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UNIVERSITY OF CALIFORNIA, SAN DIEGO

The Role of Resident Fishes in Linking Habitats of a Southern California Salt Marsh

**A dissertation submitted in partial satisfaction of the
requirements for the Degree of Doctor of Philosophy
in
Oceanography**

by

Drew M. Talley

Committee in charge:

Lisa A. Levin, Chair
Paul K. Dayton
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2000

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2000

In memory of

Jennifer Lark Talley

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ABSTRACT OF THE DISSERTATION

The Role of Resident Fishes in Linking Habitats of a Southern California Salt Marsh

by

Drew Matthew Talley
Doctor of Philosophy in Oceanography
University of California, San Diego, 2000

Professor Lisa A. Levin, Chair

Natural environments are not homogenous, but instead are mosaic landscapes often comprised of quite environmentally distinct habitats. They harbor distinct biological communities, which vary across a number of spatial and temporal scales. These habitats are not isolated, but are connected through physical and biological linkages which themselves vary through time and across spatial scales. This study addressed the effect of habitat heterogeneity on the resident fish community of a tidal salt marsh in Mission Bay, CA, and examined how fish-utilization patterns mediated linkages between habitats. First, reproductive and habitat utilization data were combined with a comprehensive review of the literature on *F. parvipinnis* to highlight major gaps in our understanding of this important species. Next, small- (decimeter) and larger-scale (100's of meter) patterns of habitat utilization within the marsh landscape were examined. Physical environments differed among microhabitats (seagrass beds, unvegetated flat, subtidal creeks, intertidal creeks, and intertidal pools), and changed over short (tidal) through longer (interannual) time scales. Small resident fishes recognized and responded to these habitats, showing preferences in

utilization even at the smallest spatial scales examined. *Fundulus parvipinnis* habitat preferences changed through ontogeny, with small juveniles preferring intertidal pool and shallow creek habitats, while larger juveniles selected deeper habitats. Nighttime foraging of *Fundulus parvipinnis*, a numerical dominant in the southern California marsh fish community, was also investigated. *Fundulus parvipinnis* was found to feed nocturnally, but with reduced efficiency, ingesting more detritus at night than during daytime. Further, *F. parvipinnis* was shown to spawn on nighttime spring tides in Mission Bay. Thus, habitat value changes for this species over diel time scales. Finally, the potential consequences of microhabitat availability were explored in a study of ichthyofaunal colonization of a newly-created marsh was examined in Mission Bay, CA. This highly-modified habitat was rapidly colonized by fishes, but in the created marsh size-structure of the fish communities was skewed towards larger individuals. Lack of juveniles was attributed to absence of critical pool and shallow creek (microhabitat) availability. The results of this study indicate that the activities of resident fishes can create linkages at multiple scales between habitats within the wetland mosaic.

CHAPTER 1

Introduction to the Dissertation

Most natural habitats are not homogenous, but rather are mosaics of microhabitats that occur on a number of spatial and temporal scales (e.g., Pickett and White 1985). Salt marshes are clear examples of such a mosaic, in that they are comprised of visibly distinct microhabitats (Mitsch and Gosselink 1986). These microhabitats can vary in biological and environmental character over diel, tidal, seasonal, and interannual time scales (e.g., Bertness 1992, Allison 1995, Rountree and Able 1993, Ruiz-Campos 2000). Further, these habitats may be linked through both physical and biological processes. "[M]ost ecological structure is composed of patches or components which will decay in isolation." (Dayton 1992).

Despite habitat complexity in coastal wetlands, these ecosystems and their inhabitants have often been examined without regard to their heterogeneous microhabitats, either by (a) integrating across habitats or (b) restricting study to a single habitat within the wetland complex. Most studies of cross-habitat linkages have focused on the larger spatial scale of outwelling, attempting to understand how the production of a wetland may contribute to nearshore and offshore production (Nixon 1980, Deegan 1993), or on the importation of juveniles to wetland habitats ("nursery function", e.g., Baltz et al. 1992, Kneib and Knowlton 1995). There is presently

limited information about how marsh habitats interact, and how these interactions ("linkages") might affect the organisms that reside in or use them.

Developing an understanding of these habitat linkages may be particularly crucial for southern California's wetlands. California's coastal wetlands are among the most threatened habitats on Earth, with less than 10% of their historical acreage remaining (Schoenherr 1992). While these wetlands are thought to provide a nursery habitat for relatively few commercially important species, they function as critical habitat for a number of threatened and endangered birds, plants, and fishes, as well as for resident invertebrates (Zedler 1996, Swift et al. 1993). Understanding the linkages between the habitats that make up the wetland ecosystem will provide knowledge needed to effectively preserve and restore these threatened habitats.

The lessons to be gained from teasing apart these habitat linkages may extend beyond wetland habitats, however. It is likely that some larger generalizations can be derived through obtaining a mechanistic understanding of the processes driving linkages in wetland habitats.

Due to their mobility, conspicuous presence, abundance, and various life-history traits, fishes are likely to be important in mediating linkages between habitats in southern California salt marshes. Despite their recognized importance in other wetland systems (e.g., see Kneib 1997), resident wetland fishes in southern California are not very well studied. Thus, this research will have the additional benefit of improving our understanding of the ecology and biology of these species.

The overall goal of this research is to identify habitat utilization patterns and ichthyofaunally-mediated linkages between wetland habitats. **Chapter II** is a review of current knowledge of the biology and ecology of the California killifish, and provides novel data on diel patterns of utilization of marsh habitats and the timing of reproduction in *F. parvipinnis*. This chapter focuses on gaps in our understanding of this fish's functional role in wetland and associated communities. In **Chapter III** linkages formed through ichthyofaunal habitat use patterns over tidal, seasonal, ontogenetic, and interannual time scales are examined using quantitative drop-traps, stable isotopic analysis of tissues, and diet experiments. Sampling at decimeter spatial scales within creeks provides insight into utilization patterns of southern California ichthyofauna in relation to small-scale heterogeneity of creek habitats. Short-term temporal variation in habitat use and foraging value for *F. parvipinnis* is described in **Chapter IV**, which assesses differences between daytime and nighttime feeding success. In **Chapter V** the colonization of created marsh creeks by fishes is examined, and compared to the adjacent natural marsh using stable isotope analysis, mark-recapture studies, and baited trap sampling. The potential effects of creek geomorphology on fish size-structure and site fidelity are also inferred by comparison of created and natural systems. The implications of this research for understanding connectivity of habitats and the conservation of Pacific coast wetlands are discussed in the final chapter, **Chapter VI**.

Finally, Appendix I includes additional information related to habitat utilization of wetland fishes, both in a relatively pristine lagoon and highly-modified environment (salt ponds) in Laguna Ojo de Liebre, Baja California Sur, Mexico.

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CHAPTER II

The Ecology and Biology of the California killifish, *Fundulus parvipinnis*

Abstract

The California killifish, *Fundulus parvipinnis*, is an abundant and conspicuous member of the fish community of the threatened coastal wetlands of southern and Baja California. Due to its high density, occurrence in a wide range of environmental conditions, and middle trophic position, it is likely that this species plays a critical role in ecosystem function. This paper reviews our current understanding of the biology and ecology of the California killifish, and presents new data on *F. parvipinnis* reproduction and habitat utilization patterns in a tidal salt marsh in Mission Bay, CA. Finally, it summarizes the gaps in our knowledge of this species, pointing to directions for new research.

Introduction

Wetland resident fishes play a critical role in ecosystem function, exerting influence on distributions and population dynamics of their prey (Kneib 1986, Kelso 1979), acting as prey for other species (Haaker 1975, Zembal and Fancher 1988), and serving as vectors for transmission of parasites (Lafferty and Morris 1997). In addition, there is an increasing recognition that wetland resident fishes play a key role

in the transfer of production and nutrients off of the marsh surface (Kneib 1997, Lefevre et al. 1999).

Fishes of the genus *Fundulus* are ubiquitous in North American salt marshes, with the exception of the Pacific coast north of Morro Bay, CA. There are over 35 recognized species in the genus *Fundulus* (Bernardi and Powers 1995), of which 20 occur in North America (Fritz 1975). Only one of these, the California killifish (*Fundulus parvipinnis* Girard), occurs in the salt marshes of the Pacific coast.

Fundulus parvipinnis is a numerically dominant resident fish in wetlands of southern and Baja California, representing as much as 80% of the individuals captured during studies (e.g., see Allen 1982, De la Cruz Agüero et al. 1996, Ambrose and Meffert 1999, Chapter V). Due to its high abundance, middle trophic position, and common occurrence in bays and estuaries of southern and Baja California, it is likely that *F. parvipinnis* plays critical trophic roles in wetland ecosystems, structuring prey and predator assemblages.

Despite their probable ecological importance, there is surprisingly little published research on the ecology and biology of the California killifish, particularly when compared to the rich literature on the dominant Atlantic-coast congener, *F. heteroclinus*. As of this writing, there are 609 records in the BIOSIS Previews database from 1982-2000 which contain "*Fundulus heteroclinus*" in the title, abstract, or keywords section, but only 19 records for "*Fundulus parvipinnis*". These figures highlight our limited understanding of the ecology and biology of the California

killifish. Because *Fundulus parvipinnis* inhabits one of the most threatened habitats on Earth (Pacific coast salt marshes), knowledge of its function is particularly important.

It has been over a quarter century since the last publication to described the natural history of *F. parvipinnis* (Fritz, 1975). Since that time, our understanding of the biology and ecology of this species has grown. In this paper, I review current knowledge about the biology and ecology of the California killifish, drawing on published material, gray literature, and my own unpublished data, emphasizing current gaps in our knowledge. My goal is to provide in a condensed form what is known about the natural history of *F. parvipinnis*, including habitat utilization, foraging patterns, reproduction, and community roles.

Materials and Methods

Study site

The new data in this paper were derived from sampling performed in the Northern Wildlife Preserve/Kendall Frost Marsh Reserve (NWP/KFMR) in the northern part of Mission Bay, San Diego, California (32° 47' N, 117° 14' W; Figure II-1). The NWP/KFMR is a natural marsh of approximately 12 hectares which is managed by the City of San Diego and the University of California, San Diego. The marsh vegetation is predominantly composed of *Spartina foliosa*, *Salicornia bigelovii* and *Salicornia virginica* (Levin et al. 1998; Talley and Levin 1999). The vegetated

marsh is bordered at the bayward side by unvegetated tidal flat and, at lower tidal heights, by seagrass bed (mostly comprised of *Zostera marina* and *Ruppia maritima*).

Field Protocol

Gill Nets

The tidal migrations of adult *F. parvipinnis* between seagrass beds and vegetated marsh were examined using experimental gill nets. During August and September of 1999 (Table II-1), gill nets were set approximately 30 minutes prior to slack high or low tides in either the vegetated marsh or seagrass bed at high tide, or in the seagrass bed at low tide. Nets were 10 meter long x 2 meter tall Baltic Sea-type gill nets of two mesh sizes: two each of 8 mm and 19 mm mesh. Nets in the vegetated marsh were set with one end at the creek edge, and oriented such that they extended 10 meters up into the vegetated marsh. Low tide nets in the seagrass bed were oriented such that one end was near the waterline, with the net extending out towards deeper water. High tide nets were haphazardly placed in the seagrass bed, but oriented in the same direction as low tide nets. Nets were left for one hour, after which they were cleared, with all fish being identified and counted. Minimum, maximum, and mean water depth for each net was recorded.

Timing of reproduction

To assess temporal patterns of spawning, female *F. parvipinnis* were sampled from subtidal creeks of the NWP/KFMR during June through August of 1998 (Table

II-1). Fish were collected during daytime low tides using a 3 meter-diameter monofilament cast net made of 9.5 mm mesh. The net was thrown into subtidal creek habitat and the first 10 females captured were immediately transported to the lab for analysis. Fish were euthanized, then the wet weight was taken by placing the fish in a slot cut into a large sponge, to wick away water. The sponge containing the fish was placed on a scale, and the weight measured to the nearest milligram. The fish was then removed from the sponge, and the sponge was re-weighed to obtain the body weight of the fish by difference. Ovaries were removed from the fish, and weighed to the nearest milligram.

A gonadosomatic index (GSI) was calculated as:

$$(\text{gonad weight/body weight [g]}) * 100.$$

Maximum tidal heights for each day were calculated using Harbor Master® 5.0 (Zihua Software Inc).

Diel patterns of habitat use

Baited minnow traps were used to test the high tide utilization of subtidal creek, vegetated marsh, and intertidal pool habitats in day versus night during July through September 1997 (Table II-1). *Fundulus parvipinnis* were sampled with Gee® minnow traps, 22-cm diameter at the center, tapering to 19 cm at each end, made of 0.6-cm wire mesh with 2-cm openings. Each habitat received 3 traps baited with

canned cat food at each sampling (N=9). An exception was July 22 1997, when only creek and vegetated marsh habitats were sampled. Traps were left undisturbed for one hour, after which they were recovered. During recovery, all fish were counted, identified to species, and measured (total length) to the nearest mm. Analyses were performed on transformed ($\log [x+1]$) count data from traps.

Analysis of growth and production from literature

The relevant studies addressing growth and production of *F. parvipinnis* were not consistent in the calculation or presentation of these values. For that reason, when necessary and practical, values were converted using conversion equations provided within the text of the study.

Results and discussion

General facts- morphology, range, lifespan

Fundulus parvipinnis derives its name from the Latin *fundus* for "bottom", as the first described species of this genus had a habit of burrowing into mud (Moyle 1976). *Parvi-pinnis*, also from Latin, is translated as "small-finned" (Moyle 1976). The etymology of the common name "killifish" for members of the Cyprinodontidae is less clear, but may be a contraction of the words "killing fish", since the word "killing" was used in colonial times for exceptionally effective bait (Moyle 1976). Common names for *F. parvipinnis* include Pacific killifish (Wells and Zobell 1934, Miller

1943), California mud-fish (Ritter and Bailey 1908), and most commonly, California killifish (Miller and Lea 1976).

Fundulus parvipinnis is a small (up to 115 mm standard length) fish that occurs in shallow bays and salt marshes from Morro Bay, California (35° 21' N) to Bahía Almejas, Baja California Sur, Mexico (24° 20' N, Figure II-1; Miller and Lea 1976). It is a robust-bodied fish, with small pelvic and rounded caudal and dorsal fins. *Fundulus parvipinnis* has 12 to 15 dorsal fin rays, 11-13 anal fin rays, and 31-37 midlateral scales, with 0-1 anterior gill rakers on the upper limb of the first gill arch, 7-10 on the lower limb, and 34-37 vertebrae (Miller and Lea 1976). The overall color is an olive green on the back and sides, with lighter yellowish brown on the underside. Males become darker on the back, and are brighter yellow laterally and on the underside. They develop scale ctenii when breeding, and are distinguished by much longer anal fins than females (Myers 1930). Markings vary between populations. Girard (1854) and Jordan and Evermann (1896) stated that females possess a dark dusky lateral band, while males possess olive-green bars laterally. However, males, females, and juveniles of the population in Anaheim bay possess bars (Fritz 1975), and juvenile fishes taken from Laguna Ojo de Liebre (BCS, Mexico) also possess distinct bars (Talley, personal observation; Figure II-1).

Osburn and Nichols (1916) recognized two subspecies of *F. parvipinnis*, a classification that subsequently has been supported by other researchers (Myers 1930, Miller 1943, Miller and Hubbs 1954). The southern form, *Fundulus parvipinnis brevis*, is distinguished from the northern form (*F. parvipinnis parvipinnis*) by having

fewer vertebrae, fewer lateral line scales, and a deeper body. The break between subspecies occurs near Ensenada, BCN, Mexico (31° 51' N, Figure II-1; Miller and Hubbs 1954). However, Dumke (1976) has argued that the morphological differences between subspecies are the result of temperature changes, and points out that these differences vary clinally, with anomalies in locations where the north-south temperature gradient is interrupted. Dumke (1976) proposed that the subspecific designation of *F. parvipinnis* was unwarranted.

A fully freshwater, land-locked species of *Fundulus*, *Fundulus lima* Vaillant, exists on the Baja California peninsula (Myers 1930). *Fundulus lima* is endemic to the Baja California Peninsula, and is thought to be an isolated derivative of *F. parvipinnis* (Myers 1930). It is found in oases of the Pacific drainage of Baja California Sur (e.g., the Oasis of San Ignacio, Figure II-1; Reynoso-Mendoza 1994, Ruiz-Campos 2000). This species is the closest relative of *F. parvipinnis* (Myers 1930, Bernardi and Powers 1995).

Genetic and morphological characters of *F. parvipinnis* reflect strong differences between individuals collected north and south of Punta Eugenia, Baja California, Mexico (27° 50' N Latitude, Bernardi and Talley in press; Figure II-1). While this finding neither confirms nor disputes the designation of subspecies for *F. parvipinnis*, no support was found in the genetic data for a break near Ensenada.

Allen (1980) felt that there was strong evidence from length-frequency data in Upper Newport Bay, CA (Figure II-1), that *F. parvipinnis* is an annual species (lifespan of 1 year). Fritz (1975), based on reading of scale annuli, maintained that the

population in Anaheim Bay (Figure II-1) had a longevity of approximately 18 months, with roughly 3% of the population living to 30 months of age. A maximum age of 3.2 years was estimated for a population in Ojo de Liebre lagoon, Baja California (27° 45' N, Figure II-1), by Pérez-España et al. (1998) through extrapolation of their data and calculations of growth. It should be noted here that there are two potential difficulties with this interpretation of the data. First, the authors used the literature value of maximum size for *F. parvipinnis* (110 mm total length (TL), Eschmeyer et al. 1993), and yet did not capture any fish that were greater than 85 mm total length in their sampling (i.e., approximately 1.2 years of age by their calculated growth rates). It is unknown if these smaller sizes were caused by sampling bias, smaller maximum size, or shorter lifespan in Ojo de Liebre relative to other populations. Second, the authors used a size at hatching of 2 mm in their calculations, which is considerably shorter than the 5-7 mm standard length (SL) at hatching reported for Upper Newport Bay, CA (33° 37' N, Figure II-1) and Mission Bay, CA (32° 46' N, Figure II-1; Rao 1974, Watson 1992). While these difficulties require that the results of the Pérez-España et al. study be interpreted cautiously, this study is nonetheless important and novel, both in subject matter and approach.

Physiology

Several studies on the physiology of *F. parvipinnis* appear in the literature, mostly related to this hardy fish's tolerance to extremes of temperature, salinity, and sulfide. One of the earliest was the work of Keys (1931), who examined the effects of

low salinity on oxygen requirements in killifish. Among his findings was the tolerance of *F. parvipinnis* for freshwater. It was stated that a "considerable portion" of any group of fish transferred to freshwater will eventually become acclimated (Keys 1931, p. 472), and that a gradual decrease in salinity over several weeks normally results in acclimation of nearly all individuals. This ability of *F. parvipinnis* to acclimate to freshwater suggests the appearance of reproductive freshwater populations (Miller 1939,1943; Eigenmann 1892) could occur fairly rapidly. Keys (1931) further noted that smaller fish are more tolerant of sudden decreases in salinity than are larger fish, but that larger fish are more resistant to asphyxiation.

Wells (1935a) demonstrated that there is a seasonal change in metabolic rate for *F. parvipinnis*, even for individuals maintained at constant temperature throughout the year, with metabolic rates high during February and March, and low during July and August. The rate of metabolism was also dependent on the temperature at which the fish had been raised. It was further shown that the increase in oxygen consumption with increasing temperature is more pronounced in small individuals than it is in larger ones (Wells 1935b).

Douderoff (1945) performed studies of *F. parvipinnis* response to heat and cold, and found that fish acclimated at ambient local temperatures (20°C) could achieve 100% survivorship for 7 days at temperatures as low as 7°C, and 62% survivorship for six days at temperatures as high as 34°C. He further noted that survivorship in cold water increased with a decrease in salinity.

Hubbs (1965) examined the effect of temperature and light on development of *F. parvipinnis* eggs, and found that successful hatching occurred at temperatures ranging from 16.6 to 28.5 °C. He further noted a decrease in time to hatching with increases in temperature, from 45.5 days when incubated at a constant 17.2 °C, to 14 days when incubated at 28.5 °C. Thermal effects on development were minimal, however, at temperatures above 21°C, with hatching times ranging from 14-22 days (Hubbs 1965). Eggs of *F. parvipinnis* were observed to hatch more quickly when exposed to light than when maintained in darkness.

Later studies of osmoregulation in California killifish established a range of tolerances for salinities ranging from freshwater to greater than 70 (Valentine and Miller 1969). It was noted that there is some loss in the ability of *F. parvipinnis* to osmoregulate at salinities below 25, and a rapid breakdown at salinities above 60 (Valentine and Miller 1969). This study was considered to support the findings of Carpelan (1961), who inferred that the maximum salinity tolerance for *F. parvipinnis* was above 55, based on populations sampled in Los Peñasquitos Lagoon, San Diego, CA (Figure II-1). However, Feldmeth and Wagoner (1972) reported on field measurements of California killifish in shallow ponds of Bolsa Chica Bay (Orange County, CA, Figure II-1), where a population was "plentiful" in ponds with a salinity of 128. Sampling in the Ojo de Liebre Lagoon (BCS, Mexico) yielded apparently self-sustaining populations of *F. parvipinnis* in waters with salinity as high as 48.4 (Appendix I). Ruiz-Campos et al. (2000) found populations along the northern coast of Baja California in waters with salinities ranging from 1 to 88. Although there seems to

be some variation in estimates of salinity tolerance for *F. parvipinnis*, the general picture that emerges is that this species is extremely euryhaline, able to reproduce in salinities probably as high as 60, and can survive for some time in salinity as high as 128. No studies have examined whether salinity tolerance differs among populations of *F. parvipinnis*.

Another set of studies examined the influence of salinity on fertilization, hatching, and early development of *F. parvipinnis* (Rao 1972, 1974, 1975, 1977). Fertilization success was highest in water with a salinity of 5-33, and lower at salinities of 55 or 0 (Rao 1974). *Fundulus parvipinnis* larvae were shown to be extremely tolerant of freshwater immediately after hatching, but become susceptible to higher mortality in freshwater 2-4 weeks after hatching, subsequently regaining tolerance when 6-8 months of age (Rao 1972). This suggests that the response to low salinity is actually somewhat more complex than Keys' (1931) finding of lower tolerance with increased size. Additional work on the effects of salinity on growth of larval (Rao 1977) and juvenile (Rao 1972) *F. parvipinnis* revealed that the highest growth rates occur in hypersaline water, and the lowest in freshwater.

Fundulus parvipinnis tolerates high levels of sulfide, with a 96 hour LC_{50} (lethal concentration for 50% of the fish) of 700 μM total sulfide (Bagarinao and Vetter 1989). Sulfide is a toxicant that can affect the health, distribution, and survival of marine organisms, and is present at relatively high concentrations in marsh environments (Bagarinao 1992). *Fundulus parvipinnis* has a much higher tolerance to sulfide than do open-coast fishes, and the mechanisms of oxidative detoxification of

sulfide in this species have been identified as being coupled to ATP production (Bagarinao and Vetter 1990).

Although we know the effects of environmental factors such as temperature, salinity, and sulfide concentration on aspects of the biology and physiology of *F. parvipinnis*, there is still little understanding of how these responses change through time and space, and how they translate into changes in the behavior, distribution, and abundance of populations.

Abundance

Fundulus parvipinnis is one of the numerically dominant members of the wetland fish community in southern and Baja California, representing as much as 80% of the average catch in some studies (Ambrose and Meffert 1999), and commonly representing more than a third of the individuals captured for a given sampling period (e.g., Desmond et al. 2000, Allen 1982, Chapter V). Mean density estimates of *F. parvipinnis* in wetland habitats range from 0.05 individuals m^{-2} to more than 60 individuals m^{-2} (Table II-3). Pérez-España et al. (1998), using seines to census small fishes, calculated the mean density of *F. parvipinnis* to be 0.11 individuals m^{-2} in shallow waters (<3 m deep) of Ojo de Liebre lagoon (Table II-3). Using similar methodology (seines), Ambrose and Meffert (1999) recorded densities of approximately 2.2 and 6.9 *F. parvipinnis* m^{-2} in the restored and natural marshes (respectively) at Malibu Lagoon (Figure II-1), Horn and Allen (1981) recorded 1.53 m^{-2} in Upper Newport Bay (Figure II-1), and Nordby and Zedler (1991) found 0.49 m^{-2}

in sampling at Tijuana Estuary, CA, and 0.05 m^{-2} in Los Peñasquitos Lagoon, CA (Figure II-1, Table II-3). Talley (Chapter III) used quantitative drop-traps (0.64 m^2) to examine the ichthyofauna in a marsh in Mission Bay, CA (Figure II-1), and found a mean density of 1.7 juvenile *F. parvipinnis* m^{-2} in the creek and intertidal pool habitats at high tide in the summer and fall of 1999, and 15.5 m^{-2} at low tide, with one low tide sample containing over 2,000 m^{-2} (Table II-3). In 1998, a mean of 0.69 and 43.1 *F. parvipinnis* m^{-2} were recovered at high and low tide, respectively (Talley Chapter III, Table II-3).

It is unclear to what degree the variation in estimates of *F. parvipinnis* density is due to differences in sampling methodology, microhabitats sampled, temporal variation in densities, or actual between-site variability. Future studies assessing densities of *F. parvipinnis* should attempt to use comparable quantitative methodologies to previous work, and should record the microhabitat (e.g., seagrass, unvegetated flat, subtidal creek), tidal stage, and information about the hydrology (e.g., tidal range) and landscape parameters (e.g., drainage density, intertidal vegetation) of the sampling site, in order to tease apart the potential effects of these parameters on *F. parvipinnis* density.

Utilization and movement patterns

Intramarsh

Tidal migrations

In Fritz's (1975) paper on the ecology of *F. parvipinnis*, he noted, through observation of float-tagged fish and mark-recapture returns, that killifish make tidally-induced migrations, moving into intertidal creeks and marsh flats on incoming tides, and back into deeper channels as the tide ebbs. Since that time, we have learned little more about the details of these migrations. Other studies have confirmed the general trend of tidal migrations for *F. parvipinnis* (Chapter III, West and Zedler in press). California killifish generally follow the waterline when migrating between intertidal and subtidal habitats, as suggested by Fritz's (1975) observations and supported by gill net data from Mission Bay, CA (Table II-2), but this behavior may be related more to water depth and tidal state than to distance from waterline per se, and there seems to be an additional ontogenetic component to the pattern of movement. Work by Talley (Chapter III) and Desmond et al. (2000) suggests that water depth plays an important role in governing habitat utilization patterns, with smaller size-classes of *F. parvipinnis* selecting shallower habitats than do larger individuals. However, small juvenile size classes of *F. parvipinnis* in Mission Bay very rarely migrate into unvegetated flat and seagrass habitats even when depths are comparably shallow to the intertidal pools in which they are abundant (Chapter III). Adult killifish do migrate into these habitats, but only at low tide (Table II-2). *Fundulus parvipinnis* was not captured in seagrass habitat at high tide, nor at low tide in water deeper than 30 cm,

indicating that when they do migrate to the seagrass beds, they remain near the waterline. Conversely, there was no apparent depth-related difference in catches in gill nets set on the intertidal marsh at high tide, with fish taken in water from 6 to 65 cm of water. This finding suggests that once the intertidal habitats are flooded, adult killifish are not constrained to as narrow a depth range in their movements, supporting a similar observation by Fritz (1975).

These migrations do not appear to be a simple movement with the flow of tidal currents, but are only generally driven by tidal movement and habitat availability. Adult killifish moving in channels on flooding or ebbing tides will regularly reverse direction and swim against the current, often feeding while doing so, and then reverse direction again, such that their net movement is in the direction of the tide (D. Talley, personal observations). Further, in areas with large, permanent pools in the high intertidal, adult killifish move against the ebbing tide and up tidal creeks, spending the low tide phase in the pool habitat (D. Talley, unpublished data).

The general preference of *F. parvipinnis* for shallow-water habitats is likely a function of protection from predation, as shallow water has been shown to provide refuge habitat for fish and crustaceans (e.g., see Ruiz et al. 1993). This habitat selection may involve a fitness trade-off, as subtidal seagrass beds may provide better foraging habitat than the preferred shallow-water habitats do (Chapter III).

Nonetheless, gill-net catches suggest that adult *F. parvipinnis* make tidal migrations not only between channels and vegetated marsh, as noted by Fritz (1975), but also between upper marsh and subtidal seagrass beds. How far an individual

killifish will migrate during tidal cycles is not known. Mark-recapture-release and stable isotopic analysis data from Mission Bay, CA (Chapter V), suggests that *F. parvipinnis* do exhibit site fidelity, as there is relatively little exchange between populations in a created and contiguous natural marsh.

There is little understanding of what drives these short-term movements of *F. parvipinnis*, and how ecoscape-level properties (*sensu* Kneib 1994) affect killifish behavior and population dynamics. Comparative studies between wetlands with different configurations and areal coverage of creeks, intertidal pools, unvegetated flat, and seagrass beds would help to illuminate the mechanisms underlying these migrations.

Diel patterns

Fundulus parvipinnis migrate between the intertidal and subtidal environments with the tide at night as well as during the day (Chapter IV), although the mechanisms driving these migrations may differ between diel stages. High-tide minnow trap catches of *F. parvipinnis* from intertidal pool and vegetated marsh habitats in Mission Bay, CA at night were significantly lower than those during the day (ANOVA $F_{1,13}=14.5$, $p<0.01$ for pool habitats, and $F_{1,16} = 7.6$, $p<0.02$ for vegetated habitats), while there was no difference between day and night catches for subtidal creek habitat ($p>0.2$; Figure II-2). While this suggests that fewer adult *F. parvipinnis* utilize intertidal habitats at night, gill-net catches of *F. parvipinnis* in Mission Bay, CA showed no significant difference between day and night sampling (Chapter IV). This

lack of congruence between sampling methods could be the result of a lack of power in the gill net experiment, as replication was low and variability was high; the trend was towards higher numbers in day versus night (Chapter IV). Alternatively, the behavior that induces *F. parvipinnis* to enter minnow traps may differ between day and night, resulting in a change in trap efficiency depending on diel conditions.

Catches of *F. parvipinnis* in the same wetland were found to be unrelated to presence or absence of bait in the traps (D. Talley unpublished data), suggesting that killifish are attracted to minnow traps by the structure they provide, possibly as refuge from predation. Migration between the subtidal and intertidal habitats may be driven by foraging needs during night high tides, and by some combination of foraging and refuge during daytime. This pattern could also suggest that shallow water alone (without physical structure) provides sufficient refuge during night-time excursions into the intertidal, as avian predation would be expected to be less efficient in darkness. Controlled experiments examining predation pressure and *F. parvipinnis* behavior under differing light and microhabitat conditions are needed to untangle these processes.

Ontogenetic migrations

Fundulus parvipinnis also exhibit ontogenetic migration, with small juveniles preferentially using shallow creek and intertidal pool habitats, and larger individuals using deeper creek and subtidal habitats (Desmond et al. 2000, Chapter III, this study). This is similar to the ontogenetic patterns described for *F. heteroclinus* on the Atlantic

coast (Kneib 1997 and references therein). These movements promote the transfer of energy across the marsh landscape on a number of spatial and temporal scales (see Kneib 1997, Kneib 1994, and Chapter III).

Movement patterns – intermarsh

Bernardi and Talley (in press) found high levels of genetic differentiation between populations of California killifish along the coast of Alta and Baja California, and inferred low dispersal between marshes. A low level of genetic exchange is consistent with the reproductive behavior (see below) and large size at hatching (Watson 1992) of *F. parvipinnis*, and with the observation that California killifish are rarely found along the open coast as larvae or adults (Watson 1992), even immediately offshore of a large estuary (Nordby 1982).

Genetic differentiation between populations could also arise from natural selection, as has been shown for *F. heteroclitus* on the Atlantic coast of North America (reviewed in Powers et al. 1993). There is evidence for differentiation among California killifish, as some populations in southern California may have developed resistance to chemical contaminants (R. Ambrose, UCLA, personal communication).

Future work should focus on determining the relative importance of genetic drift versus selection in the differentiation of populations of *F. parvipinnis*, through both field and laboratory experimentation. Further, efforts should be made to resolve more

thoroughly the spatial scale of differentiation of populations (e.g., intra-bay), as well as the relationship between population differentiation and oceanographic and environmental features. Coupling these genetic techniques with the use of new tools available for identifying the environmental history of individual fishes (e.g., chemical otolith signatures, Thorrold et al. 1998) will aid not only our understanding patterns of evolution, but also protection of the overall (gamma) genetic diversity of this species.

Foraging

There have been at least 8 studies that have included an examination of gut contents to determine foraging habits of *F. parvipinnis*. One consistent finding across these studies is that arthropods (in particular crustaceans) make up a large proportion of the gut contents (Fritz 1975, Allen 1980, Hartney and Tumyan 1998, Pérez-España 1998, West and Zedler in press, Chapter IV, Chapter III). However at higher resolution and including various habitats and temporal patterns, there is less concordance between studies.

Fritz (1975), examining *F. parvipinnis* in Anaheim Bay, CA, found that crustaceans and insects together comprised on average over 80% of the gut content of *F. parvipinnis* (as measured by "calorically equivalent food items"). While it was not specifically tested, he did not note any obvious differences in composition between day and night sampling, but suggested that there may have been lower levels of feeding at night relative to day (G. Fritz, personal communication). Insects (larval and adult) on average made up over 25% of the gut content in this study, while amphipods

and microcrustaceans (copepods and ostracods) comprised 18% and 32%, respectively (Fritz 1975). Fritz argued, based on frequency of occurrence data, that there was no ontogenetic shift in food habits for *F. parvipinnis*, when comparing small individuals (22–40 mm SL) to the overall population sampled (Fritz 1975).

Allen (1980) reported that *F. parvipinnis* in Upper Newport Bay, CA consumed a wide range of foods, including amphipods, insects, and gastropods, but showed an apparent preference for gastropods (48%), polychaetes (23%) and microcrustaceans (18.8%) when measured as percentage of dry weight. Allen further noted a "seasonal-ontogenetic" shift in diet, with juveniles feeding on microcrustaceans and shifting to larger prey as they grew (Allen 1980).

A study of *F. parvipinnis* feeding habits in Marina del Rey, CA (Figure II-1) also identified California killifish as low-level "microcarnivores", consuming mostly crustaceans and insects (Hartney and Tumyan, 1998). The authors further argued for shifts in prey choice from juvenile and small adult fish in the October sampling consuming largely planktonic copepods, to larger adult fish in April principally consuming benthic prey (mostly tanaids; Hartney and Tumyan 1998). As with the study by Allen (1980), the changes in diet here were difficult to attribute reliably to ontogeny, seasonal changes, or some combination of the two.

Pérez-España et al. (1998) examined 8 individual *F. parvipinnis* in their work in Ojo de Liebre lagoon, BCS, Mexico, and found a similar overall pattern of prey items, with crustaceans dominating the total gut contents at 90%. The authors state

that 16 crustacean species were identified in guts, but they did not provide any further details on the composition.

West and Zedler (in press) used baited minnow traps to examine foraging of *F. parvipinnis* related to vegetated marsh access in a tidal wetland in San Diego Bay, CA (Figure II-1). Stomach contents of fish examined in their study showed differences in prey composition depending on whether they had access to intertidal marsh. Differences in composition of gut contents could also be attributable to location of capture (creek versus vegetated marsh), as these two factors were confounded in this study. Fishes with marsh access consumed largely isopods, amphipods, and insects, while those without marsh access (feeding in creeks) consumed largely ostracods, polychaetes, and detritus (West and Zedler, in press). There were also differences in overall gut fullness between fish with and without marsh access; those fish captured on the marsh surface had more food in their guts than those captured in creeks. The authors found no evidence of ontogenetic shift in food habits in this study.

Using short-term (~2 hour) enclosure experiments, Talley and Sylvester (Chapter IV) and Talley (Chapter III) looked at patterns of feeding between diel stages and among microhabitats, respectively, for California killifish in a tidal salt marsh in Mission Bay, CA. In these studies crustaceans were a dominant component of *F. parvipinnis* prey, but more detritus was consumed at night relative to day, and more detritus consumed in intertidal pools and creeks relative to subtidal habitats. Given the low nutritional value of detritus for congeners of *F. parvipinnis* (Prinslow et al.

1974, Fritz personal communication), this indicates that foraging value of habitats likely differs between diel stages and among microhabitats.

There is also indirect evidence of feeding habits of *F. parvipinnis* inferred from stable isotope analysis of food webs in Tijuana Estuary and San Dieguito Lagoon, CA (Kwak and Zedler 1997, Figure II-1) and Mission Bay, CA (Chapter V, Levin et al. unpublished data, Chapter III). Kwak and Zedler (1997) concluded, based on location of capture and $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$ values of marsh producers and consumers, that juvenile killifish were feeding on *Trichocorixa reticulata* (water boatmen) in marsh pools. $\delta^{15}\text{N}$ values of muscle tissues suggest that *F. parvipinnis* in Mission Bay undergo ontogenetic shifts in diet, related to changing prey preference, changing habitat from which prey items are taken, or both (Chapter III). More work is needed to tease apart the relationship between changes in prey availability, changes in habitat use, and feeding changes with ontogeny. Further, a better understanding of the trophic value of various components of killifish diets is needed to determine fitness value of various foraging regimes.

Growth and production

While the information available on growth and production of *F. parvipinnis* is scarce in the published literature, what exists confirms the potential importance of this species for wetland ecosystems. Pérez-España et al. (1998) examined growth rates for a population of *F. parvipinnis* in Ojo de Liebre, BCS Mexico, estimating Von Bertalanffy Growth Function parameters and secondary production. The authors'

estimate of growth ($K \cdot \text{year}^{-1}$) as 0.93 for this population is fairly high (in the top 4% of values) when compared to the values of K for 75 species reviewed in Pauly (1989).

The only other published study presenting individual growth rates of *F. parvipinnis* was by Fritz (1975), who did not calculate Von Bertalanffy growth parameters, but instead presented his findings as a linear relationship between time and length. The Anaheim Bay population mean growth rate (Fritz 1975) is similar to that of the Ojo de Liebre population (Pérez-España et al, 1998; Figure II-3). It is unknown by how much growth rates may differ between populations, between microhabitats, or through time, but there are known relationships between growth and environmental factors such as temperature and salinity that suggest rates may differ through the range of California killifish occurrence (see Physiology section above).

A bioenergetics model of *F. parvipinnis* growth in relation to access to pickleweed (*Salicornia*) vegetated marsh habitat calculated by Madon (2000) estimated that access to the marsh surface for feeding provides 30% more growth relative to fish without access. While this model apparently did not address potential effects of diel differences in foraging pattern, and used water temperatures from subtidal rather than intertidal habitats in its calculations, it nonetheless strongly supports the importance of vegetated marsh habitats for enhancing growth in *F. parvipinnis*. Experimental testing of the effects of vegetated marsh to *F. parvipinnis* growth and production (e.g., see Irlandi and Crawford 1997) and comparative studies across wetlands with differing vegetation types and inundation regimes are needed to fully understand the value of vegetated marsh to killifish growth and production.

Pérez-España et al. (1998) also estimated total population numbers, total consumption, and total production values for *F. parvipinnis* in Ojo de Liebre lagoon. From this (using conversion factors for wet weight to dry weight from Allen 1980) it is possible to derive an estimate of productivity for *F. parvipinnis* in Ojo de Liebre of 1.09 g DW m⁻² yr⁻¹. Allen (1980) also estimated productivity for *F. parvipinnis* in the entire littoral zone of Upper Newport Bay, CA, and arrived at an estimate of 0.393 g DW m⁻² yr⁻¹ (which was less than 40% the value given for fishes in Ojo de Liebre). Allen's (1980) estimate of productivity for *F. parvipinnis* from only the intertidal pool ("panne") habitat in Upper Newport Bay was much higher, at 1.317 g DW m⁻² yr⁻¹, possibly due to higher productivity of the smaller size classes that were found there. These differences in productivity underscore the need to understand how production and growth might differ among microhabitats in the marsh landscape. Further, it is known that *F. parvipinnis* densities fluctuate seasonally, with highest densities in September and October, and lowest numbers and biomass from December through May (e.g., Allen 1980, West and Zedler in press), as well as interannually (Nordby and Zedler 1991, Chapter V, Chapter III). Production is related to growth and abundance, indicating that the production estimates we currently have represent only snapshots of this species' dynamics.

Nonetheless, the magnitude of these production values hints at the potential importance of killifish in this system, and underscores the need to more thoroughly understand the patterns of growth and production in this species. For example, Pérez-España et al. estimate that each year 1,930 tons of biomass (mostly microcrustaceans)

is consumed and 187 tons of biomass produced (~10% transfer efficiency) by *F. parvipinnis* in the Ojo de Liebre lagoon. Similar studies throughout the range of *F. parvipinnis*, and similar analyses using data already generated from other studies, are needed to clarify our understanding of killifish production dynamics. Despite studies of otolith analyses for embryo, larva, and juvenile stages of *F. heteroclinus* on the Atlantic coast that yielded information about reproductive periodicity and daily age (Radtke and Dean 1982), no studies of otolith analysis for ageing of *F. parvipinnis* have been published. California killifish possess otoliths that are relatively large and easy to remove (D. Talley personal observation), thus similar studies should be possible. Incorporating otolith analysis and validation into estimates of age and growth could greatly increase our knowledge about the growth and production dynamics of *F. parvipinnis*, and how these dynamics are related to environmental conditions.

Reproduction

The major source for information about reproduction in *F. parvipinnis* comes from a study performed on 424 individual fish taken in Anaheim Bay, CA in 1969 (Fritz 1975). In that study, it was determined that *F. parvipinnis* mature at a minimum standard length of 46 mm (average 59.5 mm for males, and 60.1 mm for females). Females produced between 61 and 439 ova (mean = 178 ova per fish), and there was a positive relationship between size of fish (SL) and number of ova produced (Fritz 1975). Eggs of California killifish have short, adhesive threads (Hubbs 1965, Rao

1972) which become less adhesive within approximately one day following fertilization (H.J. Walker, personal communication).

The Anaheim Bay population of killifish spawned from April through September (Fritz 1975). Based on a time to hatching of 3 to 4 weeks (Hubbs 1965), monthly length-frequency distributions, and the observation that the ovaries in *F. parvipinnis* matured sequentially in 3 regions, Fritz (1975) determined that there were 3 distinct periods of spawning in April, May, and June for this population, with spawning activity decreasing thereafter through September. Based on a shift in sex ratio (females/males) of the population through time (from roughly unity in April through July, with an overall increasing trend to a maximum of almost 7 in November), Fritz (1975) hypothesized that males may spawn only once and die, while females spawn at least three times. He further posited that a relative lack of reproductive males late in the summer may account for the reduced spawning at that time.

Keys (1931), studying a population of *F. parvipinnis* in Mission Bay, CA, stated that the spawning period was from May to June, possibly extending as late as the beginning of August "[i]f the preceding winter has been unusually prolonged." Sampling in the same bay in 1997-2000 revealed at least some ripe females and males well into September each year, but the proportion of individuals that were reproductive was not quantified, and spawning events were not witnessed (D. Talley personal observation).

Pérez-España et al. (1998) estimated the months of hatching for *F. parvipinnis* in Ojo de Liebre lagoon to be April and May, based on backwards extrapolation of cohorts from length-frequency histograms. Given the estimate of time to hatching from Hubbs (1965), the authors suggest that spawning occurs there in March and April. The authors do not quantify or note the appearance of ripe individuals in their sampling, and base their spawning dates solely on this inference.

These varying estimates of spawning season for *F. parvipinnis* may be an artifact of differing methodologies, or they may represent real variability in the timing of spawning, either changing through time or changing with geographic location. *Fundulus heteroclitus* on the Atlantic coast is known to have spawning seasons that vary in response to local temperatures, with spawning occurring earlier in the year and being more protracted in warmer waters (Able and Fahay 2000). *Fundulus heteroclitus* spawns from May through June in Massachusetts, April through August in New Jersey, and March through August in North Carolina (Able and Fahay, 2000 and references therein). The range of *F. parvipinnis* along the Pacific coast includes numerous upwelling zones, which can create strong gradients in water temperature over short distances of shoreline (CalCOFI 1963). Water temperature can also change along a gradient from the head to the mouth of the bays. For example, in Bahía Falsa (San Quintín, BCN, Mexico, Figure II-1) water temperature between the mouth and head of the bay (a distance of approximately 10 km) differed by 7°C, from 13°C at the mouth to 20 °C at the head (Farreras and Cabrera 1979). If temperature is a factor controlling spawning season in *F. parvipinnis*, as it is in *F. heteroclitus*, it is possible

that nearby populations may exhibit strong differences in reproductive season. This is an area of investigation that would benefit from controlled studies of spawning behavior across multiple populations.

While it has been suggested that *F. parvipinnis* may selectively spawn on spring high tides (Rao 1972, Foster 1967), this has not previously been confirmed. Gonadosomatic indices (GSI) of female killifish from Mission Bay, CA indicate that fish spawn during spring tidal cycles, within 2-3 days of a full or new moon (Figure II-4). Further, during the reported spawning season for *F. parvipinnis*, (April through September), spring high tides occur at night through the range of distribution for this species (Harbor Master® 5.0, Zihua Software Inc). Thus, spawning should occur at night.

The courtship behavior and spawning of *F. parvipinnis* in the wild has never been recorded in published literature. During summer spring high tides in Mission Bay, when GSI values indicated spawning was taking place, ripe males and females could be captured in shallow waters of the vegetated marsh (often < 10 cm deep; D. Talley, personal observation). At these times it was common to hear splashing; presumably related to courtship or spawning of killifish (D. Talley personal observation). It has been suggested that *F. parvipinnis* females deposit their eggs a few centimeters below the sediment surface on mudflats (Rao 1972). However, the presence of large numbers of small juvenile fish in intertidal pool habitats (Chapter III, Fritz 1975), and faster hatching rates in warmer, lighted environments (Hubbs 1965) suggest that *F. parvipinnis* uses vegetated marsh or intertidal pool habitats for

spawning (personal observation, Fritz 1975). This implies that variation in the availability of these habitats between individual marshes (e.g., areal coverage of intertidal pool) may affect reproductive success of this species.

It has been proposed that the spawning schedule of *F. parvipinnis* is such that it provides warmer water temperatures for more rapid growth of eggs and larvae, as well as higher marsh inundation times (thus greater foraging availability) and more night-time high tides (thus lower predation risk) during periods of peak *F. parvipinnis* abundance (West and Zedler in press). While it is likely that these factors play an important role in *F. parvipinnis* life history, other factors may also explain the observed pattern.

Fundulus parvipinnis spawns on spring high tides (Figure II-4), possibly to allow access to the high intertidal pools, where eggs would experience relatively warm water temperatures (Chapter III) and lowered risk of advection, as subsequent tides would not inundate the spawning site as long. Further, food resources for larval fish may be replenished by the tides (Kneib 1993), therefore synchronizing spawning such that larvae hatch during spring tides and maximum inundation of upper marsh would promote growth. These advantages favor spawning during April-June, which Fritz (1975) considered the peak season.

From April through September along the range of *F. parvipinnis* distribution, spring high tides occur at night. While the shallow waters of the intertidal may provide refuge from piscivorous fishes (Ruiz et al. 1993), visually-feeding birds are likely more effective predators on the marsh during daylight, and therefore spawning

on night-time high tides may offer additional protection from predation. Additionally, while the spring is a period during which water temperatures generally are rising (e.g., see West and Zedler in press), it is also a period of minimum daytime inundation for high intertidal habitats (Harbor Master® 5.0 Zihua Software Inc). This low inundation time during daylight means the intertidal pools will be isolated under insolation for long periods, allowing them to warm and become hypersaline (Lennon 1995, Chapter III). As warm temperature and high salinity promote rapid hatching and growth for killifish eggs and larvae, spawning in April through June (the reported peak spawning periods in Fritz 1975) would be another selective advantage. Finally, it should be mentioned that densities of temperate, soft-bottom macrofauna, which are common prey items for *F. parvipinnis*, tend to peak during the Spring and Fall (L. Levin personal communication), and this may provide greater nutrition, promoting egg and sperm production.

Some of these putative selective pressures could be tested by examining multiple populations through time. For example, there is a shift towards earlier season of maximum night-time inundation with increases in tidal elevation (Harbor Master® 5.0, Zihua Software Inc). Therefore if night-time inundation is a strong influence on the timing of spawning in *F. parvipinnis*, populations utilizing marshes with higher tidal elevations should spawn consistently earlier than those spawning in lower marshes. Similarly, through correlating changes in prey densities, intertidal pool temperatures, or salinity with the timing of spawning in various populations, much could be learned about the proximate factors driving the patterns of *F. parvipinnis* life

history. Manipulative experiments with laboratory-reared populations under varying temperature, salinity, and feeding regimes could help verify mechanisms controlling spawning pattern.

Much of what we know about reproductive habits of *F. parvipinnis* is based on inference, and studies of small numbers of populations or individuals. We are lacking firm knowledge of such basic information as what substrate is used for attachment of eggs, and how *F. parvipinnis* populations differ in reproductive behavior and biology between and among populations.

Larval ecology

With the exception of the research on physiology and morphology (e.g., Rao 1972, Watson 1992; see sections above), there have been no published studies of *F. parvipinnis* larvae. No research has examined larval feeding, major sources of larval mortality, nor cues driving recruitment of *F. parvipinnis*. *Fundulus parvipinnis* larvae probably utilize intertidal pools, small depressions, and shallow creek habitats. This is supported by the probable location of spawning and the preference of juvenile fish for these habitats (see above). Nordby (1982) provides supporting evidence; his data suggest that *F. parvipinnis* larvae are not strongly utilizing subtidal or nearshore habitats. Nordby (1982) sampled ichthyofauna of tidal creeks, subtidal channels, and nearshore habitats in Tijuana Estuary, CA. Over the course of this one-year study, over 21,000 larvae were captured, of which only 2 were *F. parvipinnis*. Further, this sampling recovered over 50,000 fish eggs, of which none belonged to *F. parvipinnis*.

This supports the contention that *F. parvipinnis* larvae remain on the intertidal marsh habitat, as has been demonstrated for *F. heteroclitus* on the Atlantic coast (Kneib 1993).

Difficulties associated with sampling ichthyoplankton on the marsh surface, as well as the short larval stage (~ 2 weeks, Watson 1992) undoubtedly have led to our lack of knowledge of this life-history stage. Nonetheless, small changes in larval mortality and growth rates can drive large changes in fish recruitment (Houde 1987). Thus, teasing apart the processes controlling these factors will be a critical step in understanding the population dynamics of *F. parvipinnis*.

Role in marsh community

Research to date on *F. parvipinnis* has focused almost exclusively on autecological studies, with little attention paid to the synecology of this species. Studies including species or community interactions of *F. parvipinnis* have been generally in the form of records of killifish as prey items (e.g., Haaker 1975, Zembal and Fancher 1988), as predators (e.g., Hartney and Tumyan 1998, West and Zedler in press, Chapter IV), or in species associations (Allen 1982, Horn and Allen 1981). One important exception is a study by Lafferty and Morris (1996), which looked at the behavioral effects of a parasite on behavior in *F. parvipinnis*. It was found that the parasite induced behaviors in killifish which made the fish more vulnerable to avian predation, and thus increased the transmission of the parasite to its final avian host. This observation demonstrates potential interactions among *F. parvipinnis* distribution

and behavior and population dynamics of the parasite (*Euhaplorchis californiensis*), the first intermediate host (*Cerithidia californica*), and the final avian hosts (Lafferty and Morris 1996).

Studies investigating the broader ecological role and interspecific interactions of *F. parvipinnis* in wetland communities are lacking. There have been numerous studies of interspecific and community interactions of *F. heteroclitus* on the Atlantic coast, including work on interspecific competition (Weisberg 1986, Dunson and Rowe 1996), effects of *F. heteroclitus* predation on prey populations (Kelso 1979, Kneib 1988), and transport of production across habitat boundaries (Cicchetti 1998). Similar work should be carried out using controlled studies of *F. parvipinnis*.

It has been stated that *F. parvipinnis* "occupies the same ecological niche" as *F. heteroclitus* (Weaver 1976). I know of no published studies which have critically examined that proposal. While the general habits and morphology appear to be similar, there are reasons to expect some possible differences. Environmentally, the habitats on the Pacific coast differ substantially from those on the Atlantic coast, with southern and Baja California having smaller, more isolated marshes, relatively little freshwater input (Zedler 1996a), higher elevation for *Spartina* (Callaway and Josselyn 1992), mixed semidiurnal as opposed to semidiurnal tides (Open University 1989), and a suite of different prey and predator species, among others. Studies examining co-occurring species of *Fundulus* on the Atlantic and Gulf coasts have revealed habitat partitioning and inter-specific variation in physiological tolerances (e.g., Werne 1975, Weisberg 1986, Crego and Peterson 1997). It is unknown if *F. parvipinnis*, living in

habitats without sympatric congeners, has a broader niche than is displayed by these other species of *Fundulus*.

Future directions

Despite its high abundance, conspicuous presence, and likely importance in wetland ecosystems, there have been relatively few published studies on *F. parvipinnis* since the seminal paper written more than 25 years ago (Fritz 1975). Based on this review of the literature, I would suggest that the particularly large gaps in our knowledge of *F. parvipinnis* ecology fall into three broad areas:

1. Causes of temporal and spatial variation in abundance. The densities of *F. parvipinnis* vary strongly between seasons, years, and locations, but it is still unclear what drives these variations at both small and large spatial and temporal scales. Efforts must be made to conduct research that provides us with a mechanistic understanding of how *F. parvipinnis* populations are regulated, focusing on fitness values of varying microhabitats within the marsh landscape, larval stages and recruitment, as well as the effects of larger-scale differences between drainages and years. There is a wealth of information in the form of monitoring surveys and technical reports that should be consulted as well to help illuminate these issues.
2. The consequences of temporal and spatial variation in abundances. Little is known about the functional role of *F. parvipinnis* in wetland and associated communities.

Efforts must be placed in learning how killifish directly and indirectly affect potential predators, prey and competitors. In particular, manipulative studies of this species and its ecological role are lacking.

3. Learning more about the basic biology of *F. parvipinnis* is a critical step towards attaining these larger goals. For example, we are particularly lacking in understanding of the reproductive behavior and biology of California killifish. It is currently unknown precisely where and how spawning takes place, and what drives the timing of reproduction. Similarly, very little is known about the assimilation rates of various food items in *F. parvipinnis* diets: if or how well *F. parvipinnis* can utilize detritus or algae for maintenance or growth, or how various common components of their diet (e.g., ostracods, gastropods, amphipods) differ in trophic value. Comparative studies of reproduction between populations of *F. parvipinnis* and controlled studies of assimilation efficiency are needed.

Developing a clearer understanding of the ecology of *F. parvipinnis* may be a critical component of learning to successfully preserve, protect, and create the threatened wetland habitats and their associated faunas in southern and Baja California.

Table II-1. Sampling dates and gear used in collections of *Fundulus parvipinnis* in Mission Bay, CA during this study.

Sampling gear	Sampling dates
Gill nets	August 10-12, 26, and September 24-27 1999
Cast net (gonad index)	June 3,9,13,21,23,26,28, July 12,20-24,28,31, August 3-7,11,6-21,24, and 26 1998
Minnow trap	Night sampling July 22 and August 9 1997, Daytime sampling August 4, 7, September 17 and 20, 1997

Table II-2. Mean number of *Fundulus parvipinnis* (± 1 standard error) captured by each gill net in vegetated marsh and seagrass habitats at high and low tides in Mission Bay, CA.

	High Tide		Low Tide	
	Mean # fish/net	Mean depth (cm)	Mean # fish/net	Mean depth (cm)
Vegetated Marsh	10.9 $\pm$ 2.5	41.3 $\pm$ 2.3	N/A	N/A
Seagrass	0	114.4 $\pm$ 9.1	6.2 $\pm$ 3.2	30.1 $\pm$ 3.0

Table II-3. Estimates of density of *Fundulus parvipinnis* in Pacific coast wetlands.

Location	Sampling method	Tidal phase	Habitat	Density (m ⁻²)	Study	Note
Upper Newport Bay, CA	seines	not given	panne (pool)	1.53	Horn and Allen 1981	
Upper Newport Bay, CA	seines	not given	inshore	0.069	Horn and Allen 1981	
Upper Newport Bay, CA	otter trawl	not given	channel	<0.001	Horn and Allen 1981	
Tijuana Estuary, CA	seines (w/blocking nets)	moderate to low	creek	0.49	Nordby and Zedler 1991	
Los Peñasquitos Lagoon, CA	seines (w/blocking nets)	moderate to low	creek	0.05	Nordby and Zedler 1991	
Laguna Ojo de Liebre, Mexico	seines	not given	water depths ≤ 3 m	0.11	Pérez-España et al. 1998	
Malibu Lagoon, CA	seines (w/blocking nets)	not given	creek	6.9	Ambrose and Meffert 1999	restored
Malibu Lagoon, CA	seines (w/blocking nets)	not given	lagoon	2.2	Ambrose and Meffert 1999	natural
Mission Bay, CA	0.64 m ² drop traps	low	creek and pool	15.5	Talley Chapter III	1999, sub-adults only
Mission Bay, CA	0.64 m ² drop traps	high	creek and pool	1.7	Talley Chapter III	1999, sub-adults only
Mission Bay, CA	0.64 m ² drop traps	low	creek	43.1	Talley Chapter III	1998, sub-adults only
Mission Bay, CA	0.64 m ² drop traps	high	creek	0.69	Talley Chapter III	1998, sub-adults only

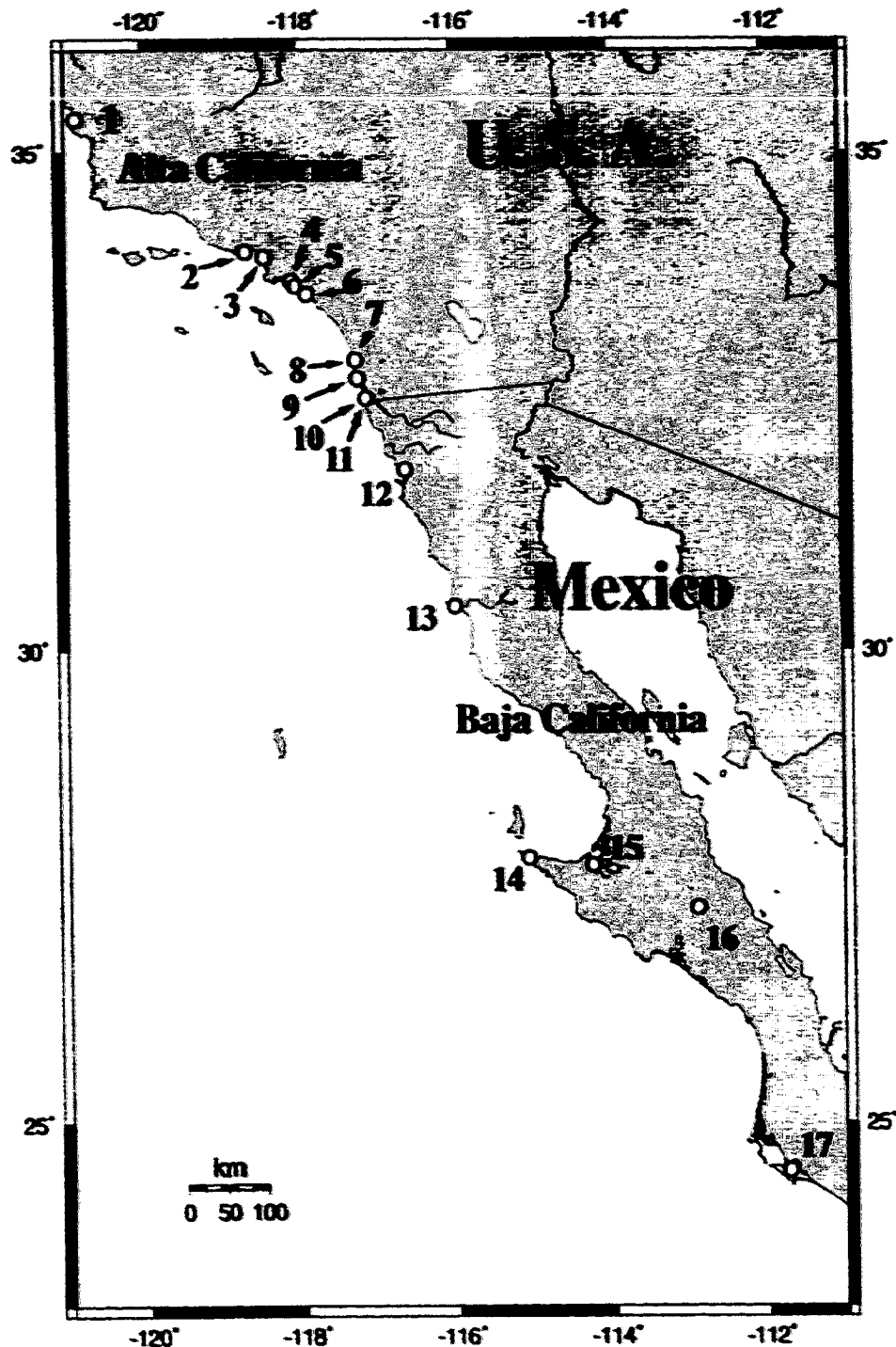


Figure II-1. Locations of *Fundulus* studies referred to in the text. 1. Morro Bay, 2. Malibu Bay, 3. Marina Del Rey, 4. Anaheim Bay, 5. Bolsa Chica, 6. Newport Bay, 7. San Dieguito Lagoon, 8. Los Peñasquitos Lagoon, 9. Mission Bay, 10. San Diego Bay, 11. Tijuana Estuary, 12. Ensenada, 13. San Quintín, 14. Punta Eugenia, 15. Laguna Ojo de Liebre, 16. Oasis de San Ignacio, 17. Bahía Almejas.

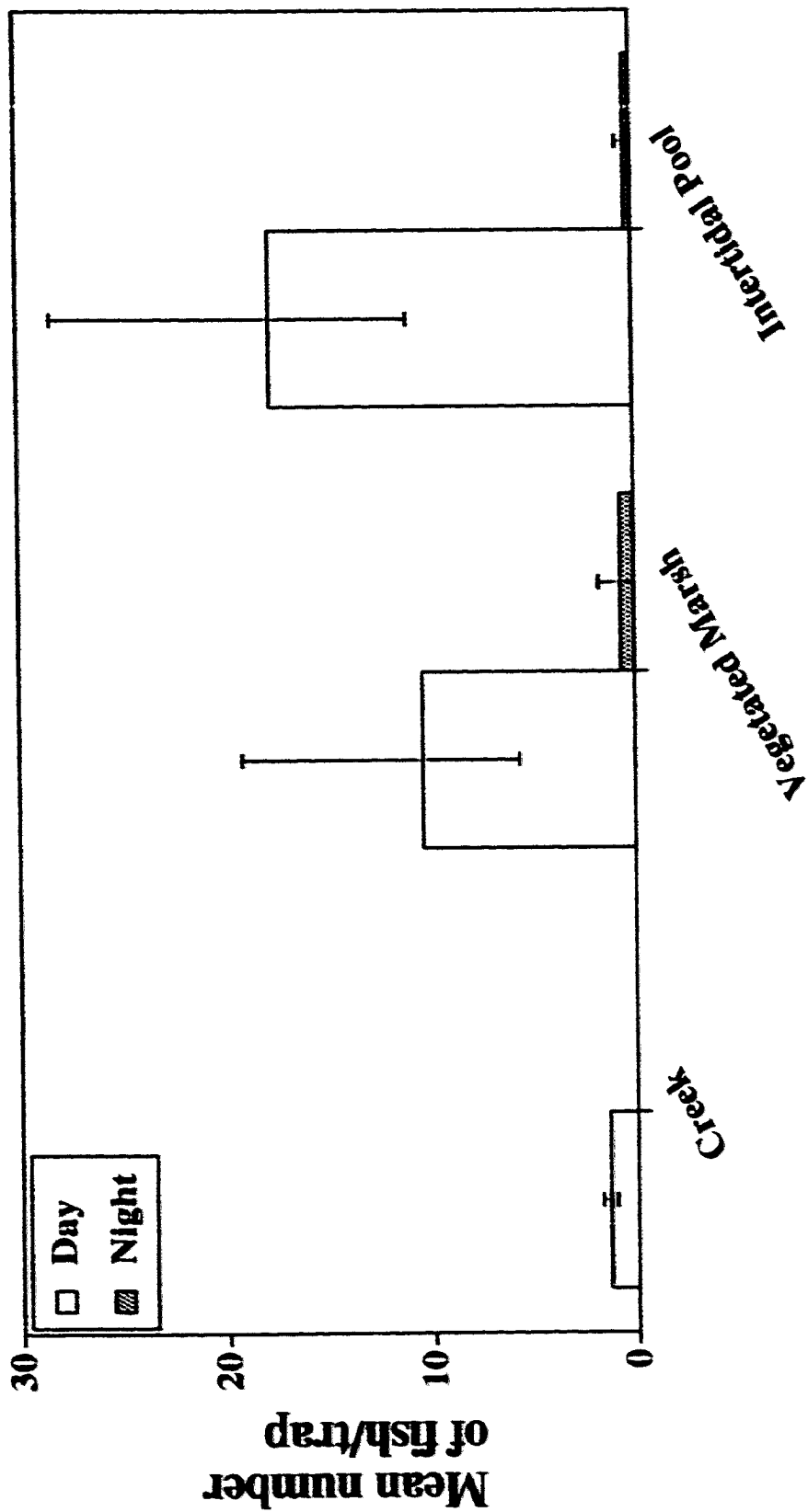


Figure 11-2. Mean numbers of *F. parvipinnis* per trap in each of three habitats in Mission Bay, CA during daytime and nighttime high-tide sampling. More fish were trapped in the Spartina-vegetated marsh and intertidal pools than creeks, and more fish were caught during daytime than at night. Error bars are ± 1 s.e.

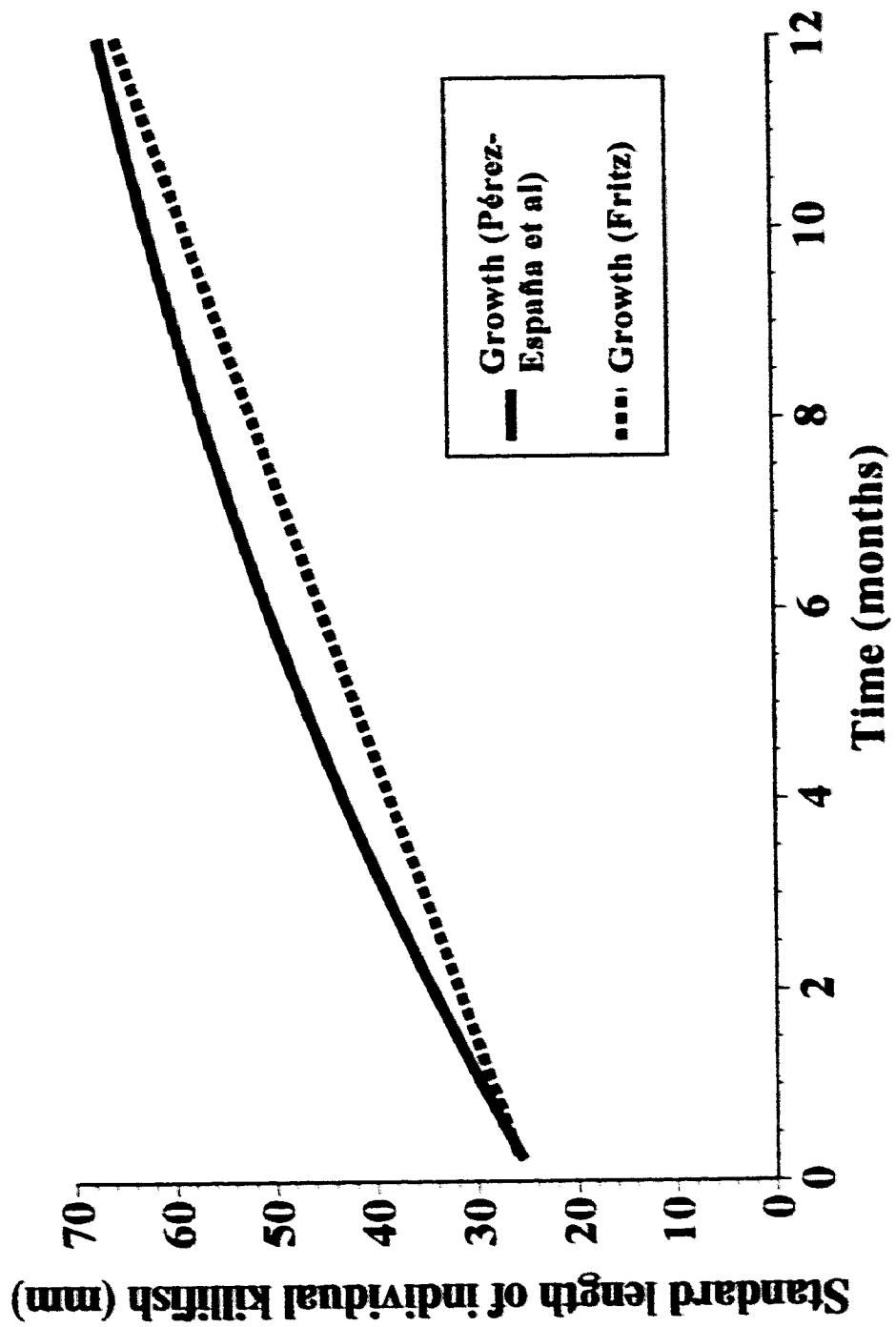


Figure II-3. A comparison of the estimates of growth rates for *F. parvipinnis* from Pérez-España et al 1998 and Fritz 1975. Only lengths for which growth was estimated in both studies are presented.

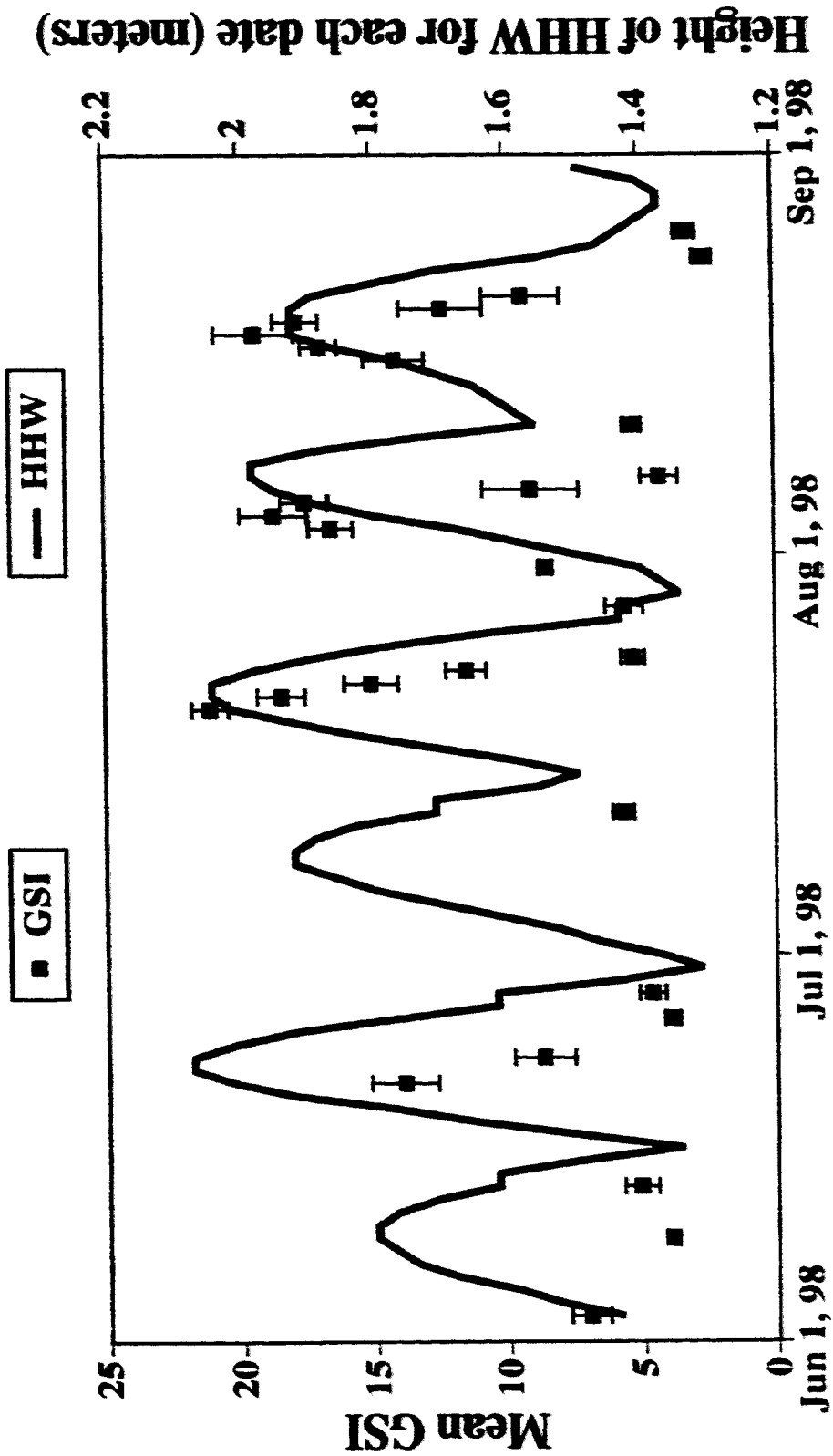


Figure II-4. The mean value of gonadosomatic indices (GSI) of female *F. parvipinnis* from Mission Bay, CA for sampled dates and height (in meters) of higher high water (HHW) during the period from Jun 1, 1998 to Sep 1, 1998. Sudden decreases in GSI are interpreted as spawning events. Peaks of HHW occur at full and new moons.

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CHAPTER III

The role of utilization patterns of fishes in linking habitats within a wetland mosaic

Abstract

Many natural environments are comprised of a complex mosaic of habitats, with distinct environmental and biological characteristics, connected by linkages spanning a range of temporal and spatial scales. This study utilized drop-traps, caging experiments, and stable isotopic analyses to examine habitat linkages mediated by small resident fishes in a southern California wetland. Habitats examined included seagrass beds, unvegetated tidal flats, subtidal creeks, intertidal creeks, and intertidal pools. These habitats differed with regard to environmental parameters: higher elevation habitats have generally higher mean water temperature and salinity and lower mean depth, but these parameters changed on tidal, seasonal, and interannual time scales. Fishes showed distinct habitat preferences. Gobiids (mostly *Clevelandia ios* (arrow goby) and *Gillichthys mirabilis* (long-jawed mudsucker)) dominated seagrass and unvegetated flat habitats, while juvenile *Fundulus parvipinnis* (California killifish) remained in creek and pool habitats at both high and low tides. Stable isotopic analysis of tissues, showing enrichment in ^{15}N with size for *F. parvipinnis*, accompanied by size-specific distribution patterns, indicated that *Fundulus parvipinnis* undergoes ontogenetic habitat shifts, moving from intertidal pools to creek habitats. These movements may be accompanied by diet shifts. Experimental caging of

Fundulus parvipinnis within each habitat revealed no difference in overall gut fullness (g. food/g. fish), however pool and intertidal creek fish consumed a lower diversity of food items and higher percentage detritus than in other habitats. These patterns of habitat use suggest trade-offs between habitats within the wetland mosaic.

Introduction

All natural systems are composed of mosaics of patches and microhabitats (Giller et al. 1992). These patches are reticulately-connected, with the connections mediated by both physical and biological processes spanning a wide range of spatial and temporal scales (Polis and Strong 1996).

The physical processes forming these linkages broadly involve the transport of material between habitats. For example, wind-transported marine aerosols have been shown to influence terrestrial productivity thousands of kilometers away (Swap et al. 1992), and sediment and nutrients transported by rivers can affect coastal marine benthic communities far downstream (Hall et al. 1992).

These habitat linkages can also be mediated by biological processes, with animals connecting systems through their movements and utilization patterns. Between-habitat movements will be determined by habitat quality and the biological needs of the species, including foraging value, predation risk, and reproductive value.

Thus habitat boundaries (and therefore habitat linkages) are species-specific. These linkages commonly occur on spatial scales from a few meters (e.g., reef fish community impacts on adjacent soft-bottom benthos, [Jones et al. 1991]) to thousands

of kilometers (e.g., for migrating birds, Hunt and Schneider 1986). They also occur across a spectrum of temporal scales, ranging from hours (e.g., for lizards feeding in the intertidal at low tide, Arndt 1999) to years (e.g., for leatherback turtles, *Dermochelys coriacea*, Musick 1997). While traditional analyses of habitat function and community ecology have often focused on single habitats, recent attention has focused on the importance of the ubiquitous interactions between habitats (e.g., Polis and Strong 1996), and on the role of spatial pattern in shaping these interactions (e.g., Wiens et al. 1993).

There may also be distinct habitat-use and between-habitat movement patterns that change during ontogeny. In some cases, intraspecific differences in functional roles among ontogenetic stages can be greater than interspecific differences in function (Livingston 1988). An understanding of habitat linkages therefore requires a knowledge of the temporal and ontogenetic patterns of utilization by organisms. Habitat patches may themselves be heterogeneous, and provide microhabitats that can be partitioned by species and life stages. This wealth of variability needs to be evaluated and incorporated into models if we are to understand population dynamics in a spatially-heterogeneous world.

Recent models of population dynamics incorporate between-habitat (patch) movement (e.g., see Hanski and Gilpin 1997 and references therein). However, metapopulation theory has paid little attention to the complexity of patch quality and distribution beyond two habitat types. Landscape ecology does address these issues, but its theoretical development has been slow due to the diversity and complexity of

habitat shape, type, quality, distribution, and connectivity. The understanding of complex systems and the development of a testable spatial ecological theory should include empirical data obtained from complex ecosystems with interconnected habitats.

Pacific coastal wetlands are clear examples of such spatial diversity. They are comprised of a mosaic of habitats, including subtidal and intertidal creeks, submerged aquatic vegetation (SAV), unvegetated tidal flat, intertidal vegetated marsh, and permanent pools. Each of these habitats are potentially linked through a number of biological and physical processes, including the movement of water, sediment, and detritus between habitats, and the movement and activities of plankton and nekton.

Fish movements may be of particular importance in linking habitats within a wetland and in linking wetlands with coastal or offshore habitats. This has been better-studied on the Atlantic and Gulf coasts of North America, where the role of wetlands in providing essential fish habitat for commercially important species, and the reciprocal role of those species in affecting wetland community structure and function, has received much attention (e.g., Weinstein and Brooks 1983, Scharf and Schlicht 2000). Much of this work has its genesis in Odum's (1968) "outwelling" hypothesis, where he suggested that expanded fisheries in coastal areas may result from the outwelling "of nutrients and organic detritus from shallow water nutrient traps such as...salt marshes" (as quoted in Odum 1980). While the original focus of this hypothesis was on organic detritus as the source of "outwelled" material (see Nixon 1980 for a review), later studies suggested the importance of mobile fishes and

invertebrates in the transport of energy and carbon between habitats (e.g., Cicchetti 1998, Rountree and Able 1992).

A number of taxa use wetlands as nursery areas or as foraging habitat, including commercially important species such as menhaden, spot, croaker, and shrimp (Weinstein 1979). Through these activities, these species are not only exporting production from wetland habitats, but have also been shown to have effects on the structure and function of marsh resident communities (e.g., Service et al. 1992). In this manner, changes in the environment or ecology of one habitat can potentially be linked to changes in a spatially and temporally distant habitat. For example, *Pomatomus saltatrix* (bluefish) require estuarine systems as nursery habitat (Minello 1999). These fish live offshore as adults, where they are important predators on other fishes and invertebrates (Buckel et al. 1999). Adults spawn on the shelf, and their larvae migrate back to estuarine nursery habitats (Able and Fahay 2000). A loss or degradation of estuarine habitat could therefore have important effects on offshore communities mediated by changes in abundance or population structure of *P. saltatrix*.

Ichthyofauna which complete their entire life cycle within the wetland ("marsh residents") also transfer energy and nutrients across the marsh surface, but receive much less attention than the commercially-harvested, migratory taxa (Kneib 1997). These resident fishes are important components of linkages on this larger (between wetland) scale (Kneib 1997), as well as within and among habitats in the wetland mosaic (Kneib 1994). To address linkages between wetlands and coastal regions, as

well as intra-marsh linkages, it is necessary to determine the pattern and process of temporal and spatial habitat utilization by southern California resident fish species.

A number of underlying ecological and physiological factors may drive habitat utilization patterns in wetland fishes. Proximate factors such as the presence or absence of vegetation (Rozas and Odum 1987), differences in prey availability (Hartney and Tumyan 1998), water depth (Ruiz et al. 1993), inundation time (McIvor and Rozas 1996), or creek order (Desmond 1996), have all been shown to affect fish utilization of habitats. These factors ultimately affect fishes in a number of ways, including changing susceptibility to predation (McIvor and Odum 1988), physiological stress (Evans et al. 1999), reproductive fitness, and foraging success (Kneib 1997, Hsiao et al. 1996, Rozas and Odum 1988).

Habitat utilization patterns of individual fishes change through time, both on longer (e.g., interannual, seasonal, or ontogenetic) and shorter (e.g., tidal) time scales (Baltz et al. 1993, Kneib and Wagner 1994, Chapter V). Proximate factors such as light availability, water depth, temperature, and predation pressure change across a range of time scales. For example, wetland fish use of microhabitats may vary with light availability (Chapter IV), which varies not only on diel time scales, but also seasonally. Temperature, which has been shown to be a factor in fish habitat selection and growth (Sogard 1992, Lankford and Targett 1994), can change dramatically through a single day, but also shows strong interannual variability (e.g., with El Niño events), as well as changes through geologic time, with long-term global warming and cooling cycles (Seibold and Berger 1982). Biological factors affecting fishes, such as

the presence and abundance of predators and prey, change over time scales ranging from tidal and diel (Rountree and Able 1993), through geological (Jablonski and Sepkoski 1996). The same pattern of variability across scales applies to the presence of algae and vegetation, which can serve as forage or refuge for many wetland fishes (e.g., Minello and Zimmerman 1992). Evaluation of habitats at multiple temporal scales is required to capture the range of utilization patterns.

An important tool for testing for potential changes in habitat utilization is stable isotope analysis. Stable isotope analysis is based on the finding that the ratio of isotopes incorporated in an organism's tissues reflect that of their food source; either by remaining the same as that of the food ingested, or by changing in a predictable manner during assimilation into tissues (Fry and Sherr 1984). Given variability in isotopic composition between food sources or locations, this allows isotopic composition of animal tissues to be used in a number of ways. Stable isotopes have been used in ecology to examine large-scale migrations (e.g., Fry et al 1999), local site fidelity (Chapter V), spatial variability in food webs (Deegan and Garrit 1997), trophic structure (Vander Zanden et al 2000), and ontogenetic changes in diet (Vander Zanden et al 1998). In this study, analysis of isotopic signatures will be used to explore ontogenetic shifts in microhabitat use patterns of small resident fishes.

The goal of this paper is to use habitat utilization patterns of wetland resident fishes to test hypotheses about linkages in wetland mosaic habitats. The following hypotheses were examined using drop-traps, stable isotope analyses, and enclosure experiments: (1) wetland resident fishes perceive the wetland as a mosaic of habitats,

partitioning the landscape on spatial scales ranging from centimeters to hundreds of meters; (2) there are changes in these fish utilization patterns on tidal, seasonal, and/or inter-annual time scales; (3) ontogenetic shifts in habitat utilization by wetland resident fishes lead to trophic linkages through "life-history omnivory" (*sensu* Polis and Strong 1996); (4) key mechanisms driving the observed spatial and temporal distributions include (a) physiological/environmental conditions and (b) differential food availability.

Materials and Methods

Study site

Sampling was performed in the Northern Wildlife Preserve/Kendall Frost Marsh Reserve (NWP/KFMR) in the northern part of Mission Bay, San Diego, California (32° 47' N, 117° 14' W; Figure III-1). The NWP/KFMR is a natural marsh of approximately 12 hectares which is managed by the City of San Diego and the University of California, San Diego. The marsh vegetation was predominantly composed of *Spartina foliosa*, *Salicornia bigelovii* and *Salicornia virginica* (Levin et al. 1998; Talley and Levin 1999).

Microhabitats

Five classes of wetland micro-habitat were examined in this study (Figure III-2): (1) seagrass bed, (2) unvegetated tidal flat, (3) subtidal creek (4) intertidal creek, and (5) intertidal pools. Subtidal seagrass bed (Figure III-2A) included areas vegetated

with both *Zostera marina* (eelgrass) and *Ruppia maritima* (widgeon grass).

Unvegetated tidal flat (Figure III-2B) bordered the seaward edge of the marsh. There were two main predominantly subtidal creeks in the wetland system (Figure III-1, III-2C). Sections of creeks were designated as intertidal if they appeared to drain completely at MLW. Intertidal creeks (Figure III-2D) occurred throughout the marsh, but were more numerous on the western side of the wetland, and were generally narrower and shallower than subtidal sections of creeks. Pools sampled were unvegetated depressions ranging from $\approx 0.7 \text{ m}^2$ to 68 m^2 (Figure III-2E). Pools were surrounded by vegetation (generally *Salicornia spp* or *Spartina foliosa*), and usually had abundant colonies of coccoid cyanobacteria growing on the sediment surface, something seen only occasionally in shallow creek habitats, and never in other habitats. Vegetated sediments were excluded from this study because the quantitative drop-traps used (see below) were unreliable in vegetated marsh habitats.

Drop-trap sampling

Quantitative drop traps were used to sample fishes from each of the 5 microhabitats described above. Drop traps were constructed of four 11-gauge stainless-steel panels, each 23 cm high and 80 centimeters long, forming a square of 0.64 m^2 . A float collar constructed of 80 cm by 80 cm PVC pipe (2" inner diameter) was connected to the drop trap by a 2 m long sock of 3 mm delta-mesh netting. The traps were deployed from moveable four-legged stands constructed of 1.25 cm diameter aluminum tubing (height 2.5 m). Traps were attached to the stands by two

ropes threaded through a pair of brass rings, with the rings in turn attached to a shackle, held in place by a cotter-pin. Traps were put in place between 3 and 24 hours prior to each deployment, and were triggered at slack high and low tide (± 30 minutes). The trap was released from the stand during deployment by removing the cotter pin through means of a 20 meter long rope, so that there was no human presence in the immediate vicinity at the time of trap release. Immediately after dropping, the metal frame of each trap was checked to ensure that it formed a complete seal with the substratum.

Trapping was performed during the summer of 1998 (Jul 22-28, Jul 30, Aug 1-3, Aug 9-11, and Sept 15 1998), the summer of 1999 (Jul 15-19, Aug 10-14, Aug 25-29, and Sept 8-11) and the fall of 1999 (Sept 23-26, Oct 8-11, and Nov 6-9). Traps were deployed at both high and low tide in each of the 5 microhabitats on each sampling date, with the exception of the summer 1998 sampling, which was only conducted in creek habitats. Trapping in 1999 (which was used to test high versus low tide distribution patterns) was conducted during periods in which the high-tide elevation was $\geq 4.5'$ above MLLW during daylight hours, to ensure that nekton had access to all habitats at high tide. In an effort to include unvegetated flat on very low spring tides, but retain the ability to compare across habitats, all traps were dropped simultaneously prior to slack low tide when it appeared the low tide would leave unvegetated flat habitat exposed.

Water temperature and salinity were measured once within the trap; water depth was measured at 5 points within the trap (each corner and in the center). Trap

location was noted on a map, and distance to the bay, distance to the nearest creek, pool widths (longest dimension and perpendicular axis), distance to marsh edge, and creek width (where applicable) were measured. Traps were cleared using a large-framed (0.7 x 0.7 m) dip-net constructed of 3 mm delta mesh on a large (0.7 x 0.7 m) stainless-steel frame, attached to a 2 m long, 5 cm diameter wooden handle. The net was swept through the trap until 3 successive sweeps in at least 2 directions captured no fish. Fishes were removed from the dip nets, identified, measured, and released in the field, to minimize impact on the reserve. Sediments and plant material in the dip net were examined closely for small fishes prior to being returned to the water.

Within-creek habitat selectivity

Paired trap deployments were used to compare fish use of shallow subtidal creek microhabitats in relation to proximity to junctions with low-order creeks (= "rivulets"). On each of five dates (Aug 3, Aug 11, and Sept 16, 1998, and Oct 9-10 1999), two traps were deployed ("rivulet" and "non-rivulet") at daytime low tide within shallow subtidal creekbeds. Traps were set such that one was immediately adjacent to where a rivulet joined the creek being sampled. The paired trap was set immediately adjacent (< 1.0 m away) from the first trap (Figure III-3), and more distant from the junction (= "non-rivulet"). Both traps were positioned so that they were the same distance from the creek edge. Traps were deployed and cleared following the same protocol described above for other drop-trap samples.

Foraging experiments

Enclosure experiments were conducted with *F. parvipinnis* to examine potential differences in foraging quality of microhabitats examined here. Enclosures were constructed from clear plastic storage boxes (47 cm wide x 80 cm long x 33 cm tall) modified in the following manner. The bottoms were removed using a handheld rotary saw, and removable lids were constructed of 1 mm plastic mesh, with a small rim of plastic (~3 cm wide) creating a seal with the body of the box.

One hour prior to daytime high tides on October 9-11 1999, enclosures were placed in the NWP/KFMR in Mission Bay, CA, in each of the 5 microhabitats: seagrass bed, unvegetated tidal flat, subtidal creek, intertidal creek, and intertidal pool. Two divers using SCUBA deployed enclosures in the three deepest habitats. Enclosures were pushed approximately 8 cm into the sediment to ensure a complete seal, 3 *F. parvipinnis* were introduced into each enclosure, and the lids were affixed. The experimental fish were starved for 24 hours prior to the experiment to allow complete gut clearance. To verify that all food items were obtained in the field, a subsample of 5 control fishes was maintained in an aquarium with filtered seawater, then processed simultaneously with experimental fishes.

One hour after high tide, temperature and salinity were measured from inside and outside the enclosures using a YSI® 30 handheld gauge. Fish were then removed from the enclosures using a small dip net, and immediately placed in liquid nitrogen to halt digestion and preserve gut contents. To ensure that the fish were allowed to feed for approximately equal periods of time, efforts to remove the fish were discontinued

either when all 3 fish had been successfully recovered or after ten minutes of searching, whichever was shorter. Fish were allowed to feed within the enclosures for a total of approximately 2 hours.

In the laboratory, fish were thawed and blot-dried before gut content analysis. Total length, standard length, and total wet weight was recorded for each fish. Only the first section of the gut ("foregut") was removed for analysis, to minimize error associated with differential digestion of gut contents (Babkin and Bowie 1928, Cicchetti 1999). Immediately upon removal, gut fullness was subjectively estimated, with each gut being given a rating from 1 to 5 (1 = empty, 2=25% full, 3=50% full, 4=75% full, 5 = 100% full). Gut contents were then identified to the lowest taxonomic group possible, and wet weight of each taxonomic group was measured to the nearest milligram. A gut content index, the wet weight of the pooled gut contents expressed as a percentage of the wet body weight of the fish (Hyslop 1980), was also calculated for each fish sampled.

Stable Isotope Analyses

Stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$) were used to explore dietary differences of *Fundulus parvipinnis* through ontogeny by examining size- (age) specific differences in isotopic composition. Fish were sampled for isotope analysis at low tide from the marsh creeks and pools using a monofilament cast net, a small seine, and an aquarium dip net on Oct 8, 10, & 15 1996, Apr 14 1997, Oct 22 & 23 1997, and Apr 16, 1998. During Oct 1997, *F. parvipinnis* also were sampled by seine from

the subtidal *Zostera marina* (seagrass) beds in the bay adjacent to the marshes (Figure III-1). Only one individual from each cast net throw or seine pull was analyzed for stable isotopic composition, to increase independence of samples. *Fundulus parvipinnis* with a total length greater than 40 mm were filleted to remove muscle tissue for isotope analysis. For fishes under 40 mm in length, the gut was removed and the remainder of the fish was analyzed. To examine the potential for possible changes in isotopic values because of the inclusion of scale and bone material in smaller (non-filleted) fish, one adult (72 mm total length) and one juvenile (40 mm total length) fish were filleted on one side, with the remaining half of the fish analyzed separately for comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. To determine if female *F. parvipinnis* fractionate isotopes when developing eggs, muscle tissue and gonads were analyzed from four ripe females collected in spring 1998.

Fish were washed in distilled water, dried at 60°C to constant weight, ground with a mortar and pestle, and then sent to R. Michener at the Stable Isotope Laboratory at Boston University for analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Analyses were carried out on a Finnigan Delta-S isotope ratio mass spectrometer using standard methods (Lajtha and Michener 1994). All international standards were obtained from the National Bureau of Standards, Gaithersburg, Maryland, USA. Internal instrument precision is 0.014‰, and typical sample precision is better than 0.1‰ (R. Michener pers. comm.).

^{34}S isotopic analyses were performed by Kris Tholke at the Stable Isotope Laboratory of the Marine Biological Laboratory in Woods Hole, Massachusetts. After

combustion, sulfate was precipitated as BaSO₄, converted to SO₂, and the isotopic ratio determined by mass spectrometry.

Stable isotope ratios are reported in standard δ notation as follows:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$$

where X is ¹³C, ¹⁵N, or ³⁴S, and R is ¹³C/¹²C, ¹⁵N/¹⁴N, or ³⁴S/³²S, respectively. Values are expressed on a per mil (‰) basis.

Data analysis

Due to the large expected variability in biological and environmental factors related to tidal state (high versus low) and season, data analyses were performed for four different environmental "states", unless otherwise indicated: (1) summer high tide (SHT), (2) summer low tide (SLT), (3) fall high tide (FHT), and (4) fall low tide (FLT). Because only subtidal creek and intertidal creek habitats were sampled in 1998, these samples were compared only against similar habitats for 1999 when assessing interannual variability.

All *F. parvipinnis* individuals captured in this study were post-larval stage, and most (>99%) were sub-adult (<46 mm standard length, as defined by Fritz 1974). Therefore, unless otherwise stated, analyses of patterns of utilization in *F. parvipinnis* in this study were performed on distribution data based on 2 size-classes of *F. parvipinnis*, relative to the median size captured (25 mm total length): those with a

total length ≤ 25 mm were designated as “small juvenile” or “J1” *F. parvipinnis*, and those > 25 mm were designated “juvenile” or “J2” *F. parvipinnis*. Further, due to the difficulty of identifying very small gobiids accurately in the field, gobies were grouped for analyses based on two size classes - “small gobiids” (< 35 mm total length) and “large gobiids” (≤ 35 mm total length). The median size captured in this study was 34.5 mm total length. As fishes of different sizes generally have distinct prey preferences, subdividing the data by size class not only allows the testing of hypotheses about intraspecific partitioning of habitats, but effectively creates ecologically relevant groupings of individuals (Livingston 1988).

Ordination of presence-absence data was performed using correspondence analysis (CA, JMP 4.0 statistical software, SAS Inc.) to evaluate patterns of utilization among habitats. Significance of the ordinations was determined by use of a G test on the presence-absence data. If the test was significant at $\alpha = 0.05$, the ordination diagram was further examined to evaluate trends in the data.

Several drop-trap deployments were considered flawed, due to: (1) difficulties prior to deployment (e.g., the netting was hanging in the water, potentially attracting or frightening fishes), (2) early deployment difficulties, such as the trap release mechanisms sticking, leading to movement of the trap and associated disturbances early in deployment, and (3) incomplete sealing with substratum, potentially allowing egress of fishes. Biological data (species composition, abundance, and length information) from flawed trap samples were not used in any analyses. However,

environmental data (e.g., depth, temperature, salinity) from these samples were used in the analyses of environmental characteristics of habitats.

Non-metric multidimensional scaling (MDS) was used to examine similarities and differences for environmental variables within each of the different habitats (see Clarke and Greene, 1988; Clarke, 1993). These analyses were based on Bray-Curtis similarity indices of $\log(x+1)$ transformed, unstandardized data. Stress values, measures of how well the 2 dimensional MDS plots represents the distances between the data, are given. Clarke (1993) suggests values <0.1 are good and <0.2 are useful.

Statistical analyses of abundances were performed on $\log(x+1)$ transformed data, unless otherwise specified. This transformation emphasizes relative rather than absolute differences in abundance (Mead 1988).

Multivariate analyses of gut content from enclosure experiments were carried out using Primer Statistical software (Clarke and Warwick, 1994). Non-metric multidimensional scaling (MDS) was used to explore gut content similarities and differences for fish within each of the different habitats (see Clarke and Greene, 1988; Clarke, 1993). These analyses were based on Bray-Curtis similarity indices of $\log(x+1)$ transformed, unstandardized data. Gut content data were wet weights of each food item.

Results

Environmental variation

Habitats differed in water depth for all sampling periods (summer and fall, high and low tides), with seagrass habitats generally being deepest, and intertidal pools the shallowest (ANOVA, $p < 0.05$ for each state; Figure III-4 A-D). There were also differences in mean water temperature among habitats for the fall low tide sampling (ANOVA, $F_{1,39} = 6.71$, $p < 0.001$; Figure III-4D), as well as differences in salinity among habitats for both low tide sampling sessions in 1999 ($p < 0.05$, Figure III-4B,D).

There were seasonal differences in both low-tide temperature (ANOVA $F_{1,83} = 29.6$, $p < 0.0001$) and salinity (ANOVA $F_{1,71} = 34.9$, $p < 0.0001$), when examined across all habitats, with both temperature and salinity being higher in summer relative to fall (28.0 vs 23.5 °C and 36.6 vs 33.2, respectively, Figure III-5B). At high tide the habitats differed in mean temperature between seasons (ANOVA $F_{1,92} = 83.3$, $p < 0.001$), with summer temperatures being higher than fall (mean = 25.7 and 21.3 °C, respectively), but salinity was not significantly different (ANOVA, $F_{1,82} = 2.3$, $p > 0.10$; Figure III-5A).

Multidimensional scaling (MDS) provided additional evidence that differences in water depth, temperature, salinity, and distance from the bay edge created distinct environments within the marsh complex (Figure III-6A-D). Samples from each habitat tended to cluster together when examined with MDS, with unvegetated flat and

seagrass beds often overlapping, and pools appearing the most distinct (stress < 0.02 for all plots).

Habitats also varied over interannual time scales, as seen by comparing temperature and salinity for creek habitats (subtidal and intertidal combined) between summer 1998 and summer 1999 (Figure III-7A-B). High-tide creek samples from summer 1998 had significantly lower mean water temperatures (ANOVA $F_{1,44}=18.7$, $p<0.0001$, Figure III-7A) and salinity (ANOVA $F_{1,44}=4.9$, $p=0.03$, Figure III-7 B) than samples from the summer of 1999. Similarly, low-tide salinity values were significantly higher in 1999 creek samples ($F_{1,30}=13.1$, $p<0.005$, Figure III-7 B).

At the smallest spatial scale examined in this study (decimeters), there was no significant difference for measures of mean depth, water temperature, or salinity between low-tide samples taken from creeks adjacent to rivulets versus those creek samples approximately 1 meter away ($p>0.29$, Figure III-8).

Fish Distributions

A total of 3,801 fishes representing eight species were captured in 248 successful trap deployments over the course of this study (Table III-1). *Fundulus parvipinnis* was the dominant fish captured in this study, representing 76.7% of the total catch. Almost half of the fish taken, however, (1406 individual *F. parvipinnis*) were from a single creek sample in the summer of 1998. As this density was an order of magnitude higher than that in the next highest sample, it was considered an outlier, and was not used in any of the statistical analyses of general habitat use patterns.

Clevelandia ios and small, unidentified gobies (likely *C. ios* or juvenile *Gillichthys mirabilis*, although a small number of *Quietula y-cauda* and *Ilypnus gilbertii* were also taken) represented the majority of the remaining catch, at 12.8% and 15.4%, respectively (Table III-1). *Paralichthys californicus* and *Sygnathus auliscus* were caught only in the tidal flat and seagrass habitats, and represented only a small fraction (less than 1%) of the total catch (Table III-1).

Habitat specificity

Small wetland resident fishes showed habitat selection (based on analyses of presence/absence data) for each environmental state sampled. In each case, (SHT, SLT, FHT, and FLT), there were significant differences in distribution among habitats for the four broad groups of fishes (J1 *F. parvipinnis*, J2 *F. parvipinnis*, large gobiids, and small gobiids) and for traps without any fishes (Figure III-9A,B), based on G tests of presence/absence data. Both size classes of *F. parvipinnis* were associated with intertidal pools, and small gobiids with seagrass habitat, at each environmental state, (as determined by the relative direction on the first and second canonical analysis axes). Further, unvegetated flat and seagrass habitats tended to be similar at both low and high tides (Figure III-9A,B).

On a scale of decimeters, the densities of *F. parvipinnis* were two orders of magnitude higher in sections of creek adjacent to rivulets (mean of 330.8 fish per trap) relative to samples not adjacent to rivulets (mean of 3.4 fish per trap), when examined at low tide (paired t-test, $t_4 = -3.16$, $p < 0.05$, Figure III-10).

Tide effects

There were significant differences in total fish densities among habitats at both high and low tides, when examined across all times, but the patterns of utilization differed with tidal stage. During high tides, there were significant differences in overall fish densities ($F_{4,95}=3.33$, $p=0.013$), with the highest density occurring in the seagrass habitats (mean of 6.4 fish per trap, Figure III-11). Fish in seagrass samples at high tide were comprised almost exclusively of small gobiids (Figure III-11). At low tide, habitats also exhibited differences in ichthyofaunal abundance ($F_{3,88}=3.87$, $p=0.012$), with the highest densities found in the creek habitat (mean of 15.8 fish per trap). Low-tide creek samples were dominated by both *Fundulus parvipinnis* (54.7%) and small gobiids (43.3%).

Fundulus parvipinnis densities exhibited habitat-specificity at high tide when evaluated across all times ($F_{4,95}=3.33$, $p=0.013$), with the pool and unvegetated tidal flat habitats significantly different from seagrass habitats when further examined with post-hoc tests (Student's t-test, $P<0.05$). The highest mean number of *F. parvipinnis* per trap was in the shallow creek habitat (mean = 1.4 fish per trap), and the lowest was in the seagrass and tidal flat habitats (mean of 0.0 individuals per trap; Figure III-11). At low tide, *F. parvipinnis* densities also differed between habitats ($F_{3,88}=9.24$, $p<0.0001$), with the highest numbers occurring in pools (mean = 10.9 per trap), and the lowest in samples from the unvegetated tidal flat (0.0 fish per trap, Figure III-11).

The abundance patterns of small gobiids contrasted that that of *F. parvipinnis*. While high-tide distributions of small gobiids exhibited significant differences across habitats ($F_{4,98}=7.63$, $p<0.0001$), the highest mean density was in the seagrass habitats (5.7 per trap) and the lowest in pool habitats (mean=0.5 per trap; Figure III-11). At low tide, the highest small gobiid density per trap occurred in the tidal flat habitat (mean = 4.8 individuals per trap), and the lowest in pool habitats (mean = 0.1 individuals per trap; Figure III-11).

Habitat utilization changes as a function of tidal stage (Figure III-11). The tidal flat had higher densities of total fish at low tide relative to high tide ($F_{1,29}=10.93$, $p<0.003$), with a mean density of 6.1 fish per trap at low tide, compared to a mean of 2.1 fish per trap at high tide (Figure III-11). These differences were driven by changes in gobiid densities (Figure III-11), suggesting that the unvegetated tidal flat provides habitat for tidally migrating fishes. Samples from subtidal creeks had higher densities of fish at low tide relative to high tide ($F_{1,53}=19.26$, $p<0.0001$), with a trend towards greater abundances at low tide for all groups (Figure III-11). Finally, intertidal pools had higher densities of fish at low tide (mean abundance = 10.7 fish per trap) relative to high tide (mean abundance = 3.9 fish per trap, $F_{1,55}=4.69$, $p=0.035$). This difference was due mostly to much higher densities of *F. parvipinnis* (mean per trap of 10.5 at low tide, 1.1 at high tide, $F_{1,55}=7.37$, $p<0.009$; Fig 11). In contrast, the densities of gobiids in pools tended to be lower at low tide (Figure III-11). Seagrass habitat exhibited no difference in density between tides for any fish group ($p>0.2$ for all contrasts), suggesting that the small fishes using this habitat (almost exclusively

gobiids) are either not migrating with the tides, or are replaced by similar numbers of gobiids when they migrate (Figure III-11).

Seasonal patterns

Drop-trap data revealed no evidence of seasonal variation in habitat utilization patterns over the time period of this study. There were no significant differences in density for any of the four main groups (small gobiids, large gobiids, J1 *F. parvipinnis*, and J2 *F. parvipinnis*) or for total ichthyofaunal densities when compared between seasons (and across all habitats combined) at low or high tide ($p > 0.1$ for all contrasts; Figure III-12). When analyzed between seasons but within each habitat and tidal state individually, only 2 habitat/taxa combinations were significantly different; juvenile *F. parvipinnis* were more abundant in fall relative to summer in both high-tide pool samples ($p < 0.05$) and low tide creek samples ($p < 0.03$).

Ontogenetic patterns in California killifish

Fundulus parvipinnis showed distinct patterns of utilization related to size class, with smaller individuals (J1 *F. parvipinnis*) selecting different habitats than larger juveniles (J2). For low-tide traps that captured *F. parvipinnis*, there were significant differences in the proportion of J1 individuals among habitats ($F_{2,38} = 9.7$, $p = 0.0009$). Pool samples were dominated by J1 *F. parvipinnis* (85.0% $\pm$ 4.7 of the killifish in pools), while creek samples were almost evenly-divided between J1 and J2 *F. parvipinnis* (J1 *F. parvipinnis* represented 56.3% $\pm$ 9.0; Figure III-14). At high tide

there was no difference in utilization of habitats by J1 *F. parvipinnis* (ANOVA, $p>0.45$), but the trend was also towards small size classes being more prevalent in pools (Figure III-14).

Interannual patterns

There is strong evidence for interannual variability in creek ichthyofaunal abundances based on comparison of densities between years (summer 1998 vs summer 1999; Figure III-15 A,B), but little evidence of changes in relative distributions of taxa. Mean low tide creek abundance for all taxa combined was 53.2 individuals per trap in the summer of 1998, but only 9.0 individuals per trap in the summer of 1999 ($F_{1,30} = 22.07$, $p<0.001$; Figure III-15 A). These differences resulted both from higher densities of both J1 *F. parvipinnis* (mean of 18.9 per trap in the summer of 1998, 3.2 per trap in the summer of 1999, $F_{1,30} = 7.4$, $p=0.01$) and higher densities of large juvenile (J2) *F. parvipinnis* (mean 24.2 per trap in summer 1998 samples, 0.8 per trap in summer 1999 samples, $F_{1,30} = 4.88$, $p<0.035$). While not statistically significant, there was also a trend towards higher low-tide densities of small gobiids in creeks during summer 1998 relative to summer 1999 (Figure III-15 A).

During high tide, none of the fish groups exhibited significant differences in density between years ($p>0.05$, Figure III-15B). There was however a nonsignificant trend mirroring the pattern of low-tide samples, with higher densities of total fishes, *F. parvipinnis*, and small gobiids in the 1998 samples relative to 1999 (Figure III-15 B).

Stable isotope data

Ontogenetic changes in source of nutrition are revealed by stable isotopic composition of *F. parvipinnis* tissue. There was a strong positive relationship between body size (age) and $\delta^{15}\text{N}$ for killifish in this marsh, with large adults being enriched in ^{15}N ($r^2=0.45$, $p<0.0001$; Figure III-16). $\delta^{15}\text{N}$ of food items generally undergo a shift of approximately +2-4‰ during assimilation into an organism's tissues, and therefore higher $\delta^{15}\text{N}$ values are often considered indicative of organisms feeding at a higher trophic level (e.g., DeNiro and Epstein 1981).

If the samples are examined by "large" and "small" size classes separately, using the same size-classes utilized for drop-trap analyses in this study (total length < 25 mm being "J1", ≥ 25 mm being "J2"), an additional pattern emerges. J1 fish showed a decrease in $\delta^{15}\text{N}$ with increasing size ($r^2=0.90$, $p=0.0004$), while larger fish show an increase ($r^2=0.52$, $p<0.0001$; Figure III-16). Ova of female *F. parvipinnis* examined in this study had lighter carbon signatures (mean $\delta^{13}\text{C}=-18.1$) than the muscle tissue of the same fish (mean $\delta^{13}\text{C}=-15.2$, paired t-test, $t_6=-6.91$, $p=0.0062$). There was no detectable difference in fractionation of nitrogen or sulfur (paired t-test, $p>0.80$ for both contrasts) between these tissues (Figure III-17). Mean $\delta^{15}\text{N}$ for muscle tissue was 11.5‰, and for ovary tissue was 11.4‰. Mean $\delta^{34}\text{S}$ for muscle tissue was 10.1‰, and for ovary tissue was 9.9‰. These results and the enriched $\delta^{15}\text{N}$ in the smallest fish sampled suggest that nitrogen and sulfur isotopic signatures of larvae may closely resemble those of the parent fish.

This trend of ^{15}N enrichment with size is unlikely to be an artifact of processing, despite the finding that fish under 40 mm total length were processed differently (gutted and processed whole) than larger fish (filleted). There was no apparent difference in $\delta^{15}\text{N}$ values for filleted samples (muscle only) versus the remaining tissue from the same individual fish processed whole, although there was the suggestion of a shift to lighter $\delta^{15}\text{C}$ in whole samples (Figure III-18).

Enclosure experiment

There was no difference among habitats in overall gut fullness (g. food/g. fish) of caged fishes (ANOVA, $p>0.9$, Figure III-19). Fish with empty guts did not differ in representation among habitats (ANOVA on arcsin-transformed mean proportion of fishes with empty guts, $F_{4,11}=0.97$, $p=0.46$), and were not included in remaining analyses. There were differences in the diversity of food items obtained, with the highest mean number of food categories per fish observed in fish caged in the seagrass habitat (mean = 4.4, ± 1.0), and the lowest (mean = 1.9 ± 0.1) from cages in pool habitats (ANOVA, $F_{4,11}=3.83$, $p<0.05$, Figure III-19).

There were also differences in consumption of detritus for fishes enclosed within different habitats; fish from pool and intertidal creek habitats had a high percent of their gut content made up of detritus (mean = 92% and 64%, respectively) relative to fish enclosed in deep creeks (7%), unvegetated flat (17%), or seagrass habitats (2%; ANOVA on arcsin-square root transformed proportions, $F_{4,11}=7.9$, $p<0.005$, Figure III-20). Since detritus is probably a lower-quality food than invertebrates, these results

suggest that the deeper habitats may provide better foraging opportunities for *F. parvipinnis* than do the shallower intertidal creeks and pools. (Prinslow et al. 1974) demonstrated that *F. heteroclitus* was unable to use detritus either for growth or maintenance of body weight. *Fundulus parvipinnis* has a very similar digestive tract morphology to that of *F. heteroclitus*, and their relatively simple guts are not consistent with detritivorous feeding (Bowen, 1983). Thus, it is likely that detritus provides similarly low nutritional value for *F. parvipinnis*.

General differences in foraging among habitats were revealed by multidimensional scaling. Fish from pool habitats had the most similar within-habitat gut contents, and were generally similar to those in intertidal creek habitats (Figure III-21, stress=0.10, overall analysis of similarity [ANOSIM], $p < 0.01$). Fish from seagrass and unvegetated flat habitats were variable and overlapping in their gut contents, while those from subtidal creek habitats were distinct (Figure III-21). These findings suggest that foraging value may be quite similar for pool and creek habitats, as well as for intertidal flat and seagrass habitats, while deeper creeks may be distinct with regard to habitat value.

Discussion

The Kendall-Frost salt marsh is a complex habitat mosaic, with microhabitats evident on a number of spatial and temporal scales. In this respect it is typical of many natural habitats, with environmental and biological factors creating ecotopes which are

often embedded within physical gradients – in this case gradients of inundation, temperature, salinity, and light, forced by tidal, diel, seasonal, and climatic regimes.

These microhabitats displayed spatial and temporal environmental variability which suggests that they have the potential to provide distinct fitness costs and benefits to wetland fauna. These ecotopes exist at a number of spatial scales, and exist within a hierarchy of micro-, meso-, and macro-environments within the marsh landscape. For example, physical structures on the scale of millimeters, in the form of animal burrows or plant stems, have been shown to influence the chemistry and water flow of the surrounding areas in soft-bottom benthic environments (Leonard and Luther 1995). On broader spatial scales than those examined here, change in inundation times across hundreds of meters of intertidal marsh (from low to high marsh elevations) have been demonstrated to dramatically affect soil, sediment, and plant characteristics (Mitsch and Gosselink 1986).

These ecotopes also have a temporal component to them, changing on tidal, diel, seasonal, interannual, and interdecadal time scales. In this study, environmental parameters were found to vary strongly on tidal (e.g., Figure III-7) through seasonal (e.g., Figure III-5) time scales. This implies that not only might these microhabitats confer varying degrees of fitness, but that relative fitness levels are dynamic, and change on a number of temporal scales.

Linkages

Small resident fishes recognize ecotopes within the wetland landscape, and utilize these ecotopes in size- and species- specific patterns (Figures 9, 10). Fishes are thus contributing to the formation of biotopes, with microhabitat communities being comprised of distinct ichthyofaunal assemblages, which change on a number of time scales. It is through these changes in utilization that fishes help link habitats within the marsh mosaic. For example, in this study intertidal pools at low tide represented a favored habitat for J1 *F. parvipinnis*, but harbored relatively few other small resident marsh fishes (Figure III-9). At high tide, this same habitat was still preferentially utilized by J1 *F. parvipinnis*, but at densities almost an order of magnitude lower (Figure III-13). Thus, the boundaries between the pools and adjacent habitats, while generally impermeable to fishes at low tide, were quite porous at high tide. Another interpretation is that the habitat value of pools for J1 *F. parvipinnis* changed dramatically with tidal stage, becoming less important when the marsh is flooded, and more important at low tide.

Patterns of shifting habitat value and utilization indicate that the intertidal pool habitat is both physically and functionally linked to other marsh habitats. Specifically, pools are linked to other marsh habitats through a number of processes, including (a) developmental dynamics, (b) trophic transfer, and (c) physical linkages.

Linkages through changes in population dynamics are likely in this system, as the ontogenetic changes in habitat utilization suggest that intertidal pools play an important nursery function for *F. parvipinnis*. Areal extent of pool habitat, as well as

habitat quality, are likely to affect population densities and survivorship of J1 *F. parvipinnis*. Lowered survivorship of small size classes could in turn have demographic consequences for later life-stages, reducing densities of J2 and adult *F. parvipinnis*, which preferentially utilize other habitats, (e.g., creeks for J2 *F. parvipinnis* [Figure III-9], and deep creeks and subtidal habitats for adults [D. Talley, unpubl. data]). A created marsh, which lacked pools and low-order creeks, had a *F. parvipinnis* size-structure skewed towards large individuals relative to the adjacent natural marsh (KFMR/NWP; Chapter V). These changes in juvenile and adult fish densities would affect both killifish prey and predators in these other marsh habitats.

Fish-mediated trophic transfer between pools and other habitats was also demonstrated in this study. The ichthyofaunal utilization pattern features both movement into and out of pools with change in tides, and movement out of pools with ontogeny for *F. parvipinnis*. Thus there is a linkage between microhabitats on both short (tidal) and longer (order of months) time scales. Stable isotope data offer additional support for these trophic linkages through ontogeny. Two of the possible interpretations of the change in $\delta^{15}\text{N}$ signal with size for *F. parvipinnis* (Figure III-16) are: (a) a change in diet with ontogeny, potentially involving a shift to higher trophic levels with age, or (b) a change in the base of the food web between habitats. It is likely that both of these are factors in the enrichment of ^{15}N with size in *F. parvipinnis*. That the different size classes of *F. parvipinnis* display (1) distinct differences in nitrogen signatures and (2) distinct habitat preferences, suggests a trophic linkage through ontogeny between pools and other habitats in the marsh mosaic.

These habitats may be linked by physical processes as well. Movement of organisms across habitats by "rafting" on masses of detached plant material (or "wrack") has been documented in numerous studies of intertidal and shallow subtidal ecosystems (see Worcester, 1994 and references therein). Wrack from the shallow subtidal can have direct physical effects on neighboring habitats, creating regions of anoxia (Bonsdorff 1992), damaging wetland plants (Valiela and Rietsma 1995), and even forming sand dunes (Hemminga and Nieuwenhuize 1990). Wrack mats of seagrass and *Spartina* plants are also thought to be important in the formation of intertidal pools on the marsh surface (Pethick 1974, Hartman et al. 1983), and have biological effects such as dispersing organisms (Highsmith 1985) and subsidizing terrestrial habitats (Polis and Hurd 1996). Given the importance of intertidal pool habitat to wetland fishes indicated in this study, the health, proximity, and extent of seagrass habitats in relation to the vegetated marsh probably has indirect effects on fish population dynamics via pool formation. These effects would be in addition to any direct effects of shallow subtidal habitat (e.g., the habitat support for small gobiids at low tide, [Figure III-9]).

There are broader conservation implications of *F. parvipinnis* pool use. Invasive *Spartina alterniflora* on the Pacific coast of North America has greater aboveground biomass relative to the native cordgrass, and thus creates greater quantities of wrack (Callaway and Josselyn 1992). *Spartina alterniflora* is thus likely to alter pool formation in native *S. foliosa* and *Salicornia* spp. habitat, thereby indirectly affecting wetland fish populations.

The linkages between habitats in the marsh ecosystem are unique only in their details; trophic, demographic, and physical linkages are ubiquitous in nature. Linkages through demographic changes are likely in any system in which there are ontogenetic shifts in habitat utilization. Such shifts have been well-documented in numerous aquatic species, including bluegill sunfish (Werner and Hall 1988) and salmon (Groot and Margolis 1991), but are also common in terrestrial systems. For example, juvenile Oregon garter snakes (*Thamnophis atratus hydrophilus*) in North America have been shown to utilize habitats and food resources distinct from that used by adults (Lind and Welsh, 1994), and little brown bats (*Myotis lucifugus*) have also been shown to partition their habitats between adults and juveniles (Adams 1996).

Linkages related to ontogeny and reproduction have also been well established for a number of wetland fish species on the Gulf and Atlantic coasts of North America. *Fundulus heteroclitus* preferentially uses shallow depressions on the marsh surface when young, moving into deeper waters of tidal creeks as it ages (Kneib 1997, Kneib 1984). Many commercially important fishes use wetlands as nursery habitats, migrating offshore through ontogeny (Able and Fahay 2000).

Similarly, trophic transfers are a common component of ecological communities. Trophic linkages are inherent in any organism that obtains nutrition in different habitats at different life stages ("life history omnivory", *sensu* Polis 1984); they transport biomass across habitats. But trophic linkages can result from a number of activities unrelated to ontogeny. Seasonal changes in the distribution and availability of food resources, for example, can lead to trophic linkages between

distant habitats. Examples include such disparate groups as ungulate mammals (Fryxell and Sinclair 1988), birds (Cox 1985 and references therein), and reptiles (Madsen and Shine 1996) migrating in response to changing distributions of food resources. Migrations on short timescales (e.g., diel migrations of tadpoles between microhabitats in freshwater pools (Schley et al. 1998), or flamingos migrating daily over 300 km between foraging and nesting habitats (Rendon-Martos et al. 2000) are also common, while migrations on longer than seasonal time scales are less common, and are usually connected to ontogeny or reproduction (e.g., in leatherback turtles, *Dermochelys coriacea*, (Waller 1996)).

Factors promoting habitat linkages

Physical

There are a number of aspects of the physical environment in southern California wetlands that promote habitat linkages, but which can be generalized to other habitats and patterns of connectivity as well. These include aspects of temporal change in physical conditions, temporal changes in habitat availability, proximity and arrangement of environments, and input of directional energy.

Temporal changes in the environment

In this study, water temperature varied by as much as 10.8 °C and salinity by as much as 2.8 within the same habitats sampled at low and high tide on the same day. This variation was as high as 14.6 °C and 7.4 salinity within different microhabitats

sampled at low tide on the same day . This is a considerable change in temperature and salinity over such a short time scale – more than twice the change in sea-surface temperature and salinity observed off of southern California during the 1997-1998 El Niño Southern Oscillation event (Barnston et al. 1999, <http://www-mrlrg.ucsd.edu/shoresta/>). Growth, reproduction, and behavior of fishes is strongly related to temperature and salinity (e.g., Crego and Peterson 1997, Graham 1970), so it is expected that environmental differences in microenvironments should promote movement between habitats.

In this study, key movements between habitats were general tidally-driven movement of fish between subtidal and intertidal habitats, movements of small *F. parvipinnis* to microhabitats adjacent to creeks at low tide, and movements of *F. parvipinnis* from intertidal pool habitats to the subtidal through ontogeny. Temporal changes in the wetland environment have been shown to affect the distribution of fishes in other studies. For example, temperature influenced seasonal occurrence of fish taxa in an estuary in New Jersey (Szedlmeyer and Able 1996); *Fundulus heteroclitus* moves to intertidal pools during the winter, likely to avoid the colder water temperatures in creek habitats (Smith and Able 1994). On shorter time scales, some fishes in an Atlantic coast marsh utilize wetland habitats differently based on diel stage (day vs. night), possibly due to differences in predation pressure (Rountree and Able 1993). This illustrates that the temporal changes in the environment that can give rise to habitat linkages may be biotic, as well as abiotic.

Habitat availability

Temporal changes in habitat availability should also promote habitat linkages. Intertidal sections of creek in this study were by definition inaccessible during part of the spring tidal cycle, therefore fish presence during high tide demonstrates a habitat linkage between these intertidal habitats and the subtidal. Other studies of wetland nekton have demonstrated the use of variably available habitat. Killifish and gobies were documented foraging on high intertidal vegetated marsh in southern California (Johnson 1999), *Fundulus heteroclitus* forage on vegetated habitats on the Atlantic coast (Weisberg and Lotrich 1982), and pinfish (*Lagodon rhomboides*) use intertidal habitats adjacent to seagrass (Irlandi and Crawford 1997). These patterns of variation in accessibility have analogues in other systems as well, such as snow or ice cover altering habitat availability over seasonal time scales (Reid et al. 1994), or organisms utilizing ephemeral pools at a range of time scales (e.g., Pyke and White 1996).

Habitat proximity and configuration

A relationship between proximity of habitat elements and utilization pattern was clearly demonstrated at small spatial scales in his study. Fishes showed preferential utilization of creek microhabitats within just a few meters of rivulets (Figure III-8). This behavior could: (a) allow feeding on prey being swept from the marsh surface along rivulets, (b) provide close proximity to preferred access to high marsh on flooding tide (e.g., Rozas et al. 1988), or (c) maintain fish in a physical environment (e.g., temperature, dissolved oxygen) which is preferred. Habitat

preferences have been noted at larger spatial scales in other studies of wetland fishes on the Gulf and Atlantic coasts. For example, Peterson and Turner (1994), in a study of a Louisiana tidal marsh, found that while nekton were using the vegetated marsh, those densities were highest in the "marsh edge" habitat, within 3 meters of the water's edge. It is expected that habitat linkages in wetlands and other ecosystems would be promoted by short distances between habitats.

The effect of the spatial arrangement of habitat on ecosystems and communities is widely-recognized, and is the focus of the growing field of landscape ecology (Polis et al. 1997). Proximity and configuration of habitats have been shown to affect populations and communities across a wide range of taxa, habitat types, and geographic regions. For example, the arrangement of seagrass beds relative to vegetated marsh has been suggested to influence the health of pinfish (*Lagodon rhomboides*) in North Carolina (Irlandi and Crawford 1997); fish were both more abundant and grew larger when in habitats with access to both vegetated marsh and submerged aquatic vegetation. Other studies have found effects of location of wetland habitat on fish species or densities, due to provision of refuge, foraging habitat, or appropriate physico-chemical conditions (e.g., Bell et al. 1988, Baltz et al. 1993). There are numerous terrestrial examples as well; the spatial distribution of urban canyons in southern California has been shown to affect utilization by coyotes: coyotes are more likely to visit small habitat fragments that are in close proximity to larger fragments than those which are more isolated. This in turn has consequences for populations of feral cats and songbirds, as high coyote abundance tends to lower feral

cat abundance, and thus increase songbird densities through "mesopredator release" (Crooks and Soulé 1999)

Input of physical energy

Physical energy, in the form of wind or water flow could also be expected to promote habitat linkages through passive transport of abiotic materials or organisms, or through subsidizing active transport of organisms between habitats. This latter mechanism has been theorized to be of major importance for wetland habitats, where the tides are thought to provide nutrient input to the intertidal and transport or subsidize the energy required for migration of organisms onto and off of the intertidal zone ("tidal subsidy", *sensu* Odum 1968, as quoted in Odum 1980). Tidal and stream currents have also been implicated in linking wetland habitats to nearshores productivity through promoting outwelling of nutrients and dissolved organic matter (Odum 1980).

Tidal flow is likely an important physical mechanism driving the habitat linkages examined in this study, both directly by providing access for organisms and nutrients to intertidal habitats, and indirectly through movement of seagrass and *Spartina* drift material ("wrack") that creates the pool habitat discussed above. The overall patterns of movement for small resident fishes in this study were consistent with the direction of tidal flow, suggesting that tidal subsidy may be a factor in the observed distributions. Linkages driven by the input of wind or water energy are not

unique to the intertidal zone; the input of physical energy, particularly in situations where that input is cyclic or predictable, should promote linkages between habitats.

Biological

The biology of organisms within communities will affect the strength, probability, and distance of linkages between habitats. These biological factors include mobility, changes in habitat requirements with ontogeny, and habitat requirements that include trade-offs in habitat occupancy.

Mobility

In this study, intra-marsh habitats were linked through the movements of small resident fishes over distances from a few meters to as much as 200 meters, and over times ranging from just a few hours (tidal linkages) to months (ontogenetic linkages). Linkages across other spatial and temporal scales would undoubtedly be observed if a different suite of organisms, scales, or habitats were examined. For example, Bernardi and Talley (in press) examined genetic exchange between populations of *F. parvipinnis* across 9 lagoons in Alta and Baja California. They found that killifish apparently experience very low dispersal rates between lagoons, suggesting that direct inter-marsh linkages with regard to this species is very low. In contrast, Huang and Bernardi (submitted) found relatively high levels of gene flow between populations of long-jawed mudsuckers (*Gillichthys mirabilis*) at different sampling locations (marshes). This difference in dispersal ability is probably due to *G. mirabilis* larvae

having a pelagic dispersal stage (Barlow 1963). In contrast, *F. parvipinnis* has relatively large larvae, presumably capable of maintaining their position in an estuary, and a life-history strategy that promotes retention in wetlands (Chapter II). This further suggests that mobility at all life stages, both passive and active, must be taken into account when considering the effects of life history on habitat linkages of any given taxa.

Ontogeny

Organisms that undergo strong changes in predation risk, feeding, environmental tolerances or environmental optima are also likely to generate habitat linkages. In this study, each of these factors may be responsible for the observed changes in distribution of *F. parvipinnis* with ontogeny.

Size-dependent differences in relative predation risk between habitats is likely, as avian and piscine predators show general differences in size-selection (Sogard 1997). Shallow water has been shown to afford a refuge from aquatic predators (e.g., Ruiz et al. 1993), but fish may be more vulnerable to avian or terrestrial predators. Since birds exhibit positive size-selection of prey, smaller fishes may suffer lower mortality remaining in shallow habitats (pools and shallow creeks) at low tide than they would remaining in subtidal creek, intertidal flat, or seagrass habitats. These deeper habitats would be more likely to be occupied by piscivorous fishes, which generally exhibit negative size-selection of prey (Sogard 1997).

As fishes grow, however, they would become more vulnerable to predation from positively size-selective avian predators, and simultaneously less so to piscivorous fishes, obtaining a refuge in size in subtidal habitats (Sogard 1997). There is even evidence that, for Atlantic coast killifishes, younger age-classes seek refuge from cannibalism by older age-classes (Kneib 1987). These factors together suggest that killifish in this system can decrease their risk of predation by utilizing different habitats at different life stages, and that this is therefore a factor in linking habitats within the wetland complex. Similar cases of ontogenetic changes in predation risk appear to be common in aquatic organisms (e.g., Werner and Hall 1988), but occur in terrestrial ecosystems as well (e.g., Sharp 1997).

Ontogenetic changes in environmental tolerance or optima may also be a mechanism driving habitat linkages in this study. Fishes have been shown to have the ability to detect changes in temperature and salinity as small as 0.03 °C and 0.06, respectively (Norris 1963, Bull 1938). Further, tolerances for high temperature and salinity change with size in many species (Brett 1979). It is possible that differences in temperature or salinity between habitats (Figure III-4) may be partly responsible for the differential use patterns seen with ontogeny in this study. Organisms that undergo ontogenetic shifts in environmental requirements or optima would likely promote linkages between habitats that meet their requirements at different times or life stages.

Given the substantial difference in size between J1 and adult *F. parvipinnis* (8 mm - 108 mm TL) , some change in diet with ontogeny seems likely, and is suggested by isotope analysis in this study (Figure III-16). Work by Hartney and Tumyan (1998)

suggested that *F. parvipinnis* may undergo such an ontogenetic shift in diet.

Ontogenetic changes in diet occur across a vast range of taxa and habitats (Polis 1984 and references therein), and likely increase the probability and strength of linkages between habitats wherever those different dietary items are associated with distinct habitat.

"Trade-off" habitats

Close or adjacent habitats that have complementary or "opposing" fitness values should also be expected to increase the degree of linkage in a system. For example, a habitat with high refuge value and low foraging value, adjacent to a habitat with low refuge but high foraging value, should promote movement between habitats in order to maximize overall fitness. Enclosure experiments in this study suggest that there is a potential for this mechanism to be operating among the small resident wetland fishes examined here. Pool and shallow creek habitats may provide lower foraging value at high tide than do nearby subtidal habitats (Figure III-20), while the deeper creek habitats likely harbor a higher predation risk for these small fish. Despite this, the proportion of J1 *F. parvipinnis* in pools is lower at high tide than it is at low tide (Figure III-14), suggesting that fish may be using these deeper habitats to forage at high tide (in addition to any other habitats not examined here, such as the vegetated intertidal). There are numerous examples of these linkages due to trade-offs in other ecosystems, ranging from kangaroo rats balancing refuge in shrubs against forage in

the open (Bouskila 1995) to squirrels trading reproductive fitness for protection from predation (Macwhirter 1991).

These physical and biological factors can strongly affect the presence and strength of linkages, but are dependent on the spatial and temporal scales of the processes and organisms involved (Kneib 1994). Assessing the likelihood, direction, and strength of linkages between habitats requires study at a scale (or often multiple scales) appropriate to the habitats, organisms, and processes being examined, if one is to make their results general (Thrush et al. 2000, Turner et al. 1999).

Table III-1. Fishes captured during this study (percent of total individuals captured listed in parentheses).

Species	High Tide	Low Tide	Total Captured
<i>Fundulus parvipinnis</i>	89 (21.5)	*1417 (71.6)	1506 (62.9)
Unidentified gobiids	166 (40.1)	203 (10.3)	369 (15.4)
<i>Clevelandia ios</i>	90 (21.7)	217 (11.0)	307 (12.8)
<i>Gillichthys mirabilis</i>	13 (3.1)	106 (5.4)	119 (5.0)
<i>Quietula y-cauda</i>	12 (2.9)	27 (1.4)	39 (1.6)
<i>Atherinops affinis</i>	38 (9.2)	1 (<1.0)	39 (1.6)
<i>Ilypnus gilbertii</i>	6 (1.4)	2 (<1.0)	8 (<1.0)
<i>Syngnathus auliscus</i>	0 (0.0)	6 (<1.0)	6 (<1.0)
<i>Paralichthys californicus</i>	0 (0.0)	1 (<1.0)	1 (<1.0)
Total	414	1980	2394

*Does not include single sample of 1,407 *F. parvipinnis* captured in July of 1998. See text for details.

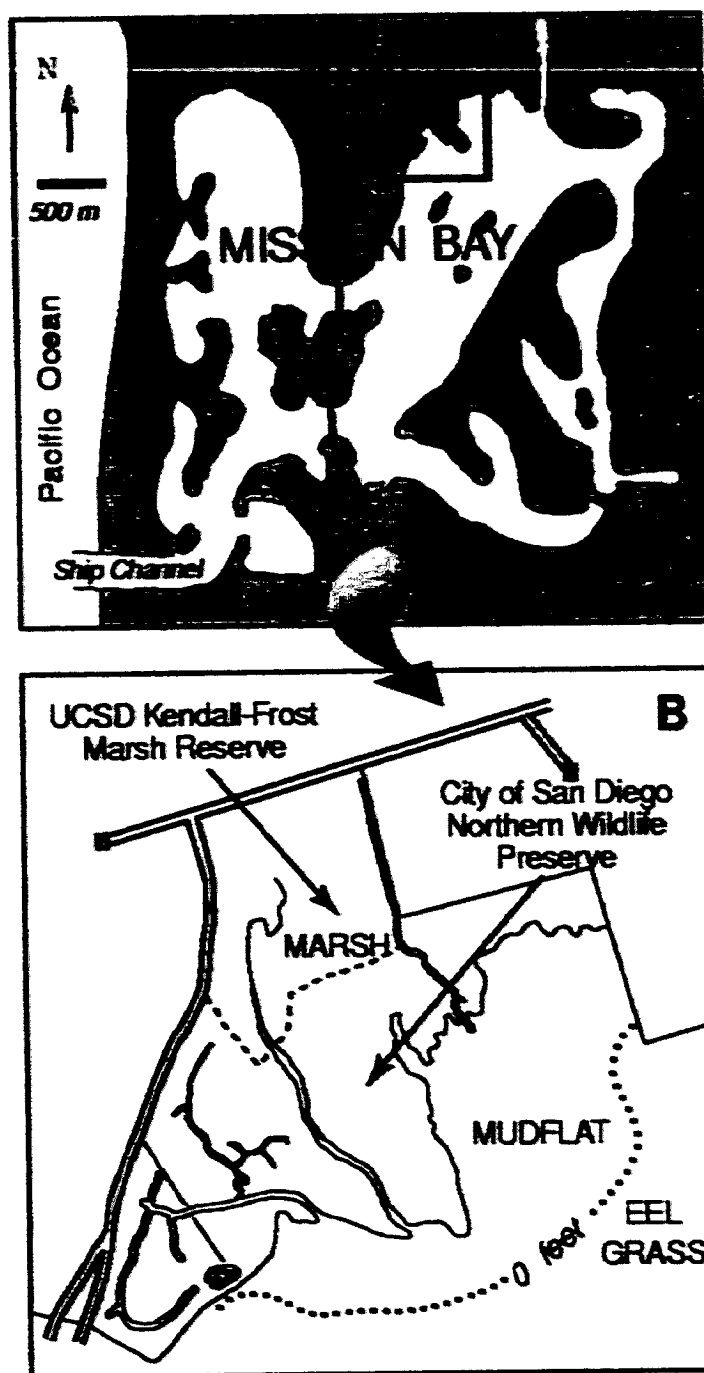
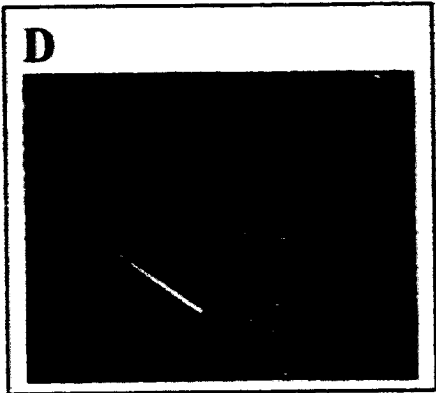
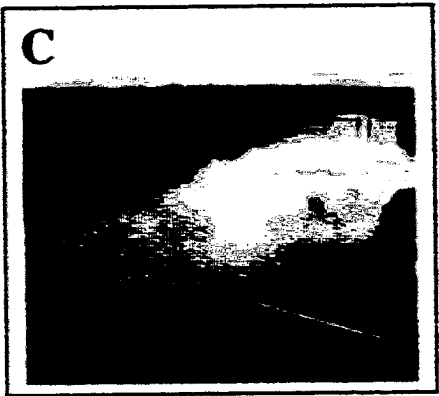
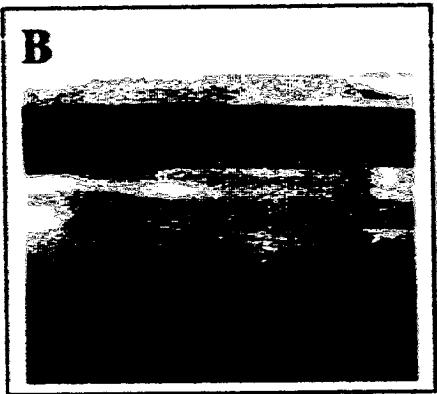
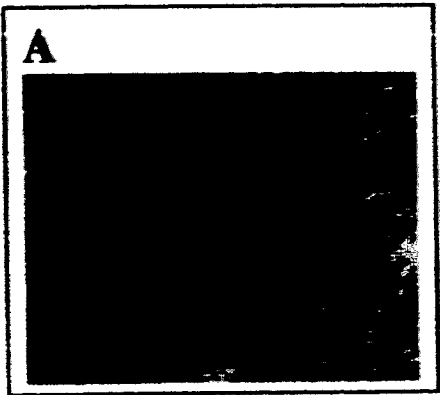


Figure III-1. Map of study site, showing (A) Mission Bay, San Diego, CA and (B) the Kendall-Frost/Northern Wildlife Preserve.



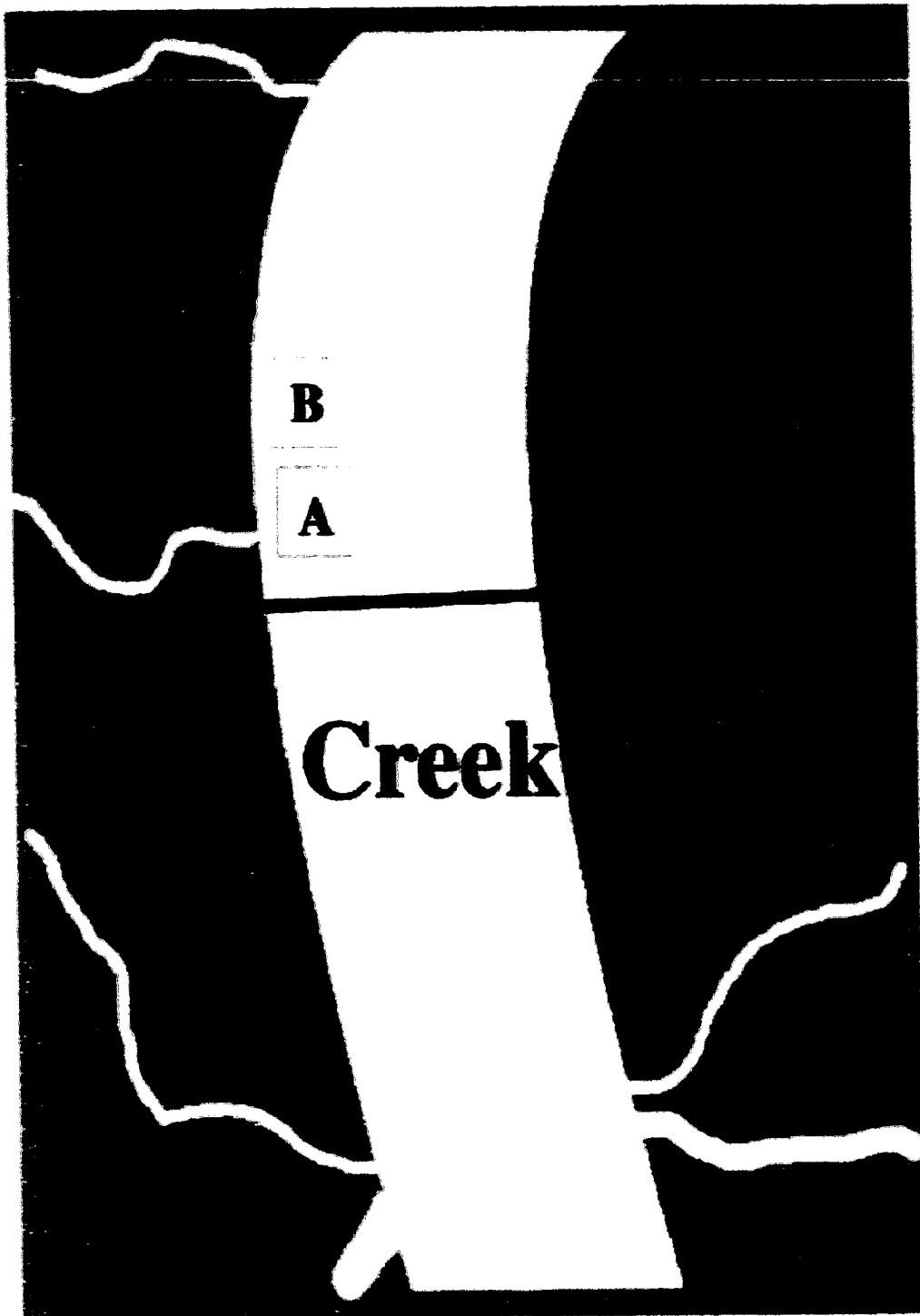


Figure III-3. Schematic diagram of sampling for differences in fish density between creek habitat adjacent to rivulet (A) and "non-rivulet" creek (B). Boxes represent drop traps (0.8 m on each side).

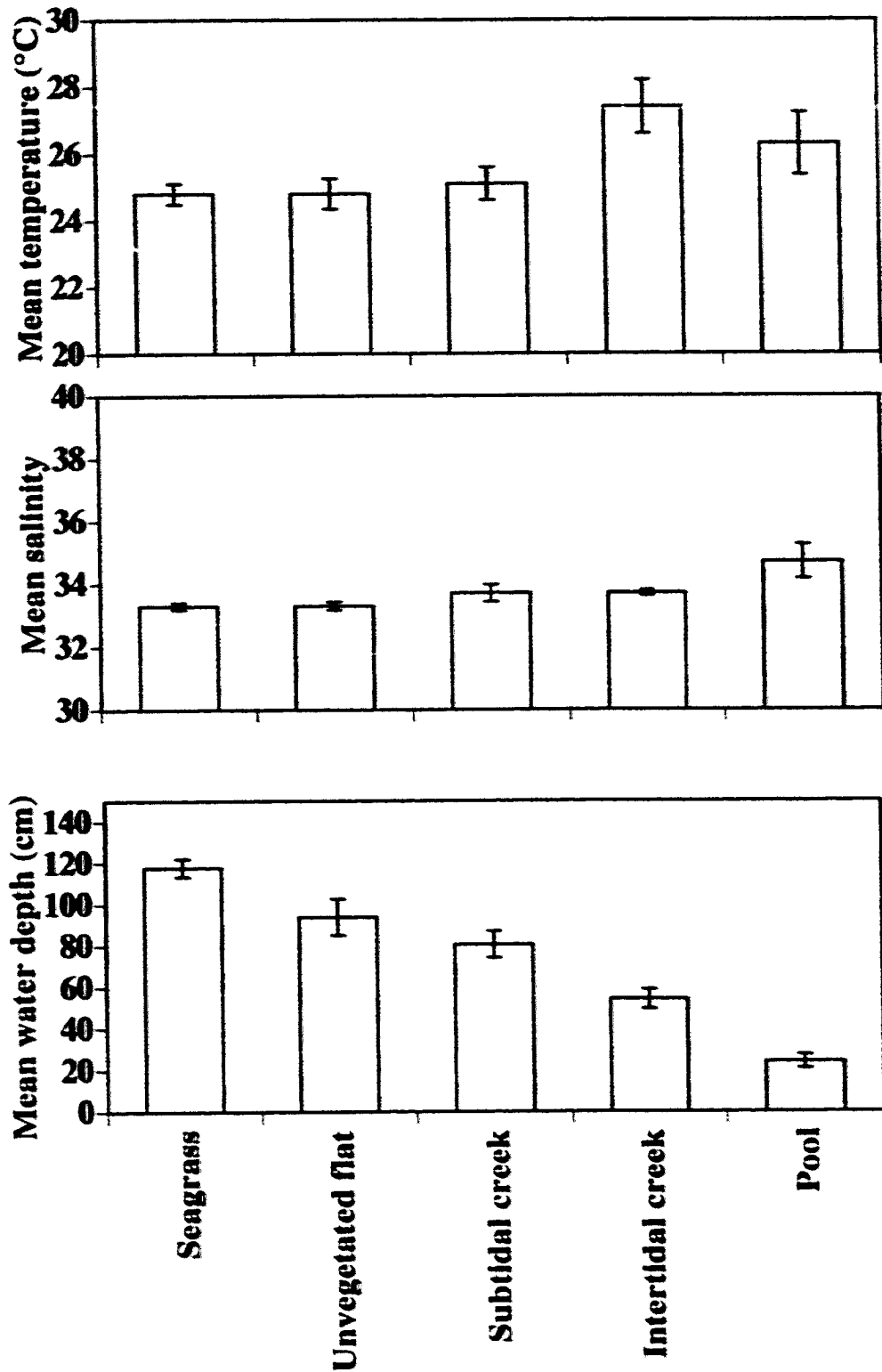


Figure III-4A. Mean temperature, salinity, and water depth for each habitat at summer high tide. Error bars are ± 1 s.e.

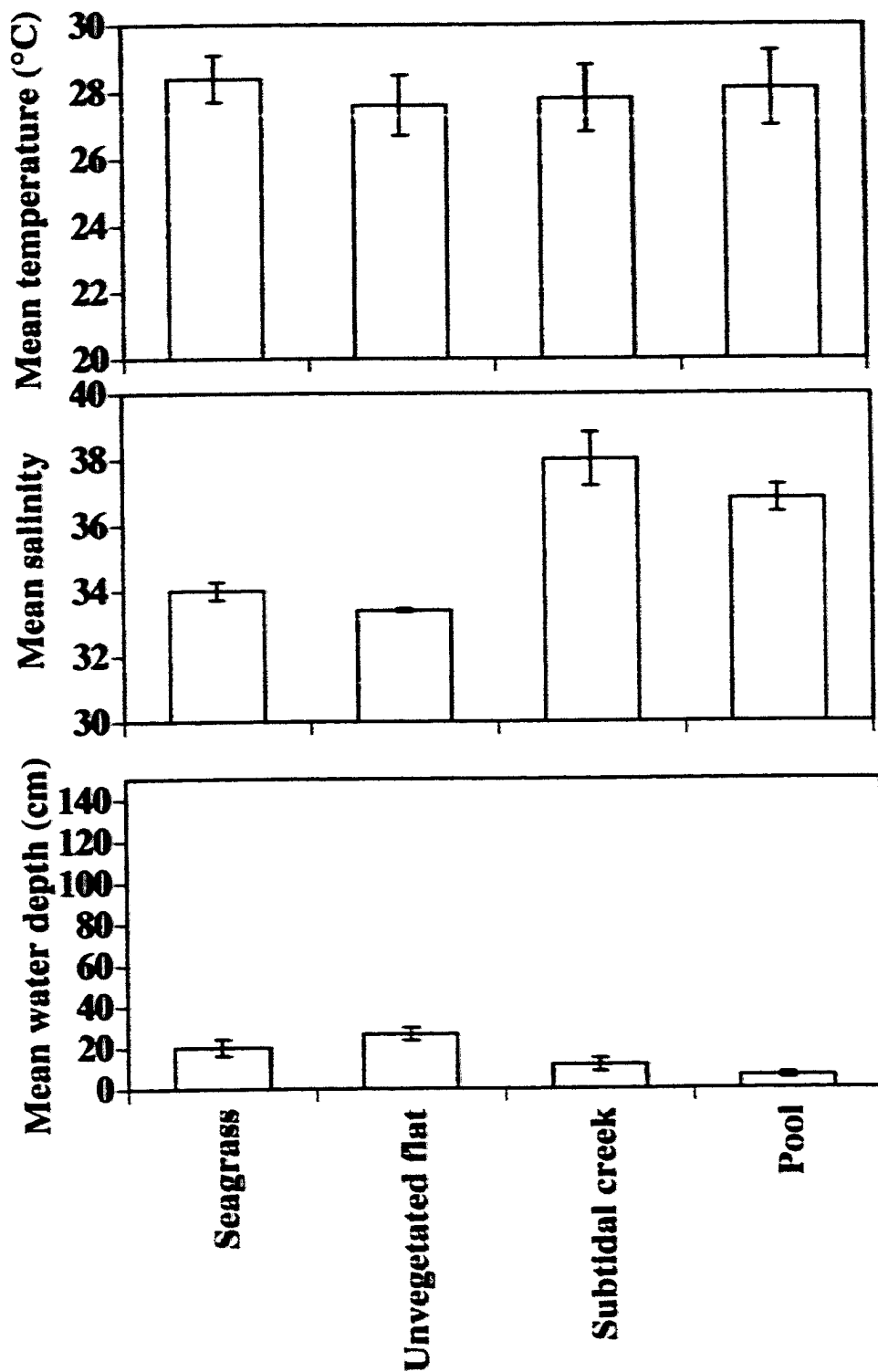


Figure III-4B. Mean temperature, salinity, and water depth for each habitat at summer low tide. Error bars are ± 1 s.e.

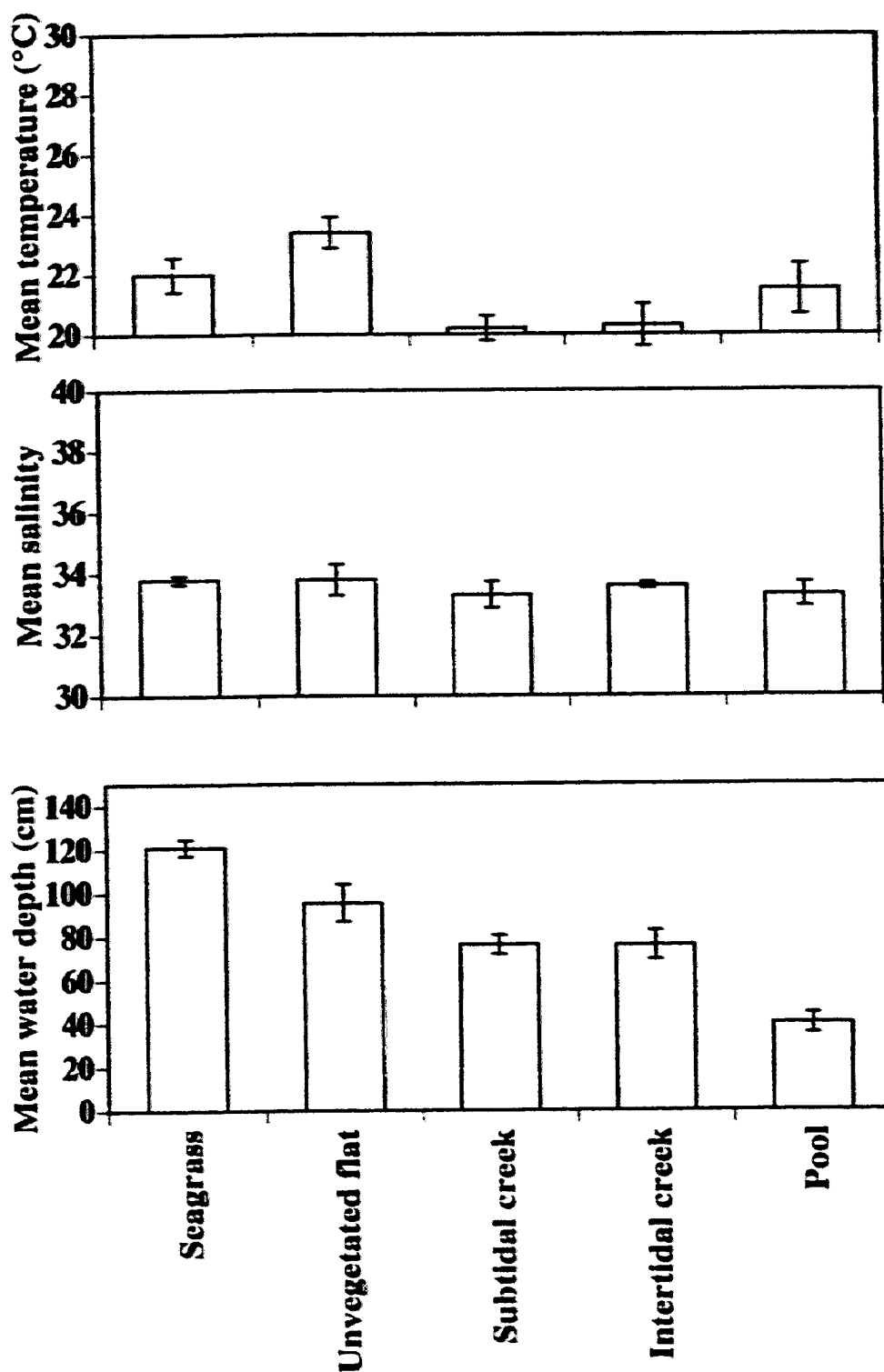


Figure III-4C. Mean temperature, salinity, and water depth for each habitat at fall high tide. Error bars are ± 1 s.e.

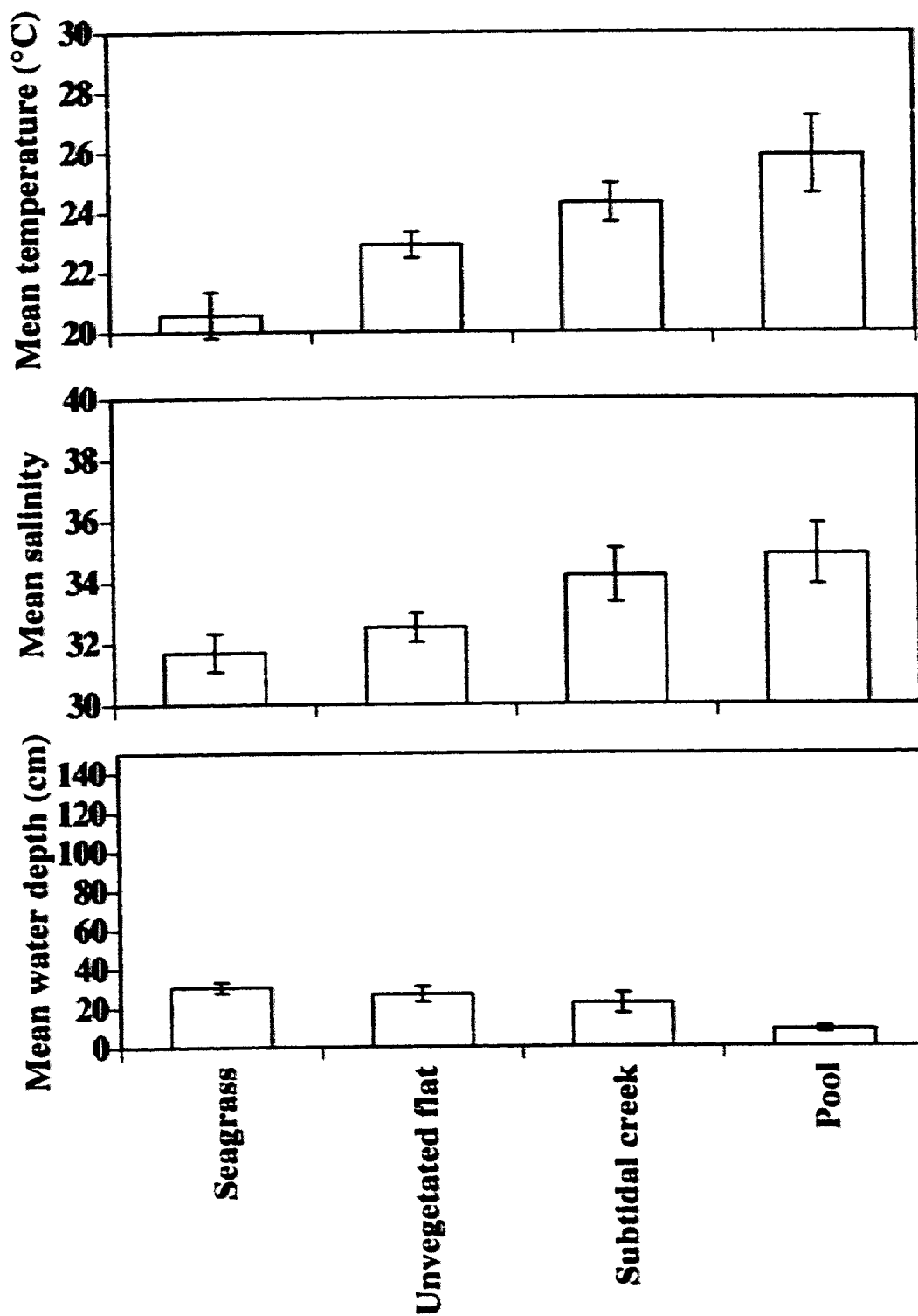


Figure III-4D. Mean temperature, salinity, and water depth for each habitat at fall low tide. Error bars are ± 1 s.e.

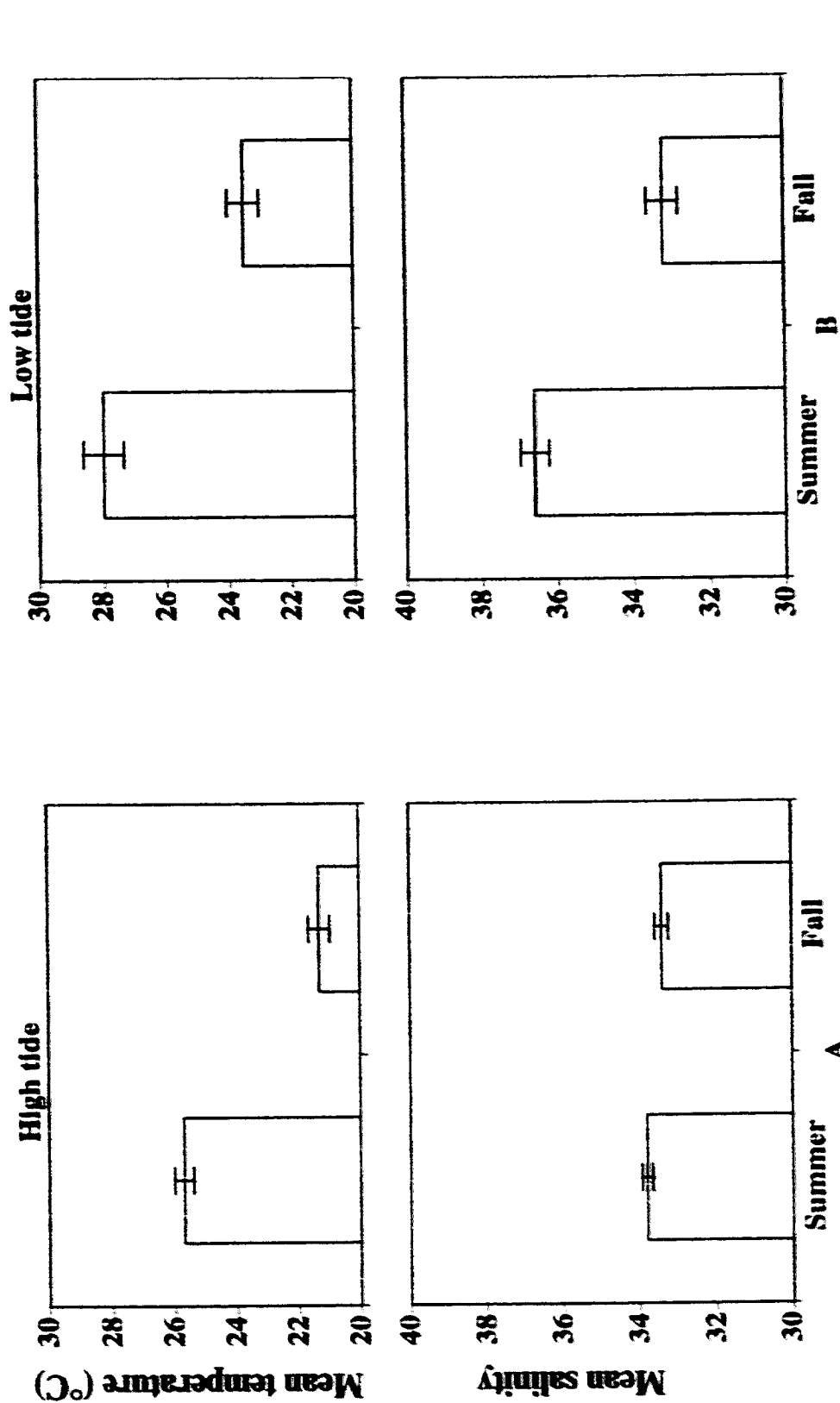


Figure III-5. Mean water temperature and salinity (across all habitats) in summer 1999 versus fall 1999 samples at high (A) and low (B) tides. Error bars are ± 1 s.e.

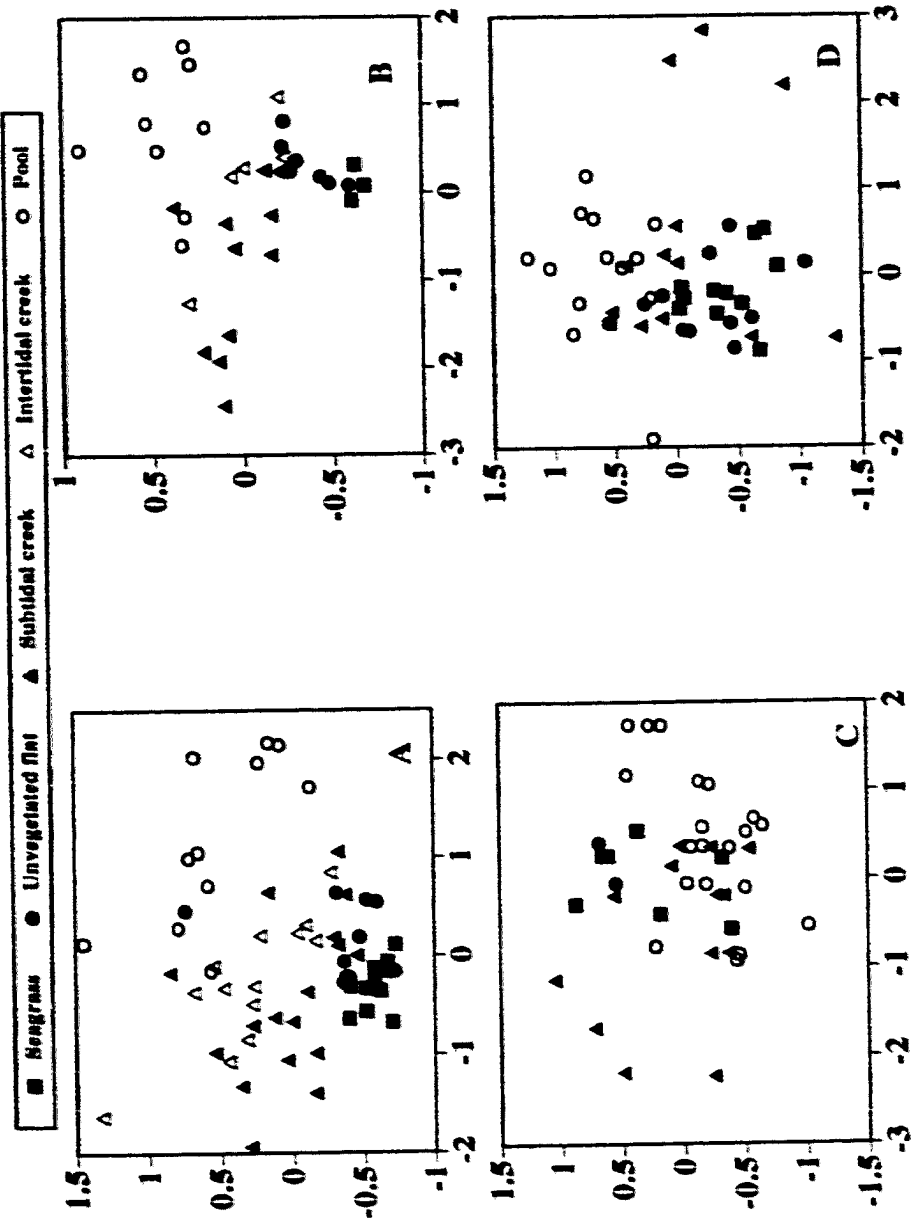


Figure III-6. MDS plot of environmental data (mean water depth, temperature, salinity, and distance from marsh edge) for each environmental state. (A) SHT, (B) SLT, (C) FHT, and (D) FLT. Stress < 0.02 for all plots.

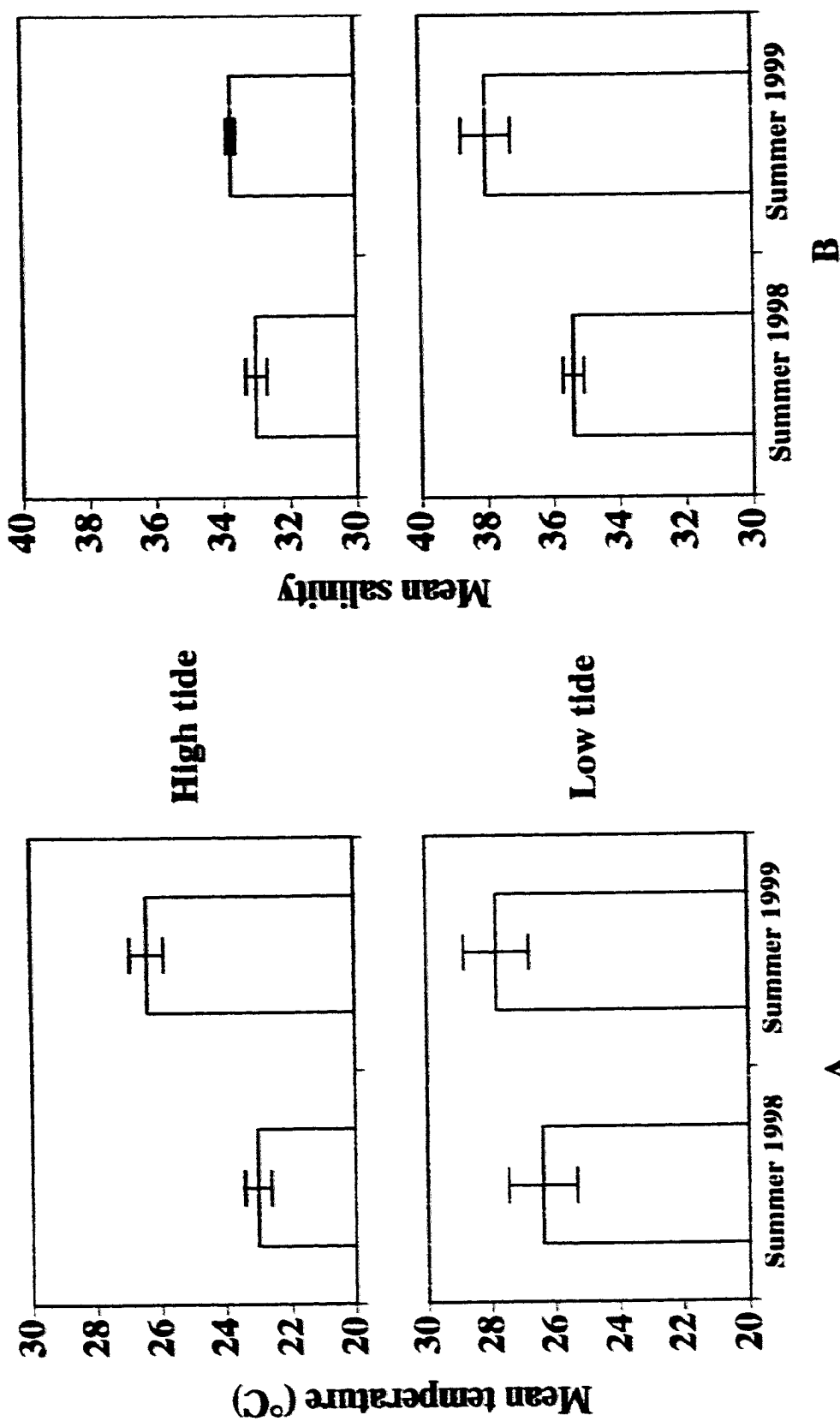


Figure III-7. Mean water temperature (A) and salinity (B) for creek samples (subtidal and intertidal combined) from summer of 1998 vs. summer 1999 at both high and low tides. Error bars are ± 1 s.e.

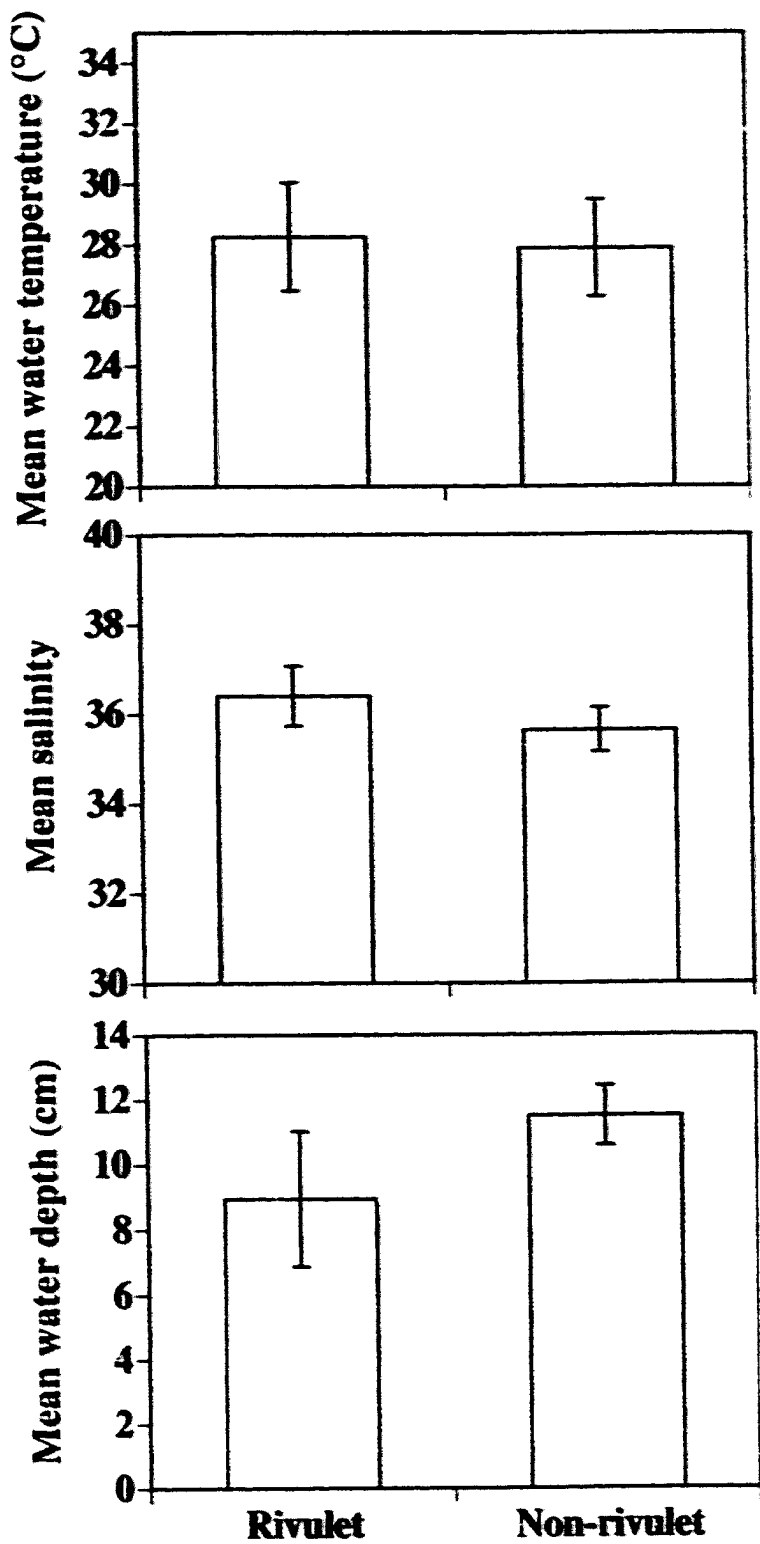


Figure III-8. Mean temperature, salinity, and water depth for rivulet and non-rivulet samples. Error bars are ± 1 s.e.

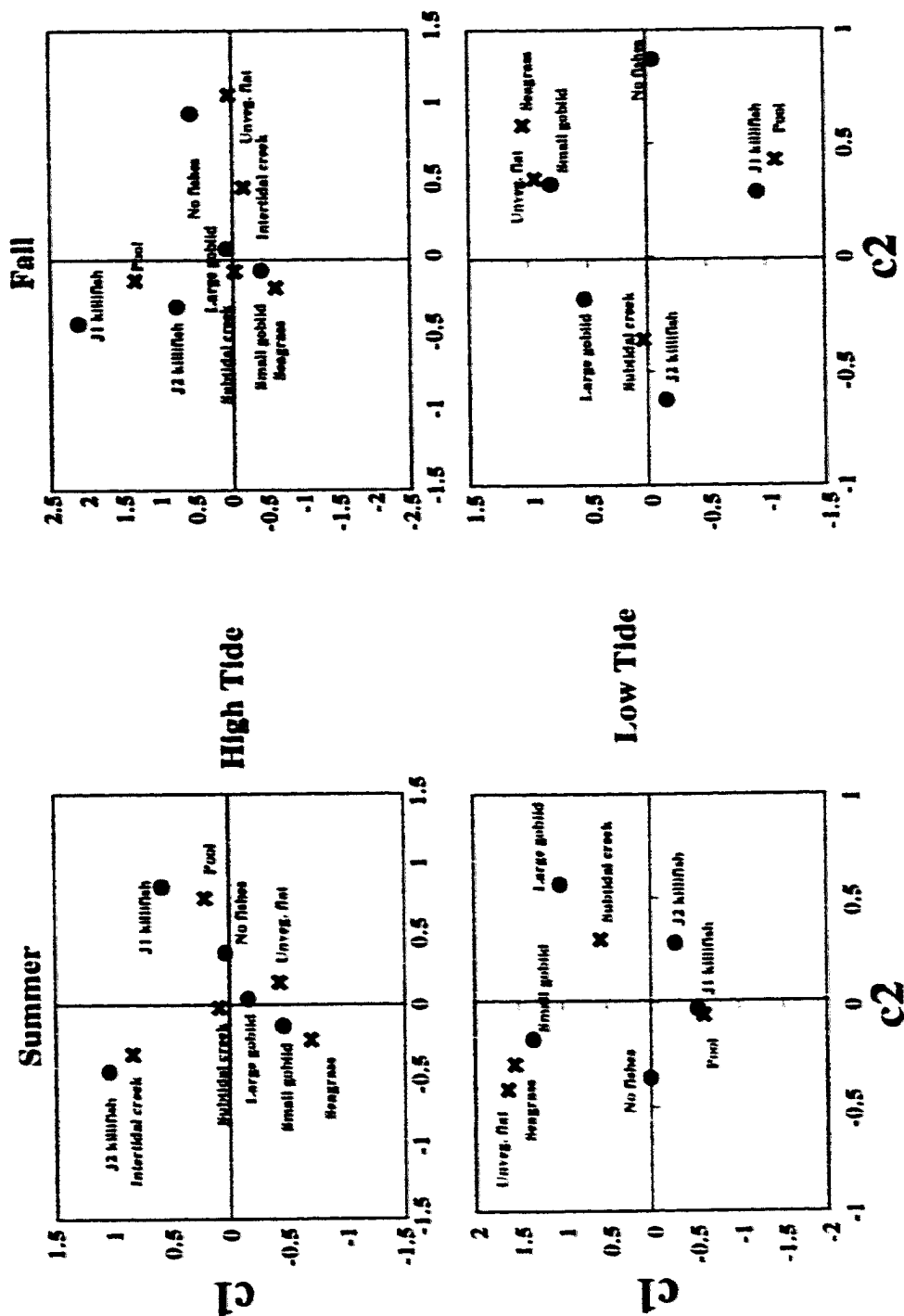


Figure III-9. Ordination of presence/absence data for the four main groups of fishes and empty traps from correspondence analysis at each environmental state.

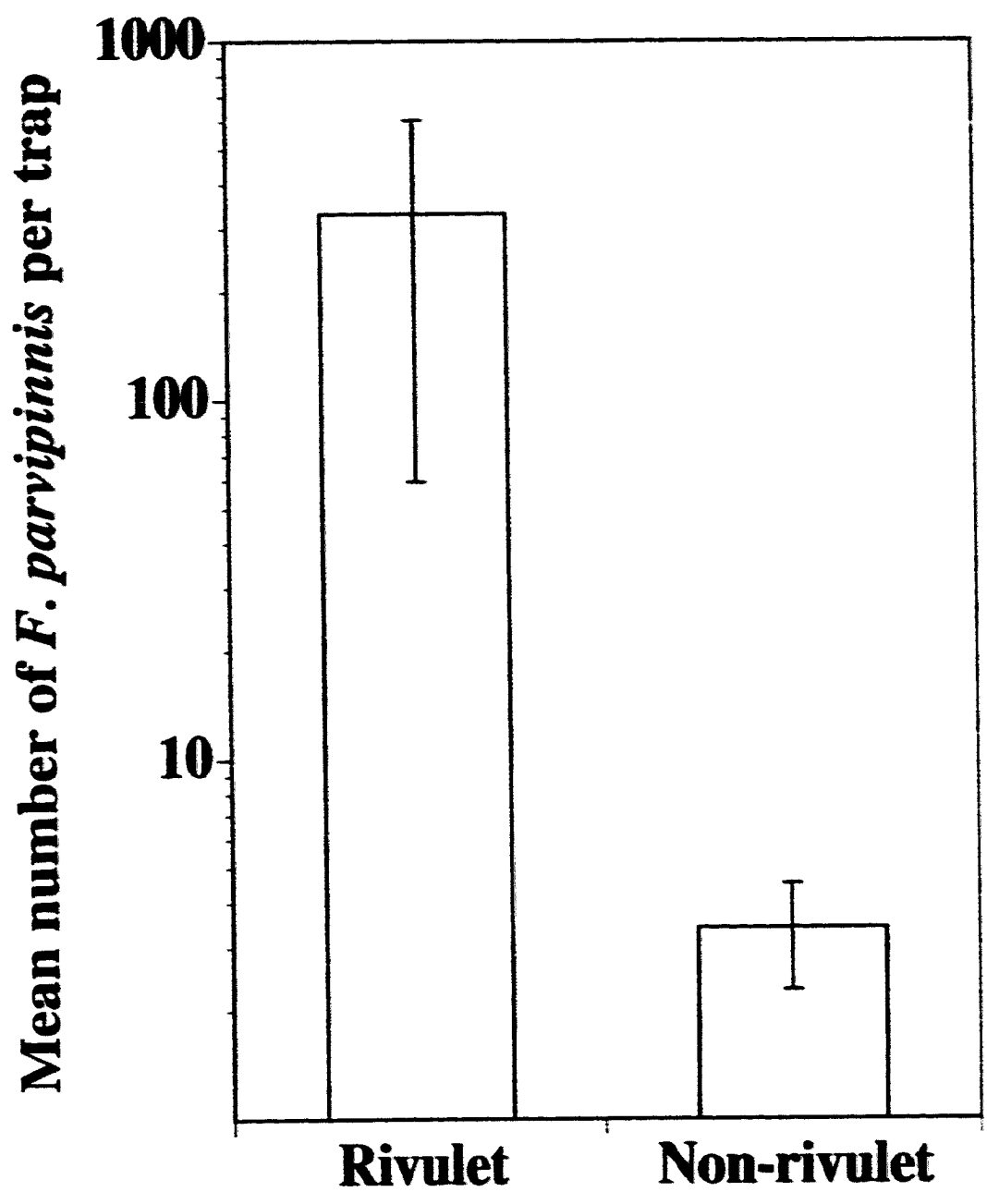


Figure III-10. Mean number of *F. parvipinnis* per trap from rivulet and non-rivulet samples. Error bars are ± 1 s.e.

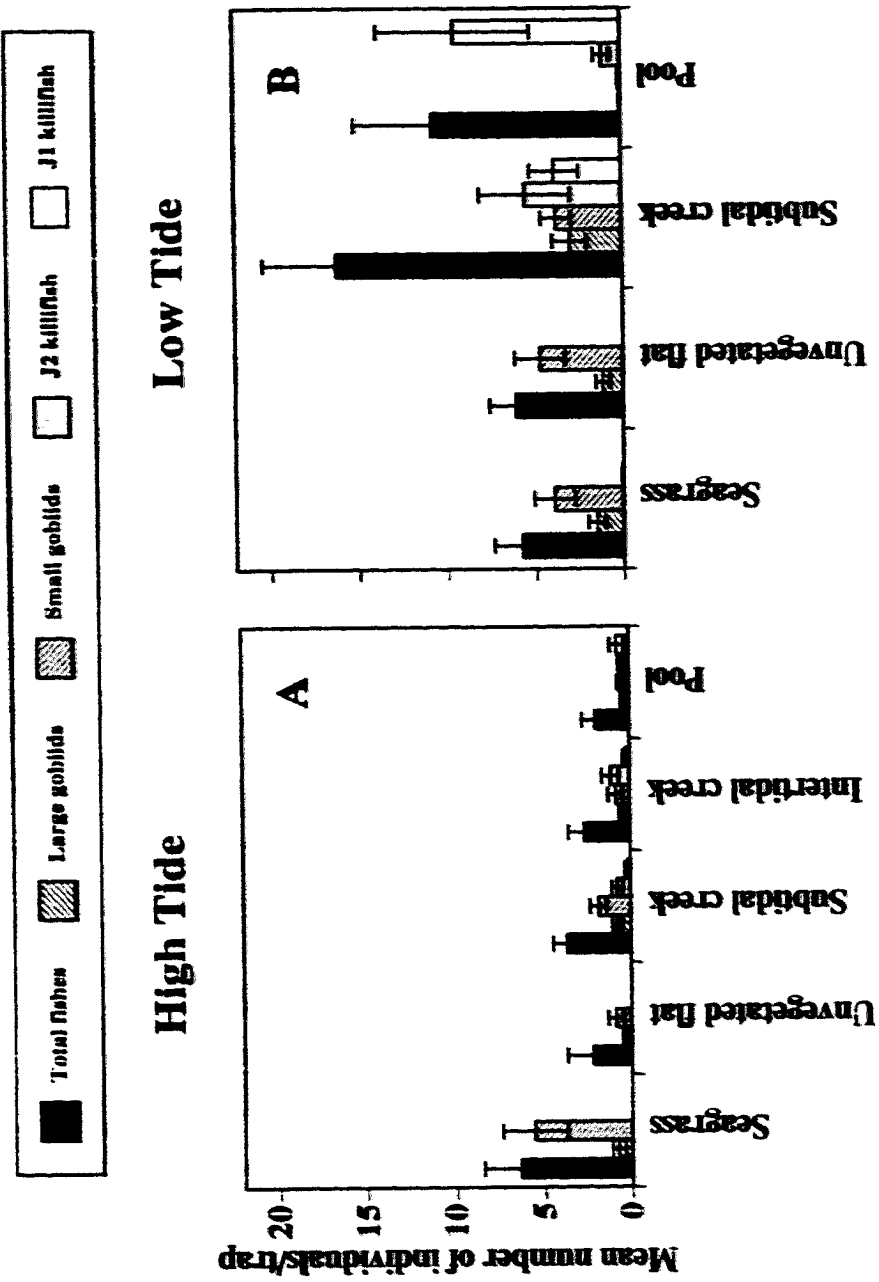


Figure III-11. Mean number of individuals per trap from each habitat (collapsed across season) for total fishes as well as the four main groups at high and low tides. Error bars are ± 1 s.e.

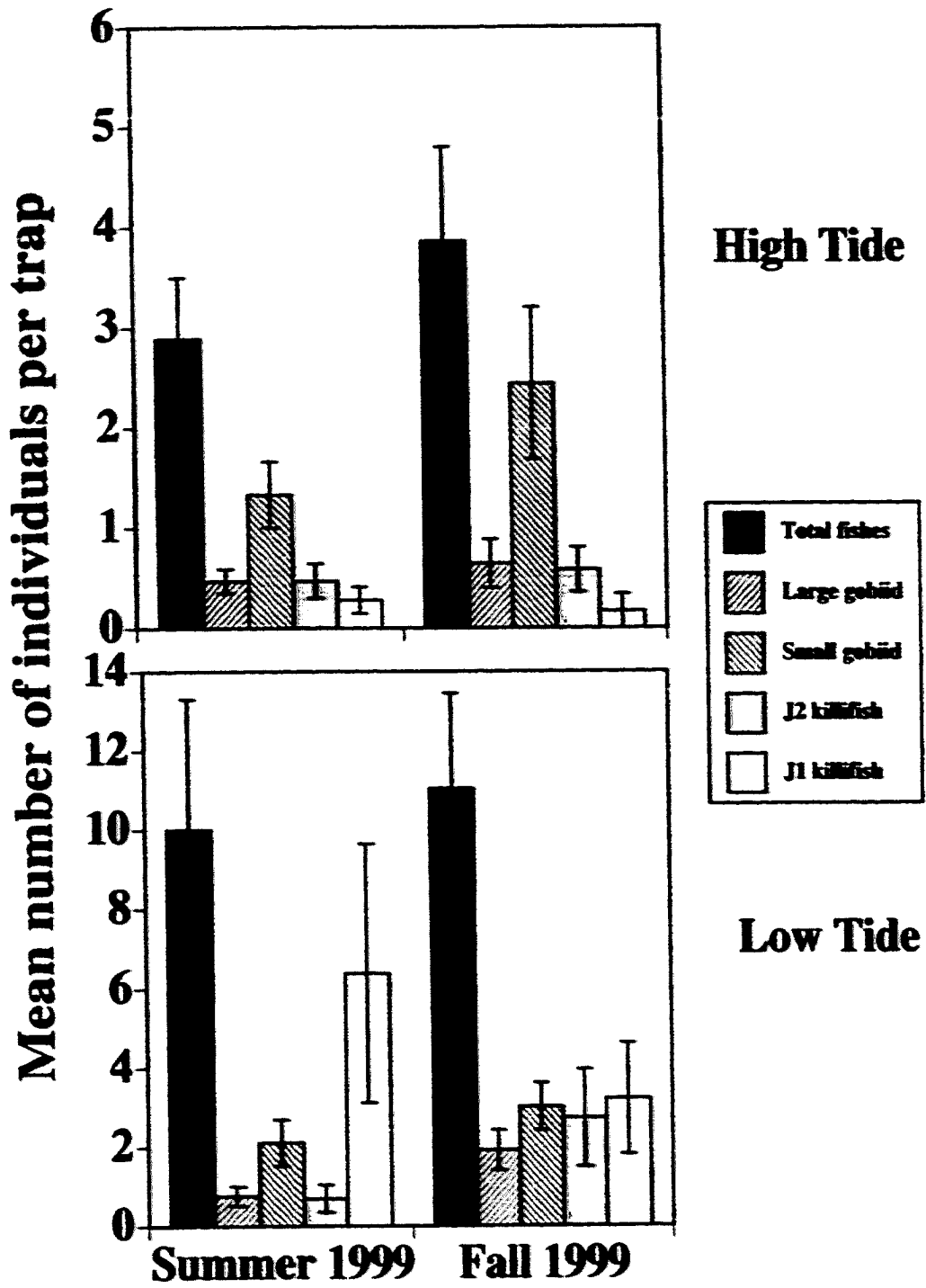


Figure III-12. Mean number of individuals per trap across habitats compared between seasons (summer 1999 and fall 1999) for total fishes as well as the four main groups at high and low tides. Error bars are ± 1 s.e.

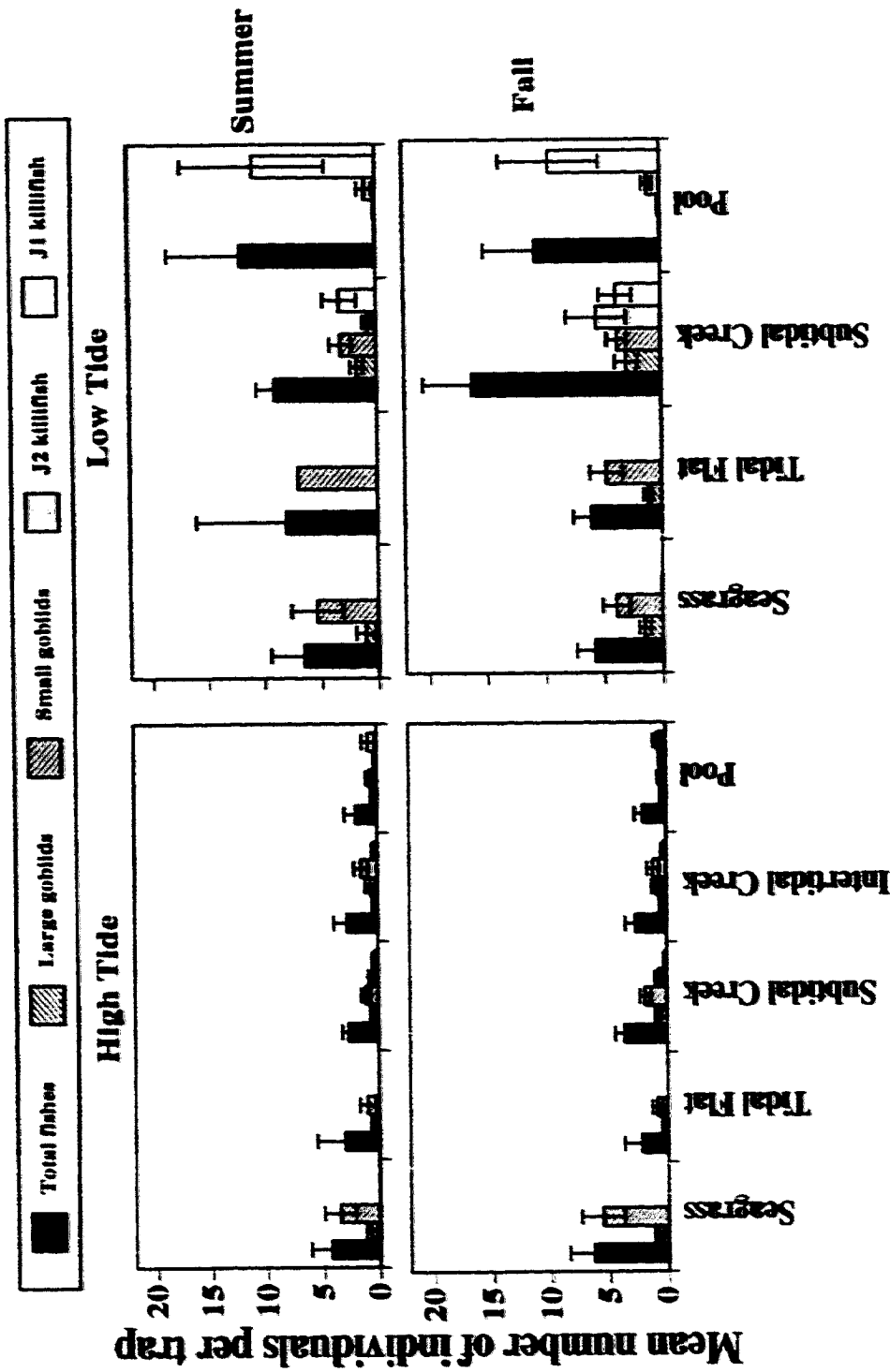


Figure III-13. Mean number of individuals per trap from each habitat at each environmental state. Shown are total fishes as well as the four main groups at high and low tides. Error bars are ± 1 s.e.

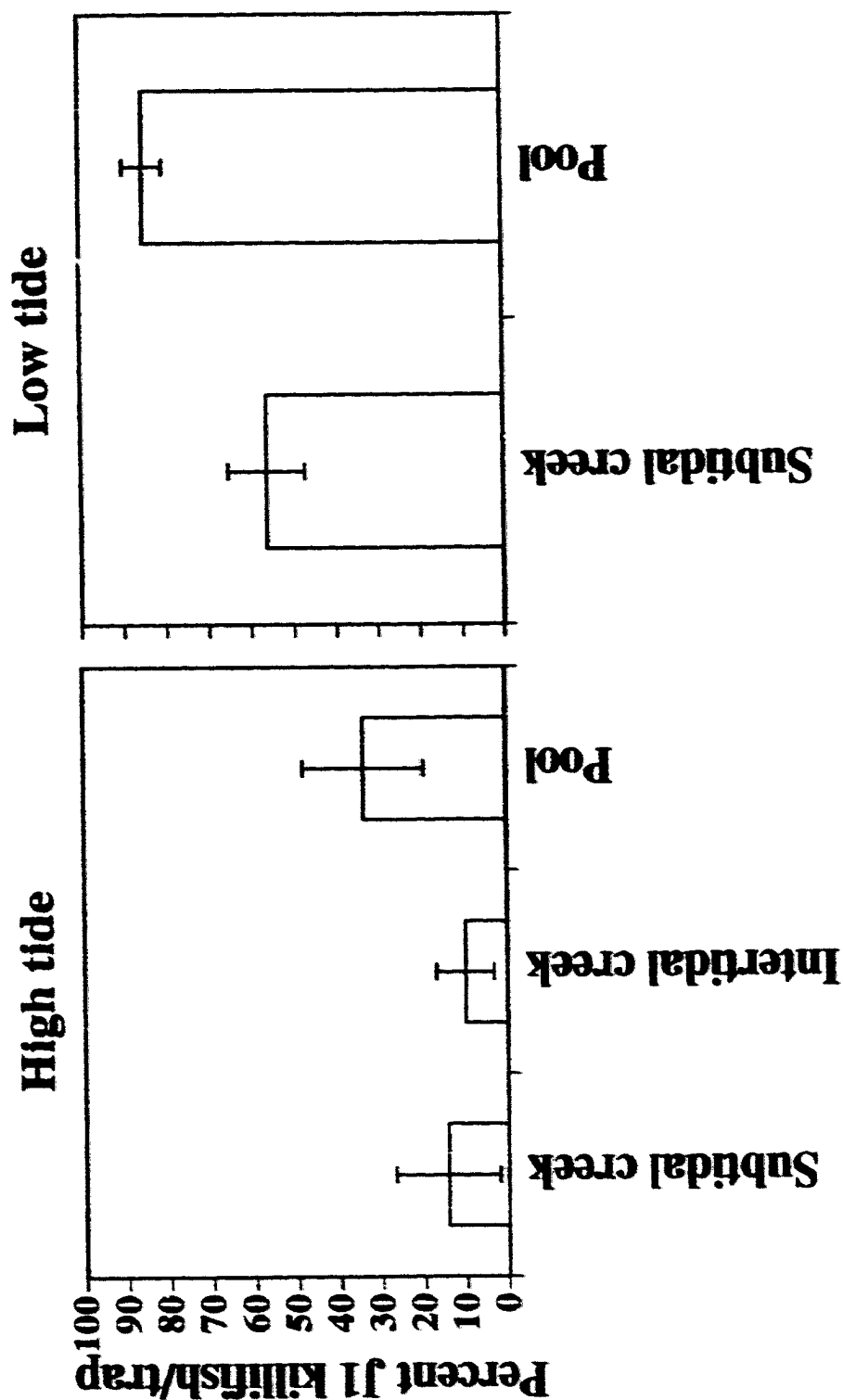


Figure III-14. Mean percentage of *F. parviphinis* from each trap which were from the smallest size class (J1 killifish, <25 mm TL) collapsed across season, at both high and low tide. Error bars are ± 1 s.e.

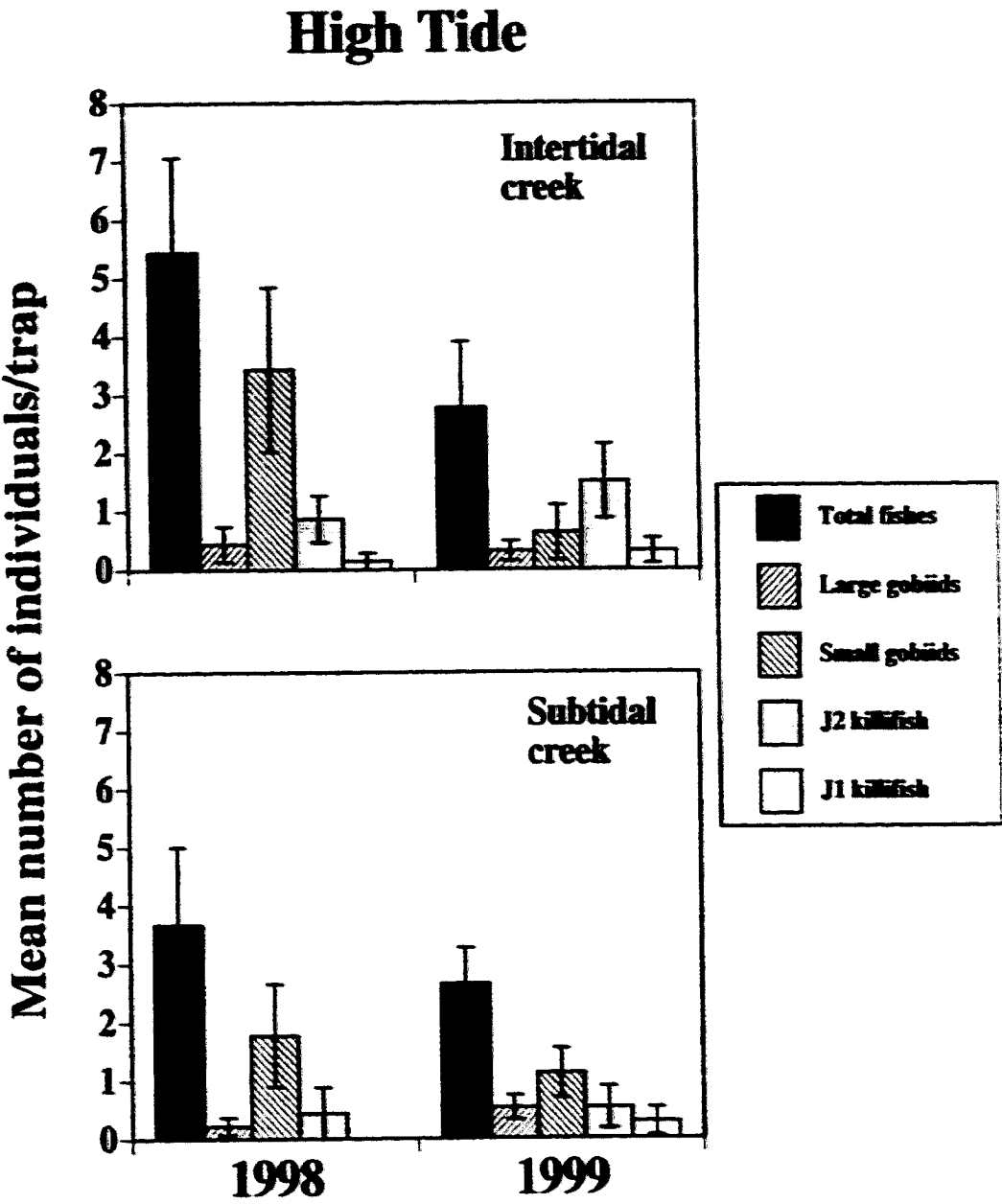


Figure III-15A. Mean number of individuals per trap from creek habitats in the summer of 1998 vs. the summer of 1999 at high tide. Shown are total fishes as well as the four main groups. Error bars are ± 1 s.e.

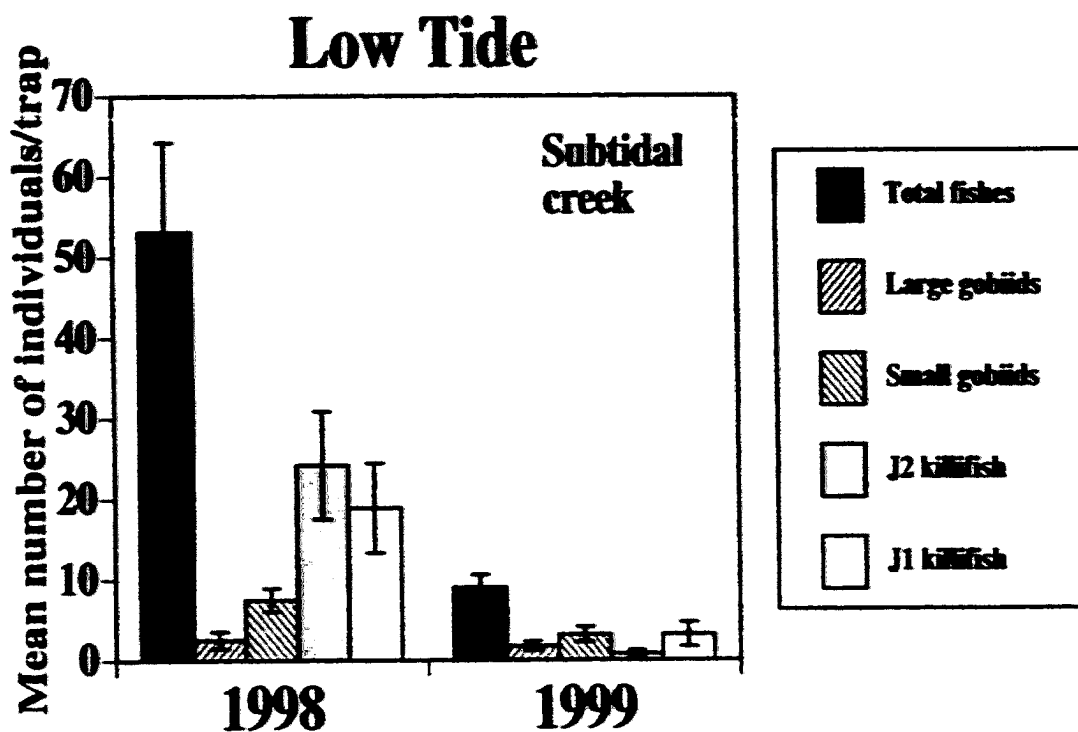


Figure III-15B. Mean number of individuals per trap from creek habitats in the summer of 1998 vs. the summer of 1999. Shown are total fishes as well as the four main groups at low tide. Error bars are ± 1 s.e.

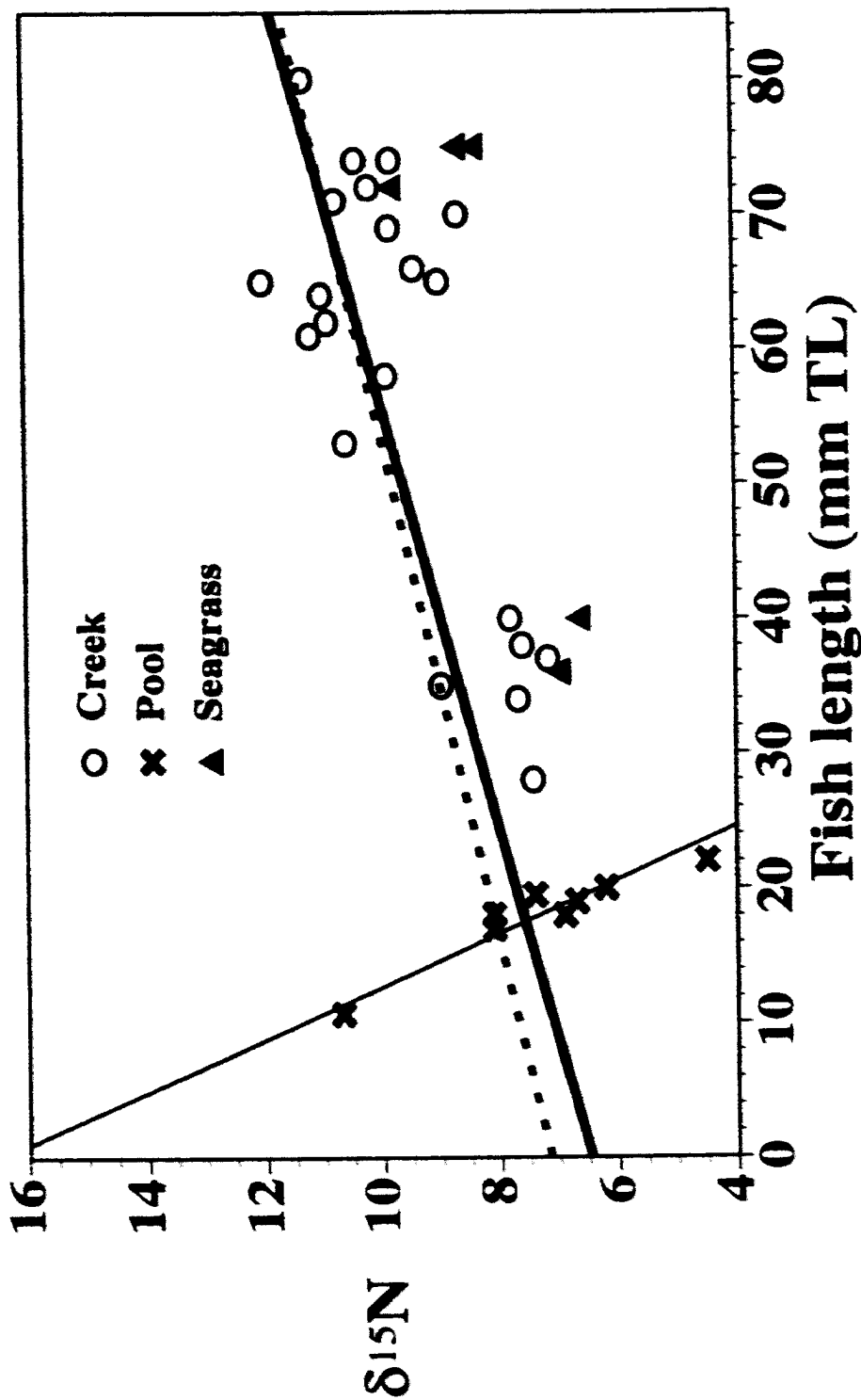


Figure III-16. Relationship between $\delta^{15}\text{N}$ and body size for *F. parvipinnis* captured in each of 3 habitats: creek, pool, and seagrass. Thick solid line is overall regression, dashed line is regression of individuals > 25 mm TL only, and thin solid line is regression of postlarval individuals only (< 25 mm TL).

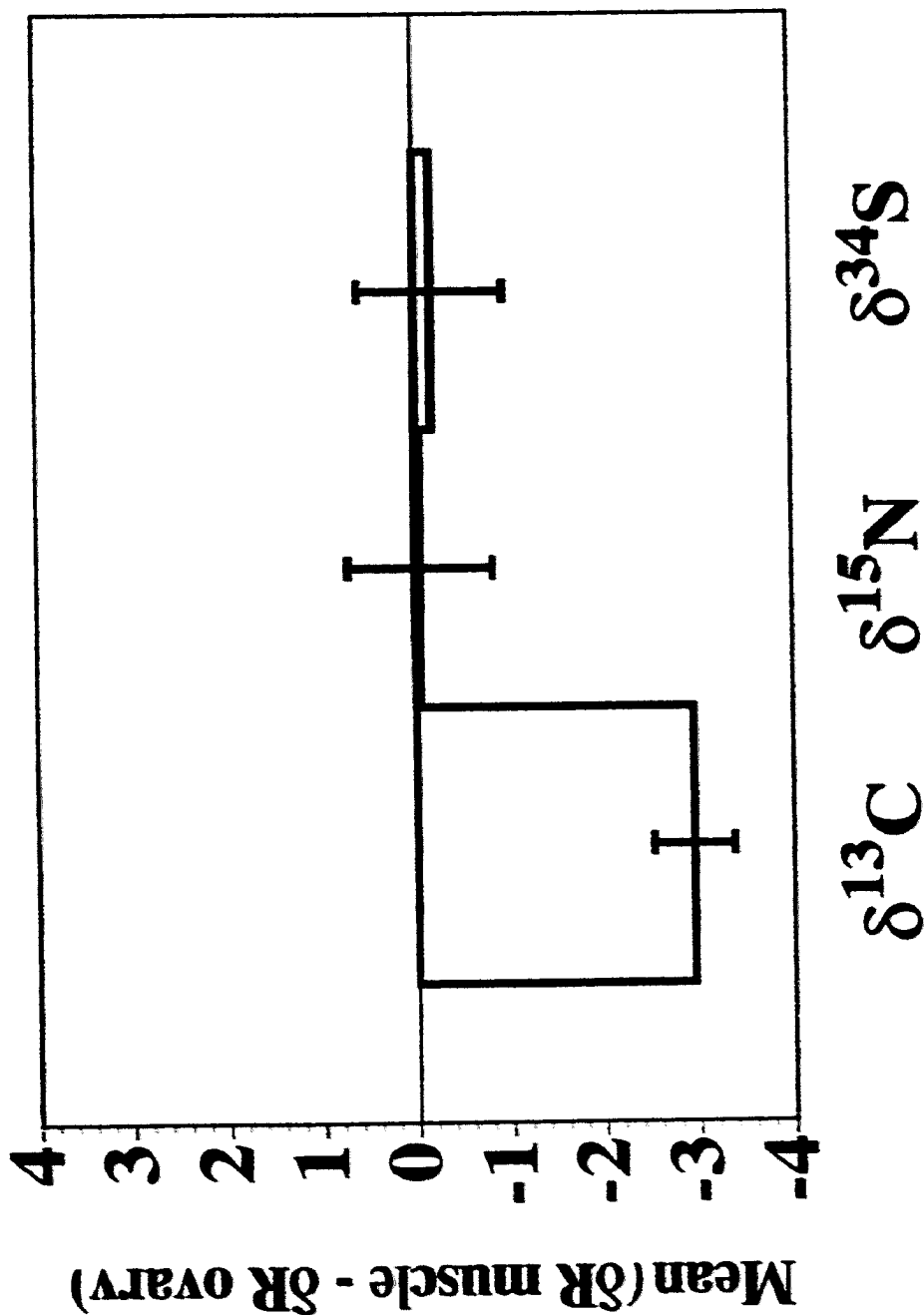


Figure III-17. Mean change in isotopic signature between muscle and ovary tissue for ripe female *F. parvipinnis*. Error bars are ± 1 s.e.

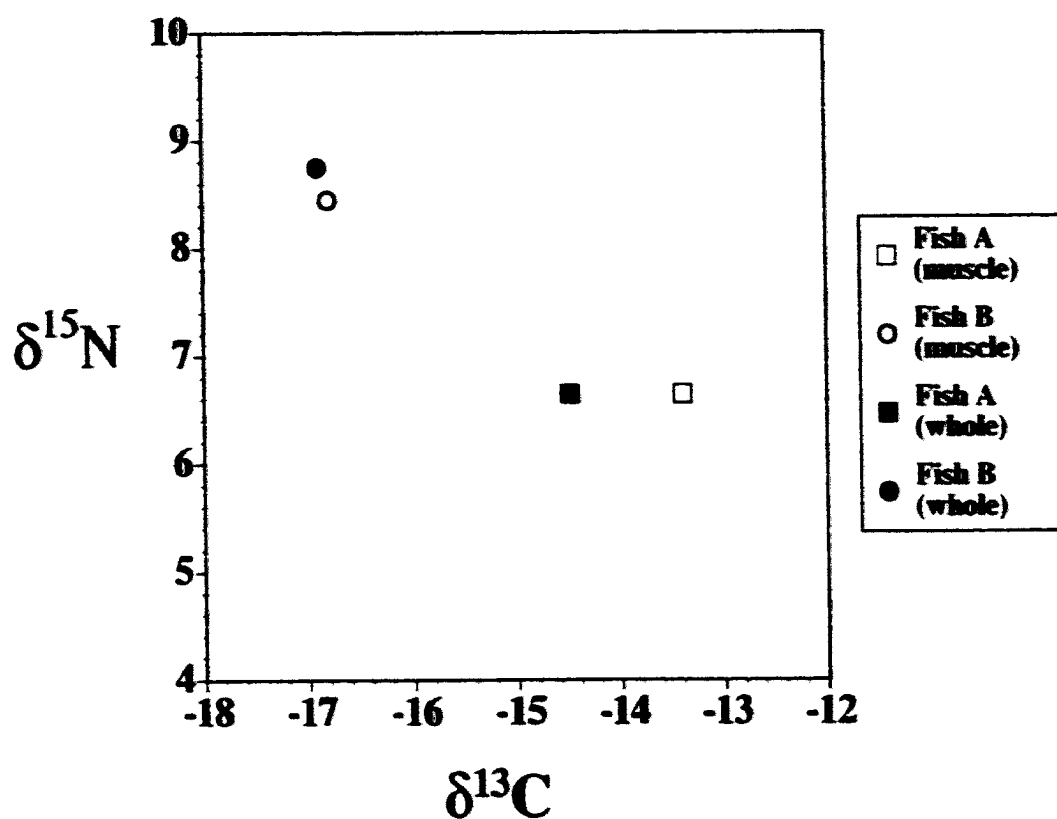


Figure III-18. Isotope biplot (^{13}C vs ^{15}N) for fish samples processed as fillet (muscle) and remainder (whole). Same individual fish are represented by the same shape symbol.

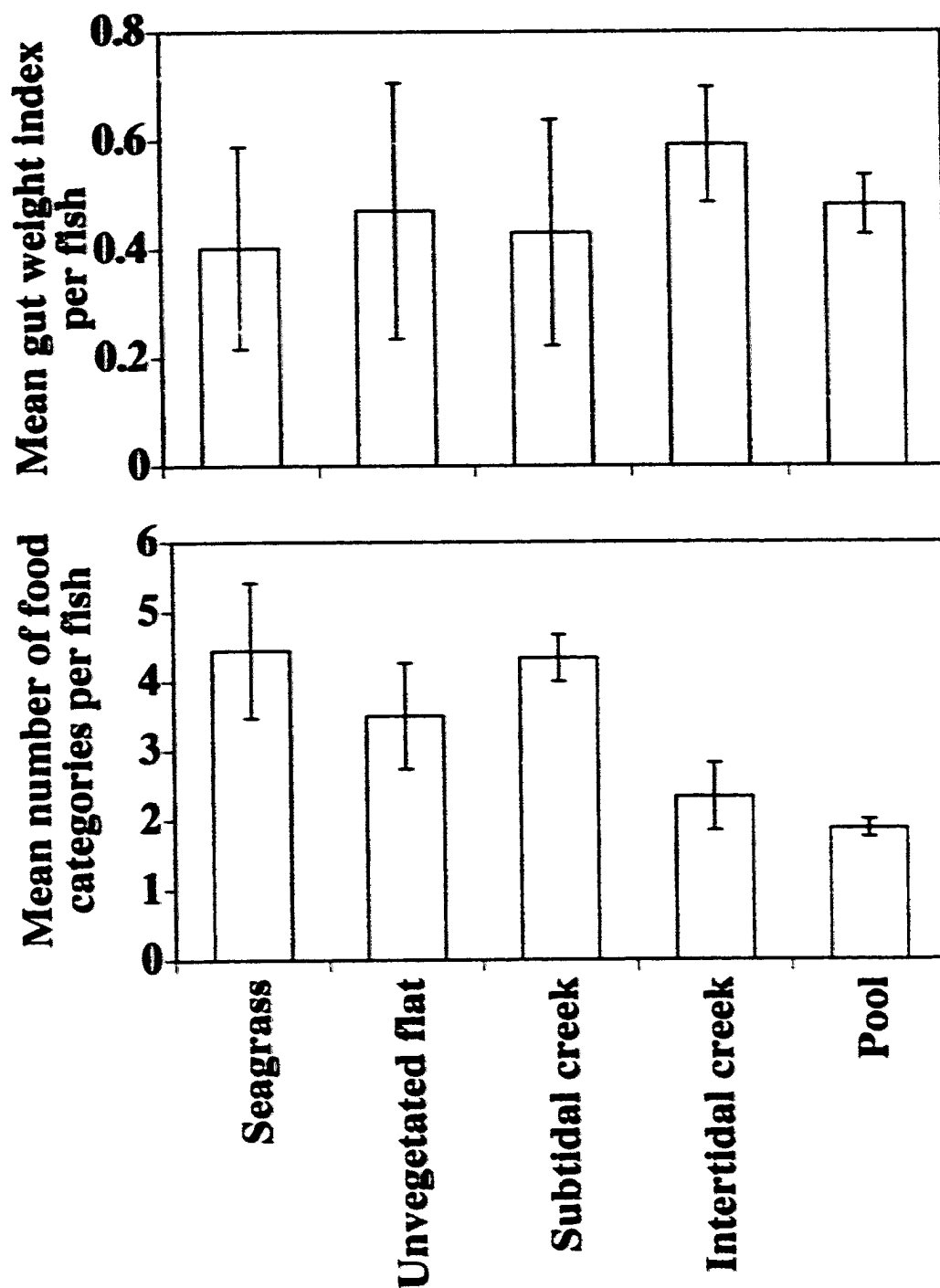


Figure III-19. Mean gut weight index (g. food/g. fish X 100) and mean number of food categories per fish for fish from enclosures in each habitat examined. Error bars are ± 1 s.e.

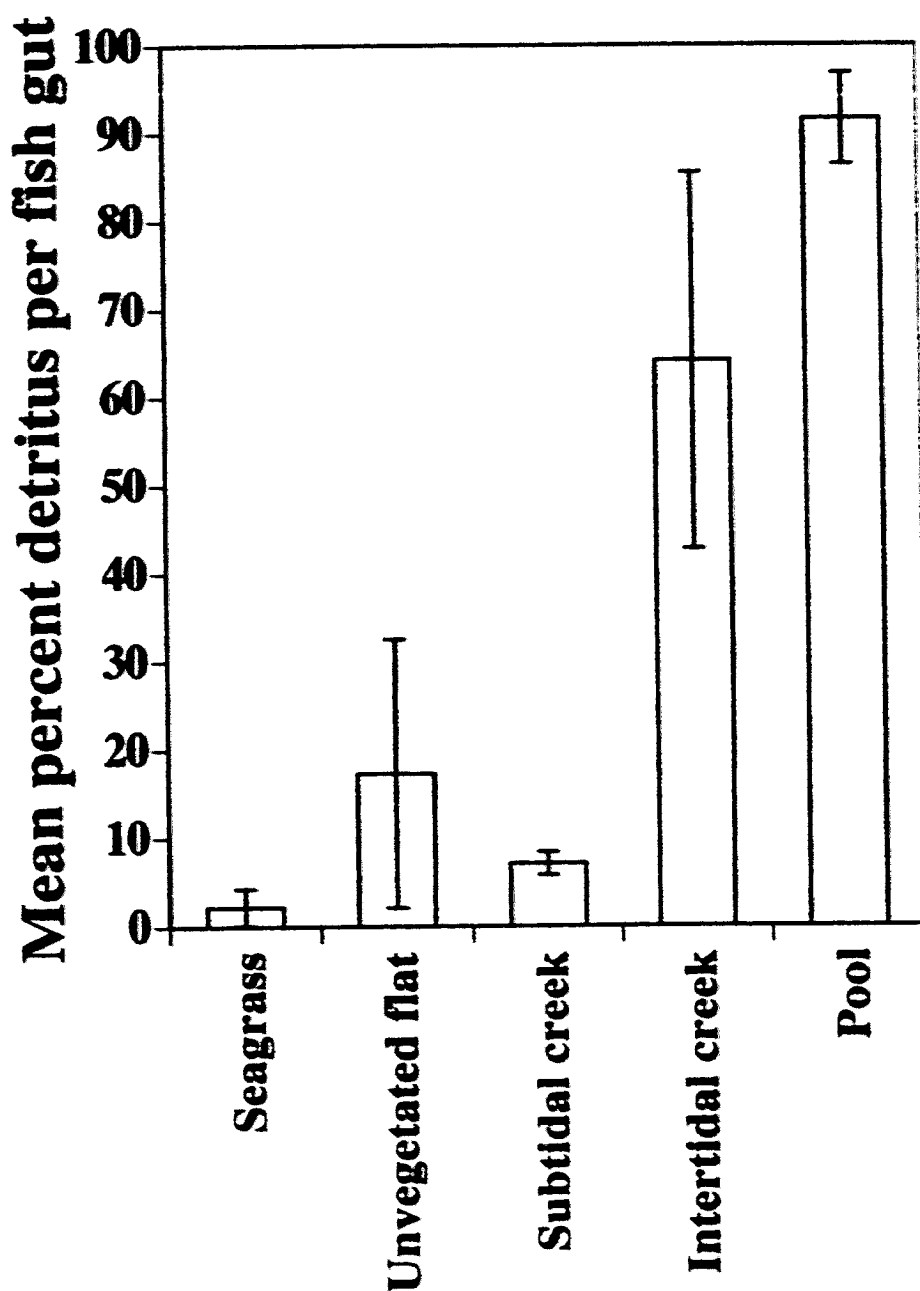


Figure III-20. Mean percent detritus per fish gut from each habitat examined. Error bars are ± 1 s.e.

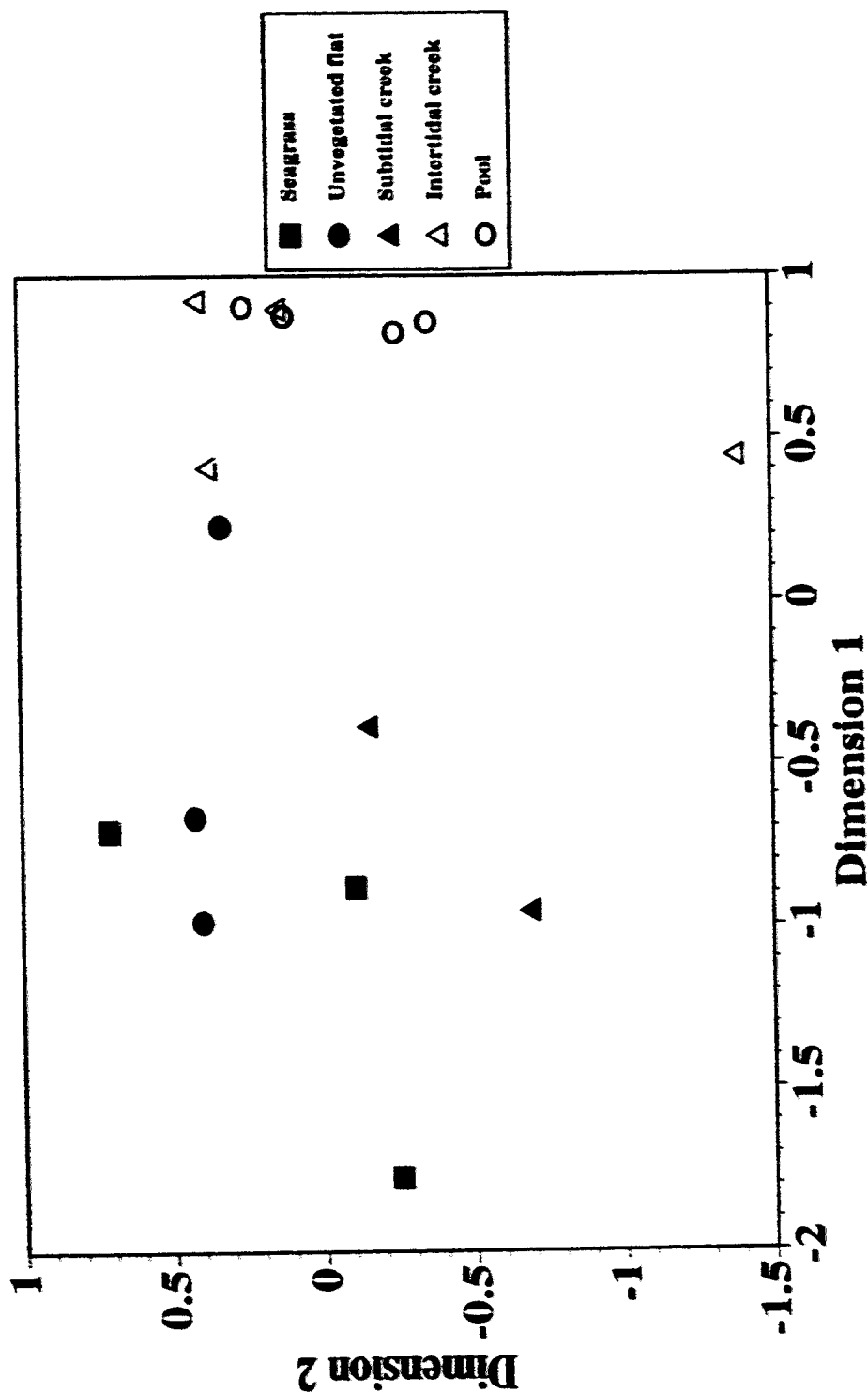


Figure III-21. MDS plot of similarities for gut content of fishes from enclosure experiment. Points represent means from each cage. All cages from the same habitat have the same symbol. Stress < 0.01.

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CHAPTER IV

Diel patterns of feeding in the California killifish, *Fundulus parvipinnis*, and implications for defining essential fish habitat

Abstract

Intertidal fishes in southern California face a suite of environmental conditions distinct from those encountered on the Atlantic and Gulf coasts. This is particularly evident with regard to the timing and availability of the rich foraging resources of the tidal wetlands. This study investigates the foraging biology of the California killifish (*Fundulus parvipinnis*), an important and numerically-dominant southern California wetland resident fish. Gill nets, enclosure experiments and gut content analyses were used to evaluate the presence of *F. parvipinnis* in intertidal habitats during night versus day, to determine their ability to forage at night, and to assess diel differences in food ingested. No difference in gut fullness between fish feeding nocturnally and those feeding diurnally was found. However, nocturnally-feeding fish had significantly more detritus in their guts (32% by weight) relative to those feeding diurnally (10.1 % by weight). Possible mechanisms contributing to this difference are differential prey availability and reduced efficiency of visual predation at night. Quantification of the temporal changes in habitat value and utilization by wetland

fishes is required for defining Essential Fish Habitat for resident fish species in the threatened wetlands of southern California.

Introduction

Fishes that complete their entire life-cycle within the wetland ("marsh residents") have critical ecological roles in these habitats. Resident marsh species act as predators, prey, and vectors for parasites in wetlands (Haaker 1975, Kneib 1988, Lafferty and Morris 1996). Further, through participation in a "trophic relay", resident nekton play an important role in the transfer of marsh production to coastal waters (Kneib 1997).

Despite their apparent ecological importance, the ecology of wetland resident fishes on the Pacific coast of North America has not been studied extensively. The vast majority of studies on wetland resident fishes in North America have been performed on the Atlantic and Gulf coasts of the U.S. (Kneib 1997, but see Chamberlain and Barnhart 1993, Fritz 1975, Desmond et al 2000, Chapter V).

Quantification of temporal and spatial variation in foraging habits of resident fishes is needed to delineate not only the transfer and cycling of energy within and across marsh and estuarine systems, but also to evaluating Essential Fish Habitat (EFH) for these species. Intertidal habitats are rich sources of food for many estuarine fishes. However, the trophic value of the habitat may vary not only with tidal and seasonal cycles (Fritz 1975, Hartney and Turnyan 1998), but also with respect to diel

cycles. For example, different prey may be available during daytime (Haase 1993), or predation risk of a habitat may vary with time of day, leading to changes in the relative value of habitats (Metcalf 1999). *Fundulus parvipinnis* (California killifish), one of the numerically dominant southern California salt marsh resident fishes, is a particularly useful model for examining diel habitat utilization effects. Both through its numerical dominance (Ambrose and Meffert 1999, Chapter V) and intermediate trophic level (generally a 2d level carnivore), *F. parvipinnis* likely exerts considerable influence on its predators and prey in the marsh habitat, and will affect the transfer of production offshore as well. Although some studies examining the diet of *F. parvipinnis* have been conducted, these have either not considered (Fritz 1975, Hartney and Tumyan 1998) or not analyzed nighttime feeding (Johnson 1999).

Most of the work on wetland fishes has concentrated on describing the spatial distribution of species on either tidal or seasonal time scales (Kneib and Wagner 1994, Rozas 1995, Ambrose and Meffert 1999), but has not considered the potential for variation in habitat use patterns related to diurnal cycles. Studies that have examined diel patterns in habitat utilization of wetland fishes show strong temporal differences in utilization related to feeding (Weisberg et al. 1981) or predator-avoidance (Rountree and Able 1993). Fishes utilizing intertidal environments face unique challenges related to tidal cycles. Tidal regimes interact with diel and seasonal cycles of habitat value, availability, and predation risk (e.g., Gibson 1993), and so patterns of habitat use may not be as simple as those in the better-studied subtidal systems, where

most fishes have evolved strictly nocturnal, diurnal, or crepuscular activity patterns (Helfman 1993).

The purpose of this study is to (1) determine if *F. parvipinnis* is present at night in the intertidal in wetlands of Mission Bay, CA, (2) determine if *F. parvipinnis* is capable of feeding at night, and (3) determine if there is a difference in the amount or quality of the food obtained during nighttime versus daytime feeding. These questions were addressed by examining gut contents of starved *F. parvipinnis* placed in enclosures during daytime and nighttime high tides.

Materials and Methods

Study Site

Enclosure experiments were performed in intertidal creeks (~90 cm above MLLW) of the Kendall Frost/Northern Wildlife Preserve, a 12 hectare natural salt marsh in the northern part of Mission Bay, San Diego, California (32° 47' N, 117° 14' W). The vegetated marsh is dominated by *Spartina foliosa* in the area immediately surrounding this experiment. The marsh is fully tidal, with slight seasonal freshwater input, and creek salinities near that of full seawater (~33).

Enclosure Design

Enclosures were constructed from clear plastic storage boxes (47cm wide x 80cm long x 33 cm tall) modified in the following manner. The bottoms were removed using a handheld rotary saw, while removable lids were constructed of 1 mm plastic

mesh, with a small rim of plastic (~3 cm wide) creating a seal with the body of the box.

Field Protocol - Enclosures

On July 15 and 16 1999, adult *F. parvipinnis* were captured from the Kendall Frost/Northern Wildlife Preserve, and placed in tanks of flowing filtered seawater for 48 hours to allow complete gut clearance (Weisberg et al 1981, Talley unpublished data). Six of these fish were maintained in these aquaria during the field experiment as controls. These fish were sacrificed and analyzed simultaneously with the experimental fish (three for each treatment), to verify that the guts were empty and to ensure that food items in enclosure fish gut content studies were obtained in the field alone.

On the afternoon of July 17 and pre-dawn hours of July 18, 1999, 5 enclosures were placed in a shallow intertidal creek one hour prior to high tide. Enclosures were pushed approximately 8 cm into the sediment to ensure a complete seal, five fish were introduced into each enclosure, and the lids were affixed. One hour after high tide, temperature and salinity were taken from inside and outside the enclosures using a YSI® 30 handheld salinity and temperature gauge. Fish were then removed from the enclosures using a small dip net, and immediately placed in liquid nitrogen to halt digestion and preserve gut contents. To ensure that the fish were allowed to feed for approximately equal periods of time, efforts to remove the fish were discontinued either when all five fish had been successfully recovered or after five minutes of

searching, whichever was shorter. Fish were allowed to feed within the enclosures for a total of approximately 2 hours.

Field Protocol - Gill Nets

On September 25, 1999 and May 11, 2000, four experimental gill nets were set in the marsh at Mission Bay, CA approximately 30 minutes prior to both the nighttime and daylight high tides. Nets were 10 meter long x 2 meter tall Baltic Sea type gill nets of two mesh sizes: two each of 8 mm and 19 mm mesh. Nets were set with one end at the creek edge, and oriented such that they extended 10 meters up into the vegetated marsh. Nets were left for one hour, after which they were cleared, with all fish being counted and measured. Day and night catches were compared using a one-way ANOVA on $\log(x+1)$ transformed counts.

Lab Protocol

Fish were thawed and blot-dried before gut content analysis. For each fish, total length, standard length, and total wet weight was recorded. Only the first section of the gut ("foregut") was removed for analysis, to minimize error associated with differential digestion of gut contents (Babkin and Bowie 1928, Cicchetti 1999). Immediately upon removal, gut fullness was subjectively estimated, with each gut being given a rating from 1 to 5 (1 being empty, 5 being completely full). Gut contents were then identified to the lowest taxonomic group possible, and wet weight of each taxonomic group was measured to the nearest milligram. A gut content index (Hyslop

1980) was also calculated for each fish sampled. The gut content index describes the wet weight of the pooled gut contents as a percentage of fish wet body weight.

Inundation Time

Comparisons of inundation times for vegetated marsh habitat were performed using 1999 tide data for representative sites from the central Atlantic coast of North America (Roosevelt Inlet, DE, 38° 49' N, 75° 12' W) and for this study site (Crown Point, Mission Bay, CA), using Harbormaster software (Zihua Software, LLC, Rockport MA). The Atlantic coast site was chosen for its proximity to the location of the study on tidal and diel feeding patterns of *F. heteroclitus* by Weisberg et al (1981). However, the general trends in the tide data are consistent regardless of the specific Atlantic-coast location chosen. Atlantic coast (*Spartina alterniflora*) marshes were considered available for fish feeding at tides greater than 0.8 meters above MLLW, and southern California (*Spartina foliosa*) marshes were considered available at tides greater than 1 meter above MLLW.

Results

Water temperatures were on average 9.5 °C higher inside cages during daylight sampling relative to nighttime (31.6 °C day, 22.1 °C night, ANOVA, $p < 0.001$), and salinity was 0.5 higher (35.4 day, 34.9 night, ANOVA $p < 0.01$). Mean water temperature and salinity measures inside the enclosures were similar to those outside (26.9 °C and 35.2 inside, 26.5 °C and 25.9 outside).

Only one of the six control fish had any material in its guts (a small amount of sediment in a single nocturnal control sample), supporting the assumption that all gut contents in experimental fish were derived from the field.

The majority of fish from both daytime and nighttime enclosure experiments had food in their guts (Table IV-1). Percent occurrence data were calculated using the mean number of guts containing each food item per enclosure (Table IV-1). Overall, gut contents were comprised mostly of unidentified crustacean parts (percent composition by weight across both treatments = 39.9%). These are likely to have included harpacticoid copepods, tanaids, and amphipods, based on other guts examined (D. Talley, unpublished data). It is likely that the majority of these parts are from amphipods, as identifiable amphipods represented an additional 19.3% of the overall fish gut content by weight. Gut fullness and relative gut weight did not differ between diurnally and nocturnally feeding fish (Figure IV-1).

Percent detritus in gut contents was compared between the diurnally and nocturnally feeding fish, using a one-way ANOVA on arcsin-transformed mean proportions. The enclosures, and not individual fish, were considered experimental units for these analyses. Detritus represented a higher proportion by weight of the gut content of fishes feeding at night (mean = 31.8%) than in those feeding during daylight (mean = 10.1%, $p < 0.05$; Figure IV-2).

There were no statistically significant day-night differences in number of *F. parvipinnis* captured by gill nets (Figure IV-3).

Discussion

Like *F. heteroclitus*, the dominant killifish in the Atlantic coast salt marshes of North America (Kneib 1986), *F. parvipinnis* has been previously shown to feed predominantly during high tides and on the vegetated marsh (Fritz 1975). While no studies have addressed diel patterns of feeding in California killifish, there are reasons to expect that optimal feeding patterns would not precisely follow those of *F. heteroclitus*, which also feeds mostly on the vegetated marsh during high tides, but almost exclusively diurnally (Weisberg et al. 1981). The Pacific coast of North America generally experiences mixed semi-diurnal tides, in contrast to the relatively even semi-diurnal tides of the Atlantic coast (Open University 1989). Vegetated marshes on the Atlantic coast are therefore more accessible to fishes during both daylight and nighttime on any given day, while marshes on the Pacific coast are not consistently accessible to fishes during daylight (Figure IV-4). This is also because the dominant lower marsh vegetation, *Spartina foliosa* (Pacific cordgrass), has a much higher minimum elevation than the comparable Atlantic cordgrass, *S. alterniflora* (Callaway and Josselyn 1992). If southern California wetland fishes limited their feeding to daylight hours when the vegetated marsh is inundated (tides greater than 1.0 meters above MLLW for Mission Bay *Spartina foliosa* habitat, Zedler (1982)), their foraging opportunities would be extremely limited from December through May (Figure IV-4). Winter and Spring are likely to be important foraging seasons for adult *F. parvipinnis*, both because this species begins spawning in April (Fritz 1975), and because densities of temperate, soft-bottom macrofauna, which are common prey

items for *F. parvipinnis*, tend to peak during the Spring (Talley and Levin 1999, Levin et al 1998). If *F. parvipinnis* was unable to feed nocturnally, populations in southern California marshes, unlike their congeners on the Atlantic coast, would have no access to the intertidal foraging habitat for extended periods during the Winter and Spring.

Balancing risk and energy

Nocturnal foraging on southern California intertidal wetlands during the winter and spring months could be adaptive for reasons other than energetics. Animal behavior is often considered to be driven in large part by tradeoffs between foraging benefits and risk of predation, where animals seek to minimize the ratio of mortality risk to food gained (μ/f ratio, Gilliam and Fraser 1987). This often involves the use of sub-optimal foraging habitats in cases where the perceived risk of predation in higher-quality foraging areas is high (e.g., Sogard 1994, Brown 1999). During the winter and early spring months, *F. parvipinnis* populations are dominated by larger fish, with few very small individuals present (Perez-Espana et al. 1998). While shallow water can provide a refuge habitat from piscivorous fishes (Ruiz et al. 1993), wading birds forage in the marsh habitat during the daytime (Bent 1963). Since piscivorous birds, unlike fish, show positive size-selection for prey (Sogard 1997), the relatively large *F. parvipinnis* in the winter and spring would be particularly vulnerable to these selective and efficient predators when feeding on the vegetated marsh surface during daylight high tides. These individuals might be able to maximize their fitness by using the rich food resources of the vegetated marsh during the night, when predation risk is lower.

Our data demonstrate that killifish have the potential to take advantage of food in intertidal habitats despite the fact that these habitats are inundated predominantly during the night throughout much of the year. The presence of *F. parvipinnis* in gill net samples demonstrates that this species is present on the vegetated marsh during both the day and night (Figure IV-3). This reinforces the hypothesis that the vegetated marsh may be a significant trophic resource for fishes in Pacific coast marshes, despite the relatively short inundation times (Johnson 1999).

The increased proportion of detritus in the guts of nocturnally-feeding *F. parvipinnis* suggests that the nutritional value of food obtained during night feeding may be lower than that obtained during daytime foraging. Prinslow et al (1974) demonstrated that *F. heteroclitus* was unable to use detritus either for growth or maintenance. *Fundulus parvipinnis* has a very similar digestive tract morphology to that of *F. heteroclitus*, and their relatively simple guts are not consistent with detritivorous feeding (Bowen 1983). Thus, it is likely that detritus provides similarly low nutritional value for *F. parvipinnis*.

The presence of more detritus in the guts of fish feeding at night also suggests less efficient prey capture under nighttime conditions. Two potential mechanisms of lowered capture efficiency are: (1) lower light levels and (2) differential prey availability at night relative to day. Lowered light levels might reasonably be assumed to reduce prey capture efficiency or handling ability by reducing the reactive distance (distance from prey item at which predator begins strike) for predators. No studies have examined *F. parvipinnis* feeding at low light. However, studies of other estuarine

fishes, including *Fundulus grandis* from the Gulf of Mexico, suggest that reactive distance is reduced by very low light levels (Benfield and Minello 1996 and references therein). Reduced reactive distance at low light levels may underlie the differences in gut contents between day- and night-feeding fish.

Differential prey availability between day and night may also contribute to the greater percentage of detritus consumed by night-feeding *F. parvipinnis*. Studies of diel patterns of macrofaunal activity in wetlands have revealed differences between day and nighttime behavior (e.g., Haase 1993, Thiel et al. 1995). Of particular relevance to nighttime feeding by fishes is a study by McNeil et al (1995), which revealed that amphipods in a sub-tropical salt marsh were more than 10 times as abundant on the sediment surface at night than during the day. Fish striking at prey items resting on the sediment surface, coupled with potentially shorter reaction distances, could cause the incidental ingestion of surface material, and explain the greater abundance of detritus in the guts of night-feeding *F. parvipinnis*.

Diel variation as a component of EFH

The importance of identifying EFH has recently begun to receive national attention in the United States, as a result of a 1996 amendment to the Magnuson-Stevens Fishery Conservation and Management Act. This amendment includes specific provisions for determination of EFH for fishery species which are under federal fisheries management plans, and defines EFH to include waters and substrate necessary for spawning, breeding, feeding, or growth to maturity (NOAA 1996). This

increased interest in EFH for federally managed fisheries has also instigated research into defining EFH for non-target species, such as *Fundulus* spp., since they provide forage for target species, and because EFH offers a useful framework in which to look at habitat utilization patterns (e.g., Minello 1999).

An understanding of the differences in foraging ability and pattern among marsh fishes of different species or in different regions is critical to assessment of EFH, to quantifying transfer of production across the marsh landscape, and to energetics models of wetland populations. If fishes gain different nutritional or fitness benefits from specific areas depending on the time of day, then this temporal/spatial requirement should be a defined part of their EFH. Lack of nighttime habitat sampling, coupled with an assumption that habitat-specific abundances reflect habitat value, may hinder the accurate assessment of habitats classified as EFH. Only by including either habitat-related measures of fitness (e.g., growth, survivorship, or reproduction) or accurate proxies for such measures, can EFH be correctly evaluated. Further, efforts to model or estimate transfer of production or fish energetics require a complete understanding of how the species involved forage throughout the diel cycle. This is a crucial component of the EFH model.

Conclusion

This study demonstrates that *F. parvipinnis* can take advantage of the rich food resources of the vegetated intertidal salt marsh during both night and day. We further show that the nutrition derived from those habitats at night may differ from that

derived through daytime foraging in the same habitat. Night feeding may improve fitness for *F. parvipinnis* by increasing the μ/f ratio, despite the lower quality of food obtained during nocturnal feeding. These short-time scale differences in habitat utilization and quality should be incorporated into assessments of EFH. Further study is needed to determine the mechanisms driving the differences in day versus night diets for *F. parvipinnis*, as well as the consequences for growth, reproduction, and habitat utilization patterns.

Table IV-1. Frequency of occurrence (in percent) of food items in the guts of fish from this experiment, $\pm$ one standard error.

	Day	Night
Amphipods	54 $\pm$ 8.3	67 $\pm$ 9.1
Algae	72.0 $\pm$ 18.5	66.7 $\pm$ 9.1
Unidentifiable crustacea	72.0 $\pm$ 18.5	66.7 $\pm$ 13.1
Insects	48 $\pm$ 12.3	10 $\pm$ 6.1
Polychaete	28.0 $\pm$ 9.7	48.3 $\pm$ 13.5
Detritus	42.0 $\pm$ 9.8	53.3 $\pm$ 9.4
Empty Guts	10.7 $\pm$ $\pm$ 6.9	19.0 $\pm$ 9.3

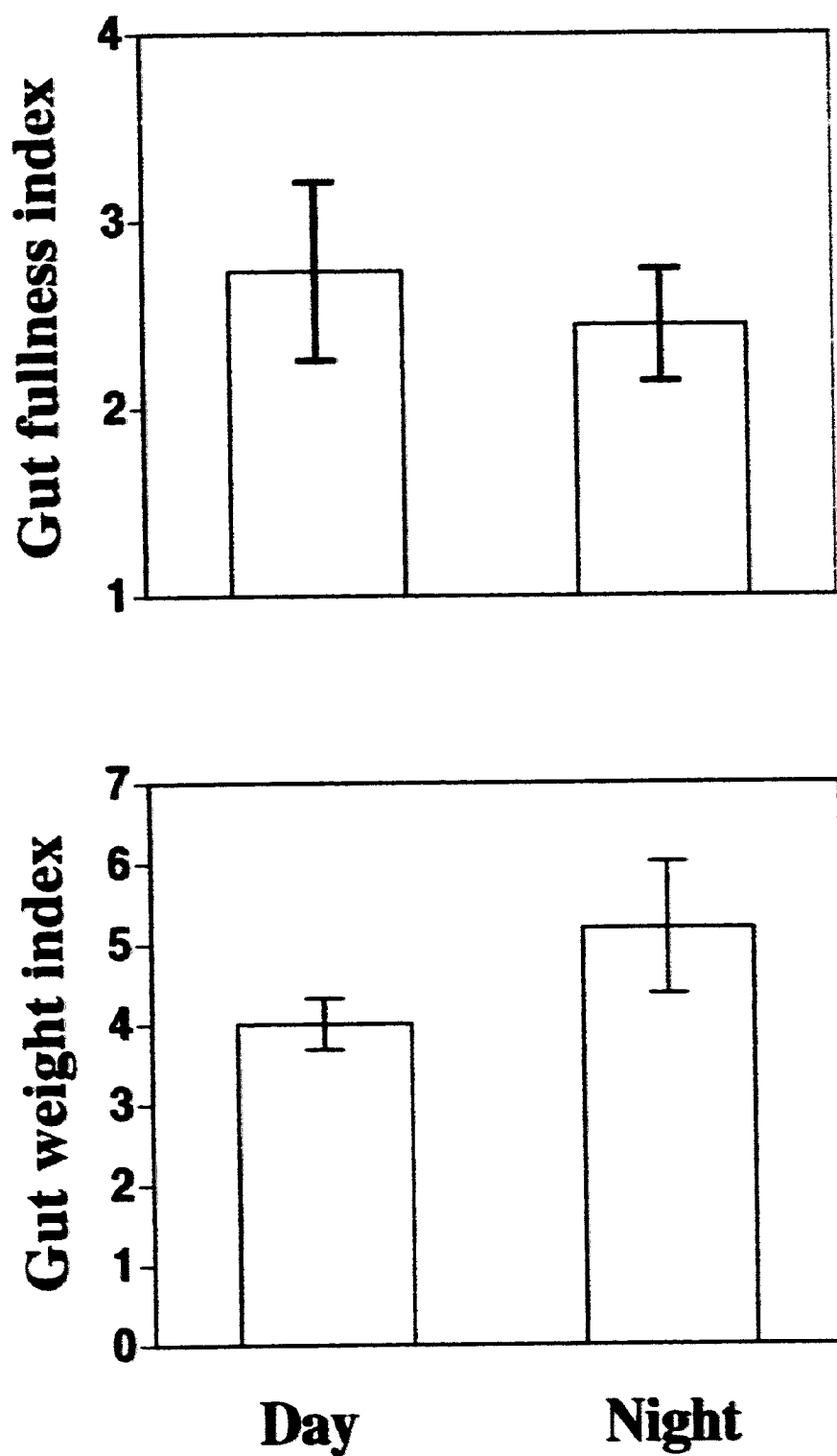


Figure IV-1. Relative gut fullness and gut weight indices for fish from both day and night enclosure experiments. No significant differences between treatments for either index were found (one-way ANOVA, $p > 0.2$).

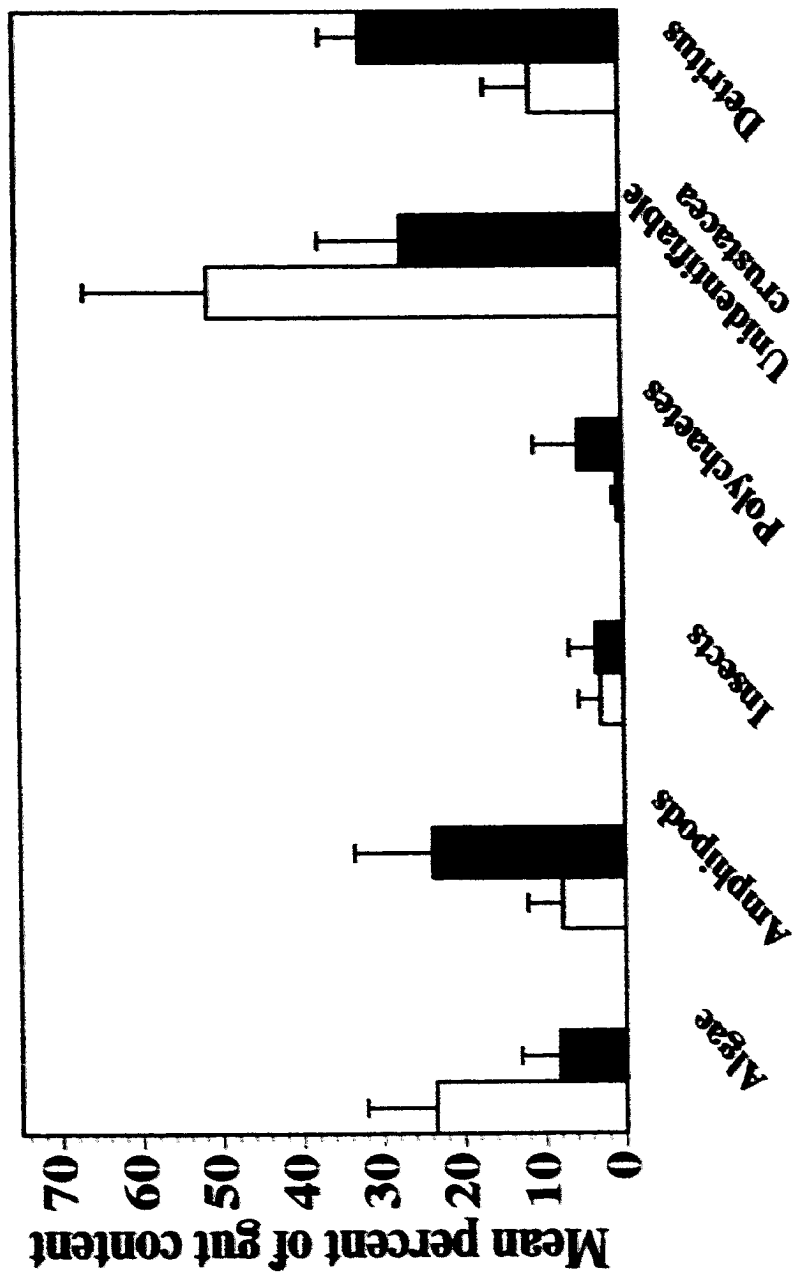


Figure IV-2. Percentage of stomach content (by weight) $\pm$ one standard error for food items in fish from day (light bars) and night (dark bars) feeding enclosures. Percent detritus is significantly different between day and night fish at $p < 0.05$ (ANOVA on arcsin-transformed proportions)

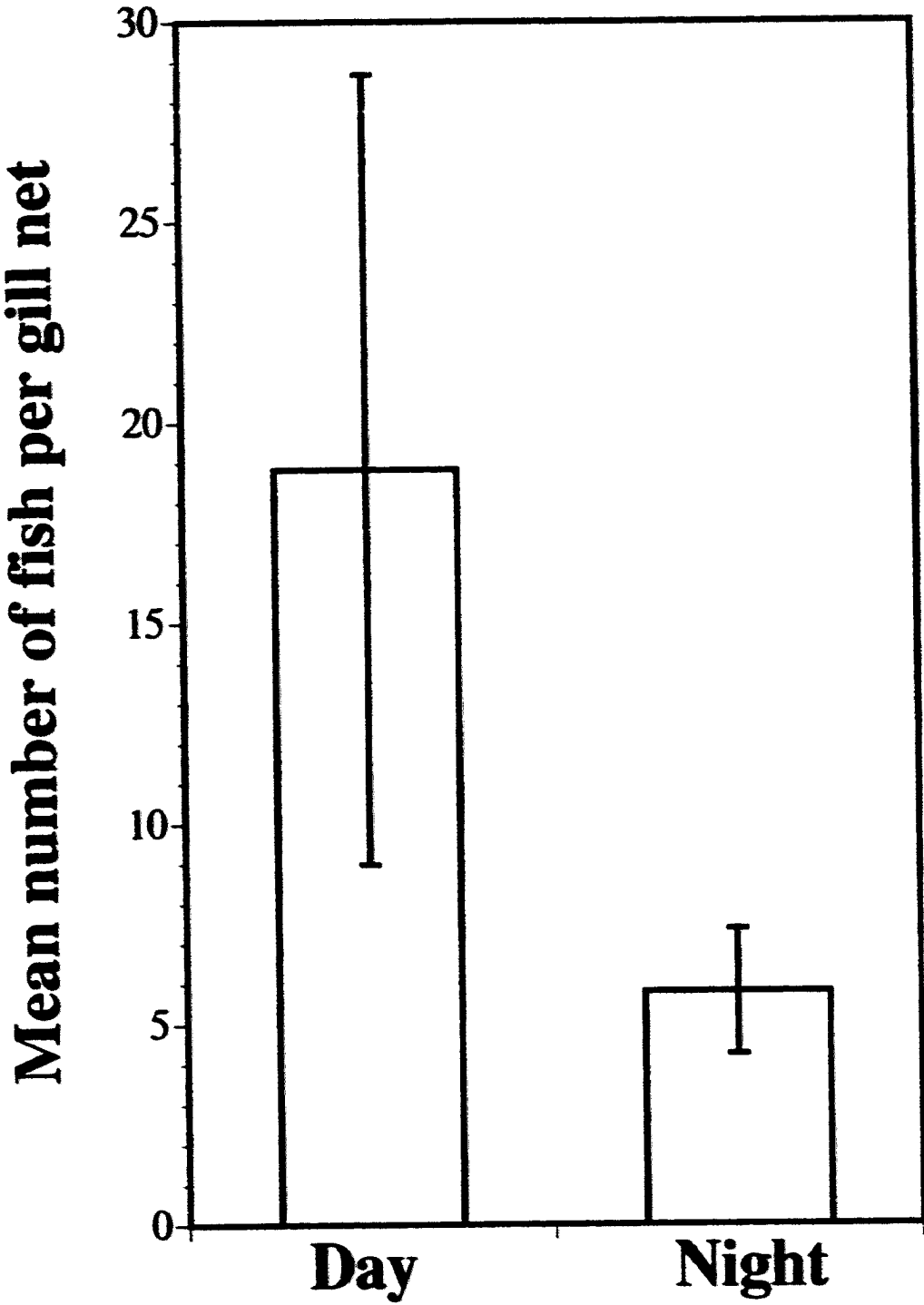


Figure IV-3. Mean number of *Fundulus parvipinnis* caught on the vegetated marsh (*Spartina foliosa* and *Salicornia* spp.) by gill nets set during day and night high tides in Mission Bay, CA. No significant differences between treatments were found (one-way ANOVA, $p = 0.2$).

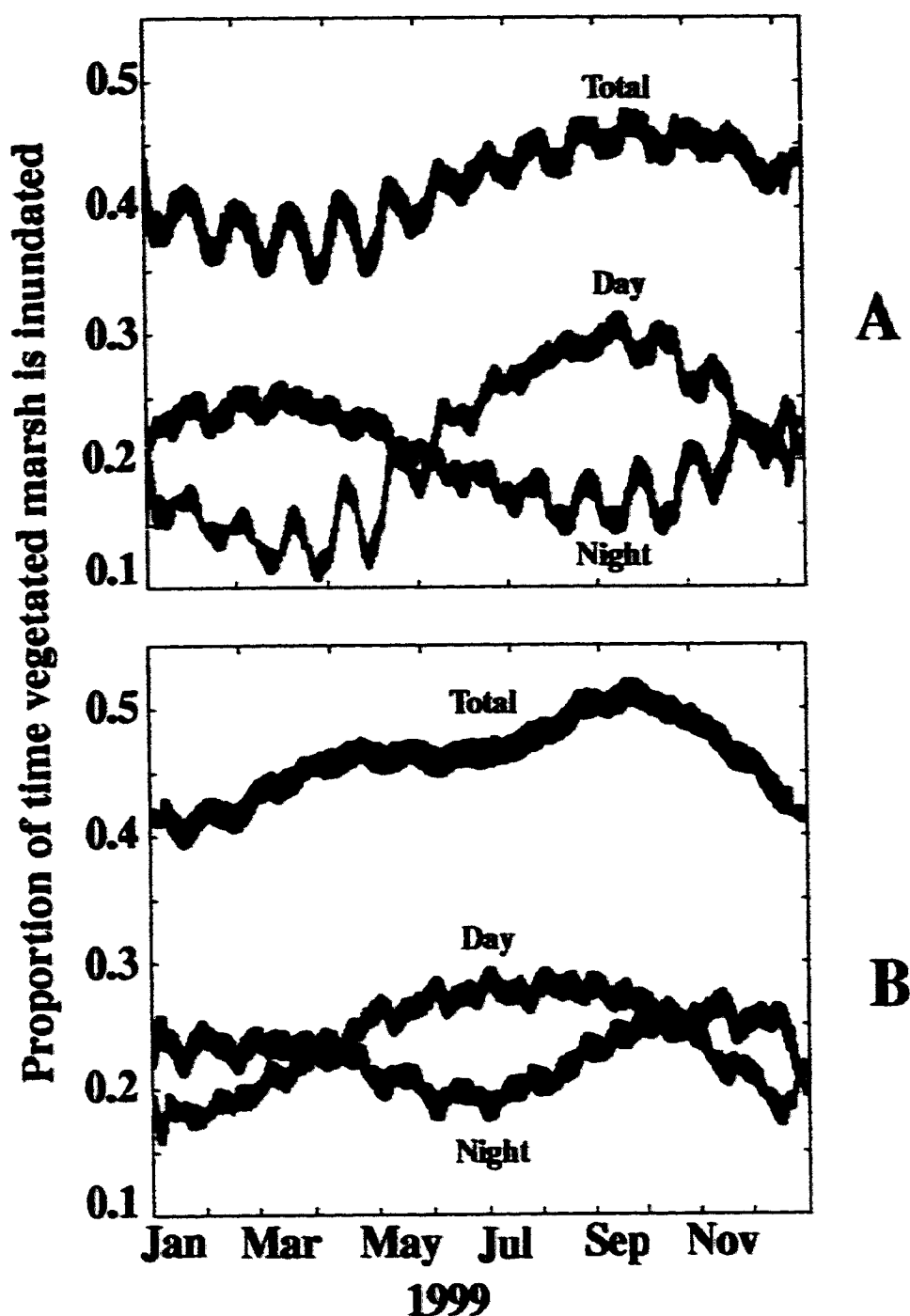


Figure IV-4. Mean proportion of time *Spartina*-vegetated marsh is available to *Fundulus parvipinnis* for foraging in (A) Mission Bay, CA and (B) Roosevelt Creek, DE during 1999. Red line represents total inundation, green is daylight inundation, and black is night inundation. Lines are smoothed (14 day) running averages, using lower limit of Pacific coast *S. foliosa* and Atlantic coast *S. alterniflora* as 0.8 and 1.0 feet above MLLW, respectively.

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CHAPTER V

Ichthyofaunal utilization of newly-created versus natural salt marsh creeks in Mission Bay, CA.

Abstract

The ichthyofaunal assemblages in a created and adjacent natural marsh in Mission Bay, San Diego, California were compared in order to evaluate functional equivalence of created systems. Fishes trapped in both marshes included *Fundulus parvipinnis*, *Gillichthys mirabilis*, *Acanthogobius flavimanus*, *Ctenogobius sagittula*, *Atherinops affinis*, and *Mugil cephalus*. *Fundulus parvipinnis* was numerically dominant in both systems, representing on average 69% of all fishes trapped in the created marsh and 65% of all fishes trapped in the natural marsh. *Gillichthys mirabilis* was the second-most abundant species, representing on average 31% of all fishes trapped in the created marsh and 28% of all fishes trapped in the natural marsh. Species richness and dominance measures were similar between the two systems, while abundances were higher in the natural relative to the created marsh. The size-structure of *F. parvipinnis* and *G. mirabilis* differed between the created and natural marsh creeks, with the created marsh populations being skewed towards larger size classes. These size differences are believed to arise from differences in creek morphology between the created and natural systems, and potentially affect both predators and prey of these species in the marsh. Mark-release-recapture revealed

considerable marsh fidelity, with as many as 35% of the *F. parvipinnis* tagged in a marsh being recovered one day later in the same marsh. Stable isotope analyses of *F. parvipinnis* revealed similar $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ values between marshes; however there was a consistent enrichment in ^{13}C (>3 per mil) in tissues of *F. parvipinnis* from the created marsh, supporting the high marsh fidelity suggested by tagging results. This first published documentation of the Mission Bay marsh resident fishes suggests that the created marsh ichthyofaunal assemblage was distinct in density and size structure from the adjacent natural marsh, and provides lessons for future restoration efforts.

Introduction

California's wetlands are among the most threatened habitats on earth, having lost 90% of their historical acreage to human activities (Schoenherr 1992). This habitat loss and fragmentation is particularly acute in southern California, and has pushed several wetland bird and plant species to the brink of extinction (Zedler 1996a). Mission Bay, in San Diego, CA, was largely intertidal marsh and mudflat habitat as recently as 1940, but now consists of only three small, isolated remnant marshes (Marcus 1989). Marsh restoration and creation have become increasingly common methods to mitigate losses such as these.

The success of mitigation in restoring function of resident marsh fish communities is of interest both to ecologists and resource managers. Resident fishes play a pivotal role in marsh ecosystems, directly and indirectly affecting both

organisms on which they prey (e.g., Kneib 1986, Vince et al. 1976, Kelso 1979) and those which feed on them (e.g., Lafferty and Morris 1996, Kersten et al. 1991). Additionally, resident marsh ichthyofauna play a critical role in the transfer of energy and nutrients off of the marsh surface (Kneib 1997).

Despite their ecological importance, there is limited information on the ecology of marsh-resident ichthyofauna of southern California, in particular for the numerical dominant, *Fundulus parvipinnis* (California killifish). There are even fewer studies of the effectiveness of marsh creation in restoring ichthyofaunal populations, although recent work by Williams and Zedler (in press), Desmond (1996), and Zedler et al. (1997) has begun to provide insight into these issues in California.

The first comprehensive account of the basic ecology of *F. parvipinnis* was provided by Fritz (1975). Allen (1980, 1982) and Horn and Allen (1985) examined the seasonal changes in abundance, composition, and productivity of a fish assemblage in Upper Newport Bay, southern California, which included marsh residents. Desmond (1996) examined the relationship between "creek order" (*sensu* Horton's (1945) "stream order") and fish assemblages in two southern California wetlands. Creek order is a function of the number and arrangement of tributaries, and is strongly correlated with creek size, with low-order creeks being smaller than high-order creeks. Desmond (1996) observed a strong relationship between creek order and utilization by *F. parvipinnis*, with higher proportions of small individuals occurring in low-order creeks. The same pattern was not found for *Gillichthys mirabilis* (mudsucker) or *Clevelandia ios* (arrow goby). It also was noted that low-order creeks are not usually

included in the design of restored marshes, and therefore these systems may be missing critical habitat for juvenile *F. parvipinnis*. Southern California native fishes have been found not to directly distinguish created from natural wetland channels *per se*, but instead seemed to respond to a suite of physical characteristics including salinity, geomorphology, and sediment composition, which often differ between created and natural systems (Williams and Zedler *in press*, Zedler et al. 1997).

Fish in Atlantic coast estuaries appear to utilize restored marshes differently than natural or reference systems. These differences are manifested as changes in density (e.g., Landin et al. 1989, Havens et al. 1995); changes in diet (e.g., Allen et al. 1994 ; Moy and Levin 1991); or more general changes in habitat utilization when compared to the natural system (Meyer et al. 1993).

However studies by Lasalle et al. (1991), Minello and Zimmerman (1992), Simenstad and Thom (1996), Shreffler et al. (1990, 1992) and Zedler (1996b) all suggested that at least some critical habitat functions characteristic of natural systems, such as prey resource and refuge from predation, can develop in restored wetlands after several years.

In this paper, I examine ichthyofaunal establishment in a created-marsh creek of the Crown Point Mitigation Site (CPMS), Mission Bay, California, during the first 2.5 years following marsh creation and make comparisons with an adjoining natural marsh system, the Northern Wildlife Preserve (NWP)(Figure V-1). The study addresses the following questions: (1) Is there evidence for succession in the created-marsh creek ichthyofaunal assemblage? (2) What are the patterns of inter-annual

variability in ichthyofaunal assemblages in the created and natural marsh creeks? (3)

Does the resident fish community composition and abundance in the created creek

come to resemble that in the natural creek? (4) Does the size-structure of the dominant

marsh-resident fish taxa in the created creek come to resemble that in the natural

creek? And (5) Does *F. parvipinnis* exhibit marsh creek fidelity, and is this the same

between created and natural marsh creeks? The answers to these questions are used to

suggest strategies and considerations for salt marsh restoration.

Materials and Methods

Study site

Fishes were sampled in creeks of a natural (Northern Wildlife Preserve)(NWP) and adjacent created (Crown Point Mitigation Site)(CPMS) marsh in the northern part of Mission Bay, San Diego, California (32° 47' N, 117° 14' W)(Figure V-1A). The NWP is a natural marsh of approximately 12 hectares which is managed by the City of San Diego and the University of California, San Diego. The NWP has three discrete creek systems; the system closest to the mitigation marsh was used for this study (Figure V-1B). The CPMS is a created salt marsh system (approximately 2.8 hectares of intertidal and subtidal habitat and approximately 0.8 hectares of upland habitat), established by the City of San Diego to mitigate for losses of intertidal habitat. The created marsh was built by grading dredge spoils on what was formerly an unsuccessful least tern nesting site, although this area historically was tidal wetland (Marcus 1989). The site was planted with *Spartina foliosa* (cordgrass) and upland

vegetation. The CPMS was first opened to tidal flushing on December 14, 1995, and planting took place from March 22-26, 1996.

Estimates of length of deep subtidal creek (>20 cm deep at MLLW) and shallow subtidal creek (<20 cm deep at MLLW) were made from aerial photographs and maps of the study site. The CPMS has approximately 375 meters of deep subtidal channel and 80 meters of shallow subtidal creek (Figure V-1C). The study site in the NWP has approximately 150 meters of deep subtidal channel and 630 meters of shallow subtidal creek (Figure V-1B).

As part of the restoration evaluation effort, plant densities were estimated in selected blocks on either side of the creeks in both the natural and created systems. The vegetation of the created system was dominated by *S. foliosa* and *Salicornia bigelovii*, while the natural marsh vegetation was predominantly composed of *S. foliosa*, *S. bigelovii* and *Salicornia virginica* (Levin et al., unpublished data). *Spartina foliosa* in the CPMS was patchy; densities ranged from 0-96 stems/m² in 1996, 0-480 stems/m² in 1997, and 0-1216 stems/m² in 1998 (McCray et al., submitted). *Spartina foliosa* densities in the NWP were more homogenous, ranging from 91-160 stems/m² in 1996, 96-208 stems/m² in 1997, and 43-85 stems/m² in 1998 (McCray et al., submitted). *Salicornia bigelovii* distribution was seasonal, with new recruits appearing in January and senescing in the Fall. *Salicornia bigelovii* was generally absent in the CPMS during 1996, and ranged from 32-656 stems/m² in 1997 and 50-981 stems/m² in 1998 (Levin et al., unpublished data). In the NWP, *S. bigelovii* densities in ranged from 62-323 stems/m² in 1996, 32-416 stems/m² in 1997, and 49-

200 stems/m² in 1998, while *S. virginica* densities ranged from 0-50 stems/m² in 1996, 0-45 stems/m² in 1997, and 0-117 stems/m² in 1998 (Levin et al., unpublished data).

Both marshes are fully tidal, with only seasonal freshwater input, and creek salinities slightly higher than that of full seawater (mean=34.3 psu).

Sampling methods

Ichthyofauna were sampled with Gee® minnow traps, 22-cm diameter at the center, tapering to 19 cm at each end, made of 0.6 cm wire mesh with 2 cm openings. Traps were baited with canned cat food, attached to stakes with 2-3 m of rope, and placed at four locations in the creek at CPMS and four locations in the NWP (Figure V-1B,C). Between December 31, 1995 and September 21, 1998, traps were placed in creeks on 32 days during daytime low tide, and recovered the following day at low tide (i.e., soak time = 24 hours). During recovery, all fish were counted, identified to species, and measured (total length) to the nearest mm.

Mark and recapture methods were used to examine fidelity of *F. parvipinnis* to each marsh and exchange of individuals between marshes. Fish were collected for mark-release-recapture (MRR) sampling on June 2, June 29, August 1, September 4, and October 3, 1996, and on June 19, 1997. All fish were tagged by clipping a small part of the caudal fin to identify location of capture (NWP or CPMS), and were immediately released at the same location. Re-sampling at the same locations took place once between 1-5 days later, whereupon fish were counted, measured, checked for tags, and re-released. In both field and laboratory observations, fin-clipped fish re-

grew a substantial portion of their fins in less than one month. This new growth had a transparent appearance quite distinct from marks on freshly-tagged fish. Thus, it is unlikely that fish tagged from different sampling periods would have been mistakenly counted during resampling. Analyses of MRR data were performed on arcsin-transformed proportion data. The use of proportion data allows for the comparison between marshes with unequal sample sizes.

Stable Isotope Methods

Habitat fidelity was also investigated by examining stable isotope composition from fish tissues. For these analyses, individual *F. parvipinnis* were sampled at low tide from the marsh creeks using a monofilament cast net and a small seine on October 8, 10, & 15 1996, April 14 1997, and October 22 & 23 1997. During October 1997, *F. parvipinnis* were also sampled by seine from the subtidal *Zostera marina* (seagrass) beds in the bay adjacent to the marshes (Figure V-1B). Only one *F. parvipinnis* from each cast net throw or seine pull was used for stable isotope analysis, to increase independence of samples. *Fundulus parvipinnis* with a total length greater than 40 mm were filleted to remove muscle tissue for isotope analysis. For fishes under 40 mm in length, the gut was removed and the remainder of the fish was analyzed. The mean size (total length) of fish used in the stable isotope analyses did not differ between marshes ($p>0.2$), and therefore all size classes were pooled within each marsh for statistical analysis.

Fish were washed in distilled water, dried, ground with a mortar and pestle, and then sent to R. Michener at the Stable Isotope Laboratory at Boston University for analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Analyses were carried out on a Finnigan Delta-S isotope ratio mass spectrometer using standard methods (Lajtha and Michener 1994). All international standards were obtained from the National Bureau of Standards, Gaithersburg, Maryland, USA. Internal instrument precision is 0.014‰, and typical sample precision is better than 0.1‰ (R. Michener pers. comm.).

^{34}S isotopic analyses were performed by Kris Tholke at the Stable Isotope Laboratory of the Marine Biological Laboratory in Woods Hole, Massachusetts. After combustion, sulfate was precipitated as BaSO_4 , converted to SO_2 , and the isotopic ratio determined by mass spectrometry.

Stable isotope ratios are reported in standard δ notation as follows:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$$

where X is ^{13}C , ^{15}N , or ^{34}S , and R is $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, or $^{34}\text{S}/^{32}\text{S}$, respectively. Values are expressed on a per mil (‰) basis.

Results

Species Composition

A total of six fish species were collected over the course of the sampling. *Fundulus parvipinnis*, *Gillichthys mirabilis*, *Mugil cephalus* (mullet), *Atherinops affinis* (topsmelt), *Acanthogobius flavimanus* (yellowfin goby), and *Ctenogobius sagittula* (long-tailed goby) were captured in each marsh. For the first month following marsh creation, only *F. parvipinnis* was recovered in the CPMS. Evaluated across all sampling dates, ichthyofaunal species richness was the same in both the created and natural marshes, with an average of 2 species per trap in both creeks (repeated-measures ANOVA, $F_{1,6}=0.14$, $p=0.72$) (Table V-1). *Fundulus parvipinnis* was the most common species collected, occurring in 89% of all traps in the CPMS and 87% of all traps in the NWP. *Fundulus parvipinnis* represented 69% of the total number of individual fishes caught in the CPMS and 65% of the total number of individual fishes caught in the NWP. *Gillichthys mirabilis* occurred in 73.2% of all traps in the CPMS and 67% of all traps in the NWP, representing 31% of the total number of individual fishes caught in the CPMS and 28% of the total number of individual fishes caught in the NWP. The proportions of each species captured per trap were not significantly different between marshes when examined over the entire sampling period (repeated-measures ANOVA on each species' proportion, $p>0.05$). There was interannual variability in species' proportions, with spring and summer

1998 samples from both marshes containing a large number of young-of-the-year (YOY) *G. mirabilis* (Table V-1). This increase in *G. mirabilis* abundances, coupled with a trend towards fewer *F. parvipinnis* in both systems in 1998 (Table V-1), shifted the mean percentage representation per trap of *G. mirabilis* from 13% in the CPMS and 5% in the NWP during 1996-1997 to 48% and 49% (respectively) during May-September of 1998. The highest species richness in both marshes occurred in the spring and summer of 1998, with as many as five species present in each marsh creek.

Pielou's estimator of Simpson's index ($1-D$) was used to assess the dominance of the ichthyofaunal assemblage sampled (Krebs 1989). This measure can be interpreted as the probability that 2 randomly-selected individuals will be of different species, and is sensitive to changes in the more abundant species (Krebs 1989). The average index value evaluated across all times was almost identical between the created and natural marshes ($1-D=0.34$ for both marshes) (repeated-measures ANOVA, $F_{1,6}=1.87$, $p=0.22$). Values were lower in both marshes in 1996 and 1997 (0.19 and 0.10 in the CPMS and 0.04 and 0.05 in the NWP) compared to 1998 samples (0.53 in CPMS, 0.51 in NWP).

Abundance Patterns

Total ichthyofaunal abundances per trap (Figure V-2) were higher in the NWP than in the CPMS (repeated-measures ANOVA, $F_{1,6}=10.1$, $p<0.02$).

Population Size-Structure

There were differences in *F. parvipinnis* population size-structure between the created and natural creeks. For 12 of 15 sampling dates (those with greater than 50 fish captured per marsh), *F. parvipinnis* populations in the CPMS were skewed towards larger individuals relative to the NWP (Kolmogorov-Smirnov test, $p < 0.05$) (Figure V-3). *Gillichthys mirabilis* showed a similar trend (Figure V-4). The number of fish captured per sampling date was generally low except in the summer of 1998, and therefore distributions were only tested on those 11 dates for which both marshes had >20 *G. mirabilis* (all in the summer of 1998). On 9 of those 11 dates *G. mirabilis* were significantly larger in the CPMS than in the NWP (Kolmogorov-Smirnov test, $p < 0.025$) (Figure V-4).

Mark-recapture

Over the course of the mark-recapture sampling, an average of 14.6% of the *F. parvipinnis* marked in the created system were recovered in the same marsh on the sampling date following marking, while 9.4% of those marked in the natural system were recaptured in the natural marsh (Table V-2). On 5 of the 6 MRR sampling dates, fish marked in the natural marsh were recovered in the created marsh (from 0.5%–3.6% of those marked), while only once were fish from the created marsh recaptured in the natural system (2.7%) (Table V-2). Evaluated across all sampling dates, the percentage of fish captured in the opposite marsh from which they were tagged was

higher for fish marked in the NWP (repeated-measures ANOVA, $F_{1,5}=36.8$, $p<0.001$)(Table V-2).

Stable Isotope Analyses

Fundulus parvipinnis from the created marsh had heavier carbon signatures (overall mean difference =3.4 per mil) compared to fish taken from the natural system (Figure V-5 A,B). $\delta^{13}\text{C}$ values for *F. parvipinnis* averaged -12.1 (range -9.4 to -16.7) in the CPMS and -16.0 (range -8.3 to -18.7) in the NWP over all sampling periods. This difference was observed in the Fall 1996 ($F_{1,4}=30.7$, $p<0.01$) and Fall 1997 ($F_{1,3}=36.8$, $p<0.001$) samples, but not in the Spring 1997 samples ($F_{1,13}=2.0$, $p=0.18$)(Figure V-5 A,B). The same trend was observed for insects, annelids and amphipods (overall mean $\delta^{13}\text{C}=-15.4$ (CPMS), -12.8 (NWP)), which serve as prey for *F. parvipinnis* (Levin et al. 1999). *Fundulus parvipinnis* from the subtidal seagrass (Fall 1997) had $\delta^{13}\text{C}$ values (mean $\delta^{13}\text{C}=-15.7$) indistinguishable from NWP *F. parvipinnis* ($F_{1,30}=0.17$, $p>0.6$), but significantly lighter than those of CPMS *F. parvipinnis* ($F_{1,30}=38.1$, $p<0.001$)(Figure V-5 A,B). Mean $\delta^{15}\text{N}$ (8.4 vs 8.7) and $\delta^{34}\text{S}$ values (11.5 vs 11.7) were not significantly different between the CPMS and NWP on any date (ANOVA, $p>0.5$).

Discussion

Assemblage Composition

Although baited trap catches are a biased subsample of the ichthyofaunal assemblage (e.g., Harvey and Jackson 1997), they offer a rapid means of assessing the relative abundance of those species which are susceptible to capture. *Fundulus parvipinnis* and *G. mirabilis* (the numerical dominants in this study) are readily captured by baited minnow traps. This methodology has been used commercially, recreationally, and in scientific research to catch these species and congeners (e.g., Halpin 1997, Eschmeyer and Herald 1983, Black 1980). The trends observed here are discussed with the understanding that only a subset of the ichthyofaunal assemblages are being compared, and it is the relative comparison across marshes which is of interest here.

The overall ichthyofaunal species composition was quite similar between the created and natural marsh creeks. The creeks of both systems were dominated by *G. mirabilis* and *F. parvipinnis*, which together represented over 90% of the individual fishes captured. Other measures of assemblage composition were also similar, including percentage representation of each species, evenness measures, and species richness.

The greater numbers of species present in both marshes beginning in the spring and summer of 1998 relative to the preceding sampling periods was largely driven by the appearance of two gobiids, *C. sagittula* and *A. flavimanus*, and an increase in the

abundance of a mugilid, *M. cephalus* (Table V-1). *Ctenogobius sagittula* is normally rare in southern California, but is common in the warmer waters of central and southern Baja California, Mexico (Fitch and Lavenberg 1975). *Mugil cephalus* is a species with warm-water affinities (Miller and Lea 1972) which is usually present in Mission Bay, but was unusually abundant during 1998 (Table V-1). This was accompanied by the recruitment of other warm-water species to the Mission Bay marshes that were not collected by minnow traps, including *Callinectes arcuatus* (arched swimming crab) and *Albula vulpes* (bonefish) (pers. obs). Shifts in the marsh-creek ichthyofaunal community towards species with warm-water affinities came at the end of a period of increased water temperature and sea level associated with the 1997-1998 El Niño event, which ended in the late Spring/early Summer of 1998 (<http://www-mlrg.ucsd.edu/shoresta/>, Barnston et al. 1999). This suggests that these changes may represent a lagged pulse in recruitment of species with warm-water affinities. Such a lag could have resulted from the time required for El Niño conditions to cause increased reproductive success or transport into Mission Bay, combined with the time required for subsequent growth of individuals to sufficient size to become available to capture.

The decrease in dominance measures for both marshes during 1998 was largely driven by the heavy recruitment of *G. mirabilis* beginning in the spring of 1998. The increases in percent representation and absolute abundances of an already relatively abundant species (*G. mirabilis*), lower absolute and relative abundances of the marsh numerical dominant (*F. parvipinnis*), and the appearance of 3 rarer species (see above)

combined to create more evenness in the marsh-creek ichthyofaunal assemblages. This pattern may have been reversing towards the end of 1998 when numbers of *G. mirabilis* decreased and the numbers of *F. parvipinnis* increased in each marsh (Table V-1).

Created Marsh Creek Utilization

Results from this study support the emerging view that fish readily utilize channels in southern California created marshes, as noted in Zedler (1997), and in that respect are similar to the results of Williams and Zedler (in press). Nonetheless, functional equivalence of a created marsh requires more than simply abundance or diversity similarities. In this study, the different size-structure of the dominant species, *F. parvipinnis* and *G. mirabilis*, probably resulted from a lack of low-order creeks and other shallow-water habitat in the created marsh. Shallow areas provide critical nursery habitat for juvenile *F. parvipinnis*, and small individuals have been shown to prefer shallow water (Desmond 1996, Fritz 1975, Horn and Allen 1985). This is consistent with the idea that predation risk increases for most fish species with increasing water depth and decreasing fish size (e.g., Ruiz et al. 1993, Kneib 1987, Sogard 1994). Shallow-water habitat in the CPMS during low tides was mostly limited to three small areas (Figure V-1C). Lack of shallow-water habitat could confer lower survivorship on eggs laid in the CPMS, if the larvae and juveniles are not able to move to the appropriate habitat in the NWP. The size-structure differences between the CPMS and NWP creeks further implies different trophic support function

for piscivores in the two systems. For piscivorous fish, there may be a tradeoff between foraging in the NWP versus foraging in the CPMS. Piscivorous fish generally select for smaller individuals (Sogard 1997, Juanes 1994), and may therefore forage more effectively in the NWP, which is dominated by smaller prey fishes. However, the lack of shallow-water refuge habitat in the CPMS may make those prey fishes encountered in that system more easily captured.

Differences in *F. parvipinnis* and *G. mirabilis* could also generate differences in the predation pressure they exert on infauna and epifauna in the created and natural marsh creeks. A congener of *F. parvipinnis*, *F. heteroclitus*, has been shown to have strong direct and indirect effects on the abundance and distribution of numerous invertebrate species and, moreover, these effects change with fish body size (Kneib 1988; Kneib and Stiven 1982; Gerking 1994; Vince et al. 1976). It is likely that *F. parvipinnis*, which attains high densities in both the CPMS and the NWP, also affects prey populations, and that the smaller fish of the NWP are likely to select different prey than do the larger CPMS fish. The vast majority of teleost fishes, including *F. parvipinnis*, go through at least one major dietary shift through their ontogeny. (Gerking 1994, Allen 1980, Hartney and Tumyan 1998). *Gillichthys mirabilis* is known to play a critical trophic role in estuarine environments, both as predator and prey, and undergoes changes in diet and habitat during ontogeny (Horn 1980), and therefore may also differ in its effects on prey populations between the two systems.

Stable isotope analyses revealed considerable variation in $\delta^{13}\text{C}$ values among individuals of the same species (*F. parvipinnis*), something not noted in previous

studies of wetland fishes of southern California (Kwak and Zedler 1997). This variation could result from different habitat or feeding histories among individuals, or from differences in individual assimilation or fractionation of isotopes. The ^{13}C enrichment noted in *F. parvipinnis* from the created marsh occurred across all consumers measured in the CPMS, including infauna and epifauna, as well as among their microalgal food sources (Figure V-5 A,B)(Levin et al. 1999). That these differences in ^{13}C enrichment occurred at all trophic levels suggests that they arose at least in part at the level of the primary producers through differential fractionation, differences in dissolved inorganic carbon (DIC) pools, or different producer species. Further, there was seasonality to the heavy carbon signal in the CPMS; the $\delta^{13}\text{C}$ values shifted in the direction of the natural marsh (lighter) in samples taken in the spring of 1997, but were significantly heavier in the preceding and following fall samples (Figure V-5 A,B). Because there was no overall trend towards an increase in isotopic similarity among marshes between 1996 and 1997, it is difficult to predict whether the created marsh organisms will achieve stable isotopic values similar to those of the natural system.

Kwak and Zedler (1997) interpreted *S. foliosa* as being the primary producer largely supporting *F. parvipinnis* in Tijuana Estuary (TJE), located approximately 21 km south of Mission Bay. The mean isotope values for *S. foliosa* from TJE were $\delta^{13}\text{C} = -15.1 \pm 0.2$, $\delta^{15}\text{N} = 10.3 \pm 0.3$, and $\delta^{34}\text{S} = 11.5 \pm 0.5$ (Kwak and Zedler 1997), compared to mean values for *S. foliosa* from Mission Bay of $\delta^{13}\text{C} = -14.3$ (no replicates), $\delta^{15}\text{N} = 3.6 \pm 0.1$, and $\delta^{34}\text{S} = -0.9 \pm 0.6$ (Levin et al. unpublished data). The

mean isotope values for *F. parvipinnis* from the tidal creeks of TJE were $\delta^{13}\text{C} = -17$, $\delta^{15}\text{N} = 17$, and $\delta^{34}\text{S} = 9.2$ (Kwak and Zedler 1997), compared to mean values for *F. parvipinnis* from the NWP in Mission Bay of $\delta^{13}\text{C} = -16.0 \pm 0.4$, $\delta^{15}\text{N} = 8.7 \pm 0.4$, and $\delta^{34}\text{S} = 11.7 \pm 0.4$ (Fig. 5, Levin et al. unpublished data). Sulfur isotope values in consumers closely track those of their food (Peterson et al. 1986), thus the sulfur data from the NWP strongly suggest that *S. foliosa* is not a primary food source for *F. parvipinnis* in the Mission Bay study site.

Site Fidelity

The MRR data suggest that while there was some exchange of *F. parvipinnis* between the two systems, overall fidelity was quite high (Table V-2). Exchange between systems was likely asymmetrical, with *F. parvipinnis* marked in the created marsh being less likely to be recaptured in the opposite system than vice-versa (Table V-2). This suggests the possibility that there was a source-sink relationship between the two systems, at least during the summer months of 1996 and 1997. This could involve heavier recruitment of small fishes into the natural marsh creeks (Figure V-3), and subsequently greater migration of individuals into the created marsh. The lower abundances of *F. parvipinnis* in the CPMS supports the possibility of differential size-specific mortality between sites. Site fidelity for feeding is further supported by the distinct $\delta^{13}\text{C}$ signatures of *F. parvipinnis* from the CPMS and NWP (Figure V-5 A,B). The shift towards lighter carbon values for *F. parvipinnis* in the Spring 1997 CPMS samples (Figure V-5 A,B) could alternatively be interpreted to suggest that there was a

seasonal component to marsh fidelity, possibly driven by spawning movements.

However, the infauna (Figure V-5 A,B) and many of the primary producers, including benthic microalgae and macroalgae (Levin et al. 1999), exhibited a similar seasonal shift in $\delta^{13}\text{C}$.

Greater CPMS fidelity could have resulted from the greater area of deep-water habitat in the CPMS, allowing resident fishes to avoid leaving the marsh at low tide. In the NWP, large natant fauna had few deep-water refugia during spring low tides. At low tide fishes presumably must either have (a) shared these few refugia, (b) migrated across the mudflat and into the subtidal seagrass beds, or (c) migrated into the CPMS. This latter behavior is not supported by $\delta^{13}\text{C}$ data, as daily migrations (and feeding) in the CPMS should have homogenized the isotopic signatures. Similarity of $\delta^{13}\text{C}$ values of *F. parvipinnis* collected in the nearby subtidal seagrass habitat to those of fish in the NWP supports the idea that individuals may have been migrating between the subtidal seagrass and the NWP, but not between the CPMS and the seagrass (Figure V-5 A,B). Differences in daily migration patterns could lead to different sources and intensity of *F. parvipinnis* mortality between the two marshes.

Conclusions

No evidence was seen for succession among the ichthyofaunal species examined in the created marsh. However, large interannual variability was observed in the species composition of both the natural and created marshes in this study, likely

associated with large-scale climatic events. This implies the need for long-term monitoring of these dynamic systems, to assess equivalence under a wide range of natural variation in environmental settings.

Ichthyofaunal species dominance and richness measures were not significantly different between the two systems. Resident marsh fish abundances were significantly lower in the created marsh relative to the natural marsh. After 2.5 yrs the ichthyofaunal assemblage of the created channel met the assessment criteria established for another mitigation marsh in southern California, the Sweetwater Marsh Wildlife Refuge, that of having 75% of the abundance and diversity of the natural system for 2 consecutive years (Zedler 1996b).

The size-structure of the numerical dominants, *F. parvipinnis* and *G. mirabilis*, was skewed towards larger size classes in the created marsh. The differences in size-structure between the created and natural systems suggest that marsh and creek geomorphology may affect both the suitability of habitat for small fishes and fish migration patterns, and so should be considered when designing marsh restoration projects.

Fundulus parvipinnis exhibits considerable habitat fidelity in both marshes, as evidenced by MRR and stable isotope data. The observed fidelity and distinctive isotopic signatures imply that this created marsh may function in relative isolation with respect to resident wetland ichthyofauna.

Table V-1. The mean number of individuals (total and by species) and mean number of species per trap from created (Crown Point Mitigation Site (CPMS)) and natural (Northern Wildlife Preserve (NWP)) salt-marsh creeks in Mission Bay, San Diego. Numbers in parentheses are ± 1 standard error.

Date	Marsh	<i>Acanthogobius flavimanus</i>	<i>Atherinops affinis</i>	<i>Pundulus parvipinnis</i>	<i>Gillichthys mirabilis</i>	<i>Ctenogobius sagittula</i>	<i>Mugil cephalus</i>	Total Individuals	No. species
12/31/95	CPMS	0	0	1.33 (± 0.88)	0	0	0	1.33 (± 0.88)	1.00 (± 0.00)
	NWP	0	0.33 (± 0.33)	9.00 (± 7.51)	0.67 (± 0.67)	0	0	10.00 (± 7.55)	1.67 (± 0.33)
	CPMS	0	0	2.25 (± 1.44)	0	0	0.67 (± 0.29)	2.25 (± 1.44)	1.00 (± 0.00)
1/23/96	NWP	0	1.25 (± 0.95)	7.25 (± 2.53)	0.75 (± 0.48)	0	0	9.25 (± 2.17)	2.00 (± 0.00)
	CPMS	0	1.50 (± 0.96)	35.25 (± 7.97)	10.00 (± 2.86)	0	0	46.75 (± 9.46)	2.50 (± 0.29)
	NWP	0	0.25 (± 0.25)	21.50 (± 6.03)	3.50 (± 2.18)	0	0	25.25 (± 8.07)	1.75 (± 0.48)
6/4/96	CPMS	0	0.33 (± 0.41)	31.00 (± 12.97)	3.50 (± 2.07)	0	0	32.25 (± 6.30)	2.25 (± 0.25)
	NWP	0	0	32.25 (± 12.60)	1.50 (± 1.19)	0	0	33.75 (± 13.17)	1.50 (± 0.29)
	CPMS	0	0.33 (± 0.33)	24.67 (± 5.36)	6.67 (± 3.76)	0	0	31.67 (± 8.76)	2.00 (± 0.00)
6/29/96	NWP	0	1.33 (± 0.88)	26.33 (± 9.87)	1.67 (± 0.67)	0	0	29.33 (± 9.84)	2.67 (± 0.33)
	CPMS	0	0	25.67 (± 13.44)	4.00 (± 3.16)	0	0	44.50 (± 10.18)	1.50 (± 0.29)
	NWP	0	0	35.25 (± 8.40)	1.50 (± 0.87)	0	0	36.75 (± 8.77)	1.75 (± 0.25)
8/1/96	CPMS	0	0	37.50 (± 16.54)	6.25 (± 2.66)	0	0	43.75 (± 15.26)	1.75 (± 0.25)
	NWP	0	0	194.50 (± 86.73)	0.50 (± 0.50)	0	0	195.00 (± 86.45)	1.25 (± 0.25)
	CPMS	0	0.25 (± 0.25)	15.00 (± 9.08)	2.00 (± 1.08)	0	0	17.25 (± 10.04)	2.00 (± 0.41)
8/6/96	NWP	0	0	30.00 (± 9.12)	0.50 (± 0.50)	0	0	30.50 (± 9.37)	1.25 (± 0.25)
	CPMS	0	0	10.00 (± 2.86)	1.75 (± 1.03)	0	0	11.75 (± 3.12)	1.50 (± 0.29)
	NWP	0	0.75 (± 0.25)	50.50 (± 22.48)	0	0	0	51.25 (± 22.48)	1.50 (± 0.29)
9/4/96	CPMS	0	0	62.25 (± 36.09)	4.25 (± 2.21)	0	0	66.50 (± 33.97)	1.75 (± 0.25)
	NWP	0	0.25 (± 0.25)	203.00 (± 38.51)	0	0	0	203.25 (± 38.30)	1.25 (± 0.25)
	CPMS	0	0	35.50 (± 26.51)	0.75 (± 0.75)	0	0	36.25 (± 26.38)	1.25 (± 0.25)
10/3/96	NWP	0	0	82.33 (± 32.56)	0	0	0	82.33 (± 32.56)	1.00 (± 0.00)
	CPMS	0	0.25 (± 0.25)	76.25 (± 19.18)	0	0	0	76.50 (± 19.27)	1.25 (± 0.25)
	NWP	0	0	109.50 (± 19.12)	0.50 (± 0.29)	0	0	110.00 (± 19.27)	1.40 (± 0.29)
10/5/96	CPMS	0	2.25 (± 1.60)	36.50 (± 11.53)	3.50 (± 1.55)	0	0	42.25 (± 10.27)	2.75 (± 0.25)
	NWP	0	0	25.50 (± 11.15)	3.75 (± 3.12)	0	0	39.00 (± 6.93)	1.25 (± 0.48)
	CPMS	0	0.25 (± 0.25)	36.75 (± 16.02)	1.75 (± 1.11)	0	0	38.75 (± 15.17)	2.00 (± 0.41)
6/21/97	NWP	0	0.5 (± 0.29)	30.75 (± 12.17)	1.50 (± 0.29)	0	0	32.75 (± 12.17)	2.50 (± 0.29)
	CPMS	0	0	99.75 (± 20.25)	2.25 (± 2.25)	0	0	102.00 (± 39.07)	1.25 (± 0.25)
	NWP	0	0	166.00 (± 79.94)	0	0	0	166.00 (± 79.94)	1.00 (± 0.00)

Table V-1. Continued

4/19/98	CPMS	1.00 (±1.00)	0	33.25 (±13.76)	3.25 (±3.25)	0	1.00 (±0.41)	38.50 (±13.94)	2.25 (±0.25)
	NWP	0.5 (±0.5)	0	26.00 (±19.55)	7.75 (±3.36)	0	0	34.25 (±19.91)	2.00 (±0.41)
5/20/98	CPMS	0	1.25 (±0.48)	16.75 (±7.51)	7.75 (±3.36)	0	0.25 (±0.25)	26.00 (±10.35)	3.00 (±0.41)
	NWP	0	0	26.25 (±5.17)	30.50 (±8.39)	0	0	56.75 (±6.41)	2.00 (±0.00)
6/2/98	CPMS	0.25 (±0.25)	0.25 (±0.25)	6.25 (±2.02)	13.75 (±2.78)	0	1.25 (±0.63)	21.75 (±5.02)	3.25 (±0.48)
	NWP	0.75 (±0.75)	0	28.50 (±6.06)	42.50 (±13.12)	0	0.25 (±0.25)	72.00 (±15.55)	2.50 (±0.29)
6/19/98	CPMS	0.50 (±0.50)	0	7.50 (±2.60)	11.25 (±5.65)	0	2 (±0.82)	21.25 (±7.76)	3.00 (±0.41)
	NWP	0.75 (±0.48)	0	14.75 (±3.17)	54.00 (±17.59)	0	0.75 (±0.75)	70.25 (±19.88)	2.75 (±0.25)
6/27/98	CPMS	0	0	5.25 (±3.35)	10.50 (±1.76)	0	0.25 (±0.25)	16.00 (±4.32)	2.00 (±0.00)
	NWP	0	0	7.00 (±5.40)	37.50 (±15.31)	0	0.50 (±0.50)	45.00 (±19.74)	2.00 (±0.41)
7/1/2/98	CPMS	0.25 (±0.25)	0	13.25 (±4.46)	12.50 (±1.50)	0.25 (±0.25)	0.25 (±0.25)	26.50 (±6.14)	2.75 (±0.48)
	NWP	0.25 (±0.25)	0	6.75 (±1.75)	41.00 (±6.07)	0.50 (±0.50)	0.75 (±0.75)	49.25 (±6.87)	2.75 (±0.25)
7/16/98	CPMS	1.00 (±1.00)	0	9.25 (±2.56)	9.00 (±3.54)	0	2 (±1.15)	21.25 (±6.18)	2.50 (±0.65)
	NWP	0.5 (±0.29)	0	18.00 (±7.99)	48.75 (±6.69)	0	0.25 (±0.25)	67.50 (±6.74)	2.75 (±0.48)
7/23/98	CPMS	0.50 (±0.29)	0	0.75 (±0.25)	6.75 (±1.31)	0.25 (±0.25)	0	8.25 (±1.80)	2.50 (±0.50)
	NWP	0	0	14.50 (±1.06)	11.50 (±1.06)	0	0	26.00 (±0.00)	2.00 (±0.00)
7/31/98	CPMS	0	0	8.25 (±5.79)	6.00 (±1.63)	0	0	14.25 (±4.42)	1.75 (±0.25)
	NWP	0.25 (±0.25)	0	21.50 (±13.18)	22.25 (±4.61)	0.50 (±0.50)	0.50 (±0.50)	45.00 (±9.57)	2.50 (±0.29)
8/6/98	CPMS	0.75 (±0.48)	0	5.75 (±2.95)	6.50 (±2.40)	0.25 (±0.25)	0	13.25 (±3.07)	2.50 (±0.65)
	NWP	1.00 (±0.71)	0	9.25 (±1.80)	16.25 (±7.08)	2.00 (±0.41)	0.50 (±0.50)	29.00 (±6.60)	3.75 (±0.48)
8/11/98	CPMS	0	0	12.75 (±10.47)	5.25 (±0.85)	0	0.5 (±0.29)	18.50 (±9.91)	2.25 (±0.48)
	NWP	0.33 (±0.29)	0	69.67 (±16.30)	9.00 (±2.00)	1.33 (±0.58)	1.67 (±0.76)	82.00 (±18.38)	2.75 (±1.11)
8/20/98	CPMS	0	0.25 (±0.25)	6.25 (±4.01)	7.25 (±1.93)	0.25 (±0.25)	0	14.00 (±4.02)	2.25 (±0.25)
	NWP	0.25 (±0.25)	0	27.50 (±6.17)	9.00 (±3.19)	2.75 (±1.6)	1 (±0.71)	40.50 (±3.97)	3.25 (±0.48)
8/28/98	CPMS	0	0	7.50 (±2.40)	4.00 (±1.63)	0.25 (±0.25)	0	11.75 (±2.02)	2.00 (±0.41)
	NWP	0	0	85.50 (±2.02)	3.75 (±1.65)	0.5 (±0.29)	0	89.75 (±40.68)	2.25 (±0.48)
9/3/98	CPMS	0	0	6.75 (±4.15)	6.75 (±0.25)	0	0	13.50 (±4.29)	1.50 (±0.29)
	NWP	0	0	12.50 (±3.59)	4.00 (±0.41)	0	0.25 (±0.25)	16.75 (±3.90)	2.25 (±0.25)
9/12/98	CPMS	0.5 (±0.5)	0	13.75 (±7.60)	5.75 (±3.20)	0	0	20.00 (±8.13)	2.25 (±0.25)
	NWP	0	0	53.00 (±26.44)	10.25 (±8.61)	0	0	63.25 (±23.86)	1.75 (±0.25)
9/15/98	CPMS	0.5 (±0.5)	0.25 (±0.25)	23.50 (±7.56)	4.25 (±0.75)	0	0	28.50 (±7.33)	2.50 (±0.29)
	NWP	0	0	13.75 (±4.35)	7.25 (±1.80)	0	0	21.00 (±3.67)	2.00 (±0.00)
9/21/98	CPMS	0	0.25 (±0.25)	14.25 (±8.38)	3.75 (±3.42)	0	0	18.25 (±8.49)	1.75 (±0.25)
	NWP	0.25 (±0.25)	0	38.67 (±17.90)	5.00 (±1.46)	0	0	44.00 (±15.32)	2.33 (±0.29)

Table V-2. Mark-release-recapture data for *Fundulus parvipinnis* from created (Crown Point Mitigation Site (CPMS)) and natural (Northern Wildlife Preserve (NWP)) salt-marsh creeks in Mission Bay, San Diego. First number is number of tagged individuals recovered, bold indicates percent of marked fish recovered.

Date	Marsh	Marked	Recovered in marsh in which tagged	Recovered in opposite marsh
June 2 1996	CPMS	137	33 (24.1)	0 (0.0)
	NWP	84	14 (16.7)	3 (3.6)
June 29 1996	CPMS	71	25 (35.2)	0 (0.0)
	NWP	76	7 (9.2)	6 (7.9)
August 1 1996	CPMS	148	10 (6.8)	4 (2.7)
	NWP	775	71 (9.2)	4 (0.5)
September 4 1996	CPMS	40	2 (5.0)	0 (0.0)
	NWP	202	25 (12.4)	4 (2.0)
October 3 1996	CPMS	141	7 (5.0)	0 (0.0)
	NWP	247	17 (6.9)	9 (3.6)
June 19 1997	CPMS	146	23 (15.8)	0 (0.0)
	NWP	102	6 (5.9)	0 (0.0)
Total	CPMS	683	100 (14.6)	4 (0.6)
	NWP	1486	140 (9.4)	26 (1.7)

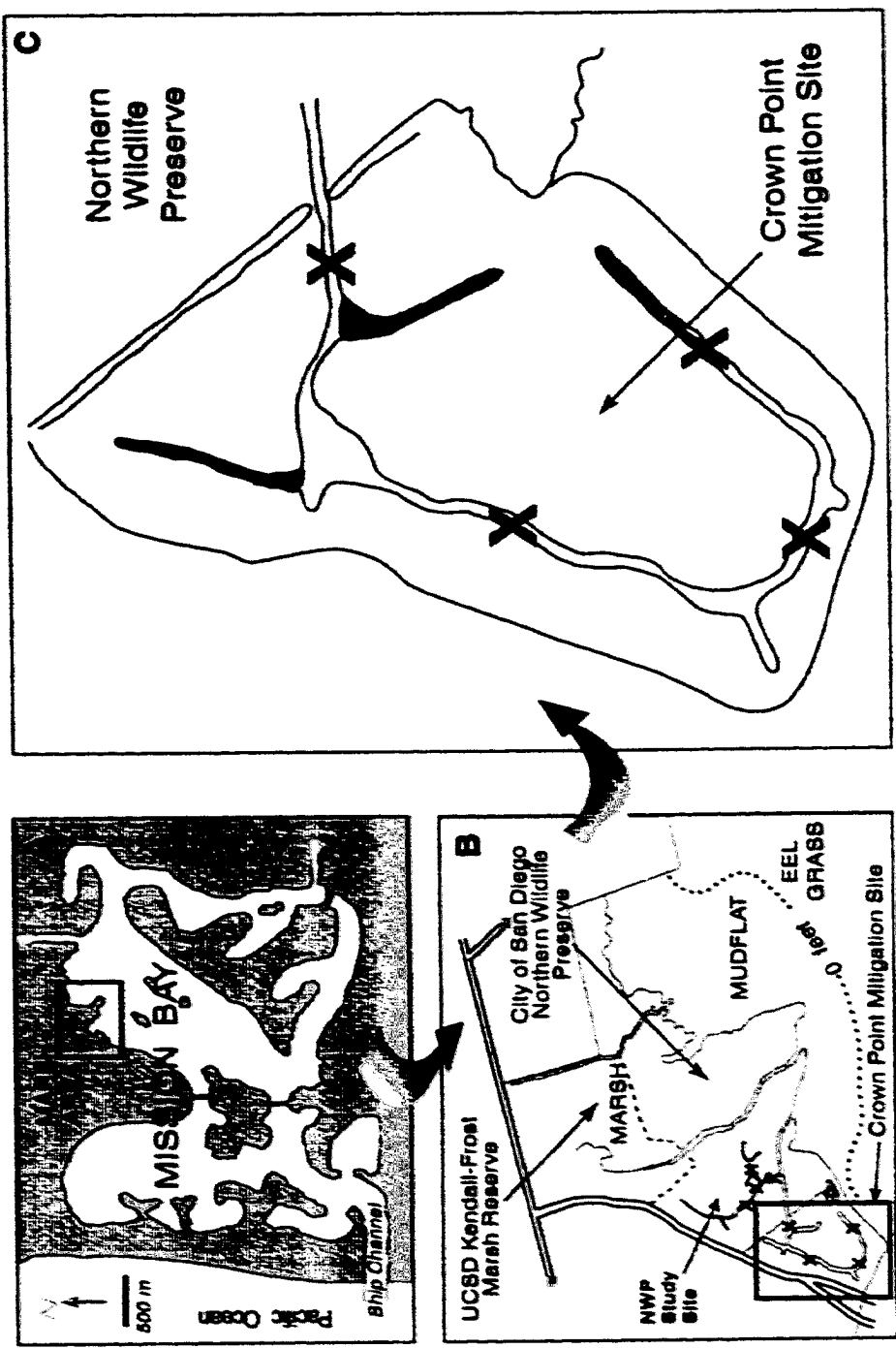


Figure V.1. Map of study site, showing (A) Mission Bay, San Diego, CA (B) the Crown Point Mitigation Site (CPMS) and Northern Wildlife Preserve (NWP), and (C) the CPMS study site. Xs mark the locations of minnow traps. Shaded area in (C) indicates shallow subtidal habitat.

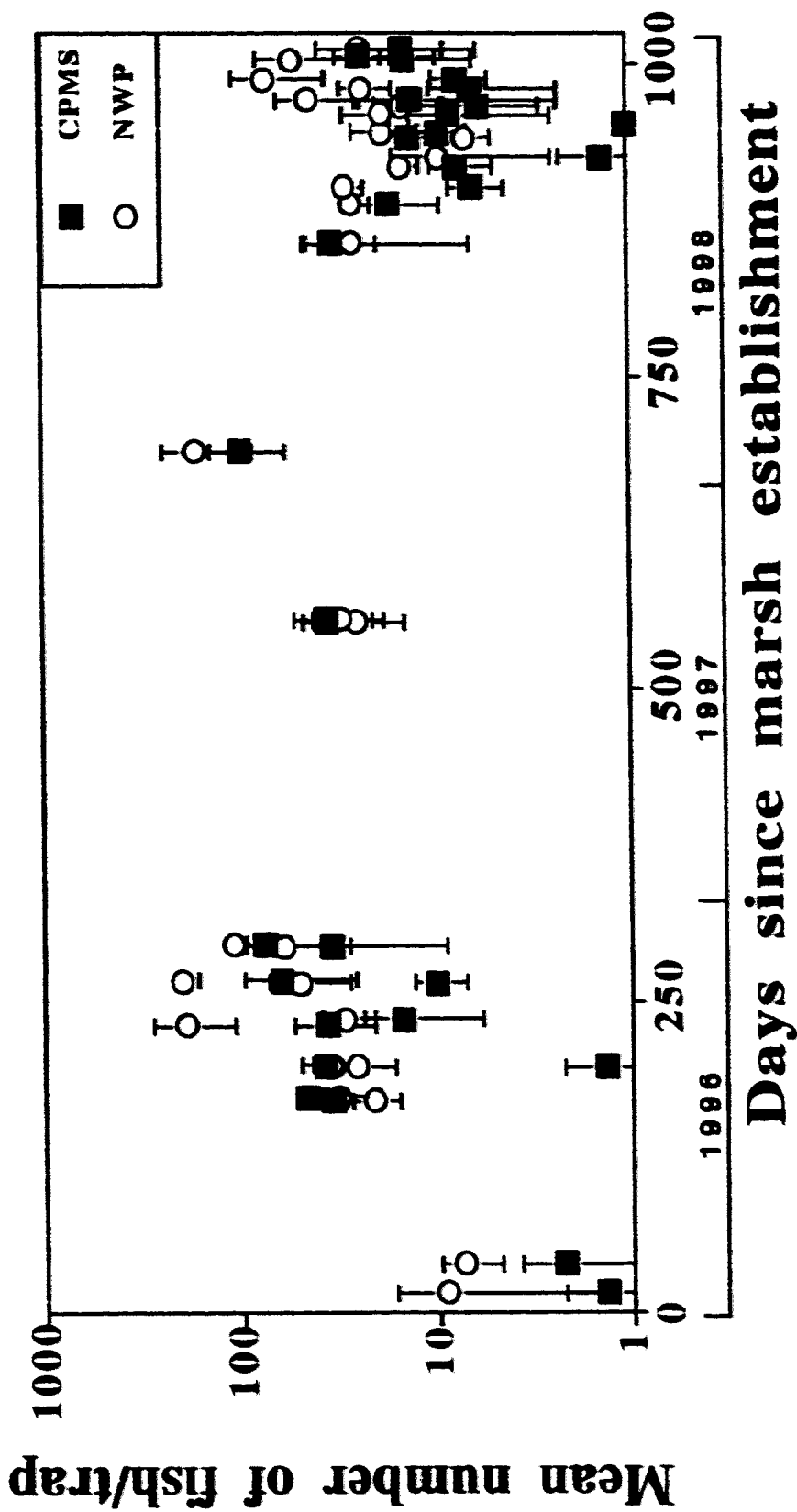


Figure V-2. Mean number of fish per trap at each sampling time for the Crown Point Mitigation Site (CPMS) and Northern Wildlife Preserve (NWP). Error bars are ± 1 standard error.

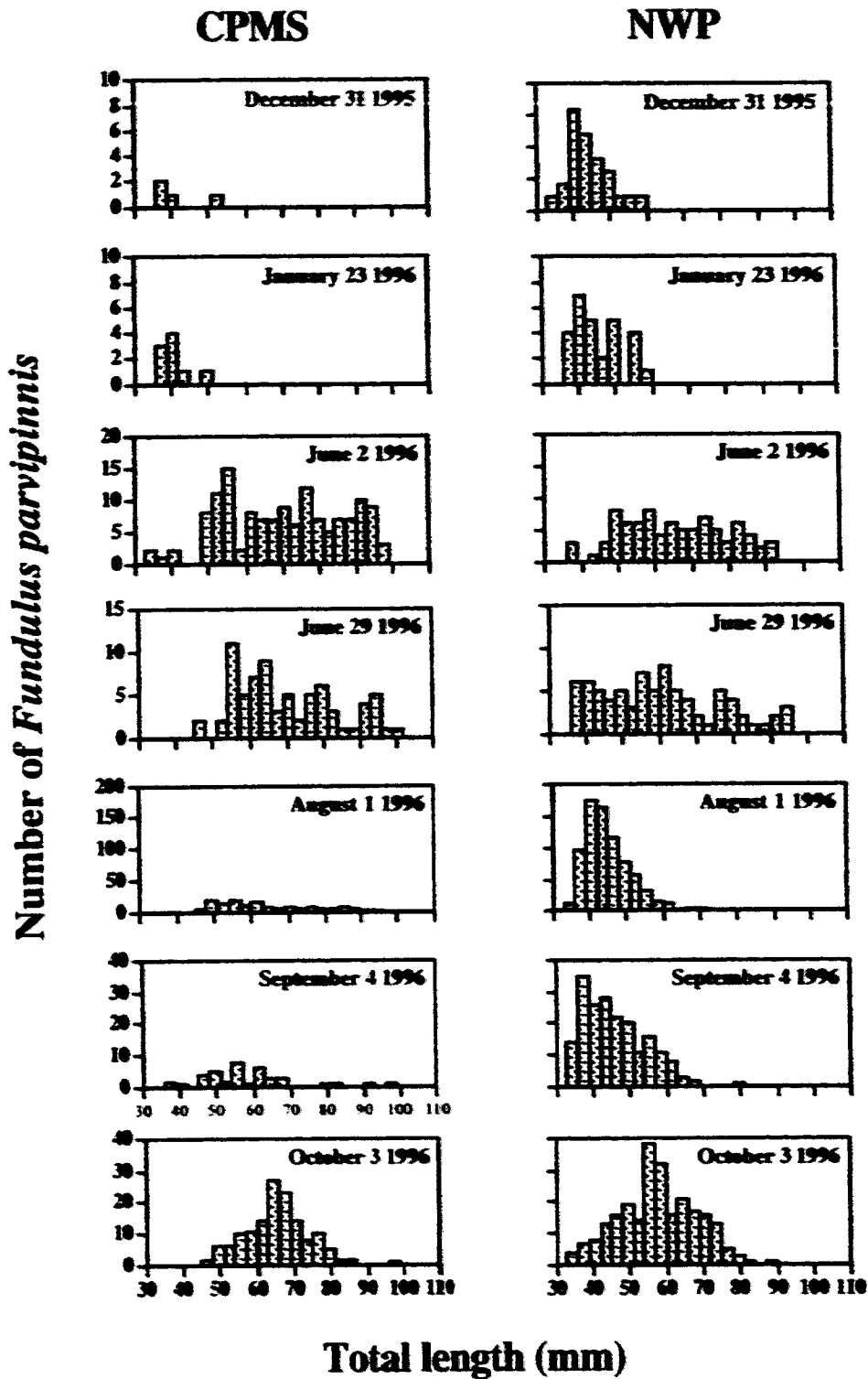


Figure V-3A. Length-frequency histograms for *Fundulus parvipinnis* from the Crown Point Mitigation Site (CPMS) and the Northern Wildlife Preserve (NWP) creeks (1995 and 1996 samples). Note that scales on Y axes differ across times.

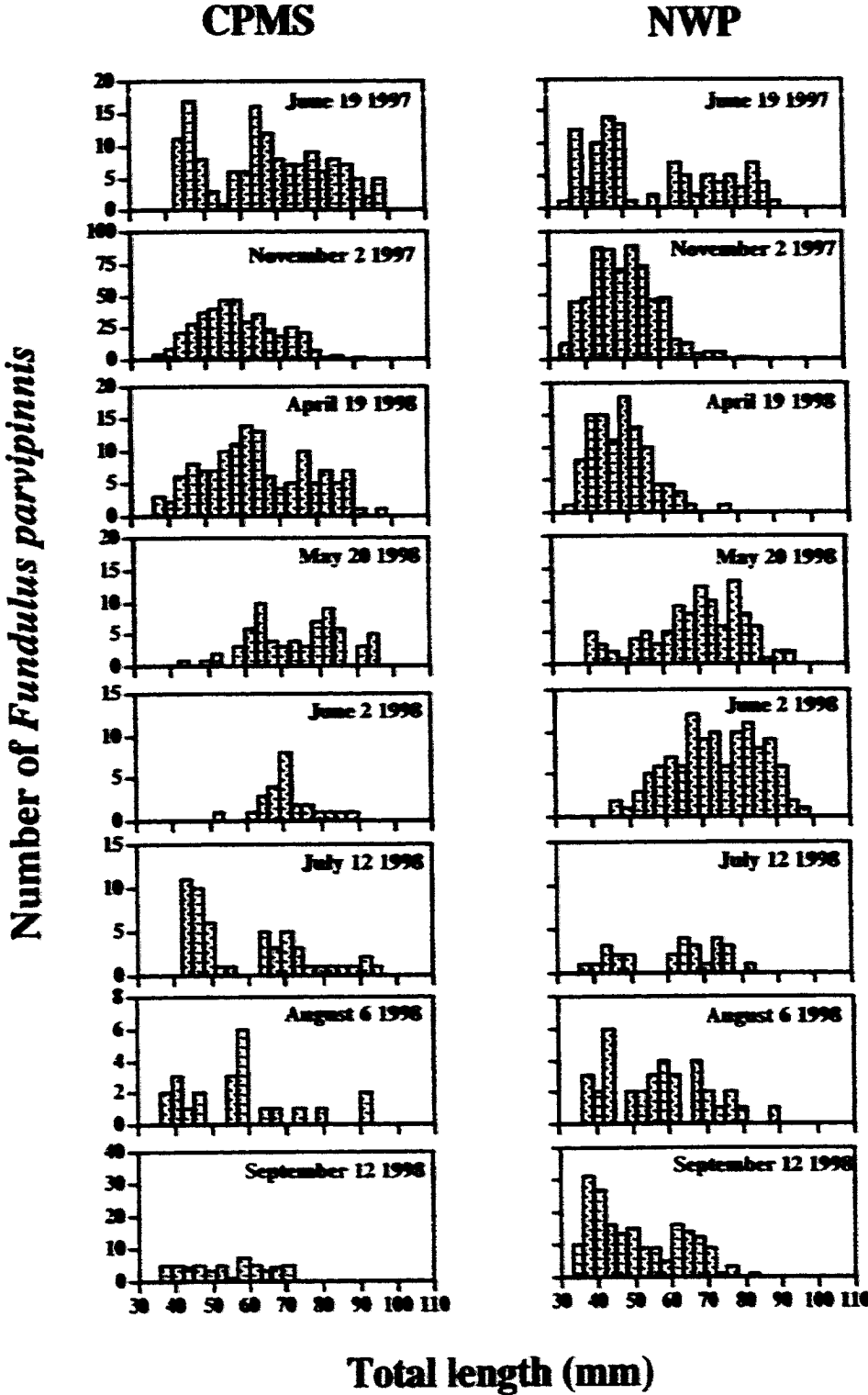


Figure V-3B. Length-frequency histograms for *Fundulus parvipinnis* from the Crown Point Mitigation Site (CPMS) and the Northern Wildlife Preserve (NWP) creeks (1997 and 1998 samples). Note that scales on Y axes differ across times.

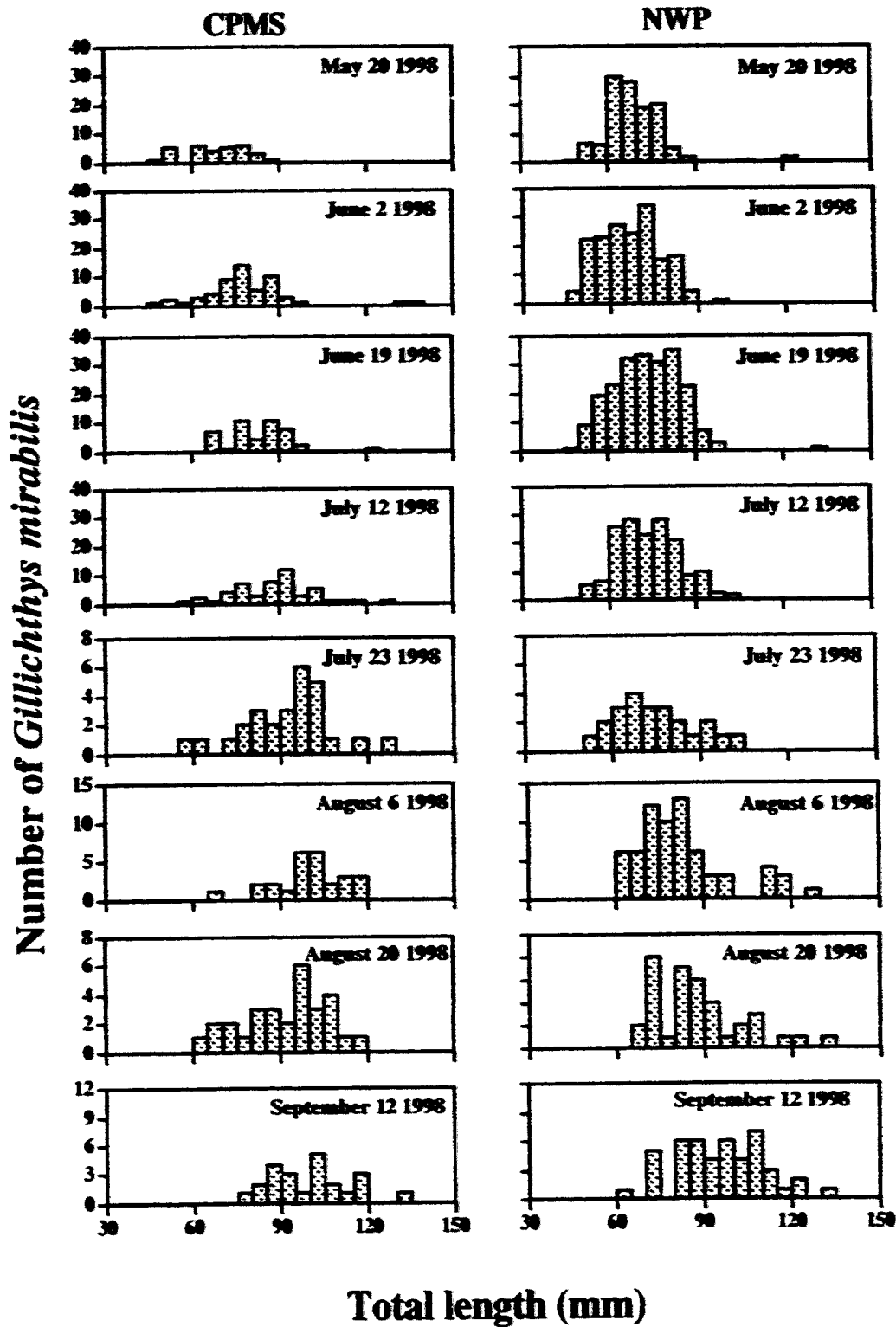


Figure V-4. Length-frequency histograms for *Gillichthys mirabilis* from the Crown Point Mitigation Site (CPMS) and the Northern Wildlife Preserve (NWP) creeks. Note that scales on Y axes differ across times.

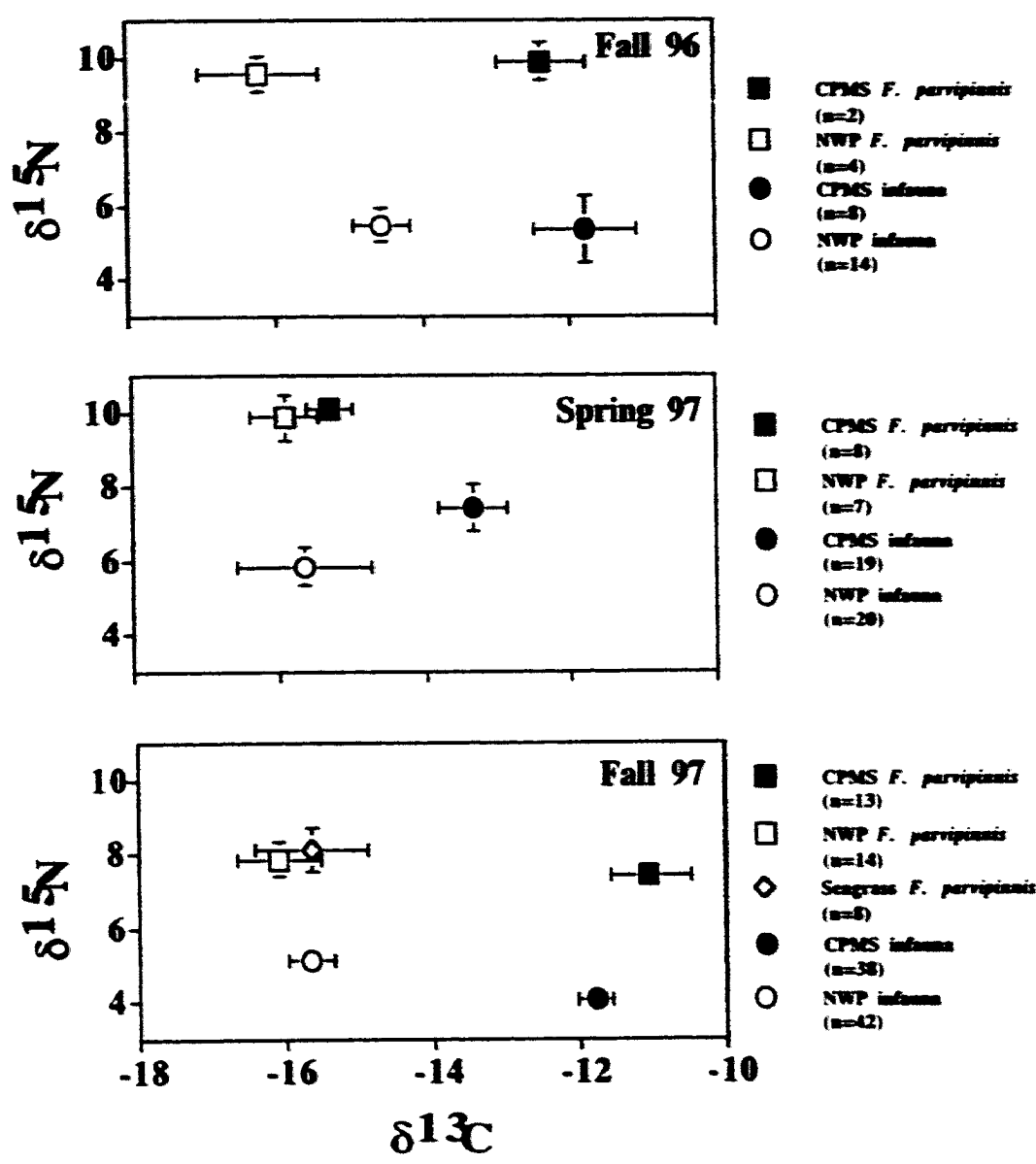


Figure V-5. Biplots of $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ for *Fundulus parvipinnis* and infauna from the Crown Point Mitigation Site (CPMS) and the Northern Wildlife Preserve (NWP) on three sampling dates, and from the subtidal seagrass beds for Fall 1997. Infauna data are from Levin et al (1999). Error bars are ± 1 standard error.

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CHAPTER VI

Conclusions

Establishing a rigorous and predictive theory of how spatial heterogeneity influences ecological systems requires empirical research on "carefully selected model systems that occupy key positions in environmental matrices" (Wiens et al 1993). This work shows that wetland resident fishes are an ideal model for such empirical research, because they are important members of a mosaic ecosystem, and because they influence habitat linkages on a number of spatial and temporal scales. Further, research on California's wetlands provides ecological data needed to preserve these ecosystems, which are among the world's most threatened habitats.

The tidal salt marsh in Mission Bay is comprised of a mosaic of habitats, each having distinct environmental characteristics defined by water temperature, depth, salinity, and the relative distance or distribution of each habitat with respect to other marsh landscape components (Chapter IV). This habitat heterogeneity exists across a range of spatial scales, and provides microenvironments which promote differential utilization by marsh fauna. Further, these microenvironments change through time, leading to temporal heterogeneity in landscape elements across time scales from tidal through interannual (Chapter IV).

The heterogeneity of habitats described here for southern California marshes affects habitat function for resident fishes. These fishes have distinct habitat

preferences and utilization patterns that change over both short (tidal) time scales and longer (interannual) time scales.

Fishes use microhabitats in size- and taxon-specific manners. Large numbers of gobies migrated into the intertidal at high tide, and returned to the unvegetated flat at low tide (Chapter IV). Small juvenile (J1) *F. parvipinnis* exhibited strong preferences for intertidal pool habitats, in particular at low tide, with larger juveniles (J2) selecting deeper creek habitats (Chapter IV). Adult *F. parvipinnis* migrated with the tide between seagrass and vegetated marsh (Chapter IV, V; Figure VI-2). In addition to these tidal shifts, habitat-use patterns were modified by diel stages, lunar periodicity, and interannual changes (Chapters III, IV, V).

In Mission Bay there were differences in *F. parvipinnis* habitat-utilization patterns related to diel stage, with nocturnally-feeding fish consuming a higher percentage of detritus relative to diurnally feeding fish. This increase in detrital consumption, which appears related to a lower prey capture efficiency in darkness, has potential effects on growth and behavior of *F. parvipinnis* (Chapter III).

Fundulus parvipinnis in Mission Bay also makes use of intertidal habitats for spawning, with a semilunar periodicity corresponding to summer (nighttime) spring high tides (Chapter V). It is unknown how widespread this pattern of spawning is for *F. parvipinnis*, or how plastic this behavioral trait is. This behavior presumably allows eggs to incubate in pools or in vegetated marsh high in the intertidal. These habitats provide favorable environmental conditions, and more protection from aquatic predators (including conspecific adults, [Fritz 1975]). Laying eggs in this habitat also

affords close proximity to favored shallow habitats in the intertidal for post-hatch larvae.

Mark-recapture and stable isotope studies document that *Fundulus parvipinnis* adults exhibit site fidelity, with relatively few individuals migrating between adjacent created and natural marshes (Chapter II). The extensive subtidal habitat within the created marsh creek may eliminate the need for low-tide refuge outside the created marsh. Alternatively, the geomorphology of the connection between these two systems may reduce *F. parvipinnis* exchange, as the two marshes are connected by only a single channel at all but the highest spring tides. In either case, these observations support the idea that there may be some homing behavior in *F. parvipinnis* (Fritz 1975), and suggest that this may be related to microhabitat (subtidal refuge) distribution.

Trade-offs of opposing fitness functions (e.g., refuge versus foraging value) may ultimately be driving these patterns of utilization. Evidence for such tradeoffs exist as among-habitat differences in foraging value and putative size-specific differences in predation risk (Chapter IV).

External forcing can also alter wetland ecoscapes, and thus affect use patterns. El Niño-associated changes in temperature and sea-level, global warming, algal blooms induced by non-point source pollution, exotic species introductions, or other anthropogenic and natural alterations to the marsh can potentially change the relative coverage or suitability of habitats. Further, biological alterations induced by external forcing may have important consequences for the fitness value of habitats. For

example, the appearance in shallow creeks and pools of an aggressive piscivorous crab during El Niño events (*Callinectes arcuatus*, Chapter II), may mitigate the refuge value of that habitat, and thereby induce a change in behavior and linkage patterns for *F. parvipinnis*.

Small resident fishes influence populations of invertebrates via predation (Kelso 1979, Kneib 1986), and are themselves important prey species (Kneib 1986, Haaker 1975). *Fundulus parvipinnis* is ubiquitous and abundant in southern California wetlands, and is therefore undoubtedly important in these roles (Figure VI-1)(Chapter II). Thus, changes in the size structure or abundance of fishes in salt marshes, due to changes in habitat availability or landscape pattern, will affect other marsh biota, through top-down effects on the prey of resident fish, bottom-up effects on their predators, or both. This in turn forms functional linkages between habitats, where the condition, size, and proximity of one habitat will affect biota in linked habitats through the activities of small wetland fishes.

These linkages scale with the temporal and spatial scales of utilization of wetland fishes. For example, habitat linkages between the vegetated marsh, pools, creeks, unvegetated flat, and subtidal seagrass beds differ with the life-stage of *F. parvipinnis*. Small juveniles, larger juveniles, and adults form linkages between different habitats and at different scales (Chapter III, Figure VI-2). At yet another set of spatial and temporal scales, these habitats are therefore linked through the ontogeny of *F. parvipinnis* (Chapter III, Figure VI-2). Further, the subtidal seagrass beds are likely linked to the marsh plain through the formation of wrack mats. Wrack mats are

precursors to high intertidal pools, thus they link seagrass beds to other habitats by provision of habitat for small juveniles *F. parvipinnis* (Chapter III, Figure VI-2).

In Mission Bay, CA, the resident fish community rapidly colonized a created wetland which was adjacent to a natural marsh. This indicates that over these short distances, dispersal does not limit ichthyofaunal recovery, even for species with quite limited dispersal, such as *F. parvipinnis* (Bernardi and Talley in press). While this lack of recruitment-limitation has not been explicitly tested in created marshes, results from other marsh construction projects, such as the Connector Marsh in the Sweetwater Marsh National Wildlife Refuge, Chula Vista, CA (Zedler 1996) support the suggestion that intra-bay colonization of created marsh habitats can be quite rapid for the dominant resident species. Establishment of marsh ichthyofaunal communities with equivalent size-structures and composition of rarer species, however, may depend upon natural configurations of microhabitats within the created wetland. This was demonstrated in the created marsh in Mission Bay, where the population of *F. parvipinnis* was skewed towards larger sizes due to lack of small creek and pool habitats (Chapter V).

An important lesson for management and conservation is that marsh creation and preservation efforts must account for spatially- and temporally-explicit patterns of habitat utilization. Targeting marsh habitats too broadly for creation or preservation, such as "subtidal area" and "low marsh" (e.g., U. S. Army Corps of Engineers 1990) may well miss important microhabitats and affect wetland function. Incorporation of habitat heterogeneity into planning, (e.g., pools and rivulets in marsh plain habitats)

will promote more natural function and linkages. To my knowledge, no mitigation project in California has included mandated construction of intertidal pool habitats, despite this having been shown to be important habitat for Atlantic coast *Fundulus heteroclitus* (e.g., Kneib 1997). Such issues may be critical for a proposed marsh creation effort in a developed area ("Campland") in Mission Bay, CA. This site has great potential to support a natural wetland fish community, because the proposed location exists adjacent to a ready source of colonizers. Providing habitat for southern California wetland resident fishes in created marshes will require a mechanistic understanding of the role of landscape elements in the life history of these fishes.

In sum, the scale of linkages may be expected to be related to the spatial and temporal scale of habitat heterogeneity, which is intimately related to the scale of the individual organism. Levin and Pacala (1997) argue that species have evolved such that each "experiences the environment at its own set of spatial and temporal scales". I would add that those scales are themselves dynamic, changing both through time and across populations.

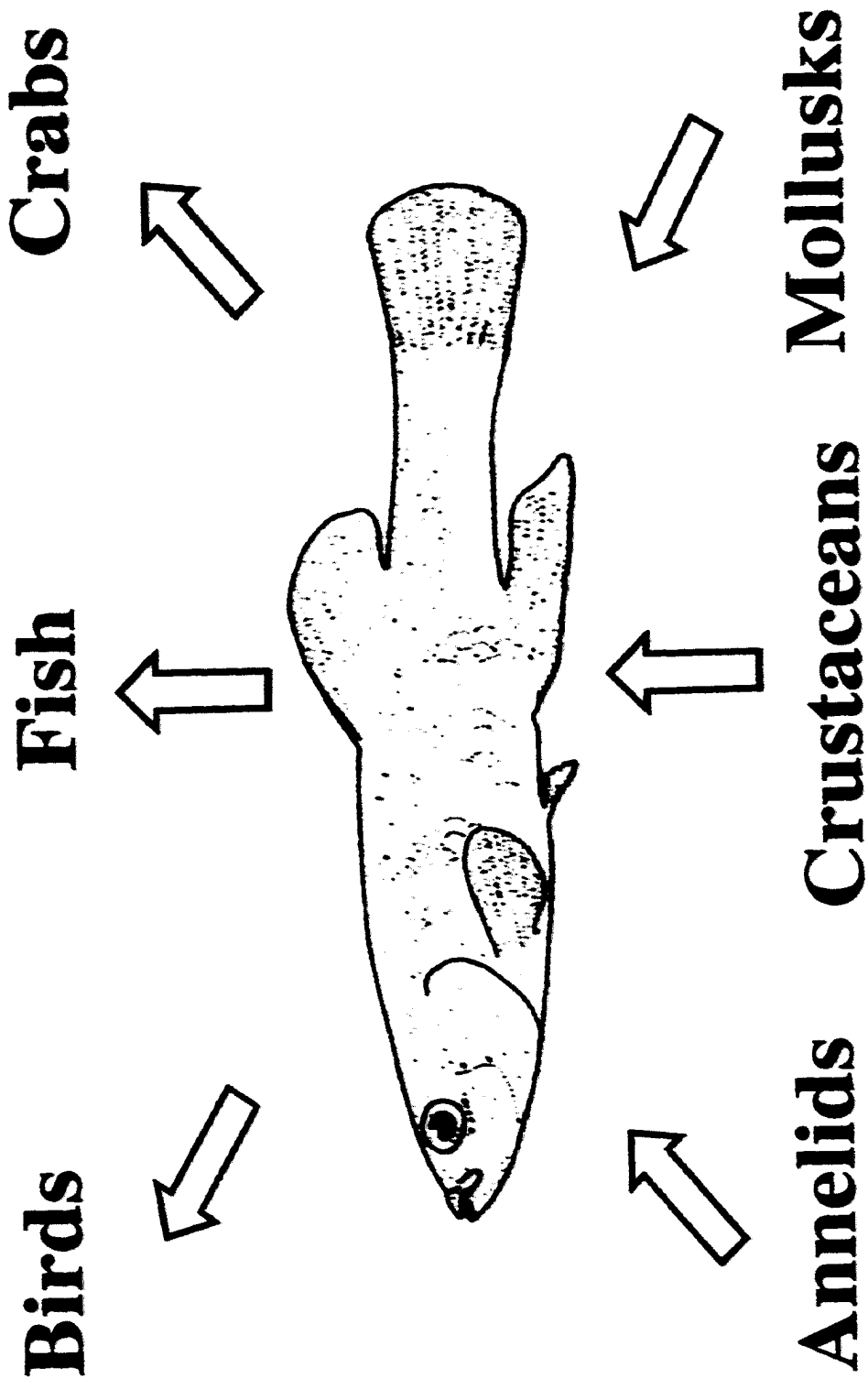


Figure V1-1. A conceptual diagram illustrating the central role of *Fundulus parvipinnis* in salt marsh trophic dynamics. Arrows indicate direction of energy flow (i.e. point from prey to predator).

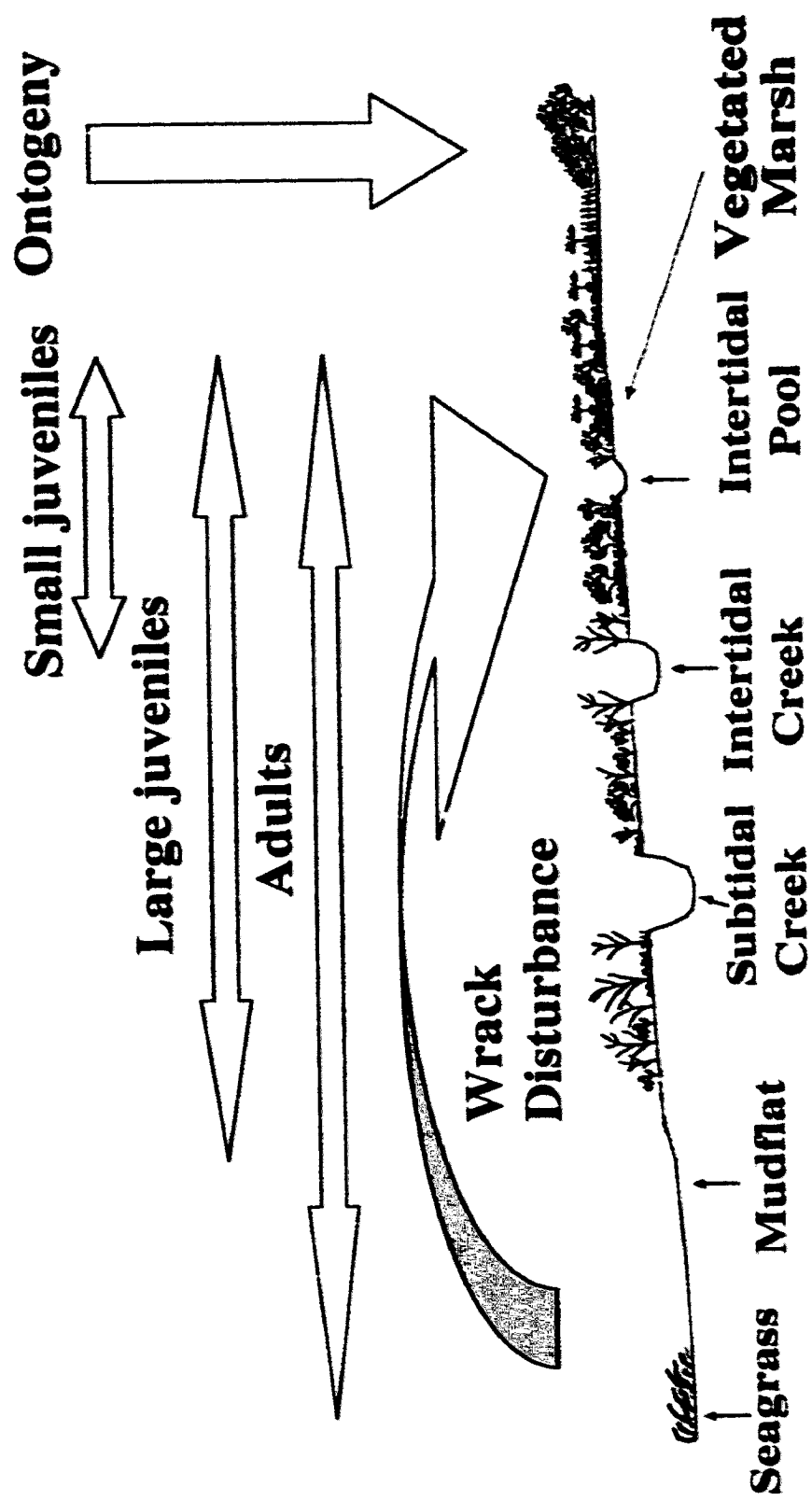


Figure VI-2. Conceptual model of habitat linkages mediated by *Fundulus parvipinnis* and seagrass in southern California salt marshes. See text for details.

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APPENDIX I

The fishes of the lagoon and vasos of Ojo de Liebre, Baja California, Mexico

Introduction

Exportadora de Sal, S.A. (ESSA) has proposed building a salt-production facility in San Ignacio Lagoon, B.C.S. This proposed plant would be located in a portion of the Vizcaino Biosphere Reserve. Due to the environmentally sensitive nature of the location of the proposed plant, an Environmental Impact Assessment (EIA) has been commissioned to evaluate a number of possible environmental effects. This report details one part of that assessment: the effect that the pumping of seawater from the lagoon into the evaporative ponds (or "vasos") may have on the lagoon's ichthyofaunal communities.

During salt production, water is pumped from the lagoon at extremely high rates. This could entrain fish larvae, juveniles, or food resources into the vasos, and remove them from the local lagoon environment. Ultimately, salt production could lead to a reduction in fish populations within the lagoon, with potential top-down and bottom-up effects throughout the ecosystem.

As part of the effort to assess this potential impact on San Ignacio Lagoon, the ichthyofaunal communities surrounding an existing salt production facility in Ojo de

Liebre, (at Guerrero Negro, B.C.S.) were examined (Figure A-1). The Guerrero Negro salt plant has been in operation for more than 40 years, so it is reasonable to expect that negative impacts of a pumping station on the fishes might be evident there. To address this question, I examined: (1) the abundances and community composition of fishes within the concentrating ponds ("vasos", Ocho Bombas and Salitrales), and (2) within the natural lagoon (Ojo de Liebre), the relationship between distance from the pumping stations and ichthyofaunal densities. Sampling was performed in the winter of 1998-1999.

Materials and Methods

Sampling was conducted on November 7-10 1998 and January 7-8 1999 in the initial collecting ponds (Ocho Bombas and Salitrales) at the Guerrero Negro salt facility and in the Ojo de Liebre lagoon outside of these ponds (Table A-1, Figure A-1). A large bag seine (13.3 m x 2.1 m, 3 mm mesh) was used for the majority of the sampling in the following manner: two persons walked into the water carrying the seine until reaching a distance 20 meters from shore, or until the water depth was greater than 2 meters (whichever came first). One person then remained in place, while the other unfurled the net such that it was parallel to the shoreline. The net and the operators remained in place for 5 minutes to minimize disturbance to fishes. The net was then pulled rapidly towards the shore, with the aid of bridles being pulled by workers standing on shore. Fish were enumerated, identified, and re-released on site.

when possible. Fishes not identifiable in the field were preserved in buffered formalin for identification in the lab. Reported water depth for each sample refers to the mean depth at the beginning of the seine haul.

Additional non-quantitative sampling was undertaken using baited Gee® minnow traps (22 cm diameter at the center, tapering to 19 cm at each end, made of ca. 0.6 cm wire mesh with ca. 2 cm openings) and cast-nets. These data were not used in the statistical analyses or estimates of density, due to unequal sampling effort between sites and lack of replication. However, the minnow trap catches were added to the species list and total count of individuals.

Temperature and salinity measurements were made using a YSI 30 electronic temperature/salinity/conductivity meter (YSI Incorporated, Yellow Springs, Ohio, USA). Measurements were made within 10 centimeters of the surface in an undisturbed portion of the water prior to sampling, and are given in practical salinity units (psu). In some cases measurements were not taken, due to equipment difficulties.

Fish species diversity in the vasos and the lagoon was compared using rarefaction curves (Hurlbert 1971). Calculations were performed using the freeware program SpeciesRichness on a Macintosh computer (program available via anonymous ftp from ftp://roswell.sdsu.edu/pub/download/Species_richness.sea.hqx). Samples from seines which were determined in the field to be unacceptable (e.g., when the net leadline did not maintain contact with the sediment) were excluded from the rarefaction analysis. *Sphoeroides lispus* and *Sphoeroides annulatus* were lumped.

since on the initial sampling dates the two species were identified only to genus.

Proportional data were arcsin transformed prior to running statistical tests.

Densities were calculated using the area swept by the seine and the number of fish captured per sweep. Statistical comparisons of densities were performed on data that were log-transformed, to satisfy the assumptions of homogeneity of variance and to normalize the data. Because both sampling dates were in the same season (winter), and there was no apparent difference in density or composition between sampling dates, therefore data from all dates were lumped for statistical analysis.

Overall fish densities were calculated as follows. The vasos were divided into regions based on the locations of the samples. By using each sample (or set of samples) at a given location to estimate the density for that region of the vaso, and then multiplying that density by the total area that region represented, an overall abundance of fishes per vaso could be estimated. Adjusted average densities were then calculated by dividing the total area of the vaso by the estimated number of fish per vaso.

Results

Physical parameters

The mean depth of water sampled was not significantly different between the vasos and the lagoon: depth in both cases was close to 1.0 meter ($F_{1,20}=1.7$, $p>0.2$) (Figure A-2). Salinity values were higher in the vasos (mean of 44.3 psu) than in the

lagoon (mean of 39.3 psu, Figure A-2) ($F_{1,14}=25.4$, $p<0.001$), and there was a significant positive relationship within the vasos between distance from the pumps and salinity ($r^2=0.35$, $p<0.04$)(Figure A-3). The mean water temperature was higher in the vasos (20.5 °C) than in the lagoon (17.0 °C, Figure A-2) ($F_{1,16}=15.6$, $p<0.01$), and a positive relationship exists within the vasos between temperature and distance ($r^2=0.65$, $p<0.001$, Figure A-3).

Biological parameters

In total, 14,815 individual fishes belonging to 19 species were captured during this study (Table A-2). Of these, 14,532 fishes (18 species) were taken from the vasos, and 283 fishes (14 species) from the Ojo de Liebre lagoon. Diversity (as measured by rarefaction analysis) was higher inside the lagoon than in the vasos (Figure A-4).

Fish density was higher in samples from inside the vasos (mean of 5.8 fish/m²) than samples taken in the lagoon (mean of 0.09 fish/m²) ($F_{1,21}=28.6$, $p<0.001$, Figure A-5). Inside the vasos, there was a significant negative relationship between fish density and distance from the pumps ($r^2=0.35$, $p=0.03$). The estimated mean density of fish within the vasos is 2.1 ind/m². A significantly higher proportion of the individuals captured in the lagoon were edible or "food fish" species (as determined by Emmett et al 1991, Goodson 1988, and D. Talley, personal observation: 35.4% $\pm$ 9.2), compared to those captured from within the vasos (0.04% $\pm$ 0.03; $F_{1,21}=23.6$, $p<0.001$; Table A-2). In the lagoon, there was no significant relationship between distance from the vaso and density of fishes. However, when the only small creek ("low-order creek", *sensu*

Horton 1945) seined in this study is omitted from the analysis, the relationship is positive and significant ($r^2=0.67$, $p<0.01$, Figure A-6).

This study estimates that there are approximately 59.7 million fishes in both vasos (30.3 million in Ocho Bombas, and 29.4 million in Salitrales). Using the intermediate value for lagoon area that is less than 3 meters in depth given by Pérez-España et al. (1998: 401.8 million m^2), and dividing that area by 2/3 to estimate depth sampled by gear in this study (less than 2 meters in depth), the overall ichthyofaunal abundance in Ojo de Liebre during this sampling is estimated to be 24.1 million fishes.

Species composition differed between samples taken from the vasos and the lagoon. The vasos were dominated by small, non-commercial species, including *Atherinops affinis* (topsmelt: 57.1%), *Fundulus parvipinnis* (California killifish: 22.1%), and *Quietula y-cauda* (shadow goby: 12.5%; Figure A-7). Samples from the lagoon also had high proportions of *A. affinis* (18.3%) and *F. parvipinnis* (14.2%), but was dominated by *Hypsopsetta guttulata* (diamond turbot: 34.7%; Figure A-7), which is an important food fish.

Discussion

Abundances and density

This survey indicates that while the vasos at Ojo de Liebre represent only 10% of the lagoonal area less than 2 meters deep, they have twice as many fishes as the lagoon itself. Additionally, the estimated mean density in the vasos was much higher

than that in the lagoon (2.1 ind/m² versus 0.09 ind/m²). These numbers must be taken as a very rough estimate, since only a few areas of the lagoon were sampled, and different sampling gears are highly selective for different species (e.g., Rozas and Minello 1997). Furthermore, the densities and abundances reported here are likely underestimates, both in the lagoon and in the vasos, as numerous large, fast-moving fishes were observed escaping our gear, and benthic and burrowing fishes are often missed by seines (Zedler 1996). Nonetheless, the high densities of fishes residing within the vasos suggests that there is at least some input of fish or fish larvae from the lagoon through the pumps. It is not unprecedented to find fishes being pulled into intake pipes from industrial sources. The San Onofre Nuclear Generating Station (SONGS) in the United States has intake pipes which pump just over 52 m³ of seawater per second (compared with 30 m³ per second peak flow into the vasos), and thousands of fish per day are estimated to go through pipes at SONGS (Love et al., 1989).

The number of fishes living in the vasos cannot be simply translated into a loss term for the lagoon unless there is no reproduction inside the vasos, and the lagoon populations are recruitment limited. Since these conditions are either not met or unknown, interpretation of these results becomes more difficult.

At least one of the dominant species, *Fundulus parvipinnis*, appears to be able to complete its life cycle within the vaso. During the course of this sampling, *F. parvipinnis* of all size classes, juvenile through adult, were captured, and several of the adults were reproductive. While this could be argued to be the result of all size classes

being pulled in through the pumps and surviving, this could also indicate that *F. parvipinnis* is completing its life cycle within the vasos. *Fundulus parvipinnis* has been shown to survive in waters of high temperature and salinity (Valentine 1969, Fritz 1975), and its eggs hatch more rapidly in high-salinity waters (Hubbs 1965). The mean density of *F. parvipinnis* in the vasos was an order of magnitude higher (0.21 ind/m²) than in the lagoon (0.02 ind/m²). These values bracket the mean *F. parvipinnis* density of 0.11 ind/m² found in Ojo de Liebre lagoon by Pérez-España et al (1998).

There are no published data on the temperature and salinity tolerances of *Quietula y-cauda*, but it is reasonable to suspect that those populations are also reproducing within the vasos, as all size classes were captured in this sampling. It is less certain that the numerical dominant of the vasos, *Atherinops affinis*, could be reproducing within the vasos. *Atherinops affinis* is reported to mature at 2-3 years of age, at a length of 15 cm. (Emmett et al 1991), and the largest individual captured in this study was only 7.9 cm.

This evidence suggests that while there is undoubtedly some reproduction occurring within the vasos, it probably does not account for all of the fishes living there. At least some larvae, juveniles, and possibly adults are being pumped into the vasos and away from appropriate habitats in the lagoon.

Composition

The vasos had a distinct ichthyofaunal community, comprised largely of small, euryhaline species, while the lagoon fish community had a much higher proportion of

larger, food-fish species (Table A-2, Figure A-7). These differences in community composition could be due to selective impingement through the pumps, selective survival, or some combination of the two. Selective impingement would require that some species are more susceptible to being pulled into the pumps than others, due to behavior, swimming ability, or larval development mode (e.g., planktonic versus benthic).

While this is impossible to address directly with the data at hand, it has been shown that larval dispersal is at least in part dependent on behavior (e.g., Johannes 1978), and there is a wide range of sizes and presumably swimming abilities among the larvae of species captured in this study (Moser 1996), so it is probable that there is some degree of selective impingement occurring at the larval stage. Further, it has been demonstrated that there is a size and species-specific survivorship for adult fishes passing through intakes (Love et al 1989), which supports the idea that selective differential survivorship from passing through the intakes may play a role. Finally, the higher temperature and salinity within the vasos supports the proposal that fish surviving passage through the pumps may be subject to additional selective mortality. Other research on wetland fishes has shown that the major factors structuring ichthyofaunal communities were temperature and salinity tolerances (see Saiki 1997 and references therein). It is worth noting in that regard that the two most abundant fishes within the vasos were *Atherinops affinis* (mean=57% of the catch per seine) and *Fundulus parvipinnis* (mean=22% of the catch per seine). *Atherinops affinis* has been shown to tolerate salinities in excess of 80 psu, living in salt-producing ponds in

northern California (Carpelan, 1955), while *F. parvipinnis* has been shown to osmoregulate at salinities up to 70 psu (Valentine, 1969).

Although the species found within the vasos were generally not commercially valuable, they are nonetheless ecologically important. The two species representing over 79% of the catch from the vasos (*A. affinis* and *F. parvipinnis*) are eaten by birds, seals, crabs, and fishes, including commercially valuable species such as *Paralichthys californicus* and *Sebastes* spp (e.g., Haaker 1975, Emmett et al 1991, Lafferty and Morris 1996, Horn 1980, D. Talley personal observation). Small euryhaline fishes such as these have also been shown to affect infaunal and epifaunal populations, including crustaceans (e.g., Kneib 1982).

A strong dominance of *A. affinis* and *F. parvipinnis* has been recorded from Ojo de Liebre and Guerrero Negro lagoons (De La Cruz-Agüero 1996). The findings in the vasos of this study were qualitatively similar. Lack of similar sampling methodologies, temporal differences in sampling, and a lack of information about abundances in each of those specific sampling locations prevents comparison between that study and this one.

Distance/density relationship

Excluding the data point from the narrow tidal creek in the lagoon, there was a significant positive relationship between distance from the pumps and lagoon ichthyofaunal densities (Figure A-5). There are at least two possible (non-mutually exclusive) explanations for this pattern. This decrease in density could be the result of

loss of larvae, juveniles, or food resources to the pumps, leading to lowered recruitment or survival in the vicinity of the intakes to the vasos. Alternatively, the change in density could be a function of the increasing distance from the open waters of the lagoon as one moves through the wetlands towards the pumps. It is not possible to distinguish between these two alternative explanations based on the data at hand.

Summary

1. Mean water temperature was higher in the vasos (20.5 °C) than in the lagoon (17.0 °C).
2. Mean salinity was higher in the vasos (44.3 psu) than in the lagoon (39.3 psu).
3. The vasos in Ojo de Liebre had average ichthyofaunal densities of 2.1 ind/m², and an estimated total abundance of 59.7 million fish, while the lagoon had an average ichthyofaunal density of 0.09 ind/m², and an estimated total abundance of 24.1 million fishes (in waters ≤ 2 meters deep).
4. Ichthyofaunal densities within the vasos decreased with distance from the pumps.
5. Ichthyofaunal densities outside the vasos increased with distance from the pumps.
6. The ichthyofaunal community in the vasos was distinct from that of the lagoon, with a lower proportion of food fishes and a higher proportion of small, euryhaline species living in the vasos.

7. More species were captured in the vasos (18 species) than in the lagoon (14 species), yet rarefaction analysis indicates a more diverse assemblage in the natural marsh.

Table A-1. List of seine samples and summary measurements from this study. Note that not all samples were included in all statistical analyses (see Materials and Methods).

Sample ID	Date	Nearest Vaso	Location	Distance to Pumps (km)	Area Seined (m ²)	Temp (°C)	Salinity (psu)	Depth (m)	Total Fishes	Fishes/m ²	No. of Species
A	11/7/98	Ocho Bombas	Vaso	0.05	260	16.9	43.4	1	1716	6.60	5
B	11/7/98	Ocho Bombas	Vaso	10	260	21.8	48.4	0.7	69	0.27	2
C	11/8/98	Ocho Bombas	Vaso	0.1	260	19.7	43.6	1	2641	9.77	6
D	11/8/98	Ocho Bombas	Vaso	0.05	40			3	4	0.10	1
E	11/9/98	Salitrales	Vaso	0.05	260	19.2	43.5	1.5	2843	10.93	13
F	11/9/98	Salitrales	Vaso	4	260	23	46.8	0.4	317	1.22	5
G	11/9/98	Salitrales	Vaso	2	260			0.5	252	0.97	4
H	11/10/98	Salitrales	Vaso	0.05	130	20.1	43.4	0.7	141	1.08	5
I	11/10/98	Salitrales	Lagoon	0.1	260			2	5	0.02	1
J	11/10/98	Salitrales	Vaso	0.05	195	20.3	42.6	2	6258	32.10	7
K	11/10/98	Salitrales	Vaso	0.1	260			0.3	296	1.14	6
L	1/23/99	Salitrales	Lagoon	3.5	220	15.1	40.2	2	17	0.08	5
M	1/23/99	Salitrales	Lagoon	3.5	220	16.9	39.6	2	35	0.16	4
N	1/23/99	Salitrales	Lagoon	2.5	400	16.9	39.8	1.4	23	0.06	4
O	1/23/99	Salitrales	Lagoon	2	400	19.5	36	1.1	13	0.03	3
P	1/23/99	Salitrales	Lagoon	1.75	400	17.4	39.6	0.3	7	0.02	4
Q	1/23/99	Salitrales	Lagoon	1.5	400	18.9		0.8	17	0.04	5
R	1/23/99	Salitrales	Lagoon	1	160	19		1.8	64	0.40	7
S	1/24/99	Ocho Bombas	Lagoon	2	400	14.7	40	0.5	16	0.04	3
T	1/24/99	Ocho Bombas	Lagoon	2.1	400	15.4	40.1	0.5	3	0.01	2
U	1/24/99	Ocho Bombas	Lagoon	4	400	19.1	35.2	0.1	12	0.03	2
V	1/24/99	Ocho Bombas	Vaso	2	400	20.3	41	0.4	37	0.09	4
W	1/24/99	Ocho Bombas	Vaso	3	400	23.2	46.4	0.45	63	0.16	3
X	1/24/99	Ocho Bombas	Vaso	0.01	360	19		2	247	0.69	6
Y	1/24/99	Ocho Bombas	Lagoon	4	400			0.4	71	0.18	2

Table A-2. List of all species captured during the course of this study. Common names are taken from Escobar-Fernandez and Sirl (1997), Goodson (1988), and Miller and Lea (1972). Note that the total does not precisely match the total given in the results section, since some samples were not used in the analyses. Commercial status based on Emmet et al (1991), Goodson (1988), and personal observation. *Sphoeroides* spp were lumped, although individuals from both species were captured.

Species	Common Name (English)	Common Name (Spanish)	Family	Number Captured		Commercial Value?
				Vaso	Lagoon	
<i>Eucinostomus currant</i>	blackspot mojarra	mojarra tricolor	GERREIDAE	597	1	No
<i>Orthopristis reddingi</i>	bronze-striped grunt	burrito roncacho	HAEMULIDAE	0	5	No
<i>Fundulus parvipinnis</i>	California killifish	guayacán	FUNDULIDAE	622	68	No
<i>Atherinops affinis</i>	topsmelt	pejerrey grujón	ATHERINIDAE	12,343	67	No
<i>Strongylura exilis</i>	California needlefish	agujón	BELONIDAE	4	0	No
<i>Syngnathus auliscus</i>	barred pipefish	agujita	SYNGNATHIDAE	14	1	No
<i>Mugil curema</i>	white mullet	lisa blanca	MUGILIDAE	6	3	Yes
<i>Exocoetis asper</i>	sargassum blenny	blenia ocellada	LABRISOMIDAE	95	39	No
<i>Achirus mazatlanus</i>	Mexican sole	sol Mexicano, tepalcate	ACHIRIDAE	57	1	No
<i>Hypsopsetta guttulata</i>	diamond turbot	platija diamante	PLEURONECTIDAE	12	63	Yes
<i>Sphoeroides hispidus</i>	?	?	TETRAODONTIDAE			No
<i>Sphoeroides annulatus</i>	bullseye pufferfish	botete	TETRAODONTIDAE	118	16	No
<i>Oligoplites saurus</i>	yellowtail leatherjacket	zapatero siletecueros	CARANGIDAE	10	0	No
<i>Opisthonema sp.</i>	herring	machuelo	CLUPEIDAE	2	0	No
<i>Cynoscion parvipinnis</i>	shortfin corvina	corvina azul	SCIAENIDAE	3	0	Yes
<i>Quectula y-cauda</i>	shadow goby	gobio	GOBIIDAE	625	16	No
<i>Hyporhamphus rosae</i>	California halfbeak	pajarito, media agujón	HEMIRHAMPHIDAE	239	1	No
<i>Chaetodipterus zonatus</i>	Pacific spadefish	chambo	EPHIPPIDAE	1	0	No
<i>Paralichthys californicus</i>	California halibut	lenguado de California	PARALICHTHYIDAE	1	3	Yes
Total				14,749	284	



Figure A-1. Map of the study site, showing the evaporative ponds ("vasos") and lagoon at Ojo de Liebre in Baja California, Mexico. Inset shows location of study site in relation to the Baja California peninsula. Modified from a map by E.S.S.A.

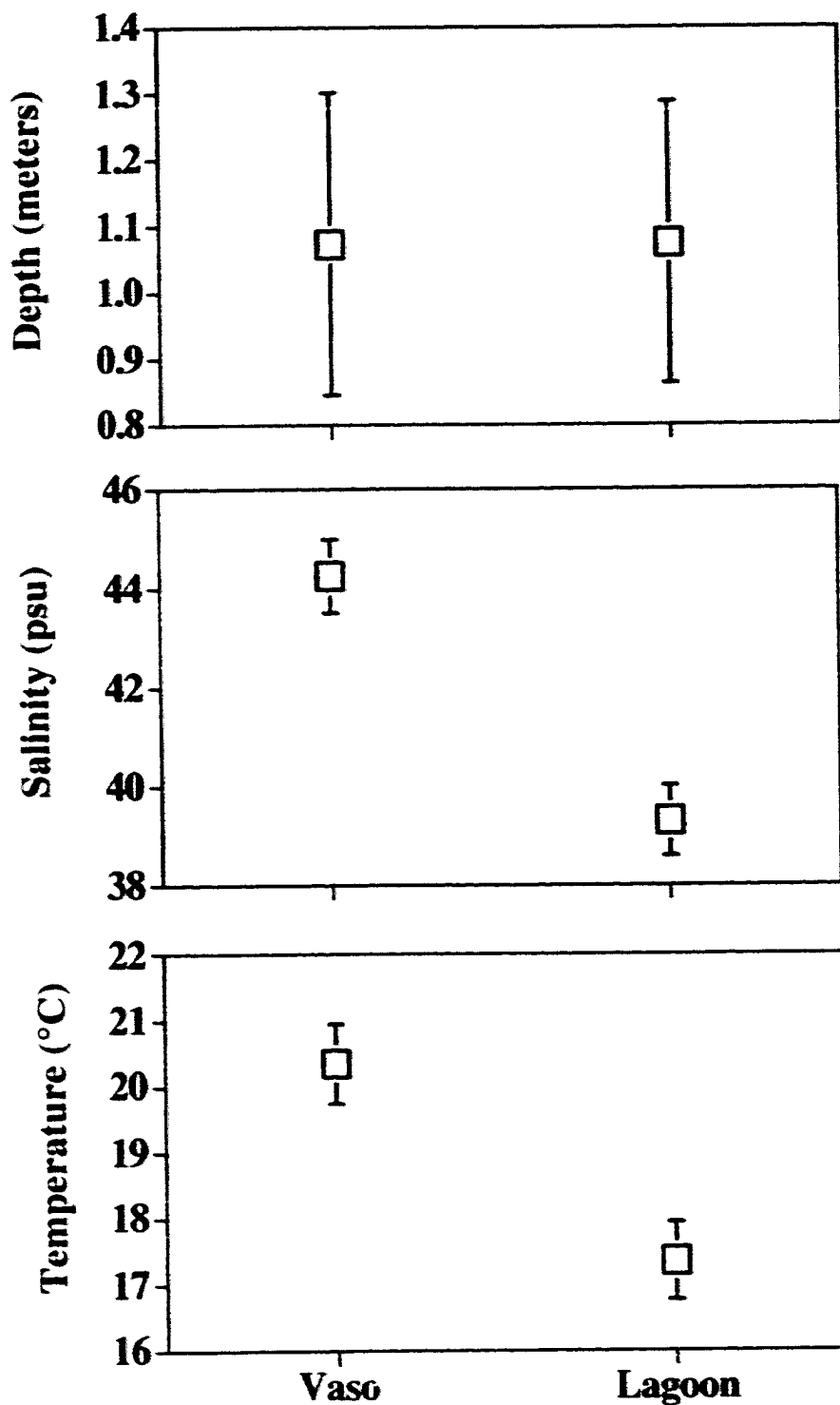


Figure A-2. Mean water depth, salinity, and temperature for samples from within the vasos and the lagoon at Ojo de Liebre. Error bars are ± 1 standard error.

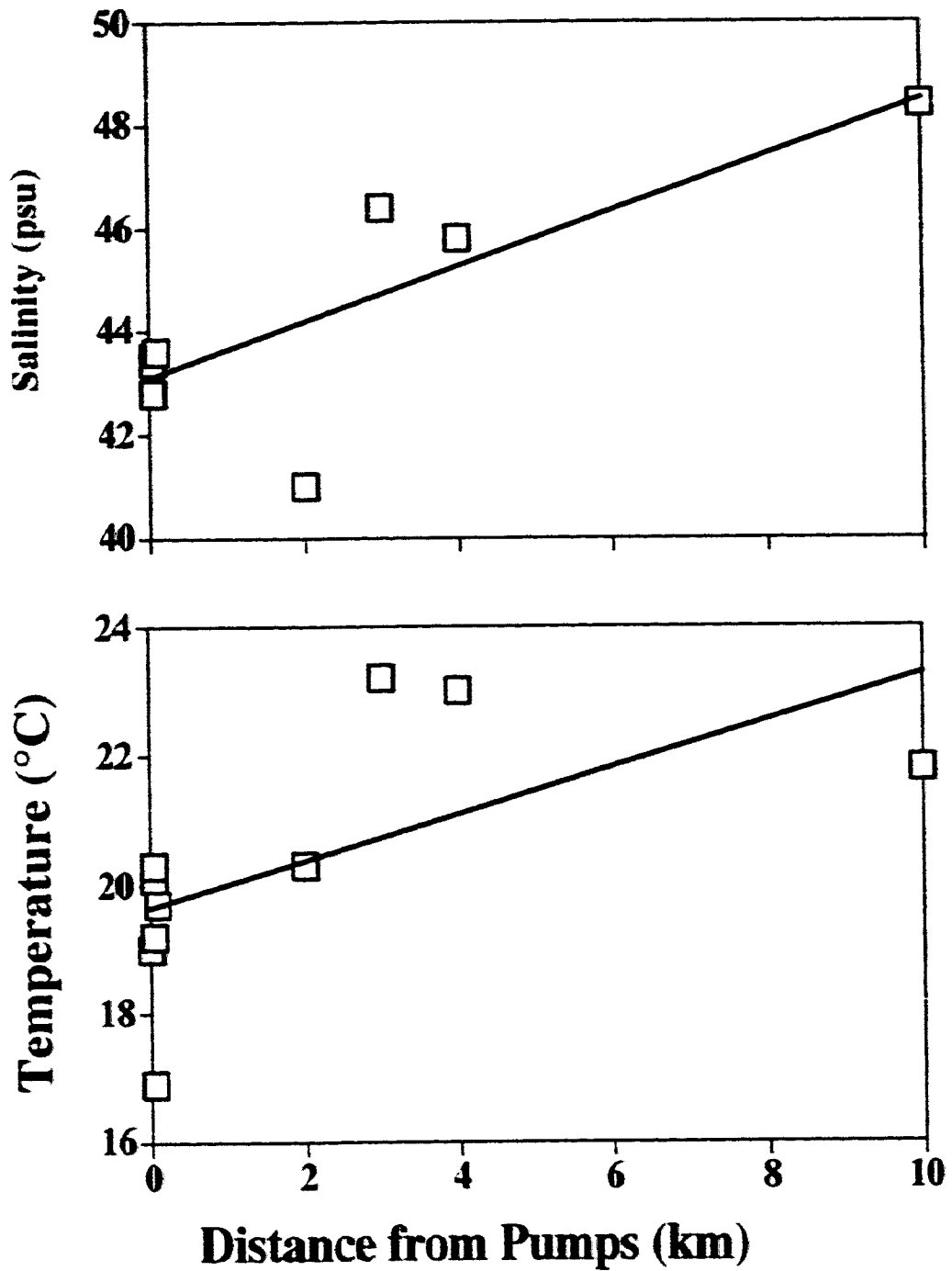


Figure A-3. Relationship between distance from pumps inside the vasos and temperature and salinity.

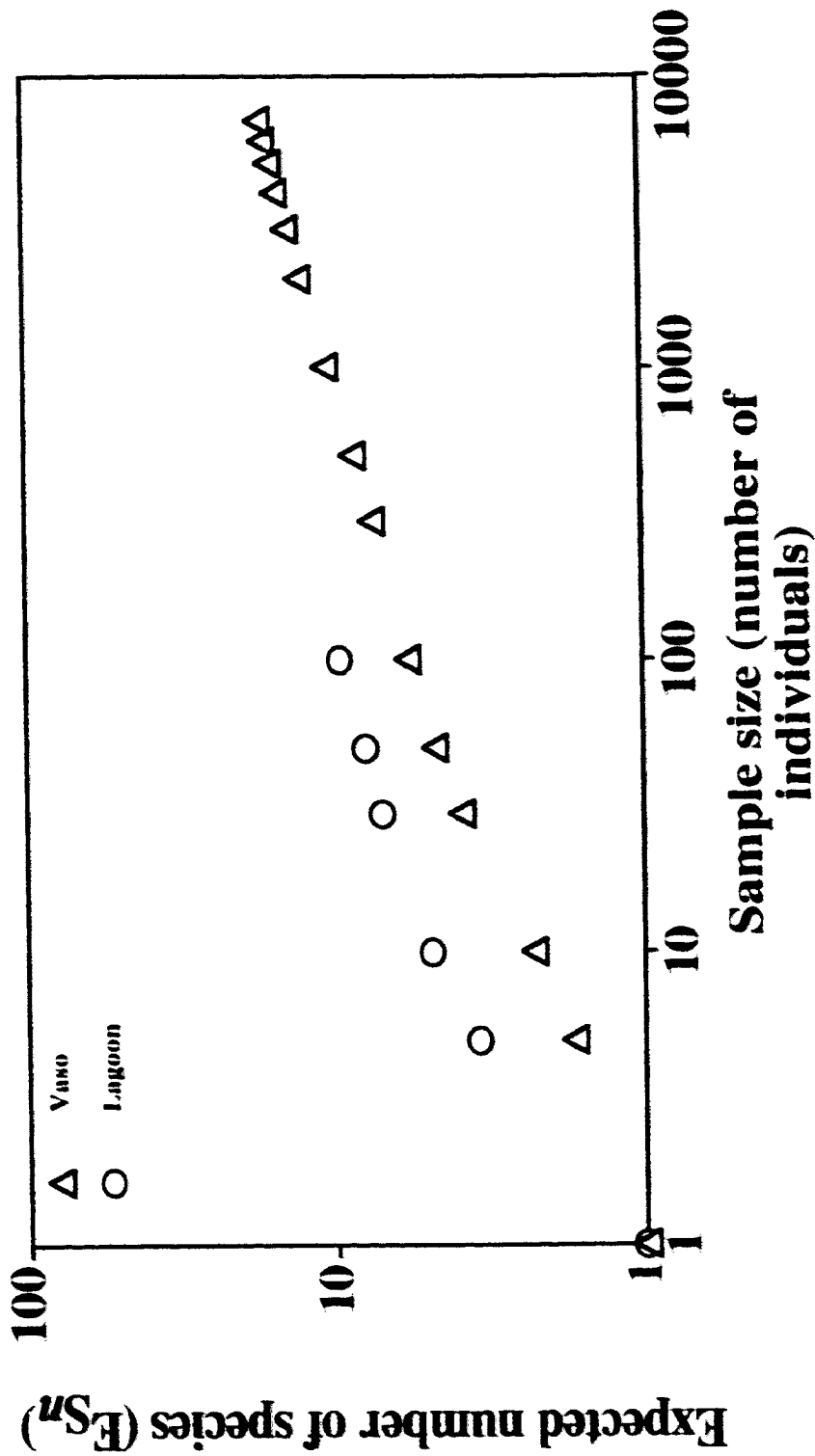


Figure A-4. Rarefaction curves showing expected number of fish species for a given sample size (number of individuals) for samples taken inside the vasos and the lagoon at Ojo de Liebre.

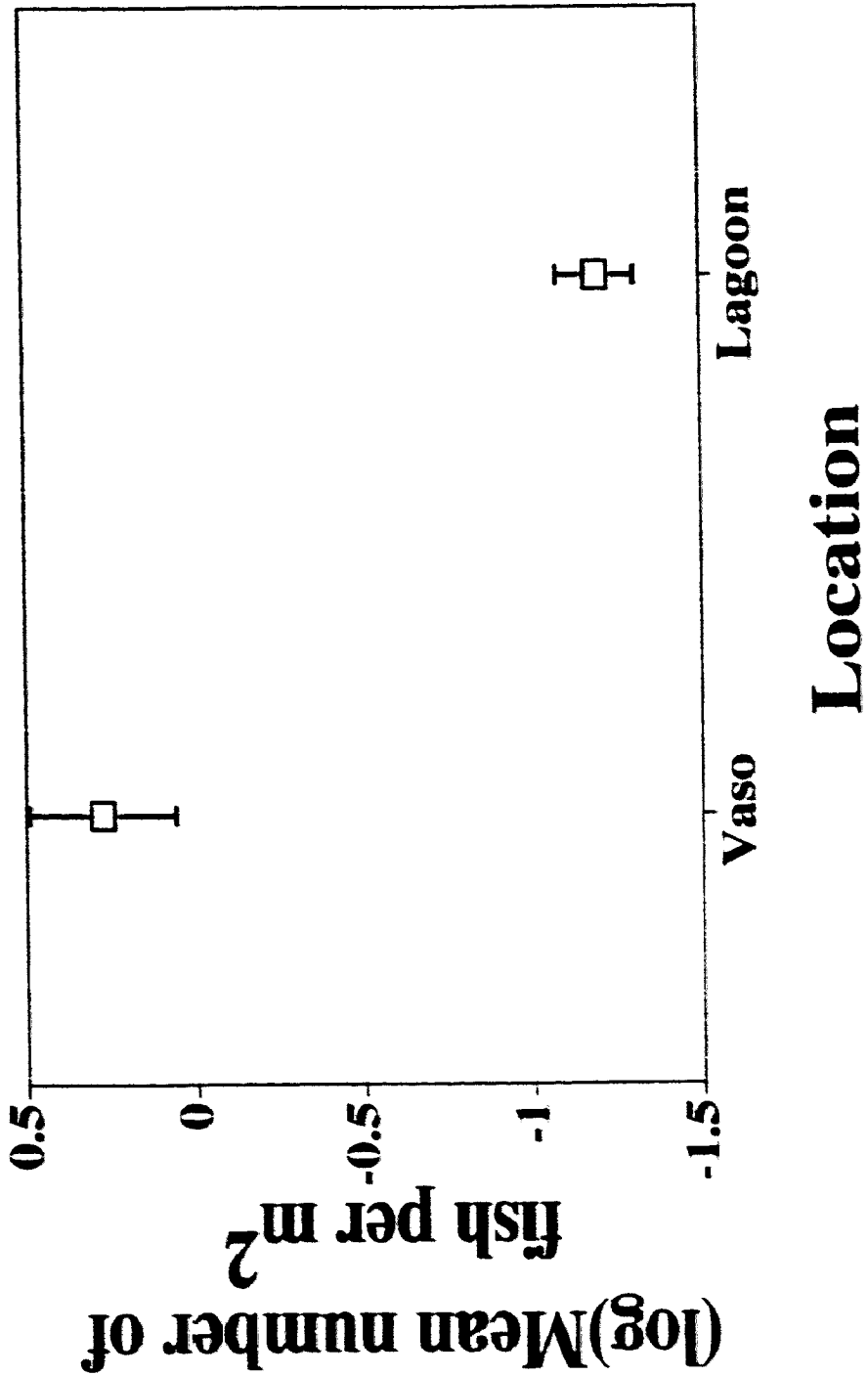


Figure A-5. The (log) mean density of fishes from samples taken inside the vasos and the lagoon at Ojo de Liebre. Error bars are ± 1 s.e.

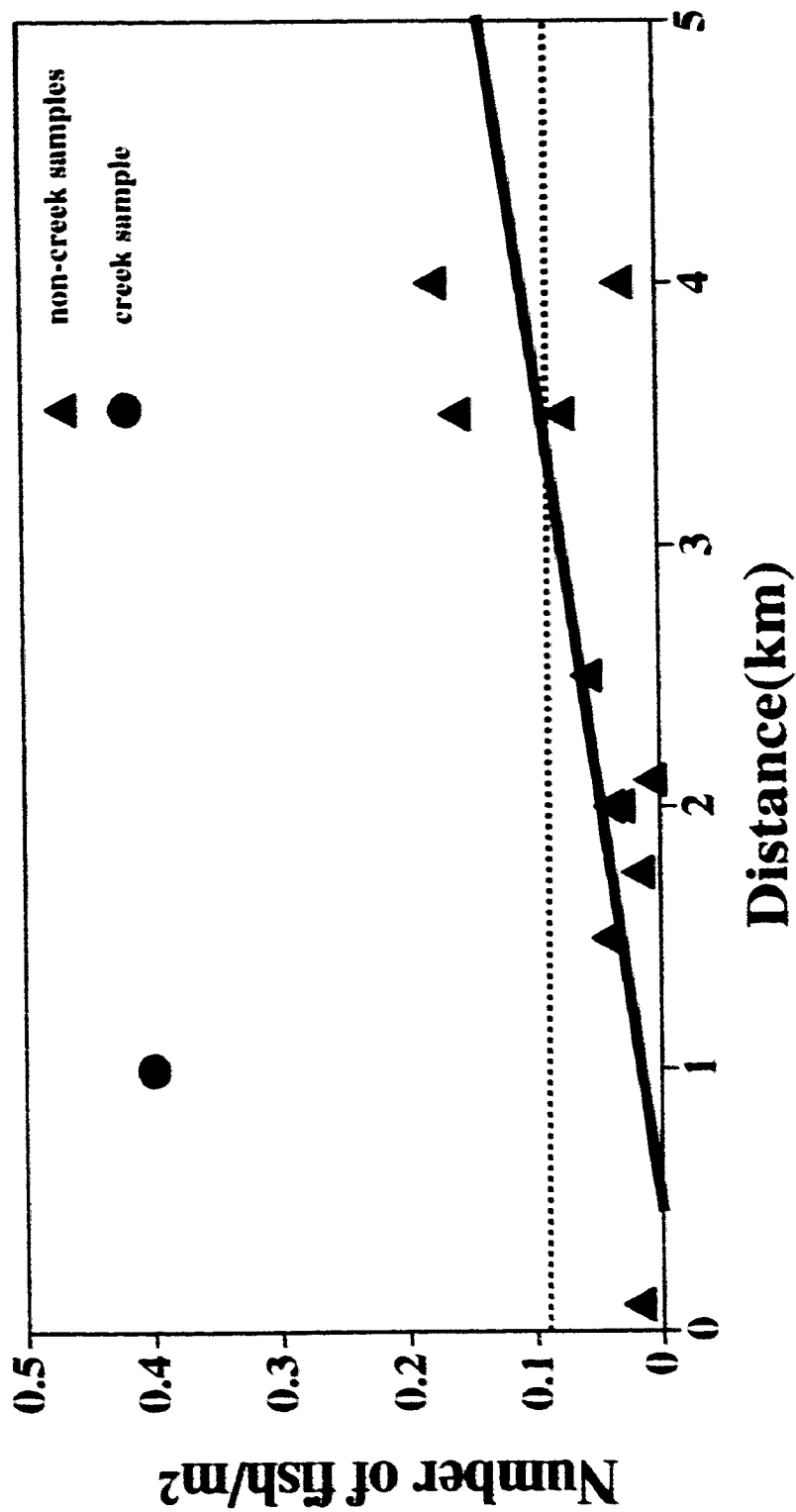


Figure A-6. Relationship between distance from vasos and number of fishes per m² in the lagoon at Ojo de Liebre. Solid line represents the fitted linear relationship excluding the tidal creek sample ($r^2 = 0.67$, $p < 0.01$), while the dashed line shows the relationship with that data point included ($p > 0.05$).

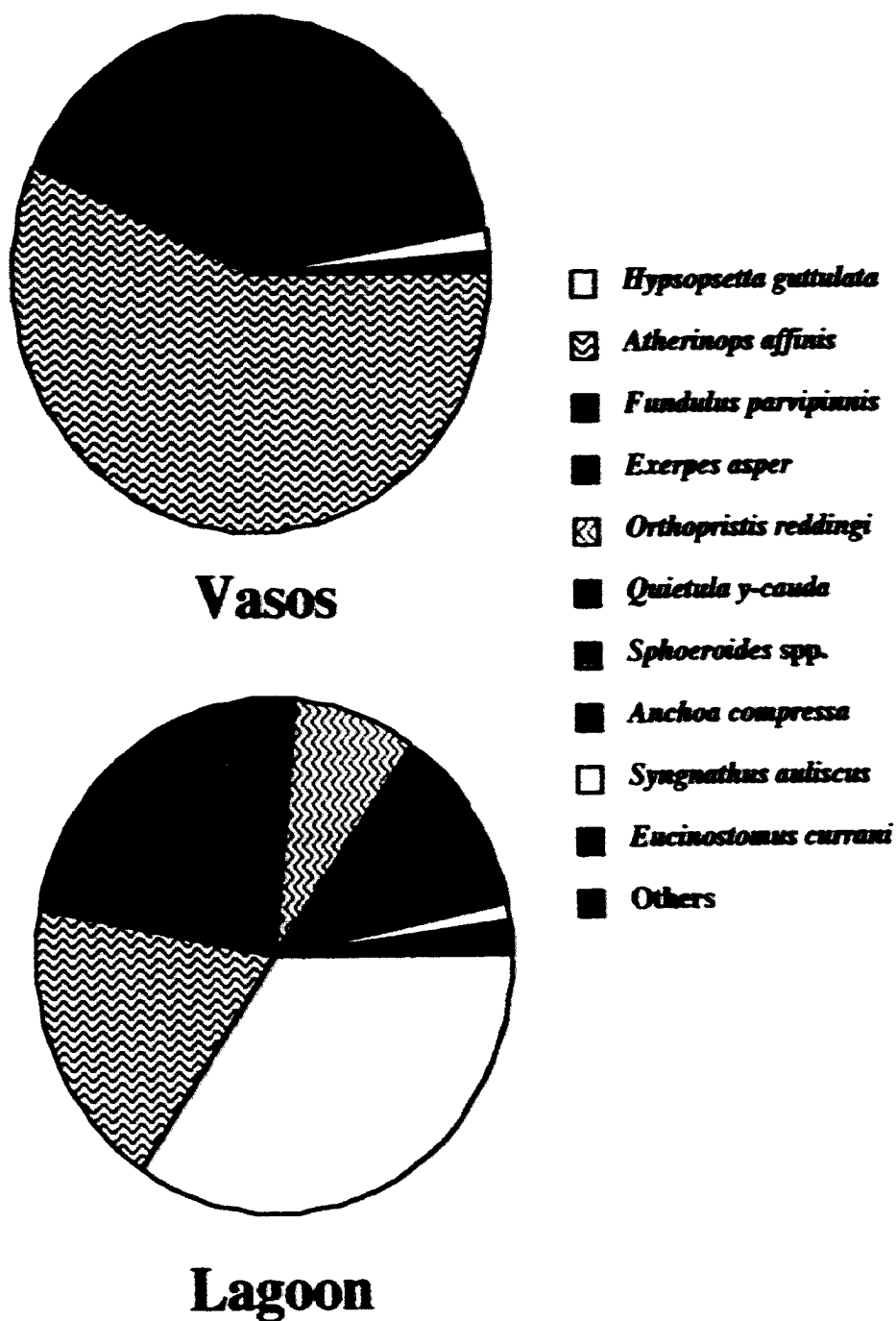


Figure A-7. Ichthyofaunal species composition for the vasos and lagoon at Ojo de Liebre. "Others" category is comprised of species which individually represent less than 1% of the total individuals captured.

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