>Lutjanus griseus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	p	-	-	-	-	-
<i>Macrobrachium ohione</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-
	i	-	-	-	-	-	p	p	0.01	0.01	p	-	0.01	0.04	0.02	-	-	-	-	0.13	-	-	-
<i>Malaclemys terrapin</i>	c	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	p	p	0.01	p	-	p	p	p	p	p	-	-	-	-	-	-	-	-	-	-	-
<i>Membras martinica</i>	c	0.65	2.73	0.53	0.42	1.51	0.28	0.21	1.85	0.70	0.26	0.23	0.07	-	0.01	0.11	0.06	0.19	0.20	0.28	0.46	1.33	0.04
	i	-	0.02	-	-	0.04	0.04	-	-	-	-	-	0.31	-	-	0.12	0.01	0.06	0.99	-	-	-	-
<i>Menidia beryllina</i>	c	4.18	2.84	2.13	2.55	1.60	1.41	0.81	2.12	1.69	10.1	21.2	6.18	6.56	2.86	3.09	3.65	2.93	5.58	12.5	12.3	4.12	4.24
	i	2.31	5.35	14.9	6.04	2.74	1.64	1.32	1.83	1.61	3.90	3.75	2.24	2.18	4.58	4.57	2.60	2.10	3.49	5.08	1.62	0.42	0.39
<i>Menippe adina</i>	c	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	-	-	-	-	-	-	0.01	p	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Menippe mercenaria</i>	c	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-
<i>a</i>	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Menticir- rhus ame- ricanus</i>	c	0.65	0.31	0.64	0.66	0.12	0.05	0.06	0.15	0.07	0.13	0.02	-	-	-	0.01	-	-	-	0.02	-	-	-
	i	p	0.02	0.01	0.01	p	-	0.01	0.01	0.01	p	0.03	0.02	-	0.04	0.03	0.04	0.01	0.02	0.02	0.01	0.01	0.03
<i>Menticir- rhus littoralis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microgo- bius gulosus</i>	c	0.44	0.62	0.53	0.05	0.01	0.02	0.01	0.01	0.01	0.02	0.09	0.03	-	-	-	-	-	-	-	-	-	0.01
	i	0.22	0.49	0.18	0.34	0.18	0.34	0.56	0.47	0.30	1.11	0.97	0.80	1.02	1.01	1.59	1.69	2.15	1.19	1.27	0.51	0.05	0.01
<i>M. thalas- sinus</i>	c	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micropan- opeus sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	p	0.13	0.06	0.03	0.04	0.16	0.11	0.09	0.06	0.11	0.14	0.02	0.02	0.02
<i>Micropo- gonias undulatus</i>	c	6.94	2.90	2.03	1.16	1.82	1.14	1.01	0.70	0.88	0.38	2.03	0.88	-	-	0.06	-	-	0.01	0.03	-	-	-
	i	0.71	1.11	2.40	1.48	1.79	0.47	3.03	1.67	1.49	0.34	3.33	1.99	2.10	1.26	3.24	10.97	8.40	2.91	1.88	2.27	1.90	0.73
<i>Micropte- rus salmoides</i>	c	-	-	-	-	-	-	-	-	-	-	0.01	0.01	-	-	-	-	-	-	0.01	-	-	-
	i	0.01	p	p	-	0.03	0.08	0.18	0.14	0.29	0.89	0.26	0.47	0.70	0.13	0.23	0.16	0.49	0.14	0.41	0.37	0.06	0.19
<i>Morone chrysops</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-
	i	p	-	-	-	p	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-
<i>Morone mississip- piensis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	p	p	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
<i>Morone saxatilis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	p	p	p	-	-	-	0.01	-	-	-	-	p	-	p	-	-	-
<i>Mugil cephalus</i>	c	1.05	1.12	1.05	2.69	0.15	0.86	0.51	0.58	0.32	0.13	0.37	0.04	-	-	-	0.04	-	-	0.02	-	-	0.09
	i	1.12	2.57	1.87	1.71	1.55	1.58	0.97	1.34	1.53	0.80	1.06	1.48	1.67	1.21	0.66	1.14	1.39	1.20	0.54	1.26	0.49	0.80
<i>Mugil curema</i>	c	0.02	-	0.03	-	-	0.02	0.01	0.03	0.01	-	0.02	-	-	-	-	-	-	-	-	-	-	0.01
	i	-	p	-	-	p	-	p	0.01	0.01	0.01	0.01	0.03	p	-	0.01	-	-	-	-	-	-	-
<i>Mugil sp.</i>	c	-	-	-	-	-	-	-	-	0.04	0.01	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myrophis punctatus</i>	c	0.01	-	0.01	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	p	-	-	-	-	-	-	p	-	-	-	-	-	-	-
<i>Mysida- cea sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notropis longi- rostris</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	0.04	-	-	-	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Oligoplites saurus</i>	c	0.03	0.02	0.01	-	0.01	0.04	0.01	-	-	-	0.08	-	0.01	-	0.01	0.02	0.03	0.01	0.02	0.01	0.10	0.02
	i	p	p	0.01	-	0.01	0.02	0.02	p	p	0.01	0.01	0.04	p	0.01	0.01	p	-	0.04	0.01	-	-	-
<i>Ophichthus gomesii</i>	c	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Opisthonema oglinum</i>	c	-	0.02	-	-	0.11	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Opsanus beta</i>	c	0.01	0.11	0.07	0.01	0.02	0.02	-	-	-	0.02	-	-	-	-	0.03	-	0.02	-	-	0.01	-	-
	i	-	p	p	0.01	-	-	-	p	-	-	-	p	-	0.01	-	-	p	-	-	-	-	-
<i>Orthopristis chrysoptera</i>	c	0.01	-	-	-	-	-	0.01	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ovalipes floridanus</i>	c	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Palaemonetes sp.</i>	c	1.47	1.79	1.50	2.25	0.40	1.70	1.40	0.87	3.06	2.40	5.90	4.79	1.96	0.19	1.02	1.94	1.27	1.80	3.35	3.76	3.22	3.67
	i	14.3	42.9	11.4	28.8	13.3	26.7	8.08	9.67	9.74	29.7	19.4	102	22.2	30.9	52.3	42.6	37.2	27.2	26.8	13.9	3.65	1.33
<i>Panopeus herbstii</i>	c	-	-	0.04	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	0.02	-	0.01	0.03	0.01	p	-	p	-	-	-	-	-	-	-	-	-	-
<i>Panopeus occidentalis</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-
<i>Paralichthys lethostigma</i>	c	0.10	0.04	0.01	0.03	-	0.07	0.03	0.02	0.03	0.04	0.03	0.01	0.01	0.02	0.02	0.01	0.03	0.02	0.03	0.01	0.01	0.01
	i	0.07	0.05	0.06	0.02	0.01	0.03	0.02	0.02	0.01	0.01	0.04	0.03	0.02	0.01	0.02	0.04	0.04	0.03	0.01	p	p	0.01
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Farfantepenaeus aztecus</i>	c	13.1	4.06	3.23	1.89	4.28	0.61	0.20	2.15	0.63	1.00	1.03	0.40	-	-	0.01	-	-	-	-	-	-	-
	i	1.78	3.07	4.11	4.16	1.36	0.50	1.25	1.49	0.55	0.61	1.31	1.87	0.50	2.63	1.09	1.55	2.82	1.72	0.95	0.41	1.38	0.44
<i>F. duorarum</i>	c	0.05	0.20	0.04	0.01	-	0.07	-	0.01	0.01	0.13	0.15	-	-	-	-	-	-	-	-	-	-	-
	i	0.02	0.04	0.06	0.01	-	0.07	0.02	0.01	p	0.08	0.04	0.03	0.01	0.03	0.04	0.02	p	-	0.02	0.01	-	-
<i>Litopenaeus setiferus</i>	c	1.05	2.38	0.16	0.34	0.08	0.08	0.04	0.20	0.25	0.53	0.06	-	-	-	-	-	-	-	-	-	-	-
	i	0.48	2.53	1.38	0.54	0.40	0.22	0.92	1.04	0.30	1.00	0.32	1.43	0.20	1.22	0.80	1.15	1.94	1.37	0.67	0.94	0.26	0.27
<i>Peprilus alepidotus</i>	c	0.02	0.02	0.03	0.01	-	-	0.03	0.04	0.01	-	-	-	-	-	0.04	0.02	0.02	-	-	0.02	0.06	0.01
	i	-	p	0.01	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. burti</i>	c	0.01	-	0.26	-	0.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	0.04
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>P. triacanthus</i>	c	-	-	-	-	-	-	-	-	0.04	0.01	0.05	0.01	-	-	0.06	-	0.01	0.01	-	-	-	0.01
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	p	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Poecilia latipinna</i>	c	0.93	2.42	1.47	0.21	-	0.01	0.01	0.01	-	0.02	0.01	0.01	0.01	0.01	-	-	0.01	0.01	0.05	0.02	-	0.04
	i	2.30	2.70	2.60	8.24	21.8	20.2	0.57	1.02	0.54	0.64	p	0.44	1.32	3.87	1.63	0.03	0.83	0.38	0.36	0.02	-	0.03
<i>Pogonias cromis</i>	c	0.11	0.06	0.04	0.04	0.01	0.03	0.17	0.08	0.03	0.09	0.06	0.01	0.05	0.02	0.01	0.06	0.09	0.05	0.15	0.34	0.15	0.18
	i	0.32	0.19	0.04	0.04	0.05	0.07	0.08	0.09	0.05	0.08	0.06	0.04	0.08	0.04	0.04	0.12	0.03	0.01	0.03	0.02	0.07	0.04
<i>Polydactylus octonemus</i>	c	0.01	-	0.07	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	p	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pomatomus saltatrix</i>	c	-	0.03	0.02	0.02	-	0.01	-	0.01	0.02	-	-	-	-	-	-	0.01	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-
<i>Porichthys plectrodon</i>	c	0.03	0.01	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prionotus scitulus</i>	c	-	0.01	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prionotus sp.</i>	c	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Prionotus tribulus</i>	c	0.04	0.11	0.01	0.04	0.01	0.02	0.02	0.01	-	-	-	-	-	-	0.01	0.01	-	-	0.01	0.01	-	-
	i	0.03	p	0.01	p	-	p	0.01	0.01	p	-	-	p	0.01	-	p	0.01	0.02	p	0.01	0.01	-	-
<i>Procambarus clarki</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	0.03	0.01	p	p	p	-	-	0.01	0.04	p	0.01	0.02	-	-	-
<i>Rachycentron canadum</i>	c	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhinoptera bonasus</i>	c	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhithropanopeus harrisi</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	p	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sardinella aurita</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-
	i	-	-	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-
<i>Sciaenops ocellatus</i>	c	0.13	0.05	0.05	0.10	0.01	0.10	0.27	0.53	0.32	0.19	0.22	0.07	0.16	0.03	0.04	0.06	0.04	0.20	0.39	0.17	0.02	0.04
	i	0.17	0.04	0.19	0.10	0.02	0.35	0.24	0.30	1.41	0.56	0.23	0.24	0.27	0.26	0.60	0.32	0.30	0.54	0.42	0.39	0.52	0.57
<i>Scomberomorus cavalla</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>S. maculatus</i>	c	0.05	0.06	0.02	0.04	0.04	0.03	0.07	0.02	0.05	0.09	0.02	-	-	-	-	-	-	-	0.01	-	0.01	-
	i	0.02	0.01	0.01	p	-	0.01	0.01	0.01	0.01	-	-	-	-	p	0.01	p	p	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Selar crumenophthalmus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.70	-	-	-	-	-	-
<i>Selene vomer</i>	c	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sesarma reticulatum</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sicyonia sp.</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sphoeroides parvus</i>	c	1.72	1.05	0.53	0.49	0.11	0.13	0.19	0.17	0.21	0.05	-	0.10	0.01	0.13	0.20	0.02	0.16	0.13	0.05	0.10	0.23	0.04
	i	0.04	0.60	0.41	0.10	-	0.01	0.03	0.01	0.02	p	-	0.04	p	0.01	0.13	p	0.05	0.02	p	-	-	0.01
<i>Squilla sp.</i>	c	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	p	-	-	-	-	-
<i>Stellifer lanceolatus</i>	c	-	0.01	0.03	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.01	-	p
<i>Stenotomus caprinus</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Morone hybrid</i>	c	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	p	-	-	-	-	-	-	0.01	-	-	-	-	-	p	-	-	-
<i>Strongylura marina</i>	c	0.15	0.14	0.08	0.04	0.02	0.08	0.01	0.03	-	0.01	0.01	0.01	-	0.13	0.03	0.05	0.02	0.02	0.04	0.01	0.01	0.02
	i	0.05	0.13	0.10	0.07	0.02	0.06	0.02	0.03	0.03	0.01	0.01	p	p	0.01	0.01	p	0.01	p	p	-	p	0.03
<i>Symphurus plagiusa</i>	c	0.17	0.18	0.07	0.07	0.06	0.12	0.01	-	0.06	0.01	0.01	0.01	0.08	0.01	0.01	-	0.01	0.01	0.01	0.02	0.02	0.06
	i	0.07	0.39	0.10	0.07	0.08	0.01	0.02	p	-	p	0.06	0.04	0.10	0.03	0.06	0.05	0.15	0.02	0.01	0.06	0.02	0.01
<i>Syngnathus floridae</i>	c	-	-	-	-	-	-	-	-	-	0.01	0.02	0.02	-	-	-	-	-	-	-	-	-	-
	i	-	-	-	-	-	-	-	-	-	-	0.01	-	-	-	0.01	0.03	-	-	-	-	-	-
<i>Syngnathus louisianae</i>	c	-	0.02	-	-	-	0.01	-	-	-	-	-	0.01	-	0.01	-	-	-	0.01	0.10	0.02	0.01	0.03
	i	-	-	0.01	0.04	0.01	0.04	p	p	p	-	-	0.01	-	1.52	0.04	0.06	0.08	0.09	0.25	0.03	-	0.06
<i>Syngnathus scovelli</i>	c	0.01	0.01	-	0.04	0.01	-	0.03	0.06	0.04	0.07	0.01	0.03	0.08	-	0.05	0.01	0.02	-	0.07	0.04	0.01	0.01
	i	p	-	0.03	0.74	0.03	0.09	0.19	0.21	0.25	0.17	0.08	0.33	0.17	0.52	0.34	0.19	0.35	0.30	0.27	0.16	0.09	0.12
<i>Syngnathus sp.</i>	c	0.01	0.06	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	i	p	p	p	p	p	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

(Table 2.1 continued)

Species	a	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	'96	'97	'98	'99	'00	'01	'02	'03	'04	'05	'06	'07
<i>Synodus foetens</i>	c i	0.01 p	0.02 p	- 0.01	0.05 -	0.01 -	- -	- p	0.01 -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
<i>Trachinotus carolinus</i>	c i	- -	- -	0.01 -	0.02 -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	0.03 -	- -	- -	- -
<i>Trichiurus lepturus</i>	c i	0.10 -	0.02 -	- -	- -	0.01 -	- -	0.01 -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
<i>Trinectes maculatus</i>	c i	1.33 p	0.12 0.03	0.02 0.10	0.01 0.01	- 0.01	- 0.01	- 0.04	0.01 0.01	- 0.04	0.01 0.02	- 0.03	- 0.06	- 0.09	- 0.20	- 0.34	- 0.04	- 0.02	- 0.05	- 0.02	- 0.01	- p	- 0.02
<i>Uca pugnax</i>	c i	- -	0.01 -	- p	- 0.01	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -	- -
<i>Xanthidae</i>	c i	- -	- -	- -	- -	- -	- p	- -	- -	- -	- -	- -	- -	- -	- -	0.01 -	- -	- -	- -	- -	- -	- -	- -

The species that contributed most to the dissimilarities in SBDs, with individual mean biomasses between 7.48 and 87.12 g., are mostly consumers such as *Sciaenops ocellatus* (red drum), *Micropterus salmoides* (largemouth bass), and *Mugil cephalus* (striped mullet), that were larger than the species contributing most to the dissimilarities in SADs (mostly *Cyprinodon variegatus* [sheepshead minnow], *Anchoa mitchilli* [bay anchovy], and *Palaemonetes sp.* [grass shrimp]). The latter had individual mean biomasses ranging from 0.012- 1.56 g.

Post-opening increases of red drum, largemouth bass and striped mullet contributed most to dissimilarities between pre- and post-opening SBD differences in the impact area (14.08 %, 5.6 %, and 4.22% respectively; Table 2.2; Figure 2.4).

Table 2.2. SIMPER output showing the species that explain > 50 % of the dissimilarity between the species biomass distributions in the impact area before and after the opening of the CFD. Species are listed in order of their contribution to the dissimilarity; the mean catch per unit effort (biomass; g) pre- and post-opening is displayed.

Species	CPUE (g) Impact (Before)	CPUE (g) Impact (After)	% contribution to dissimilarity	% cumulative contribution
<i>Sciaenops ocellatus</i>	1.27	4.75	14.08	14.08
<i>Micropterus salmoides</i>	0.19	1.57	5.6	19.68
<i>Mugil cephalus</i>	2.83	3.75	4.22	23.91
<i>Dorosoma cepedianum</i>	1.36	2.32	4.18	28.09
<i>Bagre marinus</i>	1.47	0.91	3.99	32.08
<i>Cynoscion nebulosus</i>	2.26	3.09	3.63	35.7
<i>Lepisosteus oculatus</i>	1.04	1.88	3.54	39.24
<i>Archosargus probatoccephalus</i>	2.31	1.52	3.2	42.44
<i>Arius felis</i>	2.8	2.34	2.6	45.04
<i>Lepisosteus spatula</i>	1.2	1.11	2.49	47.53
<i>Fundulus grandis</i>	0.77	0.2	2.28	49.8
<i>Lepomis microlophus</i>	0.43	0.92	2.27	52.07



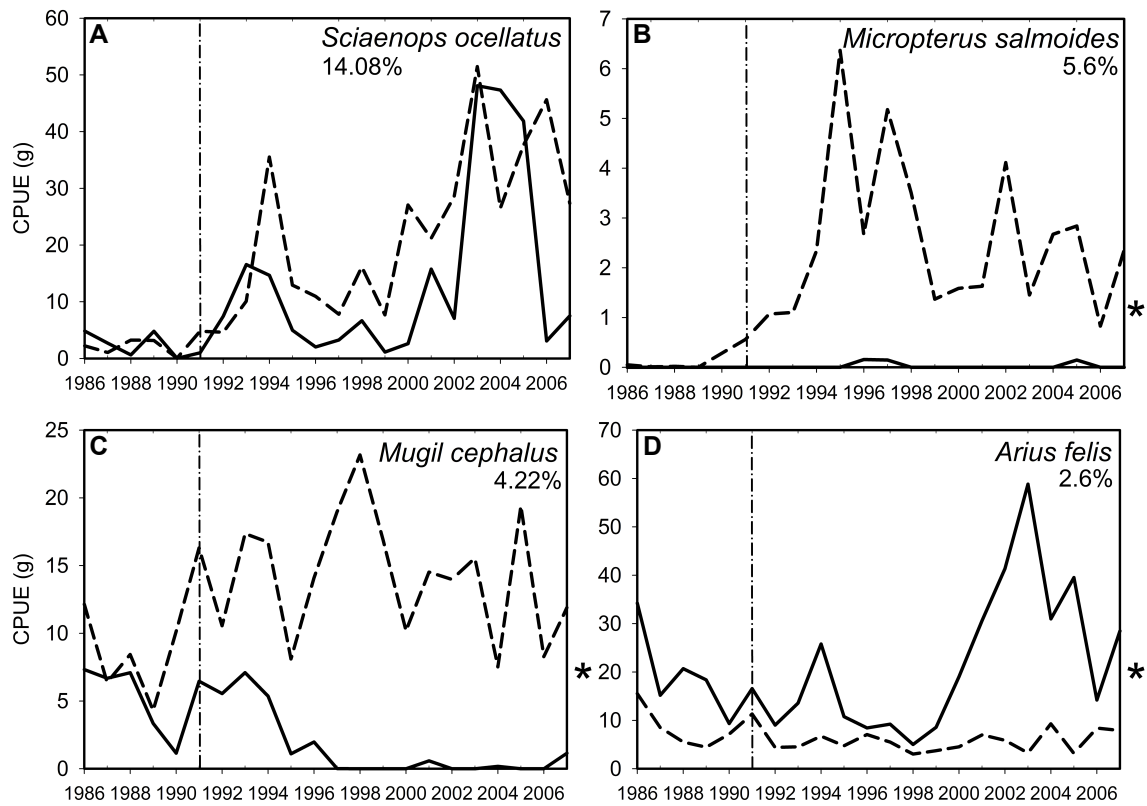


Figure 2.4. The yearly mean catch per seine tow (g) of A) *Sciaenops ocellatus*, B) *Micropterus salmoides*, C) *Mugil cephalus*, and D) *Arius felis* in the control area (solid line) and the impact area (dashed line) from 1986 to 2007. The selection consists of the species with the highest percent contribution to the dissimilarities between the species biomass distributions (see Tables 2.2 and 2.4). The opening of the CFD is indicated with a vertical dashed line, the percent contribution to the dissimilarity between the pre- and post-opening species biomass distributions in the impact area is indicated with a percentage in each figure, and significant differences between the biomass of each species in the control and impact after the opening of the CFD are indicated with an asterisk.

Decreases in abundance of sheepshead minnow, followed by increases of bay anchovy and grass shrimp contributed most to dissimilarities in SADs (8.82%, 7.84%, and 6.48% respectively; Table 2.3; Figure 2.5).

Table 2.3. SIMPER output showing the species that explain > 50 % of the dissimilarity between the species abundance distributions in the impact area before and after the opening of the CFD. Species are listed in order of their contribution to the dissimilarity; the abundance pre- and post-opening is displayed.

Species	Abundance Impact (Before)	Abundance Impact (After)	% contribution to dissimilarity	% cumulative contribution
<i>Cyprinodon variegatus</i>	3.43	0.78	8.82	8.82
<i>Anchoa mitchilli</i>	3.1	5.04	7.84	16.66
<i>Palaemonetes sp.</i>	4.54	4.9	6.48	23.14
<i>Poecilia latipinna</i>	2.46	0.68	6.16	29.3
<i>Fundulus grandis</i>	2.03	0.59	4.77	34.07
<i>Brevoortia patronus</i>	2.15	2.69	4.33	38.4
<i>Lucania parva</i>	2.15	2.57	4.06	42.46
<i>Adinia xenica</i>	1.25	0.19	3.6	46.06
<i>Menidia beryllina</i>	2.36	1.57	3.22	49.27
<i>Fundulus pulvereus</i>	0.84	0.16	2.23	51.51

Species biomass differences that accounted for more than 25% of the dissimilarity in SBDs between the control and the impact areas post-opening were higher biomass of striped mullet (10.42%) and red drum (7.89%), and lower biomass of *Arius felis* (hardhead catfish; 7.07%) in the impact versus the control area (Table 2.4; Figure 2.4).

Higher abundances in the impact area of grass shrimp, bay anchovy, and gulf menhaden contributed most (> 25%) to dissimilarity in SADs between the control and impact area post-opening (10.15%, 7.54%, and 7.34% respectively; Table 2.5; Figure 2.5).

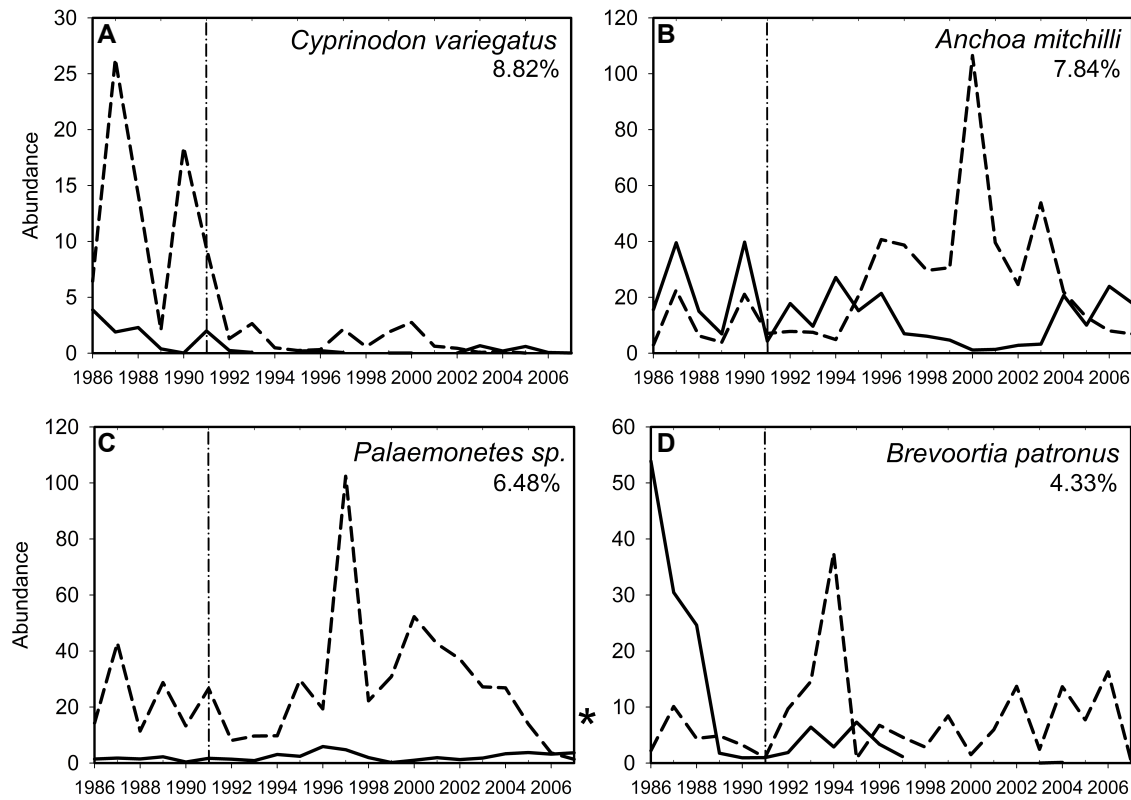


Figure 2.5. The yearly mean number of specimens per seine tow (abundance) of A) *Cyprinodon variegatus*, B) *Anchoa mitchilli*, C) *Palaemonetes sp.*, and D) *Brevoortia patronus* in the control area (solid line) and the impact area (dashed line) from 1986 to 2007. The selection consists of the species with the highest percent contribution to the dissimilarities between the species abundance distributions (see Tables 2.3 and 2.5). The opening of the CFD is indicated with a vertical dashed line, the percent contribution to the dissimilarity between the pre- and post-opening species abundance distributions in the impact area is indicated with a percentage in each figure, and significant differences between the abundance of each species in the control and impact after the opening of the CFD are indicated with an asterisk.

Table 2.4. SIMPER output showing the species that explain > 50 % of the dissimilarity between the species biomass distributions in the impact area versus the control area after the opening of the CFD. Species are listed in order of their contribution to the dissimilarity; the mean catch per unit effort (g) in the control and impact areas is displayed.

Species	CPUE (g) Control (After)	CPUE (g) Impact (After)	% contribution to dissimilarity	% cumulative contribution
<i>Mugil cephalus</i>	0.65	3.75	10.42	10.42
<i>Sciaenops ocellatus</i>	3.34	4.75	7.89	18.31
<i>Arius felis</i>	4.54	2.34	7.07	25.38
<i>Dorosoma cepedianum</i>	0.61	2.32	5.64	31.02
<i>Micropterus salmoides</i>	0.08	1.57	4.96	35.98
<i>Lepisosteus oculatus</i>	0.41	1.88	4.95	40.93
<i>Leiostomus xanthurus</i>	0.44	1.73	4.56	45.48
<i>Pogonias cromis</i>	2.16	1.16	4.08	49.57
<i>Lepisosteus spatula</i>	0.67	1.11	3.22	52.78

Table 2.5. SIMPER output showing the species that explain > 50 % of the dissimilarity between the species abundance distributions in the impact area versus the control area after the opening of the CFD. Species are listed in order of their contribution to the dissimilarity; the mean abundance per unit effort (number of individuals) in the control and impact areas is displayed.

Species	Abundance Control (After)	Abundance Impact (After)	% contribution to dissimilarity	% cumulative contribution
<i>Palaemonetes sp.</i>	1.54	4.9	10.15	10.15
<i>Anchoa mitchilli</i>	3.11	5.04	7.54	17.69
<i>Brevoortia patronus</i>	0.7	2.69	7.34	25.03
<i>Lucania parva</i>	0.18	2.57	7.06	32.09
<i>Micropogonias undulatus</i>	0.35	1.58	4.01	36.1
<i>Menidia beryllina</i>	2.41	1.57	3.25	39.35
<i>Callinectes sapidus</i>	0.28	1.1	2.73	42.08
<i>Farfantepenaeus aztecus</i>	0.33	1.09	2.72	44.8
<i>Mugil cephalus</i>	0.21	1.04	2.71	47.51
<i>Microgobius gulosus</i>	0.06	0.9	2.54	50.05

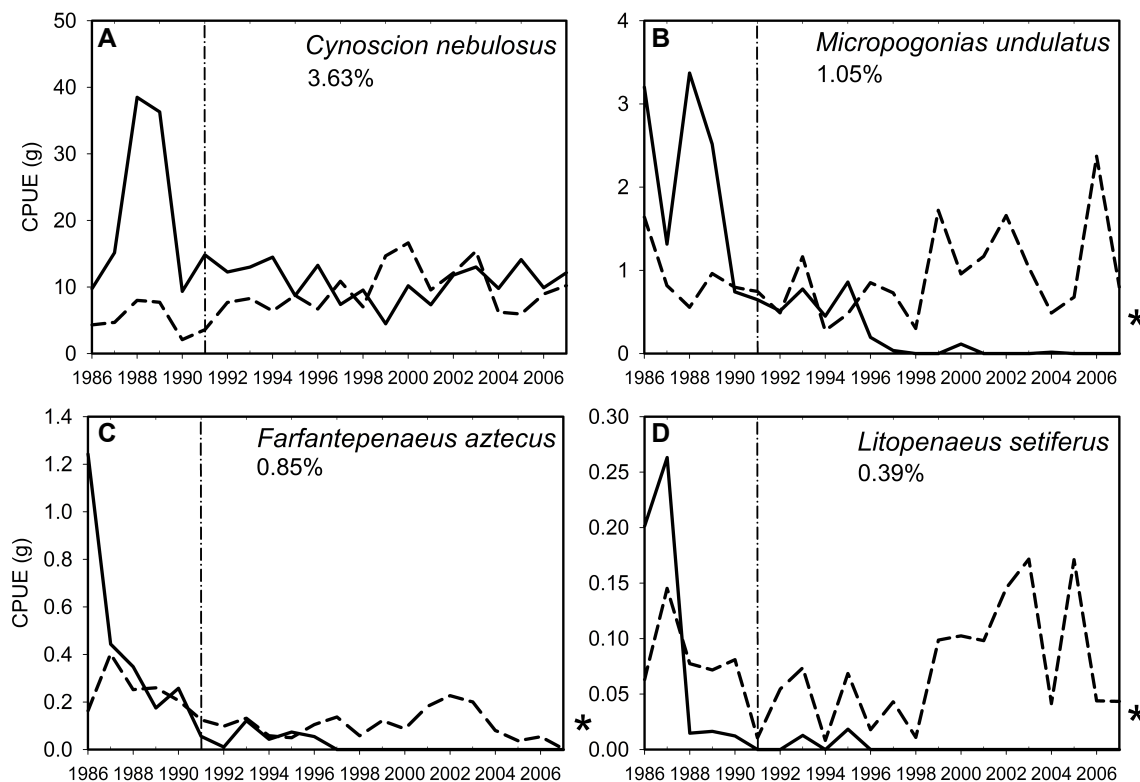


Figure 2.6. The yearly mean catch per seine tow (g) of A) *Cynoscion nebulosus*, B) *Micropogonias undulatus*, C) *Farfantepenaeus aztecus*, and D) *Litopenaeus setiferus* in the control area (solid line) and the impact area (dashed line) from 1986 to 2007. The selection consists of the species that have high ecological or economical importance and are not yet represented in Figures 2.4 or 2.5. The opening of the CFD is indicated with a vertical dashed line, the percent contribution to the dissimilarity between the pre- and post-opening species biomass distributions in the impact area is indicated with a percentage in each figure, and significant differences between the biomass of each species in the control and impact after the opening of the CFD are indicated with an asterisk.

Other species highlighted for their economical or ecological importance (spotted seatrout, Atlantic croaker, brown shrimp and white shrimp) responded either neutrally or positively to the opening of the CFD (Figure 2.6).

The impact area had significantly higher total abundance than the control area ( $t = -4.54$ ,  $p = 0.0003$ ), while there is no significant difference between the total biomass of the control and impact area after the opening of the CFD (Figure 2.7A-B). There was a significant decrease in the number of species in the control area post-opening ( $t = -5.74$ ,  $p < 0.0001$ ), while there was no

change in the number of species in the impact area during the same time period ( $t = -0.33$ ,  $p = 0.7452$ ). The mean weight of individuals was significantly lower in the impact area than the control area post-opening ( $t = 2.94$ ,  $p = 0.006$ ), while there was no significant difference between the two areas pre-opening ( $t = 1.61$ ,  $p = 0.1463$ ; Figure 2.7D).

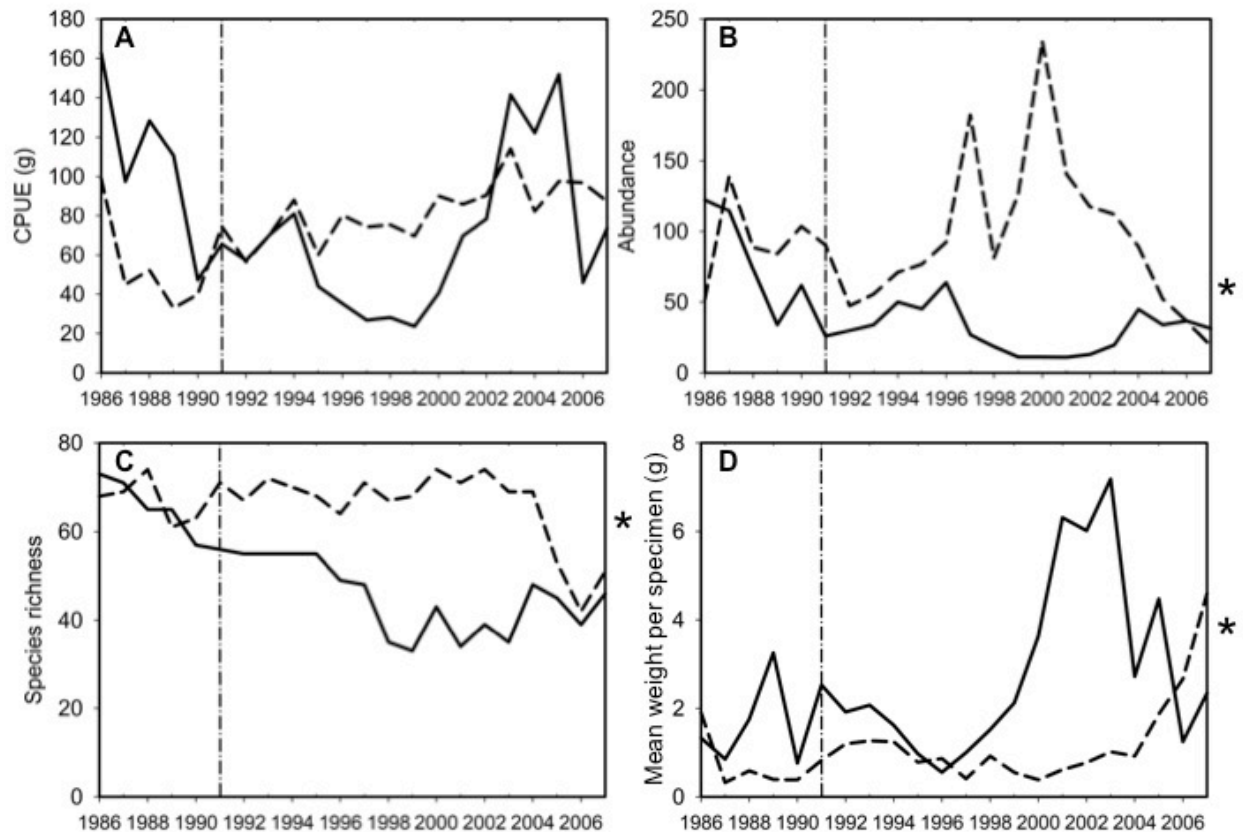


Figure 2.7. Yearly means of A) the catch per seine tow in grams, B) the abundance per seine tow in number of specimens, and D) the weight per specimen in the control area (solid line) and the impact area (dashed line) from 1986 to 2007; 7C shows the total number of species collected per year per area. The asterisk indicates significant differences between the control and impact after the opening (7A, B and D), or a significant decrease in the control area (7C). The opening of the CFD is indicated with a vertical dashed line in all figures.

No statistics were performed to test the effects of Hurricane Katrina, since only 3 years (= data points) are available for analysis. Some interesting observations can still be made (Figure 2.7). The abundance in the impact area decreased 5-fold from 2004 to 2007 until it reached the

level of abundance in the control area, while over the same time period the mean weight per specimen in the impact area increased 5-fold. No obvious changes in mean total biomass per year were visible. The number of species per year decreases by 0.33 in the inflow area due to Hurricane Katrina, while no effect was observed in the control area.

## **DISCUSSION**

The opening of the CFD caused a significant decrease in salinities in the impact area, and significant changes in the nekton community in that area. The species biomass distributions, as well as the species abundance distributions were significantly different pre- versus post-opening of the CFD. Additional pairwise comparisons revealed that both distributions were also significantly different between the control and impact area post-opening. The estuarine species showing the most significant changes, in general, exhibited increases in abundance and biomass after opening of the CFD in the inflow area.

### **Salinity**

Measurements showed that the opening of the CFD caused a decrease in salinity in both the impact as well as the control area, while the mean salinities in impact area were lower than the control area prior to opening of the CFD. This makes my analyses a comparison between two treatment levels, rather than a comparison between 'no effect' in the control area versus a freshwater effect in the impact area (Downes 2002). There is likely some freshwater seepage through the levee separating the two areas. However, The BACI analysis revealed a significantly larger decrease in salinity in the impact area compared to the control area, therefore the CFD did cause a greater effect on the impact area than the control area.

Interestingly, the mean salinity in the control area post-opening decreased to a level that is not significantly different from the mean salinity in the impact area pre-opening. Therefore, it is possible to interpret the control area as a space-for-time substitution, with similar salinity

conditions as the pre-opening impact area. Because of this, pairwise comparisons between the control and the impact area following the opening of the CFD provide additional insight in the effect of the CFD.

### **Community-wide Effects**

Significant interactions in the BACI analyses indicated the presence of an effect of observed salinity changes on nekton SBD and SAD most clearly. Additional pairwise comparisons revealed that the pre-and post-opening communities in the impact area, as well as the communities in the control and impact area after opening, differ. The finding of no significant difference between control and impact before the opening of the diversion supports the contention that the observed change is due to the opening of the CFD, but this finding could also be due, in part, to the low number of permutations possible with five pre-opening years; this is suspected due to the high R-values, which are usually an indication of significant differences (Clarke and Warwick 2001). In some selected individual species, an initial difference is seen between control and impact areas, with high biomass in the control area followed by a large decline before (and unrelated to) the opening of the CFD (Figure 2.6). Analyzing the change in difference only between control and impact areas could potentially result in a false positive effect of the CFD. Because of this, the actual biomass and abundance of the highlighted species in the control and the impact area are discussed and compared in the pairwise comparisons, instead of examining the trend in the control-impact difference in a BACIP design.

The majority of the species that contributed > 50% to the dissimilarities between pre-and post-opening SBDs and SADs, or between control and impact area SBDs and SADs, had a positive response to the CFD by increased biomass or abundance (see Individual Species Increases section). A previous study higher up the same estuary also documented higher nekton abundance and biomass with fresh-water flow compared to the area not receiving flow (Piazza



and La Peyre 2007). Other previous findings in the same estuary include increases in density and biomass of grass shrimp with freshwater flow, and no change in brown shrimp (Rozas et al. 2005b; Day et al. 2009). This concurs with the significantly higher abundance of grass shrimp in the impact versus the control area found in this study, and no significant difference between control and impact of brown shrimp. In general, Rozas et al. (2005b) found that changes in density and biomass, rather than changes in community composition, occurred as a result of the freshwater inflow.

My results demonstrate differences in allocation or distribution of biomass among nekton species, as opposed to total biomass, while for abundance both the distribution among species as well as total abundance changed. Total abundance was significantly higher in the impact versus the control area after the opening of the CFD. The combination of higher numbers of consumers without a change in total biomass may be indicative of improved nursery function in the impact area compared to the control area. The mean weight (size) per individual is significantly smaller in the impact than the control area. This difference is likely attributable to fewer marine predators using the area because of lowered salinities, thereby resulting in higher numbers of small, juvenile estuarine nektors in the impact area.

The effect of the CFD on species richness is interesting; the number of species declined in the control area post-opening, while there was no change in the impact area. The mean salinity measured in the impact area post-opening (~8) usually is associated with lower species diversity than the mean salinity in the impact area pre-opening (~11; Wetzel, 1983, Levinton 2001). Hence, no decrease in diversity in the impact may be attributable to the salinity gradient created by the diversion, which acted to create habitat for species with different salinity preferences. Post-opening, the impact area can support species typically found in the 0-5 ppt range (Wetzel 1983) in addition to species typically found in the 5-18 ppt range. Salinity distribution in the

control area is more uniform than in the impact area, and salinity declined as a function of minimal amounts of freshwater seeping through the levee separating the areas. Overall uniform salinity declines in areas normally ranging from 10-20 ppt, typically causes a drop in the number of species (Wetzel 1983); this corresponds with the species decline seen in the control area. Without sufficient flows to create areas in an estuary that have salinities  $< 5$  ppt, many primary freshwater nekton cannot occur.

### **Individual Species Increases**

The selection of species is based upon importance as defined in the analyses or by ecological or economical importance. Because their response to the CFD is mostly positive, I infer that in general, effects of opening of the CFD on the nekton community in the impact area are positive. For example, the most significant post-opening increase in biomass is that of red drum. This species, though not picked *a priori* in my study, is one of the most popular sport-fish in Louisiana (Frimodt 1995). In addition, all species chosen *a priori* as economically or ecologically important (white shrimp, brown shrimp, gulf menhaden, spotted seatrout, Atlantic croaker and largemouth bass) either increased or did not change in the impact area when compared to pre-opening conditions, or in the control area.

This result is especially encouraging concerning spotted seatrout and brown shrimp. These species are thought to be associated with relatively high estuarine salinities (Gunter 1964; Frimodt 1995), but they did not decrease in response to the opening of the CFD. In contrast, Reed et al. (2007) did find a positive relationship between brown shrimp biomass and salinity in Barataria Bay, Louisiana, but concluded that the probable cause was the association of higher salinities with more preferred broken marsh habitats, and proximity to the Gulf of Mexico source of recruitment (Etherington and Eggleston 2003). Rozas et al. (2005b) reported that the salinity preference of brown shrimp was difficult to determine in a study in Breton Sound. With poor

information on brown shrimp salinity preferences, maintaining a salinity gradient with multiple habitats seems prudent.

One species that likely is responding positively and directly to a decrease in salinity is largemouth bass. Largemouth bass is a primary freshwater species, but in Louisiana it is found in salinities of  $\leq 3.0$  ppt (Louisiana Department of Wildlife and Fisheries, unpublished data). Even though largemouth bass in Louisiana may be able to tolerate higher salinities than elsewhere, salinities were mostly too high for the bass prior to opening of the diversion in the impact area, or in the control area; its occurrence in the inflow area is therefore likely a direct effect of the decrease in salinity.

That said, it is likely that individual species responses to the CFD opening are not driven by salinity alone. Habitat changes probably also play a role. Rozas et al (2005b) found increases in SAV in the freshened Breton Sound impact area, and concluded that species that use SAV as nursery habitat most likely benefited from SAV increases. Increased abundance of small species like grass shrimp in my study are likely a reflection of the increase in SAV.

Freshwater diversion could also lead to changes in nutrient and energy transfers in the food web (Wissel and Fry 2005; Goecker et al. 2009). The observed increase of the euryhaline striped mullet is likely one example of such changes. The diet of striped mullet consists in large part of micro-algae and organisms that feed directly on micro-algae (Blaber 1976). As such, increases in nutrient concentrations with freshwater inflow (Day and Ko 2003) resulting in increased algal biomass, likely also contributed to the increase in mullet in the impact area (Cardona 2000). The occurrence of overall increases in secondary productivity in response to increased nutrient loading is well documented (Cushing 1975; Nixon 1988; Iverson 1990; Nixon and Buckley 2002; Rozas et al. 2005b). To determine the extent to which the diversion may have

altered the food web and food web pathways, a stable isotope study that includes nekton is desirable (Rozas et al. 2005b; Goecker et al. 2009). Such a study is described in Chapter 4.

### **Individual Species Decreases**

Species that contributed most to the dissimilarities between biomass distributions, but have less biomass in the impact area post-opening, as compared to pre-opening or the control area, are hardhead catfish, gafftopsail catfish (*Bagre marinus*), black drum (*Pogonias cromis*), and sheepshead (*Archosargus probatocephalus*). Of these species, hardhead catfish contributed most to the dissimilarities in SBD between the control and impact areas. The difference in biomass of hardhead catfish was caused by an increase in the control area instead of a decrease in the impact area after the opening of the CFD. The catfishes are not highly valued as sport or food fish, which means their increase is not economically important.

From an ecological point of view, all above-mentioned species are either omnivores or carnivores; their decline may increase survival of juveniles of other species in the area. Declines in black drum and sheepshead may also result in a reduction in oyster predation (Brown et al. 2008; George et al. 2008). Black drum predation on oysters has been recognized as problematic to the extent that methods to deter black drum from oyster predation have been studied (Brown et al. 2003; Brown et al. 2006; George et al. 2008). By reducing predation pressure, the CFD might provide an indirect positive effect on oysters.

The species with the most significant decrease in abundance in the impact area after the opening of the CFD (sheepshead minnow) still showed slightly higher abundances in the impact than the control area, where it is not abundant.

### **Effects of Hurricane Katrina**

Hurricane Katrina (2005) had a large impact on the abundance of juvenile estuarine nekton. It caused a surge of saltwater into the impact area, increasing salinities (Steyer et al.

2007). A 5-fold decrease in nekton abundance in the impact area coincides with a 5-fold increase in individual mean weight from 2004 to 2007, an indication that juvenile nekton may have been disproportionately affected. Such changes were not observed in the control area, where salinities remained uniformly high. It is interesting to note that increases in mean weight per specimen offset decreases in abundances in such a way that no hurricane effect can be detected in total nekton biomass in the impact area, emphasizing the need for detailed analyses when investigating ecosystem impacts on nekton.

Species richness also decreased in the impact area in response to Hurricane Katrina, down to the level in the control area. This also was likely attributable to saltwater intrusion, hence this event had less affect on the control area. Saltwater intrusion is known to cause decreases in nekton species-richness (Love et al. 2008), the effects of which in this case may have been enhanced by eliminating the aforementioned salinity gradient, turning the impact area into a uniform brackish environment that supported fewer species of nekton (Wetzel 1983, Levington 2001). Species richness has increased in the impact area since 2006, likely a result of the salinity gradient that now exists again owing to increased freshwater input through the CFD. A study directly following Hurricane Katrina demonstrated that there was a temporary shift from a tidal freshwater/resident community to a brackish/migrant community in the upper estuary of Breton Sound, which shifted back by Spring 2007 (Piazza and La Peyre 2009). This supports previous assumptions. Piazza and La Peyre (2009) also concluded that the nekton community in Breton Sound in general demonstrated resilience in the face of enduring physical habitat changes, which has likely been a factor in the mostly positive or neutral responses to the changes induced by the CFD.

## Conclusions

In conclusion, the CFD changed the salinity and nekton community, and species biomass and abundance distributions, in the Breton Sound estuary. There was no difference in total biomass between the control and impact area, which means differences lie in the allocation of biomass in the nekton communities. In addition, higher abundance and lower individual mean weight distinguished the nekton community in the inflow area from the control area. This result indicates that the CFD may have created an area with higher nursery function than the area without freshwater inflow. Selected nekton species of ecological or economical importance either: 1) increased in biomass after the opening of the CFD; 2) had higher biomass in the impact area than the control area; or 3) were not significantly affected. The saltwater intrusion caused by Hurricane Katrina caused a brief decline in the number of species and abundance of juveniles in the impact area, which emphasized the negative effect of high uniform salinities in an estuary. Restoring the salinity gradient by means of the CFD is likely reversing this process. Overall, using river diversions in restoration projects to build land and restore wetlands in Louisiana estuaries should not be discouraged because of presumed negative impacts on higher trophic levels.

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## **CHAPTER 3**

### **THE RELATION BETWEEN ENVIRONMENTAL FACTORS, NEKTON HABITAT USE, AND COMMUNITY STRUCTURE IN LOUISIANA ESTUARIES WITH DIFFERENT HYDROLOGICAL REGIMES**

#### **INTRODUCTION**

Most of coastal Louisiana has been hydrologically isolated from the Mississippi River since the early 1900s, which has caused subsidence, saltwater intrusion and coastal erosion (Mossa 1996; Lane et al. 1999; Lane et al. 2007). Learning from the historical processes that have built the vast deltaic plain during the Holocene (Roberts 1997), one practical and sustainable solution to wetland loss could be the creation of river diversions to stimulate sediment deposition in areas now starved of sediment inputs, and to institute salinity reductions in areas suffering from saltwater intrusion (Chatry and Chew 1985).

The second largest diversion that is currently operational in Louisiana is the Caernarvon Freshwater Diversion (CFD). This diversion is capable of diverting  $226 \text{ m}^3 \text{ s}^{-1}$  of Mississippi water into the Breton Sound estuary; however, the mean discharge has been  $45 \text{ m}^3 \text{ s}^{-1}$  (SUNRIS-[www.dnr.state.la.us](http://www.dnr.state.la.us)). It was originally constructed in 1991 to stimulate the oyster fishery (Chatry et al. 1983); more recently the CFD is being used as a measure to control salinity and restore the coastal wetlands of the Breton Sound estuary, an area that has been suffering heavily from habitat degradation, salt water intrusion and wetland loss (Lane et al. 1999).

Building or maintaining wetlands is believed to be beneficial to nekton and fisheries (Cowan et al. 2008), as estuaries are widely recognized as nursery areas, and catches in the Gulf of Mexico are dominated by estuarine-dependent nekton (Gunter 1967; McHugh 1967; Houde and Rutherford 1993). If the CFD successfully builds land, nekton habitat and nursery grounds could be expanded, which could have a positive effect on estuarine nekton. Even if the area of sediment deposition is too limited to expand wetlands (Wheelock 2003), given mean relative sea-

level rise in Louisiana ( $10 \text{ mm yr}^{-1}$ ; Penland and Ramsey 1990), deposition of sediments will be necessary just to sustain existing wetlands.

There are other immediate effects of the restoration of a hydrological connection to the Mississippi River. Physico-chemical factors, notably salinity and nutrients, but also temperature, water level, dissolved oxygen (DO), turbidity, and pH are likely to change with the input of Mississippi River water (Turner and Rabalais 1991; Lane 1999; Wheelock 2003; Piazza and La Peyre 2007; Day 2009b). Extensive monitoring and scientific research is needed to evaluate the effects of these alterations on wetlands functioning. The wetland function I focused on in this study is relative habitat value for estuarine nekton communities. Habitat use by nekton is often related to abiotic variables such as salinity (Rakocinski et al. 1992; Evans 1993), temperature (Neill and Magnuson 1974), DO (Pihl et al. 1991), turbidity (Benfield and Minello 1996), water level (Thomas and Connolly 2001; Piazza and La Peyre 2007; Kimmerer et al 2009), and pH (Rago and Wiener 1986), and other environmental variables such as submerged aquatic vegetation (SAV) coverage (Rozas and Odum 1988) and emergent marsh vegetation (Rakocinski et al. 1992; Thomas and Connolly 2001). Controversy about diverting Mississippi River water has included expectations of eutrophication of the estuary (Turner and Rabalais 1991; but also read Lane et al., 1999), the reduction of oyster production (Turner 2006; but also read Buzan et al. 2009 and La Peyre et al. 2009), and the displacement of recreationally and commercially important nekton species like spotted seatrout (*Cynoscion nebulosus*; Serafy et al. 1997; USACOE 2004) and brown shrimp (*Farfantepenaeus aztecus*; Rozas et al. 2005; USACOE 2004).

To evaluate the effects of the CFD since its opening, environmental variables and nekton species biomass distributions (SBD) in the inflow area were compared to those in a control area in the Breton Sound estuary that is essentially blocked from the diversion inflow by a levee. In

addition, the inflow area should be compared, if possible, to historical ecosystem conditions using data collected prior to anthropogenic impacts to the ecosystem as a benchmark (Trexler et al. 2003). However, an historic record from this area before the construction of levees along the Mississippi River is not available. To address this problem, I compared the environmental and biological characteristics of Breton Sound to an estuary (Fourleague Bay, the reference area) that receives freshwater inflow from the Atchafalaya River, which currently is the only natural freshwater diversion in Louisiana.

The goals of this study were: 1) to determine if the restored hydrological connection in Breton Sound changed the nekton community and environmental characteristics; and 2) to determine how environmental variables are related to observed differences in the nekton communities of the CFD inflow area, the control area, and the reference area. The null hypothesis is that there are no differences among the three areas. To accomplish these goals, environmental variables and nekton were monitored and sampled from October 2006 to February 2008 at the three areas. Differences among the areas based both upon environmental variables and on SBDs, as well as the relationships between the two sets of variables, were determined using multivariate analyses. Using this approach I examined habitat use of nekton in areas with different hydrological regimes.

## **MATERIALS AND METHODS**

### **Study Area**

A total of twelve study sites were established to perform this study. Eight study sites are in the Breton Sound estuary (Figure 3.1). At the northwest end of the estuary, Mississippi River water flows in through the CFD. Six sites (three pairs of replicated stations) are located in the diversion inflow area at approximately 15, 25, and 35 km from the diversion; these are referred to as the low, medium and high (salinity) inflow sites. These sites are located along the eastern

route (Figure 3.1; Lane et al. 1999; Day et al. 2009b), which is the route that the majority of the freshwater discharge follows down the estuary (Snedden et al. 2007). As such, the sites are located along a salinity gradient, with observed salinities varying from 0.2 ppt at the in the upper estuary sites to 17 ppt in the sites at the southern end of the estuary. Two sites (one pair of replicated stations) are located in Breton Sound in an area that is mostly isolated from diverted freshwater flow by a levee; these are the control sites. Four reference sites (two pairs of replicated stations) are located in the Fourleague Bay area (Figure 3.2). This area is hydrologically connected to the Atchafalaya River, and freshwater from the Atchafalaya River reaches this area seasonally. The Atchafalaya basin currently receives 30% of the Mississippi River discharge, and, in coastal Louisiana, most closely resembles an estuary with unaltered hydrological connections to upstream sources of river water. This basin is the only area in coastal Louisiana where land is being built instead of lost. More detailed information on this area can be found in Van Heerden and Roberts (1980). The reference sites were located at two different distances from the Gulf of Mexico to create low and high (salinity) reference sites. The dominant plant species in both estuaries are *Spartina alterniflora* and *Spartina patens*, which are intermixed and gradually replaced by various other plant species going upstream to lower salinity areas.

### **Field Methods**

Nekton and environmental data were collected bi-monthly in Breton Sound and quarterly in Fourleague Bay from October 2006 until February 2008. Nekton was collected by deploying a 15.24 meter bag seine (bag size 1.44 m<sup>2</sup>) with 0.63 cm mesh, two times per sampling trip at each site. One end of the net remained on the marsh edge while the other end was pulled out with a boat powered by an electric trolling motor and towed back to the marsh in a quarter circle. All

nekton collected was put on ice and weighed to the nearest 0.1 g wet weight, measured (TL in mm) and identified to the lowest possible taxonomic level once returned to the laboratory.

An YSI hydrosonde was placed at each site at  $\pm 7$  m off the marsh edge, which is the same distance from the marsh edge to which the bag of the seine extends during collections. During each sampling trip, the hydrosonde recorded temperature ( $^{\circ}\text{C}$ ), pH, conductivity (salinity; ppt), water depth (cm), turbidity (NTU) and dissolved oxygen (% and  $\text{mg l}^{-1}$ ) every 5 minutes.



Figure 3.1. Areal photograph of Breton Sound; sampling sites are indicated. The CFD is indicated at the northwest end of the estuary. The main route of freshwater flow, the 'eastern route', is indicated with a dotted line. The sites in the inflow area; L1 and L2, M1 and M2, and H1 and H2 are positioned from low to high salinity along a salinity gradient, while the control sites (C1 and C2) are separated from most of the freshwater flow by a levee.



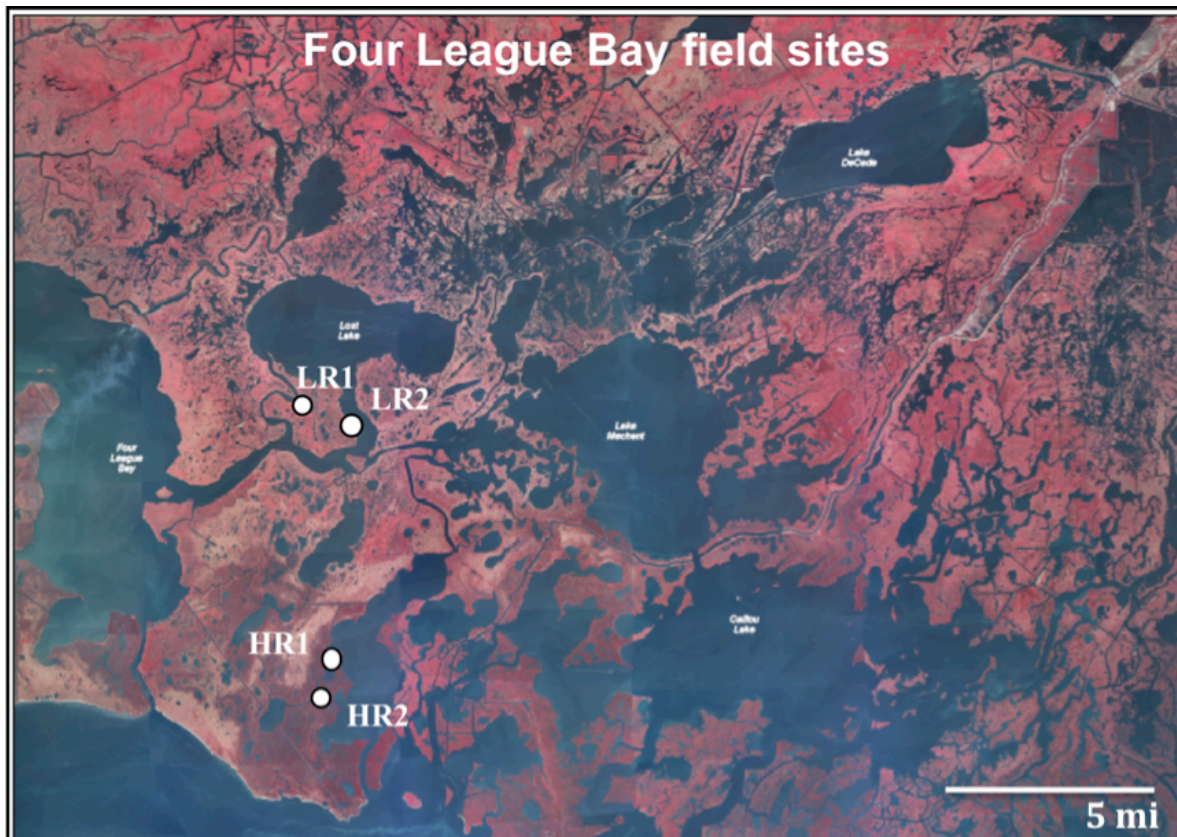


Figure 3.2. Aerial photograph of Fourleague Bay; sampling sites are indicated. The low reference sites (LR1 and LR2) are positioned higher in the estuary than the high reference sites (HR1 and HR2). The low salinity sites have a natural hydrological connection with the Atchafalaya River, while the high salinity sites are more tidal.

Submerged aquatic vegetation (SAV) was collected by raking the inside of a  $0.25 \text{ m}^2$  quadrat six times; the metal quadrat was haphazardly thrown three times into the water at the marsh edge and three times midwater ( $> 7 \text{ m}$  from the marsh edge). The same quadrat was used to collect marsh vegetation; it was haphazardly thrown onto the marsh surface near the edge three times; one quadrat of marsh vegetation was clipped at the base of the plant stem, and two quadrats were counted. Stem density was recorded for all quadrats. The collected plants and SAV were identified to the lowest taxonomic level, dried for 48 hours at  $60^\circ \text{C}$  and weighed to the nearest  $0.1 \text{ g}$  dry weight.



## Data Analysis

The data were analyzed using PRIMER 6 & PERMANOVA+ (Anderson et al. 2008). For the multivariate analyses, only trips where all of the variables were collected were included in the analysis to avoid an unbalanced dataset; this resulted in 56 samples. Each trip to each site is treated as a sample. To test for seasonal differences, I created the factor 'season' (in addition to the factor 'site') with the levels spring (March, April, and May), summer (June, July and August), fall (September, October and November), and winter (December, January and February).

I first tested for salinity differences among sites, because salinity was expected to directly reflect differences in hydrological connectivity among sites. Because the residuals of the salinity data were not normally distributed, I used a non-parametric test in PRIMER to test for salinity differences between the sites. I performed a PERMANOVA main test with a site x season design on salinity, followed by pairwise comparisons between sites across all seasons, and on all site-season combinations. These tests permitted comparison among sites within season, and between the seasonal samples of the same site. An  $\alpha$ -level of 0.01 was used for pairwise comparisons to minimize the likelihood of experiment-wide error (Sokal and Rohlf 1995).

The following environmental variables were used in the multivariate analyses: marsh vegetation biomass (g dry weight/ 0.25 m<sup>2</sup>), SAV biomass (g dry weight/ 0.75 m<sup>2</sup>), marsh vegetation stem density (number of stems/ 0.25 m<sup>2</sup>), marsh vegetation species richness (number of species/ 0.25 m<sup>2</sup>), water temperature (°C), depth (m), pH, turbidity (NTU), salinity (ppt) and dissolved oxygen (mg l<sup>-1</sup>). All variables were normalized to the mean to reduce scalar effects. A principal component analyses (PCA) on the normalized data was performed in PRIMER. After creating a resemblance matrix using Euclidean distance of the first five PCA axis scores of each multivariate sample, a PERMANOVA was performed with a site x season design to determine

whether significant differences existed among sites and seasons; pairwise tests were used to determine specific differences among sites.

Samples used in the nekton analyses are the SBD per unit effort, where one unit of effort is two seine tows per site, per sampling trip. The same 56 trips where all environmental variables were collected are samples in the nekton analyses. The values of the variables in analyses including nekton are the biomasses (g) of the species that were collected in at least one of the samples (0 when a species was not present in that particular sample); this resulted in profiles (samples) with 88 variables. The dataset was pre-treated with a fourth root transformation before analysis to create a balance between the importance of rare and abundant (and heavy and light) species. After creating a resemblance matrix using Bray-Curtis similarity, a PERMANOVA was performed using a site x season design to determine whether significant differences in SBD were detectable between sites and seasons. Pairwise comparisons were used to identify specific differences in SBD among sites. To visualize these differences, a canonical analysis of principal coordinates (CAP) was used to plot nekton SBD groupings between sites along axes that best separated the (*a priori* identified) sites. A CAP analysis is similar to a PCA but for biological data, and displays data on otherwise potentially hidden axes that delineate the greatest separation among sites (Anderson et al. 2008). A PERMANOVA analysis on the axes scores of the CAP analysis to find differences between sites would be meaningless, because this analysis is purposely informed *a priori* to find and display the best separation between the sites (Anderson 2008); therefore the PERMANOVA was performed only with the data from the resemblance matrix.

Finally, a canonical correlation analysis (CCA) was performed using environmental and SBD data simultaneously. This analysis separated nekton SBD on the basis of environmental variables, and determined which environmental variables delineated the separation among

nekton SBD. After creating a resemblance matrix using Euclidean distance of the first five CCA axis scores of each nekton sample, a PERMANOVA was performed with a site x season design to determine whether significant differences in nekton SBD existed among sites and seasons. Pairwise comparisons were used to identify specific differences in SBD among sites. An  $\alpha$ -level of 0.01 was again used for pairwise comparisons to minimize the likelihood of experiment-wide error. In each PERMANOVA test the number of permutations was set to 9999; power and precision increase with the number of permutations (Hope 1968), and a high number of permutations ( $> 4999$ ) should be done to draw inference at a level of 0.01 (Anderson et al. 2008), the number of samples per site and season always allowed for more than 4999 permutations.

## **RESULTS**

Salinity differed significantly among sites and seasons (Figure 3.3). The PERMANOVA main effects test showed that salinity differed both by site and season; pairwise comparisons reveal that salinity differed significantly in almost every combination of site and season from every other combination ( $\alpha = 0.01$ ). Sites also differed significantly from one another when salinity was pooled over season (Table 3.1). Salinities in the inflow area were lowest at the sites closest to the CFD ( $0.9 \text{ ppt} \pm \text{SD } 1.1$ ), followed by the mid-estuary sites ( $4.6 \text{ ppt} \pm \text{SD } 3.2$ ), and highest at the sites farthest from the CFD ( $10.8 \text{ ppt} \pm \text{SD } 3.2$ ). The control sites have lower salinities than expected, given that it was structurally isolated from freshwater inflow ( $3.0 \text{ ppt} \pm \text{SD } 1.9$ ). This result is likely due to freshwater seepage through the levee. The reference sites in Fourleague Bay overall had higher salinities than sites in Breton Sound (upper estuary sites  $6.4 \text{ ppt} \pm \text{SD } 4.5$ ; lower estuary sites  $15.4 \text{ ppt} \pm \text{SD } 4.3$ ), likely due to the fact that these sites are farther removed from their source of freshwater inflow (the Atchafalaya River).

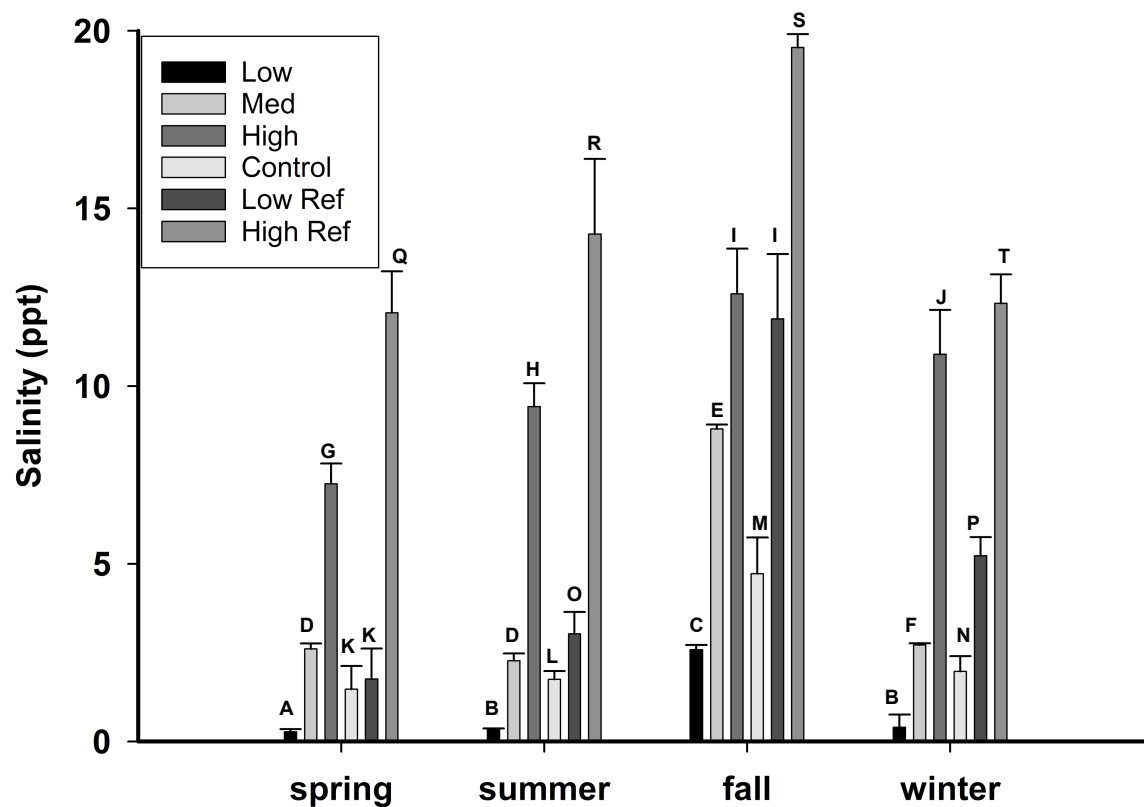


Figure 3.3. The seasonal salinities (in ppt) measured at the six different sets of sites. Measurements were done from October 2006 until February 2008. The letters indicate significant differences at  $\alpha = 0.01$ .

At all sites, highest salinities were observed in fall. Salinities began to decrease in winter, and were lowest in spring. All sites, except for the upper estuary sites in the inflow area, occurred mostly in the range described for brackish marshes (3-18 ppt; Tiner 1993). The upper estuary sites fall in the range of freshwater marshes (0-3 ppt; Tiner 1993).

Principle components analysis (PCA) on environmental variables reveals that salinity is the main variable causing separation between samples, and is responsible for between-site differences (Figure 3.4A). There are five axes (with an eigenvalue  $> 1$ ) along which meaningful separation occurs; most separation is explained by PC axis 1, then by PC axis 2 etc. Other

variables responsible for differences between sites are plant species richness, plant biomass, stem density, pH and SAV biomass. The length of each variable's vector indicates the strength of that variable explaining the separation between samples on the first two PC axes; if a vector line reaches the circle then none of that variable's other eigenvectors will differ from 0. The second longest vector explaining separation on the first PC after salinity is plant species richness, and is inversely related to salinity. This inverse relationship of salinity to plant and SAV variables indicates that, in general, higher salinity sites contained lower plant biomass distributed among fewer species when compared to lower salinity sites.

The separation along the second PC axis is attributable to seasonal differences between the samples (Figure 3.4B). Note that Figure 3.4A and 3.4B are the same PCA plot, but the symbols in Figure 3.4B indicate in which season the samples were collected; in this figure, samples with the same symbol are not necessarily collected at the same site. The main gradients along which seasonal separation occurs are temperature and dissolved oxygen (DO). Temperature varied from a mean over all sites of 14 °C ( $\pm$  SD 4.7) in winter to 32 °C ( $\pm$  SD 1.4) in summer, while DO varied from a mean of 9.2 mg l<sup>-1</sup> ( $\pm$  SD 2.0) in winter to 7.0 mg l<sup>-1</sup> ( $\pm$  SD 1.3) in summer. To a lesser extent, turbidity and depth also cause separation along this axis, and are inversely related to one other in my data.

A PERMANOVA analysis of the PCA scores on the first 5 axes of the environmental variables confirmed that separation among sites and seasons are indeed significantly different ( $\alpha$  = 0.01). Pairwise comparisons between sites revealed that all differed significantly from one other at  $\alpha$  = 0.01, with these exceptions: 1) the medium inflow sites were not significantly different from the low inflow and control sites, and the high inflow sites were not significantly different from the high reference sites (Table 3.1).

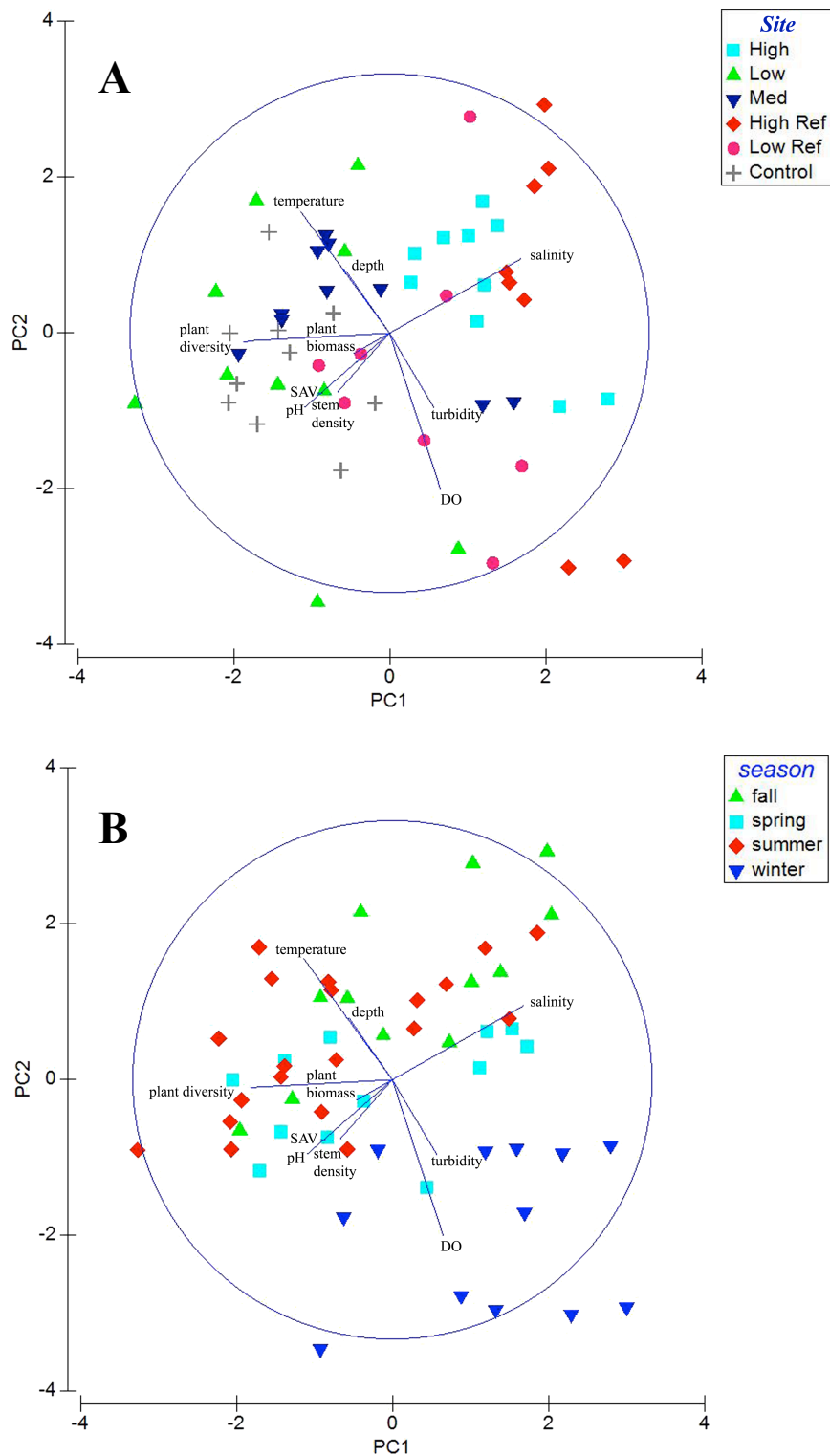


Figure 3.4. A principal component analysis (PCA) of environmental variables. Each symbol consists of the values of all environmental variables collected during one sampling trip. The contribution of each variable in separating the samples is indicated by the direction and the length of the vectors (a combination of the first two eigenvectors). The symbols indicate A) the sites at which the samples were collected, and B) the season in which the samples were collected.

Table 3.1. PERMANOVA pairwise comparisons of sites across seasons. The p-values of each comparison are shown, significant differences between the sites at  $\alpha = 0.01$  are indicated with an \*. Sites are compared with respect to observed salinities, PCA scores of the multivariate environmental variables on the first five axes, the nekton species biomass distributions, and CCA scores of the nekton SBDs on environmental variables on the first five axes.

Pairwise comparison	Salinity	Environmental variable PCA scores	Nekton SBD	Canonical correlation scores
Low-Med	0.0001*	0.0135	0.0010*	0.0048*
Low-High	0.0001*	0.0003*	0.0003*	0.0001*
Low-Control	0.0001*	0.0029*	0.0006*	0.5750
Low-Low Ref	0.0001*	0.0019*	0.0001*	0.0001*
Low-High Ref	0.0001*	0.0005*	0.0001*	0.0001*
Med-High	0.0001*	0.0003*	0.0052*	0.0001*
Med-Control	0.0001*	0.0187	0.0314	0.0684
Med-Low Ref	0.0001*	0.0013*	0.0001*	0.0001*
Med-High Ref	0.0001*	0.0001*	0.0001*	0.0001*
High-Control	0.0001*	0.0001*	0.0001*	0.0001*
High-Low Ref	0.0001*	0.0006*	0.0071*	0.0064*
High-High Ref	0.0001*	0.0392	0.0161	0.0155
Control-Low Ref	0.0001*	0.0002*	0.0001*	0.0001*
Control-High Ref	0.0001*	0.0001*	0.0001*	0.0001*
Low Ref-High Ref	0.0001*	0.0020*	0.1177	0.1613

A total of 17,940 fish and invertebrates were caught in this study, with a combined weight of 67 kg. In total, 88 species, representing 21 families, were collected. The dominant species by number, that together account for 90 % of the total, were in decreasing order: *Palaemonetes pugio* (grass shrimp), *Micropogonias undulatus* (Atlantic croaker), *Anchoa mitchilli* (bay anchovy), *Brevoortia patronus* (gulf menhaden), *Litopenaeus setiferus* (white shrimp), *Lucania parva* (rainwater killifish), *Farfantepenaeus aztecus* (brown shrimp), *Menidia beryllina* (inland silverside), *Callinectes sapidus* (blue crab), *Fundulus grandis* (gulf killifish), *Cyprinodon variegatus* (sheepshead minnow), *Cynoscion arenarius* (sand seatrout), *Leiostomus xanthurus* (spot) and *Lepomis microlophus* (redeer sunfish). The mean species richness per site ranged from 33.5 species at both the low salinity inflow sites and the high salinity reference site, to 41 species at the high salinity inflow sites (Table 3.2). The mean catch per unit effort (CPUE)

per site ranges from 761.5 grams in the high salinity inflow sites to 891.2 grams in the high salinity reference sites (Table 3.2).

Table 3.2. The total number of nekton species and the catch per unit effort (CPUE) at the 6 different field sites ( $\pm$  SE). The low, medium and high sites are in the diversion inflow area in Breton Sound, the control sites are outside the inflow area in Breton Sound, and the low and high reference sites are in Fourleague Bay. A unit of effort is the summed biomass collected in two seine tows at each site.

Site	Nekton Species Richness	CPUE (g)
Low	33.5 ( $\pm$ 4.5)	876.4 ( $\pm$ 142.4)
Medium	34.5 ( $\pm$ 5.5)	791.5 ( $\pm$ 173.5)
High	41 ( $\pm$ 0)	761.5 ( $\pm$ 115.54)
Control	37 ( $\pm$ 3)	764.9 ( $\pm$ 404.5)
Low ref	36 ( $\pm$ 1)	765.5 ( $\pm$ 219.6)
High ref	33.5 ( $\pm$ 1.5)	891.2 ( $\pm$ 280.5)

A PERMANOVA site x season main effects test on mean SBD revealed significant differences in SBD among sites, as well as seasons ( $\alpha = 0.01$ ). The test was performed on a Bray-Curtis similarity matrix created from the fourth-root transformed SBDs. To determine which sites differed significantly from others, pairwise tests were performed. At  $\alpha = 0.01$ , the low and high reference sites, the high reference and high inflow sites, and the medium inflow and control sites did not differ in pairwise comparisons. Otherwise, the 12 additional comparisons identified significant differences in SBD between sites (Table 3.1). A two-way SIMPER analysis was performed to test which species were mostly responsible for similarities within site. Species that cumulatively contribute  $\geq 50\%$  of the similarity between samples collected at the same sites are considered to be characteristic of the site at which they were collected (Table 3.3).



Table 3.3. List of species for each site that contribute  $\geq 50\%$  to SBD similarities within site. The third and fourth columns show the percent contribution to overall similarity within site of each species, and the cumulative percentage, respectively.

Site	Species	% Contribution	Cumulative %
Low	<i>Micropterus salmoides</i>	17.92	17.92
	<i>Lepomis miniatus</i>	13.32	31.24
	<i>Callinectes sapidus</i>	11.77	43.01
	<i>Fundulus grandis</i>	11.46	54.47
Med	<i>Micropogonias undulatus</i>	12.30	12.30
	<i>Farfantepenaeus aztecus</i>	10.40	22.70
	<i>Lagodon rhomboides</i>	9.82	32.52
	<i>Callinectes sapidus</i>	7.66	40.18
	<i>Lucania parva</i>	7.06	47.24
	<i>Cynoscion arenarius</i>	5.47	52.71
High	<i>Anchoa mitchilli</i>	11.56	11.56
	<i>Palaemonetes pugio</i>	9.66	21.22
	<i>Lagodon rhomboides</i>	9.36	30.58
	<i>Bairdiella chrysoura</i>	8.63	39.22
	<i>Micropogonias undulatus</i>	8.29	47.51
	<i>Fundulus grandis</i>	6.12	53.63
Control	<i>Fundulus grandis</i>	9.68	9.68
	<i>Anchoa mitchilli</i>	9.41	19.09
	<i>Callinectes sapidus</i>	9.12	28.21
	<i>Lucania parva</i>	8.39	36.60
	<i>Lepomis microlophus</i>	8.03	44.63
	<i>Lagodon rhomboids</i>	6.94	51.58
Low Ref	<i>Palaemonetes pugio</i>	12.04	12.04
	<i>Brevoortia patronus</i>	9.42	21.45
	<i>Callinectes sapidus</i>	9.14	30.59
	<i>Litopenaeus setiferus</i>	6.32	36.91
	<i>Mugil cephalus</i>	5.19	42.10
	<i>Micropogonias undulatus</i>	5.13	47.23
	<i>Anchoa mitchilli</i>	5.09	52.33
High Ref	<i>Micropogonias undulatus</i>	16.33	16.33
	<i>Mugil cephalus</i>	11.58	27.91
	<i>Leiostomus xanthurus</i>	8.60	36.51
	<i>Litopenaeus setiferus</i>	7.92	44.44
	<i>Palaemonetes pugio</i>	7.02	51.46

A CAP analysis performed to reveal which nekton species cause most of the separation between sites shows that both the low and high reference sites are mostly distinguished from the other sites by the presence of high biomass of grey mullet (*Mugil cephalus*) and Atlantic menhaden (*Brevoortia patronus*); the high inflow sites by brown shrimp (*Farfantepenaeus aztecus*) and pinfish (*Lagodon rhomboides*); the medium inflow sites by pinfish, gobies (*Microgobius gulosus* and *Gobiosoma bosc*) and rainwater killifish (*Lucania parva*); the control sites by the same gobies, rainwater killifish and pipefish (*Syngnathus scovelli*), and the low inflow sites by sunfish (*Lepomis miniatus* and *Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*; Figure 3.5). The CAP vectors indicate which species are responsible for the separation between the samples. Because of the high number of species collected, only those species that have eigenvalues higher than 0.45 are shown as vectors.

A canonical correlation analysis (CCA) indicates that differences in nekton SBD were more strongly driven by seasonal variability (separation mainly along the temperature vector) than by variability related to the sites themselves (separation mainly along the salinity vector; Figure 3.6A-B). Dissolved oxygen also contributed to the separation among seasons, and is inversely related to temperature. As none of the observed DO values [3.79-13.25 (mean = 7.78 ( $\pm$  0.05) mg l<sup>-1</sup>)] are low enough to be defined as hypoxic (< 2 mg l<sup>-1</sup>; Rosenberg and Loo 1988), it is not surprising that DO had little effect on SBDs.

Salinity is the primary gradient of separation on the second axis, and separates nekton SBDs based upon site of collection. The other vectors mainly on the second axis that further separate SBDs are pH, plant diversity and SAV biomass, which together with salinity clearly separate SBDs collected at the low inflow, medium inflow and control sites from SBD collected at the high inflow, high reference and low reference sites (Figure 3.6A).

A PERMANOVA on the resemblance matrix of first five CCA axis scores revealed a significant site and season effect ( $\alpha = 0.01$ ). Pairwise comparisons between sites across seasons indicate that the low and medium sites did not differ significantly from the control site, and the high reference sites did not differ from the low reference and the high inflow sites. All of the remaining pairwise comparisons differed significantly (Table 3.1).

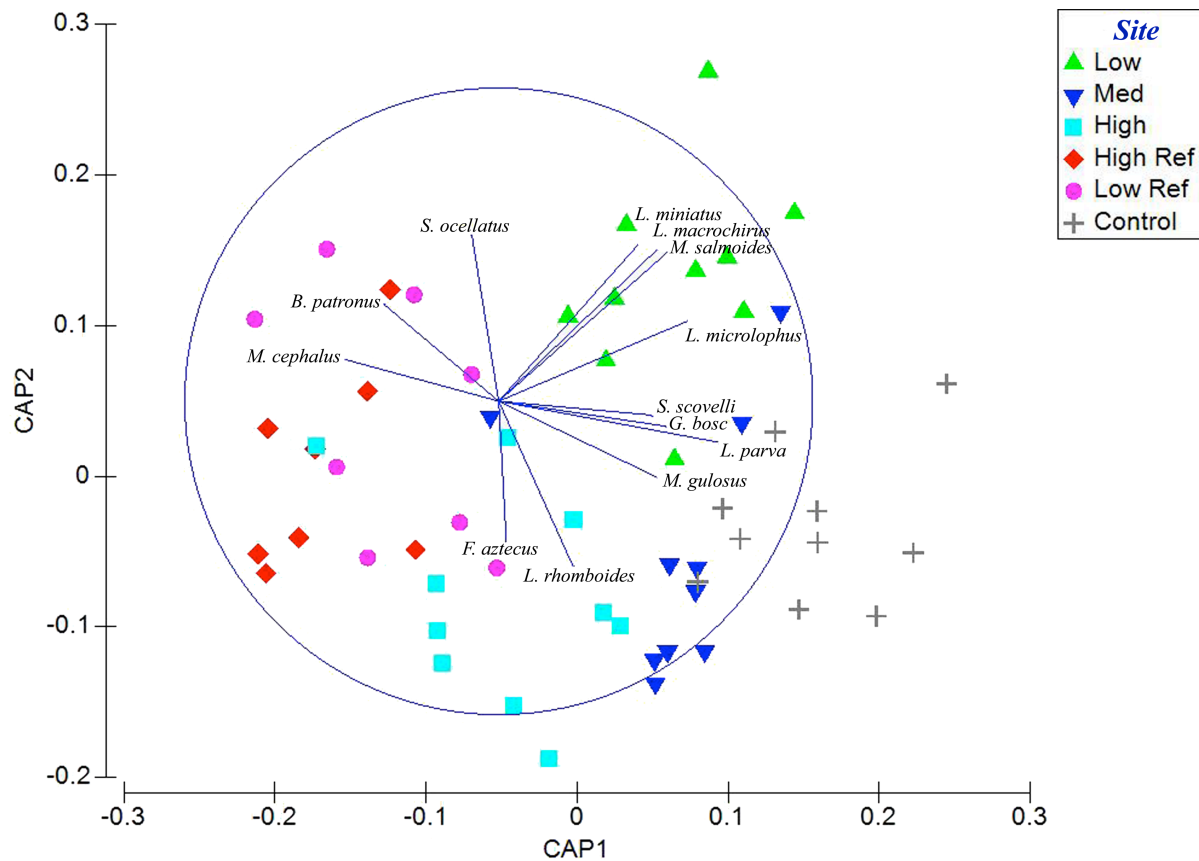


Figure 3.5. A canonical analysis of principal coordinates (CAP) performed on the nekton data collected at each site. The symbols indicate which site the SBD samples were collected. The vectors with nekton species names in the figure indicate which species define differences among groups. The direction and length of the vectors indicate the strength of association between species and sites. All species shown had eigenvalues of  $\geq 0.45$  on a CAP axis.

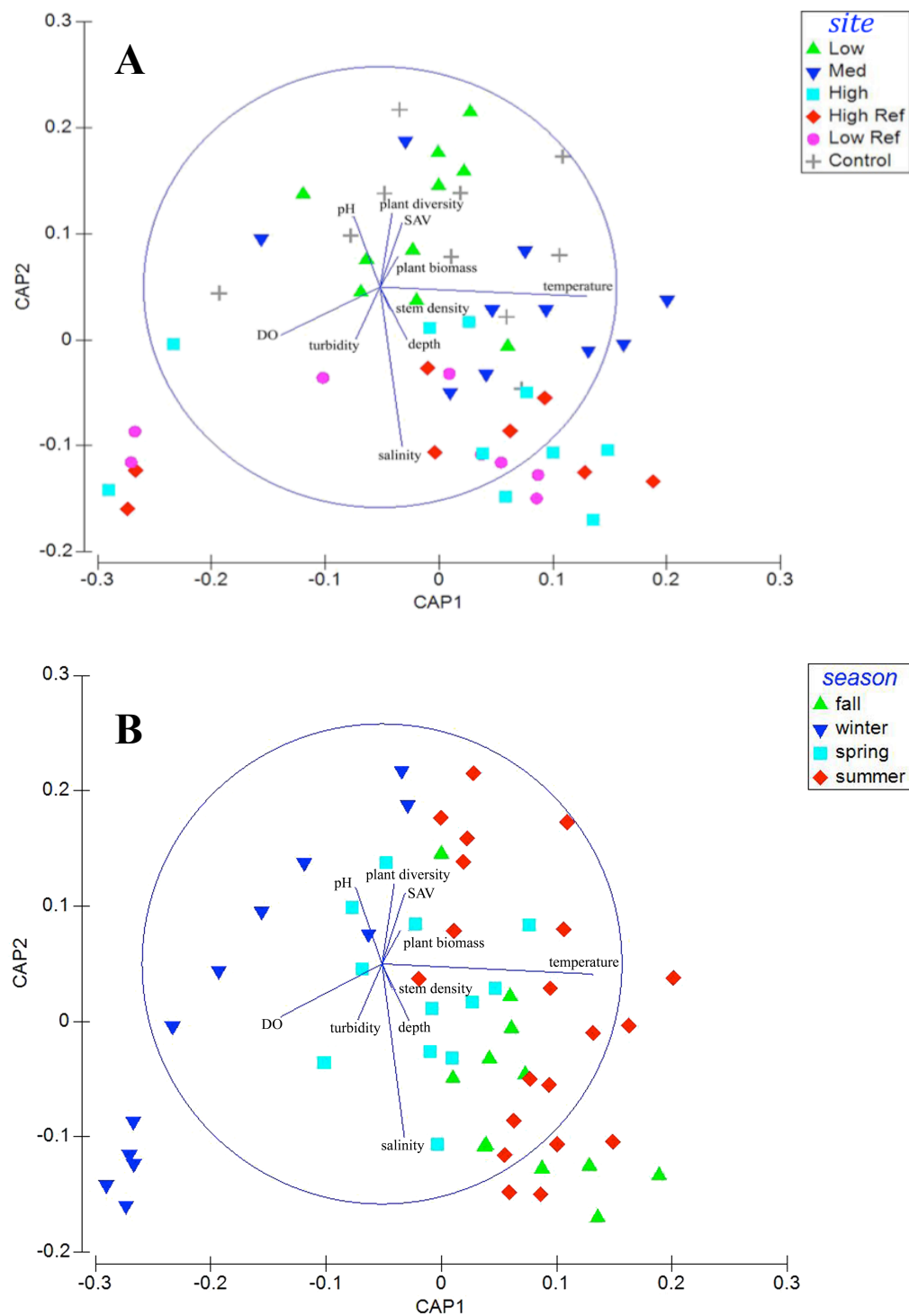


Figure 3.6. Plot of the canonical correlation analysis (CCA) displaying the separation of nekton samples based upon environmental variables. The direction and length of each vector indicates the strength of association between species biomass distributions and environmental variables. The symbols indicate A) at which site samples are collected, and B) in which season samples were collected.

## **DISCUSSION**

### **Habitat Characteristics**

The main abiotic factor affected by freshwater inflow from the CFD is salinity. Each (replicated) study site had a significantly different salinity regime, with lowest salinities observed at sites closest to the CFD. Overall the sites in Fourleague Bay (the reference area) had higher salinities than sites in Breton Sound, and in hindsight I should have selected sites closer to the source of freshwater (the Atchafalaya River). However, this mismatch was attributable to lower than expected salinities in Breton Sound due to increased flow through the CFD after Hurricane Katrina in 2005. Still, the low reference sites had salinities comparable to the mid-estuary inflow sites, the control sites and the high salinity inflow sites depending upon season. Another unexpected result was that the control area had salinities that were not higher than sites in the inflow area at similar distance from the diversion. This suggests that seepage through the levee and/or mixing through openings in the levee farther down the estuary must be occurring.

Marsh plant species richness, biomass and stem density, as well as SAV biomass and pH, were all inversely related to salinity, hence positively related to freshwater inflow through the CFD. This supports the results of Day et al. (2009a and b) who reported highest aboveground plant biomass within 20 km from the diversion, and a reduction in plant biomass with distance from the diversion, and results of Rozas et al. (2005), who found increased SAV density in the inflow area with freshwater releases from the CFD.

Two additional gradients along which separation of environmental samples occurred are temperature and DO. To a lesser extent separation was determined by water depth and turbidity. These four variables were not related to salinity, and by inference the CFD, and separate samples based upon seasonal differences rather than site of collection. However, it is impossible to conclude that the CFD has no effect on any or all of these variables in the freshwater area closer

to the diversion, as my low inflow sites were 15 km from the CFD, corresponding to the southern ‘boundary’ of the upper estuary as defined in other studies of Breton Sound (Day et al. 2009b). Rozas et al. (2005) did include lower parts of the estuary in their study, and found that DO was positively related to freshwater flow through the CFD; daytime DO levels were measurably higher in the inflow than the control area. I did not find this effect. Part of the reason for this discrepancy might be that their measurements were made in a four-day period after prolonged high releases from the CFD (Lane et al. 2004); the DO increases might dissipate in ambient conditions. In addition, their measured DO values in the control area were much lower than in my study ( $\sim 5.2 \text{ mg l}^{-1}$  versus  $7.65 \text{ mg l}^{-1}$ ). The reason for this is unknown, although I did also find higher SAV cover in the control area than Rozas et al. (2005), which could be producing the oxygen during daytime, but lower DO during nighttime. My samples were collected only during daytime. A reason for the higher SAV coverage could be the freshwater seepage through the elevated road separating the control from the inflow area. It is possible that this freshwater seepage did not occur at the time of their study, since I measured lower salinities in the control area than Rozas et al. (2005). If this is the case, the CFD might indeed have increased DO levels in Breton Sound, but this increase now is prevalent in both the inflow and the control area.

Previous studies have also reported a reduction in temperature with flow from the CFD, but this was in the above-described upper estuary. Diverted waters equilibrated with ambient temperatures in the rest of the estuary within a few kilometers from the CFD (Hyfield et al. 2008; Day et al. 2009b). Turbidity is also likely affected by diversion inflow at sites closer to the diversion, because sediment deposition is reportedly greatest at distances less than 10 km, and decreases rapidly with distance from the diversion (Wheelock 2003). Other potential effects related to freshwater inflow reported in previous studies are sediment resuspension by high flow (Zedler and Onuf 1988; Sklar and Browder 1998), thereby increasing turbidity, and an increase

in water volume as a result of a freshwater pulse, which was demonstrated to be positively correlated with water depth in vegetated marshes of the upper estuary in Breton Sound (Piazza and La Peyre 2007; Day et al. 2009b). None of the aforementioned variables (DO, temperature, turbidity, water depth) were found to be related to the CFD in my study, which may indicate that the CFD does not significantly affect these variables at distances  $\geq 15$  km from the CFD under operational conditions that occurred during my study. Rather, my data show that the aforementioned variables were affected by season. My results show that temperature was the main gradient along which seasonal separation occurs. Dissolved oxygen was inversely related to temperature, which likely occurred simply in response to differences in saturation potentials (Mortimer 1956). Water depth was positively correlated to temperature. Northerly winds push water out of the estuaries in winter, causing a reduction in water levels when temperatures are low (Walker and Hammack 2000). Turbidity in turn is inversely related to water depth and temperature; the combination of wind driven sediment resuspension and shallower water in winter can cause higher turbidity (Kristensen et al. 1992; Cho 2007).

### **Effects of Habitat on Nekton Species Biomass Distributions**

Overall, the species found to be abundant in the two Louisiana estuaries I examined are very typical for Gulf of Mexico estuaries, and have been described as dominant species in previous studies (Rakocinski et al. 1992; Rozas et al. 2007; Simonsen 2008; Day et al. 2009b). Although seasonal factors apparently explained more of the variability in SBD than spatial variability, the SBD at almost all sites differed significantly. Seasonal variability in nekton abundance and biomass has been described as so high in various studies (Rakocinski et al. 1992; Livingston 1997; Akin et al. 2003) as to obscure responses to habitat change or effects of environmental effects (Rose 2000; Rozas et al. 2007). In my study, the CFD caused enough change for spatial differences in community structure to be discernable, likely in response to the

formation of a salinity gradient. The results of the CCA confirm this; the main factor separating the nekton SBD among the sites of collection is salinity. Rakocinski et al. (1992), in a study in a neighboring estuary, also found a clear separation between nekton communities based upon salinity. In addition to the SBD differences caused by salinity, it appears that high SAV coverage that occurs in the control, and upper and mid-estuary inflow sites, attracted certain nekton species. The nekton species that distinguish these sites from the other sites (other than the species that prefer lower salinities in the upper-estuary sites) are *Microgobius gulosus*, *Syngnathus scovelli*, *Gobiosoma bosc* and *Lucania parva*; all small species that use SAV for cover (Castellanos and Rozas 2001). Previous studies report that SAV coverage increased as a result of freshwater inflow through the CFD, and may enhance secondary productivity in the inflow area (Rozas et al. 2005; Day et al. 2009b). Correspondingly, my results indicate that SAV biomass is a distinguishing factor in the environmental characteristics of low and high salinity sites, and affects SBDs. As such, the observed shift in nekton SBDs to species that use SAV in low salinity sites is likely an indirect effect of freshwater flow through the CFD.

Dissolved oxygen was not a strong a driver in distinguishing nekton communities compared to environmental characteristics, as evidenced by the shorter vector in the canonical correspondence analysis. In my results, variation in DO appears to be associated with seasonal variability rather than site; these results are similar to those of Rakocinski et al. (1992) in their study in the Barataria Basin in Louisiana, who also found that seasonal variation in DO and water temperature exceeded spatial variation in these variables within the estuary. My results indicate that DO probably did not limit the distribution of any of the species I collected, as the measured DO levels indicate that eutrophication sufficient to generate hypoxia ( $O_2 < 2 \text{ mg l}^{-1}$ ; Rosenberg and Loo 1988) did not appear to occur. That said, I did not sample during nighttime



hours, nor was my sampling frequency sufficient to capture short-term variability in DO if that occurred.

Lane et al. (1999) concluded in their water quality analysis that there is a near complete assimilation of nitrogen by the ecosystem in the Caernarvon inflow area. Through this assimilation, primary and secondary productivity within the estuarine environment could perhaps be stimulated by nutrients from the Mississippi River (Cushing 1975; Iverson 1990; Chesney et al. 2000; Nixon 1988; Nixon and Buckley 2002; Day et al. 2009a). My results support this contention. However, other studies have suggested that high nutrient loadings attributable to diversions weaken marsh plants (Swarzenski et al. 2008) and could result in harmful algal blooms and localized hypoxia (Turner and Rabalais 1991). I did not observe such effects, although I did not measure all variables that could have identified these problems.

Water depth was not related to CFD inflow and distance of my sites from the CFD. However, while I did not measure volume, other studies have reported increased water volume in the inflow area in association with a freshwater pulse through the CFD (Piazza and La Peyre 2007; Day et al. 2009b), which could affect nekton communities by increasing the extent of physical habitat for estuarine species (Kimmerer et al. 2009), and by altering marsh hydroperiod, which controls habitat use by nekton (Rozas 1995; Piazza and La Peyre 2007; Sable 2007).

Of all physical factors, salinity and temperature are most frequently cited as having the strongest influence on the structure of nekton communities (e.g. Peterson and Ross 1991; Marshall and Elliot 1998; Araujo et al. 1999; Gelwick et al. 2001). My results support the previous studies and clearly show that temperature and salinity were the dominant gradients along which nekton community structure diverged. There are various mechanisms responsible for the importance of temperature and salinity in the formation of nekton communities. In addition to species-specific tolerance ranges for both variables in juvenile and adult life stages,

temperature and salinity are important factors in the attraction of some fish larvae into the estuary (Elliot and Hemmingway 2002). The fact that temperature is the primary gradient on the first canonical axis indicates that seasonal variability caused greater separation among nekton communities than did location among the sites I studied. This indicates that even with the significant salinity differences between sites, estuarine nekton appear to respond more to seasonal as compared to spatial variation, and the overall effect of seasonal changes on species biomass distributions is still greater than the effect of the freshwater inflow through the CFD. These results are similar to those of Akin et al. (2003) in Mad Island Marsh estuary in Texas, and Simonsen (2008) in Barataria Bay, Louisiana amongst others. Although they did not look at seasonal effects, these results are also consistent with Rozas et al (2005), who only found small effects of the CFD and concluded that consumer communities from the inflow and control area were overall very similar.

Nonetheless, the small differences in SBD between sites are significant; in addition to the abiotic factors measured here, these differences could be caused by differences in food sources, predation pressure and bioenergetics between the sites. These processes also are important in determining relative habitat value (Craig and Crowder 2002), and are spatially variable in fluvial estuarine environments (Crowder and Magnuson 1983).

While most of the previous studies of the effects of the CFD were performed in the upper 15 km of the Breton Sound estuary, my study extends to the salt marsh-open water boundary of Breton Sound. The strength of this approach is that the potential for displacement of some estuarine nekton by a seaward shift of isohalines, which has been hypothesized in previous studies (Rozas et al. 2005; Reed et al. 2007; Day et al. 2009b), could be examined. Rather than displacing existing habitat and nekton communities, the flow from the CFD appears to actually create habitat for additional nekton species. Within the low salinity inflow area, different (new)

habitat types with different nekton communities were present, mainly as a result of the salinity gradient. Similarly, Peterson and Ross (1991) concluded that species richness is enhanced at coastal low salinity sites by the presence of freshwater species, because of the creation of new habitat. In my study, the species added include members of the family Centrarchidae, especially sunfish and largemouth bass, which are popular sport fishes.

Locally, species richness is greatest at the high salinity site in the inflow area, perhaps owing to lower variability in salinity in these areas (Peterson and Ross 1991). In general though, I did not find a reduction in nekton species richness in the salinity range of 3 to 8 ppt that has been frequently reported in reviews of estuarine ecosystems (Remane and Schlieper 1971; Wetzel 1983; Levinton 2001). The reason for this is unknown; perhaps other preferred habitat characteristics (e.g. food sources) offset the metabolic costs of unfavorable salinities. It is also possible that estuarine nekton species in large deltaic ecosystems experience more natural variability in salinity than those in drowned river valley estuaries and are thus locally adapted to the conditions they experience. Overall, my results are consistent with those described by Day et al. (2009b), and with their conclusion that the diversion mostly produced either neutral or positive effects in the Breton Sound estuary, and that the CFD causes local effects, but no estuarine-wide impacts.

Future research should include testing the more subtle effects of the diversion and the habitat differences described here; for example, comparing the caloric content of species at the different sites and areas to examine a potential relationship between energy density and hydrological connectivity. Similarly, elucidation of changes in foodweb pathways in relation to the factors above would be extremely useful (Deegan 2002; Rozas et al. 2005). Changes in foodweb pathways may go undetected if only nekton species biomass distributions, and even energy density, are the only metrics evaluated. These subjects are investigated in Chapter 4.

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## **CHAPTER 4**

### **USING CARBON, NITROGEN, AND SULFUR STABLE ISOTOPES AND ENERGY DENSITY OF NEKTON TO DETECT EFFECTS OF THE CAERNARVON FRESHWATER DIVERSION ON THE ESTUARINE FOOD WEB IN BRETON SOUND**

#### **INTRODUCTION**

Beginning in 1991, Mississippi River water has flowed through the Caernarvon Freshwater Diversion (CFD) into the Breton Sound estuary to restore wetlands by mitigating saltwater intrusion and introducing sediments and nutrients for marsh development (Mitsch et al. 2001; Day et al. 2000; 2007; 2009). This renewed hydrological connection to the Mississippi River is likely having effects on the estuarine food web (Wissel and Fry 2005; Piazza and La Peyre 2007; Day et al. 2009).

In this chapter I compared food webs of areas with different hydrological connectivity to the Mississippi River watershed through stable isotope and caloric content analyses. The goals of these comparisons were to determine: 1) if the opening of the CFD has caused changes in the estuarine food web of Breton Sound, and 2) if these changes have an effect on the energy density of nekton in the estuary. Reintroduction of Mississippi River water could increase energy densities of estuarine fishes and invertebrates via addition of nutrient-rich food sources with the influx of river carbon and nitrogen, and extended access to high quality habitats due to increased inundation of wetland habitats (Kneib 2000; Piazza and La Peyre 2007; Madon 2008). I contend that such changes can be detected in the isotopic composition and caloric density of consumers in the estuary (Peterson and Fry 1987, Hartman and Brandt 1995; Piazza 2009).

Isotopes are forms of the same element that differ in the number of neutrons in the nucleus (Fry 2006). Elements with ‘extra’ neutrons in the nucleus are called heavy isotopes. Since there can be a slight difference in the reaction time of heavy and light isotopes in kinetic reactions (a difference in fractionation), the ratio of heavy to light isotopes can be used as a

natural tracer in element cycling and organic matter dynamics (Fry 2006). In this chapter I use the ratio of  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$  and  $^{34}\text{S}/^{32}\text{S}$  to detect differences in food web pathways in estuaries with different hydrological connectivity to the Mississippi River deltaic ecosystem. This is measured by the difference of these ratios relative to standards; these differences are notated as  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  respectively (Fry 2006).

The isotopic composition of animals is influenced by diet, as well as by environment (Fry 2006; Newsome et al. 2007). Consumer  $\delta^{13}\text{C}$  values are a good indication of carbon sources in the food web, because primary producers can have distinct  $\delta^{13}\text{C}$  values, while there is negligible fractionation with food assimilation ( $<1\text{‰}$  per trophic level; Deegan and Garrit 1997). Distinct  $\delta^{13}\text{C}$  values of primary producers are attributable to different sources of  $\text{CO}_2$ , or differences in fractionation during plant photosynthetic carbon fixation (Peterson and Howarth 1987; Fry 2006). The relative contribution of  $\delta^{15}\text{N}$  increases with increasing trophic level ( $\sim 3.4\text{‰}$  per level; Vander Zanden and Rasmussen 2001), which makes it useful in studies of trophic structure of a community. It also increases with higher input of anthropogenic nitrogen (Fry 2002), which on one hand makes it a useful natural tracer of anthropogenic nitrogen (Costanzo et al. 2001) such as river input in estuaries (Wissel et al. 2005). On the other hand this complicates comparative trophic structure studies between consumer communities from different areas (Newsome et al. 2007). Values of  $\delta^{34}\text{S}$  differ depending upon the source of sulfate in plant uptake (Peterson and Howarth 1987), with sulfates from precipitation at the low end ( $\sim +2\text{‰}$ ) and sea-salt sulfate at the high end ( $\sim +18\text{‰}$ ; Deegan and Garrit 1997). The low fractionation of  $\delta^{34}\text{S}$  with food assimilation, similar to that of  $\delta^{13}\text{C}$ , makes this isotope another good tracer for source materials in food webs (Peterson and Fry 1987; Connolly et al. 2004).

Stable isotope analysis may reveal differences in food web complexity and food web carbon sources among areas with different hydrologic connectivity to the Mississippi River

(Visintainer et al. 2006). The relative contribution of river-derived carbon in the form of particulate organic matter or phytoplankton to the diet of estuarine consumers should be higher in an area receiving river inflow than in an area without a hydrological connection to a river (Kendall et al. 2001; Vorwerk and Froneman 2009). In addition to a direct contribution of river-derived carbon, inflow of nutrients like nitrogen, and the delivery of bioavailable nitrogen upon decomposition of river-derived carbon, can increase the growth of phytoplankton, which can in turn increase the relative contribution of phytoplankton to the diet of estuarine consumers in an area receiving river inflow (Kendall et al. 2001). If there are indeed differences in the relative contribution of carbon sources among areas with different hydrological connectivity, energy density (here measured as caloric density) of consumers can be analyzed to illuminate the presence and effects of quality differences in consumers' diets among areas (Hartman and Brandt 1995; Piazza 2009).

I used a combination of carbon, nitrogen and sulfur isotopes to detect differences in food web dynamics of the estuarine nekton communities in: 1) an area within the estuary that receives freshwater flow from the CFD (inflow), 2) an area in the same estuary that is mostly isolated from CFD freshwater inflow (control), and 3) an area with a hydrological connection to a natural river diversion (reference). I hypothesize that nekton species in the areas with a hydrological connection to river water will have a higher proportion of particulate organic matter (POM, phytoplankton is included in this term) in their diets than the nekton in the isolated area, and higher energy density. Because wetlands serve as nutrient sinks (Lane et al. 1999; Day et al. 2009; Hunter et al. 2009), and because flooding events will be less pronounced farther away from the point of inflow, I also hypothesize that the distance from the point of inflow of freshwater and nutrients will negatively affect energy density of nekton species. The null

hypothesis is that there is no difference in isotopic composition and energy density of consumers in the three areas.

In addition to food availability and quality, hydrological connectivity may affect trophic diversity and the size of the trophic niche of the consumer community (Newsome et al. 2007; Layman et al. 2007a). A niche is defined as the (trophic) position of species or populations in an ecosystem relative to other species or populations in the same ecosystem (Elton 1927). Following Hutchinson's (1957) formalization of a niche as an n-dimensional hypervolume, ecologists have developed quantitative measures to describe niche space. Recently, isotope ecologists have suggested representing the trophic niche as the relative positions of species in a community in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bi-plot space (Bearhop et al. 2004; Newsome et al. 2007; Layman et al. 2007a). The difference in variability and extent of spacing among the isotopic composition of consumer species within a community can then be compared between communities.

I hypothesize that the reference area should have the highest trophic diversity and niche breadth, which is an indication of a more complex community (Layman et al. 2007a), because it is a stable wetland area with an established natural hydrological connection to a river (Van Heerden and Roberts 1980). I expect the control area, which is, in essence, hydrologically isolated from river inflow, to have the lowest trophic diversity and niche breadth. I hypothesize the inflow area to have a niche breadth between the reference and control areas, in the expectation that it has been on a restoration trajectory since the opening of the CFD in 1991. The null hypothesis is that there is no difference in trophic diversity and niche breadth among the three areas.

## **MATERIALS AND METHODS**

### **Study Area**

The Breton Sound and Fourleague Bay study areas and sample sites are described in Chapter 3. Fourleague Bay serves as the reference area in this study. Samples from all sites (Figure 3.1 and 3.2, Chapter 3) were used for caloric content analysis. For stable isotope analysis, only samples from the medium salinity sites in the inflow area, (M1 and M2, Figure 3.1, Chapter 3), the control sites (C1 and C2, Figure 3.1, Chapter 3), and the low salinity sites in the reference area (LR1 and LR2; Figure 3.2, Chapter 3) were used. Selection of these stations allows a comparison between the isotopic compositions of consumers in similar brackish marsh environments with comparable salinities (Figure 3.3, Chapter 3). Brackish marshes are described as having salinities anywhere between 3-18 ppt (Tiner 1993); the marshes compared in the isotope analyses described here have mean salinities between 3-6.4 ppt.

### **Field and Laboratory Methods**

Samples of both producers and consumers were collected for stable isotope analysis, while only nekton samples were collected for caloric content analysis. All plant and animals collected were identified to the species level. The field collection methods of marsh plants, submerged aquatic vegetation (SAV), and nekton are described in Chapter 3. Additionally, detritus samples were collected from within the same quadrats the vegetation clippings were made by removing the upper layer (~ 2-5 cm) of mostly dead plant material after the standing vegetation was clipped. Epiphytes were collected in two ways (both methods were used in each area): 1) submerged vegetation was clipped, inserted in Nalgene bottles with distilled water and shaken to dislodge epiphytic algae. The distilled water with epiphytic algae was centrifuged, the clear supernatant decanted, and the residue dried in an oven at 60° C for 48 hours; 2) the clipped submerged vegetation was transferred to the drying oven with the epiphytes still attached. When

dry (after 48 hours at 60° C), epiphytic algae were removed from the stems with tweezers.

Macrophyte stem particles, sediment grains, etc. were removed from the epiphytic algae samples with tweezers while the samples were viewed under a stereomicroscope. Samples were taken for stable isotope analysis from all collected marsh plant species, submerged aquatic vegetation (SAV), detritus and epiphytes.

Fish samples were filleted, and muscle tissue samples were used for isotope analysis. The specimens were usually small juveniles, and typically all muscle tissue was used. Head and exoskeleton were removed from shrimp, and the muscle tissue of the tail was used for analysis. The isotope samples consisted of composite samples from at least 3, and at most 10, individuals of the same species collected on the same sampling trip and site, to ensure that the isotope value was representative for that species at that site.

In an effort to create a representative sample of each estuarine community for trophic structure analysis, members of functional groups that are not present within the plant or nekton communities were collected as well. The functional groups added were grazers (periwinkles) and filter feeders (clams and mussels). From these animals, also only muscle tissue was used for isotope analysis.

All samples for stable isotope analysis were soaked in deionized water to remove sulfates, dried at 60 °C for 48 hours, and ground to a fine powder with a Wiglebug® before analysis. Data on the stable isotope composition of particulate organic matter (POM) was obtained from Brian Fry (personal communication; Wissel and Fry 2005; Wissel et al. 2005) for Breton Sound, and from Kendall et al. (2001) for Fourleague Bay.

The  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  value of the samples was determined with an elemental analyzer (Carlo Erba 1500®) linked to a Finnigan Delta® plus isotope ratio mass spectrometer.

Isotopic abundances are given as:

$$\delta X = \left[ \frac{RSAMPLE}{RSTANDARD} - 1 \right] \times 1000 \quad (\text{Eq. 4.1})$$

where X is  $^{13}\text{C}$ ,  $^{15}\text{N}$  or  $^{34}\text{S}$  and R is the respective ratio,  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$  or  $^{34}\text{S}/^{32}\text{S}$  (Fry 2006).

All samples were used in the analysis of trophic structure (Table 4.1). A selection of nine nekton species that were collected at all sites was used in a food web comparison among the three areas using isotope and caloric content analyses. Caloric density of nekton tissue of the same nine species was determined with a Parr 6200® isoperibol oxygen bomb calorimeter. Samples were dried for 48 hours at 60°C, and ground with a combination of mortar and pestle and Wiglebug®. The samples were composite samples consisting of all specimens of a species collected at the same time at the same site to ensure both representative values and enough material for analysis. All samples were pressed into 1 g (dry weight) pellets before combustion in the bomb calorimeter to obtain caloric density ( $\text{cal g}^{-1}$ ) of the sample. Entire specimens of estuarine nekton species were dried and processed as above for analysis of caloric density.

### **Data Analysis**

To obtain information on trophic structure of consumers within each of the three areas, I calculated: 1) the area of the smallest convex polygon encompassing the mean isotopic concentration for all species of consumers in  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plot space (total area; TA); 2) the distance between each point and the center of this polygon (centroid distance, CD); 3) the largest distance between two  $\delta^{13}\text{C}$  values of consumers ( $\delta^{13}\text{C}$ -range; CR); and 4)  $\delta^{15}\text{N}$ -range (NR).



Table 4.1. Isotopic compositions of all consumers used in the calculation of trophic metrics and in MANOVA's, and all carbon sources used for 'baseline' comparisons of the control, inflow and reference area. Species names are listed with their  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values, producer or consumer 'type', and the area and season of collection. All collections were done between October 2006 and August 2008. Nekton species in bold were selected for comparison of food web pathways among the three areas because they were collected in all three study areas.

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
C3 plant	<i>Aster subulatus</i>	control	fall	-27.97	2.66	12.58
C3 plant	<i>Lythrum lineare</i>	control	fall	-27.09	1.61	5.40
C3 plant	<i>Scirpus robustus</i>	control	fall	-25.54	3.04	8.10
C3 plant	<i>Scirpus robustus</i>	control	fall	-23.13	2.52	5.85
C4 plant	<i>Distichlis spicata</i>	control	fall	-13.34	4.12	8.44
C4 plant	<i>Spartina patens</i>	control	fall	-13.24	3.17	5.64
C4 plant	<i>Spartina patens</i>	control	fall	-12.80	3.50	10.56
detritus		control	fall	-26.74	0.01	8.30
detritus		control	fall	-24.87	0.65	8.46
detritus		control	fall	-28.54	0.12	8.46
detritus		control	fall	-17.49	2.68	8.83
detritus		control	fall	-17.49	2.62	9.37
detritus		control	fall	-19.84	2.97	8.79
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>fall</b>	<b>-22.28</b>	<b>10.51</b>	<b>9.13</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>fall</b>	<b>-22.03</b>	<b>10.19</b>	<b>9.45</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>fall</b>	<b>-22.08</b>	<b>9.69</b>	<b>8.16</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>fall</b>	<b>-22.95</b>	<b>9.15</b>	<b>10.45</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>control</b>	<b>fall</b>	<b>-17.87</b>	<b>8.35</b>	<b>5.09</b>
fish	<i>Gobiosoma bosc</i>	control	fall	-22.43	9.01	9.98
fish	<i>Lucania parva</i>	control	fall	-16.67	4.39	5.69
fish	<i>Lucania parva</i>	control	fall	-18.06	4.78	5.74
fish	<i>Microgobius gulosus</i>	control	fall	-22.98	7.86	7.64
POM		control	fall	-22.00	4.30	18.00
SAV	<i>Ceratophyllum demersum</i>	control	fall	-22.35	2.60	9.55
SAV	<i>Eleocharis parvula</i>	control	fall	-19.94	1.04	-0.20
SAV	<i>Najas guadalupensis</i>	control	fall	-23.24	2.03	5.61
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>control</b>	<b>fall</b>	<b>-24.37</b>	<b>5.79</b>	<b>9.39</b>
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>control</b>	<b>fall</b>	<b>-24.37</b>	<b>5.80</b>	<b>9.40</b>

(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
<b>shrimp</b>	<i>Litopenaeus setiferus</i>	<b>control</b>	<b>fall</b>	<b>-23.43</b>	<b>6.91</b>	<b>8.24</b>
<b>shrimp</b>	<i>Litopenaeus setiferus</i>	<b>control</b>	<b>fall</b>	<b>-24.23</b>	<b>7.23</b>	<b>9.75</b>
C3 plant	<i>Baccharis halimifolia</i>	control	spring	-29.58	1.13	9.57
C3 plant	<i>Euthamia galetorum</i>	control	spring	-29.74	2.47	9.73
C3 plant	<i>Euthamia galetorum</i>	control	spring	-31.54	1.57	6.36
C3 plant	<i>Lythrum lineare</i>	control	spring	-27.82	2.24	8.54
C3 plant	<i>Lythrum lineare</i>	control	spring	-27.86	3.84	7.15
C3 plant	<i>Scirpus robustus</i>	control	spring	-28.49	5.01	5.06
C3 plant	<i>Scirpus robustus</i>	control	spring	-28.22	3.60	3.16
C3 plant	<i>Vigna luteola</i>	control	spring	-29.02	-1.96	7.69
C4 plant	<i>Distichlis spicata</i>	control	spring	-13.68	5.62	8.98
C4 plant	<i>Spartina patens</i>	control	spring	-13.53	3.26	7.79
C4 plant	<i>Spartina patens</i>	control	spring	-12.92	2.85	-0.28
detritus		control	spring	-21.44	1.35	7.84
detritus		control	spring	-15.77	1.70	8.83
detritus		control	spring	-18.61	2.03	8.05
detritus		control	spring	-27.26	0.92	5.66
detritus		control	spring	-26.54	0.08	5.74
detritus		control	spring	-25.88	0.18	6.15
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>control</b>	<b>spring</b>	<b>-23.48</b>	<b>11.55</b>	<b>6.78</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>control</b>	<b>spring</b>	<b>-22.98</b>	<b>11.53</b>	<b>6.40</b>
<b>fish</b>	<i>Brevoortia patronus</i>	<b>control</b>	<b>spring</b>	<b>-23.95</b>	<b>10.95</b>	<b>9.64</b>
fish	<i>Gobiosoma bosc</i>	control	spring	-21.58	10.47	6.31
fish	<i>Gobiosoma bosc</i>	control	spring	-21.54	10.98	4.23
fish	<i>Lucania parva</i>	control	spring	-19.48	8.97	4.64
fish	<i>Lucania parva</i>	control	spring	-19.68	8.57	4.51
<b>fish</b>	<i>Menidia beryllina</i>	<b>control</b>	<b>spring</b>	<b>-19.20</b>	<b>9.28</b>	<b>5.08</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>control</b>	<b>spring</b>	<b>-22.89</b>	<b>11.13</b>	<b>5.84</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>control</b>	<b>spring</b>	<b>-22.93</b>	<b>10.88</b>	<b>5.81</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>control</b>	<b>spring</b>	<b>-23.29</b>	<b>11.89</b>	<b>5.46</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>control</b>	<b>spring</b>	<b>-22.63</b>	<b>11.30</b>	<b>5.52</b>

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>spring</b>	<b>-23.52</b>	<b>11.48</b>	<b>4.88</b>
POM		control	spring	-22.00	4.30	18.00
SAV	<i>Eleocharis parvula</i>	control	spring	-17.59	3.31	-2.85
SAV	<i>Eleocharis parvula</i>	control	spring	-17.13	1.35	2.96
SAV	<i>Eleocharis parvula</i>	control	spring	-17.60	2.16	3.70
SAV	<i>Eleocharis parvula</i> & algae	control	spring	-18.23	4.10	4.65
SAV	<i>Filamentous algae</i>	control	spring	-17.30	6.62	10.34
SAV	<i>Filamentous algae</i>	control	spring	-19.76	3.06	5.09
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>spring</b>	<b>-19.62</b>	<b>9.03</b>	<b>6.00</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>spring</b>	<b>-19.81</b>	<b>9.59</b>	<b>6.78</b>
C3 plant	<i>Alternanthera philoxeroides</i>	control	summer	-22.42	3.53	7.91
C3 plant	<i>Euthamia galetorum</i>	control	summer	-28.76	4.69	8.00
C3 plant	<i>Euthamia galetorum</i>	control	summer	-32.03	4.92	8.61
C3 plant	<i>Euthamia galetorum</i>	control	summer	-29.17	2.60	8.89
C3 plant	<i>Iva frutescens</i>	control	summer	-29.82	3.88	6.23
C3 plant	<i>Lythrum lineare</i>	control	summer	-27.84	4.65	7.95
C3 plant	<i>Lythrum lineare</i>	control	summer	-29.85	3.63	6.04
C3 plant	<i>Lythrum lineare</i>	control	summer	-30.29	1.59	7.68
C3 plant	<i>Scirpus robustus</i>	control	summer	-27.10	4.51	4.49
C3 plant	<i>Scirpus robustus</i>	control	summer	-27.03	5.38	7.91
C3 plant	<i>Scirpus robustus</i>	control	summer	-28.56	2.99	8.43
C3 plant	<i>Vigna luteola</i>	control	summer	-27.84	0.00	7.72
C3 plant	<i>Vigna luteola</i>	control	summer	-29.68	-0.80	6.86
C4 plant	<i>Amaranthus cannabinus</i>	control	summer	-12.93	2.84	8.14
C4 plant	<i>Distichlis spicata</i>	control	summer	-14.16	4.18	2.18
C4 plant	<i>Distichlis spicata</i>	control	summer	-13.63	4.14	4.68
C4 plant	<i>Distichlis spicata</i>	control	summer	-14.30	5.27	4.74
C4 plant	<i>Spartina patens</i>	control	summer	-13.79	4.14	7.15
C4 plant	<i>Spartina patens</i>	control	summer	-12.61	4.09	7.77
detritus		control	summer	-15.28	1.67	6.34
detritus		control	summer	-15.80	1.56	5.83

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
detritus		control	summer	-16.56	2.13	5.48
detritus		control	summer	-28.71	0.52	8.18
detritus		control	summer	-28.60	0.57	8.91
detritus		control	summer	-28.56	1.64	6.72
detritus		control	summer	-17.53	2.79	5.53
detritus		control	summer	-15.95	2.23	-0.24
detritus		control	summer	-16.87	2.61	5.74
detritus		control	summer	-28.34	2.40	6.74
detritus		control	summer	-27.98	2.40	6.84
detritus		control	summer	-28.32	3.10	7.35
epiphytes		control	summer	-20.10	1.68	6.53
epiphytes		control	summer	-19.11	1.14	0.78
epiphytes		control	summer	-23.16	1.49	4.36
epiphytes		control	summer	-20.13	1.55	6.43
epiphytes		control	summer	-22.14	2.23	3.19
epiphytes		control	summer	-21.28	2.06	4.94
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>summer</b>	<b>-24.31</b>	<b>11.55</b>	<b>7.03</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>summer</b>	<b>-20.06</b>	<b>12.40</b>	<b>13.94</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>summer</b>	<b>-22.73</b>	<b>10.77</b>	<b>8.26</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-22.34</b>	<b>10.94</b>	<b>9.45</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-21.53</b>	<b>10.64</b>	<b>8.02</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-22.56</b>	<b>10.70</b>	<b>7.81</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-22.76</b>	<b>11.02</b>	<b>8.27</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-23.16</b>	<b>11.16</b>	<b>8.37</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>summer</b>	<b>-22.51</b>	<b>10.86</b>	<b>7.79</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>control</b>	<b>summer</b>	<b>-20.25</b>	<b>9.47</b>	<b>5.24</b>
fish	<i>Gobiosoma bosc</i>	control	summer	-22.83	10.12	6.90
fish	<i>Leiostomus xanthurus</i>	control	summer	-20.88	8.89	7.45
fish	<i>Lepomis microlophus</i>	control	summer	-18.52	8.24	4.00
fish	<i>Lepomis microlophus</i>	control	summer	-19.10	8.01	6.73
fish	<i>Lepomis miniatus</i>	control	summer	-17.69	7.94	7.00

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
fish	<i>Lucania parva</i>	control	summer	-20.70	10.59	6.94
fish	<i>Lucania parva</i>	control	summer	-20.56	9.66	6.25
fish	<i>Lucania parva</i>	control	summer	-19.20	9.22	6.25
fish	<i>Lucania parva</i>	control	summer	-19.22	8.09	6.00
fish	<i>Lucania parva</i>	control	summer	-23.11	10.60	8.54
fish	<i>Lucania parva</i>	control	summer	-22.26	10.60	8.21
fish	<i>Lucania parva</i>	control	summer	-22.14	11.18	8.55
fish	<i>Lucania parva</i>	control	summer	-22.79	10.03	8.25
fish	<i>Lucania parva</i>	control	summer	-21.50	10.01	8.39
fish	<i>Lucania parva</i>	control	summer	-23.01	10.86	9.36
fish	<i>Lucania parva</i>	control	summer	-21.19	9.58	7.76
fish	<i>Lucania parva</i>	control	summer	-21.75	10.10	6.77
fish	<i>Lucania parva</i>	control	summer	-22.14	9.07	7.54
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>summer</b>	<b>-19.18</b>	<b>9.26</b>	<b>7.03</b>
fish	<i>Microgobius gulosus</i>	control	summer	-21.06	9.34	5.77
fish	<i>Microgobius gulosus</i>	control	summer	-21.75	9.81	5.73
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-23.44</b>	<b>10.79</b>	<b>6.66</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-24.68</b>	<b>8.23</b>	<b>5.07</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-24.32</b>	<b>10.56</b>	<b>6.56</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-23.76</b>	<b>10.95</b>	<b>7.08</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-23.84</b>	<b>11.07</b>	<b>6.79</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>summer</b>	<b>-24.01</b>	<b>8.06</b>	<b>4.92</b>
fish	<i>Micropterus punctulatus</i>	control	summer	-18.41	9.74	5.94
fish	<i>Micropterus punctulatus</i>	control	summer	-18.04	10.10	5.10
fish	<i>Micropterus salmoides</i>	control	summer	-19.77	9.95	7.29
fish	<i>Micropterus salmoides</i>	control	summer	-21.40	9.80	7.02
fish	<i>Micropterus salmoides</i>	control	summer	-20.15	9.84	7.83
fish	<i>Micropterus salmoides</i>	control	summer	-20.46	10.11	5.94
fish	<i>Micropterus salmoides</i>	control	summer	-20.15	11.14	2.62
fish	<i>Micropterus salmoides</i>	control	summer	-20.64	9.66	8.99
fish	<i>Micropterus salmoides</i>	control	summer	-20.84	10.48	7.45

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
fish	<i>Micropterus salmoides</i>	control	summer	-20.20	10.66	6.58
fish	<i>Micropterus salmoides</i>	control	summer	-21.06	11.52	7.24
fish	<i>Micropterus salmoides</i>	control	summer	-21.18	11.57	6.67
POM		control	summer	-22.00	4.30	18.00
SAV	<i>Ceratophyllum demersum</i>	control	summer	-21.09	3.20	4.94
SAV	<i>Ceratophyllum demersum</i>	control	summer	-20.72	4.64	5.84
SAV	<i>Ceratophyllum demersum</i>	control	summer	-18.85	4.08	4.60
SAV	<i>Ceratophyllum demersum</i>	control	summer	-19.09	3.69	2.25
SAV	<i>Ceratophyllum demersum</i>	control	summer	-20.36	3.73	3.16
SAV	<i>Ceratophyllum demersum</i>	control	summer	-20.49	3.49	1.43
SAV	<i>Eleocharis parvula</i>	control	summer	-18.31	1.76	1.31
SAV	<i>Eleocharis parvula</i>	control	summer	-18.15	1.66	1.94
SAV	<i>Eleocharis parvula</i>	control	summer	-19.10	2.92	2.97
SAV	<i>Eleocharis parvula</i> & algae	control	summer	-19.76	2.73	1.00
SAV	<i>Eleocharis parvula</i> & algae	control	summer	-18.85	2.77	2.54
SAV	<i>Filamentous algae</i>	control	summer	-16.19	3.25	2.67
SAV	<i>Filamentous algae</i>	control	summer	-18.47	3.34	1.94
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>control</b>	<b>summer</b>	<b>-23.53</b>	<b>9.29</b>	<b>8.00</b>
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>control</b>	<b>summer</b>	<b>-21.80</b>	<b>9.13</b>	<b>7.32</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>summer</b>	<b>-20.16</b>	<b>9.25</b>	<b>5.60</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>summer</b>	<b>-19.57</b>	<b>9.27</b>	<b>7.75</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>summer</b>	<b>-19.15</b>	<b>8.68</b>	<b>6.23</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>summer</b>	<b>-21.14</b>	<b>9.95</b>	<b>7.94</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>control</b>	<b>summer</b>	<b>-20.98</b>	<b>9.49</b>	<b>7.38</b>
C3 plant	<i>Alternanthera philoxeroides</i>	control	winter	-29.57	2.05	6.04
C3 plant	<i>Aster subulatus</i>	control	winter	-28.95	2.41	7.54
C3 plant	<i>Aster subulatus</i>	control	winter	-29.66	2.24	7.21
C3 plant	<i>Polygonum punctatum</i>	control	winter	-28.49	1.97	7.09
C3 plant	<i>Scirpus robustus</i>	control	winter	-28.39	2.15	-0.29
C4 plant	<i>Paspalum distichum</i>	control	winter	-14.85	5.13	7.08
C4 plant	<i>Paspalum distichum</i>	control	winter	-14.10	4.96	4.33

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
C4 plant	<i>Spartina patens</i>	control	winter	-13.78	3.46	6.72
C4 plant	<i>Spartina patens</i>	control	winter	-13.57	3.98	8.79
C4 plant	<i>Spartina patens</i>	control	winter	-13.61	4.30	8.11
C4 plant	<i>Spartina patens</i>	control	winter	-13.60	4.06	6.57
detritus		control	winter	-15.58	1.87	6.18
detritus		control	winter	-14.31	0.86	6.54
detritus		control	winter	-16.89	1.96	5.78
detritus		control	winter	-28.93	1.65	2.22
detritus		control	winter	-19.83	1.19	8.86
detritus		control	winter	-22.33	0.63	4.92
detritus		control	winter	-13.44	3.27	5.49
detritus		control	winter	-13.37	3.51	5.51
detritus		control	winter	-15.14	3.55	5.84
detritus		control	winter	-13.61	1.53	5.91
detritus		control	winter	-13.75	1.50	5.53
detritus		control	winter	-14.50	1.57	6.03
filter feeder	clam	control	winter	-20.86	5.63	8.10
filter feeder	clam	control	winter	-26.10	6.82	9.30
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>winter</b>	<b>-21.65</b>	<b>10.15</b>	<b>7.89</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>winter</b>	<b>-22.47</b>	<b>12.22</b>	<b>6.08</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>winter</b>	<b>-24.03</b>	<b>11.77</b>	<b>7.11</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>control</b>	<b>winter</b>	<b>-22.89</b>	<b>10.16</b>	<b>7.90</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>control</b>	<b>winter</b>	<b>-25.98</b>	<b>10.34</b>	<b>9.09</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>control</b>	<b>winter</b>	<b>-26.31</b>	<b>10.41</b>	<b>8.66</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>winter</b>	<b>-21.18</b>	<b>10.00</b>	<b>8.70</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>control</b>	<b>winter</b>	<b>-21.56</b>	<b>10.84</b>	<b>9.76</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>control</b>	<b>winter</b>	<b>-19.82</b>	<b>8.54</b>	<b>6.34</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>control</b>	<b>winter</b>	<b>-20.56</b>	<b>9.37</b>	<b>8.48</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>control</b>	<b>winter</b>	<b>-19.46</b>	<b>8.95</b>	<b>6.81</b>
fish	<i>Gobiosoma bosc</i>	control	winter	-22.71	9.54	7.25
fish	<i>Gobiosoma bosc</i>	control	winter	-22.27	8.41	6.96

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
fish	<i>Gobiosoma bosc</i>	control	winter	-23.16	8.99	9.78
fish	<i>Lucania parva</i>	control	winter	-20.74	9.42	8.04
fish	<i>Lucania parva</i>	control	winter	-21.01	9.40	7.53
fish	<i>Lucania parva</i>	control	winter	-19.96	8.92	5.33
fish	<i>Lucania parva</i>	control	winter	-18.45	7.97	2.13
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-19.68</b>	<b>8.82</b>	<b>5.06</b>
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-18.98</b>	<b>8.81</b>	<b>4.99</b>
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-21.59</b>	<b>9.72</b>	<b>8.59</b>
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-21.76</b>	<b>9.73</b>	<b>8.89</b>
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-18.63</b>	<b>8.32</b>	<b>6.11</b>
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>control</b>	<b>winter</b>	<b>-20.07</b>	<b>8.76</b>	<b>6.14</b>
fish	<i>Microgobius gulosus</i>	control	winter	-21.24	8.59	7.59
fish	<i>Microgobius gulosus</i>	control	winter	-20.38	8.23	6.36
fish	<i>Microgobius gulosus</i>	control	winter	-21.65	8.53	8.12
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>winter</b>	<b>-23.07</b>	<b>10.02</b>	<b>6.33</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>control</b>	<b>winter</b>	<b>-22.36</b>	<b>9.44</b>	<b>4.94</b>
fish	<i>Micropterus salmoides</i>	control	winter	-20.59	12.66	6.79
fish	<i>Micropterus salmoides</i>	control	winter	-18.24	9.35	6.69
fish	<i>Mugil cephalus</i>	control	winter	-19.32	9.18	6.37
POM		control	winter	-22.00	4.30	18.00
SAV	<i>Ceratophyllum demersum</i>	control	winter	-18.50	5.81	3.49
SAV	<i>Ceratophyllum demersum</i>	control	winter	-20.22	4.37	8.59
SAV	<i>Ceratophyllum demersum</i>	control	winter	-19.65	5.03	3.90
SAV	<i>Eleocharis parvula</i>	control	winter	-17.33	3.87	-2.12
SAV	<i>Filamentous algae</i>	control	winter	-17.69	5.62	11.64
SAV	<i>Halodule wrightii</i>	control	winter	-17.44	6.88	10.67
SAV	<i>Myriophyllum spicatum</i>	control	winter	-16.15	3.37	-4.47
SAV	<i>Myriophyllum spicatum</i>	control	winter	-21.43	3.42	8.39
SAV	<i>Najas guadalupensis</i>	control	winter	-22.35	5.48	2.68
SAV	<i>Najas sp.</i>	control	winter	-18.55	6.64	-1.98
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>control</b>	<b>winter</b>	<b>-24.03</b>	<b>7.37</b>	<b>7.52</b>



(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-19.84</b>	<b>8.28</b>	<b>7.98</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-19.62</b>	<b>7.99</b>	<b>6.55</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-21.52</b>	<b>8.53</b>	<b>7.99</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-21.04</b>	<b>9.00</b>	<b>8.47</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-18.58</b>	<b>7.94</b>	<b>7.95</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>control</b>	<b>winter</b>	<b>-19.08</b>	<b>7.76</b>	<b>6.71</b>
C3 plant	<i>Ipomoea sagittata</i>	inflow	fall	-25.46	5.65	11.22
C4 plant	<i>Paspalum distichum</i>	inflow	fall	-13.74	6.51	10.02
C4 plant	<i>Paspalum distichum</i>	inflow	fall	-13.47	6.39	10.33
C4 plant	<i>Spartina alterniflora</i>	inflow	fall	-14.08	4.71	12.39
C4 plant	<i>Spartina alterniflora</i>	inflow	fall	-13.34	5.92	10.00
C4 plant	<i>Spartina patens</i>	inflow	fall	-13.50	4.48	11.15
C4 plant	<i>Spartina patens</i>	inflow	fall	-14.04	3.72	12.73
detritus		inflow	fall	-13.29	3.78	10.82
detritus		inflow	fall	-15.63	3.83	11.92
detritus		inflow	fall	-14.38	3.56	11.38
detritus		inflow	fall	-13.63	3.21	13.50
detritus		inflow	fall	-14.12	3.51	12.61
detritus		inflow	fall	-14.08	2.99	13.29
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>fall</b>	<b>-21.45</b>	<b>11.91</b>	<b>8.96</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>fall</b>	<b>-21.83</b>	<b>11.70</b>	<b>10.44</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>fall</b>	<b>-22.14</b>	<b>12.67</b>	<b>9.23</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>fall</b>	<b>-20.07</b>	<b>11.74</b>	<b>10.13</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>fall</b>	<b>-21.01</b>	<b>11.63</b>	<b>10.39</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>fall</b>	<b>-21.34</b>	<b>11.15</b>	<b>10.89</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>inflow</b>	<b>fall</b>	<b>-20.02</b>	<b>10.35</b>	<b>10.88</b>
fish	<i>Gobiosoma bosc</i>	inflow	fall	-21.55	10.05	8.73
fish	<i>Gobiosoma bosc</i>	inflow	fall	-22.03	10.32	10.57
fish	<i>Lucania parva</i>	inflow	fall	-18.29	9.78	7.87
fish	<i>Lucania parva</i>	inflow	fall	-17.79	5.41	5.93
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>fall</b>	<b>-19.42</b>	<b>10.60</b>	<b>8.92</b>

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>inflow</b>	<b>fall</b>	<b>-19.35</b>	<b>10.50</b>	<b>9.04</b>
fish	<i>Microgobius gulosus</i>	inflow	fall	-21.52	12.29	2.45
fish	<i>Microgobius gulosus</i>	inflow	fall	-20.25	9.84	8.48
POM		inflow	fall	-22.00	4.80	18.00
SAV	<i>Ceratophyllum demersum</i>	inflow	fall	-20.11	5.29	6.61
SAV	<i>Ceratophyllum demersum</i>	inflow	fall	-21.67	4.92	10.22
SAV	<i>Filamentous algae</i>	inflow	fall	-20.75	2.33	0.40
SAV	<i>Myriophyllum spicatum</i>	inflow	fall	-18.17	4.21	2.87
SAV	<i>Najas guadalupensis</i>	inflow	fall	-24.43	0.43	0.29
SAV	<i>Najas guadalupensis</i>	inflow	fall	-22.37	3.37	12.60
SAV	<i>Najas guadalupensis</i>	inflow	fall	-22.82	2.97	5.20
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>inflow</b>	<b>fall</b>	<b>-24.05</b>	<b>7.48</b>	<b>9.27</b>
<b>shrimp</b>	<b><i>Farfantepenaeus aztecus</i></b>	<b>inflow</b>	<b>fall</b>	<b>-20.61</b>	<b>7.85</b>	<b>10.26</b>
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>inflow</b>	<b>fall</b>	<b>-23.19</b>	<b>8.36</b>	<b>9.56</b>
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>inflow</b>	<b>fall</b>	<b>-22.50</b>	<b>7.52</b>	<b>9.45</b>
C3 plant	<i>Alternanthera philoxeroides</i>	inflow	spring	-29.04	3.68	11.45
C3 plant	<i>Juncus roemerianus</i>	inflow	spring	-28.21	2.90	2.01
C3 plant	<i>Lythrum lineare</i>	inflow	spring	-29.30	4.11	6.39
C3 plant	<i>Scirpus robustus</i>	inflow	spring	-26.77	4.04	8.88
C3 plant	<i>Scirpus robustus</i>	inflow	spring	-28.26	6.20	2.34
C4 plant	<i>Distichlis spicata</i>	inflow	spring	-14.73	4.30	9.30
C4 plant	<i>Distichlis spicata</i>	inflow	spring	-14.00	5.45	9.38
C4 plant	<i>Distichlis spicata</i>	inflow	spring	-14.33	4.82	5.07
C4 plant	<i>Spartina alterniflora</i>	inflow	spring	-13.54	4.76	-0.62
C4 plant	<i>Spartina alterniflora</i>	inflow	spring	-13.60	4.59	4.18
C4 plant	<i>Spartina patens</i>	inflow	spring	-13.47	3.07	8.37
C4 plant	<i>Spartina patens</i>	inflow	spring	-13.67	3.99	5.93
detritus		inflow	spring	-13.53	2.13	7.47
detritus		inflow	spring	-13.33	1.25	9.08
detritus		inflow	spring	-14.36	2.69	7.58
detritus		inflow	spring	-20.92	2.93	7.81

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
detritus		inflow	spring	-21.02	2.78	6.45
detritus		inflow	spring	-24.27	2.45	5.48
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>spring</b>	<b>-22.12</b>	<b>12.75</b>	<b>8.12</b>
<b>fish</b>	<i>Brevoortia patronus</i>	<b>inflow</b>	<b>spring</b>	<b>-23.73</b>	<b>10.62</b>	<b>7.54</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>spring</b>	<b>-19.38</b>	<b>10.54</b>	<b>8.16</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>inflow</b>	<b>spring</b>	<b>-20.47</b>	<b>11.10</b>	<b>6.53</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>inflow</b>	<b>spring</b>	<b>-21.08</b>	<b>11.37</b>	<b>7.08</b>
POM		inflow	spring	-22.00	4.80	18.00
SAV	<i>Filamentous algae</i>	inflow	spring	-20.42	6.60	8.21
SAV	<i>Filamentous algae</i>	inflow	spring	-20.06	6.50	2.75
SAV	<i>Filamentous algae</i>	inflow	spring	-20.66	1.76	7.55
<b>shrimp</b>	<i>Farfantepenaeus aztecus</i>	<b>inflow</b>	<b>spring</b>	<b>-20.74</b>	<b>10.14</b>	<b>7.52</b>
C3 plant	<i>Euthamia galetorum</i>	inflow	summer	-28.62	4.43	11.46
C3 plant	<i>Lythrum lineare</i>	inflow	summer	-27.22	5.17	11.16
C3 plant	<i>Scirpus robustus</i>	inflow	summer	-27.85	5.55	8.49
C3 plant	<i>Vigna luteola</i>	inflow	summer	-29.73	-1.39	11.07
C4 plant	<i>Distichlis spicata</i>	inflow	summer	-14.18	5.91	8.05
C4 plant	<i>Distichlis spicata</i>	inflow	summer	-14.68	5.54	8.54
C4 plant	<i>Distichlis spicata</i>	inflow	summer	-13.46	6.43	8.00
C4 plant	<i>Distichlis spicata</i>	inflow	summer	-14.50	3.55	10.95
C4 plant	<i>Spartina alterniflora</i>	inflow	summer	-13.48	5.40	7.45
C4 plant	<i>Spartina alterniflora</i>	inflow	summer	-13.32	6.23	10.00
C4 plant	<i>Spartina alterniflora</i>	inflow	summer	-14.34	6.24	14.01
C4 plant	<i>Spartina alterniflora</i>	inflow	summer	-13.84	5.20	12.75
C4 plant	<i>Spartina patens</i>	inflow	summer	-13.70	4.35	5.95
C4 plant	<i>Spartina patens</i>	inflow	summer	-13.62	4.59	9.92
C4 plant	<i>Spartina patens</i>	inflow	summer	-12.85	4.40	5.78
C4 plant	<i>Spartina patens</i>	inflow	summer	-13.61	4.24	11.90
detritus		inflow	summer	-13.79	2.28	8.37
detritus		inflow	summer	-13.70	2.89	7.10
detritus		inflow	summer	-14.07	2.65	6.96

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
detritus		inflow	summer	-26.47	4.10	5.70
detritus		inflow	summer	-26.79	4.62	9.02
detritus		inflow	summer	-22.58	4.79	5.49
detritus		inflow	summer	-15.65	3.74	6.70
detritus		inflow	summer	-15.38	3.46	7.16
detritus		inflow	summer	-15.50	3.32	6.54
detritus		inflow	summer	-13.78	3.09	8.22
detritus		inflow	summer	-13.73	2.00	7.10
detritus		inflow	summer	-14.30	3.08	8.11
epiphytes		inflow	summer	-19.16	3.69	11.80
epiphytes		inflow	summer	-17.31	2.54	1.72
epiphytes		inflow	summer	-18.81	3.44	6.93
epiphytes		inflow	summer	-20.20	3.90	12.93
epiphytes		inflow	summer	-19.13	2.68	14.32
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>inflow</b>	<b>summer</b>	<b>-22.50</b>	<b>12.79</b>	<b>7.16</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>inflow</b>	<b>summer</b>	<b>-19.76</b>	<b>10.69</b>	<b>10.79</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>inflow</b>	<b>summer</b>	<b>-20.93</b>	<b>11.51</b>	<b>9.67</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.29</b>	<b>12.68</b>	<b>9.66</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>inflow</b>	<b>summer</b>	<b>-18.59</b>	<b>10.30</b>	<b>8.45</b>
fish	<i>Leiostomus xanthurus</i>	inflow	summer	-21.64	8.27	8.28
fish	<i>Lepomis macrochirus</i>	inflow	summer	-15.29	8.64	9.64
fish	<i>Lepomis microlophus</i>	inflow	summer	-19.03	8.76	7.24
fish	<i>Lepomis microlophus</i>	inflow	summer	-16.63	8.99	10.13
fish	<i>Lepomis miniatus</i>	inflow	summer	-16.54	9.15	9.25
fish	<i>Lepomis miniatus</i>	inflow	summer	-16.67	8.70	10.21
fish	<i>Lucania parva</i>	inflow	summer	-17.65	9.35	5.56
fish	<i>Lucania parva</i>	inflow	summer	-17.06	9.40	7.90
fish	<i>Lucania parva</i>	inflow	summer	-19.13	10.28	4.96
fish	<i>Lucania parva</i>	inflow	summer	-20.12	10.83	10.04
fish	<i>Lucania parva</i>	inflow	summer	-20.87	10.88	9.04
fish	<i>Lucania parva</i>	inflow	summer	-20.89	11.58	8.70

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
fish	<i>Lucania parva</i>	inflow	summer	-20.84	10.85	11.18
fish	<i>Lucania parva</i>	inflow	summer	-19.35	10.29	10.58
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>inflow</b>	<b>summer</b>	<b>-19.27</b>	<b>11.06</b>	<b>7.77</b>
fish	<i>Microgobius gulosus</i>	inflow	summer	-19.06	9.98	4.99
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.38</b>	<b>11.45</b>	<b>8.92</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.29</b>	<b>11.55</b>	<b>8.67</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-22.45</b>	<b>11.12</b>	<b>7.66</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.53</b>	<b>11.90</b>	<b>8.18</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.60</b>	<b>11.70</b>	<b>8.29</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.88</b>	<b>10.25</b>	<b>6.04</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-20.70</b>	<b>10.65</b>	<b>7.96</b>
<b>fish</b>	<b><i>Micropogonius undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-20.05</b>	<b>10.77</b>	<b>8.99</b>
<b>fish</b>	<b><i>Micropogonius undulatus</i></b>	<b>inflow</b>	<b>summer</b>	<b>-21.10</b>	<b>10.72</b>	<b>7.45</b>
fish	<i>Micropterus punctulatus</i>	inflow	summer	-16.72	9.50	6.12
fish	<i>Micropterus punctulatus</i>	inflow	summer	-15.81	9.65	7.38
fish	<i>Micropterus salmoides</i>	inflow	summer	-18.31	12.96	7.72
fish	<i>Micropterus salmoides</i>	inflow	summer	-18.45	12.59	7.22
fish	<i>Micropterus salmoides</i>	inflow	summer	-18.55	13.21	5.66
POM		inflow	summer	-22.00	4.80	18.00
SAV	<i>Ceratophyllum demersum</i>	inflow	summer	-18.76	8.44	11.10
SAV	<i>Ceratophyllum demersum</i>	inflow	summer	-21.27	6.31	6.98
SAV	<i>Ceratophyllum demersum</i>	inflow	summer	-19.40	4.69	5.51
SAV	<i>Ceratophyllum demersum</i>	inflow	summer	-18.58	6.62	2.27
SAV	<i>Eleocharis parvula</i>	inflow	summer	-17.84	3.97	8.38
SAV	<i>Eleocharis parvula</i>	inflow	summer	-18.52	4.43	4.67
SAV	<i>Eleocharis parvula &amp; algae</i>	inflow	summer	-20.16	5.62	7.24
SAV	<i>Filamentous algae</i>	inflow	summer	-18.66	5.41	1.45
SAV	<i>Filamentous algae</i>	inflow	summer	-16.71	5.47	4.46
SAV	<i>Filamentous algae</i>	inflow	summer	-18.96	5.06	2.78
SAV	<i>filamentous algae</i>	inflow	summer	-17.91	3.57	2.19
SAV	<i>Najas guadalupensis</i>	inflow	summer	-22.75	6.67	9.28

(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
SAV	<i>Najas guadalupensis</i>	inflow	summer	-19.14	4.32	4.68
<b>shrimp</b>	<i>Farfantepenaeus aztecus</i>	<b>inflow</b>	<b>summer</b>	<b>-22.69</b>	<b>9.22</b>	<b>7.97</b>
<b>shrimp</b>	<i>Farfantepenaeus aztecus</i>	<b>inflow</b>	<b>summer</b>	<b>-19.29</b>	<b>6.97</b>	<b>11.17</b>
<b>shrimp</b>	<i>Farfantepenaeus aztecus</i>	<b>inflow</b>	<b>summer</b>	<b>-19.98</b>	<b>8.78</b>	<b>9.98</b>
<b>shrimp</b>	<i>Litopenaeus setiferus</i>	<b>inflow</b>	<b>summer</b>	<b>-20.01</b>	<b>9.52</b>	<b>10.02</b>
<b>shrimp</b>	<i>Litopenaeus setiferus</i>	<b>inflow</b>	<b>summer</b>	<b>-20.29</b>	<b>8.51</b>	<b>8.60</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>summer</b>	<b>-20.07</b>	<b>10.94</b>	<b>7.94</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>summer</b>	<b>-18.04</b>	<b>9.57</b>	<b>7.73</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>summer</b>	<b>-18.17</b>	<b>9.36</b>	<b>7.54</b>
C4 plant	<i>Distichlis spicata</i>	inflow	winter	-14.20	7.31	8.84
C4 plant	<i>Paspalum distichum</i>	inflow	winter	-14.26	5.42	12.41
C4 plant	<i>Spartina alterniflora</i>	inflow	winter	-14.09	5.31	6.64
C4 plant	<i>Spartina alterniflora</i>	inflow	winter	-14.01	7.17	-0.07
C4 plant	<i>Spartina alterniflora</i>	inflow	winter	-13.44	6.57	1.34
C4 plant	<i>Spartina alterniflora</i>	inflow	winter	-13.48	7.32	8.56
C4 plant	<i>Spartina patens</i>	inflow	winter	-13.84	4.08	13.07
C4 plant	<i>Spartina patens</i>	inflow	winter	-13.72	4.42	12.80
detritus		inflow	winter	-15.19	3.18	4.45
detritus		inflow	winter	-14.69	3.67	5.54
detritus		inflow	winter	-14.40	3.90	4.09
detritus		inflow	winter	-14.12	3.32	7.59
detritus		inflow	winter	-14.68	3.51	9.48
detritus		inflow	winter	-16.58	3.63	5.42
detritus		inflow	winter	-13.84	5.50	1.74
detritus		inflow	winter	-15.09	5.26	0.87
detritus		inflow	winter	-15.15	7.55	7.58
detritus		inflow	winter	-14.52	3.85	10.63
detritus		inflow	winter	-15.11	3.56	7.53
detritus		inflow	winter	-15.01	3.06	7.70
filter feeder	mussel	inflow	winter	-24.64	7.33	10.78
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>winter</b>	<b>-21.27</b>	<b>11.78</b>	<b>10.20</b>

(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>inflow</b>	<b>winter</b>	<b>-21.32</b>	<b>10.76</b>	<b>10.30</b>
<b>fish</b>	<i>Brevoortia patronus</i>	<b>inflow</b>	<b>winter</b>	<b>-24.52</b>	<b>10.58</b>	<b>11.06</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>winter</b>	<b>-20.83</b>	<b>13.19</b>	<b>11.56</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>winter</b>	<b>-21.67</b>	<b>12.40</b>	<b>11.73</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>inflow</b>	<b>winter</b>	<b>-20.45</b>	<b>12.24</b>	<b>10.84</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>inflow</b>	<b>winter</b>	<b>-16.99</b>	<b>10.90</b>	<b>9.64</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>inflow</b>	<b>winter</b>	<b>-16.90</b>	<b>9.80</b>	<b>7.79</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>inflow</b>	<b>winter</b>	<b>-17.77</b>	<b>8.88</b>	<b>6.26</b>
fish	<i>Gobiosoma bosc</i>	inflow	winter	-21.10	10.51	10.78
fish	<i>Lucania parva</i>	inflow	winter	-19.31	11.31	10.55
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-18.65</b>	<b>10.72</b>	<b>9.80</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-19.14</b>	<b>10.29</b>	<b>8.58</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-20.03</b>	<b>11.22</b>	<b>10.43</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-19.53</b>	<b>11.04</b>	<b>9.12</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-19.24</b>	<b>11.11</b>	<b>10.48</b>
<b>fish</b>	<i>Menidia beryllina</i>	<b>inflow</b>	<b>winter</b>	<b>-18.80</b>	<b>9.80</b>	<b>8.59</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>inflow</b>	<b>winter</b>	<b>-19.05</b>	<b>10.68</b>	<b>8.78</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>inflow</b>	<b>winter</b>	<b>-19.94</b>	<b>11.01</b>	<b>9.11</b>
fish	<i>Micropterus salmoides</i>	inflow	winter	-18.49	14.08	4.14
grazer	periwinkle	inflow	winter	-16.90	8.80	13.35
POM		inflow	winter	-22.00	4.80	18.00
SAV	<i>Chara sp.</i>	inflow	winter	-18.48	8.17	11.29
SAV	<i>Chara sp.</i>	inflow	winter	-17.23	7.74	5.94
SAV	<i>Cymodocea manatorum</i>	inflow	winter	-16.37	6.93	2.57
SAV	<i>Myriophyllum spicatum</i>	inflow	winter	-15.88	4.61	10.56
SAV	<i>Myriophyllum spicatum</i>	inflow	winter	-15.07	6.48	7.02
SAV	<i>Myriophyllum spicatum</i>	inflow	winter	-15.79	5.03	4.64
SAV	<i>Myriophyllum spicatum</i>	inflow	winter	-14.91	6.29	11.62
SAV	<i>Najas sp.</i>	inflow	winter	-20.26	7.74	2.58
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>winter</b>	<b>-19.16</b>	<b>10.01</b>	<b>10.04</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>winter</b>	<b>-18.28</b>	<b>9.88</b>	<b>9.53</b>

(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>winter</b>	<b>-18.38</b>	<b>10.47</b>	<b>10.32</b>
<b>shrimp</b>	<i>Palaemonetes pugio</i>	<b>inflow</b>	<b>winter</b>	<b>-18.63</b>	<b>10.63</b>	<b>11.13</b>
C3 plant	<i>Scirpus robustus</i>	reference	fall	-28.91	7.06	13.78
C3 plant	<i>Scirpus robustus</i>	reference	fall	-25.50	2.06	12.96
C4 plant	<i>Distichlis spicata</i>	reference	fall	-14.06	7.19	13.47
C4 plant	<i>Spartina alterniflora</i>	reference	fall	-13.96	6.58	18.32
C4 plant	<i>Spartina patens</i>	reference	fall	-13.34	7.37	14.63
C4 plant	<i>Spartina patens</i>	reference	fall	-13.06	5.41	14.55
detritus		reference	fall	-15.12	3.95	14.67
detritus		reference	fall	-20.31	3.03	14.08
detritus		reference	fall	-16.12	4.65	16.13
detritus		reference	fall	-13.67	4.60	13.12
detritus		reference	fall	-13.75	5.59	12.12
detritus		reference	fall	-14.18	4.35	12.38
filter feeder	mussel	reference	fall	-24.91	6.49	12.14
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>reference</b>	<b>fall</b>	<b>-20.94</b>	<b>13.17</b>	<b>14.15</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>reference</b>	<b>fall</b>	<b>-22.32</b>	<b>11.30</b>	<b>11.76</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>reference</b>	<b>fall</b>	<b>-23.81</b>	<b>12.58</b>	<b>13.29</b>
<b>fish</b>	<i>Anchoa mitchilli</i>	<b>reference</b>	<b>fall</b>	<b>-22.93</b>	<b>11.10</b>	<b>13.39</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>reference</b>	<b>fall</b>	<b>-19.42</b>	<b>9.07</b>	<b>9.98</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>reference</b>	<b>fall</b>	<b>-20.10</b>	<b>9.73</b>	<b>10.01</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>reference</b>	<b>fall</b>	<b>-20.50</b>	<b>9.74</b>	<b>10.18</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>reference</b>	<b>fall</b>	<b>-21.28</b>	<b>10.74</b>	<b>11.73</b>
<b>fish</b>	<i>Cynoscion nebulosus</i>	<b>reference</b>	<b>fall</b>	<b>-22.70</b>	<b>10.56</b>	<b>10.92</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>reference</b>	<b>fall</b>	<b>-17.23</b>	<b>9.39</b>	<b>8.71</b>
<b>fish</b>	<i>Fundulus grandis</i>	<b>reference</b>	<b>fall</b>	<b>-17.21</b>	<b>8.55</b>	<b>8.50</b>
fish	<i>Lucania parva</i>	reference	fall	-16.71	4.60	5.75
<b>fish</b>	<i>Menidia beryllina</i>	<b>reference</b>	<b>fall</b>	<b>-21.10</b>	<b>10.82</b>	<b>9.79</b>
<b>fish</b>	<i>Micropogonias undulatus</i>	<b>reference</b>	<b>fall</b>	<b>-23.56</b>	<b>12.75</b>	<b>11.43</b>
POM		reference	fall	-26.80	5.60	18.00
<b>shrimp</b>	<i>Farfantepenaeus aztecus</i>	<b>reference</b>	<b>fall</b>	<b>-23.58</b>	<b>6.82</b>	<b>9.44</b>



(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>reference</b>	<b>fall</b>	<b>-19.52</b>	<b>6.13</b>	<b>8.69</b>
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>reference</b>	<b>fall</b>	<b>-20.55</b>	<b>6.23</b>	<b>7.86</b>
C3 plant	<i>Scirpus americanus</i>	reference	spring	-27.23	5.93	9.08
C4 plant	<i>Distichlis spicata</i>	reference	spring	-13.90	9.12	5.61
C4 plant	<i>Spartina patens</i>	reference	spring	-13.22	10.39	4.40
C4 plant	<i>Spartina patens</i>	reference	spring	-13.19	7.82	1.24
detritus		reference	spring	-13.67	4.72	7.77
detritus		reference	spring	-13.98	4.46	9.34
detritus		reference	spring	-14.01	6.54	8.78
detritus		reference	spring	-13.84	3.11	7.71
detritus		reference	spring	-14.80	2.55	8.36
detritus		reference	spring	-17.29	4.41	9.64
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>reference</b>	<b>spring</b>	<b>-20.68</b>	<b>12.70</b>	<b>12.33</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>spring</b>	<b>-22.92</b>	<b>10.37</b>	<b>11.49</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>reference</b>	<b>spring</b>	<b>-18.07</b>	<b>7.45</b>	<b>5.20</b>
fish	<i>Gobiosoma bosc</i>	reference	spring	-21.72	11.28	10.44
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>reference</b>	<b>spring</b>	<b>-20.64</b>	<b>10.90</b>	<b>9.19</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>reference</b>	<b>spring</b>	<b>-21.30</b>	<b>10.60</b>	<b>9.38</b>
grazer	periwinkle	reference	spring	-15.60	5.74	10.36
POM		reference	spring	-26.80	5.60	18.00
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>spring</b>	<b>-19.53</b>	<b>8.98</b>	<b>8.93</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>spring</b>	<b>-19.49</b>	<b>9.09</b>	<b>8.96</b>
C3 plant	<i>Lythrum lineare</i>	reference	summer	-29.12	7.61	13.41
C4 plant	<i>Distichlis spicata</i>	reference	summer	-14.10	5.87	12.78
C4 plant	<i>Spartina patens</i>	reference	summer	-14.00	3.19	12.11
C4 plant	<i>Spartina patens</i>	reference	summer	-13.63	7.36	14.13
detritus		reference	summer	-14.13	1.38	8.54
detritus		reference	summer	-14.38	1.54	8.20
detritus		reference	summer	-14.32	1.96	8.26
detritus		reference	summer	-22.20	4.52	11.64
detritus		reference	summer	-22.85	4.84	14.21

(Table 4.1 continued)

Type	Species	Site	Season	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{34}\text{S}$
detritus		reference	summer	-20.73	4.08	10.89
epiphytes		reference	summer	-25.01	8.26	8.12
epiphytes		reference	summer	-21.09	5.34	0.28
epiphytes		reference	summer	-21.24	4.98	0.06
epiphytes		reference	summer	-28.76	6.60	10.04
epiphytes		reference	summer	-19.91	4.67	1.58
epiphytes		reference	summer	-21.32	4.36	1.60
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>reference</b>	<b>summer</b>	<b>-23.32</b>	<b>12.21</b>	<b>12.89</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>reference</b>	<b>summer</b>	<b>-24.16</b>	<b>11.53</b>	<b>11.71</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>reference</b>	<b>summer</b>	<b>-21.78</b>	<b>11.62</b>	<b>9.58</b>
<b>fish</b>	<b><i>Anchoa mitchilli</i></b>	<b>reference</b>	<b>summer</b>	<b>-22.71</b>	<b>12.67</b>	<b>4.26</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>summer</b>	<b>-25.26</b>	<b>9.52</b>	<b>10.01</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>summer</b>	<b>-22.74</b>	<b>10.16</b>	<b>11.90</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>summer</b>	<b>-24.76</b>	<b>9.61</b>	<b>10.40</b>
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>summer</b>	<b>-27.67</b>	<b>10.64</b>	<b>4.23</b>
<b>fish</b>	<b><i>Cynoscion nebulosus</i></b>	<b>reference</b>	<b>summer</b>	<b>-20.62</b>	<b>11.89</b>	<b>11.42</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>reference</b>	<b>summer</b>	<b>-21.67</b>	<b>9.77</b>	<b>8.69</b>
POM		reference	summer	-26.80	5.60	18.00
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>reference</b>	<b>summer</b>	<b>-20.94</b>	<b>8.85</b>	<b>10.49</b>
<b>shrimp</b>	<b><i>Litopenaeus setiferus</i></b>	<b>reference</b>	<b>summer</b>	<b>-23.23</b>	<b>8.78</b>	<b>8.53</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>summer</b>	<b>-19.04</b>	<b>8.18</b>	<b>10.10</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>summer</b>	<b>-19.98</b>	<b>8.54</b>	<b>10.44</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>summer</b>	<b>-20.52</b>	<b>9.31</b>	<b>8.32</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>summer</b>	<b>-23.14</b>	<b>10.67</b>	<b>8.32</b>
C3 plant	<i>Scirpus robustus</i>	reference	winter	-26.04	5.38	12.62
C4 plant	<i>Paspalum distichum</i>	reference	winter	-14.49	8.33	9.69
C4 plant	<i>Paspalum distichum</i>	reference	winter	-14.18	8.06	8.85
C4 plant	<i>Spartina patens</i>	reference	winter	-13.92	8.18	9.28
C4 plant	<i>Spartina patens</i>	reference	winter	-13.45	7.23	8.64
detritus		reference	winter	-14.04	7.47	9.43
detritus		reference	winter	-14.00	5.42	10.23

(Table 4.1 continued)

Type	Species	Site	Season	d <sup>13</sup> C	d <sup>15</sup> N	d <sup>34</sup> S
detritus		reference	winter	-14.16	6.59	9.36
detritus		reference	winter	-14.74	5.57	8.94
detritus		reference	winter	-14.16	5.69	9.49
detritus		reference	winter	-15.93	5.07	11.06
<b>fish</b>	<b><i>Brevoortia patronus</i></b>	<b>reference</b>	<b>winter</b>	<b>-24.25</b>	<b>6.73</b>	<b>10.78</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>reference</b>	<b>winter</b>	<b>-18.89</b>	<b>8.33</b>	<b>6.31</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>reference</b>	<b>winter</b>	<b>-18.14</b>	<b>8.56</b>	<b>6.25</b>
<b>fish</b>	<b><i>Fundulus grandis</i></b>	<b>reference</b>	<b>winter</b>	<b>-18.01</b>	<b>8.98</b>	<b>6.72</b>
fish	<i>Gobiosoma bosc</i>	reference	winter	-22.03	10.29	11.67
fish	<i>Lucania parva</i>	reference	winter	-19.82	8.13	6.74
<b>fish</b>	<b><i>Menidia beryllina</i></b>	<b>reference</b>	<b>winter</b>	<b>-21.10</b>	<b>9.88</b>	<b>9.64</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>reference</b>	<b>winter</b>	<b>-20.91</b>	<b>8.96</b>	<b>7.94</b>
<b>fish</b>	<b><i>Micropogonias undulatus</i></b>	<b>reference</b>	<b>winter</b>	<b>-20.46</b>	<b>9.89</b>	<b>7.75</b>
fish	<i>Mugil cephalus</i>	reference	winter	-17.03	5.13	5.62
fish	<i>Mugil cephalus</i>	reference	winter	-17.18	6.98	7.14
fish	<i>Mugil cephalus</i>	reference	winter	-16.91	5.10	2.92
grazer	periwinkle	reference	winter	-13.28	5.81	13.01
POM		reference	winter	-26.80	5.60	18.00
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>winter</b>	<b>-18.56</b>	<b>8.29</b>	<b>10.01</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>winter</b>	<b>-19.17</b>	<b>8.33</b>	<b>9.68</b>
<b>shrimp</b>	<b><i>Palaemonetes pugio</i></b>	<b>reference</b>	<b>winter</b>	<b>-19.75</b>	<b>9.08</b>	<b>9.71</b>

Before the use of these metrics in isotope ecology (Bearhop et al. 2004; Layman et al. 2007a, b; Newsome et al. 2007; Simonsen 2008), these metrics have been applied and discussed in the field of ecomorphology (Findley 1973; Ricklefs and Travis 1980; Winemiller 1991). Calculations were made using MATLAB® (2005) based upon techniques described in Layman et al. (2007a). Previous studies provide more details on theory and calculations of these metrics (Findley 1973; Ricklefs and Travis 1980; Winemiller 1991; Cornwell et al. 2006).

I used ANOVA (SAS 2005) to determine significant differences between the mean CD of each area. The  $\alpha$  level was 0.05 in all statistical tests performed, unless otherwise indicated. To increase power I also performed an ANOVA on the centroid distances of all individuals in the consumer community, rather than on the means for each species. For both models the residuals were normally distributed and no transformations were necessary. In addition, I tested for significant differences in trophic diversity among the areas based upon a combination of all four trophic structure metrics. I normalized the data to the mean to correct for scalar differences and tested for among-area differences with an ANOVA in SAS, followed by a Tukey's pairwise comparisons test. The residuals were normally distributed. To ensure that the differences in dispersion of consumers in C-N space was not an artifact of differences in isotopic base values and divergence of carbon sources between different areas, I calculated TA, CD, CR and NR for the carbon sources in the sites as well. I normalized these metrics to the mean and tested the transformed data for significant differences among the areas using ANOVA. The residuals were normally distributed. I also tested with a Pearson correlation test in SAS for significant differences between the normalized consumer and producer metrics.

To test for significant differences between the consumers' mean isotopic composition among the three areas based upon all three stable isotope ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$ ), I used MANOVA with both area and season in the model to account for seasonal differences. To clarify

where specific differences occurred, I performed multiple comparisons with a Bonferroni adjustment because of the high number of pairwise comparisons (144) in the two-way MANOVA with interactions. The residuals of this model were normally distributed and no transformations were necessary. I performed the same MANOVA on the producers' isotopic compositions. In this case, I did not find a seasonal main effect or an area\*season interaction, so I reduced the producers' model to a one-way MANOVA with area as the main effect.

To identify basal resources in the food web in each area, consumers that occurred in all three areas were plotted in  $\delta^{13}\text{C}$  -  $\delta^{34}\text{S}$  biplot space together with all producers/carbon sources. Only nekton species that were collected in all three areas were used in the source contribution and energy density analyses so as to create comparable nekton communities. The nekton species I used in this analysis include: *Anchoa mitchilli* (bay anchovy), *Brevoortia patronus* (Gulf menhaden), *Cynoscion nebulosus* (spotted seatrout), *Farfantepenaeus aztecus* (brown shrimp), *Fundulus grandis* (Gulf killifish), *Litopenaeus setiferus* (white shrimp), *Menidia beryllina* (silverside), *Micropogonias undulatus* (Atlantic croaker) and *Palaemonetes pugio* (grass shrimp). Included in this group are primary consumers, secondary consumers, detritivores, omnivores and an apex predator.

To determine the fractional contribution of river-associated carbon to each of the food webs, the existing carbon sources (primary producer groups) were aggregated into three sources with comparable  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  ranges. This resulted in two aggregations of local carbon sources, and one source of river-associated particulate organic matter (POM). From each source, I chose the extreme value to form a three-source triangle that contained all of the consumers from each area. The carbon sources were combined in the following way: source 1 is POM only and represents river-associated carbon; source 2 is an aggregate of local carbon sources---C4 plants, detritus (consisting mainly of C4 plant material), SAV, and epiphytes; and source 3 is another

aggregate of local carbon sources---C3 plants, detritus (consisting mainly of C3 plant material) and epiphytes. Even though two of the sources are large aggregates, useful information could be derived from the fractional contribution of these sources to the diets of consumers, because high  $\delta^{34}\text{S}$  values of POM separates the river-associated carbon source from local carbon sources.

I performed MANOVA using the  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of the consumers to test whether food webs in the three areas differed significantly. Pairwise comparisons were made using Tukey's multiple comparisons test; the residuals were normally distributed. To determine the contribution of each of the aggregate sources to the food webs in each area, the following set of linear equations was solved:

$$f_1 + f_2 + f_3 = 1, \quad (\text{Eq. 4.2})$$

$$f_1 * \delta^{13}\text{C}_1 + f_2 * \delta^{13}\text{C}_2 + f_3 * \delta^{13}\text{C}_3 = \text{observed } \delta^{13}\text{C} \text{ of the sample, } (\text{Eq. 4.3})$$

$$f_1 * \delta^{34}\text{S}_1 + f_2 * \delta^{34}\text{S}_2 + f_3 * \delta^{34}\text{S}_3 = \text{observed } \delta^{34}\text{S} \text{ of the sample; } (\text{Eq. 4.4})$$

where the three sources are denoted by the subscripts 1-3, and  $f$  is the fractional contribution of a source (Fry 2006).

Whether the average fractional contribution of each source to the diet of consumers was significantly different among the three areas was tested using MANOVA. To determine which of the individual comparisons differed significantly from among all pairwise comparisons, I performed Tukey's multiple comparisons test. The residuals were normally distributed and no transformation was necessary.

The caloric content of the nekton species was compared among the three areas to determine whether the caloric density of tissue of the consumer community differed significantly by using ANOVA with Tukey's multiple comparisons test. Unlike the stable isotope analyses,

caloric density was analyzed from samples collected in all study sites (Figure 3.1 and 3.2; Chapter 3) to further differentiate changes in caloric content in consumers in the areas that are, and are not exposed to river inflow. In the comparison of mean caloric density among areas, the results from all sites were included. First, I performed one one-way ANOVA to compare the mean caloric density per area, followed by a Tukey's comparisons test to determine which areas were significantly different. The residuals were normally distributed. Then, I performed a one-way ANOVA for each species (resulting in 9 ANOVA's) followed by a Tukey's comparisons test to determine which species were significantly different among the areas. The residuals were normally distributed. An  $\alpha$ -level of 0.01 was used for these pairwise comparisons to minimize the likelihood of experiment-wide error (Sokal and Rohlf 1995). Additionally, samples collected for caloric content from the low, medium and high salinity sites within the inflow area were compared to each other with a one-way ANOVA followed by Tukey's multiple comparisons. This was followed again with one-way ANOVA's for each species, followed by Tukey's comparisons test with  $\alpha = 0.01$ . The residuals were normally distributed.

In an effort to relate energy density to hydrological connectivity, caloric density of consumers in the inflow area was correlated with  $\delta^{34}\text{S}$  values of consumers using Pearson correlation, since  $\delta^{34}\text{S}$  values distinguish local plant sources ( $\sim +2 - +6 \text{ ‰}$ ) from POM/phytoplankton ( $\sim +17 - +21 \text{ ‰}$  in brackish marshes; Peterson and Fry 1987; Wissel and Fry 2005). I also performed a Pearson correlation between caloric density of consumers in all areas and salinity as a proxy for hydrological connectivity and distance from the river input. For these analyses the mean caloric density per species, site and season was used. Higher salinities indicate a larger distance from the point of river inflow, and (by inference) less influence by river water.

## **RESULTS**

### **Trophic Structure**

Trophic diversity of the consumers' community was highest in the reference area, followed by the inflow area and lowest in the control area (Figure 4.1). An effort was made to sample a large and representative community in each area for the trophic metric calculations, and to sample as many carbon sources as possible in each area (Table 4.1). All trophic structure metrics analyzed in C-N biplot space, namely total area (TA), centroid distance (CD),  $\delta^{13}\text{C}$ -range (CR) and  $\delta^{15}\text{N}$ -range (NR), were largest in the reference area, followed by the inflow area and smallest in the control area (Figure 4.1; Table 4.2). Unlike the other metrics, CD is a mean of multiple measurements (the centroid distance of each point in the polygon), which provided the opportunity to perform an ANOVA on CD alone. While the differences in CD between the reference, inflow and control area (3.12, 2.55 and 2.15, respectively) were not significant, this was mainly due to the low number of samples when the mean per species were used. When the CD was calculated based upon the values per each consumer specimen, the reference area had a significantly higher CD than the control and inflow areas ( $F = 7.50$ ,  $p = 0.0007$ ), even while absolute differences between the mean CD's of the reference, inflow and control areas were smaller (2.86, 2.07 and 2.07, respectively).

Testing trophic structure differences on the combination of all four metrics (after normalizing the data to the mean) revealed that there were significant differences in trophic structure among the areas ( $F = 173.31$ ,  $p < 0.0001$ ). All areas were significantly different from one another ( $p = 0.0002$  in the inflow-reference comparison,  $p < 0.0001$  in the other two pairwise comparisons).



Figure 4.1. C-N biplots with the mean isotopic composition of consumer species (●) and carbon sources (●) in the control, inflow and reference areas. Two trophic structure metrics are indicated in the figure; total area (TA), which is represented by the smallest convex polygon that could be placed around the consumer species in the figure, and centroid distance (CD), which is the mean distance of the consumer species to the centroid of the polygon. Carbon sources are C3 plants (C3), particulate organic matter (POM), epiphytes (Epi), two detritus groups (D1 and D2; depending on dominant material), submerged aquatic vegetation (SAV), and C4 plants (C4). All plant and animal species used in this figure are listed in Table 4.1.

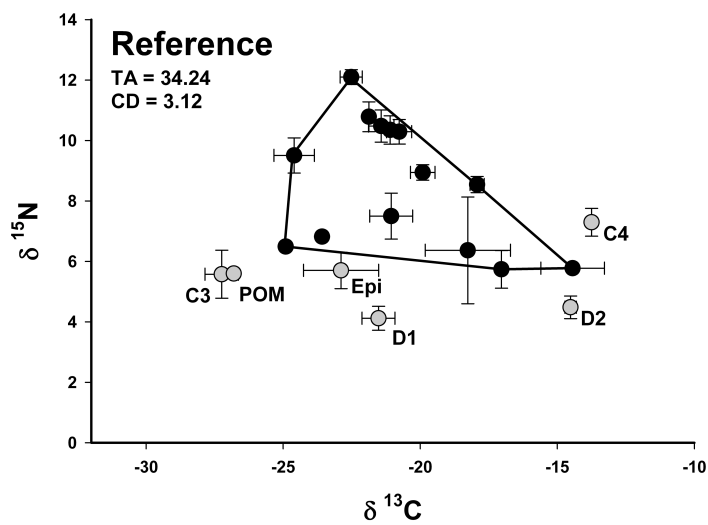
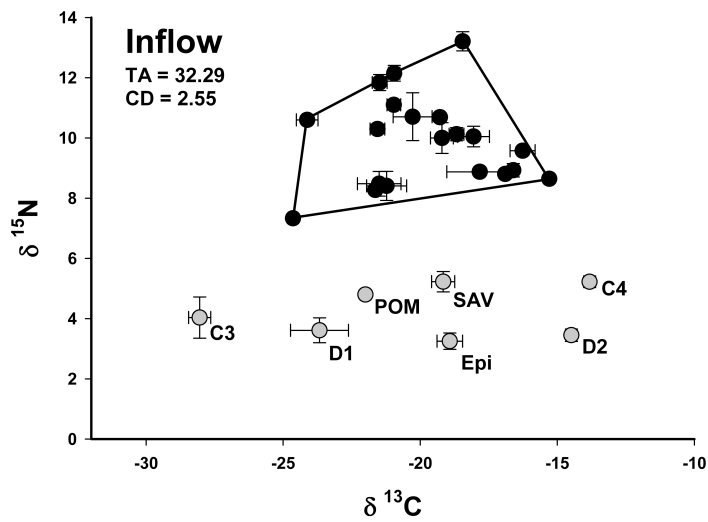
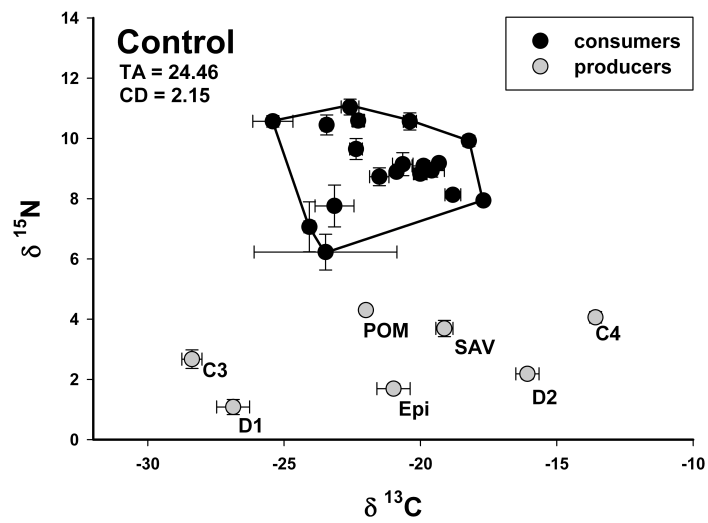
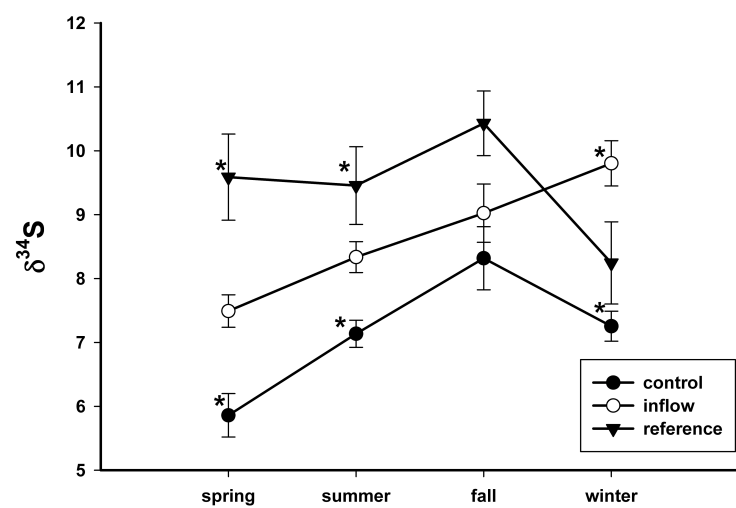
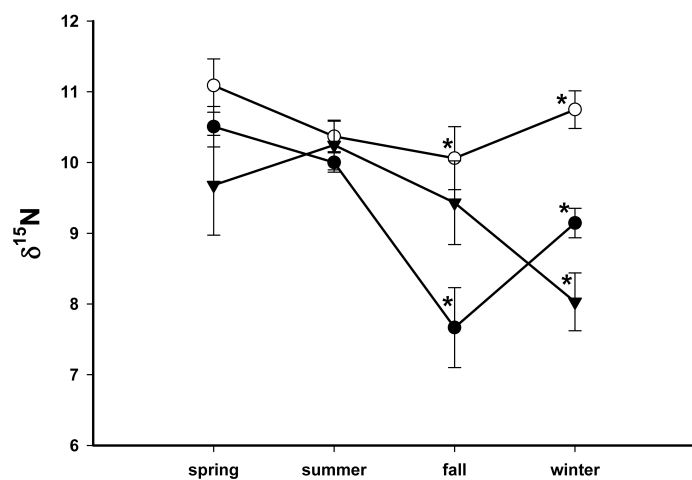
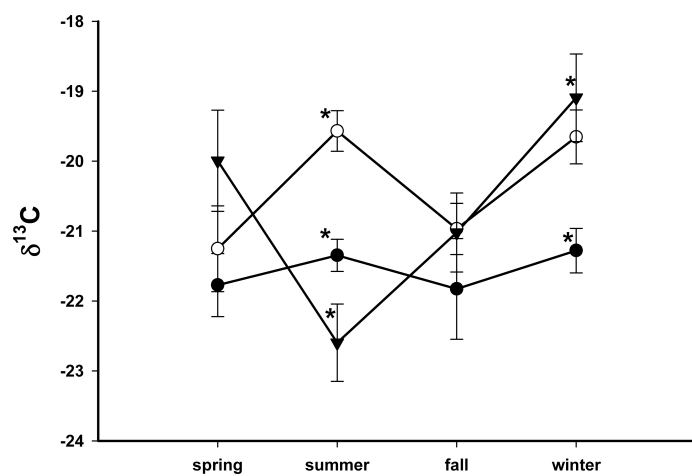


Table 4.2. Comparison of four trophic structure metrics among the control, inflow and reference areas. The metrics derived for the consumer groups indicate the extent of trophic diversity, while the metrics derived for the producer groups indicate divergence in stable isotope compositions of carbon sources in each area. The normalized value of each metric that is used in analyses is indicated in the table.

Metric	Group	Control		Inflow		Reference	
		value	normalized	value	normalized	value	normalized
Total Area (TA)	Producers	29.20	0.95	18.27	-1.04	24.46	0.09
	Consumers	24.46	-1.13	32.29	0.38	34.24	0.76
Centroid	Producers	4.43	-0.06	4.06	-0.96	4.88	1.03
Distance (CD)	Consumers	2.15	-0.94	2.55	-0.12	3.12	1.05
$\delta^{13}\text{C}$ Range (CR)	Producers	14.80	0.96	14.22	0.08	13.49	-1.04
	Consumers	7.72	-1.06	9.35	0.12	10.47	0.93
$\delta^{15}\text{N}$ Range (NR)	Producers	0.15	-1.13	0.49	0.76	0.42	0.37
	Consumers	4.82	-1.10	5.88	0.25	6.36	0.85

The same metric calculations and tests were performed for the primary producers and other carbon sources, to ascertain that divergence in consumers did indeed indicate trophic diversity and niche breath. There was no significant difference in divergence of carbon sources among the areas ( $F = 0.31$ ,  $p = 0.7383$ ). This result, and the finding that there was no correlation between the size of each metric calculated for the consumer community and the carbon sources group within the same area ( $p = 0.8864$ ) supports the conclusion that the differences in trophic structure among the areas were not an artifact of differences in isotopic base values among the areas.

Figure 4.2. Comparison of the mean  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values per season of all consumers (see Table 4.1 for listing) in the control, inflow and reference areas. This elucidates the nature of the season\*area interaction in a MANOVA performed to compare the consumers from the three areas based upon all three stable isotopes. The asterisks (\*) indicate significant differences ( $\alpha = 0.05$ ) among the areas per season based upon multiple comparisons with a bonferroni adjustment following the MANOVA.



## Isotopic Composition Comparisons

The mean isotopic composition of all consumers based upon three stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$ ) was significantly different among areas. Comparing the isotopic composition of consumers with a MANOVA by area and season revealed significant differences among areas, seasons and within the area\*season interaction ( $p < 0.0001$  for all three). Even though there is an interaction between area and season, the inflow area had consistently higher  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values than the control area (Figure 4.2). The main cause of an interaction effect was the strong seasonal variability in isotopic compositions in the reference area (Figure 4.2). When calculated over seasons,  $\delta^{13}\text{C}$  was significantly lower in the control area than the reference and inflow areas ( $p = 0.0339$  and  $p = 0.0016$  respectively), as were  $\delta^{15}\text{N}$  ( $p < 0.0001$ ) and  $\delta^{34}\text{S}$  ( $p < 0.0001$ ); the inflow and reference area did not differ significantly from one another.

The primary producers in the control area also had significantly lower  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  values ( $p < 0.0001$ ) than the inflow and reference areas; there was no significant seasonal effect on the isotopic compositions of primary producers. The producers in the reference areas had similar  $\delta^{13}\text{C}$  values as compared to producers in the inflow area, but significantly higher  $\delta^{15}\text{N}$  ( $p = 0.0012$ ) and  $\delta^{34}\text{S}$  ( $p < 0.0001$ ) values. These types of base value differences among areas do not affect trophic structure metrics calculated for consumers, as it influences the position of the whole consumers community in C-N biplot space, not the variability.

To help identify the source material in each food web, the consumer communities'  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values were compared with their local primary producers. Sulfur isotopes were significantly different between consumers and producers in each area, and the carbon isotopes differed between producers and consumers only in the inflow and reference areas ( $p < 0.0001$  and  $p = 0.0002$ , respectively), while they were not significantly different in the control area. This

is one indication that consumers rely on a non-local (ultimate) carbon source in their diet, and the consumers in the reference and inflow areas do so more than consumers in the control area.

### **Food Web Sources**

A MANOVA on the mean  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of selected nekton species revealed significant differences among the three areas ( $F = 14.87$ ,  $p < 0.0001$ ; Figure 4.3). For better comparison, only nekton species that were collected in all areas were used for these analyses (see data analysis section for selection). Mean nekton  $\delta^{13}\text{C}$  values were significantly lower in the control area than the inflow area ( $p = 0.0018$ ), while those of the reference area were not significantly different than those of either the control or inflow area. Mean nekton  $\delta^{34}\text{S}$  values were significantly lower in the control area than either the reference or the inflow area ( $p < 0.0001$ ).

By aggregating carbon sources (see data analysis section), a three-source, two-isotope model was created to calculate the fractional contribution of each carbon source to each species' diet using a mixed-model approach (Fry 2006; Figure 4.3; Table 4.3). The mean relative contribution of carbon sources to diets of each consumer community was significantly different among areas ( $F = 10.75$ ,  $p < 0.0001$ ). There was a significantly higher mean contribution of POM to diets of consumers in the inflow (~36%) and reference areas (~39%) than the control area (~24%;  $p < 0.0001$ ); the inflow and reference areas did not differ significantly from one another. Analyses of POM in both Breton Sound and Fourleague Bay indicate that it mostly consists of phytoplankton (Wissel et al. 2005 and Kendall 2001 respectively).

The relative contribution of Source 2 (C4 plants, detritus, SAV and epiphytes) was significantly lower in the reference area (~31%) than in the control area (~35%) and inflow area (~39%;  $p = 0.0478$ ), which is likely attributable to the lack of SAV in the sites of collection in the reference area (Chapter 3). The relative contribution of source 3 (C3 plants, detritus and

epiphytes) was significantly higher in the control area (~41%) than the inflow (~25%) and the reference areas (~30%;  $p < 0.0001$ ).

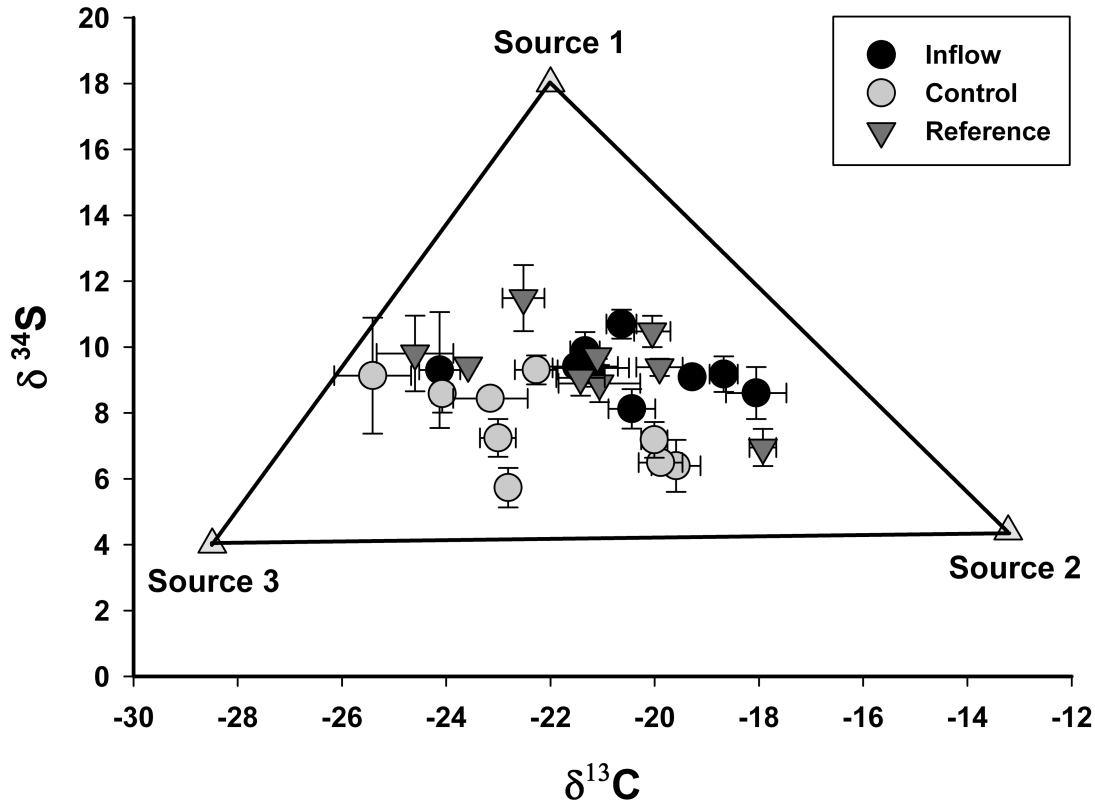


Figure 4.3. Comparison of the mean  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values per species of *Anchoa mitchilli* (bay anchovy), *Brevoortia patronus* (Gulf menhaden), *Cynoscion nebulosus* (spotted seatrout), *Farfantepenaeus aztecus* (brown shrimp), *Fundulus grandis* (Gulf killifish), *Litopenaeus setiferus* (white shrimp), *Menidia beryllina* (silverside), *Micropogonias undulatus* (Atlantic croaker) and *Palaemonetes pugio* (grass shrimp) in the inflow (●), control (●) and reference (▼) areas. They are plotted within a polygon created with the extreme values of aggregated carbon sources, which is used to calculate the relative contribution of each carbon source in each species' diet with a mixed model approach. Source 1 is particulate organic matter (POM), and represents the river-associated carbon source. Source 2 and 3 are aggregates of local carbon sources. Source 2 is an aggregate of C4 plants, detritus (consisting mainly of C4 plant material), SAV, and epiphytes. Source 3 is an aggregate of C3 plants, detritus (consisting mainly of C3 plant material), and epiphytes.



Table 4.3. Mixed model results of the mean proportional contribution per species ( $\pm 1$  S. E.) of the three carbon sources in the control, inflow, and reference areas. See Figure 4.3 for detail on source material.

Species	Site	Source 1	Source 2	Source 3
<i>A. mitchilli</i>	control	0.29 ( $\pm 0.04$ )	0.26 ( $\pm 0.01$ )	0.45 ( $\pm 0.04$ )
<i>A. mitchilli</i>	inflow	0.38 ( $\pm 0.03$ )	0.30 ( $\pm 0.01$ )	0.32 ( $\pm 0.03$ )
<i>A. mitchilli</i>	reference	0.53 ( $\pm 0.07$ )	0.17 ( $\pm 0.04$ )	0.30 ( $\pm 0.05$ )
<i>B. patronus</i>	control	0.37 ( $\pm 0.02$ )	0.05 ( $\pm 0.04$ )	0.59 ( $\pm 0.06$ )
<i>B. patronus</i>	inflow	0.38 ( $\pm 0.13$ )	0.13 ( $\pm 0.08$ )	0.50 ( $\pm 0.05$ )
<i>B. patronus</i>	reference	0.41 ( $\pm 0.08$ )	0.08 ( $\pm 0.02$ )	0.51 ( $\pm 0.09$ )
<i>C. nebulosus</i>	control	0.37 ( $\pm 0.05$ )	0.25 ( $\pm 0.05$ )	0.38 ( $\pm 0.00$ )
<i>C. nebulosus</i>	inflow	0.47 ( $\pm 0.03$ )	0.31 ( $\pm 0.03$ )	0.22 ( $\pm 0.02$ )
<i>C. nebulosus</i>	reference	0.45 ( $\pm 0.03$ )	0.36 ( $\pm 0.04$ )	0.19 ( $\pm 0.01$ )
<i>F. aztecus</i>	control	0.32 ( $\pm 0.04$ )	0.15 ( $\pm 0.03$ )	0.53 ( $\pm 0.01$ )
<i>F. aztecus</i>	inflow	0.37 ( $\pm 0.04$ )	0.32 ( $\pm 0.04$ )	0.31 ( $\pm 0.06$ )
<i>F. aztecus</i>	reference	0.38 (-)	0.16 (-)	0.46 (-)
<i>F. grandis</i>	control	0.16 ( $\pm 0.04$ )	0.52 ( $\pm 0.04$ )	0.33 ( $\pm 0.03$ )
<i>F. grandis</i>	inflow	0.31 ( $\pm 0.06$ )	0.55 ( $\pm 0.06$ )	0.14 ( $\pm 0.03$ )
<i>F. grandis</i>	reference	0.19 ( $\pm 0.04$ )	0.61 ( $\pm 0.01$ )	0.20 ( $\pm 0.04$ )
<i>L. setiferus</i>	control	0.31 ( $\pm 0.05$ )	0.22 ( $\pm 0.07$ )	0.47 ( $\pm 0.02$ )
<i>L. setiferus</i>	inflow	0.38 ( $\pm 0.02$ )	0.30 ( $\pm 0.05$ )	0.32 ( $\pm 0.05$ )
<i>L. setiferus</i>	reference	0.34 ( $\pm 0.04$ )	0.34 ( $\pm 0.05$ )	0.32 ( $\pm 0.06$ )
<i>M. beryllina</i>	control	0.16 ( $\pm 0.04$ )	0.49 ( $\pm 0.04$ )	0.34 ( $\pm 0.02$ )
<i>M. beryllina</i>	inflow	0.35 ( $\pm 0.02$ )	0.45 ( $\pm 0.01$ )	0.20 ( $\pm 0.01$ )
<i>M. beryllina</i>	reference	0.40 ( $\pm 0.01$ )	0.31 ( $\pm 0.00$ )	0.29 ( $\pm 0.00$ )
<i>M. undulatus</i>	control	0.11 ( $\pm 0.02$ )	0.32 ( $\pm 0.02$ )	0.56 ( $\pm 0.00$ )
<i>M. undulatus</i>	inflow	0.28 ( $\pm 0.03$ )	0.41 ( $\pm 0.02$ )	0.31 ( $\pm 0.03$ )
<i>M. undulatus</i>	reference	0.35 ( $\pm 0.04$ )	0.31 ( $\pm 0.05$ )	0.33 ( $\pm 0.01$ )
<i>P. pugio</i>	control	0.21 ( $\pm 0.02$ )	0.46 ( $\pm 0.02$ )	0.32 ( $\pm 0.02$ )
<i>P. pugio</i>	inflow	0.36 ( $\pm 0.04$ )	0.49 ( $\pm 0.02$ )	0.15 ( $\pm 0.03$ )
<i>P. pugio</i>	reference	0.37 ( $\pm 0.02$ )	0.40 ( $\pm 0.03$ )	0.22 ( $\pm 0.04$ )

## Energy Density

The energy densities ( $\text{cal g}^{-1}$ ) of the aforementioned select group of nekton species did not differ significantly between the control and inflow areas, while the mean energy density in the reference area was significantly lower than either area in Breton Sound ( $p < 0.0001$ ; Figure 4.4A). A closer look at the inflow area revealed that distance from the CFD (river water source) had an effect on energy density in consumers. Within the inflow area, mean nekton energy density in low salinity sites (closest to the diversion) was significantly higher than in high salinity sites farthest from the diversion ( $p = 0.0107$ ). The mean energy density of nekton from medium salinity sites did not differ from either the low or high salinity sites (Figure 4.4B), which indicates a modest gradient in energy enhancement to the food web with distance from the CFD. This is further evidenced by a negative correlation between salinity and caloric content of consumers (Pearson Correlation Coefficient = 0.53,  $p = 0.0084$ ; Figure 4.5A).

Because diets with a high contribution of POM are reflected in high  $\delta^{34}\text{S}$  values of consumers (Figure 4.3), the  $\delta^{34}\text{S}$  values of each species in the medium salinity inflow sites were correlated with caloric density per species as well. Only samples from the inflow sites were used because the nekton in the reference area were shown above to have lower energy density compared to the inflow area, likely due to distance from the river source. There was a significant positive correlation between the consumers'  $\delta^{34}\text{S}$  values and their caloric density (Pearson Correlation Coefficient = 0.58,  $p = 0.0149$ ; Figure 4.5B).

## **DISCUSSION**

I demonstrated that restored hydrological connectivity in Breton Sound increases total niche width and trophic diversity, alters foodweb pathways, and increases energy density in the estuarine nekton community.

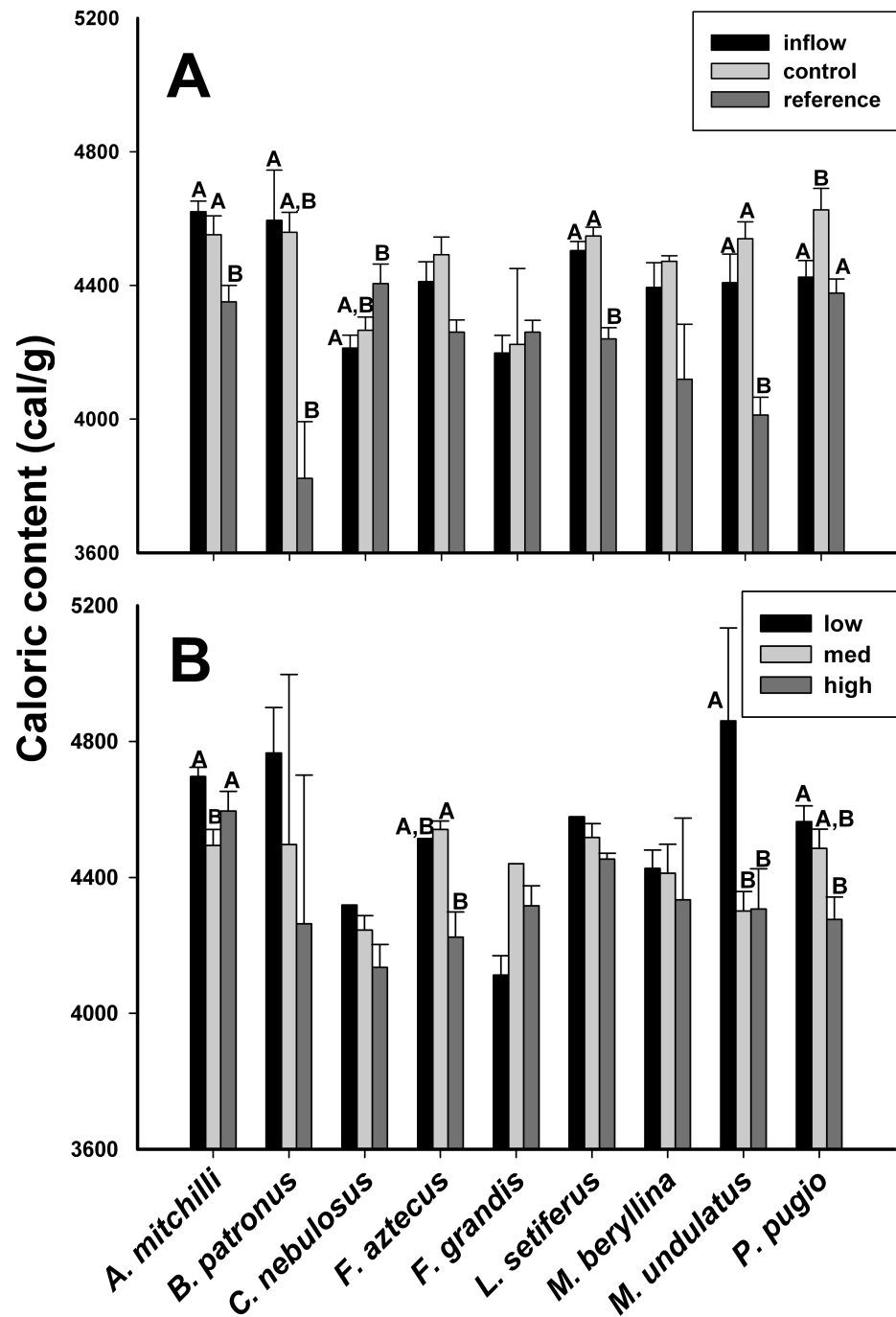


Figure 4.4. Comparison of the mean energy density (cal g<sup>-1</sup>) of nine nekton species among A) the inflow, control, and reference areas, and B) the low, medium, and high salinity sites in the inflow area. Significant differences ( $\alpha = 0.05$ ) based on Tukey's multiple comparisons following an ANOVA are indicated by letters (A and B) in the figures.

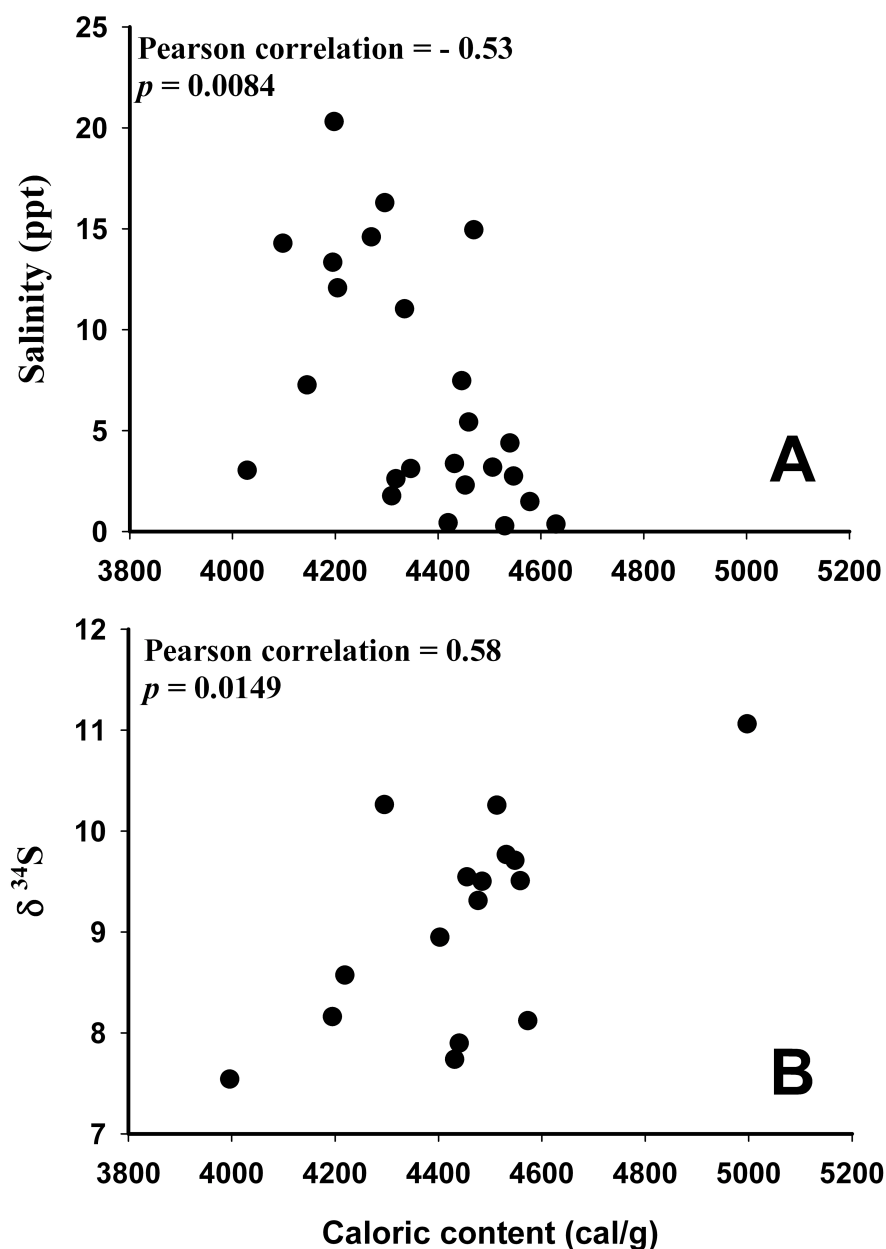


Figure 4.5. Correlations between A) the mean energy density ( $\text{cal g}^{-1}$ ) of nine nekton species collected in all areas, and the salinity at the site of collection, based upon samples collected in all sites and areas, and B) between the mean energy density of the same nekton species, now only from the specimens collected at the medium salinity site in the inflow area, and the mean  $\delta^{34}\text{S}$  values of the same species in the same site. The Spearman correlation coefficient and p value of this correlation are indicated in the figures.

The area with restored flow (inflow area) seems to be on a restoration trajectory with intermediate trophic metric values compared to the control area (mostly isolated from the flow) and the reference area (an estuary with natural hydrological connectivity).

Highest energy densities in nekton were observed at sites closest (~ 15 km) to the point of inflow; energy densities significantly decreased with distance from the source of freshwater inflow. River-associated alterations in foodweb pathways are evidenced by an increase in relative contributions of POM as the ultimate carbon source in diets of estuarine nekton.

Trophic structure metrics, based upon variability in C-N bi-plot space of consumers' isotopic composition within a community, revealed that the reference area has the largest trophic diversity, followed by the inflow and control areas. High variability within a community in  $\delta^{15}\text{N}$  values is mainly indicative of a multitude of trophic levels and thereby, functional groups, within the community, while high variability in  $\delta^{13}\text{C}$  values is mainly indicative of a multitude of carbon sources at the base of the food web (Layman et al 2007a). High C and N variability and niche breadth are an indication of an established, complex and resilient community because of high trophic diversity and ample possibilities for niche diversification (Layman et al 2007a). Layman et al. (2007b) showed reduced resilience of top predators due to loss of hydrological connectivity, which they demonstrated by using the same metrics as applied here.

It is interesting that the values of all trophic structure metrics from the consumer community in the inflow area were between the values of the community in the reference area and the control area, and that lowest values all were from the community in the control area. The control area is in the same estuary (Breton Sound) as the inflow area, but is separated by a levee that blocks most of the freshwater flow from the CFD, while the reference area is in another estuary approximately 150 km away. This demonstrates that hydrological connectivity plays a large role in the trophic structure of consumer communities. A recent study by Armitage and

Fourqurean (2009) showed an increase in food web complexity in a seagrass community as a result of nutrient enrichment; increased nutrients as a result of hydrological restoration also could be a factor in the increase in food web complexity in the Breton Sound inflow area. Food web complexity has a non-linear response curve with allochthonous material and nutrient inputs; although these subsidies enable greater biomass than supported by local productivity, too much input can have the opposite effect on estuarine food web complexity and stability (Jefferies 2000; Caddy 1993). Currently, the food web in Breton Sound seems to be on the increasing slope of curve. The even higher trophic diversity in Fourleague Bay indicates that this estuary probably is not on the declining slope of this curve, despite discharge of approximately  $5000 \text{ m}^3 \text{ s}^{-1}$  from the Atchafalaya River (Van Heerden and Roberts 1980). This suggests that much higher than current discharge through the CFD may be possible before negative effects will become evident, although the approximate 3-fold higher nutrient loading in the Mississippi River compared to the Atchafalaya River (Goolsby et al. 1999) should be taken into account when optimizing CFD discharge.

The importance of hydrological connectivity to estuarine food webs has been emphasized in the literature (Power et al. 1996; Hein et al. 2003; Freeman et al. 2007; Howe and Simenstad 2007), and has been shown to have a positive effect on nekton abundance and biomass in Breton Sound (Wissel and Fry 2005; Piazza and La Peyre 2007; Day et al. 2009; Chapter 2). In addition to nutrient enrichment, the increased frequency of inundation of flooded high-quality marsh habitat as a result of freshwater inflow also could be contributing to increases in trophic diversity (Piazza and La Peyre 2007; Kimmerer et al. 2009).

Previous critiques on comparing trophic structure metrics between different areas point out the effect of potential differences in divergence of isotopic composition of carbon sources between areas, which could result in between-area differences in trophic structure metrics of the

consumer community unrelated to niche breath (Newsome et al. 2007). For this reason, an effort was made to collect samples in each area of as many carbon sources as possible. There was no difference in the divergence of the carbon sources among areas based upon four trophic structure metrics, and there was no correlation between the metrics calculated for carbon sources and consumers collected in the same areas. This confirms that the differences in trophic metrics are indeed caused by trophic diversity and niche breath differences among the consumer communities in my study areas.

Comparing the actual stable isotope values of the consumers and producers in the three different areas revealed that both environmental and biological factors are causing differences in isotopic compositions. The elevated  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$  levels in the reference and inflow areas (as compared to the control area) are partially caused by environmental factors, evidenced by the fact that the isotope values of both consumers and producers were significantly higher than in the control area. Anthropogenic nitrogen associated with Mississippi River water is known to elevate  $\delta^{15}\text{N}$  values in estuarine ecosystems (McClelland et al. 1997; Kendall et al. 2001; Fry and Allen 2003; Costanzo et al. 2001).

Based on the  $\delta^{13}\text{C}$  and  $\delta^{34}\text{S}$  values of a representative selection of nine nekton species that occur in all areas, a significantly higher contribution of particulate organic matter (POM) in the food webs of the inflow and the reference area was found, as compared to that in the control area. This was corroborated with significantly higher  $\delta^{34}\text{S}$  values of nekton in the inflow and reference areas compared to the control area, and significantly higher  $\delta^{34}\text{S}$  values in consumers compared to local primary producers. The  $\delta^{15}\text{N}$  values are not used in this analysis, because  $\delta^{15}\text{N}$  values change with trophic level by 2 to 5‰ (Minagawa and Wada 1984; Peterson and Fry 1987; Deegan and Garritt 1997), and the exact fractional correction for each of the consumer species is unknown. Applying a correction factor can cause additional errors when different areas are

compared (Newsome et al. 2007), because biogeochemical processes also can cause differences in  $\delta^{15}\text{N}$  increase per trophic level among areas (Peterson and Fry 1987; Vander Zanden and Rasmussen 1999). Using a combination of C and S stable isotopes is the best approach to differentiate carbon sources at the base of a food web (Connolly 2004).

Proliferation of new primary producers with nutrient addition, plus a shift toward these new producers in consumers' diets has been shown in previous studies (Keats 2004; Armitage and Fourqurean 2009). The distinction between the isotopic composition of POM and local carbon sources could be made because  $\delta^{34}\text{S}$  values of POM are elevated to +18 ‰ in the brackish marshes the samples were taken (Peterson and Fry 1987; Wissel and Fry 2005). Values of  $\delta^{34}\text{S}$  of POM are known to increase with increasing salinity until salinity is ~3 ppt, after which values remain steady at ~ +17 - +21 ‰, even when salinities are variable (Peterson and Fry 1987; Wissel and Fry 2005). The three areas compared had mean salinities that exceed 3 ppt where the samples were taken, thus differences observed in  $\delta^{34}\text{S}$  values of consumers are not related to salinity differences. The significant positive correlation between  $\delta^{34}\text{S}$  values and caloric density in nekton in medium salinity sites, in combination with the significantly negative correlation between salinity and caloric density, supports this conclusion.

This also supports the conclusion that the nutritional value of a diet high in POM depends upon the distance from the source of river inflow. The energy density of nekton was significantly lower in the reference area than the control and inflow area, while that of the control and inflow area was not significantly different from one another. Even though the reference and inflow areas both are connected to a river source, the distance of the reference sample sites from their freshwater source is > 2-fold higher than that for the inflow sample sites (52 vs 25 km). The above mentioned ~ 3-fold higher nutrient loading of the Mississippi River as compared to the Atchafalaya River could contribute to the overall higher energy density in nekton in the inflow



area as compared to the reference area as well. A closer look at the inflow area revealed that the energy density in the inflow area was significantly higher in nekton sampled at sites closest to the diversion, and significantly lower in nekton sampled farthest away from the diversion. Of note is that the inflow of freshwater with a high nutrient concentration (Turner and Rabalais 1991; Goolsby et al. 1999) only causes modest increases in the relative proportion of river-associated carbon sources at the base of the estuarine food web, and modest increases in energy density in consumers. This observation and the decrease in energy density in nekton with distance from a source of freshwater input are likely owed to the fact that wetlands act as nutrient sinks (Lane et al. 1999; Lane et al. 2002; Hunter et al. 2009); diminished nutrient availability with distance from the freshwater inflow point could subsequently result in lower energy transfer to consumers. As previously noted, the negative correlation between salinity and energy density of nekton based upon samples from all sites in all areas support this conclusion. Variability in this relationship indicates between-species variability in energy density; the species selected as representative for Louisiana estuaries have different salinity optima. However, even with different salinity preferences, all species in the inflow area have either higher or similar energy density in sites closest to the CFD (~ 15 km) when compared to sites farther down the estuary (~ 35 km from the CFD).

While continued monitoring of Breton Sound for possible adverse effect of the increased nutrients on nekton is advised (Turner and Rabalais 1991; Rozas et al. 2005), the present level of nutrient enrichment does not appear to be adversely affecting the Breton Sound estuary, and may be directly contributing to higher energy density in nekton, as well as increased numbers and biomass (Piazza and La Peyre 2007; Chapter 2). In a previous study tracing Mississippi River influences in the same estuary, Wissel and Fry (2005) concluded that the CFD accounted for an average of 25% of food web support and concluded that the freshwater inflow increased

secondary production. They also found a decline in influence of the diversion away from the CFD, starting with approximately 50% food web support in the upper parts of the estuary to approximately 10% food web support in lower Breton Sound.

In conclusion, consumers in the Breton Sound estuary appear to have access to more nutritional diets after restoration of the hydrological connection to the Mississippi River, which is evidenced both by a higher niche breadth, and by an increased proportion of particulate organic matter in the estuarine food web. With the present flow regime, the CFD increases the energy density of estuarine nekton, likely through bottom up effects, rather than causing a negative effect on nekton through either eutrophication or sub-optimal salinities. These findings might be surprising, but are not new in estuarine ecology. As Nixon and Buckley (2002) stated: “The recent demonizing of N ignores the fact that nutrients are a fundamental requirement for producing biomass”. The freshwater inflow in Breton Sound through the CFD changes the estuarine consumer community by increasing: 1) the food web complexity and trophic diversity, 2) the contribution of POM to the estuarine food web, and 3) the energy density of estuarine nekton.

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## **CHAPTER 5**

### **USING ECOPATH WITH ECOSIM TO EXPLORE NEKTON COMMUNITY RESPONSES TO FRESHWATER INPUT FROM A MISSISSIPPI RIVER DIVERSION IN BRETON SOUND, LOUISIANA**

#### **INTRODUCTION**

Fisheries scientists are more frequently turning to ecosystem based approaches while studying ecosystems and advising fisheries managers (Walters et al. 1997). The complexity of estuarine ecosystems necessitates a holistic approach; ecosystem-based modeling approaches explicitly account for ecological interactions that can reveal unexpected indirect effects or impacts (Walters et al. 1997; 2008).

Here I use an ecosystem-based modeling approach to study the effects of a coastal restoration effort on estuarine nekton communities and species biomass distributions (SBD). The Caernarvon Freshwater Diversion (CFD) can mimic flooding of the Mississippi River and is being used to restore the Breton Sound estuary in Louisiana by inputting freshwater, sediments and nutrients (Mossa 1996; Lane 1999). The reduction in salinity associated with freshwater input is likely affecting estuarine nekton (Helfman et al. 1997; Moyle and Cech 2000; Alber 2002; Day et al. 2009).

The purpose of this study is to determine whether the inflow of freshwater into the Breton Sound estuary changes estuarine nekton communities and SBD, and if so, how. The added advantage of using a modeling approach is that once a base model is created, different scenarios that have the potential to affect nekton communities and SBD can be evaluated, and the effects of individual environmental parameters, in this case salinity, can be emphasized.

To this end, a balanced ecosystem base model of Breton Sound was built based upon five years of fisheries independent monitoring data before the opening of the CFD. This functional

ecosystem model was then used to test different freshwater flow scenarios by entering different monthly salinity time series, and simulating the response of the nekton community through time.

I have employed the software Ecopath with Ecosim (EwE) for this study. This software was created to estimate biomasses and food consumptions of the modeled groups through trophic flows or food web interactions, and the effects of fishery and fisheries management on these estimates. The Ecopath model was originally designed by Polovina (1984a; 1984b) to create steady-state trophic models of ecosystems, then transferred to researchers at the University of British Columbia's Fisheries Centre who combined it with theoretical ecology concepts, mainly the network models proposed by Ulanowicz (1986; 1995). The Ecopath approach was optimized for use in fisheries management, and for addressing environmental questions, by including a temporal component, Ecosim and a temporal and spatial component, Ecospace (Walters et al. 1997; 1999; 2000; Pauly et al. 2000). A more detailed explanation of Ecopath with Ecosim (EwE) can be found in the user guides (Christensen et al. 2004; 2009), available online at [www.ecopath.org](http://www.ecopath.org). A brief explanation of the working of EwE is included in the Methods section below.

Two main components of the EwE software are used in this study---Ecopath, to create a static, mass-balanced snapshot of the biomass pools and trophic flows in the Breton Sound estuary, and Ecosim to create time dynamic simulations of changes to this model for exploration of different scenarios (Christensen et al. 2004). The addition of a new function in Ecosim, specifically developed for this study, makes this approach especially useful to test effects of freshwater input on nekton in estuaries. With this new function, salinity data can be entered as a forcing function, along with user specified salinity optima and tolerance ranges for each species or species group (i.e., biomass pool) in the model. This allows for simulation of species-specific



responses to salinity changes in addition to the trophic interactions that are simulated in Ecosim. This study is the first test case of this new application of the EwE software.

I hypothesize that within the estuarine nekton community, some species with a preference for higher salinities will be displaced by species with a preference for lower salinities at sites closest to the CFD. In addition, predator-prey relationships will influence this simple response; indirect effects of salinity through trophic interactions will be important (Walters et al. 2008).

In addition to addressing my research questions, this study also will result in a model of the Breton Sound ecosystem, which describes species relationships by visualizing energy transfers, trophic fluxes and assimilation efficiency (Villanueva et al. 2006), and can be used to study nekton community response in a variety of additional scenarios. The added salinity function in Ecosim that is used here provides estuarine scientists with a valuable tool to assess the state and dynamics of nekton populations in ecosystems with variable salinities.

## **METHODS**

### **Study Area**

The 1,100 km<sup>2</sup> Breton Sound estuary is located south of New Orleans, Louisiana. It is bounded by the levee of the Mississippi River on the west side, and the levee of the Mississippi River Gulf Outlet (MRGO) on the east side. The CFD is a water control structure located in a bend in the Mississippi River at the north end of the estuary. From there, Mississippi River water flows directly into the estuary with a mean discharge of 45 m<sup>3</sup> s<sup>-1</sup>, and a maximum flow of 226 m<sup>3</sup> s<sup>-1</sup>. The Louisiana Department of Wildlife and Fisheries (LDWF) has sampled nekton and measured salinity monthly at several fixed stations in Breton Sound since 1986. The six stations chosen for this study are located in a salinity gradient along the main flow path of the diverted freshwater flow (Snedden et al. 2007; Figure 5.1).

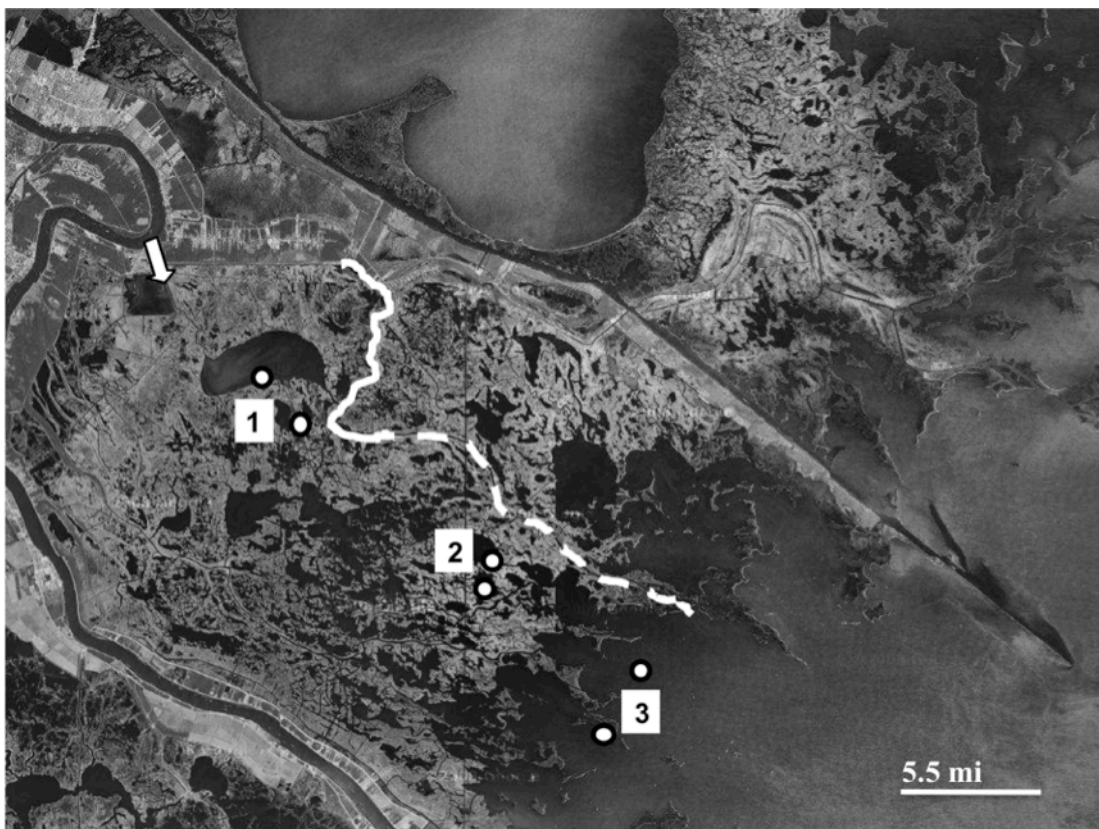


Figure 5.1. Aerial photograph of the research area. The circles indicate the sites at which the nekton collections and salinity measurements were done monthly from 1986 to 2007. The numbers refer to the three Ecosim scenarios, and indicate from which sites the salinity data (as forcing functions), and the nekton data (as comparative time series) are used to create each Ecosim scenario. To create the Ecopath model, nekton data from all sites from 1986-1990 were used.

## Ecopath

A balanced ecosystem model of the Breton Sound estuary before the opening of the diversion was built starting with EwE v. 5.1, and continued in EwE v.6, both downloadable at [www.ecopath.org](http://www.ecopath.org). This Ecopath model of Breton Sound simulates biomass dynamics of 39 groups. Ecopath as used here requires the following input variables for each group: biomass, and where applicable, P/B (production to biomass) and Q/B (consumption to biomass) ratios, stanza age breaks (split between juvenile and adult in months), Von Bertalanffy growth function (VBGF) K value (Von Bertalanffy 1928), optimum salinity, and the standard deviation of the salinity tolerance range of the group (Table 5.1). With this information, plus information on each

group's diet, a possible working ecosystem model can be developed in Ecopath. There are two master equations at the basis of Ecopath, plus the assumption of mass balance over an arbitrary period, here (and usually) a year. The first equation describes the production term and can be expressed as:

$$B_i \cdot (P / B)_i \cdot EE_i - \sum_{j=1}^n B_j \cdot (Q / B)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \quad (\text{Eq. 5.1})$$

where  $B_i$  and  $B_j$  are the biomasses of the prey (i) and predators (j) respectively;  $P/B_i$  the production/biomass ratio, equivalent to total mortality ( $Z$ );  $EE_i$  the ecotrophic efficiency, which is the proportion of the production that is utilized in the system;  $Q/B_j$  the consumption/biomass ratio;  $DC_{ji}$  the fraction of prey (i) in the diet of predator (j);  $Y_i$  the total fishery catch rate of (i);  $E_i$  the net migration rate (emigration-immigration); and  $BA_i$  the biomass accumulation rate for (i).

This first equation only includes the production of each group. The second master equation ensures energy balance within each group as follows:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad (\text{Eq. 5.2})$$

Respiration is estimated by the model from the difference between consumption and production, as well as unassimilated food terms. A more detailed explanation on the workings of Ecopath can be found at [www.ecopath.org](http://www.ecopath.org).

The choice of which nekton species and biomass to use for the groups in the Breton Sound Ecopath base model was based upon five years of fisheries independent data collected monthly by the Louisiana Department of Wildlife and Fisheries (LDWF). Nekton was collected using 15.24 meter bag seines with 6 mm mesh deployed from a boat by setting and anchoring

one end of the seine, and circling that point with the boat three times with the seine extended. Fish and crustaceans were identified to the lowest possible taxonomic level, counted and weighed to the nearest 0.1 g wet weight.

The five-year mean biomass ( $\text{g m}^{-2}$ ) of all species collected at the study sites in the estuary from 1986-1990 was calculated. These are the five years just prior to the opening of the CFD in 1991. To control for between-year differences in effort, total biomass (g) per year was first divided by the number of net tows (units of effort) in that year, and consequently divided by the area (m) swept in one unit of effort to gain  $\text{g m}^{-2}$ .

Based upon these data, species were selected to be a part of the ecosystem model. Species selection was firstly based on dominance in the estuary; the species that together comprised 75% of the nekton biomass in the estuary are modeled as their own biomass group. Secondly, species with low biomass that were expected to increase in biomass with inflow of freshwater were included in the model, e.g., largemouth bass (*Micropterus salmoides*) and sunfish (*Lepomis sp.*) were added. Thirdly, a large enough forage base for the predators had to be present in the model. To achieve mass balance, some adjustments were made to the biomass of important forage groups in the system. Bay anchovy (*Anchoa mitchilli*) is the dominant forage fish, but their total biomass is not sufficient to sustain all predators, because other forage fish like Gulf killifish (*Fundulus grandis*) and silversides (*Menidia beryllina*) are part of their diet as well. Instead of adding many groups, each with low biomass, to the model, the biomass of all small forage fish collected in the system was pooled with the biomass of bay anchovy.

For the same reason, biomass of all penaeid shrimp present in the system was combined, creating a penaeid shrimp group consisting of brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*) and pink shrimp (*Farfantepenaeus duorarum*). *Farfantepenaeus aztecus* was the dominant species of the three, and represented 98% of the penaeid shrimp

biomass in the LDWF collections. Altogether, the nekton groups in the Ecopath model represents 98% of the yearly mean nekton biomass present in the system based upon the LDWF collections from 1986-1990. The zoobenthos group biomass consists of zoobenthos biomass derived from an Ecopath model of Weeks Bay, a shallow sub-estuary of Mobile Bay, AL (Althausen 2003), plus the biomass of grass shrimp (*Palaemonetes sp.*) estimated from LDWF data in the research area.

Consumer groups consist of fish, crustaceans, zooplankton and zoobenthos. Lastly, producers including phytoplankton, submerged aquatic vegetation (SAV), benthic algae, and a detritus group were included in the model. The biomass of zooplankton, zoobenthos, phytoplankton, benthic algae and detritus was borrowed from the Weeks Bay model (Althausen 2003). Biomass of SAV was determined from collections made from 2006-2008 (Chapter 3) in an area in Breton Sound that does not receive freshwater flow from the diversion (as a proxy for 'before' conditions).

Each nekton group was split into adults and juveniles with the multi-stanza feature in Ecopath with Ecosim (Christensen et al. 2004). Adults and juveniles of the same species often have different functions in a food web, and are therefore best split into separate groups, having separate diets, predators, and salinity ranges. This separation also allows for cannibalism of adults on juveniles in the model. For each juvenile-adult combination, species-specific VBGF parameters (Von Bertalanffy 1928), total mortality rates, and the stanza break (months) are required.

Each consumer group has a diet consisting of one or more of the other groups. Each prey item was entered proportionally to a consumer's diet on a scale from 0 to 1. Diets of each species or consumer group are based upon information obtained in the published literature, fishbase, and local stomach content analysis. Diets were adjusted to create a model of one possible working, balanced ecosystem. Within realistic boundaries, the exact relative proportion of prey items a

predator eats is a function of availability of these prey items. Diets were adjusted until the Ecopath-generated ecotrophic efficiency of each group was between 0 and 1, where zero indicates that the group is not being consumed, and one indicates the group is being heavily preyed upon (Christensen et al. 2004). An Ecopath model will not balance when any ecotrophic efficiency value is above one; this prevents having more of a modeled biomass pool consumed than is present in the model. While balancing the model, the trophic level of each group is calculated by Ecopath based upon its diet. These values were also used to determine if the diet choices were plausible.

### **Network Analysis**

In Ecopath, various network analysis indices developed by theoretical ecologists (Ulanowicz 1986), can be calculated. For this, the entire system is aggregated into discrete trophic levels as proposed by Lindeman (1942). Results of this analysis are the calculated absolute flows, which can be aggregated to create useful summary statistics that can then be compared to other systems. In addition to straightforward summary statistics (e.g. the sum of all consumption; Table 5.2), the following indices were calculated: the connectance index, which is the ratio of the number of actual links between groups to the number of possible links; the system omnivory index, which is calculated as the mean omnivory of all consumers weighted by the logarithm of each consumer's food intake (Christensen et al. 2004) and the transfer efficiency, which is calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from one trophic level to the next, and the throughput of the trophic level (Christensen et al. 2009; Table 5.2). The summary statistics provide information on the size of various trophic flows, while the omnivory and connectance indices are measures of the distribution of feeding interactions among trophic levels. These indices characterize the extent to which a system displays web-like features (Cruz-Escalona et al. 2007), and high values

indicate that the groups are not highly specialized and feed on many different trophic levels. Ratios of some of these statistics can provide information as well. The ratio of total system biomass to the total system throughput is directly proportional to system maturity (Christensen 1995; Villanueva et al. 2006), which becomes higher with increasing maturity. Another maturity index is the ratio of net primary production to total respiration, which decreases to 1 with increasing maturity (Odum 1969; 1971).

## **Ecosim**

Ecosim allows time-dynamic simulations of the initial parameters from the Ecopath base model expressed through a series of coupled differential equations derived from the first Ecopath master equation (see Christensen et al. 2004; 2009; Equation 5.1). When no time forcing data are entered as part of an Ecosim scenario, the Ecosim run creates a flat line indicating no change from the initial Ecopath base model, but only if the Ecopath base model is indeed balanced.

In my Ecosim scenarios the effects of salinity are investigated; fishing and other forcing and mediation functions are not included in the model at present. Three Ecosim scenarios were created to test different salinity regimes on the nekton community structure and SBD in the Breton Sound estuary. Monthly salinity (ppt) measurements, made by the LDWF from 1986-2007 at three different distances from the CFD along a salinity gradient within the main flow path of the diversion (Figure 5.1), were used in the three scenarios. Measurements at approximately 10, 25 and 35 km from the opening of the CFD were used, creating low (scenario 1), medium (scenario 2) and high (scenario 3) salinity scenarios based upon real data (Figure 5.2). These monthly mean salinities from 1986-2007 representing each of the scenarios were entered as forcing functions in the model, together with species-specific salinity tolerance ranges.

The tolerance range of each species is based upon extensive LDWF metadata, derived from monthly collections from 1966-2007 in all of coastal Louisiana. Using the collected nekton

and salinity data, abundance of each nekton species in the model was plotted against the salinity measured at the time of collection. This created roughly dome-shaped curves, from which an optimum and a standard deviation (SD) could be derived. For most species, there was considerably more variability at the optima of the curve, with decreasing variability at the tails of the curve. Variability in abundance at the optima is inferred to occur in response to salinity as well as other factors, whereas at the tails of the curve, salinity is believed to have a greater effect on simulated abundance.

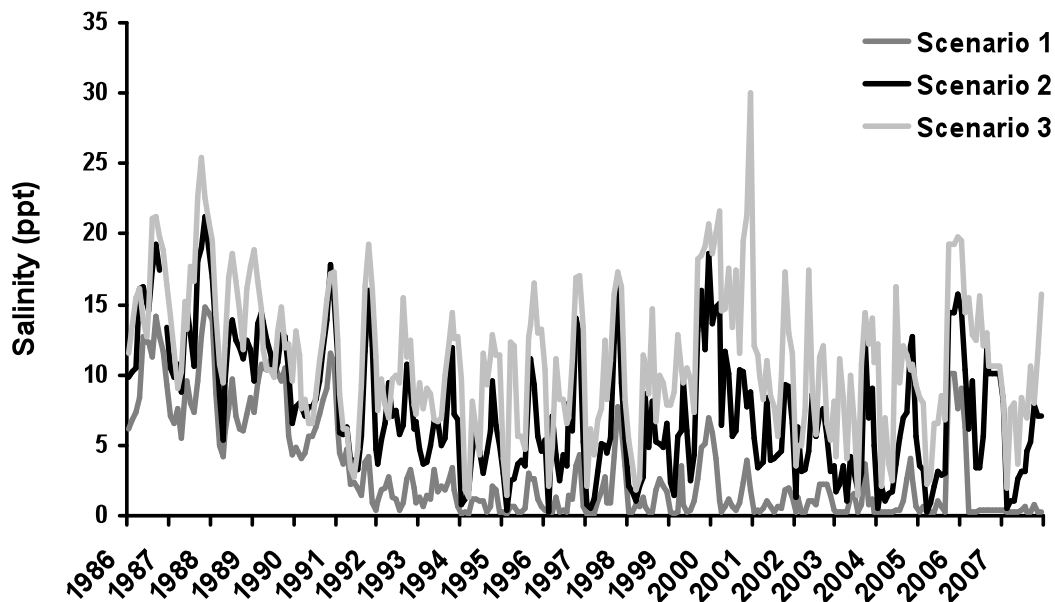


Figure 5.2. Salinity time series, created with the monthly mean salinity measurements from 1986-2007, which are used as forcing functions in the model. The three time series (scenarios) are indicated with different grey scales.

This function was then used to modify feeding rate in such a way that optimum feeding rate occurs at the optimum salinity, with feeding rate declines from the optimum at a rate determined by the SD. Examples of this function are shown for spotted seatrout (*Cynoscion nebulosus*) and largemouth bass (*Micropterus salmoides*; Figure 5.3); all salinity optima and



standard deviations are given in Table 5.1. Sub-optimal feeding rate affects performance and participation in the ecosystem, thus leading to reduced biomass.

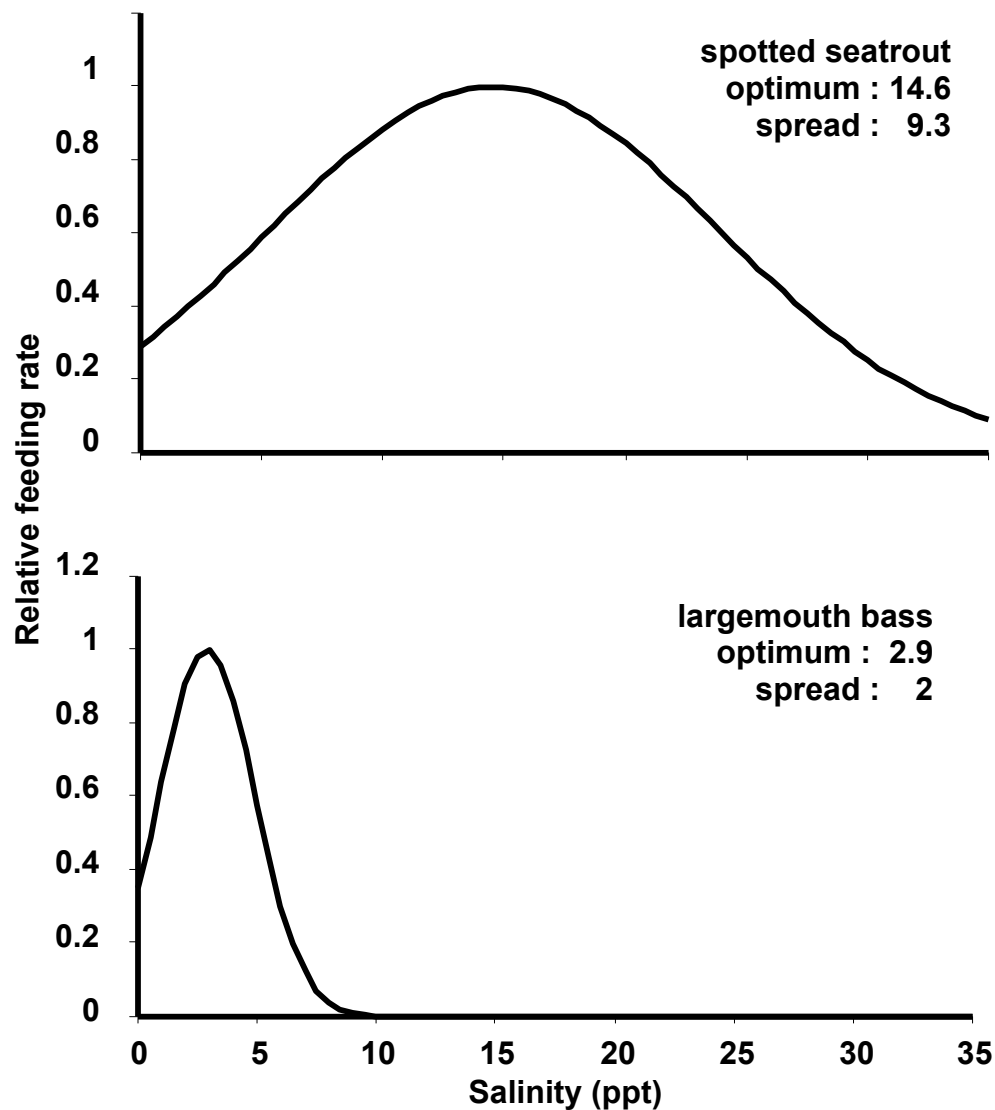


Figure 5.3. Two examples of the species-specific response curves to salinity, with spotted seatrout (*Cynoscion nebulosus*) in the top figure, and largemouth bass (*Micropterus salmoides*) in the bottom figure. The relative feeding rate is 1 at optimum salinity and declines away from the optimum at a rate determined by the standard deviation. The curves are based on abundance versus salinity plots of each species created with data collected by LDWF in the entire Louisiana coastal area from 1966-2007.

Because the response curve of feeding rate to salinity is a dome shaped curve (Figure 5.3), moving away from optimum salinity has little penalty on the feeding rate of a species up to one half SD removed from the optimum, after which feeding rate declines rapidly until it trails off asymptotically. As such, species can recover if salinities return to favorable levels, and the responses to slight salinity changes away from the selected optimum are moderate.

Model runs to evaluate the simulation scenarios begin in 1986 with the community composition and SBD described in the Ecopath base model and were run until 2007. The combination of salinity and species-specific salinity ranges, together with trophic interactions that follow foraging arena theory (Walters and Martell 2004), determine the outcome of the SBD for each scenario run.

### **Statistical Analysis**

To test whether salinities used in the scenarios were indeed significantly different from one another, an ANOVA (analysis of variance) followed by a Tukey test was performed in SAS 9.1.3 (2005). The residuals were normally distributed, so no transformations were performed.

The Monte Carlo routine in Ecosim was used as a sensitivity analysis both for Ecopath and Ecosim. This routine tests the sensitivity of Ecosim's output to Ecopath input parameters by drawing input parameters from a uniform distribution centered on the base Ecopath value with coefficient of variation set (in this case) at 0.1 (Christensen et al. 2009). Because each Monte Carlo run creates a different Ecosim output, these outputs can be used as samples in statistical analyses. Each of the three scenarios was run repeatedly with the Monte Carlo application in Ecopath with Ecosim. The five best outcomes (= trials with the lowest weighted sum of squared deviations) of 10 Monte Carlo runs (totaling  $5 \times 10 = 50$  Monte Carlo runs) were treated as samples in the statistical software PRIMER 6 (Clarke and Warwick 2001). Five samples of the Ecopath SBD (run start), as well as five samples of each Ecosim salinity scenario SBD output, were used

in an ANOSIM analysis, which is a non-parametric equivalent of ANOVA. The ANOSIM procedure was used to test if nekton SBDs at the end of the salinity scenario runs differed significantly from one another, and from those used in the Ecopath base model. The ANOSIM analysis was performed on a Bray-Curtis similarity matrix of the square root transformed data. The number of permutations was set at 9999, and was between 126 and 9999 in practice depending on the number of possible permutations. The alpha level was set at 1% (equivalent to 0.01 in a parametric test). This alpha level is lowered from the conventional 5% to reduce the chance for type II error in the pairwise comparisons (Sokal and Rohlf 1994). Two analyses were done; one one-way analysis with four factor levels: start, scenario 1, scenario 2 and scenario 3; and one one-way analyses with two factor levels: before (start) and after (pool of 3 scenario outcomes). The second analysis tests the diversion's effect on the whole estuary. The level 'start' or 'before' refers to the nekton SBD of the Ecopath model, samples were derived with Monte Carlo runs as described above. The level 'after' refers to all pooled SBDs at the end of each run; all five samples of all three scenarios are samples of the level 'after' in this analysis.

Following the ANOSIM analysis, a SIMPER analysis was performed to determine which species, if any, contributed most to dissimilarities between the SBDs at the end of each scenario run and the SBD in the base model. Only nekton species were included in the ANOSIM and SIMPER analyses, i.e., detritus, plant, plankton and benthic groups were excluded because high biomass pools of these groups obscure information in the nekton SBD in analyses.

## **RESULTS**

### **Ecopath and Network Analysis**

After adjusting diet data (Kavanagh et al. 2004), the Ecopath model balanced. During the balancing process, Ecopath generates missing parameter values to complete a functioning ecosystem (Table 5.1, Ecopath generated values indicated with an \*).

Table 5.1. A listing of the biomass groups included in the Breton Sound Ecopath model. The table reports the biomass ( $\text{g m}^{-2}$ ), production to biomass ratio (P/B), consumption to biomass ratio (Q/B), the age in months at which a juvenile becomes an adult (stanza break), and the K parameter used for each group in the Von Bertalanffy growth function (VBGF K value). The optimum and SD of the salinity tolerance range of each species based upon field monitoring data are displayed in the last two columns. Symbols and numbers in superscript indicate the source of the values: \* = values generated by Ecopath; <sup>1</sup> data collected in this system; <sup>2</sup> data from the Weeks Bay Ecopath model (Althausen 2003); <sup>3</sup> data from the Gulf of Mexico Ecopath model (Walters et al. 2008); <sup>4</sup> C. Walters, personal communication; <sup>5</sup> FishBase.

Group name	Biomass (g/m <sup>2</sup> )	P/B	Q/B	Stanza break (m)	VBGF K value	Optimum sal. (ppt)	SD salinity
juvenile gar	0.000531*	2 <sup>4</sup>	9.649*		0.2 <sup>4</sup>	3	4
adult gar	0.0376 <sup>1</sup>	0.193 <sup>2</sup>	1.490 <sup>2</sup>	12 <sup>4</sup>		7	5.6
juvenile spotted seatrout	0.527*	3.7 <sup>3</sup>	6.442*		0.2 <sup>5</sup>	15.6	8.3
adult spotted seatrout	1.88 <sup>1</sup>	0.7 <sup>3</sup>	1.6 <sup>3</sup>	18 <sup>3</sup>		14.6	9.3
juvenile red drum	0.280*	2.2 <sup>3</sup>	4.870*		0.4 <sup>5</sup>	26.5	13.5
adult red drum	1.526 <sup>1</sup>	0.62 <sup>3</sup>	1.86 <sup>3</sup>	18 <sup>3</sup>		9.2	6.8
juvenile largemouth bass	0.000210*	2 <sup>4</sup>	9.011*		0.4 <sup>4</sup>	0.1	1.5
adult largemouth bass	0.0063 <sup>1</sup>	0.6 <sup>4</sup>	2.814 <sup>2</sup>	12 <sup>4</sup>		2.9	2
juvenile sheepshead	0.00357*	2 <sup>4</sup>	28.9*		0.25 <sup>4</sup>	12.5	7.1
adult sheepshead	0.396 <sup>1</sup>	0.417 <sup>2</sup>	6.359 <sup>2</sup>	12 <sup>4</sup>		12.5	7.1
juvenile sunfish	0.000361*	2 <sup>4</sup>	12.280*		0.6 <sup>4</sup>	3.1	2
adult sunfish	0.0004 <sup>1</sup>	0.8 <sup>4</sup>	4.966 <sup>2</sup>	12 <sup>4</sup>		1.5	2.5
juvenile ladyfish	0.00984*	2.8 <sup>3</sup>	18.147*		0.26 <sup>5</sup>	15	5.2
adult ladyfish	0.0932 <sup>1</sup>	1.6 <sup>3</sup>	6 <sup>3</sup>	10 <sup>3</sup>		15	5.2
juvenile Atlantic croaker	0.0136*	2 <sup>4</sup>	20.035*		0.75 <sup>4</sup>	17	7
adult Atlantic croaker	0.0454 <sup>1</sup>	1.5 <sup>3</sup>	10 <sup>3</sup>	12 <sup>4</sup>		17	7
juvenile spot	0.00510*	2 <sup>4</sup>	25.452*		0.75 <sup>4</sup>	13.9	8.5
adult spot	0.0268 <sup>1</sup>	1.1 <sup>3</sup>	12 <sup>3</sup>	12 <sup>4</sup>		15.5	5.5
juvenile catfish	0.00878*	2 <sup>4</sup>	22.403*		0.4 <sup>4</sup>	13.1	8.4
adult catfish	0.156 <sup>1</sup>	0.8 <sup>3</sup>	7.6 <sup>3</sup>	12 <sup>4</sup>		15	7
juvenile black drum	0.00209*	2 <sup>4</sup>	34.129*		0.15 <sup>4</sup>	8.9	6.7
adult black drum	0.274 <sup>1</sup>	0.5 <sup>4</sup>	6.359 <sup>2</sup>	12 <sup>4</sup>		8.9	6.7
juvenile southern flounder	0.000278*	2 <sup>4</sup>	26.189*		0.3 <sup>4</sup>	7	5
adult southern flounder	0.0241 <sup>1</sup>	0.417 <sup>2</sup>	6.359 <sup>2</sup>	12 <sup>4</sup>		14	5
juvenile gulf menhaden	0.0113*	2.3 <sup>3</sup>	11.536*		0.8 <sup>4</sup>	14.2	6.4
adult gulf menhaden	0.023 <sup>1</sup>	1.9 <sup>3</sup>	6 <sup>3</sup>	12 <sup>3</sup>		15.2	5.4
juvenile striped mullet	0.741*	2.4 <sup>3</sup>	22.417*		0.3 <sup>4</sup>	9.4	7.3
adult striped mullet	3.167 <sup>1</sup>	0.8 <sup>3</sup>	8 <sup>3</sup>	18 <sup>3</sup>		9.4	7.3
bay anchovy	1.750 <sup>1</sup>	2.530 <sup>3</sup>	14 <sup>3</sup>			15	8
juvenile blue crab	0.0551*	3 <sup>4</sup>	17.037*		0.7 <sup>4</sup>	11.5	6.4
adult blue crab	0.07 <sup>1</sup>	2.4 <sup>3</sup>	8.5 <sup>3</sup>	12 <sup>4</sup>		7.6	7.4
juvenile penaeid shrimp	0.00991*	3 <sup>4</sup>	66.651*		1.5 <sup>4</sup>	17	6.6
adult penaeid shrimp	0.750 <sup>1</sup>	2.4 <sup>3</sup>	19.2 <sup>3</sup>	3 <sup>4</sup>		9.8	6.6
zooplankton	0.609 <sup>2</sup>	28.772 <sup>2</sup>	84.87 <sup>2</sup>			15	40
zoobenthos	3.22 <sup>2</sup>	4.5 <sup>3</sup>	22 <sup>3</sup>			15	40
phytoplankton	1.946 <sup>2</sup>	101.702 <sup>2</sup>				1	15
macroalgae/SAV	60.24 <sup>1</sup>	9.014 <sup>3</sup>				5	40
benthic algae	12.876 <sup>2</sup>	3.909 <sup>2</sup>				15	40
detritus	4 <sup>2</sup>						

Ecosystem parameters derived from network analysis indicate that the Breton Sound model is a possible working ecosystem with parameters within the range of previously described coastal ecosystems (Table 5.2).

Table 5.2. A summary of ecosystem statistics derived from the Breton Sound Ecopath model, compared to summary statistics from other Ecopath models of coastal ecosystems in the Gulf of Mexico for which such data are available.

Parameter	Breton Sound	Laguna Alvarado	Tamiahua lagoon	Celestun lagoon	Yucatan northern shelf	Units
Sum of all consumption	224.4	1265	380.4	2801	1050	$\text{g m}^2 \text{yr}^{-1}$
Sum of all respiratory flows	130.9	987.5	244.9	1687	602.3	$\text{g m}^2 \text{yr}^{-1}$
Sum of all flows into detritus	714.5	249.6	185.6	2998	394.6	$\text{g m}^2 \text{yr}^{-1}$
Total system throughput	1730	2683	822.4	8969	2049	$\text{g m}^2 \text{yr}^{-1}$
Sum of all production	839.9	1574	315.8	2443	692.0	$\text{g m}^2 \text{yr}^{-1}$
Calculated total net primary production	791.2	1291	254.7	1890	-	$\text{g m}^2 \text{yr}^{-1}$
Total primary production/total respiration	6.04	1.30	1.04	1.12	0.75	
Net system production	660.3	303.5	-	-	-148.1	$\text{g m}^2 \text{yr}^{-1}$
Total primary production/total biomass	8.72	16.50	12.10	6.21	6.97	
Total biomass/total throughput	0.05	0.03	0.02	0.05	0.03	
Total biomass (excluding detritus)	90.8	78.1	16.5	448.5	65.2	$\text{g m}^2$
Connectance Index	0.16	0.30	0.38	0.29	0.28	
System Omnivory Index	0.15	0.25	0.13	0.18	-	
Source	This study	Cruz-Escalona et al. 2007	Abarca-Arenas et al. 1993	Chavez et al. 1993	Arreguin- Sanchez et al. 1993	

A graphical representation of all trophic flows and biomasses shows that the highest trophic level in the ecosystem model is 3.46, while the mean (of the nekton species) is 2.67 (Figure 5.4). The proportion of total flow originating from detritus is 0.45. The mean transfer efficiencies from primary producers and from detritus of 8.5 and 6.4% respectively are low compared to Lindeman's suggested transfer efficiency of 10% (Lindeman 1942). Christensen

and Pauly (1993) found the mean of 41 systems to be 9.2%, but the range was very large with mean trophic transfer efficiencies as low as 3.2% and as high as 17.6 %. Therefore, the transfer efficiencies in Breton Sound seem plausible. The system omnivory index (0.15) and the connectance index (0.16) generated from the Breton Sound model are low to average compared to other modeled systems in coastal areas of the Gulf of Mexico (Table 5.2). The information contained about the stability or maturity of the system in simulations that produce low connectance indices is unclear. Christensen and Pauly (1993) provide several different explanations for high and low values of both indices, and conclude interpretation of these indices is ambiguous. A summary of network analysis parameters in the Breton Sound model, compared with other modeled coastal ecosystems in the Gulf of Mexico, is displayed in Table 5.2.

### **Ecosim**

The differences between the Ecosim scenario-run outcomes are solely a factor of the differences between the salinity forcing values of each scenario and their effect on trophic interactions; fishing and other mediation factors are not included. When no salinity scenario was selected during an Ecosim run, the biomass pools remained constant over time; this is a confirmation that the Ecopath model is balanced.

There is a significant difference between salinity scenarios ( $F = 330.04, p < 0.0001$ ; all three scenarios differed from one another with  $p < 0.05$ ; Figure 5.2). Mean salinities after the opening of the diversion are  $1.4 \text{ ppt} \pm \text{SD } 3.6$  in scenario 1,  $6.0 \text{ ppt} \pm \text{SD } 4.6$  in scenario 2 and  $10.3 \text{ ppt} \pm \text{SD } 3.6$  in scenario 3. The mean salinity before and after the opening of the diversion also differs significantly ( $F = 312.73, p < 0.0001$ ). The mean salinity of the whole estuary was  $11.9 \text{ ppt} \pm \text{SD } 3.6$  before the opening of the CFD, and  $5.9 \text{ ppt} \pm \text{SD } 5.1$  after the opening of the CFD.

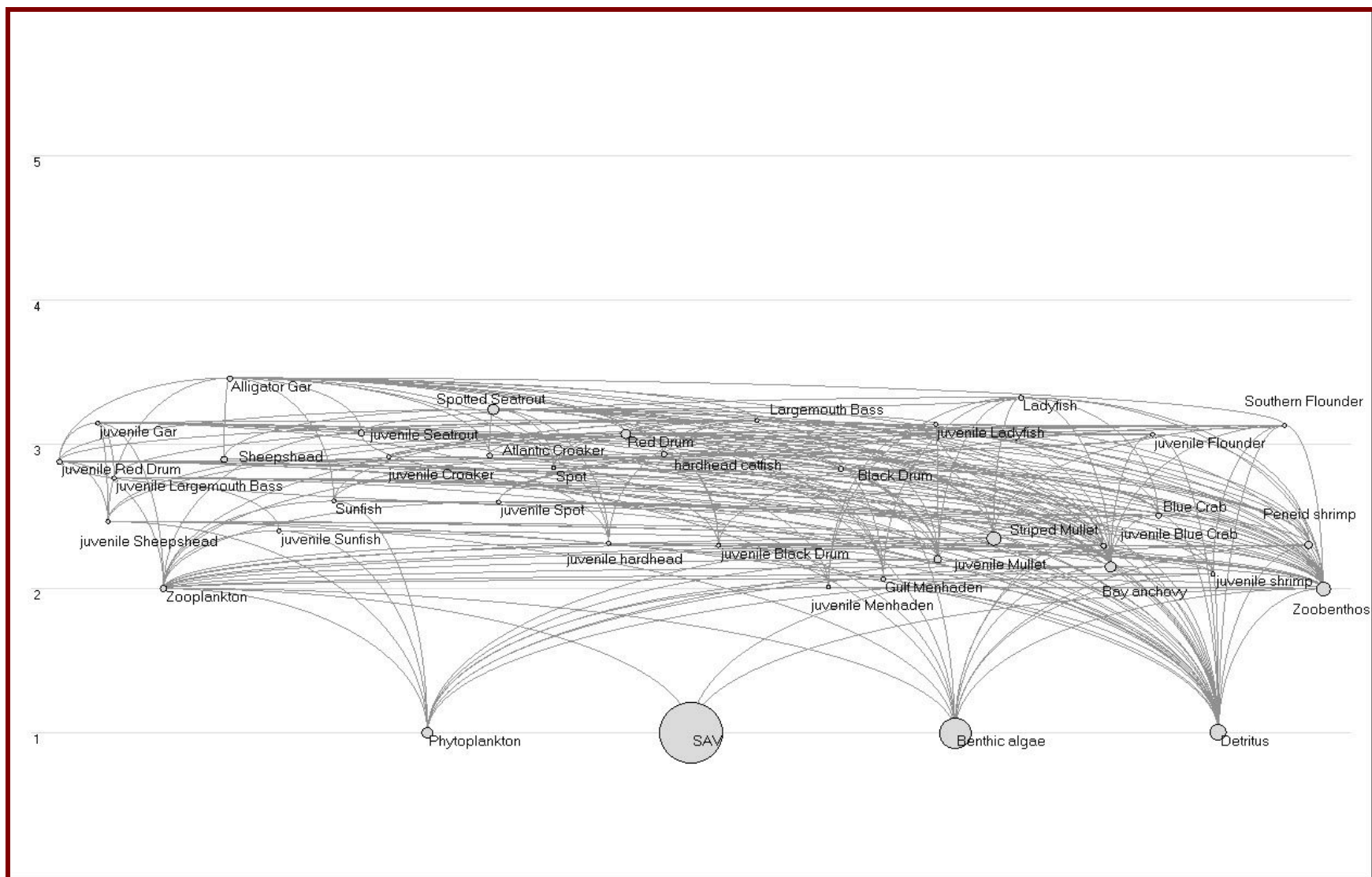


Figure 5.4. Flow diagram of all biomass pools and flows in the Breton Sound Ecopath model. The size of the dots refer to the size of the biomass pools, and the y-axis indicates the model generated trophic levels of the biomass pools based on the diets entered in the model.



Table 5.3. Mean biomass ( $\text{g m}^{-2} \pm \text{SD}$ ) per species of the five best trials (each based upon ten Monte Carlo runs) of the Ecopath base model, and of each salinity scenario. The lowest sums of squared deviations of each scenario when fitted to real time series are shown in the table heading. Total nekton biomass from each scenario is shown at the end of the table.

	Start ( $\text{g m}^{-2}$ )		Scenario 1 ( $\text{g m}^{-2}$ )		Scenario 2 ( $\text{g m}^{-2}$ )		Scenario 3 ( $\text{g m}^{-2}$ )	
	Before		After					
Lowest SS			752.0		296.7		398.1	
Group	Mean	SD	Mean	SD	Mean	SD	Mean	SD
juv. gar	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
alligator gar	0.036	0.002	0.173	0.140	0.049	0.009	0.012	0.003
juv. sp. Seatrout	0.543	0.084	0.014	0.010	0.286	0.057	0.279	0.049
spotted seatrout	1.953	0.172	0.103	0.076	1.125	0.319	1.445	0.261
juv. red drum	0.209	0.037	0.041	0.020	0.107	0.031	0.080	0.021
red drum	1.474	0.113	0.436	0.235	0.878	0.324	0.644	0.120
juv. LMB	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000
largemouth bass	0.004	0.000	0.016	0.010	0.002	0.001	0.000	0.000
juv. sheepshead	0.004	0.001	0.003	0.000	0.004	0.001	0.004	0.001
sheepshead	0.407	0.044	0.286	0.061	0.414	0.031	0.405	0.052
juv. sunfish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
sunfish	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
juv. ladyfish	0.009	0.003	0.003	0.004	0.006	0.004	0.006	0.001
ladyfish	0.087	0.013	0.066	0.089	0.091	0.072	0.061	0.013
juv. croaker	0.014	0.003	0.008	0.006	0.010	0.003	0.013	0.001
Atlantic croaker	0.044	0.005	0.106	0.123	0.057	0.013	0.049	0.005
juv. spot	0.005	0.000	0.008	0.003	0.003	0.001	0.004	0.001
spot	0.025	0.002	0.105	0.089	0.021	0.007	0.025	0.003
juv. hardhead	0.009	0.001	0.002	0.001	0.009	0.002	0.009	0.001
hardhead catfish	0.155	0.018	0.018	0.011	0.104	0.027	0.139	0.016

(Table 5.3 continued)

Lowest SS Group	Start (g m <sup>-2</sup> )		Scenario 1 (g m <sup>-2</sup> )		Scenario 2 (g m <sup>-2</sup> )		Scenario 3 (g m <sup>-2</sup> )	
	Before		752.0		296.7		398.1	
	Mean	SD	Mean	SD	Group	Mean	SD	Mean
juv. black drum	0.002	0.001	0.004	0.001	0.003	0.000	0.003	0.001
black drum	0.258	0.019	0.597	0.060	0.437	0.059	0.291	0.032
juv. flounder	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
southern flounder	0.023	0.002	0.034	0.018	0.037	0.006	0.035	0.003
juv. menhaden	0.009	0.001	0.018	0.006	0.009	0.006	0.006	0.001
gulf menhaden	0.019	0.002	0.500	0.863	0.047	0.070	0.021	0.006
juv. mullet	0.703	0.076	1.116	0.138	0.616	0.065	0.345	0.048
striped mullet	2.944	0.127	3.297	0.360	2.245	0.275	1.595	0.062
bay anchovy	1.764	0.134	3.887	0.355	2.185	0.193	1.534	0.165
juv. blue crab	0.050	0.005	0.057	0.010	0.071	0.010	0.069	0.007
blue crab	0.067	0.004	0.087	0.012	0.082	0.009	0.069	0.008
juv. shrimp	0.008	0.001	0.003	0.001	0.006	0.000	0.008	0.002
penaeid shrimp	0.687	0.076	1.327	0.259	0.864	0.053	0.743	0.065
zooplankton	0.435	0.062	0.556	0.065	0.628	0.086	0.587	0.137
zoobenthos	3.425	0.287	3.881	0.168	3.543	0.211	3.579	0.384
phytoplankton	1.455	0.189	2.043	0.204	1.812	0.074	1.508	0.113
SAV	60.419	0.254	60.522	0.110	60.966	0.294	61.425	0.121
benthic algae	13.004	1.618	10.978	1.598	13.985	0.305	13.470	1.225
detritus	3.946	0.035	3.979	0.027	3.967	0.024	3.920	0.048
Total	94.193	2.188	94.275	2.759	94.669	0.569	92.385	1.664
Total nekton only	11.510	0.513	12.316	1.849	9.768	0.310	7.895	0.514

The Monte Carlo routine was able to create a balanced model for each trail when varying the input parameters within 10% confidence intervals (Table 5.3). The sums of squared deviations of the best fit between the scenario runs and their respective measured time series nekton biomass data also are shown in Table 5.3.

The ANOSIM analysis reveals that there are significant differences in SBDs among the three scenario runs, and the Ecopath base model ( $R = 0.805$ ,  $p = 0.01\%$ ). All pair-wise comparisons indicate significant differences; all  $R$ -values were higher or equal to 0.78, with  $p$  in each comparison 0.8%. However, when all SBD scenario outcomes were pooled and compared to the Ecopath base model, the SBD of ‘before’ versus ‘after’ did not differ significantly ( $R = 0.101$ ,  $p = 18.9\%$ ; Figure 5.5). The total biomass in the Ecopath base model is  $11.51 \text{ g m}^{-2}$ . Total predicted nekton mean biomass at the end of each run was highest at the low salinity scenario ( $12.32 \text{ g m}^{-2}$ ), intermediate at the medium salinity scenario ( $9.77 \text{ g m}^{-2}$ ) and lowest at the high salinity scenario ( $7.86 \text{ g m}^{-2}$ ; Table 5.3).

## **DISCUSSION**

By using the Monte Carlo routine in Ecosim, the Ecopath base model was shown to be robust, as each Monte Carlo trial balanced, and there was small variation between the five best trials of each scenario (expressed as standard deviation in Table 5.3). This indicates that the Ecopath model was insensitive to small changes in input values, thus potential small errors in input values likely did not significantly affect Ecosim run outcomes. The Monte Carlo routine in Ecosim is the best available sensitivity analysis for Ecopath and has replaced Ecoranger for this purpose in EwE version 6 (Christensen, pers. comm.).

The flows, more than the size of biomass pools, represent the contribution of each biomass pool to the estuarine foodweb (Figure 5.4); ecosystem functioning can be viewed in terms of biomass fluxes between trophic levels (Villanueva et al. 2006). For example, submerged

aquatic vegetation (SAV) has a large biomass pool with few flows, and contributes much less to the food web than phytoplankton, which in contrast, has a small pool but many flows. Estuarine nekton species generally are members of either a detritus-based or phytoplankton-based food web (De Sylva 1985), which makes the low contribution of SAV to energy flows not surprising. It is useful to keep SAV in the model because it is a visible component of the Breton Sound estuary. In addition, it could play an important role in nekton biomass distribution and trophic interactions, as it serves as a refuge from predation for small forage species and juveniles, thus decreasing predation mortality (Castellanos and Rozas 2001; Rozas et al. 2005). This can be modeled in future versions of Breton Sound Ecosim simulations by including SAV as a mediation factor.

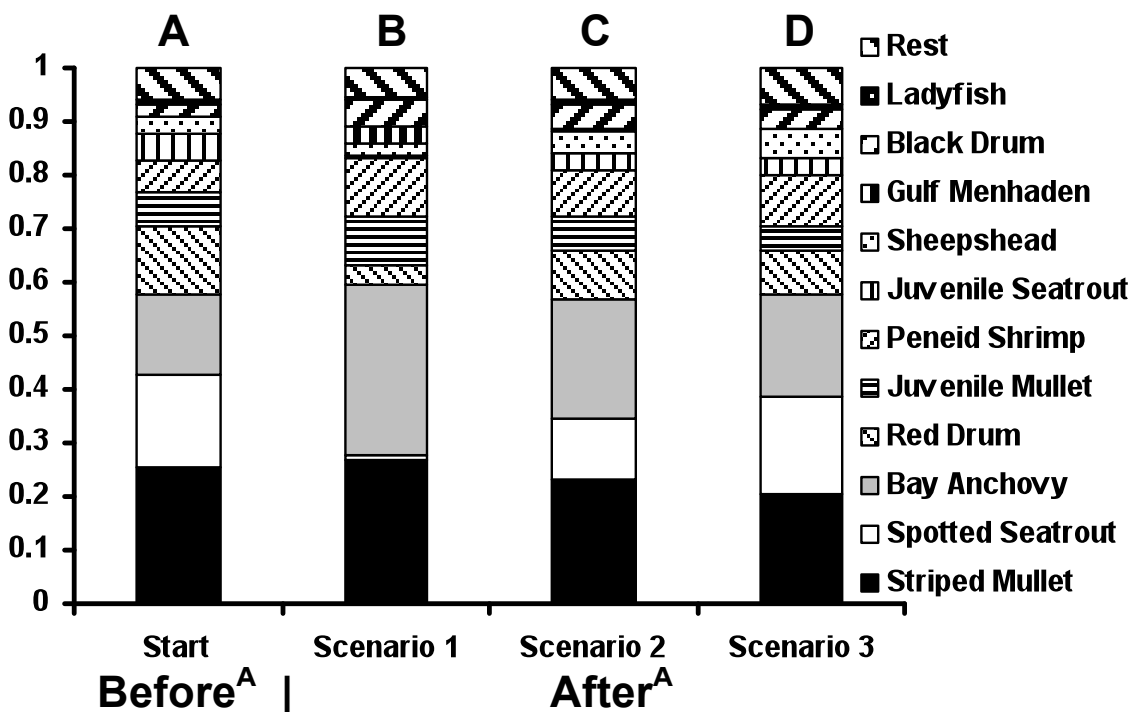


Figure 5.5. The relative SBD of the Ecopath base model and the three Ecosim scenarios in Breton Sound. The letters A-D indicate that all individual scenarios are significantly different from each other; <sup>A</sup> indicates there is no significant difference 'before' (Ecopath model) and 'after' (combination of the three end scenarios) the opening of the diversion. The species are listed in the legend from bottom to top in order of their contribution to the dissimilarity between the four SBDs. The last category ('Rest') is a compilation of species that together contribute less than 10% to the dissimilarities between the distributions.

When other coastal ecosystems in the Gulf of Mexico are compared with those of Breton Sound, the network analysis summary statistics of Breton Sound are within possible ranges (Table 5.2). However, the high total primary production to total community respiration (PP/R) ratio in Breton Sound (6.04) is noteworthy. This ratio in Breton Sound does not exceed, but is on the high end of the range of 0.8-6.4 reported by Christensen and Pauly (1993) in a comparative study of 41 aquatic systems. Most likely the before-mentioned high primary production produced by SAV that is not used in the system by consumers elevates this ratio.

While Ecopath models are well represented in the literature, the specific Ecosim salinity forcing functions are presented here for the first time. Therefore, the results of these simulations will be compared with other modeling efforts and published field data. The sums of squared deviations (Table 5.3) of the best fit between the Ecosim scenario runs and their respective measured time series data are high, and likely could be lowered if other factors influencing nekton biomass are added as forcing or mediation functions in Ecosim. Modifications to improve fit will be one future effort as part of the development of Ecosim runs with forecasting capabilities. While salinity is often the major factor influencing nekton distribution in estuaries (Bulger et al. 1993; Wagner 1999), other factors influence observed SBDs (Neill and Magnuson 1974; Cushing 1975; Rozas and Odum 1988; Pihl et al. 1991; Benfield and Minello 1996; Chesney et al. 2000; Thomas and Connolly 2001; Piazza and La Peyre 2007), and the option of including other factors (e.g. fishing) certainly exists, which will be important in future developments of Ecosim runs with forecasting capabilities.

However, because the purpose of this modeling effort was to study the effects of the CFD on estuarine nekton mainly as a result of salinity changes, this simple model is appropriate. The advantage of the present simple model is that the effects of salinity are explicit and separated out

from other factors potentially affecting fish biomass. This model thereby demonstrates potential SBDs resulting from salinity changes, and trophic interactions in response to salinity changes.

The results of the present model reveal that the low, medium and high salinity scenarios create significantly different nekton SBDs. The SBD at the end of each scenario can be interpreted as that which is expected to occur when each salinity scenario is played out estuary-wide. However, when all scenario results were pooled and compared to the base model, there was no significant difference. Since each salinity scenario is based upon real salinity data measured at three different distances from the diversion, this indicates that salinity changes due to the CFD with its current flow regime likely has not significantly altered nekton community composition in the Breton Sound estuary, although the distribution of biomass within the estuary may have changed. A separate modeling effort in Barataria Bay, which is adjacent to Breton Sound, also revealed that there was no significant reduction in populations of fisheries species due to salinity changes beginning there in 1990 (Reed et al. 2007).

It is an interesting result in the Breton Sound Ecosim scenario runs that small forage fish, represented by the dominant bay anchovy, achieve highest biomass in the lowest salinity scenario (Figure 5.5). This is especially interesting because this group has an optimum salinity of  $15 (\pm 8)$  ppt in the model (Table 5.1), indicating that this SBD is likely caused by trophic interactions, and thus is not directly driven by the salinity forcing function. This reveals that predation pressure on some biomass pools can be lowered indirectly by salinities that displace more stenohaline predators, many of which are marine transients. This mechanism may enhance the nursery function of the estuary, as these areas serve as refuge for forage fish and, especially juveniles of estuary-dependent nekton species (Gunter 1967; McHugh 1984; Houde and Rutherford 1993). A similar result was demonstrated in Chapter 2, where more small individuals were present in the inflow area of the CFD than the higher salinity control area.

In contrast, Reed et al. (2007) predicted a positive relation between bay anchovy and salinity in Barataria Bay; however, they pointed out that this was a result of a positive correlation between bay anchovy and the ratio of open water, and open water was found more in saline marshes than freshwater marshes. In both cases, salinity is only indirectly responsible for the distribution of bay anchovy, but may drive other mechanisms (decrease in predation pressure in lower salinities, increase in open water due to higher salinities) to which bay anchovy respond. The fact that opposite responses to salinity are found may be that the salinity gradient in Barataria Bay is much less distinct, and overall salinities there are higher than in Breton Sound, and may be too high to deter marine predators. MacRae (2006) showed that bay anchovy, based upon the LDWF metadata, have decreased in Barataria Bay over time, perhaps owing to rebuilding stocks of predators such as spotted seatrout and red drum (due to changes in fishing regulations). These results highlight the importance of trophic interactions, and why a holistic ecosystem scale approach is necessary to study nekton response to environmental changes (Cowan et al. 2008). In future modeling efforts in Breton Sound, both salinity and landscape patterns will be included explicitly by using the time-and spatially dynamic Ecospace.

The results in Breton Sound furthermore suggest that under the current flow regime, total nekton biomass is positively related to freshwater input from the CFD, as the highest total nekton biomass was predicted for the low salinity scenario, while the highest salinity scenario produced the lowest biomass (Table 5.3). The fact that a freshwater diversion can increase secondary production is not surprising (Cushing 1975; Iverson 1990; Nixon and Buckley 2002, Day et al. 2009). The effect of the Mississippi River on estuarine and coastal ecosystems is likely the basis for the high fishery productivity in Louisiana (Chesney et al. 2000). A study conducted closer to the CFD in Breton Sound also documented higher nekton densities and biomass in the CFD inflow area compared to a control area (Piazza and La Peyre 2007). Because their study took

place during a freshwater flood pulse event, they could correlatively link higher nekton densities to riverine input (Piazza and La Peyre 2007). In future improvements of my model, river nutrient inputs will be added explicitly, which will likely result in higher nekton biomass values than currently estimated by the model.

The nekton species that were expected to be most likely negatively affected by the CFD are spotted seatrout and brown shrimp (Gunter et al. 1964; Serafy et al. 1997; USACOE 2004; Rozas et al. 2005). Biomass of spotted seatrout was indeed predicted to have an inverse relationship with salinity, but still is predicted to occur at before-diversion densities at the high salinity end of the estuary. Brown shrimp biomass, represented in the model as 98% of the biomass of the penaeid shrimp group, actually shows a slight positive relationship with lower salinities in the simulations, which might be due to a reduction in predation pressure as described above. With optimum salinities in the model of 9.8 ppt for adults and 17 ppt for juveniles, and SD in both cases of 6.6 (compared to mean salinity in scenario 1 of  $1.4 \pm \text{SD } 3.6$ ), the penaeid shrimp group is certainly not *a priori* expected to prefer low salinities. However, it is relatively euryhaline, which results in a tolerance for lower salinities. With more information, a more complex response curve could potentially be created for each penaeid shrimp species individually, increasing the accuracy of shrimp biomass and distribution predictions. Currently however, the relationship with brown shrimp distribution and freshwater inflow is unclear; Rozas et al. (2005) concluded from their study in Breton Sound that evidence for an effect of freshwater inflow from the CFD on brown shrimp distributions was inconclusive, and that the response of brown shrimp to salinity patterns in estuaries is still a matter of debate. They suggested a BACI study and a modeling approach to come to an answer in this matter. Results from my BACI study (Chapter 2) show that brown shrimp are not negatively affected by the current flow regime of the CFD. Biomass showed declines starting before the opening of the diversion, but appears now to



be increasing in the inflow area since 1996 (Chapter 2). With that, no previous studies in the area have detected a conclusive negative effect of the CFD on brown shrimp (Rozas et al. 2005; Day et al. 2009).

Future research should include testing different hypothetical freshwater flow rate scenarios; currently the simulations were based upon actual salinity data measured in the estuary. Such numerical experiments are possible by coupling a hydrodynamic model that can simulate salinity distribution based upon CFD flow rates, to Ecosim and Ecospace, which then can be used to simulate nekton distributions based upon the salinity output as well as changes in habitat. In this way, it may be possible to evaluate in a relative sense, which flow regime is optimal to achieve wetland restoration without losing nekton biomass and species of interest that prefer higher salinities. Results of the combined models could then be used as a flexible gaming tool (Walters et al. 2008) to provide advice to managers about flow regimes in this and other planned diversion projects in coastal Louisiana (USACOE 2008). The results of this and other studies (e.g. Kim et al. 2009; Reed et al. 2007; Day et al. 2009) appear to indicate that freshwater diversions can be operated in a way that can benefit wetlands and promote land-building, without negatively affecting nekton populations in Louisiana's estuarine ecosystems.

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## SUMMARY AND CONCLUSIONS

Since 1991, the Caernarvon Freshwater Diversion (CFD) has been used to stimulate sediment deposition in areas now starved for sediment inputs, and to institute salinity reductions in areas suffering from saltwater intrusion as part of efforts to restore Louisiana's estuaries. I examined the effects of freshwater input through the CFD on estuarine nekton communities in Breton Sound. Because freshwater diversion may be the most tractable solution for restoration of coastal wetlands, positive as well as neutral effects of freshwater inflow on nekton are positive outcomes.

In the first chapter I assessed the current state of northern Gulf of Mexico (GOM) fisheries and Louisiana estuarine nekton communities using the mean trophic level index (MTLI). A previously reported low and declining MTLI for the GOM appeared to be a reflection of high targeting of shrimp and menhaden in the commercial fisheries landings rather than an indication of overfishing and poor ecosystem health. Examining long-term trends in the MTLI was still deemed a useful approach to assess ecosystem status when fisheries independent data are used for calculations, or when selective targeting and other human decisions concerning fishing practices are taken into account. Evaluating the MTLI of Breton Sound alone revealed no causal relationships between short-term variability in the index and environmental factors or hurricane disturbances; this variability is likely just a factor of using a fisheries independent dataset with a small catch (g) per year; an indication that the Breton Sound index might only be informative for inference about long-term trends. Comparing the long-term trend in the MTLI of Breton Sound with that of Fourleague Bay, which serves as the reference area throughout this body of work, indicated that the MTLI of Breton Sound is lower than that of Fourleague Bay, but that it has been increasing and approaching the level of the Fourleague Bay index. This may

indicate that the restored hydrological connectivity through the CFD is improving the health of the Breton Sound food web.

In Chapter 2, I concentrated on Breton Sound and the CFD, and investigated a potential causal relationship between the opening of the CFD and changes in nekton species biomass distributions (SBD) by using a Before-After-Control-Impact (BACI) design. The most significant biomass changes since opening the CFD were increases in *Sciaenops ocellatus*, *Micropterus salmoides* and *Mugil cephalus*, and a decrease in *Arius felis*. The most significant abundance changes were a decrease in *Cyprinodon variegatus* and increases in *Anchoa mitchilli*, *Palaemonetes* sp. and *Brevoortia patronus*. There was no extirpation of economically important species, including *Cynoscion nebulosus* and *Farfantepenaeus aztecus*. Six species chosen *a priori* for their ecological or economical importance either showed a relative increase in biomass or abundance in the inflow area compared to the control area (*M. salmoides*, *B. patronus*, *F. aztecus*, *Micropogonias undulatus*, *Litopenaeus setiferus*), or no change (*C. nebulosus*) after the opening of the CFD. In addition, abundance and the proportion of smaller individuals in the nekton community was higher in the inflow area compared to the control area. This indicates that the CFD may be creating an area with higher nursery function than areas in Breton Sound that are isolated from freshwater inflow. Overall, the BACI study showed that the CFD has caused shifts in SBD, but did not show a negative impact on the nekton community in Breton Sound in the years since opening.

In Chapters 3 and 4, I studied the mechanisms behind the changes in the estuarine nekton community by investigating the relationship between environmental variables and nekton SBD, and the effects of hydrological connectivity on the estuarine food web structure. In Chapter 3, I identified differences in environmental variables among areas in Breton Sound and Fourleague Bay with different connectivity to, and distance from, a source of freshwater input, and

demonstrated how these environmental variables affected SBD. The main abiotic factor affected by freshwater inflow was salinity. With that, marsh plant species richness, biomass and stem density, as well as submerged aquatic vegetation (SAV) biomass and pH, were positively related to freshwater inflow. Other environmental variables were more affected by seasonal variability than freshwater inflow at sites where they were measured; these were temperature, dissolved oxygen, water depth and turbidity. Previous studies have demonstrated that these variables are affected by the CFD in the upper Breton Sound estuary; this study investigated these relationships in Breton Sound at distances  $> 10$  km from the CFD. Temperature was the main abiotic factor that distinguished SBD samples, this is an indication that estuarine nekton responded more to seasonal variation as compared to the variation caused by freshwater inflow or lack thereof. Salinity was the second most important factor distinguishing SBD, indicating that spatial differences in community structure were also discernable, mostly caused by the influence of freshwater. These results are in accordance with other studies that have reported salinity and temperature as having the strongest influence on the structure of estuarine nekton communities. The finding that dissolved oxygen had very little influence on SBD, and was related to seasonal instead of spatial variation, is an indication that eutrophication related hypoxia due to nutrient inputs through the CFD likely was not occurring or affecting nekton community structure in Breton Sound during my study.

In Chapter 4 I demonstrated by means of a stable isotope study that the trophic diversity and niche breadth of the consumer community in the CFD inflow area were higher than those of the community in an area mostly blocked from the inflow. The indices of trophic structure in the CFD inflow area were closer to those of Fourleague Bay, which has an established natural hydrological connection and had the highest trophic diversity. In addition, I demonstrated with a three-source mixing model that areas with a hydrological connection (the CFD inflow area as



well as Fourleague Bay) had a significantly higher relative contribution of particulate organic matter at the base of the food web. The energy density of nekton species was negatively related to salinity, which indicates an energy benefit to consumers of a hydrological connection to a river, and of proximity to freshwater input. With that, there was a positive correlation between energy density in nekton and the relative contribution of POM at the base of the food web, as indicated by stable isotope analysis. This suggests that reconnection of the river to the estuary increased flow of nutrients and POM, which, at this intensity, had a positive effect on the storage of energy in consumers.

In Chapter 5, I used information gathered on Breton Sound to build an ecosystem model of the estuary. A model version of Breton Sound was completed using Ecopath with Ecosim, which visualizes the important carbon pools and flows and food-web links in the ecosystem. I then used it to simulate the effects of three salinity scenarios on SBD, which responded due to a combination of species-specific salinity tolerance ranges and trophic interactions. In general, the addition of a salinity function in Ecopath with Ecosim, which is unique to my study, provides estuarine and fisheries ecologists with an important tool in understanding the dynamic environment in estuaries. By using the salinity forcing function on the Breton Sound model, two important discoveries were made. Firstly, nekton species present in the estuary were predicted to redistribute rather than disappear from the system in response to the CFD, which was revealed by using measured salinities as forcing functions in the model runs. This response is likely to hold true as long as all preferred habitats (the right combination of landscape and salinity) can be found somewhere in the estuary. Secondly, the predicted redistribution of marine predators to the saltier ends of the estuary increased the nursery function of the estuary in simulations by creating a refuge in areas with salinities below the predator's preferences.

The multitude of approaches applied in these five chapters provided insight about several of the same processes that were operating at different spatial scales. Firstly, the Breton Sound estuary seems to be on a restoration trajectory towards a healthier ecosystem with a more complex consumer community. This is evident from the MTLI calculated for Breton Sound in Chapter 1, which showed an increasing slope, approaching the level of Fourleague Bay. It is also apparent from the trophic structure indices calculated in Chapter 4, which indicated that the consumer community in the inflow area in Breton Sound had a niche breadth and trophic diversity in between the control area in Breton Sound, and the reference area in Fourleague Bay.

Secondly, The CFD apparently stimulates secondary productivity in the inflow area. This is evident from Chapter 3 and Chapter 5, because the highest biomass sampled (Chapter 3) and predicted (Chapter 5) occurred in sites in the inflow area closest to the CFD, while this was lower in the mid-estuary sites, and lowest in sites that are farthest away from the CFD. This is also reflected in increasing energy density in nekton with proximity to the CFD (as shown in Chapter 4) and by biomass increases in some nekton species after opening of the CFD (as shown in Chapter 2).

Thirdly, salinity changed as a result of freshwater inflow through the CFD, and this change affected species biomass distributions. In Chapter 3, both spatial variation in salinity and its effect of salinity on SBD were shown using principal component analysis and canonical correspondence analysis, respectively. These shifts in SBD were also made evident on a larger time scale with a BACI design in Chapter 2. Similar shifts in SBD were found by modeling the effect of salinity in Chapter 5. All of these approaches support the conclusion that these shifts in SBD likely have not resulted in extirpation of economically or ecologically important nekton species from the estuaries due to the reduced salinity.

Fourthly, the CFD likely is increasing the nursery function for estuarine nekton in the Breton Sound estuary. This is made evident by increased abundance, and proportion of smaller individuals in the inflow area as shown in Chapter 2. It also emerged from the model predictions in Chapter 5, as biomass of small forage fish and shrimp increased in the upper estuary, even when their species-specific tolerance ranges revealed that the salinities in this area were sub-optimal. This may be attributable to reduced pressure from marine predators in the areas with low salinity (Chapter 2 and 5), and increased cover of SAV close to the CFD (Chapter 3) that likely provides refuge from predators.

In conclusion, the CFD affects the estuarine nekton community in Breton Sound, mostly by generating shifts in SBD within the estuary. Effects shown were mostly caused by changes in salinity, and the addition of energy to the estuarine food web, either in the form of nutrients or particulate organic matter. Both parameters are expected to have a non-linear response curve; too much nutrient loading or freshening is likely to have negative effects on the estuarine nekton community. It is of note though, that no negative impacts were observed in Fourleague Bay either, which receives two orders of magnitude more freshwater discharge from the Atchafalaya River than the amount of freshwater diverted through the CFD. This might be an indication that the Breton Sound estuary is not near the tipping point of the non-linear response curve. With the present information I can conclude that with its current flow regime, the CFD did not show a net negative impact on the nekton community, as it did not extirpate species, and apparently had a positive effect on the nursery function of the estuary.

## VITA

Kim de Mutsert was born in March in Rotterdam, the Netherlands. She graduated from High School in Krimpen aan den IJssel in 1997, and moved to Amsterdam to study biology at the University of Amsterdam. After coursework, she partook in one research project in the Netherlands under the supervision of Dr. Wim Admiraal, in which she studied light competition in benthic algae of floodplain lakes of the Waal River; and one in Canada, to study the effect of eutrophication on fish communities in Great Lakes coastal wetlands, in cooperation with Dr. Patricia Chow-Fraser from the McMaster University in Hamilton, Ontario. Kim earned a Master of Science degree/*Doctorandus* in biology from the University of Amsterdam in 2003. She moved to Louisiana in 2003 to start a doctoral program at the University of Louisiana at Lafayette. She gained research experience in biogeochemistry as a research assistant in the laboratory of Dr. Robert R. Twilley, and field experience in mangrove swamps in the Florida coastal Everglades. She transferred to the Department of Oceanography and Coastal Sciences at the Louisiana State University, and continued her doctoral study under the supervision of Dr. James H. Cowan Jr. in May 2006. Here she gained research experience in fisheries ecology, and field experience in Louisiana salt marshes. Kim will earn a Doctor of Philosophy degree from the Department of Oceanography and Coastal Sciences at LSU in May 2010. She will continue to work with Dr. James H. Cowan Jr. as a postdoctoral researcher at LSU after graduation, and has also agreed to work on a research project concerning the implementation of river diversions in Louisiana in cooperation with the Engineer Research and Development Center of the United States Army Corps of Engineers.