

DEC 28 2000

THE WINTER ECOLOGY OF PIPING PLOVERS (*CHARADRIUS MELODUS*)
ALONG THE TEXAS GULF COAST

A Dissertation
presented to
the Faculty of the Graduate School
University of Missouri - Columbia

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by
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JULY 2000

The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

THE WINTER ECOLOGY OF PIPING PLOVERS (*CHARADRIUS MELODUS*)
ALONG THE TEXAS GULF COAST

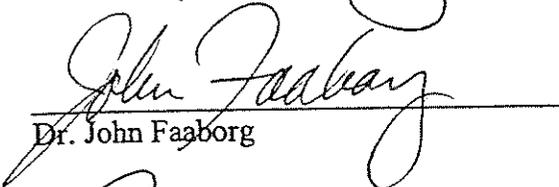
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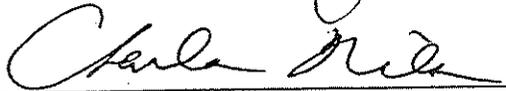
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ACKNOWLEDGEMENTS

Never in my life have I spent so much time counting things. Birds, worms, beachcombers...I have a hard time looking at anything anymore without trying to count it. Few things, however, have been as challenging for me to count as the number of people that helped me with this project.

Let me begin by thanking my thesis advisor, Mark Ryan. Mark was a great facilitator, patient listener and inspiring mentor. One of my great regrets with this project was that I was in Texas most of the time and unable to benefit more often from Mark's wisdom and company. My other committee members, Drs. John Faaborg, Gerald Summers, Charles Nilon and Charles Rabeni were extremely helpful and supportive of the project, and I feel very fortunate to have benefited from the advice of such a distinguished group of scientists.

I was lucky to have the help of several fine field assistants. Keith Walsh, my first field assistant, endured the challenges of the hectic first field season, and became a good friend in the process. Tim Menard, Shawn Farry, and John Hoffman also helped collect data on the project. I'm grateful for all of their dedication and camaraderie.

A most pleasant surprise was the large number of talented, and friendly biologists I came to know in Texas as they helped in one way or another with the project. Foremost among these was Lee Elliott, then with the Texas Parks and Wildlife Department (TPWD). Lee is a true naturalist and one of the finest people I've had the pleasure to know. I can't even begin to describe the number of ways Lee provided support during the project. I also owe Ted Eubanks (Piping Plover Recovery Team) a large debt of gratitude. The project simply would not have succeeded without Ted's initial support and enthusiasm. Others that provided expertise and moral support included Mary Ellen Vega, Lee Ann Linam, and Dick Harrington with TPWD, Robyn Cobb, Johnny French, Pat Clements, David Peterson, Phil Glass, Karen Myers, Claire Lee, and Theresa Barrera

with the U.S. Fish and Wildlife Service Field Offices, Steve Thompson, Marie Fernandez, Linda Laack, and Dina, Freddie, Sam, Arturo, Rudy and the rest of the staff of Laguna Atascosa National Wildlife Refuge, Chris Pease with Matagorda Island National Wildlife Refuge, Mike Farmer and Rex Wahl with the National Audubon Society, Jake Dameron and Angela Deaton with Galveston Island State Park, and Dr. James Teer and the rest of the staff at the beautiful Rob and Bessie Welder Wildlife refuge.

At the Texas A&M University – Corpus Christi, Dr. Edward Jones provided valuable statistical advise and Dr. Kim Withers provided many interesting opportunities for discussion, and Tony Amos, at the University of Texas Marine Science Institute, was both informative and inspiring.

I would like to thank the Texas Parks and Wildlife Department, the U.S. Fish and Wildlife Service the National Fish and Wildlife Foundation, the Edward K. Love Foundation, the Rob and Bessie Welder Wildlife Foundation, and Ted Eubanks for their financial support of the project.

I would like to thank my family for their support during the project. My parents, Connie and Chuck Zonick, sister Michelle, grandfather Tony and grandmother Ruth, and in-laws Mary and Bill were always there to help me face the challenges of the project and ask me when I was going to finally get around to finishing.

Finally, I would like to dedicate the project, to my wonderful wife and friend Dr. Veronica Counihan, and to my new son Brett Anthony. They helped me realize that there are things that are actually more important than science, which, ironically motivated me to be a better scientist. Veronica helped me in so many ways, enduring the heat and other challenges of Texas and the long hours I had to dedicate to the project. I couldn't have finished this dissertation without her love and support.

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ABSTRACT

Piping Plovers were monitored along the Texas Gulf Coast during the nonbreeding season (July – April) from 1991-1994. Groups of study sites were established within Texas' 2 coastal ecosystems (bay and lagoon ecosystems) and a coastal ecotone. Plovers were regularly counted at these sites and observed to determine habitat use patterns, diet, foraging effort, foraging efficiency, energy expenditure and factors influencing site abundance. Prey populations were sampled in areas used by foraging plovers for comparison to plover diets in different habitats and ecosystems.

Plovers were found to use bayshore tidal flats when bayshore tides were low and tidal flats were emergent. As bayshore tides inundated tidal flat habitat, plovers moved to beach habitat at most sites. Plovers density at beach and bayshore habitat varied in the 2 ecosystems and the ecotone. Plovers occurred at disproportionately high density at ecotone beaches and bay ecosystem tidal flats. In the lagoon ecosystem, where tides were controlled predominantly by winds, plovers used beaches less frequently, apparently also using mainland tidal flats and washover passes as secondary habitats.

Plover diet differed considerably in the 2 ecosystems. In the bay ecosystem, plovers fed predominantly on polychaetes, whereas plovers in the lagoon ecosystem were observed to feed largely on insects and other arthropods. Plovers in the ecotone exhibited a mixed diet of polychaetes and insects. Prey samples established that plover diets in these areas closely reflected the available prey communities. Plover flock size was

positively correlated with total benthic density and polychaete density in the bay ecosystem and the ecotone, but negatively correlated with these prey in the lagoon ecosystem, where plovers fed to a much greater extent on insects.

Plovers captured about 10 animals/minute in both ecosystems and the ecotone, and at beach and bayshore habitats. However, plovers foraging at beach habitat appeared to invest much more energy responding to human disturbance, territorial aggression, avoiding the swash. This additional energy investment likely resulted in a substantially lower energy intake rate for plovers foraging at beach habitat, and may explain why beaches were generally used only when bayshore flats were inundated. Plovers spent approximately 77% of their time foraging during daylight hours, and were more likely to roost during high bayshore tides and at beach and washover pass habitat.

Mean plover study site abundance was related to several environmental parameters (beach benthic density, bayshore benthic density, bayshore surface prey density, bayshore area, beach length, beach vehicular density). A stepwise multiple regression model selected beach length (positive) and beach vehicular density (negative) as the factors most strongly influencing plover site abundance. These results suggest that, although plovers may use beaches as a secondary habitat, degradation to this habitat may be limiting plover carrying capacity on Texas barrier islands. Given these findings, the large number of Piping Plovers wintering in Texas (~50% of the global population), and the extended length of the nonbreeding period (9-10 months), the protection of beach habitat should be among the highest priorities for Piping Plover recovery.

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CHAPTER I. INTRODUCTION AND STUDY AREA

INTRODUCTION

Few animals better symbolize the challenges associated with preserving biodiversity than the federally-protected Piping Plover (*Charadrius melodus* Ord). Like many other American species, the Piping Plover was reduced to near extinction in the late 1800's by unregulated hunting (Bent 1929). Plover populations recovered in the early 1900's after the establishment of the Migratory Bird Treaty Act and other laws designed to control the harvest of wildlife only to suffer another more recent decline caused by habitat loss and other impacts associated with human encroachment (U.S. Fish and Wildlife Service 1985).

In 1985, the Piping Plover was added to the group of plants and animals on the list of federally threatened and endangered species protected under the Endangered Species Act (ESA). There are now over 1,200 species on this list (U.S. Fish and Wildlife Service 2000), but in the 27 year history of the ESA, only 6 species have recovered to the point that they have been removed from the list (Mann and Plummer 1995). As is the case for most other species still on the federal list, the Piping Plover persists in the wild but continues to decline.

The federal agency responsible for enforcing the ESA for terrestrial species, the U.S. Fish and Wildlife Service (Service), admits on their worldwide web site that the ESA has succeeded in doing little more than preventing the extinction of listed species:

"Of all the species listed between 1968 and 1993, only 7 -- or less than 1 percent -- have been recognized as extinct, and subsequently de-listed. The fact that almost 99 percent of listed species have not been lost speaks to the success of the Act as a mechanism for conservation of species that are at risk of extinction."

Millions of dollars have been spent toward Piping Plover recovery, no doubt greatly reducing the species' decline and improving its recovery potential. In this regard the Piping Plover is not typical of other listed species, most of which have received little or no funds for research or recovery efforts. More is known about the Piping Plover, and more protective measures have been undertaken on behalf its recovery, than for most of the other listed species combined. Despite such disproportionate investments, however, demographic models project the extinction of the Great Lakes/Great Plains populations sometime near the middle of the current century (Ryan et al. 1993, J. Plissner, pers. comm.).

The Piping Plover is one of about 650 species with an approved recovery plan. A recovery plan is essentially a set of goals and strategies, written by a group of biologists (i.e., a recovery team) with species-related expertise, and designed with the goal of recovering the listed species. The research described in this manuscript addresses many of the winter recovery goals set in the Piping Plover recovery plans.

Project Description

This dissertation details research I conducted between July 1991 and April 1994 describing the ecology of the federally - protected Piping Plover (*Charadrius melodus*) on wintering grounds along the Texas Gulf Coast (TGC). The northern and southern regions of the TGC present 2 different coastal ecosystems to nonbreeding Piping Plovers. One of the primary focuses of my research was to determine whether Piping Plover ecology differed substantially among these two coastal ecosystems. I approached this question by studying plover populations at 18 study sites along the TGC. I monitored plovers at 3 or more representative study sites within each coastal ecosystem, and within the ecotone region where the 2 ecosystems meet. I evaluated the effects of several habitat parameters and environmental variables on plover abundance and density, studied the diet and foraging ecology of plovers, and collected samples to describe the prey populations³

used by plovers at the 18 study sites. I used these measures to estimate and compare the resources available to plovers and the foraging success of plovers among the two coastal ecosystems.

The Focus of Piping Plover Recovery Efforts

On 11 December 1985, the Service issued a final rule recognizing 3 distinct breeding populations of Piping Plovers worldwide (U.S. Fish and Wildlife Service 1985). The larger 2 populations, breeding along the Atlantic Coast of North America and the North American Great Plains, were listed as threatened. A third population, much smaller than the others and breeding only along the shores of the North American Great Lakes, was listed as endangered. Two recovery teams were created by the Service, one to plan the recovery of the Atlantic Coast Population, and a second to do the same for both interior populations. Recognizing the link between species conservation and habitat conservation, both recovery teams placed a high priority on determining the habitat requirements of each population. Most research and management efforts focused on breeding populations (e.g., Prindiville-Gaines and Ryan 1988, MacIvor 1990, Nordstrom 1990, Mayer and Ryan 1991a, Mayer and Ryan 1991b), despite the fact that Piping Plovers spend the vast majority of their life cycle away from the breeding grounds (Bent 1929). The early bias toward breeding ecology was necessary to stem the species' steep decline (Ryan et al. 1993). The major causes for the decline of Piping Plovers were attributed primarily to the loss of breeding habitat (to development and water-control projects), increased depredation on eggs and juveniles, and the direct destruction of nests by human activities (Haig and Oring 1985).

More recently though, it has become apparent that the recovery of the Piping Plover may hinge on an understanding of the species non-breeding ecology and responsible stewardship of winter habitat. Recent events have focused increasing attention on the potential for a catastrophic loss of Piping Plovers during the 9-month nonbreeding period.

These include a series of hazardous material spills near Galveston Island and a persistent brown tide episode in the Texas Laguna Madre (Dunton 1994, Edwards 1995). Piping Plover winter habitat is threatened by hydrological changes associated with the Gulf Intracoastal Waterway (GIWW; Farmer 1991, Diaz and Kelly 1994), commercial development, and predicted sea level rises (Bildstein et al. 1991). These events pose less immediate, but potentially greater threats to the long-term population viability of the Piping Plover.

Research has begun to fill in the gaps in our understanding of the key aspects of Piping Plover winter ecology. Most work has focused on defining the species' winter range (Haig and Oring 1985, Nicholls and Baldassarre 1990a, Haig 1992). Early investigations have begun into such aspects of Piping Plover ecology as habitat associations (Nicholls and Baldassarre 1990b), movement patterns (Johnson and Baldassarre 1988), and activity budgets (Johnson and Baldassarre 1988). Most of these studies, however, have been limited by either time (a single field season; Nicholls and Baldassarre 1990b), or geography (a single study location; Johnson and Baldassarre 1988).

The winter distribution of Piping Plover populations is becoming clearer due to several recent census efforts (Haig and Oring 1985, Nicholls and Baldassarre 1990b, Haig and Plissner 1993, Eubanks 1994, Zonick and Ryan 1995, Elliott 1996). The first International Piping Plover Census (IPPC) was conducted in 1991. The winter portion of the 1991 IPPC accounted for a total of 3,451 Piping Plovers during a 2-week census of the presumed winter range of the species. The 1991 IPPC count represented approximately 60% (3,451 out of 5,482) of the number of breeding Piping Plovers recorded during the 1991 IPPC summer count of breeding Piping Plovers (not counting the number of young produced in 1991). Wintering Piping Plovers were observed along the Atlantic Coast from the southern tip of Florida to the upper portion of North Carolina.

Wintering birds also were recorded on the shores of the Bahamas and Cuba, but the majority of the winter population was observed along the Gulf Coast of the United States. Over 92% (3,206 out of 3,451) of all of the Piping Plovers observed during the non-breeding portion of the IPPC occurred along the Gulf Coast. Of these, nearly 60% (1,905 out of 3,206) were observed along the TGC. Several large regions of the TGC (e.g., the Land-Cut, Baffin Bay, and North Padre Island) received only partial coverage during the 1991 IPPC. Also, despite admirable efforts by a few individuals, the Gulf Coast of Mexico has yet to be surveyed to the extent of the United States Gulf Coast. It is very possible that a large portion of the birds unaccounted for on the winter portion of the IPPC occurred in these areas.

The second IPPC was conducted in 1996 (Elliott 1996). A total of 1333 Piping Plovers were recorded in Texas in 1996, down substantially from the 1991 count of 1905. Several factors varied between the 2 counts, however, and the 1996 count is almost certainly a less accurate count than was the 1991 IPPC. Whereas many sites that were missed in the 1991 IPPC were covered in the 1996 count, many areas that were covered in 1991 were omitted from the 1996 count. The difference in the coverage in 1996 was due in large part to an extended period of extremely low tides that made many areas inaccessible, and to a government furlough that greatly reduced the manpower available for the 1996 IPPC.

Piping Plover winter habitat requirements also have been recently investigated. Johnson and Baldassarre (1988) and Nicholls and Baldassarre (1990) described aspects of the major habitat types utilized by Piping Plovers, as well as some of the microhabitat characteristics that are predictive of Piping Plover presence. Johnson and Baldassarre (1988) observed Piping Plovers in the Mobile Bay complex of the Alabama Gulf Coast to use "sandflats," "mudflats," and "beaches" as winter habitats. Their research indicated that sandflats and mudflats were "used for feeding", and sandy beaches were used for

"resting and probably roosting" (Johnson and Baldassarre 1988).

Nicholls and Baldassarre (1990b) used discriminant function analysis (DFA) to investigate the relationship between a number of microhabitat characteristics and the presence/absence of Piping Plovers throughout most of their winter range. Their analyses selected "...greater beach width, greater % mudflat, lower % beach and more small inlets..." as the winter habitat characteristics predictive of Piping Plover presence/absence along the Gulf Coast of the United States. Along the Atlantic Coast, DFA selected "...the number of large inlets and passes, number of tide pools, % mudflat, beach width, and % sandflat as the major factors affecting (Piping Plover) presence or absence." (Nicholls and Baldassarre 1990b).

The nonbreeding behavior of Piping Plovers has been described for only selected locations. Piping Plovers wintering along the Alabama Gulf Coast were observed to spend the majority (76%) of their time foraging (Johnson and Baldassarre 1988). Tidal height was negatively correlated with plover foraging activity in Alabama. After resighting 12 of 19 plovers color-banded at Dauphin Island, Alabama, Johnson and Baldassarre (1988) concluded that Piping Plovers exhibit "relatively high site-fidelity...to wintering sites in coastal Alabama." Elliott and Teas (1996) described the behavior of plovers using beach habitat at 3 locations along the central Texas coast. Plovers at these 3 sites spent most of their time foraging (86.7%, 89.5%, and 96.2%). Elliott and Teas estimated levels of human disturbance at the sites based upon counts of vehicles and pedestrians and found pedestrian encounters caused plovers to shift from foraging behavior to some other activity. Vehicles did not have the same effect, suggesting plovers were less affected by this form of disturbance. However, Elliott and Teas found plover abundance to be negatively correlated with vehicle abundance.

Unanswered Questions

Most of the previous work done on nonbreeding Piping Plovers has been spatially or

temporally restricted. For example, the conclusions by Nicholls and Baldassarre (1990a, 1990b) were founded primarily upon data collected from a collection of onetime visits to a large number of study sites throughout the winter range. Conversely, the research by Johnson and Baldassarre (1988) addressed specific aspects of Piping Plover ecology through multiple visits to a very small portion of the winter range. Whereas these approaches were appropriate for the scope of each project, and provided a foundation toward an understanding of the winter requirements of Piping Plovers, they did not answer several key questions.

The habitat associations derived by Nicholls and Baldassarre (1990b) reflect only a portion of the parameters that might play a role in habitat selection by Piping Plovers. For instance, they did not consider such factors as tidal stage, prey density, and human disturbance in their analyses, yet these factors have been shown to significantly influence shorebird site-use and behavior (Burger et al. 1977, Connors et al. 1981, Hicklin and Smith 1984).

Johnson and Baldassarre (1988) provided new insight into the winter movements and winter activity of Piping Plovers. However, the limited spatial scale of their research constrains the degree to which their results can be used to describe general winter movements and behaviors of Piping Plovers, particularly within markedly different ecosystem types like the Laguna Madre systems in Texas and Mexico. Here also, the habitat descriptions were general in nature (e.g., sandflat, beaches) and were not related to proximate influences such as prey density or human disturbance.

Of central relevance to the recovery of the Piping Plover is the identification and protection of high quality winter sites. Generally, the quality of a particular habitat or location to Piping Plovers has been determined indirectly, based upon survey information or the presence of habitat features commonly associated with Piping Plover presence. In 1990, Nicholls and Baldassarre broadened the criteria for appraising a location's value to

Piping Plovers by ranking winter sites using a formula that incorporated judgments about the quality of local habitat features. According to their formula, sites having more than 40 plovers were ranked as "1" (i.e. most important sites). Sites were ranked as "2" (i.e. of secondary importance) if the site had between 20 and 40 plovers and met at least 2 of 3 criteria. The criteria were:

"(1) habitat quality, i.e., excellent, with expansive mudflats adjacent to sandy beach; (2) historical data, i.e., presence on Christmas Bird Count at least once in previous five years; and (3) disturbance level, i.e. moderate to no disturbance at site (e.g., < 1.4 people and/or 0.2 off-road vehicles observed per km)."

Although the system's measure of habitat quality was subjective (by their own admission) and relied heavily on census data, the consideration of habitat features by Nicholls and Baldassarre resulted in a more credible ranking scheme by reducing the likelihood that a site might be given inflated stature based upon a single anomalous census. The consideration of human disturbance as one of the ranking criteria added another important dimension to the scheme. Nicholls and Baldassarre recognized that, when appraising a site's value to Piping Plovers, it was important to determine not only how many plovers occurred at a site, but also whether the habitat at that site was of sufficient quality to support the population (or an expanding population during the recovery process), and whether other environmental variables (e.g., human disturbance) were present that might compromise the site's apparent value.

Study Focus

In this study I present a site appraisal model predicting Piping Plovers abundance, and compare the quality of different habitat types and ecosystem types for Piping Plovers. I support these models by relating 3-year measures of Piping Plover site quality estimators (e.g., Piping Plover abundance, foraging efficiency) to an assemblage of simultaneously

monitored habitat components (e.g., estimates of available habitat, prey population measures) and environmental variables (e.g., human disturbance measures) that are most likely to affect Piping Plover site quality.

My research focused on describing the effects of key habitat components and environmental variables on the abundance and foraging ecology of Piping Plovers in different habitats and ecosystem types along the TGC. I evaluated Piping Plover foraging success using several approaches and used these measures as a means of appraising the relative success of nonbreeding populations. I contend that, in addition to abundance, foraging success is one of the most appropriate means of appraising the quality of different habitats, sites and landscapes for Piping Plovers. Foraging activity has been shown to occupy the largest proportion of the diurnal activity of wintering Piping Plovers (Johnson and Baldassarre, Teas and Elliott unpublished data, pers. obs.). Maintaining fat stores is of primary importance to plovers and other migratory shorebirds (Evans 1976, Davidson 1981, Myers et al. 1987, Helmers 1992). Furthermore, because Piping Plovers are a federally-protected species, other means of appraising the relative condition of plovers (e.g., by direct measurement of fat stores from harvested birds) in different areas or habitats were not justifiable.

Research Objectives

The primary objectives of the research were as follows.

Objective 1. Characterize and compare the relative density of Piping Plovers among 2 coastal ecosystems and their ecotone.

Because Piping Plovers winter over a wide geographic range, encompassing several ecosystem types, this comparison is expected to guide Piping Plover recovery by determining how ecosystem type affects plover density.

Objective 2. Identify the spatial, temporal, and environmental factors that affect Piping Plover densities.

A specific goal associated with this objective was to determine whether differences in Piping Plover density can be explained by specific spatial, temporal or environmental parameters, or combinations of these conditions acting together. This will greatly extend the current knowledge associated with Piping Plover winter habitat use patterns.

Objective 3. Characterize the prey resources potentially available to Piping Plovers among the habitats and ecosystems used by Piping Plovers along the TGC.

These data will help determine the relationship between potential prey density and Piping Plover density and will support habitat quality appraisals.

4. Characterize the foraging ecology of Piping Plovers along the TGC, and identify the factors affecting foraging success.

Specific goals associated with this objective were to determine and compare:

- a. The amount of time Piping Plovers spend foraging among major habitat types along the TGC;
- b. Piping Plover diets among major habitat types and ecosystems along the TGC;
- c. Estimated energy expenditures by Piping Plovers among major habitat types and ecosystems along the TGC;
- d. Piping Plover foraging efficiency among major habitat types and ecosystems along the TGC;
- e. Agonistic behavior by Piping Plovers among major habitat types and ecosystems along the TGC;

This information will provide additional knowledge about Piping Plover diets in different habitats and ecosystems and will allow for a comparison of the quality of the habitat types and ecosystems used by Piping Plovers along the TGC as appraised by the relative costs and benefits associated with foraging.

Objective 5. Identify the habitat components and environmental conditions that most strongly influence Piping Plover abundance at sites along the TGC.

Accomplishing this objective will help prioritize sites, or perhaps entire ecosystems, for conservation. This model will help direct the preservation or restoration of areas with quality habitat for wintering Piping Plovers by identifying the habitat components that are most likely to influence Piping Plover carrying capacity. With this knowledge, high quality habitat might be preserved in areas that are subject to development or other human modifications by guiding the design of future projects in a manner that is likely to minimize impacts to key habitat components. Similarly, this model will allow resource managers to more accurately predict the effects of changes associated with environmental conditions (e.g., bayshore tidal regimes, human disturbance), potentially leading to more effective habitat management for Piping Plovers during the nonbreeding season.

The research associated with these objectives is presented in 3 different, but interrelated chapters. Chapter 2 describes research addressing Piping Plover population density and the environmental factors affecting Piping Plover habitat use along the TGC (Objectives 1-3). Chapter 3 describes Piping Plover foraging ecology, and the factors that influence foraging success (Objective 4). Chapter 4 describes the factors influencing Piping Plover site abundance (Objective 5). In a summary chapter I discuss the implications of the findings on efforts to recover the Piping Plover, and recommend steps to improve the management of habitat along the TGC for plovers.

STUDY AREA

I selected the Texas coast as the geographic focus of this research because Texas supports the largest known portion of the Piping Plover winter population (Haig and Plissner 1993, Nicholls and Baldassarre 1990b). I examined the non-breeding ecology of Piping Plovers at 18 study sites along the Texas Gulf Coast (TGC). Three or more sites

each were located within the 2 coastal ecosystems represented in Texas, the estuarine bay ecosystem, and the hypersaline lagoon ecosystem (Figure 1). Four more sites were located within the ecotonal transition between the 2 coastal ecosystems.

All sites but one (Laguna Atascosa National Wildlife Refuge) contained a stretch of ocean beach. Although site beaches differed somewhat with regard to prey population densities, levels of human disturbance, and beach width, beach habitat structure was similar at all study sites.

In contrast, bayshore habitat structure differed greatly among my study sites. Changes associated with a few key geomorphologic and environmental factors along the TGC have produced 2 markedly different coastal ecosystems, each characterized by very different bayshore habitats. Two factors, tidal regime and salinity, strongly influence the habitats that occur along the TGC.

Tidal amplitudes are attenuated along the entire TGC relative to other, less sheltered North American coastlines (Britton and Morton 1989). Tides affecting beach shore are similar along the Texas Gulf coastline. In contrast, the bayside tides vary markedly in different regions of the TGC, and often are not synchronized with beach tides.

The salinities of Texas bays also varies markedly. From Galveston Bay in the north to South Bay bordering Mexico, there is a progressive increase in salinity. Southern bays are saltier because they receive less freshwater from rains and riparian inflows, and lose greater relative volumes of freshwater to evaporation.

In the northern region of the TGC, extending from the Houston Ship Channel Pass south to Aransas Pass (Figure 1), tides are controlled predominantly by astronomical forces, baywater salinities are generally brackish (15 - 30 ppt), and the climax intertidal community is dominated by cordgrass (*Spartina alterniflora*). This region can most accurately be described as an estuarine bay ecosystem, and is referred to by this term, or by the term "bay ecosystem" hereafter in this report.

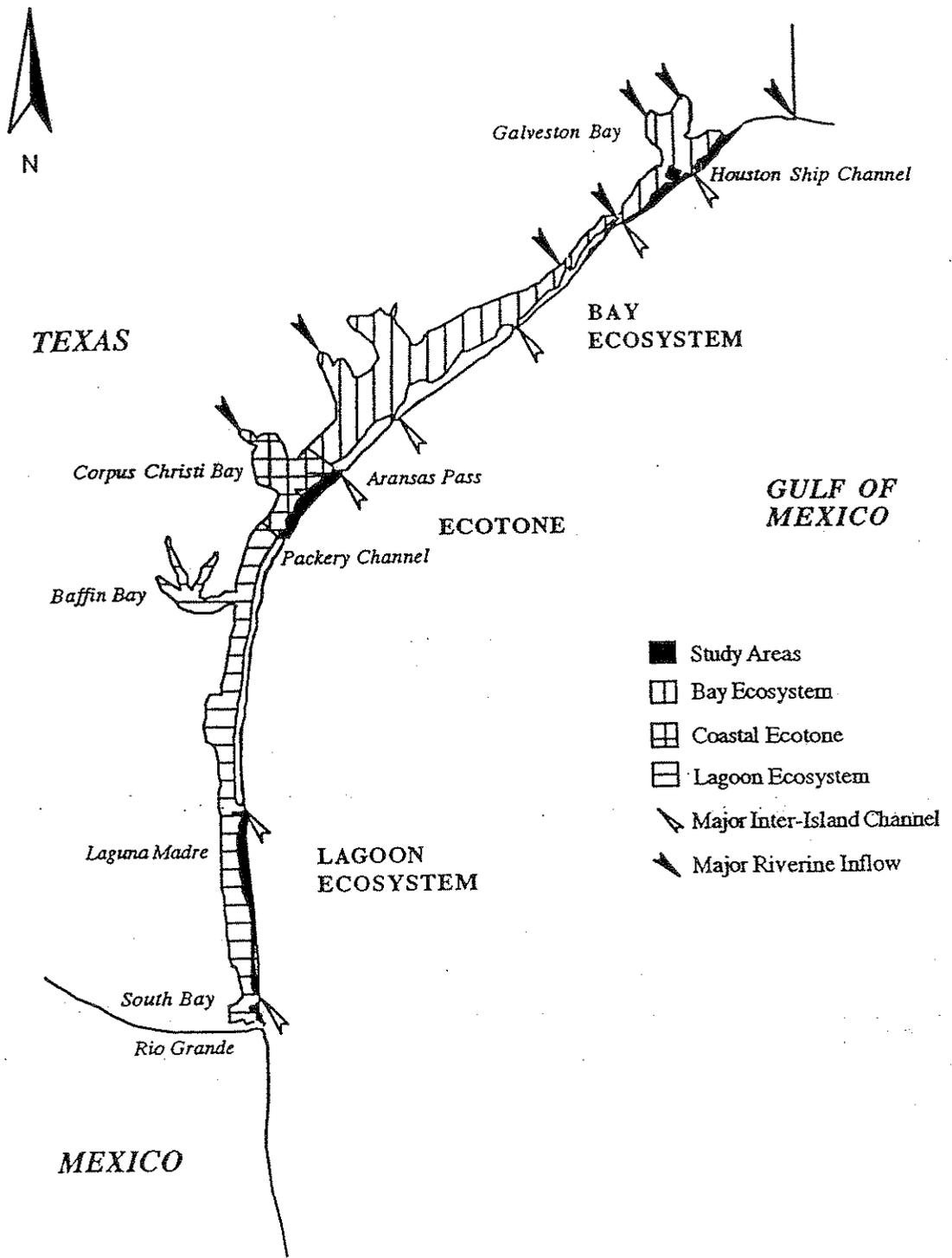


Figure 1. Schematic diagram of the Texas Gulf Coast illustrating the relative positions of the two major coastal ecosystems and the coastal ecotone.

About 50 km to the south, a different ecosystem becomes evident near Packery Channel and extends to the Rio Grande (Figure 1). In this region, tides are controlled mostly by shifts in winds and atmospheric pressure, particularly those accompanying winter cold fronts. Baywater salinities are often extreme (> 50 ppt), and the climax intertidal community is dominated by blue-green algal flats. This unique ecosystem is best described as a hypersaline lagoon ecosystem because it is characterized and maintained by recurrent periods of hypersalinity due to relative geographic isolation from other permanent bodies of water. This region is referred to as either the "hypersaline lagoon ecosystem" or the "lagoon ecosystem" hereafter.

Between these 2 ecosystems exists a transitional region where the tides are affected in mixed fashion by both winds and astronomical forces, salinities fluctuate between brackish and extreme, and the intertidal community is dominated neither by cordgrass, nor algal flats, but a mixture of both communities (Figure 1). This region can best be described as a coastal ecotone and is identified by this term, or by the term "ecotone" hereafter.

The Estuarine Bay Ecosystem and Study Sites.

The Galveston Bay system of the upper Texas Coast typifies the landscape and habitat features of the estuarine bay ecosystem. The climate in this ecosystem ranges from humid to subhumid with average annual rainfalls between 80 - 125 cm (Texas General Land Office 1994). Temperatures generally range from winter minimum lows near 7°C to average summer highs near 35°C (Texas General Land Office 1994). Baywaters within the estuarine bay ecosystem are deeper than those in the lagoon ecosystem. Maximum depths of primary bays in the estuarine bay ecosystem range from about 1.3 m (Galveston Bay) to 4.0 m (Matagorda Bay) compared to the hypersaline lagoon ecosystem's shallow primary bay (Laguna Madre) which reaches a maximum depth of only about 1 m (Britton and Morton 1989). Primary bay salinities range from

about 18 ppt in Galveston Bay to 23 ppt in Matagorda Bay (Texas General Land Office 1994). The intertidal regions of the bayshore in the estuarine bay ecosystem are dominated by densely-vegetated cordgrass marshes. Other typical plant species that flourish within this ecosystem include Marshhay cordgrass (*Spartina patens*), Glasswort (annual: *Salicornia bigelovii*, perennial : *Salicornia virginica*), Saltwort (*Batis maritima*) and Gulf cordgrass (*Spartina spartinae*). Unvegetated sand and mud flats appear as a narrow fringe along the marsh's border during periods of low tide. A few large (> 20 ha) unvegetated sand and mud flats occur in the bay ecosystem, usually adjacent to large tidal channels, or on the accreting side of jetties, but these flats comprise only a small percentage of the total area of bayshore habitat, most of which occurs as cordgrass marsh. The tides occur at a diurnal to semi-diurnal frequency, so that the unvegetated flats become available to shorebirds once or twice every 24 hours. The 3 sites monitored in the bay ecosystem were Bolivar Flats, Big Reef, and San Luis Pass (Figure 2).

Bolivar Flats. This site, located at the southeastern tip of Bolivar Peninsula in Galveston County, was composed of a single muddy sand flat, sandwiched between the northern jetty along the Houston Ship Channel and a cordgrass marsh (Figure 3). The marsh and sand flats at this site were growing as a result of the accretion of sediment transported by the Gulf longshore current, and trapped by the north jetty. Bolivar Flats was accorded protection via a 100-year lease to the National Audubon Society in 1992.

Big Reef. This site, located on Galveston Island in Galveston County, was an accreting wetland situated along the northern edge of the Houston Ship Channel's southern jetty (Figure 3). This site contained a small lagoon surrounded by a vegetated sandy spit. However, salinities in the lagoon were usually well below that of seawater (i.e., < 35 ppt). The lagoon was bordered by several small muddy sand flats fringed by patches of cordgrass marsh. A small tidal channel at the site's west side maintained a constant tidal exchange between the lagoon and the Houston Ship Channel. The City of

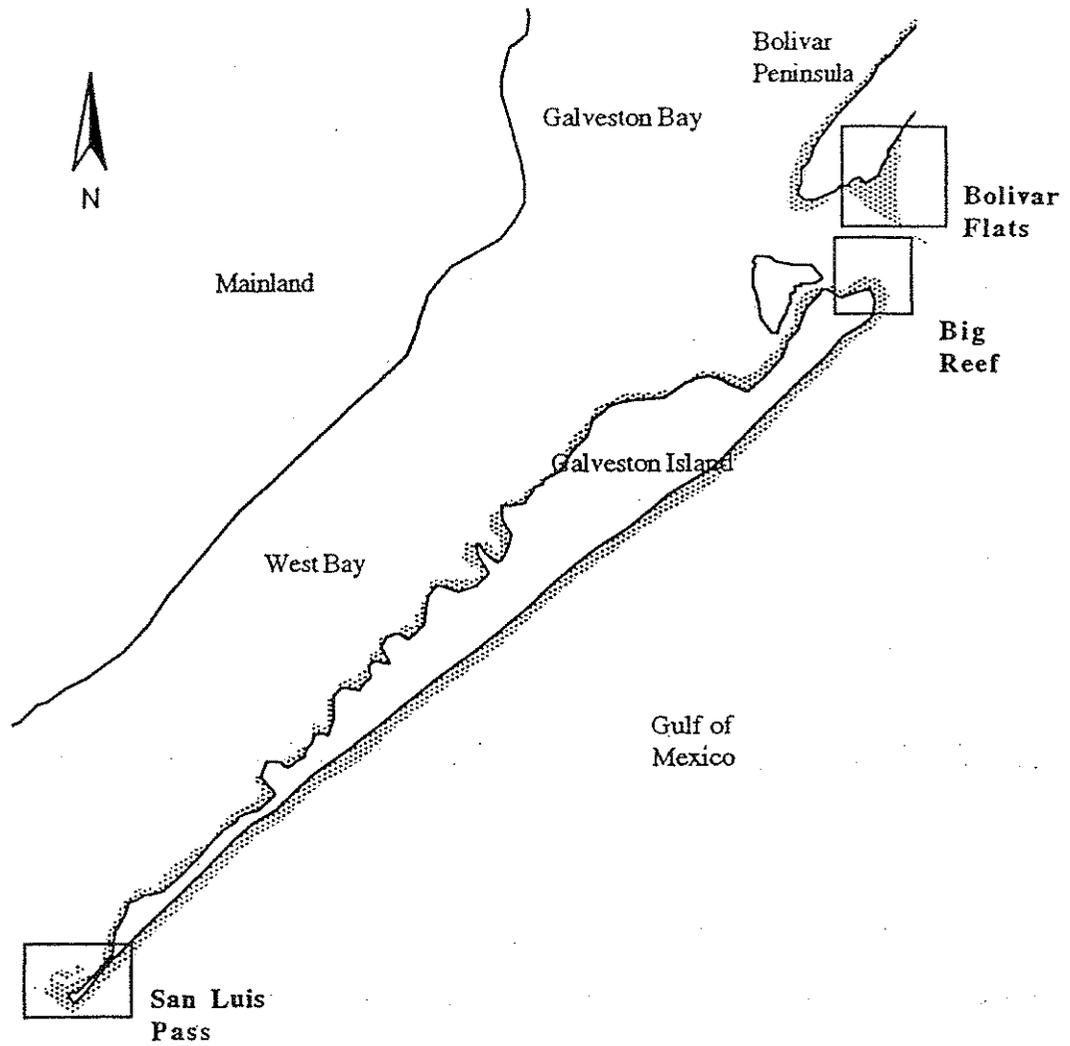


Figure 2. The relative locations of the study sites representing the bay ecosystem are illustrated. Bolivar Flats is located on Bolivar Peninsula. Big Reef and San Luis Pass are located on Galveston Island.

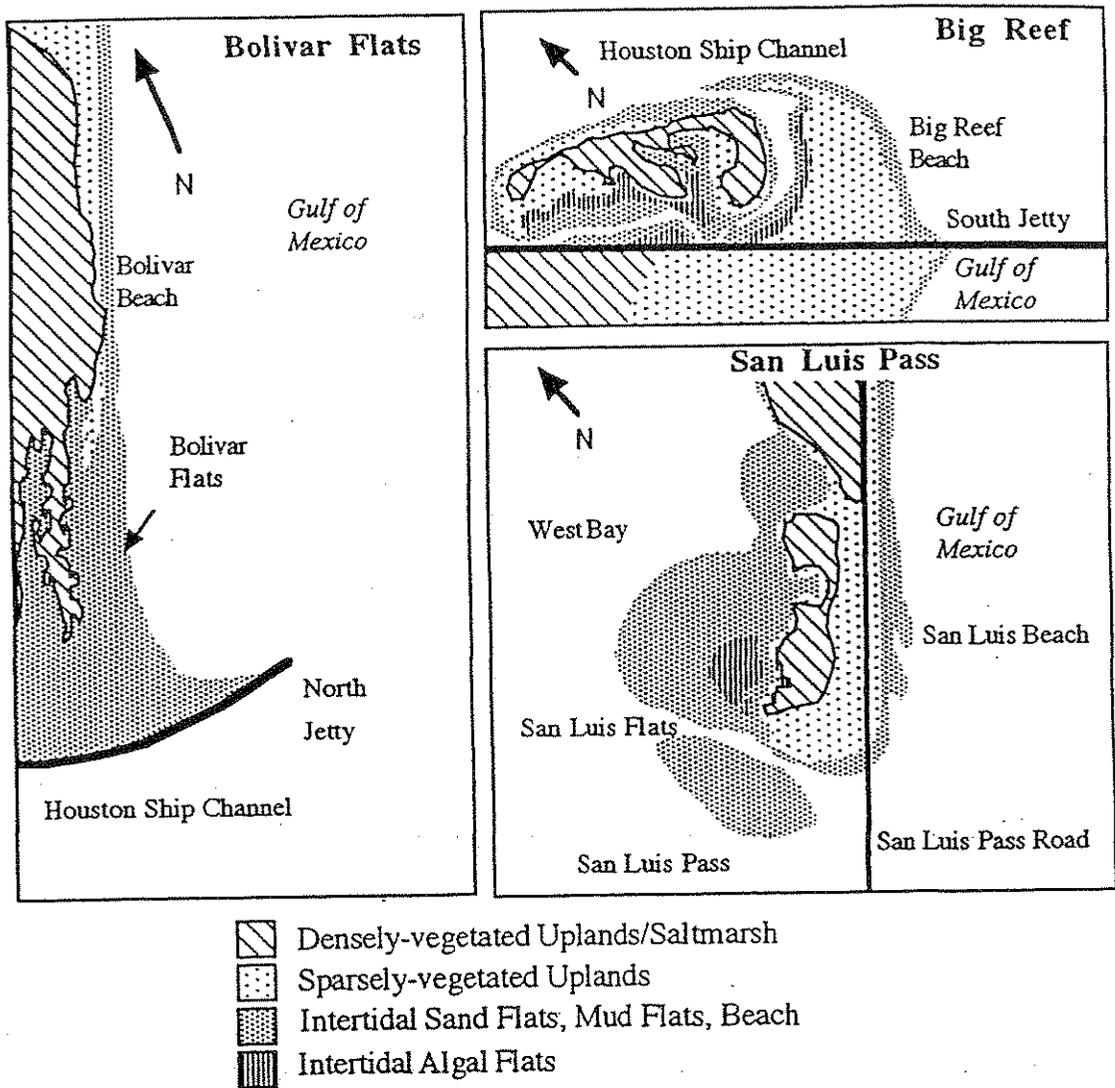


Figure 3. Schematic maps of the 3 Estuarine Bay Ecosystem Sites.

Galveston established the Big Reef study site as the Big Reef Nature Park soon after the conclusion of the study in 1994.

San Luis Flats. This site, located along San Luis Pass on the southwest tip of Galveston Island in Galveston County, was composed of several large sand flats bordered by coastal prairie (Figure 3). It was the only estuarine bay ecosystem study site that was not largely created by a man-made structure.

The Central Ecotone and Study Sites.

The ecotone exhibits habitat features diagnostic of each bordering ecosystem. Cordgrass marshes are present, but reduced in comparison to the bay ecosystem. The ecotone also is reflective of the lagoon ecosystem, as permanent algal flats occur in many locations. The vegetative community and baywater salinities are a blend of those typifying the 2 ecosystems, and tides are driven by both winds and astronomical forces. The 3 sites monitored in the ecotone were East Flats, Mustang Island State Park, and Packery Channel (Figure 4).

East Flats. This site, located near the northern tip of Mustang Island in Nueces County, was composed of a series of algal flats and mud flats separated by small patches of upland, and fingers of cordgrass and cattail (*Typha* spp.) marsh (Figure 5). A wastewater reclamation facility released a treated, low-salinity effluent into this wetland from its eastern border. Once sharing a broad tidal exchange with the waters of Corpus Christi Bay and Redfish Bay, this wetland had been surrounded to such a great extent by dredge spoil from the Corpus Christi Ship Channel and a residential access channel that the only remaining tidal exchange between the site's tidal flats and the surrounding baywater occurred through a few small channels along the site's southern border. The periodicity and magnitude of inundation experienced by the flats was erratic due to the restricted tidal flow.

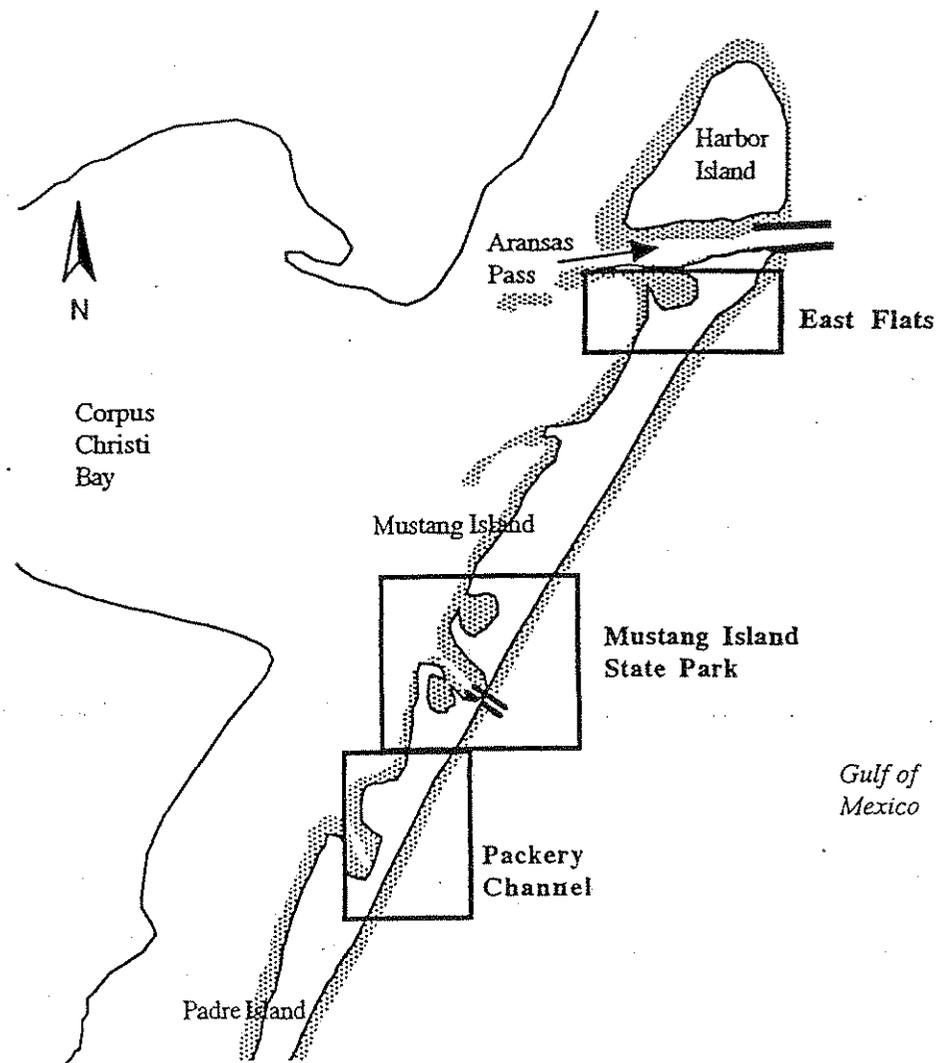


Figure 4. The locations of the study sites representing the Coastal Ecotone. All 3 sites are located on Mustang Island.

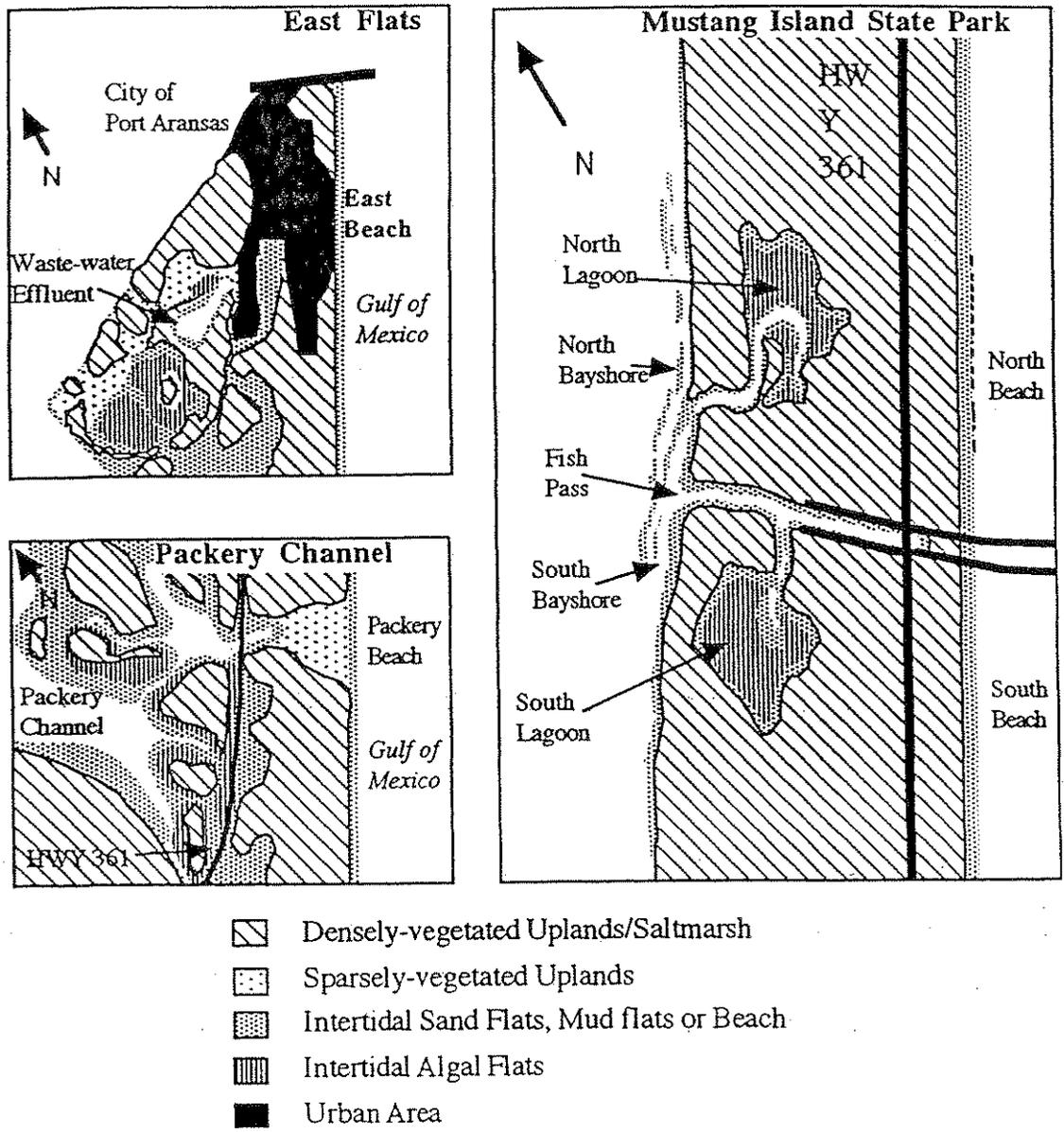


Figure 5. Schematic maps of the 3 Coastal Ecotone Sites.

Effluent released by the treatment facility into the wetlands probably contributed as much to the regular inundation of the wetland as did baywater swells.

Mustang Island State Park. This site, contained within the boundaries of the Mustang Island State Park (MISP), Nueces County, was divided by a man-made boat channel, identified on most maps as Fish Pass (Figure 5). The elevated banks along Fish Pass had eliminated most of the tidal exchange between the Park's tidal flats and the waters of Corpus Christi Bay, effectively splitting 1 large lagoon into 2 small lagoons, 1 each on the north (MISP - North) and south (MISP - South) side of the pass. An artificial channel re-established an effective tidal exchange between the northern lagoon and the bay, but the southern lagoon remained isolated from baywater tidal exchanges to a large extent during the study.

Packery Flats. This site, located along the northern shoreline of Packery Channel in Nueces County, was composed of sand flats and algal flats surrounded by coastal prairie (Figure 5). Due in part to its proximity to Corpus Christi, the beach at this site often experienced high levels of human disturbance.

The Hypersaline Lagoon Ecosystem and Study Sites.

The climate in this ecosystem ranges from subhumid to semiarid with average annual rainfalls between about 65 - 80 cm (Texas General Land Office 1994). Temperatures generally range from winter minimum lows near 9°C to average summer highs near 36°C (Texas General Land Office 1994). The lagoon ecosystem borders an extreme-saline lagoon, the Laguna Madre. The Laguna Madre has probably been without a significant riverine influence since the Rio Grande filled its estuary approximately 4,000 years ago (Rusnak 1960). The low relative amount of freshwater entering the Laguna Madre from rain or riverine inflow, coupled with a high evaporative rate, contributes to high local salinities (> 80 ppt) compared with those of the Gulf of Mexico (36 ppt), or the primary bays of the estuarine bay ecosystem (13 - 23 ppt; Britton and Morton 1989, Hedgpeth

1967). Smaller lagoons and tide pools associated with the Laguna Madre often exceeded 100 ppt during the study (pers. obs.). Few intertidal organisms flourish under these severe conditions (Copeland and Nixon 1974). The hypersaline environment of the Laguna Madre is probably most challenging to life at the lower trophic levels (e.g., plants, invertebrates), and it was at these levels that the hypersaline lagoon ecosystem appeared to differ most noticeably from the estuarine bay ecosystem (e.g., insects replacing polychaetes as the dominant intertidal macrofaunal groups). The life forms that are able to survive in this ecosystem, however, often occur in great numbers (Carpelan 1967, pers. obs.), presumably because they are released from competition with their saline-sensitive counterparts in the estuarine ecosystem.

A considerable portion of the intertidal area in the lagoon ecosystem is covered by a sheet-like matrix described as a "blue-green algal mat" or "algal mat." Flats covered by algal mats are referred to as "algal flats" (regardless of the underlying substrate) and cover hundreds of square kilometers in the lagoon ecosystem (Pulich and Rabalais 1986, Tunnell 1989). Algal mats are composed of a mix of blue-green algae, dominated by *Lyngbya confervoides*. Algal mats also contain a variety of pennate diatoms (Pulich and Rabalais 1986, Sorensen and Conover 1962). Although most algal mats are only a few millimeters thick, algal flats have been shown to be 20-40% as productive as cordgrass marshes (Pulich and Rabalais 1986).

Plant species that flourish in the lagoon ecosystem include Glasswort (annual: *Salicornia bigelovii*, perennial: *Salicornia virginica*), Saltwort (*Batis maritima*), Sea lavender (*Limonium nashii*), Key Grass (*Monanthochloe littoralis*), and Sea Purslane (*Sesuvium portulacastrum*). Only a handful of hypersaline ecosystems exist world-wide, and the Laguna Madre is one of the largest and most extensively studied (Britton and Morton 1989).

Due to several unique characteristics of the wind-tidal flats along the Laguna Madre (e.g., hypersalinity, low-human population-density), the bayshore margins of the mainland land mass also exhibit large areas of unvegetated intertidal flat habitat. In contrast, mainland shores in the bay ecosystem are generally narrow and are dominated by densely-vegetated cordgrass marsh habitat, or have been converted to human developments. Because Piping Plovers generally avoid densely-vegetated habitat (pers. obs., Brush 1995), much of the mainland intertidal habitat in the bay ecosystem is unsuitable for Piping Plovers, whereas the mainland flats in the lagoon ecosystem exhibit large areas of suitable habitat. Accordingly, both mainland and barrier landforms were represented by study sites within the lagoon ecosystem.

The 3 sites monitored in the lagoon ecosystem were Laguna Atascosa National Wildlife Refuge, South Padre Island, and South Bay (Figure 6). At 1 of the sites (South Bay), the mainland and the local barrier (Brazos Island) were connected by a land bridge formed by Highway 4, and there was no clear division between the 2 landforms. To clarify this situation, I defined all flats ≥ 5 km from the Gulf shoreline as "mainland" flats, and all flats < 5 km from the Gulf shoreline as "barrier" flats. Because the beach habitat was, by definition, always associated with the barrier landform (i.e., < 5 km from Gulf Coastline), this landform classification existed only for bayshore habitat. Furthermore, because none of the study sites in the bay ecosystem nor the ecotone were ≥ 5 km from the Gulf Coastline, mainland sites occurred only within the lagoon ecosystem, and comparisons between parameters among the mainland flats and barrier flats are restricted to those within this ecosystem.

Laguna Atascosa National Wildlife Refuge. This site, located within the boundaries of Laguna Atascosa National Wildlife Refuge (LANWR) in Cameron County, was composed of a series of large algal flats and mud flats (Rincon Buena Vista Flats, Elephant Head Cove Flats, Horse Island Flats, Redhead Cove Flats and Yucca Flats)

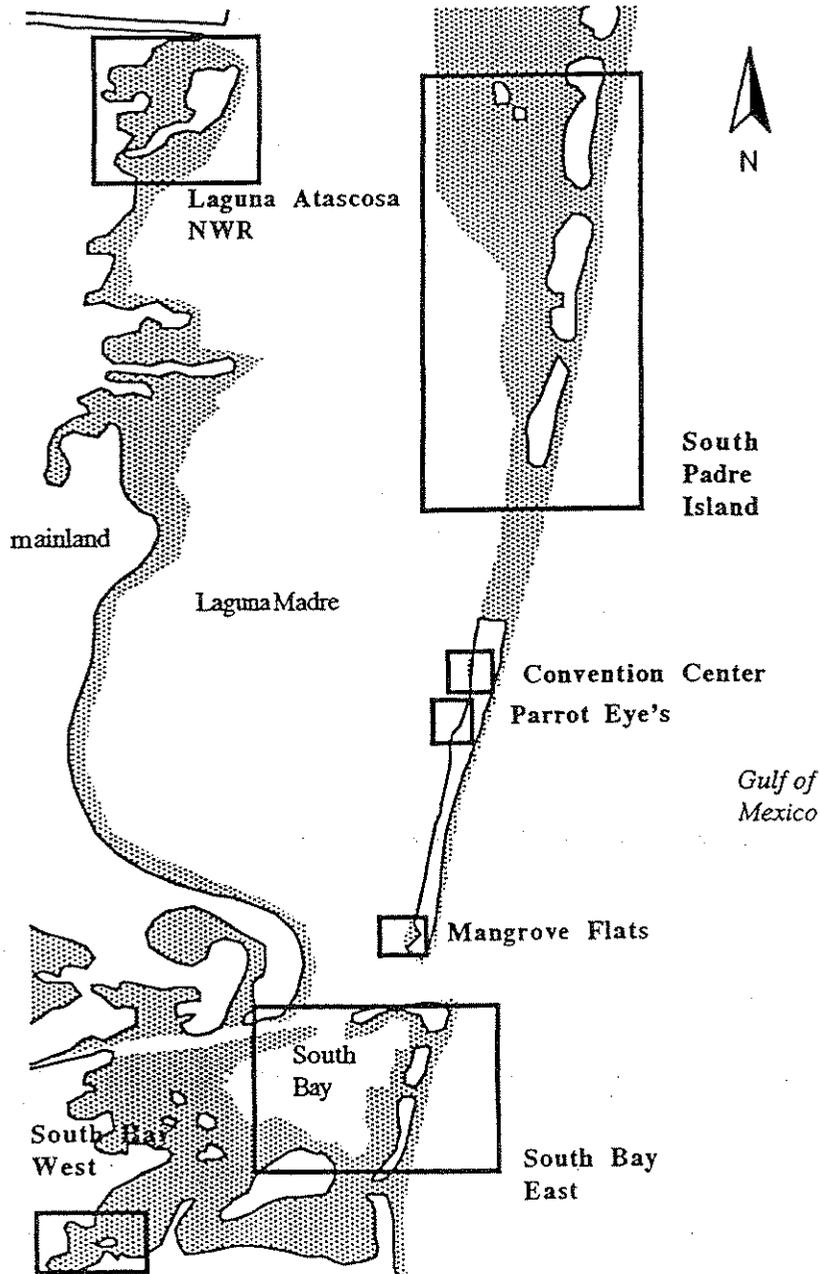


Figure 6. The locations of the study sites representing the Hypersaline Lagoon Ecosystem. Sites are located at Laguna Atascosa National Wildlife Refuge (mainland sites only), South Bay (mainland and barrier island site) and South Padre Island (barrier island sites only)

associated with a system of coves near Horse Island (Figure 7). All of the flats were ≥ 5 km from Gulf Coastline, and were thus classified as "mainland" flats. The flats were bordered by a dense coastal thicket of Tamaulipan thorn scrub elevated from the flats by a 1-3 m steep cliff-line. Like the East Flats study site, this site had been nearly removed from tidal exchange from the Laguna Madre by dredge spoil deposits and an elevated access road. This site occurred at roughly the same latitude as the South Padre Island site (Figure 6).

South Bay. This site, located along the shoreline of South Bay in Cameron County, was composed of 2 large algal flats and mud flats surrounded by an elevated coastal prairie/savanna (Figure 7). One of the flats, South Bay West, was located ≥ 5 km from the Gulf, and was classified as a "mainland" flat. The other flat, South Bay East, was located within the 5 km zone, and was classified as a "barrier island" flat. Dredge spoil deposits associated with the Brownsville Ship Channel had substantially reduced the natural tidal exchange between South Bay and the Laguna Madre.

South Padre Island. This site on South Padre Island in Cameron County, was composed of 1 large flat and a series of small, isolated flats (Figure 7). The smaller flats (Mangrove Flats, Parrot Eye's Flats and Convention Center Flats) were situated within the commercially-developed, southern tip of the island. The large flat (North Flat) was located immediately north of all development at the northern terminus of highway P100. All of the flats were within the 5 km zone of the Gulf and were classified as "barrier island" flats. Algal flats and sand flats were the dominant habitat types at all of the locations on South Padre Island.

Wetland Classification of Study Sites

I classified the landscape and wetland habitat features at the sites (Table 1) using a slightly modified version of the wetland classification system developed by Cowardin et

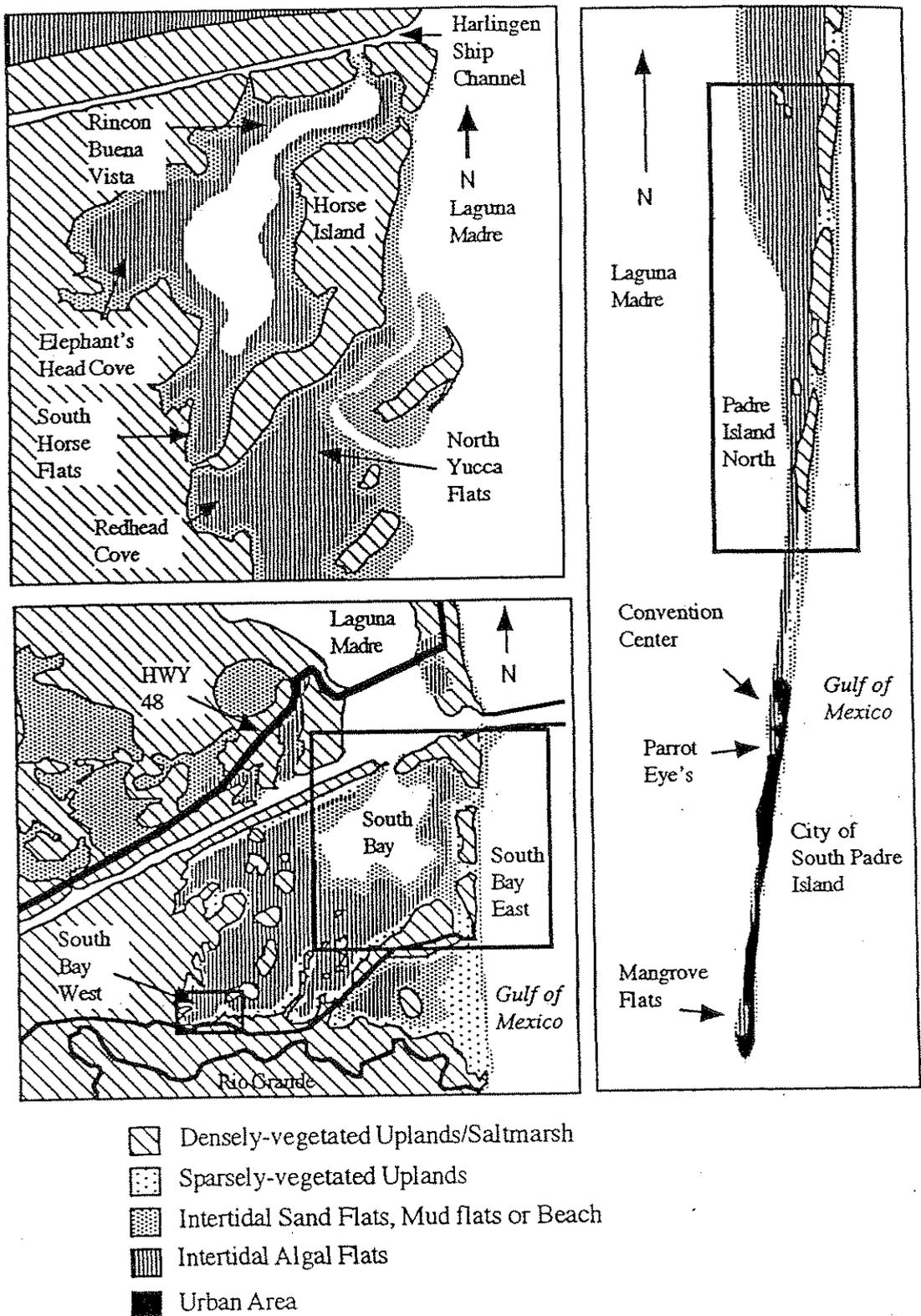


Figure 7. Schematic maps of the 3 Hypersaline Lagoon Study Sites.

Table 1. Classification of beach and bayshore habitat among study sites based on a modification of the wetland classification system designed by Cowardin et al. (1979). Modifiers for such parameters as tidal regime and algal mat prevalence have been added to augment the wetland characteristics that provide distinction among study locations.

Study Site	System	Subsystem	Tidal Regime	Tidal Force	Substrate Subclass	Salinity Modifier	Algal Mat
Beaches							
<u>Estuarine Bay Ecosystem</u>							
Bolivar Flats	Marine	Intertidal	Regular	Astronomical	Sand	Polyhaline	Absent
Big Reef	Estuarine	Intertidal	Regular	Astronomical	Sand	Polyhaline	Absent
San Luis	Marine	Intertidal	Regular	Astronomical	Sand	Polyhaline	Absent
<u>Coastal Ecotone</u>							
East Flats	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent
MISP	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent
Packery	Marine	Intertidal	Regular	Astronomical	Sand	Polyhaline	Absent
<u>Hypersaline Lagoon Ecosystem</u>							
South Bay	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent
South Padre	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent
Tidal Flats							
<u>Estuarine Bay Ecosystem</u>							
Bolivar Flats	Estuarine	Intertidal	Regular	Astronomical	Sand/Mud	Polyhaline	Absent
Big Reef	Estuarine	Intertidal	Regular	Astronomical	Sand/Mud	Polyhaline	Ephemeral
San Luis	Estuarine	Intertidal	Regular	Astronomical	Sand/Mud	Polyhaline	Ephemeral
<u>Coastal Ecotone</u>							
East Flats	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Euhaline	Present
MISP	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Euhaline	Present
Packery Flats	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Polyhaline	Present
<u>Hypersaline Lagoon Ecosystem</u>							
LANWR	Marine	Intertidal	Irregular	Wind	Mud	Euhaline	Dominant
South Bay	Marine	Intertidal	Irregular	Wind	Mud	Hyperhaline	Dominant
South Padre	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Hyperhaline	Dominant

al. (1979). Modifiers were added to the classification system to describe the tidal regime, tidal force, salinity and presence of algal mats at each site.

Site Visitation Schedule

The bay ecosystem, lagoon ecosystem, and the ecotone were visited in alternating fashion throughout the nonbreeding period, with visits to each area lasting approximately 1 month. In this way, each area was visited for approximately 3 months during each 9 month field season. During each of the 1 month visits, the sites within the site group were visited in alternating fashion. Because some sites were more difficult to access, and required the availability of an ATV, or relatively dry roads, some sites were visited more frequently than others. For example, the large, northern flat on South Padre Island (Figure 7) was accessible only with an ATV. Because ATVs were not always available, this site was visited less frequently than were the other 2 sites in the lagoon ecosystem. The East Flat site (Figure 5), located in the ecotone, was added to the study late in the second year, and was visited less frequently than were the other 2 sites in the ecotone.

Site Selection Criteria

I selected study sites that were reasonably accessible (e.g., by car, ATV or walking) and supported large numbers of Piping Plovers and Snowy Plovers (*Charadrius alexandrinus*) during either the 1991 IPPC, or during preliminary surveys I conducted between July 1991 - September 1991. In general, natural land formations were used to delineate site boundaries (e.g., habitat transitions, water boundaries, lomas [islands of upland prairie surrounded by tidal flats]). I selected sites that were representative of their respective ecosystems. The lagoon ecosystem study sites were larger than the sites within the bay ecosystem, reflecting the more expansive nature of the wind-tidal flats of the Laguna Madre. The bay ecosystem sites were composed predominantly of sparsely vegetated and unvegetated sand flats. The lagoon ecosystem sites were composed predominantly of sparsely vegetated and unvegetated mud flats, sand flats and algal flats.

The sites within the ecotone were intermediate in size compared to the sites in the 2 ecosystems, and contained a combination of sand flats and algal flats.

Human-engineered Alterations

To varying degrees, all of the study sites owe their present form to the influences of human-engineered manipulations. Bolivar Flats and Big Reef are supplied by sediment that is either trapped or redirected by the jetties erected to maintain the channel depth of the Houston Ship Channel. In contrast, the tidal flats at San Luis Pass may have been reduced by the presence of the jetties which trap sediment at Bolivar Flats and Big Reef that normally may have accreted at San Luis Pass. The flats associated with the East Flats, Mustang Island State Park, Laguna Atascosa National Wildlife Refuge, and South Bay study sites all appear to have been substantially affected by dredge spoil (pers. obs). Portions of Packery Channel are occasionally deepened by dredging.

Without question, the large northern flat on South Padre Island has been less affected by human manipulation than any of the other study sites I monitored for this research. But this site too, was has been substantially altered by human design. Spoil dredged from Mansfield Channel erodes onto the flats during periods of strong north winds associated with winter fronts. The foredunes along the flat's Gulf border, stripped of large tracts of stabilizing vegetation by ATVs, release large volumes of sand into the prevailing southeastern winds (F. Judd, pers comm.). The sand, in turn, has begun to swamp hundreds of hectares of intertidal habitat. Waters entering the Laguna Madre through the Mansfield Channel, the Harlingen Ship Channel, and the Land Cut (a section of the GIWW connecting the once isolated upper and lower Laguna Madre systems) have reduced the overall salinity of the Laguna Madre (Diaz and Kelly 1994). The Harlingen Ship Channel carries hazardous materials from the Rio Grande Valley agricultural industry into the lagoon.

Study Period

I collected these data over a period of 3 consecutive years incorporating large portions of 3 consecutive nonbreeding seasons beginning in July 1991 and ending in April 1994. Although I collected some data during very early (i.e., July) and very late (i.e., April) portions of the nonbreeding period, most of the data were collected between mid-August and late-March.

CHAPTER II. PIPING PLOVER DENSITY

INTRODUCTION

The largest concentrations of nonbreeding Piping Plovers occur along the western Gulf Coast, particularly in Texas (Nicholls and Baldassarre 1990b, Haig and Plissner 1993, Elliott 1996). The local distribution of nonbreeding Piping Plovers along the Gulf Coast has been linked to such habitat features as wide beaches, large mudflats and small inlets (Nicholls and Baldassarre 1990a). However, other habitat and environmental features that are known to affect shorebird abundance have not been studied in association with Piping Plover distribution. Climatic factors and tide cycles often strongly influence shorebird activity and habitat use patterns (Pienkowski 1983, Puttick 1984, Colwell 1993). Human disturbance also has been shown to alter shorebird behavior in ways that might affect population density (Burger and Gochfeld 1991, Pfister et al. 1992, Elliott and Teas 1996). Spatial and temporal factors, such as habitat interspersion (Connors et al. 1981, Handel and Gill 1992, Farmer and Parent 1997), time of day (Robert et al. 1989, Thibault and McNeil 1994, McNeil and Rompre 1995), and time of year (Baker and Baker 1973, Withers and Chapman 1993) also can affect shorebird behavior, habitat use, and population density.

Identifying the habitat and environmental parameters that most strongly influence Piping Plover habitat use patterns and population density will provide valuable insight for the process of preserving locations and habitat types important to Piping Plovers. To address this goal I monitored Piping Plover density and abundance in association with the factors described above. I monitored plovers at different times of the day during the winter period and both migratory periods (spring and fall) to address temporal variations in nonbreeding ecology. I focused my research within 4 nested spatial scales: 1) the ecosystem scale, 2) the site scale, 3) the habitat scale, and 4) the microhabitat scale.

METHODS

Objective 1. Piping Plover Density

In objective 1, I proposed to establish and compare the relative densities of Piping Plovers among the dominant habitat types and ecosystem types along the TGC. To accomplish this objective, I conducted regular censuses at the 2 dominant habitat types (beach and bayshore) at 18 study sites located within the 2 ecosystems and the ecotone zone between the 2 ecosystems.

I counted Piping Plover populations during each site visit (see Study Areas for site visitation schedule). Because beach and bayshore habitats were spatially disjunct at most of the sites, I counted these areas separately. However, within each of these 2 habitats, bird counts were of the entire site. In general, I conducted only 1 survey/habitat during each site visit, however when tide levels changed dramatically during a site visit, I occasionally conducted a second survey under the altered tidal condition.

Beach Piping Plover density was calculated by dividing plover beach by the length of beach surveyed. Bayshore Piping Plover density was calculated by dividing plover bayshore counts by the average area of bayshore habitat available at each site during the study. The average area of available bayshore habitat was estimated by multiplying the total potential area of bayshore habitat at each site by the average percent bayshore tidal amplitude (described below) recorded at that site during the study.

Objective 2. Factors affecting Piping Plover density.

In objective 2, I sought to identify the factors affecting Piping Plover density. To accomplish this objective, I monitored an array of environmental, temporal, and spatial variables.

Variables evaluated for their effects on Piping Plover density were: 1) bayshore tidal amplitude, 2) beach tidal amplitude, 3) climatic conditions, 4) human disturbance,

5) season, 6) time of day, 7) habitat and microhabitat types, and 2 spatial variables: 8) landform and 9) ecosystem.

Bayshore tidal amplitude

During each site visit, I recorded the level of bayshore tidal inundation as one of 5 ranked values. The ranks corresponded to visual estimates of percent tidal inundation of the total available area of Piping Plover habitat at each site. The ranks (very low, low, moderate, high and very high) corresponded to estimated percent tidal inundation levels equal to 0, 1 - 24, 25 - 75, and 76 - 99, and 100, respectively. During very low tides (i.e., ~ 0% inundation) the tidal flats were judged to be emergent to the maximum extent possible. During very high tides (i.e., 100% inundation), the flats were completely submerged, and only upland habitat remained emergent. Very high tide conditions usually were associated with storm tides during the summer-fall hurricane season or strong north fronts during the winter period.

Visual estimates of tidal inundation were used instead of tide gauges because the substrate associated with most of the bayshore habitat was often unstable, preventing the use of permanently located tide gauges on many of the tidal flats. Initial attempts to place site-associated tide markers resulted in almost complete loss due to tidal erosion in some areas and vandalism in others. Whereas professional tide monitors are maintained in some locations along the Texas coast these gauges measure the tidal amplitude in areas that were often far removed from the study sites. These monitors were designed to measure tide levels within the deeper regions of the bays, and would have provided very poor estimates of tidal inundation of the broad wind tidal flats at many of the sites. For these reasons, I determined visual estimation to be the best method for accurately documenting the local bayshore tidal conditions.

For the purpose of data analyses, I ranked bayshore tidal conditions as either emergent or inundated. Bayshore conditions were considered emergent if the tide was

either very low, low or moderate (i.e., if inundation was estimated to be <75%). If the tide was estimated to be high or very high (i.e., $\geq 75\%$ inundation) the bayshore tidal conditions were ranked as inundated.

I appraised the total potential area of bayshore habitat at each site by digitizing the boundaries of all intertidal and sparsely-vegetated supratidal habitat from U.S. Geological Survey Topographic Quadrangle Maps into a geographic information system (Atlas Geographic Information System, Strategic Mapping Inc., Santa Clara, California). I referred to aerial infrared photographs to guide the delineation of tidal boundaries. In many cases, man-made or natural structures (e.g., seagrass beds, upland vegetation transitions, duck blinds) helped locate the extreme low and high tide boundaries.

Beach Tidal Amplitude

I estimated beach tidal amplitude by measuring beach width. I measured beach width at 3 sites (Bolivar Flats, Mustang Island State Park North Beach, and Packery Channel). These were the only sites that had stable beach landmarks, such as beach mileage signs, that I was able to use as consistent reference points to collect comparable beach width measures. I defined beach width as the distance between the swash boundary and the vegetation line on the upper beach.

Climatic Conditions

During each site visit, I measured air temperature, wind speed, and precipitation and used these data to classify climatic conditions as either harsh or mild. All three of these variables have been shown to adversely affect the foraging effectiveness of plovers and other visually foraging shorebirds, often reducing their net energy intake rates (Goss-Custard 1984, Davidson 1981, Pienkowski 1981). Plovers and other visually foraging shorebirds have been observed to feed more slowly during cold periods and rainy periods, possibly due to reduced prey activity (Goss-Custard 1970, Pienkowski 1981).

Air temperatures ranged from near 0°C to greater than 30°C during the study (data not shown). Winter precipitation varied from very dry during drought periods to very wet during El Niño cycles, or during months when the coast experienced heavy rain in association with tropical storms or winter north fronts. Winds were generally most strong during storm events or winter north fronts, often topping 30 knots during these periods.

Rather than attempt to analyze the effects of individual climatic variables on Piping Plovers, my analyses focused on comparing the ecology of Piping Plovers during periods of severe climatic stress (i.e., those typical of winter storm events) against that during periods of more clement conditions (i.e. those between winter storm events).

I classified climatic conditions as harsh if the air temperature was \leq the average associated with north fronts (10-14°C), and if the wind speed was also \geq the average associated with north fronts (5 - 20 knots). Climatic conditions also were considered harsh if it was extremely cold (0 - 4°C), regardless of the wind speed or precipitation, or if it was raining, regardless of the air temperature or wind speed. Between 5 - 14°C, the wind speed-temperature combination determined my ranking. Harsh conditions were judged to have occurred if the air temperature was between 10 - 14°C, and the wind speed was $>$ 20 knots, or if the air temperature was between 5 - 9°C, and the wind speed was above 5 knots.

Human Disturbance

I recorded the number of vehicles present during each of the plover surveys and used vehicular density (vehicles/ha at bayshore habitat and vehicles/km at beach habitat) as an estimate of human disturbance.

Season and Time of Day

I classified seasons according to the migratory period and the winter period, which are the 2 major stages of the annual life cycle when Piping Plovers occur in Texas. The winter period was defined as 1 November - 20 February, and the migratory period was

defined as 1 July - 30 October, and 21 February - 15 May. These periods closely reflect the boundaries of the migratory and winter periods reported by others (Eubanks 1994, Haig 1992). I classified surveys as either morning (<12:00) or afternoon (>12:00).

Habitats and Microhabitats

During bird counts, I classified habitat as either beach or bayshore habitat. I considered beach habitat to be that directly bordering the Gulf of Mexico. All other foraging habitat (i.e., that directly bordering baywater) was considered bayshore habitat. At locations where the two habitats meet, such as at the end of a barrier island (e.g., San Luis Beach and San Luis Flats), the point at which the shoreline bends away from the Gulf was considered the transition between the two habitats.

I distinguished 2 microhabitats on beaches, both occurring within the intertidal zone where the sand was still moist at the surface due to recent inundation. I classified the portion of the intertidal zone where the swash regularly wetted the substrate as the swash zone. The moist portion of the intertidal zone that lies adjacent to, but above, the swash zone was classified as the upper beach.

I recognized 2 microhabitats on bayshore flats. Flats with an algal mat were classified as algal flats, and those without an algal mat were classified as sand flats.

Data Analysis

All analyses were performed using JMP, version 3.1. JMP is a statistical program written by SAS Institute Inc., Cary, NC. Advanced statistical analyses (i.e., beyond the calculation of means, standard errors, etc.) consisted of one-way and multi-factor analyses of variance (ANOVA), linear regressions, and multiple regressions.

One-Way ANOVA

One-way ANOVAs were employed to compare numerous relationships, primarily the effects of habitat components, environmental variables, temporal variables and spatial variables on the density of Piping Plovers or prey populations. Where appropriate, one-

way ANOVAs were accompanied by multi-factor ANOVAs to support the evaluation of a particular parameter's effect either alone, or in combination with other related parameters.

Multi-factor ANOVA

Multi-factor ANOVA models were constructed to investigate the relative influences of habitat components, environmental variables, temporal variables and spatial variables on the density of Piping Plovers, total benthic prey, polychaetes, crustaceans, and insects. To build models incorporating all of the relevant parameters, it was necessary to omit some of the sites with smaller data sets from some of the models. For example, a model investigating the full complement of environmental factors affecting Piping Plover bayshore densities must contain data collected at each site during each of the following 8 different sets of conditions:

1. Emergent bayshore habitat, migratory season, mild climate;
2. Emergent bayshore habitat, migratory season, harsh climate;
3. Emergent bayshore habitat, winter season, mild climate;
4. Emergent bayshore habitat, winter season, harsh climate;
5. Inundated bayshore habitat, migratory season, mild climate;
6. Inundated bayshore habitat, migratory season, harsh climate;
7. Inundated bayshore habitat, winter season, mild climate;
8. Inundated bayshore habitat, winter season, harsh climate;

In this particular example, all 8 condition sets did not occur at all of the sites during the study. Therefore, I developed a multi factor ANOVA model using data collected at a smaller group of sites (4 sites, in this example) where I had obtained data under all of the above conditions.

Nested Parameters

The study site variable was built into the multi-factor ANOVA model as a nested

parameter. Each site contributing data to the model was nested within the ecosystem (or ecotone) in which it occurred. Nesting the study site parameter within the ecosystem parameter instructed the model to assess the contribution of intra-ecosystem (i.e., inter-site) variability as a component of the effect of the ecosystem parameter on the response variable.

Regression Analysis

Relationships between 2 continuous variables were investigated using linear regression (e.g., the relationship between Piping Plover beach density and beach vehicular density).

RESULTS

Objective 1. Piping Plover Density

Beach Density

Piping Plover beach density varied from about 0.4 birds/km to > 3.5 birds/km (Table 2). When only foraging birds were considered, the smallest average spacing between plovers ranged from about 1 bird every 50 m at the Mustang Island State Park - South site to about 1 bird every 840 m at the South Padre Island - North site. At most sites, plovers were spaced 100 - 200 m apart during the period of high abundance of foraging birds.

Mean Piping Plover density was below 3 birds/km at all but one of the sites within the bay and lagoon ecosystems, but exceeded 3 birds/km at all of the ecotone sites (Figure 8).

Bayshore Density

Piping Plover bayshore density varied from 0 birds/100 ha to almost 150 birds/100 ha (Table 3; Figure 9). The highest average densities throughout the study were observed at the 3 small flats on South Padre Island. Of the flats larger than 10 ha, high plover densities (> 49 birds/100 ha) were recorded at all 3 bay ecosystem sites, and at the South Padre Island - North site (Table 3; Figure 9).

Objective 2. Factors Affecting Piping Plover Density

Ecosystem Type and Bayshore Tidal Amplitude

Ecosystem type ($P < 0.0001$) and bayshore tidal amplitude ($P < 0.0001$) had a significant effect on Piping Plover beach density. Plover populations were significantly higher at ecotone beaches than at bay beaches ($P < 0.0001$; Table 4) or lagoon beaches ($P = 0.0002$; Table 4). There was no difference in plover density at bay and lagoon beaches ($P = 0.5787$; Table 4).

Ecosystem type ($P = 0.0448$) and bayshore tidal amplitude ($P < 0.0001$) had a significant effect on Piping Plover bayshore density. I performed this analysis using barrier island data only. Piping Plover density was significantly higher on barrier island

Table 2. Abundance, spacing, and density estimates of Piping Plovers at beach habitats at sites along the Texas Gulf Coast, 1991-1994. The length of beach (BL) monitored at each site is presented in kilometers. Abundance is presented as the mean and maximum (Max.) number of Piping Plovers recorded at each site. Spacing describes the minimum (Min.) average distance (m) between Piping Plovers as estimated by dividing the maximum abundance of foraging Piping Plovers only (data not shown) by the length of beach at each site. Mean and maximum density were estimated by dividing the mean and maximum abundance estimates by the length of the beach monitored at each study site.

Study Location	N	BL (km)	Abundance			Spacing		Density	
			Mean	SE	Max.	Min.	Mean	SE	Max.
<i>Bay Ecosystem</i>									
Bolivar Flats	35	4.8	15.3	3.96	83	177.8	3.19	0.81	17.3
Big Reef	17	3.2	1.2	5.63	12	237.5	0.37	0.22	3.8
San Luis Pass	64	6.3	12.3	4.47	32	240.0	1.87	0.21	5.1
<i>Ecotone</i>									
East Flats	7	2.8	9.9	8.78	24	133.3	3.54	1.27	8.6
Mustang Island State Park - North	66	3.2	10.3	2.86	38	88.9	3.22	0.49	11.9
Mustang Island State Park - South	32	2.6	8.5	4.11	55	47.3	3.26	1.00	21.2
Packery Channel	58	3.9	14.0	3.05	87	70.9	3.59	0.75	22.3
<i>Lagoon Ecosystem</i>									
South Bay East	25	7.6	22.6	4.65	254	233.3	2.97	1.54	33.4
South Padre Island North Area	27	25.1	12.3	4.47	171	836.7	0.49	0.26	6.8

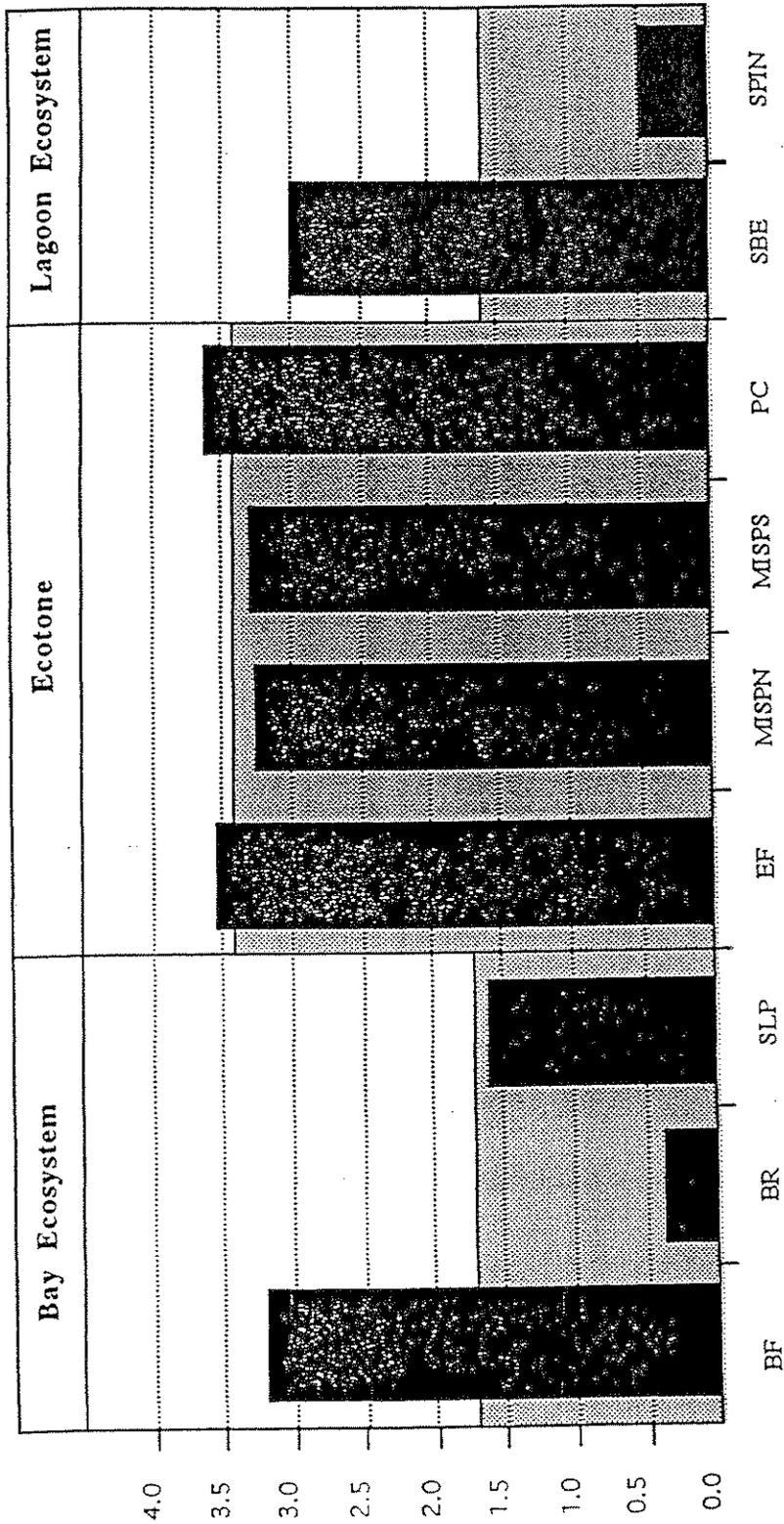


Figure 8. Mean site density and ecosystem density of Piping Plover at beach habitat along the Texas Gulf Coast, 1991 - 1994. Black bars represent site density estimates, gray bars illustrate mean density estimates for each ecosystem (calculated as the average of the mean density estimates for each site in each ecosystem).

*Site Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISPN = Mustang Island State Park - North, MISPS = Mustang Island State Park - South, PC = Packery Channel, SBE = South Bay East, SPIN = South Padre Island - North.

Table 3. Total abundance, highest study counts, and densities of Piping Plovers on bayshore tidal flats at sites along the Texas Gulf Coast, 1991 - 1994. Piping Plover (PIPL) density is expressed as the number of birds/100ha. The area of bayshore habitat at each site (BA) report the total potential area of bayshore habitat at each site (Max.) and the mean area of bayshore habitat at each site throughout the study (see page 27 for more information on this estimate).

Study Location	N	BA		Abundance			Density		
		Max.	Mean	Mean	SE	Max.	Mean	SE	Max.
<i>Bay Ecosystem</i>									
Bolivar Flats	40	188	102	50.2	4.26	119	49.2	5.2	116.7
Big Reef	23	58	29	19.7	6.78	54	68.1	13.2	203.4
San Luis Pass	65	72	42	23.4	4.03	75	56.3	6.3	192.3
<i>Ecotone</i>									
East Flats	7	246	136	49.3	12.29	189	36.2	19.8	139.0
Mustang Island State Park - North	30	61	33	7.4	4.79	39	22.3	5.1	118.2
Mustang Island State Park - South	13	69	40	0.0	0.0	0	0.0	0.0	0.0
Packery Channel	47	179	107	14.7	4.74	75	13.7	2.6	70.1
<i>Lagoon Ecosystem</i>									
LANWR - Rincon Buena Vista	31	161	95	17.4	5.37	100	18.5	5.5	112.4
LANWR - South Horse Flats	35	28	16	1.2	5.49	40	7.9	6.7	235.3
LANWR - Redhead Cove	37	36	27	5.7	5.34	130	21.0	13.7	500.0
LANWR - North Yucca Flats	43	91	50	17.1	4.96	97	34.4	7.4	167.2
South Bay - West	21	100	51	0.0	0.00	0	0.0	0.0	0.0
South Bay - East	29	642	270	19.1	3.17	202	7.8	3.4	82.8
SPI - North Area	6	812	508	355.3	13.27	543	69.9	11.5	106.9
SPI - Convention Center	19	4	2	2.9	3.91	18	144.7	65.3	900.0
SPI - Parrot Eye's	21	4	2	2.5	3.72	16	123.8	50.4	800.0
SPI - Mangrove Flats	25	8	4	3.1	3.41	17	78.0	25.1	425.0

Abbreviations: LANWR = Laguna Atascosa National Wildlife Refuge, SPI = South Padre Island.

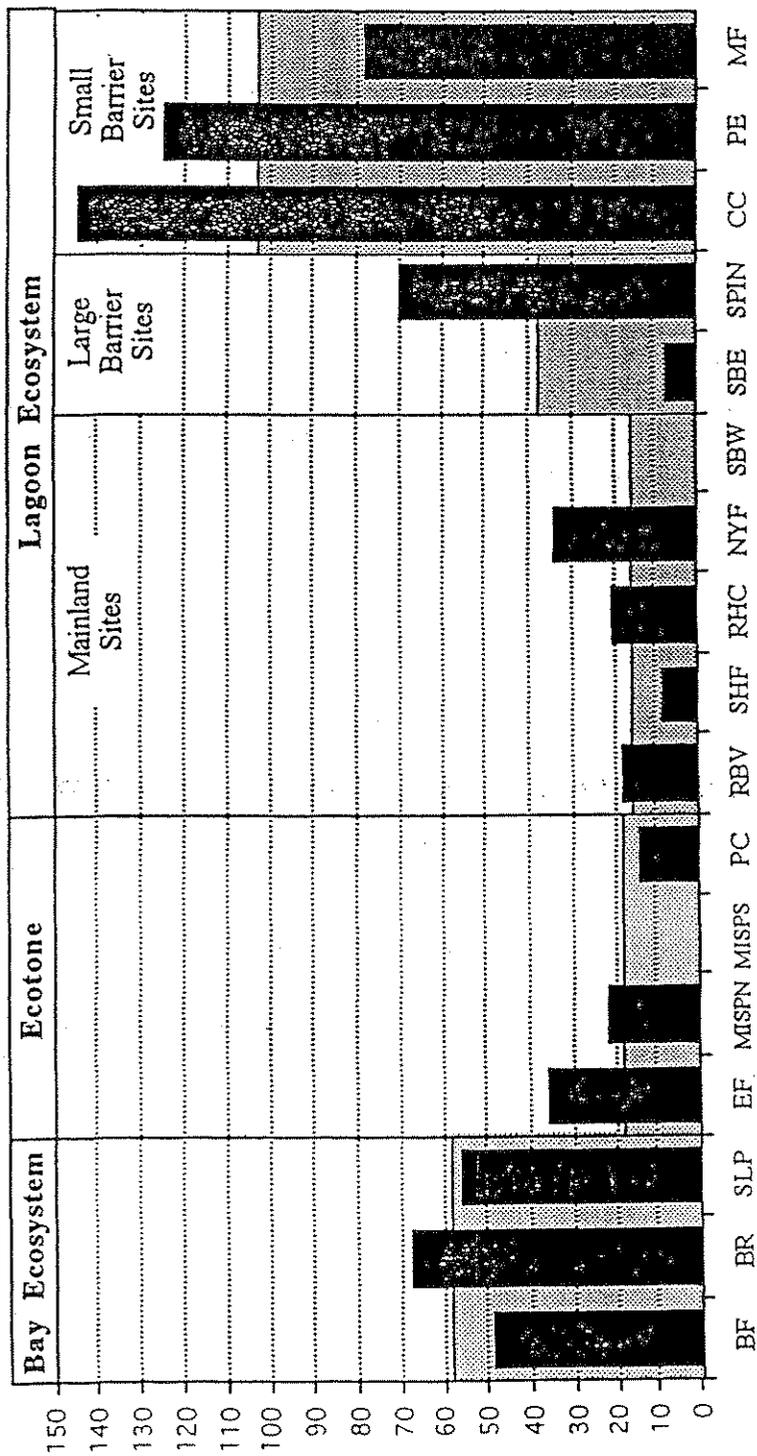


Figure 9. Mean site density and ecosystem density of Piping Plover at bayshore habitat along the Texas Gulf Coast, 1991 - 1994. Black bars represent site density estimates, gray bars represent ecosystem density estimates. Different lagoon ecosystem density estimates are presented for mainland sites, large barrier island sites and small barrier island sites.

*Site Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISPN - Mustang Island State Park - North, MISPS = Mustang Island State Park - South, PC = Packery Channel, RBV = Rincon Buena Vista, SHF = South Horse Flats, RHC = Redhead Cove, NYF = North Yucca Flats, SBW - South Bay - West, SBE = South Bay East, SPIN = South Padre Island - North, CC = Convention Center, PE = Parrot Eye's, MF = Mangrove Flats.

Table 4. Piping Plover population density and human disturbance at beach and bayshore habitat from the 2 ecosystems and the ecotone along the Texas Gulf Coast. Parameters are summarized as means for each location. Multi-factor ANOVA results of pair-wise comparisons between the ecosystems and the ecotone are presented in the last 3 columns. Piping Plover site density is represented as the number of plovers/km at beach habitat, and as the number of plovers/100ha at bayshore habitat. Human disturbance was estimated as the mean number of vehicles/km at beach habitat, and as the mean # vehicles/100ha at bayshore habitat.

Parameter	Bay Ecosystem		Ecotone		Lagoon Ecosystem		Bay vs. Lag.	Bay vs. Eco.	Eco. vs. Lag.			
	mean	N	SE	mean	N	SE						
Beach Density	1.90	119	0.41	3.37	163	0.35	1.68	52	0.62	0.5787	< 0.0001	0.0002
Beach Disturbance	1.89	87	0.29	2.65	109	0.26	1.97	35	0.46	0.5045	0.4341	0.9413
Bayshore Density	58.2	127	7.1	42.0	135	8.4	69.5	100	8.1	0.0284	0.0304	0.7835
Bayshore Disturbance	8.8	69	1.9	4.8	90	1.6	2.3	81	1.7	0.0027	0.0834	0.3729

Bay = bay ecosystem, Eco = ecotone, Lag = lagoon ecosystem.

+flats than on mainland flats within the lagoon ecosystem during emergent tide conditions ($P = 0.0139$). For this reason, data from the lagoon ecosystem mainland sites were excluded from other analyses to avoid compromising comparisons using data from sites in the bay ecosystem and ecotone which were located exclusively on barrier islands.

I observed a significantly higher mean density of Piping Plovers at bay ecosystem flats than at lagoon ecosystem flats ($P = 0.0284$; Table 4) or at ecotone flats ($P = 0.0304$; Table 4). I detected no difference in the density of Piping Plovers at lagoon ecosystem flats and ecotone flats ($P = 0.7835$; Table 4).

Piping Plovers used beaches when the bayshore tides were high and bayshore tidal flats were inundated. Bayshore tidal amplitude was strongly associated with Piping Plover density at beach habitat in both ecosystems and the ecotone (Table 5). As bayshore flats became inundated, the density of Piping Plovers at beaches increased significantly at the bay ecosystem ($P < 0.0001$), ecotone ($P < 0.0001$), and lagoon ecosystem ($P = 0.0021$).

Bayshore tidal amplitude also strongly influenced the density of Piping Plovers at bayshore habitat (Table 5). As bayshore flats became inundated, the total density of Piping Plovers using bayshore habitat decreased in the bay ecosystem ($P = 0.0011$; Table 5) and the lagoon ecosystem ($P = 0.0046$; Table 5). However, there was no detectable tide effect in the ecotone ($P = 0.3652$; Table 5).

Climatic Conditions, Time of Day and Season

With one exception, climatic conditions (Table 6), time of day (Table 7), and season (Table 8) were not related to Piping Plover density at beach habitat. Piping Plover density was higher at ecotone beaches during migration than during the winter period ($P = 0.0173$; Table 8). Human disturbance also did not significantly affect Piping Plover density at beach habitat ($P = 0.3817$; Figure 10).

Climatic conditions (Table 6), time of day (Table 7), season (Table 8) and bayshore

Table 5. The effects of bayshore tidal amplitude on Piping Plover density. Mean Piping Plover beach and bayshore densities are presented for the bay ecosystem, lagoon ecosystem, and ecotone as they were recorded during emergent and inundated tidal conditions. Beach densities are expressed as the number of plovers/kilometer. Bayshore densities are expressed as the number of plovers/100 hectares. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing plover densities between the 2 tide ranks.

Ecosystem	Emergent			Inundated			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Beach Habitat							
Bay Ecosystem	0.60	89	0.26	3.91	46	0.36	< 0.0001
Ecotone	1.81	118	0.39	7.48	45	0.64	< 0.0001
Lagoon Ecosystem	0.35	40	0.79	6.12	12	1.44	0.0021
Bayshore Habitat							
Bay Ecosystem	71.5	85	4.9	31.4	42	7.0	0.0011
Ecotone	40.0	87	8.9	31.1	38	14.9	0.3652
Lagoon Ecosystem	46.6	211	8.5	23.7	74	14.9	0.0046

Table 6. The effects of climate on Piping Plover density along the Texas Gulf Coast, 1991 - 1994. Mean Piping Plover beach and bayshore densities are presented for the bay ecosystem, lagoon ecosystem, and ecotone as they were recorded during mild and harsh climatic conditions. Beach densities are expressed as the number of plovers/kilometer. Bayshore densities are expressed as the number of plovers/100 hectares. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing plover densities between the 2 climate ranks.

Ecosystem	Mild			Harsh			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Beach Habitat							
Bay Ecosystem	1.40	69	0.32	1.24	34	0.45	0.9169
Ecotone	3.54	94	0.53	3.38	53	0.71	0.5241
Lagoon	0.92	27	0.71	2.14	12	1.06	0.8601
Bayshore Habitat							
Bay Ecosystem	68.0	60	6.7	60.6	31	9.3	0.6845
Ecotone	31.7	93	9.2	28.7	47	13.0	0.6816
Lagoon Ecosystem	53.2	166	9.4	25.1	82	13.4	0.4427

Table 7. The effects of time of day on Piping Plover density along the Texas Gulf Coast, 1991 - 1994. Mean Piping Plover beach and bayshore densities are presented for the bay ecosystem, lagoon ecosystem, and ecotone as they were recorded during morning (0600 - 1200) and afternoon (1200 - 1800) periods. Beach densities are expressed as the number of plovers/kilometer. Bayshore densities are expressed as the number of plovers/100 hectares. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing plover densities between the 2 time of day ranks.

Ecosystem	Morning			Afternoon			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Beach Habitat							
Bay Ecosystem	1.75	86	0.32	2.50	23	0.62	0.5289
Ecotone	3.83	73	0.54	2.37	21	1.00	0.3657
Lagoon	0.67	26	1.13	3.61	19	1.33	0.1596
Bayshore Habitat							
Bay Ecosystem	53.2	75	5.3	56.7	29	8.5	0.9422
Ecotone	30.6	46	18.4	72.2	45	18.6	0.9724
Lagoon Ecosystem	45.6	131	10.9	48.2	122	11.3	0.5154

Table 8. Piping Plover densities during the winter and migratory periods at sites along the Texas Gulf Coast, 1991 - 1994. Mean Piping Plover beach and bayshore densities are presented for the bay ecosystem, lagoon ecosystem, and ecotone as they were recorded during migratory and winter periods. Beach densities are expressed as the number of plovers/kilometer. Bayshore densities are expressed as the number of plovers/100 hectares. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing plover densities between the 2 season ranks.

Ecosystem	Migration			Winter			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Beach Habitat							
Bay Ecosystem	1.84	77	0.33	1.58	58	0.38	0.6149
Ecotone	4.61	58	0.64	2.69	105	0.48	0.0173
Lagoon Ecosystem	1.50	24	1.14	1.83	28	1.05	0.8314
Bayshore Habitat							
Bay Ecosystem	55.0	76	5.6	63.0	51	6.9	0.3724
Ecotone	38.3	70	11.7	37.2	94	10.1	0.9452
Lagoon Ecosystem	37.7	110	11.6	43.2	175	9.7	0.7163

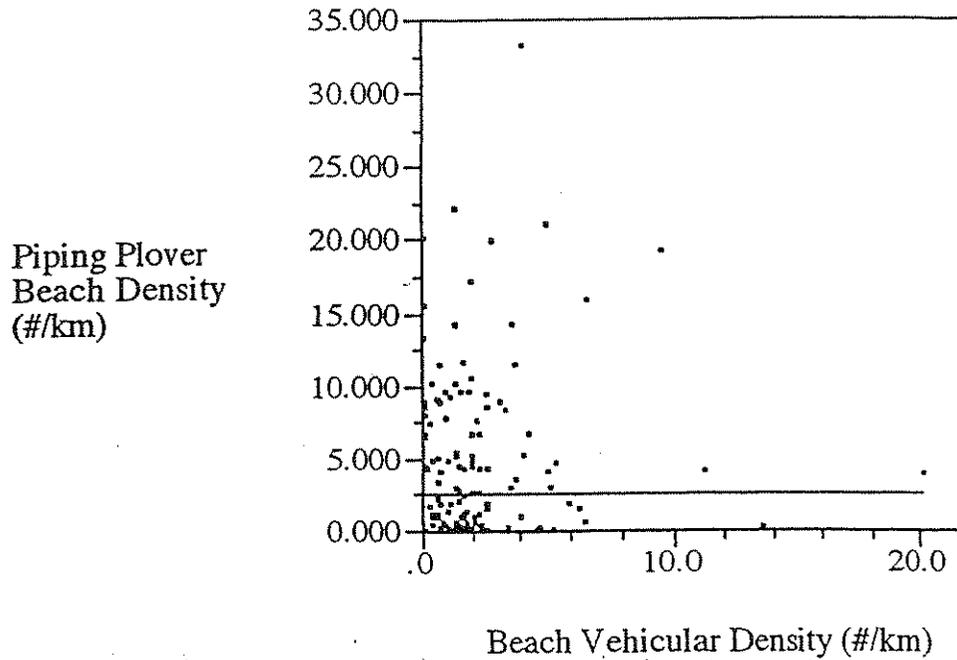


Figure 10. The effects of human disturbance on Piping Plover beach density at sites along the Texas Gulf Coast, 1991-1994. A solid regression line illustrates the relationship between human disturbance (estimated as the density of vehicles present at site beaches during the beach plover counts) and Piping Plover beach density. The analyses suggests that human disturbance had no direct effect on the use of beach habitat by Piping Plovers ($P = 0.3817$).

human disturbance (# vehicles/ha; Figure 11) seemingly were not related to Piping Plover density at bayshore habitat.

Beach Tidal Amplitude

I analyzed Piping Plover beach density in relation to beach tidal amplitudes at 3 sites where I was able to accurately monitor beach tidal amplitude during at least a portion of the study. As beach tidal amplitude increased, Piping Plover beach density also increased at Mustang Island State Park - North ($P = 0.0051$; Table 9). However, Piping Plover beach density was unrelated to beach tidal amplitude at Packery Channel ($P = 0.8764$; Table 9) and at San Luis Pass ($P = 0.6419$; Table 9). In comparison, bayshore tidal amplitude was significantly associated with Piping Plover beach density at Mustang Island State Park - North ($P = 0.0099$; Table 9) and Packery Channel ($P = 0.0017$; Table 9), but not San Luis Pass ($P = 0.3278$; Table 9).

Whereas the tidal regime influenced both beach and bayshore habitats, the most salient effect of the tides appeared to be how they affected the local availability of bayshore tidal flats. Distinguishing between the effects of the tidal regime on beach and bayshore was confounded by the fact that beach and bayshore tides were synchronous along many portions of the Texas coast (pers. obs.). That is, as tides rose and covered bayshore tidal flats, the high tide changed the level of the beach intertidal zone (i.e., swash zone) at many of the sites. This situation raises the possibility that plovers used beaches not because the tides made bayshore tides unavailable, but rather because high tides increased the availability of preferred habitat along the beach shoreline. This might result, for example, if the availability of prey populations residing within higher zones of the forebeach habitat increased significantly as high tides inundated these zones. If this were true, plovers should use beach habitat in response to beach tidal amplitude and not bayshore tidal amplitude at a site where the beach and bayshore tidal regimes are asynchronous. Fortunately, one of the sites I monitored exhibited asynchronous tides.

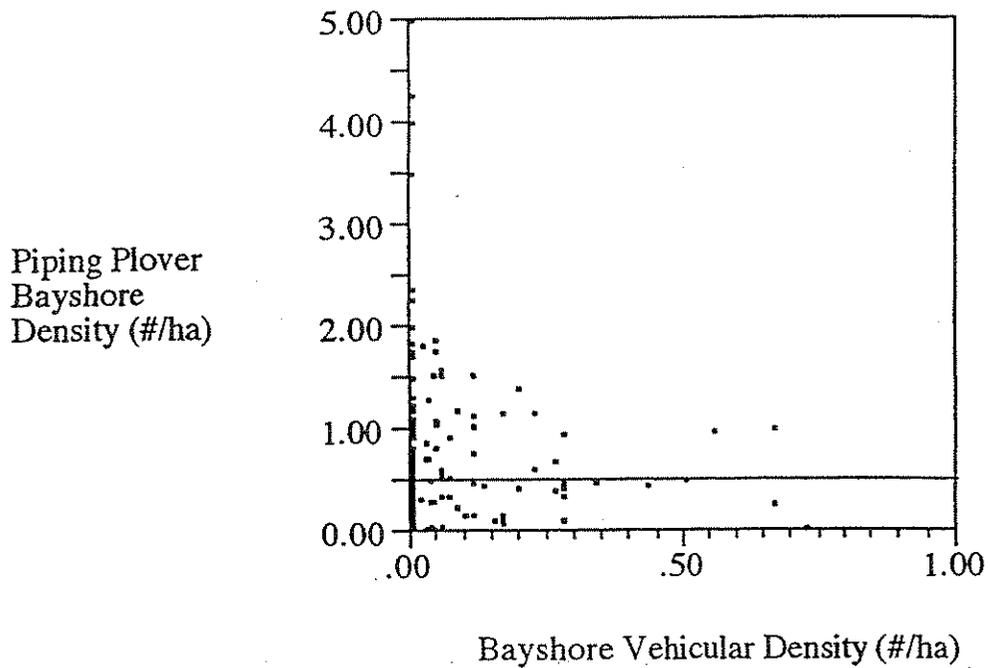


Figure 11. The effects of human disturbance on Piping Plover bayshore density at sites along the Texas Gulf Coast, 1991-1994. A solid regression line illustrates the relationship between human disturbance (estimated as the density of vehicles present at site bayshore habitat during the bayshore plover counts) and Piping Plover bayshore density. The analyses suggests that human disturbance had no direct effect on the use of bayshore habitat by Piping Plovers ($P = 0.9984$).

Table 9. The effects of beach tidal amplitude on Piping Plover density. Mean Piping Plover density at beach and bayshore habitats are presented for the 3 sites where beach tidal amplitude was measured. The proportional effect on Plover density caused by beach tidal amplitude is expressed as R^2 . The significance of the effect is expressed as a P -value in the last column. Abbreviations: MISP = Mustang Island State Park.

Ecosystem	N	R^2	P-value
Beach Density			
MISP - North	22	0.2624	0.0051
Packery Channel	27	0.0008	0.8764
San Luis Pass	24	0.0148	0.6419
Bayshore Density			
MISP - North	22	0.2221	0.0099
Packery Channel	27	0.2916	0.0017
San Luis Pass	24	0.0638	0.3278

Among the 3 sites I monitored for beach tidal amplitude, beach and bayshore tides were synchronous at San Luis Pass ($P < 0.0001$, $N = 17$) and Mustang Island State Park - North ($P = 0.0170$, $N = 29$), but asynchronous at Packery Channel ($P = 0.8764$, $N = 31$). At Packery Channel, Piping Plover density was correlated with bayshore tides but not beach tides. Considered together, these data suggest that bayshore tidal amplitude was a better predictor of Piping Plover habitat use than was beach tidal amplitude.

DISCUSSION

Objective 1. Piping Plover Density

Beach Habitat

My estimates of Piping Plover density compare closely with most estimates from other studies in Texas. With 2 exceptions (Big Reef and South Padre Island), I found Piping Plovers to use beach habitat at a higher density than the 1.4 - 1.6 birds/km estimate reported for Texas by Nicholls and Baldassarre (1990b). Elliott and Teas (1996) reported beach densities of 1.11 birds/km, 3.13 birds/km and 4.51 birds/km at 3 Texas coastal sites. One of the sites monitored by Elliott and Teas (1996) was the same site I refer to as Packery Channel (the site was called Surfer Beach by Elliott and Teas). Their 2-year mean estimate of 3.13 plovers/km at Packery Channel beach compares closely with my 3-year mean of 3.59 plovers/km.

Lee (1995) reported a mean density of 3.41 Piping Plovers/km at the Mustang Island State Park - North site during portions of the nonbreeding season in 1990 and 1991. This estimate compares closely with my estimate of 3.22 plovers/km at the same site. Chapman (1984) reported a diurnal mean of 3.0 Piping Plovers/km along an 8.1 km stretch of beach located just south of the Packery Channel site. During surveys conducted between 1992 - 1995, Chaney et al. (1995) reported that the annual Piping Plover beach density on Padre Island National Seashore (located just south of the Packery

Channel site, and the same area counted by Chapman [1984]) varied from 0.48 plovers/km to 2.1 plovers/km. Their estimates were based upon counts made throughout the year, however, including the summer period when many Piping Plovers were at breeding sites away from Texas. For this reason, the density values reported by Chaney et al. (1995) almost certainly underestimated the mean beach density of plovers on North Padre Island during the winter period.

Whereas the southern portion of the Padre Island National Seashore can be accurately classified as belonging to the lagoon ecosystem, most of the density estimates described above were measured at ecotone beaches. My data suggest that Piping Plovers used beaches in the ecotone at greater densities than those located in the bay or lagoon ecosystem. Plovers occurred at an average density of about 1.75 plovers/km in the bay ecosystem and lagoon ecosystem. Whereas my density estimates for beach sites in the 2 ecosystems more closely approximate those by Nicholls and Baldassarre (1990b), the average beach density of Piping Plovers at all of the sites, 2.29 plovers/km, was appreciably higher than their estimate of 1.4 - 1.6 plovers/km.

Bayshore Habitat

Density estimates for Piping Plover use of bayshore habitat are rare, probably due to the difficulty associated with accessing bayshore sites, and accurately quantifying the area of tidal flat habitat being counted. Garza (1997) reported bayshore densities for Piping Plovers using 15 sites on South Padre Island in 1994. With a single exception (Site 9, which supported an average of about 48 plovers/100 ha), all of the sites monitored by Garza were estimated to support fewer than 20 plovers/100 ha. Surprisingly, these findings contrast starkly with my estimates of approximately 78 - 145 plovers/100 ha at many of the same locations.

In the Laguna Madre, the mainland sites I monitored supported a much lower density of Piping Plovers than did the barrier island sites. However, under certain conditions the

mainland flats supported very large flocks (> 95 birds) of Piping Plovers. Peak use of mainland sites by Piping Plovers occurred during emergent conditions. On the mainland, these conditions were most common during the passage of winter north fronts. The strong winds accompanying these fronts often caused mainland flats to become emergent, and barrier island flats to become inundated. These conditions presumably caused plovers to migrate across the Laguna Madre from barrier islands flats to mainland flats. Until recently, such movement patterns were largely speculative. However, a radiotelemetry study investigating the movement patterns of Piping Plovers in the Lower Laguna Madre has confirmed that many Piping Plovers regularly migrate between the barrier island and mainland flats during the same winter period (Zonick et al. 1998).

Objective 2. Factors affecting Piping Plover density.

The local density of Piping Plovers at the beach and bayshore sites was most strongly influenced by 2 parameters, bayshore tidal amplitude and ecosystem type.

Bayshore Tidal Amplitude

Bayshore tidal amplitude affected density in a proximate fashion by directing the short-term movements of Piping Plovers between beach and bayshore habitat. As rising bayshore tides covered local bayshore feeding areas, plovers sought out alternative feeding habitat or suitable roost sites. Beach habitat was frequently used as a secondary habitat during periods of bayshore inundation, but washover passes and mainland tidal flats also appeared to provide important secondary habitats for Piping Plovers.

Lee (1995) found Piping Plover beach density to increase with falling beach tidal amplitude and decreasing availability of bayshore habitat (i.e., increasing bayshore tidal amplitude). My observations at the Mustang Island State Park and Packery Channel sites, which together encompass both of Lee's beach sites, suggest that bayshore tidal amplitude, and not beach tidal amplitude, directs the movements of plovers between beach and bayshore habitats. This finding suggests that plovers used beach habitat as a

secondary feeding site, preferring bayshore habitat when available. Connors et al. (1981) reported a similar tidal response by Sanderlings (*Calidris alba*) and Snowy Plovers (*Charadrius alexandrinus*) along the California coast. There, Sanderlings and Snowy Plovers cycled between beach and bayshore habitat, using beaches during periods of bayshore tidal inundation.

Interestingly, Elliott and Teas (1996) reported no relationship between Piping Plover beach density and bayshore tidal amplitude at 2 ecotone beaches, but did find a positive relationship between bayshore tidal amplitude and Snowy Plover beach density. Furthermore, Withers (1994) reported a positive relationship between bayshore tidal amplitude and Piping Plover bayshore density at Corpus Christi Pass, a site situated between the Packery Channel and Mustang Island State Park - South sites. In fact, Withers observed all shorebird species but Snowy Plovers to increase in abundance at bayshore habitat with increasing bayshore tide height. Withers detected a decrease in Snowy Plover abundance with bayshore tidal inundation (Withers 1994). These findings contrast with my findings and with those reported by Lee (1995) regarding the response by Piping Plovers to bayshore tidal conditions.

Withers' observations were restricted to bayshore habitat, so I will limit comparisons of our findings to that habitat. My data suggest high bayshore tides caused Piping Plover bayshore density to drop in the bay and lagoon ecosystems, but not in the ecotone. In the ecotone, I observed plover bayshore abundance to decline somewhat during periods of tidal inundation relative to periods of emergence (by ~ 23%; Table 5), but the difference was not significant. Furthermore, Piping Plovers often declined at the ecotone sites as bayshore tide levels dropped from moderate - very low. I scored bayshore tidal amplitude into 1 of 5 ranks (very high, high, moderate, low and very low; ranks are described in the Methods section). At Packery Channel, the mean number of Piping Plovers using bayshore habitat during very high, high, moderate, low and very low

bayshore tides was 2.3, 10.4, 18.9, 16.9, and 14.6, respectively. Therefore, plover bayshore abundance peaked near the moderate-low tide ranks, and declined somewhat if the tide dropped to a very low state. Presumably, during low and very low tides Piping Plovers moved to rarely-exposed off-site feeding areas.

The reduction in plover abundance at ecotone sites during extreme low tide episodes complicated the relationship between bayshore tidal amplitude and the use of bayshore habitat by plovers. However, my data suggest that plovers were much more common at bayshore habitat during emergent conditions (i.e., very low - moderate bayshore tides), even though they occasionally sought out off-site feeding areas during very low tide events. Plovers moved to beach habitat and washover pass habitat during periods of bayshore inundation (i.e., high-very high bayshore tides).

The Elliott and Teas (1996) study was restricted to beach habitat where they initially reported Piping Plover beach density to be unaffected by bayshore tidal conditions. My findings disagree with their reported findings and indicate bayshore tides strongly affect plover beach use. At Packery Channel, I recorded mean Piping Plover beach abundance during very high, high, moderate, low and very low bayshore tides of 44.1, 27.8, 9.9, 2.6, and 0, respectively. Furthermore, at Mustang Island State Park - North, a site lying just north of Elliott and Teas' Surfer Beach site (i.e., Packery Channel), the mean number of Piping Plovers using beach habitat during very high, high, moderate, low and very low bayshore tides was 16.7, 23.0, 5.3, 2.6, and 0, respectively. I never visited Mustang Island State Park - South during very high or high bayshore tides, and therefore have data only for moderate-very low tide ranks. However, during moderate, low and very low bayshore tides, I found 13.0, 1.0, and 0 Piping Plovers using beach habitat, respectively. Thus, at 3 south ecotone sites located near Elliott and Teas' Surfer Beach site, I observed a steady and significant ($P < 0.0001$ for Packery Channel and Mustang Island State Park - North, $P = 0.0105$ for Mustang Island State Park - South; data not shown) decline in the

abundance and density of plovers on beaches as the bayshore habitat became emergent.

Based upon these findings, the authors (L. Elliott) conducted a revised analysis of their data and concluded that bayshore tides did correlate with Piping Plover beach density ($R^2 = 0.403$, $P < 0.0001$), and the contrary finding in Elliott and Teas (1996) was inaccurate (L. Elliott, pers. comm.).

The apparent preference by Piping Plovers for bayshore habitat is supported by another observation. Whereas beach use clearly appeared to be controlled by bayshore tidal amplitude, high bayshore tides did not always cause plovers to move to beach habitat. I was occasionally unable to locate Piping Plovers during periods of high bayshore tide. Such occurrences were most common in the lagoon ecosystem where bayshore tides were influenced to a much greater degree by wind forces and where mainland tidal flats were much more suitable as feeding areas than were those in the bay ecosystem and in the ecotone. Wind tides often had local effects, inundating one flat while exposing a neighboring flat (e.g., this would occur at 2 flats on opposing sides of a small lagoon). With the exception of those associated with tropical storms, wind tides in the lagoon ecosystem usually exposed new areas of bayshore habitat as others were becoming flooded. Therefore, plovers feeding in the lagoon ecosystem often had an alternative to beach habitat during periods of locally high bayshore tides. They were able to move to alternative bayshore habitat sites that had become emergent by the same tide that inundated the site they were forced to abandon. Under this scenario, a plover being forced off of a tidal flat along a lagoon might fly into the wind to cross the lagoon and light on the opposite shoreline where baywaters were being blown off of the flats.

During the study, I observed several Piping Plovers that had been color banded by other biologists. Among those plovers that I was able to resight more than once during the study was an individual that used all 3 of the lagoon ecosystem sites during the same winter. These observations suggest that, in addition to crossing the Laguna Madre to

move between mainland and barrier island sites, some Piping Plovers appeared to use a mosaic of many bayshore sites throughout the winter. Radiotelemetric tracking of Piping Plovers in the lagoon ecosystem has further supported this hypothesis (Zonick et al. 1998). Presumably, movements among these sites are directed to a great extent by the local availability and productivity of bayshore feeding areas.

Ecosystem Features and Landscape

Piping Plover density was also affected by ecosystem and landscape features along the Texas Gulf Coast. Plovers were more common at ecotone beaches than in either ecosystem. Whereas my data do not directly demonstrate why plover beach density was highest in the ecotone, I believe indirect inferences can be drawn from information presented in this chapter and that presented in the following chapter.

As previously demonstrated, one of the major features distinguishing the 3 coastal regions was the tidal regime, and the way the tides influenced local bayshore feeding areas. The discussion above describes clearly why plovers may have been less common at lagoon ecosystem beaches than at those in the ecotone throughout the tidal cycle. Plovers in the lagoon ecosystem were more likely to seek out alternative bayshore feeding areas in preference to beach habitat when local bayshore feeding sites became inundated.

However, tidal variations among the 2 ecosystems and the ecotone did not appear to explain all of the differences in local plover density. Multi-factor ANOVA models identified an ecosystem effect on plover density that was independent of the bayshore tidal effect, suggesting some other factor may affect the use of beach habitat. As I describe in the next chapter, the bayshore prey communities at the sites also differed markedly among 2 ecosystems and the ecotone. Bayshore habitat in the bay ecosystem supported a much higher mean prey density than did that in the ecotone or the lagoon ecosystem. Therefore, plovers wintering within the bay ecosystem may have been able to

build sufficient fat stores to allow them to seek roost refugia during many high tides rather than risk predation and other potential deleterious effects that might be incurred by periods of extended feeding. Bayshore flats in the ecotone may not have been sufficiently productive to allow resident plovers to avoid as many high tide foraging episodes as plovers in the bay ecosystem.

An alternative explanation may be that periods of bayshore inundation lasted longer in the ecotone than in the bay ecosystem, thereby forcing plovers in the ecotone to seek alternative feeding sites (e.g., beach habitat) more often. Unfortunately, my data allow for only a crude investigation of this hypothesis. I encountered inundating tides during 33.6% of all censuses in the bay ecosystem, but during only 26.9% and 25.5% of all censuses in the ecotone and lagoon ecosystem, respectively. These data suggest that ecotone tidal flats (and lagoon tidal flats) were not inundated longer than bay ecosystem tidal flats and probably were inundated for shorter periods of time. Tidal flats in the ecotone and lagoon ecosystem may often have been subject to only partial inundation. This, combined with higher baywater salinities relative to the bay ecosystem, may have limited the availability of productive bayshore habitat in the ecotone and forced plovers to use beach habitat to a greater extent.

Finally, Piping Plovers were more common on emergent barrier island tidal flats than on emergent mainland tidal flats. The prey density data I collected can be used to suggest an hypothesis as to why this might be so. As I discuss in Chapter III, benthic prey density was significantly higher at lagoon ecosystem barrier island flats than at mainland flats. Therefore, the observed higher use of barrier islands may simply reflect a preference by Piping Plovers for more productive feeding areas.

CHAPTER III. PREY DYNAMICS AND PIPING PLOVER BEHAVIOR

INTRODUCTION

Perhaps more than any other parameter, prey density has been associated with shorebird ecology and linked to local abundance and fitness (Goss-Custard 1984, Hicklin and Smith 1984, Wilson 1990, Colwell 1993). This is particularly true for wintering shorebirds (Duffy et al. 1981, Myers and McCaffery 1984, Myers et al. 1987). Because of their demanding life strategy, involving long migratory journeys and the reliance upon numerous ephemeral staging sites, the winter period is considered critical for shorebirds (Myers et al. 1987). During winter, shorebirds must rebuild fat stores that have been depleted during fall migration to levels that will allow them to survive the winter period and help power a return migration to their breeding grounds in the spring (Blem 1990). Individuals that are best able to find and capture prey during the winter and maintain optimal fat stores are presumably most likely to arrive early and fit at their breeding grounds. Thus, shorebirds benefit reproductively by occupying winter sites with a reliable food supply. For this reason, estimating the availability of food to plovers among the different habitats and ecosystems of the Texas Coast was an important goal of my research.

The diet of wintering Piping Plovers had only been partially characterized at the time this study was initiated (Nicholls and Baldassarre 1990a). A better understanding of the species diet in Texas was required to evaluate what portions of the available prey community were available to the plovers. The task of describing and quantifying prey availability to plovers was complicated by observations indicating plovers fed in large part on surface prey populations (e.g., flies and other non-burrowing insects), particularly in the lagoon ecosystem (pers. obs, T. Eubanks pers. comm.). I addressed these problems by documenting the diet of plovers while concurrently sampling the prey community in areas where plovers were feeding using several different techniques.

Due to the rarity of the Piping Plover, some techniques commonly employed to evaluate bird diets (e.g., the evaluation of stomach contents from dissected birds or birds palpated to induce regurgitation) could not be used. The analysis of fecal dropping is a non-invasive technique that has been used to evaluate Piping Plover diet (Nicholls 1989, Shaffer and LaPorte 1994). Nicholls (1989) analyzed a small number of fecal samples from Piping Plovers wintering in Texas. From 4 samples collected from habitats at Bolivar Flats and 1 sample collected at San Luis Pass (all at bayshore habitat), Nicholls observed fragments of polychaetes in all samples, insects in 3 samples, and fragments of bivalves, ostracods, and copepods in 2 -3 samples each. In 2 samples collected at beach habitat on Mustang Island, Nicholls found polychaetes and crustaceans (Copepoda) in 1 sample, and insect fragments (Diptera) and amphipods (Haustoriidae) in another. From 2 samples collected at bayshore habitat in the lagoon ecosystem, Nicholls found insect fragments in 1 and polychaete fragments in the other.

Unfortunately, fecal sample analysis provides only a crude assessment of a shorebird's diet. Soft-bodied organisms are rapidly and nearly totally digested, resulting in an under-representation of annelids and other soft-bodied animals in the description of the diet (e.g., Shaffer and Laporte 1994). Additionally, shell and carapace fragments residing in the sediment can be ingested incidentally by foraging plovers leading to the inaccurate inclusion of non-prey taxa. I evaluated the Piping Plover diet among different habitats and ecosystem types by observing feeding plovers and directly characterizing the prey they captured into 2 categories (polychaetes and arthropods).

Another important aspect of Piping Plover foraging ecology is foraging success. The rate at which plovers capture prey (i.e., gross intake rate) and the energy plovers expend while feeding are both important factors in determining the net energy return (i.e., net intake rate; Goss-Custard 1984) plovers experience during foraging bouts. Plovers are visual foragers, relying upon visual cues to detect prey (Pienkowski 1979). Factors that

reduce the surface activity of prey animals (e.g., soil desiccation, low air temperature, high winds, precipitation) can also reduce the rate at which plovers capture prey (Pienkowski 1981).

One of the primary focuses of my research involved evaluation of Piping Plover diet in the 2 ecosystems and the ecotone. I also analyzed foraging success to determine whether plovers were able to forage more efficiently in either ecosystem. Additionally, I compared prey populations and plover foraging success at bayshore tidal flats and beaches, the 2 major habitat types used by plovers along the TGC.

I addressed these goals by monitoring 1) the amount of time plovers spent foraging, 2) an index of the amount of energy plovers expended while foraging, and 3) the rate at which plovers captured prey among ecosystems and habitat types. Collectively, these data allowed me to describe the prey resources that were most available to Piping Plovers, as well as investigate how these prey resources differed in availability among habitat types, ecosystem types and landscape types along the TGC, and how well plovers were able to exploit these resources. These observations address large gaps in the current understanding of Piping Plover winter ecology.

Data from this section also were used in the development of the model predicting the factors that most strongly affected Piping Plover site abundance. This model is presented in Chapter IV.

METHODS

Prey Dynamics

I sampled potential prey populations from areas that were being used by foraging Piping Plovers at the time of sample collection. During preliminary observations, I found Piping Plovers to forage on prey animals occurring below the ground (benthic prey), and also on prey animals occurring at or above the ground surface (surface prey).

To address this, I sampled prey populations in several different ways. Sampling strategies consisted of the collection of soil cores (benthic prey), the deployment of sticky traps (surface prey), visual surveys of prey using a spotting scope (surface prey), and the collection of algal mat cores (benthic to surface prey, depending upon the developmental stage of the prey animal).

Transect Layout

All prey samples were collected along transects established within areas recently (within minutes) used by one or more foraging Piping Plovers (Figures 12 and 13). The dimensions of the transects were dictated by either the dimensions of the foraging flock being sampled, or the area used by an isolated plover subject (if the plover was foraging alone).

Plovers often fed in large flocks at bayshore habitat. Foraging flocks were sampled in order of size, beginning with the largest flock. The number of samples/day I collected was limited only by the number of foraging flocks of Piping Plovers observed, by the time required to collect and transport the samples back to research vehicles from the study area, and by the physical weight of the samples I was capable of carrying. Prey samples also were collected in areas where individual plovers were foraging alone, particularly at beach habitat where plovers aggressively defended foraging territories. Samples collected in association with solitary plovers using bayshore habitat were compared to those collected in association with foraging plover flocks.

My samples were specifically directed at appraising the prey community locally available to Piping Plovers during foraging episodes. They do not necessarily reflect the prey density available throughout the study site.

Benthic Prey Samples

Macroscopic benthic (i.e., subsurface) animals were sampled via a series of 5 soil cores/transect (Figures 12 and 13). Each core was 10 cm deep x 7.5 cm in diameter.

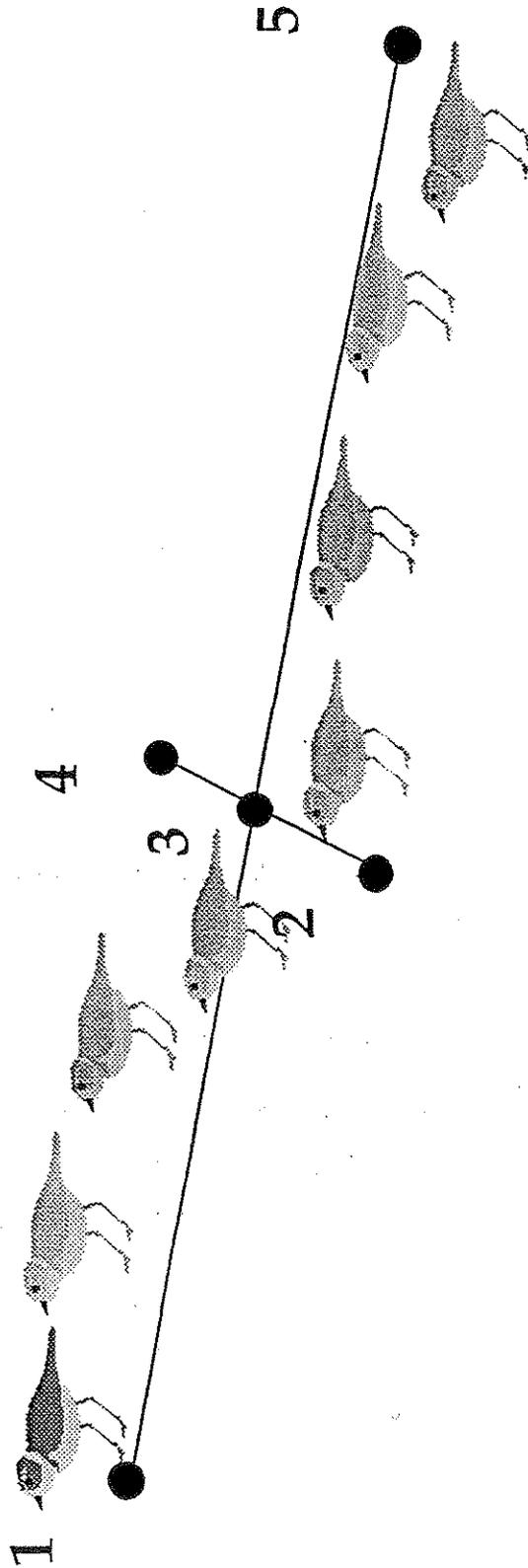


Figure 12. Strategy used to collect prey samples in areas occupied by a single foraging Piping Plover. A +-shaped transect was positioned within the area used by the plover immediately preceding sample collection. In this figure, the single foraging Piping Plover is represented by a darkly shaded figure on the extreme left. To its right, are several lightly shaded figures representing the hypothetical path of the plover immediately prior to sample collection. The sample locations are depicted by filled circles, labelled 1 - 5. I collected sample 3 from the center of the area covered by the plover. Samples 1 and 5 were collected from the outer limits of the area's long dimension. Samples 2 and 4 were collected 3 - 5 meters on each side of the center sample (sample 3) along an axis perpendicular to the area's long dimension.

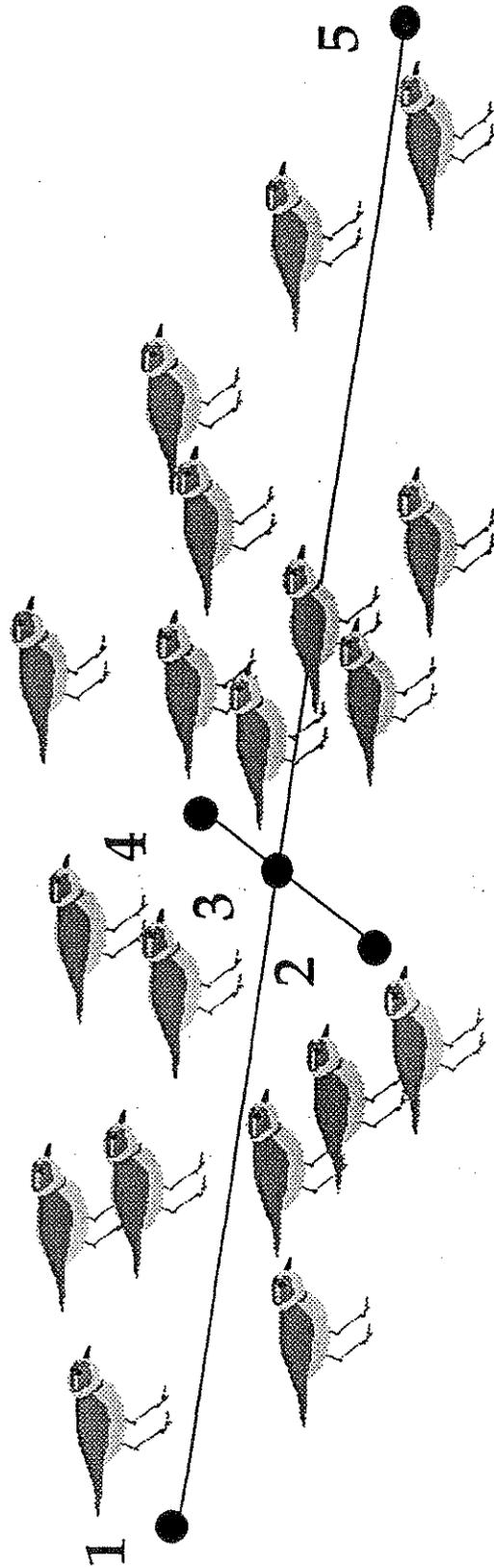


Figure 13. Strategy used to collect prey samples in areas occupied by a flock of foraging Piping Plovers. A + shaped transect was positioned within the flock. The sample locations are represented by filled circles, labelled 1 - 5. I collected sample 3 from the center of the flock. Samples 1 and 5 were collected from the outer limits of the flock's long dimension. Samples 2 and 4 were collected 3 - 5 meters on each side of the center sample (sample #3) along an axis perpendicular to the flock's long dimension.

After retrieval, cores were placed in plastic bags and sieved (600 μm) and scored later the same day or early the next morning. Each prey item was classified into one of 4 prey groups (polychaetes, crustaceans, insects, other). Benthic prey were investigated in this way on both beach and bayshore habitat.

Surface Prey Samples

During the 1991 IPPC, I observed Piping Plovers foraging on flies and other prey located above the ground, especially on bayshore habitat. Because these animals (mostly adult insects and spiders) were highly mobile, and could not be accurately represented in core samples, I employed 2 additional techniques, sticky traps and spotting scope sampling, to obtain systematic samples of this portion of the prey community.

Sticky Trap Samples

To estimate surface insect abundance, I used modified sticky traps (Southwood 1996, MacLean and Pitelka 1971, Nordstrom 1990). Each foraging flock was sampled using five square flooring tile pieces (each $\sim 2 \text{ m} \times 15 \text{ cm} \times 15 \text{ cm}$) placed directly on the ground along the same transect used to sample benthic prey (Figure 13). Each tile was displaced approximately 1 m from the position where a soil core was retrieved. The tiles were coated with a 1-2 mm layer of Stickem SpecialTM (Seabrite Enterprises, Emeryville, CA 94608) filling a 12.5 cm diameter circle. These sticky traps were left in position along the transect for 60 minutes. During this period, small animals crawling onto, or landing within the layer of adhesive became trapped and were collected and scored later that night or early the next morning. Because sticky traps were "active" for a full hour, tallies could not be used to estimate above-ground prey density, but were used only as relative measures of abundance.

Spotting Scope Samples

I developed and implemented a second technique during the final year of the study to collect instant counts of the above-ground fauna and allow for instantaneous density

estimates of this portion of the prey community. A spotting scope was positioned at a consistent and reproducible height (tripod legs fully extended, center tripod support fully retracted) near the spot of each sampling position within the transect. The scope was then near-focused to its limit, and pointed down toward the surface until the ground became focused. The scope/tripod-head complex was spun and allowed to come to rest. The radius of ground that the scope was pointing to was "angled into focus" to reveal a 0.95 m² patch of ground that was surveyed (without moving the scope) for surface animals. Animals walking or flying into the field of view during the survey were not counted.

Algal Mat Samples

Where Piping Plovers were observed feeding on algal flats, a single core was taken of the mat near the center of the transect (i.e., sample location #3; Figure 13). Each core was ~ 2 cm deep, and 7.5 cm in diameter. Each core was sealed in a separate Zip-lock™ bag with trapped air, and incubated under a controlled light cycle of 12 hours light /12 hours dark. Each core was checked once per week, throughout a six week period. All emergent animals were collected and scored.

Behavior

I characterized the foraging ecology of Piping Plovers along the TGC, and identified the factors affecting foraging success. One of my goals under this objective was to describe the diets of Piping Plovers in the 2 ecosystems and the ecotone, and among the major habitat types. The other goals of this objective related to foraging effort and foraging success.

To estimate foraging effort and success, I identified Piping Plovers involved in foraging activity during daily bird counts. I approached foraging groups of plovers and monitored randomly selected subjects with regard to their style of locomotion and the efficiency with which they captured different types of prey. The parameters I monitored are described in more detail below under "Piping Plover Foraging Locomotion" and

"Piping Plover Foraging Efficiency".

I used multi-factor models to investigate the relative effects of habitat type, ecosystem type and season on each estimate of foraging success. Additionally, I evaluated the foraging effort of Piping Plovers in relation to the density of different benthic prey groups. Finally, I measured the frequency with which foraging Piping Plovers exhibited aggressive behavior and investigated its expression among the different habitats and microhabitats used by plovers.

Piping Plover Activity

During daily bird counts, I scored the activity of each Piping Plover as either "foraging" or "roosting." I considered foraging plovers to be those that were actively feeding, or that were nearby other foraging plovers during the same count, and were not bathing, roosting or preening (i.e., plovers that appeared to be momentarily pausing between foraging attempts). Plovers scored as "roosting" were birds that were either bathing, roosting, or preening during the count.

Piping Plover Diet

I evaluated the Piping Plover diet from observations of those individuals that I was able to approach closely enough during the foraging efficiency records to identify the types and frequencies of prey that were captured.

I scored prey captured into 1 of 3 classes: 1) polychaetes and other worm-like prey, 2) arthropods and other non-worm-like prey, or 3) unknown. Polychaete captures were usually very obvious, as plovers often pull them out of the sand slowly to avoid breaking the worm.

Piping Plover Foraging Locomotion

I observed Piping Plovers to use 2 predominant styles of foraging motions. One motion, henceforth described as reserved foraging locomotion (RFL), consisted of repeated, short, conserved movements toward prey animals located within 1-2 body

lengths of the plover. The second type of motion was more prolonged, and was often very rapid, and is henceforth described as prolonged foraging locomotion (PFL). Plovers engaged in PFL moved beyond the normal 1-2 body lengths typical of RFL, often not pausing until it reached an area far beyond its initial location.

Because plovers presumably expend more energy during PFL periods relative to RFL periods, I monitored this type of locomotion, as a factor potentially affecting a foraging plover's energy costs, and thereby its net energy intake rate. To document PFL, I watched randomly selected, foraging Piping Plovers for a period of 120 seconds and recorded the amount of time the plover spent in PFL. I defined PFL as any movement beyond 2 plover body lengths, and I timed the duration of all such movements using a stopwatch. I recorded a maximum of 10 records/habitat during each site visit.

During the 120 second period, I also recorded 1) the number of times the plover took flight, 2) the number of aggressive interactions involving the plover, and 3) the number of noticeable human disturbances (e.g., passing vehicles, beachcombers walking by, low-flying airplanes).

Piping Plover Foraging Efficiency

To appraise foraging efficiency, I observed foraging Piping Plovers at close range with a high-resolution spotting scope. During foraging efficiency records, a single, randomly selected plover was observed until it made 50 attempts to capture prey (pecks). Occasionally plovers moved beyond the range necessary for accurate observation, and the record was discontinued before 50 attempts were observed. Among the data recorded during the record were 1) the number of animals captured, 2) the number of pecks [if < 50], 3) the time of record, 4) the number of each prey type captured, 5) the species of nearest shorebird neighbor and 6) the number of aggressive interactions involving the plover during the record. As many records as possible were collected, up to a maximum of 10/habitat/site visit.

To score captures with accuracy it was usually necessary to approach birds to ≤ 50 m. Rather than attempting to sequentially approach each bird present, I sampled plovers by moving in increments of about 100 m through or around foraging flocks. Records were collected by scanning the flock in a complete 360° circle, pausing throughout the scan to monitor each bird that was close enough to accurately monitor foraging efficiency. After all of the plovers within viewing range were monitored at one position, I moved another 100 m to the next position and waited a short period to allow the birds to become accustomed to my presence before data collection resumed.

Foraging Ecology and Prey Density

Foraging efficiency and foraging effort were compared to benthic prey density and surface prey abundance (prey density and abundance are described in Chapter IV). Foraging effort was estimated as the mean number of pecks/minute exhibited by foraging plovers. For these comparisons, the daily means for benthic prey density and surface prey abundance were regressed against the daily mean for foraging efficiency and foraging effort. All data were collected in areas occupied by foraging Piping Plovers.

Intraspecific and Interspecific Interactions

To investigate associations between foraging Piping Plovers and other nearby birds, I recorded the species identification of the bird located closest to the plovers I was monitoring during foraging efficiency and foraging locomotion records. I recorded all acts of aggression involving Piping Plovers (i.e., intraspecific and interspecific aggressions) that I observed during the foraging locomotion and foraging efficiency records.

Data Analysis

All analyses were performed using JMP, version 3.1. JMP is a statistical program written by SAS Institute Inc., Cary, NC. Advanced statistical analyses (i.e., beyond the calculation of means, standard errors, etc.) consisted of one-way and multi-factor

Table 10. Mean macrobenthic polychaete, crustaceans and total prey density collected at beach habitat at sites along the Texas Gulf Coast, 1991 - 1994. Density represented as the mean number of animals per square meter based upon core samples collected along transects associated with foraging Piping Plovers. Abbreviations: MISP = Mustang Island State Park.

Study Location	N	Polychaetes		Crustaceans		Insects		All Prey	
		mean	SE	mean	SE	mean	SE	mean	SE
Bolivar Flat	100	1577.5	182.81	1710.8	228.28	13.8	2.73	3304.1	347.76
Big Reef	35	3383.5	420.16	490.7	93.34	0.0	7.05	3887.2	385.46
San Luis Pass	155	2140.4	229.62	1278.7	197.23	0.0	2.19	3425.0	343.51
East Flats	35	678.0	117.20	1607.8	297.32	0.0	4.62	2298.7	338.21
MISP - North	165	920.4	111.93	880.7	170.56	0.0	2.13	1845.0	222.03
MISP - South	52	1799.3	236.41	1303.9	259.97	0.0	3.79	3155.3	307.45
Packery Channel	175	732.2	70.84	2005.6	241.97	0.0	2.06	2783.0	250.83
South Bay - East	45	693.1	121.98	597.64	117.18	0.0	4.07	1295.7	166.04
South Padre Island	45	783.5	118.37	838.71	106.20	0.0	4.07	1622.2	174.66

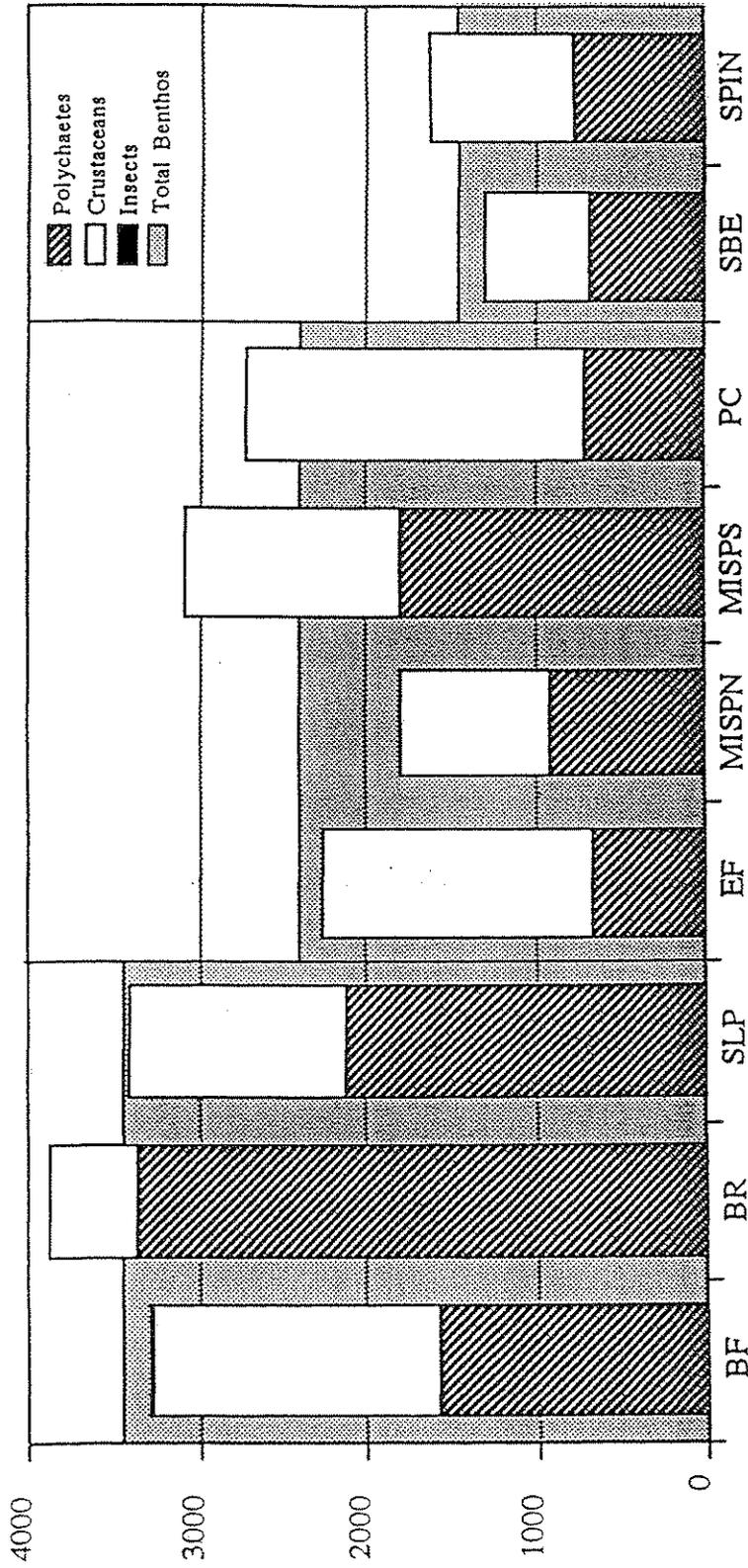


Figure 14. Macrobenthic density at beach habitat at sites along the Texas Gulf Coast, 1991 - 1994. Stacked bars illustrate polychaete density, crustacean density, insect density, and (collectively) total mean benthic density recorded at locations occupied by foraging Piping Plovers. Wide gray bars in background illustrate mean total benthic density for both ecosystems and the ecotone.

*Site Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISP = Mustang Island State Park - North, MISPS = Mustang Island State Park - South, PC = Packery Channel, SBE = South Bay East, SPIN = South Padre Island - North.

Total beach benthos differed significantly among both ecosystems and the ecotone (Table 11). Total benthic prey density was much higher in the bay ecosystem than the lagoon ecosystem ($P < 0.0001$) or the ecotone ($P < 0.0001$). Much of the variation in total benthos among the 3 regions was due to variation in polychaete populations. Polychaete densities were higher at bay beaches than at ecotone beaches ($P < 0.0001$) or lagoon beaches ($P < 0.0001$). I also recovered more polychaetes in samples from ecotone beaches relative to lagoon beaches ($P = 0.0020$). There were fewer crustaceans at lagoon ecosystem beaches than at those in the bay ecosystem ($P = 0.0210$) or the ecotone ($P = 0.0033$), however, crustacean density did not differ between the bay ecosystem and the ecotone ($P = 0.5893$). None of the 3 coastal regions differed with regard to benthic insect density at beach habitat.

There was no difference in total benthic density ($P = 0.1528$), polychaete density ($P = 0.1057$), or crustacean density ($P = 0.9846$) in the swash zone and upper beach zone (Table 12). There also was no detectable difference in the density of the dominant beach benthic prey groups in the winter and migratory periods (Table 13).

Bayshore Benthos

Benthic prey density ranged widely at bayshore habitats from just over 100 animals/m² to over 7000 animals/m² (Table 14; Figure 15). Total benthic prey varied significantly among the 3 coastal regions (Table 11). I detected higher benthic prey density in the bay ecosystem relative to the lagoon ecosystem ($P < 0.0001$) and the ecotone ($P < 0.0001$). Total benthic density also was greater in the ecotone than the lagoon ecosystem ($P = 0.0010$).

Polychaetes were often the most numerous prey group in samples, but polychaete density ranged widely from 0 to over 7,000 worms/m². Polychaete density was higher in the bay ecosystem than in either the lagoon ecosystem ($P < 0.0001$; Table 11) or the ecotone ($P < 0.0001$; Table 11) and was lower in the lagoon ecosystem than the ecotone

Table 11. Piping Plover bayshore flock size and prey population measures at beach and bayshore habitat from the 2 ecosystems and the ecotone along the Texas Gulf Coast. Parameters are summarized as study means for each location. Multi-factor ANOVA results of pair-wise comparisons between the ecosystems and the ecotone are presented in the last 3 columns. Bayshore flock size represents the mean number of Piping Plovers within foraging flocks as recorded during prey sampling periods at bayshore habitat. Benthic prey parameters are represented as the mean number of animals/m². Surface prey, as estimated by sticky traps (ST), and scope surveys (SS), are represented as the mean number of animals/100m². Insect larval density, as estimated by algal mat cores samples (AC) is represented as the mean number of larva/m².

Parameter	Bay Ecosystem			Ecotone			Lagoon Ecosystem			Bay		Eco. vs. Lag.
	mean	N	SE	mean	N	SE	mean	N	SE	vs. Lag.	vs. Eco.	
Bayshore Flock size	12.8	550	0.6	9.4	401	0.7	16.6	230	0.9	0.1945	0.2608	0.0714
Beach Total Benthos	3439.1	290	185.9	2426.2	427	153.2	1459.0	90	333.7	< 0.0001	< 0.0001	0.0010
Beach Polychaetes	2096.3	290	106.6	930.5	427	87.8	738.3	90	191.3	< 0.0001	< 0.0001	0.0020
Beach Crustaceans	1332.6	290	139.1	1452.9	427	114.6	718.2	90	249.6	0.0210	0.5893	0.0033
Beach Insects	4.7	290	1.6	0.0	427	1.3	0.0	90	2.9	0.1719	0.4369	0.3750
Bayshore Total Benthos	5067.7	550	168.0	1317.7	401	196.7	864.7	230	259.8	< 0.0001	< 0.0001	0.0010
Bayshore Polychaetes	5041.9	550	155.3	796.1	375	188.1	495.2	230	240.1	< 0.0001	< 0.0001	< 0.0001
Bayshore Crustaceans	18.9	550	59.0	604.1	370	71.9	211.3	230	91.2	0.0309	< 0.0001	< 0.0001
Bayshore Insects	6.2	550	5.0	15.9	370	6.1	158.2	230	7.7	< 0.0001	0.3925	< 0.0001
Surface Prey - ST	15.5	401	17.2	160.9	330	16.3	225.6	445	16.3	0.0082	0.0296	0.0142
Surface Prey - SS	0.6	206	8.0	81.4	95	11.8	58.1	205	8.0	0.0330	0.1638	0.4710
Insect Larva - AC	--	--	--	522.6	32	162.6	838.1	72	108.4	--	--	0.0865

Bay = bay ecosystem, Eco. = ecotone, Lag. = lagoon ecosystem.

Table 12. Comparison between the swash zone and the upper beach, the 2 microhabitats used most frequently by Piping Plovers along the Texas Gulf Coast. All numbers represent means for all sites and years. Piping Plover (PIPL) abundance is reported as the number of plovers/transect as measured during prey sampling. Benthic parameters are reported as the number of animals/m². Foraging efficiency estimates are reported as the number of captures/minute, and foraging locomotion is reported as the number of seconds/minute spent in prolonged locomotion.

Ecosystem	Swash Zone			Upper Beach			P-value
	mean	N	SE	mean	N	SE	
PIPL Abundance	1.42	315	0.10	1.20	346	0.09	0.0224
Total Benthos	2621.6	315	189.3	2641.5	346	180.6	0.1528
Benthic Polychaetes	1427.8	315	110.8	1224.7	346	105.8	0.1057
Benthic Crustaceans	1151.5	315	136.9	1401.1	346	130.6	0.9846
Benthic Insects	0.0	315	1.7	3.9	346	1.6	0.0558
Foraging Efficiency	13.7	66	0.8	7.0	38	1.1	< 0.0001
Foraging Locomotion	10.0	54	0.8	5.7	81	0.7	0.0002

Table 13. The effects of season on benthic prey density along the Texas Gulf Coast, 1991 - 1994. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing benthic prey density among the 2 seasons.

Ecosystem	Migration			Winter			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Beach Habitat							
Total benthos	2468.9	397	161.7	2888.9	410	159.1	0.7602
Polychaetes	1247.8	397	95.4	1405.6	410	93.9	0.6069
Crustaceans	1186.4	397	119.1	1464.6	410	117.2	0.2898
Insects	3.4	397	1.4	0.0	410	1.4	0.0417
Bayshore Habitat							
Total benthos	2176.2	561	179.7	3186.4	725	158.1	0.3858
Polychaetes	2031.5	540	176.9	2905.4	720	153.2	0.7270
Crustaceans	182.9	540	58.0	261.4	715	50.4	0.8616
Insects	46.5	540	6.0	42.7	715	5.2	0.5662

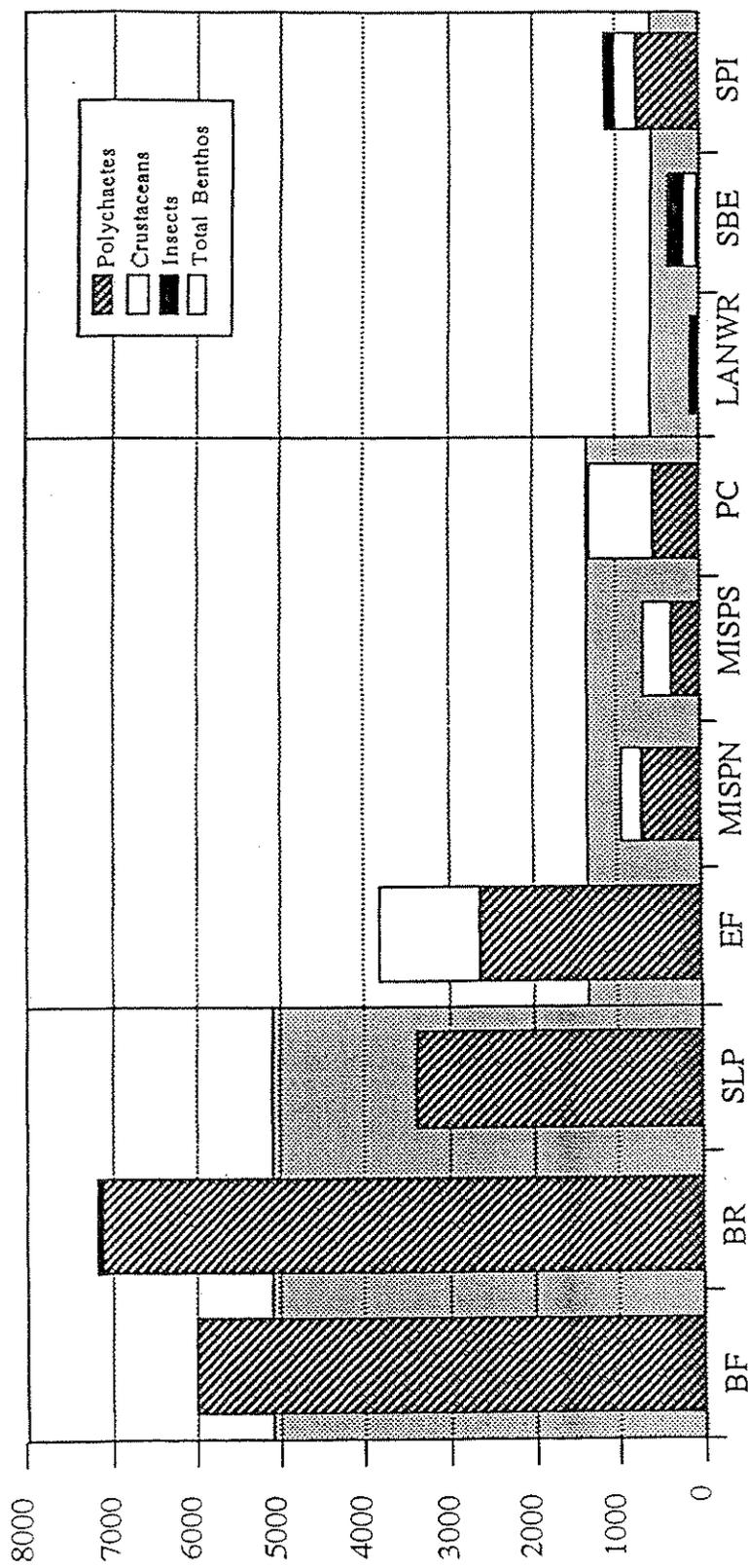


Figure 15. Mean site density and ecosystem density of Piping Plover at bayshore habitat along the Texas Gulf Coast, 1991 - 1994. Stacked bars illustrate polychaete density, crustacean density, insect density, and (collectively) total mean benthic density recorded at locations occupied by foraging Piping Plovers. Wide gray bars in background illustrate mean total benthic density for both ecosystems and the ecotone.

*Site Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISPN = Mustang Island State Park - North, MISPS = Mustang Island State Park - South, PC = Packery Channel, LANWR = Laguna Atascosa National Wildlife Refuge, SBE = South Bay East, SPI = South Padre Island.

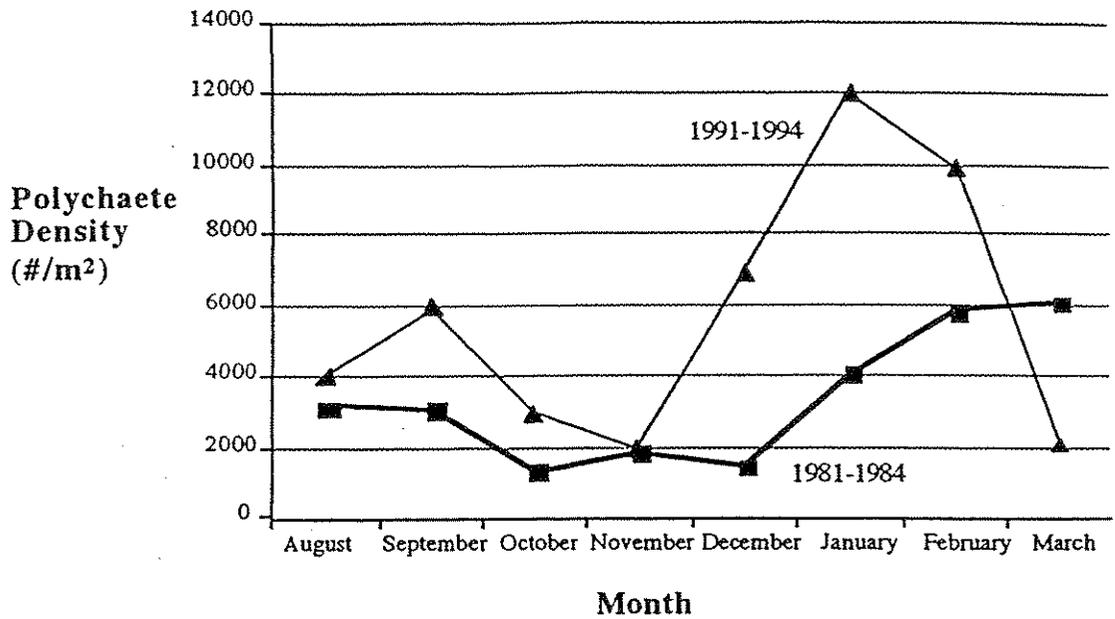
($P < 0.0001$; Table 11). Polychaete density in my samples from Bolivar Flats and Big Reef was similar to polychaete density estimates reported by Sears and Mueller (1989) for those 2 sites (Figure 16). Sears and Mueller sampled polychaetes along a fixed transect, and therefore their samples were not necessarily associated with areas recently used by foraging Piping Plovers. When the samples from both studies are compared on a monthly basis (as the data from Sears and Mueller (1989) were summarized) polychaete density was higher in my samples in 7 out of 8 months at Bolivar Flats, but just 3 out of 6 months at Big Reef. Both studies suggest that peak polychaete density occur in winter (January - February) in the bay ecosystem.

Crustacean density ranged from 0 to over 1,100 animals/m² at bayshore habitat (Table 14). Large crustacean counts were usually associated with local blooms of tanaids. Crustacean density was much higher in the ecotone ($P < 0.0001$; Table 11) and the lagoon ecosystem ($P = 0.0309$; Table 11) relative to the bay ecosystem. The highest crustacean density occurred in the ecotone, where I collected nearly 3 times as many crustaceans as in the lagoon ecosystem ($P < 0.0001$; Table 11).

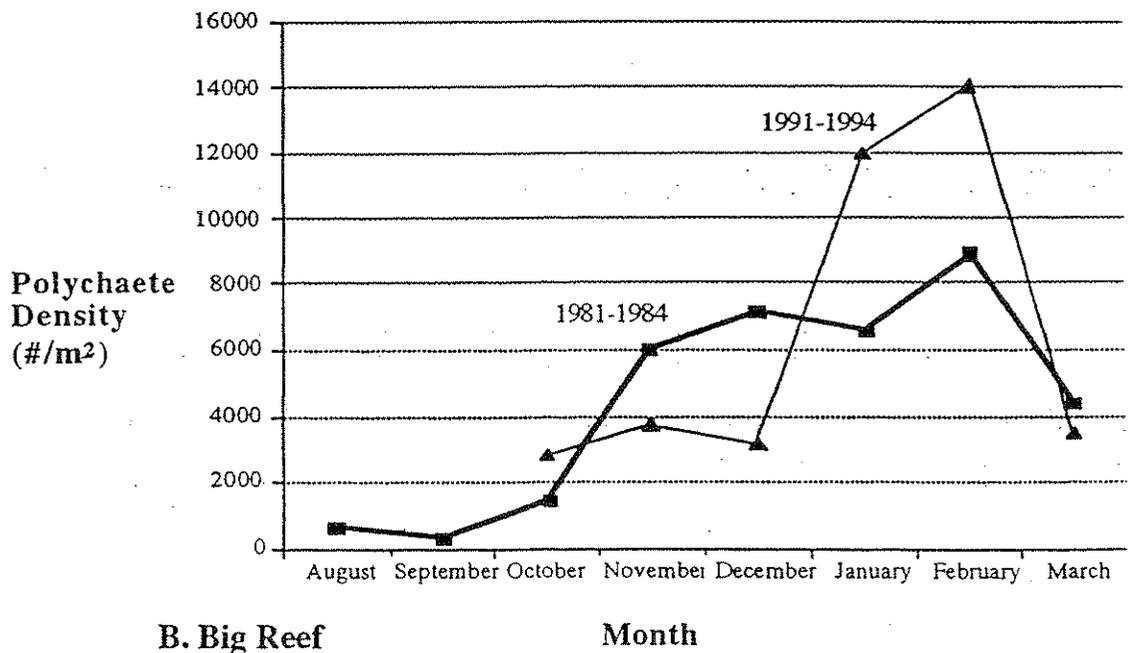
Insects were much less common in bayshore benthic samples relative to polychaetes or crustaceans, and most insects collected in subsurface samples were fly larva. I recorded densities of < 100 insects/m² at most of my sites, however, insect density exceeded this amount at all 3 study areas in the lagoon ecosystem (Table 14; Figure 16).

Total benthic prey density was similar in areas used by flocks and individual plovers ($P = 0.4925$; Table 15). Crustacean density was greater in areas used by plover flocks ($P = 0.0015$; Table 15), but neither polychaete density ($P = 0.3829$; Table 15) nor benthic insect density ($P = 0.2408$; Table 15) differed among areas used by flocks or solitary plovers.

Total benthic prey density ($P < 0.0001$) and polychaete density ($P < 0.0001$) were higher at sand flats than at algal flats (Table 16). Benthic insect density was higher at



A. Bolivar Flats



B. Big Reef

Figure 16. Polychaete density at Bolivar Flats (A) and Big Reef (B) as measured in 1981 - 1982 (thick line with rectangles) by Sears and Mueller (1989) and in 1991 - 1994 (thin line with triangles) for this study.

Table 15. Comparison of prey populations collected in association with flocks of Piping Plovers and solitary Piping Plovers. All numbers represent means for all sites throughout the study. Benthic parameters are reported as the number of animals/m². Sticky trap (ST) estimates of surface prey are reported as the number of insects captured/100 trap hours.

Ecosystem	Plover Flocks			Solitary Plovers			P-value
	mean	N	SE	mean	N	SE	
Total Benthic Prey	2895.8	1066	130.9	2018.6	220	288.2	0.4925
Benthic Polychaetes	2636.7	1048	127.5	2007.4	212	283.4	0.3829
Benthic Crustaceans	260.9	1048	41.6	59.0	207	93.6	0.0015
Benthic Insects	47.0	1048	4.3	30.6	207	9.7	0.2408
Surface Prey - ST	141.8	1028	11.1	94.6	148	29.2	0.9687

Table 16. Comparison between sand flat and algal flat habitat with regard to several study parameters. All numbers represent means for all sites throughout the study. Piping Plover (PIPL) abundance is reported as the number of plovers/transect during prey sampling. Benthic parameters and spotting scope survey (SS) estimates of surface prey are reported as the number of animals/m². Sticky trap estimates of surface prey are reported as the number of insects captured/100 trap hours. Foraging efficiency estimates are reported as the number of captures/minute, and foraging locomotion is reported as the number of seconds/minute spent in prolonged locomotion.

Ecosystem	Sand Flats			Algal Flats			P-value
	mean	N	SE	mean	N	SE	
PIPL Abundance	12.7	754	0.5	12.7	532	0.6	0.8373
Total Benthos	4316.5	754	140.5	519.6	532	167.2	< 0.0001
Benthic Polychaetes	4021.5	754	135.1	309.5	506	165.0	< 0.0001
Benthic Crustaceans	275.8	754	49.1	155.2	501	60.2	0.1037
Benthic Insects	18.6	754	5.0	83.0	501	6.1	< 0.0001
Surface Prey - ST	87.0	604	15.0	187.0	572	14.0	< 0.0001
Surface Prey - SS	0.27	336	0.6	0.71	140	0.1	0.0002
Foraging Efficiency	10.3	336	0.3	9.8	168	0.4	0.9114
Foraging Locomotion	1.25	167	0.22	1.54	118	0.26	0.0027

algal flats than at sand flats ($P < 0.0001$). Crustacean density did not differ among bayshore microhabitat types ($P = 0.1037$). All types of benthic prey were more abundant at barrier island sites relative to mainland sites (Table 17).

Bayshore Surface Prey as Estimated Using Sticky Traps

With the exceptions of a few spiders, all of the animals captured by the sticky traps were flies and other small adult insects. My samples suggest that surface prey density varied widely along the coast. The mean number of insects captured using sticky traps ranged from < 10 to nearly 1000 insects/100 trap hours (Table 18; Figure 17).

Surface prey abundance was lower in the bay ecosystem than the ecotone ($P = 0.0296$) or the lagoon ecosystem ($P = 0.0082$). The lagoon supported the highest abundance of surface prey, where levels exceeded those collected at sites in the ecotone ($P = 0.0142$). Total surface prey abundance was similar in areas used by flocks and individual plovers ($P = 0.9687$; Table 15).

Bayshore Surface Prey as Estimated Using Spotting Scope Surveys

Mean surface animal density, as estimated by spotting scope surveys, varied from 0 to over 200 animals/m² (Table 18; Figure 17). I observed significantly more surface prey in the lagoon ecosystem than in the bay ecosystem ($P = 0.0330$). However, surface prey density did not differ significantly between bay ecosystem and the ecotone ($P = 0.1638$) or the ecotone and the lagoon ecosystem ($P = 0.4710$).

Bayshore Emergent Prey Density as Estimated Using Algal Cores

I collected and monitored 104 algal mat core samples for emerging prey animals (Table 18; Figure 17). I did not collect any samples from the bay ecosystem because algal mats were extremely rare in this ecosystem and plovers were never observed to feed at algal flats during the 2 years algal cores were collected. Because there were no adult prey on the surface of the algal mat cores when they were collected, the insects scored from algal cores were mostly adult stages that had developed from eggs, larvae or pupae

Table 17. Mean prey population estimates on barrier island and mainland bayshore tidal flats in the lagoon ecosystem, 1991 - 1994 as estimated from samples collected in association with foraging Piping Plovers. Benthic prey density is expressed as the mean number of prey/m². Surface prey is expressed as the number of prey/100 trap hour for sticky traps, and the number of prey/m² for scope surveys and algal core samples. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing benthic prey density among the 2 landform types.

Ecosystem	Barrier Island			Mainland			<i>P</i> -value
	mean	N	SE	mean	N	SE	
Benthos							
Total benthos	831.5	240	89.5	109.0	85	150.4	< 0.0001
Polychaetes	474.6	240	79.1	0.0	85	133.0	< 0.0001
Crustaceans	202.5	240	32.1	0.0	85	54.0	< 0.0001
Insects	154.4	240	14.5	109.0	85	24.4	0.0147
Surface Prey							
Sticky Traps	191.6	215	29.1	257.8	230	28.1	0.4908
Scope Surveys	0.40	180	0.07	1.86	25	0.21	< 0.0001
Algal Cores	1013.6	33	239.0	1321.2	39	219.8	0.7320

Table 18. Mean surface prey density collected at bayshore habitat at sites along the Texas Gulf Coast, 1991 - 1994. Surface prey populations are represented as relative abundance (# animals/100 trap hours) as estimated by sticky traps, and prey density (# animals/100 m²) as estimated by spotting scope counts and incubated algal core samples. Abbreviations: LANWR = Laguna Atascosa National Wildlife Refuge, MISP = Mustang Island State Park.

Study Location	Sticky Traps			Spotting Scope			Algal Mat Cores		
	N	mean	SE	N	mean	SE	N	mean	SE
Bolivar Flats	150	60.0	22.7	75	0.0	12.2	0	--	--
Big Reef	90	42.2	29.3	55	0.0	14.2	0	--	--
San Luis Pass	161	9.3	21.9	99	28.8	10.6	0	--	--
East Flats	31	971.0	499.7	25	223.7	211.0	4	1299.5	658.5
MISP North Area	121	75.2	25.3	25	19.0	21.1	2	1356.0	931.2
Packery Flats	168	81.5	21.5	39	42.7	16.9	26	1451.6	258
LANWR	220	266.8	34.5	25	185.6	21.1	39	1321.2	210.9
South Bay East	50	78.0	39.3	35	23.8	17.8	13	851.9	365.2
South Padre Island	100	230.0	27.8	117	30.5	9.8	20	1118.7	294.5

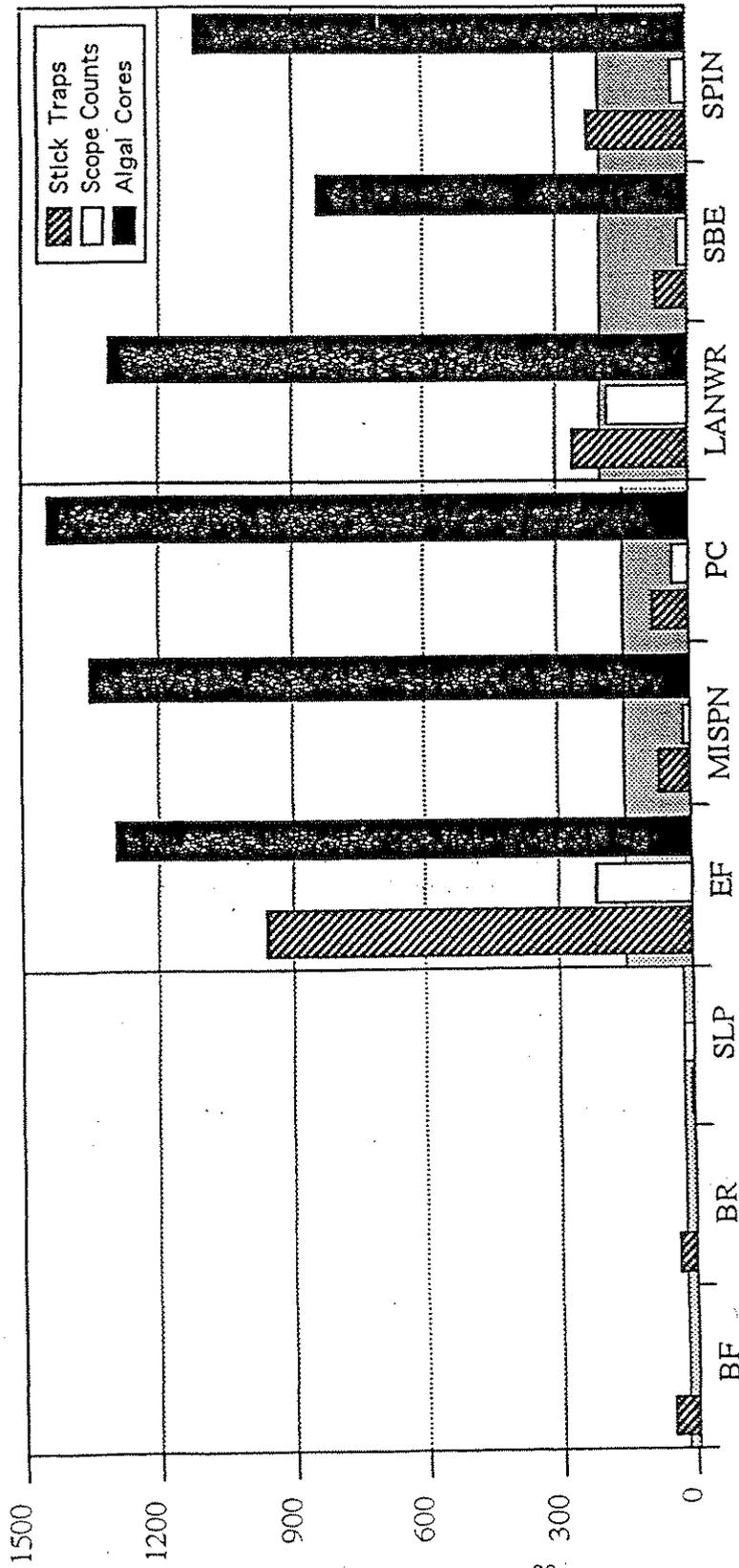


Figure 17. Mean surface prey density collected at bayshore habitat at sites along the Texas Gulf Coast, 1991 - 1994. Surface prey populations are represented as relative abundance (striped bars (# animals/100 trap hours) as estimated by sticky traps, and prey density (# animals/100 square meter) as estimated by spotting scope counts (white bars) and incubated algal core samples (black bars). Wide gray bars in background illustrate mean relative surface abundance from sticky traps at each ecosystem and the ecotone.

*Site Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISPN = Mustang Island State Park - North, MISPS = Mustang Island State Park - South, PC = Packery Channel, LANWR = Laguna Atascosa National Wildlife Refuge, SBE = South Bay East, SPI = South Padre Island.

present in the mat. Therefore, these samples estimate the short-term (6 week) insect productivity potential of algal mats.

Emergent insect density ranged from about 850 to nearly 1,500 insects/m² (Table 18; Figure 16). Emergent insect density was somewhat lower in the ecotone than the lagoon ecosystem ($P = 0.0865$; Table 11).

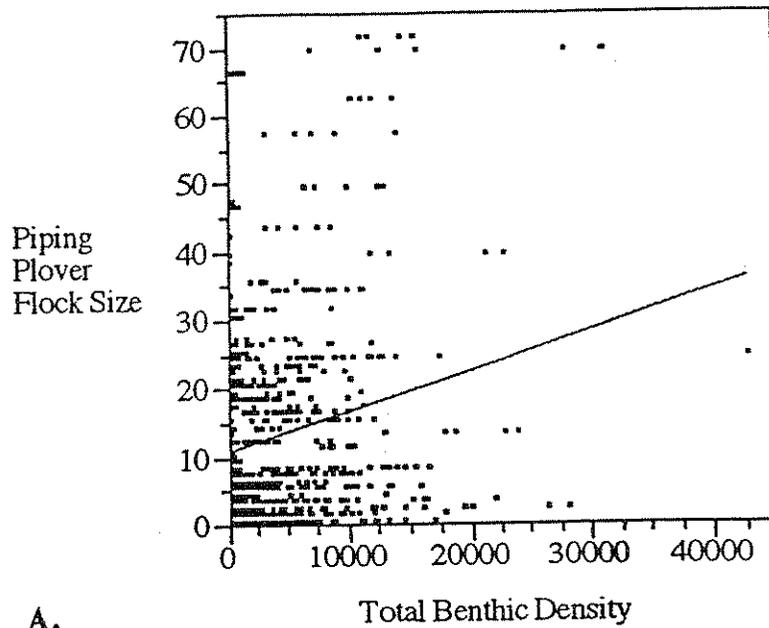
Relationship Between Prey Density and Piping Plover Flock Size

Whereas bayshore plover flock size did not differ significantly in the 2 ecosystems and the ecotone (Table 11), there was a strong relationship between Piping Plover foraging flock size and total benthic prey density. When I pooled data from both ecosystems and the ecotone I detected a positive relationship between the number of Piping Plovers feeding in an area and the density of total benthos ($P < 0.0001$; Figure 18A) and polychaetes ($P < 0.0001$; Figure 18B) within the area used by the flock. There was no such relationship between plover flock size and benthic crustacean density ($P = 0.0885$; Figure 19A) or benthic insect density ($P = 0.0594$; Figure 19B).

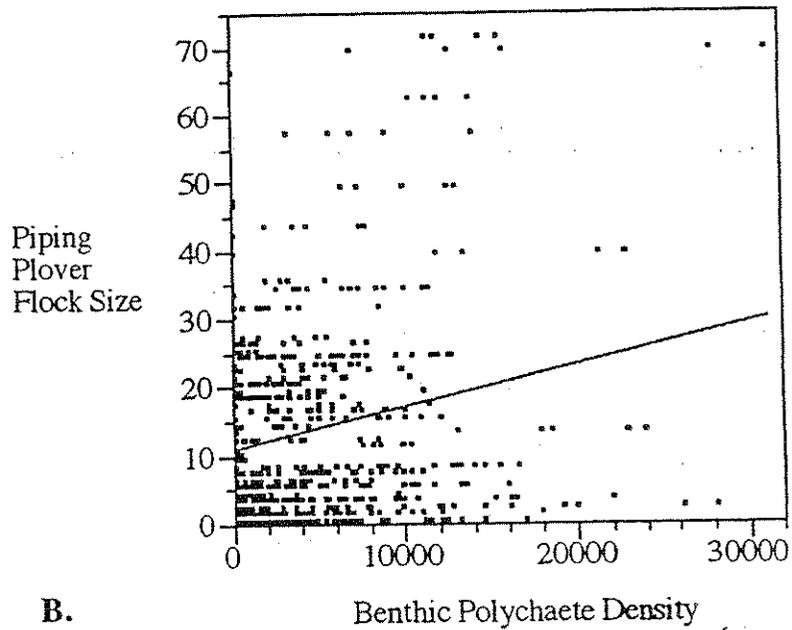
Different relationships become apparent when the data from each of the ecosystems and the ecotone were investigated independently. Within the bay ecosystem, Piping Plovers were attracted to concentrations of polychaetes. Flock size increased in areas with high total benthic density ($P < 0.0001$; Figure 20A), high benthic polychaete density ($P < 0.0001$; Figure 20B), and low benthic insect density ($P = 0.0035$; Figure 21B). There was no relationship between flock size and benthic crustacean density in the bay ecosystem ($P = 0.2420$; Figure 21A).

In the ecotone, plover flocks were associated with concentrations of total benthos ($P = 0.0003$; Figure 22A), polychaetes ($P = 0.0054$; Figure 22B) and crustaceans ($P = 0.0016$; Figure 23A). Benthic insect populations were not related to Piping Plover concentrations in the ecotone ($P = 0.1034$; Figure 23B).

In the lagoon ecosystem, the larger flocks of Piping Plovers were associated with

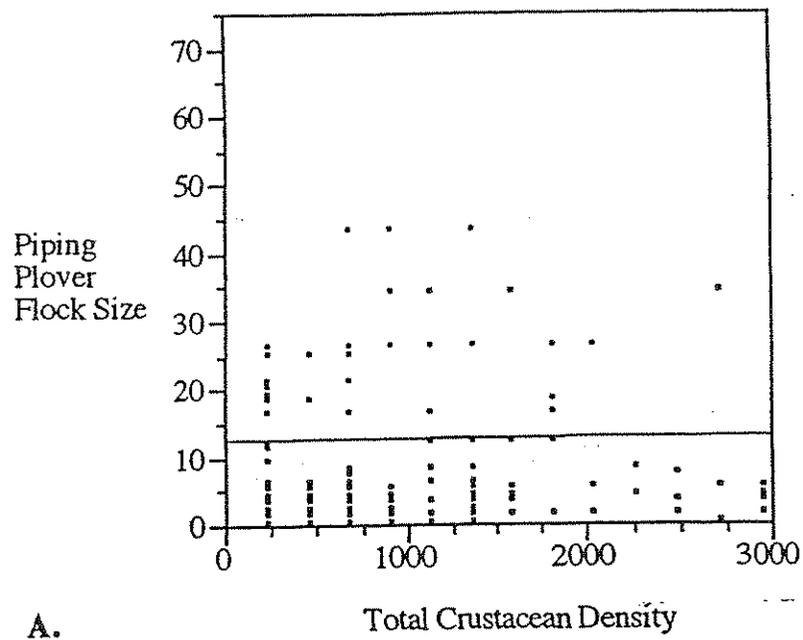


A.

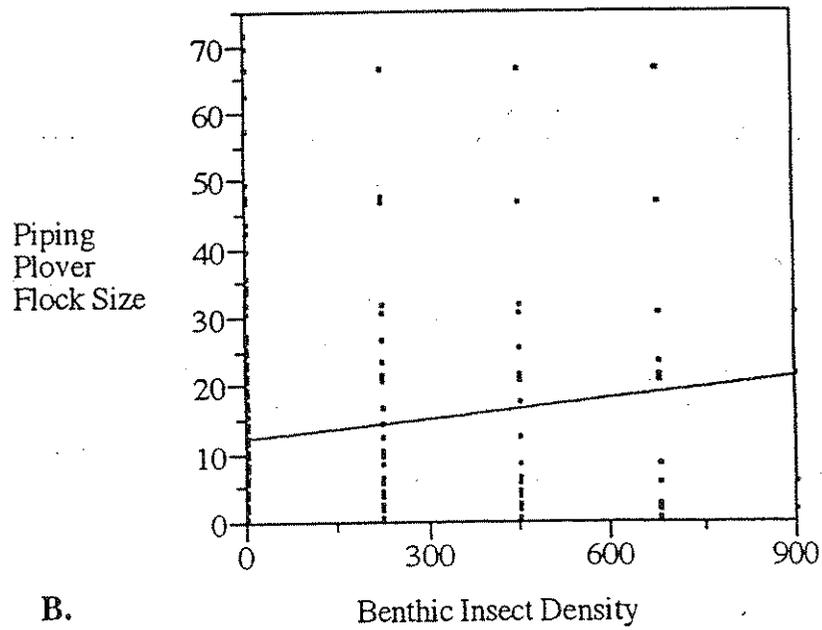


B.

Figure 18. Linear regressions illustrating the relationship between Piping Plover foraging flock size and total benthic prey density (A; $P < 0.0001$) and benthic polychaete density (B; $P < 0.0001$). Data are pooled from all sites.

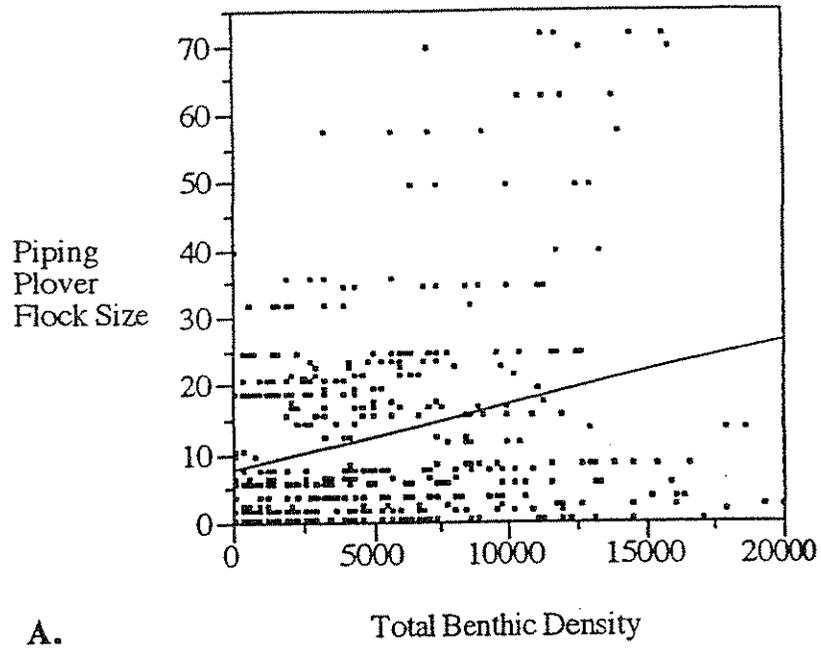


A.

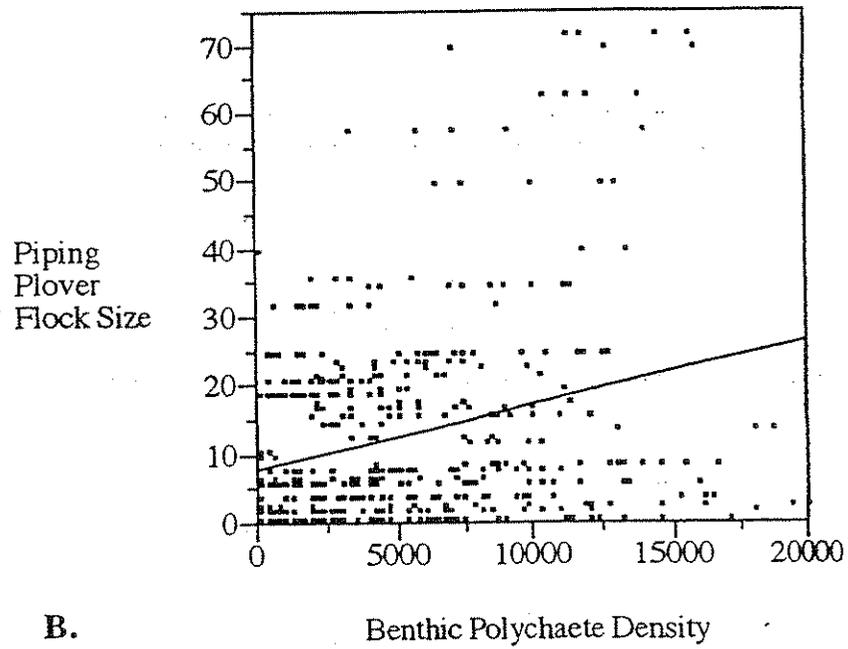


B.

Figure 19. Linear regressions illustrating the relationship between Piping Plover foraging flock size and benthic crustacean density (A; $P = 0.0885$) and benthic insect density (B; $P = 0.0594$). Data are pooled from all sites.

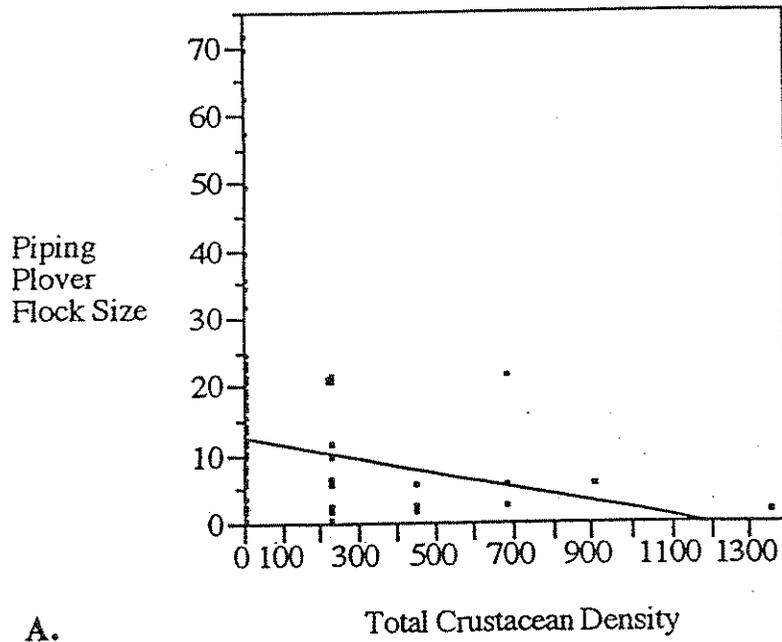


A.

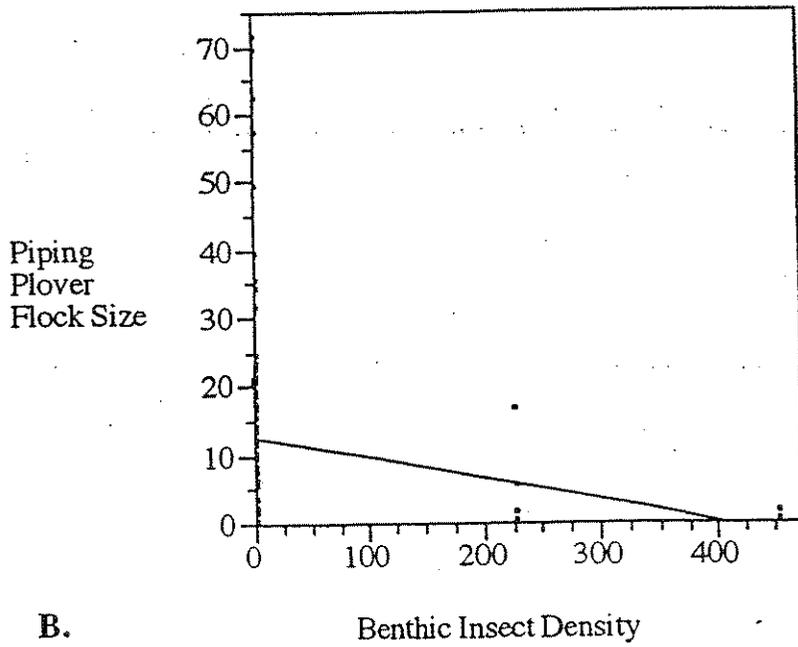


B.

Figure 20. Linear regressions illustrating the relationship between Piping Plover foraging flock size and total benthic prey density (A; $P < 0.0001$) and benthic polychaete density (B; $P < 0.0001$). Data are from bay ecosystem sites only.

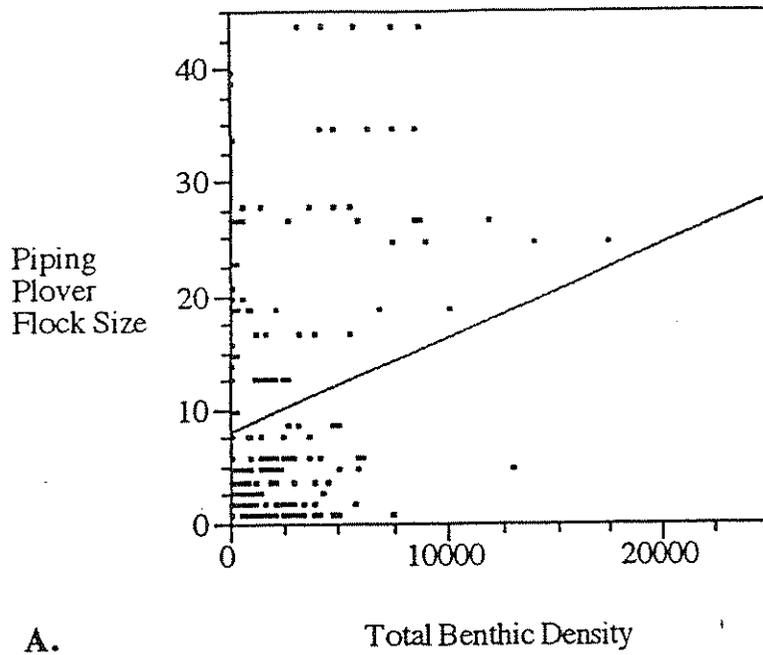


A.

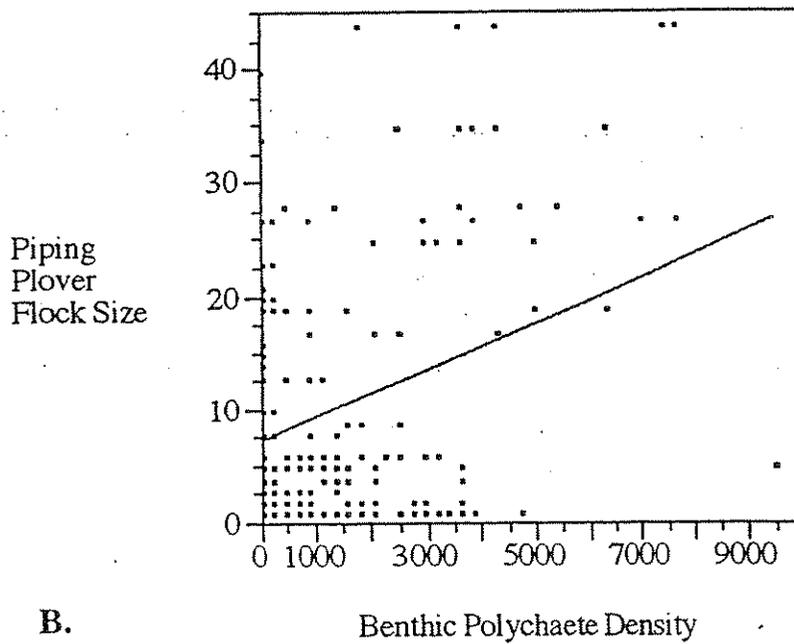


B.

Figure 21. Linear regressions illustrating the relationship between Piping Plover foraging flock size and benthic crustacean density (A; $P = 0.2420$) and benthic insect density (B; $P = 0.0035$). Data are from bay ecosystem sites only.



A.



B.

Figure 22. Linear regressions illustrating the relationship between Piping Plover foraging flock size and total benthic prey density (A; $P = 0.0003$) and benthic polychaete density (B; $P = 0.0054$). Data are from the ecotone sites only.

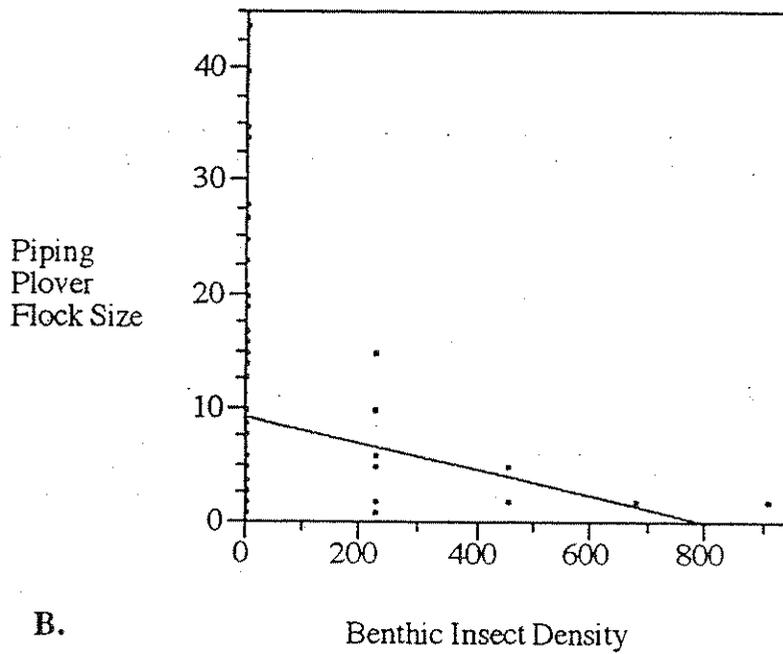
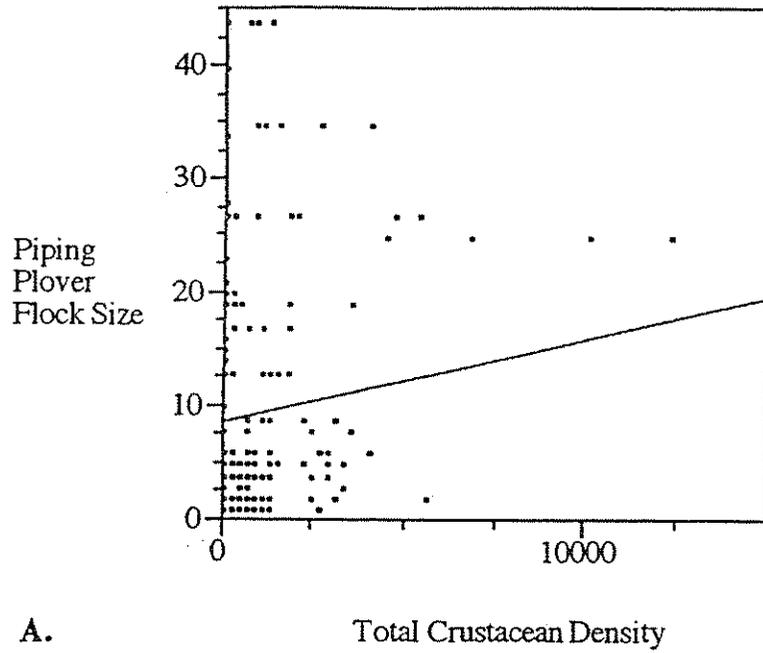


Figure 23. Linear regressions illustrating the relationship between Piping Plover foraging flock size and benthic crustacean density (A; $P = 0.0016$) and benthic insect density (B; $P = 0.1034$). Data are from ecotone sites only.

areas of the flats that exhibited the lowest concentrations of total benthos ($P = 0.0004$; Figure 24A), polychaetes ($P = 0.0019$; Figure 24B) and crustaceans ($P = 0.0048$; Figure 25A). Benthic insect density did not significantly affect Piping Plover flock size in the lagoon ecosystem ($P = 0.2845$; Figure 25B).

There was no relationship between flock size and surface prey abundance at all sites combined ($P = 0.9568$; Figure 26A) or in the bay ecosystem ($P = 0.9568$; Figure 26B) or the ecotone ($P = 0.1402$; Figure 27A). Surprisingly, flock size was negatively associated with surface prey abundance in the lagoon ecosystem ($P < 0.0001$; Figure 26B).

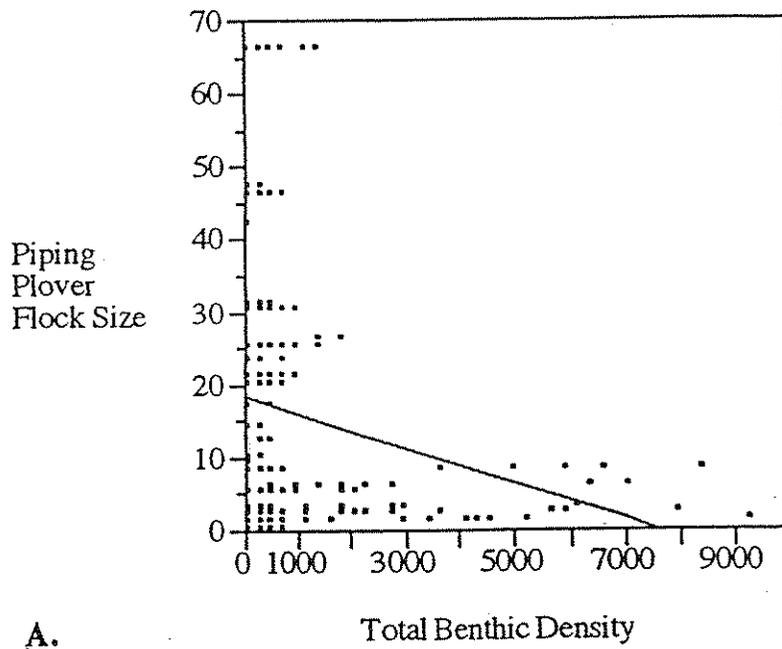
Behavior

Piping Plover Activity

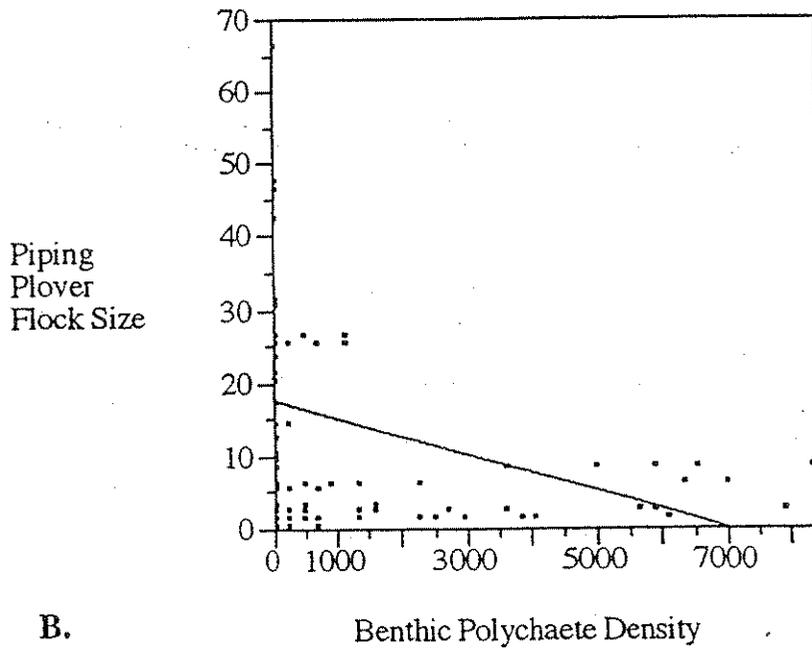
The majority of the Piping Plovers I encountered during shorebird counts were engaged in foraging activity (Figure 28). Plovers using beach habitat were more likely to be roosting than were plovers using bayshore habitat ($P < 0.0001$).

Most roosting activity by Piping Plovers at my sites occurred during high bayshore tide conditions ($P < 0.0001$). Piping Plovers roosted most commonly in washover pass regions of beach habitat and on high flat areas of bayshore habitat. Washover passes are broad, unvegetated barrier island landscapes that are formed and maintained by hurricanes and tropical storms. Because they occur at higher elevations than the forebeach, and receive less human disturbance, they provide ideal roost habitat for plovers. In washover passes, plovers often roosted along the front (Gulfward) margin of the pass in *Sargassum*-based coppice dune fields. Roosting in washover passes also occurred in areas where trash and other flotsam accumulated, and in tire tracks and other depressions. Unfortunately, these latter associations caused plovers to be more susceptible to disturbance as these areas were popular driving corridors for people seeking to access the bayshore areas for fishing, windsurfing, etc.

On bayshore flats, plovers often roosted in patches of dried algal mat and seagrass



A.



B.

Figure 24. Linear regressions illustrating the relationship between Piping Plover foraging flock size and total benthic prey density (A; $P = 0.0004$) and benthic polychaete density (B; $P = 0.0019$). Data are from lagoon ecosystem sites only.

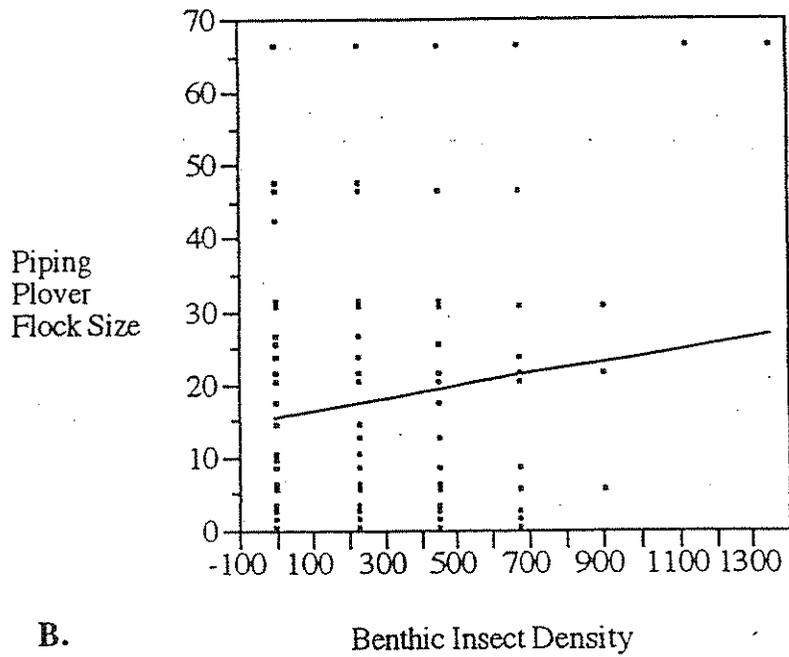
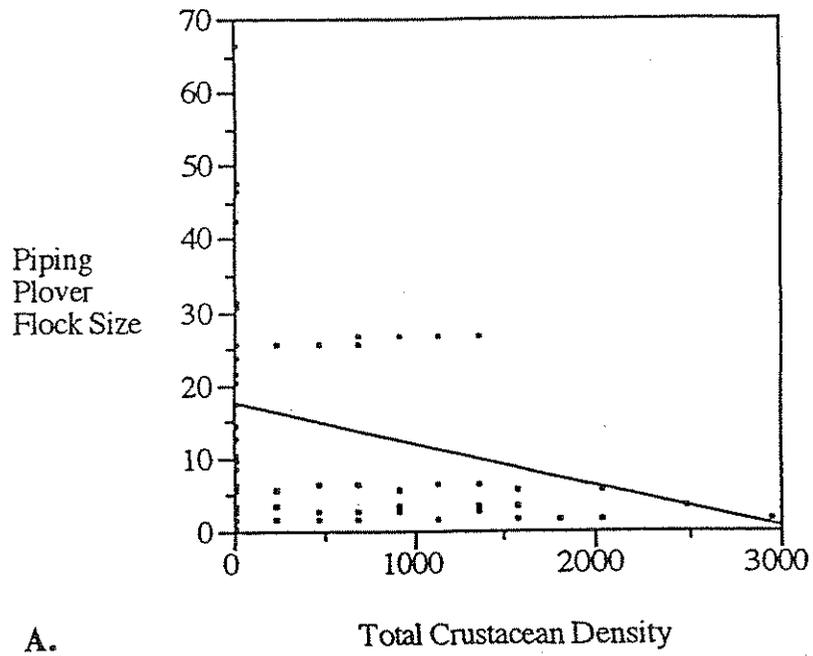


Figure 25. Linear regressions illustrating the relationship between Piping Plover foraging flock size and benthic crustacean density (A; $P = 0.0048$) and benthic insect density (B; $P = 0.2845$). Data are from lagoon ecosystem sites only.

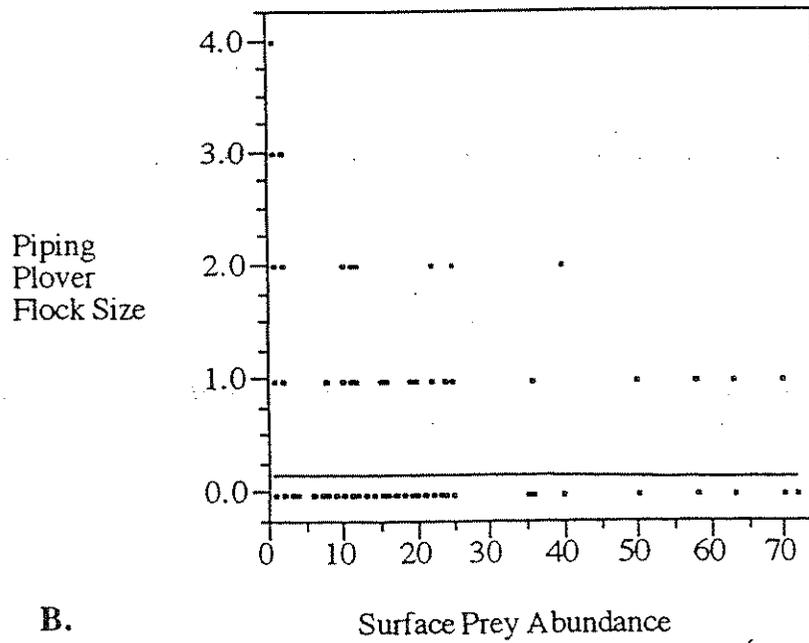
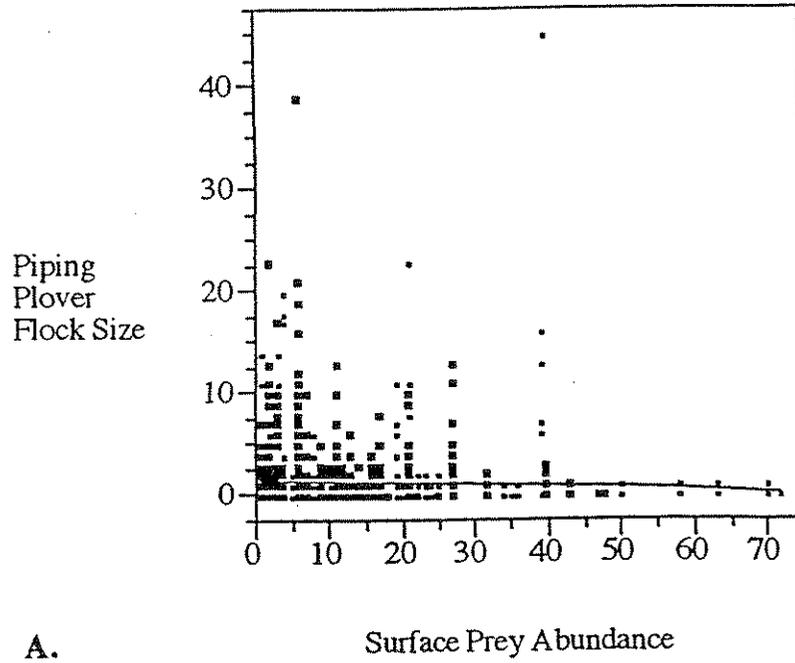


Figure 26. Linear regressions illustrating the relationship between Piping Plover foraging flock size and surface prey abundance at all sites (A; $P = 0.0501$) and at bay ecosystem sites (B; $P = 0.4080$).

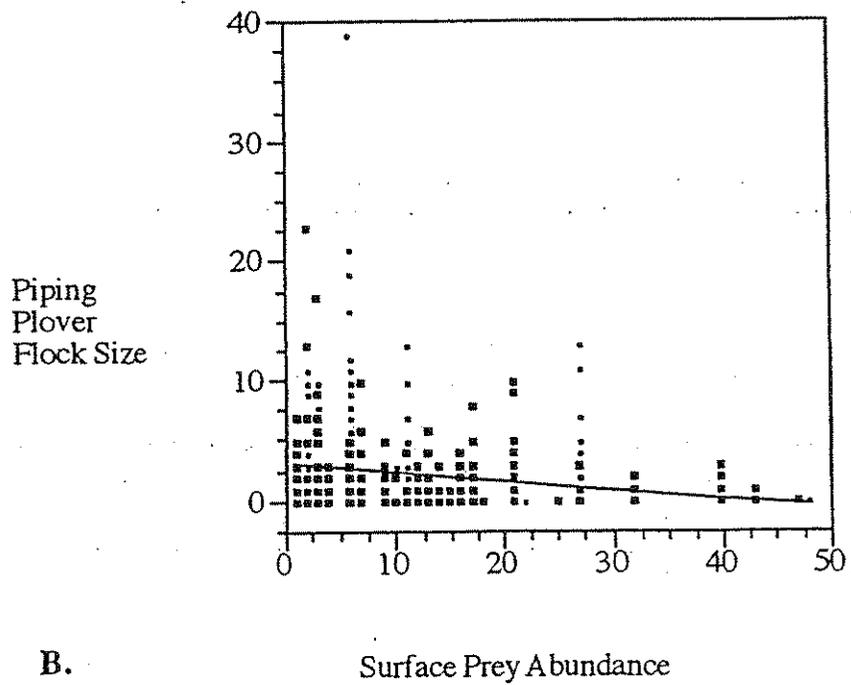
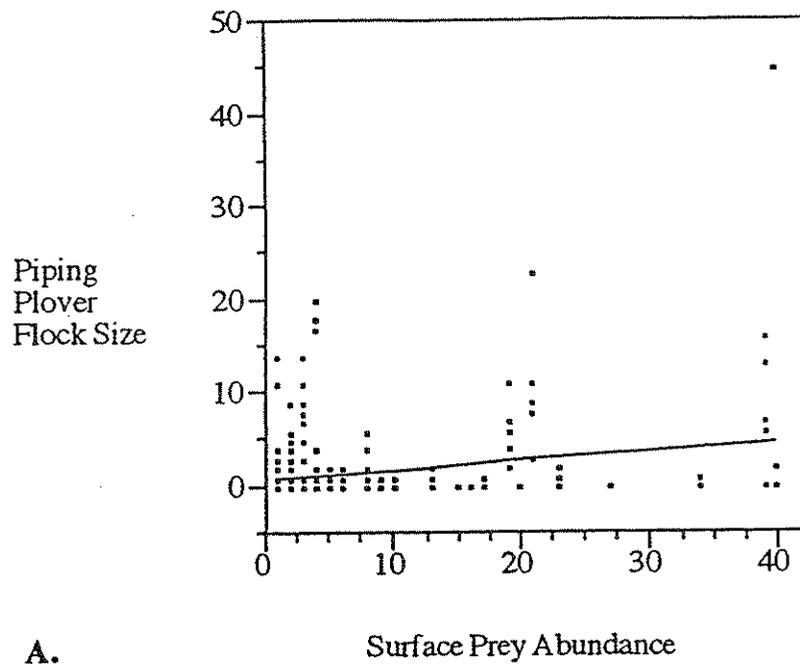
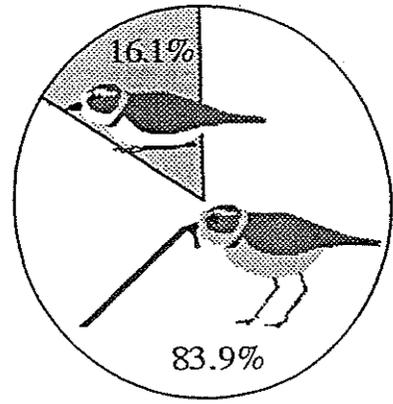
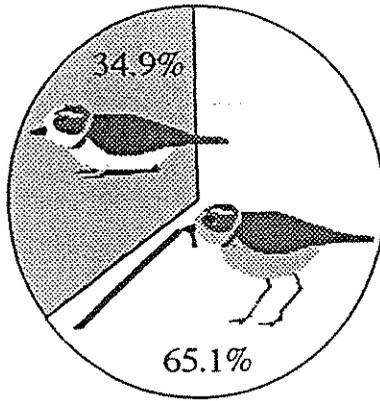
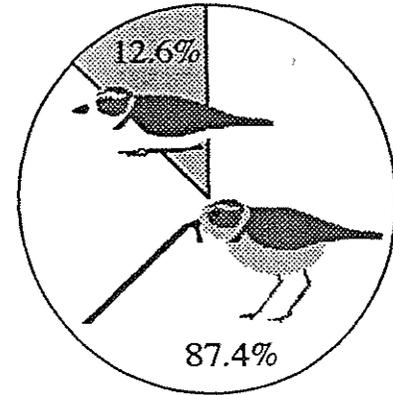
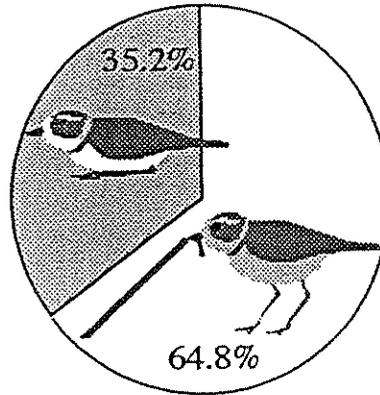


Figure 27. Linear regressions illustrating the relationship between Piping Plover foraging flock size and surface prey abundance at ecotone sites (A; $P = 0.1402$) and at lagoon ecosystem sites (B; $P < 0.0001$).

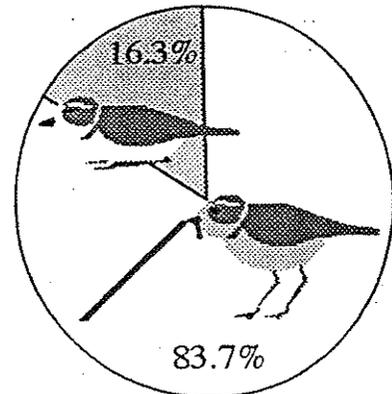
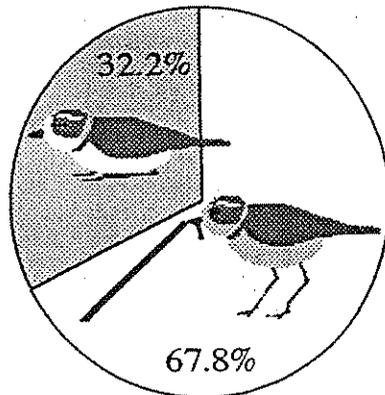
Bay
Ecosystem



Ecotone



Lagoon
Ecosystem



Beach Habitat

Bayshore Habitat

Figure 28. Mean Piping Plover activity for beach and bayshore habitat at the bay and lagoon ecosystem and the ecotone. Activity was assessed during daily, sites-wide shorebird counts. The area of each unshaded pie wedge is proportionate to the percentage of plovers that were foraging during the counts. Shaded pie wedges reflect the proportion of plovers that were roosting, preening or bathing during the counts.

wrack (primarily shoalgrass, *Halodule wrightii*). As higher areas of the algal mat became desiccated, the mat cracked and separated into pieces. As these pieces dried further, their corners curled upward creating small windbreaks behind which plovers often roosted. The colors of the Piping Plover nonbreeding plumage are ideally suited for all of these roosting environments. Despite great efforts, I often became aware of many roosting plovers only after one or more of the birds in the roosting flock moved into the open. Fortunately, in most cases, roosting plovers tolerated some disturbance, and often settled back into roosts if they were not unduly disturbed. The exception to this rule occurred in washover passes, where plovers were often more easily flushed. Plovers flushed from washover pass roost sites usually flew completely out of the pass to the bayshore.

Piping Plover Diet at Beach Habitat.

Polychaetes were the dominant prey group captured by Piping Plovers at beach habitat. Nearly 70% of all identifiable prey captured by Piping Plovers at beach habitat were polychaetes (Table 19; Figure 29). At beach habitat, the polychaete group included all worm-like animals captured by plovers. I was able to identify most polychaete captures at beach habitat as *Scolecopsis squamata* based on size and color characteristics.

Arthropods composed just under 30% of the known beach diet of Piping Plovers (Table 19; Figure 29). The arthropod prey group included amphipods, mole crabs and other crustaceans, as well as insects (larvae, pupae, and adults). The large majority of captures scored as arthropods at beach habitat appeared to be amphipods.

Plover diet at beach habitat in the 2 ecosystems and the ecotone was fairly similar (Figure 30). Polychaetes made up over half of the diet of plovers in all 3 regions. The higher proportion of polychaetes in the diet of plovers using lagoon ecosystem beaches may be an artifact of the small sample size (N = 9).

Piping Plover diet differed strongly at the 2 distinct beach microhabitats. Piping

Table 19. The relative proportions of polychaetes and arthropods in the diet of Piping Plovers at different locations and habitat types along the Texas Coast.

Parameter	Polychaetes			Arthropods		
	mean	N	SE	mean	N	SE
All sites and habitats	59.1	609	1.7	28.9	609	1.7
Bay Ecosystem - all habitats	77.7	308	1.9	7.6	308	1.3
Ecotone - all habitats	55.2	155	3.0	28.3	155	3.1
Lagoon Ecosystem - all habitats	23.9	146	3.3	74.7	146	3.4
Beach	68.7	123	2.9	18.9	123	2.8
Beach - swash zone	84.8	67	2.6	5.9	67	1.9
Beach - upper zone	38.1	32	5.9	39.3	32	7.4
Bayshore Flats	56.6	486	2.0	31.5	486	2.0
Sand Flats	75.0	340	2.0	13.1	340	1.7
Algal Flats	13.8	146	2.4	74.3	146	3.5

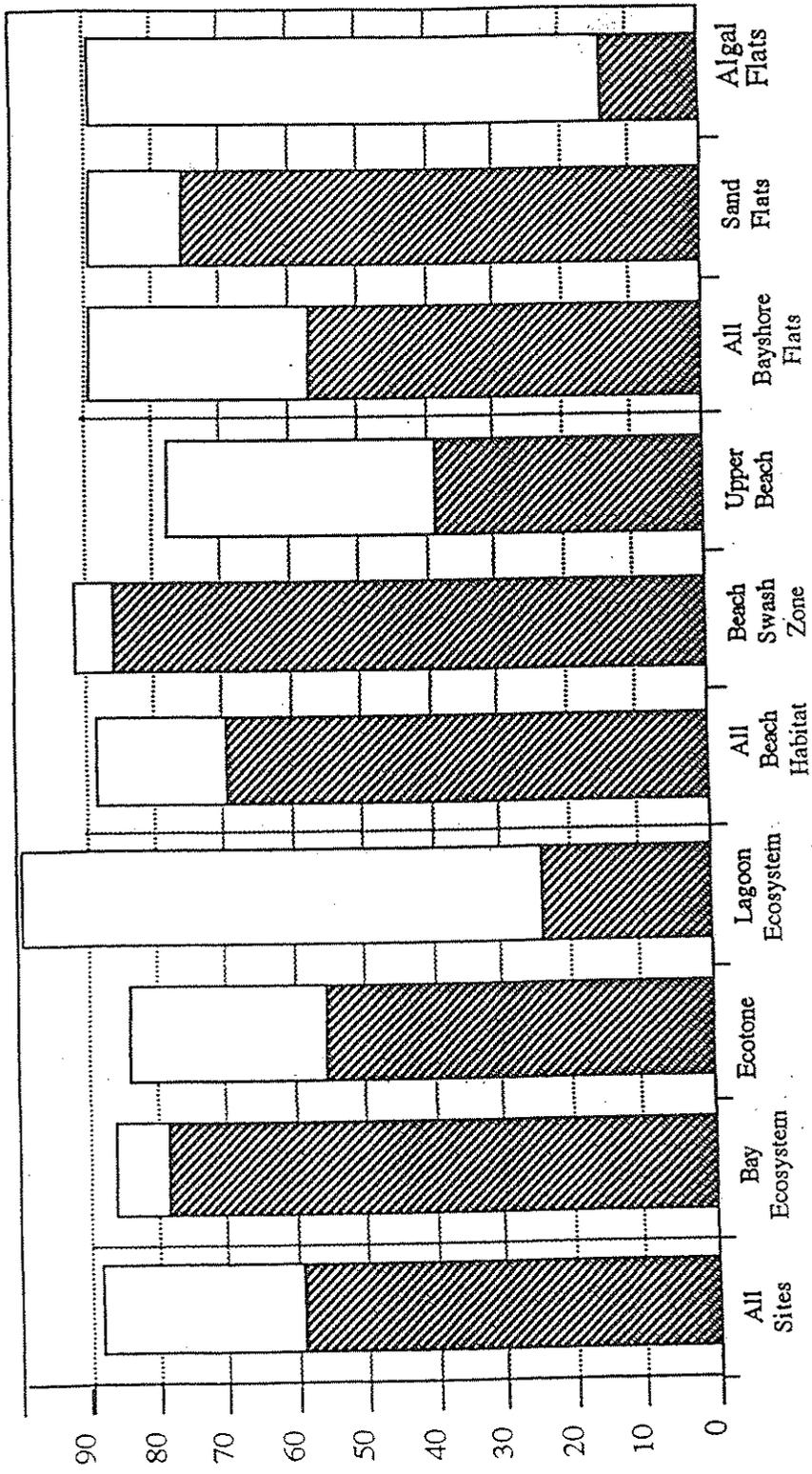


Figure 29. The proportion of polychaetes (▨) and arthropods (□) in the diet of Piping Plovers along the Texas Coast. Bars illustrate the identifiable proportion of plover prey captures.

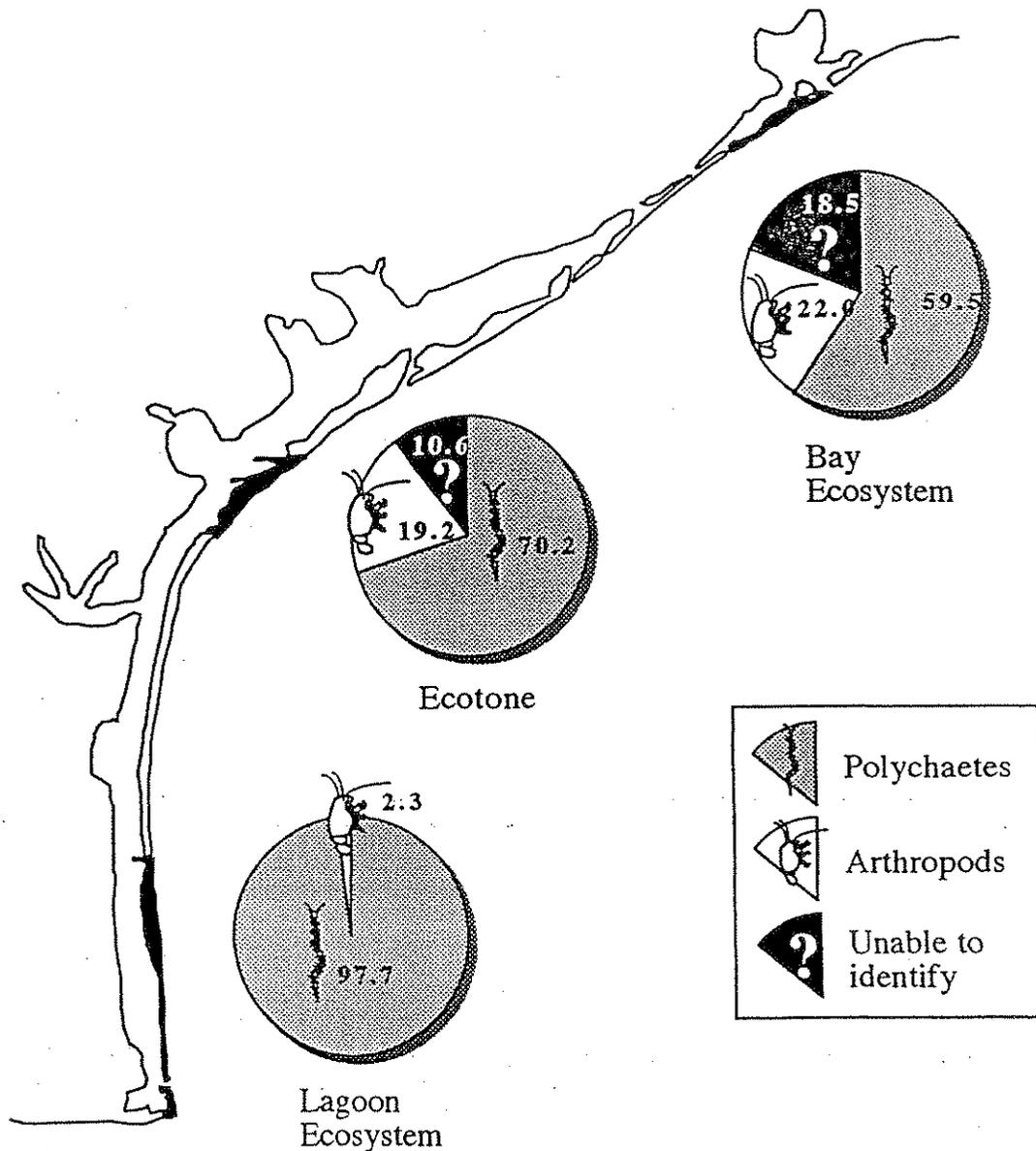


Figure 30. Piping Plover diet at beach habitat in the 2 ecosystems and the ecotone. Pie charts illustrate the proportion of polychaetes and arthropods captured by foraging plovers.

Plover captured mostly polychaetes in the lower beach swash zone ($P < 0.0001$; Table 19; Figure 29). Plovers foraging higher up on the beach captured a much greater proportion of arthropods ($P < 0.0001$). Above the swash, plovers captured a similar proportion of polychaetes and arthropods (Table 19; Figure 29).

Piping Plover Diet at Bayshore Habitat.

Piping Plovers captured more polychaetes than arthropods on bayshore flats. However, the ratio of these 2 prey types was not as pronounced as at beach habitat (Table 19; Figure 29). At bayshore habitat, the arthropod prey group was very broad including tanaids and all other types of crustaceans, spiders and insects (larvae, pupae, and adults). Strong dietary changes were observed when Piping Plovers moved among bayshore microhabitats. At sand flats, plovers fed mostly on polychaetes, capturing approximately 5 polychaetes for every arthropod (Table 19; Figure 29). At algal flats, the reverse was true, as plovers captured about 5 arthropods for every polychaete (Table 19; Figure 29).

Plover diet among the 2 ecosystems and the ecotone reflected the relative availability of sand flats and algal flats, the 2 dominant types of bayshore microhabitat used by Piping Plovers along the Texas Gulf Coast (Figure 31). In the bay ecosystem, where sand flats were much more common, polychaetes made up over 75% of the diet of Piping Plovers (Figure 31). In the lagoon ecosystem, where algal flats were much more common, arthropods comprised about 75% of the diet (Figure 31). At the ecotone sites, where a mosaic of sand flats and algal flats occurred, polychaetes and arthropods both comprised substantial portions of the Piping Plover diet (Figure 31).

Foraging Locomotion

Piping Plovers foraging at beach habitat spent $> 12\%$ of their time in prolonged foraging locomotion (PFL), compared to $< 3\%$ for plovers foraging on bayshore flats ($P = 0.0413$; Table 20). PFL bouts often occurred when plovers were engaged in territorial interactions with other Piping Plovers or when plover that were feeding in the beach

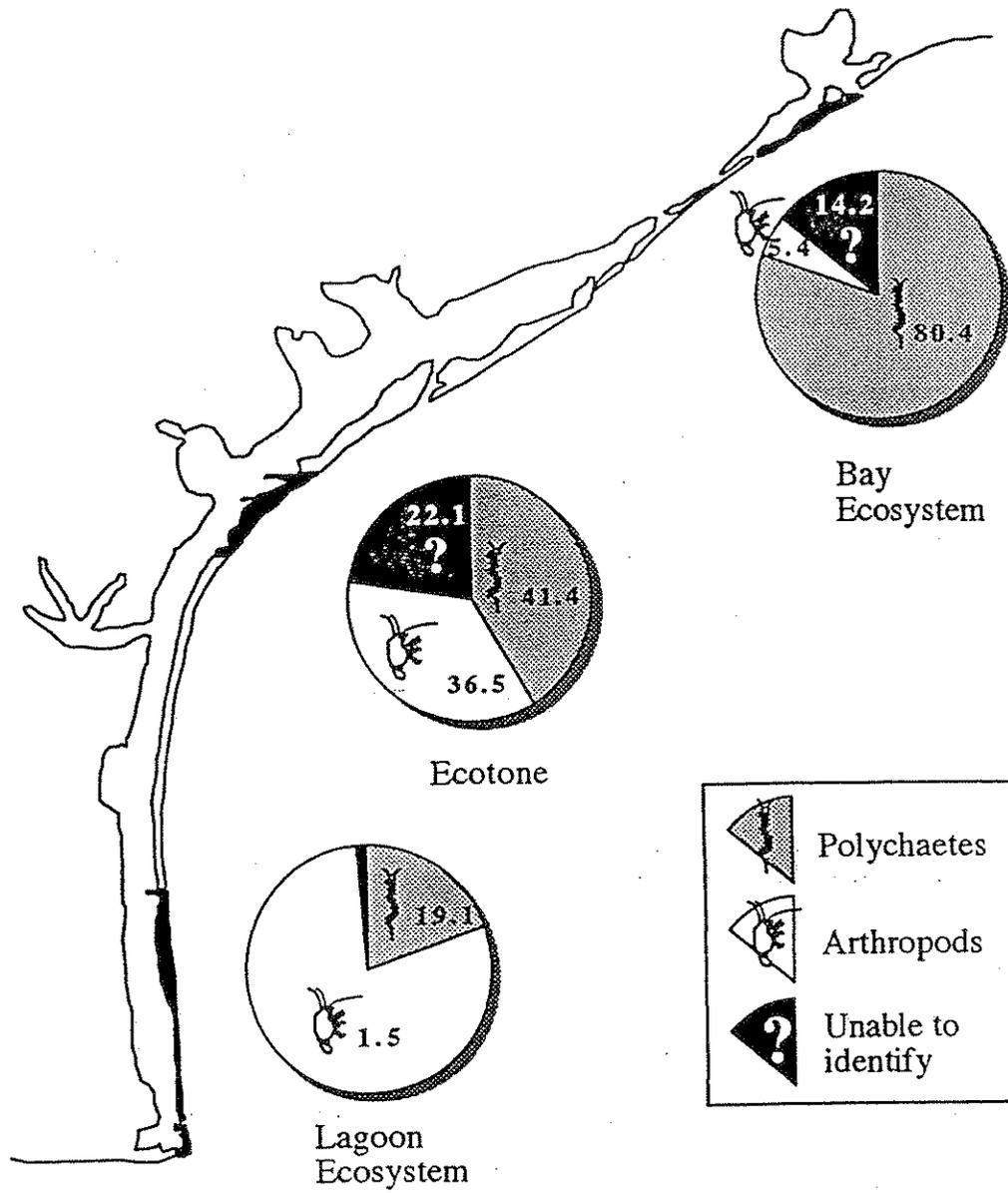


Figure 31. Piping Plover diet at bayshore habitat among the 2 ecosystems and the ecotone. Pie charts illustrate the proportion of polychaetes and arthropods captured by foraging plovers.

Table 20. Foraging efficiency (FE) and prolonged foraging locomotion (PFL) among different habitats and coastal regions of the Texas Gulf Coast, 1991 - 1994. All numbers represent means for all sites throughout the study. Foraging efficiency estimates are reported as the number of prey captured/minute, and foraging locomotion is reported as the % time plovers spent in PFL.

Parameter	FE			P	PFL			P
	mean	N	SE		mean	N	SE	
Beach	11.0	127	0.5	0.3726	12.5	154	0.7	0.0413
Bayshore	10.1	504	0.2		2.3	285	0.5	
Sand Flats	10.3	336	0.3		2.1	167	0.4	
Algal Flats	9.8	168	0.4	0.9114	2.6	118	0.4	0.0027
Beach Swash Zone	13.7	66	0.8	<0.0001	16.6	54	1.3	0.0002
Upper Beach Zone	7.0	38	1.1		9.5	81	1.2	
<u>All Beach:</u>								
Bay Ecosystem	10.2	40	1.1	0.1285	11.8	47	1.5	0.1626
Ecotone	10.9	78	0.8		13.5	90	1.1	
Lagoon Ecosystem	16.2	9	2.3		9.2	17	2.6	
<u>All Bayshore:</u>								
Bay Ecosystem	10.8	272	0.3	0.2321	1.9	141	0.4	0.2454
Ecotone	11.2	95	0.5		2.5	99	0.5	
Lagoon Ecosystem	8.0	137	0.4		3.2	45	0.7	

swash zone were forced to retreat to the upper beach to avoid an incoming swell of water. I also observed PFL as a response to the approach of a beachcomber walking through a feeding territory. The effect of the swash on PFL is supported by the fact that plovers foraging in the swash zone spent nearly twice as much time in PFL as did plovers feeding on the upper beach ($P = 0.0002$; Table 20). However, movements to avoid the swash did not completely account for elevated PFL at beach habitat. Piping Plovers foraging on upper beach habitat (i.e., those plovers that were not forced to move to avoid the swash) still exhibited significantly greater PFL than did plovers foraging at bayshore tidal flats ($P < 0.0001$; Table 20). Territorial interactions ($P < 0.0001$) and human disturbance ($P = 0.0002$) also were important factors contributing to PFL. Plovers that exhibited at least 1 display of aggression toward another plover spent an average of 9.3% ($N = 16$, $SE = 0.6$) of their time in PFL compared to just 1.8% ($N = 269$, $SE = 0.2$) for nonaggressive plovers. Plovers that experienced at least 1 encounter with a beachcomber or other type of pedestrian spent more time in PFL (mean = 11.8%, $N = 16$, $SE = 1.3$) than did plovers that did not encounter pedestrians (mean = 5.6%, $N = 423$, $SE = 0.3$).

Foraging locomotion did not differ significantly at beach habitat among the 2 ecosystems and the ecotone ($P = 0.1626$; Table 20). I detected no difference in foraging locomotion between the migratory and winter seasons at beach habitat ($P = 0.5584$; Table 20).

At bayshore habitats, plovers spent slightly more time in PFL on algal flats than on sand flats ($P = 0.0027$; Table 20). Territorial displays also affected foraging locomotion at bayshore habitat. Plovers that exhibited at least 1 display of aggression toward another plover during the record spent an average of 9.3% ($N = 16$, $SE = 1.1$) of their time in PFL compared to just 1.8% ($N = 269$, $SE = 0.3$) for nonaggressive plovers ($P < 0.0001$).

Plovers in both ecosystems and the ecotone spent similar amounts of time in PFL at bayshore habitat ($P = 0.2454$; Table 20). I detected no difference in foraging locomotion

between the migratory and winter seasons at bayshore habitat ($P = 0.2672$).

Foraging Efficiency

Piping Plovers captured an average of about 10 animals/minute among all habitats at my study sites (Tables 21 and 22). Foraging efficiencies were similar at beach and bayshore habitats ($P = 0.3726$). Plovers also foraged with similar efficiency among the 2 ecosystems and the ecotone at beach habitat ($P = 0.1285$; Table 21). However, Piping Plovers foraged more efficiently within the swash zone of the beach habitat relative to the upper beach zone ($P < 0.0001$; Table 12).

Plovers foraged with similar efficiency among the 2 ecosystems and the ecotone at bayshore habitat ($P = 0.1626$; Table 22). Plovers captured prey at about the same rate on sand flats and algal flats ($P = 0.9114$; Table 18).

Piping Plovers were more efficient at capturing polychaetes than arthropods ($P < 0.0001$; Table 23). At beach habitat, plovers captured *Scolecopsis squamata* and other polychaetes more efficiently than amphipods and other beach arthropods ($P = 0.0351$; Table 23). At bayshore habitat, plovers captured polychaetes more efficiently than insects and other types of arthropods ($P < 0.0001$; Table 23).

Foraging Ecology and Prey Density

Piping Plovers foraged more actively and efficiently in areas of high benthic prey density. At beach habitat, plover foraging effort increased from about 10 pecks/min in areas of low prey density (< 1000 animals/m²) to about 20 pecks/min in areas of high prey density (> 5000 animals/m²; $P = 0.0208$; Figure 32A). Foraging effort was positively related to polychaete density ($P = 0.0306$; Figure 32B) but was not related to crustacean density ($P = 0.1642$; Figure 33A) or insect density ($P = 0.5953$; Figure 33B). Plovers also captured more prey in areas of the beach with dense prey populations ($P = 0.0132$; Figure 34A).

Table 21. Mean foraging efficiency of Piping Plovers at beach habitat at sites along the Texas Gulf Coast, 1991 - 1994. Capture efficiency of all prey types, polychaetes, and arthropods are represented as the number of prey captured/minute. Abbreviations: MISP = Mustang Island State Park.

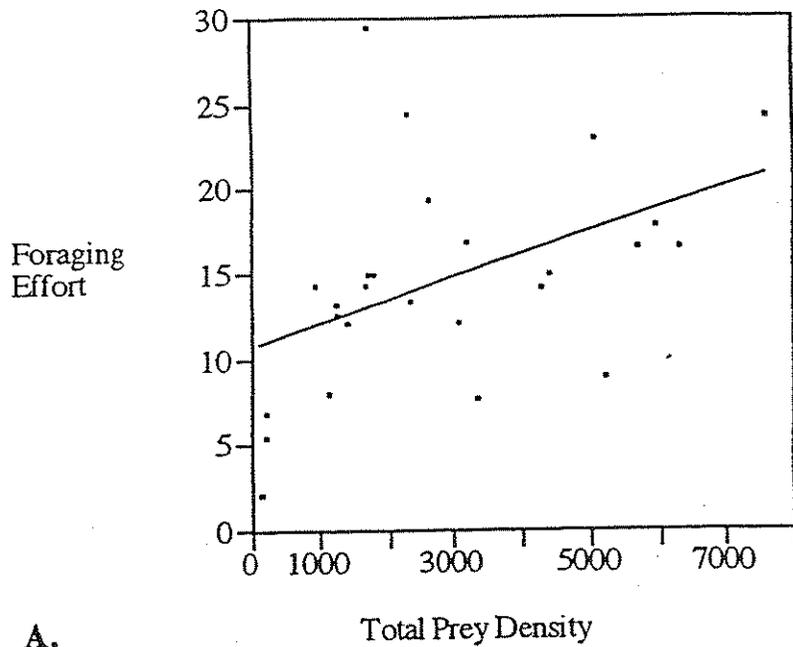
Study Location	All Prey			Polychaetes			Arthropods		
	mean	N	SE	mean	N	SE	mean	N	SE
Bolivar Flat	11.9	20	1.5	8.6	20	1.7	1.7	20	0.7
Big Reef	4.9	6	2.7	1.7	6	3.1	1.4	6	1.3
San Luis Pass	10.0	14	1.8	7.9	14	2.0	1.7	14	0.9
East Flats	5.2	2	4.8	4.0	2	5.4	0.0	2	2.3
MISP - North	10.5	28	1.3	7.8	24	1.5	1.9	24	0.7
MISP - South	11.8	20	1.5	9.7	20	1.7	1.0	20	0.7
Packery Channel	11.1	28	1.3	8.7	22	1.6	3.3	22	0.7
South Bay - East	14.9	2	4.8	13.9	2	5.4	1.0	2	2.3
South Padre Island	16.5	7	2.5	16.5	7	2.9	0.0	7	1.2

Table 22. Mean foraging efficiency of Piping Plovers at bayshore habitat at sites along the Texas Gulf Coast, 1991 - 1994. Capture efficiency of all prey types, polychaetes, and arthropods are represented as the number of prey captured/minute. Abbreviations: MISP = Mustang Island State Park.

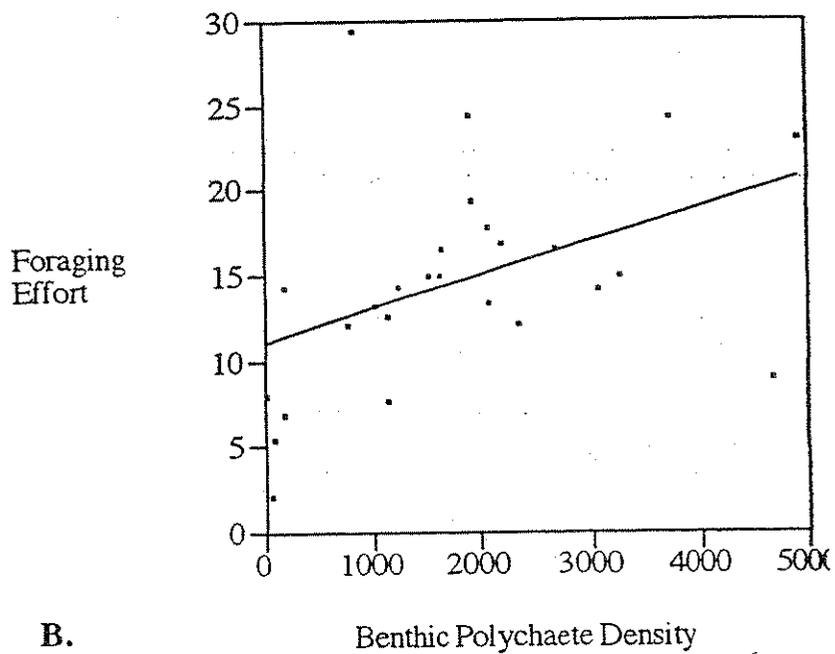
Study Location	All Prey			Polychaetes			Arthropods		
	mean	N	SE	mean	N	SE	mean	N	SE
Bolivar Flat	11.9	143	0.4	9.9	142	0.5	0.7	142	0.3
Big Reef	8.7	42	0.8	6.5	41	1.0	1.2	41	0.5
San Luis Pass	10.0	127	0.5	8.5	121	0.6	0.1	121	0.3
East Flats	8.5	8	1.8	1.0	8	2.2	7.2	8	1.2
MISP - North	10.4	59	0.7	7.2	45	0.9	1.1	45	0.5
Packery Channel	11.6	86	0.6	5.7	67	0.8	3.3	67	0.4
South Bay - East	9.3	8	1.8	6.3	8	2.2	2.7	8	1.2
South Padre Island	9.9	64	0.7	3.3	64	0.8	6.6	64	0.4

Table 23. Comparison of foraging capture rate (number of prey captured/minute) among different prey groups. Data represented are from only those records in which each prey group represented at least 75% of the total captures. For example, arthropods comprised 75% or more of the prey captured at beach habitat for 16 foraging efficiency records, compared to 321 records at beach habitat in which polychaetes comprised 75% or more of the prey captured.

Parameter	Polychaetes			Arthropods			P-value
	mean	N	SE	mean	N	SE	
All Habitats	12.3	243	0.3	8.6	143	0.5	< 0.0001
Beach Habitat	11.7	321	0.3	8.8	16	1.5	0.0351
Bayshore Habitat	12.3	243	0.4	8.5	137	0.5	< 0.0001



A.



B.

Figure 32. Linear regressions illustrating Piping Plover foraging effort (number of pecks/minute) in relation to total benthic density (A; $P = 0.0208$) and benthic polychaete density (B; $P = 0.0306$) at beach habitat. Data are from all sites.

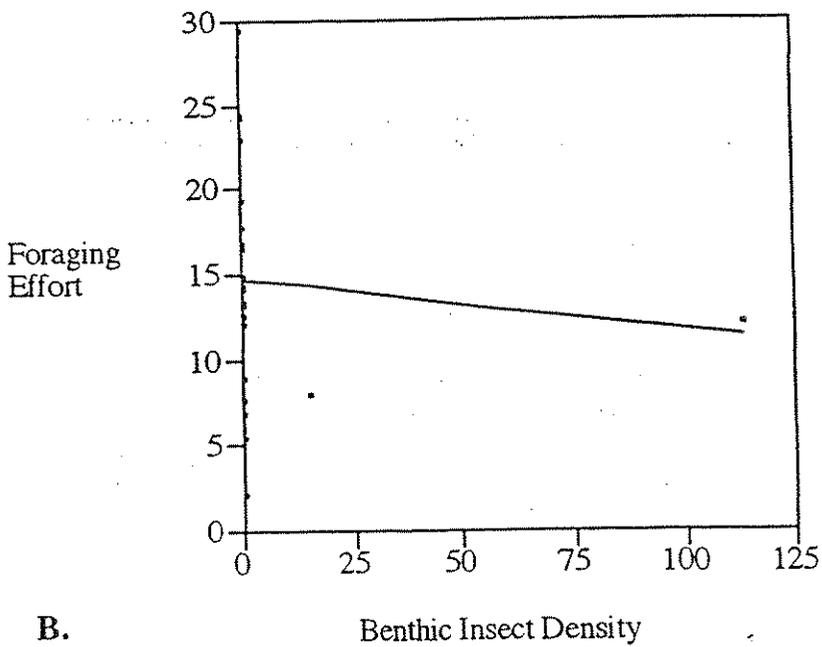
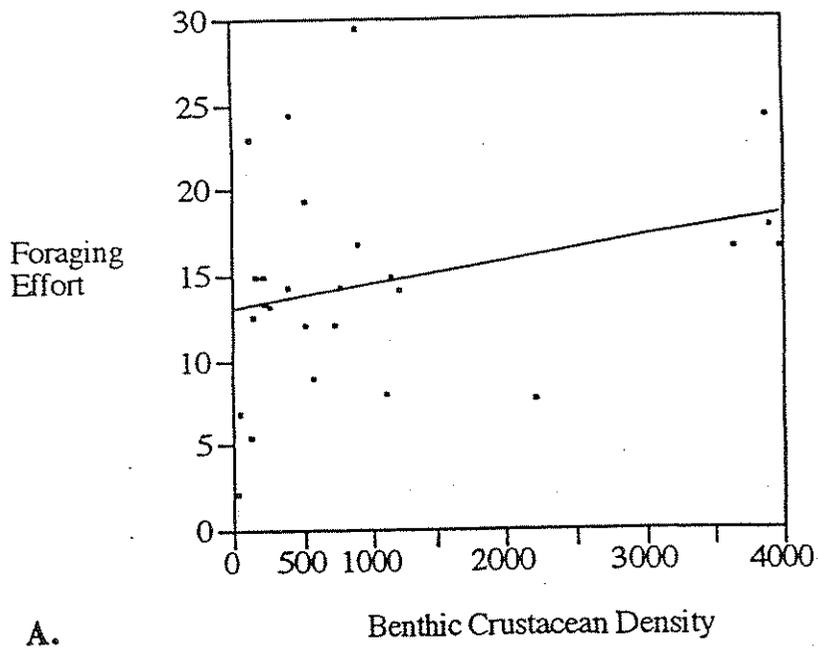
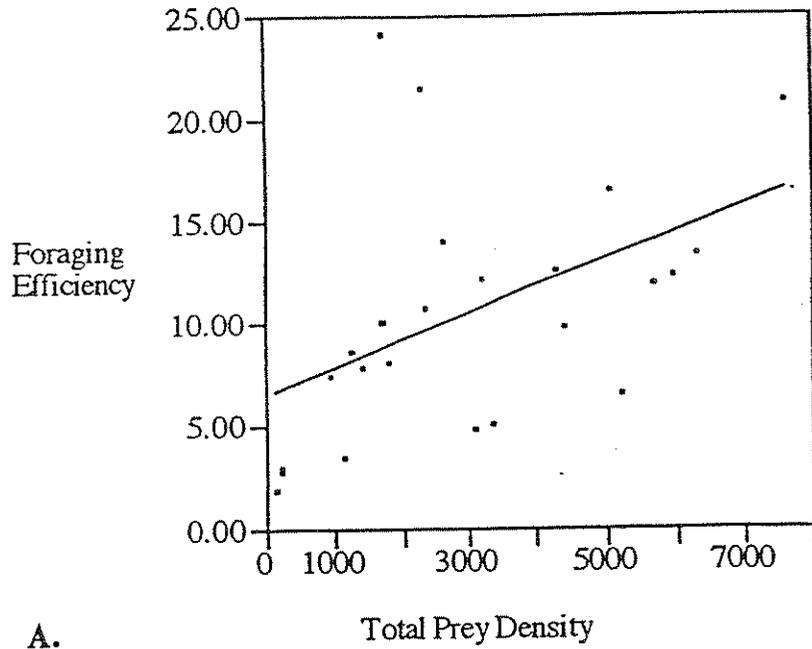
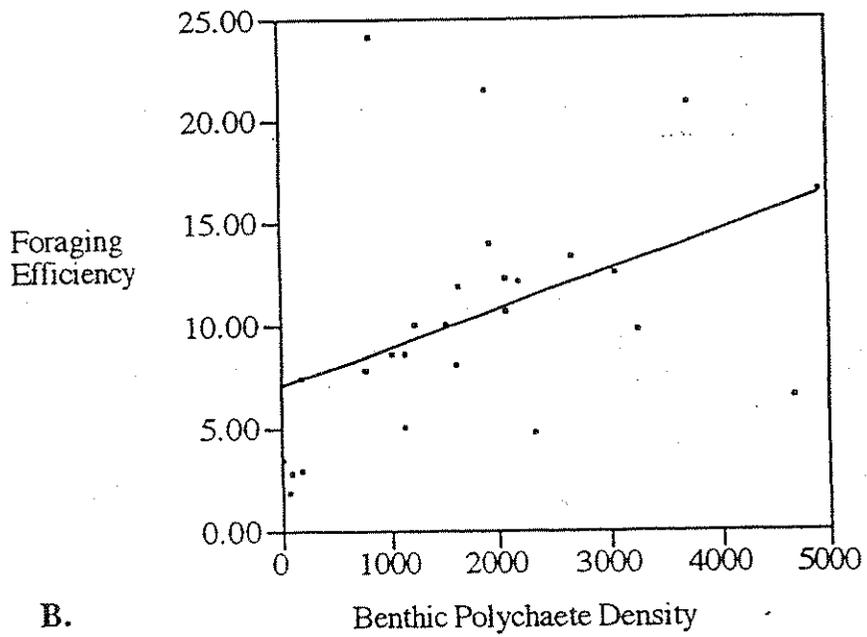


Figure 33. Linear regressions illustrating Piping Plover foraging effort (number of pecks/minute) in relation to benthic crustacean density (A; $P = 0.1642$) and benthic insect density (B; $P = 0.5953$) at beach habitat. Data are from all sites.



A.



B.

Figure 34. Linear regressions illustrating Piping Plover foraging effort (number of pecks/minute) in relation to total benthic density (A; $P = 0.0132$) and benthic polychaete density (B; $P = 0.0245$) at beach habitat. Data are from all sites.

Foraging efficiency was positively related to polychaete density ($P = 0.0245$; Figure 34B), but was not related to crustacean density ($P = 0.1206$; Figure 35A) or benthic insect density ($P = 0.5636$; Figure 35B).

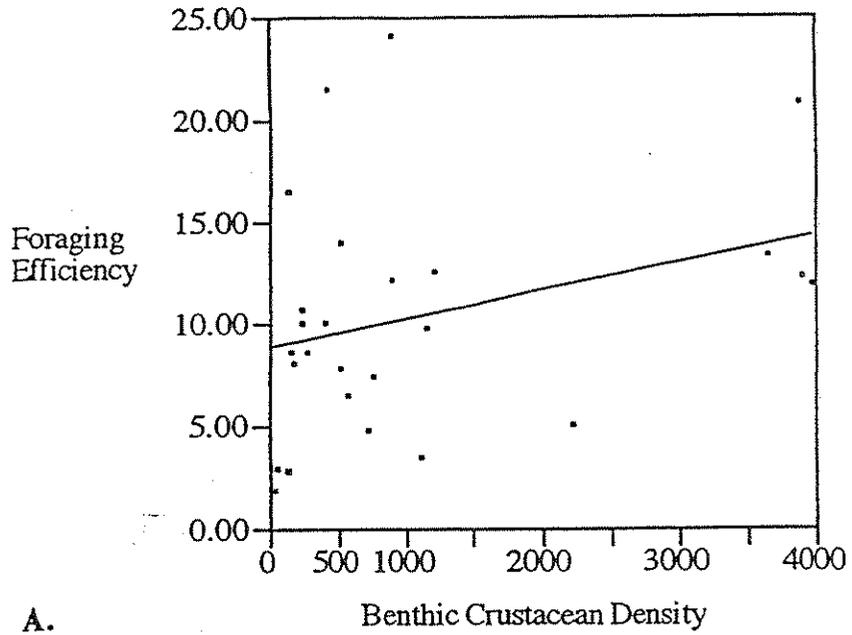
At bayshore habitat, foraging effort also was positively related to total benthic prey density ($P < 0.0001$; Figure 36A) and polychaete density ($P < 0.0001$; Figure 36B), but was unrelated to benthic crustacean density ($P = 0.5222$; Figure 37A) or benthic insect density ($P = 0.2858$; Figure 37B). Plovers captured more prey on tidal flats with high total prey density ($P = 0.0094$; Figure 38A) and polychaete density ($P = 0.0109$; Figure 38B). Foraging efficiency on tidal flats was not affected by crustacean density ($P = 0.8491$; Figure 39A), or benthic insect density ($P = 0.9731$; Figure 39B).

Interestingly, plovers foraged less actively ($P = 0.0096$; Figure 40) and less efficiently ($P = 0.0183$; Figure 41) in areas of the tidal flat with high surface prey abundance. However, polynomial fits explained the greatest amount of variability among the data (e.g., quartic fit, $P = 0.0784$, $R^2 = 0.113$; Figure 41B) and suggest the existence of a threshold abundance of surface prey, above which plovers may have foraged less efficiently.

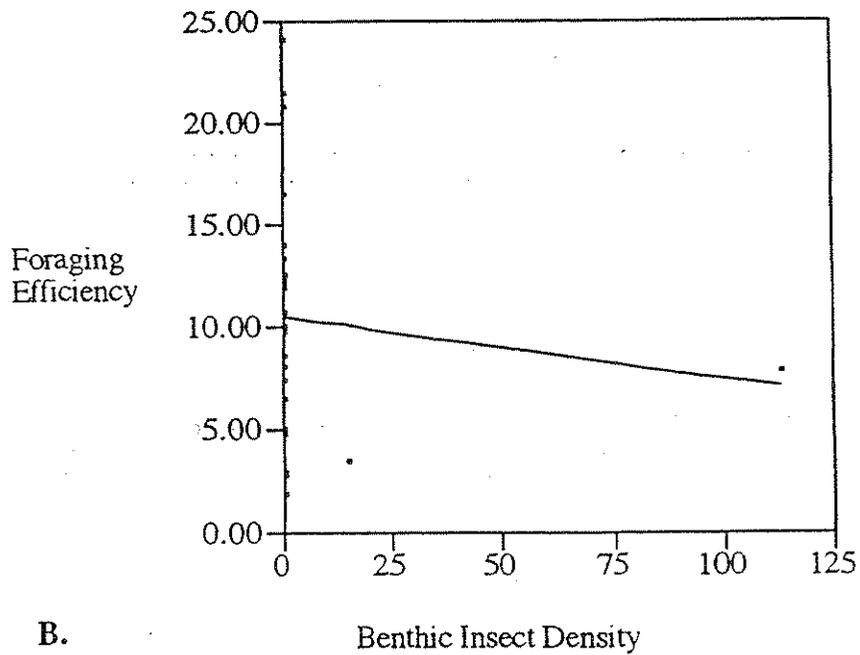
Intraspecific and Interspecific Interactions

Piping Plovers were more likely to occur in close proximity to another Piping Plover at bayshore habitat than at beach habitat ($P < 0.0001$; Figure 42). At beaches, the nearest species to Piping Plovers were Sanderlings (*Calidris alba*). Western Sandpipers (*C. mauri*) and other Piping Plovers were the most common nearest neighbors at sand flats, and *C. mauri*, Least Sandpipers (*C. minutilla*) and other Piping Plovers were the most common nearest neighbors at algal flats.

The large majority of aggressive interactions I observed during the study were intraspecific. The majority of interspecific aggressions involving Piping Plovers were with another *Charadrius* spp., usually Snowy Plovers (*Charadrius alexandrinus*) or

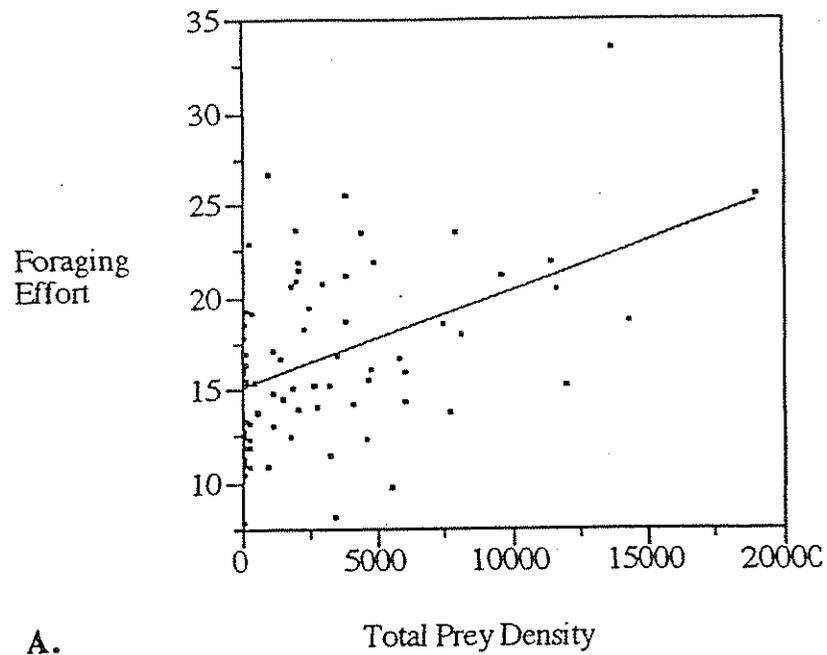


A.

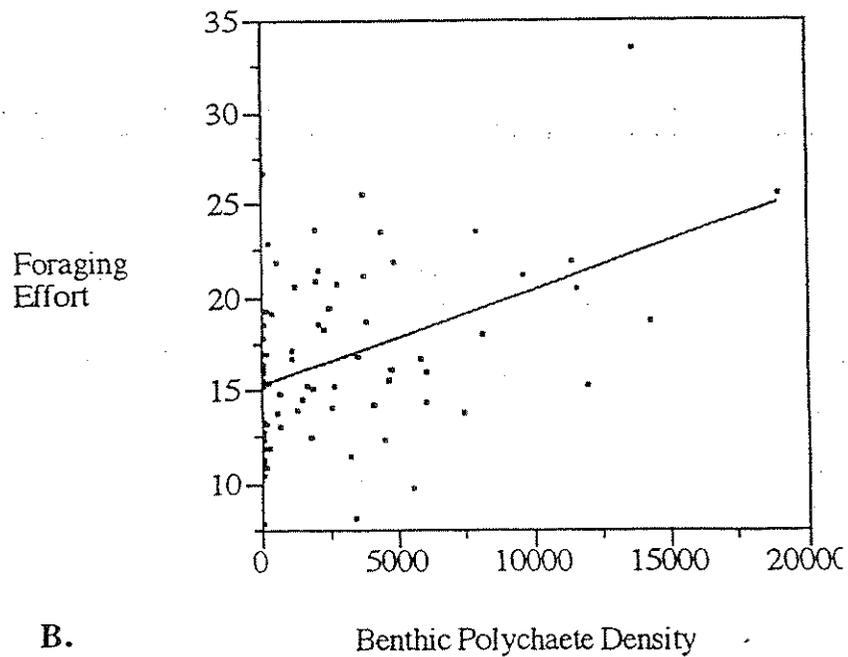


B.

Figure 35. Linear regressions illustrating Piping Plover foraging efficiency (number of captures/minute) in relation to benthic crustacean density (A; $P = 0.1206$) and benthic insect density (B; $P = 0.5636$) at beach habitat. Data are from all sites.

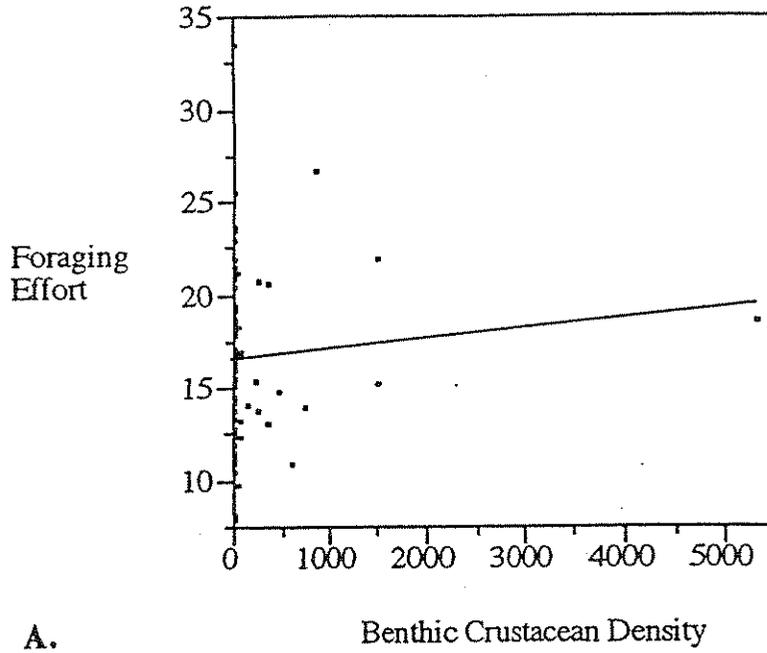


A.

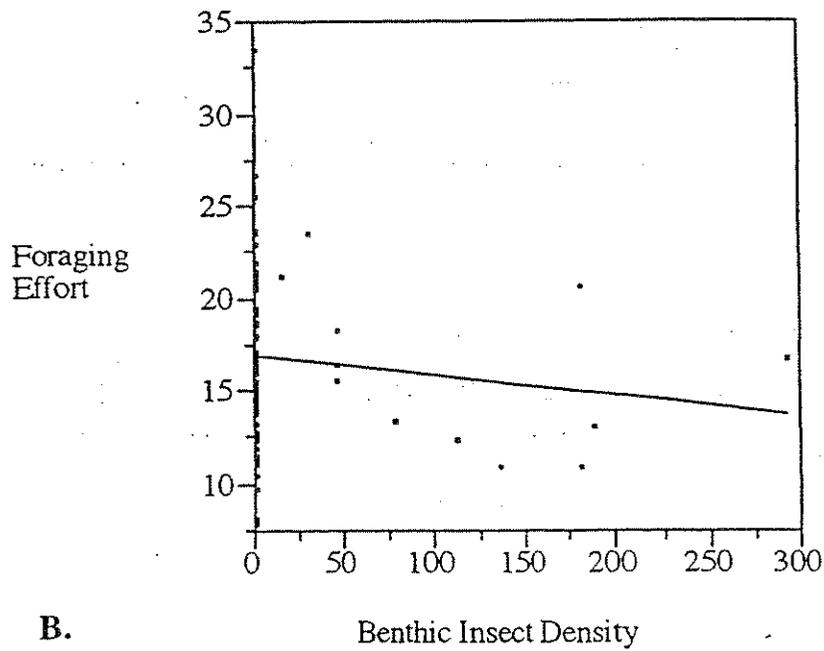


B.

Figure 36. Linear regressions illustrating Piping Plover foraging effort (number of pecks/minute) in relation to total benthic density (A; $P < 0.0001$) and benthic polychaete density (B; $P < 0.0001$) at bayshore habitat. Data are from all sites.

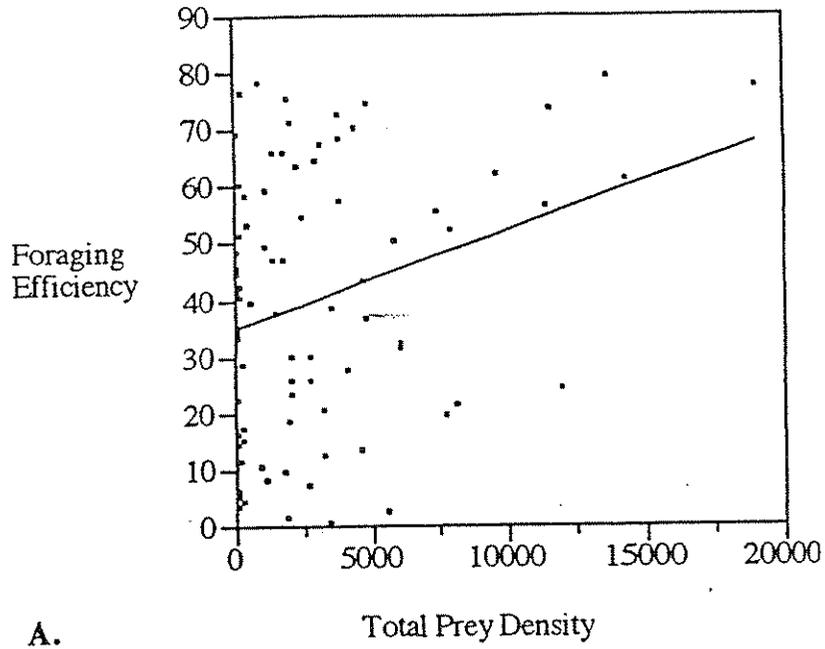


A.

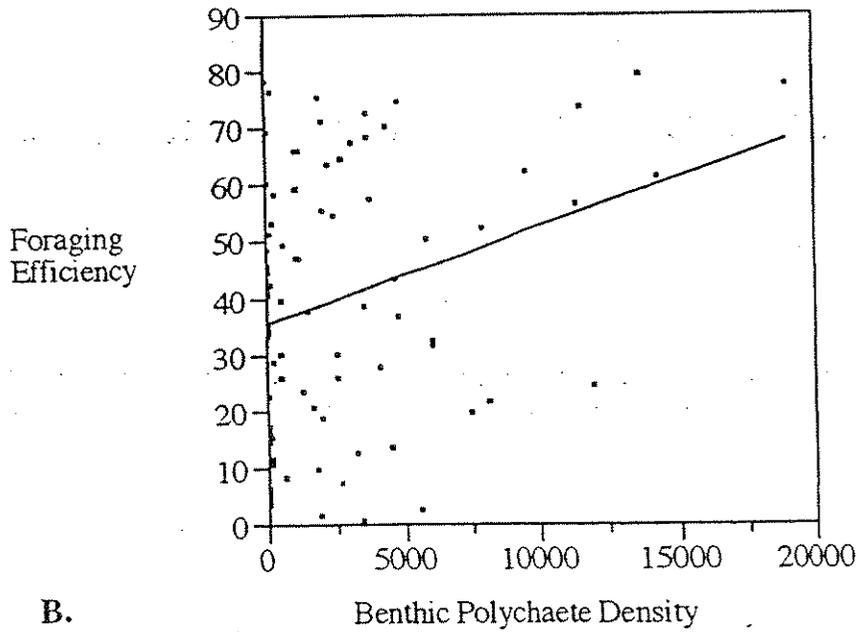


B.

Figure 37. Linear regressions illustrating Piping Plover foraging effort (number of pecks/minute) in relation to benthic crustacean density (A; $P = 0.5222$) and benthic insect density (B; $P = 0.2858$) at bayshore habitat. Data are from all sites.

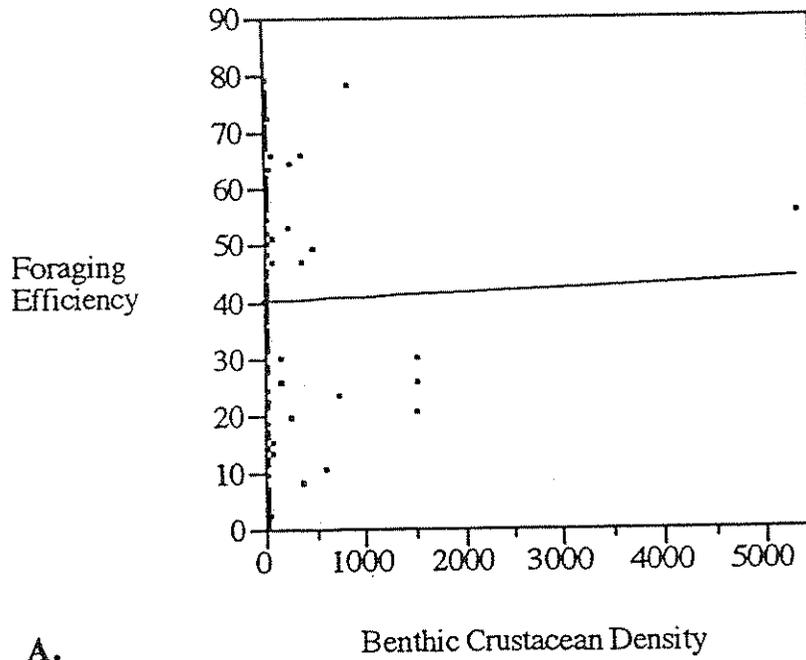


A.

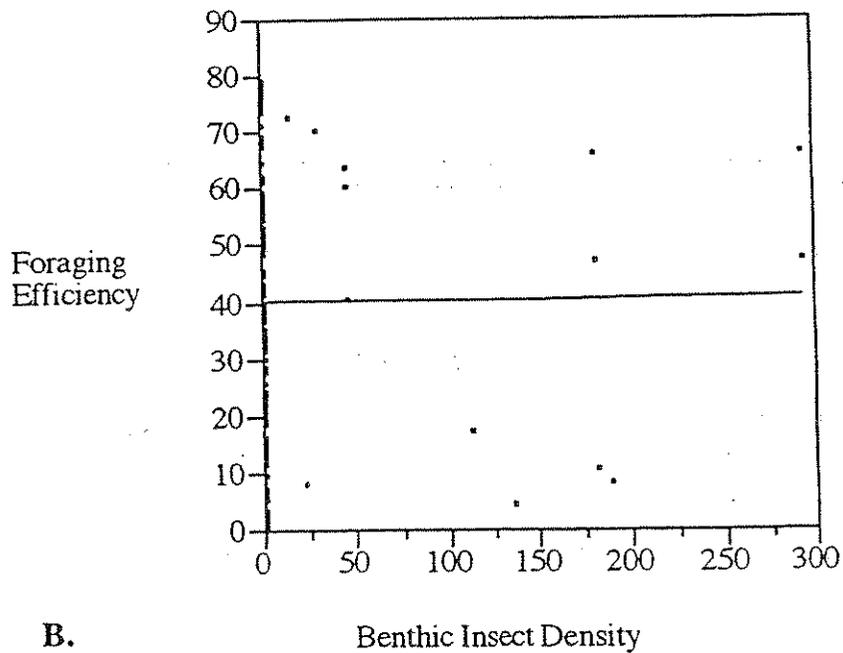


B.

Figure 38. Linear regressions illustrating Piping Plover foraging efficiency (number of captures/minute) in relation to total benthic density (A; $P = 0.0094$) and benthic polychaete density (B; $P = 0.0109$) at bayshore habitat. Data are from all sites.



A.



B.

Figure 39. Linear regressions illustrating Piping Plover foraging efficiency (number of captures/minute) in relation to benthic crustacean density (A; $P = 0.8491$) and benthic insect density (B; $P = 0.9731$) at bayshore habitat. Data are from all sites.

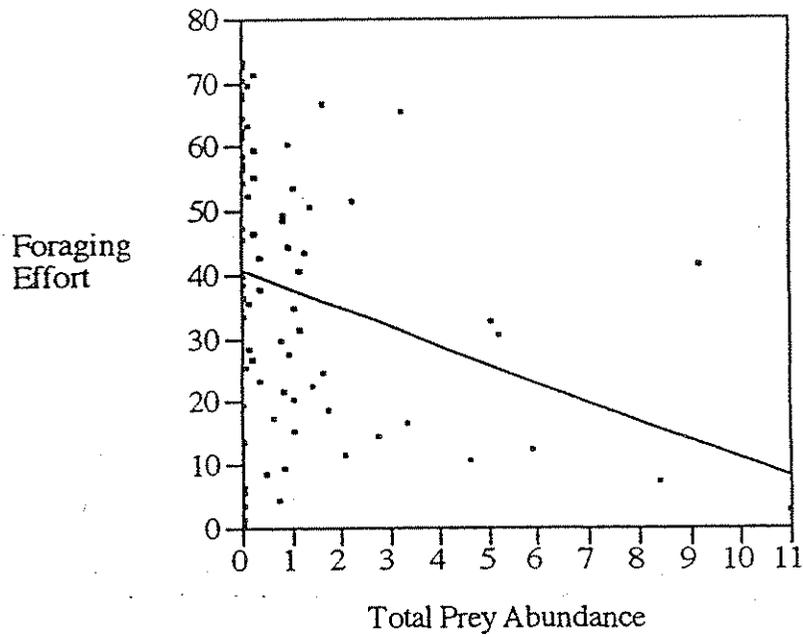


Figure 40. Linear regressions illustrating the relationship between Piping Plover foraging effort (number of pecks/minute) and total surface prey abundance at bayshore habitat ($P = 0.0096$). Data are from all sites as appraised by sticky trap prey assays.

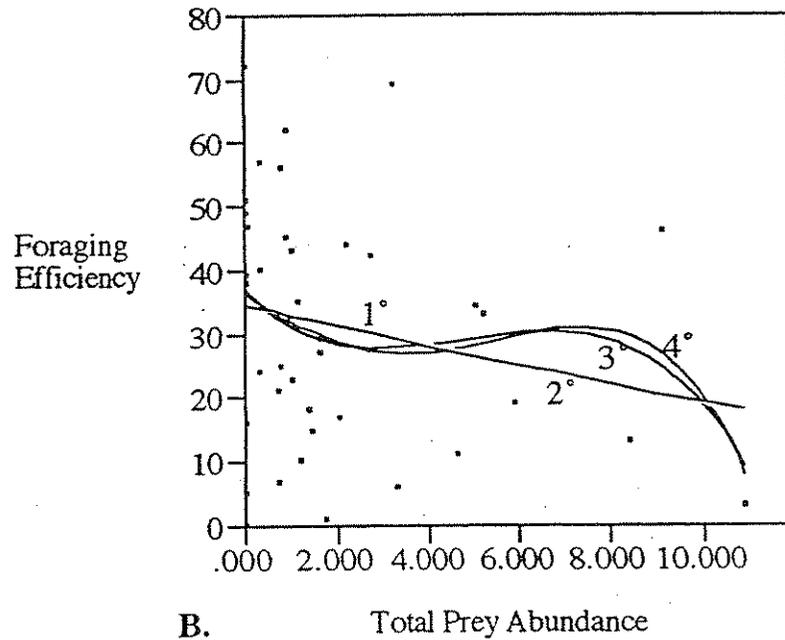
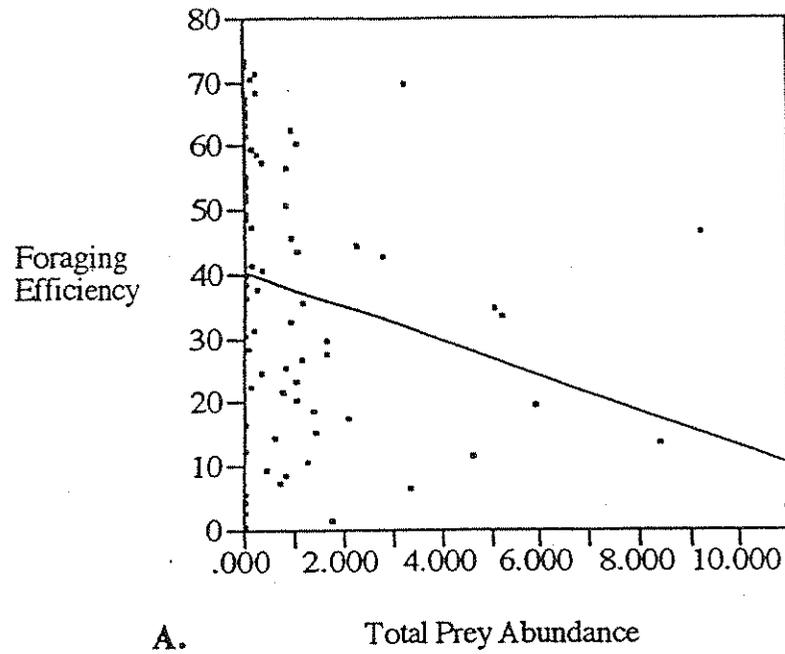


Figure 41. Linear regressions illustrating the relationship between Piping Plover foraging efficiency (number of captures/minute) and total surface prey abundance at bayshore habitat at all sites as appraised by sticky trap prey assays. Figure A illustrates a linear regression line ($P = 0.0303$, $r^2 = 0.064$), and (B) the linear fit in relation to various polynomial fits. The quartic fit (4° ; $P = 0.0784$, $r^2 = 0.113$) and cubic fit (3° ; $P = 0.0436$, $r^2 = 0.109$) explain a greater amount of variation in the data relative to the linear fit or quartic fit ($P = 0.0589$, $r^2 = 0.077$).

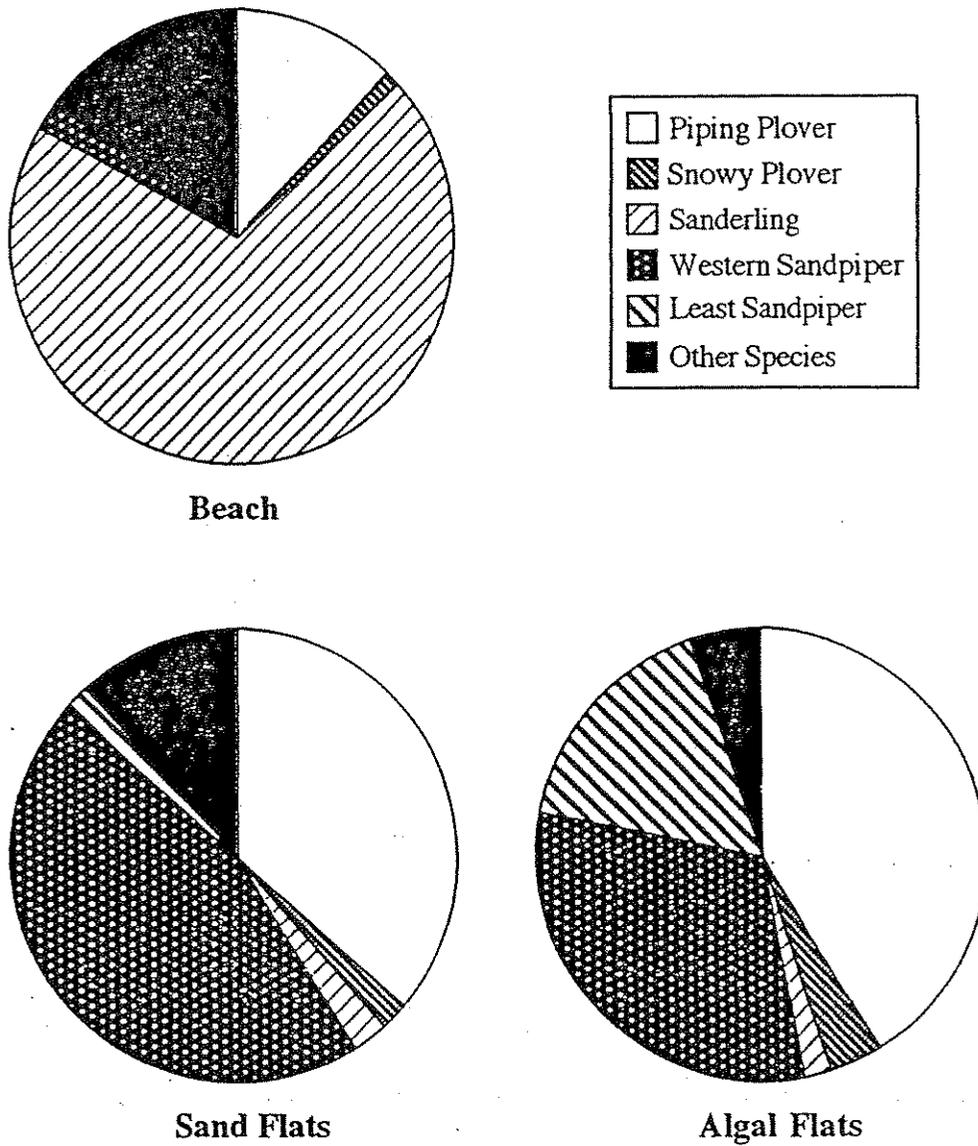


Figure 42. Species that were closest to Piping Plovers foraging at beach, sand flat, and algal flat habitat. Pie sections correspond to the 4 shorebird species most commonly associated with foraging Piping Plovers. The area of the pie wedge is proportional to the frequency with which each species occurred as the nearest neighbor to a Piping Plover as it was observed during a foraging efficiency record.

Semipalmated Plovers (*C. semipalmatus*). Interspecific interactions were generally restricted to bayshore habitat, as *C. alexandrinus* and *C. semipalmatus* only rarely utilized beaches as foraging habitat at my study sites (pers. obs.). Interactions between Piping Plovers and Sanderlings (the other common shorebird utilizing beach intertidal habitat) occurred, but were rare (pers. obs.).

Foraging Piping Plovers were observed to exhibit some form of aggression about once every 8 minutes (mean = 0.119 acts of aggression/min., SE = 0.019, N = 533 records [1926.8 minutes of observation]) as appraised via FE records, and about once every 15 minutes (mean = 0.068 acts of aggression/min., SE = 0.014, N = 441 records [882 minutes of observation]) as appraised via PFL records.

Using FE data, I found Plovers to be no more aggressive at beach habitat (mean = 0.066 acts of aggression/min, SE = 0.044, N = 102) than at bayshore habitat (mean = 0.131 acts of aggression/min, SE = 0.021, N = 431; $P = 0.3065$). However plovers were significantly more aggressive during the migratory period than during the winter period ($P = 0.0018$; Table 24) at beach habitat. Season did not affect plover behavior at bayshore habitat (Table 24).

Using PFL data, I found Plovers to be no more aggressive at beach habitat (mean = 0.075 acts of aggression/min, SE = 0.025, N = 154) than at bayshore habitat (mean = 0.0645 acts of aggression/min, SE = 0.018, N = 287; $P = 0.1162$). Plovers were no more aggressive during the migratory period than during the winter period at beach or bayshore habitat based upon the PFL data (Table 24).

DISCUSSION

Prey Dynamics

Piping Plovers wintering in the bay and lagoon ecosystems of the TGC encountered very different bayshore prey communities. In the bay ecosystem plovers fed at tidal flats

Table 24. Seasonal variation in the frequency of aggressive displays by Piping Plovers along the Texas Gulf Coast, 1991 - 1994. The mean number of aggressive displays/minute as recorded during foraging efficiency (FE) and foraging locomotion (PFL) records is reported by season among different habitat types. The *P*-values presented in the last column are associated with one-way ANOVA analyses comparing plover aggression between the 2 seasons. N = the number of FE or PFL records supporting the estimates.

	Migration			Winter			<i>P</i> -value
	mean	N	SE	mean	N	SE	
FE Data							
Beach	0.124	54	0.030	0.000	48	0.032	0.0018
Bayshore	0.121	231	0.032	0.144	200	0.034	0.6281
Sand Flats	0.141	187	0.040	0.225	125	0.049	0.5958
Algal Flats	0.033	44	0.016	0.008	75	0.012	0.5607
PFL Data							
Beach	0.077	84	0.031	0.071	70	0.034	0.6413
Bayshore	0.034	119	0.030	0.086	168	0.025	0.3727
Sand Flats	0.024	83	0.042	0.157	86	0.041	0.1424
Algal Flats	0.056	36	0.032	0.012	82	0.021	0.8977

that supported an extremely rich benthic food base dominated by polychaetes but containing only a sparse population of insects and other types of surface prey. Conversely, plovers wintering in the lagoon ecosystem fed at tidal flats that were benthos-poor, but rich in surface prey relative to the bay ecosystem. Prey populations in the ecotone were mixed, offering both benthic and surface prey to plovers.

Withers (1994) also reported abundant populations of polychaetes, crustaceans, and insects (adults and larvae) between 1991 - 1993 at Corpus Christi Pass (a small tidal flat situated in the ecotone between my Packery Channel and Mustang Island State Park - South sites). Withers recorded between 225 polychaetes/m² and 1335 polychaetes/m² in 3 microhabitat types. In samples collected in association with foraging Piping Plovers I recovered an average of 339 polychaetes/m² at the Mustang Island State Park - North site and 557 polychaetes/m² at Packery Channel site. Although surface prey populations were not sampled, Withers found between 455 insects/m² and 729 insects/m² in benthic samples. Benthic insect density was much lower among samples collected in association with foraging Piping Plover flocks, ranging from 3 insects/m² at the Packery Channel site to 41 insects/m² at Mustang Island State Park - North site.

Diet

In general, I found the diet of Piping Plovers to reflect the relative availability of the major prey groups. Plovers in the bay ecosystem fed primarily on polychaetes, whereas plovers in the lagoon ecosystem relied more heavily on surface prey. Plovers wintering in the ecotone, where a mix of habitats and prey communities occurs, exhibited a mixed diet, incorporating more surface prey than the diet of plovers wintering in the bay ecosystem and more polychaetes than the diet of plovers wintering in the lagoon ecosystem.

On beaches, plovers fed primarily on the polychaete *Scolelepis squamata* and on small amphipods. These organisms, along with small clams (*Donax* spp.; not regularly

eaten by plovers), dominated the beach invertebrate community at all of my sites. Polychaete densities were highest in the bay ecosystem, lowest in the lagoon ecosystem, and intermediate in the ecotone. Crustacean densities were also lower in the lagoon ecosystem than the bay ecosystem and the ecotone.

At McFaddin Beach (a site located in the bay ecosystem ~ 50 km north of Bolivar Flats) and Malachite Beach (a site located in the ecotone ~ 10 km south of Packery Channel) Shelton and Robertson (1981) found *S. squamata* and haustoriid amphipods to be the most abundant fauna in random samples of the mid and upper intertidal zones. These are the 2 zones I found plovers to use most frequently. They found *S. squamata* to be more abundant at their bay ecosystem site (McFaddin Beach), and amphipods to be more abundant at their ecotone site (Malachite Beach). They reported an average of 591 *S. squamata*/m² and 436 amphipods/m² at their bay ecosystem beach and ~ 313 *S. squamata*/m² and 2598 amphipods/m² at their ecotone beach (based upon 6 visits to each site). These findings compare reasonably well with the data I gathered from samples collected in association with foraging plovers at beach habitat. The higher relative density of polychaetes in my samples at bay ecosystem and ecotone beach compared to the random samples collected by Shelton and Robertson (1981) may indicate a selection by plovers for areas where *S. squamata* were most abundant.

I rarely observed plovers feeding on any prey other than amphipods and polychaetes at beach habitat. Therefore, despite their abundance, bivalves appeared to comprise a very small part of the Piping Plover diet. The bivalve fragments Nicholls (1989) recovered from plover fecal pellets may have been incidentally ingested by plovers along with sand as they were capturing other prey. Shelton and Robertson (1981) found *Donax* sp. to be the most abundant prey at both of their sites, but found them to be concentrated at lower tidal zones, which are often not available to Piping Plovers.

Foraging Efficiency

Interestingly, plovers foraged with similar efficiency at both major habitats, and in both ecosystems and the ecotone. Piping Plovers captured about 10 animals/min. whether feeding at beach habitat or bayshore habitat, or whether feeding in the polychaete-rich bay ecosystem flats, the insect-rich lagoon ecosystem flats or the mixed community ecotone flat.

The only detectable shift in foraging efficiency occurred at beach habitat when plovers moved from the upper beach microhabitat into the lower swash zone. After such a move, the primary diet of plovers shifted from amphipods to polychaetes, and foraging efficiency nearly doubled from about 7 animals/min. to 14 animals/min. My prey samples suggest that *S. squamata* were present at equal densities in both microhabitats. By closely watching *S. squamata* feed, however, it seems likely that this polychaete is much more readily available to plovers in the swash zone. *S. squamata* appeared to actively forage at the surface only when they were covered with water. As the swash zone became covered, *S. squamata* extended palps into the thin film of water in the receding swash in order to trap food particles. Presumably, *S. squamata* became visually detectable to plovers under these conditions, for it was during the period when the swash was receding that plovers ran into the swash zone and switched from amphipods to *S. squamata*. Once in the swash zone, plovers collected as many *S. squamata* as they could before an incoming swell forced them to again move up into the upper beach zone and shift back to an amphipod diet.

Prolonged Foraging Locomotion

The repeated movement between the swash zone and the upper beach illustrates another distinguishing feature in Piping Plover behavior at beach habitat and bayshore habitat along the Texas coast. Plovers appeared to expend much greater energy on beach habitat than at bayshore habitat. Plovers spent about 12% of their time in prolonged

foraging locomotion (PFL) at beaches compared to less than 3% at bayshore habitats. Much of the PFL appeared to be explained by movements in and out of the swash, territorial defense (which was much higher on beach habitat), and running to avoid people using the beach.

These results complement and perhaps partially explain my findings in Chapter II suggesting Piping Plovers preferred bayshore habitat over beach habitat in Texas. One hypothesis for this preference is that plovers suffered a lower net energy intake at beaches. The lower net energy intake may be due, not to a lower direct energy intake since plovers captured about the same number of prey in both habitats, but to an increased energy investment required to capture the same number of prey at both habitats.

Connors et al. (1981) demonstrated a directed response by Sanderlings to tides and prey availability along the California coast. They found Sanderlings to forage on beach habitat at high and mid-level tides but switch to protected bayshore sand flats as the tides receded. They related these movements to the availability of prey at different tide levels and found a strong correlation between prey availability and Sanderling density at both beach and bayshore habitats, suggesting birds were visiting each habitat type when it was most productive.

Because the beach and bayshore sites monitored by Connors et al. (1981) were closely situated and the tides synchronous, they were unable to evaluate whether Sanderlings shifted to beach habitat because bayshore flats were inundated, or because beach sites became more productive. In this way their study area was similar to my bay ecosystem sites and my 2 northern ecotone sites (East Flats and Mustang Island State Park), where bayshore tides and beach tides were synchronous. At these sites, Piping Plovers behaved like the Sanderlings in California, using beaches during high tides and bayshore flats at low tides. However, one of my ecotone sites (Packery Channel) experienced asynchronous beach and bayshore tides. At Packery Channel, Piping

diet in the lagoon ecosystem.

A negative correlation between flock size and prey abundance might have occurred if plovers foraging in large flocks were able to rapidly deplete local surface prey populations. Therefore, an alternative hypothesis is that plovers were attracted by locally abundant surface prey populations, but harvested these populations to such an extent that my prolonged sampling technique (1 hour sticky traps) measured the depleted population rather than the initial population abundance that attracted the plover flock.

Another important feature to consider when comparing benthic and surface prey communities is prey mobility and the way it affects a plover's ability to detect and capture prey. Most of the benthic prey eaten by plovers (polychaetes and crustaceans) were sessile or sedentary. The detectability of these prey to Piping Plovers may have been governed simply by whether these organisms were present at the surface (when feeding or defecating) or were not (when burrowing or residing in a tube, etc.) Surface prey were probably more detectable to Piping Plovers than most benthic prey, but may have been more difficult to catch due to their mobility. The mobility feature of surface prey also may have reversed the effect of prey density on Piping Plover foraging efficiency. Perhaps, at some point, too many mobile surface prey caused a reduction in the intake rate by plovers. Plovers may have become confused about which prey to pursue, just as do predators foraging on schooling fish or flocking birds (Page and Whitacre 1975).

Could there have been a maximum surface prey density threshold above which foraging efficiency was compromised? Some support for this hypothesis is found in the negative relationship between foraging efficiency and surface prey abundance and the apparent existence of a threshold of foraging efficiency for plovers feeding on surface prey. The predicted threshold, 10 animals/sticky trap, was higher than I commonly observed among most of my samples, but suggests that a threshold might exist and may affect how plovers select local feeding areas in the lagoon ecosystem.

I did not assess the caloric value of different prey groups to Piping Plovers, but this measure clearly affects the net energy plovers realize and presumably governs their selection of prey from among the available population. Pienkowski (1981) found Ringed Plovers (*Charadrius hiaticula*) and Black-bellied Plovers (*Pluvialis squatarola*) to feed selectively on large lugworms (*Arenicola marina*) when environmental conditions increased the activity of this species. The plovers fed at greater rates on lugworms, even though a smaller polychaete species (*Notomastus latericeus*) was more common than *Arenicola*, and also became more available to plovers under the same conditions that increased *Arenicola* availability.

Withers (1994) measured both biomass and prey density at 2 ecotone sites. Withers found benthic density rather than biomass to most often affect shorebird abundance. However, the biomass measures reported by Withers provide a means of estimating the relative caloric potential of the major prey groups eaten by plovers. At Corpus Christi Pass, Withers found polychaetes to have a biomass of about 0.86 mg/animal. Adult insects and amphipods had about 1/2 the biomass of polychaetes (0.48 mg/animal and 0.36 mg/animal, respectively). Larval insects and tanaids had only a fraction of the biomass available from polychaetes (0.27 mg/animal and 0.07 mg/animal, respectively). Based upon the biomass estimates by Withers, polychaetes appear to offer a substantially higher relative energy return to plovers than do insects, amphipods and tanaids. This may explain the ability of plovers wintering in the bay ecosystem to spend less time at beach habitat relative to plovers wintering in the ecotone. Polychaetes comprised a much greater proportion of the bayshore diet of plovers wintering in the bay ecosystem relative to plovers wintering in the ecotone (Figure 31). Whereas the diet of plovers in the lagoon ecosystem contained an even smaller proportion of polychaetes, beach habitat may have offered a poor alternative to these birds. Beach benthic populations were apparently less dense in the lagoon ecosystem (Figure 14). The increased energy expenditures required

of plovers foraging at beach habitat coupled with the reduced benthic populations occurring there may partially explain why lagoon plovers also used beaches less than ecotone plovers. However, my data suggest that when Piping Plovers did use lagoon beaches, they fed almost exclusively on polychaetes (Figure 30).

Roosting Behavior

I found Piping Plovers to spend about 34% of the diurnal period roosting or preening while at beach habitat and about 18% of the diurnal period roosting or preening while at bayshore habitat (i.e., foraging rates of 66% and 82% for beach and bayshore habitats, respectively). These estimates compare well with those reported for plovers wintering in Alabama (Johnson and Baldassarre 1988). Elliott and Teas (1996) reported a much higher estimate of foraging activity for Piping Plovers using 3 Texas beaches (86.7%, 89.5%, and 96.2%). This apparent incongruity may stem from the way in which beach habitat was delineated in both studies. I included all washover passes that occurred at my sites as a part of the beach habitat. Because they occur at higher elevations than the beach, and receive less human disturbance, washover passes provide ideal roost habitat and many of the plovers I found roosting at beach habitat at my sites occurred in washover passes. The foraging activity estimates developed by Elliott and Teas (1996) were for only those plovers using the forebeach habitat, and did not account for the activity of plovers using nearby washover passes, where roosting behavior was more common (L. Elliott, pers. comm.).

Human Disturbance

My data suggest human activity reduced the net foraging success of Piping Plovers at beach habitat by increasing the amount of energy plovers had to expend while foraging. Vega (1988) reported an apparent reduction in the abundance of *S. squamata* and *Haustorius* sp. at beaches experiencing vehicular traffic, suggesting human activity at beach habitat may be the source of both direct and indirect impacts to Piping Plovers.

Elliott and Teas (1996) reported a negative relationship between Piping Plover beach density and vehicular density at the Packery Channel site (referred to as Surfer Beach in Elliott and Teas 1996). Whereas Elliott and Teas (1996) detected no relationship between Piping Plover density and pedestrian density, they found pedestrian encounters reduced the amount of time plovers were able to spend foraging. Elliott and Teas (1996) concluded that "Reductions in time spent foraging may be sufficient to cause birds to move to habitats where time budgets are unaffected by human disturbance. This may entail moving to bayshore habitats or beaches occupied by fewer pedestrians." I found no relationship between Piping Plover density and vehicular density at beach habitat. In fact, the trend between plover density and beach vehicular density was positive at the Packery Channel site. My data indicate that plover movements between beach and bayshore habitat were predominantly controlled by bayshore tidal amplitude. However, in addition to disrupting foraging efforts, human disturbance appeared to have a significant effect on Piping Plover abundance at my sites. This relationship is described further in Chapter IV.

CHAPTER IV. PIPING PLOVER SITE ABUNDANCE

INTRODUCTION

The recovery of rare plants and animals must be founded on thorough knowledge of the features that define and threaten the species' niche. This knowledge guides both the preservation of sites that exhibit optimal habitat and the sound management of sites where habitat quality has been compromised. The final objective of my study was to identify the habitat components and environmental conditions that affect the abundance of Piping Plovers along the TGC. Accomplishing this objective will identify the environmental features that are most important to winter recovery throughout a major portion of the species nonbreeding range.

Nicholls and Baldassarre (1990b) used discriminant function analysis (DFA) to investigate the relationship between a number of microhabitat characteristics and the presence/absence of Piping Plovers throughout most of their winter range. Their analyses selected "...greater beach width, greater % mudflat, lower % beach and more small inlets..." as the winter habitat characteristics predictive of Piping Plover presence/absence along the Gulf Coast of the United States. Along the Atlantic Coast, DFA selected "...the number of large inlets and passes, number of tide pools, % mudflat, beach width, and % sandflat as the major factors affecting (Piping Plover) presence or absence." (Nicholls and Baldassarre 1990b).

However, Nicholls and Baldassarre's conclusions were founded primarily upon data collected during single visits to a large number of study sites throughout the winter range. Furthermore, the habitat associations evaluated by Nicholls and Baldassarre (1990b) include only a portion of the parameters that may play a role in habitat selection by Piping Plovers. For instance, such factors as tidal stage, prey density, and human disturbance were not considered in their analyses, yet these factors have been shown to

significantly influence shorebird site-use and behavior (Burger et al. 1977, Connors et al. 1981, Hicklin and Smith 1984). I sought to build upon the foundation developed by Nicholls and Baldassarre. I did this by developing a site abundance model that incorporated several factors that were not considered by Nicholls and Baldassarre's model, and supported the new model with data collected from multiple visits to several sites.

METHODS

To address this objective I developed a multiple regression model predicting local Piping Plover abundance based upon the following 6 habitat and environmental parameters measured at each study site:

1. Available beach habitat area.
2. Available bayshore habitat area.
3. Macrobenthic prey density at beach habitat.
4. Macrobenthic prey density at bayshore habitat.
5. Surface prey abundance at bayshore habitat.
6. Human disturbance at beach habitat.

I employed a step-wise regression model to select, from among these 6 parameters, those that most significantly predicted variation in the number of Piping Plovers occurring at all of the barrier island study sites I monitored. Data collected at Laguna Atascosa National Wildlife Refuge, the 3 southern sites on South Padre Island and the South Bay -West site were omitted from this model because these sites either did not possess beach habitat, or because data were not collected at beaches for these sites. Including these sites would not have allowed the incorporation of beach-associated parameters in the model. Additionally, the Mustang Island State Park -South site was omitted from this analysis because this site was not representative of its geographic region (the ecotone), and Piping Plovers were never found at this site. This site was

monitored only to support comparisons to the Mustang Island State Park - North site.

I selected the habitat parameters because they have all been associated with shorebird abundance or quality shorebird habitat (e.g., habitat area; Goss-Custard et al. 1995, prey abundance; Cullen 1994, Withers 1994, Connors et al. 1981, human disturbance; Staine and Burger 1994), and were variables that had the potential to vary substantially among my study sites.

To support the model, I monitored Piping Plover populations and the above 6 independent variables at my study sites from July - May in 1993 and 1994 (i.e., the last 2 years of the study). Whereas many of the above parameters were monitored during the study's first field season (July 1991- May 1992), human disturbance and surface prey were not measured until the second year of the study, and therefore data collected in the first year of the study are not incorporated into the model.

To maximize the number of samples used to support the model, I partitioned the study period into 4 temporal periods comprised of the migration season (fall and spring) and the winter season for each of the last 2 years of the study. Season and study year also were built into the model as independent variables to factor variability associated with these parameters into the analysis. Thus, each of the 8 barrier island study sites could potentially be represented by as many as 4 samples, yielding a potential maximum of 32 samples. However, because weather and other factors limited access to some of the sites during one or more of the 4 periods, most sites were represented in the model by fewer than 4 samples, and the model was supported by a total of 19 samples.

Piping Plover site abundance for each period was estimated as the sum of the mean number of Piping Plovers recorded during all beach and bayshore surveys conducted during each temporal sampling period at each site. For instance, during the 1993 fall migratory season at Bolivar Flats, I recorded an average of 46.0 plovers using bayshore habitat and 17.4 plovers using beach habitat, yielding an estimated site abundance for that

period of 63.4 plovers.

I selected the most robust model using backwards stepwise regression analysis. To investigate the effects of autocorrelation, I compared the relationships among the means of the 6 variables and Piping Plover abundance among the 19 samples using nonparametric correlation (Spearman Rho test).

Data Analysis

The analyses were performed using JMP, version 3.1 (SAS Institute Inc., Cary, NC). I programmed entry and exit criteria for the backward stepwise analyses to initially incorporate all 8 parameters (year, season, beach vehicular density, bay area, beach length, beach benthos, bayshore benthos, bayshore surface prey). Through backward stepwise regression, all parameters were removed from the model, beginning with the parameter that least affected plover abundance, and ending with the parameter that explained the greatest amount of variation in abundance. Akaike's Information Criterion was used to determine which parameters collectively constituted the model that best fit my data.

RESULTS

Mean abundance at beach habitats varied from < 1 birds/count to > 20 birds/count (Table 25). The highest single day counts at beach habitats were of roosting flocks and occurred at washover passes in the lagoon ecosystem or at the Packery Channel site, which was the only site outside of the lagoon ecosystem that had a washover pass (Table 26).

Mean abundance at bayshore habitats ranged from 0 plovers to > 355 plovers (Table 25). Nine of the 10 highest single day counts in bayshore habitat were in the lagoon ecosystem, most of these counts coming at the South Padre - North Area site (Table 26). In contrast to my observations of plovers at beach habitat, most plovers counted during

Table 25. Estimated mean site abundance of Piping Plovers on bayshore tidal flats and beach habitats at sites along the Texas Gulf Coast, 1991 - 1994. Mean site abundance was estimated as the sum of the mean bayshore flat abundance and the mean beach abundance at each site. Abbreviations: LANWR = Laguna Atascosa National Wildlife Refuge, MISP = Mustang Island State Park, NB = no beach at site, ND = do data, NYF = North Yucca Flats, RBV = Rincon Buena Vista, RHC = Redhead Cover, SHF = South Horse Flats, SPI = South Padre Island.

Study Location	Beach Abundance			Bayshore Abundance			Total
	N	mean	SE	N	mean	SE	
<i>Bay Ecosystem</i>							
Bolivar Flats	35	15.3	3.9	40	50.3	5.3	65.5
Big Reef	17	1.2	0.7	23	18.4	3.8	19.6
San Luis Pass	64	12.3	6.5	65	27.4	2.5	39.7
<i>Ecotone</i>							
East Flats	7	9.9	3.5	7	49.3	26.9	59.2
MISP - North	66	10.3	1.6	30	7.4	1.7	17.7
MISP - South	32	8.5	2.6	13	0.0	0.0	8.5
Packery Channel	58	14.0	2.9	47	14.7	2.8	28.7
<i>Lagoon Ecosystem</i>							
LANWR - RBV	NB	0.0	--	31	17.4	4.9	17.4
LANWR - SHF	NB	0.0	--	35	1.2	1.1	1.2
LANWR - RHC	NB	0.0	--	37	5.7	3.6	5.7
LANWR - NYF	NB	0.0	--	43	17.1	4.3	17.1
South Bay - West	NB	0.0	--	21	0.0	0.0	0.0
South Bay - East	25	22.6	11.7	29	19.1	8.2	41.7
SPI - North Area	27	12.3	6.5	6	355.3	58.3	367.6
SPI - Convention Center	ND	--	--	19	2.9	1.3	2.9
SPI - Parrot Eye's	ND	--	--	21	2.5	1.0	2.5
SPI - Mangrove Flats	ND	--	--	25	3.1	1.0	3.1

Table 26. High single day counts of Piping Plovers at beach and bayshore habitats along the Texas Gulf Coast, 1991 - 1994.

Location	Date	# Piping Plovers	
		Total	Roosting
Beach Habitat			
South Bay - East	2/10/93	254	254
South Padre Island - North	2/4/93	171	171
South Bay - East	2/26/93	153	121
Packery Channel	2/25/93	87	87
Bolivar Flats	2/18/93	83	56
Bolivar Flats	1/22/93	80	80
Packery Channel	11/2/92	76	76
South Bay - East	10/8/93	74	45
Packery Channel	2/11/93	63	63
Packery Channel	2/5/93	61	6
Bayshore Habitat			
South Padre Island - North	3/2/93	543	0
South Padre Island - North	1/27/94	489	223
South Padre Island - North	12/5/91	400	no data
South Padre Island - North	12/9/93	254	0
South Padre Island - North	10/15/93	251	13
Laguna Atascosa NWR - Yucca Flats	1/28/93	238	0
South Bay - East	3/3/92	202	no data
South Padre Island - North	3/1/92	195	no data
East Flats	3/26/93	189	0
Laguna Atascosa NWR - Redhead Cove	11/18/91	130	0

the high single day counts at bayshore habitats were engaged in foraging behavior.

Mean total site abundance (i.e., beach and bayshore counts combined) ranged from 0 plovers to over 350 plovers (Table 25). With one exception, all of the sites with small plover populations (< 10 plovers) were either very small (e.g., the 3 sites on the southern end of South Padre Island) or were situated away from the barrier island chain on the mainland coastline (e.g., the South Bay-West site and the Laguna Atascosa National Wildlife Refuge sites).

The exception to this rule was one of the Mustang Island State Park (MISP) sites. Whereas the MISP - South site was neither small (40 ha tidal flats, 2.6 km beach) nor on the mainland, it supported a site population of just 8.5 plovers. All of the plovers in this mean population estimate were observed at beach habitat. No Piping Plovers were observed using bayshore flats at this site during the study. The MISP - North site, which was similar in size (33 ha tidal flats, 3.2 km beach) and borders the south site, supported a much larger site population (17.7 plovers). Furthermore, Piping Plovers consistently used bayshore flats at the MISP - North site (Table 3).

The difference in plover site abundance at these 2 sites is less confounding when the habitat features of the sites are compared more closely. The bayshore portions of the MISP sites consist of 2 lagoons, one lagoon forms part of MISP - North, and a second lagoon forms part of MISP - South (Figure 5). The 2 lagoons were once part of a single large lagoon, but they were isolated by a man-made channel (Fish Pass). In addition to splitting the large lagoon into 2 smaller lagoons, the channel also interrupted tidal flow into both lagoons. A second artificial channel was dredged into the north lagoon to re-establish a tidal exchange between the MISP - North lagoon and Corpus Christi Bay, but the MISP - South lagoon remained relatively isolated from tidal influences throughout the study. The MISP - South site was drier and more heavily vegetated, and these factors appear to have affected the value of the site to Piping Plovers.

Factors Affecting Piping Plover Site Abundance

Data from 8 sites were evaluated to investigate the relationship between Piping Plover site abundance and habitat and environmental conditions occurring at the sites. Mean Piping Plover site abundance at the 8 sites varied from < 3 plovers to > 370 plovers (Table 27).

The habitat and environmental parameters also varied widely. Mean bayshore area at the sites varied from about 20 ha to > 500 ha (Table 27). Beach length for most of the sites ranged from about 3 km to about 7 km, with the long (> 25 km) South Padre Island - North site being the exception (Table 27). Human disturbance, estimated as beach vehicular density, ranged from 0 vehicles/km to almost 6 vehicles/km (Table 27). Bayshore benthic density ranged from 0 animals to > 12,000 animals/m² (Table 27). As expected, beach benthic populations were more consistent, ranging from about 560 to about 7,000 animals/m², with most samples ranging from about 1,000 to about 3,500 animals/m² (Table 26). Finally, insects and other surface prey ranged from 0 to nearly 1400 animals captured/100 trap hr. (Table 27).

Pairwise correlation analyses revealed that some of the independent parameters were significantly correlated with each other (Figure 43). Among these were bay area/beach vehicular density ($P= 0.0007$), bay surface prey/beach length ($P= 0.0112$), and bay surface prey abundance/bay benthic density ($P= 0.0243$). All of these correlations were negative.

The effects of each of the measured parameters on Piping Plover abundance were independently evaluated. The area of bayshore habitat (positive relationship; $R^2 = 0.3770$, $P = 0.0052$) explained the greatest amount of variability in plover abundance at my sites (Figure 44). Beach vehicular density (negative relationship; $R^2 = 0.3277$, $P = 0.0104$; Figure 44), and beach length (positive relationship; $R^2 = 0.2259$, $P = 0.0397$; Figure 45) also each explained over 20% of the variability in Piping Plover abundance at

Table 27. Mean values for the environmental and habitat variables used in the multiple regression models. Each figure represents the mean value of the variable over the 3 year study period.

Study Site	Yr.	Sea.	Beach Variables						Bayshore Variables						Surface Prey			Piping Plover Abundance			
			BL		Benthic Density		Vehicular Density		Bayshore Area		Benthic Density		Surface Prey		Piping Plover Abundance						
			mean	SE	N	mean	SE	N	mean	SE	N	mean	SE	N	mean	SE	N	mean	SE	N	
BF	Y2	Mig	4.8	1239	25	203	1.56	0.54	7	78.3	6	23.2	4765	35	697	0.07	0.05	30	63.4	7	18.0
BF	Y2	Wint	4.8	6418	40	564	0.83	0.30	7	100.7	7	15.5	11998	45	841	0.13	0.06	45	90.6	7	29.2
BF	Y3	Mig	4.8	1266	30	167	2.22	0.38	7	105.8	8	21.1	2757	30	469	0.03	0.02	30	59.0	7	14.7
BF	Y3	Wint	4.8	949	5	512	0.58	0.23	5	131.6	5	27.4	7110	35	843	0.00	0.00	10	55.2	5	21.3
BR	Y2	Wint	4.4	7142	5	361	3.65	0.83	3	34.8	5	5.3	12340	15	734	0.73	0.28	15	2.8	3	5.8
BR	Y3	Mig	4.4	3104	15	939	5.10	1.13	6	19.3	6	5.3	2260	15	669	1.00	0.20	15	7.1	6	7.9
SLP	Y2	Mig	6.3	3633	40	560	5.83	2.17	13	27.0	12	5.2	4076	30	670	0.35	0.15	20	30.8	13	5.4
SLP	Y2	Wint	6.3	3824	90	511	1.24	0.13	24	47.1	21	3.7	4294	90	322	0.12	0.05	66	29.7	24	6.3
SLP	Y3	Mig	6.3	1654	25	484	2.75	0.66	6	33.0	6	7.6	2296	25	470	0.00	0.00	25	32.5	6	7.2
EF	Y2	Mig	2.8	3345	10	559	0.00	0.00	2	123.0	2	0.0	0	6	0.0	13.83	6	2.52	34.5	2	61.5
EF	Y3	Mig	2.8	2140	15	437	0.00	0.00	2	123.0	2	35.5	0	25	0.0	8.72	25	0.99	74.0	2	38.9
MISPN	Y2	Wint	3.2	3464	55	531	1.21	0.26	25	25.9	20	17.4	329	55	102	0.54	0.15	80	16.2	20	11.0
MISPN	Y3	Wint	3.2	1695	10	324	4.06	2.19	2	44.8	2	13.2	1996	25	318	1.04	0.25	25	18.0	2	13.5
PC	Y2	Wint	3.9	563	45	90	1.73	0.39	30	102.0	25	10.5	600	125	132	0.68	0.37	125	32.1	25	8.3
PC	Y3	Mig	3.9	2066	35	341	2.91	1.51	3	29.8	3	16.7	0	5	375	5.00	0.46	5	43.0	3	15.2
PC	Y3	Wint	3.9	4449	35	317	2.65	1.37	3	89.5	3	25.8	3179	15	298	0.73	0.21	15	46.0	3	15.4
SBE	Y3	Mig	7.6	712	20	200	1.49	0.48	3	267.5	3	40.1	859	20	341	0.70	0.21	20	47.3	3	27.4
SBE	Y3	Wint	7.6	1808	20	238	2.57	0.59	2	120.4	4	76.8	181	5	132	0.00	0.00	5	4.5	4	4.5
SPIN	Y3	Wint	25.1	1740	40	185	0.00	0.00	3	507.5	2	01.5	663	45	107	1.09	0.35	45	372.8	3	118.8

Abbreviations: BF = Bolivar Flats, BR = Big Reef, SLP = San Luis Pass, EF = East Flats, MISPN = Mustang Island State Park, PC = Packery Channel, SBE = South Bay - East, SPIN = South Padre Island - North, Wint = Winter, Mig. = Migration, Y = year.

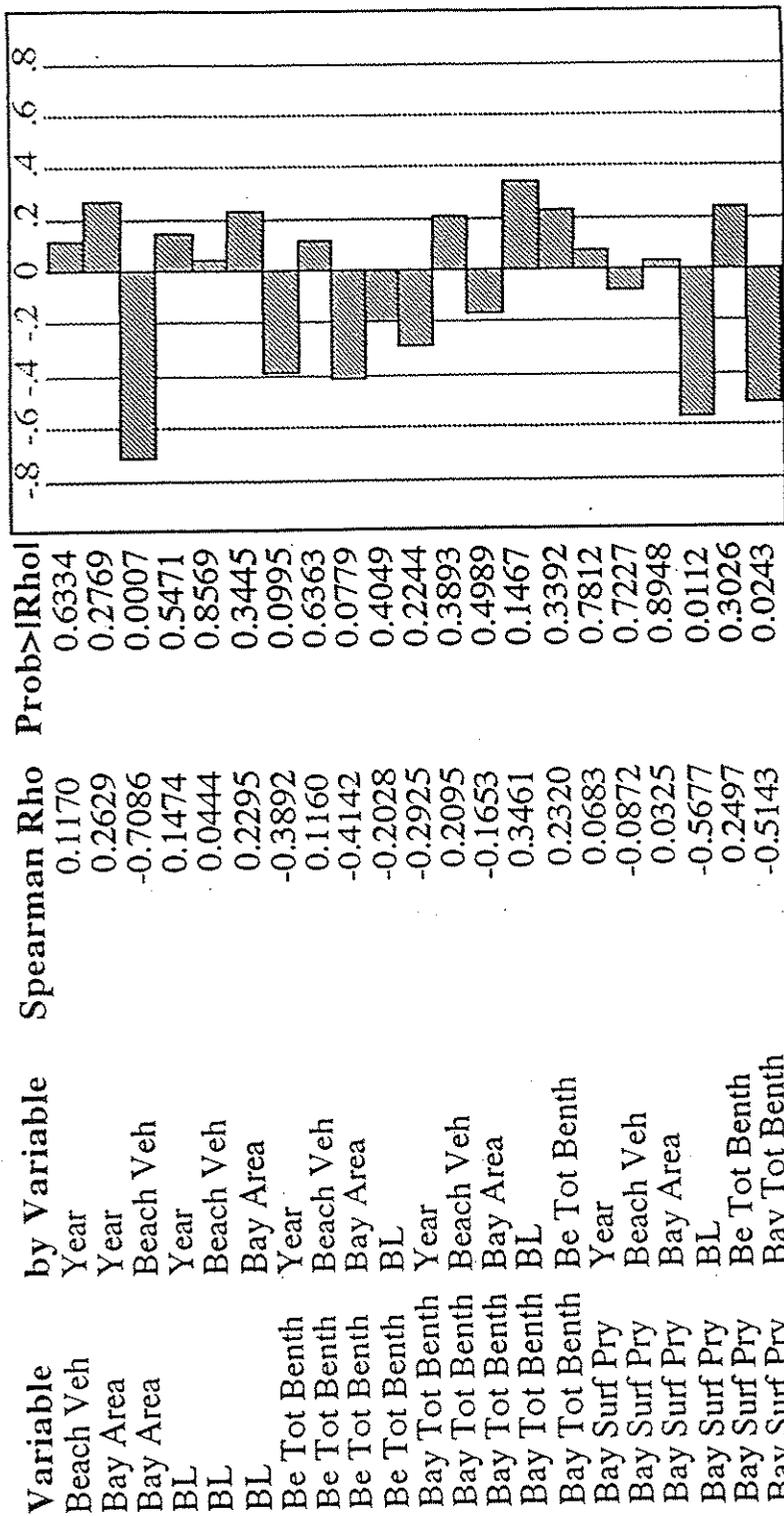


Figure 43. Nonparametric pairwise correlations between the 6 independent environmental parameters evaluated for their effect on Piping Plover abundance. Year and season are also shown. Abbreviations: Veh = vehicle density, BL = beach length, Be Tot Benth = beach benthos density estimate, Bay Tot Benth = bayshore benthos density estimate, Bay Surf Pry = relative bayshore surface prey abundance estimate.

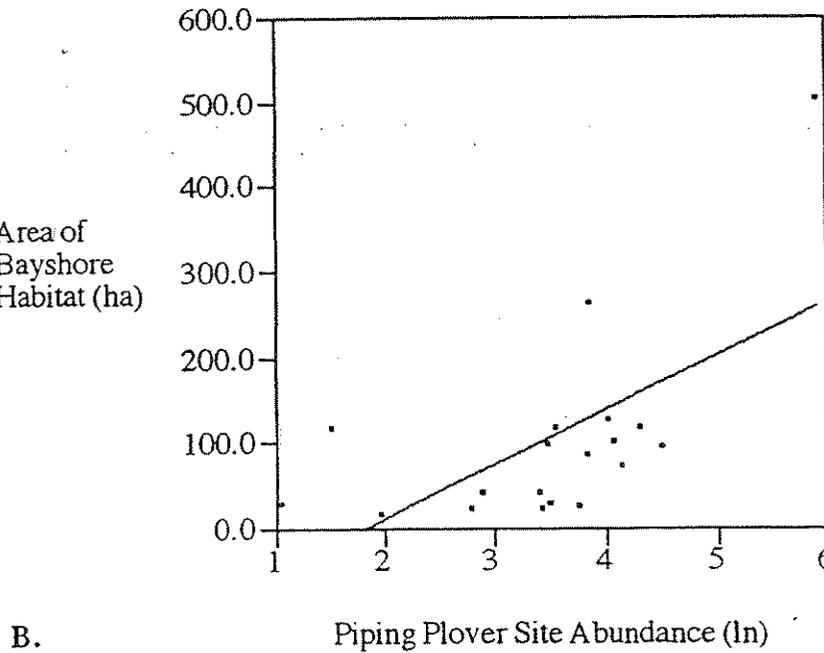
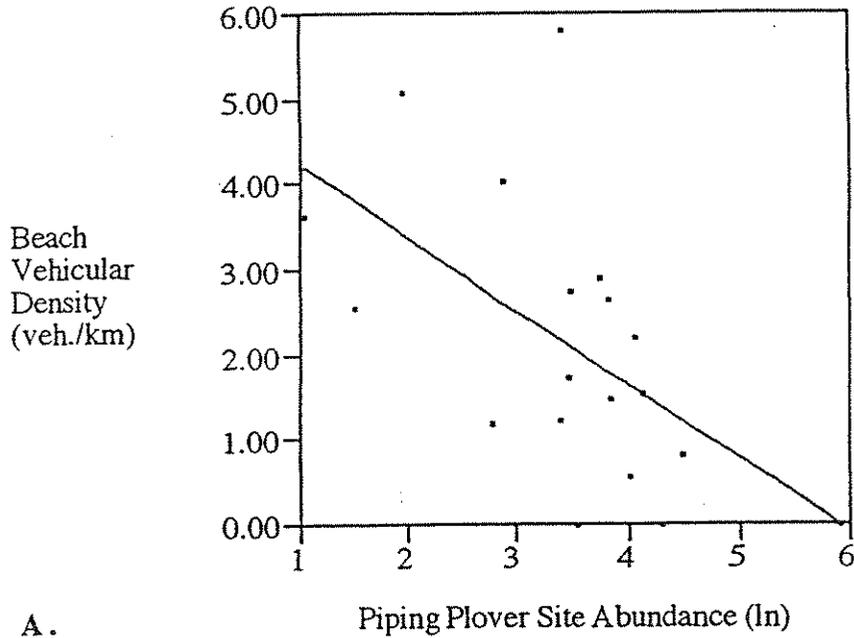
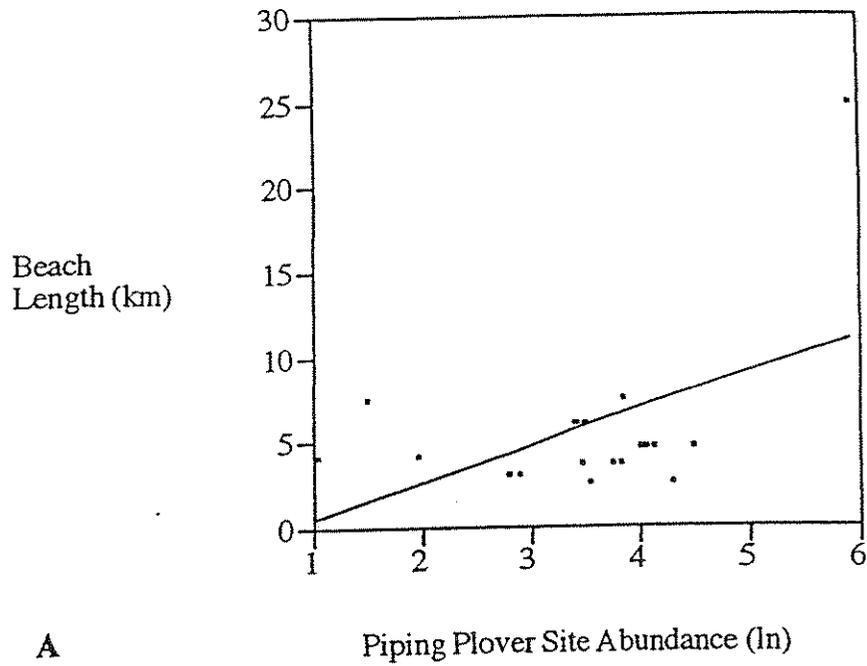
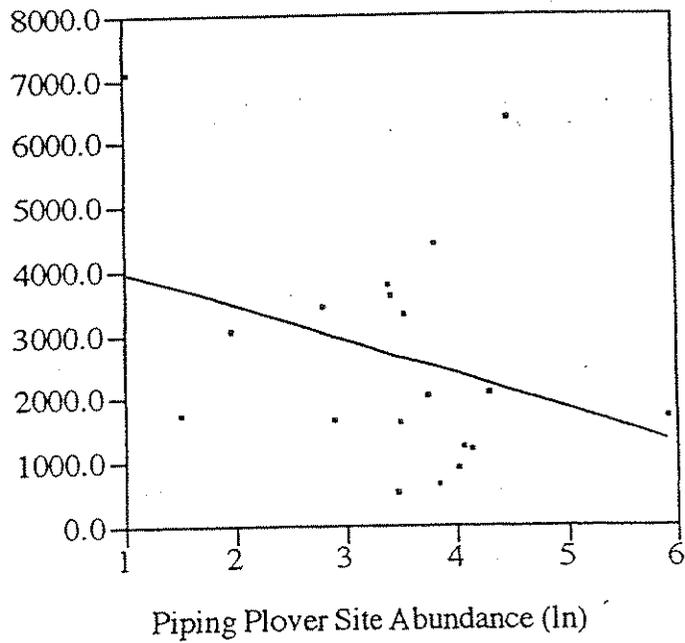


Figure 44. Simple regressions evaluating the effects of (A) beach vehicular density (vehicles/kilometer; $P = 0.0104$, $R^2 = 0.3277$) and (B) bayshore area (hectares; $P = 0.0052$, $R^2 = 0.3770$) on Piping Plover site abundance.



A



B

Figure 45. Simple regressions evaluating the effects of (A) beach length (kilometer; $P = 0.0397$, $R^2 = 0.2259$) and (B) beach benthic density (# animals/square meter; $P = 0.1762$, $R^2 = 0.1049$) on Piping Plover site abundance.

my sites.

None of the prey measures strongly or significantly influenced plover abundance (Figures 45 and 46). Beach benthic density (negative relationship; $R^2 = 0.1049$, $P = 0.1762$), bayshore benthic density (negative relationship; $R^2 = 0.0232$, $P = 0.5333$), and bayshore surface prey density (positive relationship; $R^2 = 0.0151$, $P = 0.6157$) all explained only a small amount of the variability in the abundance of Piping Plovers at my sites. The sites with the largest plover populations were those that had the largest area of bayshore flat, the largest area of beach habitat, and the lowest level of human disturbance.

The most robust multiple regression model selected by stepwise regression identified beach vehicular density ($P = 0.0106$), beach length ($P = 0.0396$), and season ($P = 0.1105$) as the most important factors explaining Piping Plover site abundance. This 3-factor model explained over half of the variability associated with Piping Plover abundance at my sites ($P = 0.0052$; $R^2 = 0.5396$). The regression formula describing the effect of these parameters on Piping Plover abundance was:

$$\begin{aligned} \ln \# \text{ Piping Plovers} &= 3.69 \text{ (y - intercept)} \\ &- 0.3525 \text{ (beach vehicular density [\#/km])} \\ &+ 0.3309 \text{ (Season [Fall = 1, Winter = 2])} \\ &+ 0.0934 \text{ (beach length [km])} \end{aligned}$$

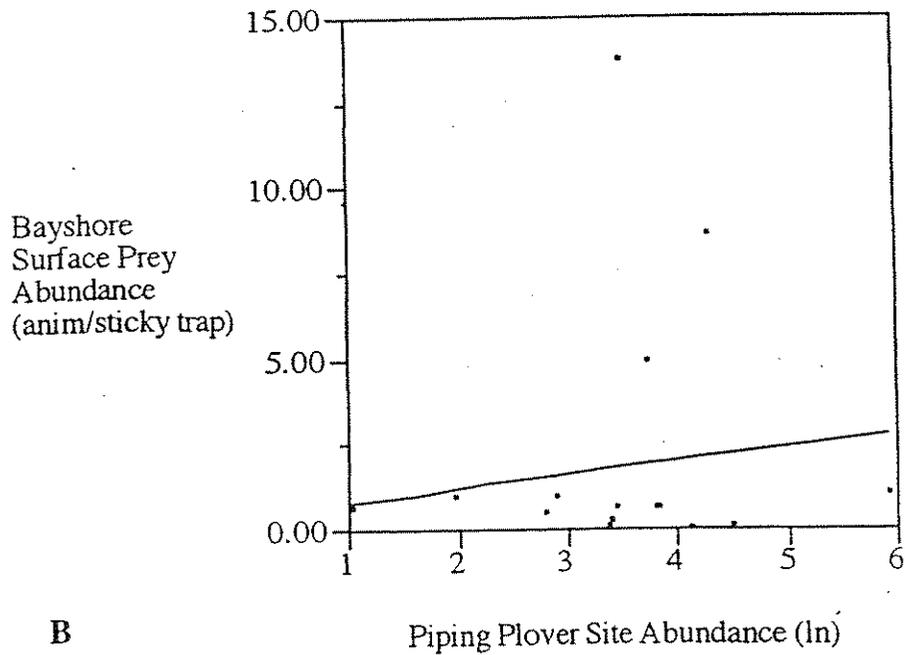
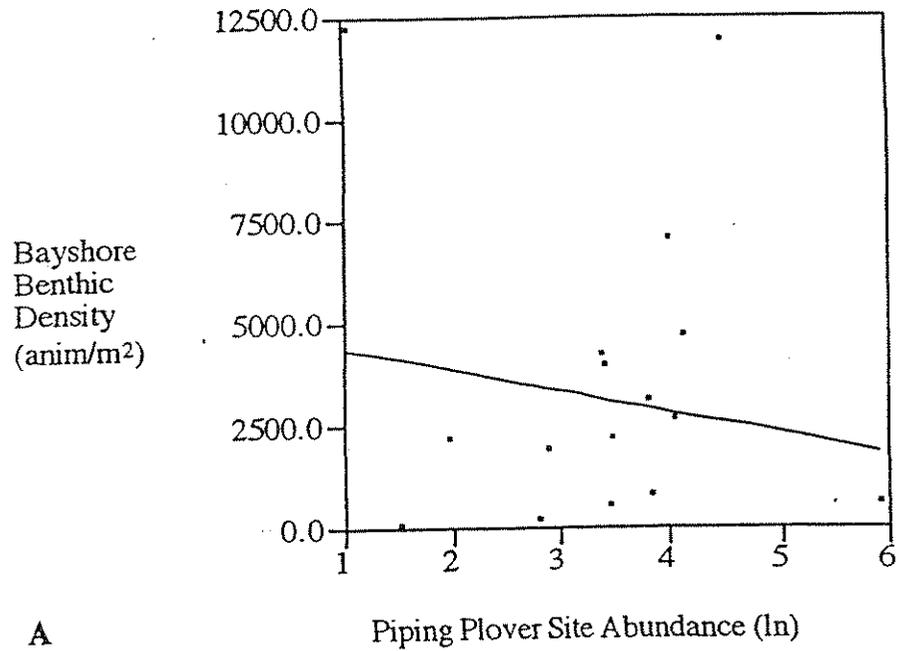


Figure 46. Simple regressions evaluating the effects of (A) bayshore benthic density (# animals/square meter; $P = 0.5333$, $R^2 = 0.0232$) and (B) bayshore surface prey abundance (# animals/sticky trap; $P = 0.6157$, $R^2 = 0.0151$) on Piping Plover site abundance.

The full model, incorporating all 6 habitat and environmental parameters and the seasonal effect into the analysis was only marginally better at predicted Piping Plover abundance ($P= 0.2210$; $R^2 = 0.5714$) than was the 3 parameter model:

$$\begin{aligned} \ln \# \text{ Piping Plovers} &= 3.90 \text{ (y - intercept)} \\ &- 0.3475 \text{ (beach vehicular density [\#/km])} \\ &+ 0.3753 \text{ (season [Fall = 1, Winter = 2])} \\ &+ 0.0581 \text{ (beach length [km])} \\ &+ 0.0016 \text{ (bayshore habitat area [ha])} \\ &+ 0.000038 \text{ (bayshore benthic density [\#/m}^2\text{])} \\ &- 0.000074 \text{ (beach benthic density [\#/m}^2\text{])} \\ &- 0.0348 \text{ (bayshore surface prey density [\#/sticky trap])} \end{aligned}$$

DISCUSSION

My site abundance estimates compare well with counts from the 1991 and 1996 International Piping Plover Censuses (IPPC). Piping Plover site abundance was estimated at Bolivar Flats, Big Reef and San Luis Pass during the 1991 and 1996 International Piping Plover Census. Seventy-three Piping Plovers were counted at Bolivar Flats in 1991 and 101 were counted in 1996 (mean = 87). Nicholls and Baldassarre (1990a) found 66 Piping Plovers at Bolivar Flats. I used data from the last 2 years of my study for the regression models presented in this chapter, resulting in an abundance estimate of 65.5 plovers at Bolivar Flats.

At Big Reef, 25 Piping Plovers were counted during the 1991 IPPC, while none were found there in 1996 (mean = 12.5). My 2-year estimate of plover abundance at Big Reef was 19.6. Bolivar Flats and Big Reef are separated only by the Houston Ship Channel, and plovers often move between these sites (pers. obs.). This probably explains why the number of plovers counted during the 1996 IPPC rose by 28 plovers at Bolivar Flats

while it dropped by 25 at Big Reef. The cumulative 1991 and 1996 IPPC counts for both sites were very similar (98 and 101), and the mean of these 2 counts (99.5) was similar to my mean estimate for both sites (85.1).

Forty-one Piping Plovers were counted during the 1991 IPPC at San Luis Pass (beach and bayshore portions of the count), and 29 were counted in 1996 (mean = 35). Both IPPC counts were similar to my 2-year estimate of 39.7 Piping Plovers for the site.

Nicholls and Baldassarre (1990a) found 39 Piping Plovers at San Luis Pass.

Unfortunately, comparative site abundance data are not available from the 1991 or 1996 IPPC to support comparisons with my other study sites because the boundaries of those counts differed from the boundaries of my study sites.

The regression model I present in this chapter indicates Piping Plover recovery efforts may need to be reevaluated. In Texas, most recovery activity for the federally-listed Piping Plover has focused on preserving bayshore habitat on barrier islands. Examples of this trend include the establishment of the Mollie Beattie Sanctuary in 1997 (which includes the bayshore portion of the Packery Channel site), the 1992 establishment of a Western Hemispheric Shorebird Reserve Network (WHSRN) site at Bolivar Flats, the establishment of preserves at Big Reef in 1995 and San Luis Pass (in progress, P. Glass pers comm.), and the acquisition by the U.S. Fish and Wildlife Service of the eastern portion of South Bay in 1998. Preserving habitat for the Piping Plover was one of the primary goals of each of these actions. However, most of these sites include large tracts of barrier island bayshore tidal flat habitat, but contain very little of the other habitat types used by Piping Plovers (e.g., beaches, mainland tidal flats, washover passes).

Indeed, my data do strongly suggest barrier island tidal flats are the preferred habitat of Piping Plovers wintering in Texas. Beach habitat, washover passes and mainland tidal flats (in the lagoon ecosystem) clearly appeared to be secondary habitats that primarily were used by plovers during periods when barrier island tidal flats were unavailable due

to tidal inundation. Clearly any site that supports Piping Plovers must have bayshore tidal flats. In fact, plover abundance and bayshore tidal flat area were positively correlated at my sites, indicating that a reduction in the amount of bayshore tidal flat habitat may reduce a site's plover population. By itself, bayshore area explained 38% of the variability in plover abundance.

The strong correlation between bayshore area and beach vehicular density further muddies an appraisal of the isolated effects of bayshore area on plover abundance. However, the 3-factor model presented above (that excluded bayshore area) was generated by backward stepwise regression analysis. Backward stepwise regression evaluates interactions among parameters before removing the parameters one at a time in reverse order of fit. This approach identifies those parameters that best explain plover abundance while also considering how these parameters interact. Whereas bayshore area explained a large amount of variation in plover abundance, when evaluated in combination with the other parameters, its effect was diminished, and it was omitted from the most robust model.

The fact that bayshore area was not incorporated into the best-fit model does not mean that protecting large areas of bayshore habitat is fruitless. However, my data suggest that the carrying capacity of barrier island sites is presently limited to a greater extent by the availability of protected beach habitat than bayshore habitat. Therefore, the present strategy of protecting barrier island tidal flats to the exclusion of beach habitat may prove ineffective in the long-term recovery of the Piping Plover.

There is recent evidence to suggest that mainland tidal flats and washover passes also function as important secondary habitats for Piping Plovers, particularly in the lagoon ecosystem (Zonick 1997, Zonick et al. 1998). Mainland tidal flats in the lagoon ecosystem are seriously threatened by human-induced alterations. Broad areas of mainland flats once experienced numerous flooding and drying cycles throughout the

winter as winter fronts pushed Laguna Madre waters into and out of the mainland coastline (Farmer, 1991). Large tracts of mainland flats, however, have become extensively isolated from these waters by miles of continuous dredged spoil banks associated with Gulf Intracoastal Waterway (GIWW) and the Harlingen Ship Channel. Rincon Buena Vista, Elephant's Head Cove, South Horse Flats (Figure 7) and other mainland tidal flats used by Piping Plovers during my study have undergone an extensive and progressive encroachment by Glasswort (*Salicornia bigelovii*), Saltwort (*Batis maritima*), and other salt-tolerant plants. Whereas these plants are not unusual in the tidal flat landscape, tidal flats surrounded by dredged spoil appear to exhibit much higher levels of encroachment. These, and perhaps several other mainland tidal flats may require expeditious management (e.g., removal of dredged spoil banks blocking tidal waters) if they are to remain intertidal wetlands.

However, the trend associated with human influences on beach habitat is most alarming. The Texas Gulf Coast supports thriving petrochemical refining and offshore drilling industries. Texas beaches are exposed to small scale oil and tar exposure on a constant basis. Bolivar Flats and other sites situated nearby the mouths of ship channels are particularly vulnerable to catastrophic oil spills.

Human presence on beaches, however, may be a greater long-term threat to Piping Plovers in Texas. Piping Plovers primarily used beaches during periods when bayshore flats were flooded. The availability of high quality beach habitat to plovers during these periods may be critical to their survival. Human disturbance at beach habitat was identified by stepwise regression as the most important factor affecting the abundance of Piping Plovers at my sites. By itself, beach vehicular density explained 33% of the variability in Piping Plover abundance among my study sites. The area of beach habitat (i.e., beach length) also significantly affected plover abundance, independently explaining 23% of the variability in Piping Plover abundance among my study sites.

CHAPTER V. CONCLUSIONS & MANAGEMENT RECOMMENDATIONS

Along the TGC, Piping Plovers occupy sparsely-vegetated beach, and bayshore tidal flat habitat (e.g., sand flats and algal flats) throughout a 9-10 month non-breeding period (Haig 1992). At my study sites, plovers used both beach and bayshore habitat, but preferred bayshore habitat when both habitat types were emergent and thereby available to plovers. During periods of high bayshore tides, when tidal flats were inundated and were not available, Piping Plovers moved to beach habitat at most sites and foraged within the beach intertidal zone until bayshore tides receded and bayshore habitat was again available to plovers.

The preference for bayshore habitat could not directly be explained by differences in prey availability or plover foraging efficiency in the 2 habitat types. Whereas prey were more abundant at bayshore habitat than at beach habitat in the bay ecosystem, the relationship was reversed in the lagoon ecosystem and the ecotone. Furthermore, Piping Plovers foraged with similar efficiency at beach and bayshore habitats. Plovers also foraged with similar efficiency at bayshore tidal flats in the bay and lagoon ecosystems, even though these ecosystems supported starkly different bayshore prey communities.

The preference for bayshore habitat may have been due to factors that reduced net energy intake rates of plovers using beach habitat. Piping Plovers were much more territorial when feeding at beach habitat, often interacting aggressively to defend feeding areas along the forebeach from other Piping Plovers. Plovers also experienced greater levels of human disturbance at beach habitat than at bayshore habitat. Finally, to feed on their preferred prey at beach habitat, plovers had to repeatedly run into and out of the swash zone. These factors caused plovers to spend considerably more time in prolonged foraging locomotion (PFL), and presumably expend more energy to obtain a similar rate

of prey intake. The result was probably a lower net energy intake rate on beaches relative to bayshore flats, resulting in the observed preference for bayshore habitat.

The importance of beach habitat to Piping Plovers

Although plovers preferred to feed at bayshore habitat, beaches provided alternative feeding and roosting habitat for plovers during periods when bayshore feeding areas were unavailable. Changes in atmospheric pressure and wind conditions accompanying winter cold fronts often created extremely high bayshore tides that covered all bayshore tidal habitat at many of my sites. A plover's ability to survive the harsh conditions accompanying these fronts may depend on its ability to find suitable roost sites or alternative feeding sites. In many parts of the Texas coast, beaches appeared to provide the only suitable alternative to bayshore tidal flats. The importance of beaches is underscored by the habitat model described in Chapter IV, which identified undisturbed beach habitat as the key component affecting local Piping Plover abundance at my study sites. Beaches appeared to be most critical in the ecotone, where plovers occurred at higher densities relative to the bay or lagoon beaches.

The importance of mainland habitat in the lagoon ecosystem

Plovers used beaches somewhat less frequently in the lagoon ecosystem, particularly along the long (25.4 km) South Padre Island study site. There is recent evidence to suggest that, in the lagoon ecosystem, mainland tidal flats may serve the same role for plovers as do beaches in the bay ecosystem and ecotone (Zonick et al. 1998). My mainland study sites had lower average densities of plovers throughout the year, but occasionally supported large plover flocks (> 90 birds). As described in the Study Area section, tides in the lagoon ecosystem were controlled to a much greater extent by wind forces which often created new emergent flats at mainland sites just as flats on the barrier island became flooded. Plovers in the lagoon ecosystem appeared to react to this tidal regime by moving among several barrier island and mainland tidal flats as they became

emergent under the wind-tidal regime. This hypothesis is supported by my observations of what appeared to be the same color banded Piping Plover using all 3 of my lagoon ecosystem sites during the same non-breeding period (Zonick and Ryan 1994, 1995), and by a recent study demonstrating the use of both barrier island and mainland sites by radiofitted plovers (Zonick et al. 1998).

Large areas of mainland tidal flats in the lagoon ecosystem are threatened by indirect effects of maintenance operations on the Gulf Intracoastal Waterway (GIWW). Dredged material removed from the GIWW is placed on dredged material placement areas (DMPAs; also referred to as "spoil islands") that lie along the channel. DMPAs located near Laguna Atascosa National Wildlife Refuge and South Bay have formed barriers that have greatly altered the natural tidal inundation regime of neighboring mainland tidal flat systems (Farmer 1991, pers. obs.). These flats began exhibiting unusually dense blooms of *Salicornia bigelovii* and other vascular plant species in 1992 (Zonick and Ryan 1994). These blooms have persisted and may represent the first stage in the successional replacement of tidal flats by upland habitat (Zonick and Ryan 1994, Brush 1995). The importance of mainland tidal flats to Piping Plovers in the lagoon ecosystem underscores the need for remedial measures to restore a more natural tidal regime to these mainland systems (Zonick et al. 1998).

Washover pass habitat

The washover pass is another habitat that appeared to offer critical high tide refugia to Piping Plovers. Washover passes were used by Piping Plovers both as feeding and roosting areas during the study and also provide important roosting, feeding and nesting habitat for other plover species (e.g., Snowy Plovers and Wilson's Plovers; Zonick 1997). During tropical storm events, all tidal flat habitat in the lagoon ecosystem may be submerged for days or weeks. Such a phenomenon occurred in the fall of 1992 following Hurricane Andrew. Though Hurricane Andrew did not strike the Texas Coast directly, it

caused extreme high tides in the Laguna Madre which inundated South Bay and other rarely submerged tidal flats for a period lasting several weeks. A similar episode occurred following Tropical Storm Josephine in 1997 (Zonick 1997). During these events, washover passes provided critical foraging and roosting habitat for Piping Plovers and other waterbirds. Newport Pass, one of the washover passes at the Packery Channel site, consistently supported large flocks of Piping Plovers during and beyond the study period (Zonick 1997).

Threats associated with the human use of Piping Plover habitat

The increasing human use of Texas beaches appears to be the greatest immediate threat to the long term recovery of Texas Piping Plover populations. For example, human use of Nueces County beaches (Nueces County includes Mustang Island, including all 3 ecotone sites, and the city of Corpus Christi) has increased at an annual rate of nearly 10% in the last decade. The rate of human use of Mustang Island may soon increase. Nueces County has recently announced its intent to elevate the causeway connecting Mustang Island to Corpus Christi, and reopen Packery Channel as a recreational waterway connecting Corpus Christi Bay with the Gulf of Mexico. These projects would clearly stimulate greater human use of the barrier island, further degrading the quality of beaches along the Texas coastal ecotone, where plovers are most dependent on protected beach habitat.

The Great Lakes and Northern Great Plains Piping Plover Recovery Plan requires that the 1998 interior population of Piping Plovers be nearly doubled (from ~ 2,500 breeding pairs to ~ 4,000 breeding pairs) before the Piping Plover interior population be delisted (U.S. Fish and Wildlife Service 1988). It is logical to expect that the Texas Gulf Coast will need to support many of these additional birds. The potential for the TGC to support an expanding Piping Plover population may hinge on the availability of protected beach habitat, particularly in the ecotone and the bay ecosystem where plovers have no

alternative habitat during high tide episodes. Piping Plovers are highly territorial at beach habitat. Whereas the mean Piping Plover density approached or exceeded 3 birds/km at 6 of my 9 beach sites, none of the beaches supported an average > 3.6 birds/km. During maximum use, plovers were spaced less than 90 m apart at 3 of the 4 ecotone beaches. These sites may already be at or near their carrying capacity due to limitations in beach habitat.

In 1997, Nueces County, in cooperation with the U.S. Fish and Wildlife Service, the Texas Parks and Wildlife Department, and the National Audubon Society designated Newport Pass, one of the 2 washover passes at the Packery Channel site, as a sanctuary to protect an important Piping Plover roost site. Vehicular barriers and interpretive signs will reduce disturbance at the roost site and educate visitors to the beach about the importance of beach and washover pass habitat to Piping Plovers and other coastal species. The Newport Pass Sanctuary was the first area preserved with the goal of protecting secondary habitat for Piping Plovers, but must not be the last if the species is to expand to recovery levels.

Mainland tidal flats, washover passes, and particularly beach habitat must be protected along with barrier island tidal flats, and these habitats must be managed to reduce or mitigate human impacts. The broad tidal flats in the ecotone and lagoon ecosystem must be preserved to support recovering plover populations. The system of washover passes on Matagorda Peninsula, San Jose Island, Mustang Island, Padre Island and Brazos Island must be protected as high water refugia for Piping Plovers and nesting habitat for the Snowy Plover. The effects of the GIWW on mainland tidal flats must be understood and, if necessary, corrected before these crucial alternative winter sites are no longer suitable for Piping Plovers.

However, the transformation of Texas' beaches from free-access lands to pedestrian-only beaches should be the highest priority for the recovery of Piping Plovers on the

wintering grounds. It is true that pedestrian traffic has been shown to reduce plover habitat quality, and the conversion to pedestrian-only beach access might increase pedestrian traffic along some areas of the coast. However, the areas that are likely to suffer the greatest level of pedestrian disturbance following such a conversion already face very high levels of both pedestrian and vehicular disturbance (e.g., Packery Channel, San Luis Pass). Many other beach areas located away from public parking facilities would likely experience a reduction in human disturbance were vehicles prohibited on Texas beaches. Furthermore, if Texas beaches were established as pedestrian-access only, there would be no need to manage the beaches for vehicular access. Vehicular traffic appears to reduce the abundance of important Piping Plover prey species at beach habitat (Vega 1988). A reduction in mechanical scraping and raking would likely reduce the erosion of beach habitat, and allow the beach benthic community to recover from impacts that may be associated with beach grooming practices, potentially increasing the carrying capacity of such beaches for Piping Plovers. Piping Plovers would clearly benefit from these changes.

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