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The ecology of two estuarine-dependent tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*), in coastal Louisiana

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THE ECOLOGY OF TWO ESTUARINE-DEPENDENT TONGUEFISHES, THE
BLACKCHEEK TONGUEFISH (*SYMPHURUS PLAGIUSA*) AND THE OFFSHORE
TONGUEFISH (*S. CIVITATIUM*), IN COASTAL LOUISIANA

A Dissertation

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in

The Department of Oceanography and Coastal Sciences

by

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ABSTRACT

The pattern and process of wetland loss in coastal Louisiana has the potential to influence the distribution and abundance of fishes and macroinvertebrates that utilize inshore estuarine habitat as nurseries during their early life histories. Current management plans designed to stabilize marsh elevations, such as freshwater diversions, may also influence the distribution and abundance of estuarine-dependent nekton. Given the importance of nursery function of inshore estuaries in coastal Louisiana, it is of interest to explore the response of estuarine-dependent organisms to environmental gradients. To this end I examined the ecology of two sympatric tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*), in coastal Louisiana. Both species are common transients, occupying estuarine waters from post-settlement to early adulthood. Examination of patterns of resource utilization within the Barataria study area identified significant differences between species with respect to microhabitat selection. Offshore tonguefish were generally more abundant than blackcheek tonguefish in the Barataria study area. Blackcheek tonguefish used lower salinities, higher temperatures, finer substrates, shallower depths, and were found closer to shore than offshore tonguefish. Ontogenetic shifts in resource utilization were also evident for both species; larger individuals typically utilized warmer waters with lower dissolved oxygen concentrations and higher salinities, and were collected farther from shore in deeper water over coarser substrates. Blackcheek tonguefish were abundant along the marsh edge while offshore tonguefish were rare, indicating the apparent avoidance of marsh-edge habitat by offshore tonguefish. In a similar study conducted in the Vermilion system, blackcheek tonguefish were more abundant than offshore tonguefish, indicating that salinity can substantially alter the distribution and abundance

of these tonguefishes. Examination of growth rates within the Barataria system indicated that offshore tonguefish grew at a significantly higher rate than did blackcheek tonguefish. Growth of both species was significantly affected by various biotic and abiotic factors. Qualitative loop analyses indicate that tonguefish abundances are potentially affected by the input of nutrients, changes in emergent marsh habitat, and alterations in salinity. Environmental changes associated with wetland loss and associated management alternatives have the potential to affect these sympatric tonguefishes as well as other estuarine-dependent species.

CHAPTER I.

INTRODUCTION: WETLAND DYNAMICS, NURSERY HABITAT AND THE ECOLOGY OF TONGUEFISHES

Numerous ecologically and economically important fishes and macroinvertebrates rely on shallow, estuarine habitat at some point during their early life histories (Weinstein 1979; Rakocinski et al. 1992; Baltz et al. 1993; Peterson and Turner 1994). The importance of inshore habitat is especially evident in coastal Louisiana, from which a majority of the total commercial marine fisheries harvest in the northern Gulf of Mexico is derived. Many species common to the region, including some of the most economically important fisheries species (i.e., shrimp and menhaden), are strongly dependent on these inshore nurseries, and share a common estuarine-dependent life history with juvenile and adult stages separated by great distances (Gunter 1967). Adult populations reside in offshore waters where they spawn, with the pelagic larvae moving into inshore nurseries and eventually settling over highly productive estuarine habitat. These estuaries function as nurseries, and juveniles typically remain within the estuary for the better part of a year, eventually migrating offshore to recruit into adult populations at maturity.

To fully understand the ecology of estuarine-dependent fishes it is important to consider the geological and hydrological framework of the region. Deposition of sediments from the Mississippi River has dominated the geology of the southeastern and central coast of Louisiana for much of the past 6,000 years (Frazier 1967) and to a lesser extent the entire area known as the Fertile Fishery Crescent (Gunter 1963) that also encompasses large areas of Texas and Mississippi. During this time, the river has changed course on numerous occasions (Frazier 1967), after which a new deltaic lobe was formed via a well-defined series of events known as the deltaic cycle (Scruton 1960; Coleman and Gagliano 1964; Kolb and Lopik 1966).

The deltaic cycle can be broken down into two major components: the constructional phase and the destructional phase (Coleman et al. 1998). The constructional phase begins once the river has shifted course to a new depositional point in a process called delta switching. The initial prodeltaic deposits are the first terrigenous sediments introduced into a new delta lobe, and continue to accrete both in thickness and in area. During the period of land formation the delta front continuously progresses seaward until deposition of sediments reaches the continental shelf. Once shelf delta formation begins, the delta enters a period of relative stability until the course of the river switches to a shorter, more favorable path and constructional processes begin anew. Once a shift in river course occurs, local land-building processes cease due to decreased river discharge, and marine processes dominate the coastal geology. Dewatering and compaction result in subsidence of depositional sediments, eventually resulting in significant land loss throughout the abandoned deltaic lobe.

Although reworking of sediments and coastal land loss are part of the natural deltaic cycle, current land loss rates of $0.86\% \text{ yr}^{-1}$ (Turner 1990) are substantially higher than can be explained by subsidence alone (Hatton et al. 1983). Four major hypotheses exist as to the most important contributing factors to the observed rates of wetland loss in coastal Louisiana: (1) land loss is due to indirect consequences of extensive canal dredging; (2) a decline in the suspended sediment load of the Mississippi River has led to observed land losses; (3) extensive levee construction along the Mississippi River has contributed to land loss; and (4) land losses are due to extensive saltwater intrusion into typically fresher areas (Turner 1997). Although it is generally accepted that these factors are all somewhat important contributors to the high rates of land loss observed in coastal Louisiana, there is substantial debate as to the relative importance of each factor (Turner 1997; Day et al. 2000; Gosselink 2001).

A direct link between canal dredging and wetland loss has been demonstrated for several estuarine basins throughout coastal Louisiana (Bass and Turner 1997; Turner 1997). Increased incidences of land loss are common near dredged canals, and the creation of spoil banks from deposition of dredged material along these canals may also contribute to the problem by altering the natural frequency and duration of tidal events. These hydrological changes ultimately stress wetland vegetation, with the associated reduction in vegetated biomass contributing to decreased sediment accretion rates. While canal dredging undoubtedly contributes to wetland loss in Louisiana, the high rates of land loss cannot be solely attributed to dredging activities in all areas (Day et al. 2000). Since the mid 1800's, there has been an overall decline in the suspended sediment load of the Mississippi River due partly to declining discharge and partly due to changing land use practices (Kesel 1988), so the amount of sediment available for deposition has decreased. Construction of levees and other coastal impoundments have also contributed to the overall reduction in sediment deposition by preventing spring flooding events that are an important sediment source (Day et al. 1995). Levees also prevent the formation of crevasses, or breaks along the course of the river, which also contribute large quantities of sediment to the system.

Other factors, such as saltwater intrusion and eustatic sea level rise, may also be contributing to the observed rates of land loss in Louisiana. The movement of high salinity waters into traditionally freshwater wetlands stresses vegetation intolerant to salinity, and the resulting plant mortalities contribute to decreased sedimentation. The effects of compaction and subsidence that are common throughout coastal Louisiana can also be magnified by an overall increase in sea level. In reality the high rates of land loss in coastal Louisiana cannot be attributed to any single one of these factors; rather wetland loss is a result of a dynamic interplay

among anthropogenic alterations to the hydrology of the region and the geologic processes at work in the deltaic plain.

The recent trends of coastal land loss are especially important to those species that utilize vegetated habitat along the marsh edge (Weinstein 1979; Zimmerman et al. 1984; Baltz et al. 1993; Peterson and Turner 1994). Individuals occupying the marsh edge are thought to benefit from increased food availability, decreased threat of predation or both, although the relative importance of these benefits is not yet clear (Boesch and Turner 1984). As intact marsh habitat begins to disintegrate, the amount of edge increases (Chesney et al. 2000), potentially resulting in enhanced productivity among marsh-edge species (Browder et al. 1985; Browder et al. 1989). Unfortunately edge quantities cannot increase indefinitely; eventually a point is reached after which additional marsh loss will result in a corresponding loss of edge. Simulation modeling indicates that we may be approaching this peak in the amount of available edge habitat, and productivity of species that rely on the marsh edge may soon decline sharply as edge is lost (Browder et al. 1989). Given the importance of inshore nursery habitat to so many species, it is critical to gain an understanding of the underlying ecological processes at work.

My dissertation research involves a detailed examination of the ecology of tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*). Both tonguefishes are congeners and frequently occur sympatrically (Allen and Baltz 1997), so allow for the examination of the ecology of potential estuarine-dependent competitors. Both species are also among the most commonly occurring flatfishes in coastal Louisiana, and are persistent throughout most of the year (Allen and Baltz 1997), which allows for meaningful comparisons across space and time.

Both tonguefishes are morphologically similar, but can generally be distinguished by a suite of physical characteristics (Munroe 1998; Munroe et al. 2000). Blackcheek tonguefish can

readily be identified by few (5 – 7) broad, indistinct bands of pigmentation on the eyed side (Figure 1.1), pigmentation along the dorsal and ventral margins of the body on the blind side, 10 caudal fin rays, and dark pigmentation in the cheek area. In contrast, offshore tonguefish typically possess more (10-13) and narrower distinct bands of pigmentation on the eyed side (Figure 1.2), lack pigmentation along the dorsal and ventral margins of the blind side, possess 12 caudal fin rays, and lack dark pigmentation in the cheek area. Correct identification is generally possible using pigmentation patterns only, although examination of caudal fin rays is occasionally required.

Munroe (1998) recently published a thorough review of the ecology of tonguefishes, including both blackcheek and offshore tonguefish. Within coastal Louisiana both blackcheek and offshore tonguefish are within the middle of their geographic range. The blackcheek tonguefish has a relatively wide distribution in the western Atlantic. Individuals have been captured along the eastern seaboard of the United States as far north as New York. The geographic range of blackcheek tonguefish extends throughout the Gulf of Mexico to the Campeche Peninsula, Mexico, as well as in the Caribbean. The distribution of offshore tonguefish is similar to that of blackcheek tonguefish, although not nearly as extensive. Offshore tonguefish occur along the eastern seaboard of the United States as far north as North Carolina, and their range extends throughout the Gulf of Mexico to the Yucatan Peninsula, Mexico, but have not been reported in Caribbean waters (Munroe 1998).

Little is known about the age distribution and growth rates of tonguefishes (Miller et al. 1991). Recent work with blackcheek tonguefish in Chesapeake Bay indicates longevity of adults of 5 – 6 years (Terwilliger and Munroe 1999). Blackcheek tonguefish can exceed 200 mm total length (TL), although few individuals reach this size (Munroe 1998). Individuals achieve most



Figure 1.1. The blackcheek tonguefish (*Symphurus plagiusa*).



Figure 1.2. The offshore tonguefish (*Symphurus civitatum*).

of their total growth during the time spent within inshore nursery areas, reaching lengths on the order of 100 mm TL following a year spent within the estuary (Allen and Baltz 1997; Terwilliger and Munroe 1999). Less is known about the age and growth of offshore tonguefish, although they reach somewhat smaller maximum lengths than do blackcheek tonguefish (Munroe 1998), which may be due to a slower overall growth rate, shorter longevity or both.

Newly settled juveniles first appear within estuarine nurseries during summer (Reichert and van der Veer 1991; Allen and Baltz 1997; Jones et al. 2002) following a spawning period from spring through summer (Olney and Grant 1976). The juveniles remain within the estuary for the better part of a year, and eventually vacate the shallow, inshore habitat, presumably to recruit into offshore adult populations (Baltz et al. 1993). Tonguefishes that emigrate from the estuary are of sufficient size to be mature as sexual maturity of both blackcheek and offshore tonguefish occurs at approximately 85 mm TL (Munroe 1998; Terwilliger and Munroe 1999).

My dissertation research focuses on the utilization of nursery habitat by young-of-the-year blackcheek and offshore tonguefish in coastal Louisiana. Analyses were typically conducted for size-specific groupings of tonguefishes due to potential changes in resource utilization that may be masked by analyses at the species level (Livingston 1988), and the fact that ontogenetic changes in environmental requirements are particularly important among estuarine-dependent species. My analyses involved the examination of population responses to environmental gradients by identifying patterns of resource utilization at the microhabitat level (Baltz 1990). By examining a specific suite of environmental conditions at numerous sites occupied by one or more individuals, it then becomes possible to broaden the understanding of resource requirements at the population level and to changing requirements across life history stages.

Throughout my dissertation I borrow data sets originally published in Baltz et al. (1993), Allen and Baltz (1997), and Baltz and Jones (in press). In chapter two I examined size-specific patterns in resource utilization by blackcheek and offshore tonguefish along environmental gradients in Barataria Bay, Louisiana. I focused on the examination of seasonal, spatial and ontogenetic patterns in resource utilization between species and among size classes as well as differences in habitat suitabilities between the two species. In chapter three, I examined the utilization of marsh-edge habitat by blackcheek and offshore tonguefish in Barataria Bay, and compared tonguefish densities along the marsh edge with those obtained along depth and distance-from-shore gradients from other research in the region. In the fourth chapter, I conducted age and growth analyses for both species of tonguefish. In this chapter I analyzed the basic relationship between fish growth and otolith growth, examined length at age relationships for young individuals, and related recent daily growth to a suite of environmental variables. In chapter five, I compared resource utilization of blackcheek and offshore tonguefish collected in Barataria Bay as well as Vermillion Bay to determine if the separate tonguefish populations respond similarly to one another. In addition, I examined whether principal components analysis (PCA) models obtained from one study region can accurately predict changes in distribution and abundance patterns under different environmental conditions. Chapter six addresses the qualitative modeling of the ecology of blackcheek and offshore tonguefish in coastal Louisiana. I incorporated direct interactions between tonguefishes and the components of a benthic food web, and modeled the effects of specific habitat variables on abundances of blackcheek and offshore tonguefish. A brief summary is given in chapter seven. These combined results shed some light on the relationships between closely related estuarine-dependant species in coastal Louisiana, and provide information that may be applicable to other species of interest.

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CHAPTER II.

HABITAT SELECTION BY SYMPATRIC TONGUEFISHES (*SYMPHURUS*: *CYNOGLOSSIDAE*) IN COASTAL LOUISIANA: UNRAVELING SEASONAL, SPATIAL, AND ONTOGENETIC PATTERNS IN RESOURCE UTILIZATION

Introduction

Estuaries function as nursery grounds for numerous post-larval and juvenile fishes and macroinvertebrates (Weinstein 1979; Valesini et al. 1997; Jones et al. 2002), including flatfishes (Allen and Baltz 1997; Walsh et al. 1999). These transient life-history stages of estuarine-dependent flatfishes exhibit a separation in habitat utilization between young and adults (Gunter 1967). Reproductive adults typically reside in offshore, marine waters that are separated spatially from inshore nurseries. Once transported into the estuary, pelagic larvae of flatfishes transform and settle, assuming a benthic lifestyle and responding to a different set of environmental requirements (Fuiman 1997). Juveniles typically occupy the highly productive nursery habitat until maturity, during which time they may undergo ontogenetic changes in environmental requirements until they eventually move offshore, mature, and recruit into adult populations.

Within the estuary, the environmental conditions occupied by an individual are crucial to its long-term survival. At the finest scale, the microhabitat of an individual fish is the site it occupies at a given point in time (Baltz et al. 1993). Similarly sized individuals of a species select similar microhabitats; therefore careful measurements of many individuals and associated physical, chemical, and biological variables should define the response of a species or life history stage to environmental gradients (Hurlbert 1981; Baltz 1990). The specific microhabitat that an individual occupies is limited by the physiological tolerances of the species; within such tolerances specific sites are presumably selected in response to factors that optimize the net

energy gain of an individual while minimizing predation risks (Boesch and Turner 1984).

Selection of specific environmental conditions during and immediately following settlement can have an important impact on early growth rates of flatfishes (Manderson et al. 2002) and may ultimately affect the probability of their survival. Although processes affecting early life history stages of flatfishes may be important in controlling recruitment (Miller et al. 1991), processes operating during the juvenile period can be just as important (Houde 1989). Given the importance of Louisiana's highly productive estuarine nurseries, it is of interest to determine how juveniles of two congeneric species partition resources within the estuary.

Two species of tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*), are among the most commonly occurring flatfishes in coastal Louisiana (Allen and Baltz 1997), and so are ecologically important members of the demersal fish community. While both species have been known to occupy estuarine waters in coastal Louisiana (Thompson and Forman 1987), blackcheek tonguefish were believed to be the only commonly occurring species of tonguefish and offshore tonguefish were viewed as rare within inshore waters (Munroe et al. 2000). The high abundance of offshore tonguefish in coastal Louisiana (Allen and Baltz 1997) indicates that they are not rare; in fact, they were the most abundant flatfish species collected. The prior belief that offshore tonguefish rarely occurred in coastal Louisiana may be due to a recent change in the distributional patterns of offshore tonguefish, or may have resulted from misidentification as blackcheek tonguefish due to their morphological similarity (Munroe 1998; Munroe et al. 2000). Due to the difficulties in identifying these two species, previous reports of the distribution and abundance of tonguefishes in coastal Louisiana may be confounded by the potential misidentification of offshore tonguefish.

I approached the question of resource partitioning (Ross 1986) between two juvenile congeneric tonguefishes by fine-scale studies of distribution and abundance at the microhabitat level (Baltz 1990). By comparing environments occupied by size-specific classes (Livingston 1988) of blackcheek and offshore tonguefishes with environmental availability, I tested whether: 1) these two tonguefishes shared similar patterns of seasonal and/or spatial resource utilization within inshore nurseries; 2) there was evidence of ontogenetic shifts in resource utilization by these tonguefishes along environmental gradients; and 3) whether these ontogenetic shifts were due to seasonal/spatial patterns of environmental variation or actual changes in environmental preferences. By addressing these hypotheses, I can begin to characterize the range of environmental conditions that are tolerated and required by these tonguefishes (Minello 1999), and gain a better understanding of the influence that environmental variability may have on tonguefish recruitment (Miller et al. 1991), an area where little information is currently available for the 130 + species of cynoglossids.

Materials and Methods

Study Area

The Barataria Basin is the first major estuary west of the Mississippi River (Figure 2.1). Located between the natural levees of the river and the abandoned Bayou Lafourche distributary, the basin is roughly 110 km long and 50 km wide and has a saltmarsh area of 145,000 ha (Conner and Day 1987). The basin has been deprived of the overland flow of river water and sediments by closure of the Bayou Lafourche-Mississippi River connection in 1902 and by a levee system completed in the 1930s – 40s. The absence of riverine input of fresh water, sediments and nutrients combined with canal construction, saltwater intrusion, and subsidence has contributed to an annual loss of wetlands in Louisiana of $65 \text{ km}^2 \text{ yr}^{-1}$ (Day et al. 1989).

Currently, the main source of freshwater input into the basin is from precipitation, which averages 160 cm per year (Conner and Day 1987). The climate of the basin is subtropical, and the hydrography and salinity are primarily influenced by local precipitation, tidal flux, and prevailing winds. The recent opening of the Davis Pond freshwater diversion in 2002 has provided an additional source of fresh water and sediment into the basin in an attempt at reversing the decades-long trend of land loss in the region (LDNR 2002).

The saltmarsh portion of Barataria Bay has salinities that vary both seasonally and spatially between 6 and 22 psu (Baltz et al. 1993). Water in the basin is turbid and shallow, with water depths generally less than 2 m. Seasonal winds easily dominate the microtidal system, which has a mean tidal range of 0.32 m (Childers et al. 1990). The dominant marsh vegetation is *Spartina alterniflora* (smooth cord grass), with *Juncus roemerianus* (black rush), *Distichlis spicata* (saltgrass), *Batis maritima* (saltwort), and *Salicornia virginica* (glasswort) also common to the study area.

Field Methods

Juvenile tonguefishes were quantitatively collected over 24 months in the Barataria Bay system from September 1992 to August 1994 using a 1-m beam trawl with a uniform mesh size of 5 mm (Kuipers 1975). Kuiper's design was modified by the addition of a pair of polyvinyl chloride skids (10 x 50 cm) for use on fine substrates. To facilitate sampling the broad saline-to-brackish estuary of Barataria Bay, sampling effort was divided into six strata ranging from the near shore zone in the Gulf of Mexico to the brackish marsh some 30 km inland (Figure 2.1). Within each stratum a randomized location was selected each month to sample fishes associated with a variety of substrates and environmental conditions (Figure 2.1). This approach enabled me to describe patterns of resource utilization for blackcheek and offshore tonguefish along environmental gradients within the study area.

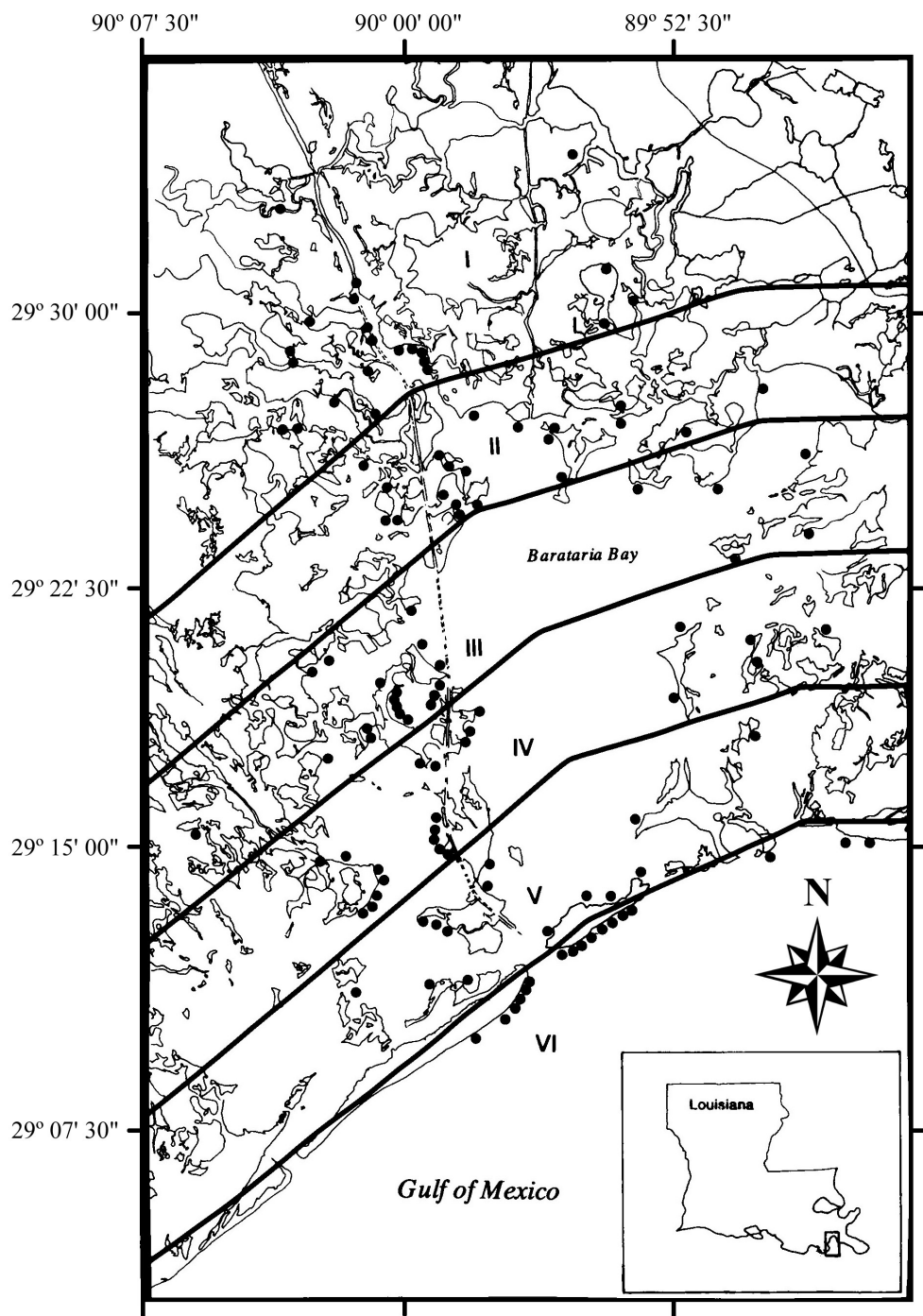


Figure 2.1. The Barataria Bay, Louisiana, USA study region indicating strata designations (I – VI). Black dots represent sampling locations.

Sampling at a location involved making a series of five tows at sites parallel to the shoreline, typically the marsh edge. Each subsequent tow was more distant from shore and generally in deeper water. Tow duration at each site was typically 2 min (range 1-2 min.), and tow direction was parallel to the shoreline to minimize environmental heterogeneity within a sample. A sample of towed distances was measured between stakes to estimate coverage over substrate types (Allen and Baltz 1997). Each tow covered a mean (\pm 1SD) area of approximately $152 \pm 14.8 \text{ m}^2$, which varied substantially ($\text{CV} = 9.7\%$) over substrate types: silt (138 m^2), clay (142 m^2), sand (158 m^2), and plant detritus (170 m^2). Measurements of salinity (psu) and temperature ($^{\circ}\text{C}$) were taken in the middle of the water column at each tow site using a Yellow Springs Instrument (YSI) Model 33 salinity, conductivity, and temperature meter, and dissolved oxygen concentration was measured using a YSI Model 57 oxygen meter. The hydrology of the study area is dominated by wind stress, which minimizes vertical stratification within the shallow bays (Hopkinson et al. 1985). All samples were collected during daytime hours when photosynthesis results in elevated dissolved oxygen concentrations. The substrate type was identified during each tow from surficial samples that were characterized in terms of dominant and subdominant components and coded on an ordinal scale of particle size as 1: clay, 2: silt, 3: sand, 4: plant detritus (primarily *Spartina alterniflora*), and 5: shell. Minimum and maximum water depths (m) between the beginning and end of each tow were noted and used to calculate median depth, and an estimate of the distance from shore (m) was also recorded.

Trawl samples were sorted in the field to separate all fishes and macroinvertebrates, and have been previously summarized by Allen and Baltz (1997) and Jones et al. (2002). Specimens were preserved in 95% ethanol. All tonguefishes were identified in the laboratory using keys and descriptions by Hoese & Moore (1977) and Munroe (1991), and were measured to the nearest mm standard length (SL).

Analytical Methods

Multivariate analysis of variance (MANOVA), using general linear models and the least-square-mean method (SAS Institute 1996), was used to compare means of environmental variables. Transformed environmental variables ($\log_{10} x + 1$) were used when the assumption of normality was not met. When normality of the residuals was unattainable, careful visual examination of residual plots and residual biplots was conducted to identify potential patterns of unexplained variability and to confirm variance homogeneity. MANOVA is relatively robust with respect to moderate violations of the assumption of normality (Johnson and Field 1993), and I detected no problems with heteroscedasticity. Two separate MANOVAs compared environmental conditions among seasons and strata. Seasons were defined as: fall (September – November), winter (December – February), spring (March – May), and summer (June – August), and strata classifications were assigned from I – VI based on sampling location (Figure 2.1). Additionally, two separate MANOVAs compared mean environmental usage between species: one analysis between species and the other among size classes within and between species. Tonguefishes were assigned to four size classes (SC I – IV) to examine size-related patterns of microhabitat use (Livingston 1988) as SC I: ≤ 15 mm, SC II: > 15 to 30 mm, SC III: > 30 to 85 mm, and SC IV: > 85 mm SL. The first three size classes represent juvenile tonguefishes, while the largest size class included individuals at or approaching sexual maturity (Munroe 1998; Terwilliger and Munroe 1999). Univariate means and standard errors of environmental variables for species and size classes were calculated by treating each beam-trawl collection as an independent sample. For between-species comparisons I generated one record for each species present in each sample, while for size-class comparisons I generated one record for each size class of a species present in each sample. Because of differences in tow duration, I attempted to

standardize the data by calculating relative abundances of species and size classes as number of individuals captured per minute (total number of individuals divided by tow duration). For the statistical analyses I weighted the means for species or size-class abundance (SAS Institute 1996) by catch per minute to estimate species or size class responses to environmental gradients without increasing degrees of freedom (Hurlbert 1984). *A posteriori* testing of environmental variables found to differ significantly among seasons, strata, species and size classes was conducted using Tukey's adjustment for multiple pairwise comparisons. Separate analyses were conducted for each season; however, results did not differ greatly among seasons, so only annual results are reported.

Following Schoener (1970), I calculated overlaps in temporal, spatial, and size-structured (Livingston 1988) distributions among species and size classes to assess overlap and resource partitioning (Ross 1986) across four seasons, six strata, and four size classes in the Barataria Bay system. Schoener's index of overlap (C_{xy}) was calculated as:

$$C_{xy} = 1 - 0.5 (\sum | p_{xi} - p_{yi} |),$$

Where p_{xi} is the proportion of resource i used by species x and p_{yi} is the proportion of resource i used by species y . Overlap was estimated as the proportional similarity in relative abundance (based on catch per minute) between all species pairs in 4 x 6 x 4 arrays (i.e., seasons, strata, & size classes). Pairwise overlaps by season and strata were also estimated without regard to fish size.

Variation in patterns of microhabitat use by blackcheek and offshore tonguefishes were examined in a principal component analysis (PCA) of six environmental variables (temperature, dissolved oxygen, salinity, distance from shore, median depth and substrate) based on the correlation matrix. The PCA was conducted using the Factor Procedure in SAS, and the first

four factors were rotated using the varimax option to facilitate the interpretability of each separate component (SAS Institute 1996). The PCA was used to resolve six intercorrelated environmental variables into four orthogonal variables to facilitate visualization and simplify comparisons between species and among size classes. Environmental variables in 594 samples without missing data were used to calculate variable loadings and generate principal component scores for each sample. Mean principal component scores for each size class within species were calculated by treating each sample as an independent observation and weighting the analysis by catch per minute. I then plotted size classes in PCA space using calculated means as centroids. The variance about the centroids was estimated as the means of standard errors on each of four principal component axes for each size class within species. I then estimated 95 % confidence intervals about the centroids by doubling the standard errors. These confidence intervals allow for visual comparisons of resource utilization between species and among classes along several gradients of environmental variation. Separate analyses were conducted for each season; however, results did not differ strongly among seasons, so only the annual results are presented.

Habitat suitability curves were constructed to describe selection along individual environmental gradients by blackcheek and offshore tonguefishes (Baltz 1990). These curves allow for an examination of resource use that accounts for non-uniform sampling across environmental gradients. Habitat suitability curves were constructed for each of the six environmental variables measured: temperature, dissolved oxygen, salinity, distance from shore, median depth and substrate. A number of equal intervals along each environmental variable were chosen to provide the smoothest habitat suitability curves possible. Habitat suitability (S) for each interval was calculated as:

$$S = P(E|F) / P(E),$$

where $P(E|F)$ is the probability (resource use for a species or life history stage) of finding a value for environmental variable (E) given the presence of a fish (F), and $P(E)$ is the probability (resource availability) of finding that value regardless of whether a fish is present or not (Baltz 1990). Interval values were then normalized by dividing by the highest suitability to range from zero (intolerable) to one (optimal). Due to insufficient sample sizes for several size classes, suitabilities were only calculated for SC III.

Results

Seasonal and Spatial Environmental Variation

Environmental conditions differed significantly on a seasonal basis (MANOVA: $F = 34.64$, $p < 0.0001$). Median depth, salinity, dissolved oxygen and temperature differed among seasons, whereas distance from shore and substrate did not (Table 2.1). Mean depths sampled were significantly shallower in winter than in spring or fall, but were similar to those sampled in summer. Salinities were significantly higher in fall than they were in the other three seasons, and dissolved oxygen was significantly higher in winter than in other seasons. Temperature was significantly different among all seasons. Highest mean temperatures occurred in summer, followed by fall and spring, and lowest temperatures occurred during winter months.

Environmental conditions also differed among strata (MANOVA: $F = 24.75$, $p < 0.0001$). Median depth, distance from shore, substrate, salinity and dissolved oxygen differed among strata, whereas temperature did not (Table 2.2). Median depth and distance from shore were significantly greater in the lowermost stratum than in all other strata. Distances were significantly lower in the uppermost stratum than in Strata III and IV, but were similar to distances in Strata II and V. Substrates were significantly coarser in the two lower strata than in the upper four strata. Salinities were significantly different among all strata except the lowermost two strata. Salinities were highest in the lowermost two strata, and were

Table 2.1. Seasonal patterns in resource availability estimated by least-square means (\pm SE) for six environmental variables. Significant differences ($p \leq 0.025$) among seasons are indicated by different letters reading horizontally (NS indicates that differences were not significant). Seasonal ranges are reported below the mean for each variable.

Variable				
Season	Winter	Spring	Summer	Fall
Median depth (m)	1.6 \pm 0.05 A (0.8 - 4.2)	1.8 \pm 0.06 BC (0.7 - 4.5)	1.7 \pm 0.06 AB (0.7 - 6.1)	1.9 \pm 0.06 C (0.8 - 5.9)
Distance from shore (m)	343 \pm 30.7 NS (9 - 3660)	270 \pm 33.4 NS (8 - 1400)	297 \pm 34.3 NS (5 - 3215)	279 \pm 35.6 NS (5 - 2010)
Substrate code	2.2 \pm 0.08 NS (1 - 5)	2.0 \pm 0.09 NS (1 - 5)	2.0 \pm 0.09 NS (1 - 5)	1.9 \pm 0.10 NS (1 - 5)
Salinity (psu)	11.5 \pm 0.49 A (0.9 - 23.8)	11.9 \pm 0.53 A (0.1 - 22.8)	10.9 \pm 0.55 A (0.0 - 25.0)	14.5 \pm 0.57 B (2.3 - 29.2)
Dissolved Oxygen (mg l ⁻¹)	9.3 \pm 0.10 B (4.4 - 12.4)	8.3 \pm 0.11 A (4.5 - 10.2)	7.9 \pm 0.12 A (4.4 - 11.7)	8.1 \pm 0.12 A (5.1 - 11.3)
Temperature (° C)	15.7 \pm 0.28 A (10.2 - 21.0)	21.4 \pm 0.30 B (13.1 - 30.5)	30.0 \pm 0.31 D (27.5 - 32.4)	23.9 \pm 0.32 C (14.0 - 31.0)
Sample Size	174	147	139	134

progressively lower in the upper strata. Dissolved oxygen concentration was lower in the uppermost stratum than in all other strata.

Species and Size Class Occurrence

Blackcheek and offshore tonguefishes are among the four most commonly collected flatfish species (Allen and Baltz 1997). In 594 individual beam-trawl samples, 2897 offshore tonguefish and 631 blackcheek tonguefish were collected. Offshore tonguefish were found in 229 separate trawls and blackcheek tonguefish in 231 trawls, both with an equal frequency of occurrence of 0.39. Both species co-occurred in 92 trawl samples, for a joint frequency of occurrence of 0.15.

Only one blackcheek tonguefish was collected from size class I (SC I) and so this size class of blackcheek tonguefish was excluded from further analyses (Table 2.3). Numerous blackcheek tonguefish were collected in all other size classes. Substantially more offshore tonguefish were collected in SC III than in any other size class, and offshore tonguefish in SC I and IV were less common, only occurring in twelve and sixteen samples, respectively.

Species-Level and Size Class Comparisons

Significant differences were detected between blackcheek and offshore tonguefish (MANOVA: $F = 35.83$, $p < 0.0001$) with respect to all environmental variables except dissolved oxygen (Table 2.4). Blackcheek tonguefish used significantly lower salinities, higher temperatures, and finer substrates than did offshore tonguefish, and used shallower depths nearer to shore. Significant differences among species and size classes (MANOVA: $F = 10.76$, $p < 0.0001$) were detected for all six microhabitat variables measured (Table 2.3).

Within species differences for blackcheek tonguefish were significant for two of six environmental variables. The largest blackcheek tonguefish (SC IV) were found in higher

Table 2.2. Spatial patterns in resource availability estimated by least-square means (\pm SE) for six environmental variables. Significant differences ($p \leq 0.047$) among strata are indicated by different letters reading horizontally (NS indicates that differences were not significant). Spatial ranges are reported below the mean for each variable.

Variable						
Strata	I	II	III	IV	V	VI
Mean depth (m)	1.6 \pm 0.06 A (0.7 - 6.1)	1.5 \pm 0.06 A (0.8 - 2.8)	1.5 \pm 0.06 A (0.8 - 2.6)	1.6 \pm 0.05 A (0.7 - 2.5)	1.7 \pm 0.07 A (0.8 - 5.0)	2.5 \pm 0.06 B (1.2 - 4.5)
Distance from shore (m)	156 \pm 38.0 A (5 - 1000)	209 \pm 38.7 AB (9 - 915)	291 \pm 37.1 AB (8 - 1465)	368 \pm 36.0 B (9 - 3660)	273 \pm 47.6 B (6 - 1610)	517 \pm 41.5 C (20 - 2415)
Substrate code	1.7 \pm 0.10 A (1 - 5)	1.6 \pm 0.10 A (1 - 5)	1.6 \pm 0.09 A (1 - 5)	1.9 \pm 0.09 A (1 - 5)	2.8 \pm 0.12 B (1 - 5)	3.0 \pm 0.11 B (1 - 5)
Salinity (psu)	4.8 \pm 0.40 A (0.0 - 17.5)	7.6 \pm 0.40 B (3.0 - 17.0)	11.5 \pm 0.39 C (5.4 - 19.0)	14.3 \pm 0.38 D (5.7 - 27.5)	18.1 \pm 0.50 E (10.4 - 29.2)	19.5 \pm 0.43 E (10.9 - 28.3)
Dissolved Oxygen (mg l ⁻¹)	7.7 \pm 0.14 A (4.4 - 10.8)	8.7 \pm 0.14 B (6.0 - 11.3)	8.6 \pm 0.14 B (4.4 - 12.1)	8.8 \pm 0.13 B (5.1 - 12.4)	8.5 \pm 0.17 B (5.9 - 10.6)	8.3 \pm 0.15 B (5.5 - 10.6)
Temperature (° C)	21.3 \pm 0.63 NS (10.5 - 31.0)	22.9 \pm 0.64 NS (13.0 - 32.4)	22.8 \pm 0.61 NS (11.5 - 32.4)	22.3 \pm 0.59 NS (10.2 - 31.0)	22.1 \pm 0.78 NS (11.4 - 32.0)	22.2 \pm 0.68 NS (14.0 - 31.0)
Sample Size	105	101	112	118	70	88

Table 2.3. Weighted means (\pm SE) of environmental variables used by size classes of blackcheek and offshore tonguefish in Barataria Bay, Louisiana. N is the number of independent samples used in the analysis. Posterior testing ($p \leq 0.028$) of means among size classes is based on least-square-means comparisons, with significantly different means lacking at least one letter in common (i.e., A, B & C), reading vertically.

Common name	N	Median depth (m)	Distance from shore (m)	Substrate Code	Salinity (psu)	Dissolved oxygen (mg l ⁻¹)	Temperature (° C)
Blackcheek Tonguefish							
≤ 15 mm	1	1.6 --	75 --	2.0 --	8.0 --	9.2 --	17.9 --
> 15 ≤ 30 mm	50	1.4 ± 0.16 A	225 ± 123.8 A	1.5 ± 0.19 A	10.9 ± 1.26 A	9.1 ± 0.23 CD	17.8 ± 0.96 AB
> 30 ≤ 85 mm	158	1.5 ± 0.07 A	222 ± 57.8 A	1.6 ± 0.09 A	10.2 ± 0.59 A	8.9 ± 0.11 CD	19.4 ± 0.45 B
> 85 mm	76	1.8 ± 0.15 AB	333 ± 118.8 AB	2.0 ± 0.18 AC	13.9 ± 1.21 AB	8.0 ± 0.23 AB	25.6 ± 0.92 C
Offshore Tonguefish							
≤ 15 mm	12	2.4 ± 0.38 ABC	567 ± 303.0 AB	1.7 ± 0.46 AB	19.2 ± 3.09 AB	9.3 ± 0.57 BD	19.0 ± 2.36 ABC
> 15 ≤ 30 mm	90	1.9 ± 0.10 B	383 ± 77.7 A	2.1 ± 0.11 A	11.7 ± 0.80 A	9.2 ± 0.15 D	17.1 ± 0.60 A
> 30 ≤ 85 mm	198	2.2 ± 0.04 C	616 ± 29.4 B	2.6 ± 0.04 B	16.8 ± 0.30 B	8.7 ± 0.06 C	16.5 ± 0.23 A
> 85 mm	16	2.1 ± 0.27 ABC	254 ± 213.3 AB	3.0 ± 0.32 BC	21.2 ± 2.17 B	6.8 ± 0.40 A	27.1 ± 1.66 C

temperatures and lower dissolved oxygen concentrations than were smaller individuals (SC II & III). No significant differences were detected within blackcheek tonguefish with respect to substrate use; blackcheek tonguefish used fine substrates throughout all size classes examined. Within offshore tonguefish, significant differences were detected for all six environmental variables. Most notably, the largest offshore tonguefishes (SC IV) used significantly higher temperatures and lower dissolved oxygen concentrations than did all smaller individuals (SC I, II & III). Larger-sized offshore tonguefish (SC III & IV) also used significantly coarser substrates and higher salinities than did smaller individuals (SC II). Additionally, offshore tonguefishes in SC III were found in deeper waters farther from shore than were individuals in SC II. Size-class differences between species were significant for all six environmental variables. In comparisons of similarly sized individuals between species, offshore tonguefish were typically found in deeper waters farther from shore than were blackcheek tonguefish. Offshore tonguefish were also collected in generally higher salinity waters over coarser substrates than were blackcheek tonguefish.

Temporal and Spatial Distribution

Distributions of both species overlapped broadly on a seasonal basis (Schoener's index of overlap = 0.78); both species were found in the study area in all seasons, and were most abundant in winter months (Figure 2.2). The temporal occurrence of size classes is similar for both species, indicating that differential appearance of size classes within the estuary is not the primary form of segregation between species. On a spatial basis, the distribution of both species did not overlap as much (Schoener's index of overlap = 0.35). Blackcheek tonguefish were most abundant in the upper three strata of the study area where approximately 83 % of the individuals collected were found on an annual basis (Figure 2.3). Offshore tonguefish were most common in

Table 2.4. Weighted means (\pm SE) of environmental variables used by blackcheek and offshore tonguefishes in Barataria Bay, Louisiana. N is the number of independent samples and total number is the number of individuals. Significant differences ($p \leq 0.028$) of means between species are indicated by different letters reading vertically (NS indicates that differences were not significant).

Common name	N	Total number	Median depth (m)	Distance from shore (m)	Substrate code	Salinity (psu)	Dissolved oxygen (mg l^{-1})	Temperature ($^{\circ}\text{C}$)
Blackcheek Tonguefish								
all sizes	231	631	1.5 ± 0.07 A	241 ± 55.0 A	1.7 ± 0.08 A	10.9 ± 0.54 A	8.8 ± 0.11 NS	20.2 ± 0.45 A
Offshore Tonguefish								
all sizes	229	2897	2.3 ± 0.04 B	582 ± 31.1 B	2.6 ± 0.05 B	16.3 ± 0.33 B	8.7 ± 0.06 NS	16.8 ± 0.26 B

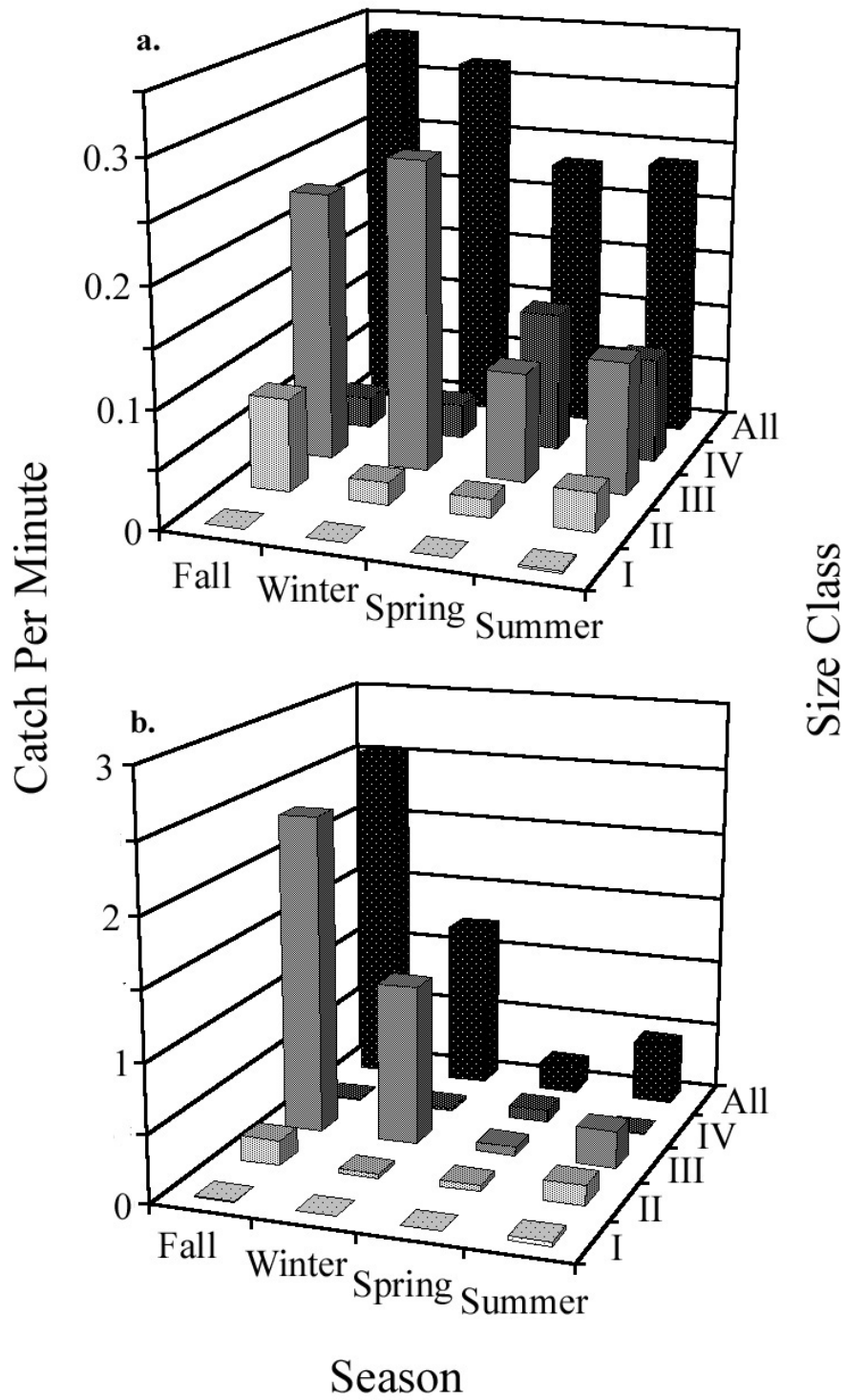


Figure 2.2. Seasonal distribution of total and size-specific catch per minute data for (a) blackcheek tonguefish and (b) offshore tonguefish. Note that the catch per minute scale differs by an order of magnitude between the two graphs.

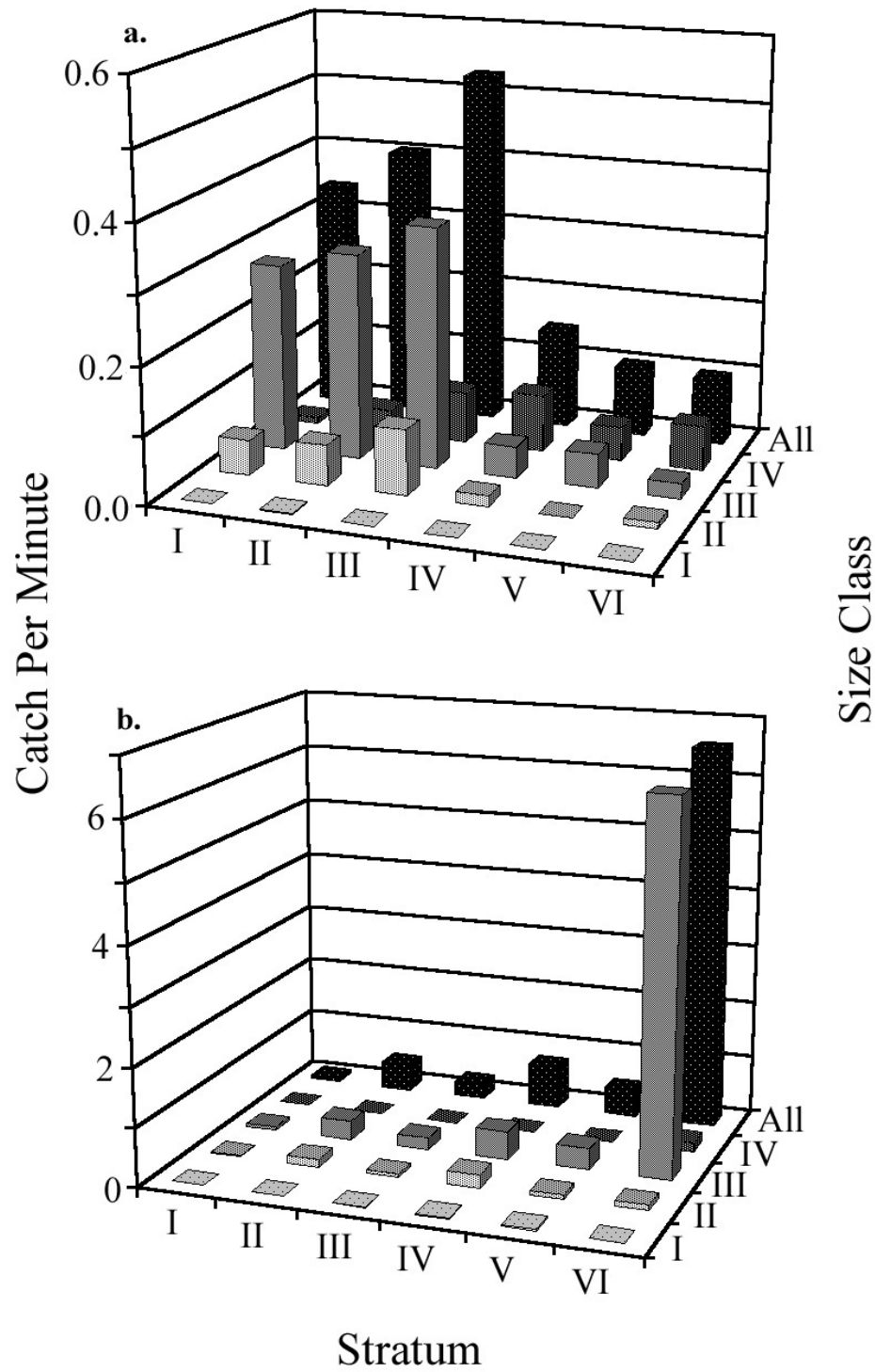


Figure 2.3. Spatial distribution of total and size-specific catch per minute data for (a) blackcheek tonguefish and (b) offshore tonguefish. Note that the catch per minute scale differs by an order of magnitude between the two graphs.

the lowermost stratum, where almost 64 % of collections were made. When spatial and seasonal distributions were considered together, overlap was reduced to 0.30, and when size-class distributions were also considered with season and strata, the overlap between species of comparably sized individuals was reduced to approximately 0.23.

Principal Component Analysis

The principal component analysis (Table 2.5) identified four major axes of environmental variation (eigenvalues > 1). Together, they explained 81 % of the variability of the environmental data. The first principal component had a large positive loading for temperature and a large negative loading for dissolved oxygen, and was interpreted as a seasonal axis. The second principal component had large positive loadings for median depth and distance from shore, and was interpreted as a spatial axis. The third principal component had a large positive loading for substrate, while the fourth principal component had a large positive loading for salinity.

A plot of species and size classes in principal component space identified differences in resource use among groups (Figure 2.4). Environmental conditions used by smaller blackcheek tonguefish were similar, and occurred in cool, highly oxygenated, shallow, near-shore waters of low salinity. The largest blackcheek tonguefish (SC IV) differed from other blackcheek tonguefish (SC II & III) by using warmer waters with lower dissolved oxygen concentration, and were typically found in deeper waters farther from shore. They were also found in higher salinities than were the two smaller size classes. Smaller offshore tonguefish (SC I, II & III) were found in cooler, highly oxygenated waters, and were typically in deeper waters farther from shore than were the largest offshore tonguefish (SC IV). Smaller offshore tonguefish were also found over finer substrates, although the smallest sized offshore tonguefish (SC I) were found in

Table 2.5. Principal component scores for environmental variables in Barataria Bay, Louisiana. Magnitudes and signs of individual component loadings indicate strength and direction of each variables influence on a principal component. The variance explained by the eigenvalue associated with each principal component is expressed as absolute, proportional and cumulative values.

Environmental variable	Principal Component			
	1	2	3	4
Median depth	0.12	0.72	0.21	0.25
Distance from shore	-0.14	0.86	-0.09	-0.00
Substrate code	-0.05	0.05	0.98	0.11
Salinity	-0.05	0.15	0.11	0.97
Dissolved oxygen	-0.84	0.15	-0.01	-0.02
Temperature	0.85	0.10	-0.06	-0.08
Variance explained	1.47	1.32	1.02	1.02
Proportion of variance explained	0.25	0.22	0.17	0.17
Cumulative variance explained	0.25	0.47	0.64	0.81

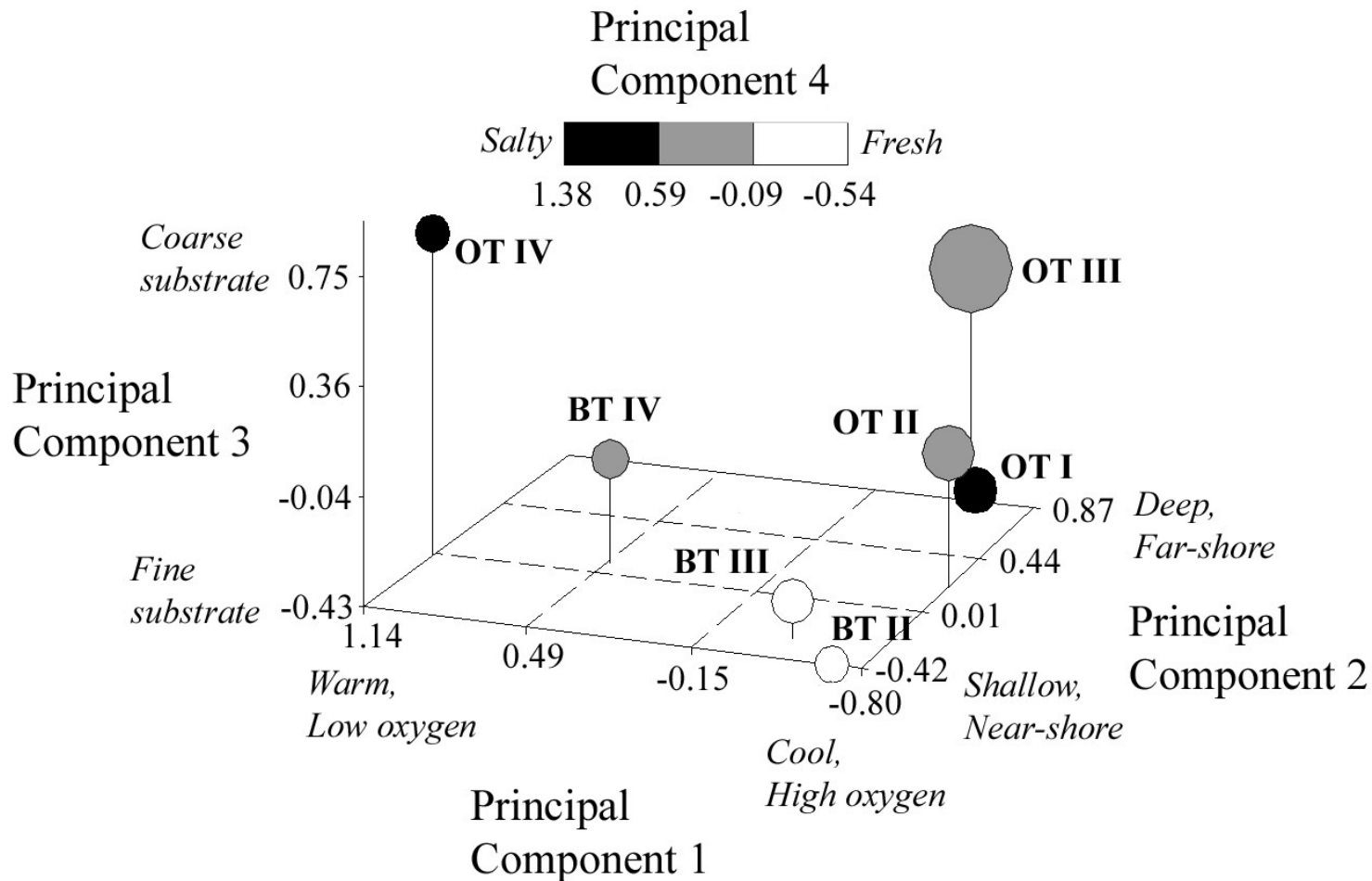


Figure 2.4. Size-specific microhabitat use patterns of blackcheek and offshore tonguefish in four-dimensional principal component space. Balloons indicate location of centroids, with balloon radii representing two standard errors about the mean. Species codes are: BT: blackcheek tonguefish, and OT: offshore tonguefish. Size class intervals are I: ≤ 15 mm; II: > 15 to 30 mm; III: > 30 to 85 mm, and IV: > 85 mm SL.

higher salinities than were those of SC II. Offshore tonguefish in SC III differed primarily from smaller offshore tonguefish (SC I & II) in that they were found on coarser substrates. The largest offshore tonguefish (SC IV) were found in higher salinity waters than were intermediately sized offshore tonguefish (SC II & III), and were found over coarser substrates than offshore tonguefish in SC II. For both species and all size classes plotted in Figure 2.4, the centroids (± 2 SE) are well separated in PCA space, indicating a high degree of segregation between and within species and size classes.

Resource utilization differed substantially among separate life history stages for both tonguefishes. Increasingly larger blackcheek tonguefish typically were collected in deeper water farther from shore, and over coarser substrates than were smaller blackcheek tonguefish. Larger individuals were also collected in warmer, higher salinity waters with a low dissolved oxygen concentration. Ontogenetic patterns in resource use along environmental gradients were not as clearly defined for offshore tonguefish. As sizes increased, individuals were collected in warmer waters with lower dissolved oxygen concentrations and over coarser substrates. No clear ontogenetic trends were evident along the depth/distance-from-shore axis, and the smallest and largest offshore tonguefish used higher salinities than did intermediately sized individuals.

Habitat Suitabilities

Habitat suitability curves for tonguefishes in SC III identified differences between species with respect to resource utilization and selection for several environmental variables. Shallow water sites were most suitable for blackcheek tonguefish, whereas deeper sites were more suitable for offshore tonguefish (Figure 2.5). Near-shore sites were most suitable for blackcheek tonguefish, and sites more distant from shore were more suitable for offshore tonguefish (Figure 2.6). Clay substrates were most suitable for blackcheek tonguefish, whereas

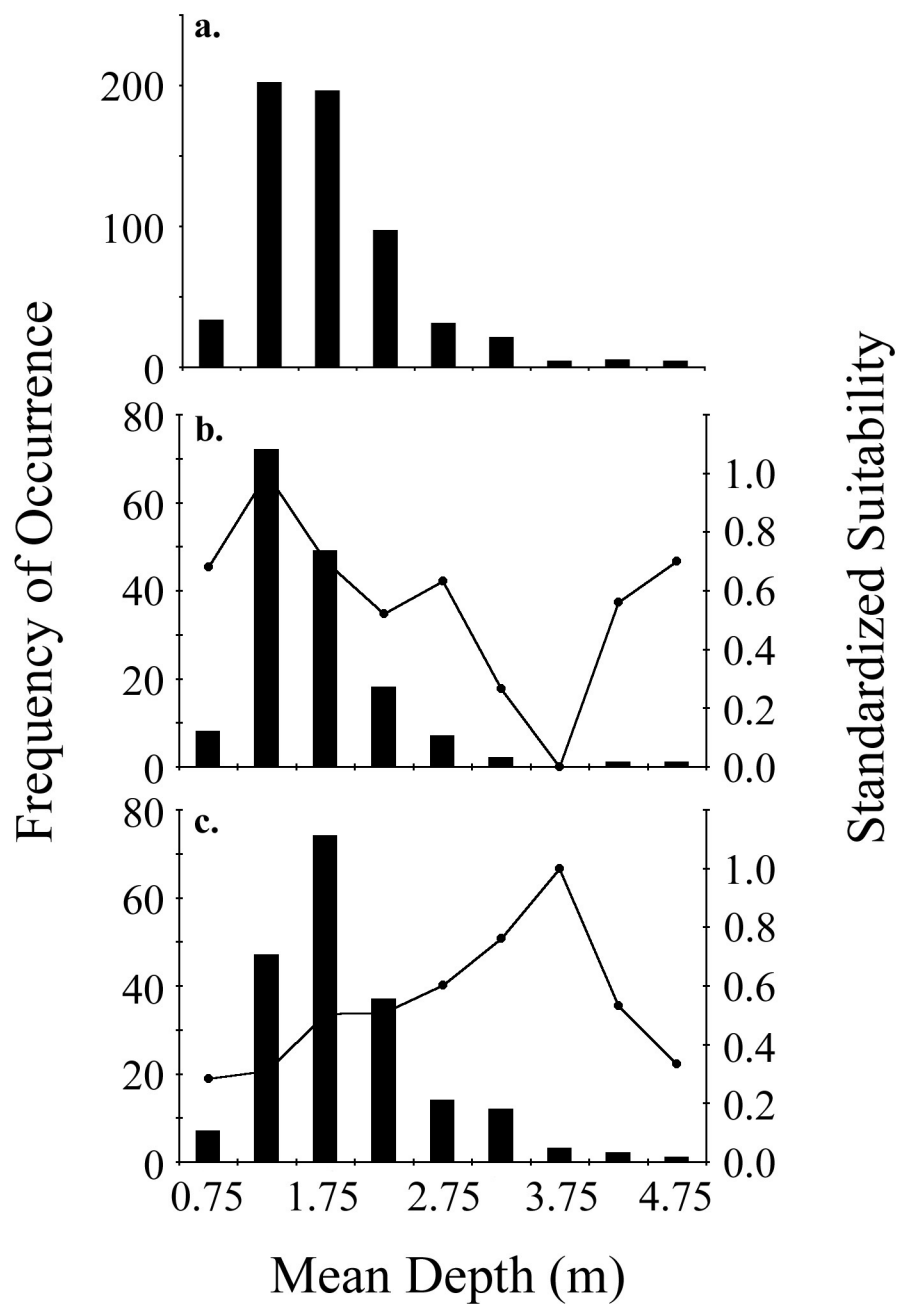


Figure 2.5. Depth availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

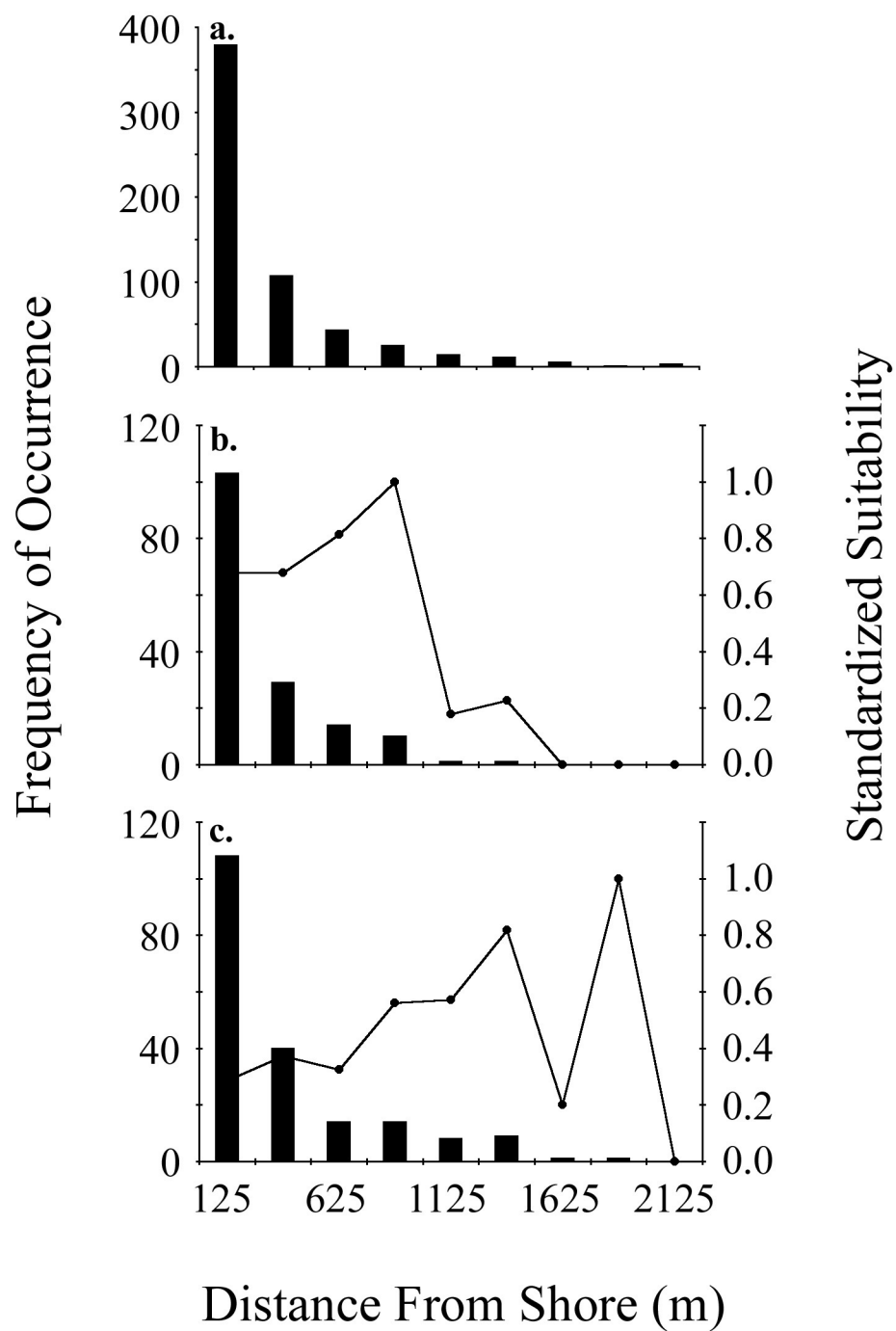


Figure 2.6. Distance availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

sand substrates were most suitable for offshore tonguefish (Figure 2.7). Intermediate salinities were more suitable for blackcheek tonguefish, while highest salinities were most suitable for offshore tonguefish (Figure 2.8). Higher dissolved oxygen concentrations were most suitable for both species (Figure 2.9). Intermediate temperatures were most suitable for both species, although lower temperatures were more suitable for offshore tonguefish than they were for blackcheek tonguefish (Figure 2.10).

Discussion

Several distributional patterns were identified for blackcheek and offshore tonguefish within the Barataria Bay system. Seasonal patterns were similar for both species, but blackcheek tonguefish tended to occupy different spatial regions of the estuary than did offshore tonguefish. Concurrently, significant differences between species were evident with respect to all environmental variables except dissolved oxygen. Differences in mean environmental conditions were also evident among size classes within species, and these differences reflected ontogenetic changes in resource utilization. Ontogenetic patterns of resource utilization coincide with spatial patterns of environmental variability for all variables except temperature and dissolved oxygen. Ontogenetic shifts in temperature and dissolved oxygen usage did not parallel seasonal or spatial changes, and may reflect actual differences in environmental selection.

Blackcheek and offshore tonguefish did not exhibit patterns of seasonal segregation, but segregation along a spatial gradient was evident. The two species overlapped broadly on a seasonal basis (Schoener's index of overlap = 0.78), owing to the fact that both species occupied the estuary throughout the year. Newly settled juveniles of both species began appearing in samples during summer following a late spring – early summer spawning period that coincides with peaks in thermal maxima (Olney and Grant 1976; Munroe 1998). This closely parallels

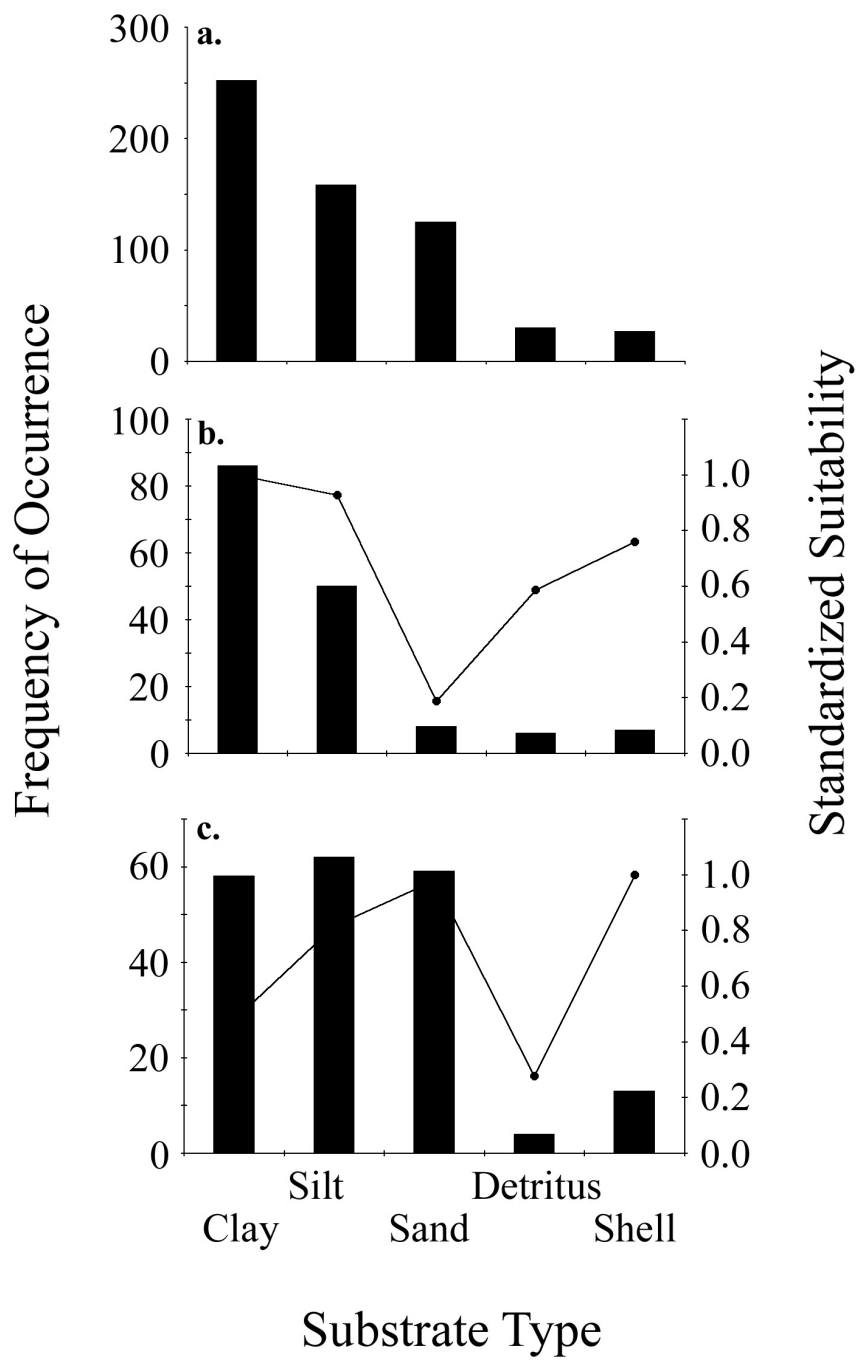


Figure 2.7. Substrate availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

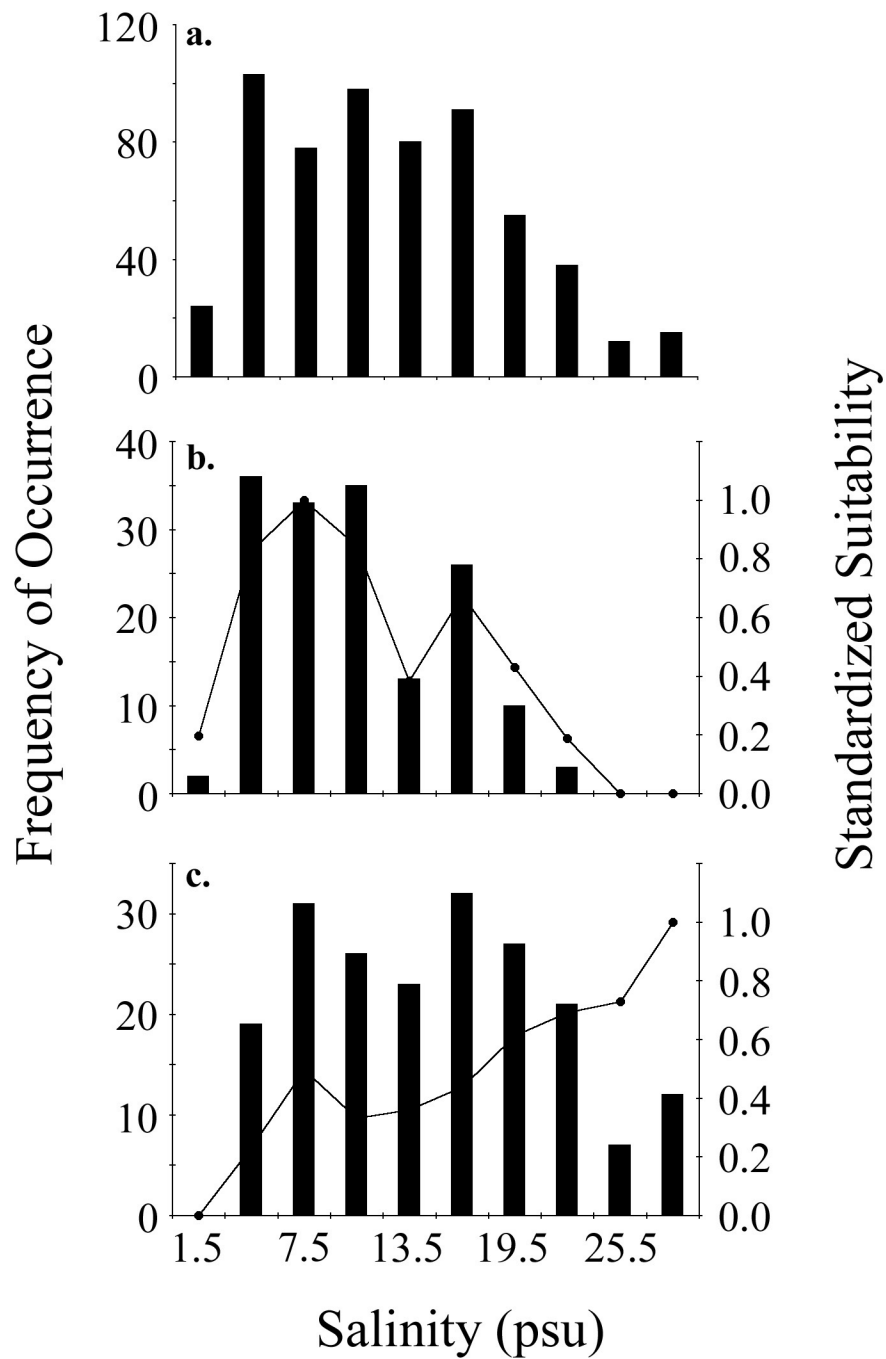


Figure 2.8. Salinity availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

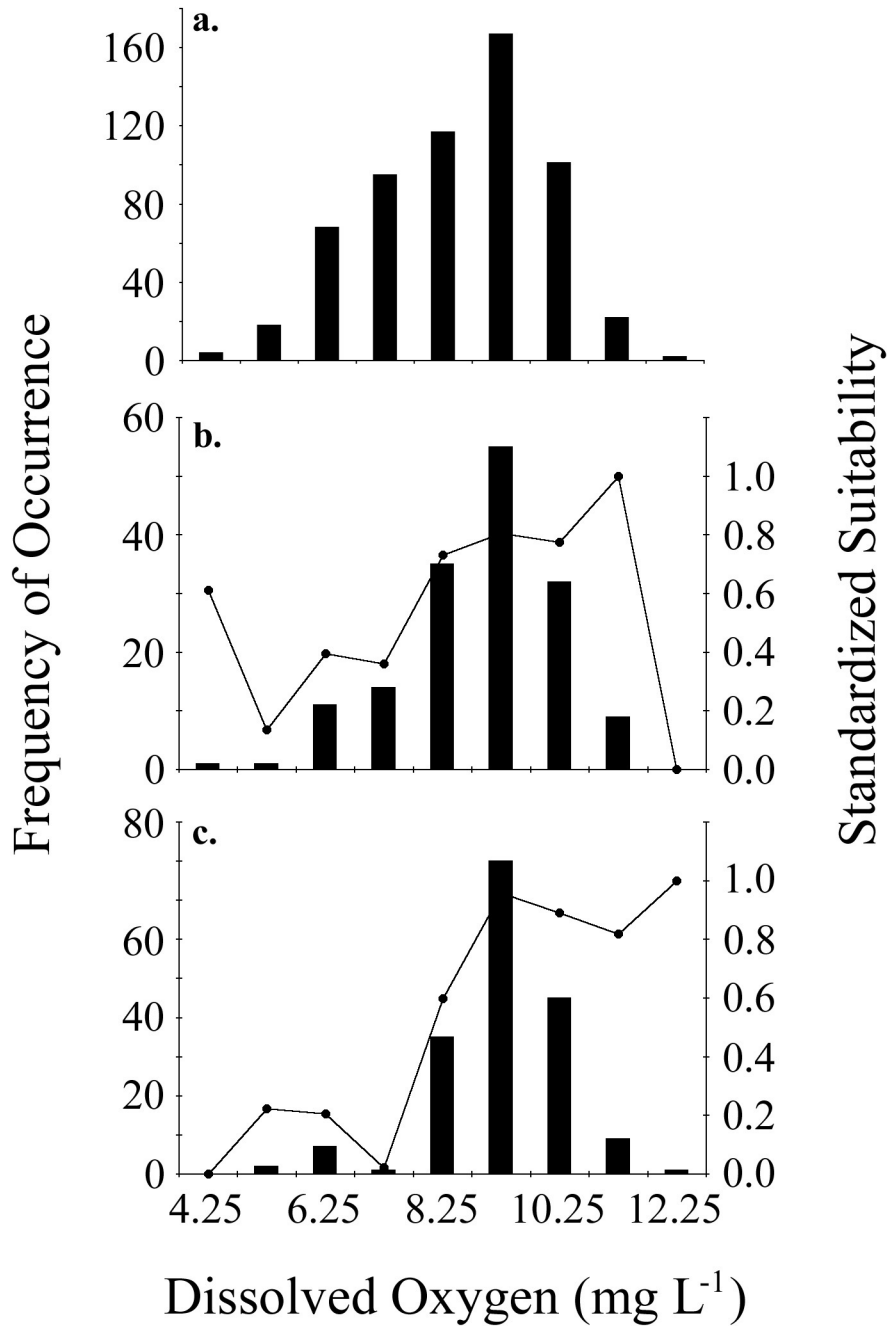


Figure 2.9. Dissolved oxygen availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

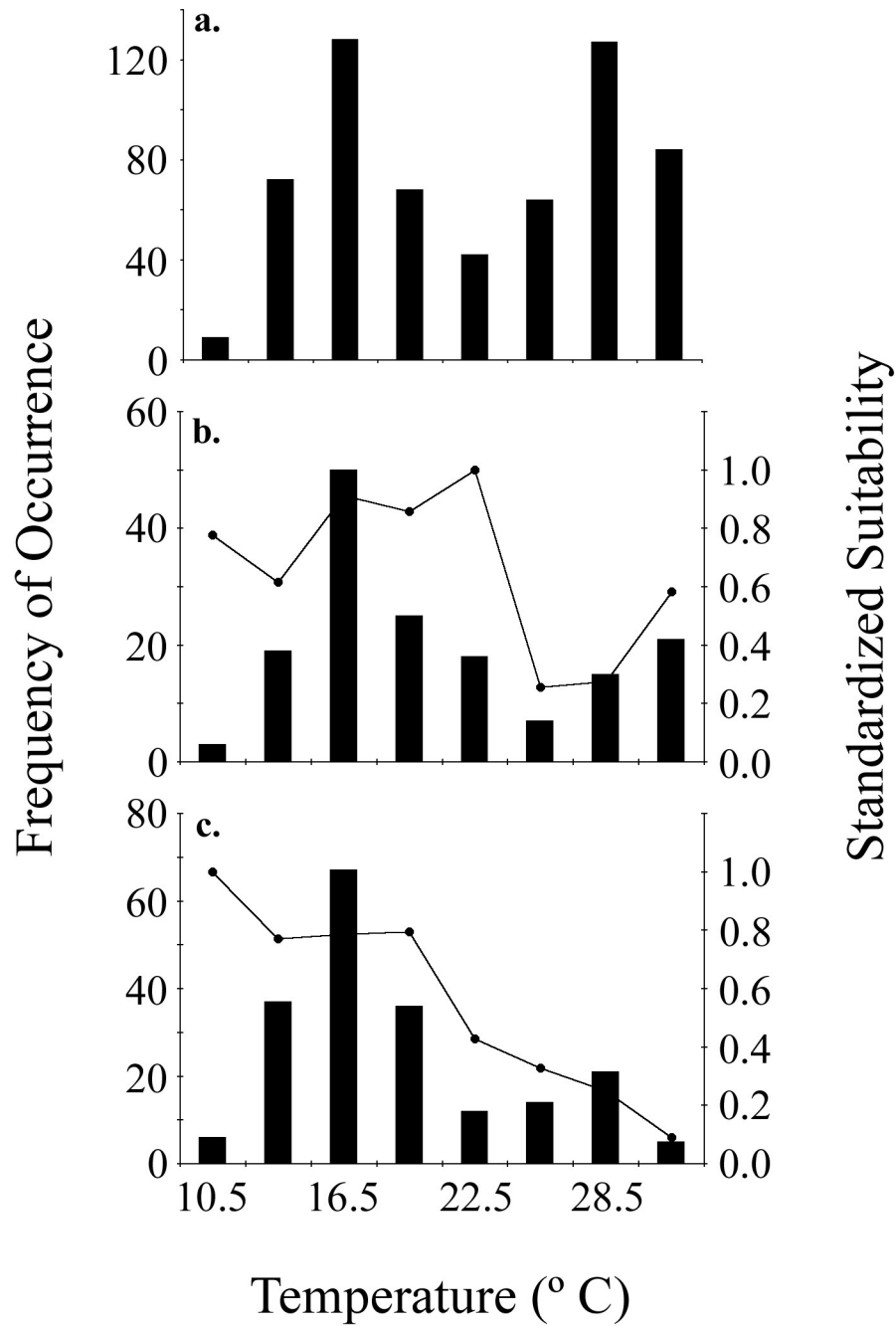


Figure 2.10. Temperature availability (a) and microhabitat suitability curves for size class III blackcheek (b) and offshore (c) tonguefish. Histograms illustrate frequency of occurrence, and curves illustrate standardized suitabilities.

settlement periods of blackcheek tonguefish in Georgia, USA (Reichert and van der Veer 1991). Seasonal changes in abundances were similar for both species, with peak abundances occurring in fall and winter months followed by a decrease in abundance in spring. The seasonally concordant utilization of inshore waters by these congeneric tonguefishes is not surprising, since temporal segregation is generally more important among species that are not closely related (Ross 1986). There was, however, evidence of spatial segregation between species (Schoener's index of overlap = 0.34). Most blackcheek tonguefish were collected in the uppermost strata (I – III), whereas offshore tonguefish were most abundant in the lowermost stratum (VI). Spatial differences in distribution may have contributed to differences between species with respect to resource use. Offshore tonguefish occupied deeper waters farther from shore than did blackcheek tonguefish, and used warmer, higher salinity waters over coarser substrates. Microhabitat suitability curves identified differences between species with respect to resource use along all measured environmental gradients except dissolved oxygen (Figures 2.5 – 2.10). All of these differences paralleled spatial differences in environmental variation (Table 2.2), and may be due to bathymetric preferences of each species. Blackcheek tonguefish are primarily a shallow-water species with most adults occurring in depths ranging from 1 to 30 m, whereas adult offshore tonguefish typically occupy deeper waters, occurring most commonly in depths from 11 to 45 m (Munroe 1998). It is interesting that differential habitat selection was manifested in each species at relatively small sizes and apparently maintained throughout the rest of their life histories.

Both species demonstrated ontogenetic shifts in environmental resource utilization. Shifts along environmental gradients were most clearly defined for blackcheek tonguefish. As size increased, a clear transition developed towards deeper, high salinity waters farther from

shore for both species. Additionally, larger blackcheek tonguefish also moved into warmer, low dissolved oxygen concentration waters over coarser substrates. Only one newly settled (SC I) blackcheek tonguefish was collected in the study, and was excluded from this analysis; however, individuals of this size class were collected previously in Barataria Bay along the marsh edge (Baltz et al. 1993). Settling blackcheek tonguefish may prefer shallow, inshore areas that are outside the range of conditions sampled via trawling. Reichert and van der Veer (1991) found that blackcheek tonguefish settlement within a tidal creek typically occurs in shallow areas over muddy substrates. Size-related patterns in resource use were less clear for offshore tonguefish. Excluding the first size class of offshore tonguefish, they showed transitions similar to those seen in blackcheek tonguefish for all environmental variables, except there was not a clear movement to deeper waters farther from shore. The smallest offshore tonguefish did not follow these trends in that they were collected in warmer, higher salinity waters than were intermediately sized (SC II & III) individuals. These smallest individuals may have been collected shortly after settlement and while still moving into the estuary during summer months in lower strata. Differences between juvenile and adult size classes for both species were most likely due to offshore movement as individuals approach maturity and recruit into adult populations.

Utilization of temperature and dissolved oxygen gradients were not concordant with temporal or spatial patterns of environmental variability. It is often difficult to determine whether differences in resource use among size classes are due to actual ontogenetic shifts in resource requirements or due to changes in environmental conditions (Miller 1979). I can begin to unravel ontogeny and phenology by comparing seasonal and spatial trends in environmental variability with similar size-specific distributional trends in tonguefishes. If size-specific patterns of resource use in tonguefishes are different from observed spatial and temporal

environmental variability then ontogeny should be important. Ontogenetic patterns in resource use did not correspond well to observed seasonal changes in environmental variation from the time of settlement (summer) to disappearance from the estuary (spring/summer) for either species. Utilization of depth, distance from shore, salinity and substrate gradients did correspond with spatial environmental gradients, although temperature and dissolved oxygen did not. Ontogenetic changes in temperature and dissolved oxygen concentration appear to be important to these tonguefishes, and temperature is probably the most important variable, whereas trends in dissolved oxygen usage are most likely due to the inverse relationship between temperature and dissolved oxygen. Temperature is an important ecological gradient along which competition may exist (Magnuson et al. 1979; Baltz et al. 1982), and separation of species and/or size classes within a species along temperature gradients may be a means of reducing interspecific or intraspecific competition (Connell 1980). Changes in temperature also serve as cues for spawning and migratory activities in marine fishes (Gunter 1938, Gunter 1945, Miller 1965, Olney & Grant 1976). Larger tonguefishes virtually disappeared from the study area during warm, summer months. Low abundances of larger tonguefishes in colder months indicate that adults were not returning to the estuary, and so were most likely moving offshore to recruit into adult populations rather than avoiding warmer water temperatures (Gunter 1945, Miller 1965).

Several additional factors not addressed in the present study may also be important in determining the distribution of tonguefishes in coastal Louisiana. One such factor thought to be important to estuarine-dependent fishes is turbidity (Blaber and Blaber 1980; Chesney et al. 2000). Although previous research indicated that turbidity was not a major gradient of environmental variation in the Barataria Bay system (Baltz et al. 1993), turbidity is often an influential factor in determining distributions of estuarine-dependent fishes by reducing potential

predation pressures. Highly turbid waters provide cover for fishes by limiting the reactive distance of potential predators (Cyrus and Blaber 1987), so the highly turbid waters of coastal Louisiana should enhance protection to juvenile tonguefishes from predators.

Natural and anthropogenic factors, such as trawling and hypoxia, may also affect the distribution and abundances of tonguefishes in coastal Louisiana. While fisheries in Louisiana do not explicitly target tonguefishes, they are commonly caught as bycatch in the trawl fishery (Baltz and Chesney 1996). Significant changes to the inshore demersal trawl assemblages have been identified (Chesney et al. 2000), and some of these changes are most likely attributable to the effects of trawling. Blackcheek tonguefish were among the most commonly collected species in the Louisiana Department of Wildlife and Fisheries shrimp sampling program between 1972 and 1992 (Baltz and Chesney 1996), so bycatch mortalities for tonguefishes are probably high. In addition to actively removing individuals as bycatch, the trawl fishery disturbs the substrate within the estuary, which may reduce the suitability of habitat available for demersal fishes and cause changes in prey assemblages. The lowest abundances of blackcheek and offshore tonguefish occurred during periods of heightened trawling activity in coastal Louisiana, suggesting that trawling-related mortalities are important factors in their population dynamics.

Hypoxia may also influence the distribution of demersal fishes, although its direct effects are not easily quantified (Chesney and Baltz 2001). The presence of hypoxia is thought to affect demersal fishes more strongly than pelagic fishes, which can escape hypoxic waters by altering their vertical position in the water column. Offshore tonguefish had not been identified as a common species in inshore Louisiana waters until recently (Munroe et al. 2000), perhaps due to misidentification of offshore tonguefish as blackcheek tonguefish (Munroe 1998; Munroe et al. 2000). Another possibility is that the persistent and increasing presence of hypoxic waters in

coastal Louisiana may have altered the spatial distribution of offshore tonguefish populations, favoring the inshore distribution of juveniles.

Although I have unraveled evidence of resource partitioning among species and size classes for two congeneric tonguefishes in coastal Louisiana along environmental gradients, the importance of feeding cannot be ignored (Ross 1986). Partitioning of food resources is often the most important factor separating ecologically similar species, and has generally been found to be more prevalent than the combined effects of habitat and temporal differences in interspecific partitioning of resources. Food resource distribution may also influence microhabitat occurrence of non-interacting species. Munroe (1998) noted that many tonguefishes are found over specific substrates. These patterns may be due to: differential survival, active substrate selection by the fishes, and passive substrate selection in response to active substrate selection by their invertebrate prey. The relative influence of microhabitat selection and feeding and their effect on growth and potential recruitment has previously been identified for two estuarine-dependent fishes in coastal Louisiana (Baltz et al. 1998), so the importance of food resources especially as these relate to differences in microhabitat selection between blackcheek and offshore tonguefish warrants further study.

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CHAPTER III.

UTILIZATION OF MARSH-EDGE HABITAT BY TWO SYMPATRIC TONGUEFISHES (*SYMPHURUS*: CYNOGLOSSIDAE) IN COASTAL LOUISIANA

Introduction

Numerous commercially and recreationally important fishes and macroinvertebrates utilize marsh-edge habitat as a nursery ground during their early life histories (Weinstein 1979; Rakocinski et al. 1992; Baltz et al. 1993; Peterson and Turner 1994). The marsh-edge ecotone functions as an avenue by which organisms can move onto the inundated marsh during rising tides and vacate the marsh during falling tides. Juvenile fishes and macroinvertebrates occupying this habitat may benefit from increased food availability, decreased risk of predation or both, although the relative importance of these two factors is not yet clear (Boesch and Turner 1984).

Given the importance of the edge ecotone to many estuarine-dependent species, an increase in the amount of available edge habitat may generally result in increased productivity (Browder et al. 1985). The conversion of intact marsh into open water habitat is a natural process of the destructional phase of the deltaic cycle beginning at the onset of delta abandonment (Coleman et al. 1998). During the initial period of marsh disintegration, the amount of available edge habitat increases as intact marsh is lost, which may potentially result in increased nekton productivity among species utilizing the marsh edge (Browder et al. 1985). If this is a benefit, it may only be temporary; once marsh area falls below a critical level any additional loss of marsh will result in a loss of edge. With current wetland loss rates estimated at $0.86\% \text{ yr}^{-1}$ (Turner 1997), it is important to determine the relative value of edge habitat to estuarine-dependent nekton prior to substantial decreases in the availability of marsh-edge habitat.

This study re-examines the utilization of habitat along the marsh edge by two estuarine-dependent tonguefishes that are known to commonly occur in inshore waters throughout Louisiana: the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*). These tonguefishes represent ideal candidates to examine interspecific relationships between closely related species in coastal Louisiana due to their frequent co-occurrence as well as their year-round persistence in the area (Allen and Baltz 1997). Numerous species of tonguefish utilize inshore estuarine habitat during some part of their life history (Munroe 1998). In coastal Louisiana, both blackcheek and offshore tonguefish are transients, with individuals moving as larvae into the estuary where they settle and occupy this highly productive nursery habitat through early adulthood (Baltz et al. 1993; Allen and Baltz 1997). Individuals spend the better part of a year within the estuary, migrating into deeper coastal waters as they approach maturity and recruit into adult populations.

Potential misidentifications may confound current understanding of the ecological relationships among tonguefishes in coastal Louisiana (Munroe et al. 2000). Until recently, the blackcheek tonguefish was regarded as the only common tonguefish species in inshore Louisiana waters. In fact, offshore tonguefish also commonly occur inshore, and are numerically dominant to blackcheek tonguefish in some areas of Louisiana (Allen and Baltz 1997). The two species are morphologically similar, but can be distinguished by certain physical characteristics (Munroe 1998; Munroe et al. 2000). Blackcheek tonguefish can readily be identified by few (5 – 7) broad, indistinct bands of pigmentation on the eyed side, pigmentation along the dorsal and ventral margins of the body on the blind side, 10 caudal fin rays, and dark pigmentation in the cheek area. In contrast, offshore tonguefish typically possess more (10-13) narrower, distinct bands of pigmentation on the eyed side, lack pigmentation along the dorsal and ventral margins of the

blind side, possess 12 caudal fin rays, and lack the dark pigmentation in the cheek area. Correct identification is generally possible using pigmentation patterns only, although examination of caudal fin rays may occasionally be required.

Resource utilization at the microhabitat level (Baltz 1990) for tonguefishes along the marsh edge was characterized by a drop-sampling approach (Zimmerman et al. 1984). I re-identified all tonguefishes collected during a four-year study of the utilization of marsh-edge habitat by fishes in Barataria Bay, Louisiana (Baltz et al. 1993). I also re-analyzed tonguefishes collected during a complimentary beam-trawl study (Allen and Baltz 1997). These two species occupy sites across depth and distance gradients that cannot effectively be sampled by a single quantitative gear type, so it is necessary to conduct analyses from separate data sets to fully describe population responses along these gradients. The comparison of patterns of resource utilization along the marsh edge allowed for the examination of three main questions: (1) Do blackcheek and offshore tonguefish differ with respect to utilization of marsh-edge habitat? (2) Do either blackcheek or offshore tonguefish express ontogenetic shifts in resource utilization along the marsh edge? (3) Do tonguefish densities along the marsh edge obtained by drop sampling coincide with patterns along depth and distance from shore gradients obtained by beam trawling? Based on my re-evaluation of both data sets, the marsh edge appears to be important for juvenile blackcheek tonguefish; however, juvenile offshore tonguefish do not depend heavily on the marsh edge and only rarely ($< 5\%$ of the population) occur in water less than a meter deep.

Materials and Methods

Study Area

The Barataria Basin is the first major estuary west of the mouth of the Mississippi River (Figure 3.1). Within the basin, sampling sites included the saltmarsh portions within Barataria

and Caminada bays. Located between the natural levees of the Mississippi River and the abandoned Bayou Lafourche distributary, the basin is approximately 110 km long, and is 50 km at its greatest width where it opens into the Gulf of Mexico (Conner and Day 1987). Influx of riverine water and suspended sediment into the basin from overbank flooding has been reduced since the closure of the Bayou Lafourche-Mississippi River connection in 1902 and the construction of the current river levee system in the 1930's and 40's. As a result, precipitation has been the primary source of freshwater input into the system, averaging approximately 160 cm per year (Conner and Day 1987). Since these alterations to the hydrology of the region, land building processes have been reduced while the area has continually been reworked by coastal erosion and subsidence, resulting in significant conversion of emergent marsh into open water over the past several decades (Baumann 1987). The recent completion of the Davis Pond freshwater diversion is intended to provide input of freshwater and suspended sediments in an attempt to reduce or reverse recent trends of habitat disintegration (LDNR 2002).

Field Methods: Drop Sampling

Tonguefishes were quantitatively sampled along two transects in the Barataria Basin running from the Gulf of Mexico inland for 25 km (Figure 3.1). The western transect was located within Caminada Bay, covering fairly intact marsh habitat intersected with areas of open water. The eastern transect was located within Barataria Bay, and covered areas rapidly undergoing submergence and dominated by open water habitat. Sampling effort was stratified among upper, middle, and lower reaches within each transect to characterize response along a salinity gradient.

Drop sampling (Zimmerman et al. 1984) was used to collect fishes along the marsh edge. A total of 1336 samples were collected during monthly sampling that began in October 1987 and

extended through November 1991. Initial samples were collected using a 0.5 m² plexiglass box, and samples from August 1988 onward were collected using a cylindrical fiberglass drop sampler measuring 1.188 m² in area. Comparisons of samples collected with the two devices indicated an overlap of the 95% confidence intervals of mean fish densities, so both devices were sampling the same assemblage, and were combined for statistical analyses. The drop sampler was suspended 3 m from the bow of a small boat and approximately 0.5 m above the surface of the water. A release mechanism was incorporated into the design, allowing for the dropping of the sampler at a specific site. The use of a drop sampler allowed us to collect all sizes of fishes and macroinvertebrates, and near-complete sampling allowed for accurate estimation of densities. Additionally, since the sampling area was small, microhabitat variables were homogenous throughout the sample.

During each sampling trip, samples were taken at all three reaches within a given transect (Barataria or Caminada bay), and transects were alternated between sampling trips. Several environmental variables were measured at each sampling location, including minimum distance to the marsh edge (m), and minimum and maximum depths (cm). Sample depth was then calculated as the midpoint between minimum and maximum depth. Dominant substrate type was categorized and coded on an ordinal scale of particle size as (1) clay and silt, (2) sand, (3) organic detritus, and (4) shell or shell fragments. Dominant and emergent grasses were identified when present, and a stem count was also made. Additional environmental variables measured included salinity (ppt), water temperature (° C), dissolved oxygen (DO mg l⁻¹), current velocity (cm s⁻¹), and turbidity (NTU). YSI model 33 S-C-T and model 57 oxygen meters, an AO temperature compensated refractometer, a Montedoroe-Whitney PVM-2 current meter, and a Monitek model 21 PE portable nephelometer were used to make environmental measurements.

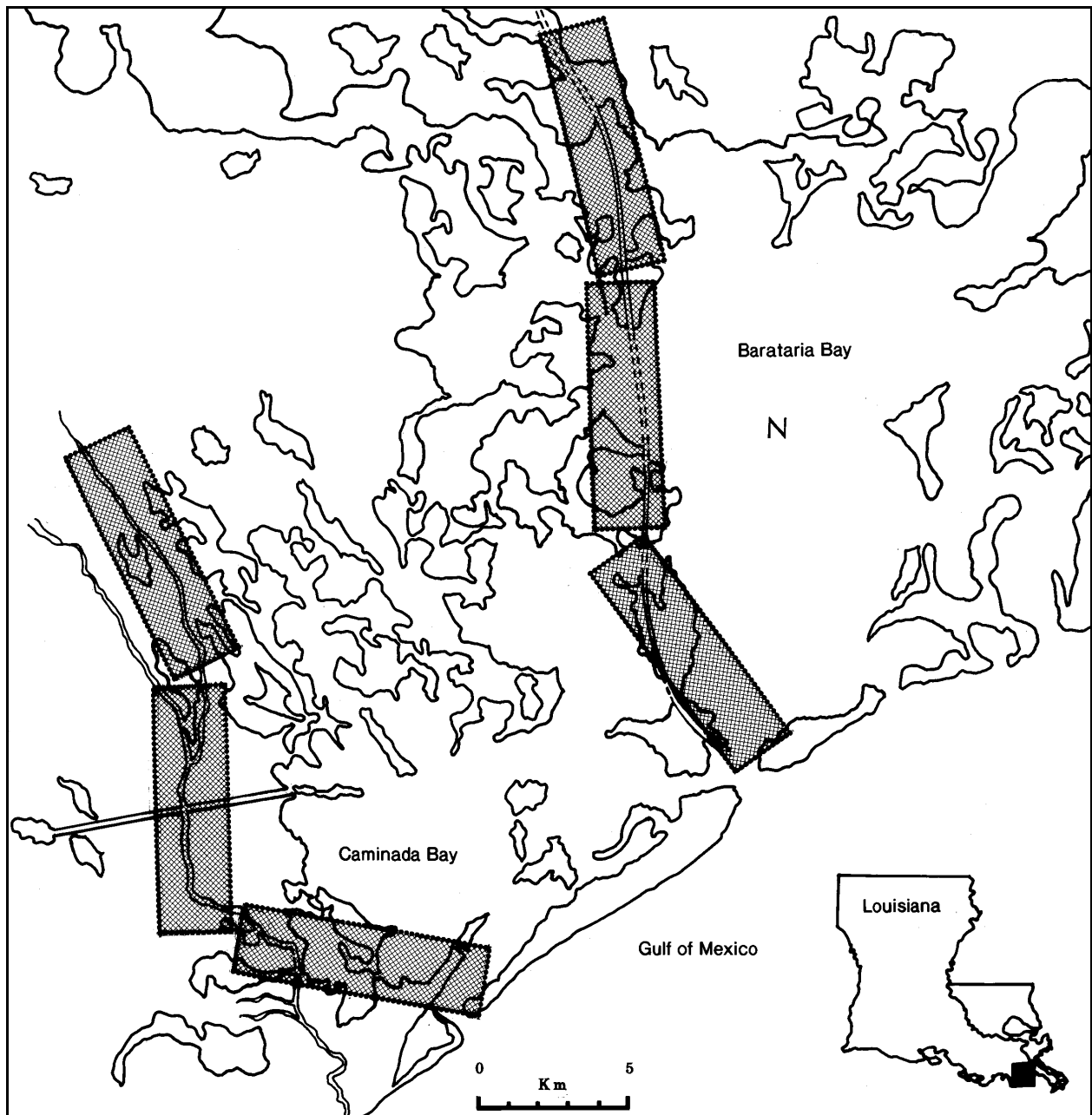


Figure 3.1. Drop-sampling study site west of the Mississippi River deltaic system, with sampling locations within the Barataria-Caminada Bay System highlighted by gray boxes.

All fishes and macroinvertebrates collected were preserved in formalin. Identification of all tonguefishes collected were identified in the laboratory using keys and descriptions by Hoese & Moore (1977) and Munroe (1998), and were measured to the nearest mm standard length (SL).

Field Methods: Beam Trawling

In a complimentary study, tonguefishes were quantitatively collected in Barataria Bay from September 1992 to August 1994 using a 1-m beam trawl with a uniform mesh size of 5 mm (Kuipers 1975). Kuiper's design was modified by the addition of a pair of polyvinyl chloride skids (10 x 50 cm) to facilitate sampling over fine substrates. Sampling effort was divided into six strata ranging from the near shore zone in the Gulf of Mexico to the brackish marsh some 30 km inland (Figure 3.2). Within each stratum a randomized location was selected each month to sample fishes associated with a variety of substrates and environmental conditions.

Sampling at a location involved making a series of five tows at sites parallel to the shoreline, typically the marsh edge. Each subsequent tow was farther from shore and generally in deeper water, which allowed me to compare the response of blackcheek and offshore tonguefish populations along depth and distance gradients. Tow duration at each site was typically 2 min (range 1-2 min.), and tow direction was parallel to the shoreline to minimize environmental heterogeneity within samples. Environmental variables were measured as previously reported for drop sampling, except that turbidities, water velocities, and stem densities were not determined.

Trawl samples were sorted in the field to separate all fishes and macroinvertebrates, and were previously reported by Allen and Baltz (1997) and Jones et al. (2002). Specimens were preserved in 95% ethanol. All tonguefishes were identified in the laboratory using keys and descriptions by Hoese & Moore (1977) and Munroe (1998).

Analytical Methods

Multivariate analysis of variance (MANOVA), using general linear models and the least-square-mean method (SAS Institute 1996), was used to compare means of environmental variables among seasons. Transformed environmental variables ($\log_{10} x + 1$) were used when the normality of the residuals was improved. When normality of the residuals was unattainable, careful visual examination of residual plots and residual biplots was used to ascertain the degree of violation of the normality assumption and to confirm variance homogeneity. MANOVA is relatively robust with respect to moderate violations of the assumption of normality (Johnson and Field 1993), and no problems with heteroscedasticity were detected.

A MANOVA was fit to compare resource use by tonguefish species and size classes along the marsh edge. Individual fish were assigned to separate size classes since species level comparisons are often inadequate (Livingston 1988). Size classes (SC) were broken down as: SC I ≤ 15 mm, SC II > 15 to 30 mm, SC III > 30 to 85 mm, and SC IV > 85 mm SL. The first three size classes represented stages in the development of juvenile tonguefishes, while the fourth size class represented individuals nearing maturity (Terwilliger and Munroe 1999). Each sample was treated as an independent observation to eliminate pseudoreplication (Hurlbert 1984). *A posteriori* testing of means found to be significantly different among species and size classes was conducted using Tukey's adjustment for multiple comparisons to control the overall alpha level. Adequacy of the model was examined by univariate and biplot analysis of the residuals.

Comparisons of blackcheek and offshore tonguefish densities were made along depth and distance-from-shore gradients by including both drop sampler and beam-trawl samples. Tonguefish densities were calculated as the number of individuals m^{-2} at the species level.

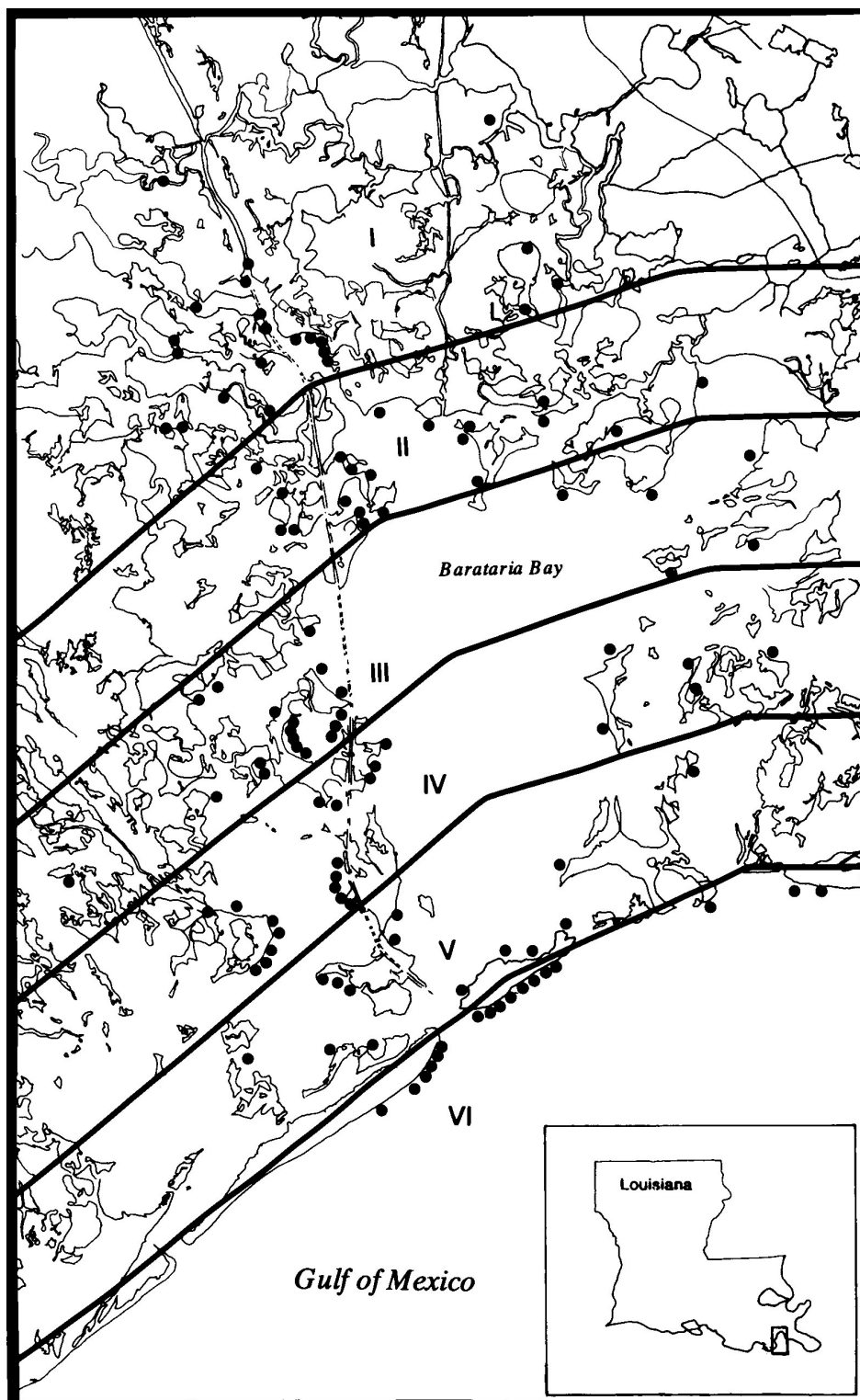


Figure 3.2. The Barataria Bay study site, with beam-trawling locations identified by black dots.

Densities from the drop sampling study were grouped due to the narrow range of depths and distances sampled; all depths were less than 1 m and all distances were less than 10 m. Densities from the beam-trawl study were calculated in 1 m intervals along the depth gradient and in 250 m intervals along the distance gradient.

Variation in microhabitat use by each species and size class of tonguefish occurring in the drop-sampler study was examined in a principal component analysis (PCA) with varimax rotation of nine environmental variables (temperature, salinity, dissolved oxygen, median depth, distance from shore, substrate, stem density, water velocity and turbidity) based on the correlation matrix. Environmental variables from 1194 samples without missing data were used to construct variable loadings and generate principal component scores for each sample. Principal components scores for each sample were then used to construct species and size class centroids, which were then plotted in three-dimensional PCA space. Densities of the species and size classes were used to weight the calculation of centroids, and confidence intervals (± 2 SE) around the centroids were estimated as the mean standard error on three PCA axes.

Results

MANOVA of the drop-sampling data identified significant seasonal differences in environmental variability along the marsh edge ($F = 82.62$, $p < 0.0001$). Seasonal differences were detected with respect to all environmental variables examined except substrate (Table 3.1). Mean depth was lowest during winter months, and distance from shore was highest during winter months. The lowest salinities occurred during spring, and salinity was highest during the fall. Temperatures were highest during summer and lowest during winter; conversely dissolved oxygen concentrations were highest during winter and lowest during summer and fall. Turbidities were highest during spring and summer months and lower during winter. Current

velocities were higher in winter than in fall, and stem densities were lower during winter months than throughout the remainder of the year.

A total of 537 tonguefishes were collected during the drop-sampling study, including 365 that have been analyzed previously (Baltz et al. 1993). Blackcheek tonguefish were the numerically dominant species collected by drop sampling. A total of 534 blackcheek tonguefish compared to only 3 offshore tonguefish were collected during four years (Table 3.2); all tonguefish analyzed by Baltz et al. (1993) were correctly reported as blackcheek tonguefish. Blackcheek tonguefish were present in the sampling area throughout the year, although numbers caught were highest during summer and fall. Older juveniles (SC II and III) were the dominant size classes. Post-settlement juveniles (SC I) were caught on occasion, and adult tonguefishes (SC IV) were relatively rare. Juveniles of SC II and III were collected in the highest densities (Figure 3.3). Blackcheek tonguefish in SC I were rare in winter, but were found in increasing densities during spring, summer, and fall months. Size class II individuals were found in highest densities during summer and fall, and SC III individuals were found in highest densities during fall and winter. Densities of adults (SC IV) were low in all seasons. All three offshore tonguefish collected were of SC II, and were collected during summer and fall months (Table 3.2).

A one-way MANOVA identified significant differences among species and life history stages collected via drop-sampling with respect to resource utilization at the microhabitat level ($F = 2.16, p < 0.0001$). Differences were detected for four environmental variables: temperature, distance from shore, velocity, and stem density (Table 3.3). Blackcheek tonguefish of SC I typically occupied sites farther from the marsh edge than did individuals of SC II. Juvenile blackcheek tonguefish of SC III were found in cooler waters than were smaller juveniles, and

Table 3.1. Seasonal patterns in resource availability estimated by least-square means (\pm SE) for nine environmental variables. Significant differences ($p \leq 0.05$) among seasons are indicated by different letters reading horizontally (NS indicates that differences were not significant).

Variable				
Season	Winter	Spring	Summer	Fall
Mean Depth (cm)	34.3 \pm 1.21 A	42.2 \pm 0.84 B	42.9 \pm 0.75 B	40.0 \pm 0.86 B
Distance from shore (m)	2.2 \pm 0.16 C	1.3 \pm 0.11 A	1.6 \pm 0.10 B	1.7 \pm 0.12 B
Substrate	1.7 \pm 0.07 NS	1.9 \pm 0.05 NS	1.9 \pm 0.04 NS	1.9 \pm 0.05 NS
Salinity (ppt)	16.0 \pm 0.45 B	14.3 \pm 0.31 A	15.8 \pm 0.28 B	20.3 \pm 0.32 C
DO (mg l ⁻¹)	9.8 \pm 0.12 C	8.0 \pm 0.08 B	6.9 \pm 0.07 A	7.1 \pm 0.08 A
Temperature (°C)	15.0 \pm 0.25 A	24.4 \pm 0.18 B	29.9 \pm 0.16 D	25.5 \pm 0.18 C
Turbidity (NTU)	12.9 \pm 1.08 A	20.4 \pm 0.75 C	17.6 \pm 0.67 C	14.4 \pm 0.77 B
Velocity (cm sec ⁻¹)	3.2 \pm 0.25 A	2.9 \pm 0.17 AB	2.8 \pm 0.15 AB	2.5 \pm 0.18 B
Stems m ⁻²	1.0 \pm 2.42 A	13.9 \pm 1.68 B	8.5 \pm 1.49 B	12.1 \pm 1.72 B
Number of samples (N)	172	349	458	357

Table 3.2. Summary of tonguefishes collected by drop-sampling along the marsh edge by taxon, size class, and season.

Species and size class	Season				
	Winter	Spring	Summer	Fall	Total
Blackcheek tonguefish					
≤ 15 mm	0	7	18	21	46
$> 15 \leq 30$ mm	15	5	152	116	288
$> 30 \leq 85$ mm	28	33	49	82	192
> 85 mm	0	1	4	3	8
Total	43	46	223	222	534
Offshore tonguefish					
$> 15 \leq 30$ mm	0	0	1	2	3

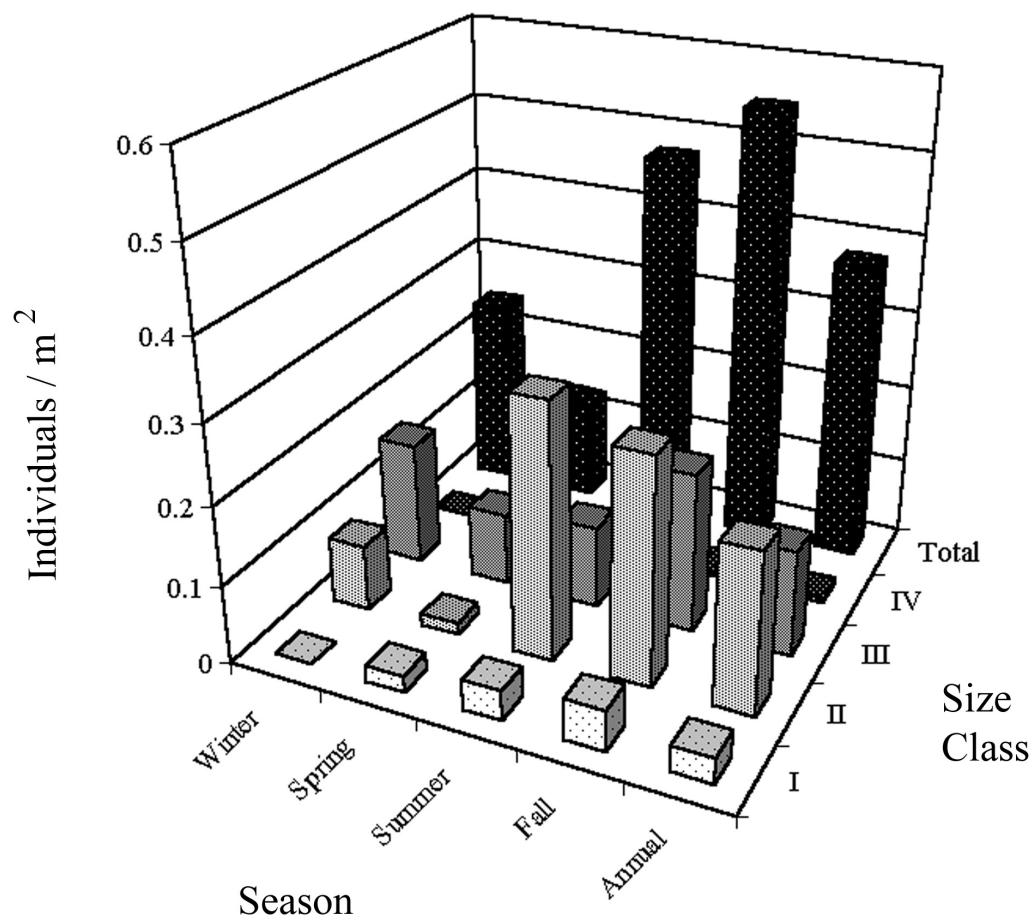


Figure 3.3. Seasonal size specific densities of blackcheek tonguefish along the marsh edge.

Table 3.3. Least-square means (\pm SE) of environmental variables for each species and size class. N is the number of independent samples used in the analysis. Posterior testing of means found to differ significantly ($p < 0.05$) were conducted using Tukey's adjustment for multiple comparisons, with means that are not different having at least one letter in common, read vertically (NS indicates that differences were not significant).

Species and size class	Number of samples (N)	Mean Depth (cm)	Distance from shore (m)	Substrate	Salinity (ppt)
Blackcheek tonguefish					
≤ 15 mm	36	46.8 ± 3.0 NS	2.3 ± 0.3 B	2.1 ± 0.2 NS	16.3 ± 1.1 NS
$> 15 \leq 30$ mm	158	41.7 ± 1.2 NS	1.3 ± 0.1 A	1.9 ± 0.1 NS	17.7 ± 0.4 NS
$> 30 \leq 85$ mm	130	39.8 ± 1.5 NS	1.5 ± 0.1 AB	2.0 ± 0.1 NS	17.6 ± 0.5 NS
> 85 mm	8	33.5 ± 6.2 NS	1.3 ± 0.6 AB	1.6 ± 0.4 NS	19.1 ± 2.3 NS
Offshore tonguefish					
$> 15 \leq 30$ mm	3	40.5 ± 11.7 NS	1.9 ± 1.1 AB	2.3 ± 0.7 NS	19.5 ± 4.3 NS
Species and size classes	D.O. (mg l^{-1})	Temperature ($^{\circ}\text{C}$)	Turbidity (NTU)	Velocity (cm sec^{-1})	Stems m^{-2}
Blackcheek tonguefish					
≤ 15 mm	7.8 ± 0.3 NS	27.4 ± 1.0 B	13.1 ± 2.2 NS	1.8 ± 0.8 AB	1.5 ± 3.0 AB
$> 15 \leq 30$ mm	7.5 ± 0.1 NS	27.2 ± 0.4 B	15.4 ± 0.9 NS	2.3 ± 0.3 B	7.1 ± 1.2 B
$> 30 \leq 85$ mm	7.5 ± 0.1 NS	23.6 ± 0.5 A	16.8 ± 1.1 NS	3.6 ± 0.4 A	2.7 ± 1.5 A
> 85 mm	6.3 ± 0.6 NS	28.0 ± 2.1 AB	16.5 ± 4.4 NS	1.6 ± 1.5 AB	6.0 ± 6.2 AB
Offshore tonguefish					
$> 15 \leq 30$ mm	8.4 ± 1.1 NS	28.3 ± 3.9 AB	10.0 ± 8.4 NS	1.7 ± 2.9 AB	0.7 ± 11.7 AB

were present under higher velocity conditions and lower stem densities than were individuals of size class II. No significant differences were detected between the two species.

Blackcheek and offshore tonguefish densities near the marsh edge coincided with observed patterns along distance-from-shore gradients obtained from a separate beam-trawl survey (Figure 3.4). Blackcheek tonguefish densities from the beam-trawl collections were higher among near shore samples, and densities along the marsh edge were substantially higher than those reported from the beam-trawl study. Offshore tonguefish densities were typically higher among beam-trawl collections made farther from shore, and densities were substantially lower along the marsh edge. Tonguefish densities along the marsh edge also coincided with observed patterns along a depth gradient (Figure 3.5). Blackcheek tonguefish densities were typically higher in shallower sites, and densities along the marsh edge were substantially higher. Offshore tonguefish densities were typically higher in deeper sites, with lowest densities occurring along the marsh edge.

In the PCA of the drop sampling study, four principal components had eigenvalues greater than 1, and combined explained 60.1% of the variability in the nine environmental variables (Table 3.4). All variables except velocity had an intermediate loading (absolute value > 0.40) on at least one principal component. The first component had a positive loading for temperature and a negative loading for dissolved oxygen, which was interpreted as a seasonal axis. The second principal component had a positive loading for mean depth and distance from shore and a negative loading for stem density, and identified a gradient of environmental variability away from the marsh edge. The third axis had a positive loading for salinity and a negative loading for mean depth. The fourth variable had a positive loading for substrate and turbidity; species and size classes did not differ with respect to mean scores for this component,

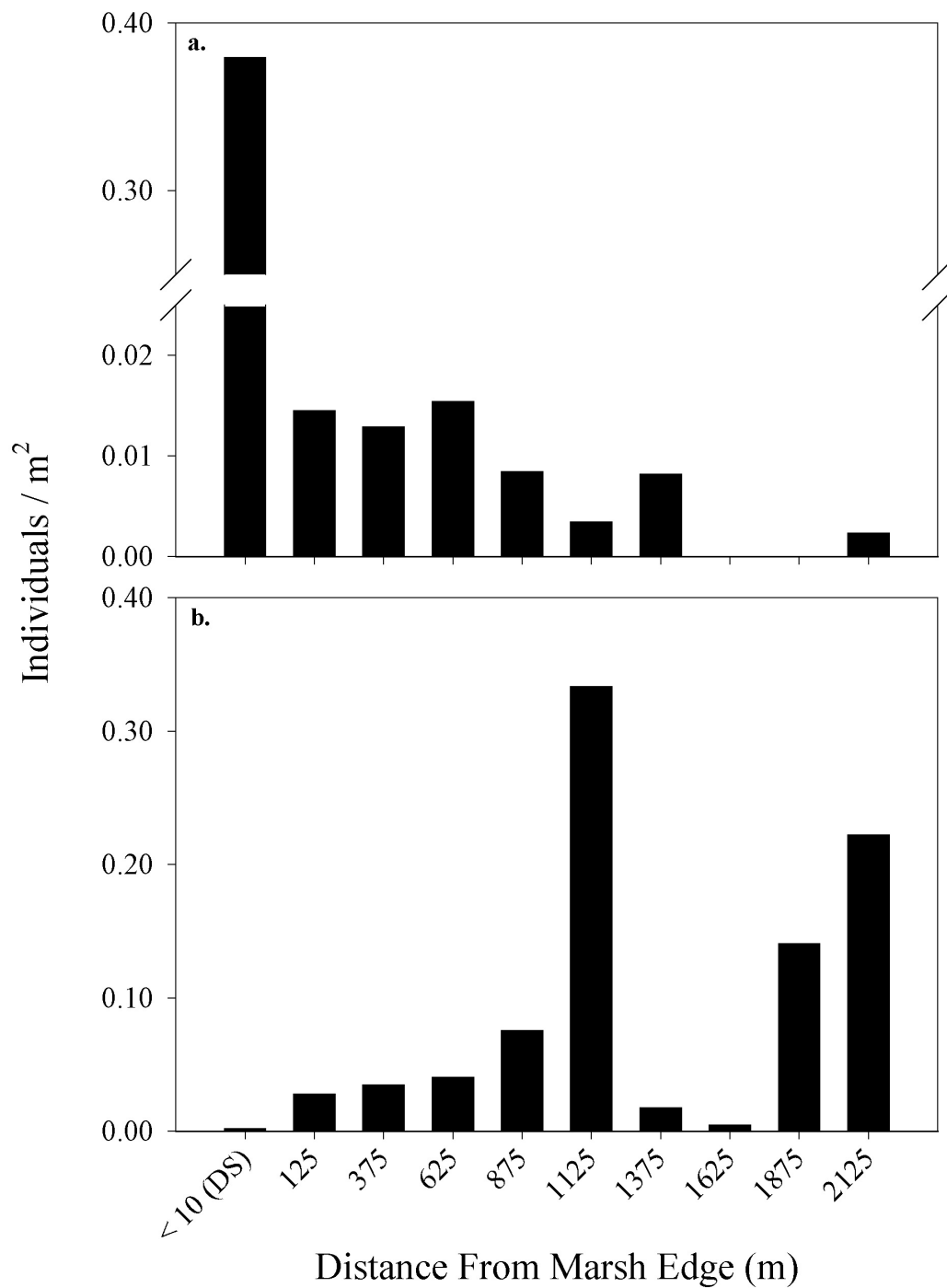


Figure 3.4. Densities of (a) blackcheek tonguefish and (b) offshore tonguefish along a distance gradient. Densities in the first column represent those obtained from the drop-sampling study, while densities in the remaining columns represent those calculated from a beam-trawl study conducted in the same area.

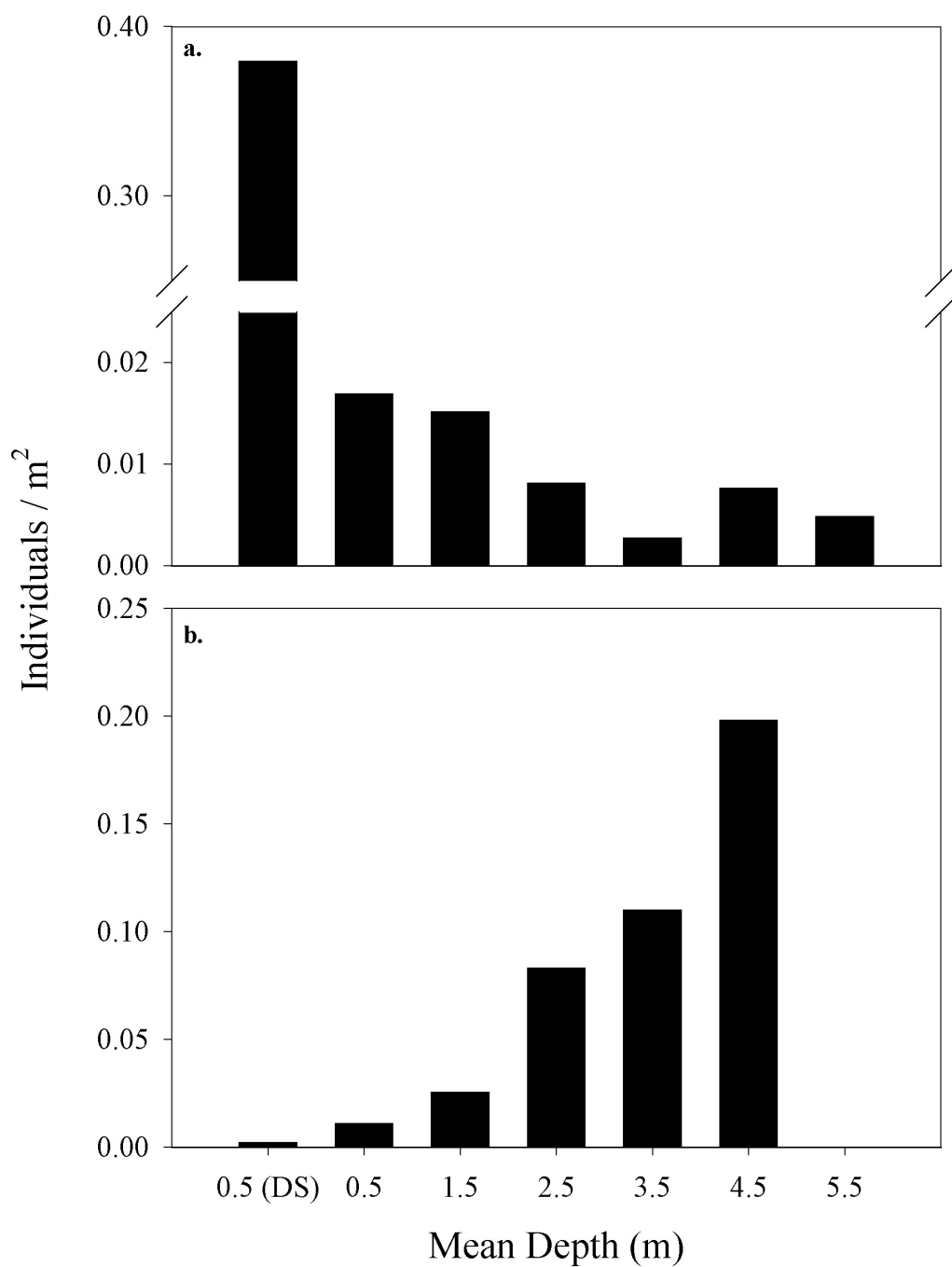


Figure 3.5. Densities of (a) blackcheek tonguefish and (b) offshore tonguefish along a depth gradient. Densities in the first column represent those obtained from the drop-sampling study, while densities in the remaining columns represent those calculated from a beam-trawl study conducted in the same area.

Table 3.4. Variable loadings and variance explained in a principal components analysis of microhabitat data. Variables considered to be important contributors to each principal component are identified by **bold** type.

Variable	Principal Component			
	1	2	3	4
Mean depth	0.35	0.54	-0.56	-0.16
Distance from shore	-0.07	0.69	-0.06	0.05
Substrate	0.01	0.41	0.07	0.64
Salinity	0.00	0.20	0.84	-0.14
Dissolved Oxygen	-0.85	0.06	-0.27	-0.03
Temperature	0.87	-0.06	-0.08	0.10
Turbidity	0.06	-0.22	-0.10	0.78
Velocity	-0.12	0.09	-0.38	-0.02
Stem Density	0.06	-0.64	-0.04	0.03
Variance Explained	1.62	1.44	1.27	1.09
Cumulative variance (%)	18.1	35.0	48.5	60.1

and so it was excluded from further analyses. Scores for the first three principal components were used to plot the centroids of each species and size class in principal component space, and indicated differences in environmental usage within and among species (Figure 3.6). Differences in resource utilization along two environmental axes were detected among juvenile blackcheek tonguefish; individuals of size classes II and III utilized shallower, near-shore sites with higher stem densities and higher salinities than did the smallest juveniles. Young blackcheek tonguefish adults (size class IV) utilized shallower, near-shore sites with higher stem densities than did juveniles, and were found in higher salinity at higher temperatures and lower dissolved oxygen concentrations. Although offshore tonguefish juveniles were rarely collected, those collected utilized deeper sites that were farther from shore and contained lower stem densities than did comparable size classes of blackcheek tonguefish, and were also found in higher salinity waters.

Discussion

The marsh-edge ecotone appears to be important to juvenile blackcheek tonguefish. Post-settlement juveniles are generally found in shallow waters with muddy sediments, and have been recorded in highest densities in sites with a cover of plant material (Reichert and van der Veer 1991). Whether blackcheek tonguefish utilizing edge habitat benefit from increased food availability, decreased risk of predation, or both, is not yet clear (Boesch and Turner 1984), although food is generally thought to be more important in controlling flatfish recruitment in lower latitudes than is predation (Miller et al. 1991). Blackcheek tonguefish occupying the marsh edge feed primarily on epibenthic harpacticoid copepods (Toepfer and Fleeger 1995). Food availability appears to be sufficient due to the infrequent occurrence of individuals with empty stomachs. The species of harpacticoid copepods commonly found in the stomachs of blackcheek tonguefish (Toepfer and Fleeger 1995) do not coincide with species found associated

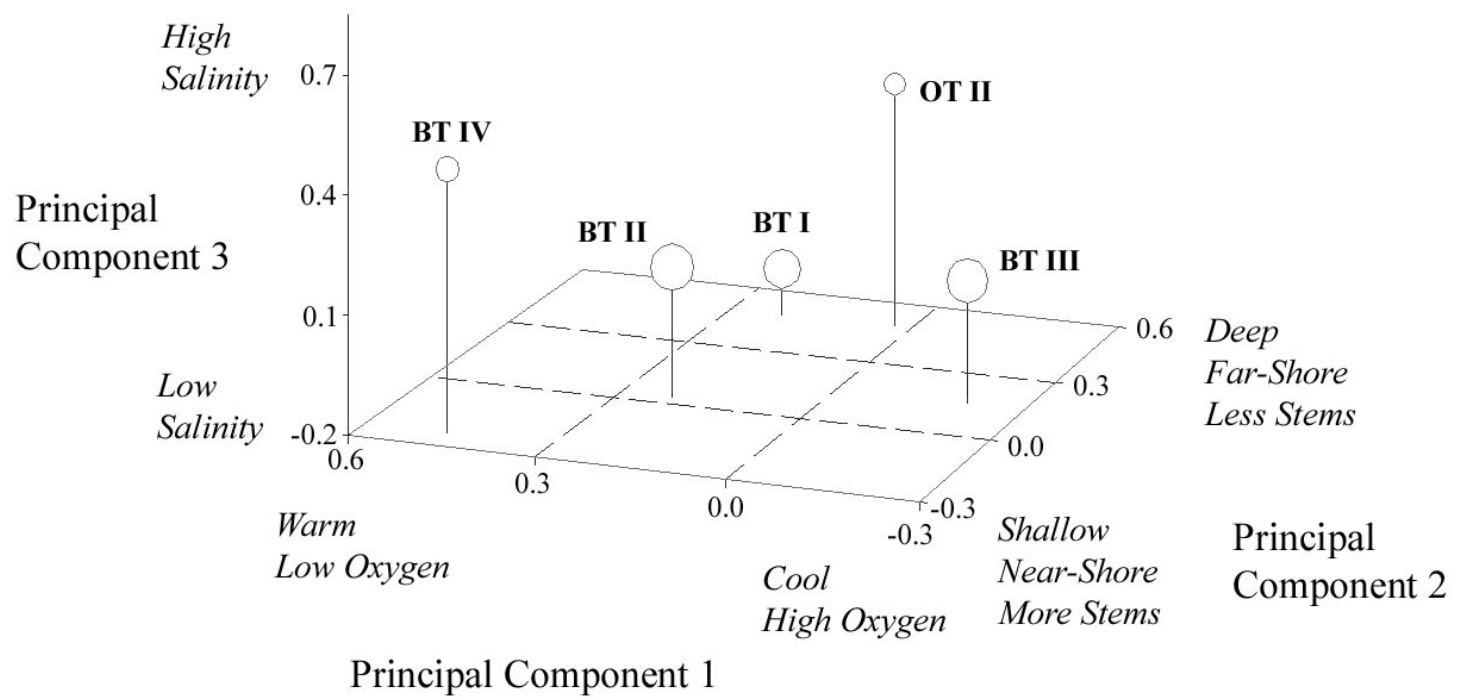


Figure 3.6. Microhabitat plot of centroids for each species and size class of tonguefish collected via drop sampling in three-dimensional principal component space. Balloon radii estimate two standard errors about the centroid.

with *Spartina alterniflora* in coastal Louisiana (Rutledge and Fleeger 1993). Apparently blackcheek tonguefish feed primarily in the surrounding sediments along the marsh edge and not directly on the flooded marsh itself.

While blackcheek tonguefish that utilize marsh-edge habitat may or may not benefit from increased food availability, further research is required to determine the relative importance of the role of refugia. Little is known about piscivory on tonguefishes, although blackcheek tonguefish constitute a small portion of the diets of juvenile (Meyer and Franks 1996) and adult (Franks et al. 1996) cobia in the northern Gulf of Mexico. Juvenile subtropical flatfishes, including the blackcheek tonguefish, are potential prey for blue crabs (*Callinectes sapidus* and *C. similis*) and sea robins (*Prionotus* sp.) in inshore areas (Reichert and van der Veer 1991). Blackcheek tonguefish are most active at night, and generally spend daylight hours buried in the sediment where their cryptic pigmentation reduces detection by potential predators. Flatfishes are typically nocturnal (Nash et al. 1994), and appear to exhibit greatest feeding rates during nighttime hours (Gibson et al. 1998). Juvenile plaice move nearer to shore at dusk to avoid larger predatory fishes and return to deeper waters at dawn (Gibson et al. 1998). All samples were collected during daylight hours, and the high daytime densities of blackcheek tonguefish do not support a movement into deeper waters during the day by this species. Even though the marsh edge may provide protection from large piscivorous fishes, utilization of near-shore habitat may result in increased susceptibility to predation by wading shorebirds (Kneib 1982; Leopold et al. 1998).

Size-specific peaks in seasonal densities indicate key periods of movement into and away from marsh-edge habitat for blackcheek tonguefish. Newly settled juveniles (SC I) were most abundant during summer and fall months, which coincides with a typically protracted spawning

season that extends from early spring through early fall during periods of high temperatures (Munroe 1998). Densities of blackcheek tonguefish in SC II were also highest during summer and fall, and large juveniles (SC III) were found in highest densities during fall and winter. Densities of these largest juveniles decreased in spring months, indicating growth into young adult tonguefish (SC IV). Adult blackcheek tonguefish were notably sparse in samples collected along the marsh edge.

Clear ontogenetic patterns of resource utilization were evident for blackcheek tonguefish. Larger juveniles typically occurred in shallower sites nearer to the marsh edge and with higher vegetation coverage. The occurrence of larger juveniles closer to the marsh edge may discount protection from predators as the primary benefit to tonguefishes occupying the shallow edge habitat. Presumably individuals would move into deeper waters as they outgrow potential predators (Boesch and Turner 1984). Larger juveniles are found in higher salinity waters, indicating movement along the salinity gradient down the estuary as individuals grow. Clear differences exist between resource utilization of juvenile and adult blackcheek tonguefish as well. While mean resource utilization of those adult blackcheek tonguefish collected corresponds closely to observed trends among juveniles, the scarcity of adults along the marsh edge indicates movement away from edge habitat. These adults are most likely leaving the estuary to recruit into the adult population (Munroe 1998). Alternatively, individuals may be moving into deeper water as they grow to avoid predation from wading shorebirds (Kneib 1982).

While marsh-edge habitat appears to be essential for juvenile blackcheek tonguefish, juvenile offshore tonguefish do not appear to depend heavily on the marsh edge. Only three individuals were collected in 1300 samples, all of which co-occurred with blackcheek tonguefish. The infrequent occurrence of offshore tonguefish along the edge was somewhat

surprising, considering their numerical abundance in beam-trawl samples (Allen and Baltz 1997). Mean water depth and distance from shore were significantly lower in this study than in other studies examining the ecology of offshore tonguefish (Allen and Baltz 1997), due primarily to the fact that sampling focus was on the utilization of marsh edge habitat, which restricted the depths and distances examined. Previous research in Louisiana indicated that juvenile offshore tonguefish utilized deeper waters that were farther from shore than did blackcheek tonguefish (Allen and Baltz 1997), and observed densities along the marsh edge fit well with observed densities along depth and distance-from-shore gradients obtained from that study.

While closely related species are expected to utilize similar environmental conditions, the apparent value of marsh edge habitat, combined with the dominance of offshore tonguefish in coastal Louisiana, makes their avoidance of the marsh edge all the more surprising. Most notably, I expected that more than a few individuals had been misidentified in the previously examined drop samples (Baltz et al. 1993). Clearly, some underlying factor allows blackcheek tonguefish to thrive along the marsh edge, but discourages offshore tonguefish from doing the same. Perhaps this discrepancy lies in physiological differences between the species. Shallow edge habitat experiences much greater temperature variability than does deeper water, so perhaps blackcheek tonguefish may be better able to acclimate to such rapidly changing environmental conditions. Offshore tonguefish may be less tolerant of high light levels, and so may occupy deeper waters with attenuated light intensity. Food and substrate differences may also play important roles. Offshore tonguefish are generally found over coarser substrates, and so may avoid the finer bottom sediments that are dominant along the marsh edge. Alternatively, interactions between species may displace one species into less favorable areas. Further research is required to adequately explain differences in utilization of marsh-edge habitat between tonguefishes in coastal Louisiana.

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CHAPTER IV.

AGE AND GROWTH OF YOUNG-OF-THE-YEAR TONGUEFISHES (*SYMPHURUS*: *CYNOGLOSSIDAE*) IN BARATARIA BAY, LOUISIANA

Introduction

Seven species of flatfishes utilize estuaries as nurseries in Louisiana (Allen and Baltz 1997) as well as elsewhere throughout the southeastern United States (Reichert and van der Veer 1991; Walsh et al. 1999). Flatfishes in coastal Louisiana are typically transient to inshore estuaries, with juveniles occupying the highly productive nursery habitat from post-settlement through early adult stages. Flatfishes generally exhibit significant variation among and within species with respect to environmental conditions at individual capture sites (Allen and Baltz 1997; Walsh et al. 1999). Individuals are limited to a range of environmental conditions defined by the physiological tolerances of the species; within such limits individuals can select sites based on increased food availability, reduced risk of predation or both, although the relative importance of these factors is not entirely clear (Boesch and Turner 1984). For some species, the threat of predation drives habitat use even when growth rates are compromised (Halpin 2000). Other species actively occupy areas with increased food availability (Roundtree and Able 1992; Wennhage and Gibson 1998).

Food is generally considered to be more important than predation in controlling recruitment among flatfishes in lower latitudes (Miller et al. 1991). Enhanced growth can theoretically influence future recruitment by decreasing the exposure time to size-specific predation during early life history stages as well as increasing future reproductive output due to either a shortened time to maturity or increased fecundity among larger adults. In lower latitudes, flatfishes typically have an extended spawning period, and as a result exhibit increased

variation in the size distribution of individuals within a given age-0 cohort (van der Veer et al. 1994). This variability is thought to result in an increased importance of size-selective mortality among young-of-the-year flatfishes in subtropical estuaries when compared to similarly aged flatfishes at higher latitudes. However, these competing hypotheses are difficult to test due to the limited availability of data on growth and predation of subtropical flatfishes (Miller et al. 1991; van der Veer et al. 1994).

Two congeneric tonguefishes commonly use inshore estuarine habitat as a nursery in coastal Louisiana (Allen and Baltz 1997). Both the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civatium*) have similar life-history patterns (Allen and Baltz 1997; Munroe 1998). Adults reside in deep, offshore waters (1 to 30 m for blackcheek tonguefish, 11 to 45 m for offshore tonguefish) where spawning occurs during an extended period that begins in late spring and continues through late summer (Munroe 1998). Spawning coincides with seasonal peaks of high temperatures. Pelagic eggs and larvae are transported into inshore nurseries where settlement occurs beginning in late summer and extending through fall (Reichert and van der Veer 1991; Baltz et al. 1993; Allen and Baltz 1997). Individuals reside within the estuary for nearly a year through late juvenile/early adult stages, eventually recruiting offshore to adult populations. The high abundances of tonguefishes in coastal Louisiana as well as the presence of only 0-class individuals (Allen and Baltz 1997) facilitates examination of the influence of nursery conditions on the age and growth of these species.

This paper compares age and growth patterns of blackcheek and offshore tonguefish juveniles collected within Barataria Bay from September 1992 through August 1994. I examined the basic morphometric relationships between otolith growth and somatic growth and estimated mean daily growth rates for both species within the estuary. I also tested three hypotheses: (1)

growth rates are not related to biotic and abiotic variation in environmental conditions measured at the microhabitat level (Baltz 1990); (2) growth rates of juvenile blackcheek and offshore tonguefish within the Barataria Bay estuary are not different; and (3) growth rates as determined by otolith analysis and indirect cohort analysis are not different.

Materials and Methods

Study Area

The Barataria Basin is the first major estuary west of the mouth of the Mississippi River (Figure 4.1), and is located between the natural levees of the river and the abandoned Bayou Lafourche distributary. The drainage basin is approximately 110 km long, and is 50 km at its greatest width where it opens into the Gulf of Mexico (Conner and Day 1987). Influx of riverine water and suspended sediment into the basin has been minimal since the closure of the Bayou Lafourche-Mississippi River connection in 1902 and the completion of the river levee system in the 1940s. As a result, precipitation has long been the primary source of freshwater input into the system. Since the 1940s land building processes have been reduced while the area has continually been reworked by coastal erosion and subsidence, resulting in significant conversion of marsh habitat into open water over the past several decades (Baumann 1987). With the recent opening of the Davis Pond freshwater diversion in 2002, there is now an additional source of fresh-water and sediment input in the system intended to alleviate the decades-long trend of land loss in the area (LDNR 2002).

Field Methods

Juvenile tonguefishes were collected from September 1992 to August 1994 as part of a beam-trawl survey examining distribution and microhabitat use by fishes and macroinvertebrates within Barataria Bay (Allen and Baltz 1997; Jones et al. 2002). Samples of benthic fishes and

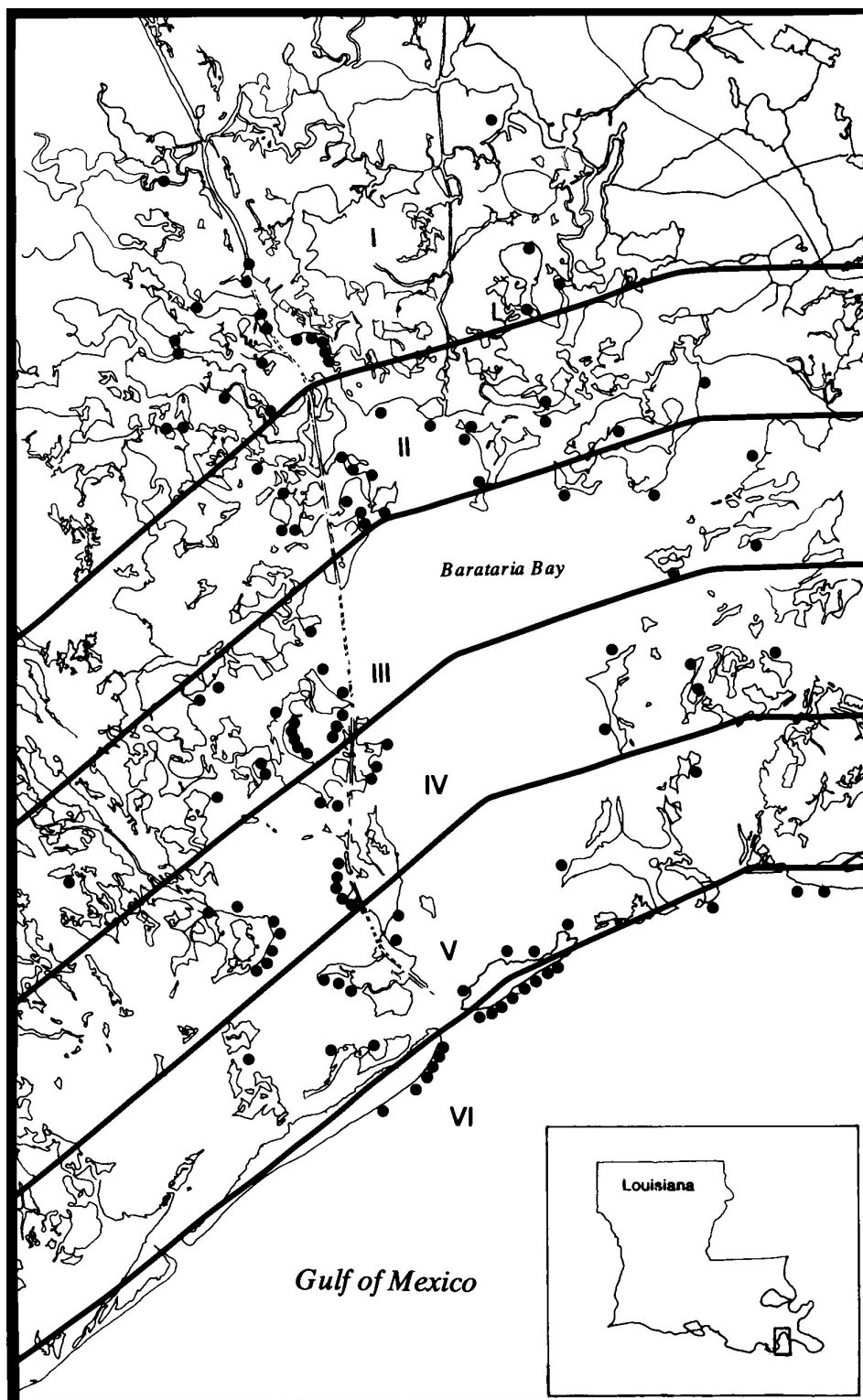


Figure 4.1. Sampling locations within the Barataria Bay, Louisiana study region. Strata designations are given by Roman numerals (I – VI).

invertebrates were collected using a 1-m beam trawl with a uniform mesh size of 5 mm (Kuipers 1975), and sampling effort was divided into six strata ranging from brackish inland sites near the northernmost reaches of Barataria Bay to the near-shore zone in the northern Gulf of Mexico (Figure 1). A randomly selected sampling location was chosen within each stratum during each month. Sampling at each location involved collecting a series of five tows at sites increasingly distant from the shoreline, and each tow was made parallel to shore to minimize habitat heterogeneity within samples. Tow duration was typically short (range 1-2 min, mean 1 min 24 sec), and for a subset of the tows, distance covered was measured over each substrate type to estimate mean towed distance (Allen and Baltz 1997). Each tow covered a mean (\pm 1SD) area of approximately $152 \pm 14.8 \text{ m}^2$, which varied substantially ($\text{CV} = 9.7\%$) over dominant substrate types: silt (138 m^2), clay (142 m^2), sand (158 m^2), and plant detritus (170 m^2).

At each sampling site salinity (psu), temperature ($^{\circ}\text{C}$), and dissolved oxygen (mg L^{-1}) were measured using a YSI model 33 S-C-T meter and a YSI model 57 oxygen meter. Median water depth (m) was calculated from minimum and maximum depth values determined during the tow, and distance from shore (m) was estimated. The dominant substrate type was identified at each sampling site and coded on an ordinal scale of particle size as 1 = silt, 2 = clay, 3 = sand, 4 = plant detritus, and 5 = shell. Organisms were sorted in the field to separate all fishes and macroinvertebrates, and specimens were then preserved in 95% ethanol. Tonguefishes were identified to species in the laboratory using keys by Hoese and Moore (1977) and Munroe et al. (2000), and were measured to the nearest mm standard length (SL).

Laboratory Methods

Tonguefishes were systematically sub-sampled from all samples collected, and both the left and right sagittal otoliths were removed when possible. Otoliths were removed from a total

of 276 blackcheek and 350 offshore tonguefish ranging in size from 10 mm to 119 mm SL. Maximum otolith diameters (MOD) were measured using digital calipers to determine the relationship between otolith growth and somatic growth as well as to determine whether left and right otoliths were symmetrical.

The limited research conducted on the age and growth of members of the family Cynoglossidae (Miller et al. 1991) has focused on otolith material from adult tonguefishes (Terwilliger and Munroe 1999). Although daily otolith increment formation was not independently validated in these tonguefishes, daily growth increments have generally been validated without difficulty for other juvenile flatfishes (Sogard 1991; Stewart and Jenkins 1991; Szedlmayer and Able 1992), including other subtropical flatfish (Reichert et al. 2000), so visible increments were assumed to be deposited daily. I only used otoliths for subsampled individuals less than 40 mm SL for our subsequent age and growth analyses. Otoliths were prepared for microstructural analysis following procedures outlined by Secor et al. (1991). Otoliths were soaked briefly in a 10% bleach solution to remove any adhering tissue, and then rinsed sequentially with distilled water and 95% ethanol before air drying. Otoliths were then embedded in araldite resin, and excess resin was trimmed using a Buehler Isomet low-speed saw equipped with a diamond wafering blade. Resin blocks containing embedded otoliths were mounted on microscope slides using Crystal-Bound thermoplastic adhesive. Transverse sections of each mounted otolith were sanded with 600 and 1200 grit sandpaper and then polished with 0.3 μm silica paste until the otolith core and daily increments were clearly visible (Figures 4.2 and 4.3). Images of otolith sections were captured electronically using a compound microscope and were then digitally modified to improve the visibility of daily increments. Daily increments were counted to provide an estimate of age in days. Recent daily growth rates were estimated by

measuring the width of the next-to-last increment to ensure that only complete daily increments were measured. Increment widths were measured on three separate occasions to account for variability in the plane of focus as well as to develop the reader's ability to measure widths more accurately.

Analytical Methods

Simple linear regression analyses were conducted to examine the relationship between MOD and SL for both blackcheek and offshore tonguefish to test for direct proportionality between otolith growth and somatic growth over the sizes encountered within the study area. Because left and right otoliths are not always symmetrical in flatfishes (Sogard 1991), separate linear regression analyses were conducted relating MOD of both the left and right sagittae to SL to test for asymmetry.

I conducted stepwise multiple regression analyses to examine the linear relationship between recent daily growth rates and several biotic and abiotic variables: mean depth, distance from shore, temperature, salinity, dissolved oxygen, substrate, blackcheek tonguefish density and offshore tonguefish density. The most recent otolith increment width was used as an estimate for somatic growth (Reichert et al. 2000). Increment width was measured on three separate occasions, and the variability of these measurements did not differ substantially between blackcheek (CV = 9.7 %) and offshore tonguefish (CV = 8.5 %). Although there was not a significant relationship between increment width and SL for either blackcheek ($F = 0.25$, $p = 0.6181$) or offshore tonguefish ($F = 0.87$, $p = 0.3523$) over the size range examined, I adjusted for differences in otolith increment widths among differently sized individuals. I conducted simple linear regression analyses relating increment width to SL, and used the raw residuals from each species as the new dependent variables. These residuals represent the excess variability in

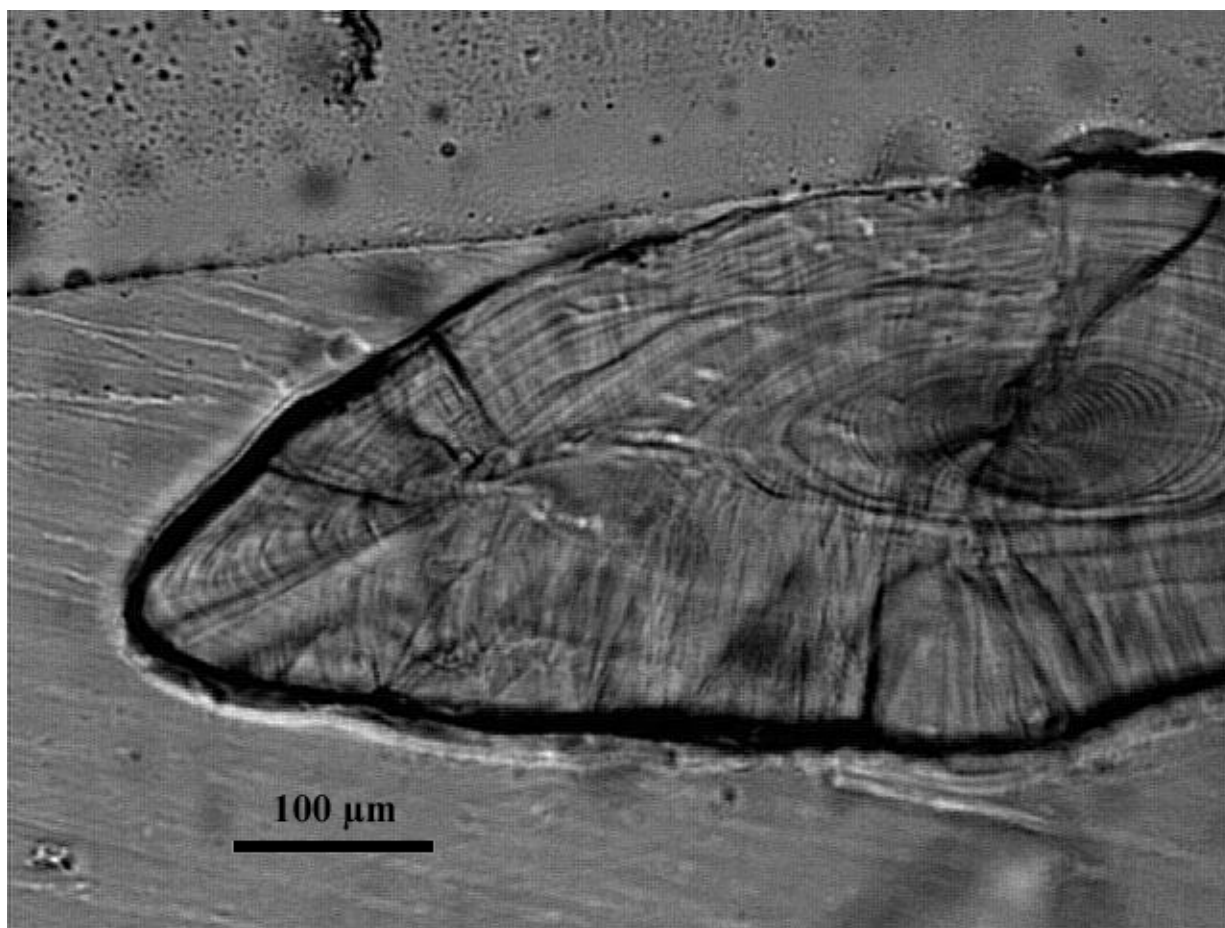


Figure 4.2. Transverse section through the left sagittal otolith of a blackcheek tonguefish juvenile (31 mm SL) indicating the visibility of daily increments.

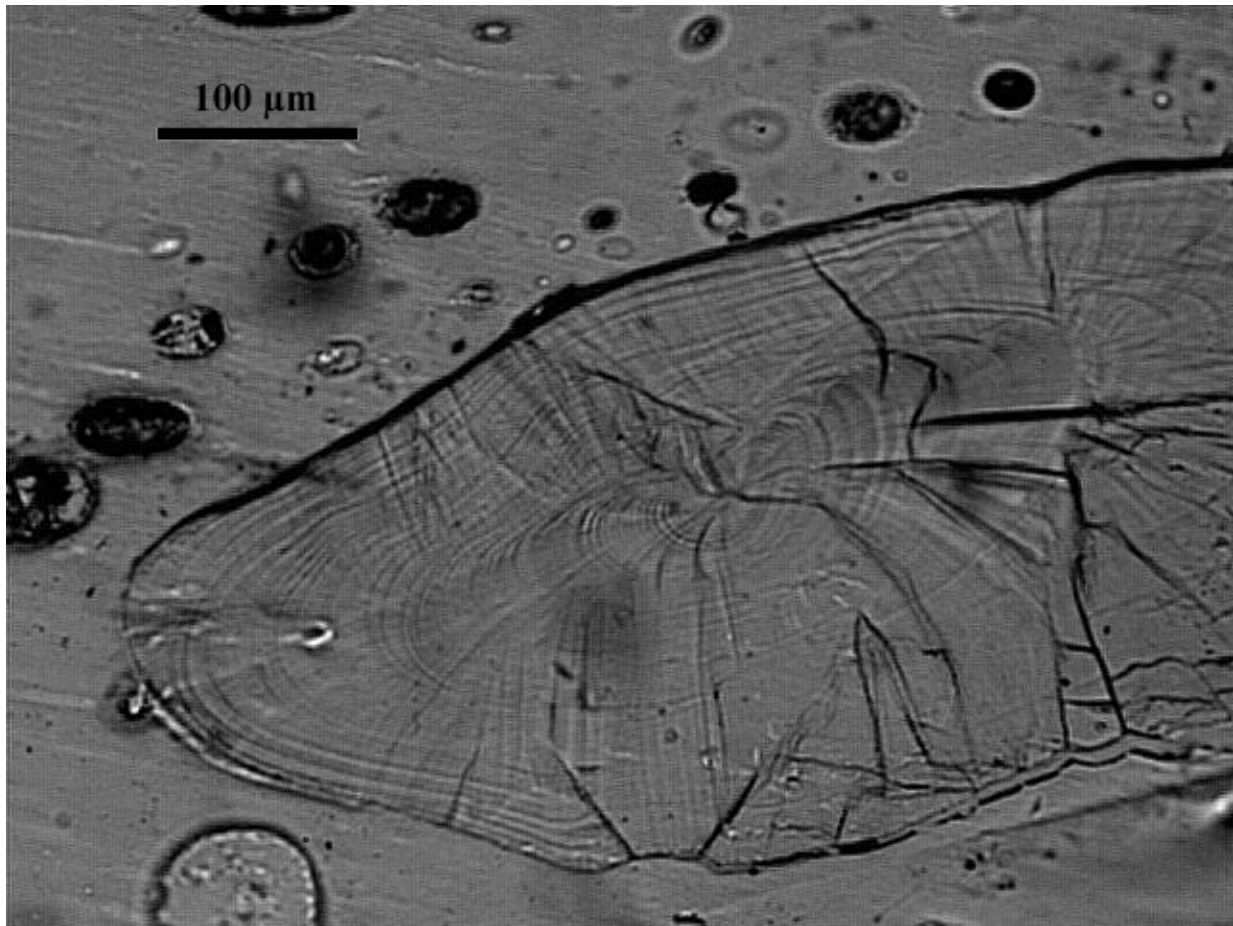


Figure 4.3. Transverse section through the left sagittal otolith of an offshore tonguefish juvenile (32 mm SL) indicating the visibility of daily increments.

increment width unaccounted for by changes in SL; presumably environmental conditions resulting in decreased growth would prevail among individuals with large, negative residuals and environmental conditions contributing to increased growth would prevail among individuals with large, positive residuals. Raw residuals were then related to the biotic and abiotic variables using stepwise regressions. A decision rule of $\alpha = 0.15$ was used to identify biotic and abiotic variables that may marginally influence growth rates. Transformed biotic and abiotic variables ($\log_{10} x + 1$) were used to improve the normality of the residuals in the step-wise models. Additionally, separate analyses of variance (ANOVA) were used to test whether recent daily growth rates differed significantly on a seasonal and/or spatial basis for either species.

Separate multi-source regression analyses were conducted for each species to examine the linear relationship between age and SL as well as age and MOD for subsampled individuals less than 40 mm SL using species as a covariate. Significance testing was conducted using sequential (Type I) sums of squares, which allows for the comparison of slopes and intercepts between species in addition to testing for linear relationships between dependent and independent variables. I also estimated daily otolith and somatic growth rates from these relationships for both blackcheek and offshore tonguefish. All analyses were conducted using the SAS statistical software package (SAS Institute 1996).

Monthly size-frequency distributions were examined for both species to evaluate changing peaks in abundance and size to provide a secondary estimate of daily growth rates. Relative densities were calculated monthly for each species in 5 mm size intervals to account for differential sampling effort among months. The median of each monthly size-frequency distribution was used to derive an estimate of mean daily growth rate throughout the year.

Results

I was unable to detect asymmetry in the sagittal otoliths of either species. Linear relationships were significant between MOD and SL for left ($\text{MOD} = 0.222 + 0.018 \text{ SL}$; $R^2 = 0.97$; $p < 0.0001$) and right otoliths ($\text{MOD} = 0.211 + 0.018 \text{ SL}$; $R^2 = 0.97$; $p < 0.0001$) for blackcheek tonguefish. For offshore tonguefish, linear relationships were also significant for left ($\text{MOD} = 0.251 + 0.018 \text{ SL}$; $R^2 = 0.95$; $p < 0.0001$) and right otoliths ($\text{MOD} = 0.259 + 0.018 \text{ SL}$; $R^2 = 0.95$; $p < 0.0001$). All slopes were nearly identical, so otolith growth appears to be symmetrical and otolith growth appears similar for both species. Accordingly, either the left or right otolith was used for age and growth determination.

Stepwise analyses were fit according to the multiple regression model: $y = a + b_1x_1 + b_2x_2 \dots + b_ix_i + \epsilon$, where y is the daily growth residual (DGR), b_0 is the y-intercept, $b_1 - b_i$ are the partial regression coefficients (slopes) for the relationship between DGR and the biotic and abiotic variables ($x_1 - x_i$) included in the model, and ϵ is the unexplained residual term. Separate analyses by species detected significant relationships between DGR obtained from simple linear regressions relating otolith increment width to SL and several transformed biotic and abiotic variables ($\log_{10} x + 1$) at the $\alpha = 0.15$ level of significance. For blackcheek tonguefish, the stepwise-regression model ($F = 2.65$, $p = 0.0623$, $R^2 = 0.17$) predicted 17 % of the variability in recent daily growth residuals using a non-zero intercept ($b_0 = 2.89$, $p = 0.0956$), blackcheek tonguefish density ($b_1 = -0.67$, $p = 0.0386$), offshore tonguefish density ($b_2 = 0.60$, $p = 0.0631$) and dissolved oxygen ($b_3 = -2.64$, $p = 0.1302$). For offshore tonguefish, the stepwise-regression model ($F = 5.79$, $p = 0.0044$, $R^2 = 0.12$) predicted 12 % of the variability in recent daily growth using temperature ($b_1 = 1.06$, $p = 0.0173$) and median depth ($b_2 = -1.28$, $p = 0.0276$); an intercept was included in the model, although it was not significantly different from zero ($b_0 = -0.81$, $p =$

0.1974). In separate ANOVAs, I did not detect any seasonal or spatial differences in recent daily growth for either blackcheek ($F = 1.03$, $p = 0.3893$) or offshore tonguefish ($F = 1.58$, $p = 0.2001$).

Multi-source regression identified significantly different linear relationships between age and SL for both species (Figure 4.4); blackcheek tonguefish grew at approximately 0.34 ± 0.024 mm d⁻¹, whereas offshore tonguefish grew significantly faster at approximately 0.42 ± 0.015 mm d⁻¹. Slopes differed significantly between species ($F = 8.44$, $p = 0.0044$), whereas the Y-intercepts did not ($F = 0.53$, $p = 0.4681$). Multi-source regression also identified significant linear relationships between age and MOD (Figure 4.5); blackcheek tonguefish MOD increased at a mean rate (\pm SE) of 0.0085 ± 0.0008 mm d⁻¹, whereas the MOD in offshore tonguefish increased at a mean rate of 0.0095 ± 0.0005 mm d⁻¹. However, neither slopes ($F = 1.09$, $p = 0.2991$) nor Y-intercepts ($F = 3.39$, $p = 0.0680$) differed significantly between species. In general, the linear relationships were stronger between age and SL than between age and MOD as evidenced by slightly higher R^2 values (Figures 4.4 and 4.5).

Blackcheek tonguefish first appeared in collections in the study area as post-settlement juveniles in September (Figure 4.6). The youngest blackcheek tonguefish that I was able to determine age for was 20 mm SL and 40 days old, although fully transformed and settled individuals as small as 13 mm SL were collected (otolith was destroyed during the sectioning process). Newly transformed recruits continued to immigrate and settle within the estuary through late winter. Although the extended spawning period of blackcheek tonguefish complicated the process due to increased variability of monthly size-frequency distributions, cohort distributional patterns could be followed from post-settlement through the emigration of sub-adult blackcheek tonguefish from the study region in August. From these distributional

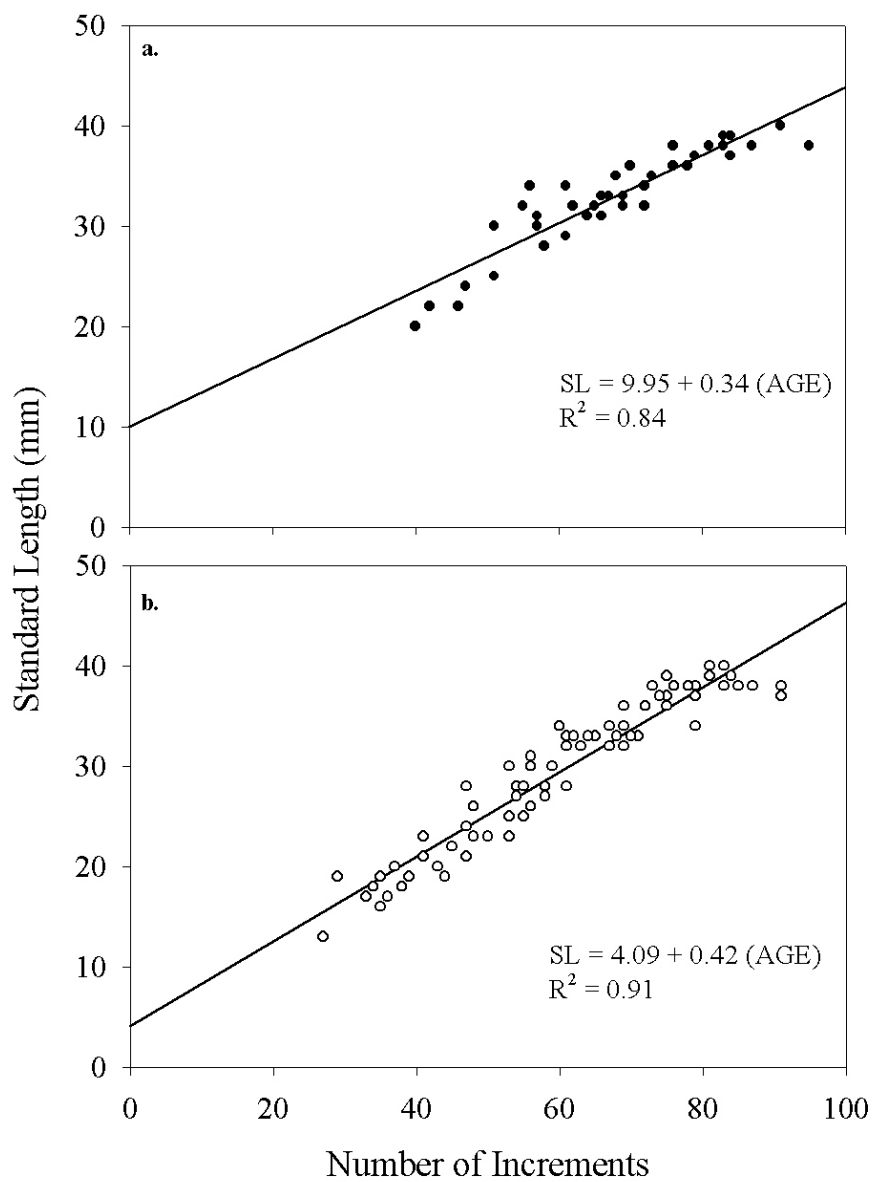


Figure 4.4. Linear regression of standard length on the number of observed otolith increments for (a) blackcheek and (b) offshore tonguefish.

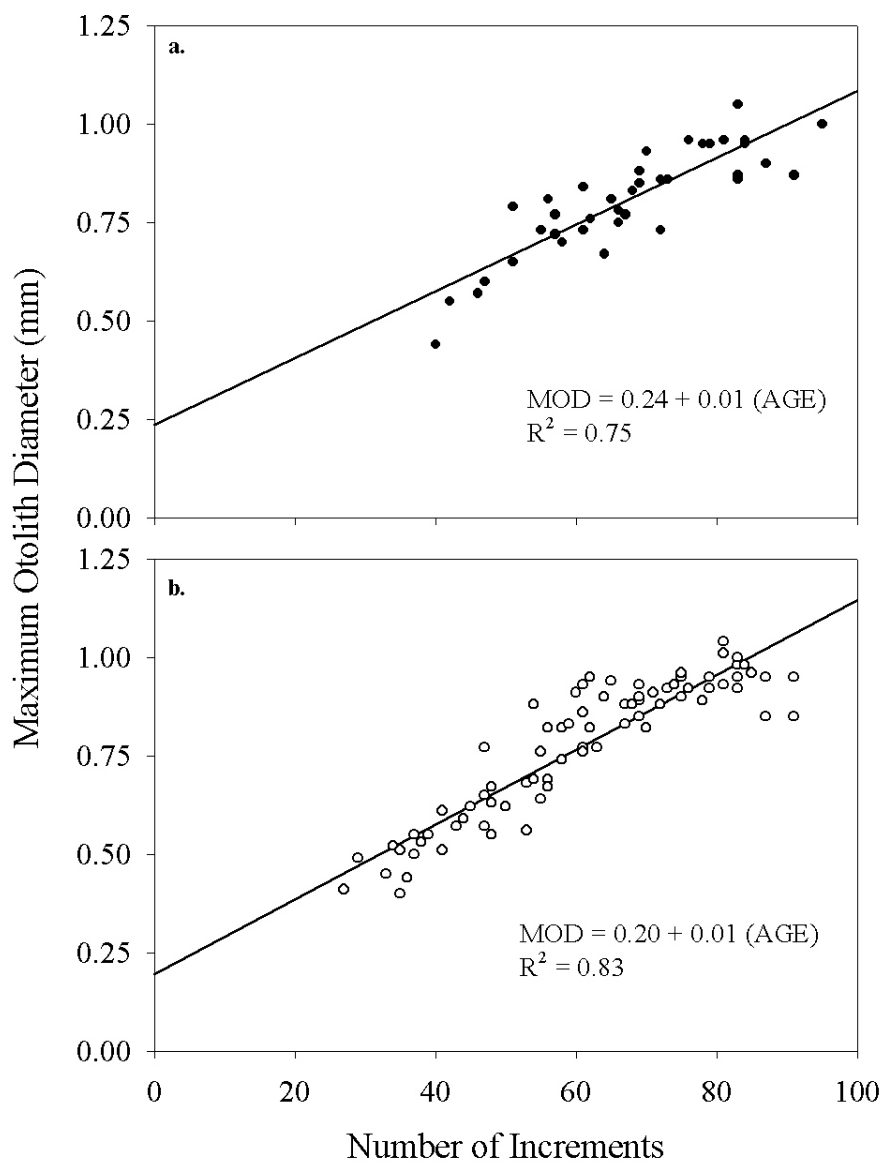


Figure 4.5. Linear regression of maximum otolith diameter on the number of observed otolith increments for (a) blackcheek and (b) offshore tonguefish.

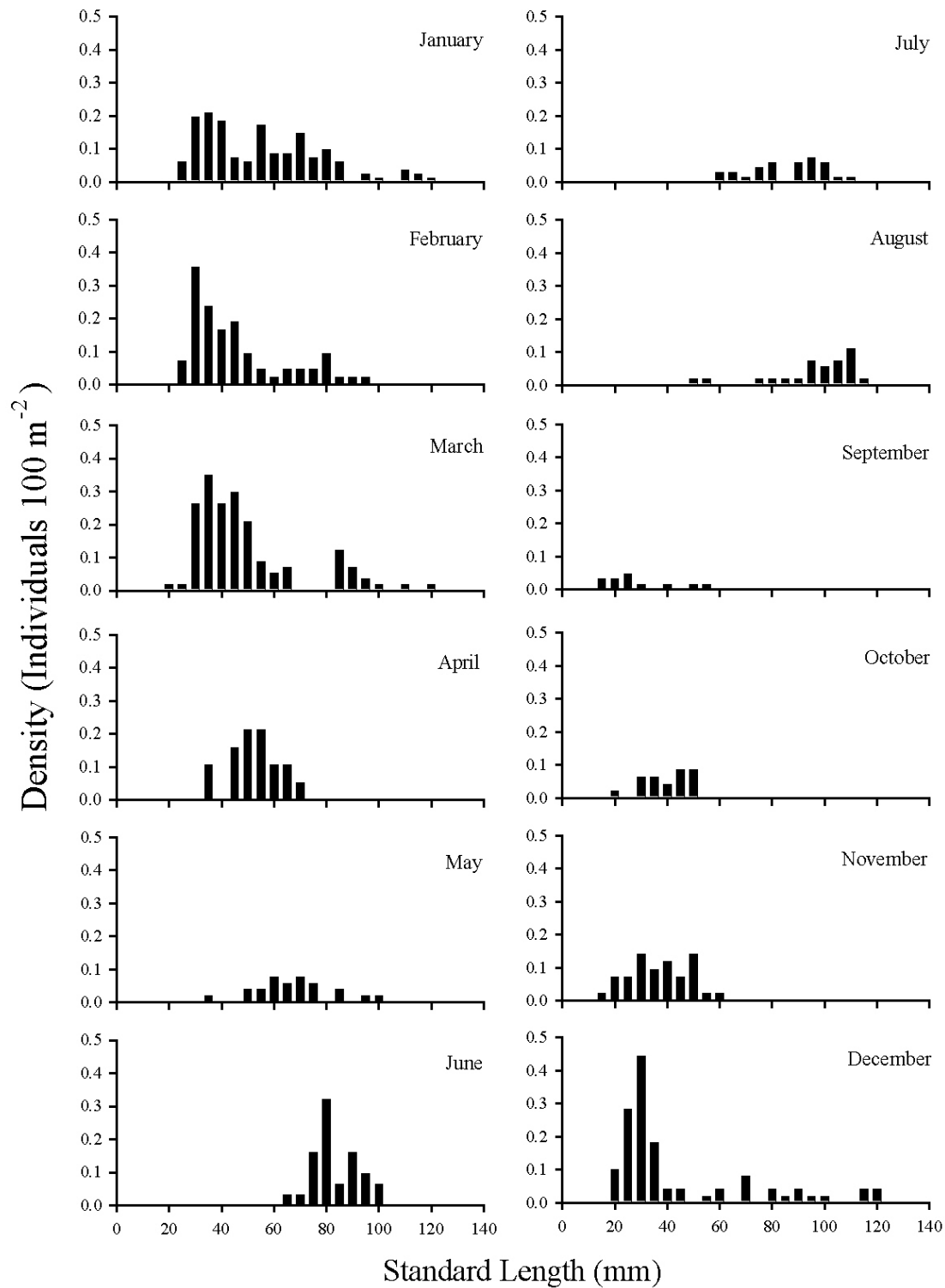


Figure 4.6. Monthly size-frequency distributions in 5 mm SL intervals for blackcheek tonguefish.

patterns I calculated a mean (\pm SE) growth rate of $0.23 \pm 0.107 \text{ mm d}^{-1}$ for blackcheek tonguefish. Similar distributional patterns were also evident for offshore tonguefish, with newly settled juveniles also appearing in collections in the study region during September and October (Figure 4.7). The youngest offshore tonguefish that I was able to determine age for was 13 mm SL and 27 days old, although fully transformed and settled individuals as small as 10 mm SL were collected (otolith was destroyed during the sectioning process). Monthly size-frequency distributions clearly indicated growth of the offshore tonguefish cohort from initial settlement through the emigration of adults from the estuary in late summer. Based on examination of monthly distributional patterns of offshore tonguefish, individuals occupying the study area had a mean growth rate of $0.18 \pm 0.109 \text{ mm d}^{-1}$. Results from a one-way ANOVA indicated that growth rates, as determined by monthly cohort analysis, did not differ significantly between species ($F = 0.12$, $p = 0.7318$).

Discussion

The daily growth rates for blackcheek and offshore tonguefish obtained from otolith increment data were similar to previous reports for other flatfishes. Blackcheek tonguefish growth rates were calculated at 0.34 mm d^{-1} , and were significantly lower than the 0.42 mm d^{-1} growth rates for offshore tonguefish. Growth rates of 0.5 mm d^{-1} have been reported for juvenile blackcheek tonguefish in a Georgia estuary during the period of April through September (Reichert and van der Veer 1991). Comparable growth rates have been reported for other similarly sized flatfishes in the southeastern United States: juvenile bay whiff (*Citharichthys spilopterus*) grow at a mean rate of 0.7 mm d^{-1} and fringed flounder (*Etropus crossotus*) growth ranges from 0.1 to 0.5 mm d^{-1} (Reichert and van der Veer 1991; Reichert et al. 2000). Observed growth rates for blackcheek and offshore tonguefish also fall within observed ranges for

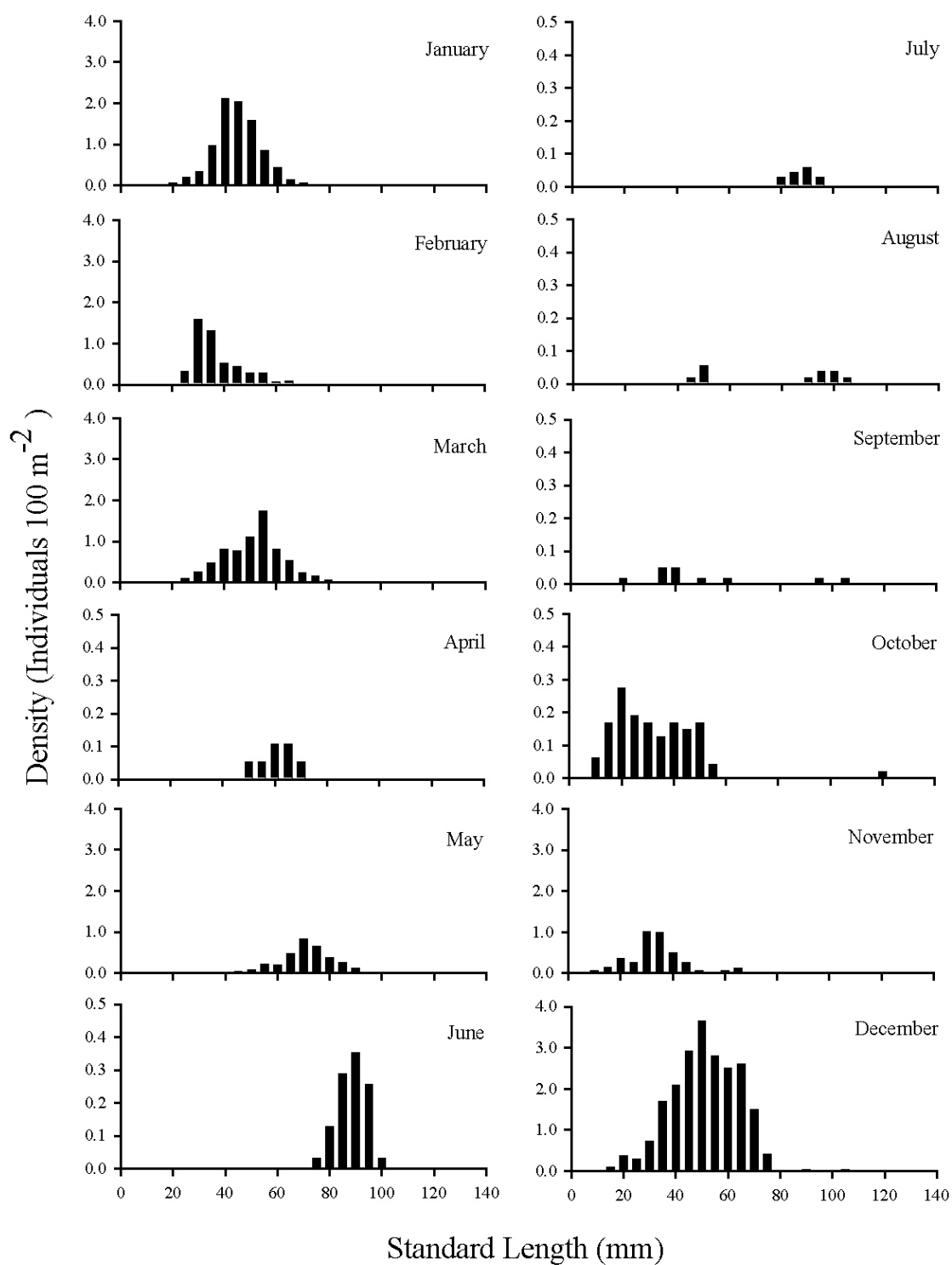


Figure 4.7. Monthly size-frequency distributions in 5 mm SL intervals for offshore tonguefish. Due to highly variable monthly densities, plots have different scales along the y-axis.

flatfishes elsewhere: juvenile greenback flounder (*Rhombosolea tapirina*) from Australia grow at a mean rate of 0.29 mm d^{-1} (May and Jenkins 1992), juvenile dab (*Limanda limanda*) growth ranges from 0.12 to 0.24 mm d^{-1} , juvenile European plaice (*Pleuronectes platessa*) growth ranges from 0.55 to 0.81 mm d^{-1} , and juvenile common sole (*Solea solea*) growth ranges from 0.5 to 0.67 mm d^{-1} in a French nursery (Amara et al. 2001).

Estimates of growth rates from monthly cohort analysis were substantially lower than growth rates obtained from direct analysis of otolith increments. Estimates of growth using monthly size-frequency distributions depend heavily on an accurate estimation of fish length distributions, which may be affected by gear selectivity. Net selectivity tends to be low for the smallest individuals due to passage through the mesh, highest for intermediately sized individuals, and low for larger individuals due to net avoidance (Kuipers 1975). Problems with net efficiency may result in an underestimation of growth rates (Reichert and van der Veer 1991). The extended spawning season of tonguefishes in coastal Louisiana (Munroe 1998) may also complicate the estimation of growth rates from monthly size-frequency distributions. The relatively constant influx of new recruits during an extended period from September through December results in high variation of monthly size-frequency distributions (Figures 4.6 and 4.7), and may produce an underestimation of monthly growth rates during this time due to downward shifts in median standard length. Growth rates calculated using monthly size-frequency distributions were also examined over the entire range of sizes encountered, not just those individuals less than 40 mm SL included in the size-at-age analyses. Highest growth rates are expected during the period following settlement, with individuals generally experiencing decreased growth as size increases (Sogard and Able 1992). Incorporation of larger, slower growing individuals in size-frequency analyses may contribute to lower calculated growth rates.

Based on otolith analysis, offshore tonguefish experienced significantly higher growth within the estuary than did blackcheek tonguefish. Increased growth in offshore tonguefish may compensate for earlier movement out of the estuary. The initial appearance of blackcheek and offshore tonguefish juveniles in collections within Barataria Bay occurs during summer (Allen and Baltz 1997). After remaining within the estuary for the better part of the year, adults move offshore to recruit into reproductive populations, presumably in response to changing temperatures (Gunter 1938, 1945, Miller 1965, Olney & Grant 1976). Adult offshore tonguefish abundances decrease substantially from spring to summer, whereas adult blackcheek tonguefish abundances remain relatively high through summer (Chapter 2). Movement of offshore tonguefish adults into reproductive populations appears to occur earlier in the season than does movement of blackcheek tonguefish; offshore tonguefish movement may be in response to lower temperatures than movement of blackcheek tonguefish. Increased growth by offshore tonguefish may offset the fact that they spend less time in the estuary than do blackcheek tonguefish.

Both tonguefishes experienced higher growth under higher temperatures and lower dissolved oxygen concentrations, two variables that are negatively correlated on a seasonal basis (Chapter 2). Blackcheek tonguefish growth was negatively related to dissolved oxygen whereas offshore tonguefish growth was positively related to temperature. The strong negative relationship between temperature and dissolved oxygen in the study area (Baltz et al. 1993; Allen and Baltz 1997; Jones et al. 2002) makes separating the effects of each factor on growth difficult; however, temperature is typically more important among flatfishes (Gibson 1994). Increased growth rates of numerous fishes, including flatfishes, have been linked to warmer temperatures. Larval and juvenile European plaice experience higher growth rates and deposit wide, clear otolith increments when held under warmer temperatures (Karakiri and Westernhagen 1989).

Growth rates of juvenile fringed flounder, another small, subtropical flatfish, increase with increasing temperatures ranging from 14 to 29 °C (Reichert et al. 2000). The positive effect of warmer temperatures on growth in flatfishes does not continue indefinitely; once optimum temperatures are exceeded warmer temperatures can actually result in slower growth rates (May and Jenkins 1992). Growth rates of juvenile blackcheek tonguefish in Georgia increase at higher temperatures, but then decline sharply at extreme temperatures (Reichert et al. 2001). I found evidence that warm temperatures positively affected growth in both tonguefishes; warmer temperatures appeared to result in increased growth over the entire range of temperatures in which tonguefishes were collected. Thus, tonguefishes that settle within the estuary earlier may benefit from longer exposure to warm temperatures in early fall than would individuals settling during cooler months. Additionally, the utilization of shallow sites near the marsh edge (Chapter 3) may expose blackcheek tonguefish to low dissolved oxygen levels during evening hours when respiration of wetland plants may cause a greater decline in dissolved oxygen concentration than is evident in deeper waters (Kemp and Boyton 1980).

Interactions between offshore tonguefish and other species may be important. Growth rates of offshore tonguefish were significantly higher in shallower waters ($p = 0.0276$) despite the fact that distributional patterns of offshore tonguefish have indicated that individuals tend to occupy deeper waters and avoid shallow sites in coastal Louisiana (Chapter 3). Although the reasons for these contrasting results are not clear, there are some plausible explanatory hypotheses. Perhaps blackcheek tonguefish are agonistic to other tonguefishes, and so offshore tonguefish are simply displaced from more favorable shallow habitat by interactions with blackcheek tonguefish. Alternatively, offshore tonguefish may be more susceptible to predation by wading shorebirds than are blackcheek tonguefish (Kneib 1982; Leopold et al. 1998). Some

fishes may select sites that minimize the risk of predation at the expense of potential growth (Halpin 2000). Pigmentation patterns differ somewhat between species (Munroe et al. 2000), so perhaps blackcheek tonguefish can more easily blend in with muddy sediments common near the marsh edge. Light and/or turbidity may also be important in determining the distribution of these estuarine-dependent species (Blaber and Blaber 1980). Additionally, there may be differences between species with respect to selected substrate type due to differential burial capabilities (Stoner and Ottmar 2003).

I detected evidence of density-dependent growth for blackcheek tonguefish ($p = 0.0386$); no such relationship was evident for offshore tonguefish. Among flatfishes, density-dependent processes are typically most important among juveniles, and generally influence growth more so than mortality (van der Veer et al. 2000). Growth rates of European plaice are density-dependent; juvenile growth is significantly lower following periods of extremely high settlement than following periods of normal settlement (Modin and Pihl 1994). Growth of young-of-the-year winter flounder is also negatively related to density (DeLong et al. 2001). Density-dependent growth has not been identified in all flatfishes; growth rates of juvenile common sole are unaffected by high variability in conspecific densities (Rogers 1994). In this study conspecific densities negatively affected growth of blackcheek tonguefish whereas growth of offshore tonguefish was not affected. The apparent differential importance of density-dependent processes may function in structuring tonguefish populations in coastal Louisiana. Within the study area, mean densities (\pm SE) of offshore tonguefish were substantially higher than were mean densities of blackcheek tonguefish; offshore tonguefish density was $0.051 (\pm 0.0090)$ individuals m^{-2} while blackcheek tonguefish density was $0.016 (\pm 0.0015)$ individuals m^{-2} . Maximum conspecific densities were also highest for offshore tonguefish, with maximum

offshore tonguefish densities of 4.75 individuals m^{-2} as compared to 0.38 individuals m^{-2} for blackcheek tonguefish. Clearly density-dependence and potential intraspecific interactions appear to be more important for blackcheek tonguefish than for offshore tonguefish. Further studies on predation, substrate selection and interactions within and between species are needed to examine these hypotheses in more detail.

While not directly examined in the study, the importance of food availability is a factor that cannot be ignored. Growth rates of numerous flatfishes, as determined from field observations, including blackcheek tonguefish, are similar to those observed in laboratory studies where individuals were maintained under *ad libitum* feeding conditions, indicating that food resources do not limit growth (Reichert and van der Veer 1991; Amara et al. 2001).

Additionally, a study on other estuarine-dependent juvenile fishes in coastal Louisiana found that abiotic factors contribute more to the prediction of growth rates than does diet (Baltz et al. 1998). The growth rates of blackcheek tonguefish presented in this paper were substantially lower than the highest growth rates for the species as reported by Reichert et al. (1991). This difference is not necessarily related to food limitation in Louisiana, since Reichert et al. (1991) examined growth during the relatively warmer periods from late March through late August whereas I examined growth throughout the year. When cohort analysis is limited to comparable months, the mean (\pm SE) growth rates of blackcheek and offshore tonguefish increased to 0.38 ± 0.040 and 0.30 ± 0.095 , respectively. Food availability has been demonstrated to influence growth in other flatfishes. Growth rates of juvenile greenback flounder from Australia are significantly higher in areas supporting higher prey abundances, and most of the variability in growth is related to food supply (Jenkins et al. 1993). Growth rates of several fishes, including winter flounder, are potentially related to food availability in a New Jersey estuary (Sogard 1992).

Since both of these studies were conducted at temperate latitudes, one would expect an increase in the importance of food for juvenile tonguefishes in coastal Louisiana (Miller et al. 1991). The relationship between feeding and growth requires further examination in these estuarine-dependent tonguefishes.

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CHAPTER V.

COMPARATIVE PATTERNS OF RESOURCE UTILIZATION OF SYMPATRIC TONGUEFISHES (*SYMPHURUS*: CYNOGLOSSIDAE) WITHIN THE VERMILION AND BARATARIA ESTUARINE SYSTEMS, LOUISIANA

Introduction

Managers are constantly striving to find new and better ways to maintain and enhance the productivity of coastal resources. Whether it involves the deployment of artificial reefs to provide hard substrate for fisheries or the construction of freshwater diversions to reverse decades-long patterns of wetland loss, the coastal environment of the northern Gulf of Mexico is constantly being modified by new management practices. Recently implemented management plans have had mixed effects; the opening of the Caernarvon freshwater diversion in 1991 has had some positive effect in reducing land loss, but has also coincided with significant expected and unexpected changes in the abundance of numerous finfish and shellfish species (LDWF et al. 1998). Due to the complex relationship between fishes and their environment, it is important to consider the response to changing ecological situations of economically and ecologically important species when making critical management decisions.

Wetlands in Louisiana are currently being lost at a rate of 0.86% annually (Turner 1990). While land loss is a natural part of the destructional phase of the deltaic cycle due to compaction and subsidence (Coleman et al. 1998), current loss rates are substantially higher than expected solely from natural processes (Hatton et al. 1983). Numerous factors have been linked to high rates of land loss in coastal Louisiana, including canal dredging, decreased suspended sediment load in Mississippi River waters, extensive levee construction along the Mississippi River, and saltwater intrusion (Turner 1997). Although the relative importance of these factors is under

substantial debate (Turner 1997; Day et al. 2000; Gosselink 2001), patterns of land loss are most likely due to a combination of these factors.

Current coastal management practices have been implemented to reverse decades-long trends of land loss in coastal Louisiana, including the implementation of freshwater diversion projects. In 1991, the Caernarvon freshwater diversion began supplying fresh water to the Breton Sound estuary (LDWF et al. 1998), and in 2002 the Davis Pond freshwater diversion began supplying fresh water to the Barataria Bay estuary (LDNR 2002). These structures are intended to resemble natural patterns of flooding of the Mississippi River (Chatry and Chew 1985) and have been designed to stabilize current marsh elevations and stimulate land building processes by providing fresh water and sediment into rapidly subsiding marsh habitat (Roberts et al. 1992). Preliminary results indicate that these projects are having positive effects; wetland loss rates have stabilized after the introduction of fresh water into some systems (LDWF et al. 1998; LDNR 2002).

Freshwater diversions may also indirectly enhance the productivity of fisheries. The stabilization of marsh elevations should benefit many fish and macroinvertebrate species that utilize emergent vegetation (Weinstein 1979; Zimmerman et al. 1984; Baltz et al. 1993; Peterson and Turner 1994) by maintaining areas that may offer increased food availability and/or protection from potential predators (Boesch and Turner 1984). Diversions also provide nutrient input that should enhance primary productivity, and subsequently fisheries productivity (Martin 1992). Additionally, the input of fresh water maintains the strong salinity gradient required for many early life-history stages of estuarine-dependent fish and macroinvertebrate species (Gunter 1961; Gunter et al. 1964). Although environmental changes associated with the implementation of freshwater diversions may enhance fisheries productivity, these benefits do not apply equally

to all species. Abundances of some commercially and recreationally important species were significantly higher following the opening of the Caernarvon freshwater diversion in 1991 whereas other species declined in abundance (LDWF et al. 1998). Significant differences in community structure have also been identified between estuaries dominated by riverine input and estuaries deprived of riverine input (Jones et al. 2002; Baltz and Jones in press). Given the potential for significant changes, it is important to develop predictive models of the potential effects of freshwater input on commercially and ecologically important species before the implementation of such large-scale projects.

I examined patterns of resource utilization of two commonly occurring estuarine-dependent tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*), in both the Vermilion and Barataria systems in coastal Louisiana. The Vermilion estuarine system is dominated by discharge of fresh water and sediment from the Atchafalaya drainage basin. Within this area land-building processes exceed the high rates of land loss currently typical of coastal Louisiana (Roberts et al. 1997) with the influx of water and sediment discharge from the Atchafalaya of $5,520 \text{ m}^3 \text{ s}^{-1}$ and $9.5 \times 10^7 \text{ tons yr}^{-1}$, respectively (Milliman and Meade 1983; Mossa and Roberts 1990). In contrast, the Barataria system has been largely deprived of riverine input of fresh water and sediment beginning in the 1930s and has subsequently experienced some of the highest rates of land loss in coastal Louisiana (Evers et al. 1992). Both tonguefishes are among the four most abundant flatfishes within both the Vermilion (Baltz and Jones in press) and the Barataria (Allen and Baltz 1997) systems, and represent an excellent system to test hypotheses regarding the response of ecologically similar species to differing environmental conditions.

Patterns of resource utilization for blackcheek and offshore tonguefish were characterized within both the Vermilion and Barataria systems in separate beam-trawl studies at the

microhabitat level (Baltz 1990). Examination of microhabitat data from these comparable studies addressed three important questions: 1) Do seasonal patterns of environmental availability differ significantly between species and/or systems, 2) Do patterns of resource utilization by blackcheek and offshore tonguefish differ significantly between Vermilion and Barataria bays, and 3) Can ecological models developed in one system predict the changes in patterns that will be found under different environmental conditions in different systems? Enhanced understanding of resource use patterns between tonguefishes under substantially different salinity regimes may identify potential effects of freshwater diversions on these flatfishes, and these results may generalize to other estuarine-dependent nekton.

Materials and Methods

Study Area: Vermilion Bay

The Vermilion system is located in south central Louisiana and includes sampling sites within Vermilion and West Cote Blanche bays that are primarily influenced by discharge from the Atchafalaya Basin (Figure 5.1). Vermilion and West Cote Blanche bays are separated from the Gulf of Mexico by Marsh Island, and Vermilion Bay is connected to the Gulf through Southwest Pass, a narrow and deep (> 25 m in some places) channel on the west end of Marsh Island. East of Marsh Island the bays are open to the Gulf. The Atchafalaya coastal area is the largest estuary in Louisiana, covering an area of nearly 400,000 ha. The basin is currently managed by the U. S. Army Corps of Engineers for flood control and navigation, which has resulted in conversion from a brackish to a nearly freshwater tidal system. The Vermilion system lies within the Atchafalaya basin, and is west of the mouth of the Atchafalaya River. Freshwater inflow is primarily from the Atchafalaya River at its mouth and at the Wax Lake Outlet. In addition, the Gulf Intracoastal Waterway carries water east and west of the main river

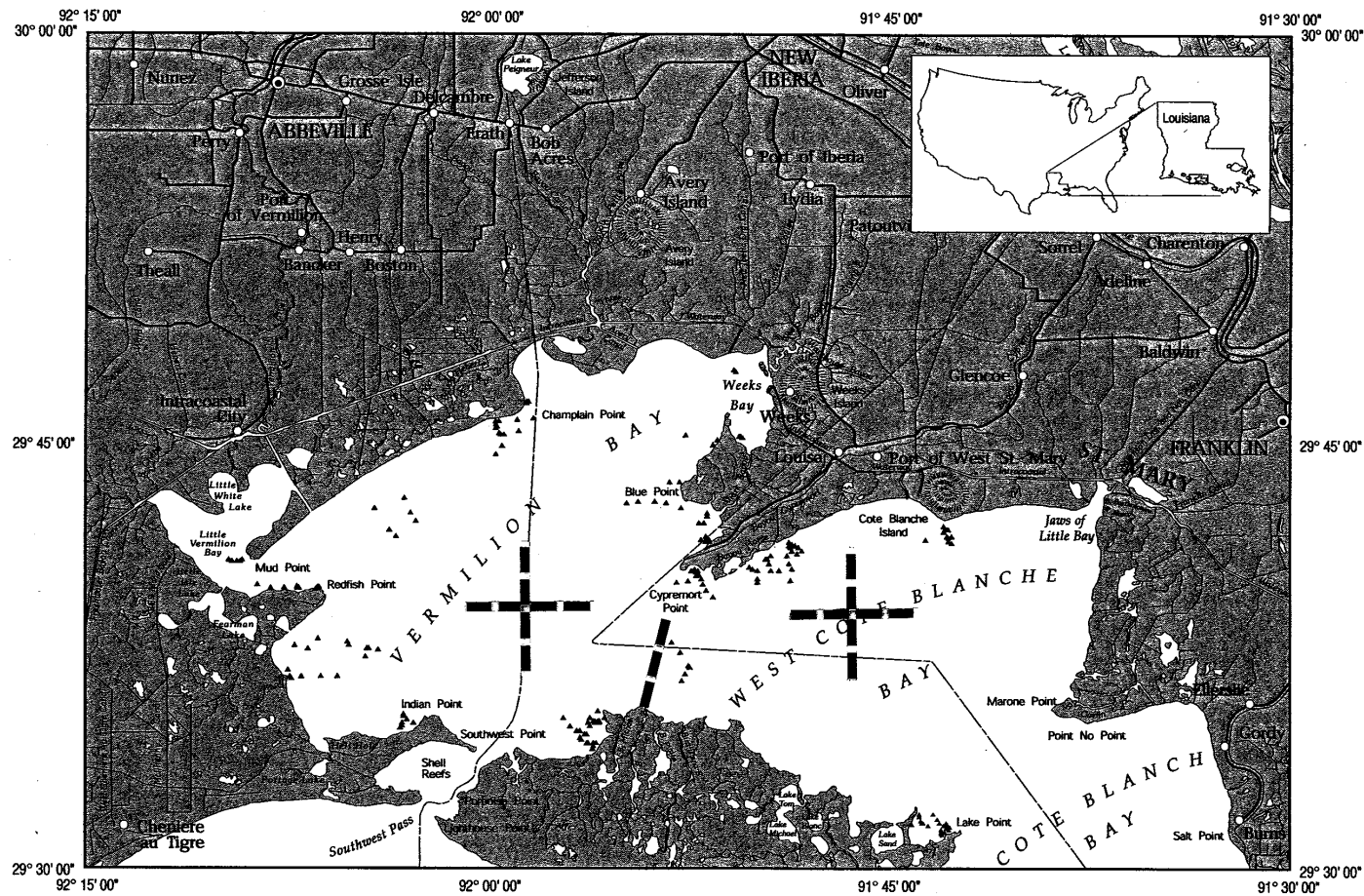


Figure 5.1. The Vermilion study area indicating beam-trawl sampling sites (triangle) and strata boundaries (crosses) for four strata in Vermilion Bay and four strata in West Cote Blanche Bay.

outlets where it enters the bays via several small channels. The Vermilion study area is shallow, with water depths rarely exceeding 4 m, and has a relatively flat bottom profile with surficial substrates dominated by fine sediments. The tidal system is microtidal (tides ≤ 0.3 m), predominantly diurnal, and generally dominated by winds. Wind direction and speed are the controlling factors for circulation, sediment transport, and suspended sediment concentrations within the system (Walker and Hammack 2000). East winds produce a westward flow of sediment-rich Atchafalaya River water along the coast, while west winds reverse the direction of plume movement and increase the area of the plume. Strong north winds, characteristic of common winter storms, cause rapid flushing from the shallow bays and water level changes in excess of 1 m.

Study Area: Barataria Bay

The Barataria system is the first major estuary west of the Mississippi River, and included sampling sites within Barataria and Caminada bays (Figure 5.2). Located between the natural levees of the river and the abandoned Bayou Lafourche distributary, the basin is roughly 110 km long and up to 50 km wide and has a saltmarsh area of 145,000 ha (Conner and Day 1987). The basin has been deprived of the overland flow of river water and sediments by a levee system completed in the 1930s – 40s and by the closure of the Bayou Lafourche-Mississippi River connection in 1902. The absence of riverine input of sediments and nutrients, combined with canal construction, saltwater intrusion, and subsidence, has contributed to an annual loss of wetlands in Louisiana of $65 \text{ km}^2 \text{ yr}^{-1}$ (Day et al. 1989). Currently, the main source of direct freshwater input into the basin is from precipitation, which averages 160 cm per year (Conner and Day 1987). The climate is subtropical, and the hydrography is primarily influenced by local precipitation, tidal flux, and prevailing winds. The recent opening of the Davis Pond Freshwater

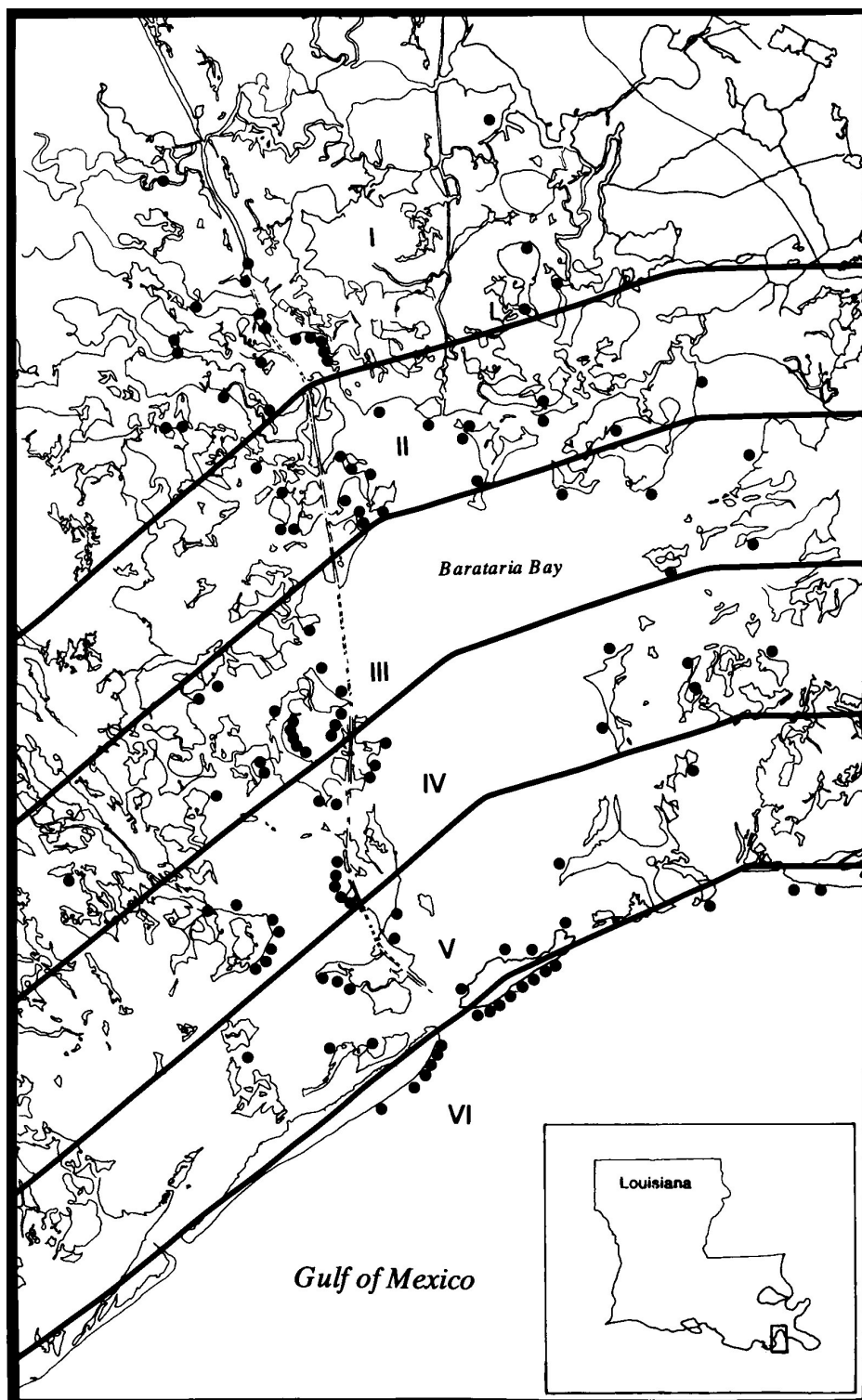


Figure 5.2. The Barataria study area indicating beam-trawl sampling locations (dots) and strata boundaries (Roman numerals I – VI).

Diversion in 2002 provides an additional source of fresh water and sediment in the basin intended to reverse the decades-long trend of land loss (LDNR 2002).

The saltmarsh portion of the Barataria system has salinities that vary both seasonally and spatially between 6 and 22 psu (Baltz et al. 1993). Water in the basin is turbid and shallow, with water depths generally less than 2 m. Seasonal winds easily dominate the microtidal system, which has a mean tidal range of 0.32 m (Childers et al. 1990). The dominant marsh vegetation is *Spartina alterniflora* (smooth cord grass), with *Juncus roemerianus* (black rush), *Distichlis spicata* (saltgrass), *Batis maritima* (saltwort), and *Salicornia virginica* (glasswort) also common to the study area.

Field Methods

Monthly collections of fishes were made from August 1998 to July 1999 in the Vermilion study area and from September 1992 to August 1994 in the Barataria study area. Juvenile tonguefishes were quantitatively collected using a 1-m beam-trawl with a uniform mesh size of 5 mm (Kuipers 1975). Kuiper's design was modified by the addition of a pair of polyvinyl chloride skids (10 x 50 cm) to facilitate sampling over the fine sediments prevalent in coastal Louisiana. Within each system a hierarchical sampling design was implemented in which the study area was broken down into strata, sampling locations and actual trawl sites. The Vermilion study area was stratified using four wedge-shaped sectors in Vermilion Bay and four rectangular sectors within West Cote Blanche Bay (Figure 5.1). Sampling locations were selected within each stratum to facilitate sampling over the range of saline-to-brackish estuarine conditions prevalent in the system (Baltz and Jones in press). During each month three to seven locations were selected to sample a variety of physiochemical conditions, and all strata were sampled seasonally. Wind and fetch within this open system often resulted in wave heights that precluded

some sampling locations from consideration. Within the more protected Barataria study area (Figure 5.2), sampling effort was divided into six strata ranging from the near shore zone in the Gulf of Mexico to the brackish marsh some 30 km inland (Allen and Baltz 1997). Within each stratum random locations were selected each month to sample fishes associated with a variety of substrates and environmental conditions. This approach allowed for the description of population responses of juvenile blackcheek and offshore tonguefish along environmental gradients in both systems.

Sampling within strata at a given location involved making a series of three to five tows at sites parallel to the shoreline, typically the marsh edge. Each subsequent tow was more distant from the shoreline and generally in deeper water. Tow direction was parallel to the shoreline to minimize environmental heterogeneity within each sample, and tow duration was kept short (1 min for Vermilion Bay and 1-2 min for Barataria Bay) to minimize environmental heterogeneity and net clogging. For tows within the Vermilion study area, sampling site positions and trawling speed over ground (SOG) were determined with a Garmin 45 GPS. At a mean SOG of 4.9 km/hr (2.7 knots), each 1-min tow covered a mean (\pm 1SD, $N = 209$) area of approximately 80 m^2 (\pm 18%) that varied with current directions and velocity as well as bottom type (Allen and Baltz 1997). For the Barataria Bay tows, a sample of towed distances was measured between stakes to estimate coverage over substrate types (Allen and Baltz 1997). Each tow covered a mean (\pm 1SD) area of approximately $152 \pm 14.8 \text{ m}^2$, which varied substantially ($CV = 9.7\%$) over substrate types: silt (138 m^2), clay (142 m^2), sand (158 m^2), and plant detritus (170 m^2). To compare relative densities at all sites, catch data were transformed to catch per minute.

Several environmental variables were examined at each tow site. In the Vermilion study area, salinity (psu), temperature ($^{\circ}\text{C}$), and dissolved oxygen concentration (mg l^{-1}) were

measured with a Hydrolab model SRV2-SU meter, while in the Barataria study area, salinity (psu) and temperature (°C) were measured using a Yellow Springs Instrument (YSI) Model 33 salinity, conductivity and temperature meter, and dissolved oxygen concentration was measured using a YSI Model 57 oxygen meter. Turbidity samples were collected in the field and maintained in cold storage until they were read on a Monitek model 21 PE portable nephelometer for the Vermilion study, whereas turbidity was not examined within the Barataria study. Substrate type was identified during each tow from surficial samples that were characterized in terms of dominant components and coded on an ordinal scale of particle size. For Vermilion samples, substrate was coded as 1: clay, 2: mud (clay + silt), 3: silt, 4: sand, 5: plant detritus, and 6: shell and shell fragments, whereas for Barataria samples, substrate was coded as 1: clay, 2: silt, 3: sand, 4: plant detritus (primarily *Spartina alterniflora*), and 5: shell and shell fragments. To facilitate comparisons between bays, mud was coded as 1.5 and the code for all other substrate types was adjusted to those used in the Barataria study. Minimum and maximum water depths (m) were used to calculate median depth, and an estimate of the distance from shore (m) was also noted.

Trawl samples were carefully sorted in the field to separate nekton. Samples collected in the Vermilion system were initially preserved in a 10% solution of stock formaldehyde solution (37%) then washed in water and transferred to 95% ethanol, whereas samples collected in the Barataria system were preserved in 95% ethanol. Tonguefishes were identified in the laboratory using keys and descriptions by Hoese & Moore (1977), Munroe (1991), and Munroe (2000), and were counted and measured to the nearest mm standard length (SL)

Analytical Methods

Multivariate analysis of variance (MANOVA), using general linear models and the least-square-mean method (SAS Institute 1996), was used to compare means of environmental

variables between systems (Barataria and Vermilion) and among seasons. Transformed environmental variables ($\log_{10} x + 1$) were used to improve the normality of residuals. When normality of the residuals was unattainable, careful visual examination of residual plots and residual biplots was conducted to ascertain the degree of violation of the normality assumption and to confirm variance homogeneity. MANOVA is relatively robust with respect to moderate violations of the assumption of normality (Johnson and Field 1993), and no problems with heteroscedasticity were detected. Seasons were defined as: fall (September – November), winter (December – February), spring (March – May), and summer (June – August). Posterior testing of environmental variables found to differ significantly among seasons and bays was conducted using Tukey's adjustment for multiple pairwise comparisons.

MANOVA was also used to compare mean resource utilization of tonguefishes between species, study areas, and size classes. Tonguefishes were assigned to four size classes (SC I – IV) to examine size-related patterns of microhabitat use (Livingston 1988) as SC I: ≤ 15 mm, SC II: > 15 to 30 mm, SC III: > 30 to 85 mm, and SC IV: > 85 mm SL. The first three size classes represent juvenile tonguefishes, while the largest size class included individuals at or approaching sexual maturity (Munroe 1998; Terwilliger and Munroe 1999). Only juveniles in SC II and SC III were included in the MANOVA since other size classes were not collected in both study areas for both species. One record was generated for each species and size class present in each sample, and data from both studies was combined for the analysis. Univariate means and standard errors of environmental variables for species were calculated by treating each beam-trawl collection as an independent sample. I attempted to standardize the data by calculating relative abundances of species and size classes as number of individuals captured per minute (total number of individuals divided by tow duration in minutes). The analysis was

weighted by the number of individuals collected per minute, which accounts for differences in abundances without artificially inflating the degrees of freedom (Hurlbert 1984). Posterior testing of environmental variables found to differ significantly between both species, both study areas and both size classes was conducted using Tukey's adjustment for multiple pairwise comparisons.

Size-specific patterns of microhabitat use by blackcheek and offshore tonguefishes between study areas were examined via principal component analysis (PCA). A PCA was conducted on the combined environmental data from both study areas to examine the variability of six environmental variables (turbidity was excluded since it was not measured within the Barataria system). The PCA was conducted using the Factor Procedure in SAS, and the first three factors were rotated using the varimax option (SAS Institute 1996). The PCA was used to resolve six intercorrelated environmental variables into three orthogonal variables based on the correlation matrix to facilitate visualization and simplify comparisons between species and bays and among size classes. Environmental variables in 805 samples without missing data were used to calculate variable loadings and generate principal component scores for each sample. Mean principal component scores for each size class within species and bay were calculated by treating each sample as an independent observation and weighting the analysis by catch per minute. I then plotted size classes in PCA space using calculated means as centroids. The variance about the centroids was estimated as the means of standard errors on each of three principal component axes for each combination of bay, species and size class. I then estimated 95 % confidence intervals about the centroids by doubling the standard errors. These confidence intervals allow for visual comparisons of resource utilization between bays and species and among classes along major gradients of environmental variation.

Results

Environmental conditions differed significantly between study areas and among seasons (MANOVA, $F = 51.08$, $p < 0.0001$). Significant differences were detected for all six environmental variables examined (Table 5.1). Salinities were generally higher in fall than in other seasons for both systems. Temperature and dissolved oxygen were negatively related, with highest temperatures and lowest dissolved oxygen concentrations occurring during summer months. No seasonal differences in distance from shore or substrate were detected within either system, although median depths sampled within the Barataria study area were highest in fall. Significant differences were detected between bays with respect to all environmental variables. Most notably, salinity was significantly higher in the Barataria study area over all seasons. Seasonal differences in temperature and dissolved oxygen concentration were also evident between systems; temperatures were higher in winter and lower in spring within the Barataria study area, while dissolved oxygen concentrations were higher during fall and winter within the Vermilion study area.

Within the Vermilion study area a total of 177 blackcheek tonguefish and 123 offshore tonguefish were collected in 211 samples from August 1998 to July 1999. Blackcheek tonguefish occurred in 50 trawls for a frequency of occurrence of 0.24, and offshore tonguefish occurred in 26 trawls for a frequency of occurrence of 0.12. Both species co-occurred in 13 samples for a joint frequency of occurrence of 0.06. Within the Vermilion system, observed densities of blackcheek and offshore tonguefish were 0.83 and 0.58 individuals min^{-1} , respectively. Blackcheek tonguefish collected within the Vermilion system ranged from 20 to 104 mm SL, while offshore tonguefish ranged from 17 to 78 mm SL. Within the Barataria study area, 631 blackcheek tonguefish and 2,897 offshore tonguefish were collected in 594

Table 5.1. Seasonal patterns of resource availability within the Vermilion and Barataria study areas as estimated by least-square means (\pm SE) for six environmental variables examined during both studies. Significant differences among seasons and bays ($P \leq 0.050$) are identified by different letters, reading horizontally. Seasonal ranges (min - max) are reported below means for each variable.

Variable	Vermilion Study Area			
	Winter	Spring	Summer	Fall
Median depth (m)	1.9 \pm 0.08 CDE (1.2 - 2.8)	1.9 \pm 0.09 BCE (1.2 - 2.7)	2.0 \pm 0.09 CDE (1.0 - 3.2)	1.7 \pm 0.09 ABD (1.0 - 2.6)
Distance from shore (m)	777 \pm 76.9 D (30 - 4723)	484 \pm 81.3 CD (30 - 2019)	509 \pm 83.7 ABCD (5 - 3148)	751 \pm 81.3 ABD (25 - 4074)
Substrate code	2.4 \pm 0.16 ABC (1 - 5)	2.8 \pm 0.17 C (1 - 5)	2.6 \pm 0.17 BC (1 - 5)	2.5 \pm 0.17 BC (1 - 5)
Salinity (psu)	3.4 \pm 0.74 B (0.0 - 6.9)	2.0 \pm 0.78 A (0.0 - 7.4)	2.0 \pm 0.81 A (0.0 - 8.5)	5.0 \pm 0.78 C (1.6 - 8.4)
Dissolved Oxygen (mg l ⁻¹)	10.4 \pm 0.18 E (9.3 - 11.9)	8.3 \pm 0.19 BC (6.0 - 12.4)	7.3 \pm 0.19 A (5.2 - 10.2)	9.2 \pm 0.19 CD (4.9 - 13.6)
Temperature (° C)	13.1 \pm 0.46 A (9.2 - 18.2)	23.9 \pm 0.49 D (15.9 - 29.9)	29.2 \pm 0.50 E (27.8 - 32.4)	24.0 \pm 0.49 D (19.1 - 31.9)
Sample Size	58	52	49	52

(Table 5.1 cont.)

Variable	Barataria Study Area			
	Winter	Spring	Summer	Fall
Median depth (m)	1.6 ± 0.05 A (0.8 - 4.2)	1.8 ± 0.06 ABC (0.7 - 4.5)	1.7 ± 0.06 AB (0.7 - 6.1)	1.9 ± 0.06 CDE (0.8 - 5.9)
Distance from shore (m)	343 ± 30.7 ABC (9 - 3660)	270 ± 33.4 AB (8 - 1400)	297 ± 34.3 A (5 - 3215)	279 ± 35.6 A (5 - 2010)
Substrate code	2.2 ± 0.08 ABC (1 - 5)	2.0 ± 0.09 A (1 - 5)	2.0 ± 0.09 AB (1 - 5)	1.9 ± 0.10 A (1 - 5)
Salinity (psu)	11.5 ± 0.49 DE (0.9 - 23.8)	11.9 ± 0.53 EF (0.1 - 22.8)	10.9 ± 0.55 BD (0.0 - 25.0)	14.5 ± 0.57 F (2.3 - 29.2)
Dissolved Oxygen (mg l ⁻¹)	9.3 ± 0.10 D (4.4 - 12.4)	8.3 ± 0.11 B (4.5 - 10.2)	7.9 ± 0.12 AB (4.4 - 11.7)	8.1 ± 0.12 B (5.1 - 11.3)
Temperature (° C)	15.7 ± 0.28 B (10.2 - 21.0)	21.4 ± 0.30 C (13.1 - 30.5)	30.0 ± 0.31 E (27.5 - 32.4)	23.9 ± 0.32 D (14.0 - 31.0)
Sample Size	174	147	139	134

independent samples collected from September 1992 to August 1994. Blackcheek tonguefish occurred in 231 trawls and offshore tonguefish occurred in 229 trawls, both with a frequency of occurrence of 0.39. Individuals of both species co-occurred in 92 trawl samples, for a joint frequency of occurrence of 0.15. Within the Barataria system, observed densities of blackcheek and offshore tonguefish were 0.76 and 3.48 individuals min^{-1} , respectively. Blackcheek tonguefish collected within the Barataria system ranged from 13 to 128 mm SL, while offshore tonguefish ranged from 10 to 120 mm SL.

Post-settlement juveniles (SC I) were not collected for either blackcheek or offshore tonguefish within the Vermilion study area (Figure 5.3). Juvenile densities were highest during fall for both species. For offshore tonguefish, juvenile densities dropped substantially during winter and were absent during spring; no adult offshore tonguefish (SC IV) were collected. Patterns of blackcheek tonguefish density were similar to those observed in offshore tonguefish, except densities were higher in winter and spring than they were for offshore tonguefish. Blackcheek tonguefish adults (SC IV) were most abundant during summer months. Seasonal patterns within the Vermilion study area were similar to observed patterns in the Barataria study area for both species, except that offshore tonguefish persisted within the Barataria system into early adulthood (SC IV), leaving the estuary between spring and summer (Chapter 2).

Mean resource utilization of tonguefishes differed significantly between species, size classes and study areas (MANOVA, $F = 15.80$, $p < 0.0001$). Significant differences were detected for all six environmental variables analyzed (Table 5.2). Several notable differences were detected when comparing resource utilization between study areas. Older blackcheek tonguefish juveniles (SC III) used significantly shallower waters than similarly sized offshore tonguefish juveniles in the Barataria study area, while this trend was reversed within the

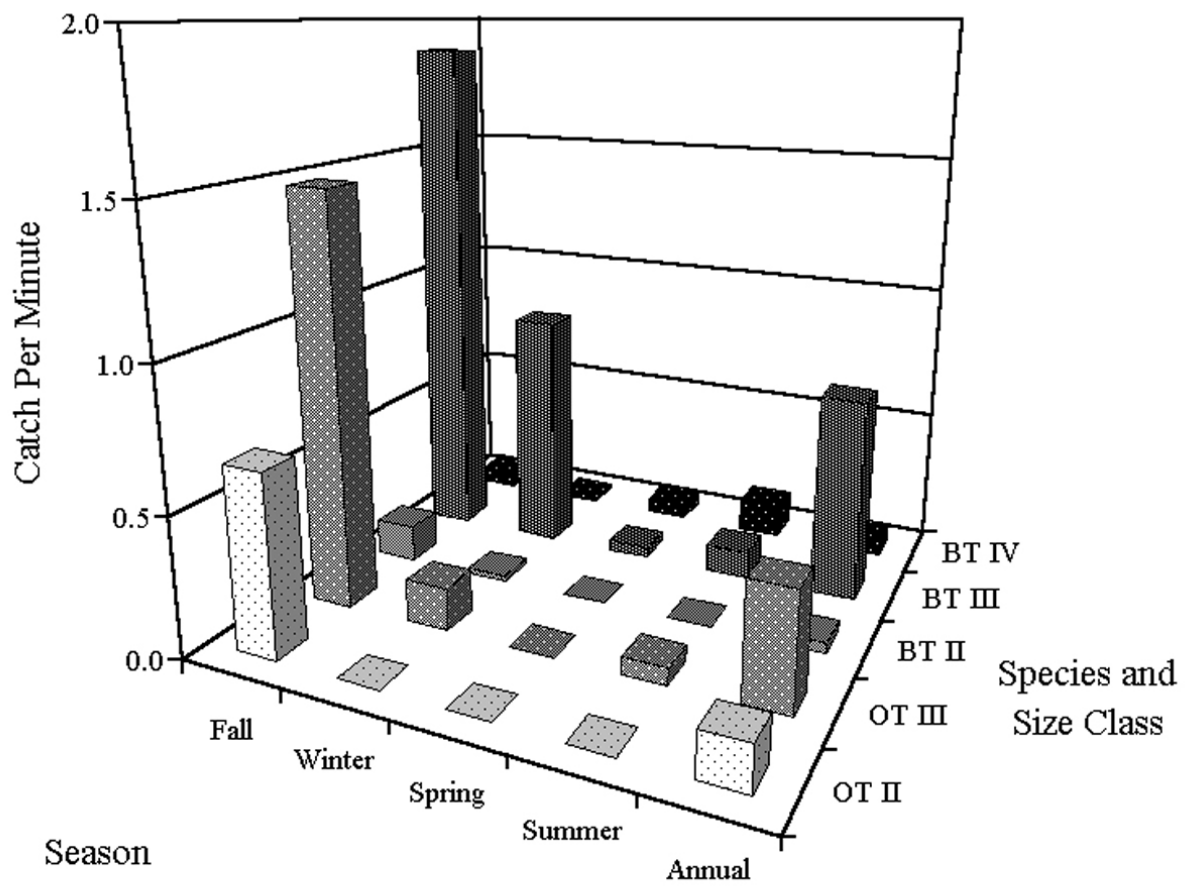


Figure 5.3. Seasonal size-specific densities for blackcheek (BT) and offshore (OT) tonguefish collected in the Vermilion study area.

Table 5.2. Comparisons of mean environmental conditions found to differ significantly among species (BT – blackcheek tonguefish, OT – offshore tonguefish), study areas and size classes. N represents the number of independent samples. Significant differences of post-hoc comparisons made using Tukey’s adjustment for pairwise comparisons ($p \leq 0.0423$) are indicated by different letters, reading vertically.

Taxon	Study Area	Size Class	N	Number of Individuals	Median depth (m)	Distance from shore (m)
BT	Barataria	$> 15 \leq 30$ mm	50	96	1.4 ± 0.25 AB	225 ± 629.6 AB
BT	Vermilion	$> 15 \leq 30$ mm	7	8	1.6 ± 0.11 AB	283 ± 264.3 AB
BT	Barataria	$> 30 \leq 85$ mm	158	408	1.5 ± 0.12 A	223 ± 294.1 AB
BT	Vermilion	$> 30 \leq 85$ mm	45	156	1.8 ± 0.02 B	836 ± 59.9 B
OT	Barataria	$> 15 \leq 30$ mm	90	254	1.9 ± 0.16 ABC	383 ± 395.2 AB
OT	Vermilion	$> 15 \leq 30$ mm	9	34	1.7 ± 0.05 AB	240 ± 128.2 A
OT	Barataria	$> 30 \leq 85$ mm	198	2593	2.3 ± 0.06 C	616 ± 149.4 AB
OT	Vermilion	$> 30 \leq 85$ mm	26	89	1.7 ± 0.03 A	601 ± 79.2 AB

Table 5.2. (cont.)

Taxon	Study Area	Size Class	Dissolved oxygen (mg l ⁻¹)	Temperature (° C)	Salinity (psu)	Substrate Code
BT	Barataria	> 15 ≤ 30 mm	9.1 ± 0.77 ABC	17.8 ± 3.78 ACD	10.9 ± 1.60 ABCD	1.5 ± 0.53 ABC
BT	Vermilion	> 15 ≤ 30 mm	9.2 ± 0.32 ABC	24.3 ± 1.58 BCD	6.9 ± 0.67 ABCD	2.4 ± 0.22 B
BT	Barataria	> 30 ≤ 85 mm	8.9 ± 0.36 AB	19.4 ± 1.76 ABC	10.2 ± 0.75 C	1.6 ± 0.25 A
BT	Vermilion	> 30 ≤ 85 mm	10.2 ± 0.07 C	20.1 ± 0.36 AB	5.8 ± 0.15 A	2.2 ± 0.05 B
OT	Barataria	> 15 ≤ 30 mm	9.3 ± 0.48 ABC	17.1 ± 2.37 AC	11.7 ± 1.00 C	2.1 ± 0.33 ABC
OT	Vermilion	> 15 ≤ 30 mm	8.3 ± 0.16 A	26.3 ± 0.77 D	7.7 ± 0.33 C	1.9 ± 0.11 ABC
OT	Barataria	> 30 ≤ 85 mm	8.7 ± 0.18 AB	16.5 ± 0.89 A	16.8 ± 0.38 D	2.6 ± 0.13 C
OT	Vermilion	> 30 ≤ 85 mm	9.1 ± 0.10 B	23.0 ± 0.48 C	6.8 ± 0.20 B	2.2 ± 0.07 B

Vermilion study area. Offshore tonguefish juveniles used significantly higher temperatures within the Vermilion system than they did in the Barataria system. Salinities used were generally lower within the Vermilion study area than they were within the Barataria study area for both species. Within the Barataria system older juvenile offshore tonguefish (SC III) used significantly higher salinities than did younger juveniles (SC II) while younger juveniles used higher salinities in the Vermilion system. In addition, older blackcheek tonguefish juveniles (SC III) used finer substrates than did similarly sized offshore tonguefish in the Barataria study area; within the Vermilion study area both species utilized similar substrates.

A PCA on the combined environmental data from the Vermilion and Barataria systems resolved six intercorrelated environmental variables into three principal components that explained 66 % of the environmental variability (Table 5.3). The first component loaded positively for temperature and negatively for dissolved oxygen, and was interpreted as a seasonal component. The second component loaded positively for median depth and distance from shore, and was interpreted as a spatial component. The third component loaded positively for substrate and salinity. There was evidence of ecological segregation (Ross 1986) between and within species in both the Vermilion and Barataria study areas along all three axes (Figure 5.4). Tonguefishes within the Vermilion study area used generally finer substrates and lower salinities than they used in the Barataria study area for all species and size classes collected. Additional patterns of environmental usage persisted between both study areas; as size increased juvenile tonguefishes of both species typically used deeper waters farther from shore. Other patterns differed substantially between the two study areas. Within the Barataria study area blackcheek tonguefish juveniles used warmer waters than did similarly sized offshore tonguefish, while in the Vermilion study area, blackcheek tonguefish juveniles used cooler waters than did juvenile

Table 5.3. Principal component scores for environmental variables in the Barataria and Vermilion study areas. Magnitude and signs of individual component loadings indicate strength and direction of each variables influence on a principal component. The variance explained by the eigenvalue associated with each principal component is expressed as absolute, proportional and cumulative values.

Environmental variable	Principal Component		
	1	2	3
Median depth	0.13	0.74	0.38
Distance from shore	-0.17	0.83	-0.14
Substrate code	0.01	0.21	0.47
Salinity	-0.07	-0.15	0.85
Dissolved oxygen	-0.86	0.10	-0.01
Temperature	0.87	0.03	-0.05
Variance explained	1.53	1.30	1.11
Proportion of variance explained	0.26	0.22	0.17
Cumulative variance explained	0.26	0.48	0.65

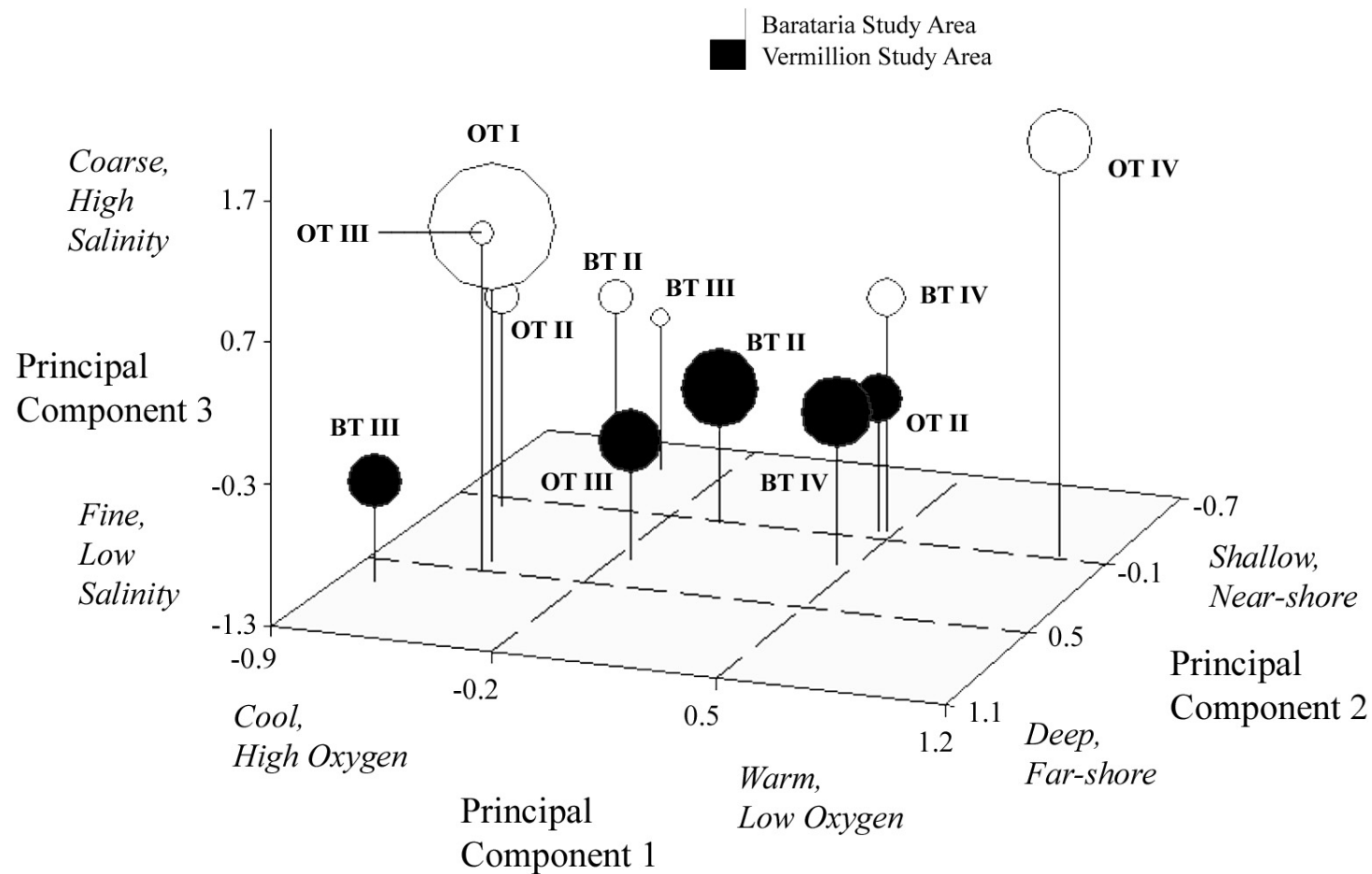


Figure 5.4. Size-specific microhabitat use patterns of blackcheek and offshore tonguefish in three-dimensional principal component space. Balloons indicate location of centroids, with balloon radii representing two standard errors about the mean. Species codes are: BT = blackcheek tonguefish, and OT = offshore tonguefish. Size class intervals are I: ≤ 15 mm; II: > 15 to 30 mm; III: > 30 to 85 mm, and IV: > 85 mm SL.

offshore tonguefish. In addition, blackcheek tonguefish juveniles generally used substantially deeper waters farther from shore than offshore tonguefish within the Barataria system; within the Vermilion system blackcheek tonguefish juveniles typically used deeper waters farther from shore than did similarly sized offshore tonguefish. Ontogenetic differences between study areas were also evident. Older juveniles of both species typically used warmer waters with lower dissolved oxygen concentrations in the Barataria system, while in the Vermilion system, older juveniles used cooler waters with higher dissolved oxygen concentrations.

Discussion

Significant differences in environmental availability were detected between the Barataria and Vermilion study areas, and potentially affected the distributional patterns of blackcheek and offshore tonguefish within these systems. Relative abundances of blackcheek tonguefish were highest within the Vermilion study area, which is characterized by lower salinities, while relative abundances of offshore tonguefish were highest in the higher salinities of the Barataria study area. Size-specific patterns of resource utilization differed substantially between systems for both species. Blackcheek tonguefish juveniles used generally warmer sites with higher dissolved oxygen concentrations than did similarly sized offshore tonguefish juveniles within the Barataria study area; these trends were reversed in the Vermilion study area. Ontogenetic shifts into deeper waters farther from shore as size increased were evident for both species in both systems.

Significant seasonal and annual differences in environmental conditions were detected between the Vermilion and Barataria study areas. Most notably, mean salinities were significantly higher within the Barataria study area than they were within the Vermilion study area across all seasons; maximum salinities encountered within the Vermilion system never exceeded the mean seasonal salinities within the Barataria system (Table 5.1). Salinity

differences are due primarily to the influence of the Atchafalaya River on the Vermilion system and the reduction of riverine input into the Barataria system. These environmental differences may be related to the vastly different hydrological properties of the two systems. Land building processes within the Atchafalaya and Wax Lake deltas offset high rates of land loss evident elsewhere in coastal Louisiana (Roberts et al. 1997), whereas land loss rates remain high within the Barataria Bay estuary (Evers et al. 1992). The combined water and sediment discharges of the Mississippi and Atchafalaya rivers are $18,400 \text{ m}^3 \text{ s}^{-1}$ and $2.1 \times 10^8 \text{ tons yr}^{-1}$ (Milliman and Meade 1983). Of this total, approximately 30% of the water flow and 40 to 50% of the sediment load are carried by the Atchafalaya River (Mossa and Roberts 1990). In contrast, the Barataria system has largely been deprived of riverine input of fresh water and suspended sediment since the early twentieth century (Conner and Day 1987). The recent opening of the Davis Pond Freshwater Diversion in 2002 has provided the Barataria system with an additional source of fresh water and suspended sediments, and although salinities will not be maintained at the low levels seen within the Vermilion system, current management plans call for substantial freshening of the upper reaches of the basin (LDNR 2002).

Resource utilization along temperature and dissolved oxygen gradients differed substantially between systems for both species. In the Barataria study area, offshore tonguefish juveniles generally were found in cooler waters than were blackcheek tonguefish; however, in the Vermilion study area offshore tonguefish used warmer temperatures than blackcheek tonguefish (Table 5.2; Figure 5.4). Additionally, offshore tonguefish life history stages were collected in substantially warmer waters in the Vermilion study area than they were in the Barataria study area. These differences in temperature utilization may play an important role in the seasonal distribution of offshore tonguefish within the Vermilion system. Juveniles began

appearing within both systems during summer months following a protracted spring – summer spawning period corresponding to periods of thermal maxima (Olney and Grant 1976; Munroe 1998). Adult offshore tonguefish were absent within the Vermilion study area; the largest offshore tonguefish collected was only 78 mm SL as opposed to 120 mm SL within the Barataria study area. Within the Barataria study area, offshore tonguefish adults moved offshore earlier than did adult blackcheek tonguefish (Chapter 2). Adults of estuarine-dependent species typically move offshore and recruit into reproductive populations in response to warm summer temperatures (Gunter 1938; Gunter 1945; Miller 1965; Olney and Grant 1976); the movement of offshore tonguefish out of inshore estuaries may potentially be initiated by cooler temperatures than similar movement of blackcheek tonguefish. Coincidentally, offshore tonguefish may have moved out of the Vermilion study area prior to maturity due to the high spring temperatures within the system.

Patterns of resource utilization along depth and distance-from-shore gradients differed substantially between species in the two study areas. Blackcheek tonguefish generally used shallower sites nearer to shore than did offshore tonguefish in the Barataria study area, whereas offshore tonguefish used shallower sites nearer to shore in the Vermilion study area. These differences appear driven by the use of deeper, far-shore waters by blackcheek tonguefish in the Vermilion system; comparisons of similarly-sized individuals indicate that offshore tonguefish used similar depths and distances between systems whereas all size classes of blackcheek tonguefish examined were found in deeper waters farther from shore in the Vermilion study area (Figure 5.4). These differences may be related to the quality and quantity of marsh-edge habitat between estuaries. Blackcheek tonguefish juveniles occur in substantial numbers along the marsh edge in Louisiana (Baltz et al. 1993). The conversion of intact marsh into open water is a

natural part of the deltaic cycle that commences after initial delta abandonment (Coleman et al. 1998). As marsh is lost the amount of available edge habitat increases, potentially resulting in increased productivity among species that utilize the marsh-edge ecotone (Browder et al. 1985). Areas in which land building processes are still dominant may have less available marsh edge than areas experiencing high rates of land loss, limiting the quantity of marsh-edge habitat available as a source of food and/or refugia (Boesch and Turner 1984). Thus the decreased availability of edge habitat in the Vermilion study area may alter the distribution of blackcheek tonguefish juveniles into deeper waters. Alternatively, dominant offshore tonguefish may displace blackcheek tonguefish into shallow areas in the Barataria system, but not in the Vermilion system where they are relatively less abundant.

The low salinities within the Vermilion system appear to favor blackcheek tonguefish while the higher salinities within the Barataria system appear to favor offshore tonguefish. This study focused on patterns of habitat utilization, and not patterns of selection or preference (Baltz 1990), so these results are not necessarily a good indication of conditions that are essential for these species (Minello 1999). Nevertheless, there are clearly some underlying factors that favor blackcheek tonguefish within Vermilion Bay and offshore tonguefish in Barataria Bay. Both tonguefishes, like many estuarine-dependent species, are generally euryhaline with respect to the salinities in which they can occur (Allen and Baltz 1997; Jones et al. 2002; Chapter 2). However, examination of salinity suitabilities from the Barataria study area indicate that lower salinities were most suitable for juvenile (SC III) blackcheek tonguefish, while higher salinities were most suitable for offshore tonguefish (Chapter 2). Salinity can have a tremendous influence on the distribution of estuarine-dependent species (Gunter 1961; Gunter et al. 1964). Given the significantly lower salinities within the Vermilion study area, the high relative

densities of blackcheek tonguefish in the Vermilion study area and of blackcheek tonguefish in the Barataria study area are expected and were predicted by PCA models describing resource utilization by both tonguefishes along salinity and other environmental gradients (Allen and Baltz 1997; Chapter 2). The abundances of several other fish and macroinvertebrate species in the Vermilion study area changed in a predictable manner based on PCA plots from the Barataria study area. Several species, including fringed flounder (*Etropus crossotus*), roughneck shrimp (*Trachypenaeus similis*), and lesser blue crab (*Callinectes similis*), used waters with relatively high salinities within the Barataria study area (Allen and Baltz 1997, Jones et al. 2002); all three species were either rare or absent within the Vermilion study area (Baltz and Jones in press). In contrast, hogchoker (*Trinectes maculatus*) were the least abundant flatfish within the Barataria system but were commonly collected in the lower salinity waters within the Vermilion system (Allen and Baltz 1997, Jones et al. 2002). Thus, at the species level, community structure changes with some predictability to differences in salinity. Accordingly, PCA models developed under a specific set of environmental conditions can be used to predict the direction of change under various environmental stresses or management scenarios.

Numerous anthropogenic stressors have been linked to changes in distribution, abundance, and community structure in coastal Louisiana (Chesney et al. 2000; Chesney and Baltz 2001), including changes in both temperature and salinity (Baltz and Jones in press). The implementation of freshwater diversions is intended to stabilize marsh habitat (LDNR 2002), but may also enhance fisheries by increasing primary and secondary productivity (Bahr et al. 1982). While this may or may not be the case, it is clear that such management practices can have deleterious effects on some species. This study indicates that changes in salinity, among other environmental factors, may affect abundances of tonguefishes within inshore estuaries, and have

the potential to influence other estuarine-dependent species as well. The magnitude of shifts in the distribution and abundances of estuarine-dependent species and life history changes are not always easily predictable; however, directional changes are more easily predicted, and so should be considered when management practices call for the alteration of environmental conditions within an estuary.

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CHAPTER VI.

QUALITATIVE MODELING OF THE ECOLOGY OF TONGUEFISHES IN COASTAL LOUISIANA

Introduction

Recent trends in fisheries ecology have involved a shift in focus from a single-species approach (Baltz 1990) to studies at the community level (Crowder 1990). These two approaches are not necessarily mutually exclusive; by characterizing patterns of resource utilization for a given species at the microhabitat level, researchers can gain an understanding of environmental conditions that are favorable for a given species or life history stage and begin to understand interactions between species and the factors that determine community structure. Nevertheless, fish populations are not isolated, and cannot be fully examined apart from other populations with which they interact. They are parts of communities, and their resource needs change as they grow and age (Livingston 1988).

Determining whether distributional patterns are due to environmental preferences of a species or interactions with other species is often difficult. Observed patterns in distribution may result from direct selection by a species for locations along environmental gradients (i.e., physiological optima and limits), or may instead result from direct or indirect interactions through other species (competitors, predators or prey). Evaluation of these interactions requires a multi-species approach that can combine the direct relationships among predators, prey and competitors as well as the influence of other environmental factors. Additionally, it is important to incorporate complex interactions involving indirect responses to accurately explore potential changes in a given community that may result from ecological or environmental disturbances.

Qualitative models, such as loop analysis, can be utilized to examine direct and complex indirect interactions at the community level without the knowledge of quantitative details (Lane

and Collins 1985; Stone 1990; Bodini 1998; Bodini 2000). In a loop model, the direct interactions among organisms and abiotic variables are represented graphically (Puccia and Levens 1991). Interactions among species and other environmental variables are represented by simple direct relationships as a positive interaction (+1), negative interaction (-1), or no interaction (0). By examining the feedback through specific loops, or circular pathways that are traced through direct interactions, one can determine the direction of changes (i.e., increase, decrease, or remain unchanged) in the community variables given a sustained change in the numbers of one or more other community variables. These analyses do not necessitate the precise quantification of direct linkages required for more complex quantitative models, and so can be constructed with a basic knowledge of the natural history of the communities being modeled. Results from a loop analysis can provide insight into the outcome of sustained alterations of the density or concentration of one or more biotic or abiotic variables (Bender et al. 1984), and can also examine confidence in model predictions arising from the analysis (Dambacher et al. 2002). Qualitative loop models are less rigorous than quantitative models, and they cannot provide quantitative predictions.

I used loop analyses to model the ecological interactions between two sympatric tonguefishes in coastal Louisiana. The blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*) commonly occur in coastal Louisiana waters throughout the year (Baltz et al. 1993; Allen and Baltz 1997; Baltz and Jones in press). Both species utilize inshore estuaries as nursery habitat; after spending nearly a year within the estuary, juveniles move offshore and recruit into adult populations. These species represent an interesting system to examine the interrelationships among ecologically similar species within highly productive estuarine habitat in coastal Louisiana.

Several loop analyses were conducted to examine direct and indirect interactions among life history stages of tonguefishes within a simplified benthic food web. Interactions were incorporated into models to examine potential effects of environmental variables such as emergent marsh habitat, open water and salinity on these estuarine-dependent tonguefishes. By modeling what is known regarding the ecology of tonguefishes in coastal Louisiana as well as what is currently unknown, it is then possible to identify potential directions for future research and modeling efforts.

Materials and Methods

Loop Analysis

Only a general overview of loop analysis is given here; for a detailed explanation of the theory and mathematical formulation behind loop analysis please refer to Puccia and Levins (1985; 1991) or Dambacher (2001).

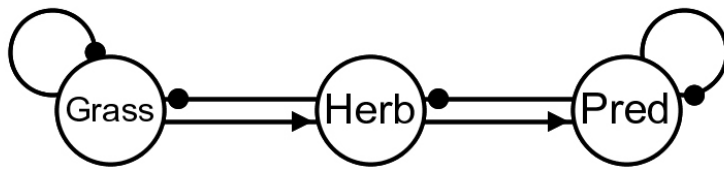
An example of a loop model is given in Figure 6.1 that incorporates interactions between grass, herbivores and predators (Dambacher et al. 1999). In loop analysis, the direct interactions among various biotic and abiotic components of an ecosystem are represented in a signed digraph, or a graphical representation of the direct interactions among organisms and abiotic variables. Interactions between various components of the system are developed graphically, and each variable included in the model is represented by a node (Grass, Herb and Pred in Figure 6.1). Lines between nodes represent non-zero interactions between variables. A positive interaction is represented by an arrow (i.e., from grass to herbivores), and indicates that an increase in grass would have an associated positive effect on herbivores. A negative interaction is represented by a line terminating with a closed circle (i.e., from predators to herbivores), and indicates that an increase in predators would have an associated negative effect on herbivores. In

this manner, all types of traditional ecological interactions can be modeled. Self-effects (interaction on one node only, such as is evident on grass and predators) can be either positive or negative, and indicate that those nodes are controlled by factors not explicitly included in the model. Once the model has been developed graphically, direct interactions between variables are entered as coefficients of the community matrix (1 for positive interaction, -1 for negative interaction, and 0 for no interaction). For a specified system consisting of n nodes, the element $a_{i,j}$ of the symbolic community matrix represents the effect directed to element j from element i . For example, in the system specified in Figure 6.1 the positive interaction from grass to herbivores is represented by a 1 in the $a_{2,1}$ element of the community matrix, and the negative self-effect on predators is represented by a -1 in the $a_{3,3}$ element of the community matrix. One of the requirements of loop analysis is that the model system be stable, or in other words, able to recover to some equilibrium point following a disturbance. Overall stability can be predicted by the feedback (F_k) at each level, k , from 1 to n . Feedback is defined by the formula:

$$F_k = \sum [(-1)^{m+1} L(m,k)]$$

where $L(m,k)$ represents the product of the elements along any set of m disjunct loops through the system that connect with k of the n total variables or nodes. Each of the k variables are included once and only once by each of the loops. For example, at $k = 3$, this product would encompass all loops that visit exactly three nodes along their pathways. System stability is dependent upon three main criteria that arise from loop theory: 1) the overall feedback of the system (F_n) must be negative, 2) feedback at all levels from 1 through n (where n represents the total number of nodes in the system) must also be negative, and 3) feedback at lower levels must be stronger than feedback at higher levels (i.e., $F_1 F_2 + F_3 > 0$).

Once the community has been adequately defined in the model, it is then possible to examine the effects of a sustained alteration (or PRESS perturbations) of specific variables



Signed Digraph

1. Grass
2. Herbivore
3. Predator

$$\begin{bmatrix} a_{1,1} & a_{1,2} & a_{1,3} \\ a_{2,1} & a_{2,2} & a_{2,3} \\ a_{3,1} & a_{3,2} & a_{3,3} \end{bmatrix}$$

Symbolic Community Matrix

$$\begin{bmatrix} -1 & -1 & 0 \\ 1 & 0 & -1 \\ 0 & 1 & -1 \end{bmatrix}$$

Community Matrix

$$\begin{bmatrix} 1 & -1 & 1 \\ 1 & 1 & -1 \\ 1 & 1 & 1 \end{bmatrix}$$

Adjoint Matrix

$$\begin{bmatrix} 1. & 1. & 1. \\ 1. & 1. & 1. \\ 1. & 1. & 1. \end{bmatrix}$$

Weighted Predictions Matrix

Figure 6.1. Example of a three-node qualitative loop model that incorporates grass, herbivores and predators.

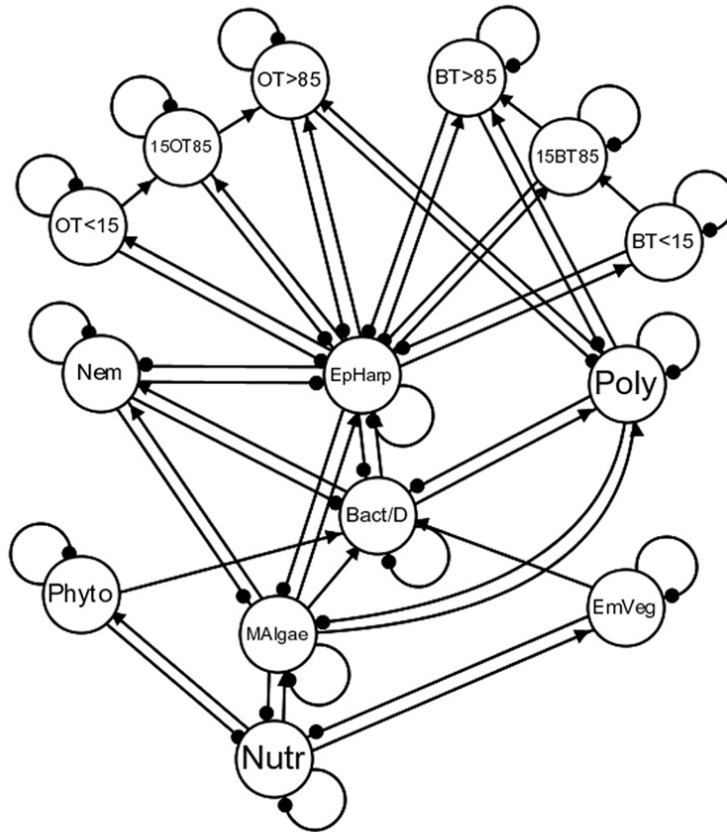
(Bender et al. 1984; Yodzis 1988). Bender et al. (1984) distinguish two general types of perturbations: PRESSES and PULSES. PRESSES are sustained perturbations of one or more variables that result in a persistent change in the abundance or concentration of a given variable and consequently affect other variables through specified interactions. Under a PRESS (e.g., the extinction of a top predator), the unperturbed variables eventually reach a new stable equilibrium point. In contrast, a PULSE perturbation is a relatively instantaneous alteration of one or more variables. After a PULSE (e.g., the occurrence of a hurricane) the system is examined as it returns to the previous equilibrium point. In community ecology, PRESS experiments yield information on both direct and indirect effects throughout the system whereas PULSE experiments generally only yield information on direct effects (Bender et al. 1984).

The relative effects (positive, negative or neutral) of a given PRESS or PRESSES on the abundances and concentrations of specified variables can be determined from the adjoint matrix (Figure 6.1). Elements of the adjoint matrix represent the product of pathways through the loop model as well as feedback at various levels. For example, a positive PRESS on predators (the third column of the adjoint matrix) would have a positive effect on grass (first row) and a negative effect on herbivores. While exact quantitative predictions cannot be obtained via loop analysis, relative effects (i.e., the direction of change) throughout the system can be determined. With a positive PRESS on predators, the positive effect on grass and the negative effect on herbivores are of the same magnitude (absolute number is the same; only the sign is different), indicating that the positive effect on grasses is similar to the negative effect on herbivores. The combined effects of PRESSing multiple variables can be estimated as the algebraic summation of the corresponding elements of each column or vector. Additionally, the determinacy of predicted responses can be examined through the weighted-predictions matrix (Dambacher et al.

2002). The weighted-predictions matrix is based on an examination of negative and positive feedback loops, and is a probability from 0 to 1 that assigns a measure of the level of confidence in each element of the adjoint matrix. Values near 0 indicate that negative and positive feedback loops nearly cancel one another, and so the corresponding values from the adjoint matrix have little predictive capabilities. Values near 1 indicate that either negative or positive feedback loops are predominant, so the corresponding values from the adjoint matrix are more capable of predicting actual changes. By examining the adjoint and weighted-predictions matrices together, it is then possible to assess a level of confidence in model predictions.

Model Description

I modeled the ecology of young-of-the-year tonguefishes within inshore estuarine habitat in coastal Louisiana. The basic model, from which all other models are based, is not comprehensive (Figure 6.2). Variables are excluded that are either unrelated to the ecology of tonguefishes in coastal Louisiana or for which there is no interest in modeling at this time. In this model system, nutrient input enhances primary production among phytoplankton, benthic microalgae (including diatoms), and emergent vegetation (Day et al. 1989). Negative interactions between primary producers and nutrients indicate consumption. Primary producers provide a net input into the detrital/bacterial pathway. Three meiofaunal groups are included in the model: epibenthic harpacticoid copepods, nematodes, and polychaetes. Interactions among the meiofauna generally represent predator-prey relationships. Epibenthic harpacticoid copepods consume a wide variety of food, but feed mainly on benthic microalgae, detritus and bacteria (Hicks and Coull 1983). These copepods are also the primary component of the diet of juvenile and adult tonguefishes (Stickney 1976; Toepfer and Fleeger 1995). Nematodes, along with copepods, are one of the most common meiofaunal groups occurring in estuarine and marine



-1	-1	-1	-1	0	0	0	0	0	0	0	0	0	0
1	-1	0	0	0	0	0	0	0	0	0	0	0	0
1	0	-1	0	0	-1	-1	-1	0	0	0	0	0	0
1	0	0	-1	0	0	0	0	0	0	0	0	0	0
0	1	1	1	-1	-1	-1	-1	0	0	0	0	0	0
0	0	1	0	1	-1	-1	0	-1	-1	-1	-1	-1	-1
0	0	1	0	1	-1	-1	0	0	0	0	0	0	0
0	0	1	0	1	0	0	-1	0	0	-1	0	0	-1
0	0	0	0	0	1	0	0	-1	0	0	0	0	0
0	0	0	0	0	1	0	0	1	-1	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	-1	0	0
0	0	0	0	0	1	0	0	0	0	0	1	-1	0
0	0	0	0	0	1	0	1	0	0	0	0	1	-1

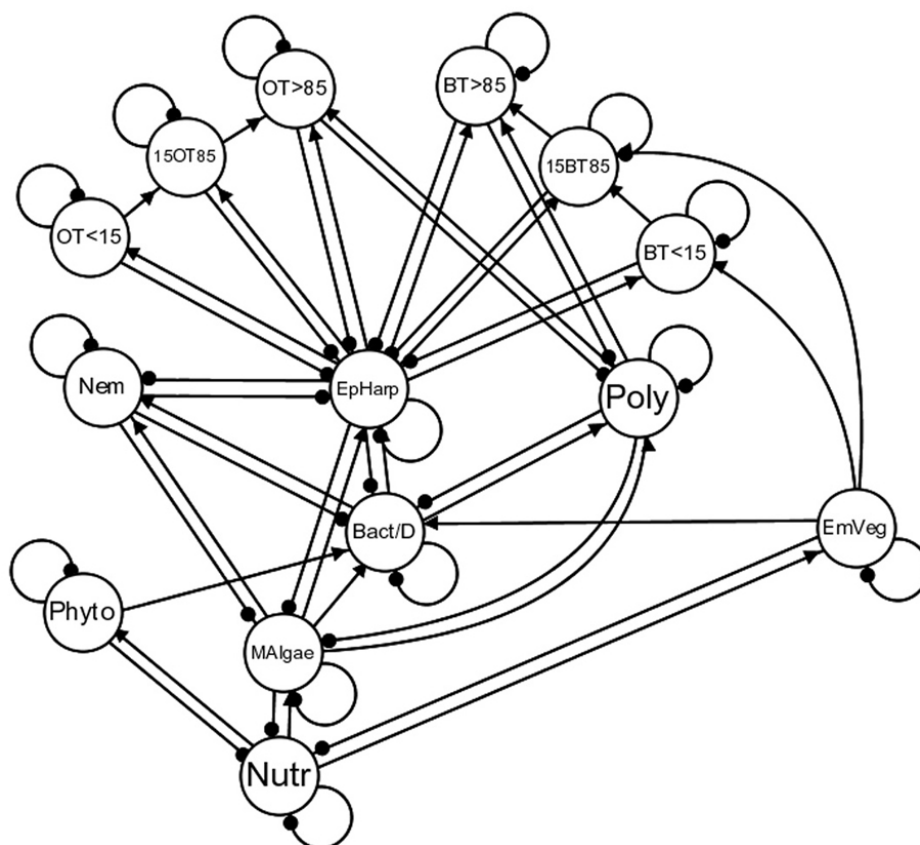
- 1: Nutrients
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Community Matrix

Figure 6.2. Basic loop model of the interactions between tonguefishes and among life history stages that includes a simple benthic food web. All other loop models are derived forms of this basic model. See text for full model description.

soft-sediment communities (Fleeger and Chandler 1983; Fleeger 1985), and may compete directly with copepods for resources (Carman et al. 1997). Nematodes are not a major component of the diet of tonguefishes, but parasitic forms are common (Stickney 1976; Toepfer and Fleeger 1995). Polychaetes are not as abundant as either copepods or nematodes in coastal Louisiana, but make up an increasingly important component of the diets of larger juvenile tonguefishes within inshore estuaries (Toepfer and Fleeger 1995). Other prey taxa are relatively rare in diets and are not incorporated into the models. Published feeding studies of tonguefish have focused primarily on blackcheek tonguefish, and no information has been reported for offshore tonguefish diets in Louisiana. I examined the stomach contents of a subsample of juvenile blackcheek and offshore tonguefishes collected sympatrically. Individuals of both species fed predominantly on epibenthic harpacticoid copepods (mostly *Coullana* spp. along with some *Halycyclops* spp.), so feeding relationships were modeled in a similar manner for both tonguefishes. Three separate size-classes of tonguefishes were incorporated into the model (Livingston 1988): post-settlement juveniles (< 15 mm SL), juveniles (15 – 85 mm SL), and individuals at or nearing maturity (> 85 mm SL; Terwilliger and Munroe 1999). The negative self-feedback loops present for all nodes indicate that these variables are not entirely controlled by factors explicitly incorporated into the models.

Three additional models were analyzed to examine interactions among tonguefishes and environmental factors. All model systems incorporate the basic tonguefish loop model (Figure 6.2), with additional direct interactions used to examine specific hypotheses. In the second model (Figure 6.3) the amount of emergent vegetation has a positive effect on blackcheek tonguefish juveniles, and is based on the fact that blackcheek tonguefish juveniles commonly use near-shore sites whereas offshore tonguefish juveniles do not (Reichert and Van der Veer 1991; Baltz et al. 1993; Chapter 3). The third model (Figure 6.4) also incorporates a negative effect of



-1	-1	-1	-1	0	0	0	0	0	0	0	0	0	0
1	-1	0	0	0	0	0	0	0	0	0	0	0	0
1	0	-1	0	0	-1	-1	-1	0	0	0	0	0	0
1	0	0	-1	0	0	0	0	0	0	0	0	0	0
0	1	1	1	-1	-1	-1	-1	0	0	0	0	0	0
0	0	1	0	1	-1	-1	0	-1	-1	-1	-1	-1	-1
0	0	1	0	1	-1	-1	0	0	0	0	0	0	0
0	0	1	0	1	0	0	-1	0	0	-1	0	0	-1
0	0	0	0	0	1	0	0	-1	0	0	0	0	0
0	0	0	0	0	1	0	0	1	-1	0	0	0	0
0	0	0	1	0	1	0	0	0	0	0	-1	0	0
0	0	0	1	0	1	0	0	0	0	0	1	-1	0
0	0	0	0	0	1	0	1	0	0	0	0	1	-1

- 1: Nutrients
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Community Matrix

Figure 6.3. Tonguefish loop model incorporating a positive effect of emergent vegetation on blackcheek tonguefish juveniles. See text for full model description.

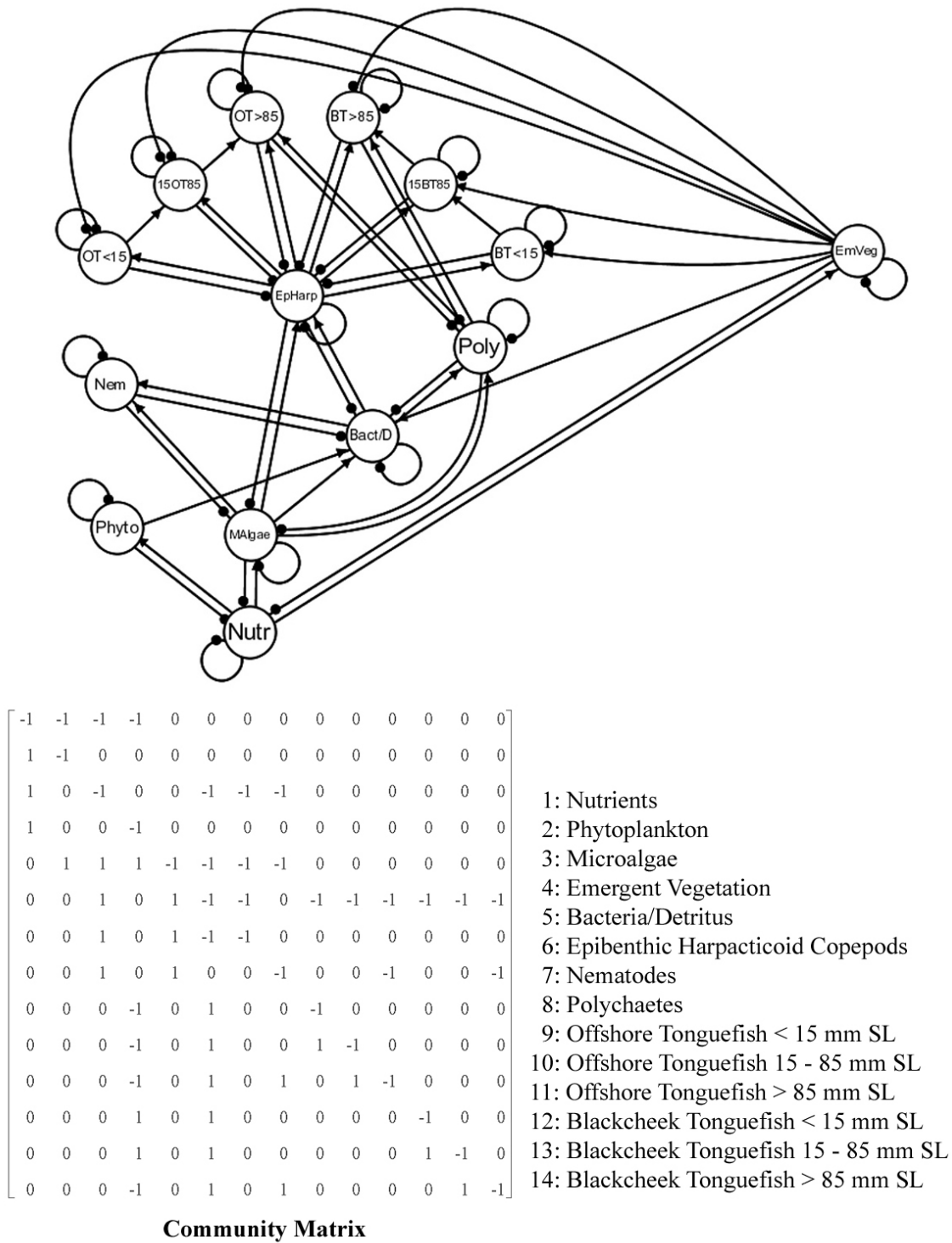
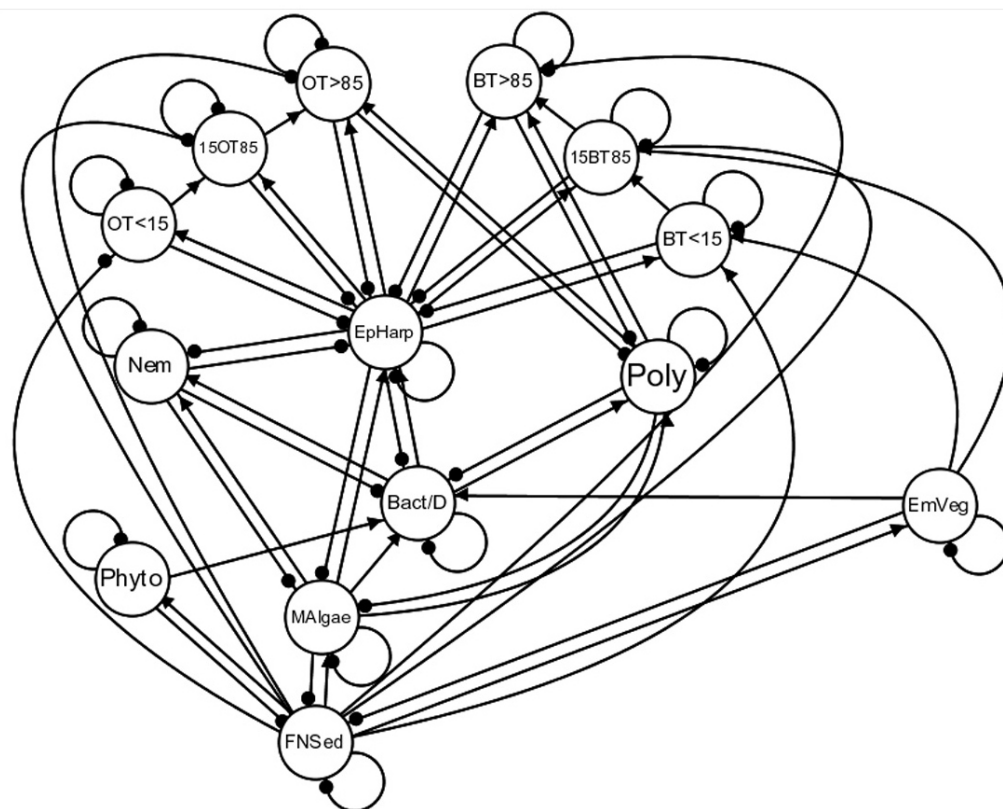


Figure 6.4. Tonguefish loop model incorporating a positive effect of emergent vegetation on blackcheek tonguefish juveniles and a negative effect of emergent vegetation on all other tonguefish life history stages. See text for full model description.

emergent vegetation on all offshore tonguefish life history stages as well as adult blackcheek tonguefish at or approaching maturity (Allen and Baltz 1997; Chapter 2). In this model, a negative press on emergent vegetation would represent conversion of marsh to open water. The fourth and final model (Figure 6.5) incorporates the potential effects of a freshwater diversion on tonguefishes. In this model, the node representing nutrients has been replaced by a node and direct interactions relating nutrients, sediment and fresh water to other nodes. This input is modeled as having a positive influence on all primary producers as well as blackcheek tonguefish, but having a negative influence on offshore tonguefish (Allen and Baltz 1997; Baltz and Jones in press; Chapter 5). Additionally, this model incorporates the benefit of edge habitat for juvenile blackcheek tonguefish. Each of the four loop models examined met the criteria for stability, so the examination of PRESS perturbations was conducted for each model. Accordingly, the adjoint matrix and the range of values from the weighted predictions matrix were reported for each model.

Results

The basic tonguefish model consisted of fourteen nodes, and contained 57 out of a possible 196 direct interactions (Figure 6.2). Criteria for system stability were met; the overall feedback was negative, feedback was negative for all levels, and negative feedback increased through level ten. For the basic tonguefish model, all size classes of blackcheek and offshore tonguefish appeared to respond to changes in life history stages of tonguefishes more strongly than to changes in the abundances of prey or primary producers (Figure 6.6). A positive PRESS on nutrients negatively affected juvenile tonguefishes (< 15 mm SL and 15 – 85 mm SL) and positively affected adult tonguefishes (> 85 mm SL); the relative influence of nutrients was similar on both species. All tonguefishes were unaffected by emergent vegetation in the basic



-1	-1	-1	-1	0	0	0	0	0	0	0	0	0	0
1	-1	0	0	0	0	0	0	0	0	0	0	0	0
1	0	-1	0	0	-1	-1	-1	0	0	0	0	0	0
1	0	0	-1	0	0	0	0	0	0	0	0	0	0
0	1	1	1	-1	-1	-1	-1	0	0	0	0	0	0
0	0	1	0	1	-1	-1	0	-1	-1	-1	-1	-1	-1
0	0	1	0	1	-1	-1	0	0	0	0	0	0	0
0	0	1	0	1	0	0	-1	0	0	-1	0	0	-1
-1	0	0	0	0	1	0	0	-1	0	0	0	0	0
-1	0	0	0	0	1	0	0	1	-1	0	0	0	0
-1	0	0	0	0	1	0	1	0	1	-1	0	0	0
1	0	0	1	0	1	0	0	0	0	0	-1	0	0
1	0	0	1	0	1	0	0	0	0	0	1	-1	0
1	0	0	0	0	1	0	1	0	0	0	0	1	-1

- 1: Fresh Water, Nutrients, Sediment
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Community Matrix

Figure 6.5. Tonguefish loop model incorporating the effects of a freshwater diversion (addition of fresh water, nutrients and sediment). These inputs resemble the effects of nutrients and emergent vegetation from the model depicted in Figure 6.3, with a positive effect of fresh water on all life history stages of blackcheek tonguefish and a negative effect of fresh water on all life history stages of offshore tonguefish. See text for full model description.

Adjoint Matrix

132	-96	-60	-96	36	-6	30	12	6	0	-6	6	0	-6
132	288	-60	-96	36	-6	30	12	6	0	-6	6	0	-6
-12	-96	180	-96	-108	18	-90	-36	-18	0	18	-18	0	18
132	-96	-60	288	36	-6	30	12	6	0	-6	6	0	-6
108	96	-84	96	204	30	-150	-60	-30	0	30	-30	0	30
-8	0	-8	0	-8	44	-28	-24	-108	-64	-20	-108	-64	-20
104	0	104	0	104	4	172	-72	60	64	68	60	64	68
48	0	48	0	48	-72	-24	144	72	0	-72	72	0	-72
-8	0	-8	0	-8	44	-28	-24	276	-64	-20	-108	-64	-20
-16	0	-16	0	-16	88	-56	-48	168	256	-40	-216	-128	-40
24	0	24	0	24	60	-108	72	132	192	252	-252	-192	-132
-8	0	-8	0	-8	44	-28	-24	-108	-64	-20	276	-64	-20
-16	0	-16	0	-16	88	-56	-48	-216	-128	-40	168	256	-40
24	0	24	0	24	60	-108	72	-252	-192	-132	132	192	252

- 1: Nutrients
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Figure 6.6. Adjoint matrix from loop model depicted in Figure 6.2. The effects of a PRESS perturbation on a given variable (1 – 14) on the model system are provided as columns of the adjoint and weighted predictions matrices, respectively.

model. Interactions between tonguefishes and meiofauna were identical for both species; all tonguefishes responded positively to PRESSES on epibenthic harpacticoid copepods and negatively to PRESSES on nematodes, and adult tonguefishes responded positively to PRESSES on polychaetes. A positive PRESS on any tonguefish species or life history stage negatively affected all life history stages of the other species as well as all earlier life history stages within the species, and positively affected later life history stages within the species. Values of the weighted predictions matrix ranged from 0 to 0.61.

The model incorporating a positive interaction from emergent vegetation to blackcheek tonguefish juveniles consisted of fourteen nodes and 59 of a possible 196 direct interactions (Figure 6.3). Criteria for system stability were met; the overall feedback was negative, feedback was negative for all levels, and negative feedback increased through level ten. Results from loop analysis changed substantially when the direct benefit of emergent vegetation to blackcheek tonguefish juveniles was incorporated into the model (Figure 6.7). A positive PRESS on nutrients enhanced numbers of blackcheek tonguefish and reduced numbers of offshore tonguefish; the determinacy of these relationships was stronger for larger juveniles and adults than for post-settlement juveniles. Similar relationships were evident for emergent vegetation; moreover, a positive PRESS on emergent vegetation produced a stronger effect than did nutrients. In this model, a negative PRESS on emergent vegetation is the equivalent of converting emergent marsh to open water and can be thought of as a positive PRESS on open water habitat. Interestingly, a combined positive PRESS on nutrients and a negative PRESS on emergent vegetation resulted in enhanced numbers for all offshore tonguefish and reduced numbers for all blackcheek tonguefish. The response of tonguefishes to PRESSES on specific life history stages remained relatively unchanged from the previous model. Values of the weighted predictions matrix ranged from 0 to 0.59.

Adjoint Matrix

132	-96	-60	-90	36	-6	30	12	6	0	-6	6	0	-6
132	282	-60	-90	36	-6	30	12	6	0	-6	6	0	-6
-18	-90	180	-108	-108	18	-90	-36	-18	0	18	-18	0	18
132	-96	-60	288	36	-6	30	12	6	0	-6	6	0	-6
96	102	-78	72	198	30	-150	-60	-30	0	30	-30	0	30
-67	43	19	-129	-24	46	-41	-29	-109	-63	-17	-109	-63	-17
145	-31	83	93	114	2	179	-67	61	63	65	61	63	65
72	-18	36	54	54	-72	-18	144	72	0	-72	72	0	-72
-67	43	19	-129	-24	46	-41	-29	269	-63	-17	-109	-63	-17
-134	86	38	-258	-48	92	-82	-58	160	252	-34	-218	-126	-34
-129	111	93	-333	-18	66	-141	57	123	189	255	-255	-189	-123
65	-53	-41	159	12	40	-11	-17	-103	-63	-23	275	-63	-23
130	-106	-82	318	24	80	-22	-34	-206	-126	-46	172	252	-46
135	-81	-27	243	54	54	-81	81	-243	-189	-135	135	189	243

- 1: Nutrients
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Figure 6.7. Adjoint matrix from loop model depicted in Figure 6.3. The effects of a PRESS perturbation on a given variable (1 – 14) on the model system are provided as columns of the adjoint and weighted predictions matrices, respectively.

The model incorporating a positive interaction from emergent vegetation to blackcheek tonguefish juveniles and a negative interaction from emergent vegetation to all other life history stages of tonguefish consisted of fourteen nodes 63 of a possible 196 direct interactions (Figure 6.4). Criteria for system stability were met; the overall feedback was negative, feedback was negative for all levels, and negative feedback increased through level ten. Predictions of this model were not substantially different from the previous model incorporating a positive interaction from emergent vegetation to blackcheek tonguefish juveniles alone, although the relative importance of nutrients and primary producers increased (Figure 6.8). Values of the weighted predictions matrix ranged from 0 to 0.50.

The model incorporating the combined effects of a freshwater diversion consisted of fourteen nodes and 65 of a possible 196 direct interactions (Figure 6.5). Criteria for system stability were met; the overall feedback was negative, feedback was negative for all levels, and negative feedback increased through level ten. Predictions from this model changed substantially from the two previous models (Figure 6.9). In this model, a positive PRESS on the freshwater diversion (input of fresh water, nutrients and sediment) resulted in increased abundances of blackcheek tonguefish and decreased abundances of offshore tonguefish. A positive PRESS on emergent vegetation positively affected blackcheek tonguefish juveniles but negatively affected blackcheek tonguefish adults and all life history stages of offshore tonguefish. A positive PRESS on nutrients and a negative PRESS on emergent vegetation (positive PRESS on open water) resulted in enhanced numbers of blackcheek tonguefish and decreased numbers of offshore tonguefish. The response of tonguefishes to PRESSES on specific life history stages remained relatively unchanged from the previous models. Values of the weighted predictions matrix ranged from 0 to 0.50.

Adjoint
Matrix

132	-96	-60	-84	36	-6	30	12	6	0	-6	6	0	-6
132	276	-60	-84	36	-6	30	12	6	0	-6	6	0	-6
-24	-84	180	-120	-108	18	-90	-36	-18	0	18	-18	0	18
132	-96	-60	288	36	-6	30	12	6	0	-6	6	0	-6
84	108	-72	48	192	30	-150	-60	-30	0	30	-30	0	30
6	-10	-14	30	-4	42	-24	-22	-104	-62	-20	-104	-62	-20
54	34	122	-102	88	6	156	-74	56	62	68	56	62	68
96	-36	24	108	60	-72	-12	144	72	0	-72	72	0	-72
-126	86	46	-258	-40	48	-54	-34	262	-62	-14	-110	-62	-14
-252	172	92	-516	-80	96	-108	-68	152	248	-28	-220	-124	-28
-282	222	162	-666	-60	72	-174	42	114	186	258	-258	-186	-114
138	-106	-74	318	32	36	6	-10	-98	-62	-26	274	-62	-26
276	-212	-148	636	64	72	12	-20	-196	-124	-52	176	248	-52
246	-162	-78	486	84	48	-54	90	-234	-186	-138	138	186	234

- 1: Nutrients
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Figure 6.8. Adjoint matrix from loop model depicted in Figure 6.4. The effects of a PRESS perturbation on a given variable (1 – 14) on the model system are provided as columns of the adjoint and weighted predictions matrices, respectively.

Adjoint
Matrix

132	-96	-60	-90	36	-6	30	12	6	0	-6	6	0	-6
132	282	-60	-90	36	-6	30	12	6	0	-6	6	0	-6
-18	-90	180	-108	-108	18	-90	-36	-18	0	18	-18	0	18
132	-96	-60	288	36	-6	30	12	6	0	-6	6	0	-6
96	102	-78	72	198	30	-150	-60	-30	0	30	-30	0	30
-67	43	19	-129	-24	46	-41	-29	-109	-63	-17	-109	-63	-17
145	-31	83	93	114	2	179	-67	61	63	65	61	63	65
72	-18	36	54	54	-72	-18	144	72	0	-72	72	0	-72
-199	139	79	-39	-60	52	-71	-41	263	-63	-11	-115	-63	-11
-398	278	158	-78	-120	104	-142	-82	148	252	-22	-230	-126	-22
-525	399	273	-63	-126	84	-231	21	105	189	273	-273	-189	-105
197	-149	-101	69	48	34	19	-5	-97	-63	-29	281	-63	-29
394	-298	-202	138	96	68	38	-10	-194	-126	-58	184	252	-58
531	-369	-207	-27	162	36	9	117	-225	-189	-153	153	189	225

- 1: Fresh Water, Nutrients, Sediment
- 2: Phytoplankton
- 3: Microalgae
- 4: Emergent Vegetation
- 5: Bacteria/Detritus
- 6: Epibenthic Harpacticoid Copepods
- 7: Nematodes
- 8: Polychaetes
- 9: Offshore Tonguefish < 15 mm SL
- 10: Offshore Tonguefish 15 - 85 mm SL
- 11: Offshore Tonguefish > 85 mm SL
- 12: Blackcheek Tonguefish < 15 mm SL
- 13: Blackcheek Tonguefish 15 - 85 mm SL
- 14: Blackcheek Tonguefish > 85 mm SL

Figure 6.9. Adjoint matrix from loop model depicted in Figure 6.5. The effects of a PRESS perturbation on a given variable (1 – 14) on the model system are provided as columns of the adjoint and weighted predictions matrices, respectively.

Discussion

Qualitative models provided insight into factors that may potentially influence abundances of sympatric tonguefishes in coastal Louisiana. By comparing results from a series of similar models, it is possible to gain a better understanding of the relative importance of biotic and abiotic variables that influence the distribution the abundances of tonguefishes.

Relationships that remain relatively stable throughout the model alterations or that change in an expected way are relationships that can be examined with some confidence; relationships that change in unexpected ways should be questioned. Results from qualitative loop analyses generate hypotheses that can then be tested experimentally or through the analysis of quantitative data.

Tonguefish responses to PRESSES on species and life history stages remained relatively unchanged throughout all models examined. Positive PRESS perturbations for all species and life history stages negatively affected all life history stages for the other species as well as earlier conspecific life history stages. These responses are most likely due to indirect interactions through food resources; no direct linkages between species or among life history stages were incorporated into the models aside for a positive linkage to later life history stages. All species and life history stages of tonguefishes feed primarily on epibenthic harpacticoid copepods in the model systems examined. Ontogenetic shifts in the diet of blackcheek tonguefish are not evident (Toepfer and Fleeger 1995); presumably the extremely small mouths of tonguefishes limit the types and sizes of prey items that can be consumed efficiently (Stickney 1976; Toepfer and Fleeger 1995). Food is generally thought to be more important than predation in limiting recruitment in flatfishes in lower latitudes (Miller et al. 1991). Food limitation has not been demonstrated for tonguefishes; growth rates of juvenile blackcheek tonguefish in a Georgia

estuary were similar to those obtained from individuals fed *ad libitum*, indicating that food limitation is not important within this area (Reichert and Van der Veer 1991). Comparison of growth rates under varying conspecific and congeneric densities are required to examine these relationships more closely.

Linkages among nutrients, emergent vegetation, and tonguefishes appeared to be extremely important. The effect of nutrients or emergent vegetation alone remained relatively unchanged throughout all models examined, although relative importances did change. A positive PRESS on nutrients or emergent vegetation positively affected blackcheek tonguefish abundances and negatively affected offshore tonguefish abundances in models that only incorporated habitat effects (Figures 6.3 and 6.4). These responses appear to be unrelated to food; a positive PRESS on either nutrients or emergent vegetation negatively affected epibenthic harpacticoid copepods. Instead, direct and indirect interactions with habitat appear to be important. Spatial segregation between tonguefishes appears to be important in describing their distributional patterns in coastal Louisiana (Chapter 2). Abundances of blackcheek tonguefish are generally higher in shallow areas near emergent vegetation, whereas offshore tonguefish abundances are higher in deeper waters farther from shore (Reichert and Van der Veer 1991; Baltz et al. 1993; Allen and Baltz 1997; Chapters 2 and 3). The observed abundance patterns among tonguefishes in coastal Louisiana are consistent with the model predictions.

A combined positive PRESS on nutrients and open water (negative PRESS on emergent vegetation) increased abundances of offshore tonguefish in models incorporating habitat effects of emergent vegetation alone (Figure 6.4), but reduced abundances of offshore tonguefish in the model incorporating the combined effect of a freshwater diversion (Figure 6.5). In habitat models (Figures 6.3 and 6.4), the strength of the effects of emergent vegetation was substantially

greater than the effects of nutrients. When the combined effects of nutrients, sediment and fresh water were incorporated this pattern did not hold; blackcheek tonguefish benefited from a combined positive PRESS on nutrients and a negative PRESS on emergent vegetation. These results appear to be associated with the effects of fresh water input (decrease in salinity) incorporated into the model. The distribution of both tonguefishes, as well as other estuarine-dependent species, is heavily dependent on salinity (Allen and Baltz 1997; Baltz and Jones in press; Chapter 5). The negative affects of lower salinities may outweigh any benefits that an increase in the amount of open water may offer for offshore tonguefish.

Results from these qualitative models have identified areas that require additional examination through other loop analyses or through direct experimentation. One area that clearly requires further study is the benefit of emergent vegetation to blackcheek tonguefish. These results support the notion that blackcheek tonguefish benefit from shallow habitat near emergent vegetation (Reichert and Van der Veer 1991; Baltz et al. 1993; Allen and Baltz 1997; Chapters 2 and 3). Whether blackcheek tonguefish benefit from increased food availability and/or decreased risk of predation is not yet known (Boesch and Turner 1984). Tonguefish predators may avoid shallow areas due to predation pressures from wading shore birds (Kneib 1982), although this does not explain the differential utilization of shallow, near-shore habitat between these tonguefishes (Chapter 3). Future qualitative loop models and/or experiments should focus on the relative importance of food and refugia to individuals that occupy shallow, near-shore habitat.

Although the loop models examined were fairly simplistic (they did not contain interactions between tonguefishes and either other potential competitors or potential predators), they did prove useful in examining the basic relationships between estuarine-dependent

tonguefishes and various biotic and abiotic variables. These models have successfully incorporated habitat and environmental variables (i.e., emergent vegetation, open water, salinity) into a basic community model. Environmental variables are generally difficult to incorporate into loop models; variables such as salinity are not consumed by species or life history stages, and so do not possess sufficient feedback required for model stability (Puccia and Levins 1985; Dambacher 2001). By combining several interrelated biotic and abiotic variables into one node, it is possible to overcome these difficulties. The distribution and abundance of these tonguefishes are related to numerous other environmental variables, such as depth, distance from shore, substrate and temperature (Allen and Baltz 1997; Chapter 2; Chapter 5). Future modeling efforts that include new and innovative ways of incorporating environmental variability into qualitative loop analyses should be explored.

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CHAPTER VII.

CONCLUSION

Various natural and anthropogenic processes have the potential to significantly alter environmental conditions within inshore estuarine habitat in coastal Louisiana. Patterns of land loss are a natural component of the deltaic cycle (Coleman et al. 1998), although numerous additional factors have contributed to observed rates of wetland loss that generally exceed rates attributable to compaction and subsidence alone (Hatton et al. 1983; Turner 1990; Turner 1997). Increased leveeing of the Mississippi River has prevented overbank flooding, largely depriving some systems of the input of fresh water and sediment (Conner and Day 1987). Freshwater diversions, which are currently being implemented as a means to stabilize current land levels, provide additional input of fresh water and sediments in some systems (LDWF et al. 1998; LDNR 2002). All of these processes alter observed environmental conditions in coastal bays and estuaries, so it is important to examine the potential effects of environmental changes on the distribution and abundance of estuarine-dependent nekton (LDWF et al. 1998; Baltz and Jones in press).

I examined the ecology of two sympatric tonguefishes, the blackcheek tonguefish (*Symphurus plagiusa*) and the offshore tonguefish (*S. civitatum*), to begin to unravel environmental variables that are most important in structuring the distribution of these estuarine-dependent tonguefishes in coastal Louisiana. Both species are common transients in coastal Louisiana (Baltz et al. 1993; Allen and Baltz 1997; Baltz and Jones in press); juveniles settle within the estuary beginning in late summer following a spawning period that coincides with periods of thermal maxima (Olney and Grant 1976; Munroe 1998), and move offshore to recruit

into reproductive populations following nearly a year spent within inshore nurseries.

Tonguefishes are also persistent in collections throughout the year (Baltz et al. 1993; Allen and Baltz 1997), so are an excellent system to examine the relationship between two ecologically similar species along environmental gradients.

Significant patterns of ecological segregation (Ross 1986) were identified between species and among life history stages within the Barataria study area (Chapter 2 and Chapter 3). Resource utilization of the two species overlapped broadly on a seasonal basis; however, overlap was reduced by spatial segregation. In 594 beam-trawl samples collected within the Barataria study area during a two-year period from September 1992 through August 1994, 2,897 offshore tonguefish and 631 blackcheek tonguefish were collected. In a complimentary study a total of 1,336 drop samples were collected along the marsh edge between October 1987 and November 1991 that contained only three offshore tonguefish along with 534 blackcheek tonguefish. In between species comparisons, blackcheek tonguefish generally used lower salinities, higher temperatures and finer substrates than did offshore tonguefish, and also occupied shallower sites nearer to shore. Both species also differed significantly with respect to utilization of marsh-edge habitat; blackcheek tonguefish appear to rely heavily on edge habitat whereas the marsh-edge ecotone was relatively unimportant to offshore tonguefish. Differences between species with respect to resource utilization appear to persist through adulthood, especially for substrate and depth; offshore tonguefish adults typically occur over sandy substrates in deeper (11 – 45 m) waters, whereas blackcheek tonguefish adults typically occur over soft mud substrates in shallower (1 – 30 m) waters (Munroe 1998). Among life history stages, ontogenetic shifts in resource utilization were evident for both species. Among both blackcheek and offshore tonguefish, larger individuals used warmer waters with lower dissolved oxygen concentrations

and were found in higher salinity waters over coarser substrates than were smaller individuals. Additionally, larger blackcheek tonguefish were typically collected in deeper water farther from shore as size increased.

Relative abundances of blackcheek and offshore tonguefish within the Vermilion study area differed substantially from abundances within the Barataria study area (Chapter 5). The Vermilion system currently receives substantial influx of fresh water from the Atchafalaya River, resulting in generally low salinities (range 0.0 – 8.5 psu) and a balance of land-building and land-loss processes (Roberts et al. 1997). In contrast, the Barataria system has been deprived of riverine input of fresh water for several decades (Conner and Day 1987), and consequently has experienced high rates of land loss (Evers et al. 1992) and generally higher salinities (range 0.1 – 29.2 psu). Within the Vermilion study area, 177 blackcheek tonguefish ($0.83 \text{ individuals min}^{-1}$) and 123 offshore tonguefish ($0.58 \text{ individuals min}^{-1}$) were collected in 211 beam-trawl samples from August 1998 to July 1999. Relative abundances within the Barataria study area were $3.48 \text{ individuals min}^{-1}$ for offshore tonguefish and $0.76 \text{ individuals min}^{-1}$ for blackcheek tonguefish. The generally lower salinities within the Vermilion system apparently favor blackcheek tonguefish, while the higher salinities within the Barataria system appear to favor offshore tonguefish. The increase in relative abundance of blackcheek tonguefish as well as the decrease in relative abundance of offshore tonguefish within the Vermilion study area coincided with predictions based on observed patterns of resource utilization from PCA plots constructed from Barataria collections (Chapter 2). In addition, no offshore tonguefish adults were collected within the Vermilion study area; significantly higher spring temperatures within the Vermilion system may have initiate offshore movement of offshore tonguefish prior to maturity (Gunter 1938; Gunter 1945; Miller 1965; Olney and Grant 1976).

Examination of growth within the Barataria study area identified significant differences between species as well as environmental influences on growth (Chapter 4). Mean growth rates (\pm SE) for early post-settlement blackcheek and offshore tonguefish within the estuary were 0.34 ± 0.024 and 0.42 ± 0.015 mm d⁻¹, respectively, and differed significantly between the two species. Growth rates of both species were significantly affected by environmental variables. In general, growth was positively related to temperature and negatively related to dissolved oxygen for both species. There was evidence of density-dependence among blackcheek tonguefish; growth rates decreased with increasing blackcheek tonguefish densities. Additionally, offshore tonguefish growth was higher in shallow waters despite the fact that offshore tonguefish appear to avoid shallow waters in favor of deeper sites.

Despite what has been learned regarding the ecology of these estuarine-dependent tonguefishes in Louisiana, there are clear avenues of future work that need to be addressed. Foremost among these is the relative role of food and refugia in structuring the distribution of these tonguefishes (Boesch and Turner 1984). Food is generally thought to be more important than predation in controlling recruitment among flatfishes in lower latitudes (Miller et al. 1991). The differential utilization of shallow, near-shore areas by blackcheek tonguefish and deep, open-water areas by offshore tonguefish is evident (Chapters 3 and 6); whether these distributional patterns are due to preference by the two species or to displacement of one species by the other is not clear from current results. Field and modeling studies that examine feeding and/or potential predation pressures on these tonguefishes as well as the potential for direct interactions between the two species may assist in addressing these hypotheses. Additionally, laboratory experiments that examine actual habitat preference by these tonguefishes along environmental gradients (i.e., temperature, salinity, turbidity etc.) may provide additional insight

into observed patterns of resource utilization at the microhabitat level (Baltz 1990). There are distinct observable patterns of resource utilization between the two species (Allen and Baltz 1997; Chapters 2, 3 and 5); it would be interesting to examine whether actual habitat preference for these tonguefishes coincides with observed patterns of resource utilization.

The results from my research indicate that both blackcheek and offshore tonguefish are sensitive to changing environmental conditions within coastal Louisiana, and can be significantly affected by changes to the hydrological properties of estuarine systems. Abundances of other species have also been affected by changing environmental conditions (LDWF et al. 1998; Jones et al. 2002; Baltz and Jones in press). Due to the importance of estuarine habitat as a nursery for numerous commercially and ecologically important species in Louisiana (Rakocinski et al. 1992; Baltz, et al. 1993; Peterson and Turner 1994; Allen and Baltz 1997), it is critical for managers to consider potential shifts in distribution or abundance when management practices call for the alteration of environmental parameters within an estuary.

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VITA

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