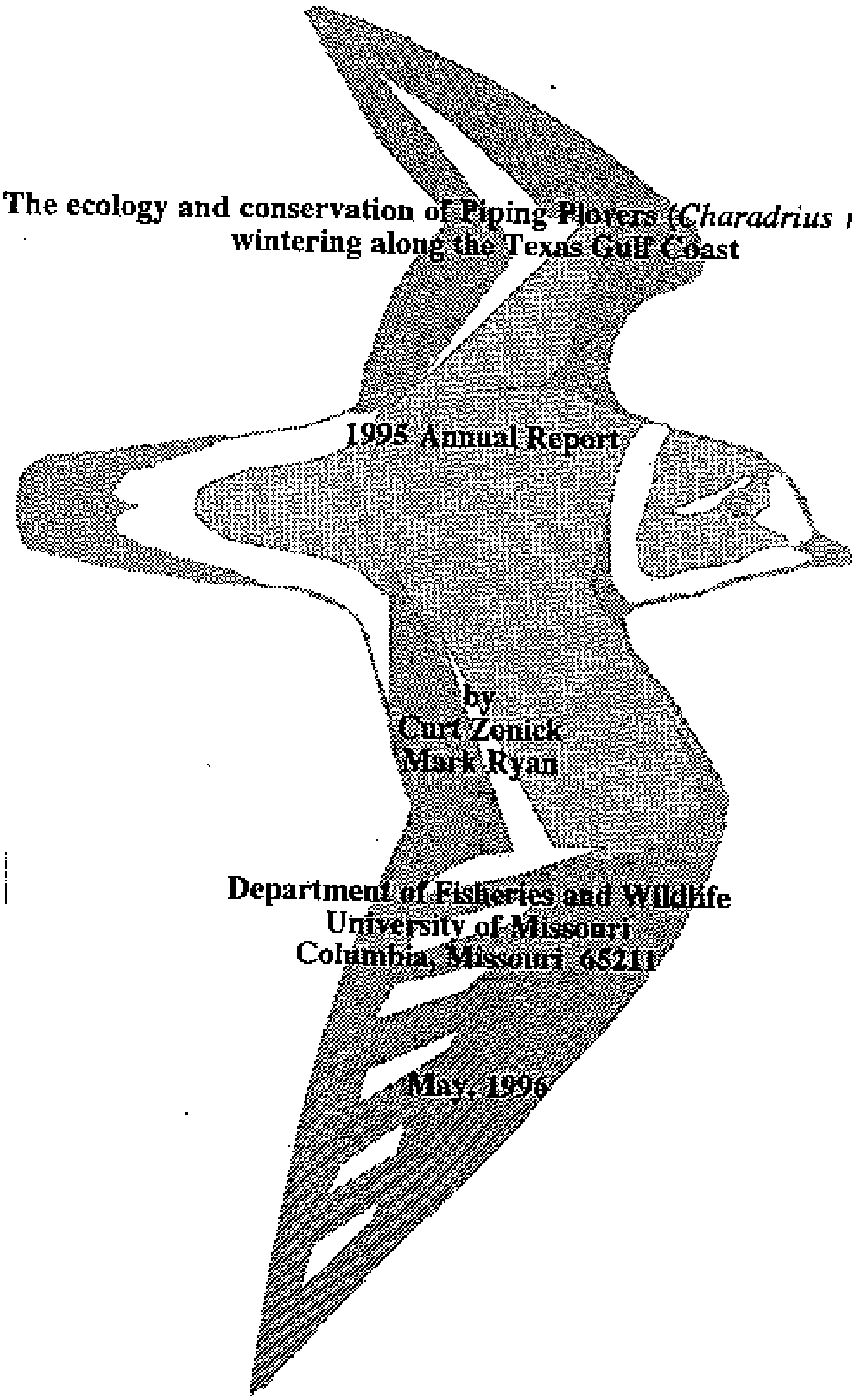

The ecology and conservation of Piping Plovers (*Charadrius melodus*) wintering along the Texas Gulf Coast

1995 Annual Report

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INTRODUCTION

To most observers, a Piping Plover (*Charadrius melodus*) is an unspectacular bird, lacking distinction in size, color, shape or behavior. Yet, among all shorebirds occurring in North America, none has received as much attention as the Piping Plover during the past decade. To its misfortune, the feature that has attracted such scrutiny to the Piping Plover is its decline toward extinction.

The Piping Plover and The Endangered Species Act

At this writing, the Piping Plover is 1 of 1,524 species listed as either "threatened" or "endangered" by the U. S. Fish and Wildlife Service [Service], the federal agency charged with implementing the Endangered Species Act [ESA] (Endangered Species Bulletin 1995). By drafting and enacting the ESA, Congress sought to "...provide a means whereby the ecosystems upon which endangered species and threatened species depend may be preserved..." (U.S Fish and Wildlife Service 1988a). Although the core of the Act has withstood 4 previous amendments (1978, 1979, 1982 and 1988) it has faced increasingly stern opposition. Regulations enforcing the ESA are viewed by a growing faction of private landowners as unreasonable obstacles to human activities that occur within the habitats used by listed species (Dwyer et al. 1995, Mann and Plummer 1995a). An opposing viewpoint contends that federal agencies have failed to uphold the ESA's direction and intent, and are "managing species for extinction" by not fully complying with the spirit of the ESA (Tear et al. 1993). Both sides agree on one thing: the ESA has fallen far short of its goals. Since the ESA's inception, only 6 species have been "saved" and subsequently delisted (Mann and Plummer 1995b). Balanced against these 6 "successes" are 7 listed species that have become extinct, and hundreds of other listed species that have continued to decline (Mann and Plummer 1995b).

The Piping Plover was listed as either federally threatened or endangered throughout its range over a decade ago (U.S. Fish and Wildlife Service 1985), and has been well-studied relative to other federally listed species. For this reason, the recovery efforts on its behalf serve to illustrate the plight faced by many endangered species and the limitations of the Act designed to save them.

Those who argue that the ESA imposes too many regulations would perhaps find allies among landowners with Piping Plovers on their property. In 1989 the sighting of a flock of 172 Piping Plovers roosting in a washover pass contributed to a decision by the Service to oppose the Playa del Rio project - a proposed multi-million dollar marina community near Brownsville, Texas (U.S. Fish and Wildlife Service 1989). The project was opposed in part because the loss of Piping Plover habitat resulting from federal activities associated with the project would "...likely jeopardize the continued existence of the Piping Plover's Great Lakes and Northern Great Plains populations" (U.S. Fish and Wildlife Service 1989). To date, this is the only project proposed within the Piping Plover's winter range determined by the Service to jeopardize its continued existence (U.S. Fish and Wildlife Service 1989), and in fact, 2 other endangered species, the Ocelot (*Felis pardalis*) and the Jaguarundi (*Felis yagouaroundi*), were also determined to be jeopardized by the Playa del Rio project. Several other ventures have proceeded only after satisfying requirements of the ESA, occasionally involving surveys to ascertain whether Piping Plovers use the project area. These surveys are often costly and can delay a project for several months.

These restrictions appear to support the landowner's viewpoint. A review of the history of the Piping Plover under the protection of the ESA, however, provides ample fodder for the attack by those stressing that the government does not go far enough to enforce the ESA to protect biodiversity. Breeding censuses have documented a steady decline of Piping Plovers worldwide, particularly populations breeding in the interior United States and Canada (Haig 1992). Intensive efforts to protect breeding populations (e.g. beach closings, predator exclusion cages) along the Atlantic Coast have met with recent success, but in most areas have only stemmed the decline of the coastal population (Line 1995). For the Atlantic Coast population to recover and remain viable, continuing efforts will almost certainly be required of countless generations of volunteers to come. The decline of the interior populations has continued, and if allowed to proceed unchecked, will result in the extinction of the interior Piping Plover within about 4 human generations (Ryan et al. 1993). The "crisis" style of management that must now be applied on behalf of the remaining Piping Plovers reflects the plight of many other listed species (Tear et al. 1993), and serves to illustrate the limited role currently played by the ESA. For the Piping Plover, the ESA has functioned at best as a reactive measure that has succeeded in slowing the species' decline, but has been largely ineffective in facilitating its recovery.

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 in 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 selected 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 were directed toward protecting breeding habitat (Mayer and Ryan 1991a, Mayer and Ryan 1991b, MacIvor 1990), 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 critical, however, in stemming the species' steep decline. 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 from rapidly expanding anthropogenic-influenced predator populations, 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, such as a series of hazardous material spills near Galveston Island (e.g. the explosions that released millions of gallons of oil from the Mega Borg in June of 1990, and the large oil release from the Shinoussa following a collision in the Houston Ship Channel in July, 1990), and a persistent brown tide episode in the Texas Laguna Madre (Edwards, 1995, Dunton 1994) have focused increasing attention on the potential for a catastrophic loss of Piping Plovers during the

9-month nonbreeding period. The progressive degradation of the Laguna Madre caused by the continuing operation of the Gulf Intracoastal Waterway (GIWW; Diaz and Kelly 1994, Farmer 1991), and the threat of habitat alterations associated with rises in sea levels (Bildstein et al. 1991) pose less immediate, but perhaps potentially greater threats to the long-term viability of the Piping Plover.

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

Study Focus

This study was designed to build upon previous research focusing on Piping Plover winter habitat requirements. To this end, we examined the non-breeding ecology of Piping Plovers over multiple field seasons at 9 major study locations along the Texas Gulf Coast. The study objectives and methods were guided by information provided by previous research on Piping Plover winter ecology and by preliminary visits to different regions of the Texas coast during the winter portion of the International Piping Plover Census [IPPC] in January, 1991. We selected the Texas coast as the geographic focus of this research because Texas supported the largest known share of the Piping Plover's winter population during the IPPC and previous winter surveys (Haig and Plissner 1993, Nicholls and Baldessarre 1990b).

Species Status

The Piping Plover was listed as either federally threatened or federally endangered throughout its current range in 1985 (U.S. Fish and Wildlife Service). Three disjunct breeding populations are recognized by the U.S. Fish and Wildlife Service (Atlantic Coast; threatened status, Great Lakes; endangered status, Upper Great Plains; threatened status). Previous research established that portions of all 3 breeding populations winter along the Texas Gulf coast (Haig and Plissner 1993). In Texas, the Piping Plover is listed as threatened by both the Texas Parks & Wildlife Department (TPWD) and the Texas Organization for Endangered Species (TOES), a non-governmental organization concerned with Texas' endangered flora and fauna.

Taxonomy of the Piping Plover

The Piping Plover, taxonomically grouped within the family Charadriidae and the order Charadriiformes, is closely related to the more familiar Killdeer (*Charadrius vociferus*). Other North American species of *Charadrius* plovers include the Snowy Plover (*C. alexandrinus*), the Semipalmated Plover (*C. semipalmatus*) and the Wilson's Plover (*C. wilsonia*). All of these species occur in Texas during all or portions of the nonbreeding period when Piping Plovers are present. Piping Plovers were originally described as a race of the Ringed Plover, *Charadrius hiaticula* (Wilson and Bonaparte no date). Recognized as a unique species in 1824, the Piping Plover was first identified as *Aegialitis meloda* (Ord 1824), and finally *Charadrius melodus* in 1931 (AOU). In 1957, the inland and Atlantic coast breeding populations were distinguished as the subspecies *C. m. circumcinctus* and *C. m. melodus*, respectively (AOU 1957). Plumage variations described as unique traits for these subspecies are subtle and inconsistent, however (Haig 1992), and a comparison of allozyme patterns between the breeding populations did not support the subspecies designation (Haig and Oring 1988).

Distribution

Historical - Piping Plovers bred across three geographic regions 1) the Northern Great Plains of the United States and Canada, 2) the beaches of the Great Lakes, and 3) the coastal Atlantic beaches of the northern United States and southern Canada (Bent 1929). Described winter locations range from the Gulf of Mexico shores from northern Mexico to south Florida, the Caribbean Islands, and the Atlantic Coast of the southern United States (Bent 1929).

Current - Piping Plovers have been recorded throughout much of their historical range during recent surveys, however, populations have declined in most areas. The Great Lakes breeding population, for example, has declined to a perilously small population of approximately 20 pairs (M. Ryan, University of Missouri, Columbia, MO pers. comm., Haig 1992).

Previous Research Focusing on the Winter Ecology of Piping Plovers

Research predating this study has contributed considerable information about the winter distribution of Piping Plovers, important winter locations, and broad habitat features associated with Piping Plover presence or absence.

Winter Distribution

The locations of several winter populations of Piping Plovers recently have been identified (Haig and Plissner 1993, Texas Parks and Wildlife Department 1993, Nicholls and Baldessarre 1990b, Haig and Oring 1985, T. Eubanks, Fermata Inc., Austin, TX pers. comm.). The 1991 IPPC accounted for a total of 3,451 Piping Plovers during a 1-2 week census throughout the majority of the predicted current winter range of the species. That represents approximately 60% (3,451 out of 5,482) of the number of breeding Piping Plovers recorded during the 1991 IPPC summer breeding census. Wintering (non-breeding) 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% (1,904 out of 3,206) were observed along the Texas Gulf Coast. Several large regions of the Texas Gulf Coast (e.g. the Land-Cut, Baffin Bay, and North Padre Island) received only partial coverage during the IPPC, however, and 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 ~2,000 birds unaccounted for on the winter portion of the IPPC occurred in these areas.

Winter Habitat Requirements

Research by Johnson and Baldessarre (1988) and Nicholls and Baldessarre (1990) have begun to develop a description 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 Baldessarre (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 Baldessarre 1988).

Nicholls and Baldessarre (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 analysis 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 Baldessarre 1990b).

Winter Behavior

Piping Plovers wintering along the Alabama Gulf Coast were observed to spend the majority (76%) of their time foraging (Johnson and Baldessarre 1988). Tidal height was negatively correlated with foraging activity. After resighting 12 of 19 plovers color-banded at Dauphin Island, Alabama Johnson and Baldessarre (1988) concluded that Piping Plovers exhibit "relatively high site-fidelity.....to wintering sites in coastal Alabama".

Questions that Remain.

Spatial and temporal scales

To offset the broad scope of their project, the research by Nicholls and Baldessarre (1990a and 1990b) was, by necessity, limited to a single visit to each "site" during a broad sweep throughout most of the Piping Plover's winter range. Their conclusions were founded primarily upon data from one-time visits to a large number of study sites. Conversely, the research by Johnson and Baldessarre (1988) addressed specific aspects of Piping Plover ecology through multiple visits to a limited number of study sites. Their conclusions were chiefly supported by data from a small geographic area. Whereas these approaches were appropriate for the scope of each project, and have provided a strong foundation toward an understanding of the winter requirements of Piping Plovers, several key questions remain to be answered.

The habitat associations derived by Nicholls and Baldessarre (1990b) reflect only a portion of the parameters that might play a role in habitat selection by Piping Plovers. Other parameters associated with a particular site or habitat such as the tidal stage at the time of the survey and the prey density at the site or habitat have been shown to significantly influence shorebird site-use and behavior (Connors et al. 1981, Burger et al. 1977, Hicklin and Smith 1984,).

The research by Johnson and Baldessarre (1988) provided new insight into the winter movements and winter activity of Piping Plovers. Their research, however, was confined to a relatively small geographic area. This constraint limits the degree to which their results can be applied to movements on a larger sale. Here too, 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.

Appraising a site's value to Piping Plovers

Two key factors hindering the effective protection of important Piping Plovers wintering sites is the uncertainty associated with judging the quality of the habitat a particular site as well as appraising the relative effects of the environmental conditions experienced by the site. Habitat quality is considered here to relate to the biotic and abiotic components of a particular site (e.g. amount of a particular habitat, prey resources), whereas environmental conditions describe the forces that mold these components or otherwise affect their availability to Piping Plovers (e.g. tidal conditions, climatic conditions, human disturbance).

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. For instance, the sand flats and beaches associated with San Luis Pass, Bolivar Flats, Packery Channel and Brazos Island State Park all supported large numbers of Piping Plovers during Christmas bird counts or other surveys, and were subsequently identified as "areas of essential habitat" for the interior populations of the Piping Plover (U.S. Fish and Wildlife Service 1988). 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 three criteria for the ranking 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 criteria's measure of habitat quality was subjective (by their own admission) and the ranking system still relied heavily on census data, the consideration of habitat features by Nicholls and Baldassarre supported a more credible ranking scheme by reducing the likelihood that a site might be given inflated stature based upon an 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 is important to determine not only how many plovers occurred at a site, but also whether the habitat at that site is of sufficient quality to support the population (or an expanding population during the recovery process), and whether other environmental variables (e.g. human disturbance) are present that might compromise the site's apparent value. Extending the use of specific habitat components and environmental variables as indicators of winter site quality, however, requires a better understanding of how Piping Plovers are affected by habitat parameters and their components. For instance, Nicholls and Baldassarre's criterion for habitat quality might be broken down to ask what the relative values of "mudflats" and "sandy beach" are to Piping Plovers. Is the relative value of these habitat types to Piping Plovers the same along different portions of the species' winter range?

What components of a habitat are important? Is total area an important component of habitat quality? Is prey density an important component of a high quality habitat or site for Piping Plovers? What environmental variables affect Piping Plover winter site use or habitat use? What importance can be attributed to the level of human disturbance normally present at a particular site or habitat? How do levels of tidal inundation or seasonal behavior patterns (e.g. migration) affect Piping Plover abundance at a particular site, or their habitat preferences?

A fundamental question associated with the long-term recovery of the Piping Plover is how the species has adapted to the diverse array of habitats to be found throughout its winter range. From the mangrove swamps along the Florida Gulf Coast, to the cordgrass marshes of Louisiana and northern Texas, to the wind tidal flats of Texas' Laguna Madre, Piping Plovers are confronted with a varied collection of habitats from which to choose during the non-breeding season. Because Texas supports so many Piping Plovers during the winter period, the recovery of the species may ultimately depend on the effective protection and management of essential winter habitat along the Texas Gulf Coast.

Important habitat features of the Texas Gulf Coast

Along the Texas Gulf Coast, changes associated with a few key geomorphological and environmental factors 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 Texas Gulf Coast.

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

Salinity - The salinity of the Texas bays varies markedly. In a comparative survey of the bays of Texas beginning with Galveston Bay in the north, and ending with South Bay bordering Mexico, there occurs a progressive increase in salinity. In general, southern bays are saltier because they receive lower amounts of freshwater from riparian inflows and rain, and lose higher amounts of freshwater from evaporation.

In the northern region of the Texas Gulf coast, extending from Sabine 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.

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 winds, 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

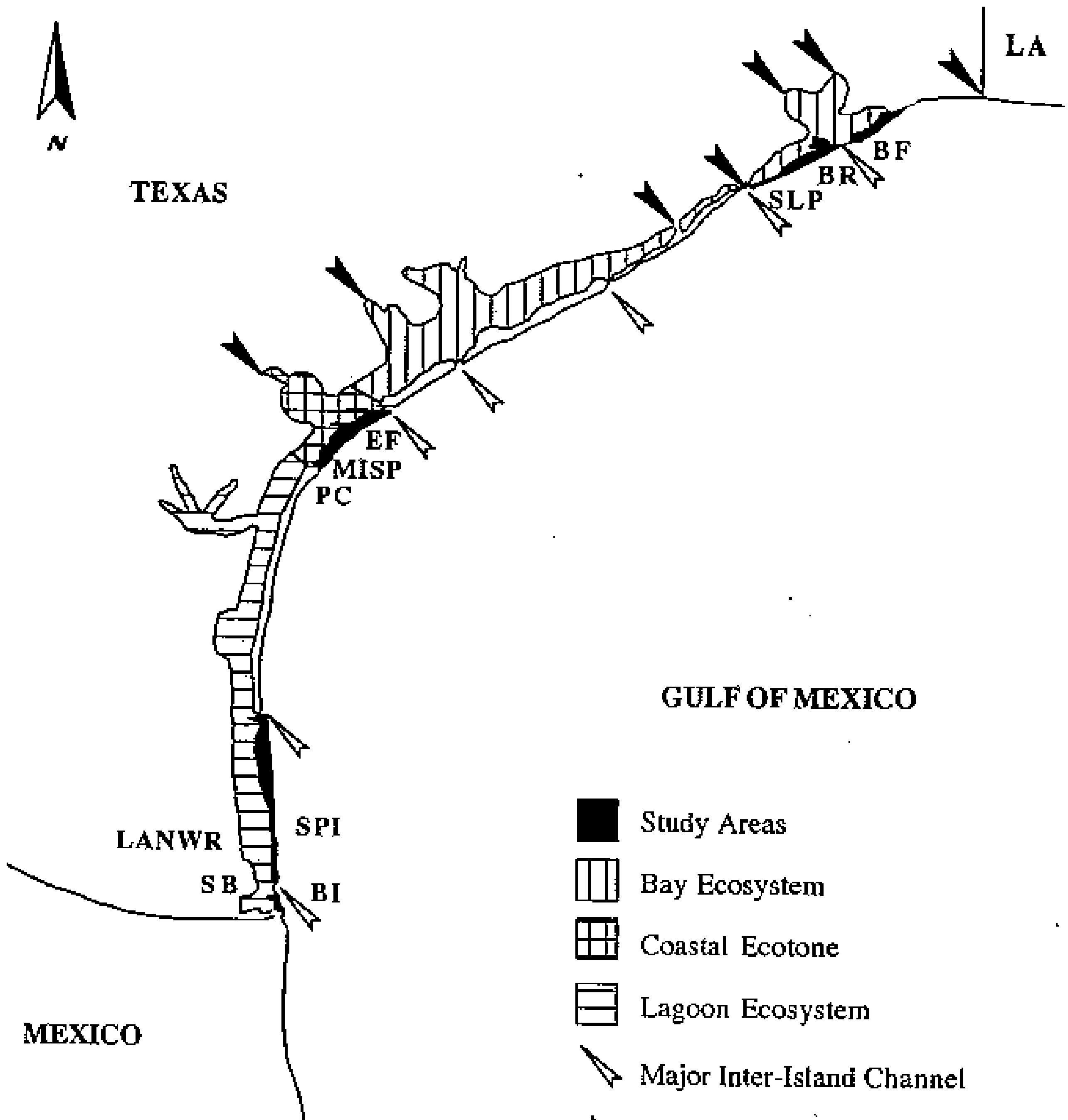


Figure 1. Schematic diagram of the Texas Gulf Coast illustrating the positions of the two major coastal ecosystems and the coastal ecotone. Locations of the study sites are identified by abbreviations (BF; Bolivar Flats, BI; Brazos Island, BR; Big Reef, EF; East Flats, LANWR; Laguna Atascosa National Wildlife Refuge, MISP; Mustang Island State Park, PC; Packery Channel, SB; South Bay, SLP; San Luis Pass, SPI; South Padre Island).

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 ecotone and the coastal ecosystems defined above are not recognized as formal divisions of the coast, however, and these terms have been conceived for the purposes of this study.

The occurrence of 2 ecosystems (the bay and lagoon ecosystems) and several large Piping Plover populations along its coast qualifies Texas as a particularly appropriate portion of the species' winter range in which to investigate the factors affecting the local abundance, habitat use and behavior of nonbreeding Piping Plovers.

Study Focus

Our research focused on evaluating the effects of key habitat components and environmental variables on the 1) occurrence, 2) foraging ecology and 3) movement patterns of Piping Plovers in different habitats and different locations. We used Piping Plover foraging ecology as a means of appraising the relative success of nonbreeding populations because this activity occupies the large majority of the average Piping Plover's time during the diurnal winter period (Johnson and Baldassarre, Teas and Elliott unpublished data, pers. obs.). Whereas Piping Plovers also spend considerable time resting and preening during the nonbreeding period, we contend that these behaviors occur only when Piping Plovers either do not need to forage, or when conditions are not favorable enough to support a net intake rate to a foraging plover. Furthermore, because Piping Plovers are a federally listed species, other means of appraising the relative condition of plovers (e.g. by measuring fat stores) in different areas or habitats are not justifiable. Therefore, we believe foraging success is the most reasonable way of evaluating and comparing the relative well being of Piping Plover Populations. As we detail in Methods, foraging success was appraised in several ways, including measures of the proportion of time plovers spend foraging in relation to resting, the amount of energy expended during foraging periods, foraging efficiency, diet, and aggressive behavior during periods of foraging.

Research Objectives

Primary Objective - The primary objective of our research was to identify the habitat components and environmental conditions that are necessary to support large numbers of Piping Plovers along the Texas Gulf Coast. We proposed to identify these parameters using a multi-factor regression model supported by data collected at 9 study sites over a period of 3 years. Accomplishing this objective will help prioritize sites, or perhaps entire ecosystems, for conservation. This model will also 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 such 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.

Secondary Objectives - Whereas the primary objective focuses on identifying the factors controlling the abundance of Piping Plovers at the scale of our study sites (58 - 812 ha), several other factors are addressed by 3 secondary objectives that we have identified for our research. The focus of these objectives address, among other things, the factors influencing Piping Plover ecology at scales other than that of our study sites, such as among habitat types, among microhabitat types, among landform types, and among ecosystems. For these objectives, we consider 6 aspects of Piping Plover ecology not addressed by our primary objective: population density, foraging activity, foraging locomotion, foraging efficiency, foraging aggressive behavior, and intra- and inter-annual movement patterns. Specifically, the secondary objectives are to:

1. Characterize the relative densities of Piping Plovers among the 2 Texas coastal ecosystems and the Texas coastal ecotone. Specific goals associated with this objective are to determine:

   a. whether Piping Plover densities are similar in the different ecosystems and in the ecotone.
   b. whether Piping Plover densities are similar at sites within ecosystems or the ecotone.

Accomplishing this objective will allow for quantitative and qualitative comparisons of the 2 coastal ecosystems in Texas as well as the ecotone transition between these ecosystems. These comparisons may guide Piping Plover recovery by identifying geographic "hot spots" of Piping Plover winter abundance, or by allowing for comparisons among habitats within the 3 areas.

2. Identify the spatial, temporal, and environmental factors that affect Piping Plover densities. A specific goal associated with this objective is to determine whether differences in Piping Plover densities under any of the comparisons described in secondary objective #1 can be explained by specific spatial, temporal or environmental conditions, or combinations of these conditions acting together.

Accomplishing this objective will greatly extend our understanding of the influences of key parameters on a location's quality to Piping Plovers (as measured by plover density).

3. Characterize the foraging ecology of Piping Plovers along the Texas Gulf Coast, and identify the factors affecting foraging efficiency. Specific goals associated with this objective are to determine:

   a. the diets of Piping Plovers on beach and bayshore habitats in both ecosystems and in the ecotone.
   b. the amount of energy expended by Piping Plovers on beach and bayshore habitats in both ecosystems and in the ecotone.
   c. the foraging efficiency of Piping Plovers on beach and bayshore habitats in both ecosystems and in the ecotone.
   d. the frequency of aggressive interactions involving Piping Plovers on beach and bayshore habitats in both ecosystems and in the ecotone.

Accomplishing this objective 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 Texas Gulf Coast as appraised by the relative costs and benefits associated with foraging.

4. Characterize the prey resources potentially available to Piping Plovers among the habitats and ecosystems used by Piping Plovers along the Texas Gulf Coast. Specific goals associated with this objective are to determine:

  a. the densities of major potential prey groups among habitats and ecosystems used by Piping Plovers
  b. whether Piping Plover densities in different habitats and ecosystems are associated with the densities of potentially available prey resources.

Accomplishing this objective will help determine the relationship between potential prey density and Piping Plover density. These analyses may help estimate the quality of different habitats, sites and ecosystem types to Piping Plovers along the Texas Coast, and potentially in other portions of the winter range.

5. Characterize the movement patterns of Piping Plovers. Specific goals associated with this objective are to determine:

  a. whether any Piping Plovers exhibit annual winter site fidelity.
  b. whether any Piping Plovers exhibit seasonal site fidelity during the nonbreeding portion of their life cycle.
  c. whether the winter home range size differs in the 2 ecosystems and the ecotone.
  d. whether changes in plover densities on different habitats under specific conditions identified in objective # 2 might be explained by interhabitat movement patterns.

Accomplishing this objective may help to predict the effect of a site's loss or degradation to occupant Piping Plovers, as well as provide information about the winter area requirements of Piping Plovers in different coastal regions. Documenting the movement patterns of individual plovers within a study site will help to establish the responses of populations to the environmental conditions investigated in objective #2.

MATERIALS AND METHODS

Habitat Characteristics of the Texas Gulf Coast Ecosystems.

The Texas Gulf coast exhibits 2 dominant ecosystems, a northern, "estuarine bay" ecosystem and a southern, "hypersaline lagoon" ecosystem (see the chapter entitled " Important habitat features of the Texas Gulf Coast" in the Introduction). Many of the research objectives were addressed by comparing these ecosystems with regard to habitat and environmental characteristics and their effects on Piping Plover density, Piping Plover foraging behavior, and Piping Plover foraging efficiency. The same types of data were collected at sites in the coastal ecotone and compared to data from the 2 ecosystems. A description of the dominant characteristics of the ecosystems and the ecotone follows.

The Estuarine Bay Ecosystem -- The climate in this ecosystem ranges from humid to subhumid with average annual rainfalls between about 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 17.6 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 maratima*) 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 Hypersaline Lagoon ecosystem - 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 a spectacular 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 exceed 100 ppt (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 is at these levels that the hypersaline lagoon ecosystem appears to differ most noticeably from the estuarine bay ecosystem (e.g. insects replacing polychaetes as one of 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 simply an "algal mat". Algal mats are not true algae, but rather are composed of a mix of blue-green algae, dominated by *Lyngbya confervoides*. Algal mats also contain a variety of pennate diatoms and other prokaryotes (Pulich and Rabalais 1986, Sorensen and Conover 1962). Algal mats form a thin layer, usually only a few centimeters thick, over the ground surface. However, the mats are extensive in many areas and cover hundreds of square kilometers in the lagoon ecosystem (Pulich and Rabalais 1986, Tunnell 1989). Flats covered by algal mats are referred to as "algal flats" (regardless of the underlying substrate). 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 maratima*), Sea lavender (*Limonium nashii*), Key grass (*Monanthochloe littoralis*), and Sea purslane (*Sesuvium portulacastrum*). Only a handful of "hypersaline" ecosystems exist worldwide, 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. Because Piping Plovers generally avoid densely-vegetated habitat (pers. obs., Brush 1995, T. Eubanks Fermata Inc., Austin, TX pers. comm.), much of the mainland intertidal habitat in the bay ecosystem is probably unsuitable to 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. At one of the sites (South Bay), the mainland and the local barrier (Brazos Island) are connected by a land bridge formed by Highway 4, and there is no clear division between the two landforms. To clarify this situation, we defined all flats $\geq$ 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 exists only for bayshore habitat. Furthermore, because none of the study sites in the bay ecosystem nor the ecotone were $\geq$ 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.

The Central Coastal Ecotone -- 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 the baywater salinities are a blend of those typifying the 2 ecosystems, and tides are driven by both winds and astronomical forces.

Study Areas

Our research was conducted at wetland sites bordering shorelines along the Gulf of Mexico or along shores of primary bays separated from the Gulf by barrier islands or peninsulas. Most sites were composed of a segment of Gulf beach habitat and an adjacent segment of bayshore habitat (Figure 2). Beach and bayshore habitats at our sites were usually separated by a row of dunes along the upper beach, a narrow (< 5 km) strip of coastal prairie, and occasionally a second row of dunes along the bayshore upland margin. At 3 sites (the Packery Channel, South Padre Island North Area, and the Brazos Island /South Bay sites) the beach and bayshore habitats were linked by washover passes (Figure 2). Although emergent for most of the study period, the washover passes were occasionally scoured into narrow, shallow washover channels by tropical storms. When emergent, the washover passes remained largely free of dunes and emergent vegetation during the study.

We monitored populations of Piping Plovers at 9 different sites. A group of 3 study sites was located within each ecosystem, and a third group of 3 study sites was located within the ecotone (Figures 3 - 5). The bayshore and Gulfshore wetlands

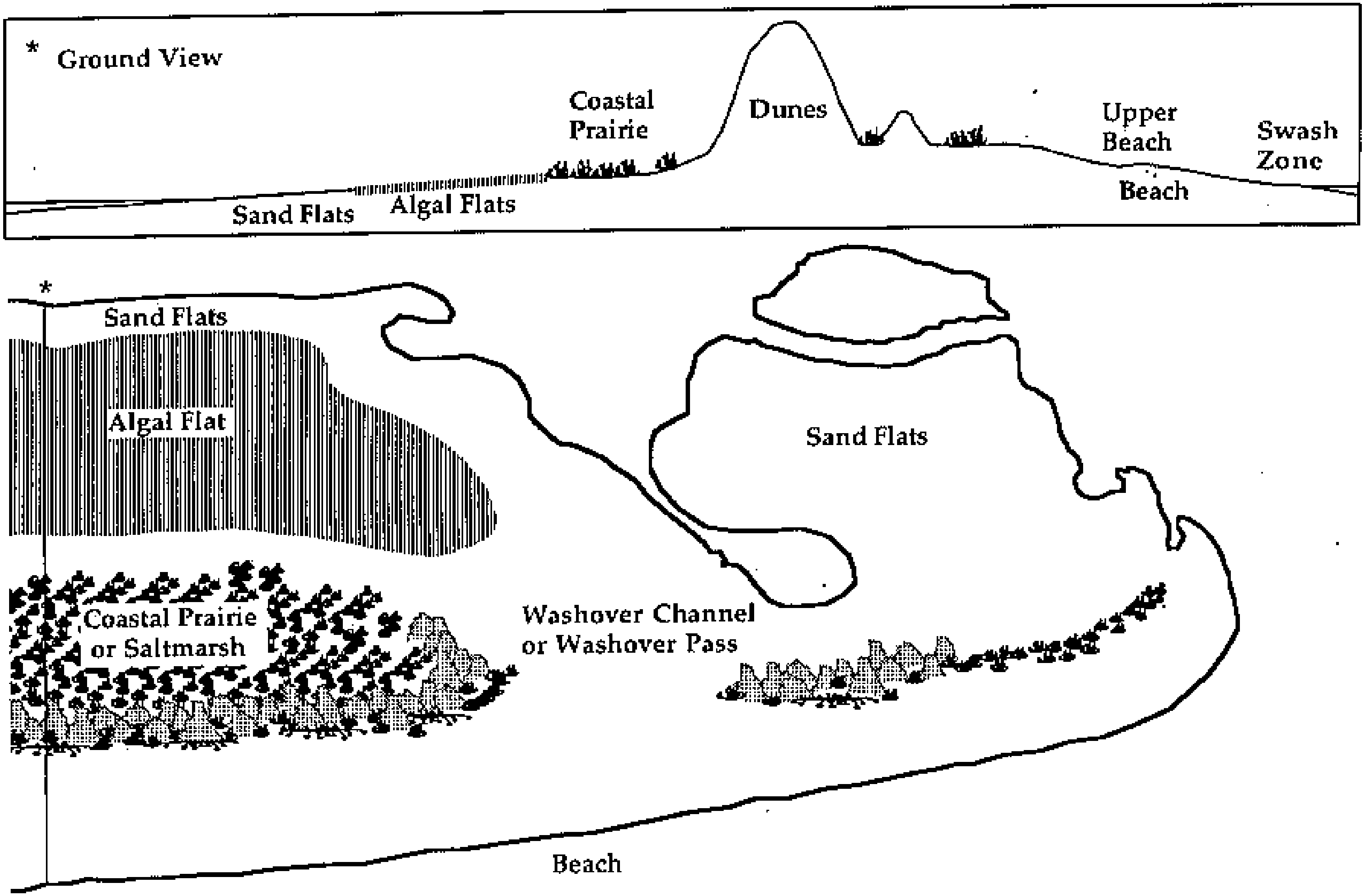


Figure 2. Schematic diagram illustrating the spatial arrangement of habitat types at most of the study sites. The intertidal habitats of the beach and the bayshore flats were usually separated by only a narrow zone of coastal prairie upland or saltmarsh bordered by dunes. In many cases, washover channels or washover passes were present, and served as corridors of sparsely -vegetated land connecting the beach and bayshore habitats to one another.

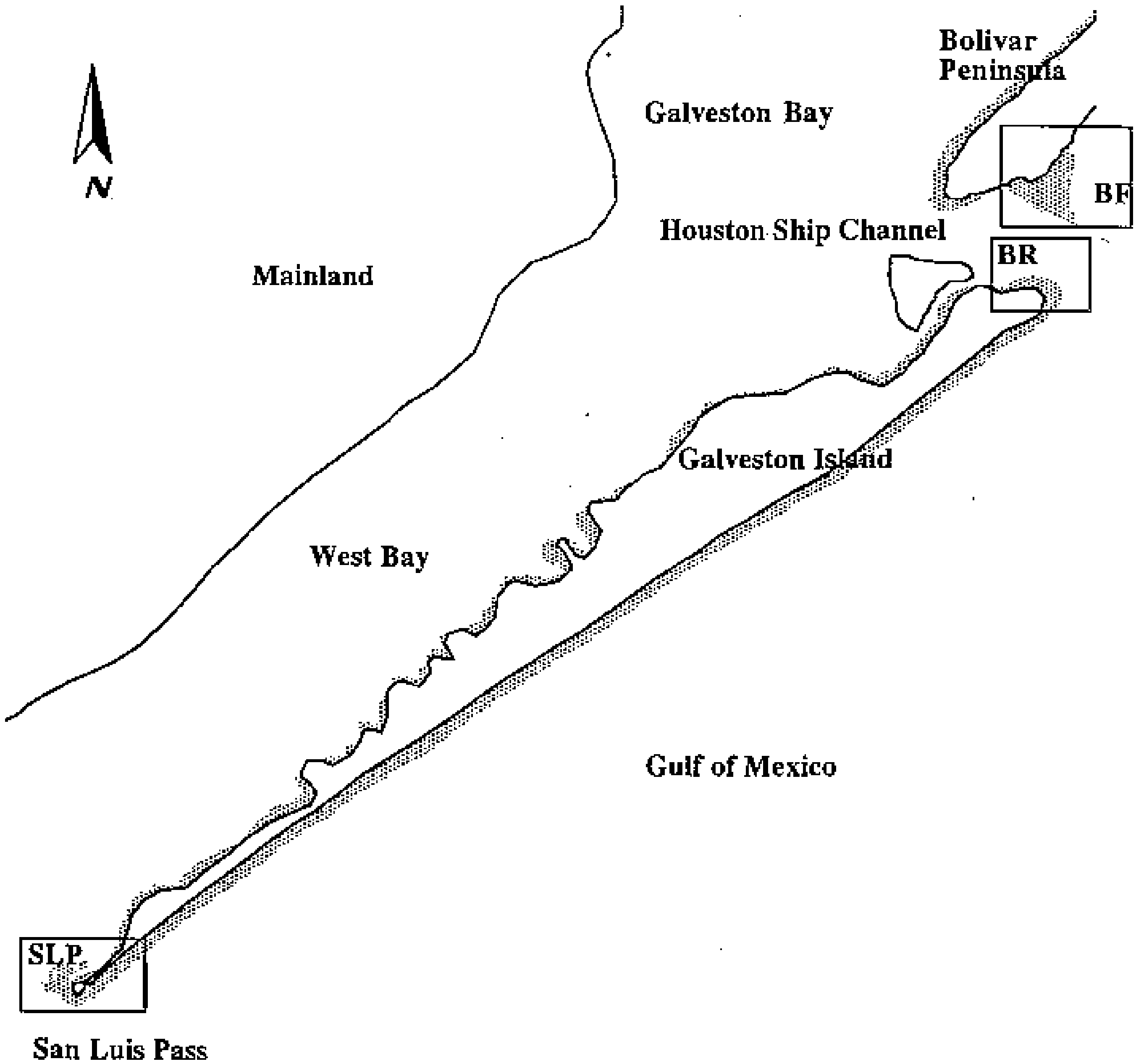


Figure 3. The locations of the study sites representing the estuarine bay ecosystem are illustrated. BF; Bolivar Flats, BR; Big Reef, SLP; San Luis Pass.

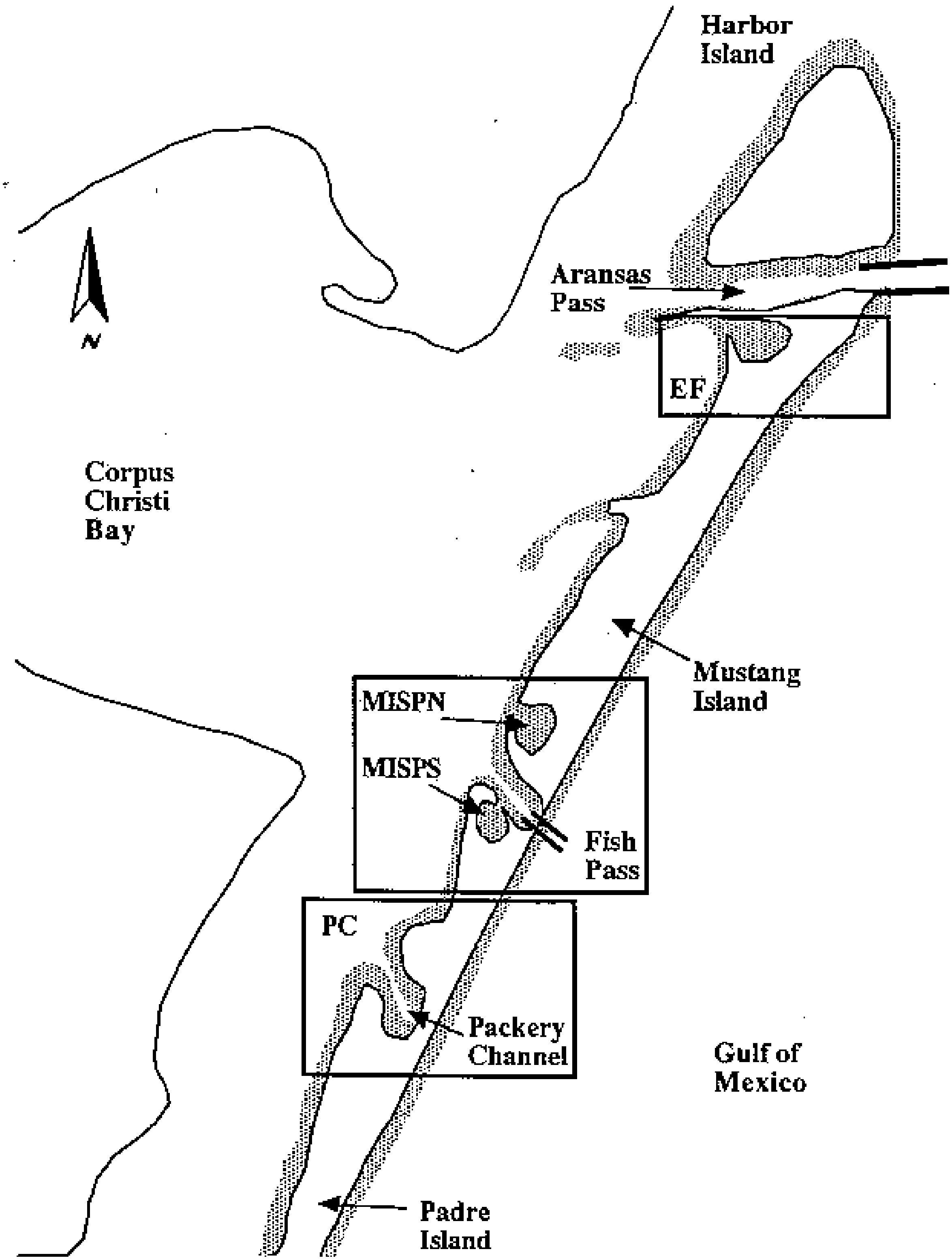


Figure 4. The locations of the study sites representing the central coastal ecotone are illustrated. EF; East Flats, MISPN; Mustang Island State Park North Area, MISPS; Mustang Island State Park South Area, PC; Packery Channel.

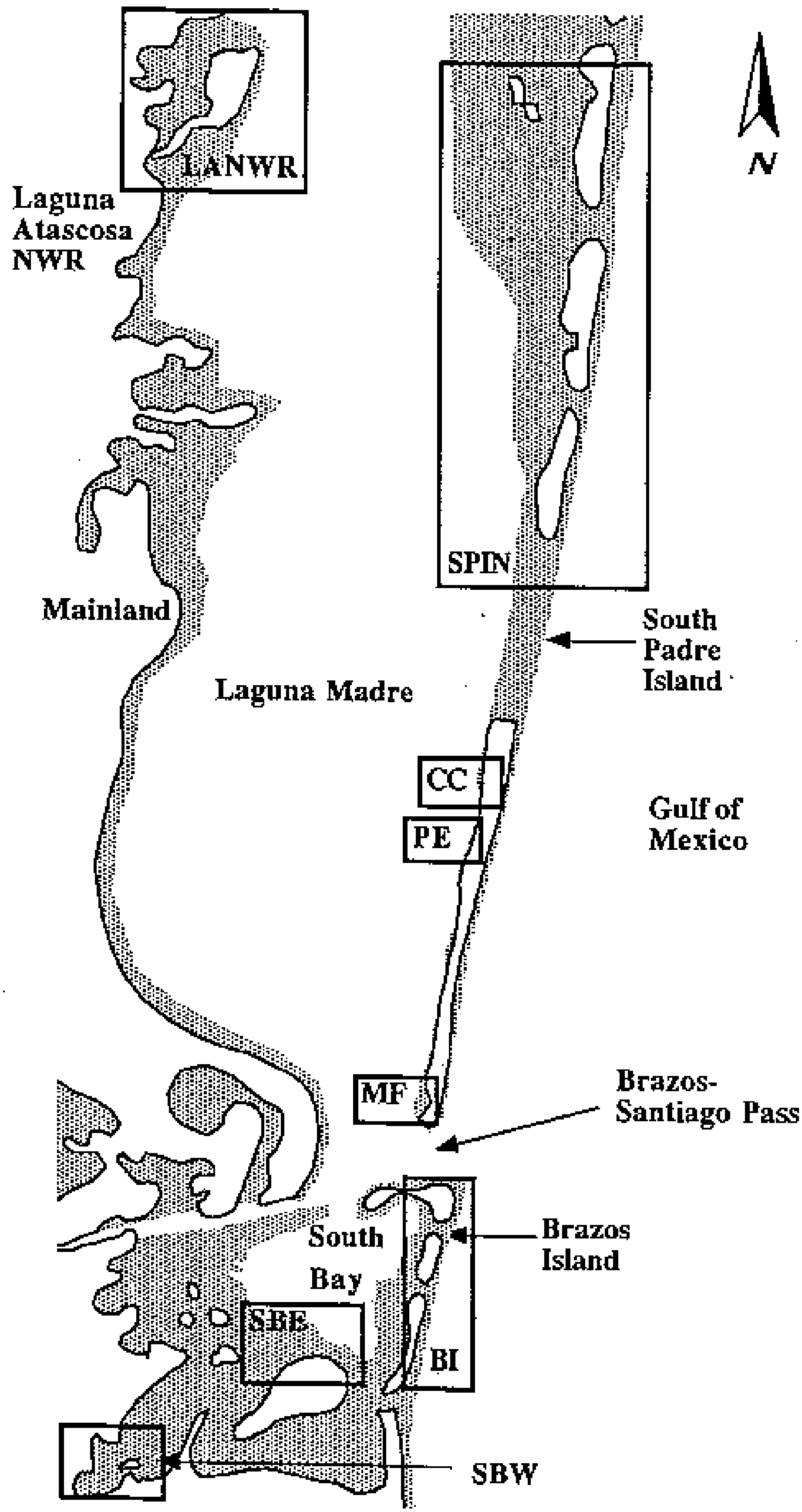


Figure 5. The locations of the study sites representing the hypersaline lagoon ecosystem are illustrated. CC; Convention Center, LANWR; Laguna Atascosa National Wildlife Refuge, MF; Mangrove Flats, PE; Parrot Eyes, SBE; South Bay East Area, SBW; South Bay West Area, SPIN; South Padre Island North Area.

associated with each of the study sites are classified in Table 1. We classified our sites according to a slight modification of the wetland classification system developed by Cowardin et al. (1979). A brief description of each study site follows below.

Estuarine Bay Ecosystem Sites.

Bolivar Flats - This site, located at the southeastern tip of Bolivar Peninsula in Galveston Co., is composed of a single muddy sand flat, sandwiched between the northern jetty along the Houston Ship Channel and a cordgrass marsh (Figure 6). The marsh and sand flats at this site are 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 conservation protection via a 100 year lease to the National Audubon Society in 1992.

Big Reef - This site, located on Galveston Island in Galveston Co., is an accreting wetland situated along the northern edge of the Houston Ship Channel's southern jetty (Figure 7). This site is composed of a small lagoon surrounded by a vegetated sandy spit. The lagoon is bordered by several small muddy sand flats. Portions of the bayshore flats associated with the lagoon exhibit ephemeral algal mats. The lagoon is fringed by patches of cordgrass marsh. Although the site is currently expanding, it cannot expand considerably without obstructing traffic in the Houston Ship Channel. Sand from the subtidal fringe of this site has been dredged in the past to replenish the eroding beaches along Galveston Island. Due to these constraints, it is unlikely that this site will expand significantly in the near future. The City of Galveston established the Big Reef study site as the Big Reef Nature Park soon after the conclusion of our study in 1994.

San Luis Flats - This site, located along San Luis Pass on the southwest tip of Galveston Island in Galveston Co., is composed of several large sand flats bordered by coastal prairie (Figure 8). It is the only estuarine bay ecosystem study site that is not largely supported by a man-made structure. The beaches associated with this site are eroding rapidly (Morton 1974). The long-term stability of the bayshore flat system is not known.

Central Ecotone Sites.

East Flats - This site, located near the northern tip of Mustang Island in Nueces Co., is composed of series of algal flats and mud flats separated by small patches of upland, and fingers of cordgrass and cattail (*Typha* spp.) marsh (Figure 9). A wastewater reclamation facility releases a treated, low-salinity effluent into this wetland from its southeastern border. Once sharing a broad tidal exchange with the waters of Corpus Christi Bay and Redfish Bay, this wetland has been surrounded to such a great extent by dredge spoil from the Corpus Christi Ship Channel that the only remaining tidal exchange between the flats and the baywater occurs through a few small channels along the wetland's southwestern border. The periodicity and magnitude of inundation experienced by the flats is erratic due to the restricted tidal flow. Effluent released by the treatment facility into the wetlands probably contributes more to the regular inundation of the wetland than do baywater swells. Expanding development along the bayshore to the south threatens to further restrict, or completely eliminate, the present remnant baywater exchanges with this site.

Due in part to the presence of park facilities and its proximity to the human population of Port Aransas, the beach at this location often experiences high levels of human disturbance.

Table 1. Classification of beach 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
Estuarine Bay Ecosystem							
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
Coastal Ecotone							
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
Hypersaline Lagoon Ecosystem							
South Bay	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent
South Padre	Marine	Intertidal	Regular	Astronomical	Sand	Euhaline	Absent

Table 1 continued. Classification of 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
Estuarine Bay Ecosystem							
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
Coastal Ecotone							
East Flats	*	*	Irregular	*	Sand/Mud	*	Present
MISP	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Euhaline	Present
Packery Flats	Marine	Intertidal	Irregular	Mixed	Sand/Mud	Polyhaline	Present
Hypersaline Lagoon Ecosystem							
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	Present

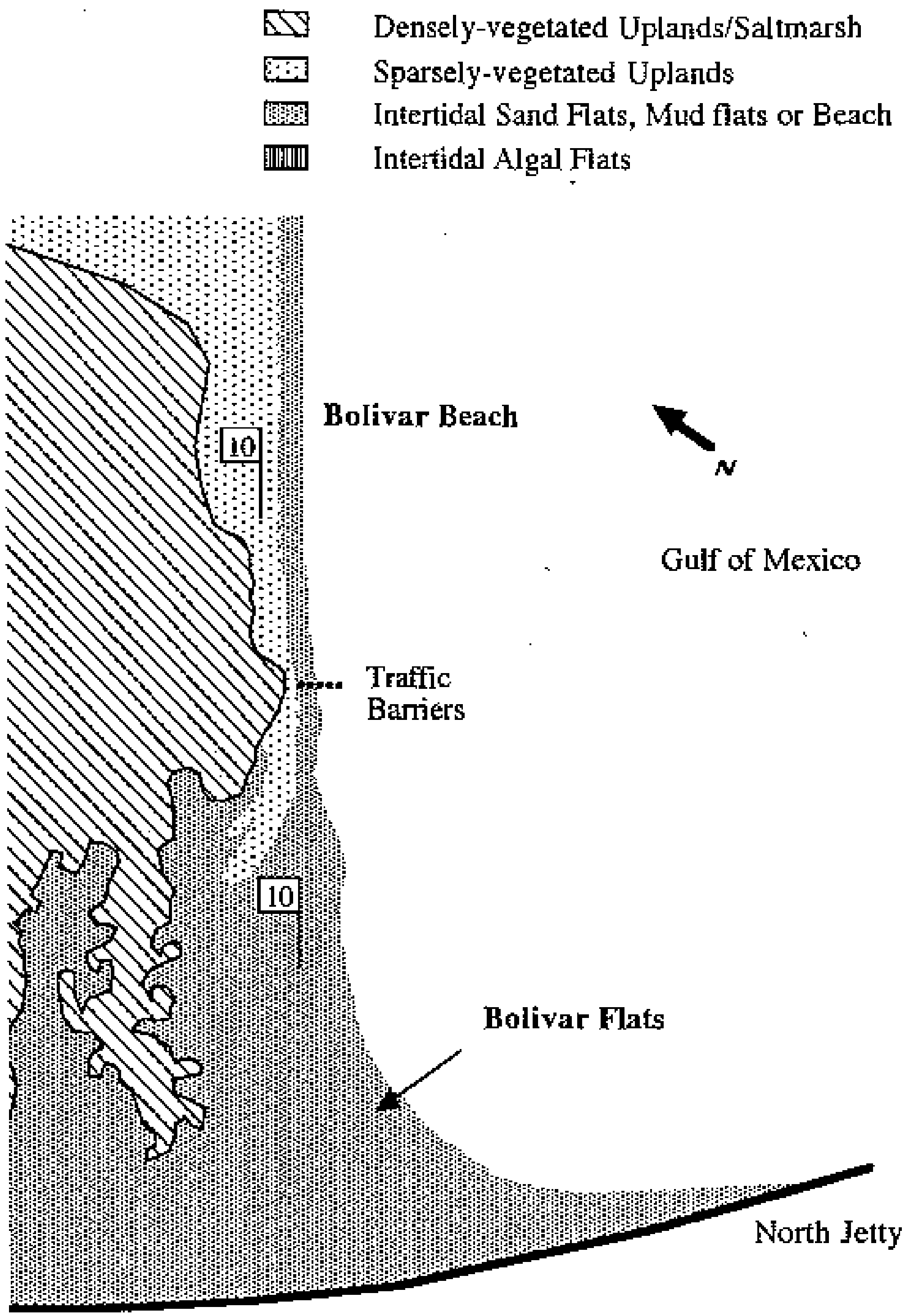


Figure 6. Schematic map of Bolivar Flats [BF] illustrating the relative locations of the habitat types associated with the study site. There were no permanent algal flats present at this site. Numbered Flags (⁋) identify the locations of color banded Piping Plovers. Refer to Table 21 for more information on sightings of color banded plovers.

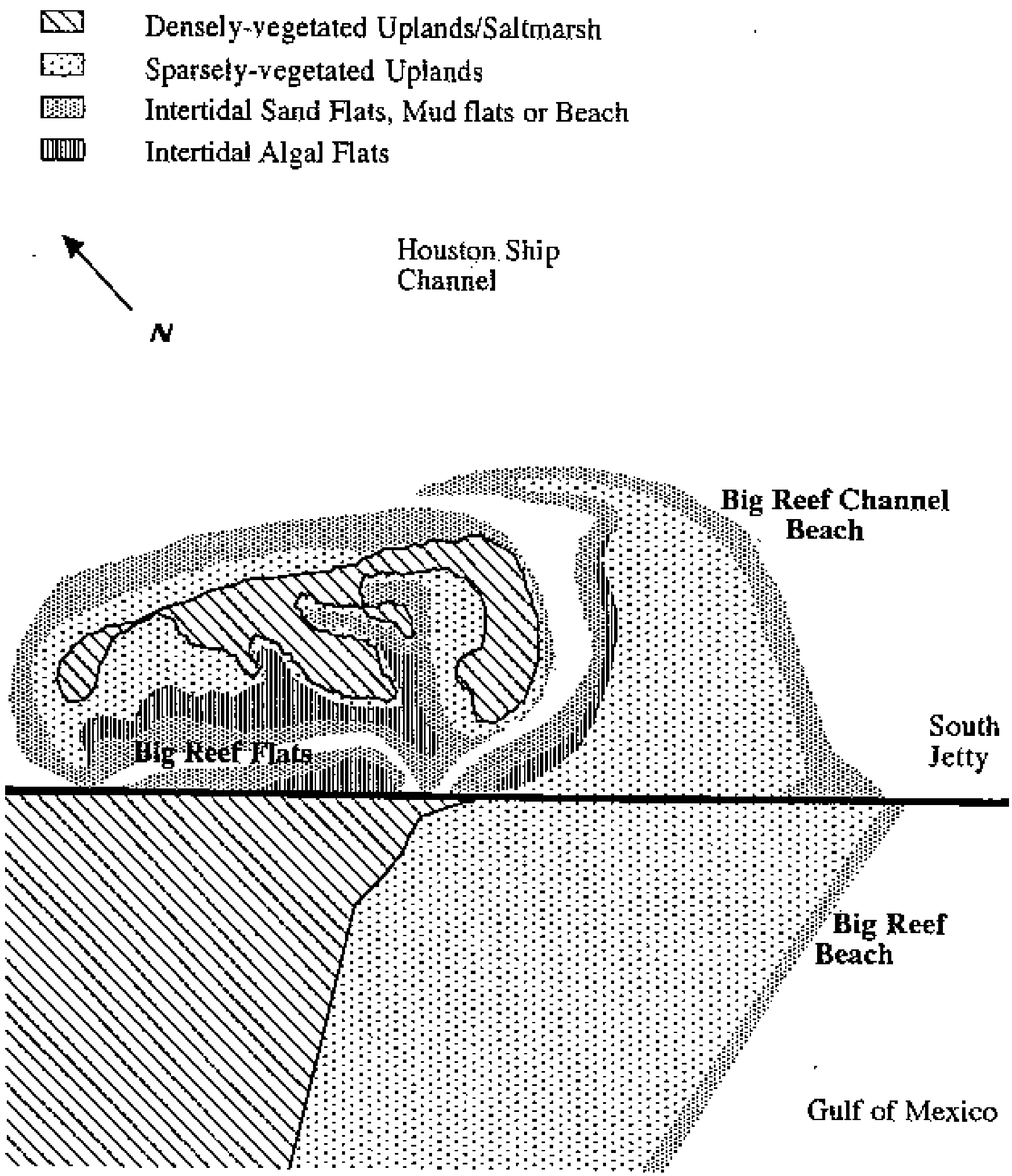


Figure 7. Schematic map of Big Reef [BR], illustrating the relative locations of the habitat types associated with the study site. No color banded Piping Plovers were seen at this study site.

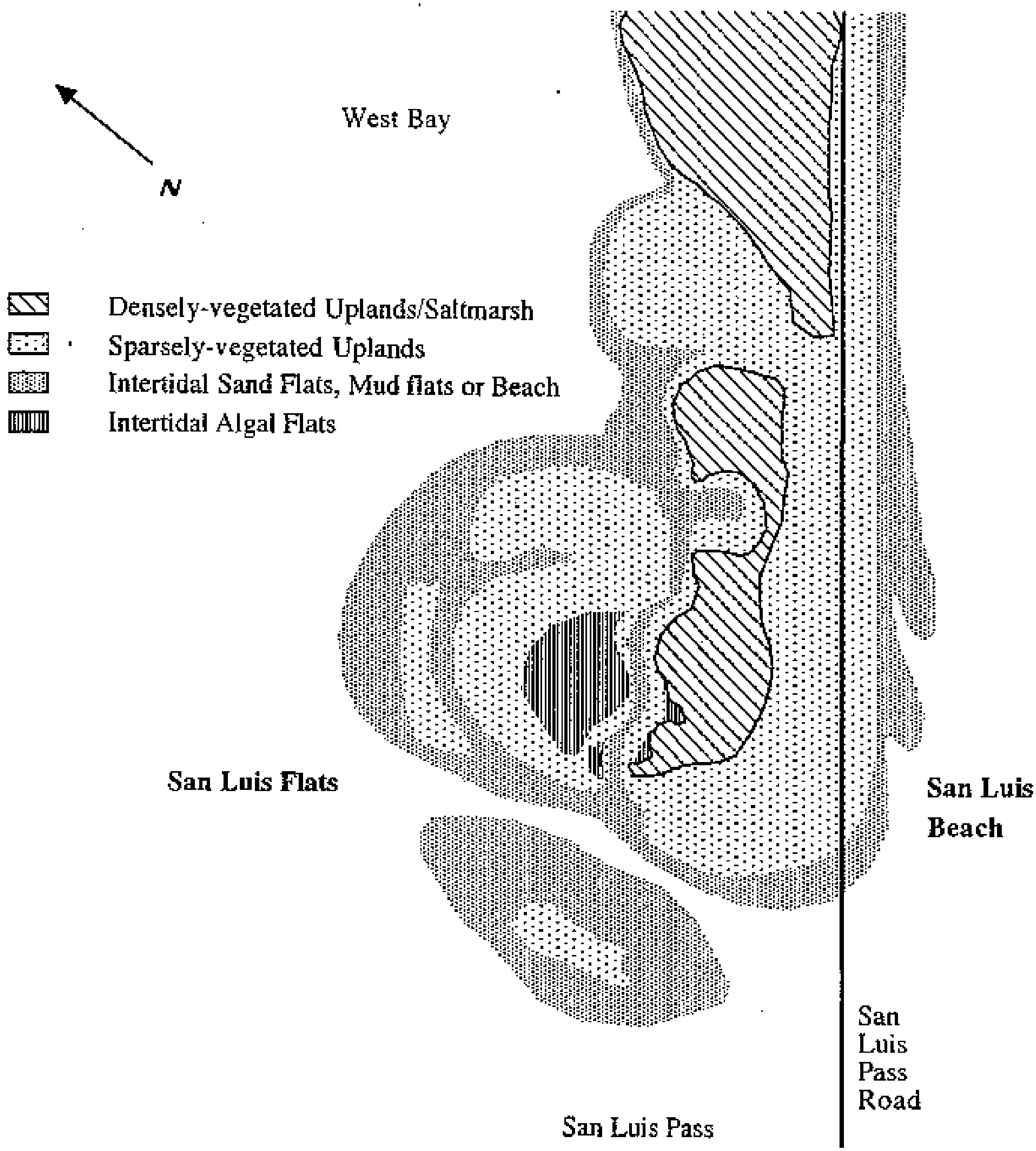


Figure 8. Schematic map of San Luis Pass [SLP] illustrating the relative locations of the habitat types associated with the study site. No color banded Piping Plovers were seen at this site during the study.

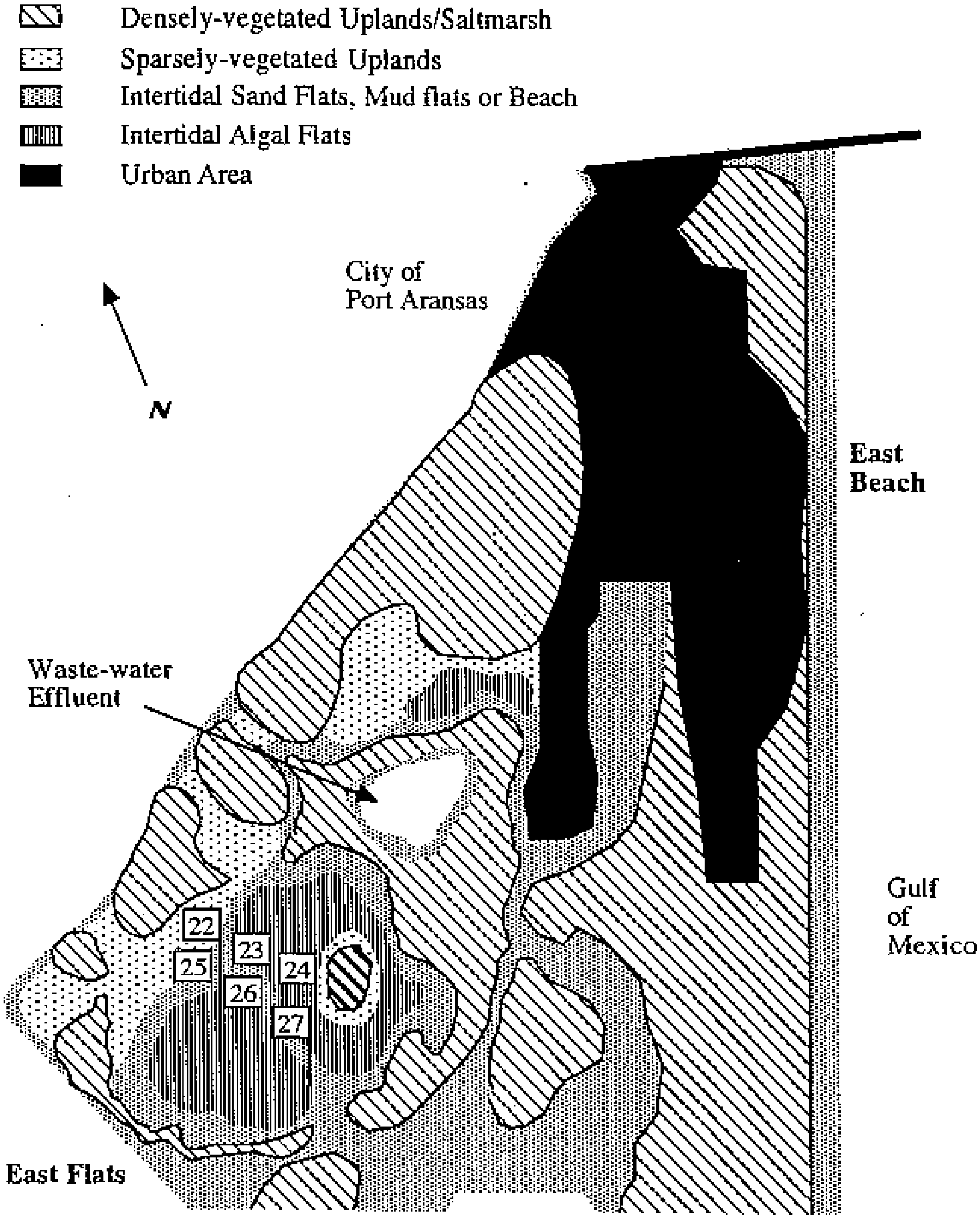


Figure 9. Schematic map of East Flats [EF] illustrating the relative locations of the habitat types associated with the study site. Numbered flags (ꟼ) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

Mustang Island State Park - This site, contained within the boundaries of the Mustang Island State Park (MISP), Nueces Co., is divided by a man-made boat channel, identified on most maps as Fish Pass (Figure 10). The elevated banks along Fish Pass have 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, one on either side of the pass. An artificial channel re-established a tidal exchange between the northern lagoon and the bay, but the southern lagoon remains isolated from baywater tidal exchanges to a large extent. Both lagoons are partially separated from Corpus Christi Bay by a line of tall sand dunes. These dunes are flanked by sand flats.

Packery Flats - This site, located along the northern shoreline of Packery Channel in Nueces Co., is composed of sand flats and algal flats surrounded by coastal prairie (Figure 11). Due in part to its proximity to Corpus Christi, this beach often experiences high levels of human disturbance.

Hypersaline Lagoon Ecosystem Sites.

Laguna Atascosa National Wildlife Refuge - This site, located within the boundaries of Laguna Atascosa National Wildlife Refuge (LANWR) in Cameron Co., is 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) associated with a system of coves near Horse Island (Figure 12). All of the flats are ≥ 5 km from Gulf Coastline, and were thus classified as "mainland" flats. The flats are bordered by a dense coastal thicket elevated from the flats by a 1-3 m steep cliff-line. Like the East Flats study site, this site has been nearly removed from tidal exchange from the Laguna Madre by dredge spoil deposits and an elevated access road. This site occurs at roughly the same latitude as the South Padre Island site, and thus shares the same stretch of Gulf beach.

South Bay - This site, located along the shoreline of South Bay in Cameron Co., is composed of 2 large algal flats and mud flats surrounded by an elevated coastal prairie/savannah (Figure 13). One of the flats is ≥ 5 km from the Gulf, and is classified as a "mainland" flat. The other flat is within the 5 km zone, and is classified as a "barrier island" flat. Dredge spoil deposits associated with the Brownsville Ship Channel have substantially reduced the natural tidal exchange between South Bay and the Laguna Madre.

South Padre Island - This site on South Padre Island in Cameron Co., is composed of one large flat and a series of small, isolated flats (Figure 14). The smaller flats (Mangrove Flats, Parrot Eye's Flats and Convention Center Flats) are situated within the commercially-developed, southern tip of the island. The large flat (North Flat) is located immediately north of all development at the northern terminus of highway P100. All of the flats are within the 5 km zone of the Gulf, and are classified as "barrier island" flats. Algal flats and sand flats are the dominant habitat types at all of the locations on South Padre Island.

Site Visitation Schedule

The 3 site groups were visited for approximately 1 month at a time (i.e. 3 months/year), and each site was visited in approximately alternate fashion during the 1 month period. However, 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. The East Flat site (EF; Figure 9), located in the ecotone, was added to the

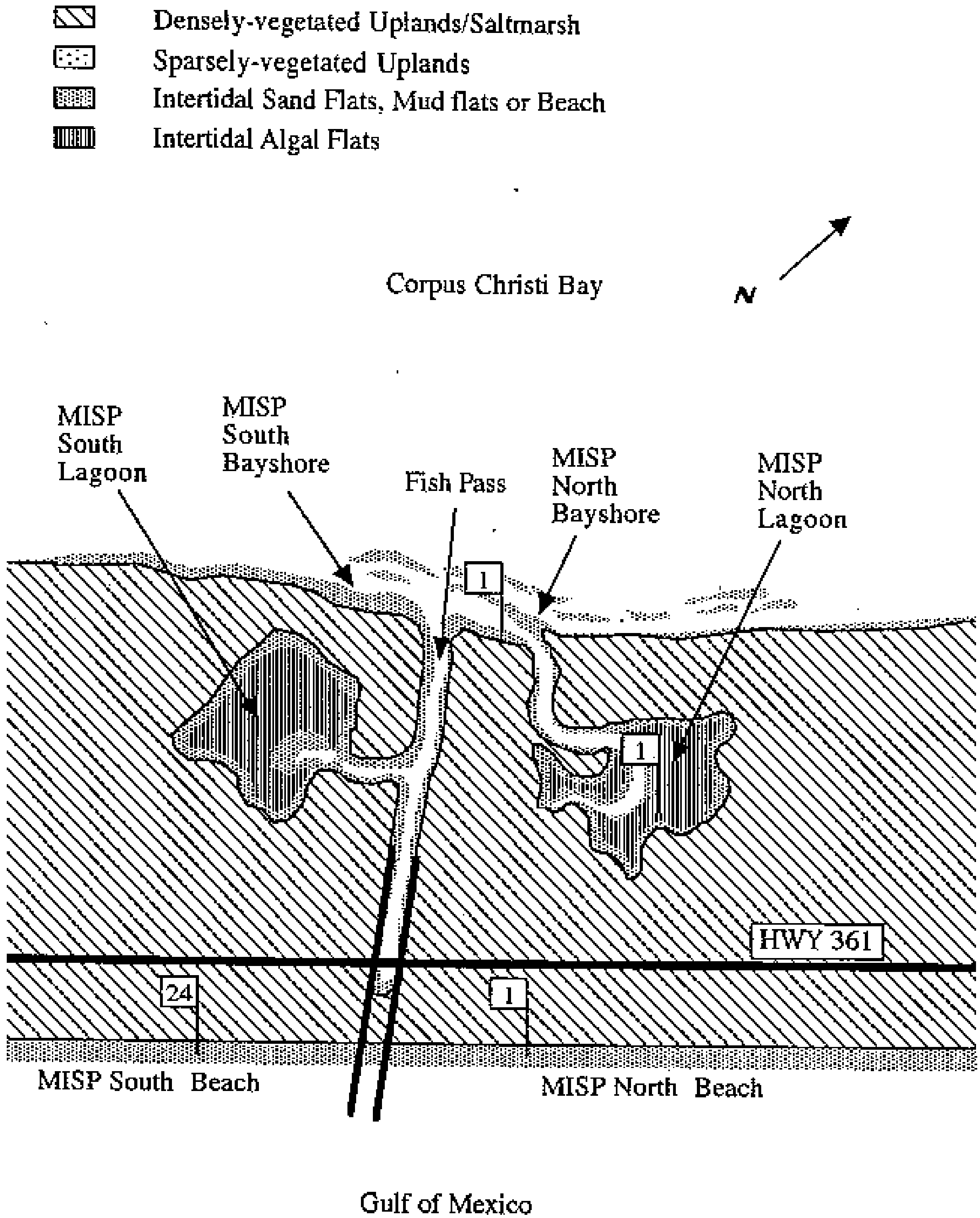


Figure 10. Schematic map of Mustang Island State Park North Area (beach. lagoon and bayshore) [MISPN] and South Area (beach, lagoon and bayshore) [MISPS] illustrating the relative locations of the habitat types associated with the study site. Numbered flags (⊣) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

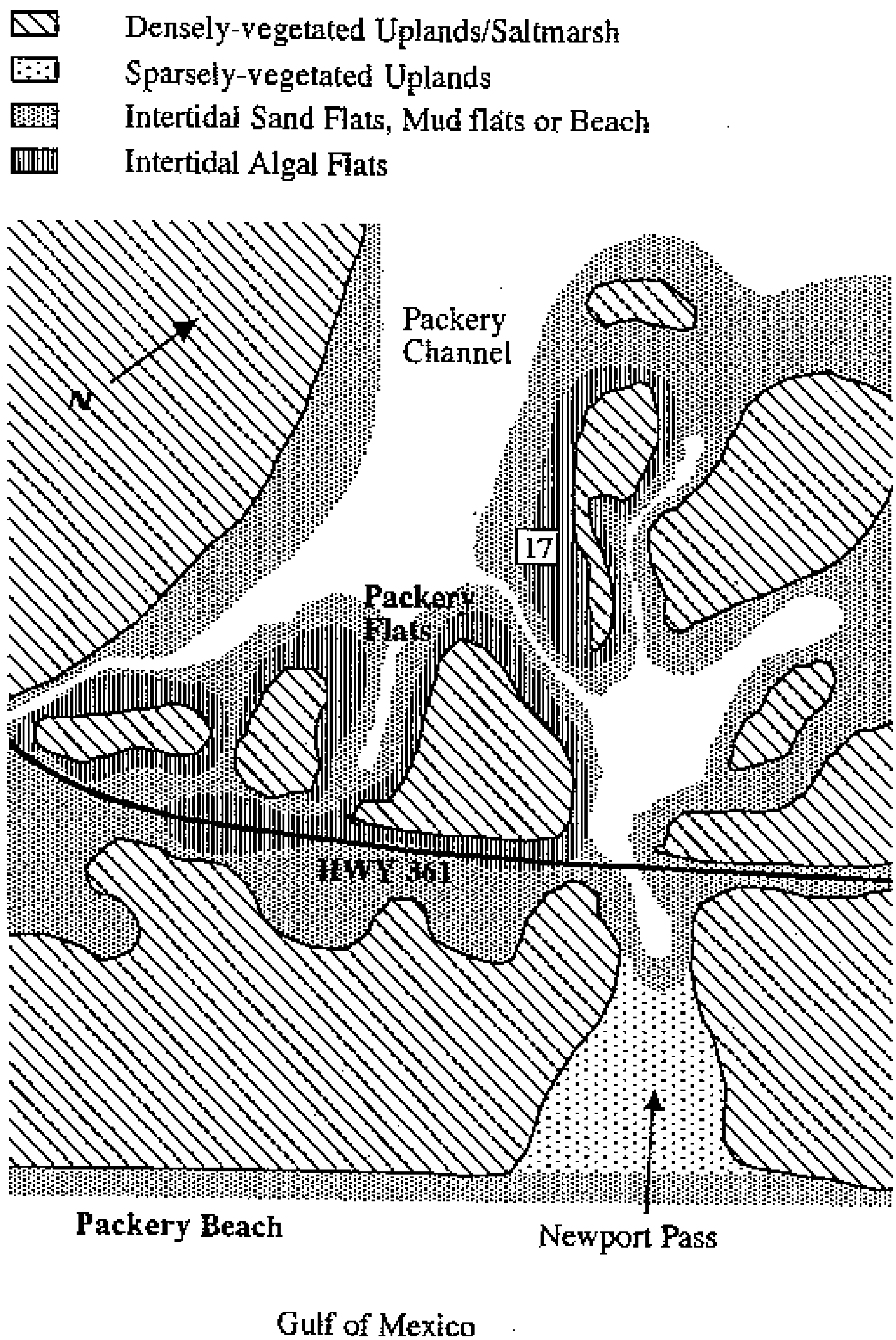


Figure 11. Schematic map of Packery Channel [PC] illustrating the relative locations of the habitat types associated with the study site. Numbered flags (⚑) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

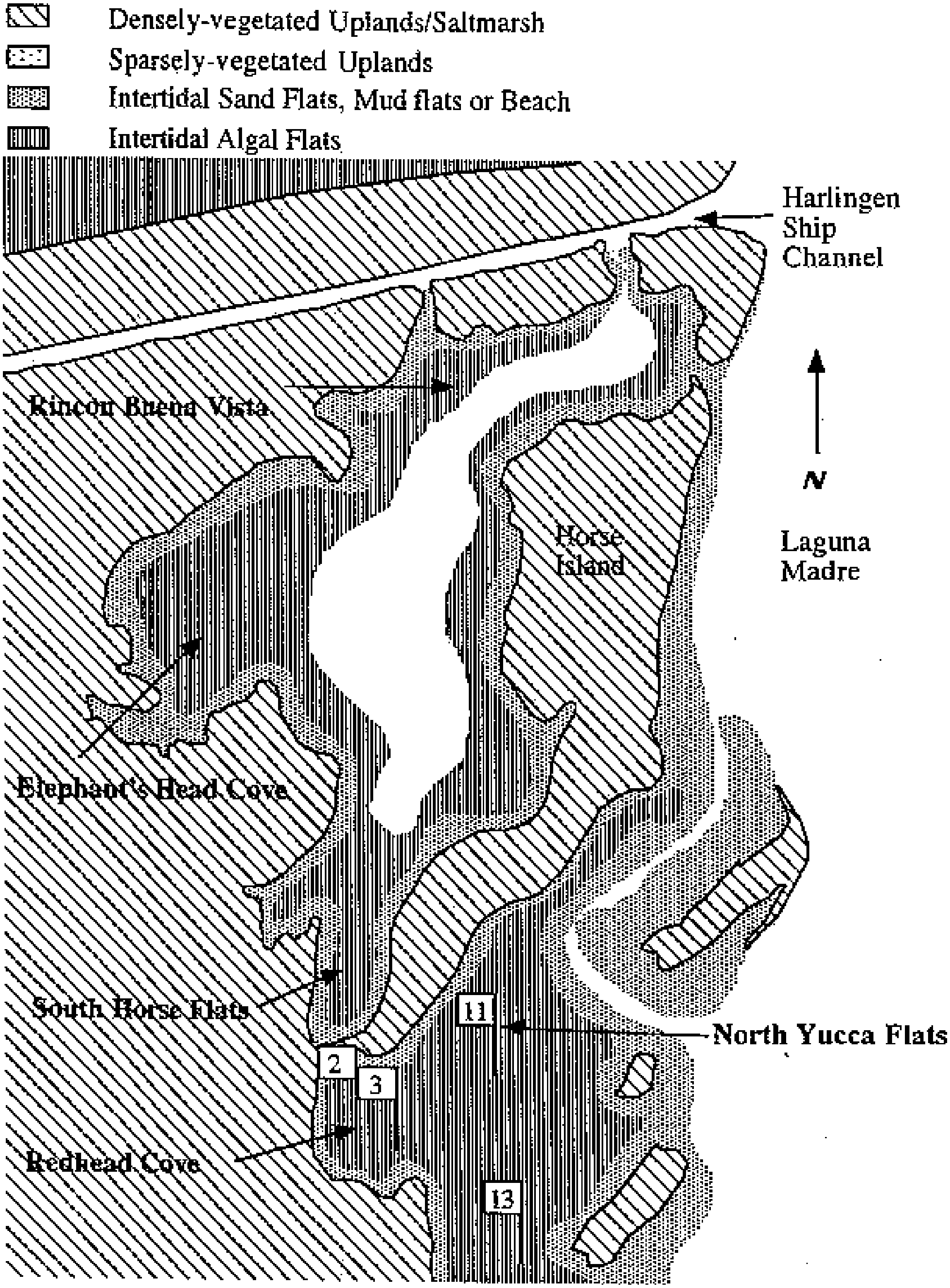


Figure 12. Schematic map of Laguna Atascosa National Wildlife Refuge [LANWR] and the subsites Rincon Buena Vista Flats [RBV], Elephant's Head Cove [EHC], South Horse Flats [SHF], Redhead Cove [RHC], and North Yucca Flats [NYF], illustrating the relative locations of the habitat types associated with the study site. There is no beach habitat associated with this study site. Numbered flags (⚑) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

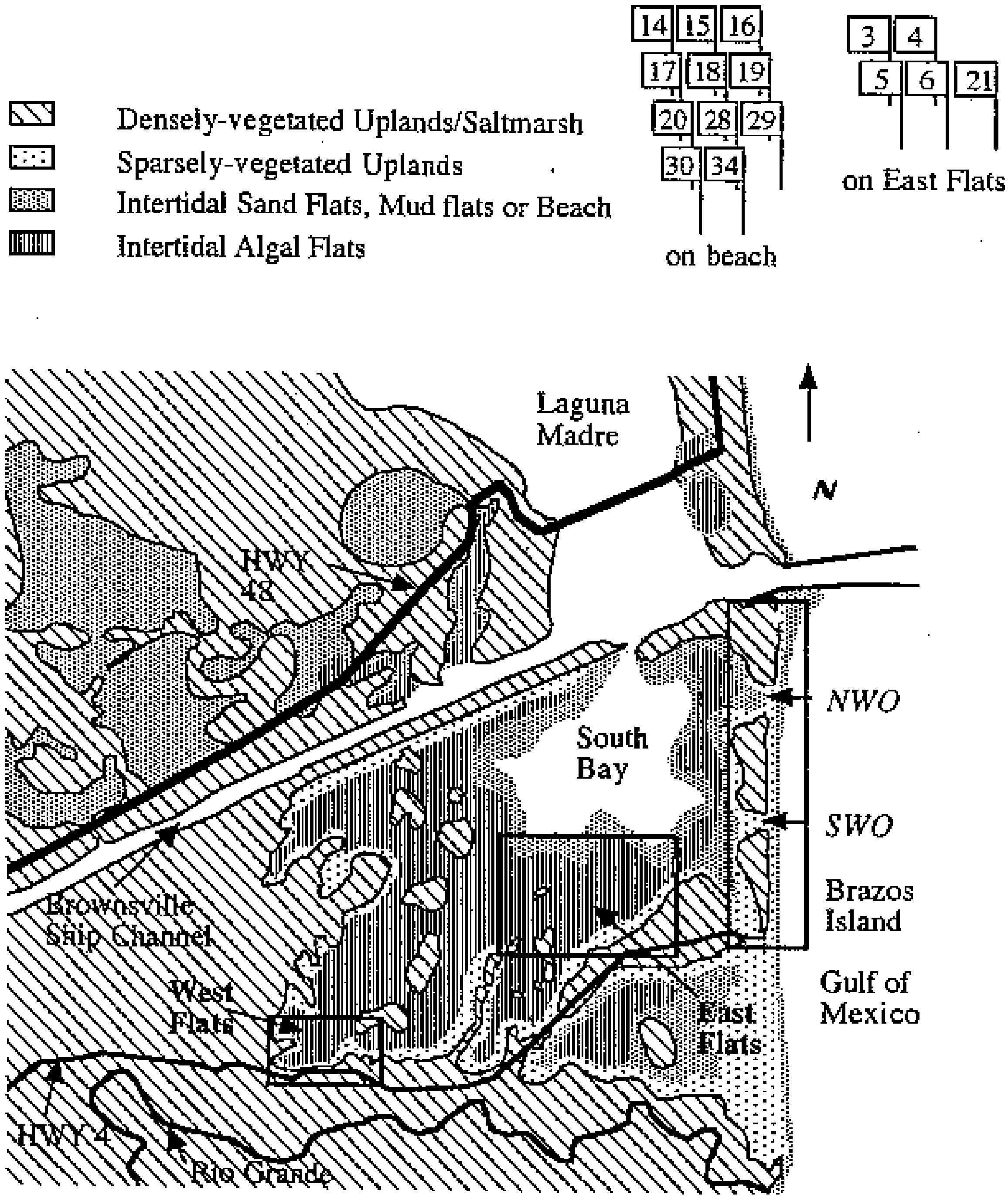


Figure 13 . Schematic map of South Bay [SB], the subsites South Bay West Area [SB-West] and South Bay East Area [SB-West], Brazos Island [BI] and the North [NWO] and South [SWO] washover passes, illustrating the relative locations of the habitat types associated with the study site. Numbered flags (⁋) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

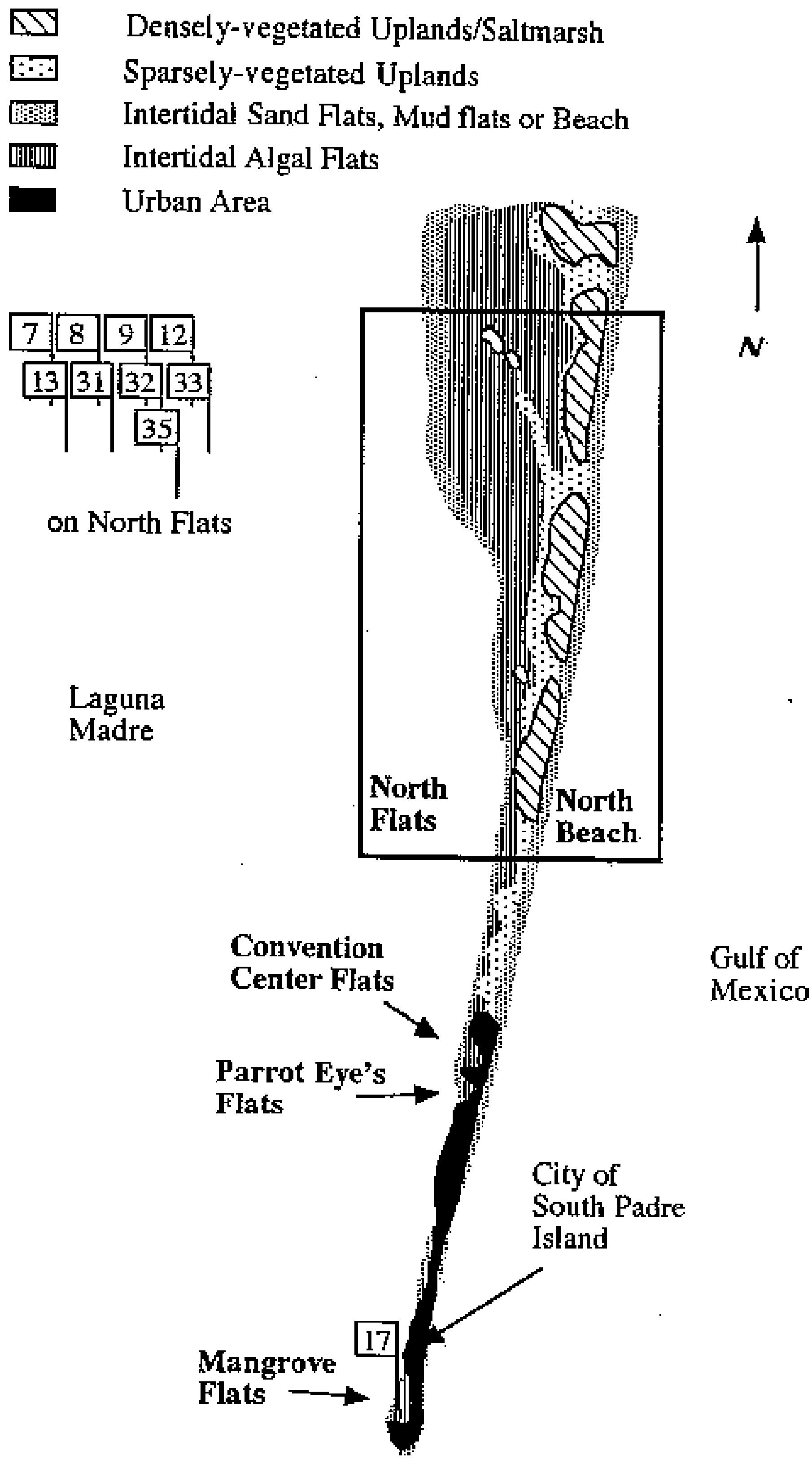


Figure 14. Schematic map of South Padre Island North Area [SPIN] and the three smaller South Padre South Area [SPIS] sites: Mangrove Flats [MF], Parrot Eye's Flats [PE] and the Convention Center Flats [CF], illustrating the relative locations of the habitat types associated with the study site. Numbered flags (꙳) identify the locations of color banded Piping Plovers that were observed on site during the study. Refer to Table 21 for more information on sightings of color banded plovers.

study late in the second year, and was visited much less frequently than were the other two sites in the ecotone. The large, northern flat on South Padre Island (SPIN; Figure 14) was accessible only with an ATV. Because ATV's were not always available, this site visited much less frequently than were the other two sites in the lagoon ecosystem.

Site Selection Criteria

All of the study sites monitored in this study were reasonably accessible (e.g. by car, ATV or walking) and supported large numbers of Piping Plovers and Snowy Plovers during either the IPPC, or during surveys 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]). 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 two ecosystems, and contained a combination of sand flats and algal flats.

Other Characteristics of the Study Sites.

Beaches

All sites but LANWR contained a stretch of ocean beach. The beach was continuous with the bayshore flats at some of the study sites, and disjunct at others. At Bolivar Flats, Big Reef, and San Luis Flats, the beach and bayshore were continuous, as these sites occur at the end of a peninsula or a barrier island. At the other 5 sites with beaches, the beach and bayshores were separated by coastal prairie. At 4 of these sites, the flats and beaches were connected by washover passes, narrow sandy "alleys" between the Gulf and the baywaters. Washover passes exhibit a low relief terrain with little or no vegetation and are created and periodically reopened by hurricanes and tropical storms. The washover passes at the sites in this study were rarely breached by high tides, but even when "dry" they remained relatively unvegetated throughout the study period.

Habitat Structure

The habitat structure of the study sites closely resembled the features characterizing their respective ecosystems (or the ecotone). Bay ecosystem study sites featured isolated, moderately sized (58 ha - 188 ha) bayshore sand flats. Cordgrass marshes occurred at higher areas of the intertidal zone at each of the three bay ecosystem study sites. Lagoon ecosystem study sites were characterized by large (280 ha - 812 ha) areas of bayshore flats, that were themselves only small parts of an expansive and nearly continuous bayshore flat system bordering the Lower Laguna Madre of Texas. The extreme saline environment of the lagoon ecosystem was too harsh to support cordgrass. In place of cordgrass, the lagoon flats featured an algal mat community. Near the upper limits of the intertidal zone, the algal mats gradually diminished and were replaced by a zone of sand or mud extending to the upland limits of the intertidal ecosystem.

The study sites associated with the coastal ecotone were intermediate in size (114 ha - 246 ha) and habitat composition. Both algal mats and cordgrass were present at the each of the study locations, but neither habitat was as abundant, nor appeared as vigorous, as they were in the heart of their respective ranges (data not shown).

Habitat Availability

The periodicity of local tides was quite different among the study sites. The bayshore flats of the estuarine bay ecosystem experienced regular cycles of tidal inundation and emergence. The tidal cycle varied from diurnal to semi-diurnal (from one high tide and one low tide per day, to two highs and two lows per day). In contrast, bayshore flats of the hypersaline lagoon ecosystem experienced a very irregular, wind-driven, tidal regime. Lagoon ecosystem flats were often in a state of continuous inundation or emergence for days at a time. Occasionally - following periods of drought or storm surges - the same tidal condition persisted for several weeks at a time at lagoon ecosystem sites (data not shown).

Direct Human Disturbance

Vehicular traffic was unrestricted on the majority of the tidal flats associated with the Big Reef, San Luis Flats, East Flats, Mustang Island State Park, Packery Channel, South Bay and South Padre Island sites. The hazards associated with driving on wetland soils, however, limited vehicular traffic on most of the flats. Only Big Reef and San Luis Flats were regularly negotiable by most types of vehicles, and these sites occasionally experienced high levels of direct human disturbance. Vehicles were allowed onto the forebeach area of all of the study beaches with the exception of East Beach (Figure 9). At East Beach, traffic barriers limited traffic to the upper beach area, but allowed pedestrian traffic on the forebeach.

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, San Luis Flats is probably smaller because is no longer receives some of the sediment trapped at Bolivar Flats. The flats associated with the East Flats, MISP, LANWR, and South Bay study sites have all been substantially affected by dredge spoil. Portions of Packery Channel are occasionally deepened by dredging.

South Padre Island is often described as near-pristine. Without question, the large northern flat on South Padre Island has been less affected by human manipulation than any of the other study sites monitored for this research. Unfortunately, this flat is far from pristine. Spoil dredged from Mansfield Channel erodes onto the flats during periods of strong north winds associated 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. The sand, in turn, has begun to swamp hundreds of hectares of intertidal habitat. Inflows of water from Mansfield Channel, and the nearby Harlingen Ship Channel/Arroyo Colorado, reduce the local salinity of the Laguna Madre, and, in the case of the latter drainage, conduct hazardous materials from the Rio Grande Valley agricultural industry into the lagoon.

The ideal setting for a study investigating the natural ecology of an organism is one that provides the opportunity to observe the organism in conditions unspoiled by man-made changes, to develop an accurate model of the organism's habitat requirements, and its niche in the ecosystem. Regrettably, the natural baseline no longer exists along the Texas Gulf Coast. "Near-pristine" is as good as it gets for Piping Plovers and other coastal species in Texas.

Study Period

We collected all of our 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 we 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.

Piping Plover Site Abundance

To address the primary objective we developed a regression model predicting local Piping Plover abundance based upon a combination of 6 independent variables comprised of key habitat components and environmental conditions. To support the model we monitored Piping Plover populations and the 6 independent variables at all study sites throughout the study period. Piping Plover site abundance was estimated as the sum of the mean number of Piping Plovers recorded during beach and bayshore surveys during the study. For instance, at Bolivar flats, we recorded an average of 50.2 plovers using bayshore habitat and 15.3 plovers using beach habitat, yielding an estimated site abundance of 65.5 plovers.

The independent variables for the regression model included: (1) area of suitable bayshore habitat, (2) bayshore macrobenthic prey density, (3) beach macrobenthic prey density and (4) human disturbance. Our data (see Results), and those from other studies (Shelton and Robertson 1981, Vega 1988) have established that crustaceans and polychaetes both dominate the beach macrobenthic community in the intertidal zone used by foraging Piping Plovers. Because Piping Plovers used crustaceans and polychaetes in a nonrandom fashion during our study (see Results), we partitioned the beach macrobenthic density variable into 2 variables for the regression model: beach crustacean density and beach polychaete density. Finally, as a sixth parameter of the regression model, we entered the length of beach we monitored at each study site (a constant measure) into the model to incorporate this variability into our analysis. We selected these factors as independent variables because they have all been associated with shorebird abundance or quality shorebird habitat in some situations (e.g. habitat area; Goss-Custard et al. 1994, 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 our study sites (e.g. prey abundance and human disturbance).

Piping Plover Density

In secondary objective #1, we sought to establish and compare the relative densities of Piping Plover among the dominant ecosystems and coastal habitat types along the Texas Gulf Coast. To accomplish this objective, we conducted regular censuses within both dominant habitat types (beach and bayshore habitat) at the study sites located within the bay and lagoon ecosystems. We also monitored a third group of 3 sites within the transition zone between the 2 ecosystems (i.e. the ecotone). For more information see "Piping Plover population density" in the "Variables" section.

Factors Affecting Piping Plover Density

In secondary objective #2, we sought to identify the factors affecting Piping Plover density. To accomplish this objective, we monitored an array of environmental, temporal and spatial variables at the 9 study sites during the study period. For this work, we selected variables that either had been shown to affect shorebird density (e.g. human disturbance; Staine and Burger 1994), or were considered by us to play potential roles in directing Piping Plover site density based upon our preliminary observations during the 1991 IPPC and discussions with other biologists in Texas before the study. The environmental variables we measured were (1) bayshore tidal amplitude, (2) beach tidal amplitude, (3) climatic conditions, and (4) human disturbance. The temporal variables considered in our analyses were (1) life cycle stage of Piping Plovers, and (2) time of day, and the spatial variables considered were (1) landform and (2) ecosystem.

We used Piping Plover population density (total and foraging density), and the Piping Plover foraging proportion during surveys (the proportion of the total number of Piping Plovers that were foraging) as response variables in our analyses. These variables are described in more detail in the "Variables" Section.

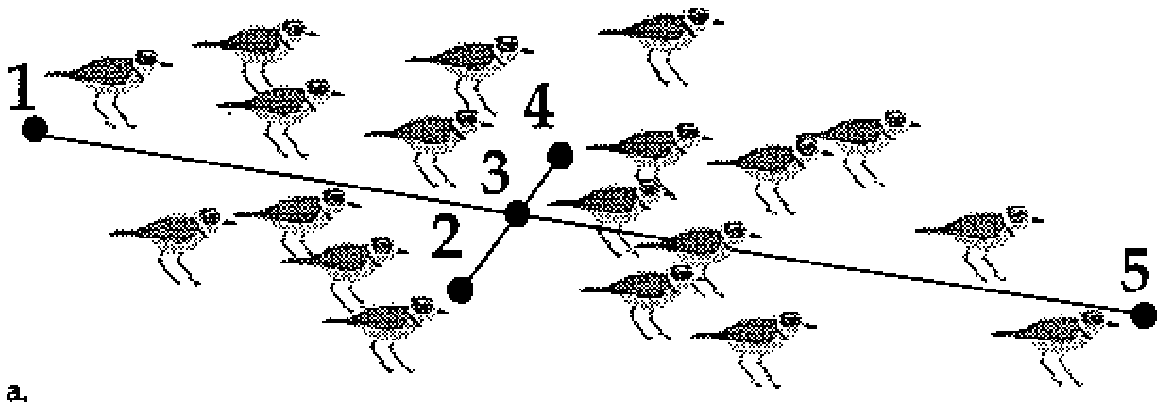
Foraging Ecology

In secondary objective #3, we sought to characterize the foraging ecology of Piping Plovers along the Texas Gulf Coast, and identify the factors affecting foraging success. One of our 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. Other goals were related to foraging success. As measures of foraging success, we observed Piping Plovers as they fed and monitored foraging locomotion, foraging efficiency and aggressive behavior. We incorporated these parameters as dependent variables into ANOVA models to investigate the relative effects of microhabitat type, habitat type, ecosystem type and Piping Plover life cycle on each measure of foraging success. Each of the variables used in these analyses are described in more detail in the "Variables" Section.

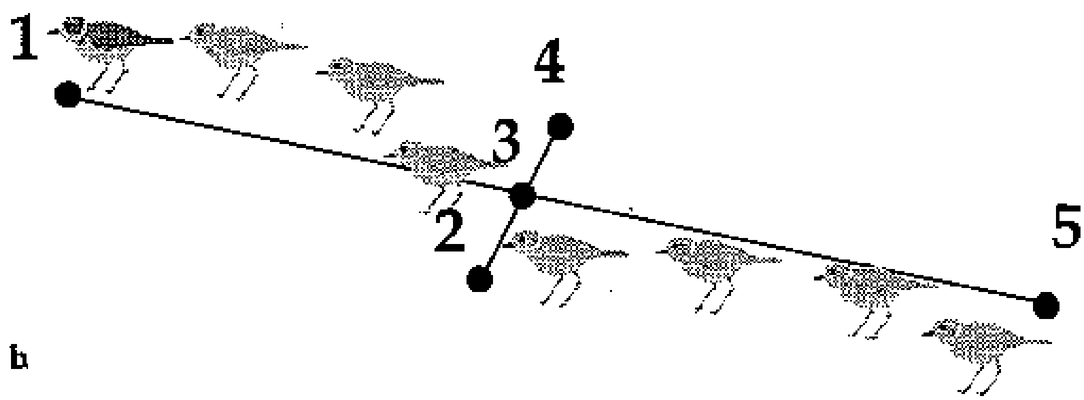
Prey Resources

To address secondary objective# 4, we sampled potential prey populations either from areas used by foraging Piping Plovers at the time of sample collection, or from microhabitats in which we consistently observed foraging Piping Plovers. Because Piping Plovers forage on prey occurring both within and above the ground (pers. obs., T. Eubanks Fermata Inc., Austin, TX pers. comm.), we employed 3 general sampling techniques to investigate prey occurring within and between both strata. Our approach sampled prey types associated with the 3 major vertical strata associated with bayshore habitat used by Piping Plovers: (1) macrobenthic prey, (2) surface prey, and (3) emergent prey from within algal mats (on algal flat habitats only). Sample strategies consisted of soil cores (density of benthic prey), sticky traps (relative abundance of surface prey), visual surveys using a spotting scope (density of surface prey), and incubated algal cores (density of emergent prey). We describe the techniques used to sample each prey type in greater detail below.

General Sampling Design - All samples were collected along X - shaped transects described in detail in Figure 15. Whereas most prey samples were collected in areas where we observed foraging Piping Plovers, to address objective #3c, we also collected



a.



b.

Figure 15. The transect design used to collect prey sampling units within an area used by a foraging flock of Piping Plovers is illustrated in (a). Plovers are represented as shaded figures. The sample locations are represented by filled circles, labelled 1 - 5. We 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.

The transect design used to collect prey sampling units within an area used by a single foraging Piping Plover is illustrated in (b). A single Piping Plover is represented by a darkly shaded figure on the extreme left. To its right, are several lightly shaded figures representing the general path of the plover immediately prior to sample collection (usually observed during a foraging efficiency record). The sample locations are depicted by filled circles, labelled 1 - 5. We collected sample 3 from the center of the area covered by the plover during the foraging efficiency record. 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.

For "unused beach samples", samples were collected along a transect that was randomly located within the boundary between the swash zone and the moist upper zone. The transect dimensions resembled those used in association with foraging Piping Plovers, but had a short axis of about six meters and a long axis of about 20 meters which was judged to be the approximate average area used by Piping Plovers in this habitat (pers. obs.).

random samples in beach habitat to support analyses comparing the prey population densities in areas used by foraging Piping Plovers with those in areas not used by Piping Plovers. Because Piping Plovers nearly always fed in the narrow intertidal zone on beaches, cores collected randomly from this zone in areas unoccupied by Piping Plovers could reasonably be regarded as samples from unused portions of suitable foraging habitat. However, potential bayshore foraging habitat was much more difficult to classify, varying in many characteristics, particularly saturation and distance from the shoreline (pers. obs.). For this reason, we were unable to compare used vs. unused bayshore habitat because it was not possible to collect meaningful random samples of unused bayshore habitat.

Beach Samples - Approximately half of the beach prey samples we collected were from areas recently used by one or more foraging Piping Plovers (henceforth referred to as "used beach samples"). The other half of the sample were collected from beaches in predetermined areas of the intertidal zone regardless of whether foraging Piping Plovers were present. These samples were collected at the upper limits of the swash zone from transects located randomly along the study beaches in the bay ecosystem and the ecotone. The locations of each transect was determined each morning by rolling dice to select a mileage position along the beach that was located using an odometer. In the lagoon ecosystem, daily beach samples were -by necessity - collected in a non-random fashion. ATV's were often used on lagoon beaches. Because these vehicles had no odometer, randomly selected positions along the beach could not be located on a day to day basis. Instead, recognizable landforms (e.g. dune formations, washover passes) were used as references to direct the researcher to locations where samples were collected. Thus, in the lagoon ecosystem, beach prey samples were collected in roughly the same locations each visit. As a result, daily beach prey estimates for the lagoon ecosystem beaches may reflect locational biases, and are more likely to be autocorrelated. However, because sample locations were not precisely positioned each visit, samples collected throughout the study at any particular location may have been separated by several hundred meters. This variation probably reduces the biases discussed above.

The daily beach samples were grouped differently, depending upon whether a foraging plover was present with a foraging territory that appeared to overlap the transect location. If a foraging Piping Plover was present, the sample was grouped with the other beach samples collected in association with foraging Piping Plovers as "used beach samples". If a foraging Piping Plover was not present, the sample was grouped separately as "unused beach samples". Unused beach samples were compared to used beach samples to determine whether plovers foraged in areas of beach with higher prey density.

Bayshore Sample Locations - All of the bayshore prey samples were collected in areas that were being used by one or more foraging Piping Plovers, or had recently (within minutes) been used.

Foraging flocks were sampled in order of size, beginning with the largest flock. The number of samples we collected was limited only by the number of foraging flocks of Piping Plovers observed after the site-wide survey, 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 we were capable of carrying. An average of approximately 5 transects were sampled per site visit (data not shown). Samples were usually collected immediately after the foraging efficiency records. These samples, therefore, 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 through the study site.

Macrobenthic Prey

Macroscopic subsurface (i.e. macrobenthic) animals were sampled via series of 5 soil cores/transect. Each core was 10 cm deep x 7.5 cm in diameter. After retrieval, cores were placed in plastic bags and sieved (600 um) and scored later the same day or early the next morning. Each prey item was classified into one of six prey groups (worm, amphipod, crab, bivalve, insect, other). Several of these groups were subdivided into size class or developmental stages to yield a total of 13 benthic prey categories (listed in Appendix). Macrobenthic prey were investigated in this way on both beach and bayshore habitat. Three other sampling techniques were used on bayshore habitat to account for the above-ground fauna from which Piping Plovers were observed to feed. Whereas Piping Plovers occasionally feed on surface animals on beaches, the large majority of their diet in this habitat is benthic. Furthermore, because Piping Plovers feed primarily within or near the swash zone on beaches, the deployment of sticky traps to capture surface prey would not have been feasible.

Surface Prey

During the 1991 IPPC, we 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 motile, and would not be accurately represented in core samples, we employed 2 additional techniques to obtain systematic samples of this portion of the prey community.

Sticky Traps - Five square flooring tile pieces (each ~2mm x 15 cm x 15 cm) were placed directly on the ground along the same transect used to sample macrobenthic prey. 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 Special" (Seabrite Enterprises, Emeryville, CA 94608) filling a 12.5 cm diameter circle. The tiles 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 into 1 of 5 groups (see Appendix). Because 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 Surveys - A second technique was implemented during the final year of the study to collect instant counts of the above-ground fauna and allow for 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 m^2 patch of ground that was surveyed (without moving the scope) for surface animals (Figure 16). All animals observed during the survey were scored into the same classes as those captured with the sticky tiles (see Appendix). Animals walking or flying into the field of view during the survey were not counted. In this way, standard visual tallies of surface fauna were collected along each

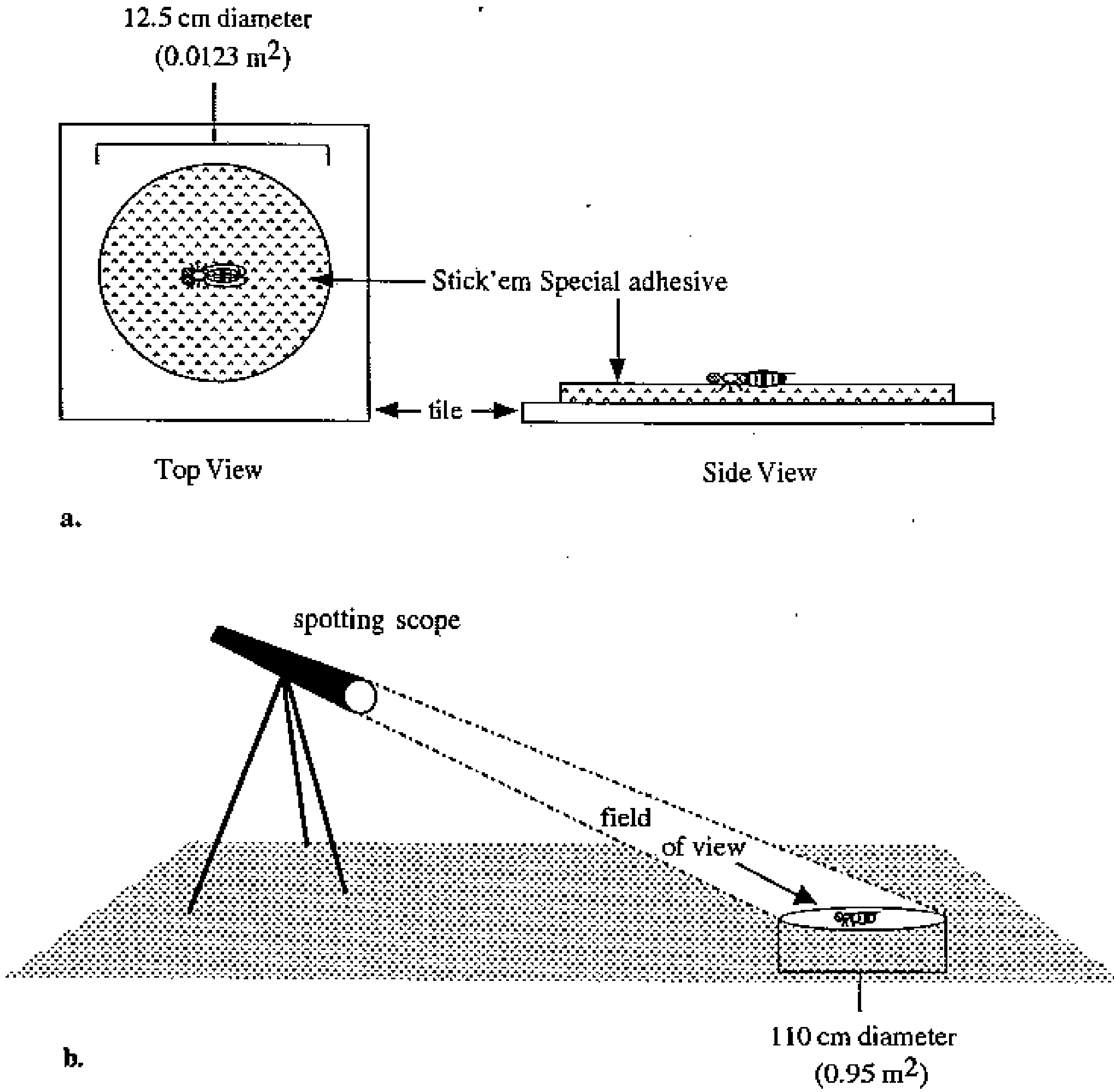


Figure 16. Schematic diagrams illustrating the methods used to sample surface animal populations are presented in this figure. An indirect sampling method using sticky trap (a), was used to estimate relative differences in the surface animal populations. The sticky traps were composed of 10 cm X 10 cm black/grey mottled linoleum tiles coated with a layer (~1mm thick) of Stick'em special adhesive (see Methods). The sticky traps were deployed along transects associated with foraging Piping Plovers, left for one hour, covered with a petri dish, and collected for scoring later in the laboratory. The sticky trap data do not allow for an estimation of surface prey density. To estimate the surface prey density, we conducted spotting scope surveys of surface prey at the 5 sample points along the same transects used to collect macrobenthic cores (b; see Figure 15 for transect information). For these surveys, spotting scopes were used to survey randomly selected areas the ground for surface animals (b).

transect.

Emergent prey from within algal mats

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). 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 into the same classes as the animal captured with "sticky tiles" (see Appendix).

Piping Plover Movement Pattern

In secondary objective #5, we sought to characterize the movement patterns of Piping Plovers, specifically addressing annual and seasonal site fidelity, and winter home range size. To address this objective, we mapped the locations of all color-banded Piping Plovers sighted during the study. Although we did not color-band any Piping Plovers during the study, we observed several birds that had been color-banded by other researchers (M. Ryan, pers. comm, T. Eubanks, pers. comm.). Multiple sightings of birds with very similar or identical band combinations were compared to establish possible movement patterns of Piping Plovers during the study (within and between study years).

Variables

In many analyses, habitat components, environmental variables, spatial variables and temporal variables were incorporated into multi-factor analysis of variance (ANOVA) models as ranked independent parameters to investigate their relative influences on the response variables (see "Data Analysis"). In some cases several parameters were combined to define a single independent effect variable. For example, the effect defined as "climatic conditions", was derived by combining the data from the air temperature, wind speed and precipitation variables into a single index. The intent behind each parameter definition and ranking strategy was to simplify the statistical models as much as possible. This allowed for the analysis of larger data sets, and focused analyses on broader, more practical parameters (e.g. harsh weather vs. mild weather, or migration period vs. winter period) than would be possible with narrowly defined effects (e.g. 20°C vs. 25°C, or September vs. October). Explanations of the data ranks for each environmental variable follow, accompanied by the rationale supporting our rank assignments.

Area of suitable bayshore habitat

During each site visit, we estimated the total area of bayshore habitat that was both available and suitable as foraging habitat to Piping Plovers. We defined suitable foraging habitat as that which was 1) composed of unvegetated or sparsely-vegetated habitat, and 2) subject to tidal inundation (citations, pers. obs.) Whereas densely-vegetated areas and supratidal areas may be regularly used by foraging Piping Plovers under some conditions (e.g. at night or in different parts of the winter range), we very rarely observed Piping Plovers foraging in these microhabitats at our sites, and therefore determined that their inclusion in measures of foraging habitat area would be inappropriate.

The total potential area of suitable bayshore habitat at each site (TPA) was estimated by digitizing the boundaries of all areas that might be both submerged and exposed by tides from U.S. Geological Survey Topographic Quadrangle Maps into the Atlas Geographic Information System (Strategic Mapping Inc., Santa Clara, California). Aerial infrared photographs were referred to as guides to improve the accuracy of the approximated positions of the lowest and highest possible tide lines. 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. The TPA was used as a baseline upon which we estimated the area of available suitable habitat, by multiplying the TPA and the estimated % of tidal inundation experienced by the site (see "bayshore tidal amplitude" in the Environmental Variables Chapter). For instance, Bolivar Flats was estimated to have a TPA of 188 ha. During visits to Bolivar Flats when the tide was estimated to be high (75% inundation), a total of 47 ha of suitable habitat was estimated to be available to Piping Plovers.

Habitats and Microhabitats

We classified foraging habitats at our sites as either beach habitat or bayshore habitat. We 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. Whereas the transition area in such cases is probably not truly abrupt, but rather a blend of the habitat components and environmental variables of each habitat, the transition areas were rarely used by Piping Plovers, and thus were not characterized in more detail.

Data were collected in beach and bayshore habitats at different times. All daily data records were collected in one habitat before moving to the other habitat. The order of habitat visitation was varied (although not randomly) to ensure each habitat was visited during different times of the day throughout the study.

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

We recognized 6 microhabitats on bayshore flats. One subdivision of flat habitat was governed upon the presence or absence of an algal mat overlying the substrate. Flats with an algal mat were classified as algal flats, and those without an algal mat were classified as sand flats. Each flat type was further classified as either dry, moist or saturated, yielding a total of 6 classifications.

Bayshore tidal amplitude

During each site visit, we estimated the level of bayshore tidal inundation as very low, low, moderate, high or very high. These tide ranks corresponded to visual estimates of tidal inundation of approximately 0%, 25%, 50%, 75% and 100% tidal inundation, respectively, or approximately 100%, 75% 50%, 25% and 0% emergence, respectively, of the total potential area of habitat suitable to foraging Piping Plovers. During very low tides (i.e.~ 0% inundation) the tidal flats were judged to be emergent to the maximum extent observed during the study period. These conditions usually were associated with seasonal low tide periods, or "spring tide" effects. During very high tides, the flats were completely submerged, and only upland (i.e. non tidally-influenced) habitat remained emergent. These conditions usually were associated with storm tides during the summer-fall hurricane season or strong north fronts during the winter period. Visual estimates were selected over tide gauges because the substrate associated with most of the bayshore habitat was often unstable, preventing the use of permanently located tide gauges on the 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 (e.g. those maintained by the Conrad Blucher Institute, based in Corpus Christi, Texas) these gauges measure the tidal amplitude in areas that are often far removed from the tidal flats. Because the tidal inundation of bayshore flats is controlled by both bay tide levels and wind conditions, the same bay tide level may result in a high tide (i.e. only ~ 25% tidal flat emergence) during one set of wind conditions, and a low tide (i.e. ~ 75% tidal flat emergence) during another set of wind conditions. For these reasons, we considered visual estimation to be the best method for accurately documenting site-localized bayshore tidal conditions. During data analyses, bayshore tidal conditions were characterized as emergent or inundated. Bayshore conditions were considered emergent if the tide was either very low, low or moderate (i.e. if the % inundation was estimated to be < 75%). If the tide was estimated to be high or very high (i.e. ≥ 75% inundation) the bayshore tidal conditions were ranked as inundated.

Beach tidal amplitude

We measured beach widths at 3 sites (Bolivar Flats, Mustang Island State Park North Beach, and Packery Channel). Beaches at these 3 sites each had at least one stable beach landmark to serve as a reference for beach width measures throughout large portions of the study. However, even these landmarks (traffic signs, posts holding trash containers) were removed or became shifted during the study by storm events or other causes. As a result, the data sets for beach tidal conditions are small. For this study we defined beach width as the distance between the swash boundary and the vegetation line on the upper beach. The distance between the upper swash zone boundary and the vegetation line in front of the foredunes was measured and recorded during surveys on the 3 beaches. Beach tidal conditions were ranked as either emergent or inundated. The beach tidal condition during a site visit was scored as emergent if the beach width for that day was ≥ 25% of the largest beach width recorded for that site during the study. For example, the widest beach recorded at the San Luis Beach site was 55 m. Therefore, all surveys conducted during conditions when the distance between the swash boundary and the vegetation line (i.e. beach width) was < 13.75 m (25% of 55 m) were recorded as having occurred during inundated beach tidal conditions. Conditions were scored as emergent at this site when the beach width was ≥ 13.75 m.

Climatic conditions

During each site visit, we 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).

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 experiences 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 (data not shown).

Rather than attempt to analyze the effects of individual climatic variables on Piping Plovers, our 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). During each Piping Plover survey, we recorded the wind direction and estimated wind in ranks associated with conditions of calm (0 knots), light winds (1-4 knots), moderate winds (5-20 knots) and strong winds (>20 knots). We estimated the air temperature during the each survey period into ranks with 5°C increments (i.e. 0-4°C, 5-9°C, 10-14°C, 15-19°C, 20-24°C, etc). The average diurnal temperature during winter north fronts along the Texas coast during our study was the rank corresponding to the interval of 10-14°C (data not shown). The average diurnal wind speed during winter north fronts along the Texas coast during our study was the rank corresponding to the interval of 5 - 20 knots (i.e. moderate wind speeds; data not shown). Rain was frequently associated with winter fronts at our sites (pers. obs). We used these average conditions as guides to rank climatic data. Our ranks are based upon the presumption that the average conditions occurring during winter north fronts represent the conditions typically occurring during the periods when Piping Plovers experience the greatest climatological stress.

Climatic conditions were considered harsh if the air temperature was equal to or less than the average associated with north fronts (10-14°C), and if the wind speed was also equal to or greater than the average associated with north fronts (5 - 20 knots). Climatic conditions were also considered harsh if it was extremely cold (0 - 4°C), regardless of the wind speed or precipitation, because plovers and other visually foraging shorebirds have been observed to feed more slowly during cold periods possibly due to reduced prey activity (Goss-Custard 1970, Pienkowski 1981). Furthermore, climatic conditions were considered harsh if it was raining, regardless of the air temperature or wind speed, because plovers and other visually foraging shorebirds appear to feed more slowly during rainfall (Goss-Custard 1970, Pienkowski 1981). Between 5 - 14°C, the wind speed-temperature combination determined our 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.

We used vehicular density as a ranked measure of human disturbance. During each site visit, we recorded the number of vehicles occurring in each habitat type and calculated the vehicular density on beaches (# vehicles/km beach) and bayshore flats (# vehicles/ha flat). Ranks of human disturbance were established by comparing the vehicular density during a site visit to the average mean vehicular density (AMVD) among all sites (calculated by computing the mean vehicle density experienced by each site, and then averaging these means). Two analyses were performed, each using a different vehicle density ranking. In one analysis, the AMVD was used as a reference measure, and human disturbance (vehicular density) was ranked as either heavy or light, depending upon whether it was above or below, respectively, this reference. Therefore, we considered a survey to have been conducted during high human disturbance only if the vehicle density was greater than the AMVD.

In a second analysis, the reference measure used for ranking data was twice the AMVD. Therefore, for this analysis, we considered a survey to have been conducted during high human disturbance only if the vehicle density was at least twice that of the AMVD. This second analysis was performed as a measure of the response of Piping Plovers to very high levels of human disturbance.

Life Cycle Stage

We classified seasons according to the two major stages of the annual life cycle of Piping Plover occurring in Texas; migration and wintering (Piping Plovers do not breed in Texas). The winter period was defined as November 1st - February 20th, and the migratory period was defined as July 1 - October 30, and February 21 - May 15. These periods closely reflect the boundaries of the migratory and winter periods reported by others (Eubanks 1994, Haig 1992, Haig et al. 1988).

Time Of Day

We classified surveys as either AM or PM, depending upon whether they were conducted before or after noon, respectively. The ranked time of day variable was incorporated into multi-factor ANOVA along with the ranked variable measuring bayshore tidal conditions, to determine which of these variables most strongly influenced Piping Plover density on beach and bayshore habitats.

Site

The study sites contributing data to an ANOVA were built into the model as a nested parameter (nested within the ecosystem in which they occur) to assess the contribution of intra-ecosystem variability to the variability of the response parameter (e.g. Piping Plover bayshore density). The study sites are described above in the "Study Area" section.

Landform

When both types of landforms (mainland and barrier) contributed data to an ANOVA we built this locational component into the model as a parameter to assess the contribution of landscape variability to the variability of the response parameter (e.g. Piping Plover bayshore density). The study sites are described above in the "Study Area" section.

Ecosystem

The ecosystems contributing data to an ANOVA were built into the model as a parameter to assess the contribution of ecosystem variability to the variability of the response parameter (e.g. Piping Plover bayshore density). The study sites are described above in the "Study Area" section.

Piping Plover population density

To support the investigation of objectives 1a, 1b, 1c, 2a, 2b, 2c, and 4 we censused Piping Plover populations during all site visits. Because we monitored beach and bayshore habitats separately, distinct censuses were conducted and maintained for each habitat. In general, we conducted only 1 survey/habitat on each site visit, however when tide levels changed dramatically during a site visit, we occasionally conducted more than one survey to assess habitat use under the different tidal conditions. All surveys were site-wide, regardless of the habitat or tidal conditions. We selected study sites that were of a size that would allow for complete coverage each visit.

For density estimates, the census total was divided by the estimated emergent tidal flat area during the census (see "Area of suitable bayshore habitat" in Habitat Components chapter of this section) to estimate bayshore total Piping Plover density. Total beach Piping Plover densities were estimated by dividing the beach census tallies by the length of beach occurring at each site.

We recorded exact tallies for Piping Plovers and other congeners [(Snowy Plover (*C. alexandrinus*), Semipalmated Plover (*C. semipalmatus*) Wilson's Plover (*C. wilsonia*) and Killdeer (*C. vociferus*)]. Other shorebird species were also counted, but their abundances were estimated, and are presented as estimates of the combined non-*Charadrius* shorebird community.

Piping Plover foraging behavior

We scored each Piping Plover observed during the site-wide censuses as either "foraging" or "not-foraging". Birds scored as "foraging" were those that were either actively feeding, or that were within habitat used by other foraging Piping Plover during the same census and were not preening or resting (i.e. appeared to be momentarily pausing between foraging attempts). Birds scored as "not-foraging", therefore, were birds that were either resting or preening during the census.

Piping Plover diet

During some of the foraging efficiency records, the prey types captured by the Piping Plover subjects were scored into major prey groups. On beaches, prey were scored into the 3 groups: 1) polychaete, 2) crustaceans or 3) unknown. The polychaete group included all worm-like animals captured by plovers, but were primarily the polychaete *Scolelepis squamata*. Polychaetes were usually very easily distinguished during capture, as Piping Plovers often pull them out of the sand slowly to avoid breaking the worm. The crustacean prey group included amphipods, and other crustaceans (e.g. mole crabs), insects (larvae, pupae, and adults), and any other, non-worm-like animals. That vast majority of captures scored into the amphipod group, however, were Haustorid amphipods.

On bayshore habitat, prey were scored into the 3 groups: 1) polychaete, 2) surface prey or 3) unknown. The polychaete group included all worm-like animals captured by plovers. The surface prey group was very broad, including tanaids and all other types of crustaceans, insects (larvae, pupae, and adults), and any other, non-worm-like animals.

We only evaluated diets for those Piping Plover subjects that were very close to the observer during the foraging efficiency record. The diet samples were further restricted to foraging efficiency records that were collected under lighting conditions that allowed prey types to be easily observed and distinguished.

Piping Plover foraging locomotion

We observed Piping Plovers to use 2 general styles of foraging motion during this study: 1) short, slow approaches toward prey animals located within 1-2 body lengths of the bird, or 2) prolonged, often rapid movement to an area several body lengths beyond the initial location. Because plovers presumably expend more energy during the prolonged foraging movement style, we propose that this may be an important parameter to consider when appraising their net energy intake during foraging periods.

To document foraging locomotion, we watched foraging Piping Plovers for a period of 120 seconds per bird and recorded the amount of time each bird spent in prolonged locomotion. We considered prolonged locomotion to be movements beyond two plover body lengths (~6 - 8 plover paces), and we timed the duration of all such movements using a stopwatch. For these records, we selected subjects by scanning a foraging flock from left to right, monitoring each Piping Plover for the 120 second period before moving on to the next. A maximum of 10 records/habitat was set for each site visit to avoid biasing the data set by records from a few visits.

During the 120 second period, we also recorded the number of times the plover took flight, the number of aggressive interactions involving the plover, and the number of noticeable human disturbances (e.g. passing vehicles, beachcombers walking by, airplane fly-overs).

Piping Plover foraging efficiency

To appraise foraging efficiency, we observed foraging Piping Plovers at close range with a high-resolution spotting scope. During foraging efficiency records, a single 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 the number of animals captured, the number of pecks (if < 50), the time of record, an estimate of the proportion of each prey type captured (e.g. worms, amphipod, etc. - when prey types were clearly identifiable), the species of nearest shorebird neighbor and the number of aggressive interactions involving the plover during the record. As many records were collected as were possible, up to a maximum of 10 per site visit.

In order to score captures with accuracy, it was usually necessary to approach birds to within about 50 m. Rather than attempting to sequentially approach each bird present, we sampled plovers by moving in increments of ~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. After all of the plovers within viewing range were monitored at one position, we moved (~100 m) to the next position and waited 15 - 30 seconds to allow the birds to become accustomed to our presence before we resumed data collection.

Piping Plover foraging aggressive behavior

We recorded all acts of aggression involving Piping Plovers (i.e. between two Piping Plovers or between a Piping Plover and another species) 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.

Multi-factor ANOVA

Many of the conclusions we present in this report were supported by multi-factor analysis of variance (ANOVA) models built to investigate the relative influences of measured habitat components, environmental variables, temporal variables and spatial variables on the response variables described above. To build models incorporating all of the important parameters together some of the sites with smaller data sets were omitted from some of the models. For instance, the model investigating the effects of tidal conditions, life cycle stage, climatic conditions, ecosystem type and site on Piping Plover bayshore densities must contain survey data collected at a site during each of the following eight 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 case, all 8 condition sets did not occur at all of our sites during the study. Thus analysis was performed on data collected at a smaller group of sites (4 sites, in this example) that each experienced all of the condition sets during our cumulative visits to the site. In the Results Section, we reference tables that inform the reader about the number of sites incorporated into each analysis as well as about the proportion of the total data collected for the response variable that was used in each analysis.

Regression Analysis

In some cases, the relationship between two variables was investigated using linear regression (e.g. the relationship between Piping Plover beach density and beach vehicular density). Multiple regression analysis was used to generate a model predicting Piping Plovers site abundance based upon mean values of several key habitat components and environmental variables.

RESULTS

Piping Plover Site Abundance

Our primary research objective was to identify the habitat components and environmental conditions necessary to support large numbers of Piping Plovers along the Texas Gulf Coast. To accomplish this objective, we developed 2 regression models predicting the abundance of Piping Plovers (the dependent variable of the model) at our 9 study sites. One regression model was supported by the independent variables (1) area of suitable bayshore habitat, (2) beach length (3) bayshore macrobenthic prey density, (4) beach crustacean density, (5) beach polychaete density and (6) human disturbance. We present this model as the most accurate predictor of Piping Plover abundance based upon our sample data. A second model was supported by only those variables that were selected by step-wise regression analysis. We present the second model as a predictor of the relative influence of each independent variable on Piping Plover abundance. Average measures for each variable were obtained from multiple visits to our 9 study sites over 3 successive years. For both models, the response variable (Piping Plover abundance) was square root transformed.

The average recorded values for each of the parameters is presented in Table 2. The regression analysis using means from all of the variables predicted Piping Plover abundance at our study sites very accurately, explaining over 99% of the variability among these locations ($R^2 = 0.9986$; Table 2; Figure 17). Beach length, bayshore area, bayshore benthic density, and beach crustacean density were all positively associated with Piping Plover abundance, whereas beach vehicular density and beach polychaete density were negatively associated with plover abundance. Using this model, several of the independent variables appear to have contributed significantly to the abundance of Piping Plovers at our study sites (Table 2; Figure 17). Beach length ($p = 0.0011$), beach crustacean density ($p = 0.0281$), and beach vehicular density ($p = 0.0058$), each were identified as variables that significantly affected Piping Plover local abundance. Bayshore macrobenthic density may have be another factor influencing Piping Plover abundance ($p = 0.0560$), although our data suggest that the effect of this parameter may not be as significant as the 3 beach variables mentioned above. The area of suitable bayshore habitat did not appear to be limiting the abundance of Piping Plovers at our study sites ($p = 0.5323$).

The model selected by backward stepwise regression identified 5 parameters as significantly affecting Piping Plover abundance (Table 3; Figure 18). Using these 5 variables, the model still predicts over 99% of the variability in Piping Plover abundance associated with our sample data. This model suggests that beach length, bayshore benthic density, beach polychaete density, beach crustacean density, and beach vehicular density all significantly influence Piping Plover abundance. Beach length bayshore benthic density, and beach crustacean density were each positively associated with Piping Plover density, whereas beach vehicular density and beach polychaete were negatively associated with Piping Plover abundance.

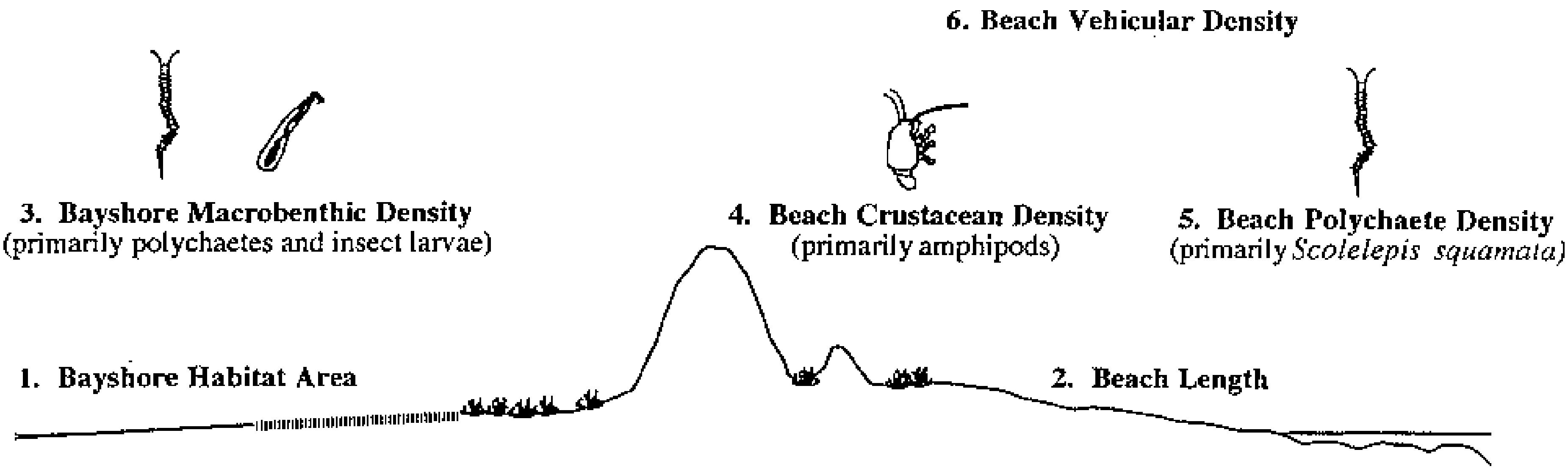
We used Mallow's Cp statistic as our model selection criterion. Theory suggests that the most appropriate model for evaluating the effects of independent variables is that in which the Cp statistic most closely approximates the number of variables in the model (Ott 1993). This method identified the 5 parameter model (i.e. 6 variables including the intercept) as having the most appropriate number of variables ($Cp = 5.4953$). Removing the beach polychaete density and bayshore benthic density variables using backward stepwise regression raises the Cp statistic to 9.1604 for 5 variables and 16.204 for 4 variables, respectively. Before including the variables into the regression analyses, we tested the independent variables for multicollinearity and found them to be uncorrelated (data not shown).

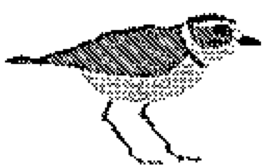
Piping Plover Density

In secondary objective #1, we focused on establishing and comparing the relative densities of Piping Plovers among the dominant landforms and ecosystems occurring along the Texas Gulf Coast. To accomplish this objective, we conducted regular censuses within both dominant habitat types (beach and bayshore habitat) at triads of study sites located within the 2 dominant coastal ecosystems (the bay and lagoon ecosystem). We also monitored a third group of 3 sites within the transition zone

Table 2. 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	Beach Variables				Bayshore Variables		Piping Plover Abundance
	beach length	polychaete density	crustacean density	vehicular density	bayshore area	macrobenthic density	
Bolivar Flats	4.8	1578	1711	1.33	102	6009	65.5
Big Reef	4.4	3384	491	2.73	29	7174	21.5
San Luis Pass	6.3	2140	1291	2.22	42	3449	35.7
East Flats	2.8	678	1608	0	136	1953	59.2
MISPN	3.2	920	881	2.07	33	970	17.7
Packery Channel	3.9	732	1304	2.15	107	1357	28.7
Rincon Buena Vista	0	0	0	0	95	260	17.4
North Yucca Flats	0	0	0	0	50	40	17.1
South Bay East Area	7.6	693	598	2.33	270	389	41.7
South Padre Island North Area	25.1	783	839	1.58	508	846	367.6





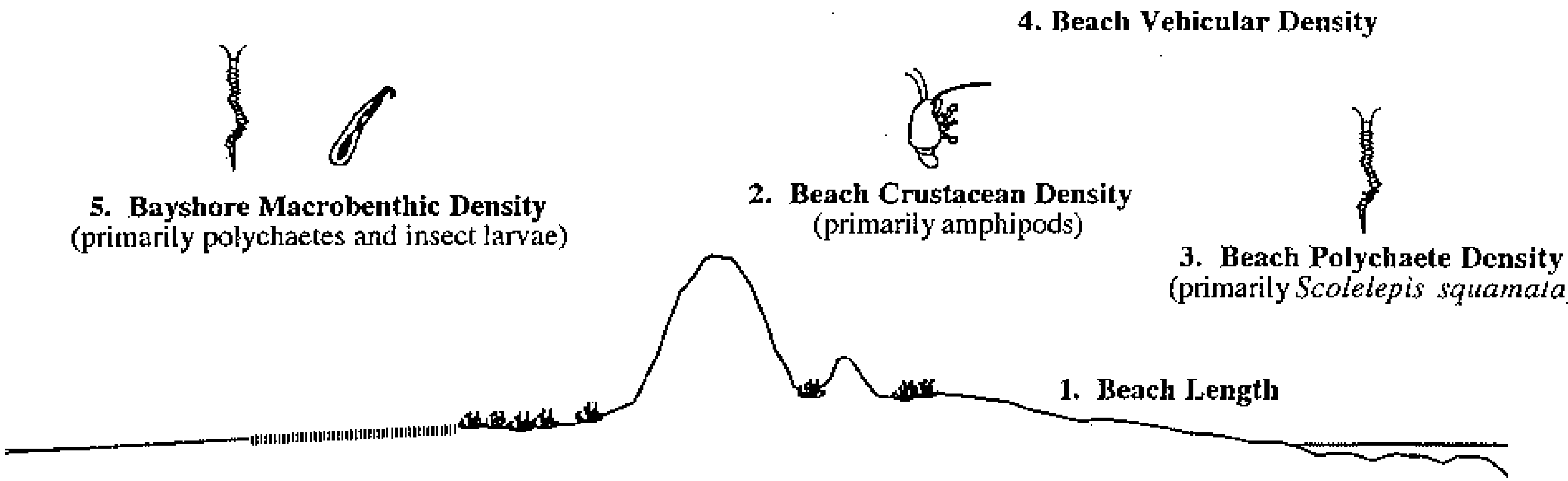
$\sqrt{\text{Piping Plover Population Size}}$ = 4.0156072 [Intercept]

+ 0.0016906 x the average area of emergent **bayshore habitat** [ha]
+ 0.6228970 x the **length of beach** [km]
+ 0.0003896 x the average density of **bayshore macrobenthos** [#/m^2]
- 0.0006880 x the average density of **polychaetes in intertidal beach habitat** [#/m^2]
+ 0.0007901 x the average density of **crustaceans in intertidal beach habitat** [#/m^2]
- 1.1718370 x the average density of **vehicles using the beach** [#/km]

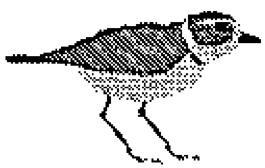
Figure 17. This figure describes the six variable multiple regression model. This model is the most accurate indicator of the average number of Piping Plovers that might be expected to use a particular area based upon our sample data. To use the model, 6 parameters must be estimated and incorporated into the regressional equation: 1) bayshore habitat area, 2) beach length, 3) bayshore macrobenthic density, 4) beach crustacean density, 5) beach polychaete density, and 6) beach vehicular density. Ideally, the benthic densities should be estimated from samples collected using methodology similar that used in this study (e.g. samples collected in areas used by foraging Piping Plovers, 10 cm deep cores, etc.). Note that the model uses a square root tranformation of Piping Plover population size. Thus the estimate from the model must be squared to predict the population size. Note also that beach polychaete density and beach vehicular density have negative effects on Piping Plover abundance. This model explains 99.6% of the variability among the mean Piping Plover populations at our study sites.

Table 3. The multiple regression evaluation of the independent variables using standard, and backward stepwise multiple regression analyses are presented in this table.

Independent Variables	coefficient	p-value	significance
6 variable model			
y- intercept	4.0156072	0.0008	***
Beach Variables:			
Beach Length	0.6228970	0.5323	--
Crustacean Density	0.0007901	0.0281	**
Polychaete Density	- 0.000688	0.1857	--
Vehicular Density	- 1.1718370	0.0058	***
Bayshore Variables:			
Bayshore Area	0.0016906	0.5323	--
Macrobenthic Density	0.0003896	0.0560	*
5-variable stepwise model			
y-intercept	4.15764066	--	--
Beach Variables:			
Beach Length	0.65605393	< 0.0001	***
Crustacean Density	0.00076274	0.0136	**
Polychaete Density	- 0.0008296	0.0636	*
Vehicular Density	- 1.1585523	0.0017	***
Bayshore Variables:			
Macrobenthic Density	0.00041460	0.0228	**



$$\sqrt{\textbf{Piping Plover Population Size}} = 4.15764066 \quad \text{[Intercept]}$$



+ 0.65605393 x the **length** of **beach** [km]
+ 0.00076274 x the average density of **crustaceans** in intertidal **beach habitat** [#/m²]
- 0.0008296 x the average density of **polychaetes** in intertidal **beach habitat** [#/m²]
- 1.1585523 x the average density of **vehicles** on the **beach** [#/km]
+ 0.00041460 x the average density of **macrobenthos** in intertidal **bayshore habitat** [#/m²]

Figure 18. This figure describes the 5-variable multiple regression model selected using backwards stepwise multiple regression. This model was used as a statistical tool to appraise the relative influences of each of the habitat and environmental variables entered into the 6-variable multiple regression model. The 5 parameters remaining in the model after backward stepwise regression (with an exit probability of $p < 0.10$) are: 1) beach length, 2) beach crustacean density, 3) beach polychaete density, 4) beach vehicular density, and 5) bayshore macrobenthic density. Note that beach polychaete density and beach vehicular density have negative effects on Piping Plover abundance. This model explains 99.6 % of the variability among the mean Piping Plover populations at our study sites.

between the 2 ecosystems (the ecotone). Densities were compared using multi-factor ANOVAs, incorporating several independent variables. At a minimum, all ANOVAs contained as independent variables the 1) ecosystem type, 2) habitat type, 3) life cycle stage, 4) bayshore tidal conditions and 5) study site. Therefore, the effects of these variables on Piping Plover densities have been incorporated into the analyses used to evaluate the effects of ecosystem type and habitat type on Piping Plover density. As a result, the relationships that have been selected as significant by these analyses should be interpreted with greater confidence than those derived from one-way ANOVAs. Whereas this section describes only the effects of ecosystem type and habitat type on Piping Plover density, the effects of other variables are described in the section entitled "Factors Affecting Piping Plover Density".

To determine whether Piping Plovers use mainland and barrier formations equally, we compared the survey results from mainland sites to barrier islands sites (see Methods). During the surveys, we distinguished between foraging and non-foraging Piping Plovers (see Methods). In this section, we have presented the survey results in the form of comparisons of total Piping Plover density, foraging Piping Plover density, and as the proportion of total Piping Plovers that were foraging during the surveys (foraging proportion). We present the results for beach habitat first, followed by the results for bayshore habitat.

Beach Habitat

General - Piping Plover beach density varied from 0.37 birds/km at Big Reef to 5.31 birds/km at the Mustang Island State Park South Area site (Table 4). Total Piping Plover densities exceeded 3 birds/km at only 1 site each within the bay and lagoon ecosystem, but at all sites within the ecotone (Figure 19). Foraging Piping Plover densities exceeded 1.5 birds/km at 3 of the 4 ecotone sites but were under 1.5 birds/km at all bay and lagoon ecosystem site beaches (Figure 20).

The largest population of Piping Plovers we observed during a single beach survey was 254 birds recorded on 10 February 1993 at Brazos Island (all birds roosting in a washover pass, Table 4; Figure 13). It is interesting to note that the site with the second largest single-survey population was the South Padre Island site (171 plovers observed while rooting in a washover pass on 4 February 1993; Table 4; Figure 14). However, throughout our 3 -year study, the average density of Piping Plovers on beach habitat at the South Padre Island site was the second lowest we recorded among our 9 sites, averaging only about 0.49 plovers/km, or about 12 plovers/survey along all 25.1 km of beach (Table 4). In contrast, we counted a high of only 55 Piping Plovers during the study at the Mustang Island State Park South Area beach (Table 4; Figure 10), yet this site had a much higher average density throughout the study, averaging 5.31 birds/km, or about 14 plovers survey along a stretch of beach that was nearly 10 times shorter (2.6 km) than that at the South Padre Island site (Table 4). Our data suggest, therefore, that some locations may support very high relative densities of Piping Plovers even though they rarely or never support very large populations. In general, Piping Plover beach densities (total and foraging) were highest within the ecotone (Figure 21).

Total Density - Our data suggest that Piping Plover total beach densities do not differ significantly along the Texas Coast. We detected no difference in the total beach density of Piping Plovers among separate pairwise comparisons between the 2 ecosystems ($p = 0.8942$; Table 5), or between the ecotone and the bay ecosystem ($p = 0.9256$; Table 5) or the ecotone and the lagoon ecosystem ($p = 0.1793$; Table 5).

Table 4. The mean abundances, maximum study tallies, and mean densities for Piping Plovers are presented for each of the study beaches are presented in this table. The length of beach (BL) monitored at each site is presented in kilometers. The density estimates are calculated by dividing the mean abundance estimates by the length of the beach monitored at each study site. * At the Big Reef study site, the portions of the beach habitat along the Houston Ship Channel and along the Gulf of Mexico were censused separately (see Figure 7).

Study Location	N	BL	Abundance		Maximum	Density
			Mean	SE		
Bay Ecosystem						
Bolivar Flats	35	4.8	15.3	3.96	83	3.19
Big Reef *:						
Ship Channel	17	3.2	1.2	5.63	12	0.37
Gulf	16	1.2	0.6	5.81	5	0.50
San Luis Pass	64	6.3	12.3	4.47	32	1.87
Ecotone						
East Flats	7	2.8	9.9	8.78	24	3.54
Mustang Island State Park North Area	66	3.2	10.3	2.86	38	3.22
Mustang Island State Park South Area	32	2.6	8.5	4.11	55	5.31
Packery Channel	58	3.9	14.0	3.05	87	3.59
Lagoon Ecosystem						
Brazos Island	25	7.6	22.6	4.65	254	2.97
South Padre Island North Area	27	25.1	12.3	4.47	171	0.49

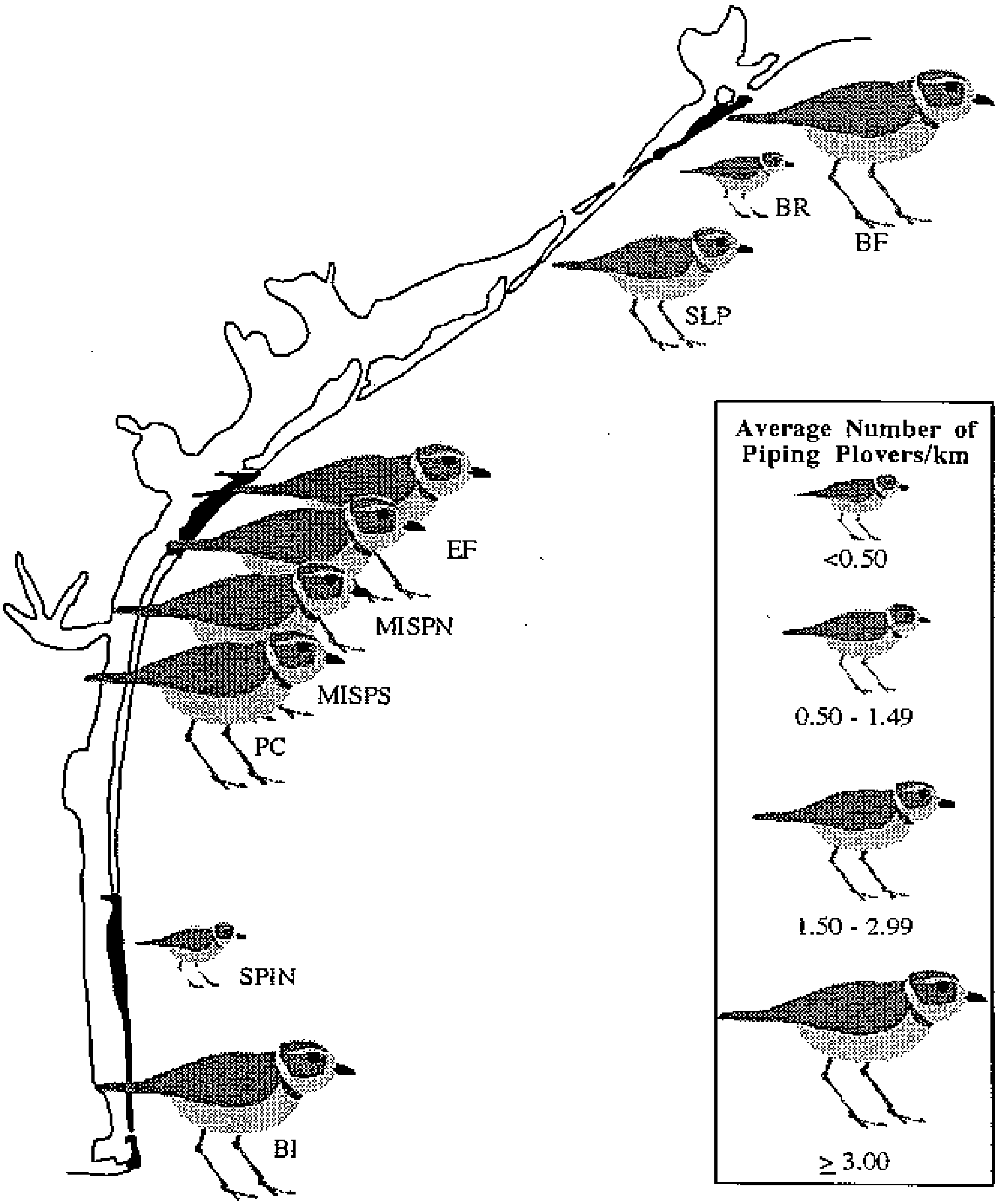


Figure 19. The relative total density of Piping Plovers observed using beach habitat at each study site is illustrated in this figure. Densities are represented as the mean number of birds per kilometer. Plover figures of increasing dimension reflect arbitrary ranks of total population densities, and are placed along the coastal map in positions that are approximately adjacent to the study sites (see Appendix for study site abbreviations).

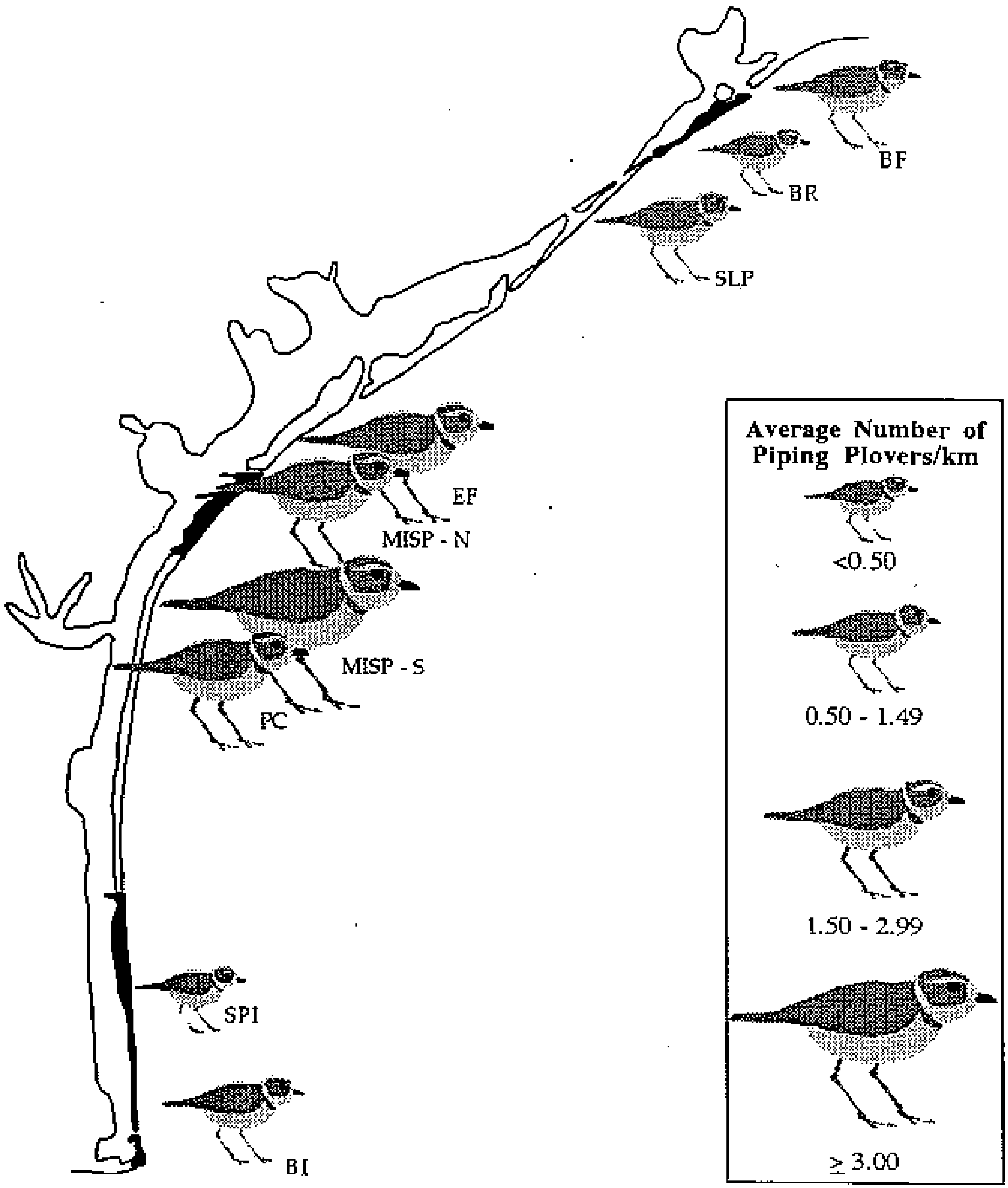


Figure 20. Average densities of foraging Piping Plovers on beach habitat at each study site are presented in this figure. Densities are represented as the mean number of birds per kilometer. Plover figures of increasing dimension reflect arbitrary ranks of total population densities, and are placed along the coastal map in positions that are approximately adjacent to the study sites (see Appendix for study site abbreviations).

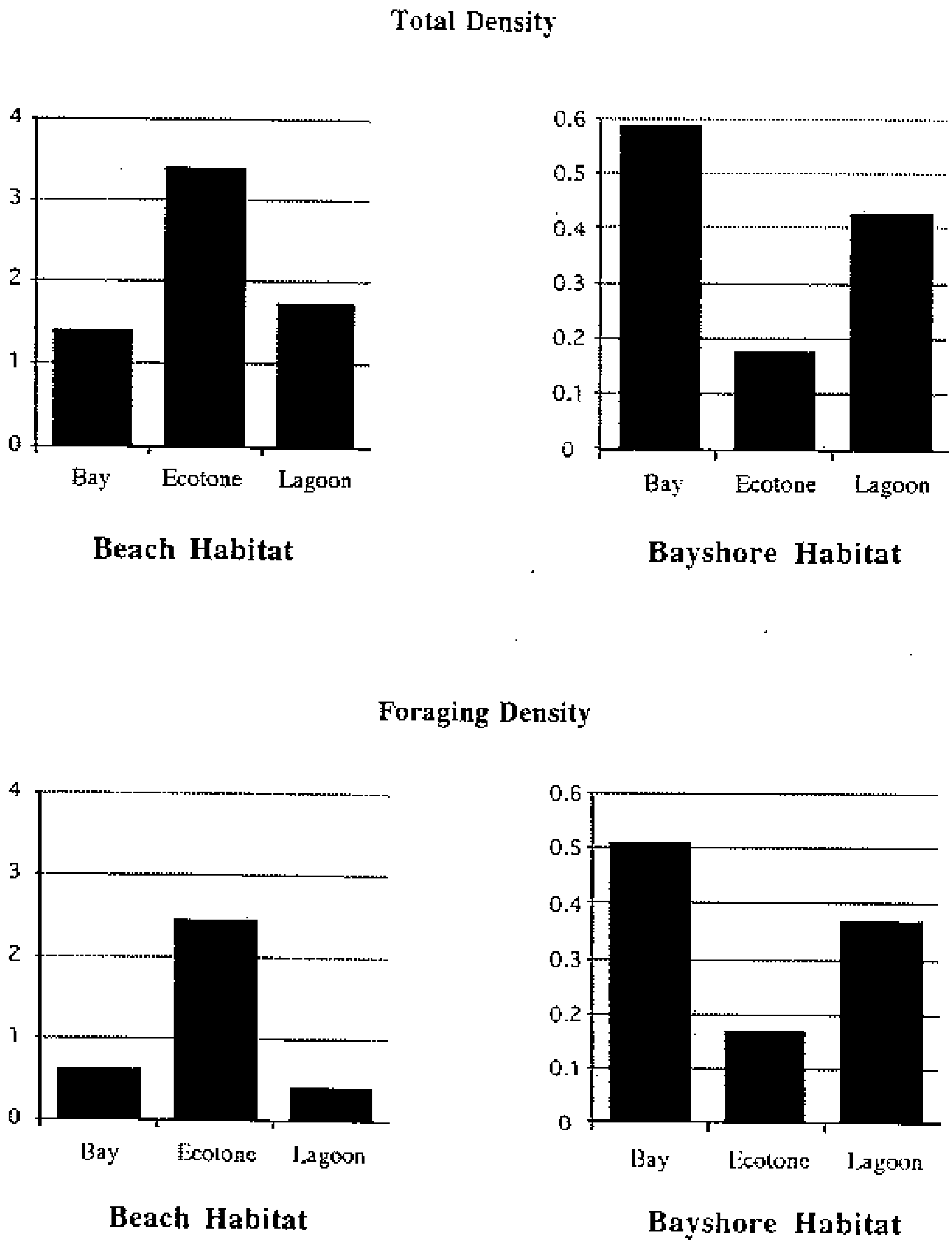


Figure 21. Mean total densities and mean foraging densities of Piping Plovers among beach and bayshore habitats within the 2 ecosystems and the ecotone are presented in this figure. Beach densities are represented as the number of Piping Plovers/kilometer. Bayshore densities are represented as the number of Piping Plovers/hectare.

Table 5. Table summarizing the ANOVA results for the Piping Plover surveys, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Survey records represent the mean # plover /km on beaches, and the mean # plovers/ha on bayshore habitat. (* = $p < 0.10$, ** = $p < 0.05$)

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
All beach surveys:	winter vs. migratory	2.23 (191) vs. 2.80 (163)	2.22 (171) vs. 2.59 (140)	0.1059
	flats: emergent vs. inundated	1.14 (251) vs. 5.73 (103)	0.78 (210) vs. 5.73 (101)	** 0.0026
	mild vs. harsh climate	2.57 (206) vs. 2.37 (148)	2.72 (123) vs. 2.59 (100)	0.6678
	AM vs. PM	2.42 (185) vs. 2.79 (63)	2.04 (71) vs. 2.83 (19)	0.9023
	light vs. heavy disturbance	2.53 (170) vs. 3.04 (76)	3.54 (71) vs. 4.42 (36)	0.6646
	bay vs. lagoon	1.73 (139) vs. 1.68 (52)	1.73 (135) vs. 1.68 (52)	0.8942
	bay vs. ecotone	1.73 (139) vs. 3.37 (163)	1.73 (135) vs. 3.39 (124)	0.1793
	ecotone vs. lagoon	3.37 (163) vs. 1.68 (52)	3.39 (124) vs. 1.68 (52)	0.3240
Bay beach surveys:	winter vs. migratory	1.58 (58) vs. 1.84 (81)	1.58 (58) vs. 1.84 (77)	0.2236
	flats: emergent vs. inundated	0.60 (93) vs. 3.91 (46)	0.60 (89) vs. 3.91 (46)	* 0.0649
	mild vs. harsh climate	1.66 (81) vs. 1.83 (58)	1.66 (81) vs. 1.83 (54)	0.8042
Ecotone beach surveys:	winter vs. migratory	2.69 (105) vs. 4.61 (58)	2.77 (85) vs. 4.75 (39)	0.3145
	flats: emergent vs. inundated	1.81 (118) vs. 7.48 (45)	1.18 (81) vs. 7.57 (43)	** 0.0013
	mild vs. harsh climate	3.54 (95) vs. 3.13 (68)	3.81 (67) vs. 2.91 (57)	0.6889
Lagoon beach surveys:	winter vs. migratory	1.83 (28) vs. 1.50 (24)	1.83 (28) vs. 1.50 (24)	0.3783
	flats: emergent vs. inundated	0.35 (40) vs. 6.12 (12)	0.35 (40) vs. 6.12 (12)	0.1512
SLP beach:	beach: emergent vs. inundated	0.18 (8) vs. 0.00 (9)	0.18 (8) vs. 0.00 (9)	** 0.0020
MISPN beach:	beach: emergent vs. inundated	0.77 (15) vs. 4.20 (14)	0.77 (15) vs. 4.20 (14)	** 0.0042
PC beach:	beach: emergent vs. inundated	2.60 (22) vs. 5.21 (9)	2.60 (22) vs. 5.21 (9)	0.8157

Table 5 continued.

Data Type	Comparisons	Total Data Set	Analzyed Data Set		p-value
All bayshore surveys:	winter vs. migratory	0.45 (314) vs. 0.42 (274)	0.41 (268) vs. 0.40 (209)		0.8204
	flats: emergent vs. inundated	0.50 (430) vs. 0.27 (158)	0.47 (342) vs. 0.24 (135)	**	0.0005
	mild vs. harsh climate	0.48 (349) vs. 0.38 (239)	0.65 (71) vs. 0.50 (56)		0.3979
	bay vs. lagoon	0.57 (130) vs. 0.40 (294)	0.58 (127) vs. 0.40 (260)	**	0.0053
	bay vs. ecotone	0.57 (130) vs. 0.38 (164)	0.58 (127) vs. 0.15 (90)	**	0.0024
	ecotone vs. lagoon	0.38 (164) vs. 0.40 (294)	0.15 (90) vs. 0.40 (260)		0.3531
Bay bayshore surveys:	winter vs. migratory	0.63 (51) vs. 0.54 (79)	0.63 (51) vs. 0.55 (76)		0.6940
	flats: emergent vs. inundated	0.70 (88) vs. 0.31 (42)	0.71 (85) vs. 0.31 (42)	**	0.0011
	mild vs. harsh climate	0.65 (71) vs. 0.49 (59)	0.65 (71) vs. 0.50 (56)		0.5341
Ecotone bayshore surveys:	winter vs. migratory	0.38 (94) vs. 0.39 (70)	0.18 (64) vs. 0.06 (26)	*	0.0887
	flats: emergent vs. inundated	0.41 (121) vs. 0.32 (43)	0.16 (63) vs. 0.12 (27)		0.3652
	mild vs. harsh climate	0.31 (99) vs. 0.49 (65)	0.13 (52) vs. 0.17 (38)		0.9996
Lagoon bayshore surveys:	winter vs. migratory	0.43 (169) vs. 0.37 (125)	0.43 (153) vs. 0.37 (107)	*	0.0674
	flats: emergent vs. inundated	0.46 (221) vs. 0.22 (73)	0.46 (194) vs. 0.27 (66)	**	0.0046
	mild vs. harsh climate	0.50 (179) vs. 0.25 (115)	0.50 (155) vs. 0.26 (105)		0.4081
	mainland vs. barrier island	0.20 (189) vs. 0.79 (105)	0.18 (166) vs. 0.80 (94)		0.6759
Lagoon Bayshore emergent:	mainland vs. barrier island	0.21 (146) vs. 0.97 (75)	0.18 (128) vs. 0.99 (66)	**	0.0044
BF bayshore:	AM vs. PM	0.56 (23) vs. 0.38 (9)	0.56 (23) vs. 0.38 (9)	**	0.0072
SLP bayshore:	AM vs. PM	0.48 (40) vs. 0.68 (16)	0.48 (40) vs. 0.68 (16)		0.3274

Foraging Density - Our data suggest that Piping Plover foraging beach densities also do not differ significantly along the Texas Coast. We detected no difference in the foraging beach density of Piping Plovers among separate pairwise comparisons between the 2 ecosystems ($p = 0.9256$; Table 6), or between the ecotone and the bay ecosystem ($p = 0.4285$; Table 6) or the ecotone and the lagoon ecosystem ($p = 0.4731$; Table 6).

Foraging Proportion - Our data suggest that Piping Plovers spent about the same amount of time foraging on beach habitat in both ecosystems and in the ecotone (Table 7). We detected no difference in the beach foraging proportions (the proportion of the total number of Piping Plovers observed during a bayshore survey that were foraging) among the bay and lagoon ecosystems and the ecotone ($p = 0.9844$; data not shown). We also detected no difference in the beach foraging proportions among separate pairwise comparisons between the 2 ecosystems ($p = 0.8974$; data not shown), or between the ecotone and the bay ecosystem ($p = .08918$; data not shown) or the ecotone and the lagoon ecosystem ($p = 0.9779$; data not shown).

Bayshore Habitat

General - Piping Plover bayshore density varied from 0.00 birds/ha at the Mustang Island State Park South Area and South Bay West Area sites to 1.45 birds/ha at the Convention Center site on South Padre Island (Table 8). The 3 sites with the greatest single day populations were on South Padre Island, South Bay, and north Mustang Island. The largest population of Piping Plovers we observed during a single bayshore survey was a group of 543 recorded on 2 March 1993 on the North Area of the South Padre Island site (Table 8; Figure 14). The 5 highest Piping Plover tallies were recorded at this site, although this is not surprising given the fact that this site had, on average, more than twice the area of bayshore flats than the next largest site, and was 5 - 10 times larger than most of the sites (compare average emergent flat areas from figures 4 - 12). The location with the sixth highest single day tally was the East Area of our South Bay site where we recorded 202 Piping Plovers on 3 March 1992 (Table 8; Figure 13). The seventh highest tally occurred at our East Flats site on 26 March 1993 where we observed 189 Piping Plovers (Table 8; Figure 9). The largest population of Piping Plovers recorded at a mainland site was 130 on 18 November 1991 at Redhead Cove flats located at Laguna Atascosa NWR (Table 8; Figure 12). The highest average densities throughout the 3-year study were observed at the 3 small flats (< 4 ha) on South Padre Island (Table 8). Of the flats larger than 10 ha, densities of 1 Piping Plover every 2 hectares or greater were recorded at all bay ecosystem sites, and on the large flat on the South Padre Island North Area site (Figure 22). In general, Piping Plover bayshore densities (total and foraging) were highest within the bay ecosystem, and lowest within the ecotone (Figure 21).

Total Density - Our analyses of Piping Plover densities on bayshore habitat were performed on data from barrier island habitat only. ANOVA comparisons among landform types using lagoon ecosystem data suggested that during emergent conditions Piping Plover densities were significantly higher on barrier island flats than on mainland flats ($p = 0.0139$; Table 5). Whereas the difference between landform types was not significant when survey data collected under conditions of bayshore tidal inundation were included in the analysis ($p = 0.6759$; Table 5), we excluded mainland data from the analyses to dispel any doubts associated with comparisons among ecosystem types.

Using barrier island surveys only, our data suggest that mean Piping Plover total densities differed significantly on bayshore habitat among the 2 ecosystems. We

Table 6. Table summarizing the ANOVA results for the foraging Piping Plover survey data, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Survey records represent the mean # plover /km on beaches, and the mean # plovers/ha on bayshore habitat. (* = $p < 0.10$, ** = $p < 0.05$)

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
All beach surveys:	winter vs. migratory	1.26 (191) vs. 1.53 (163)	1.13 (171) vs. 1.27 (140)	* 0.0566
	flats: emergent vs. inundated	0.93 (251) vs. 2.40 (103)	0.58 (210) vs. 2.38 (101)	* 0.0565
	mild vs. harsh climate	1.31 (206) vs. 1.50 (148)	1.52 (123) vs. 1.57 (100)	0.9003
	AM vs. PM	1.75 (185) vs. 0.96 (63)	1.22 (71) vs. 1.08 (19)	0.8715
	light vs. heavy disturbance	1.59 (170) vs. 1.10 (76)	2.25 (71) vs. 1.11 (36)	** 0.0104
	bay vs. lagoon	0.82 (139) vs. 0.40 (52)	0.82 (135) vs. 0.40 (52)	0.9256
	bay vs. ecotone	0.82 (139) vs. 2.26 (163)	0.82 (135) vs. 2.00 (124)	0.4285
	ecotone vs. lagoon	2.26 (163) vs. 0.40 (52)	2.00 (124) vs. 0.40 (52)	0.4731
Bay beach surveys:	winter vs. migratory	0.66 (58) vs. 0.97 (81)	0.66 (58) vs. 0.97 (77)	0.2397
	flats: emergent vs. inundated	0.44 (93) vs. 1.56 (46)	0.44 (89) vs. 1.56 (46)	0.3221
	mild vs. harsh climate	0.71 (81) vs. 1.00 (58)	0.71 (81) vs. 1.00 (54)	0.8042
Ecotone beach surveys:	winter vs. migratory	2.02 (105) vs. 2.60 (58)	1.86 (85) vs. 2.24 (39)	0.8774
	flats: emergent vs. inundated	1.60 (118) vs. 3.82 (45)	0.93 (81) vs. 3.85 (43)	** 0.0133
	mild vs. harsh climate	2.34 (95) vs. 2.16 (68)	2.24 (67) vs. 1.74 (57)	0.6889
Lagoon beach	winter vs. migratory	0.22 (28) vs. 0.57 (24)	0.22 (28) vs. 0.57 (24)	* 0.0621
	flats: emergent vs. inundated	0.22 (40) vs. 0.85 (12)	0.22 (40) vs. 0.85 (12)	0.8637
SLP beach:	beach: emergent vs. inundated	0.12 (8) vs. 0.00 (9)	0.12 (8) vs. 0.00 (9)	** 0.0020
MISPN beach:	beach: emergent vs. inundated	0.73 (15) vs. 3.42 (14)	0.73 (15) vs. 3.42 (14)	** 0.0210
PC beach:	beach: emergent vs. inundated	1.53 (22) vs. 1.99 (9)	1.53 (22) vs. 1.99 (9)	0.4794

Table 6 continued.

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
All bayshore surveys:	winter vs. migratory	0.43 (314) vs. 0.34 (274)	0.42 (268) vs. 0.30 (209)	0.3281
	flats: emergent vs. inundated	0.48 (430) vs. 0.14 (158)	0.47 (342) vs. 0.13 (135)	** 0.0014
	mild vs. harsh climate	0.41 (349) vs. 0.33 (239)	0.52 (71) vs. 0.48 (56)	0.6084
	bay vs. lagoon	0.51 (130) vs. 0.39 (294)	0.51 (127) vs. 0.38 (260)	** 0.0077
	bay vs. ecotone	0.51 (130) vs. 0.28 (164)	0.51 (127) vs. 0.15 (90)	** 0.0046
	ecotone vs. lagoon	0.28 (164) vs. 0.39 (294)	0.15 (90) vs. 0.38 (260)	0.6751
Bay bayshore surveys:	winter vs. migratory	0.61 (51) vs. 0.41 (79)	0.61 (51) vs. 0.41 (76)	0.2237
	flats: emergent vs. inundated	0.66 (88) vs. 0.23 (42)	0.65 (85) vs. 0.23 (42)	** 0.0018
	mild vs. harsh climate	0.52 (71) vs. 0.48 (59)	0.52 (71) vs. 0.48 (56)	0.6140
Ecotone bayshore surveys:	winter vs. migratory	0.24 (94) vs. 0.32 (70)	0.18 (64) vs. 0.05 (26)	** 0.0237
	flats: emergent vs. inundated	0.33 (121) vs. 0.17 (43)	0.16 (63) vs. 0.12 (27)	0.4183
	mild vs. harsh climate	0.25 (99) vs. 0.34 (65)	0.13 (52) vs. 0.16 (38)	0.9069
Lagoon bayshore surveys:	winter vs. migratory	0.44 (169) vs. 0.31 (125)	0.44 (153) vs. 0.30 (107)	* 0.0737
	flats: emergent vs. inundated	0.49 (221) vs. 0.09 (73)	0.49 (194) vs. 0.09 (64)	** 0.0137
	mild vs. harsh climate	0.45 (179) vs. 0.26 (115)	0.44 (155) vs. 0.27 (85)	0.6833
	mainland vs. barrier island	0.19 (189) vs. 0.75 (105)	0.16 (166) vs. 0.76 (87)	0.5914
Lagoon Bayshore emergent:	mainland vs. barrier island	0.22 (146) vs. 1.05 (75)	0.18 (128) vs. 1.08 (66)	** 0.0040
BF bayshore:	AM vs. PM	0.54 (23) vs. 0.47 (9)	0.54 (23) vs. 0.47 (9)	** 0.0010
SLP bayshore:	AM vs. PM	0.39 (40) vs. 0.53 (16)	0.39 (40) vs. 0.53 (16)	0.5350

Table 7. The total, foraging and roosting densities of Piping Plovers among study beaches are presented. During the first field season, birds were not distinguished with regard to behavior (i.e. foraging vs. roosting). Therefore, two total densities are reported, that from the first field season (Y1), and a second from the last two field season (Y2-3), calculated by adding the foraging and roosting densities. An index representing the foraging proportion was calculated by dividing the foraging density by the total density from Y 2-3. Parameter estimates for each ecosystem and the ecotone are represented as averages of the values of their respective study sites.

Location	Total Density	Foraging Density	Roosting Density	Foraging Proportion
	(Y1/Y2-3)			
Bolivar Beach	3.19/3.26	0.74	2.52	0.23
Big Reef Beach	0.42/0.50	0.39	0.11	0.78
San Luis Beach	1.87/2.07	1.23	0.84	0.59
East Beach	------/3.52	2.40	1.12	0.68
M.I.S.P. - North	3.23/3.33	2.33	1.00	0.70
M.I.S.P. - South	3.26/3.92	3.37	0.55	0.86
Packery Channel Beach	3.58/4.03	1.65	2.38	0.41
Brazos Island Beach	2.97/3.37	0.61	2.76	0.18
South Padre Island Beach	0.49/0.66	0.19	0.47	0.29

Table 8. The total abundances, highest study tallies, and densities for Piping Plovers are presented for each of the study bayshore flats. For reference, the maximum and mean areas of bayshore flat available at each site during the study period are listed. The density estimates are derived from mean bayshore habitat area measures.

Study Location	N	Max./Mean	Abundance		High	Density
			Mean	SE		
Bay Ecosystem						
Bolivar Flats	40	188/102	50.2	4.26	119	0.49
Big Reef	23	58/29	19.7	6.78	54	0.68
San Luis Pass	65	72/42	23.4	4.03	75	0.56
Ecotone						
East Flats	7	246/136	49.3	12.29	189	0.36
Mustang Island State Park:						
North Area	30	61/33	7.4	4.79	39	0.22
South Area	13	69/40	0.0	7.28	9	0.00
Packery Channel	47	179/107	14.7	4.74	75	0.14
Lagoon Ecosystem						
Laguna Atascosa NWR:						
Rincon Buena Vista	31	161/95	17.4	5.37	100	0.18
South Horse Flats	35	28/16	1.2	5.49	40	0.08
Redhead Cove	37	36/27	5.7	5.34	130	0.21
North Yucca Flats	43	91/50	17.1	4.96	97	0.34
South Bay:						
West Area	21	100/51	0.0	0.00	0	0.00
East Area	29	642/270	19.1	3.17	202	0.07
South Padre Island:						
North Area	6	812/508	355.3	13.27	543	0.70
Convention Center	19	4/2	2.9	3.91	18	1.45
Parrot Eye's	21	4/2	2.5	3.72	16	1.25
Mangrove Flats	25	8/4	3.1	3.41	17	0.78

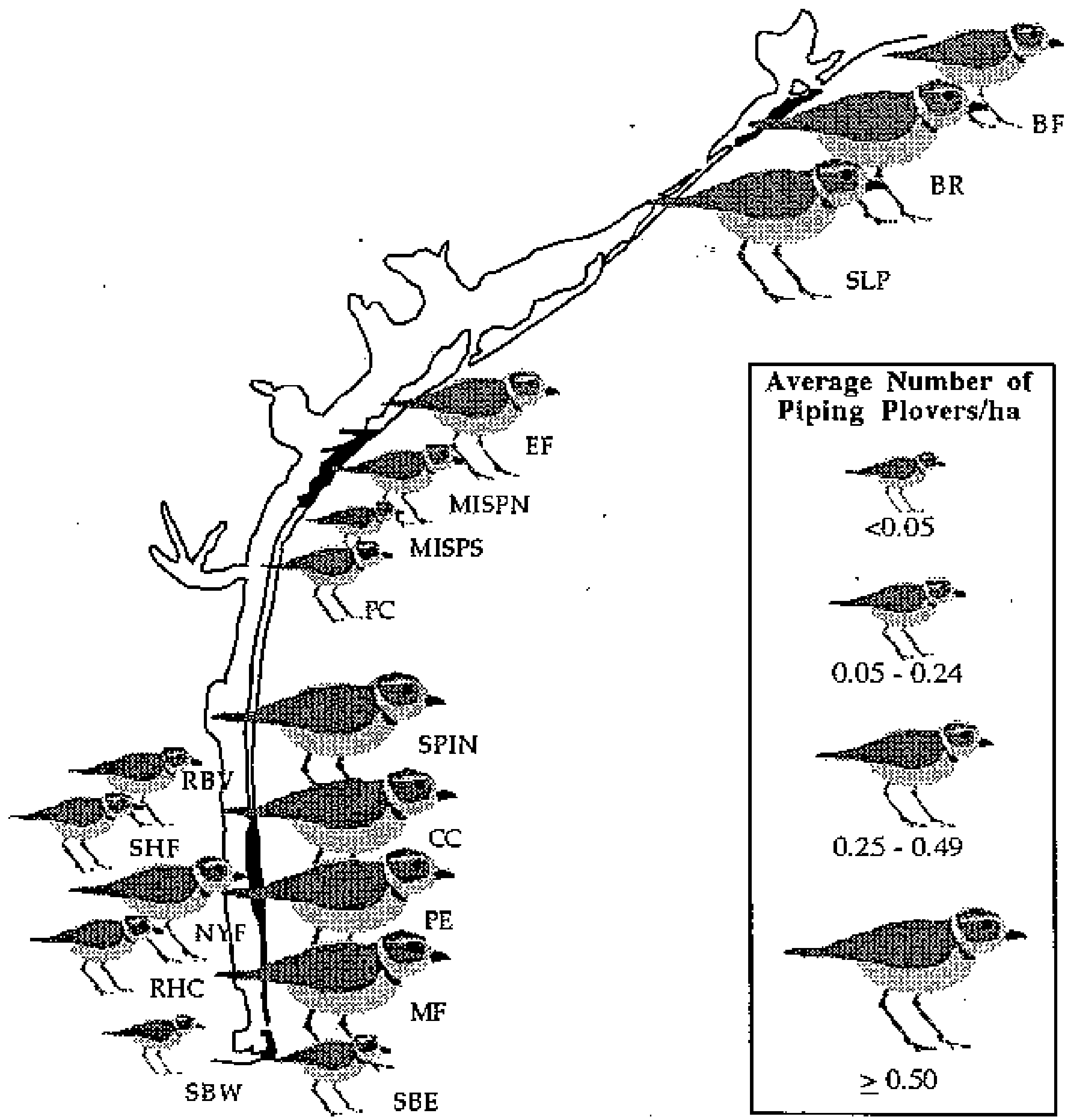


Figure 22. The relative total density of Piping Plovers observed using bayshore habitat at each study site is illustrated in this figure. Densities are represented as the mean number of birds per hectare. Plover figures of increasing dimension reflect arbitrary ranks of total population densities, and are placed along the coastal map in positions that are approximately adjacent to each study site (see Appendix for study site abbreviations).

observed a significantly higher mean total density of Piping Plovers on bay ecosystem flats than on lagoon ecosystem flats (p = 0.0053; Table 5). The mean bay ecosystem Piping Plover density was also significantly higher than the density we observed within the ecotone (p = 0.0024; Table 5). We detected no difference in the total densities of Piping Plovers at the lagoon ecosystem and the ecotone flats (p = 0.3531; Table 5).

Foraging Density - Our data suggest that Piping Plover bayshore foraging densities differed significantly among the 2 ecosystems. We recorded Piping Plovers at a significantly higher mean foraging density on bay ecosystem flats than on lagoon ecosystem flats (p = 0.0077; Table 6). The mean bay ecosystem Piping Plover foraging density was also significantly higher than the density we observed within the ecotone (p = 0.0046; Table 6). We detected no difference in the foraging densities of Piping Plovers between the lagoon ecosystem and the ecotone flats (p = 0.6751; Table 6).

Foraging Proportion - Our data suggest that Piping Plovers spent about the same amount of time foraging on bayshore habitat in both ecosystems and in the ecotone (Table 9). We detected no difference in the bayshore foraging proportions (the proportion of the total number of Piping Plovers observed during a bayshore survey that were foraging) among the bay and lagoon ecosystems and the ecotone (p = 0.1833; data not shown). We also detected no difference in the foraging proportions among separate pairwise comparisons between the 2 ecosystems (p = 0.2683; data not shown), or between the ecotone and the bay ecosystem (p = 0.0938; data not shown) or the ecotone and the lagoon ecosystem (p = 0.2569; data not shown).

Factors Affecting Piping Plover Density

In secondary objective #2, we focused on identifying the factors affecting Piping Plover density. To accomplish this objective, we monitored 4 environmental variables (bayshore tidal amplitude, beach tidal amplitude, climatic conditions, and human disturbance) and 2 temporal variables (life cycle stage, and time of day) and analyzed their influences on Piping Plover population density (total and foraging) among the ecosystems and the ecotone, and among the different landform types. In this section, we have presented the survey results in the form of comparisons of total Piping Plover density and foraging Piping Plover density. We present the results for beach habitat first, followed by the results for bayshore habitat.

Beach Habitat

Total Density - Bayshore tidal conditions markedly influenced the total density of Piping Plovers using beach habitat in both ecosystems and the ecotone (p = 0.0026; Table 5). As bayshore flats became inundated, the densities of Piping Plovers on beaches increased over six-fold in the bay ecosystem (p = 0.0649; Table 5), over four-fold in the ecotone (p = 0.0013; Table 5), and nearly twenty-fold in the lagoon ecosystem (p = 0.1512; small sample size; Table 5).

Beach tidal conditions were associated with total Piping Plover beach densities at 2 of the 3 sites where we were able to monitor beach width (see Methods). As the beach width decreased (i.e during increasing beach tidal inundation), the densities of Piping Plovers decreased significantly on beaches at the San Luis Pass site (p = 0.0020; Table 5), increased significantly at the Mustang Island State Park North Area site (p = 0.0042; Table 5), and was unchanged at the Packery Channel site (p = 0.8157; Table 5). Increasing Piping Plover beach densities were significantly associated with high bayshore tides at all 3 sites (p = 0.0106, p = 0.0042, p = 0.0027, respectively; data not

Table 9. The total, foraging and roosting densities of Piping Plovers among study bayshore flats are presented. During the first field season, birds were not distinguished with regard to behavior (i.e. foraging vs. roosting). Therefore, two total densities are reported, that from the first field season (Y1), and a second from the last two field season (Y2-3), calculated by adding the foraging and roosting densities. An index representing the foraging proportion was calculated by dividing the foraging density by the total density from Y 2-3.

Location	Total Density (Y1/Y2-3)	Foraging Density	Roosting Density	Foraging Proportion
Bay Ecosystem:				
Bolivar Flats	0.49/0.52	0.49	0.03	0.94
Big Reef	0.68/0.68	0.55	0.13	0.81
San Luis Flats	0.60/0.53.	0.50	0.06	0.89
Ecotone:				
East Flats	-----/0.36	0.31	0.05	0.86
MISP - North Bayshore	1.33/1.02	0.99	0.03	0.97
MISP - North Lagoon	0.21/0.20	0.20	0.00	1.00
MISP - South Bayshore	0.90/0.33	0.33	0.00	1.00
MISP - South Lagoon	0.05/0.07	0.01	0.06	0.14
Packery Flats	0.14/0.14	0.14	0.00	1.00
Lagoon Ecosystem:				
LANWR - Rincon Buena Vista	0.20/0.16	0.14	0.05	0.74
LANWR - South Horse Flats	0.07/0.22	0.08	0.00	1.00
LANWR - Red Head Cove	0.22/0.26	0.22	0.00	1.00
LANWR - North Yucca Flats	0.29/0.34	0.25	0.04	0.86
South Bay - West	0.00/0.00	0.00	0.00	–
South Bay - East	0.08/0.00	0.02	0.00	1.00
South Padre - North	0.70/0.76	0.64	0.12	0.84
South Padre - Conv. Center	-----/1.45	1.45	0.00	1.00
South Padre - Parrot Eye's	-----/1.29	1.00	0.24	0.81
South Padre - Mangrove	-----/0.78	0.67	0.11	0.86

shown). Linear regression analyses suggest a significant positive relationship existed between the beach and bayshore tides at the San Luis Pass site ($p < 0.0001$; data not shown) and at the Mustang Island State Park North Area site ($p = 0.0170$; data not shown), but not at the Packery Channel site ($p = 0.6258$; data not shown). Thus, in the 2 locations where Piping Plover densities were significantly associated with beach tides, they were also associated with bayshore tides, and the 2 tides were relatively synchronous. At the Packery Channel site, where the tides were asynchronous, bayshore tidal conditions were significantly associated with Piping Plover beach densities, whereas beach tidal conditions were not.

Climatic conditions ($p = 0.6678$), life cycle ($p = 0.1059$) and time of day ($p = 0.9023$; small data set) seemingly were not associated with total Piping Plover densities on beach habitat (Table 5). Human disturbance also did not significantly affect the total density of Piping Plovers on beach habitat ($p = 0.6646$; Table 5).

Foraging Density - Bayshore tidal conditions appeared to have less of an influence on foraging Piping Plover densities on beach habitat than it did on total densities. As bayshore flats became inundated, the densities of Piping Plovers on beaches increased less than four-fold in the bay ecosystem ($p = 0.3221$; Table 6), the ecotone ($p = 0.0133$; Table 6), and the lagoon ecosystem ($p = 0.8637$; Table 6). As we observed for total densities, beach tidal conditions were associated with foraging Piping Plover densities at the San Luis site($p = 0.0020$; Table 6) and the Mustang Island State Park North Area site ($p = 0.0042$; Table 6), but not the Packery Channel site ($p = 0.4794$; Table 6). Foraging Piping Plover densities were rather closely associated with bayshore tidal conditions at all 3 sites ($p = 0.0106$, $p = 0.1076$, $p = 0.0125$, respectively; data not shown).

Our data suggest that foraging Piping Plover densities were more strongly affected by the life cycle parameter ($p = 0.0566$; Table 6), than were total Piping Plover densities ($p = 0.1059$; Table 6). Climatic conditions ($p = 0.9003$) and time of day ($p = 0.9023$; small data set) seemingly were not associated with Piping Plover use of beach habitat (Table 6). Human disturbance appeared to have a strong effect on the foraging behavior of Piping Plovers on beaches. Although human disturbance did not significantly influence total Piping Plover densities (see above and Table 5), foraging Piping Plover densities declined significantly during periods of high human disturbance ($p = 0.0104$; Table 6).

Bayshore Habitat

Total Density - Bayshore tidal conditions markedly influenced the total density of Piping Plovers using bayshore habitat in both ecosystems. As bayshore flats became inundated, the total densities of Piping Plovers on flats decreased in the bay ecosystem ($p = 0.0011$; Table 5), and in the lagoon ecosystem ($p = 0.0046$; Table 5). However, the bayshore tides did not significantly affect the density of Piping Plovers using flats in the ecotone ($p = 0.3652$; Table 5).

Climatic conditions ($p = 0.3979$), and life cycle ($p = 0.8204$) seemingly were not associated with total Piping Plover densities on bayshore habitat (Table 5). Piping Plovers were as common during the mornings as they were during the afternoon on flats at the San Luis Pass site ($p = 0.3274$; Table 5) and at the South Bay East Area site ($p = 0.3740$; Table 5), but occurred at significantly higher densities during the morning hours at the Bolivar Flats site ($p = 0.0080$; Table 5).

Foraging Density - Bayshore tidal conditions markedly influenced the foraging density of Piping Plovers using bayshore habitat in both ecosystems. As bayshore flats became inundated, the total densities of Piping Plovers on flats decreased in the bay ecosystem ($p = 0.0018$; Table 6), and in the lagoon ecosystem ($p = 0.0137$; Table 6). However, the bayshore tides did not significantly affect the density of Piping Plovers using flats in the ecotone ($p = 0.4183$; Table 6).

Climatic conditions ($p = 0.6084$), and life cycle ($p = 0.3281$) seemingly were not associated with total Piping Plover densities on bayshore habitat (Table 6). Foraging Piping Plovers were as common during the mornings as they were during the afternoon on flats at the San Luis Pass site ($p = 0.5350$; Table 6), but occurred at significantly higher densities during the morning hours than during the afternoon at the Bolivar Flats site($p = 0.0010$; Table 6).

Foraging Ecology

In secondary objective #3, we focused on characterizing the foraging ecology of Piping Plovers along the Texas Gulf Coast, and identifying the factors affecting foraging success. One of our 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. Other goals were related to foraging success. As measures of foraging success, we observed Piping Plovers as they fed and monitored foraging locomotion, foraging efficiency and aggressive behavior. We incorporated these parameters as dependent variables into ANOVA models to investigate the relative effects of ecosystem type, Piping Plover life cycle, habitat type, and microhabitat type on each measure of foraging success.

Piping Plover diet

Beach habitat - Polychaetes were the dominant prey group captured by Piping Plovers during foraging efficiency records on beaches in the bay ecosystem, lagoon ecosystem and in the ecotone comprising 77%, 98%, and 79% of the identifiable captures, respectively (Figure 23). Crustaceans composed only 23%, 2% and 21% of the identifiable prey captured by Piping Plovers on the bay ecosystem, lagoon ecosystem and ecotone beaches respectively (Figure 23).

Bayshore habitat - Polychaetes comprised 94%, 48%, and 68% of the identifiable captures by Piping Plovers during foraging efficiency records on sand flats in the bay ecosystem, lagoon ecosystem and in the ecotone, respectively (Figure 24). Surface prey composed 6%, 52% and 32% of the identifiable prey captured by Piping Plovers on the bay ecosystem, lagoon ecosystem and ecotone sand flats respectively (Figure 24).

In contrast, on algal flats, polychaetes comprised only 53%, 38%, and 8% of the identifiable captures by Piping Plovers during foraging efficiency records in the bay ecosystem, lagoon ecosystem and in the ecotone, respectively (Figure 25). Surface prey composed 47%, 62% and 92% of the identifiable prey captured by Piping Plovers on the bay ecosystem, lagoon ecosystem and ecotone algal flats respectively (Figure 25).

Foraging Locomotion

Piping Plovers spent about 7.5 seconds in prolonged locomotion for every minute they spent feeding on beaches (Table 10). Piping Plovers spent about 1/5 as much time in prolonged locomotion on bayshore flat habitat as they did on beach habitat (Table 10; Figure 26). Foraging locomotion was similar on sand flats and algal flats (Table 10), and among the 2 ecosystems and the ecotone (Table 10; Figure 26).

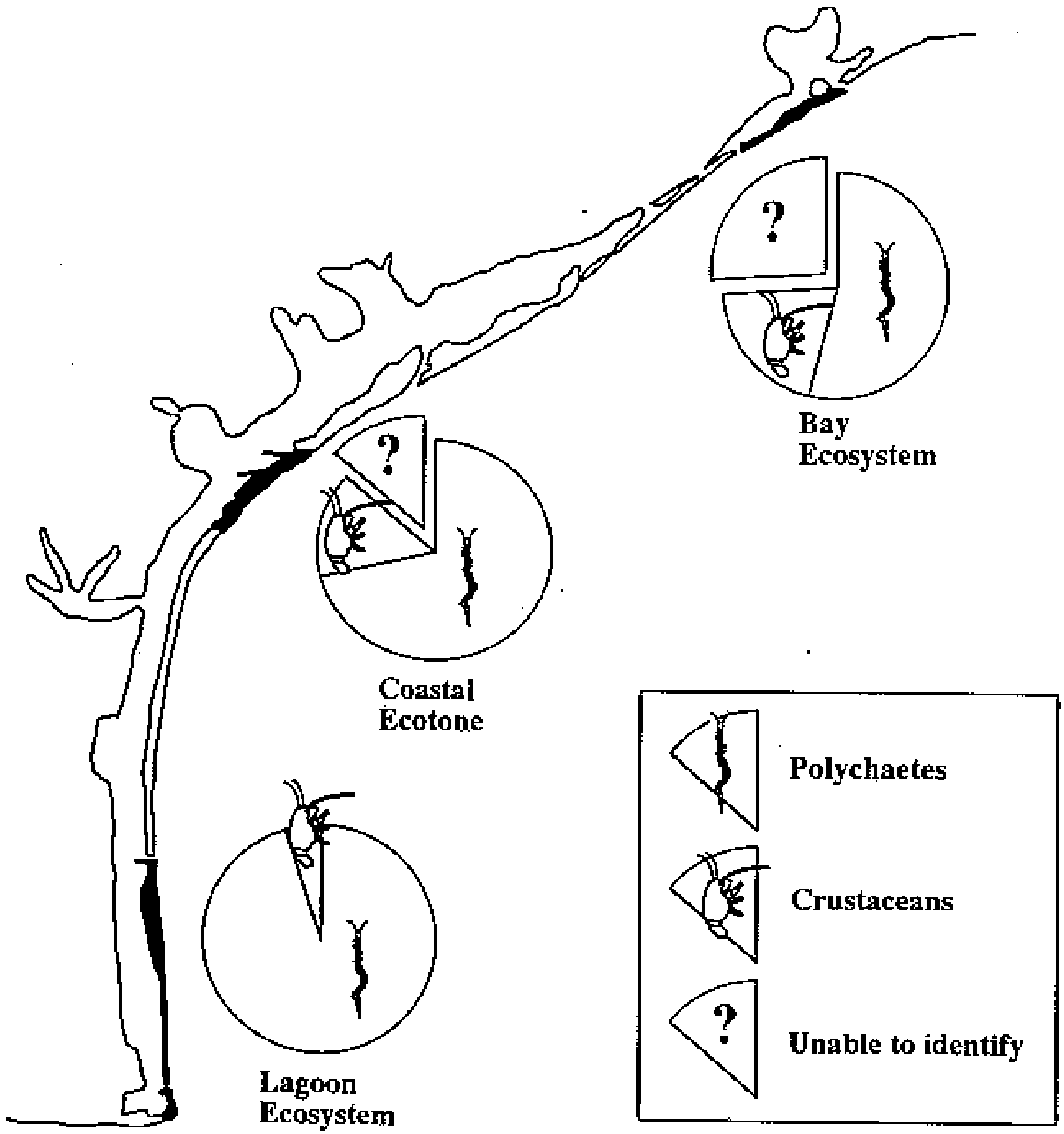


Figure 23. The pie charts in this figure illustrate the proportion of polychaetes and crustaceans in the diets of Piping Plovers on beach habitat among the 2 ecosystems and the ecotone. Diets were determined by observing foraging Piping Plovers and scoring the animals captured into one of the following three groups: 1) polychaetes (primarily the polychaete *Scolelepis squamata*), 2) crustaceans (primarily Haustorid amphipods), and 3) Unidentifiable prey. Polychaetes comprised the majority of the diet of Piping Plovers wintering in all three systems. Crustaceans were incorporated into the diet of Piping Plovers wintering in the bay ecosystem, but were only rarely captured (4.5% of total captures) by Piping Plovers wintering in the lagoon ecosystem.

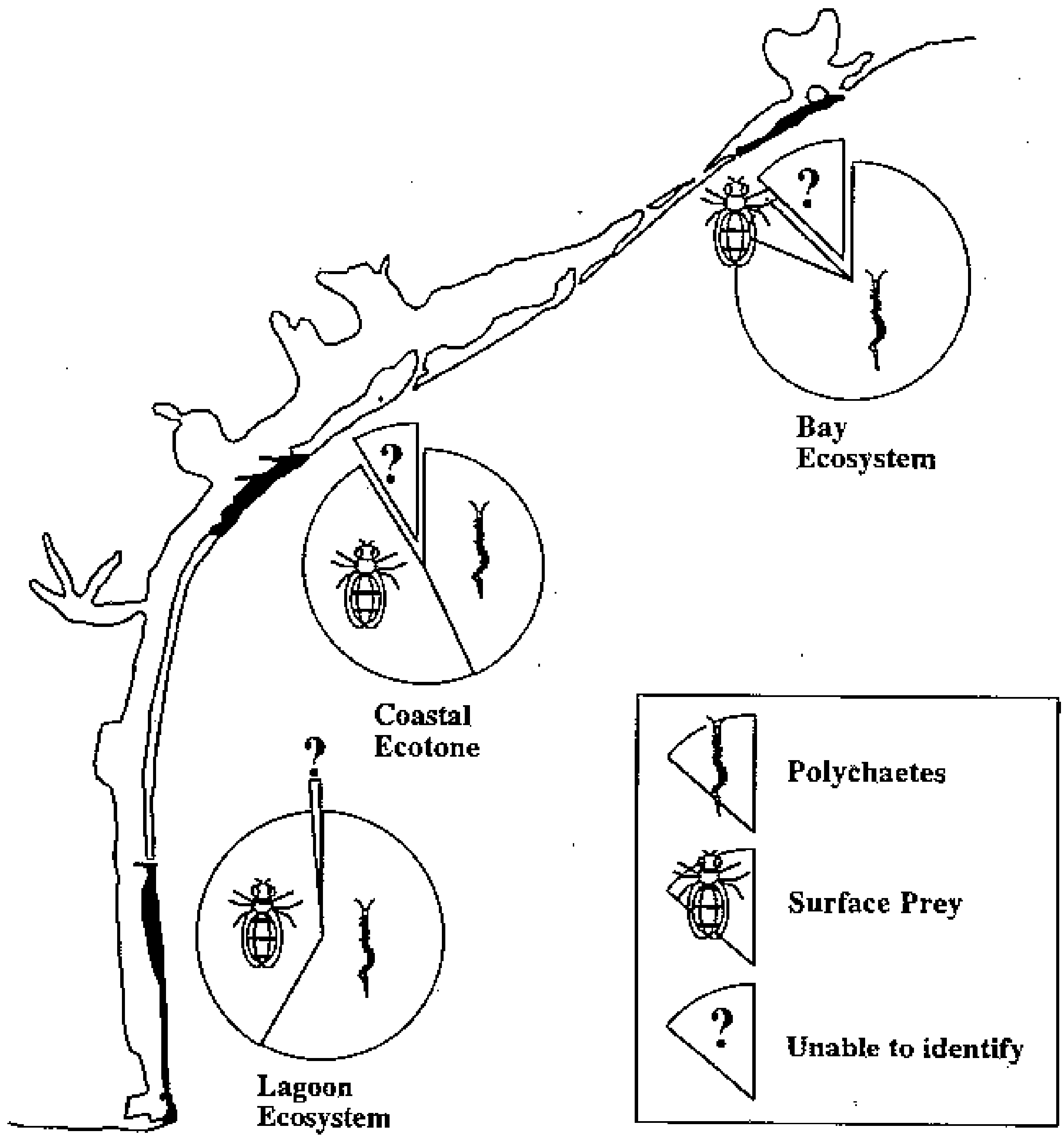


Figure 24. The pie charts in this figure illustrate the proportion of polychaetes and surface prey in the diets of Piping Plovers on sand flats among the two ecosystems and the ecotone. Diets were determined by observing foraging Piping Plovers and scoring the animals captured into one of the following three groups: 1) polychaetes, 2) surface prey (primarily insects and tanaids), and 3) unidentifiable prey. Polychaetes comprised the majority of the diet of Piping Plovers foraging on sand flats in the bay ecosystem and the lagoon ecosystem. Piping Plovers wintering within the ecotone captured polychaetes and surface prey in about equal proportions on sand flats.

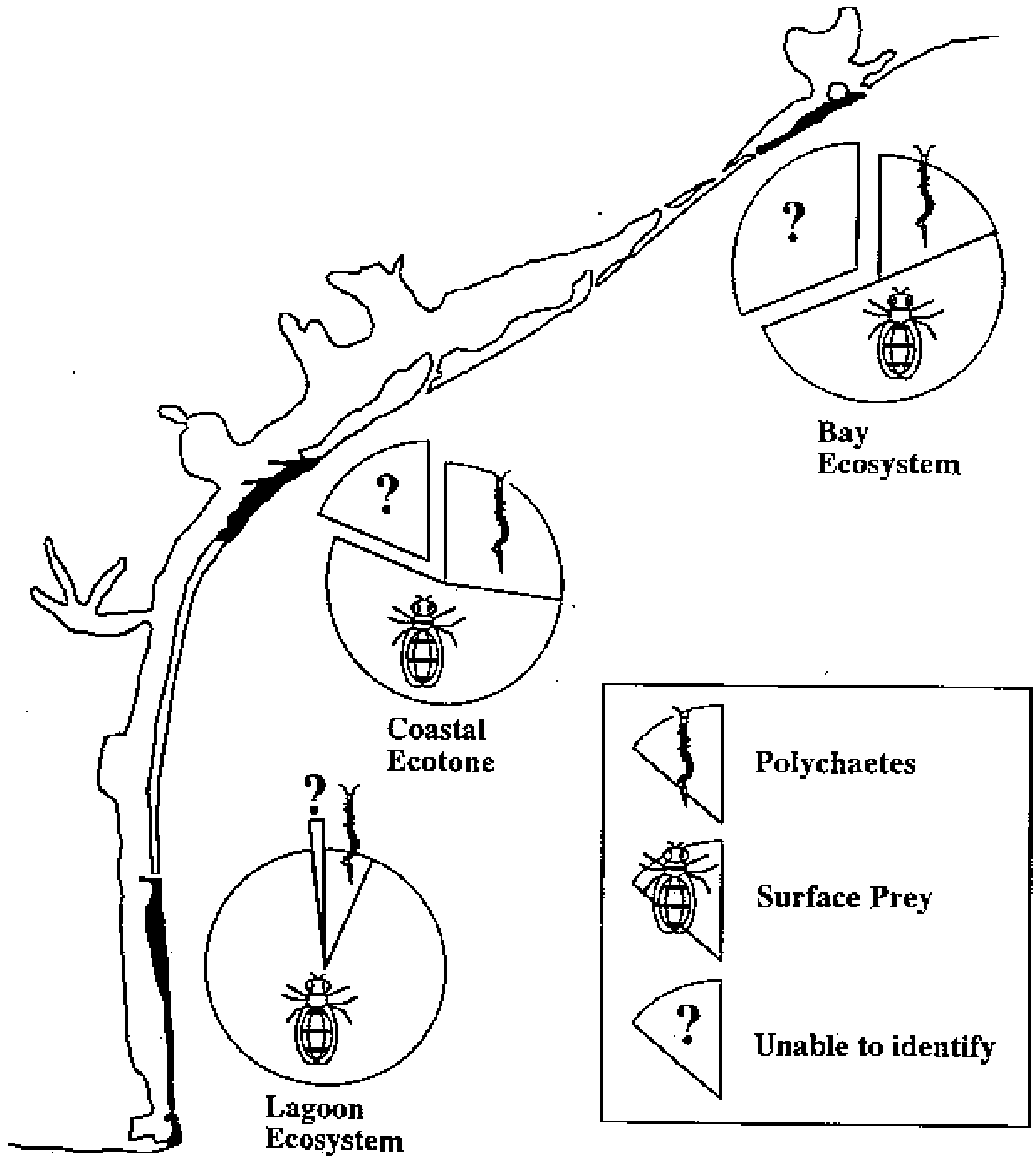


Figure 25. The pie charts in this figure illustrate the proportion of polychaetes and surface prey in the diets of Piping Plovers foraging on algal flats among the 2 ecosystems and the ecotone. Diets were determined by observing foraging Piping Plovers and scoring the animals they captured into one of the following three groups: 1) polychaetes (this group also includes worm-like animals from other taxa), 2) surface prey (primarily insects and tanaids), or 3) unidentifiable prey. Surface animals comprised the majority of the diet of Piping Plovers foraging on algal flats in all three regions.

Table 10 . This table summarizes Piping Plovers foraging locomotion in the major habitats and ecosystems used by Piping Plovers along the Texas coast.. Foraging locomotion estimates represent the mean number seconds Piping Plovers spent in prolonged locomotion/minute in each location/habitat.

Location	Beaches			Sand Flats			Algal Flats			All Flats			All Habitats		
	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
Bay Ecosystem	47	7.0	0.72	140	1.1	0.24	1	0.0	--	141	1.1	0.24	188	2.6	0.32
Coastal Ecotone	83	8.3	0.80	16	2.5	1.01	83	1.3	0.23	99	1.5	0.26	182	4.6	0.46
Lagoon Ecosystem	24	5.6	0.99	11	0.9	0.56	34	2.2	0.55	45	1.9	0.45	69	3.2	0.50
All Locations	154	7.5	0.35	167	1.3	0.56	118	1.5	0.40	285	1.4	0.17	439	3.5	0.25

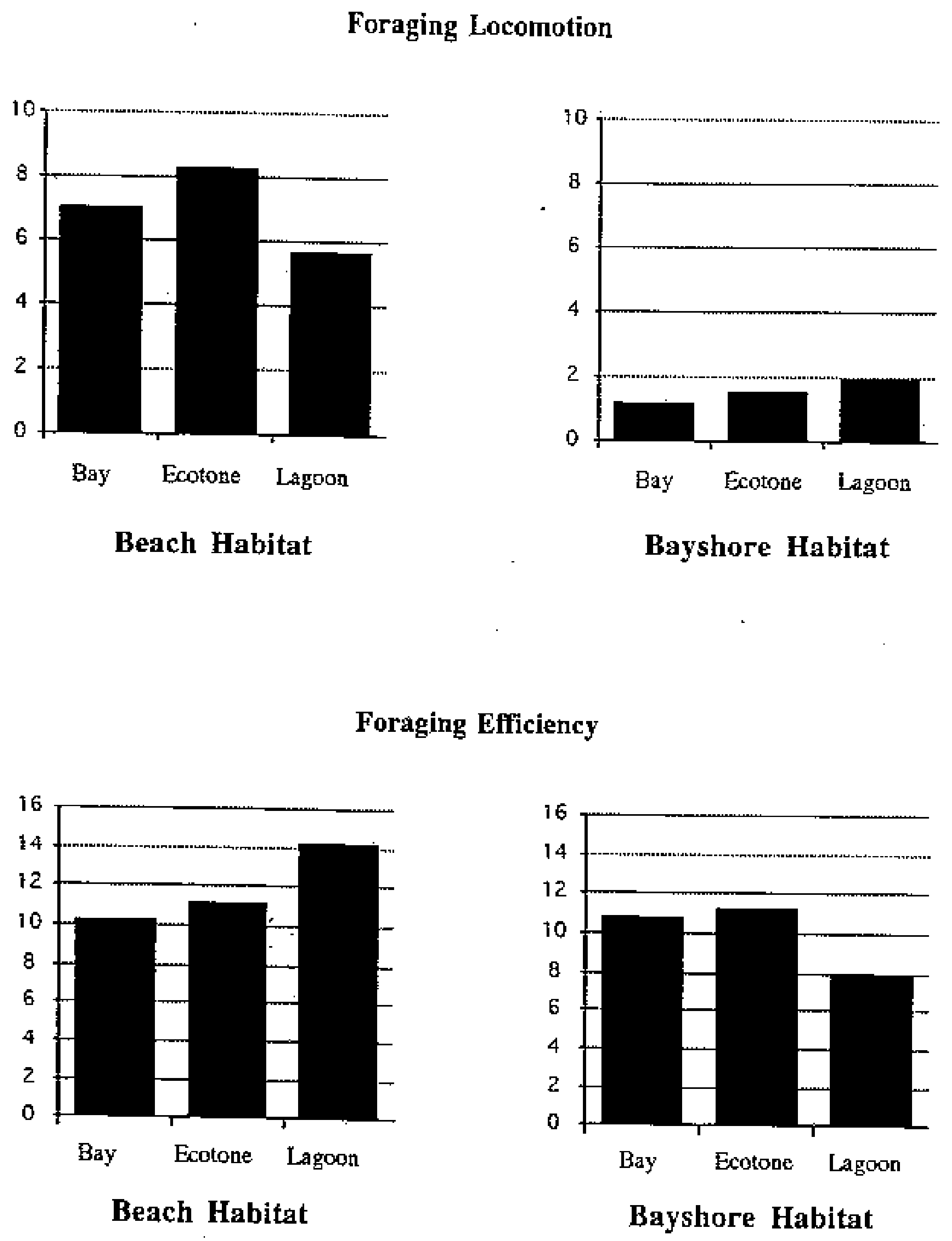


Figure 26. Mean foraging locomotion rates and mean foraging efficiencies of Piping Plovers among beach and bayshore habitats within the 2 ecosystems and the ecotone are illustrated in this figure. Foraging locomotion rates are represented as the number of seconds per minute spent in prolonged locomotion during foraging periods. Foraging efficiencies are represented as the number of animals captured/minute.

A single multi-factor ANOVA was performed for most of the relationships discussed below (a second test was run for the analysis of the effects of microhabitats). In this model, sand flats and algal flats were combined into the single data category "bayshore flats", allowing for a direct comparison between bayshore habitat and beach habitat. An analysis comparing sand flats and algal flats using data from the Mustang Island State Park North Area site (N = 77) indicated that there was no significant difference between foraging locomotion on sand flats and algal flats ($p = 0.7576$; data not shown). This was the only site where we were able to collect data associated with foraging Piping Plovers on both flat types during both the winter and migration seasons. The limited data set was due in large part to the limited availability and use of both sand and algal flats at study sites outside of the ecotone.

Data from the lagoon ecosystem were insufficient for entry into the model, due to the low frequency with which Piping Plovers foraged on beach habitat in the lagoon ecosystem. Therefore, we were only able to statistically compare foraging locomotion between the bay ecosystem and the ecotone.

Ecosystem Type - Analyses of our data suggest that plovers may spend more time in prolonged foraging locomotion in the ecotone than in the bay ecosystem, however, the difference was not significant ($p = 0.0785$; Table 11). Piping Plovers also spent more time in prolonged locomotion while foraging in the ecotone (4.64 seconds/minute) than in the lagoon ecosystem (2.90 sec/min), however we were unable to test this difference (see above).

Piping Plover Life Cycle Stage - We detected no significant difference in the foraging locomotion of Piping Plovers during the migratory and winter life cycle stages ($p = 0.3983$; Table 11).

Habitat Type - We observed Piping Plovers to spend significantly more time in prolonged locomotion while foraging on beach habitat than on bayshore habitat ($p = 0.0413$; Table 11). The difference between the two habitat types is more convincing when each ecosystem is considered independently. In the bay ecosystem, foraging Piping Plovers spent an average of 7.02 sec/min in prolonged locomotion on beach habitat, compared to only 1.13 sec/min on bayshore flats ($p = 0.0009$; Table 11). Similarly, in the ecotone, foraging Piping Plovers spent an average of 8.11 sec/min in prolonged locomotion on beach habitat, compared to only 1.48 sec/min on bayshore flats ($p = 0.0072$; Table 11). In the lagoon ecosystem, foraging Piping Plovers spent an average of 5.54 sec/min in prolonged locomotion on beach habitat, compared to 1.90 sec/min on bayshore flats, however, data were insufficient to test this difference statistically while also incorporating the potential effect of the life cycle parameter.

Microhabitat Type - The life cycle parameter was removed from the model for the analysis comparing microhabitats because it was not found to significantly affect Piping Plover foraging locomotion when considered in a model along with ecosystem type and habitat type. By removing the life cycle parameter, we were able to evaluate data from the lagoon ecosystem in the microhabitat analysis. We observed Piping Plovers to spend significantly more time in prolonged locomotion while feeding in the swash zone (SZ) than while feeding in the moist upper zone (MUZ; $p=0.0167$; data not shown). However, the differences between these microhabitats is less convincing when ecosystems are considered independently. Whereas there was a significant difference between foraging locomotion among the SZ and MUZ in the ecotone ($p=0.0167$; data not shown), the differences were not significant within bay ecosystem ($p=0.3045$; data not shown) or the lagoon ecosystem ($p=0.1788$; data not shown).

Table 11. Table summarizing the ANOVA results for the Piping Plover foraging ecology records, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for these comparisons. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Foraging aggression values represent the mean number of aggressions per minute. Foraging locomotion records represent the mean length of time spent in prolonged foraging locomotion (sec./min). Foraging efficiency records represent the mean number of animals captured per minute. (* = $p < 0.10$, ** = $p < 0.05$), *** = insufficient data for analysis.

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
All foraging aggression	winter vs. migration seasons	0.10 (293) vs. 0.11 (439)	0.11 (248) vs. 0.12 (285)	* 0.0393
	beach vs. bayshore habitats	0.08 (140) vs. 0.12 (592)	0.07 (102) vs. 0.13 (431)	0.5447
	bay vs. lagoon ecosystems	0.18 (383) vs. 0.04 (157)	0.18 (317) vs. 0.03 (64)	0.3955
	bay ecosystem vs. ecotone	0.18 (383) vs. 0.05 (192)	0.18 (317) vs. 0.03 (152)	0.3154
	ecotone vs. lagoon ecosystems	0.05 (192) vs. 0.04 (157)	0.03 (152) vs. 0.03 (64)	0.8016
Bay foraging aggression	winter vs. migration seasons	0.24 (116) vs. 0.14 (267)	0.24 (116) vs. 0.14 (201)	0.1332
	beach vs. bayshore habitats	0.05 (46) vs. 0.20 (337)	0.05 (40) vs. 0.20 (277)	0.1377
Ecotone foraging aggression	winter vs. migration seasons	0.00 (117) vs. 0.13 (75)	0.00 (105) vs. 0.10 (47)	* 0.0526
	beach vs. bayshore habitats	0.11 (85) vs. 0.00 (107)	0.08 (55) vs. 0.00 (97)	0.3000
Lagoon foraging aggression	winter vs. migration seasons	0.03 (60) vs. 0.04 (97)	0.02 (27) vs. 0.04 (37)	0.4501
	beach vs. bayshore habitats	0.00 (9) vs. 0.04 (148)	0.00 (7) vs. 0.04 (57)	0.7327
All Foraging locomotion	winter vs. migration seasons	3.20 (238) vs. 3.90 (203)	3.02 (190) vs. 4.26 (107)	0.3983
	beach vs. bayshore habitats	7.49 (154) vs. 1.37 (287)	7.25 (113) vs. 1.14 (184)	* 0.0413
	bay vs. lagoon ecosystems	2.60 (188) vs. 2.90 (62)	***	--
	bay vs. ecotone ecosystems	2.60 (188) vs. 4.64 (191)	2.29 (133) vs. 4.42 (164)	* 0.0785
	ecotone vs. lagoon ecosystems	4.64 (191) vs. 2.90 (62)	***	--

Table 11 continued.

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
Bay foraging locomotion	winter vs. migration seasons	2.22 (93) vs. 2.98 (95)	1.44 (65) vs. 3.11 (68)	0.5620
	beach vs. bayshore habitats	7.02 (47) vs. 1.13 (141)	6.26 (37) vs. 0.77 (96)	** 0.0009
Ecotone foraging locomotion	winter vs. migration seasons	3.94 (130) vs. 6.19 (61)	3.84 (125) vs. 6.27 (39)	0.4386
	beach vs. bayshore habitats	8.11 (90) vs. 1.48 (101)	7.73 (76) vs. 1.55 (80)	** 0.0072
Lagoon foraging locomotion	winter vs. migration seasons	2.90 (15) vs. 2.90 (47)	***	--
	beach vs. bayshore habitats	5.54 (17) vs. 1.90 (45)	***	--
All foraging efficiency	winter vs. migration seasons	11.83 (239) vs. 9.19 (439)	12.89 (211) vs. 8.99 (242)	* 0.0331
	beach vs. bayshore habitats	11.04 (140) vs. 10.11 (592)	10.91 (93) vs. 10.78 (360)	0.3726
	bay vs. lagoon ecosystems	10.75 (383) vs. 8.46 (157)	10.95 (254) vs. 10.06 (60)	0.3071
	bay vs. ecotone ecosystems	10.75 (383) vs. 11.05 (192)	10.95 (254) vs. 10.88 (139)	0.7859
	ecotone vs. lagoon ecosystems	11.05 (192) vs. 8.46 (157)	10.88 (139) vs. 10.06 (60)	0.3627
Bay foraging efficiency	winter vs. migration seasons	13.41 (116) vs. 9.17 (267)	14.04 (93) vs. 9.16 (161)	* 0.0833
	beach vs. bayshore habitats	10.17 (46) vs. 10.83 (337)	10.87 (36) vs. 10.96 (218)	0.2019
Ecotone foraging efficiency	winter vs. migration seasons	11.57 (117) vs. 10.35 (75)	11.90 (93) vs. 8.81 (46)	* 0.0985
	beach vs. bayshore habitats	10.91 (85) vs. 11.17 (107)	10.16 (50) vs. 11.28 (89)	0.6075
Lagoon foraging efficiency	winter vs. migration seasons	8.65 (60) vs. 8.37 (97)	12.28 (25) vs. 8.48 (35)	0.2679
	beach vs. bayshore habitats	16.18 (9) vs. 7.96 (148)	16.55 (7) vs. 9.20 (53)	* 0.0822

Foraging Efficiency

Piping Plovers captured an average of approximately 10 animals per minute during the non-breeding season at our study sites (Table 12). Foraging efficiencies were similar on beaches, sand flats, and algal flats (Table 12), and among the 2 ecosystems and the ecotone (Table 12; Figure 26).

A single multi-factor ANOVA was performed for most of the relationships discussed below (a second test was run for the analysis of the effects of microhabitats). In this model, sand flats and algal flats were combined into the single data category "bayshore flats", allowing for a direct comparison between bayshore habitat and beach habitat. An analysis comparing sand flats and algal flats using data from the Mustang Island State Park North Area site, the Packery Channel site and the South Padre Island site (N = 199) indicated that there was no significant difference between foraging efficiency on sand flats and algal flats (p=0.3919; data not shown). These were the only sites where we were able to collect data associated with foraging Piping Plovers on both sand flats and algal flats during both the winter and migration seasons. The limited data set was due in large part to the limited availability and use of both sand and algal flats at study sites outside of the ecotone.

Ecosystem Type - Analyses of our data suggest that Piping Plovers foraged with similar efficiency among both ecosystems and in the ecotone (p = 0.5456; data not shown). Pairwise comparisons of foraging efficiency among ecosystems indicated that there was no difference in foraging efficiency between the bay ecosystem and the lagoon ecosystem (p = 0.3071; Table 11), or between the ecotone and the bay ecosystem (p = 0.7859; Table 11), or the lagoon ecosystem (p = 0.3627; Table 11).

Piping Plover Life Cycle Stage - Our data suggest that Piping Plovers foraging significantly more efficiently during the winter period than during the migratory period (p = 0.0331; Table 11). However, the differences between these life cycles is less convincing when ecosystems are considered independently. The difference in foraging efficiency was not significant in the ecotone (p=0.2679; Table 11), nor were the differences quite significant within bay ecosystem (p=0.0822; Table 11) or the lagoon ecosystem (p=0.0985; Table 11).

Habitat Type - Piping Plovers appear to forage equally well on beach and bayshore habitat types (p=0.3726; Table 11). When ecosystems are considered independently, the difference in foraging efficiency among the habitat types were also not significant in the ecotone (p=0.6075; Table 11), the bay ecosystem (p=0.2019; Table 11) or the lagoon ecosystem (p=0.0822; Table 11).

Aggressive Behavior

Aggressive Interactions - We recorded the frequency of aggressive interactions in association with the foraging efficiency (FE) record (see Methods). The large majority of interactions we observed during the study were intraspecific. Although we did not record the species identity of the bird interacting with the Piping Plover subject during aggressions, some general observations can be made regarding interspecific aggressive interactions involving Piping Plovers. The majority of interspecific interactions we observed were between Piping Plovers and a congener, especially a Snowy Plover (*Charadrius alexandrinus*) or a Semipalmated Plover (*Charadrius semipalmatus*). Interspecific interactions were generally restricted to bayshore habitat, as *C. alexandrinus*, and *C. semipalmatus* only rarely utilized beaches as foraging habitat at

Table 12. This table summarizes Piping Plover foraging efficiency in the major habitats and ecosystems used by Piping Plovers along the Texas coast. Foraging efficiency estimates represent the mean number of animals of any type that was observed to be captured/minute.

Location	Beaches			Sand Flats			Algal Flats			All Flats			All Habitats		
	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE
Bay Ecosystem	40	10.2	(1.08)	264	10.9	(0.36)	8	8.2	(2.06)	272	10.8	(0.29)	312	10.7	(0.30)
Coastal Ecotone	76	11.1	(0.78)	33	9.3	(0.86)	62	12.2	(0.62)	95	11.2	(0.49)	171	11.1	(0.41)
Lagoon Ecosystem	11	14.2	(2.06)	39	6.6	(0.67)	98	8.5	(0.42)	137	8.0	(0.41)	148	8.4	(0.44)
All Locations	127	11.0	(0.61)	336	10.3	(0.29)	168	9.8	(0.31)	504	10.1	(0.22)	631	10.3	(0.22)

our study sites (data not shown).

On beaches, nearly all interactions were between two Piping Plovers. The intensity of the interactions varied from a controlled series of side-by-side pacing movements along an apparent territorial boundary, to a frantic aerial chase that occasionally led to a head-butt, or some other form of physical contact. The few interspecific interactions that we observed on beaches involving Piping Plovers usually were associated with Sanderling (*Calidris alba*). Sanderling often aggressively defended beach feeding territories from other Sanderling, but usually allowed Piping Plovers to forage within their territory without incident. Though we did not collect data to document the outcomes of interspecific interactions, Piping Plovers usually "won" interactions with Snowy Plovers, "lost" interactions with Sanderling, and "fought to a draw" with Semipalmated Plovers. We investigated the effects of Piping Plover life cycle, habitat type, and ecosystem type on the frequency of aggressive behavior.

Piping Plover Life Cycle Stage - Our data suggest that Piping Plovers were significantly more aggressive during the migratory period than during the winter period ($p = 0.0393$; Table 11). The seasonal shift in aggressive frequency is most pronounced on beach habitat, where plovers are much less aggressive during the winter period than during the migratory period ($p = 0.0072$; data not shown). No significant seasonal change in aggressive behavior was observed on bayshore habitat ($p = 0.8773$; data not shown).

The effect of life cycle on foraging aggressive frequency is less pronounced when the data from each ecosystem are considered independently. The difference in aggression frequency between the winter and migratory periods was not quite significant in the ecotone ($p=0.0526$; Table 11), and was not significant within bay ecosystem ($p=0.1332$; Table 11) or within the lagoon ecosystem ($p=0.4508$; Table 11).

Habitat Type - Our data suggest that, in general, Piping Plovers are equally aggressive on beach and bayshore habitat types ($p=0.5447$; Table 11). However, when data are viewed by life cycle, a difference is observed. We found Piping Plovers to be significantly more aggressive on bayshore habitat than on beach habitat during the winter period ($p = 0.0189$; data not shown). There was no difference between habitat types during the migratory period ($p = 0.5112$; data not shown). When data from each ecosystem are considered independently, the difference in foraging aggressive frequency between beaches and bayshore flats was not significant within the ecotone ($p = 0.3000$; Table 11), within the bay ecosystem ($p = 0.1377$; Table 11) or within the lagoon ecosystem ($p = 0.7327$; Table 11).

Ecosystem - In general, the frequency of foraging aggressive behavior involving Piping Plovers did not vary significantly among the 2 ecosystems and the ecotone ($p = 0.4914$; data not shown). Similarly, pairwise comparisons of aggressive behavior among ecosystems indicated that there was no difference in aggressive frequency between the bay ecosystem and the lagoon ecosystem ($p = 0.3955$; Table 11), or between the ecotone and the bay ecosystem ($p = 0.3154$; Table 11), or the ecotone and the lagoon ecosystem ($p = 0.8016$; Table 11).

However, our data suggest that life cycle and habitat type affect aggressive behavior (see above). When our observations on bayshore habitat are considered in isolation by life cycle stage, we observe significant difference between the ecosystems and the ecotone. When the bayshore habitat data from the winter period are used to compare foraging aggressive behavior, we find significantly higher frequencies of aggressive behavior in the bay ecosystem than in the ecotone ($p < 0.0001$; data not shown), or in the lagoon ecosystem (p = 0.0087; data not shown). The difference between aggression on bayshore habitat in the ecotone and the lagoon ecosystem is not significant during the winter period (p = 0.2849; data not shown). When the bayshore habitat data from just the migratory period are used to compare foraging aggressive behavior, we find significantly higher frequencies of aggressive behavior in the bay ecosystem than in the ecotone (p = 0.0004; data not shown), and in the lagoon ecosystem (p = 0.0002; data not shown). The difference between aggression on bayshore habitat in the ecotone and the lagoon ecosystem is not significant during the migratory period (p = 0.4616; data not shown). Thus, we observed Piping Plovers to engage in significantly higher frequencies of aggression on bayshore habitat in the bay ecosystem than in the ecotone or the lagoon ecosystem, and this difference was observed during the winter and migratory periods.

Prey Resources

In secondary objective #4, we focused on characterizing the potential prey resources among the habitats and ecosystems used by Piping Plovers along the Texas Gulf Coast. Throughout this section, these densities will be described as "prey densities", however, they accurately reflect only "potential prey densities", because we did not assess the availability of each prey group to Piping Plovers.

To accomplish secondary objective #4, we sampled animal populations either from areas used by foraging Piping Plovers at the time of sample collection, or from microhabitats in which we consistently observed foraging Piping Plovers. Because Piping Plovers forage on prey occurring both within and above the ground (pers. obs., T. Eubanks Fermata Inc., Austin, TX pers. comm.), we employed 3 general sampling techniques to investigate prey occurring within and between both strata. Our approach sampled prey types associated with the 3 major vertical strata associated with bayshore habitat used by Piping Plovers: (1) macrobenthic prey, (2) surface prey, and (3) emergent prey from within algal mats (on algal flat habitats only). Sample strategies consisted of soil cores (density of benthic prey), sticky traps (relative abundance of surface prey), visual surveys using a spotting scope (density of surface prey), and incubated algal cores (density of emergent prey).

Total macrobenthic animal populations

Macrobenthic prey densities ranged from approximately 1300 animals/square meter to nearly 4000 animals/square meter on beach habitat at our sites (Table 13). Macrobenthic animal densities generally were highest in the bay ecosystem, lowest in the lagoon ecosystem, and intermediate in the ecotone (Table 13; Figures 27 and 28). This relationship was evident for average polychaete densities (Figure 28) but not for average crustacean densities or average insect densities (Figure 29). Polychaetes were generally more numerous than crustaceans on beaches in the bay ecosystem, whereas the reverse was observed in the ecotone (Table 13; Figure 27). In general, polychaetes and crustaceans were collected in approximately equal densities from beaches with the lagoon ecosystem (Table 13; Figure 27)

On bayshore habitat, macrobenthic animal densities ranged from only about 100 animals/square meter at Laguna Atascosa NWR to over 7000 animals/square meter at the Big Reef site (Table 14). Macrobenthic animal densities generally were highest in the bay ecosystem, lowest in the lagoon ecosystem, and intermediate in the ecotone (Table 14; Figures 28 and 30). Polychaetes were generally more numerous than crustaceans on

Table 13. The mean macrobenthic densities of annelids, crustaceans and total prey animals occuring in beach habitat among the study sites are presented in this table. The densities represent estimates of the mean number of animals per square meter based upon core samples collected along transects associated with foraging Piping Plovers.

	N	Annelids	Crustaceans	Total
Study Location				
Bolivar Flat	100	1577.5 (182.81)	1710.8 (228.28)	3304.1 (347.76)
Big Reef	35	3383.5 (420.16)	490.7 (93.34)	3887.2 (385.46)
San Luis Pass	155	2140.4 (229.62)	1278.7 (197.23)	3425.0 (343.51)
Estuarine Bay Ecosystem	**290**	**2096.3 (149.96)**	**1332.6 (133.53)**	**3439.1 (223.85)**
East Flats	35	678 (117.20)	1607.8 (297.32)	2298.7 (338.21)
MISPN	165	920.4 (111.93)	880.7 (170.56)	1845.0 (222.03)
MISPS	52	1799.3 (236.41)	1303.9 (259.97)	3155.3 (307.45)
Packery Channel	175	732.2 (70.84)	2005.6 (241.97)	2783.0 (250.83)
Central Coastal Ecotone	**427**	**930.5 (62.24)**	**1452.9 (127.65)**	**2426.2 (143.44)**
Brazos Island	45	693.1 (121.98)	597.64 (117.18)	1295.7 (166.04)
South Padre Island	45	783.5 (118.37)	838.71 (106.20)	1622.2 (174.66)
Hypersaline Lagoon Ecosystem	**90**	**738.3 (84.64)**	**718.2 (79.66)**	**1459.0 (121.06)**

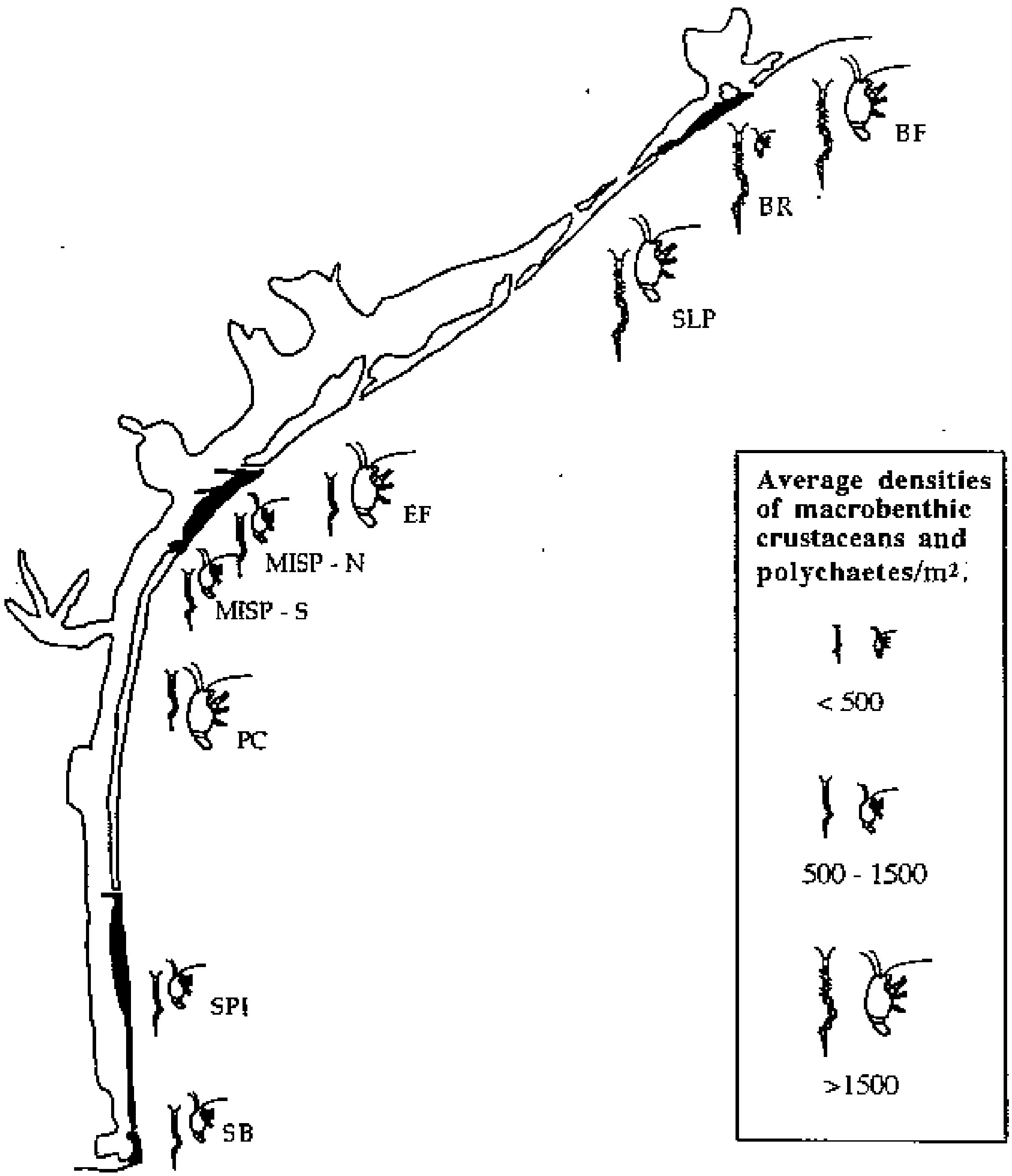
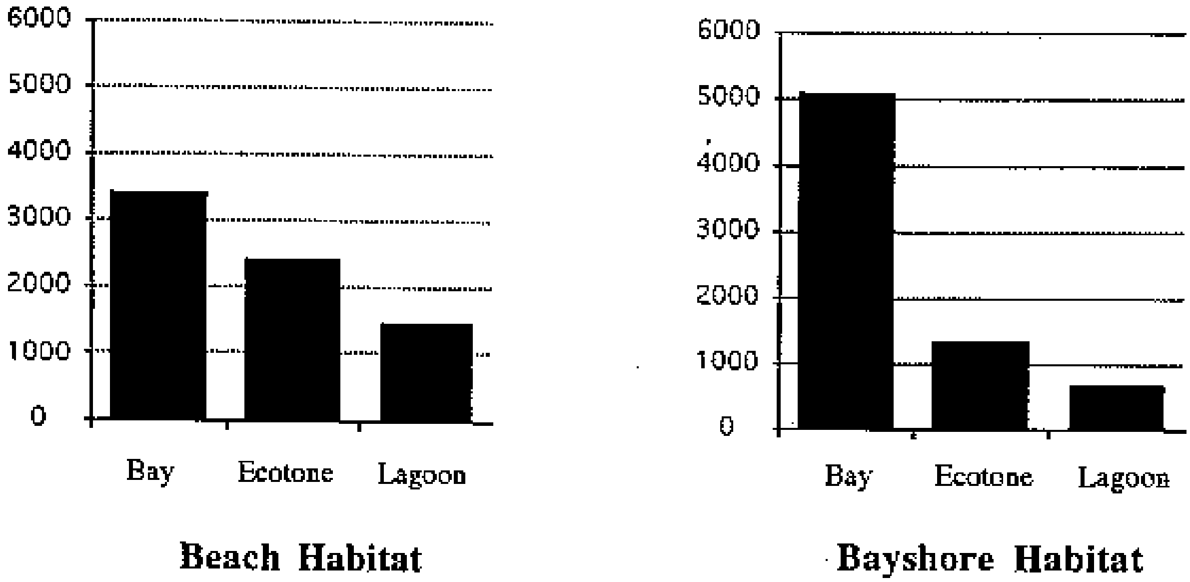


Figure 27. Mean densities of macrobenthic crustaceans and polychaetes collected in core samples associated with foraging Piping Plovers on beach habitat are illustrated in this figure. Densities are represented as the number of animals/m^2.

= crustaceans, = polychaetes.

Total Macrobenthic Density



Polychaete Density

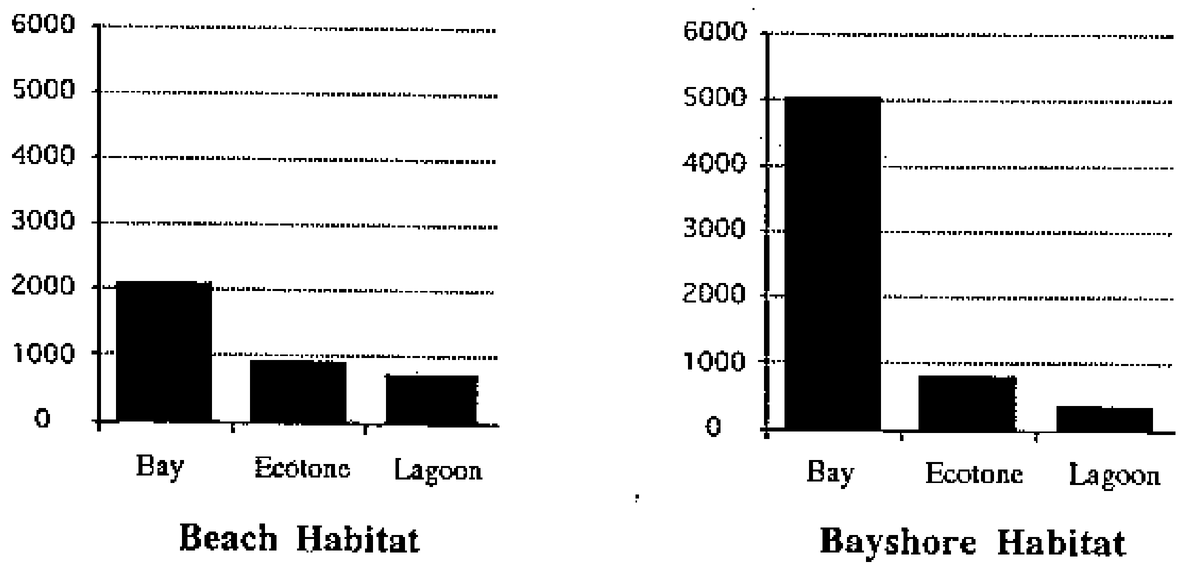


Figure 28. Mean total macrobenthic densities and mean polychaete densities among beach and bayshore habitats within the 2 ecosystems and the ecotone are illustrated in this figure. Densities are represented as the number of animals/ m^2.

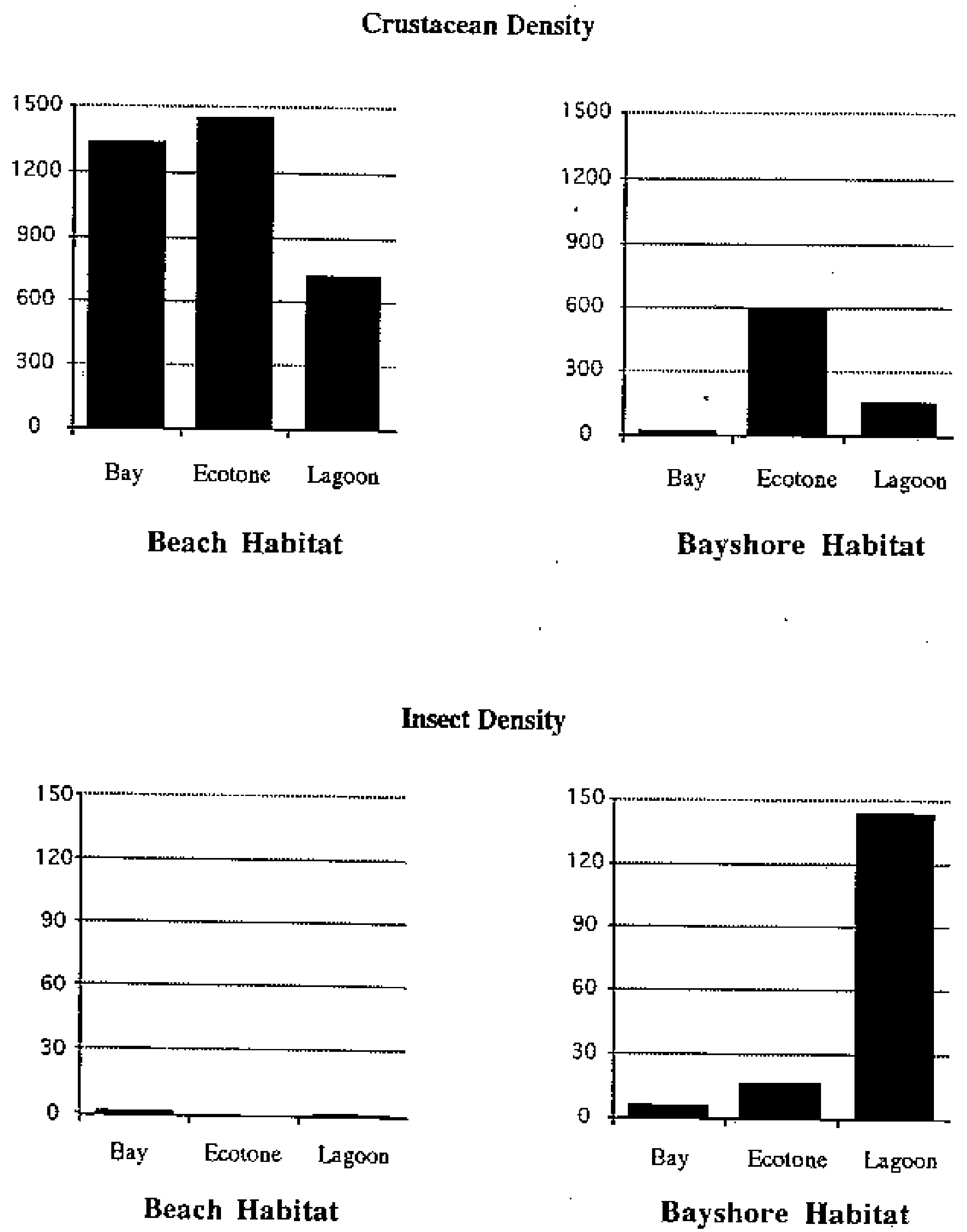


Figure 29. Mean crustacean densities and mean insect densities among beach and bayshore habitats within the 2 ecosystems and the ecotone are illustrated in this figure. Densities are represented as the number of animals/m^2.

Table 14 . The mean macrobenthic densities of annelids, crustaceans, insects (primarily larva) and total prey animals occuring in bayshore habitat among the study sites are presented in this table. The densities represent estimated of the mean number of animals per square meter based upon core samples collected along transects associated with foraging Piping Plovers.

Study Location	N	Annelids		Crustaceans		Insects		Total	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Bolivar Flats	195	5997.7	(386.97)	11.6	(6.31)	0.0	(--)	6009.3	(386.71)
Big Reef	105	7133.0	(665.87)	30.1	(9.21)	6.5	(4.79)	7173.9	(664.27)
San Luis Pass	250	3418.0	(187.76)	19.9	(7.02)	10.8	(3.56)	3448.8	(186.20)
Bay Ecosystem	**550**	**5041.9**	**(215.31)**	**18.9**	**(4.28)**	**6.2**	**(1.87)**	**5067.7**	**(214.77)**
East Flats	56	2659.3	(473.16)	1184.2	(312.42)	0.0	(--)	1953.3	(417.58)
MISP North Area	127	731.4	(104.10)	197.5	(46.38)	40.9	(11.96)	969.8	(128.19)
MISP South Area	10	339.0	(96.77)	316.4	(107.60)	0.0	(--)	655.4	(163.15)
Packery Flats	218	577.4	(82.77)	774.4	(204.70)	3.1	(1.79)	1357.0	(247.94)
Coastal Ecotone	**411**	**784.2**	**(74.03)**	**596.5**	**(121.12)**	**15.5**	**(4.22)**	**1301.6**	**(149.24)**
LANWR	85	0.0	(--)	0.0	(--)	109.0	(24.40)	109.0	(24.40)
South Bay East Area	90	55.2	(24.30)	155.7	(68.10)	178.3	(28.70)	389.2	(84.74)
South Padre Island	150	762.2	(142.72)	230.5	(43.68)	140.1	(15.66)	1096.9	(154.19)
Lagoon Ecosystem	**325**	**350.2**	**(68.87)**	**149.5**	**(28.02)**	**142.6**	**(12.53)**	**642.5**	**(78.81)**

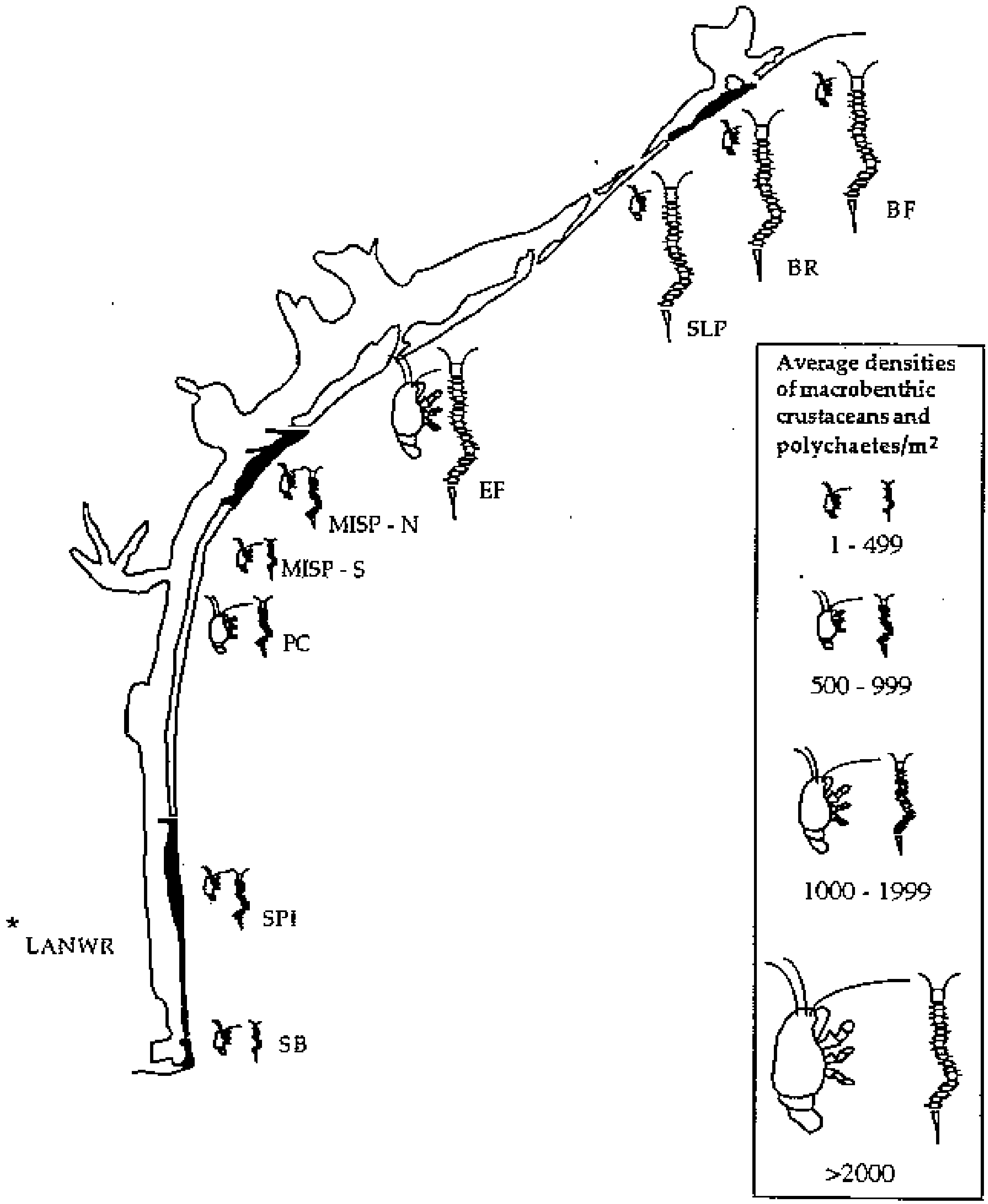


Figure 30. Mean densities of macrobenthic crustaceans and polychaetes captured in core samples associated with foraging Piping Plovers in all bayshore habitats at each study site are presented in this figure. (*) No crustaceans or polychaetes were captured in core samples at LANWR.

 = crustaceans,  = polychaetes.

bayshore flats in the bay ecosystem (Table 14; Figure 30). In general, crustaceans were collected at higher densities in the ecotone than in either ecosystem (Table 14; Figure 30), and insects (predominantly larvae) were collected at much higher densities in the lagoon ecosystem than in either the bay ecosystem or the ecotone (Table 14; Figures 29 and 31).

We performed a 3 sets of 4 ANOVAs to investigate the effects of spatial, temporal and habitat variables on macrobenthic prey densities. In one ANOVA set, we investigated the effects of life cycle, habitat type, and ecosystem on the density of macrobenthic potential prey in samples collected where Piping Plovers were feeding (used samples). Within another set of analyses, we compared macrobenthic prey density from used and unused samples. In a third ANOVA set, we compared the macrobenthic prey densities on the mainland and barrier island landforms using the data we collected from bayshore habitat in the lagoon ecosystem. For each set, we performed 4 different ANOVAs to specifically address changes in either total prey density, polychaete density, crustacean density, or insect density. We first present the results for total prey density, and follow with a summary of selected results for each of the specific prey types.

The effects of life cycle, habitat type and ecosystem on total macrobenthic prey density - Our samples suggest that there was no difference in prey densities among the winter and migratory periods ($p = 0.1556$; Table 15). When beach data are considered alone, the prey density did not differ significantly between the winter and migratory periods ($p = 0.3421$; Table 15). However, on bayshore habitat, prey densities were significantly higher during the winter period ($p = 0.0125$; Table 15). When data from each ecosystem were considered independently, the difference in prey density between the winter period and migratory period was significant within the bay ecosystem ($p = 0.0051$; Table 15), but was not significantly different within the ecotone ($p = 0.2131$; Table 15) or within the lagoon ecosystem ($p = 0.7107$; Table 15).

Our samples suggest that beach habitat supported significantly higher densities of prey in areas used by Piping Plovers than did bayshore habitat ($p = 0.0188$: Table 15). When data were evaluated by life cycle, we found prey densities to be significantly higher on beach habitat than on bayshore habitat during the migratory period ($p = 0.0030$; Table 15) and during the winter period ($p = 0.0361$; Table 15). When data from each ecosystem were considered independently, the difference in prey density between beaches and bayshore flats was not significant within the bay ecosystem ($p = 0.2222$; Table 15), but densities were significantly higher on beach habitat than bayshore habitat within the ecotone ($p = 0.0172$; Table 15) and within the lagoon ecosystem ($p = 0.0142$; Table 15).

We observed a significant difference in prey densities among the 2 ecosystems and the ecotone ($p = 0.0050$: Table 15). The samples we collected from the bay ecosystem supported significantly higher densities of prey in areas used by Piping Plovers that did samples from the ecotone ($p = 0.0034$; Table 15) or the lagoon ecosystem ($p = 0.0056$; Table 15). There was no apparent difference between the prey densities in the ecotone and the lagoon ecosystem ($p = 0.7339$; Table 15).

Comparison of used vs. unused soil core samples for total macrobenthic density - Unused samples were collected in beach habitat only (see Methods). We used a separate ANOVA to compare unused samples and used samples. We observed significantly higher densities of prey within used beach samples than in unused samples ($p = 0.0057$: Table 15). When data from each ecosystem were considered independently, we observed a significant difference in prey density between used and

Table 15 continued.

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores migratory season only	beach vs. bayshore	2469 (397) vs. 2176 (561)	2393 (350) vs. 2733 (536)	** 0.0030
	bay vs. lagoon	2912 (445) vs. 655 (175)	2912 (445) vs. 747 (291)	** 0.0283
	bay vs. ecotone	2912 (445) vs. 2340 (338)	2912 (445) vs. 2227 (415)	* 0.0524
	ecotone vs lagoon	2340 (338) vs. 655 (175)	2227 (291) vs. 747 (150)	0.2817
Used soil cores bay ecosystem only	winter vs migratory	6301 (395) vs. 2912 (445)	6301 (395) vs. 2912 (445)	** 0.0051
	beach vs. bayshore	3439 (290) vs. 5068 (550)	3439 (290) vs. 5068 (550)	0.2222
Used soil cores ecotone only	winter vs migratory	1560 (500) vs. 2340 (338)	1551 (485) vs. 2227 (415)	0.2131
	beach vs. bayshore	2426 (427) vs. 1302 (411)	2325 (375) vs. 1318 (401)	** 0.0172
Used soil cores lagoon ecosystem only	winter vs migratory	940 (240) vs. 655 (175)	1215 (180) vs. 747 (150)	0.7107
	beach vs. bayshore	1459 (90) vs. 643 (325)	1459 (90) vs. 831 (240)	** 0.0142
	mainland vs. barriers	109 (85) vs. 1003 (330)	109 (85) vs. 1003 (330)	0.1755
All samples	used vs. unused	2682 (870) vs. 1343(2360)	2700 (772) vs. 1398(1476)	** 0.0057

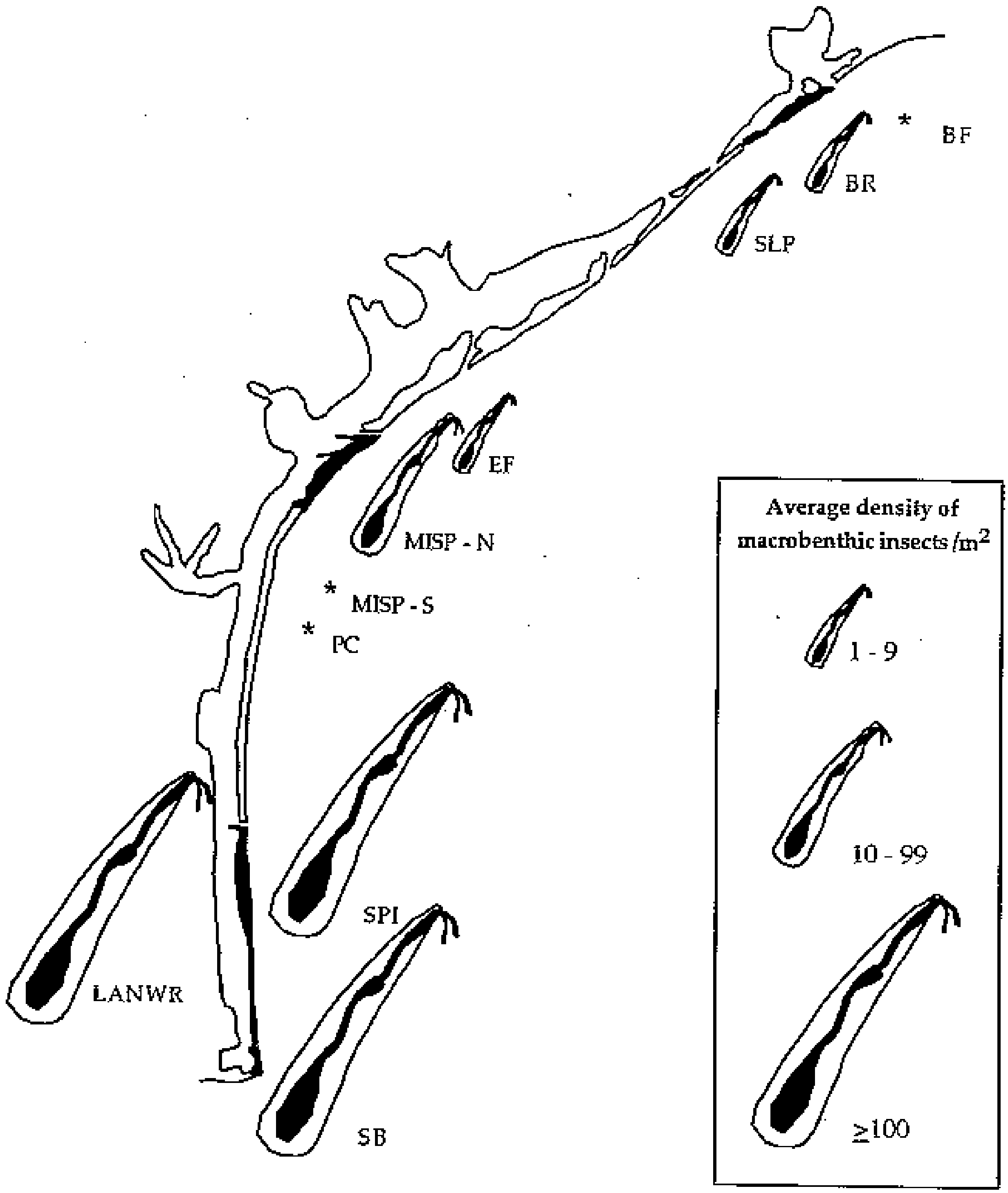


Figure 31. Mean densities of macrobenthic insect larvae and pupae captured in core samples associated with foraging Piping Plovers in all bayshore habitats at each study site. Figures of fly larvae of increasing dimension reflect arbitrary ranks of insect larvae and insect pupae densities. Densities are represented as the number of insects/m^2. (*) - No larvae were captured at BF, MISPS, or PC.

Table 15. Table summarizing the ANOVA results for total macrobenthic density, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Prey densities are represented as the mean # animals/m². (* = p < 0.10, ** = p < 0.05)

Data Type	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: full complement of samples	winter vs. migratory	3078(1135) vs. 2297 (958)	3264(1060) vs. 2320 (886)	0.1556
	beach vs. bayshore	2682 (807) vs. 2745(1286)	2650 (755) vs. 2951 (1191)	** 0.0188
	ecosystem:			** 0.0050
	bay vs. lagoon	4505 (840) vs. 820 (415)	4505 (840) vs. 1003 (330)	** 0.0056
	bay vs. ecotone	4505 (840) vs. 1875 (838)	4505 (840) vs. 1805 (776)	** 0.0034
	ecotone vs. lagoon	1875 (838) vs. 820 (415)	1805 (776) vs. 1003 (330	0.7339
Used soil cores: bayshore habitat only	winter vs migratory	3186 (725) vs. 2176 (561)	3507 (655) vs. 2273 (536)	** 0.0125
	bay vs. lagoon	5068 (550) vs. 643 (325)	5068 (550) vs. 831 (240)	**<0.0001
	bay vs. ecotone	5068 (550) vs. 1302 (411)	5068 (550) vs. 1318 (401)	**<0.0001
	ecotone vs lagoon	1302 (411) vs. 643 (643)	1318 (401) vs. 831 (240)	0.2544
Used soil cores: beach habitat only	winter vs migratory	2889 (397) vs. 2469 (397)	2872 (385) vs. 2393 (350)	0.3421
	bay vs. lagoon	3439 (290) vs. 1459 (90)	3439 (290) vs. 1459 (90)	* 0.0532
	bay vs. ecotone	3439 (290) vs. 2426 (427)	3439 (290) vs. 2325 (375)	** 0.0134
	ecotone vs lagoon	2426 (427) vs. 1459 (90)	2325 (375) vs. 1459 (180)	0.9545
Used soil cores: winter season only	beach vs. bayshore	2889 (410) vs. 3186 (725)	2872 (405) vs. 3506 (655)	** 0.0361
	bay vs. lagoon	6301 (395) vs. 940 (240)	6301 (395) vs. 1215 (180)	** 0.0010
	bay vs. ecotone	6301 (395) vs. 1560 (500)	6301 (395) vs. 1551 (485)	** 0.0009
	ecotone vs lagoon	1560 (500) vs. 940 (240)	1551 (485) vs. 1215 (180)	0.6465

unused samples within the bay ecosystem ($p = 0.0082$; data not shown), and within the ecotone ($p = 0.0636$; data not shown) but observed no difference in samples collected from the lagoon ecosystem ($p = 0.1652$; data not shown).

The effect of landform on total macrobenthic density - We observed no difference between bayshore prey densities among used samples in the mainland and barrier island landforms ($p = 0.1755$; Table 15).

Macrobenthic polychaetes

The effects of life cycle, habitat type and ecosystem on macrobenthic polychaete density - Our samples suggest that there was no difference in polychaete densities collected during the winter and migratory periods ($p = 0.1125$: Table 16). When beach data were considered alone, polychaete density did not differ significantly between the winter and migratory periods ($p = 0.3502$; Table 16). However, on bayshore habitat, polychaete densities were significantly higher during the winter period ($p = 0.0553$; Table 16).

Our samples suggest that beach and bayshore habitats supported similar densities of prey in areas used by Piping Plover ($p = 0.6008$: Table 16). When data were evaluated by life cycle, we found prey densities to be similar in both habitats during the migratory period ($p = 0.3545$; Table 16) and during the winter period ($p = 0.8201$; Table 16).

We observed a significant difference in polychaete densities among the 2 ecosystems and the ecotone ($p = 0.0027$; Table 16). The samples we collected from the bay ecosystem supported significantly higher densities of polychaetes in areas used by Piping Plovers that did samples from the ecotone ($p = 0.0042$; Table 16) or the lagoon ecosystem ($p = 0.0024$; Table 16). There was no apparent difference between the prey densities in the ecotone and the lagoon ecosystem ($p = 0.3188$; Table 16).

Comparison of used vs. unused soil core samples for macrobenthic polychaete density - We observed significantly higher densities of polychaetes within used beach samples than in unused samples ($p = 0.0016$: Table 16).

The effect of landform on macrobenthic polychaete density - We observed no difference between bayshore prey densities among used samples in the mainland and barrier island landforms ($p = 0.4865$; Table 16).

Macrobenthic crustaceans

The effects of life cycle, habitat type and ecosystem on macrobenthic crustacean density - Our samples suggest that there was no difference in crustacean densities collected during the winter and migratory periods ($p = 0.2457$: Table 17). When beach data were considered alone, crustacean density did not differ significantly between the winter and migratory periods ($p = 0.7708$; Table 17). However, on bayshore habitat, crustacean densities were significantly higher during the winter period ($p = 0.0368$; Table 17).

Our samples suggest that beach habitat supported much higher densities of crustaceans in areas used by Piping Plovers than did bayshore habitat ($p = 0.0003$: Table 17). When data were evaluated by life cycle, we found crustaceans to occur at much higher densities on beaches than bayshore habitat during during the migratory period ($p < 0.0001$; Table 17) and during the winter period ($p = 0.0002$; Table 17).

We observed no difference in crustacean densities among the 2 ecosystems and the ecotone ($p = 0.4354$; Table 17). The samples we collected from the bay ecosystem

Table 16. Table summarizing the ANOVA results for total polychaete density, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Prey densities are represented as the mean # polychaetes/m^2. (* = $p < 0.10$, ** = $p < 0.05$)

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: all used samples	winter vs migratory	2361(1135) vs. 1699 (958)	2511(1060) vs. 1751 (886)	0.1125
	beach vs. bayshore	1328 (807) vs. 2530(1286)	1295 (755) vs. 2734 (1191)	0.6008
	ecosystems			** 0.0027
	bay vs. lagoon	4024 (840) vs. 435 (415)	4025 (840) vs. 545 (330)	** 0.0024
	bay vs. ecotone	861 (840) vs. 861 (838)	4025 (840) vs. 803 (776)	** 0.0042
	ecotone vs lagoon	861 (838) vs. 435 (415)	803 (776) vs. 545 (330)	0.3188
Used soil cores bayshore habitat only	winter vs migratory	2905 (725) vs. 2031 (561)	3213 (655) vs. 2130 (536)	* 0.0553
	bay vs. lagoon	5042 (550) vs. 350 (325)	5042 (550) vs. 475 (240)	** 0.0002
	bay vs. ecotone	5042 (550) vs. 784 (411)	5042 (550) vs. 796 (401)	** 0.0045
	ecotone vs lagoon	784 (427) vs. 350 (325)	796 (401) vs. 475 (240)	** 0.0344
Used soil cores: beach habitat only	winter vs migratory	1406 (397) vs. 1248 (397)	1385 (405) vs. 1192 (350)	0.3502
	bay vs. lagoon	2096 (290) vs. 738 (90)	2096 (290) vs. 738 (90)	0.1688
	bay vs. ecotone	2096 (290) vs. 930 (427)	2096 (290) vs. 810 (375)	** 0.0280
	ecotone vs lagoon	930 (427) vs. 738 (90)	810 (375) vs. 738 (90)	0.5648
Used soil cores - winter season only	beach vs. bayshore	1406 (410) vs. 2905 (725)	1385 (405) vs. 3213 (655)	0.8201
	bay vs. lagoon	5536 (395) vs. 576 (240)	5537 (395) vs. 768 (180)	** 0.0008
	bay vs. ecotone	5536 (395) vs. 693 (500)	5537 (395) vs. 675 (485)	** 0.0026
	ecotone vs lagoon	930 (500) vs. 576 (240)	675 (485) vs. 768 (180)	0.7203

Table 16 continued.

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: migratory season only	beach vs. bayshore	1248 (397) vs. 2031 (561)	1192 (350) vs. 2130 (536)	0.3545
	bay vs. lagoon	2683 (445) vs. 240 (175)	2683 (445) vs. 280 (150)	** 0.0083
	bay vs. ecotone	2683 (445) vs. 1124 (338)	2683 (445) vs. 1030 (291)	** 0.0218
	ecotone vs lagoon	1124 (240) vs. 240 (175)	1030 (291) vs. 280 (150)	0.1409
Used soil cores: bay ecosystem only	winter vs migratory	5536 (395) vs. 2683 (445)	5537 (395) vs. 2683 (445)	** 0.0092
	beach vs. bayshore	2096 (290) vs. 5042 (550)	2096 (290) vs. 5042 (550)	* 0.0969
Used soil cores: ecotone only	winter vs migratory	693 (500) vs. 1124 (338)	675 (485) vs. 1030 (291)	0.5005
	beach vs. bayshore	930(1135) vs. 784 (958)	810 (375) vs. 796 (401)	0.6643
Used soil cores: lagoon ecosystem only	winter vs migratory	576(1135) vs. 240 (958)	768 (180) vs. 280 (150)	0.5637
	beach vs. bayshore	738 (90) vs. 350 (325)	738 (90) vs. 475 (240)	* 0.0517
	mainland vs. barriers	0 (85) vs. 545 (330)	0 (85) vs. 546 (330)	0.4865
All samples:	used vs. unused	1323 (807) vs. 757(2360)	1357 (772) vs. 650(1476)	** 0.0016

Table 17. Table summarizing the ANOVA results for total crustacean density, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Prey densities are represented as the mean # crustaceans/m^2. (* = p < 0.10, ** = p < 0.05)

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores all used samples	winter vs migratory	700(1135) vs. 608 (958)	741(1060) vs. 587 (886)	0.2457
	beach vs. bayshore	1328 (807) vs. 228 (958)	1329 (755) vs. 244 (1191)	** 0.0003
	ecosystems			0.4354
	bay vs. lagoon	472 (840) vs. 272 (415)	472 (840) vs. 343 (330)	0.2397
	bay vs. ecotone	472 (840) vs. 1049 (838)	472 (840) vs. 1042 (776)	0.4242
	ecotone vs lagoon	1049 (838) vs. 272 (415)	1042 (776) vs. 343 (330)	0.8901
Used soil cores: bayshore habitat only	winter vs migratory	261 (725) vs. 183 (561)	285 (655) vs. 192 (536)	** 0.0368
	bay vs. lagoon	19 (550) vs. 150 (325)	19 (550) vs. 202 (240)	0.1207
	bay vs. ecotone	19 (550) vs. 597 (325)	19 (550) vs. 604 (401)	0.2432
	ecotone vs lagoon	597 (325) vs. 150 (325)	604 (401) vs. 202 (240)	0.7801
Used soil cores: beach habitat only	winter vs migratory	1465 (397) vs. 1186 (397)	1468 (405) vs. 1169 (350)	0.7708
	bay vs. lagoon	1333 (290) vs. 718 (90)	1333 (290) vs. 718 (90)	0.4047
	bay vs. ecotone	1333 (290) vs. 1453 (427)	1333 (290) vs. 1474 (375)	0.7720
	ecotone vs lagoon	1453 (427) vs. 718 (90)	1474 (375) vs. 718 (90)	0.5102
Used soil cores: winter season only	beach vs. bayshore	1465 (410) vs. 261 (725)	1468 (405) vs. 285 (655)	** 0.0002
	bay vs. lagoon	760 (395) vs. 264 (240)	760 (395) vs. 352 (180)	0.3063
	bay vs. ecotone	760 (395) vs. 865 (500)	760 (395) vs. 873 (485)	0.9102
	ecotone vs lagoon	865 (500) vs. 264 (240)	873 (485) vs. 352 (180)	0.4935

Table 17 continued.

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: migratory season only	beach vs. bayshore	1186 (397) vs. 183 (561)	1169 (350) vs. 192 (536)	**<0.0001
	bay vs. lagoon	217 (445) vs. 285 (175)	217 (445) vs. 333 (150)	0.3381
	bay vs. ecotone	217 (445) vs. 1335 (338)	217 (445) vs. 1338 (291)	** 0.0331
	ecotone vs lagoon	1335 (338) vs. 285 (175)	1338 (291) vs. 333 (150)	0.4006
Used soil cores: bay ecosystem only	winter vs migratory	760 (395) vs. 217 (445)	760 (395) vs. 217 (445)	0.9709
	beach vs. bayshore	1333 (290) vs. 19 (550)	1333 (290) vs. 19 (550)	** 0.0009
Used soil cores: ecotone only	winter vs migratory	865 (500) vs. 1335 (338)	873 (485) vs. 1338 (291)	0.2185
	beach vs. bayshore	1453 (427) vs. 597 (411)	1474 (375) vs. 604 (401)	** 0.0372
Used soil cores: lagoon ecosystem only	winter vs migratory	264 (240) vs. 285 (175)	352 (180) vs. 333 (150)	0.9850
	beach vs. bayshore	718 (90) vs. 150 (325)	718 (90) vs. 202 (240)	** 0.0062
	mainland vs. barriers	0 (85) vs. 343 (330)	0 (85) vs. 343 (330)	0.1924
All samples	used vs. unused	1327 (807) vs. 503(2360)	1315 (772) vs. 733(1476)	** 0.0235

and the lagoon ecosystem supported similar densities of crustaceans in areas used by Piping Plovers ($p = 0.2397$; Table 17) There was no apparent difference between the crustacean densities in the ecotone and the bay ($p = 0.4242$; Table 17) or lagoon ecosystems ($p = 0.8901$; Table 17).

Comparison of used vs. unused soil core samples for macrobenthic crustacean density - We observed significantly higher densities of crustaceans within used beach samples than in unused samples ($p = 0.0235$: Table 17).

The effect of landform on macrobenthic crustacean density - We observed no difference between bayshore crustacean densities among used samples in the mainland and barrier island landforms ($p = 0.1924$; Table 17).

Macrobenthic Insects

The effects of life cycle, habitat type and ecosystem on macrobenthic insect density - Our samples suggest that there was no difference in insect densities collected during the winter and migratory periods ($p = 0.1577$; Table 18). Insect density did not differ significantly between the winter and migratory periods on beach habitat ($p = 0.6479$; Table 18) or on bayshore habitat ($p = 0.2325$; Table 18).

Our samples suggest that bayshore habitats supported significantly higher densities of insects than beach habitat in areas used by Piping Plover ($p = 0.0001$; Table 18). When data were evaluated by life cycle, we found insects to occur at much higher densities on bayshore habitat than on beach habitat during during the migratory period ($p < 0.0001$; Table 18) and during the winter period ($p = 0.0001$; Table 18).

We observed a significant difference in insect densities among the 2 ecosystems and the ecotone ($p < 0.0001$; Table 18). The samples we collected from the lagoon ecosystem supported significantly higher densities of insects in areas used by Piping Plovers that did samples from the bay ecosystem ($p < 0.0001$; Table 18) or the ecotone ($p < 0.0001$; Table 18). There was no apparent difference between the insect densities in the ecotone and the bay ecosystem ($p = 0.3870$; Table 18).

Comparison of used vs. unused soil core samples for macrobenthic insect density - We observed similar densities of insects within used and unused beach samples ($p = 0.8331$: Table 18).

The effect of landform on macrobenthic insect density - We observed higher bayshore insect densities among used samples from the barrier islands than from mainlands ($p = 0.0712$; Table 18).

Surface Prey

We performed 2 ANOVAs to investigate the effects of spatial, temporal and habitat variables on macrobenthic prey densities. In one ANOVA, we investigated the effects of life cycle, habitat type, and ecosystem on the abundance of surface prey collected using sticky traps deployed where Piping Plovers were feeding. In a second ANOVA, we investigated the effects of life cycle, habitat type, and ecosystem on the density of surface prey as appraised by spotting scope surveys of areas where Piping Plovers were feeding. We first present the results for surface prey abundance (sticky trap data), and follow with a summary of surface prey density (spotting scope survey data).

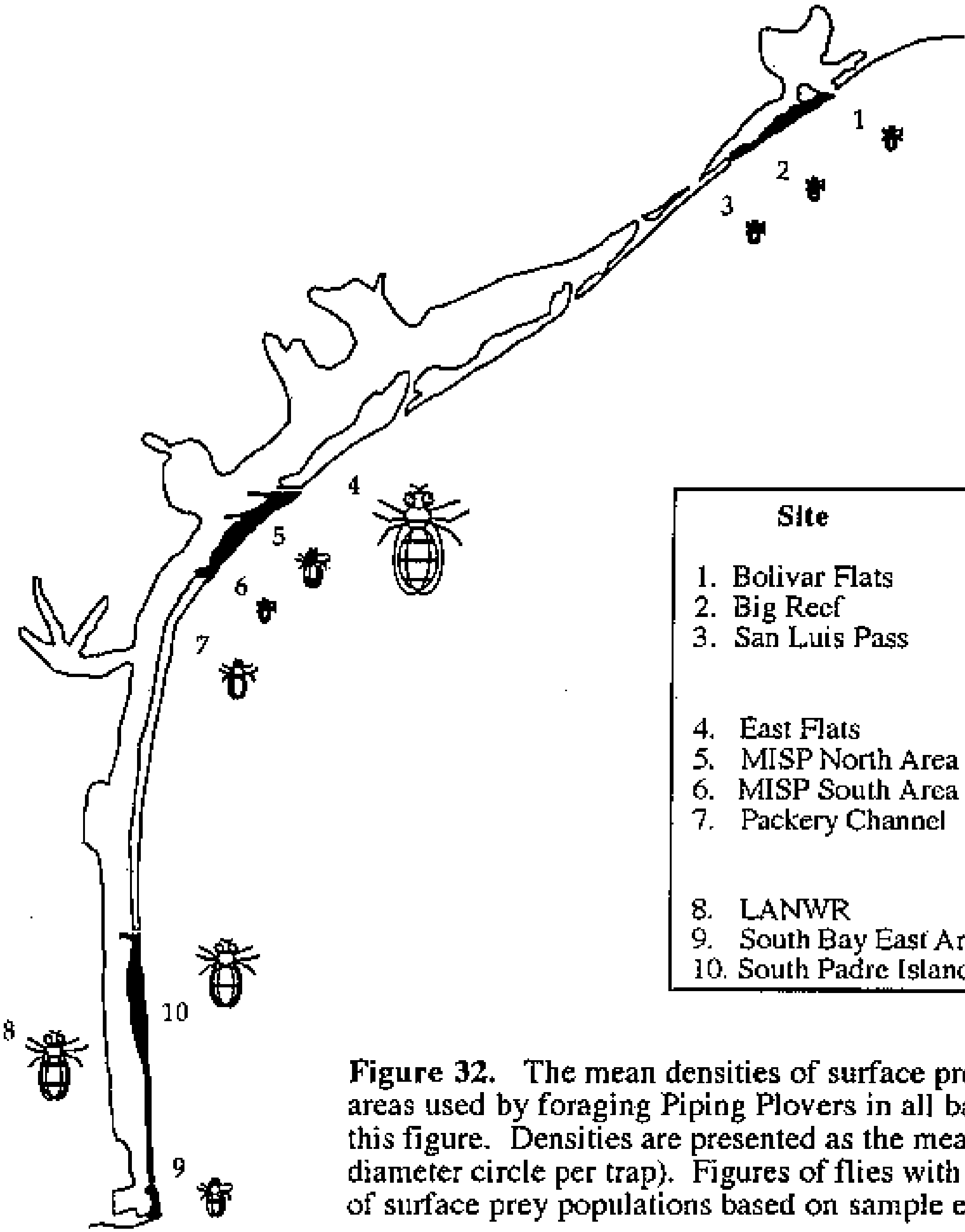
Sticky Traps - The average capture rate using sticky traps varied from less than 6 animals/100 trap hours to nearly 10 animals per trap hour (Figure 32). Our samples suggest that surface prey were significantly more abundant on bayshore habitat during

Table 18. Table summarizing the ANOVA results for total insect density, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. For the reader's comparison, we present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Prey densities are represented as the mean # insects/m². (* = p < 0.10, ** = p < 0.05)

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: all used samples	winter vs migratory	27(1135) vs. 28 (958)	22(1060) vs. 28 (886)	0.1577
	beach vs. bayshore	2 (807) vs. 44(1286)	2 (755) vs. 40 (1191)	** 0.0001
	ecosystems			**<0.0001
	bay vs. lagoon	6 (840) vs. 112 (415)	6 (840) vs. 112 (330)	**<0.0001
	bay vs. ecotone	6 (840) vs. 7 (838)	6 (840) vs. 8 (776)	0.3870
	ecotone vs lagoon	7 (838) vs. 112 (415)	8 (776) vs. 112 (330)	**<0.0001
Used soil cores: bayshore habitat only	winter vs migratory	43 (725) vs. 46 (561)	37 (655) vs. 44 (536)	0.2325
	bay vs. lagoon	6 (550) vs. 142 (325)	6 (550) vs. 154 (240)	**<0.0001
	bay vs. ecotone	6 (550) vs. 15 (411)	6 (550) vs. 16 (401)	0.5577
	ecotone vs lagoon	15 (411) vs. 142 (325)	16 (401) vs. 154 (240)	**<0.0001
Used soil cores: beach habitat only	winter vs migratory	0 (397) vs. 3 (397)	0 (405) vs. 4 (350)	0.6479
	bay vs. lagoon	5 (290) vs. 0 (240)	5 (290) vs. 0 (90)	0.8798
	bay vs. ecotone	5 (290) vs. 0 (427)	5 (290) vs. 0 (375)	0.6720
	ecotone vs lagoon	0 (427) vs. 0 (240)	0 (375) vs. 0 (90)	0.8566
Used soil cores: winter season only	beach vs. bayshore	0 (410) vs. 43 (725)	0 (405) vs. 37 (655)	** 0.0028
	bay vs. lagoon	2 (395) vs. 100 (240)	2 (395) vs. 95 (180)	**<0.0001
	bay vs. ecotone	2 (395) vs. 12 (500)	2 (395) vs. 12 (485)	0.7273
	ecotone vs lagoon	12 (500) vs. 100 (240)	12 (485) vs. 95 (180)	** 0.0008

Table 18 continued.

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
Used soil cores: migratory season only	beach vs. bayshore	3 (397) vs. 46 (561)	4 (350) vs. 44 (536)	**<0.0001
	bay vs. lagoon	9 (445) vs. 127 (175)	9 (445) vs. 133 (150)	**<0.0001
	bay vs. ecotone	9 (445) vs. 0 (338)	9 (445) vs. 0 (291)	0.1542
	ecotone vs lagoon	0 (338) vs. 127 (175)	0 (291) vs. 133 (150)	**<0.0001
Used soil cores: bay ecosystem only	winter vs migratory	2 (395) vs. 9 (445)	2 (395) vs. 9 (445)	0.3358
	beach vs. bayshore	5 (290) vs. 6 (550)	5 (290) vs. 6 (550)	0.9184
Used soil cores: ecotone only	winter vs migratory	12 (500) vs. 0 (338)	12 (485) vs. 0 (291)	0.8114
	beach vs. bayshore	0 (427) vs. 15 (411)	0 (375) vs. 16 (401)	0.8254
Used soil cores: lagoon ecosystem only	winter vs migratory	100 (240) vs. 127 (175)	95 (180) vs. 133 (150)	0.1605
	beach vs. bayshore	0 (90) vs. 142 (325)	0 (90) vs. 154 (240)	**<0.0001
	mainland vs. barriers	109 (85) vs. 112 (330)	109 (85) vs. 112 (330)	* 0.0712
All samples	used vs. unused	2 (807) vs. 1(2360)	2 (772) vs. 1(1476)	0.8331



Site	N	Animals/Trap.
1. Bolivar Flats	150	0.06
2. Big Reef	90	0.42
3. San Luis Pass	161	0.09
4. East Flats	31	9.71
5. MISP North Area	121	0.75
6. MISP South Area	10	0.20
7. Packery Channel	167	0.82
8. LANWR	220	2.67
9. South Bay East Area	60	0.75
10. South Padre Island	166	2.25

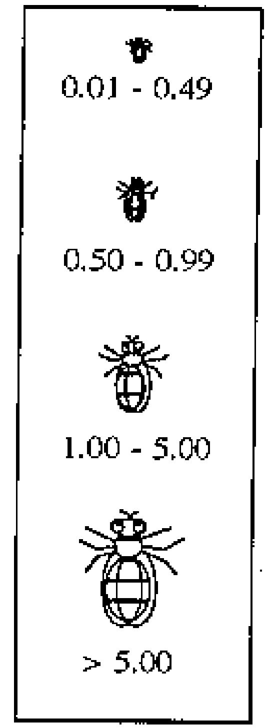


Figure 32. The mean densities of surface prey animals captured on sticky traps deployed in areas used by foraging Piping Plovers in all bayshore habitats at each study site are illustrated in this figure. Densities are presented as the mean number of animals captured per trap (12.5 cm diameter circle per trap). Figures of flies with increasing dimensions reflect arbitrary density ranks of surface prey populations based on sample estimates.

the migratory period than during the winter period ($p = 0.0035$; Table 19). When data from each ecosystem were considered independently, the difference in prey abundance between the winter period and migratory period was significant within the bay ecosystem ($p = 0.0185$; Table 19), and within the lagoon ecosystem ($p < 0.0001$; Table 19), but was not significantly different within the ecotone ($p = 0.2048$; Table 19).

Our samples suggest that algal flats supported significantly more surface prey in areas used by Piping Plovers that did sand flat habitat ($p = 0.0051$; Table 19). When data from each ecosystem were considered independently, the difference in prey density between sand flats and algal flats was not significant within the ecotone ($p=0.1080$; Table 19). Surface prey were significantly more abundant on algal flat than on sand flat habitat within the bay ecosystem ($p=0.0172$; Table 19), but were more abundant on sand flat habitat than algal flat habitat within the lagoon ecosystem ($p=0.0799$; Table 19).

We observed a significant difference in surface prey abundance among the 2 ecosystems and the ecotone ($p < 0.0001$: Table 19). The samples we collected from the bay ecosystem supported significantly fewer surface prey in areas used by Piping Plovers than did samples from the ecotone ($p = 0.0008$; Table 19) or the lagoon ecosystem ($p < 0.0001$; Table 19). The lagoon ecosystem also supported more surface prey than the ecotone ($p = 0.0490$; Table 19).

Spotting scope surveys - The average surface animal density estimated by spotting scope surveys varied from about 400 animals/square meter to about 1100 animals/square meter (Figure 33). Our spotting scope surveys suggest that there was no difference in surface prey densities among the winter and migratory periods ($p = 0.1498$; Table 20). When data from each ecosystem were considered independently, the difference in prey density between the winter period and migratory period was not significant within the bay ecosystem ($p=0.7197$; Table 20), or within the lagoon ecosystem ($p=0.6966$; Table #), but differed slightly within the ecotone ($p=0.0845$; Table 20). Our sample size was too small to compare sand flat and algal flat habitat.

We observed no difference in surface prey densities among the 2 ecosystems and the ecotone ($p = 0.1942$: Table 20). Our data suggest that the bay ecosystem supported lower densities of surface prey in areas used by Piping Plovers than did the lagoon ecosystem ($p = 0.0910$; Table 20), but there was no apparent difference between the surface prey densities in the bay ecosystem and the ecotone ($p = 0.4373$; Table 20), or the ecotone and the lagoon ecosystem ($p = 0.5870$; Table 20).

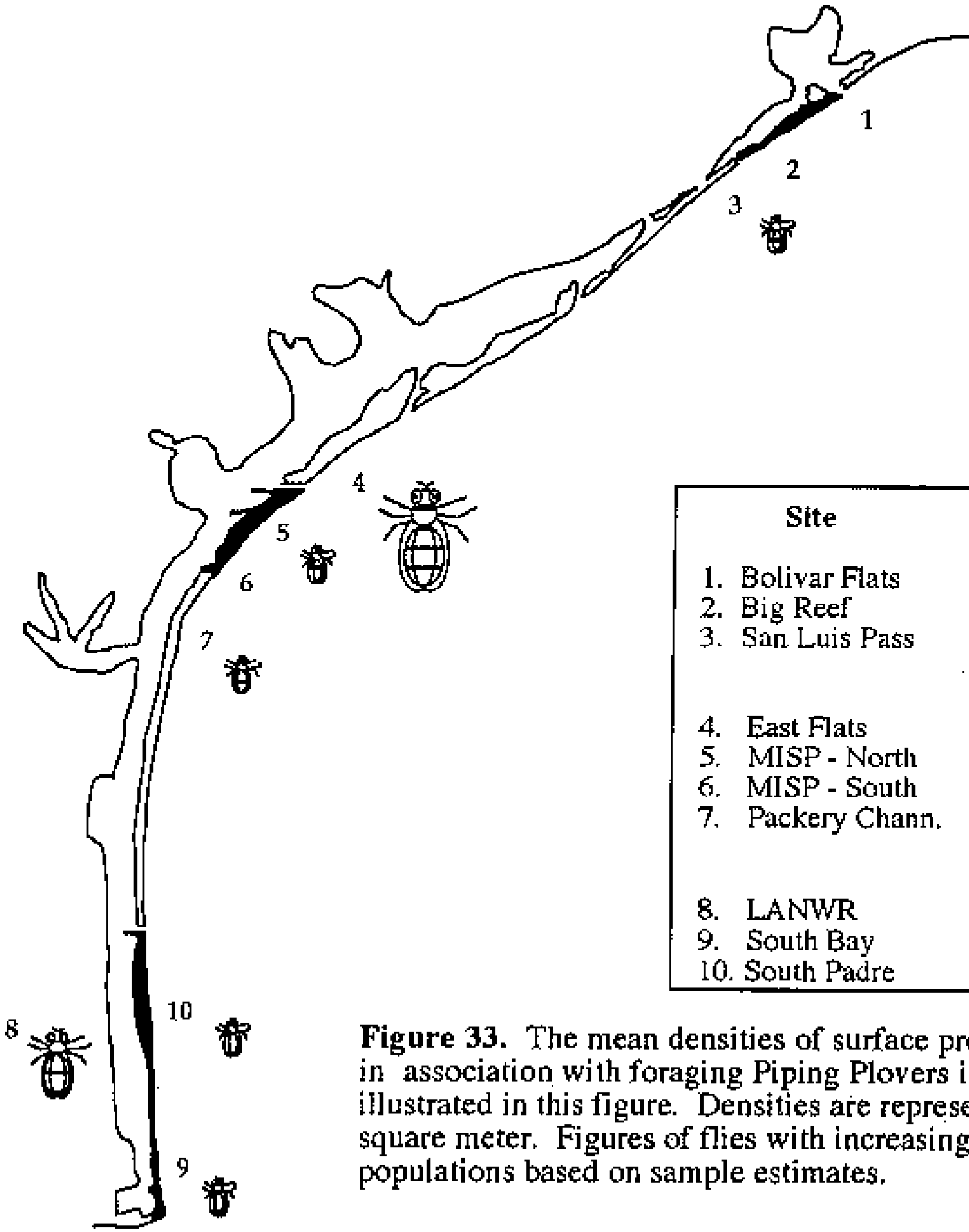
Emergent prey from within algal mats

Where Piping Plovers were observed feeding on algal flats, a single core of the algal mat and underlying sediment was collected, incubated under a controlled light cycle and evaluated for emergent prey animals (see Methods). Because these data were collected only when plovers were feeding on algal flats, and algal flats were used extensively only in the lagoon ecosystem, and rarely in the bay ecosystem, we were unable to perform many comparative analyses due to extremely small sample sizes. No samples were collected from the bay ecosystem, 32 samples were obtained from the ecotone, and 72 samples were collected from the lagoon ecosystem.

Average emergent rates from algal cores corresponded to *in situ* densities of between about 400 and 1100 emergents/square meter over a 3 week period (Figure 34). There were sufficient data to compare the emergent prey densities collected in the ecotone (476.2 animals/m^2 [N = 28]) and lagoon ecosystem (958.6 animals/m^2 [N = 29])

Table 19. Table summarizing the ANOVA results for total surface prey abundance as assessed using sticky traps, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. We present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Sticky trap prey densities are represented as the mean # animals/trap. (* = p < 0.10, ** = p < 0.05)

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
All sticky traps:	winter vs migratory	0.64 (681) vs. 2.34 (495)	0.77 (541) vs. 2.67 (294)	** 0.0035
	sand vs. algal flats	0.87 (604) vs. 1.87 (572)	1.09 (339) vs. 1.68 (496)	** 0.0051
	bay vs. lagoon	0.15 (401) vs. 2.26 (445)	0.09 (161) vs. 2.49 (385)	**<0.0001
	bay vs. ecotone	0.15 (401) vs. 1.61 (330)	0.09 (161) vs. 0.79 (289)	** 0.0008
	ecotone vs. lagoon	1.61 (330) vs. 2.26 (445)	0.79 (289) vs. 2.49 (385)	** 0.0490
Bay ecosystem traps only:	winter vs. migratory	0.12 (226) vs. 0.20 (175)	0.08 (101) vs. 0.12 (60)	** 0.0185
	sand vs. algal flats	0.13 (386) vs. 0.73 (15)	0.03 (146) vs. 0.73 (15)	** 0.0001
Ecotone traps only:	winter vs. migratory	0.65 (255) vs. 4.85 (75)	0.67 (245) vs. 1.43 (44)	0.2048
	sand vs. algal flats	1.72 (93) vs. 1.57 (237)	0.79 (73) vs. 0.79 (216)	0.1080
Lagoon ecosystem traps only:	winter vs. migratory	1.23 (200) vs. 3.10 (245)	1.23 (195) vs. 3.76 (190)	**<0.0001
	sand vs. algal flats	2.54 (125) vs. 2.15 (320)	2.57 (120) vs. 2.46 (265)	* 0.0799



Site	N	Animals/Survey
1. Bolivar Flats	75	0.00
2. Big Reef	55	0.00
3. San Luis Pass	99	0.29
4. East Flats	25	2.24
5. MISP - North	25	0.19
6. MISP - South	10	0.00
7. Packery Chann.	39	0.43
8. LANWR	25	1.86
9. South Bay	35	0.24
10. South Padre	117	0.31

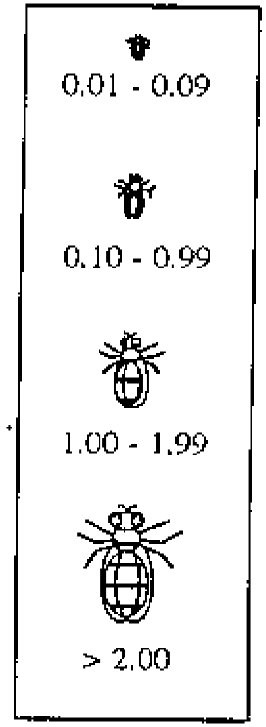
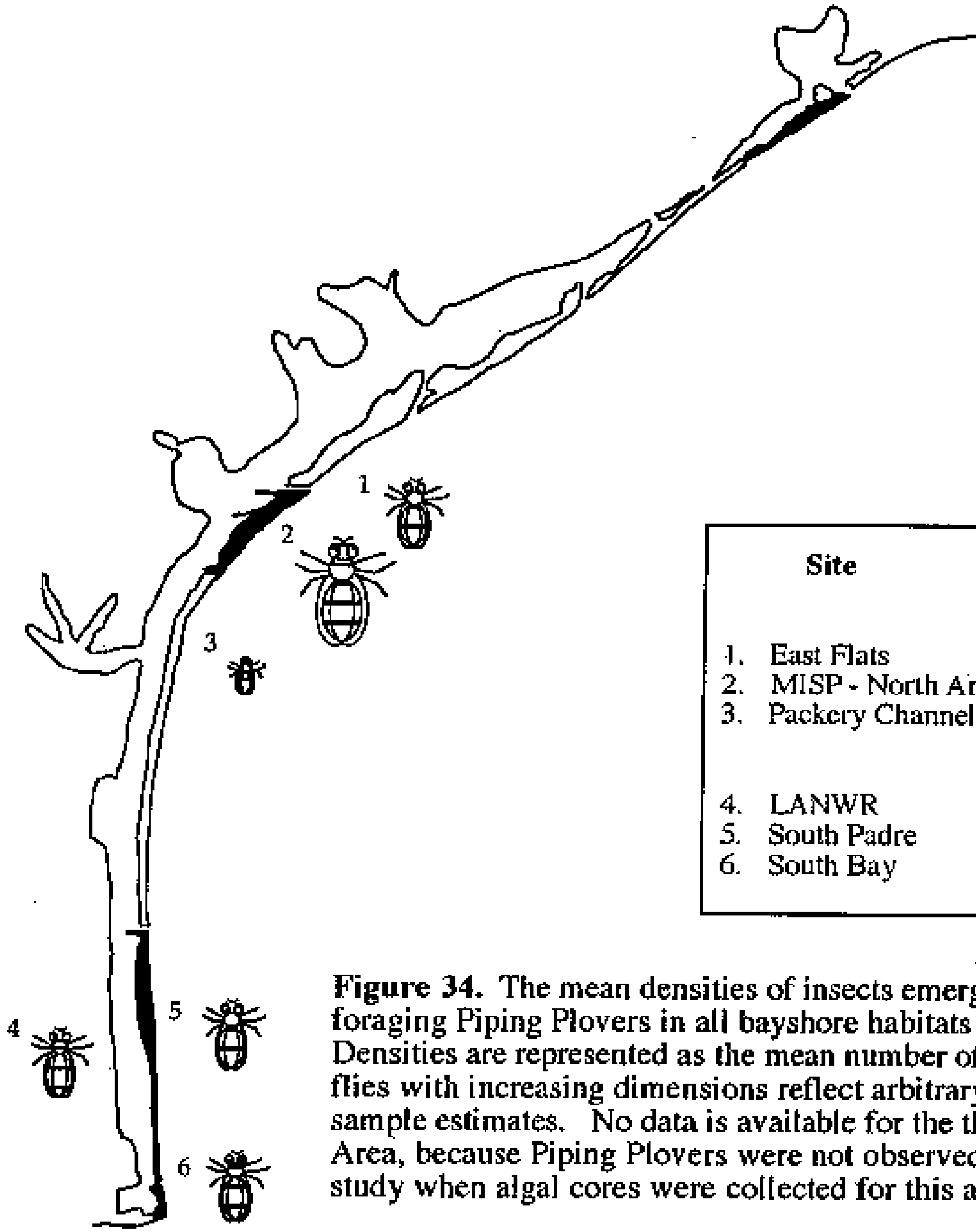


Figure 33. The mean densities of surface prey animals observed during spotting scope surveys in association with foraging Piping Plovers in all bayshore habitats at each study site are illustrated in this figure. Densities are represented as the mean number of animals observed per square meter. Figures of flies with increasing dimensions reflect arbitrary density ranks of surface populations based on sample estimates.

Table 20. Table summarizing the ANOVA results for total surface prey density as appraised by spotting scope surveys, and the data that were incorporated into the analyses. The table describes the type of data used in the analyses, the key comparisons made and the p-value associated with the F Ratio for each comparison. Also presented are the mean values for each parameter and, in parentheses, the number of samples used to derive the mean. We present mean values for the total data sets, and for the subsets of the total data sets that were incorporated into the analyses. Prey densities estimated by spotting scope surveys are represented as the mean # animals/m^2. (* = $p < 0.10$, ** = $p < 0.05$, *** = not enough data to perform analysis)

Data Set	Comparisons	Total Data Set	Analzyed Data Set	p-value
All spotting scope surveys:	winter vs migratory	0.17 (236) vs. 0.59 (270)	0.17 (201) vs. 0.25 (219)	0.1498
	sand vs. algal flats	0.27 (366) vs. 0.71 (140)	0.13 (316) vs. 0.47 (104)	***
	bay vs. lagoon	0.01 (206) vs. 0.58 (205)	0.01 (206) vs. 0.41 (175)	* 0.0910
	bay vs. ecotone	0.01 (206) vs. 0.81 (95)	0.01 (206) vs. 0.43 (39)	0.4373
	ecotone vs. lagoon	0.81 (95) vs. 0.58 (205)	0.43 (39) vs. 0.41 (175)	0.5870
Bay ecosystem scope surveys only:	winter vs. migratory	0.01 (101) vs. 0.00 (105)	0.01 (101) vs. 0.00 (105)	0.7197
	sand vs. algal flats	0.01 (206) vs. -- (0)	*** vs. ***	***
Ecotone scope surveys only:	winter vs. migratory	0.16 (45) vs. 1.40 (50)	0.24 (15) vs. 0.55 (24)	0.0845
	sand vs. algal	0.48 (65) vs. 1.55 (30)	0.32 (30) vs. 0.79 (9)	***
Lagoon ecosystem:	winter vs. migratory	0.17 (236) vs. 0.59 (270)	0.35 (85) vs. 0.46 (90)	0.6966
	sand vs. algal flats	0.27 (366) vs. 0.71 (140)	0.37 (80) vs. 0.44 (95)	***



Site	N	Animals/m^2
1. East Flats	4	848
2. MISP - North Area	2	1130
3. Packery Channel	26	426
4. LANWR	39	823
5. South Padre	20	961
6. South Bay	13	695

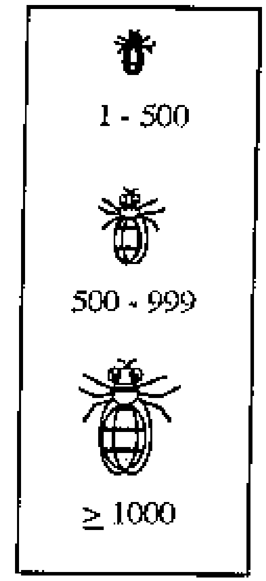


Figure 34. The mean densities of insects emerging from algal cores collected in association with foraging Piping Plovers in all bayshore habitats at each study site are illustrated in this figure. Densities are represented as the mean number of animals observed per square meter. Figures of flies with increasing dimensions reflect arbitrary density ranks of emergent population based on sample estimates. No data is available for the three bay ecosystem sites, or for MISP - South Area, because Piping Plovers were not observed foraging on algal flats during the period of the study when algal cores were collected for this assay.

during the winter period, and these did not differ significantly ($p = 0.9344$; data not shown). When data from the lagoon ecosystem alone are considered, ANOVA comparing of landform types and life cycles suggested that emergent prey densities did not differ significantly on mainland (882.9 animals/m^2 [N = 39]) and barrier island sites (856.1 animals/m^2 [N = 33]; $p = 0.1303$; data not shown), or during the winter (726.4 animals/m^2 [N = 42]) and migratory seasons (994.4 animals/m^2 [N = 30]; $p = 0.1999$; data not shown).

Piping Plover Movement Patterns

In secondary objective #5, we focused on characterizing the movement patterns of Piping Plovers along the Texas Gulf Coast. We were particularly interested in determining whether our observations of color-banded plovers supported movement patterns reflective of seasonal site fidelity (i.e. using the same site throughout a substantial portion of the same nonbreeding period) or annual site fidelity (i.e. using the same site during 2 or more nonbreeding periods). Another goal was to estimate minimum winter home range size for Piping Plovers based upon movements of color-banded birds within study years. To address this objective, we mapped the locations of all color-banded Piping Plovers sighted during the study. We evaluated the maps to determine the extent to which the movement patterns of individual birds provided support for site fidelity. Crude estimates of the minimum home range sizes for wintering Piping Plovers in each ecosystem were estimated from the largest area used by a single banded Piping Plover.

Sightings of color-banded Piping Plovers

We observed color banded Piping Plovers on 64 different occasions during the study. Color band combinations were recorded whenever it was possible to approach these birds closely enough to identify the band colors. (Table 21). Thirty-five different color band combinations were recorded, however, it is likely that some of the bands colors recorded in the field may not accurately reflect the color of each band at the time the bird was banded. Due to a recent moratorium that limited the banding of Piping Plovers, most of the color banded plovers that we encountered were banded several years prior to our study. Because of this delay, many birds sighted during the study appear to have lost 1 or more color bands, and some of the bands that they have retained appeared to have faded from their original colors. For instance, plovers originally banded with a red color band, may be recorded as having an orange or pink band in the field because the band's color has faded over time. Other factors often hindered our ability to recognize and identify color banded birds. Lighting conditions in the field during the mid-day period often caused color bands to be shaded by the plover's body, making it more difficult to accurately decipher band colors. On many occasions, we were unable to get very close to plovers because of the expansive nature of the tidal flat habitat. Heat waves emanating from the flats often severely reduced visibility. These factors acted in concert to limit our ability to accurately identify color banded birds. We recorded descriptions of several plovers wearing very similar color band combinations (Figures 35 - 37). Some of these "groups" of plovers probably represent sightings of the same plover under different field conditions leading to varied descriptions.

It is difficult to infer much about the movement patterns of Piping Plovers based upon the positions of color banded birds, because so few were ever observed more than once, and only a fraction of these resightings occurred in a different location or a

Table 21. Sightings of color-banded Piping Plovers. Color band abbreviations: FWS; U. S. Fish and Wildlife Service band, WH; white, TN; tan, YL; yellow, OR; orange, PK; pink, RD; red, LB; light blue, DB; dark blue, DG; dark green, BK; black, Fdg; dark green flag. Habitat abbreviations: Fl; bayshore flats, Be; beach. See page for a key to study site abbreviations. Observer (Obs.) abbreviations: MB; Marty Bray, LE; Lee Elliott, TM; Tim Menard, CZ; Curt Zonick.

PPL #	Left Leg Bands		Right Leg Bands		Date	Location	Habitat	Obs.
	Upper	Lower	Upper	Lower				
1	n.o.*	n.o.	FWS	BK/Fdg	10/24/91	MISPN	Fl	CZ
					11/14/91	MISPN	Fl	CZ
					1/23/92	MISPN	Fl	CZ
					1/28/92	MISPN	Fl	CZ
					2/5/92	MISPNBe	Be	CZ
					2/10/92	MISPNBe	Be	CZ
					2/25/92	MISPNBe	Be	CZ
					9/1/92	MISPN	Fl	CZ
					9/3/92	MISPNBe	Be	CZ
					9/4/92	MISPNBe	Be	CZ
					9/4/92	MISPN	Fl	CZ
2	n.o.	YL/BK/DG	FWS	BK/Fdg	11/18/91	LANWR	Fl	CZ
3	n.o.	WH/DG	n.o.	n.o.	11/18/91	LANWR	Fl	CZ
					3/4/92	SB-East	Fl	CZ
4	n.o.	[WH or YL]/DG	n.o.	[Fwh or WH]/WH	11/22/91	SB-East	Fl	CZ
5	n.o.	LG/WH	n.o.	[FWS or WH]	11/30/91	SB-East	Fl	CZ
6	n.o.	[YL or WH]/DG	n.o.	WH/WH	11/30/91	SB-East	Fl	CZ
7	n.o.	[Fdg or DG]	n.o.	BK/WH/OR	12/15/91	SPIN	Fl	CZ
8	n.o.	DG/WH	n.o.	n.o.	3/1/92	SPIN	Fl	CZ

Table 21 continued . Sightings of color-banded Piping Plovers. Color band abbreviations: FWS; U. S. Fish and Wildlife Service band, WH; white, TN; tan, YL; yellow, OR; orange, PK; pink, RD; red, LB; light blue, DB; dark blue, DG; dark green, BK; black, Fdg; dark green flag. Habitat abbreviations: Fl; bayshore flats, Be; beach. See page for a key to study site abbreviations. Observer (Obs.) abbreviations: MB; Marty Bray, LE; Lee Elliott, TM; Tim Menard, CZ; Curt Zonick.

PPL #	Left Leg Bands		Right Leg Bands		Date	Location	Habitat	Obs.
	Upper	Lower	Upper	Lower				
9	n.o.	WH/[DG or BK]	n.o.	n.o.	3/1/92	SPIN	Fl	CZ
10	FWS	Fdg	n.o.	WH/DG/BK	3/23/92	BF	Fl	CZ
					3/30/92	BFBe	Be	CZ
11	n.o.	PK/[DB or BK]/LB	n.o.	[DB or BK]/LB	10/13/92	LANWR	Fl	CZ
12	n.o.	BK/RD/WH	n.o.	BK/DG	1/13/93	SPIN	Fl	CZ
13	n.o.	BK/WH	n.o.	BK/Fdg	1/28/93	LANWR	Fl	TM
					1/27/94	SPIN	Fl	CZ
14	n.o.	WH/WH/OR	n.o.	Fdg	2/10/93	BIBe-NWO	Be	TM
					2/26/93	BIBe-NWO	Be	TM
					3/16/93	BIBe-NWO	Be	CZ
					3/31/93	BIBe-NWO	Be	CZ
					1/24/94	BIBe-NWO	Be	CZ
15	n.o.	WH/DG	n.o.	FWS	10/8/93	BIBe-NWO	Be	CZ
					2/10/93	BIBe-NWO	Be	TM
16	n.o.	n.o.	n.o.	FWS	2/10/93	BIBe-NWO	Be	TM
					2/26/93	BIBe-NWO	Be	TM
					3/16/93	BIBe-NWO	Be	CZ

Table 21 continued . Sightings of color-banded Piping Plovers. Color band abbreviations: FWS; U. S. Fish and Wildlife Service band, WH; white, TN; tan, YL; yellow, OR; orange, PK; pink, RD; red, LB; light blue, DB; dark blue, DG; dark green, BK; black, Fdg; dark green flag. Habitat abbreviations: Fl; bayshore flats, Be; beach. See page for a key to study site abbreviations. Observer (Obs.) abbreviations: MB; Marty Bray, LE; Lee Elliott, TM; Tim Menard, CZ; Curt Zonick.

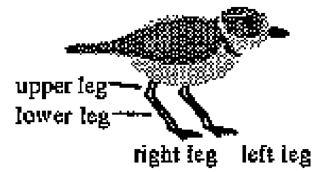
PPL #	Left Leg Bands		Right Leg Bands		Date	Location	Habitat	Obs.
	Upper	Lower	Upper	Lower				
17	n.o.	n.o.	n.o.	WH	11/3/92	PC	Fl	CZ
					12/18/92	SPIS-MF	Fl	CZ
					12/7/93	SPIS-MF	Fl	CZ
					12/9/93	BIBe-NWO	Be	TM
					2/10/93	BIBe-NWO	Be	TM
					2/26/93	BIBe-NWO	Be	CZ
					3/16/93	BIBe-NWO	Be	CZ
					3/31/93	BIBe-NWO	Be	CZ
18	n.o.	WH/RD	n.o.	RD/DG	2/10/93	BIBe-NWO	Be	TM
					2/26/93	BIBe-NWO	Be	TM
19	n.o.	WH/YL	n.o.	Fdg	2/10/93	BIBe-NWO	Be	TM
20	n.o.	FWS	n.o.	n.o.	2/10/93	BIBe-NWO	Be	TM
21	n.o.	FWS/[BK or none]	n.o.	BK/DG	3/9/93	SB-East	Fl	CZ
22	n.o.	WH	n.o.	BK/DG	3/26/93	EF	Fl	CZ
23	n.o.	DG	n.o.	WH/WH	3/26/93	EF	Fl	CZ
24	n.o.	FWS	n.o.	n.o.	9/21/93	MISPSBe	Be	CZ
					9/23/93	EF	Fl	CZ

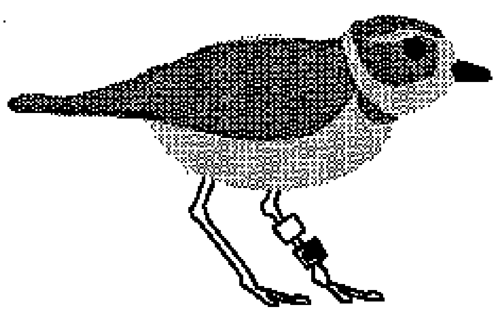
Table 21 continued. Color band abbreviations: FWS = Service band, WH = white, TN = tan, YL = yellow, OR = orange, PK = pink, RD = red, LB = light blue, DB = dark blue, DG = dark green, BK = black, Fdg = dark green flag. Habitat abbreviations: Fl; bayshore flats, Be; beach. See page for a key to study site abbreviations. Observer (Obs.) abbreviations: MB = Marty Bray, LE = Lee Elliott, TM = Tim Menard, CZ - Curt Zonick.

PPL #	Left Leg Bands		Right Leg Bands		Date	Location	Habitat	Obs.
	Upper	Lower	Upper	Lower				
25	n.o.	Fdg	n.o.	DG/WH/BK	9/28/93	EF	Fl	CZ
26	n.o.	n.o.	n.o.	Fdg	9/28/93	EF	Fl	CZ
27	n.o.	WH	n.o.	BK/Fdg	9/28/93	EF	Fl	CZ
28	n.o.	WH/TQ	n.o.	FWS	10/2/93	BIBe-NWO	Be	LE
29	n.o.	WH/DB	n.o.	n.o.	10/6/93	BIBe-NWO	Be	CZ
30	n.o.	WH/TN/PK	n.o.	Fdg	10/8/93	BIBe-NWO	Be	CZ
31	n.o.	n.o.	n.o.	FWS	10/15/93	SPIN	Fl	CZ
32	n.o.	DG/RD/WH	n.o.	BK/Fdg	10/15/93	SPIN	Fl	CZ
33	n.o.	RD	n.o.	WH	12/9/93	SPIN	Fl	CZ
34	n.o.	WH/DG	n.o.	[WH or FWS]	1/24/94	BIBe-NWO	Be	CZ
35	n.o.	WH	n.o.	WH	1/27/94	SPIN	Fl	CZ

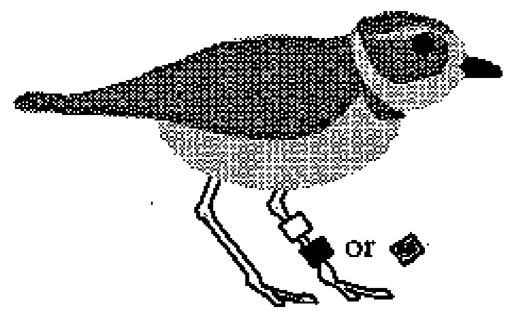
Figure 35. Six similar color band combinations recorded during the study are illustrated in this figure. Although the combinations are different, they are similar enough to perhaps represent sightings of only a couple of unique individuals, or possibly only one bird. See Table 21 for more information.

= USFWS aluminum band
= color band
= color flag

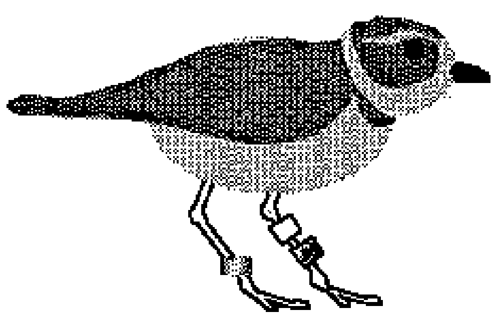




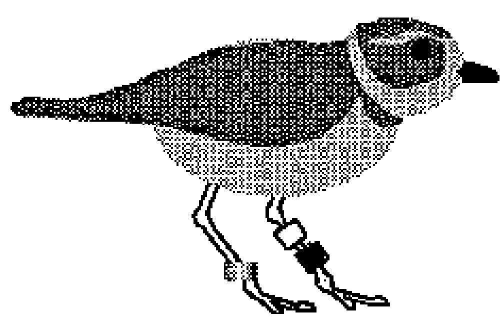
Bird # 3 - sighted at LANWR on 11/18/91 and at SB-East on 3/4/92



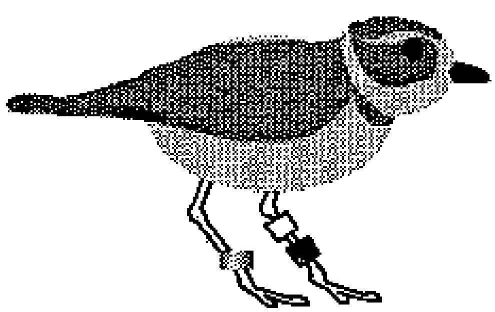
Bird # 9 - sighted at SPIN on 3/1/92



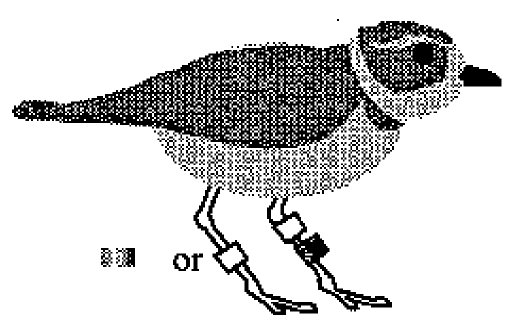
Bird # 14 - sighted at BIBe on 2/10/93 and 10/8/93



Bird # 29 - sighted at BIBe on 10/6/93

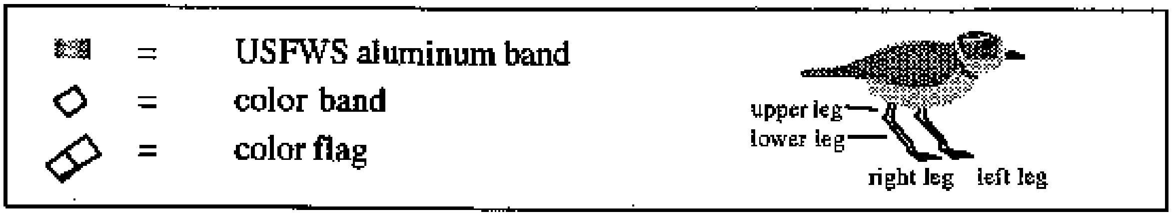


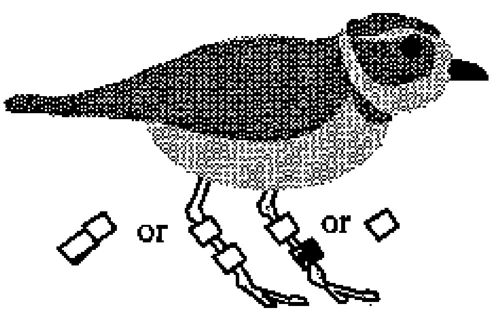
Bird # 28 - sighted at BIBe on 10/2/93



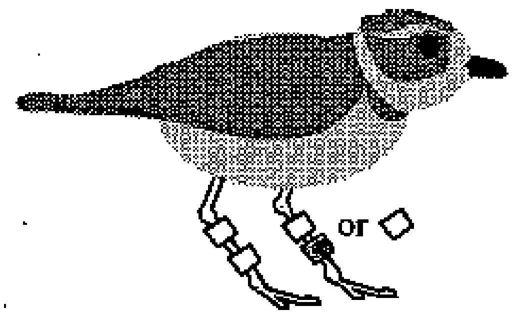
Bird # 34 - sighted at BIBe on 1/24/94

Figure 36. Three pairs of similar color band combinations recorded during the study are illustrated in this figure. Although the combinations are different, they are similar enough to perhaps represent sightings of only three unique individuals. See Table 21 for more information.

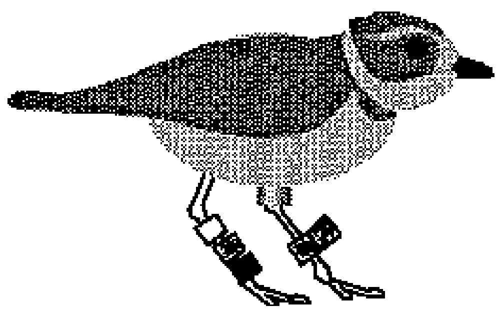




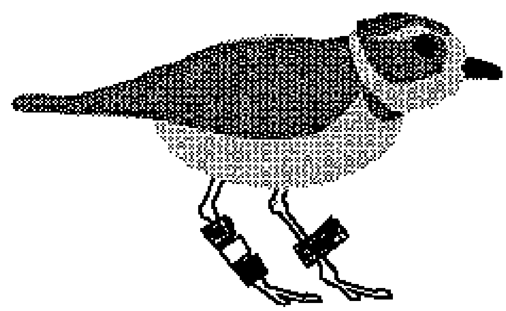
Bird # 4 - sighted at SB East Area on 11/22/91



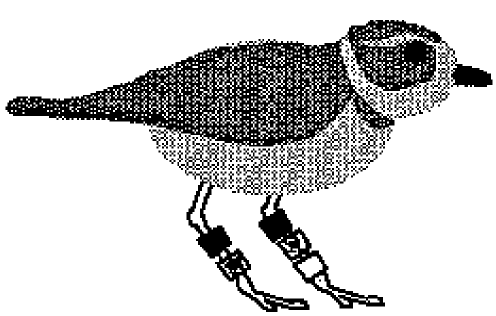
Bird # 6 - sighted at SB East Area on 11/30/91



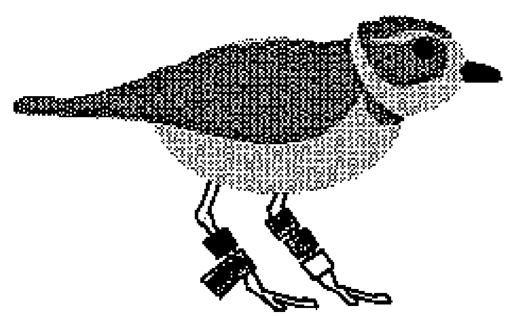
Bird # 10 - sighted at BF on 3/23/92 and at BFBe on 3/30/92



Bird # 25 - sighted at EF on 9/28/93

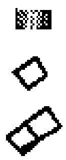


Bird # 12 - sighted at SPIN on 1/13/93



Bird # 32- SPIN on 10/15/93

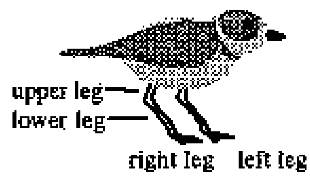
Figure 37. Two pairs of similar color band combinations recorded during the study are illustrated in this figure. Although the combinations are different, they are very similar and probably represent sightings of only two unique individuals. See Table 21 for more information.

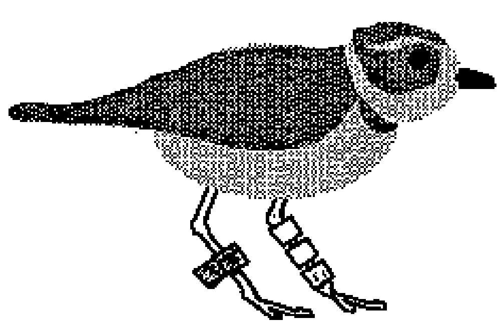


= USFWS aluminum band

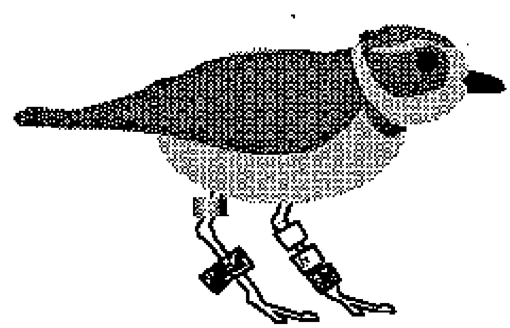
= color band

= color flag

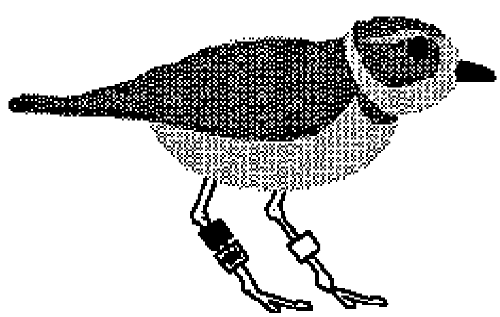




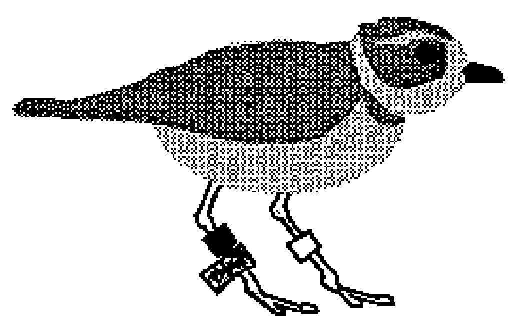
Bird # 14 - sighted at BIBe on 2/10/93



Bird # 30 - sighted at BIBe on 10/8/93



Bird # 22 - sighted at EF on 3/26/93



Bird # 27 - sighted at EF on 9/28/93

different habitat than the initial sighting. At least 7 color-banded plovers were sighted on more than one occasion, but only three of these birds were observed to use more than one habitat or multiple sites during the study. Furthermore, the loss of color bands by some birds over time may lead to artificial duplication of color band combinations. For instance, if plover # 13 lost its black band, it would wear the same color band combination as plover # 27 (Table 21). Thus, multiple sightings of plovers with only 1 or 2 color bands must be interpreted with considerable caution.

Seasonal Site Fidelity

Even though the data were very limited, our records suggest that a few Piping Plovers exhibited at least short-term seasonal site fidelity. Plover # 1 was observed on 11 different occasions over an 11 month period (Table 21; Figure 38). This bird was only seen at the Mustang Island State Park - North Area study site, despite the fact that 2 other sites were situated nearby (the Mustang Island State Park South Area site was less than 1 km away and the Packery Channel site was within ~ 7 km). Plover # 1 was observed to use beach habitat 5 times and bayshore habitat 6 times (Table 21; Figure 38). On all of the 5 occasions that this bird was observed using beach habitat the bayshore tide levels were high or very high (tide related data not shown). On 4 of the 6 occasions that this bird was observed using bayshore habitat, the bayshore tide levels were low. Of the four occasions when the tide was low, the bird was observed while foraging on sand flats along the bayshore margin. On the one occasion when the tide was low and the bird was found somewhere other than the sand flats along the bay margin, it was observed feeding on sand and algal flats associated with the site's lagoon (see Figure 10 for a schematic illustration of MISPN and the relative locations of the beach, bayshore and lagoon habitats). During the two occasions that this bird used bayshore habitat under high bayshore tidal conditions, the bird was foraging on algal flats associated with the site's lagoon. The usage pattern of bayshore and beach habitats by this bird was consistent with the hypothesis that bayshore tide levels direct movements between these two major habitat types, and reinforces the findings of analyses addressing habitat use by Piping Plovers at the site population scale that are discussed in the section entitled "The effect of bayshore tidal conditions on habitat utilization".

The observations associated with plover # 1 also suggest that at least some Piping Plovers use a very restricted area on coastal barriers during the nonbreeding period. The restricted nonbreeding range of plover # 1 illustrates the "site fidelic" behavior often attributed to Piping Plovers along the Gulf Coast (Johnson and Baldassarre 1988 Eubanks 1994, Perez 1994). However, we also recorded evidence suggesting that site fidelity may not be pervasive among Piping Plovers during the nonbreeding season. Piping Plover # 3 (Table 21; Figure 39) was sighted at LANWR on 11/18/91 and resighted later that spring (3/4/92) on the flats at South Bay - East Area site (Figure 13).

Annual Site Fidelity

Five Piping Plovers were observed during 2 nonbreeding periods, although no plovers were observed during all 3 nonbreeding periods covered by this study (Table 21). The movements of plover # 1 are described in some detail above. The black band over a green flag worn by this plover suggests that it was originally banded during the breeding season in North Dakota (M. Ryan, pers. comm.). Plovers # 14 and # 15 were sighted at the Brazos Island Beach site during the second and third field seasons of our

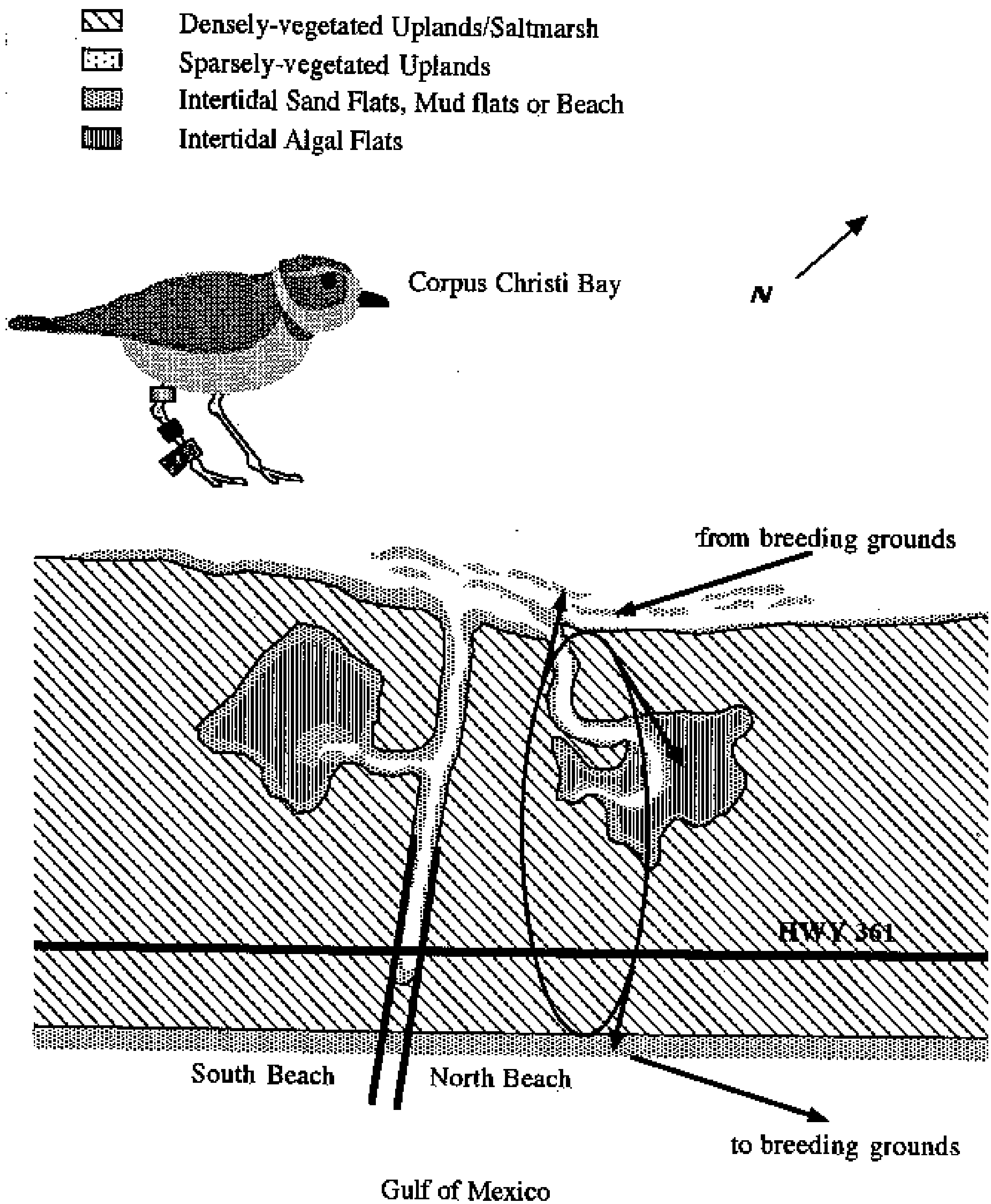


Figure 38. A schematic map illustrating the movement of color banded Piping Plover identified as PPL # 1 on Table 21 is presented in this figure. This plover was sighted 11 times during the study, only at the MISPN site. This plover's use of beach and bayshore habitats corresponded closely with the predicted habitat use patterns associated with bayshore tidal conditions as identified by ANOVA models supported by our data. Resightings over consecutive years support inter-year winter site fidelity for at least some Piping Plovers along the central Texas coast.

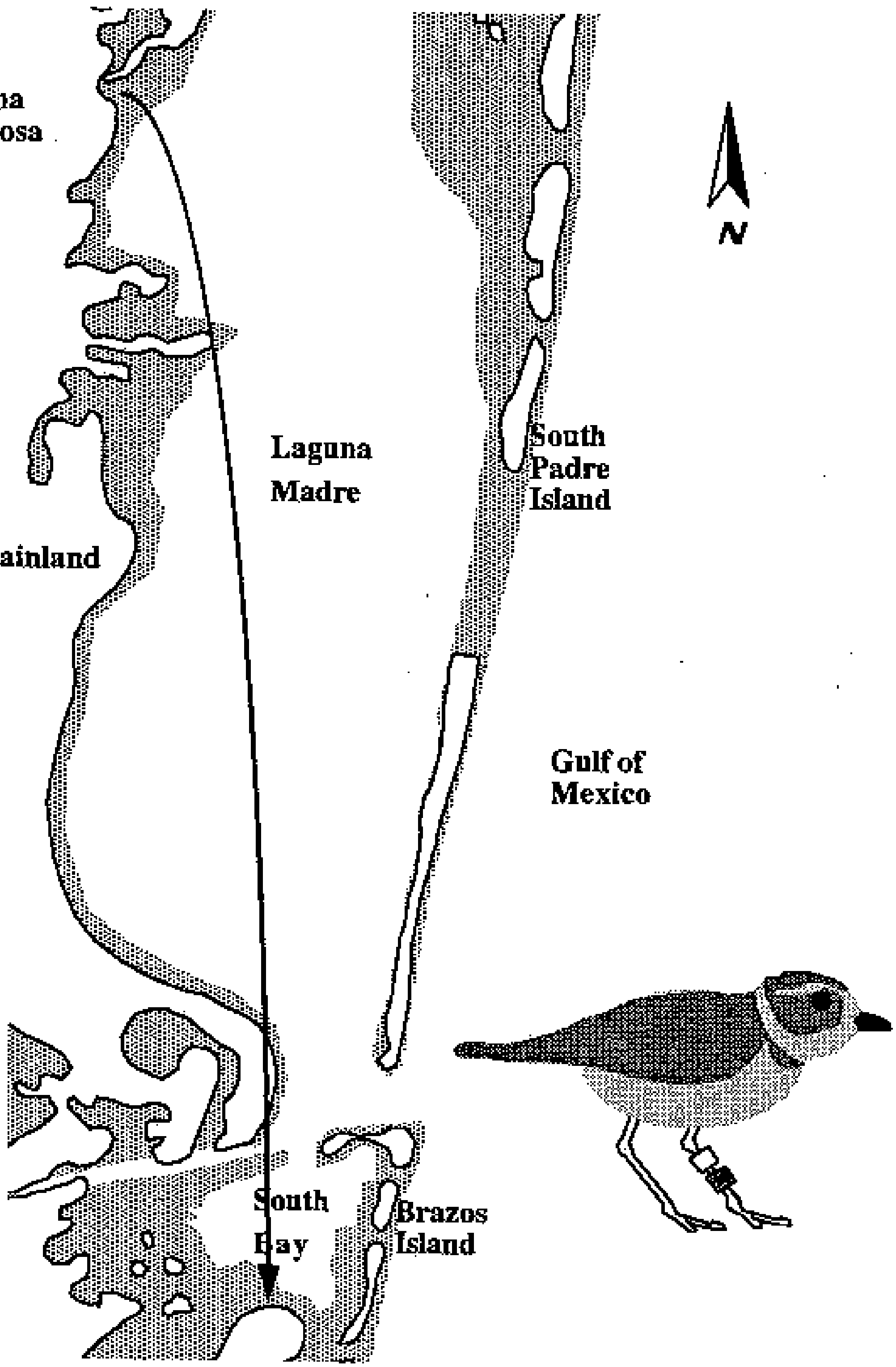


Figure 39. A schematic map illustrating the movement of a color banded Piping Plover described as PPL # 3 on Table 21 is presented in this figure. This plover was sighted while feeding on the Redhead Cove flats at Laguna Atascosa NWR on 11/18/91 and later resighted feeding on flats at the South Bay East Area site later during the same nonbreeding season (3/4/92). This movement could be associated with fall migration or might illustrate a non-migratory, intraseasonal movement among sites (perhaps in response to variable tidal conditions).

study (Table 21). Because these Piping Plovers were sighted at the same locations during consecutive nonbreeding periods, our data suggest that at least some Piping Plovers exhibit annual winter site fidelity along the Texas coast.

We also observed plovers that did not appear to exhibit annual site fidelity. Piping Plover # 13 (Table 21; Figure 40) was observed feeding at Laguna Atascosa National Wildlife Refuge (LANWR; Figure 12) on 1/28/93, and resighted approximately a year later (1/27/94) on South Padre Island North Area site (Figure 14). However, it is certainly possible that plover #13 used South Padre Island North Area site during the 1992-1993 season, and used LANWR during the 1993-1994 season without being detected. Thus, the term "site fidelity" depends largely upon how one defines a site.

Winter Home Range

Observations associated with plover # 3 (Table 21; Figure 39) indicate that some Piping Plovers may move a considerable distance during the nonbreeding period, as these sites are separated by over 35 km and are associated with different barrier islands. Because the location of the spring sighting is south of that for the fall sighting, it is difficult to explain this seasonal movement as migratory unless this bird was still staging along the coast during late November. Further indirect evidence of exaggerated winter movements might be found in the fact that very few birds were seen more than once, even though the study sites were surveyed several times over a three year period. Of the 23 Piping Plovers sighted in the lagoon ecosystem that were observed to wear at least two color bands, only 4 were resighted, and 2 of these were resighted at different location than the initial sighting. These gaps in the records suggest that the plovers sighted only once were either staging through our sites during migration (unlikely for many of the sightings) or represent sightings of plovers that were moving among our sites and other locations during the non-breeding season.

DISCUSSION

Unfortunately, we are not able to fully discuss all of our results without further delaying the delivery of this report to those parties that have provided the resources and support essential to the completion of our research. We sincerely appreciate their patience to date, and respectfully wish to test their courtesy no longer. We will be discussing the results of our research in complete detail in a future publication and in a dissertation, which we expect to make available no later than December, 1996. Until that time, we offer a brief discussion of each research focus below, and will make ourselves personally available to help explain or interpret any work that is not covered in this discussion.

Primary Objective. Identify the habitat components and environmental conditions that are necessary to support large numbers of Piping Plovers along the Texas Gulf Coast.

We developed 2 multiple regression models describing Piping Plover abundances in relation to selected habitat components and environmental conditions. The models were supported by data collected at 10 study sites along the Texas Gulf Coast over a 3 year period encompassing 3 consecutive nonbreeding seasons. Both of the models

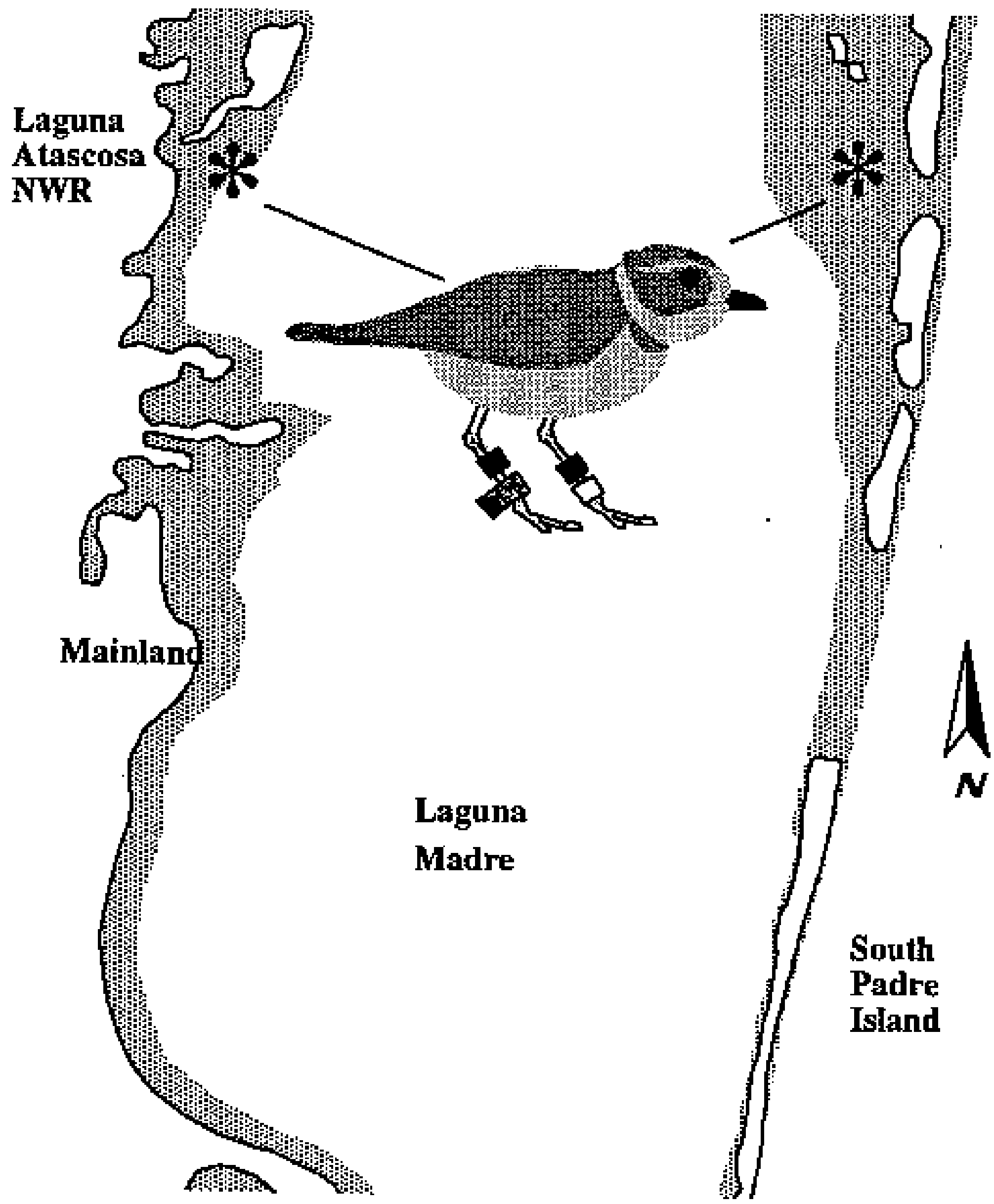


Figure 40. A schematic map illustrating the sightings of a color banded Piping Plover described as PPL # 13 on Table 21 is presented in this figure. This plover was sighted at the Laguna Atascosa NWR site and the South Padre Island North Area site on nearly the same day of the year during 1993 and 1994, respectively. These observations suggest either that some Piping Plovers winter at different sites during their lives, or that some Piping Plovers move among winter sites during the nonbreeding season.

explain over 99% of the variability associated with Piping Plover abundances at our study sites. Beach length, beach crustacean density, and bayshore macrobenthic density were positively associated with Piping Plover abundance in both models. Beach vehicular density and beach polychaete density were negatively associated with Piping Plover abundance in both models. In the non-selective full model containing all parameters, bayshore area was not significantly associated with Piping Plover abundance.

We interpret these results to suggest that high quality beach habitat may currently be limiting Piping Plover populations along the Texas coast. It is interesting to note that whereas human disturbance (as estimated by vehicular density) was not significantly associated with Piping Plover total beach densities at our sites, human disturbance was significantly associated with Piping Plover site abundance. Sites with higher levels of human disturbance had, on average, fewer Piping Plovers. Therefore, although Piping Plovers used beach habitat at similar densities at high and low disturbance sites, the sites with higher levels of disturbance either attracted or supported fewer Piping Plovers. Our research revealed that Piping Plovers foraged in greater densities at sites with lower human disturbance. It is possible to hypothesize from these findings that sites with higher levels of human disturbance limit Piping Plover energy intake rates to a greater extent relative to less disturbed sites, perhaps by limiting the time Piping Plovers can forage, or reducing the efficiency with which they forage. If true, human disturbance on Texas beaches may be limiting Piping Plover winter populations at some sites by contributing to increased winter mortality, site avoidance, or possibly even reduced recruitment into local winter populations (assuming high levels of winter site fidelity) resulting from increased mortality during migration or on the breeding grounds or from the reduced reproductive success of plovers from specific local winter populations. From a recovery or management perspective, these results suggest that Piping Plovers wintering in Texas might benefit most by efforts that reduce human disturbance on beaches and protect or restore such natural beach attributes as healthy intertidal benthic populations, especially amphipod populations. It is important to note that vehicular density may be only a modest measure of the effects of human presence on beaches on Piping Plovers. Other studies are expected to established that non-vehicular types of disturbances such as jogging, beach combing or allowing pets to roam the beach unleashed may have even greater effects on Piping Plover behavior than does vehicular traffic (L. Elliott, Texas Parks and Wildlife Department, Corpus Christi, TX, pers. comm). Furthermore, extreme forms of vehicular activity that are not distinguished in our analysis, such as the practice of raking forebeach areas to remove *Sargassum* sp. and other wrack, or the practice of scraping beach substrates into unnatural formations to improve driving conditions, probably have disproportionately large negative effects on beach quality to Piping Plovers compared to other types of vehicular activity. Therefore, the most effective recovery efforts for Piping Plovers may involve management strategies that 1) guide both vehicular and non-vehicular human activity away from selected portions of Texas beaches and 2) leave beaches in near natural conditions by reducing or eliminating activities such as the removal of beach wrack and the re-contouring of beach surface topographies.

The fact that our models did not select bayshore area as a parameter associated with Piping Plover abundance may be misleading. This parameter was incorporated into the analysis as the average area of potential intertidal bayshore area available during the study. For example, if a site had 100 hectares of bayshore habitat that was observed to be both inundated and emergent during the study period (i.e. 100 hectares of total potential bayshore area) and experienced an average tidal inundation of 50% during the study, 50 hectares was entered into the analysis as the value for the average area of bayshore habitat at that site. However, all emergent bayshore habitat is probably not the same, even that occurring at the same site. In the above example, the same site may have much higher densities of available prey on 50 hectares of very recently emergent flats during a quick drop in tide than would the same site when the same 50 hectares of flats have been exposed for hours (or days). We would expect to find more Piping Plovers using the site following recent emergence. Other factors that were not incorporated into the model due to statistical constraints, such as the climatic conditions during the surveys, the time of year, or the presence of a predator, may also affect Piping Plover abundance to a greater extent on bayshore habitat. For these and other reasons, it is possible that our model underestimates the association between Piping Plover abundance and the area of bayshore habitat. Even if this is not the case, and our model has correctly failed to identify a significant association between Piping Plover abundance and the area of bayshore habitat, it should be stressed that even though Piping Plovers may not currently be limited by available bayshore habitat, their recovery to population levels required for delisting may be dependent upon the preservation of bayshore habitat.

Objective # 1. Characterize the relative densities of Piping Plovers among the 2 Texas coastal ecosystems and the Texas coastal ecotone.

Our research indicates that Piping Plovers occurred at higher densities on bayshore flats in the bay ecosystem (~ 0.57 plovers/ha) than in either the lagoon ecosystem (0.40 plovers/ha) or the ecotone (0.38 plovers/ha). We also observed significantly higher densities of Piping Plovers on barrier island flats (~ 0.97 plovers/ha) than on mainland flats (0.21 plovers/ha) in the lagoon ecosystem during periods of tidal emergence. Beach densities were similar in both ecosystems and in the ecotone (~ 2-3 plovers/km). The higher densities in the bay ecosystem may reflect the limited area of suitable bayshore locations under most tidal conditions relative to that occurring in the lagoon ecosystem and the ecotone. In the bay ecosystem, Piping Plovers are often confined to only a small group of sites, such as San Luis Pass and Bolivar Flats. Although these sites are very productive biologically, exhibiting extremely dense macrobenthic populations, their isolation serves to concentrate Piping Plover populations, increasing the potential for catastrophic loss at one or more of these sites from an oil spill or development project. Fortunately, private and public parties interested in conservation have become increasingly aware of the importance and vulnerability of these sites and have begun taking steps to protect them (T. Eubanks, pers. comm, P. Glass, U.S. Fish and Wildlife Service, Houston, TX, pers. comm.).

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

Bayshore tidal condition was the parameter that was most consistently associated with Piping Plover densities on both beach and bayshore habitats. In general, Piping Plovers used beach habitats during periods of high bayshore tides, but usually returned to feed on bayshore flats when they became emergent (although our data did not significantly establish a association between the use of bayshore habitat and bayshore tidal emergence in the ecotone). Although high levels of human disturbance (as estimated by vehicular density) were not associated with the total densities of Piping Plovers on beach habitat, we observed Piping Plovers to forage less under conditions of high human disturbance. Climatic conditions, time of day, and life cycle stage were either not associated with Piping Plover densities, or were associated with Piping Plover densities in an inconsistent fashion.

Objective # 3. Characterize the foraging ecology of Piping Plovers along the Texas Gulf Coast, and identify the factors affecting foraging efficiency.

The diets of Piping Plover varied considerably in the 2 ecosystems when feeding on bayshore habitat. Plovers feeding on flats in the bay ecosystem ate mostly polychaetes and only a small amount of insects and other surface animals in proportion to polychaetes. In the lagoon ecosystem and the ecotone, the proportion of surface prey in Piping Plover diets was much larger in proportion to polychaetes. The difference was most pronounced on algal flats, where surface prey composed almost the entire diet of Piping Plovers in the lagoon ecosystem. In contrast, beach diets were fairly similar, composed primarily of polychaetes (predominantly *Scolelepis squamata*) and amphipods.

Foraging Piping Plovers appeared to expend significantly more energy (as estimated by prolonged foraging locomotion) on beaches than on bayshore flats. Plovers feeding on beaches spent about 5 times as much time in prolonged locomotion than did plovers feeding on sand flats or algal flats. Most of the difference in prolonged locomotion occurred within the swash zone microhabitat, where plovers must repeatedly avoid the incoming swash.

Piping Plovers captured prey at similar rates in the 2 ecosystems and the ecotone. Plovers also foraged with similar efficiencies on beach and bayshore habitats. On bayshore habitats, we observed Piping Plovers to capture prey at similar rates on sand flats and algal flats. We are in the process of incorporating the average estimated caloric values of the different prey types we monitored into our appraisal of foraging efficiency. We may find, for example, that although plovers captured prey animals at similar rates in the bay and lagoon ecosystems, the net energy intake rates in each ecosystem may differ significantly because of large differences in the caloric values of the major prey types captured in each ecosystem.

Objective # 4. Characterize the prey resources potentially available to Piping Plovers among the habitats and ecosystems used by Piping Plovers along the Texas Gulf Coast.

With the exception of the bay ecosystem, beaches supported higher macrobenthic densities than did bayshore habitats in areas used by foraging Piping Plovers. Macrobenthic densities on bayshore habitats were significantly higher in the bay ecosystem than in either the lagoon ecosystem or the ecotone in areas used by foraging Piping Plovers. We are still in the process of comparing macrobenthic populations collected from sand flats to those collected from algal flats.

Macrobenthic polychaete populations were significantly higher in the bay ecosystem than in the lagoon ecosystem or the ecotone. The lagoon ecosystem supported significantly higher densities of macrobenthic insect populations than did the bay ecosystem or the ecotone.

Above ground potential prey populations (surface prey populations) were monitored on bayshore habitats in areas used by foraging Piping Plovers suing 2 methods. Using sticky traps, we observed surface prey populations to be significantly higher in the lagoon ecosystem than in the bay ecosystem or the ecotone. Ecotone flats also supported significantly higher populations of surface prey than did bayshore flats in the bay ecosystem. Algal flats supported higher surface prey populations than did sand flats. Using a spotting scope as a second technique to estimate surface prey population densities, we estimated surface prey densities at between 400 and 1100 animals per square meter.

Objective # 5. Characterize the movement patterns of Piping Plovers.

Although few color banded Piping Plovers were sighted on multiple occasions, the movement patterns of some of these birds suggest that some Piping Plovers exhibit strong winter site fidelity whereas some apparently do not. One Piping Plover was sighted on 11 occasions at the same study site over an 11 month period covering 2 nonbreeding seasons. This plover was not observed at any other site, including 2 sites located very nearby. These observations indicate that some Piping Plovers wintering in Texas do exhibit site fidelity. Other plovers were resighted at 2 or more locations, and many more were sighted only once. If a large proportion of the Texas winter population of Piping Plovers exhibited winter site fidelity, we would have expected to observe more individuals at the same site on multiple occasions.

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APPENDIX

Abbreviations used throughout report

Study Sites

BF	Bolivar Flats
BI	Brazos Island
BR	Big Reef Channel Beach
CC	Convention Center (flat located on SPI)
EF	East Flats
EHC	Elephant's Head Cove (flat located within LANWR)
LANWR	Laguna Atascosa National Wildlife Refuge
MF	Mangrove Flats (flat located on SPI)
MISP	Mustang Island State Park
MISPN	Mustang Island State Park - North Area
MISPS	Mustang Island State Park - South Area
NYF	North Yucca Flats (flat located within LANWR)
PC	Packery Channel
PE	Parrot Eye's (flat located on SPI)
RBV	Rincon Buena Vista (flat located within LANWR)
RHC	Redhead Cove (flat located within LANWR)
SB	South Bay
SBE	South Bay - East Area
SBW	South Bay - West Area
SL	San Luis Pass
SPI	South Padre Island
SPIN	South Padre Island - North Area

Habitat

Be	Beach
Fl	Flat
MUB	Moist Upper Beach microhabitat of intertidal beach habitat
SZ	Surf Zone microhabitat of intertidal beach habitat
TPA	Total potential bayshore habitat area

Others

AOU	American Ornithologist's Union
Corps	U.S. Army Corps of Engineers
ESA	Endangered Species Act of 1973
IPPC	International Piping Plover Census
Service	U.S. Fish and Wildlife Service
TPWD	Texas Parks and Wildlife Department
TOES	Texas Organization for Endangered Species

MACRO-BENTHIC PREY CLASS	SIZE CATEGORY			
	#	Small	Medium	Large
Amphipods	(2)	2 mm		>2mm
Polychaetes	(3)	< 20 mm	20mm <x> 30mm	>30mm
Bivalves	(2)	10mm		>10mm
Crabs	(2)	<10mm		>10mm
Insects:				
	Larval	(1)	only one size class	
	Pupal	(1)	only one size class	
	Adult	(1)	only one size class	
Taniads	(1)		only one size class	
Total	(13)			

Dimensions of Prey Samples:

Sample Type:	Diameter (cm)	Depth (cm)	Surf. Area (cm2)	Time
Benthic Cores	7.5	10	44.16	~2 sec.
Surface Traps	12.5	0	122.70	1 hr.
Surface Scope		10	44.16	~2 sec.
Algal Cores	7.5	1-2	44.16	1-6 wks

Tide Levels

Tidal Amplitude	Estimated % of Tidal Flats Inundated
Very High	100%
High	75% - 99%
Moderate	50% - 74%
Low	25% - 49%
Very Low	<25%

Wind

Wind Magnitude	Estimated Wind Speeds
Strong	> 20 knots
Moderate	10-20 knots
Light	5-10 knots
Calm	< 5 knots