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Habitat Use by
Migratory Shorebirds
at the Cabo Rojo Salt Flats,
Puerto Rico

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ABSTRACT

HABITAT USE
BY MIGRATORY SHOREBIRDS
AT THE CABO ROJO SALT FLATS,
PUERTO RICO

By

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August, 1992

Chairman: Jaime A. Collazo, PhD
Major Department: Forest Resources and Conservation
(Wildlife and Range Sciences)

The Cabo Rojo Salt Flats, at the southwestern tip of Puerto Rico, provide important autumn stopover and wintering habitat for migratory shorebirds. I studied the abundance and distribution of shorebirds and their food resources at this site during autumn of 1990 and 1991.

Small calidrids (primarily *Calidris pusilla* and *C. mauri*) were the most abundant shorebirds at the salt flats. The maximum weekly counts of small calidrids in 1990 (2,690) and 1991 (3,532) occurred in mid October. Calidrids foraged primarily in the Fraternidad lagoon system; roosting took place most often at the neighboring Candelaria Lagoon.

The macroinvertebrate prey important to calidrids in the Fraternidad system were *Dasyhelea* (Diptera), *Trichocorixa* (Hemiptera), and *Artemia* (Anostraca). Changes in invertebrate abundance coincided with fluctuations in salinity.

These fluctuations were induced by the combined influences of tides, evaporation, and rainfall. On a more seasonal basis, desiccation of algal mats influences the timing of invertebrate productivity.

Shifts in the diets and among-habitat distribution of calidrids were associated with changes in food abundance; in other cases when food abundance did not change, shifts were associated with increased water levels such that prey became inaccessible to foraging calidrids. Within a preferred lagoon, differences in prey abundance among patches of differing levels of use by calidrids (high vs. low) were not strong, except in areas where only *Artemia* were present. Using mapping data, I found significant correlations between algal substrate type and the abundance of calidrids and their prey. This suggests that calidrids may select foraging sites based on algal physiognomy. The lack of clear differences between high-use and low-use patches may have been due to sampling across substrate types.

Every site within the salt flats serves as important habitat to at least one shorebird species. Conditions in these habitats are influenced by varying levels of human manipulation. Management of the salt flats must therefore be based on a clear understanding of the hydrologic regimes maintaining this broad range of habitat conditions.

CHAPTER 1
INTRODUCTION

Rationale and Objectives

Migratory shorebirds (Charadrii and Scolopaci) may spend over 65% of the year at stopover areas and wintering grounds (Senner and Howe 1984). Many individuals use the same areas year after year. The quality and availability of stopover areas and wintering grounds affect over-winter survival and are therefore critical to the stability of shorebird populations (Myers et al. 1987). The conservation of many shorebird species depends on our ability to locate, describe, and protect critical links in migration.

As an important component of wetland wildlife, shorebirds represent an international link in the global problem of wetland habitat destruction. This link has been recognized by a wide array of government and nongovernment organizations participating in the PanAmerican Shorebird Program and International Shorebird Survey (Myers 1983, Harrington et al. 1989), such as the U.S. Fish and Wildlife Service, the Canadian Wildlife Service, the Western Hemisphere Shorebird Reserve Network, and the World Wildlife Fund. The Wader Study Group and the Asian Wetlands Bureau have identified many sites important to shorebirds in the western hemisphere. The migratory routes of shorebirds have

been summarized in Pienkowski and Evans (1984), Morrison (1984), and Myers et al. (1987).

In Puerto Rico, shorebirds are one of the least-studied groups of birds. Available information consists of checklists, notes, and short-term surveys (e.g., Biaggi 1983, Danforth 1929, Leopold 1963, McCandless 1961 and 1962, Moreno and Pérez 1980, Raffaele 1989, Wetmore 1916). Pressing demands to develop wetlands and shoreline habitats for multiple uses represent the major threat to the continued existence of both migratory and resident shorebirds in Puerto Rico (Moreno and Pérez 1980, Raffaele and Duffield 1979). As a first step toward habitat protection, Raffaele and Duffield (1979) identified the Cabo Rojo Salt Flats (Figure 1.1) as one of the prime habitats for migratory and resident shorebirds. Nearly every publication and unpublished list of Puerto Rico's most valuable wetlands and wildlife habitats includes the Cabo Rojo Salt Flats (e.g., Collazo et al. 1987, Del Llano et al. 1986, Moreno and Pérez 1980, Ortiz-Rosas and Quevedo-Bonilla 1987, Raffaele and Duffield 1979).

In an effort to contribute to the knowledge of migration patterns through the eastern Caribbean, the U.S. Fish and Wildlife Service and the Commonwealth Department of Natural Resources have supported research and monitoring programs at the Cabo Rojo Salt Flats since 1985. Findings indicate that this hypersaline lagoon system is the single most important converging point for migrating shorebirds on the island during autumn migration and winter. During spring migration,

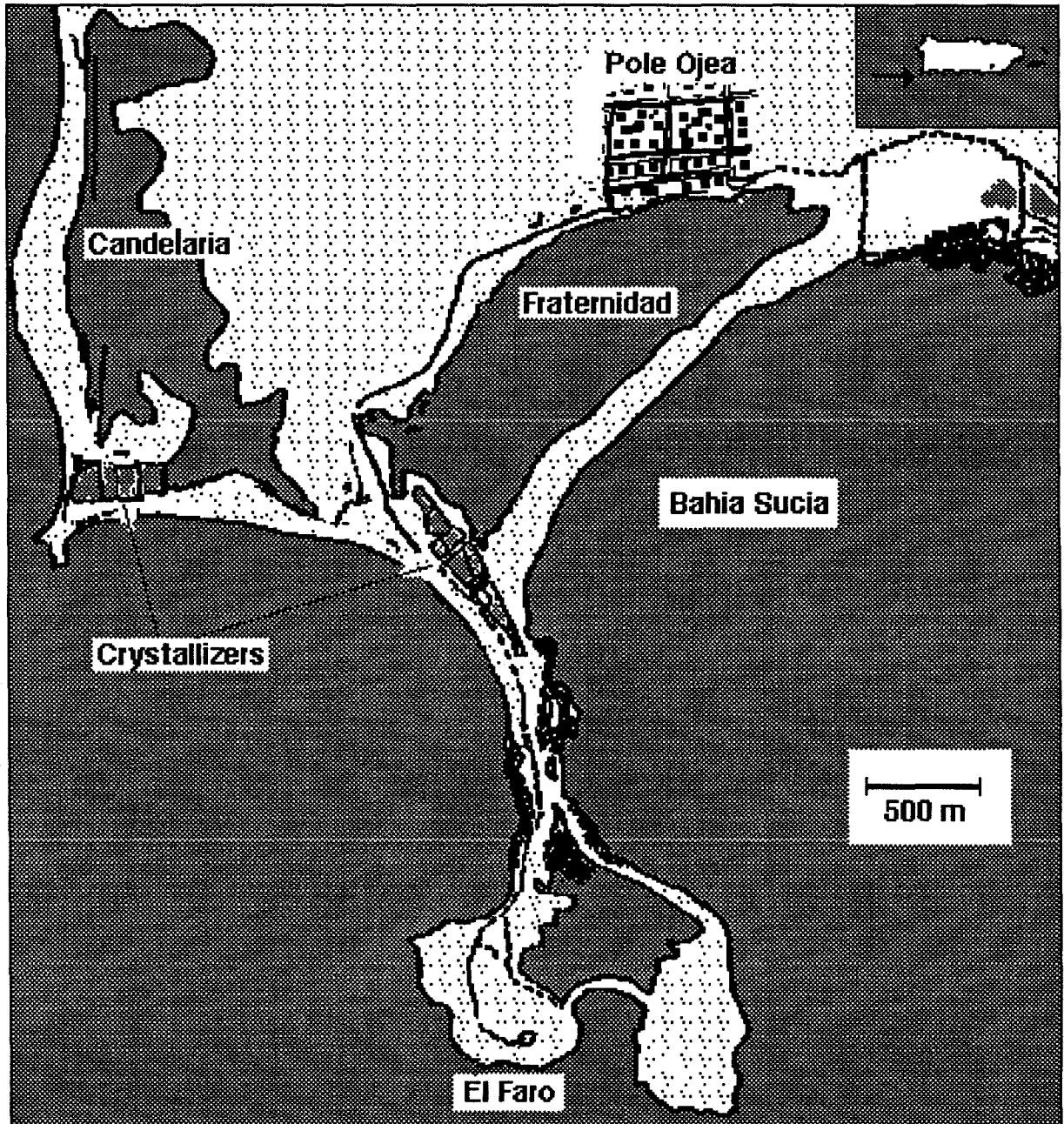


Figure 1.1. The Cabo Rojo Salt Flats, at the southwest tip of Puerto Rico.

only small numbers of migrants stop in Puerto Rico. Thirty-two species of shorebirds have been seen at the salt flats (Appendix). Small calidrids (primarily *Calidris pusilla* and *C. mauri*) comprise 60-70% of the shorebirds present on the flats during autumn migration. Harrington (1982) and Harrington and Morrison (1979) discussed the migratory patterns of *C. pusilla* in the western hemisphere (also see review by Morrison 1984). Information on the migration of *C. mauri* is less complete but has been discussed in Senner and Martinez (1982) and Senner et al. (1981).

Migratory species start to arrive at the Cabo Rojo Salt Flats in late July. Many individuals may remain through the winter, but others depart before December. Four shorebird species breed at the flats: Black-necked Stilt (*Himantopus himantopus*), Killdeer (*Charadrius vociferus*), Wilson's Plover (*C. wilsonia*), and Snowy Plover (*C. alexandrinus*). The locally threatened Snowy Plovers are found nowhere else on Puerto Rico (Biaggi 1983, Collazo et al. 1987, Lee 1989, Raffaele 1989). Numerous aquatic birds and seabirds have been seen at the area. Included among these are the White-cheeked Pintail (*Anas bahamensis*, a candidate for the federal list of endangered species), the federally endangered Brown Pelican (*Pelicanus occidentalis*), and the Least Tern (*Sterna antillarum*). The flats are also within the designated critical habitat of the federally endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*).

The apparent similarity of salt flat systems around the world widens the scope of my study. The worldwide distribution of hypersaline coastal ecosystems is described in Chapman (1977), where it is also suggested that hypersaline conditions may be prevalent on river mouth mud flats along the Patagonian coast of South America. This may be critical to the study of shorebirds, since many species winter in southern South America. Lankford (1977) devised a classification system for Mexico's 123 coastal lagoons, many of which become hypersaline at certain times of the year.

The use of coastal ecosystems throughout the tropics by migratory shorebird populations should be studied in detail. There is strong pressure for development of coastal lagoons in Puerto Rico as well as other areas in the neotropics. As of 1988, for example, 120,000 ha of shrimp ponds had been constructed within Ecuador's 3,000 km coastline (Matuszeski et al. 1988). Many of these ponds have replaced mangrove forests and lagoons.

While efforts to ensure the protection of the Cabo Rojo Salt Flats have been made by Commonwealth and Federal agencies and non-government organizations, the preparation of a management plan and the ability to assess potential impacts of habitat alterations has been hampered by the lack of basic knowledge about the use of the salt flats by shorebirds. The continued use and value of the Cabo Rojo Salt Flats as a migratory stopover and wintering area is related to the availability and abundance of food resources (Goss-Custard

1979, Hicklin and Smith 1984, Myers et al. 1980, 1987).

Thus, my study was designed to obtain baseline data on the biological resources present at the Cabo Rojo Salt Flats, the underlying factors influencing these resources, and how they are used by migratory shorebirds. These data were collected in 1990 and 1991 to address the following project objectives:

Objective 1. To describe macroinvertebrate assemblages exploited by migratory *Calidris* sandpipers and the physical patterns associated with their distribution (Chapter 2).

Objective 2. To relate the distribution of migratory *Calidris* sandpipers to habitat resource patterns at the within- and among-habitat levels (Chapter 3).

I expect that these data will strengthen conservation and management efforts at this unique stopover and wintering area in the eastern Caribbean. Furthermore, as additional data from other sites accumulate, questions such as how and why the use of tropical wetlands by migratory shorebirds differs from that of temperate wetlands will be more easily answered.

Study Area

General Description

The Cabo Rojo Salt Flats lie at the southwestern tip of Puerto Rico (Figure 1.1). The salt flats system is roughly

445 ha (1,100 acres) in area and consists primarily of two large shallow lagoon systems (Candelaria and Fraternidad) separated from the Caribbean Sea by narrow strips of mangrove and scrub vegetation. The salt flats are bordered on the east and southwest ends by the mangroves and beaches of Bosque Estatal de Boquerón (Boquerón State Forest) and on the northeast by the upland dry forest of the Cabo Rojo National Wildlife Refuge. These areas represent over 810 ha (2,000 acres) of prime habitat for the protection of Puerto Rico's resident and migratory wildlife.

Dikes and barriers are maintained in both lagoon systems by a low-intensity solar salt production company (Sal de Borinquen, Inc.). Sea water is allowed to flow into the lagoons via several narrow sluices. After dissolved salts begin to accumulate, water is pumped into diked evaporation basins (crystallizers) from the lagoon and salt precipitates are harvested for commercial sale. In the Fraternidad lagoon system (Figure 1.1), sea water enters near the east end and is pumped into crystallizers from the west end of the lagoon, where salinity levels approach saturation.

For several kilometers east of the Cabo Rojo Salt Flats, dense mangrove stands are interspersed with small open pools. It is likely that many of these pools are hypersaline. While it is clear that hypersaline lagoons often form naturally as a dynamic phase in mangrove forests of arid coastal environments (Cintrón et al. 1978), the dikes and barriers at

the Cabo Rojo Salt Flats appear to have arrested vegetation succession in several portions of the system.

Habitat Units

Shorebirds used a wide range of habitat types at the Cabo Rojo Salt Flats. Discrete habitat units within the Fraternidad system were identified (Figure 1.2). I refer to these habitat units throughout Chapters 2 and 3. Borders between habitat units are typically defined by physical features such as dikes and barriers maintained by the salt production company. A description of each unit is provided below with a summary of important characteristics at the end of the section.

Mangrove Pool. The mangrove pool is an open water area surrounded by mangroves (*Avicennia and Rhizophora*). It is bordered to the south by a narrow barrier beach. Sea water interchange with Bahia Sucia occurs through a narrow channel in the mangroves in the southeast corner of the area. At the east and west ends, dead sun-bleached mangrove snags are interspersed with shallow muddy areas. These muddy areas become exposed during periods of low water. Most of the mangrove pool area is greater than 5 cm deep.

East Lagoon. This is a large area connected at its southeastern corner to the mangrove pool by a narrow channel through mangroves. During my study, most of the area was

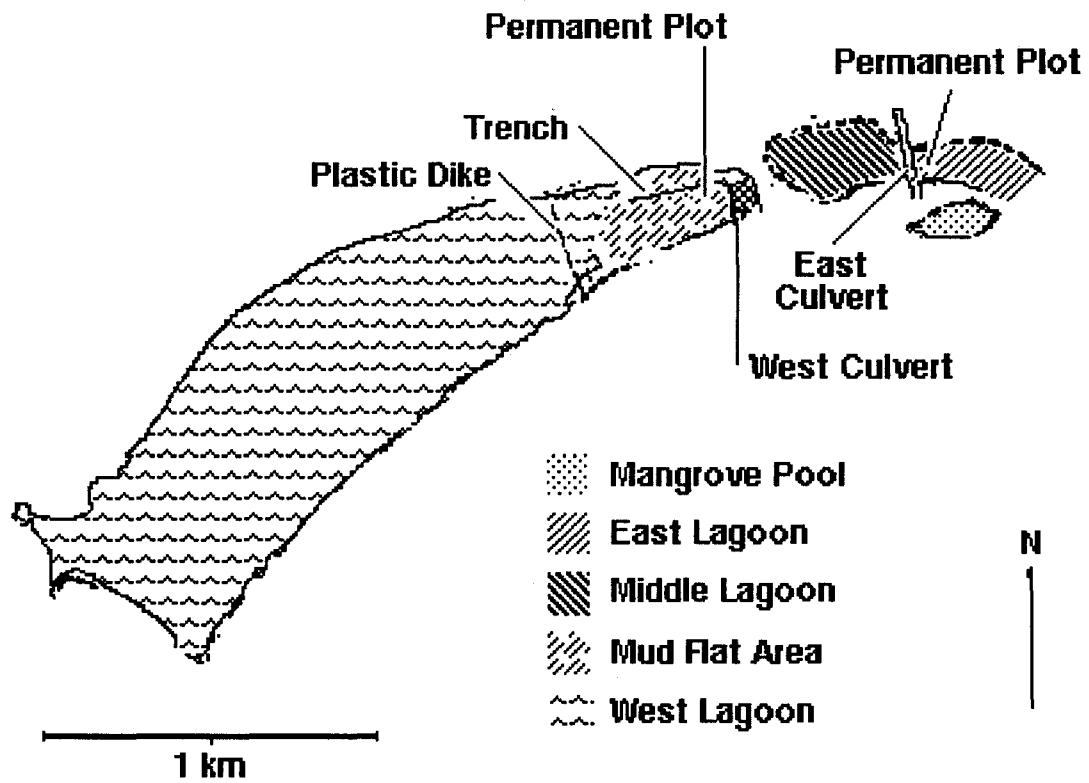


Figure 1.2. Diagram of Fraternidad system showing habitat units, measurement stations, and locations of invertebrate sampling plots.

open water greater than 5 cm deep. The shorelines are of low aspect and in areas where blue-green algal mats are well-developed (primarily the southwest, west, and northwest edges), periods of low water result in the exposure of mudflats. There is a small stand of *Acacia/Prosopis* trees beyond the southwest corner of the area and small mangrove saplings are scattered around the borders. The Cabo Rojo National Wildlife Refuge and a cattle grazing area lie 10-20 meters north of the water's edge.

Middle Lagoon. This area is separated from the east lagoon by a paved dike. The dike provides access and a utility right-of-way to a small fishing camp on the barrier beach just south of this lagoon. Water flows between the east and middle lagoons via two small culverts that pass through the dike. The northernmost culvert is partially blocked with sediments. A small stream enters the northeast corner of the lagoon from the Cabo Rojo National Wildlife Refuge, which borders the entire northern edge of this area. Dense stands of *Acacia/Prosopis* dominate this portion of wildlife refuge. A small channel connects the southwest corner of the middle lagoon to Bahia Sucia. Water movement through this channel is partially restricted by mangroves. The middle lagoon was almost completely dry in late August of 1990, except for an area roughly 50 m in diameter immediately west of the main culvert. Following increased rainfall and tidal input in mid October 1990, the lagoon became inundated

with water and lush algal mats appeared throughout much of the area.

Mud Flat. The mud flat area is bordered to the east by a dike that separates it from the middle lagoon and by a deteriorated wooden structure built by the salt production company. The intended function of this structure is to filter detritus as sea water enters the system through the west culvert (Figure 1.2). The mud flat is part of a larger lagoon that is separated from the adjacent west lagoon by a decaying plastic barrier. Since the northern end of the barrier is only partially intact, the northwest half of this lagoon is functionally part of the west lagoon. The southeast half is covered with a lush algal mat and is quite distinct from the northwest half and the west lagoon. This algal mat is referred to as the mud flat area (Figure 1.2). In late August of 1990, the mud flat area had only a shallow layer of water (less than 4 cm). Throughout late October and November of the 1990 field season, there was over 6 cm of water covering the entire mud flat area. Water levels were low during the 1991 season as a result of a tidal barrier placed at the west culvert and most of the mud flat had less than 1 cm of water overlying it.

West Lagoon. This is the largest lagoon and is bordered at its east end by the mud flat area and at the west end by the salt crystallizing basins. Most of the area is greater

than 6 cm deep and the southern edge, which is bordered by a narrow barrier beach with stands of *Acacia/Prosopis* has a rather steep aspect. The northern edge, however, is shallow with wide sandy shores and occasional stands of *Salicornia*, *Sesuvium*, and *Acacia/Prosopis*. Throughout most of the lagoon, the bottom is covered with a hard sandy crust that is often pink in color. Water levels in this lagoon are partially manipulated by the salt production company.

Summary of Habitat Units. Habitat studies focused on the east and middle lagoons, the mud flat, and the west lagoon. Of these four units, tidal flow was least obstructed at the mud flat during 1990. Ephemeral lagoons at the east end (east and middle lagoons) receive both tidal and runoff inputs. Conditions in the deeper and more permanently flooded west lagoon are maintained by the salt production company. The west lagoon is also the only unit where extensive algal mats do not occur.

CHAPTER 2
MACROINVERTEBRATES USED BY MIGRATORY CALIDRID SHOREBIRDS
AND PHYSICAL PATTERNS ASSOCIATED WITH
THEIR ABUNDANCE AND DISTRIBUTION

Introduction

The value of the Cabo Rojo Salt Flats as a migratory stopover has been established by cumulative data collected since 1985 and those contributed by this study (Chapter 3). The continued use and value of this stopover is related to the availability and abundance of food resources (Goss-Custard 1979, Hicklin and Smith 1984, Myers et al. 1980, 1987). In this chapter, I describe the salt flat macroinvertebrate community used by migratory calidrid sandpipers (*Calidris pusilla*, *C. mauri*, *C. minutilla*, *C. fuscicollis*, and *C. bairdii*).

Salt flat habitats are interspersed among mangrove forests of southern Puerto Rico from Guayama to Cabo Rojo. These hypersaline ecosystems attain landscape dominance at Cabo Rojo, where mangroves are reduced to a thin fringe. The salt flats are part of an important complex in southwest Puerto Rico that includes coral reefs, seagrass beds, mangroves and uplands. Some of the unique ecosystem characteristics of hypersaline systems were examined and

reviewed by Armstrong (1982), Copeland and Nixon (1974), Javor (1989), Nixon (1969), and Odum et al. (1971). Davis (1978, 1979) discussed basic physiological aspects of organisms inhabiting evaporation ponds of tropical and subtropical solar salt systems.

Ecosystem and physiology studies show that, in hypersaline systems, mobilization of nutrients from organic compounds may be a limiting factor to which organisms must adapt (Odum et al. 1971). This reduced mobilization of nutrients is due to the truncation of the detritivore community by hypersaline conditions. Several species of blue-green algae (Cyanophyta) and green algae (Chlorophyta) tolerate hypersaline conditions and frequent desiccation; they are the most important primary producers in the salt flat system. Large-scale commercial salt producers elsewhere in the Caribbean have recognized the importance of the algal communities for the absorption of the sun's energy that, in turn, is necessary for evaporation (J. Davis, personal communication). The algae are typically fed upon by brine shrimp (*Artemia*) and several species of salt-tolerant insects. These and many other ecosystem characteristics are shared with every documented tropical salt flat system globally (J. Davis, personal communication).

During shorebird migration at the Cabo Rojo Salt Flats in autumn 1990 and 1991, I collected baseline data on macroinvertebrate abundance and distribution, and the underlying factors influencing these parameters. These data

are necessary to formulate appropriate habitat management strategies for maintaining resource availability in the salt flats. Thus, data and analyses in this chapter address the following objective:

Objective 1. To describe macroinvertebrate assemblages exploited by migratory *Calidris* sandpipers and the physical patterns associated with their distribution.

Methods

I set up two permanent plots in 1990 to detect changes in invertebrate numbers through the season in the east lagoon and the mud flat area. I selected these units because they were considered to represent distinctly different habitat types. Within each unit, I located the permanent plots in areas that were representative of the entire habitat unit in terms of slope, depth and substrate character. Samples also were collected in the west lagoon and middle lagoon as part of other habitat use studies (Chapter 3).

Permanent plots were sampled every two weeks for a period of 10 weeks. On a sampling day, I collected six sets of samples at each plot (see Figure 2.1). Each set consisted of one water column sample and one sediment sample. Each plot was 50 m wide. I stratified the six sample sets so that two sets were taken from each of three zones: shallow water (1-2 cm); intermediate depth (3-7 cm); and deep water (8-12

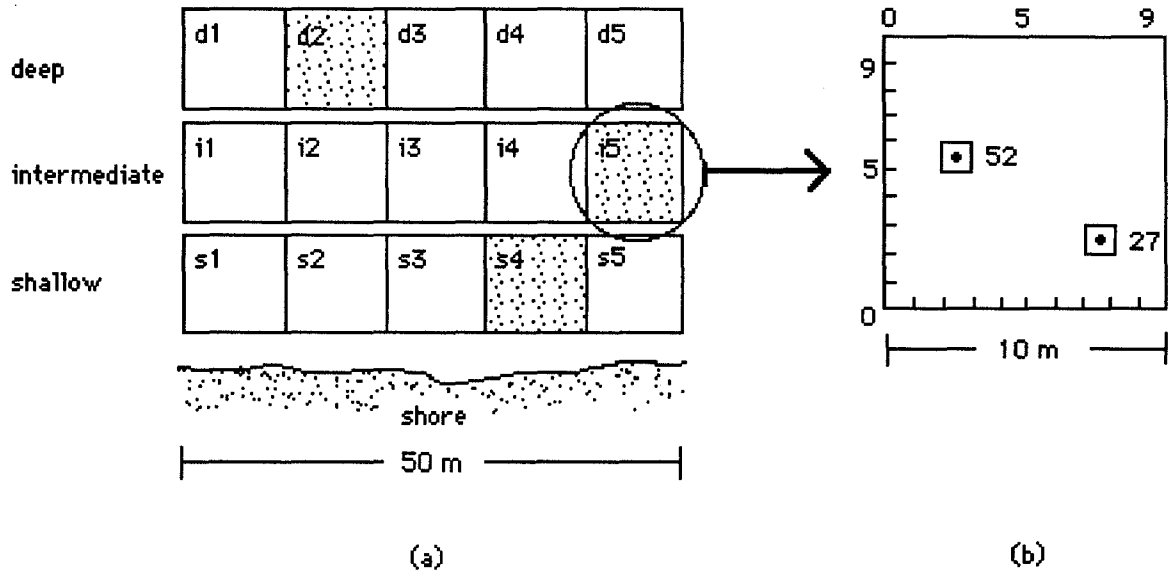


Figure 2.1. Sampling protocol for permanent plots. One 10 x 10 m quadrat was randomly chosen from within each of three zones (a). Within each 10 x 10 m quadrat, two 1 x 1 m subplots were randomly selected for sampling (b).

cm). Depth zones ran parallel to the shore for a distance of 50 m. The purpose of this depth stratification was to broaden the scope of sampling, rather than to allow between-zone comparisons. I then randomly selected one 10 x 10 m section from each of these strips for a particular sampling day. After five sampling days (8 weeks), each 10 m section of the 50 m strips had been sampled. This protocol prevented repeated sampling of each 10 x 10 m quadrat since sampling activity resulted in considerable alteration of substrata (i.e., footprints) that often persisted for several weeks. The samples taken from each zone also were randomly located within their 10 m quadrats. Thus, for each permanent plot, there are 5 sets of 6 water column samples and 5 sets of 6 mud samples.

I collected samples by first identifying the exact location of a sample from a distance of ≈ 1.5 m. Then, in a rapid motion, I placed a steel cylinder (diameter = 9.92 cm, open at both ends) vertically on the site and inserted it into the mud. This motion was done in one quick step in order to minimize the escape of swimming invertebrates. I quickly stirred the water and loose detritus inside the cylinder and transferred them into a marked plastic container using a water suction device (turkey baster). The cylinder was then reinserted into the mud adjacent to the location of the water column sample to a depth of 1.5 cm and a sediment core sample was lifted with the aid of a mason's trowel.

These samples were placed in marked plastic bags where they remained intact.

I processed all samples at the Cabo Rojo National Wildlife Refuge. Water column samples were poured into white dissecting pans and all visible invertebrates were counted and classified into morphospecies. I processed sediment samples using a "drying oven." The drying technique is similar to the use of a Berlese funnel. The intact core samples were placed on a plastic screen (1 mm mesh size) that suspended each sample over a separate bowl of water. This apparatus was enclosed within a cubical wooden box with an exhaust port and fan on its underside and a 200 watt lamp directly over the samples. The light and fan were then left on for 24 hours. As the sediment samples dried out, invertebrates burrowed downward through the underlying screen and into the bowl of water. I removed these bowls and counted and classified all visible invertebrates into morphospecies. Other processing techniques were attempted but were neither efficient nor repeatable. These included visual inspection, sieving, an agar technique (Kline et al. 1981), elutriation (Magdych 1981), and suspension of organisms in sucrose solution. Invertebrate specimens collected during the sampling efforts were preserved and identified to the lowest possible taxonomic level with the assistance of Dr. Willis Wirth and the Division of Plant Industries in Gainesville, Florida.

I monitored water level and salinity during the study. Rainfall data were obtained from the Cabo Rojo National Wildlife Refuge. I used tide prediction tables from Galveston, Texas and correction tables for Isla Magueyes, Puerto Rico (NOAA 1989) to determine tide heights at different times during the field season. Time corrections between Isla Magueyes and the Cabo Rojo Salt Flats are unknown. Tide data can therefore be compared only qualitatively to water levels within the lagoons at the study site. I measured water level and salinity daily at two sites in the study area (see Figure 1.2). One site, referred to as "east culvert," is located at a culvert that runs through a dike between the east and middle lagoons. The other site, referred to as the "west culvert" is located at a cinder block culvert running between the mud flat and Bahia Sucia (when not blocked). Salinity and water temperature were also measured at the corner of each 10 m quadrat at the time of sampling in the permanent plots and during all other invertebrate sampling activity (Chapter 3). Salinity measurements were taken with a temperature compensated refractometer (Reichert-Jung model #10419). I also obtained salinity data collected throughout 1986 at five stations in the Fraternidad Lagoon system from Willard Hill (Sal de Borinquen, Inc.).

I used Spearman correlation coefficients to examine changes through time in the invertebrate sampling data from permanent plots and relationships between salinity and

invertebrate density. I used analyses of variance to compare salinity and water temperature among different habitat units.

Results

I described the habitat units of the Fraternidad system in Chapter 1. Taxa encountered during all invertebrate sampling are listed by habitat unit in Table 2.1. The most prominent taxa were *Trichocorixa* (Hemiptera: Corixidae), *Dasyhelea* (Diptera: Ceratopogonidae), *Ephydra gracilis* (Diptera: Ephydriidae), and *Artemia* (Anostraca).

Using data from invertebrate sampling efforts only, I found a gradient in salinity among habitat units (Table 2.2). Average water temperature was significantly higher (by <2 degrees Celsius) in the west lagoon than in the other three areas (Table 2.3). *Trichocorixa* and *Artemia* occur in the narrowest ranges within the salinity gradient (Table 2.4): *Trichocorixa* occurs in the low salinity areas at the east end; *Artemia* occurs in the hypersaline west end.

Mean numbers of invertebrates per sample from the permanent plots in the east lagoon and the mud flat area during the eight-week sampling period (1990) are shown in Figures 2.2 and 2.3, respectively. I found a significant positive correlation between numbers per sample and date (N=30, 6 samples for each date) in the east lagoon for *Trichocorixa* (Rho = 0.69, p < 0.001) and a negative correlation for Stratiomyidae larvae (Rho = -0.38, p =

Table 2.1. List of macroinvertebrates encountered by site (within Fraternidad system).

<u>Taxon</u>	<u>Site(s)</u>
Anostraca	
<i>Artemia</i>	West Lake
Decapoda	
<i>Uca</i>	All sites
Chilopoda (dead adults)	Middle Lagoon
Odonata (dead nymph)	Middle Lagoon
Hemiptera	
Saldidae (adults)	Mud Flat
Hebridae (adults)	Mud Flat
Corixidae	
<i>Trichocorixa</i>	East and Middle Lagoons
Mesoveleidae (adults)	West Culvert
Coleoptera (larvae)	Middle Lagoon
Diptera	
Cecidomyiidae (adults)	East and Middle Lagoons
Ceratopogonidae	
<i>Dasyhelea</i>	East and Middle Lagoons, Mud Flat
<i>Culicoides</i> (adults)	Mangroves, East and Middle Lagoons
Chironomidae (larvae)	Middle Lagoon
Stratiomyidae (larvae)	Middle Lagoon and Mud Flat
Tephritidae (adults)	East and Middle Lagoons, Mud Flat
Ephydriidae	
<i>Ephydra gracilis</i> (adults)	East and Middle Lagoons, Mud Flat, West Lake
<i>E. gracilis</i> (larvae)	West Lake
<i>Glenanthe</i> (adults)	East and Middle Lagoons

Table 2.2. Comparison of salinity among habitat units using invertebrate sampling data. Fisher's protected least significant difference test (PLSD, $\alpha=0.05$) was used for multiple comparisons. $p = 0.000$ for overall analysis of variance (d.f. = 149, $F = 155.26$).

Unit	n	Mean	Std. Dev.	PLSD
East Lagoon	15	33	17	a
Middle Lagoon	84	41	16	a
Mud Flat	30	118	58	b
West Lagoon	24	151	49	c

Table 2.3. Comparison of water temperature among habitat units using invertebrate sampling data. Fisher's protected least significant difference test (PLSD, $\alpha=0.05$) was used for multiple comparisons. $p = 0.001$ for overall analysis of variance (d.f. = 90, $F = 5.8$).

Unit	n	Mean	Std. Dev.	PLSD
East Lagoon	12	26.6	1.9	a
Middle Lagoon	40	27.4	1.3	a
Mud Flat	18	27.4	1.3	a
West Lagoon	24	28.4	0.9	b

Table 2.4. Spearman correlations for invertebrate density vs. salinity. ($N = 306$; Diameter of each sample = 9.92 cm).

	Rho (corrected)	Z (corrected)	p
<i>Artemia</i>	0.62	10.76	0.000
<i>Trichocorixa</i>	-0.33	5.67	0.000
<i>Dasyhelea</i> larvae	-0.16	2.78	0.005
pupae	0.00	0.00	0.998
Stratiomyidae larvae	-0.26	4.59	0.000

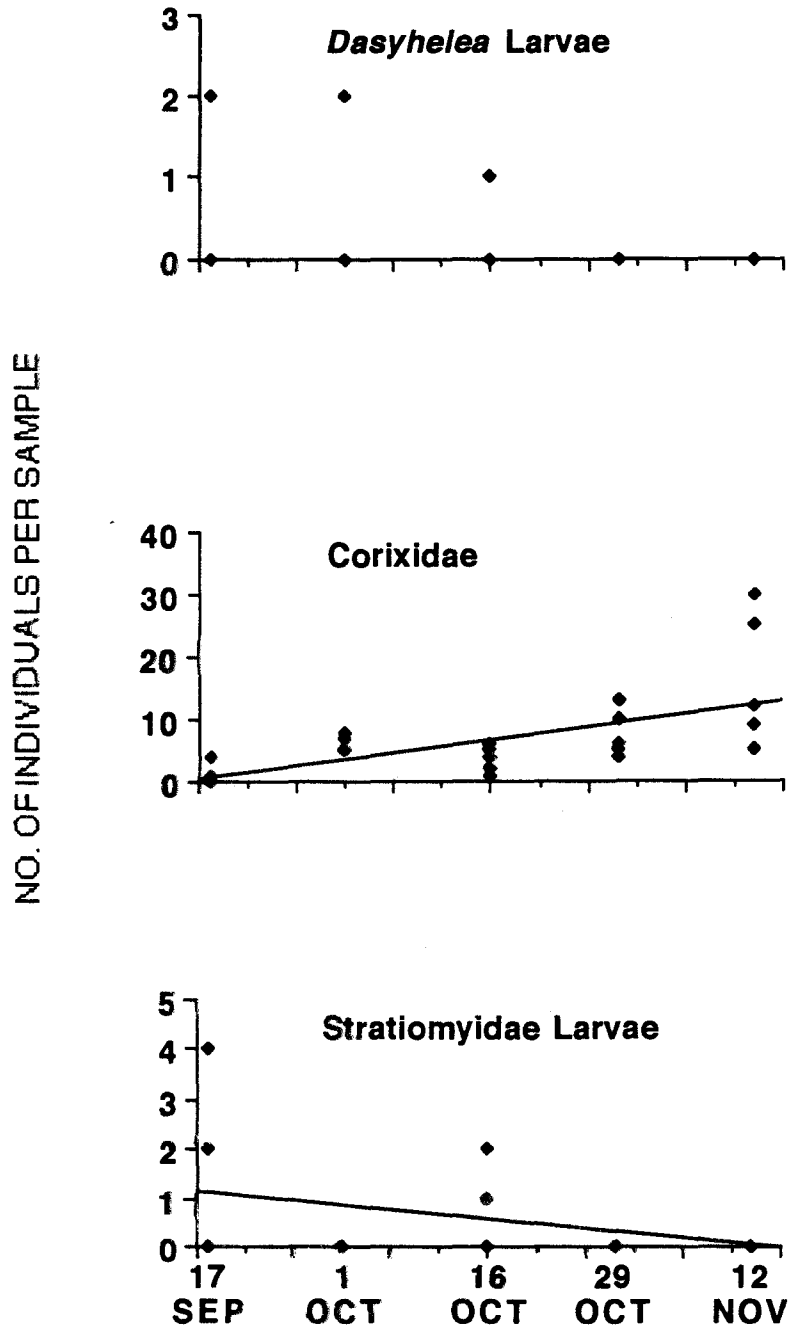


Figure 2.2. Changes in invertebrate abundance based on permanent sampling plot in the east lagoon. Regression lines shown only for those with significant Spearman correlations ($p < 0.05$). $N = 6$ for each sample date.

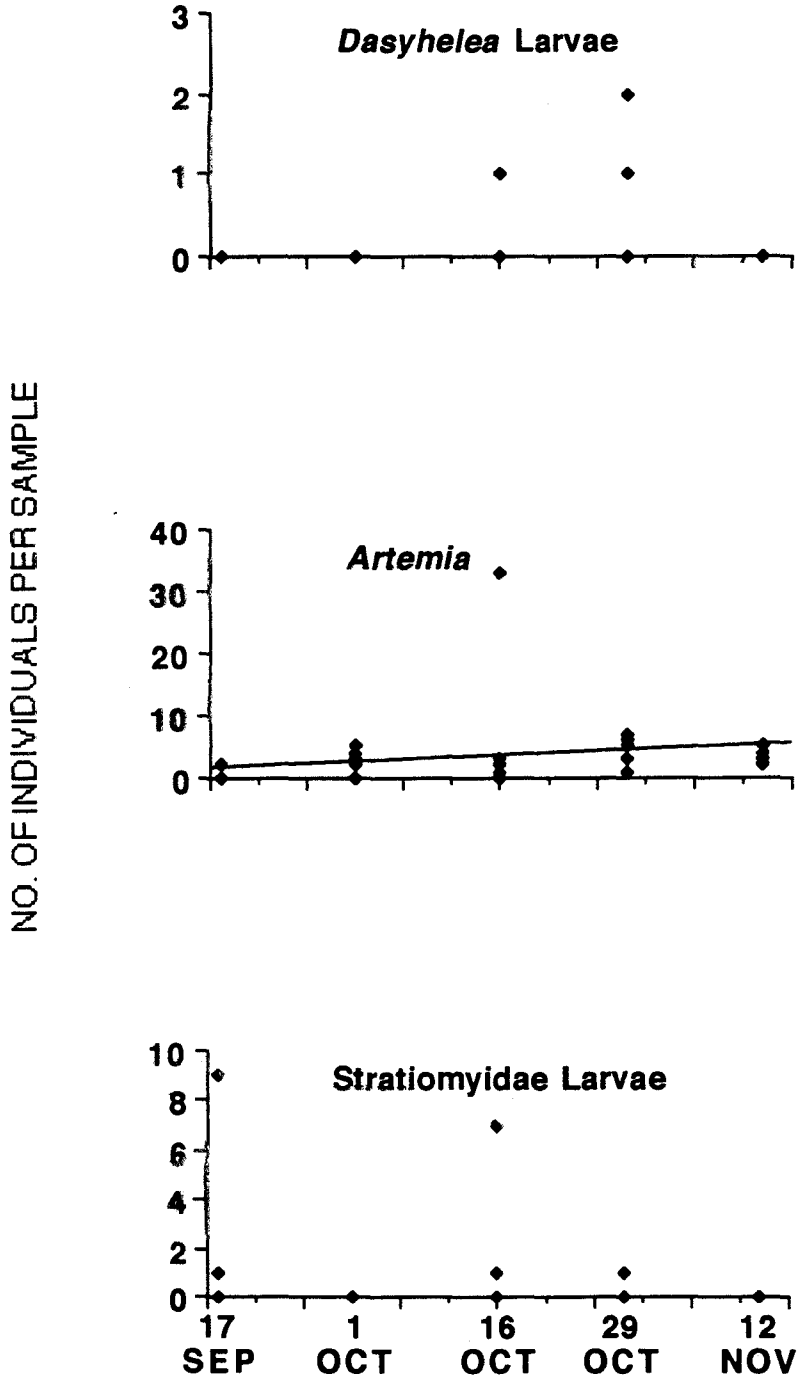


Figure 2.3. Changes in invertebrate abundance based on permanent sampling plot in the mud flat. Regression line shown only for those with significant Spearman correlations ($p < 0.05$). $N = 6$ for each sample date.

0.040). *Trichocorixa* density in the east lagoon was significantly and positively correlated with water level at the east culvert ($Rho = 0.378$, $p = 0.042$). The increase in *Trichocorixa* was noticeable even to the casual observer and also appeared to occur in the middle lagoon, which is connected to the east lagoon by culverts. In the permanent plot in the mud flat, there was a significant positive correlation between *Artemia* and sample date ($Rho = 0.57$, $p = 0.002$).

Rainfall and tide heights are shown in Figures 2.4 and 2.5, respectively. Water level and salinity fluctuations for the east and west culverts are shown in Figures 2.6a and 2.6b, respectively. Water levels increased during the 1990 season at both sites. The increase, however, was greater in the mud flat area and resulted in the flooding of large areas of previously exposed mud flats.

The decrease in salinity at the east culvert in 1990 suggests that increasing water levels in the east and middle lagoons resulted from the coincident increase in rainfall. These lagoons are connected to Bahia Sucia only indirectly through mangrove stands. Constant input of runoff into these lagoons during and after the period of high rainfall may have prevented inflow of tides and resulted in the apparent lack of association between water level at the culvert and tide level (Figure 2.5). In 1991, however, there was less rainfall. This allowed tides to have a more direct influence

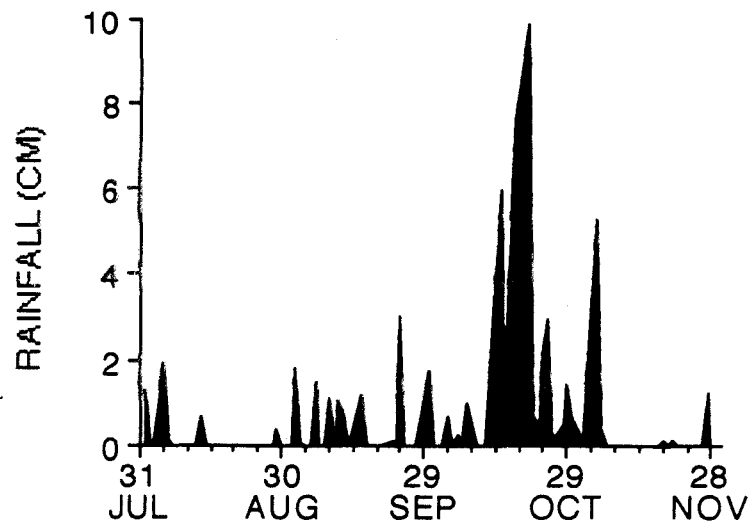


Figure 2.4. Rainfall at Cabo Rojo National Wildlife Refuge (1990).

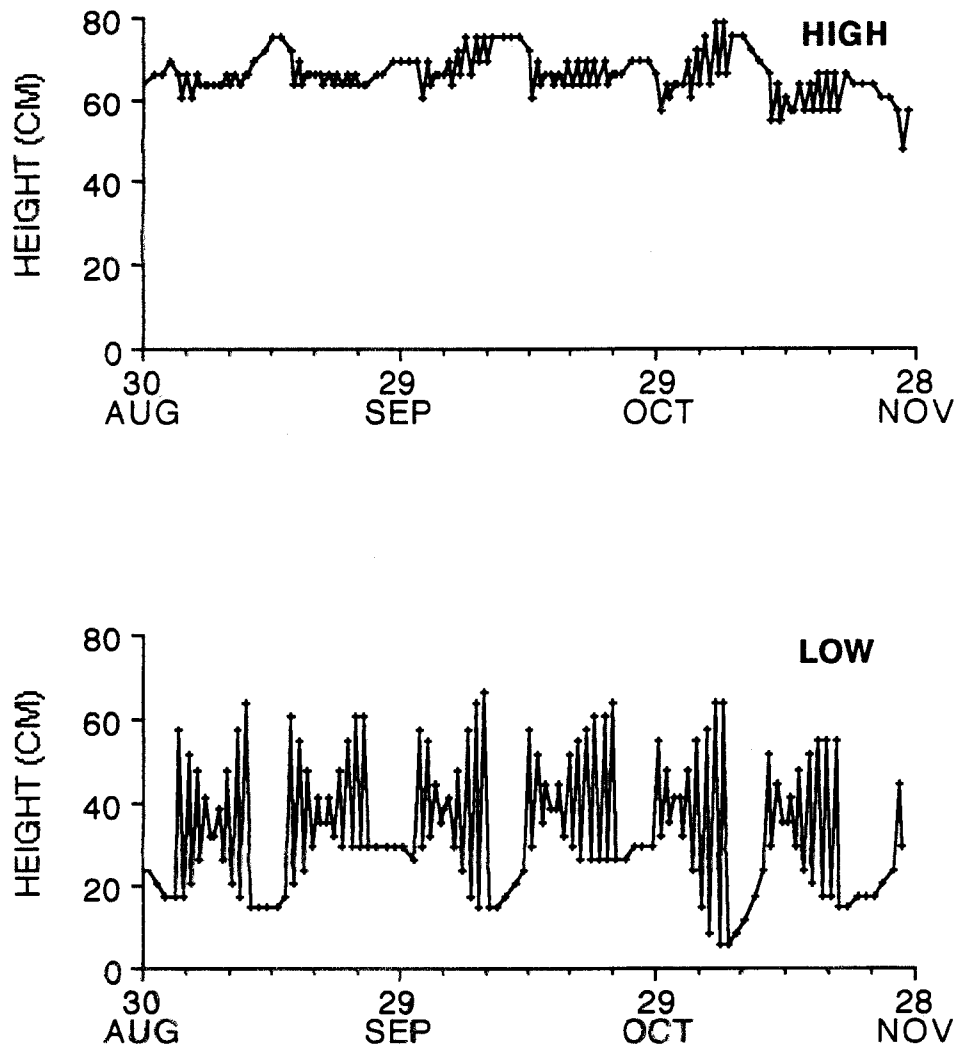


Figure 2.5. Heights of high and low tides at Isla Magueyes in 1990.

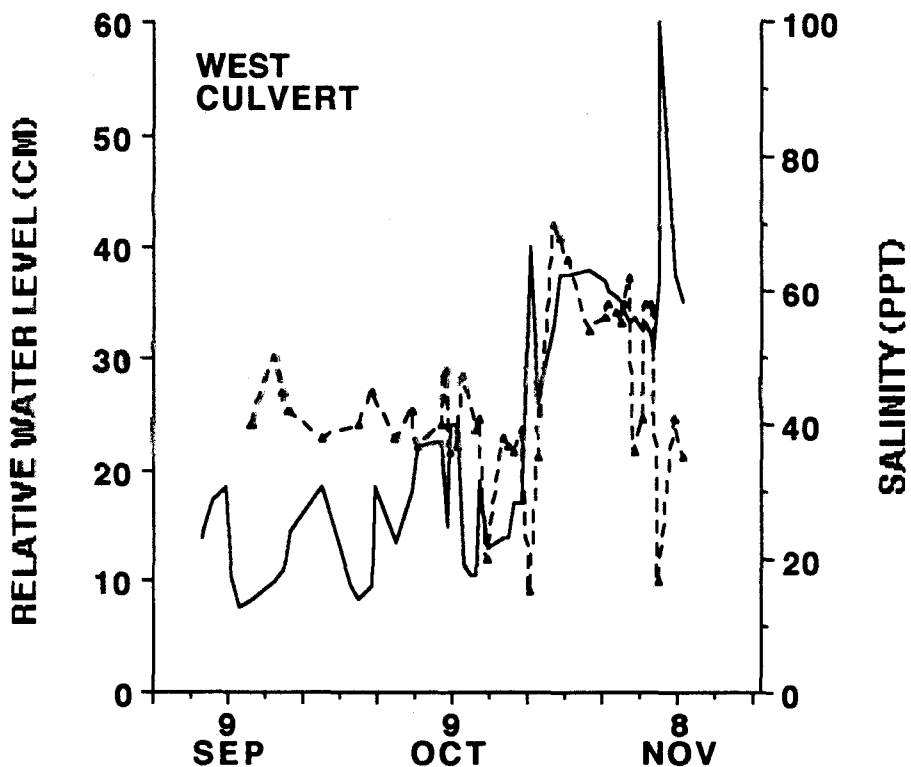
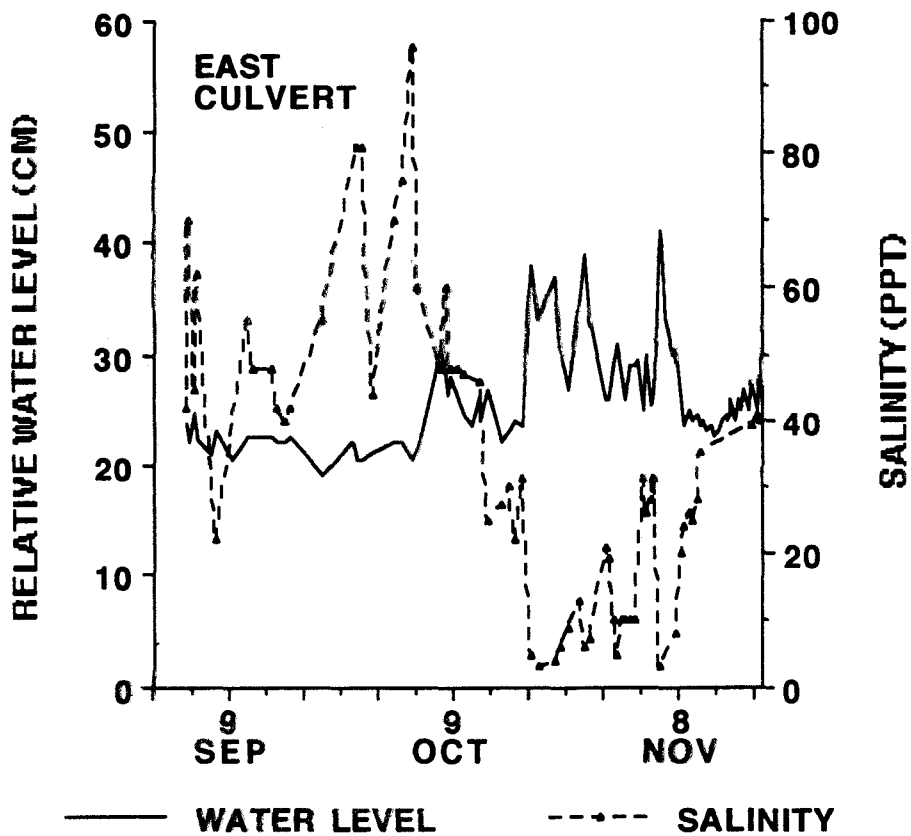


Figure 2.6. Water level and salinity at east (a) and west (b) culverts in 1990.

on the site, as indicated by fluctuating water levels and stable salinity (Figure 2.7).

Fluctuations in water level at the west culvert are, not surprisingly, related to tide cycles (Figures 2.5 and 2.6b). The dramatic increase in late October 1990, however, coincided with high rainfall. The increase in salinity at the west culvert is unexplained. Changes in direction of water flow were noticed during this time, suggesting that high salinity water from the west end of the west lagoon may have moved eastward.

Data from 1986 shown in Figure 2.8 indicate that, in those areas more distant from sea water inputs, salinity fluctuates dramatically. Site 1 in Figure 2.8 is located at the inflow culvert (west culvert). Sites 3, 4, and 5 are more distant from the culvert and are presumably influenced by changes in evaporation rates and rainfall.

Figure 2.9 shows total monthly rainfall from 1981 to 1991 at the Cabo Rojo National Wildlife Refuge. Although there is a clear seasonality of rainfall, there is also considerable variation among years in the amount of rainfall for any particular month.

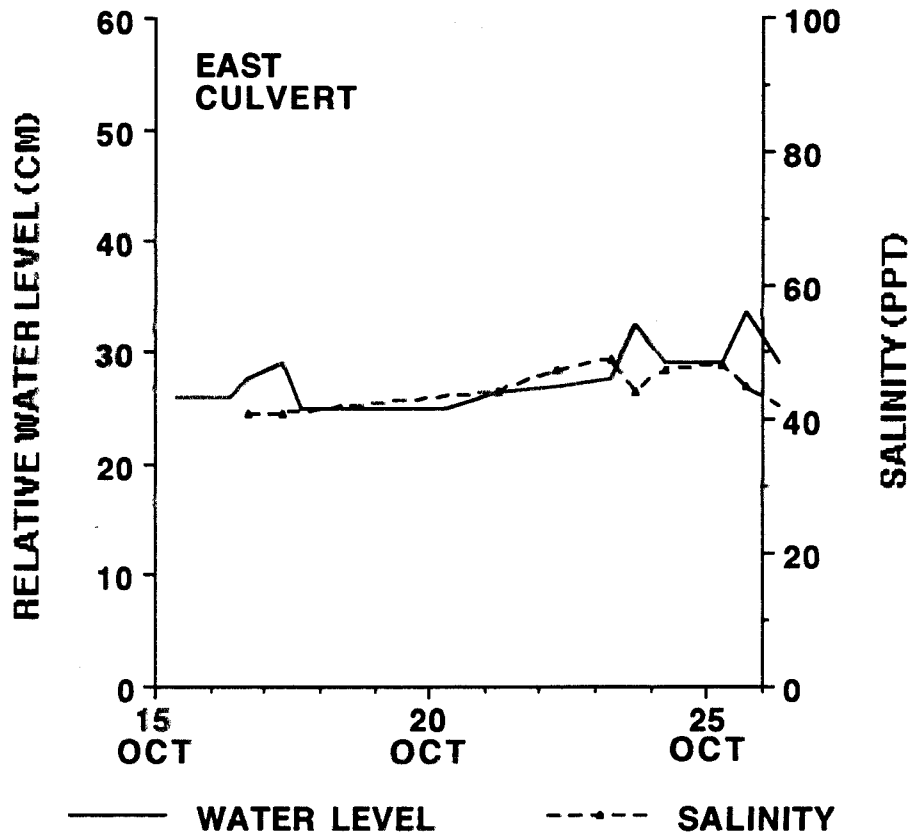


Figure 2.7. Water level and salinity at east culvert in 1991.

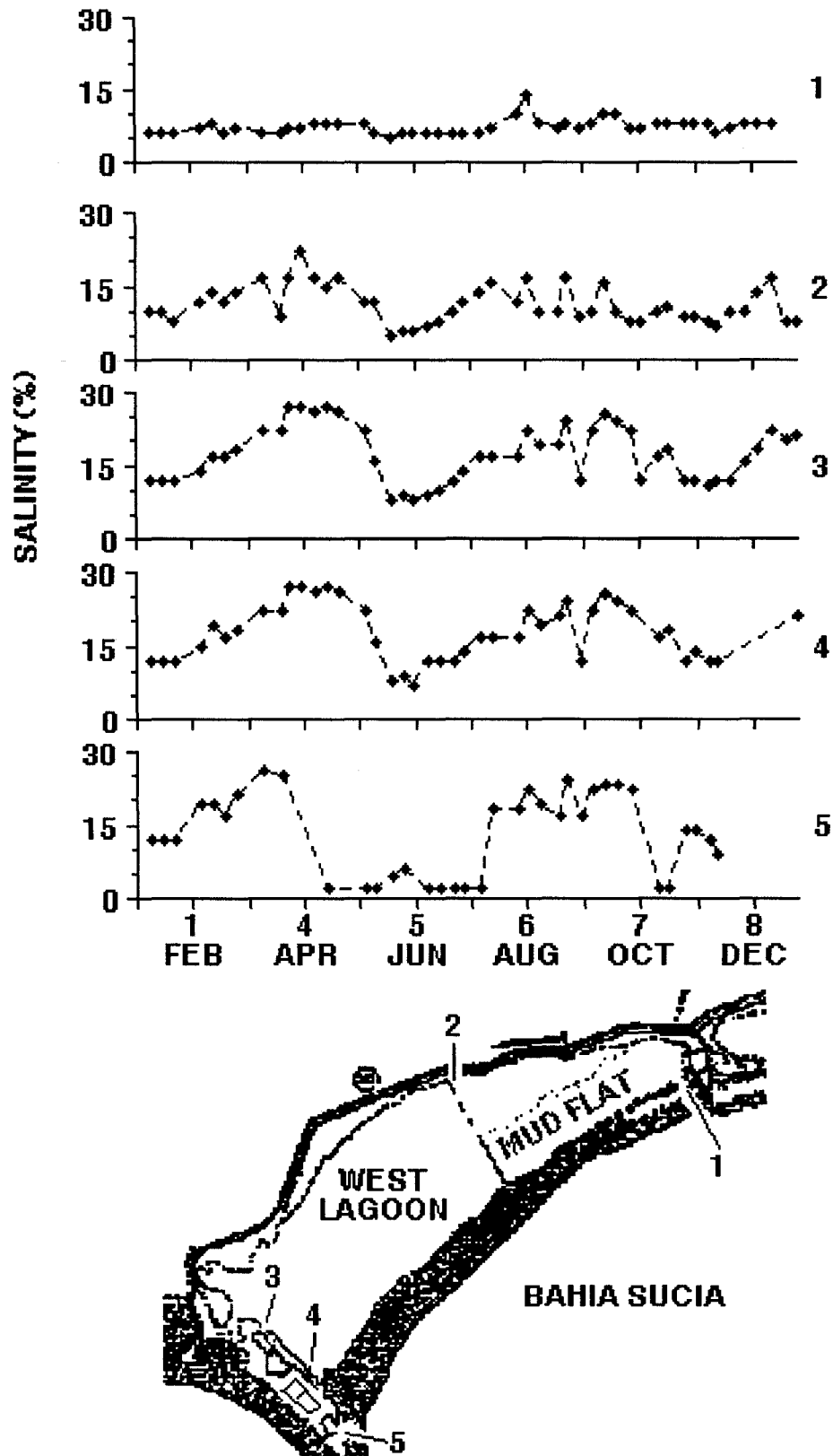


Figure 2.8. Salinity measurements from five stations in Fraternidad system during 1986 (data from Sal de Borinquen, Inc.)

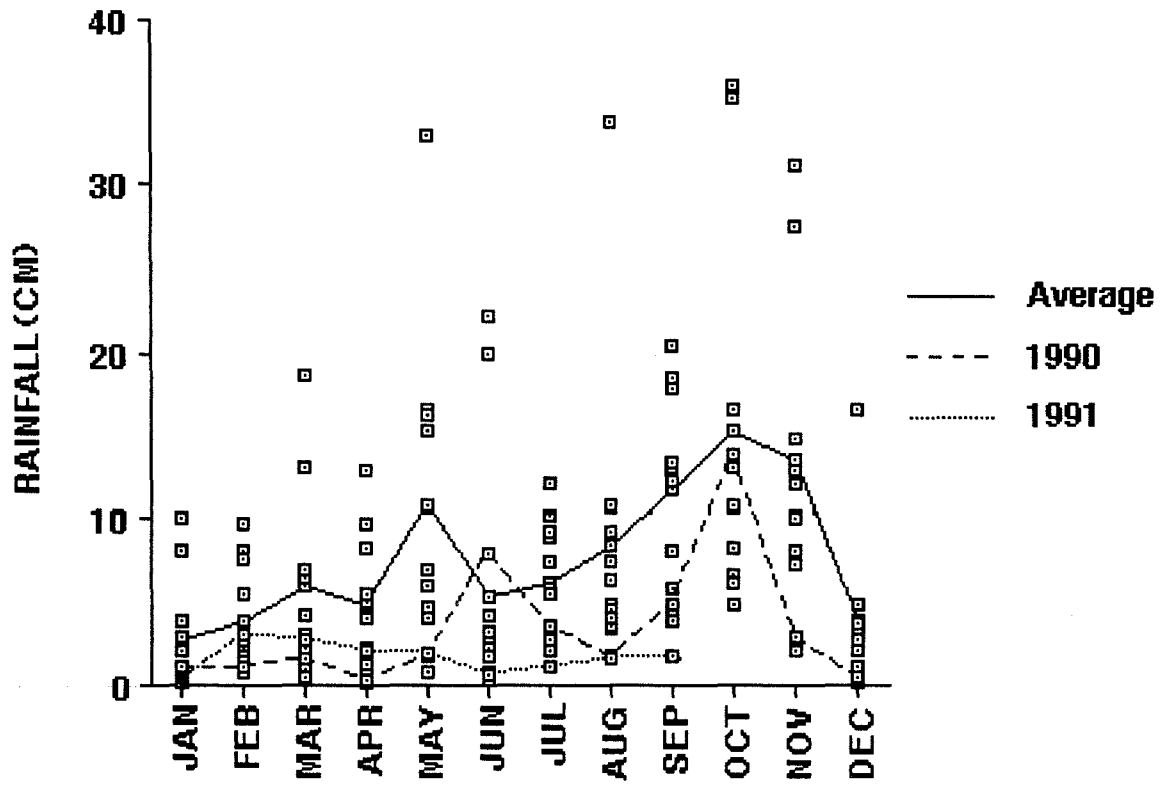


Figure 2.9. Monthly rainfall at the Cabo Rojo National Wildlife Refuge from 1981 to 1991.

Discussion

The dominant abiotic factors likely to affect the macroinvertebrate community used by shorebirds at the Cabo Rojo Salt Flats are water level and salinity. The pumps, dikes, and tidal barriers created by the solar salt company have resulted in a wide gradient in salinity across the flats. Salinity patterns at the west culvert were difficult to reconcile with rainfall and tidal patterns, perhaps as a result of filling and draining of salt crystallizer basins at the west end by the solar salt company. Furthermore, variation in autumn rainfall both within and between years causes salinity changes and the seasonal flooding and desiccation of algal mats to occur unpredictably. This poses a sharp contrast to shorebird stopover areas in higher latitudes where high-amplitude tidal cycles result in more predictable patterns. Thus, invertebrate species richness at the Cabo Rojo Salt Flats is likely to have been truncated by both the magnitude and the unpredictable timing of environmental stresses.

Linley (1976) reviewed the biology and ecology of three important genera of marine ceratopogonids (*Culicoides*, *Leptoconops*, and *Dasyhelea*), but makes few specific references to *Dasyhelea*. There are few accounts on the ecology of *Dasyhelea*. Williams (1957) provided observations on breeding habitats in the Bermuda Islands of several

ceratopogonids, including *Dasyhelea*. *Culicoides* has been studied in greater detail (e.g., Magnon et al 1990, Muirhead-Thomson 1982, Wirth and Blanton 1974, Davies 1967, 1969, Fox and Capriles 1953), but the extent to which the ecology of this group can be compared to that of *Dasyhelea* is unclear. The biology and ecology of marine corixids were reviewed by Scudder (1976). Davis (1980) considered some of the ecological aspects of *Artemia* and its importance to salt production.

Corixidae breed year round in tropical environments (Scudder 1976). Thus, life history characteristics could not be solely responsible for the increase in abundance of *Trichocorixa* in the east and middle lagoons. While some *Trichocorixa* are known to tolerate high salinity (Carpelan 1957), Davis (1966) showed that such conditions can retard the hatching of eggs in *T. reticulata* - the species likely to occur at the Cabo Rojo Salt Flats. It has been shown that in addition to having high potential for dispersal by flight, the migratory tendency of some corixids is related to the temporary nature of their habitats (e.g., Brown 1951). However, a majority of the corixids sampled early in the 1990 season were nymphal and thus incapable of flight. It is possible that either the survival and reproduction of corixid immigrants or the reproduction of residents increased as a result of changing water quality conditions. The appearance of corixid adults in parking lot puddles at the Cabo Rojo National Wildlife Refuge (1 km away) early in the season

suggests that dispersal and reproduction of immigrants may be important. However, adult *Trichocorixa* were present in the deeper areas of both the middle and the east lagoons, suggesting that reproduction of residents also may be important. In either case, abundance changes appear to result from a response to changes in the physical environment rather than from intrinsic life history patterns or adaptations. Another observation supporting this conclusion is that, even at the time when corixids were abundant in the east and middle lagoons, none were found in the higher salinity areas to the west.

As in the Corixidae, the reproduction of *Dasyhelea* in Puerto Rico is likely to be largely or entirely aseasonal. However, because egg-laying requires wet (but not flooded) substrata (Linley 1976), the effect of water level fluctuations on the abundance of larvae may be even more direct than on other taxa. Furthermore, pupation and adult emergence of many ceratopogonids can be delayed or prevented if proper water level conditions are not met (Linley 1976). In wetlands more directly affected by tides, these conditions may be met on a predictable basis. At the Cabo Rojo Salt Flats, however, differences between 1990 and 1991 field data suggest that the combined influences of rainfall, tide, and evaporation result in a somewhat less predictable availability of breeding conditions for *Dasyhelea*.

The timing and predictability of invertebrate productivity is an important aspect of the traditional use of

stopover areas by shorebirds. In many stopover areas of the temperate zone, the biological rhythms of marine invertebrates bring millions of individuals from regional populations into reproductive readiness simultaneously. Within these windows of readiness, environmental cues then bring organisms into synchronous reproduction. Intrinsic biological rhythms of invertebrates may be of critical importance to the seasonal predictability of these areas and their traditional use by shorebirds. Although the Cabo Rojo Salt Flats do not exhibit highly predictable bursts of invertebrate productivity, the site may still be relatively predictable in comparison to other tropical wetland sites in the Caribbean.

It appears that calidrid sandpipers use all of the available habitats at the Cabo Rojo Salt Flats at different times during the autumn season. In the next chapter, I examine the rapid responses of shorebirds to changes in their habitats and how invertebrate resources are exploited.

CHAPTER 3
HABITAT USE PATTERNS BY MIGRATORY CALIDRID SHOREBIRDS

Introduction

Ecologists have made considerable progress in the study of intertidal invertebrate communities exploited by shorebirds in temperate latitudes. There have been numerous studies on the foraging and territorial behavior of shorebirds, and the effects of invertebrate behavior, abundance, and distribution on shorebird activity (Bengston and Svensson 1968, Evans 1979, Goss-Custard 1977a, 1977b, 1984, Myers 1984, Myers et al. 1979, Pienkowski 1983, Puttick 1984, Wilson 1990). Research efforts also have documented the effects of shorebird predation on invertebrate abundance, populations or communities, and the potential role that prey depletion has on the migratory strategies of shorebirds (Baird et al. 1985, Castilla and Paine 1987, Evans et al. 1979, Marsh 1986a, 1986b, Peer et al. 1986, Piersma 1987, Quammen 1981, 1984, Schneider 1978, Schneider and Harrington 1981, Wilson 1989). In some cases, cumulative baseline data have allowed the development of models to estimate metabolic demands of shorebirds on the benthic biomass of estuaries (Bildstein et al. 1982, Evans et al. 1979, Grant 1981, Hockey et al. 1983, Piersma 1987, Piersma and Engelmoer 1982, Puttick 1980, Smit 1981, Summers 1977, Wolff et al. 1976).

Of particular relevance to my study are those studies that document the distribution of shorebirds in relation to habitat characteristics at the within- and among-site levels (Brush et al. 1986, Bryant 1979, Goss-Custard 1977b, Goss-Custard et al. 1977a, 1977b, Hicklin and Smith 1984, Quammen 1984, Wilson 1990, Wolff 1969). Attempts to explain the spatial distribution of shorebirds have focused on the behavior and diet of shorebirds and the effects of shorebird predation on invertebrate communities (e.g., Mallory and Schneider 1979). In North America, the Bay of Fundy represents a major migratory stopover where several aspects of shorebird habitat use have been studied in detail (Gordon et al. 1985, Hicklin and Smith 1979, 1984, Hicklin et al. 1980, Peer et al. 1986, Richardson 1979, Wilson 1990).

Parallel studies in the tropics, particularly on habitat use by shorebirds, are scarce (Ashmole 1970, Bolster and Robinson 1990, Johnson 1979, Robert et al. 1989, Schneider 1985b, Strauch and Abele 1979). Other studies have focused on migration and competition of shorebirds in the tropics (e.g., Duffy et al. 1981, Myers and McCaffery 1984, Myers et al. 1983, Schneider 1985a, Schneider and Mallory 1982, Spaans 1978, Thomas 1987). This scarcity of information is due in part to the lack of baseline information and suitable sampling techniques for tropical environments.

Hypotheses and techniques used in studies of shorebird ecology in temperate estuaries are inconsistent with observations of tropical estuaries and lagoons, and therefore

can not be applied at sites such as the Cabo Rojo Salt Flats. For example, exclosure experiments have been used to examine the effects of shorebird predation on invertebrate abundance and community structure in temperate zone wetlands. Many of these experiments, which assume there is little lateral movement of invertebrates into and out of exclosure cages, have focused on either infaunal invertebrates of coastal mud flats (Schneider and Harrington 1981, Quammen 1984, Wilson 1989) or sessile invertebrates of rocky intertidal shores (Marsh 1986a, 1986b). While existing exclosure techniques may be applicable in tropical intertidal mud flats such as those in Surinam (Swennan et al. 1982), they are inappropriate at the Cabo Rojo Salt Flats, where shorebird feeding often focuses on free-swimming aquatic invertebrates (this chapter). Shorebirds also feed on aquatic insects (or aquatic stages of insects) on their arctic breeding grounds (Baker 1977). Basic information on shorebird feeding ecology at the Cabo Rojo Salt Flats may therefore benefit future studies of both tropical and arctic shorebird habitat.

In this Chapter, I present data on numbers of migratory shorebirds and the distribution of small calidrid sandpipers (peeps) in autumn of 1990 and 1991. I investigated selection of foraging sites, at the within- and among-site levels, under the general hypothesis that calidrid distribution and density are associated with the availability and density of prey items (Goss-Custard et al. 1977b, Myers et al. 1980, Hicklin and Smith 1984).

Studies of shifts in the distribution of calidrids among sites focused on the Fraternidad system. Although alternative explanations of factors associated with habitat use focused on the east and middle lagoons and the mud flat, invertebrate abundance and habitat use in the west lagoon were also monitored (see Figure 1.2 and site descriptions in Chapter 1). I treated the eastern and middle lagoons as equivalent due to their similar area (ca. 19 ha), shared tide and rainfall inputs (Chapter 1), and because they are connected by culverts. Alternative interpretations to account for the distribution and abundance patterns of shorebirds among selected sites were based on the density and accessibility of prey. Accessibility is inferred from depth and water level measurements (i.e., prey in deep water are inaccessible to calidrids). These alternatives follow:

1. Shifts in the density of preferred prey among sites accounts for shifts in shorebird distribution. Prey accessibility (i.e., depth) among sites is similar.
2. Shifts in the accessibility of preferred prey among sites accounts for shifts in shorebird distribution. Prey densities among sites are similar.
3. Shifts in both density and accessibility of preferred prey among sites account for shifts in shorebird distribution.

I also studied the within-site level of habitat use by migratory shorebirds. To address this question, I compared

resources in patches ($\approx 600 \text{ m}^2$) of high use and low use by calidrids within habitat units. This work focused on the middle lagoon, which harbored the majority of shorebirds at peak use of the Fraternidad system. Additional work was conducted in the west lagoon. In the middle lagoon, substrata seemed less homogeneous than in the west lagoon and in intertidal mud flats visited at higher latitudes along the Atlantic seaboard. Therefore, in addition to studies of invertebrate distributions among patches of high and low levels of shorebird use, I attempted to relate shorebird habitat use to the availability of visually quantifiable wetland substrate types.

The value of the Cabo Rojo Salt Flats as a migratory stopover depends on its protection and a basic understanding of the underlying factors influencing habitat use by shorebirds. The data presented here will contribute to the hemispheric-wide need to conserve shorebird habitat (Myers et al. 1987). They will also serve as baseline information to evaluate the potential impact of habitat management practices or alterations of the system on migratory shorebird use and provide a basis for comparisons among similar hypersaline systems in the tropics. This chapter therefore addresses the second objective of the project:

Objective 2. To relate the distribution of migratory *Calidris* sandpipers to habitat resource patterns at the within- and among-habitat levels.

Methods

Numbers and Distribution of Birds

I surveyed of all shorebird species (Charadrii and Scolopaci) weekly from 22 August to 15 November 1990, covering both lagoon systems (Candelaria and Fraternidad). José Colón (research assistant) conducted these surveys from 14 October 1991 to 25 January 1992. I also surveyed foraging calidrids in habitat units of the Fraternidad system (see descriptions of units in Chapter 1) daily from 23 September to 18 November 1990 and from 14 October to 27 October 1991. Surveys were conducted between 0700 and 1000 hrs. Numbers of individuals were estimated using 10 x 40 binoculars. Distant flocks were counted using a 60x telescope. I used a four-wheel drive truck to minimize the duration of the surveys, which adhered to the route shown in Figure 3.1.

I counted small calidrid species (*Calidris pusilla*, *C. mauri*, *C. minutilla*, and *C. fuscicollis*) collectively as calidrids (peeps) due to the similarity of winter plumages among these species and the large dense flocks in which they often congregated. Species ratios within this group were estimated during several counts by myself and by Brian Harrington (Manomet Bird Observatory, pers. comm.). I determined the activity of calidrid flocks as either roosting or foraging. This determination was based on rapid scanning

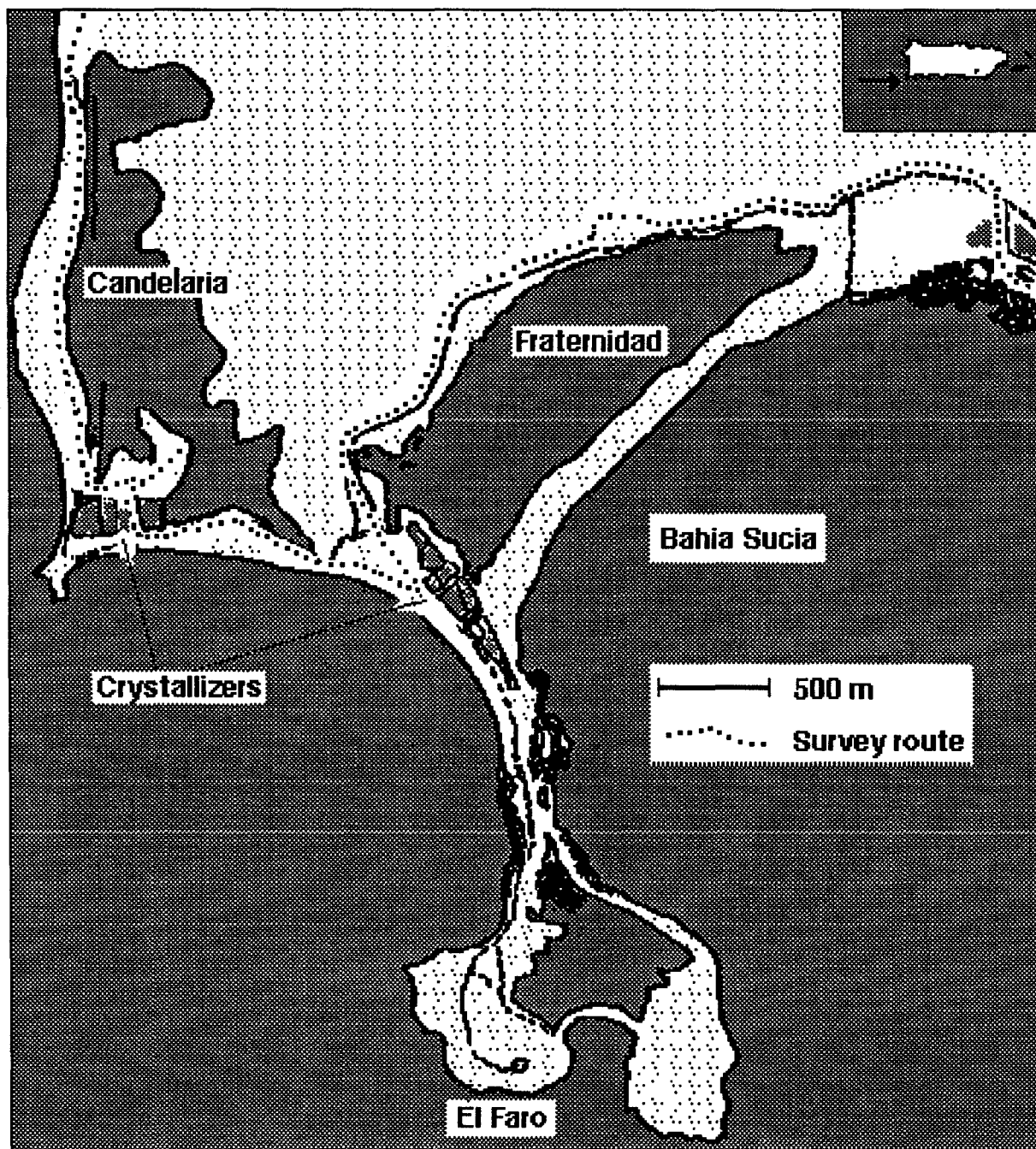


Figure 3.1. Weekly survey route.

of each flock rather than rigorous observations of each individual.

Weekly survey data are expressed as numbers of individuals per lagoon system. I used linear regression analysis to examine trends in numbers of calidrids counted within habitats during daily surveys of the Fraternidad system. Data for individual units are also expressed as proportions of all units surveyed to account for changes in total numbers of calidrids present. Spearman correlation analysis was used to compare numbers of birds within a habitat unit to water level and salinity recorded at measurement stations (east and west culverts).

Shorebird Diet and Foraging Substrata

To confirm that sampled food resources were being used by migratory shorebirds, I shot ten calidrids in 1990 and five in 1991 for diet analysis. Stomachs were injected immediately after collection with formalyn to prevent posthumous digestion. Each bird was observed foraging before collection. With the exception of one bird, which was collected at the mud flat area, all were collected in the middle lagoon. Additional stomachs of birds wounded from collision with utility cables between the east and middle lagoon also were examined (1 in 1990 and 2 in 1991). *Artemia* were the only macroinvertebrates found in areas where calidrids foraged in the west lagoon. It was therefore considered unnecessary to sacrifice calidrids for diet

analysis in these areas. In total, 8 stomachs from *C. pusilla*, 5 from *C. mauri*, and 5 from *C. minutilla* were examined. Stomach contents were examined under a dissecting microscope and identifiable particles were separated into the following groups: corixid wings; whole corixids; fragments of *Dasyhelea* larvae; whole *Dasyhelea* larvae; fragments of *Dasyhelea* pupae; whole *Dasyhelea* pupae; whole *Dasyhelea* adults; whole ephydrid larvae; whole coleopteran larvae; and whole Mallophaga. Data for each year are expressed as percent occurrence of each group among all stomachs examined and as the mean number of individuals (or fragments) per stomach.

I determined preferred shorebird foraging substrate (water column vs. bottom) through focal sampling (Altmann 1974). Individual birds were observed and foraging attempts were counted using tally meters. Unless interrupted, most individuals were observed for one minute. To avoid repeated observations of individual birds, only half as many observations were made from a single flock as there were birds in that flock. "Water foraging" included foraging attempts, or "pecks," into the water column or the water surface; "bottom foraging" included probing, multi-probing, and scything. A probe is a single peck into the algal or mud substratum and a multi-probe is a rapid series of probes discrete in time from other series or activities. Scything involves movement of the bill from side to side through muddy or algal substrata. Foraging observations were made in the

mud flat area and in the east, middle, and west lagoons. I used G-tests for goodness of fit (Sokal and Rohlf 1981) to compare data from different habitat units.

Invertebrate Sampling

I described sampling efforts for the assessment of among-site distribution patterns of invertebrates in Chapter 2. Within-site invertebrate sampling was paired on the basis of intensity of use by calidrids (high vs. low). A high-use patch was defined as an area of 20 x 30 m containing 150-200 foraging calidrids (this 20 x 30 m area often fell within a larger area used intensively by birds). I then took samples within the same habitat unit, at least 20 m away, from a randomly chosen patch of similar depth but of low use (i.e., no calidrids). For pairs taken from the middle lagoon, I recorded the location of patches using a 10 x 10 m alpha-numeric grid system. The grid system had a total of 1,094 points (alpha-numeric) in an area of 10.9 ha and included several perimeter areas that never flooded. Grid points not marked with labeled stakes were located by estimating distances from marked grid points. The location of samples within the 20 x 30 m high- and low-use patches was determined using the protocol illustrated in Figure 3.2, which resulted in a total of 12 sample sets for each high-use/low-use pair (six from high-use and six from low-use). Individual samples were collected and processed as described in Chapter 2.

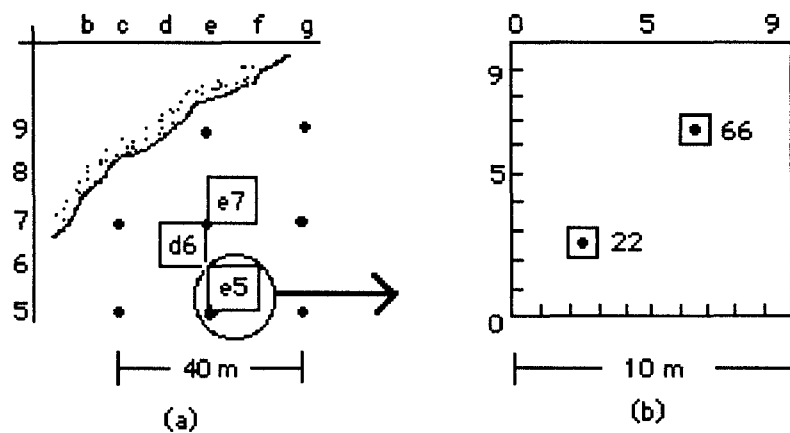


Figure 3.2. Protocol for high-use/low-use invertebrate sampling showing three 10 x 10 meter quadrats selected for sampling on alpha-numeric grid system (a) and two 1 x 1 m subplots randomly selected in each 10 x 10 m quadrat (b).

In 1991, I modified the above sampling protocol because mud samples often contained few or no invertebrates. Also, the most prevalent taxa in the stomachs of birds were rarely encountered in mud samples. I therefore sampled the water column only, which included the loose algae and detritus that lies directly over the sediment. Although I still obtained balanced pairs of six samples from each of the high-use and low-use patches, additional field time became available for the collection of samples from deep areas in the middle lagoon that were inaccessible to foraging calidrids.

I analyzed data collected for the high-use/low-use study as well as from other invertebrate sampling studies using t-tests and analyses of variance. Multiple comparisons were done using Tukey's honestly significant difference tests. I made additional post-hoc comparisons between invertebrate data from different substrata and between high-use/low-use pairs within substrate types.

Shorebird and Habitat Mapping

I monitored the use of available substrate types by calidrids in November 1990 entirely within the middle lagoon. During field observations, more than 80% of the calidrid sandpipers found in the Fraternidad system were in this lagoon, a distribution pattern also found in 1991. I quantified substrate cover by a single visit to each grid point in the alpha-numeric grid system described above during

a seven day period. During each visit, water depth was measured and total percent cover of five substrate types (rope algae, shag, amorphous algae, vascular plants, and no vegetation) was estimated. I characterized each substratum on the basis of general appearance or by species. Vascular plants included *Salicornia* sp., *Sesuvium* sp., and mangroves (*Avicennia germinans* or *Rhizophora mangle*). In order to adjust for bottom contour variability, I measured water level on a fixed depth gauge at the east culvert (Chapter 1, Figure 1.2) at the beginning of each sampling period for comparison with depth measurements from each point (Figure 3.3).

I mapped calidrid shorebirds between 0645 and 0815 hrs on 14 - 18 November 1990 at five-minute intervals. Observations during these hours avoided confounding effects of depth fluctuations caused by increasing winds (Brian Harrington, pers. comm.), usually after 0900 hrs. Some five-minute intervals were missed on several days. Mapping of flocks was accomplished with the aid of grid maps and landmarks. I used a 20 x 60 telescope for reading alpha-numerically marked grid stakes and for counting birds. Since birds within flocks were uniformly distributed, it was possible to express mapping data as sightings per quadrat. Thus, a grid cell containing a flock at three different observation times was given a sighting frequency value of three.

Most of the 10 x 10 meter quadrats contained several substrate types. It was thus difficult to develop a simple

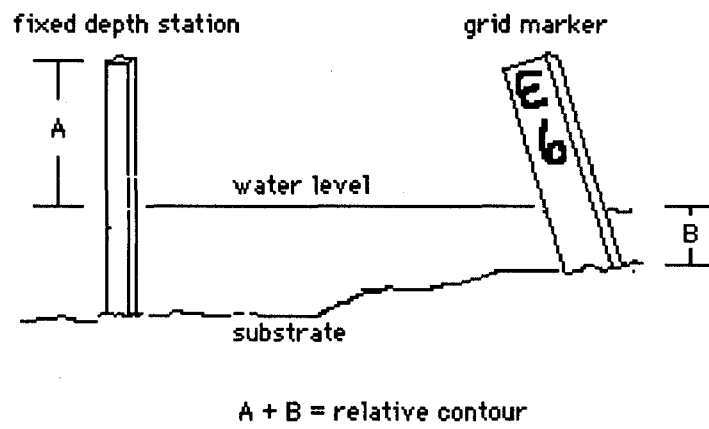


Figure 3.3. Determination of relative contour for individual grid points.

means of characterizing each of the 1,094 quadrats. To facilitate analysis of availability of habitat types and their use by shorebirds, I performed a cluster analysis (Fastclus Procedure, SAS 1982) to reduce the numerous combinations of substrate cover and relative contour values into a manageable number of habitat types. Quadrats that were more than 50% dry were excluded from the analysis since birds were not seen foraging in these areas. The cluster analysis separated the quadrats into 10 habitat types (the number of habitats was arbitrarily predetermined for the analysis to allow for aggregation of the five substrate types into several depth ranges). The Fastclus Procedure uses nearest centroid sorting methods and Euclidean distances to cluster data. After separating the quadrats into 10 types, I used the bird mapping data to determine total number of bird sightings for each type. An additional analysis was performed using data from shallow areas only (relative contour ≤ 6 cm), since deep areas are not accessible to foraging calidrids. Relative contour was then excluded from the clustering procedure, which was allowed to find five cluster types. In both the five-cluster and the 10-cluster analyses, I used G-tests of goodness of fit (Sokal and Rohlf 1981). As recommended by Neu et al. (1974), I determined Bonferroni confidence intervals for observed proportions of sightings for each habitat type to minimize Type I error rates.

Results

Numbers and Distribution of Birds

Species encountered during the weekly surveys are listed in the Appendix. Numbers of calidrids and the distribution of foraging and roosting birds among the two lagoon systems during 1990 and 1991-92 weekly surveys are shown in Figure 3.4. In 1990 numbers increased through September with a peak in early October. In both years, numbers decreased in November. December and January surveys were done in 1991-92 only and show that considerable numbers of calidrids remained at the salt flats through this period. Species percentages determined one week before peak migration in 1990 were as follows: 70% *C. pusilla*; 20% *C. mauri*; 10% *C. minutilla*; and 1% *C. fuscicollis*. These percentages were consistent with a larger data set collected by Brian Harrington (pers. comm.). *C. bairdii* was not encountered during ratio estimates although it was identified once at the Cabo Rojo Salt Flats during the course of this study (Alfredo Begazo, pers. comm.).

In the Fraternidad system, the maximum number of foraging calidrids during the 1990 weekly surveys was 2,538 ($\bar{x} = 1,229$, std. dev. = 679). Numbers of foraging calidrids in the Candelaria system never exceeded 170 during 1990 ($\bar{x} = 61$, std. dev. = 65). Although there was a single occasion during the 1991-92 surveys when numbers of foraging calidrids

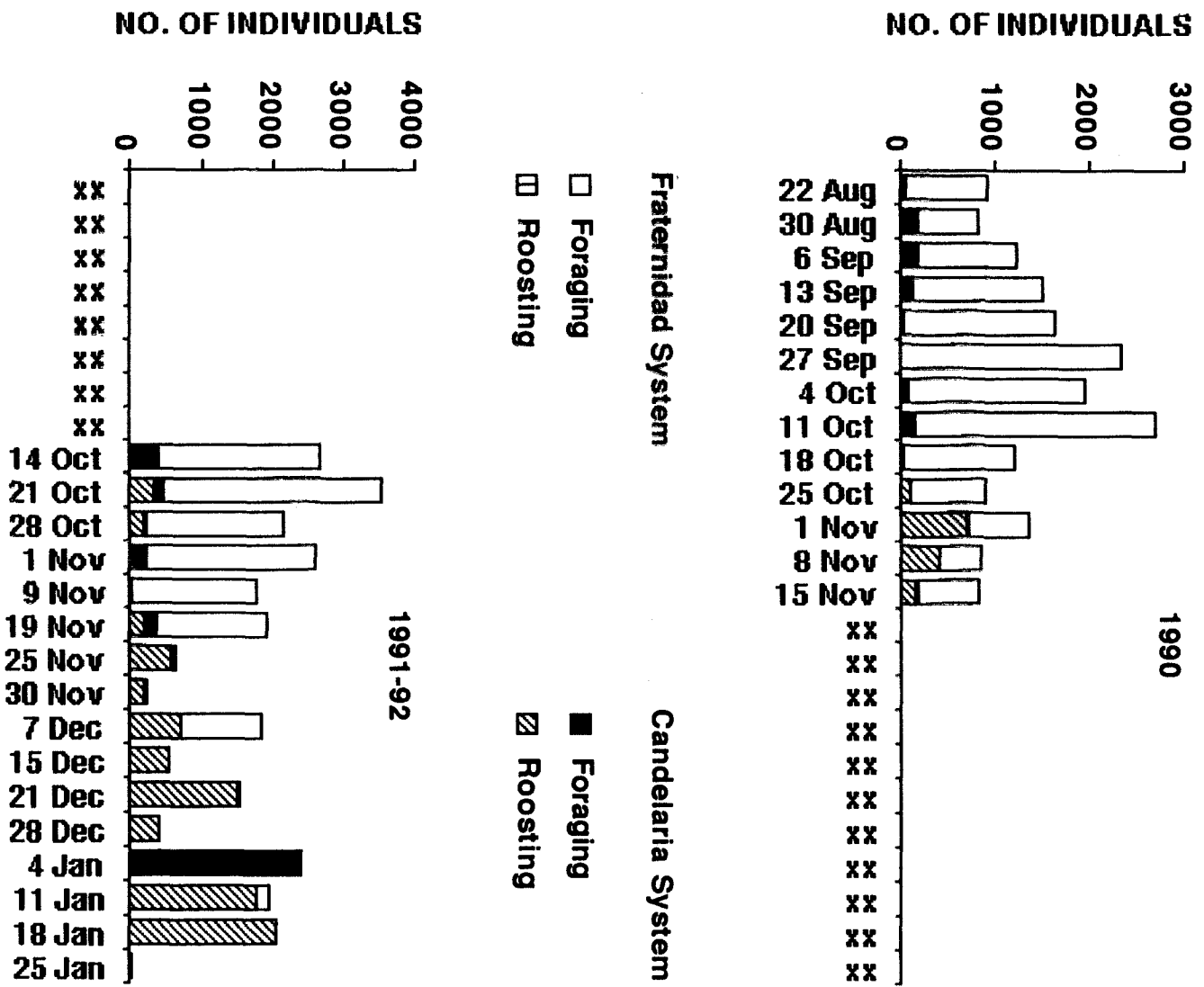


Figure 3.4. Numbers of calidrids and distribution of foraging and roosting birds among the two major lagoon systems during 1990 and 1991-92 weekly surveys.

was high in the Candelaria system (2,365), numbers were typically lower ($\bar{x} = 216$, std. dev. = 585).

Results of surveys of the Fraternidad system are shown in Figure 3.5. Data show that, although calidrids used the east and middle lagoons to some extent early in the 1990 season, a much larger proportion of birds occurred in these sites later in the season. Moderate numbers of calidrids occurred in the mud flat area through mid October when numbers dropped dramatically in this site. The highest numbers of calidrids were observed in the west lagoon. Dates of peak counts for each area and results of linear regression analyses are shown in Table 3.1. The increase in the middle lagoon and decreases in the mud flat and west lagoon were significant (Table 3.1). Numbers of calidrids in the mud flat were negatively correlated with water level at the west culvert ($N = 25$, $Rho = -0.71$, $p = 0.001$). Although I did not include the mangrove pool in habitat comparisons, calidrids used the area early in the 1990 season (maximum count of 790 on 27 September). Throughout the 1991 field season, most calidrids occurred in the middle lagoon.

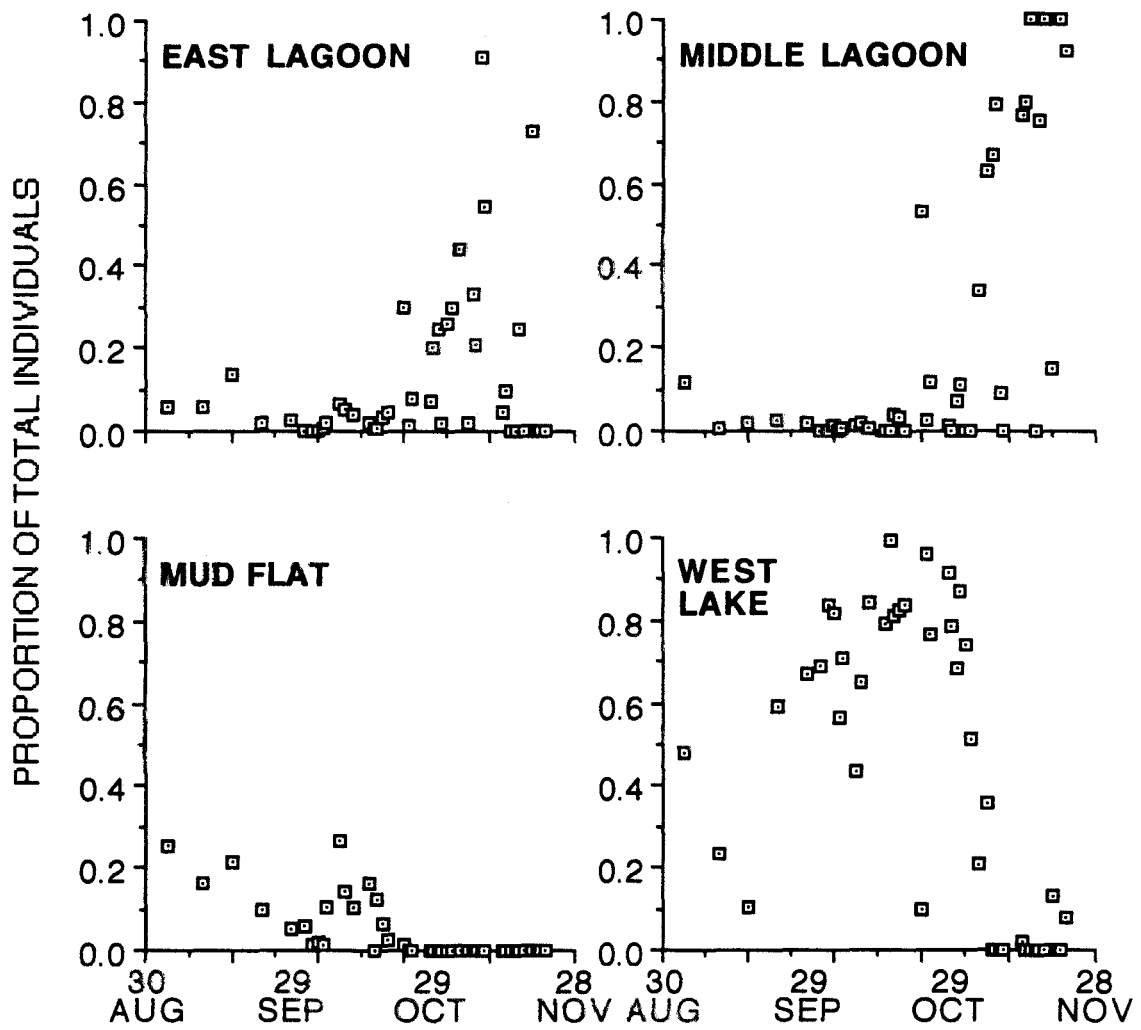


Figure 3.5. Distribution of foraging calidrids among habitat units during 1990 daily surveys.

Table 3.1. Maximum counts and regression analyses (count vs. date) on daily surveys of the Fraternidad system.

Site	Maximum Count	Date of Maximum	Slope of Regression (d.f.=1)	R ²	F	p
East Lagoon	465	15 Nov	0.78	0.03	2.03	0.162
Middle Lagoon	600	18 Nov	4.61	0.29	13.56	0.001*
Mud Flat	405	8 Oct	-2.70	0.35	21.30	0.000*
West Lagoon	3000	9 Oct	-15.15	0.20	9.37	0.004*

Shorebird Diet and Foraging Substrata

All birds collected for stomach content analyses were observed multi-probing. Several invertebrate taxa are illustrated in Figure 3.6. Data are expressed as percent frequency of occurrence in Figure 3.7. Corixids (*Trichocorixa*) were more prevalent among birds collected in 1990 but were nearly absent in 1991 birds. Conversely, *Dasyhelea* larvae (and their fragments) occurred with a much higher frequency in the stomachs of 1991 birds than in those of 1990 birds. The same patterns emerge when data are expressed as mean number of individuals or fragments per stomach (Figure 3.8).

Individual G-tests for goodness of fit (Sokal and Rohlf 1981) on foraging data from each habitat unit revealed that only those data from the west lagoon ($G = 6.75$, $n = 31$) and the middle lagoon ($G = 23.22$, $n = 15$) were sufficiently

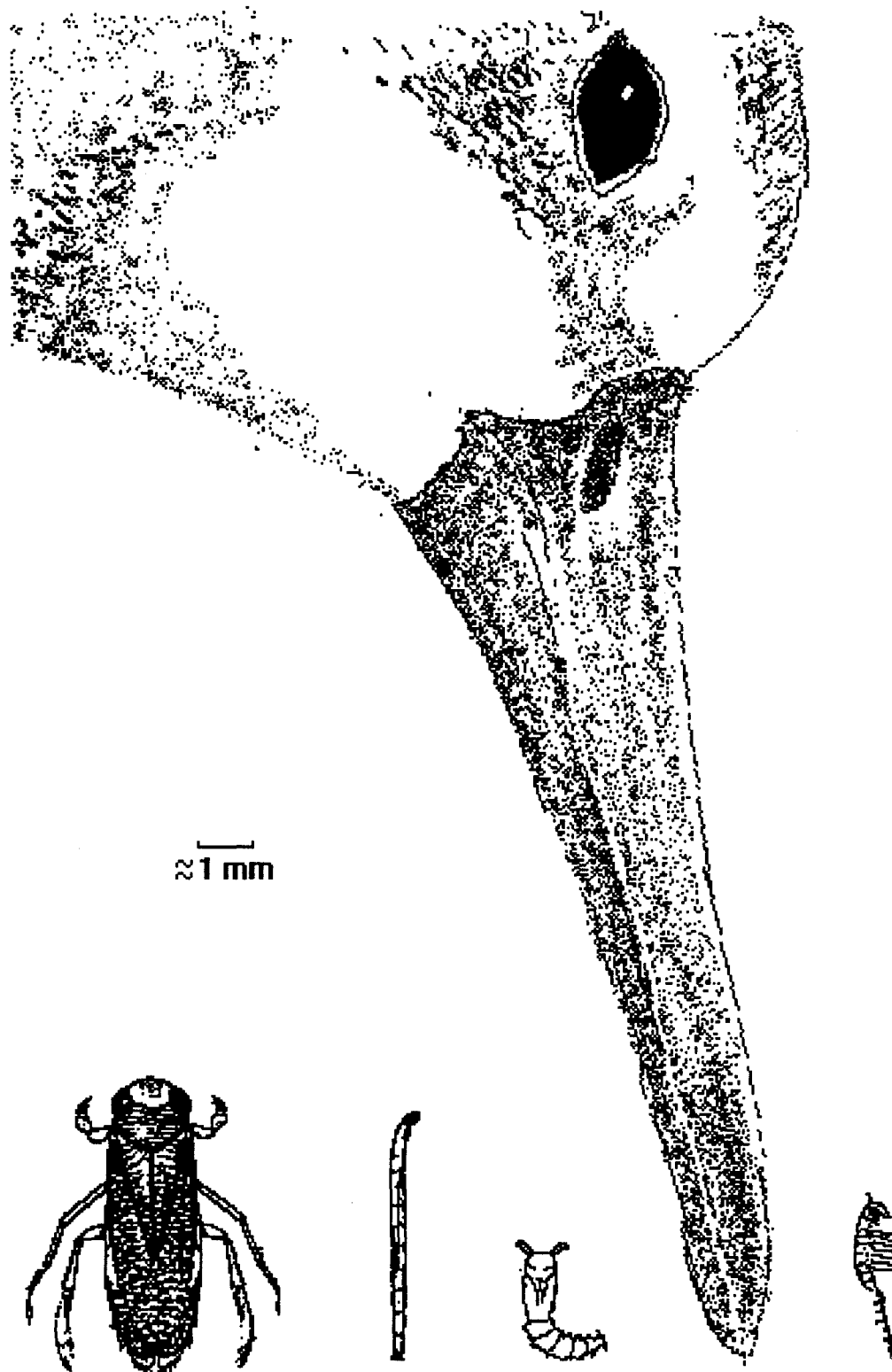


Figure 3.6. Important invertebrate taxa (*Trichocorixa*, *Dasyhelea* larvae and pupae, *Artemia*). Bill of a Semipalmated Sandpiper. *Trichocorixa* adapted from Scudder (1976). *Dasyhelea* adapted from Wirth et al. (1977).

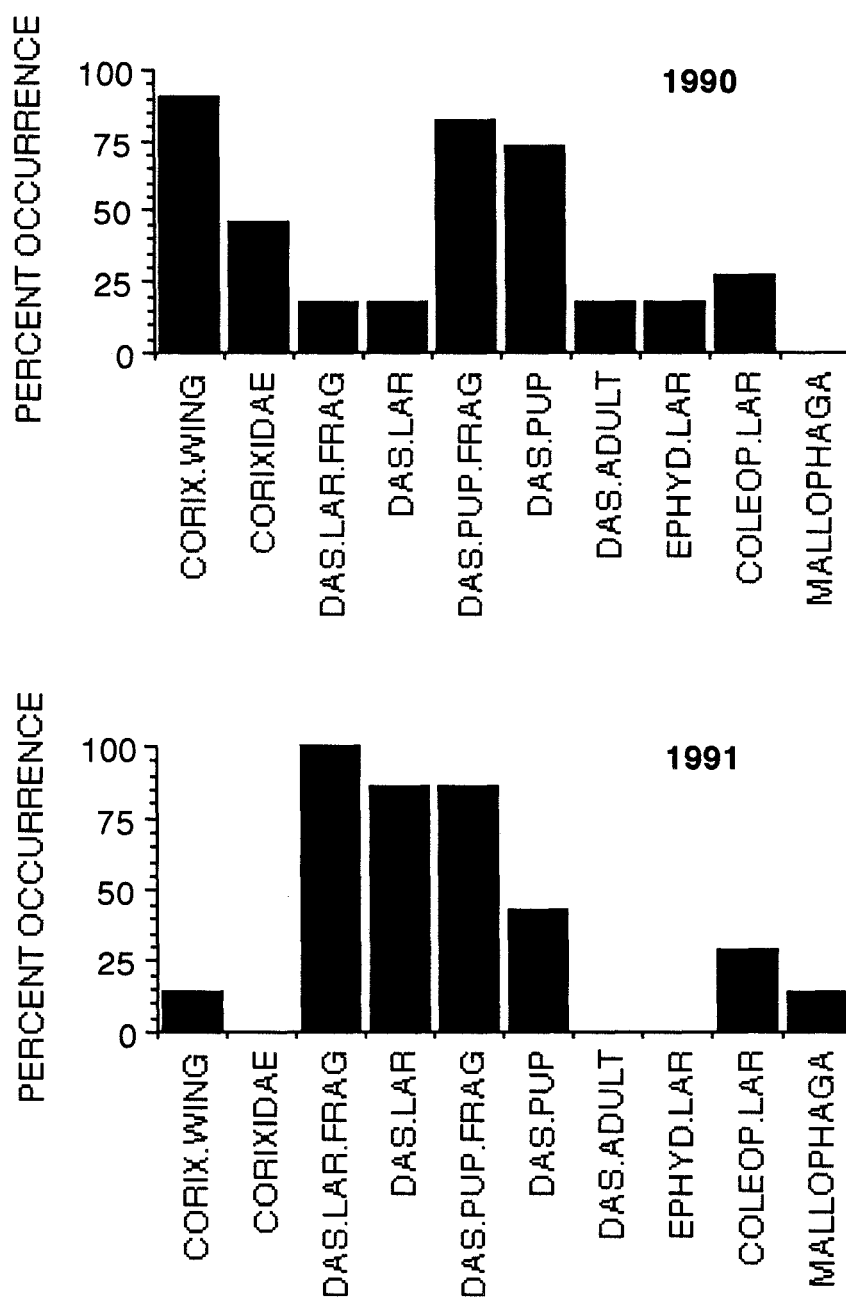


Figure 3.7. Results of diet analysis of calidrids in 1990 and 1991 expressed as percent occurrence among samples. CORIX = Corixidae (*Trichocorixa*); DAS. = *Dasyhelea*; LAR. = larvae; FRAG. = fragments; PUP. = pupae; EPHYD. = Ephydriidae; COLEOP = Coleoptera.

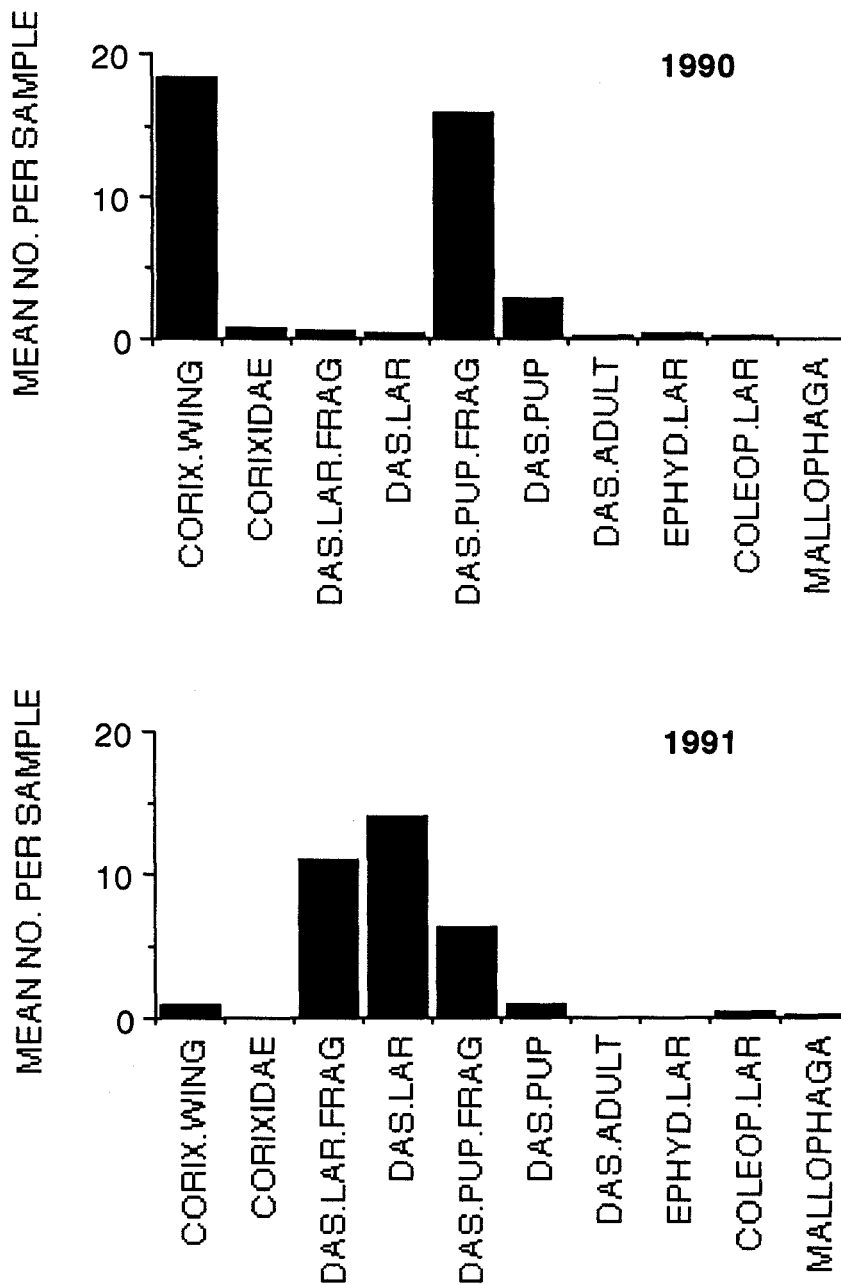


Figure 3.8. Results of diet analysis of calidrids in 1990 and 1991 expressed as mean number per sample. CORIX = Corixidae (*Trichocorixa*); DAS. = *Dasyhelea*; LAR. = larvae; FRAG. = fragments; PUP. = pupae; EPHYD. = Ephydridae; COLEOP = Coleoptera.

homogenous for between-site comparisons of foraging behavior. Frequencies of water vs. bottom foraging were significantly different ($G = 2722$, $p = 0.05$) between the two units: water foraging was more frequent in the west lagoon ($\bar{x} = 134$ water foraging attempts per minute; 1 bottom foraging attempt per minute); bottom foraging was more frequent in the middle lagoon ($\bar{x} = 0$ water foraging attempts/minute, 33 bottom foraging attempts/minute). Bottom-foraging birds collected for stomach content analysis in the middle lagoon fed upon *Dasyhelea* larvae and *Trichocorixa*, both of which are most abundant in the algal substrata lying directly over the sediments. The most regularly encountered invertebrate in the west lagoon was *Artemia*, which was extremely abundant in the water column.

Invertebrate Sampling

Mean number of invertebrates increased through time in 1990 in the eastern and middle lagoons (Chapter 2). Changes were attributed to a marked increase in *Trichocorixa*, at least in the eastern lagoon. Mean numbers of *Artemia* increased in the mud flat area.

For within-habitat comparisons, I collected a total of 228 samples from 17 sets of data (high-use/low-use pairs) during the study (11 pairs in 1990; 6 in 1991). Of the 1990 pairs, three were collected in the west lagoon and two were collected in the mud flat area. Data from the middle lagoon of both years reflect conditions of the invertebrate

community during peak use of that area by calidrids. Areas inhabited by *Artemia* (west lagoon) were sampled in 1990 only (during peak use) because calidrids were found exclusively in the middle lagoon during the shorter 1991 field season. The results of analyses of variance on high-use/low-use data are shown in Table 3.2. The differences in mean numbers of invertebrates per sample between the two seasons are shown in Figure 3.9. In 1990, mean numbers of *Dasyhelea* larvae, Stratiomyidae larvae, and *Artemia* were higher in high-use patches than in low-use patches. This difference was significant for *Artemia* and Stratiomyidae larvae. Numbers of *Trichocorixa* were significantly lower in high-use patches. In 1991, mean numbers of *Dasyhelea* larvae and *Trichocorixa* were higher in high-use areas but differences were not significant. When data from both years were pooled, mean numbers of *Dasyhelea* larvae were higher in high-use areas but differences were not significant; mean numbers of *Trichocorixa* were higher (not significant) in low-use patches. Additional samples taken in 1991 from deep areas had significantly more *Dasyhelea* larvae and pupae and *Trichocorixa* than did high-use/low-use samples taken from shallow areas.

Dasyhelea larvae and pupae were both significantly more abundant in "amorphous" algae than in "shag" and "rope" algae (Table 3.3). *Trichocorixa* were significantly more abundant in "rope" algae than in all three other types from which samples were taken. There were no Stratiomyidae larvae found

Table 3.2. Analyses of variance on high-use vs. low-use data. H = high-use; L = low-use; D = deep; HSD = Tukeys Honestly Significant Difference comparisons. Diameter of each sample = 9.92 cm.

		1990			1991				1990 & 91			
		H* n=48	L* n=48	p	H n=39	L n=39	D n=18	p	H n=87	L n=87	D n=18	p
<i>Dasyhelea</i> (larvae)	x	0.92	0.46	0.09	5.85	4.82	96.44	0.00	3.13	2.41	96.44	0.00
	sd	1.60	0.97		6.84	7.15	83.46		5.30	5.28	83.46	
	HSD	-	-		a	a	b		a	a	b	
<i>Tricho-</i> <i>corixa</i>	x	0.54	3.48	0.03	3.28	2.90	15.50	0.00	1.77	3.22	15.50	0.00
	sd	1.13	9.38		3.36	3.58	17.72		2.75	7.34	17.72	
	HSD	-	-		a	a	b		a	a	b	
<i>Artemia</i> *	x	122.50	31.39	0.04	-	-	-	-	-	-	-	-
	sd	176.10	35.16		-	-	-		-	-	-	
	HSD	-	-		-	-	-		-	-	-	
<i>Dasyhelea</i> (pupae)	x	0.25	0.40	0.53	1.15	1.15	7.72	0.00	0.66	0.74	7.72	0.00
	sd	1.06	1.18		1.48	1.88	6.00		1.34	1.57	6.00	
	HSD	-	-		a	a	b		a	a	b	
<i>Stratio-</i> <i>myidae</i> (larvae)	x	0.92	0.33	0.05	0.03	0.03	0.00	-	0.52	0.20	0.00	-
	sd	1.81	0.88		0.16	0.16	0.00		1.41	0.68	0.00	
	HSD	-	-		-	-	-		-	-	-	

* Invertebrate fauna of the lake area and of the the more eastern areas (middle lagoon and mud flat area) were mutually exclusive. Thus, high-use vs. low use comparisons for *Artemia* include lake area samples only (n=18); comparisons for other taxa include middle and mud flat areas only (n=48).

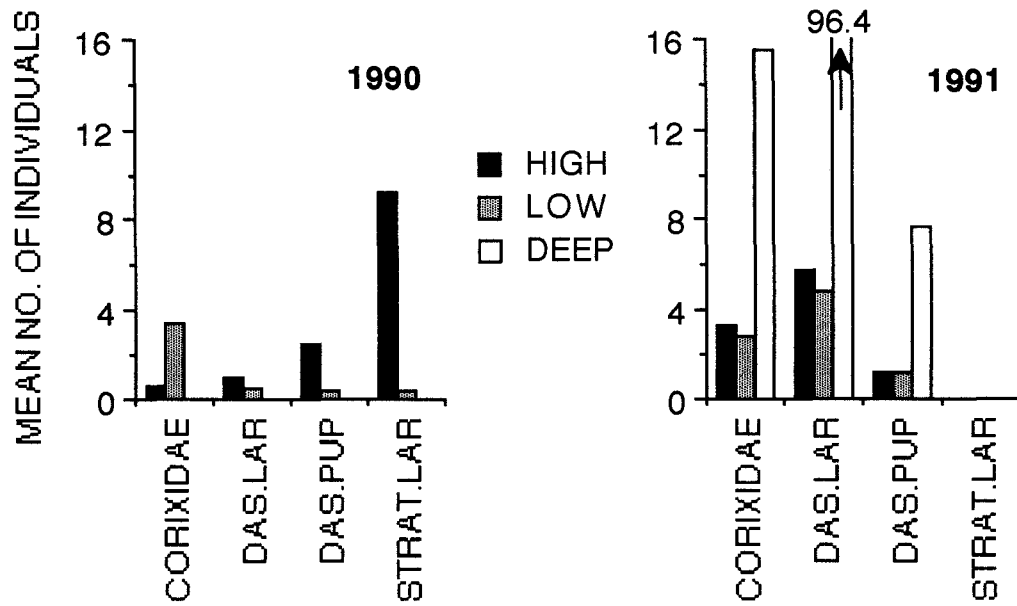


Figure 3.9. Mean numbers of individuals in high-use and low-use patches in 1990 and 1991 (deep areas for 1991 only). DAS. = *Dasyhelea*; LAR. = larvae; PUP = pupae; STRAT. = Stratiomyidae.

Table 3.3. Analyses of variance and Tukey's honestly significant difference test on invertebrate data from different substrata in the middle lagoon.

		amorph n=62	shag n=44	rope n=25	no veg n=44	p
<i>Dasyhelea</i> (larvae)	x	5.05	2.25	0.20	2.52	0.00
	sd	7.78	2.78	0.41	3.37	
	HSD	a	bc	bc	ac	
Corixidae	x	2.44	1.23	7.48	2.66	0.00
	sd	2.75	2.59	12.89	3.72	
	HSD	a	a	b	a	
<i>Dasyhelea</i> (pupae)	x	1.40	0.20	0.20	0.75	0.00
	sd	1.94	0.70	0.58	1.24	
	HSD	a	b	b	ab	

in "rope" algae, thus no test was possible. When comparisons between high-use and low-use patches were restricted to those samples from within a single substratum (i.e., amorphous algae), no significant differences were found.

Shorebird and Habitat Mapping

Mean cover values for each habitat cluster are shown in Table 3.4 (10-cluster analysis). Shorebird sightings were not distributed according to availability of habitat clusters ($G = 373, p < 0.001$). Calidrids used habitat types 4, 6, and 9 less than expected based on availability alone (Table 3.5). As indicated by mean cluster values in Table 3.4, type 4 consists primarily of shallow areas where algal mats are absent or poorly developed and which may dry out during times

Table 3.4. Mean percent cover values of substrate types for each habitat cluster (10-cluster analysis).

Habitat cluster	Relative contour (cm)	Rope algae	Shag algae	Amorphous algae	No algae	Vascular plants
1	7.6	96	1	2	1	0
2	6.9	46	0	52	1	0
3	5.5	1	2	44	52	1
4	4.4	1	2	1	96	1
5	6.2	1	1	90	8	0
6	6.0	0	54	2	44	0
7	6.1	0	51	48	1	0
8	6.7	1	97	1	1	0
9	8.6	46	0	20	34	0
10	8.1	45	48	2	4	0

Table 3.5. Simultaneous Bonferroni confidence intervals for bird sightings among ten habitat cluster types

Habitat type	Expected proportion of usage	Bonferroni intervals for observed proportions
1	0.066	0.059<=0.085<=0.110
2	0.018	*0.027<=0.045<=0.064
3	0.083	0.042<=0.064<=0.086
4	0.130	*0.013<=0.028<=0.043
5	0.209	*0.343<=0.387<=0.430
6	0.043	*0.005<=0.016<=0.028
7	0.029	0.018<=0.034<=0.050
8	0.346	0.277<=0.319<=0.361
9	0.057	*0.002<=0.004<=0.010
10	0.018	0.006<=0.019<=0.031

* indicates significant difference ($\alpha=0.05$)

of low water levels. Shallow areas also tend to be closer to edges of the lagoon and birds in those areas may be subject to greater risk of predation by raptors (personal observation). The low sighting frequency in habitat type 9 may be due to greater depth (high relative contour) in these areas. Types 2 and 5, which had higher sighting frequencies than expected, are dominated by an amorphous algal formation typically mixed with detritus particles. While the algae of this type are not attached to the bottom, they remain close to the bottom of the water column in a loose aggregate. Type 2 also has a high mean cover value for "rope algae," which is so named because it lies on the bottom in strands resembling green rope. The values for expected and observed proportions of use differed more for the amorphous algal formation (type 5) than for the amorphous/rope algae formation (type 2). The magnitude of the difference between expected and observed

bird sighting frequencies is depicted graphically in Figure 3.10.

When cover values with a relative contour depth of ≤ 6 cm are examined (5-cluster analysis), a G-test ($G = 98$, $p < 0.001$) and comparisons of Bonferroni confidence intervals still reveal rather dramatic deviations from expected distributions. As in the previous analysis, the type dominated by amorphous algae (type 5, Table 3.6) had a higher sighting frequency than expected from availability (Table 3.7), while the type having little development of algae had a lower than expected frequency. Expected and observed sighting frequencies for each type are shown in Figure 3.11.

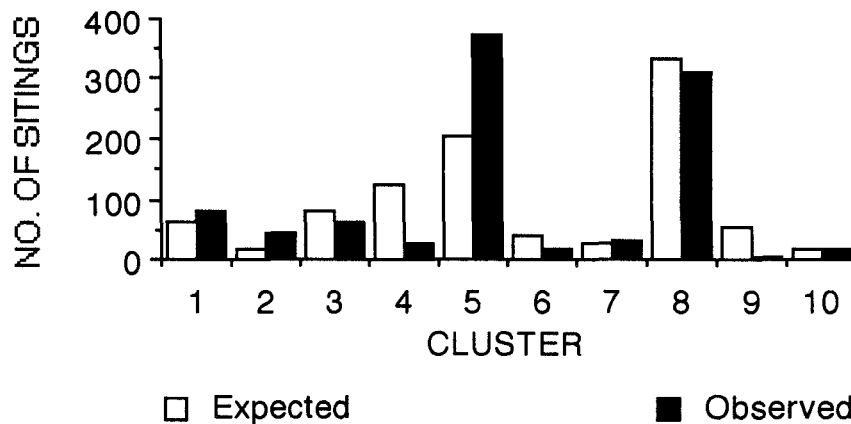


Figure 3.10. Observed and expected proportions of bird sightings among ten habitat cluster types.

Table 3.6. Mean percent cover values of substrate types for each habitat cluster (5-cluster analysis).

Habitat cluster	Rope algae	Shag algae	Amorphous algae	No algae	Vascular plants
1	73	3	16	8	0
2	3	8	35	54	0
3	1	1	2	97	1
4	1	4	85	10	0
5	0	92	4	3	0

Table 3.7. Simultaneous Bonferroni confidence intervals for bird sightings among five habitat cluster types. Habitat type 1=70% rope algae; type 2=93% shag algae; type 3=94% no algae; type 4=80% amorphous algae; type 5=100% no algae/65% vascular plants.

Habitat type	Expected proportion of usage	Bonferroni intervals for observed proportions
1	0.036	0.017<=0.044<=0.070
2	0.179	0.118<=0.167<=0.215
3	0.234	*0.032<=0.064<=0.096
4	0.283	*0.376<=0.441<=0.506
5	0.269	0.226<=0.285<=0.344

* indicates significant difference ($\alpha=0.05$).

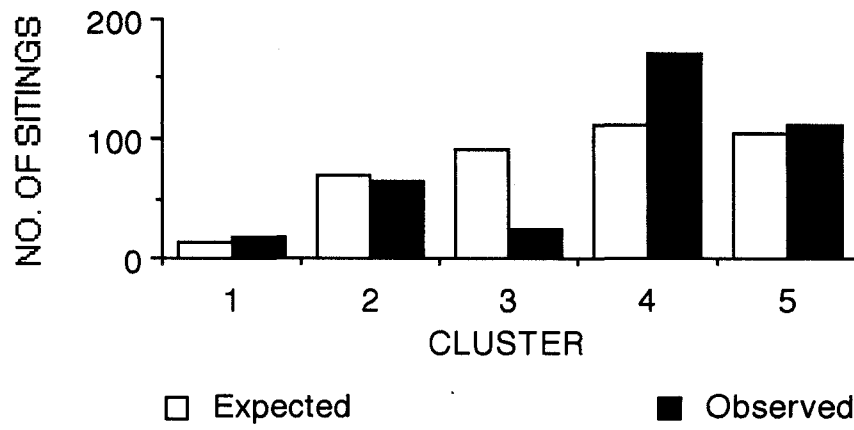


Figure 3.11. Observed and expected proportions of bird sightings among five habitat cluster types.

Discussion

Small calidrids (peeps) were by far the most abundant birds at the Cabo Rojo Salt Flats during both field seasons. Of the four species comprising this group, Semipalmated Sandpipers (*C. pusilla*) were the most numerous and comprised the majority of calidrids ($\approx 70\%$) counted during both seasons. Western Sandpipers (*C. mauri*) also accounted for a considerable proportion ($\approx 20\%$) of calidrids counted. Wunderle et al. (1989) also found that Semipalmated and Western Sandpipers were the most abundant shorebirds during autumn migration at Jobos Bay on the south central coast of Puerto Rico. As is the case at the Cabo Rojo Salt Flats, few shorebirds pass through Jobos Bay during spring migration.

As suggested by Wunderle et al (1989), shorebirds may by-pass the Caribbean during northward migration for a number of reasons that include low invertebrate productivity during spring at Caribbean wetlands and the ability of birds to accumulate large fat reserves before departing sites in northern South America (McNeil 1970). Furthermore, Morrison (1984) attributes a preponderance of juvenile Semipalmated Sandpipers at Caribbean sites in autumn to deflection by trade winds and low flight range capacities of juvenile birds following departure from North American sites. This phenomenon would not be expected during northward migration.

Calidrids appear to prefer the Fraternidad system for foraging activity, while roosting often takes place on crystallizer dikes at the Candelaria system. Although I did not make habitat comparisons between these two systems, much of the Candelaria system is deeper than the Fraternidad system. The greater use of the Candelaria system by long-legged shorebirds may be related to this difference.

Of the alternative explanations advanced to examine the distribution patterns among selected habitat units, it appears that changes in calidrid distribution were due to shifts in both densities and depth (i.e., accessibility) of preferred prey in the eastern and middle lagoons versus the mud flat (alternative 3). Thus, marked changes in the distribution of calidrids among these habitats in 1990 may be explained on the basis of physical conditions and invertebrate food resources.

Early in the 1990 season, prey were equally accessible in the mud flat and the east lagoons (i.e., both lagoons were shallow). The middle lagoon was mostly dry at this time. With the influx of rainfall, there was an increase in the prey base preferred by shorebirds in the east and middle lagoons (i.e., *Trichocorixa* and *Dasyhelea*). While prey levels at the mud flat area remained at the same level (and increased in the case of *Artemia*), an increase in depth precluded calidrids from exploiting that area. In areas in the west lagoon where birds foraged earlier in the season, *Artemia* abundance and accessibility remained high (>100

individuals per sample). These patterns suggest that when all sites were accessible for foraging (i.e., low water levels) calidrids chose the middle lagoon. Although factors such as water salinity may also directly affect site selection by calidrids, prey preference appears to be important.

The possible interaction between prey preference and accessibility also was noted in 1991 in two habitat units of Fraternidad. During a full moon high tide, productive areas in the middle lagoon were unavailable to foraging calidrids due to high water levels. Water levels in the mud flat area were relatively unaffected, since a barrier had been placed in the west culvert by the salt production company. I observed small flocks of calidrids visiting the middle lagoon, "sampling" several patches for a few moments, and returning to the exposed algal mats in the mud flat area where they pursued adult brine flies (*Ephydra gracilis*). After water levels receded in the middle lagoon, calidrids returned, even while brine flies remained plentiful in the mud flat area. In the same year, when nearly all of the calidrids using the Fraternidad system foraged in the middle lagoon, *Artemia* were still abundant in shallow waters of the west lagoon.

I documented the higher quality of deeper areas in 1991 in terms of prey abundance. Invertebrate sampling in these areas indicated that prey densities were several orders of magnitude higher than in similar areas in shallower water.

This pattern might be due to 1) predator avoidance in the case of mobile prey (*Trichocorixa*), 2) differential substrate quality or flood cycle requirements (*Dasyhelea*), or 3) prey depletion, which has been well-documented in temperate zone estuaries (e.g., Quammen 1984, Schneider and Harrington 1981).

Shifts in diet between years among birds in the middle lagoon suggest that prey abundance may affect choice of prey by shorebirds within a site. While the abundance of *Trichocorixa* remained high in high-use/low use samples from 1991 (Table 3.2), the diets of collected birds were dominated by *Dasyhelea*. The higher abundance of *Dasyhelea* in 1991 may have been due to the influence of climatic and tidal differences between the two years on water conditions in the middle lagoon (Chapter 2). In 1990, when *Dasyhelea* were less abundant, *Trichocorixa* dominated the diets of birds. Studies by Schneider (1978) and Wolff (1969) indeed suggest that shorebirds are numerically selective predators.

At first glance, calidrid distribution patterns at the within-site level were less clear than at the among-site level. In the middle lagoon, where most of the effort devoted to this part of the project was concentrated, strong significant differences were not found between high-use and low-use patches for some prey species or when 1990 and 1991 data are pooled. In one instance (*Trichocorixa* in 1990), low-use patches had significantly higher prey densities than high-use patches.

Interpretations of high-use/low-use data were elusive until substrate data were examined. At the outset of the project, I stratified the within-habitat invertebrate sampling scheme by use level (i.e., number of calidrids), depth, and general similarity of the sites. Although substrate type was recorded for high-use/low-use sampling, in some cases sampling was conducted across substrates to maintain depth uniformity and similarity. I did not perceive the heterogeneous nature of the algal substrate during the original stratification of sampling effort.

Several clear patterns still emerge from the substrate data, however, that provide insights into "within-habitat" patch selection in tropical salt water lagoons. Mapping data indicated that shorebird distribution was not random. Areas dominated by amorphous/rope algal substrata were selected by shorebirds in higher proportion than expected by chance alone. When the analysis was limited to shallow areas, the amorphous algae was still selected and the rope algae formation was selected in proportion to its availability. These substrate types harbored significantly higher number of *Dasyhelea* and *Trichocorixa*, the most important prey items in the diets of calidrids. When high-use/low-use samples were controlled for substrate type, there were no significant differences for individual taxa. This suggests that prey abundance was fairly uniform within a given substrate. In the case of *Trichocorixa* in 1990, low-use patches sampled for

several of the high-use/low-use pairs were located in rope algae, a substrate type apparently preferred by *Trichocorixa*.

These findings suggest that foraging site selection by calidrids may be based on algal substrate physiognomy, rather than an assessment of infaunal invertebrates (e.g., Goss-Custard 1977a, 1977b). Because algal formations seem so important, any significant differences in invertebrate abundance found in this study between high-use and low-use patches can not be construed to mean that birds were perceiving invertebrate distribution. It is possible that birds more readily perceived and selected substrate formations.

If migratory shorebirds can visually select "good" patches, they may be able to meet energetic demands more efficiently, particularly when foraging bouts are disrupted by predators. In 1990, predation attempts by Merlins (*Falco columbarius*) and Peregrine Falcons (*F. peregrinus*) were recorded with a frequency of up to 1 or 2 attempts per 10 minutes. As a result, calidrid flocks rarely remained in any single area on the grid system for more than 2-3 minutes. In both seasons at the Cabo Rojo Salt Flats, I regularly saw at least two Merlins and two Peregrine Falcons. Predation of shorebirds by Merlins has been well documented at wintering areas (e.g., Page and Whitacre 1975).

Data from the west lagoon showed clear positive relationships between *Artemia* and calidrid distribution. There is little variation in substrate character in the west

lake; high-use and low-use samples were taken within identical substrata. Calidrids therefore appeared to actively select foraging sites based on the abundance of *Artemia*. To the human eye, patches of greater *Artemia* abundance were readily identifiable. Whether or not calidrids visually assess *Artemia* abundance is unclear. The preferred prey in the east, middle, and mud flat areas occur within lush algal and detrital formations and their abundance would seem more difficult to perceive visually. When accessible, however, calidrids moved into these insect-dominated areas regardless of *Artemia* abundance in the west lagoon.

While the substrate types occurring at the study site likely occur elsewhere in coastal lagoons of the tropics, additional studies of shorebird feeding activity are needed in these areas. Questions such as what effect the feeding activity of extremely abundant corixids (i.e., *Trichocorixa*) has on the physical structure of algal substrata (Copeland and Nixon 1974), how shorebirds use different algal substrata, and what hydrologic regimes maintain those substrata and their invertebrate fauna deserve attention in future studies.

CHAPTER 4 CONCLUSION AND MANAGEMENT RECOMMENDATIONS

I documented the use of habitat resources at the Cabo Rojo Salt Flats by migratory *Calidris* sandpipers. Although the invertebrates fed upon by calidrids are year-round breeders, proper habitat conditions for invertebrate productivity are met unpredictably. Calidrids appear to cope with these changes in their habitat by shifting the target of their foraging activity and moving between habitats within the salt flats. In contrast, productivity at stopover areas in the temperate zone is highly predictable, both annually and seasonally, and plays a key role in the rigid annual cycles of migratory shorebirds.

From the perspectives of either shorebird migration or ecology, it may be inappropriate to compare tropical and temperate stopover areas. In the absence of a means of evaluating and comparing shorebird habitats within the tropics, our knowledge of the extent to which habitat alterations and loss affect migratory shorebirds will remain inadequate.

Shorebird conservation groups base their evaluation of stopover areas on the proportion of a particular shorebird species occurring at that site at any one time. Areas such as Delaware Bay in New Jersey and the Bay of Fundy in Canada

have thus received considerable attention from the research and conservation community. Our perception of the localized distribution of many shorebird species is at least partially affected by their absence from other areas due to habitat destruction. In Puerto Rico, the conservation significance of the Cabo Rojo Salt Flats is due in part to wetland losses elsewhere in the island as well as to the limited extent of salt flat ecosystems.

Several of the species of shorebirds seen at the salt flats are distributed among widely scattered mangrove pools and coastal lagoons throughout the neotropics. These habitats, however, are only part of a changing landscape mosaic. In most ecosystems, conservationists and park managers can rarely expect to maintain all the components of a naturally changing landscape. To cope with this problem, it is often necessary to manage different parcels of land in a relatively static state, thereby arresting "succession." In Cabo Rojo, lagoons and salt flats formed and might have persisted without human influence. However, the activities of commercial salt production over the last two centuries have likely further arrested change by maintaining the salt flat and lagoon stages of mangrove succession. Consideration of this possibility is an important component of habitat management.

Based on the conclusions of this study, my recommendations for management of shorebird habitat at the Cabo Rojo Salt Flats follow:

1. Partial (but not total) obstruction of tidal influence in the east and middle lagoons should be maintained. Under the current hydrologic regime, salinity stress and desiccation prevent growth of mangroves. Seasonal freshwater inputs enhance insect productivity.

2. Part or all of the hypersaline areas in the west lagoon should be maintained for *Artemia* (brine shrimp) productivity. *Artemia* appear to serve as a "backup" food supply when productivity is low or unavailable in the eastern areas.

3. Dikes between crystallizers or similar structures in the Fraternidad and Candelaria systems should be maintained as roosting sites for *Calidris* sandpipers.

4. Effects of water level and salinity fluctuation on *Dasyhelea* (midge flies), *Trichocorixa* (waterboatmen) and algae should be studied through controlled experiments. For example, the existing seasonal cycles of desiccation and flooding, as opposed to permanent flooding, may be critical to the maintenance of algal mats and insect productivity.

5. Manipulation of sea water inputs at the west culvert should be considered as a means of maintaining high salinity in the west lagoon and for manipulating water levels in the mud flat. Temporary exposure of algal mats in the mud flat may enhance *Ephydra* (brine fly) productivity.

6. Habitat requirements of other wildlife groups and endangered species should be determined and considered before management plans are implemented.

The Cabo Rojo Salt Flats are of immense conservation significance on a regional level. Protection of this unique

site would benefit many species of resident, migrant, and wintering shorebirds as well as other important components of Puerto Rico's wildlife.

APPENDIX
SHOREBIRD SPECIES ENCOUNTERED
AT THE CABO ROJO SALT FLATS*

<u>Species</u>	<u>Common Name</u>	<u>Source**</u>
<i>Himantopus</i> <i>himantopus</i>	Black-necked Stilt	
<i>Pluvialis</i> <i>squatarola</i>	Black-bellied Plover	
<i>dominica</i>	Lesser Golden Plover	
<i>Charadrius</i> <i>semipalmatus</i>	Semipalmated Plover	
<i>wilsonia</i>	Wilson's Plover	
<i>vociferus</i>	Killdeer	
<i>melodus*</i>	Piping Plover*	
<i>alexandrinus</i>	Snowy Plover	
<i>Tringa</i> <i>melanoleuca</i>	Greater Yellowlegs	
<i>flavipes</i>	Lesser Yellowlegs	
<i>solitaria*</i>	Solitary Sandpiper*	
<i>Catoptrophorus</i> <i>semipalmatus</i>	Willet	
<i>Actitis</i> <i>macularia</i>	Spotted Sandpiper	
<i>Phalaropus</i> <i>tricolor*</i>	Wilson's Phalarope*	

(continued)

Appendix* (continued)

<u>Species</u>	<u>Common Name</u>	<u>Source**</u>
<i>Numenius</i> <i>phaeopus</i>	Whimbrel	
<i>Limosa</i> <i>haemastica*</i>	Hudsonian Godwit	
<i>fedoa</i>	Marbled Godwit	
<i>Arenaria</i> <i>interpres</i>	Ruddy Turnstone	
<i>Calidris</i> <i>canutus*</i>	Red Knot*	
<i>alba*</i>	Sanderling*	
<i>pusilla</i>	Semipalmated Sandpiper	
<i>mauri</i>	Western Sandpiper	
<i>minutilla</i>	Least Sandpiper	
<i>fuscicollis</i>	White-rumped Sandpiper	
<i>bairdii*</i>	Baird's Sandpiper*	A. Begazo
<i>melanotus</i>	Pectoral Sandpiper	
<i>alpina*</i>	Dunlin*	
<i>himantopus</i>	Stilt Sandpiper	
<i>Tryngites</i> <i>subruficollis*</i>	Buff-breasted Sandpiper*	M. Kasprzyk
<i>Philomachus</i> <i>pugnax*</i>	Ruff*	Raffaele (1989)
<i>Limnodromus</i> <i>griseus</i>	Short-billed Dowitcher	
<i>Gallinago</i> <i>gallinago*</i>	Common Snipe*	B. Harrington

* Species not marked with an asterisk (*) were encountered during weekly surveys (those with an asterisk were seen at other times).

** Sources are listed for those species not seen during this study.

REFERENCES

- Altmann, J. 1974. Observational study of behaviour: Sampling methods. *Behaviour* 49: 227-267.
- Armstrong, N.E. 1982. Responses of Texas estuaries to freshwater inflows. Pp. 103-120 in: V.S. Kennedy (ed.). *Estuarine comparisons*. Academic Press, New York.
- Ashmole, M.J. 1970. Feeding of Western and Semipalmated Sandpipers in Peruvian winter quarters. *Auk* 87: 131-135.
- Baird, D., P.R. Evans, H. Milne, and M.W. Pienkowski. 1985. Utilization by shorebirds of benthic production in intertidal areas. *Oceanogr. Mar. Biol. Ann. Rev.* 23: 573-597.
- Baker, M.C. 1977. Shorebird food habits in the Eastern Canadian arctic. *Condor* 79: 56-62.
- Bengston, S. and B. Svensson. 1968. Feeding habits of *Calidris alpina* L. and *C. minuta* Leisl. (Aves) in relation to the distribution of marine shore invertebrates. *Oikos* 19: 152-157.
- Biaggi, V. 1983. Las aves de Puerto Rico. Editorial U.P.R. Rio Piedras, Puerto Rico.
- Bildstein, K.L., R.L. Christy, P. de Coursy. 1982. Energy flow through a South Carolina salt-marsh community. *Wader Study Group Bull.* 34: 35-37.
- Bolster, D.C. and S.K. Robinson. 1990. Habitat use and relative abundance of migrant shorebirds in a western Amazonian site. *Condor* 92: 239-242.
- Brown, E.S. 1951. The relation between migration rate and type of habitat in aquatic insects, with special reference to certain species of Corixidae. *Proc. Zool. Soc. Lond.* 121: 539-545.
- Brush, T., R.A. Lent, T. Hruby, B.A. Harrington, R.M. Marshall, and W.M. Montgomery. 1986. Habitat use by salt marsh birds and response to open marsh water management. *Colonial Waterbirds* 9: 189-195.

- Bryant, D.M. 1979. Effects of prey density and site character on estuary usage by overwintering waders (Charadrii). *Estuar. Coast. Mar. Sci.* 9: 369-384.
- Carpelan, L.H. 1957. Hydrobiology of the Alviso salt ponds. *Ecology* 38: 375-390.
- Castilla, J.C. and R.T. Paine. 1987. Predation and community organization on Eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural* 160: 131-151.
- Chapman, V.J. (ed.). 1977. *Ecosystems of the world 1. Wet coastal ecosystems.* Elsevier, Amsterdam. 428 p.
- Cintrón, G., A.E. Lugo, D.J. Pool, and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica* 10: 110-121.
- Collazo, J.A., J. Thomas, A. Knot, and J.A. Colon. 1987. Preliminary findings on several aspects of the ecology of Snowy and Wilson's Plovers at the Cabo Rojo Salt Flats. Caribbean Islands National Wildlife Refuge. U.S. Fish and Wildlife Service.
- Copeland, B.J. and S.W. Nixon. 1974. Hypersaline lagoons. Pp. 312-330 in: H.T. Odum, B.J. Copeland, and E.A. McMahan (eds.). *Coastal ecological systems of the United States, Vol 1.* The Conservation Foundation, Washington, D.C.
- Danforth, S.T. 1929. Snowy Plovers in Haiti and Porto Rico. *Auk* 46: 231-232.
- Davies, J.B. 1967. The distribution of sandflies (*Culicoides* spp.) breeding in a tidal mangrove swamp in Jamaica and the effect of tides on the emergence of *C. furens* (Poey) and *C. barbosai* Wirth and Blanton. *West Indian Med. Jour.* 41: 39-50.
- 1969. Effect of felling mangroves on emergence of *Culicoides* spp. in Jamaica. *Mosquito News* 29: 566-571.
- Davis, C.C. 1966. Notes on the ecology and reproduction of *Trichocorixa reticulata* in a Jamaican salt-water pool. *Ecology* 47: 850-852.
- Davis, J.S. 1978. Biological communities of a nutrient enriched salina. *Aq. Bot.* 4: 23-42.
- 1979. Biological management of solar saltworks. 5th Int'l Symp. on Salt, Northern Ohio Geol. Soc: 265-268.

- . 1980. Experiences with *Artemia* at solar salt works. Pp 51-55 in: G. Persoone, P. Sorgeloos, O. Roels, and E. Jaspers (eds). The brine shrimp *Artemia*. Vol. 3. Ecology, culturing, use in aquaculture. Universa Press, Wetteren. 456 pp.
- Del Llano, M., J.A. Colon, and J.L. Chabert. 1986. Puerto Rico chapter in a directory of neotropical wetlands. Compiled by D.A. Scott and M. Carbonell, IUCN, Cambridge, and IWRB, Slimbridge.
- Duffy, D.C., N. Atkins, and D.C. Schneider. 1981. Do shorebirds compete on their wintering grounds? *Auk* 98: 215-229.
- Evans, P.R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. Pp. 8-28 in: E. Naylor, and R.G. Hartnoll (eds.). Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford.
- ., D.M. Herdson, P.J. Knights, and M.W. Pienkowski. 1979. Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and Shelduck. *Oecologia* 41: 183-206.
- Fox, I. and J. Maldonado Capriles. 1953. Light trap studies on mosquitoes and *Culicoides* in western Puerto Rico. *Mosquito News* 13: 165-166.
- Gordon, D.C., Jr., P.J. Cranford, and C. Desplanque 1985. Observations on the ecological importance of salt marshes in the Cumberland Basin, a macrotidal estuary in the Bay of Fundy. *Estuarine, Coastal and Shelf Science* 20: 205-227.
- Goss-Custard, J.D. 1977a. Optimal foraging and the size selection of worms by Redshank, *Tringa totanus*, in the field. *Anim. Behav.* 25: 10-29.
- . 1977b. Predator responses and prey mortality in Redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *J. Anim. Ecol.* 46: 21-35
- . 1979. Role of winter food supplies in the ecology of common British wading birds. *Verhandlungen der ornithologischen Gesellschaft in Bayern* 23: 125-146.
- ., R.E. Jones, and P.E. Newbery. 1977a. The ecology of the Wash. I. Distribution and diet of wading birds (Charadrii). *J. Appl. Ecol.* 14: 681-700.
- ., D.G. Kay, and R.M. Blindell. 1977b. The density of migratory and overwintering Redshank, *Tringa totanus*

- (L.) and Curlew, *Numenius arquata* (L.), in relation to the density of their prey in South-east England. *Estuar. Coast. Mar. Sci.* 5: 497-510.
- Grant, J. 1981. A bioenergetic model of shorebird predation on infaunal amphipods. *Oikos* 37: 53-62.
- Harrington, B.A. 1982. Morphometric variation and habitat use of Semipalmated Sandpipers during a migratory stopover. *J. Field Ornithol.* 53: 258-262.
- and R.I.G. Morrison. 1979. Semipalmated Sandpiper migration in North America. *Studies in Avian Biology* 2: 83-100.
- ., J.P. Myers, and J.S. Grear. 1989. Coastal refueling sites for global bird migrants. Coastal Zone 89. Proc. 6th Symp. Coastal and Ocean Man., Amer. Soc. Civil Engineers: 4293-4307.
- Hicklin, P.W., L.E. Linkletter, and D.L. Peer. 1980. Distribution and abundance of *Corophium volutator* (Pallas), *Macoma balthica* (L.) and *Heteromastus filiformis* (Clarapede) in the intertidal zone of Cumberland Basin and Shepody Bay, Bay of Fundy. *Can. Tech. Rept. Fish. Aquat. Sci.* 965: 1-59.
- and P.C. Smith. 1979. The diets of five species of migrant shorebirds in the Bay of Fundy. *Proc. Nova Scotia Inst. Sci.* 29: 483-488.
- and P.C. Smith. 1984. Selection of foraging sites and invertebrate prey by migrant Semipalmated Sandpipers, *Calidris pusilla* (Pallas), in Minas Basin, Bay of Fundy. *Can. J. Zool.* 62: 2201-2210.
- Hockey, P.A.R., W.R. Siegfried, A.A. Crowe, and J. Cooper. 1983. Ecological structure and energy requirements of the sandy beach avifauna of southern Africa. Pp. 507-521 in: A. McLachlan and T. Erasmus (eds.). *Sandy beaches as ecosystems*. Junk Publishers, Den Haag.
- Javor, B. 1989. *Hypersaline environments: microbiology and biogeochemistry*. Springer-Verlag, Berlin. 328 p.
- Johnson, O.W. 1979. Biology of shorebirds summering on Enewetak Atoll. Pp. 193-206 in: F.A. Pitelka (ed.). *Shorebirds in marine environments*. *Studies in avian biology*, No. 2.
- Kline, D.L., R.H. Roberts, and D.A. Focks. 1981. Extraction of larvae of the ceratopogonid biting midge, *Culicoides mississippiensis*, from salt marsh soils with a new agar technique. *Mosquito News* 41: 94-98.

- Lankford, R.R. 1977. Coastal lagoons of Mexico: their origin and classification. Pp. 182-215 in: M. Wiley (ed.). Estuarine processes: circulation, sediments and transfer of material in the estuary, Vol. 2. Academic Press, New York.
- Lee, G. 1989. Population numbers, breeding biology and habitat use of the Snowy and Wilson's Plovers at the Cabo Rojo Salt Flats, Puerto Rico. Master's Thesis, Clemson University.
- Leopold, N.F. 1963. Checklist of birds of Puerto Rico and the Virgin Islands. Agr. Exp. Sta. Bull. 168: 1-169. University of Puerto Rico. Rio Piedras, Puerto Rico.
- Linley, J.R. 1976. Biting midges of mangrove swamps and saltmarshes (Diptera: Ceratopogonidae). Pp. 335-376 in: L. Cheng (ed.). Marine insects. North-Holland Publishing Company, Amsterdam.
- Magdych, W.P. 1981. An efficient, inexpensive elutriator design for separating benthos from sediment samples. Hydrobiologia 85: 157-159.
- Magnon, G.J., D.V. Hagan, D.L. Kline, and J.R. Linley. 1990. Habitat characteristics and phenology of larval *Culicoides* spp. (Diptera: Ceratopogonidae) from a coastal Georgia salt marsh. Environ. Entomol. 19: 1068-1074.
- Mallory, E.P. and D.C. Schneider. 1979. Agonistic behavior in Short-billed Dowitchers feeding on a patchy resource. Wilson Bull. 91: 271-278.
- Marsh, C.P. 1986a. Impact of avian predators on high intertidal limpet populations. J. Exp. Mar. Biol. Ecol. 104: 185-201.
- 1986b. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. Ecology 67: 771-786.
- Matuszeski, W., E. Perez, and S. Olsen. 1988. Structure and objectives of a coastal resources management program for Ecuador. Tech. Rep. Ser.: TR-D-2. International Coastal Resources Management Project sponsored by the United State Agency for International Development, between the University of Rhode Island and the government of Ecuador.
- McCandless, J.B. 1961. Bird life in southwestern Puerto Rico. I. Fall migration. Carib. J. Sci. 1: 3-13

- . 1962. Bird life in southwestern Puerto Rico. II. The 'winter' season. *Carib. J. Sci.* 2: 27-39.
- McNeil, R. 1970. Hivernage et estivage d'oiseaux aquatiques Nord-Américains dans le Nord-Est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). *L'oiseaux et R.F.O.* 40: 185-302.
- Meyerhoff, H.A. 1933. The geology of Puerto Rico. Monographs of the University of Puerto Rico, Physical and Biological Series B. 306 pp.
- Moreno, J.A. and N. Perez. 1980. Management plan for the seabirds and shorebirds of Puerto Rico. Puerto Rico Department of Natural Resources. San Juan, Puerto Rico. 72 pp.
- Morrison, R.I.G. 1984. Migration systems of some new world shorebirds. Pp. 125-202 in: Burger, J. and B.L. Olla (eds.). Behavior of marine animals. Vol 6: Shorebirds, migration and foraging behavior. Plenum Press, New York.
- Muirhead-Thomson, E.C. 1982. Behaviour patterns of bloodsucking flies. Pergamon Press, Oxford. 224 pp.
- Myers, J.P. 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. *Am. Birds* 37(1): 23-25.
- . 1984. Spacing behavior of nonbreeding shorebirds. Pp. 271-321 in: Burger, J. and B.L. Olla (eds.). Behavior of marine animals. Vol 6: Shorebirds, migration and foraging behavior. Plenum Press, New York.
- ., P.G. Connors, and F.A. Pitelka. 1979. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk* 96: 551-561.
- ., J.L. Maron, and M. Sallaberry. 1983. Going to extremes: why do Sanderlings migrate to the Neotropics? Pp. 520-535 in: P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely, and F.G. Buckley (eds.). Neotropical Ornithology. *Orn. Monogr.* 36.
- and B.J. McCaffery. 1984. Paracas revisited: do shorebirds compete on their wintering ground? *Auk* 101: 197-199.
- ., R.I.G. Morrison, P.Z. Antas, B.A. Harrington, T.E. Lovejoy, M. Sallaberry, S.E. Senner, and A. Tarak. 1987. Conservation strategy for migratory species. *American Scientist* 75: 18-26.

- ., S.L. Williams, and F.A. Pitelka. 1980. An experimental analysis of prey availability for Sanderlings (Aves:Scolopacidae) feeding on sandy beach crustaceans. *Can. J. Zool.* 58: 1564-1574.
- Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541-545.
- Nixon, S. 1969. Characteristics of some hypersaline ecosystems. PhD. dissertation, University of North Carolina.
- NOAA. 1989. Tide Tables 1990, east coast of North and South America, including Greenland. National Oceanic and Atmospheric Administration, U.S. Dept. of Commerce.
- Odum, H.T., S.W. Nixon, and L.H. DiSalvo. 1971. Adaptations for photoregenerative cycling. Pp 1-29 in: J. Cairns, Jr. (ed.). The structure and function of fresh-water microbial communities. American Microscopical Society Symposium. Research Division Monograph 3. Va. Poly. Inst. and St. Univ. Blacksburg, Va.
- Ortiz-Rosas, P. and V. Quevedo-Bonilla. 1987. Areas con prioridad para la conservacion en Puerto Rico. Programa Pro-Patrimonio Natuaral. Departamento de Recursos Naturales. San Juan, Puerto Rico.
- Page, G. and D.F. Whitacre. 1975. Raptor predation on wintering shorebirds. *Condor* 77: 73-83.
- Peer, D.L., L.E. Linkletter, and P.W. Hicklin 1986. Life history and reproductive biology of *Corophium volutator* (Crustacea: Amphipoda) and the influence of shorebird predation on population structure in Chignecto Bay, Bay of Fundy, Canada. *Neth. J. Sea Res.* 20: 359-373.
- Pienkowski, M.W. 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Mar. Ecol. Prog. Ser.* 11: 141-150.
- and P.R. Evans. 1984. Migratory behavior of shorebirds in the western Palearctic. Pp. 73-123 in: Burger, J. and B.L. Olla (eds.). Behavior of marine animals. Vol 6: Shorebirds, migration and foraging behavior. Plenum Press, New York.
- Piersma, T. 1987. Production by intertidal benthic animals and limits to their production by shorebirds: a heuristic model. *Mar. Ecol. Prog. Ser.* 38: 187-196.

- and M. Engelmoer. 1982. Waders and their food resources: general discussion. Pp. 161-164 in: W. Altenburg, M. Engelmoer, R. Mes, and T. Piersma (eds.). Wintering waders on the Banc d'Arguin, Mauritania. Stichting Veth tot steun aan Waddenonderzoek, Leiden.
- Puttick, G.M. 1980. Energy budgets of Curlew Sandpipers at Langebaan Lagoon, South Africa. *Estuar. Coast. Mar. Sci.* 11: 207-215.
- . 1984. Foraging and activity patterns in wintering shorebirds. Pp. 203-231 in: Burger, J. and B.L. Olla (eds.). Behavior of marine animals. Vol 6: Shorebirds, migration and foraging behavior. Plenum Press, New York.
- Quammen, M.L. 1981. Use of exclosures in studies of predation by shorebirds on intertidal mud flats. *Auk* 98: 812-817.
- . 1984. Predation by shorebirds, fish, and crabs on invertebrates in intertidal mudflats: an experimental test. *Ecology* 65: 529-537.
- Raffaele, H.A. 1989. A guide to the birds of Puerto Rico and the Virgin Islands. Princeton University Press, New Jersey. 254 pp.
- , and J. Duffield. 1979. Critical wildlife areas of Puerto Rico. Puerto Rico Department of Natural Resources. San Juan, Puerto Rico. 97 pp.
- Richardson, W.J. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. *Can. J. Zool.* 57: 107-124.
- Robert, M., R. McNeil, and A. Leduc. 1989. Conditions and significance of night-feeding in shorebirds and other water birds in a tropical lagoon. *Auk* 106: 94-101.
- SAS Institute. 1982. SAS user's guide: statistics. SAS Institute, Cary, North Carolina. 584 pp.
- Schneider, D.C. 1978. Equalisation of prey numbers by migratory shorebirds. *Nature* 271: 353-354.
- . 1985a. Migratory shorebirds: resource depletion in the tropics? Pp. 546-558 in: P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely, and R.G. Buckley (eds.). Neotropical ornithology. *Orn. Monogr.* 36.
- . 1985b. Predation on the urchin *Echinometra lucunter* (Linnaeus) by migratory shorebirds on a tropical reef flat. *J. Exp. Mar. Biol. Ecol.* 92: 19-27.

- and B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801-811.
- and E.P. Mallory. 1982. Spring migration of shorebirds in Panama. *Condor* 84: 344-345.
- Scudder, G.G.E. 1976. Water-boatmen of saline waters (Hemiptera: Corixidae). Pp. 263-289 in: L. Cheng (ed.). *Marine insects*. North-Holland Publishing Company, Amsterdam.
- Senner, S.E. and M.E. Howe. 1984. Conservation of nearctic shorebirds. Pp. 379-421 in: J. Burger and B.L. Olla (eds.). *Behavior of marine animals. Vol 5: Shorebirds, breeding behavior and populations*. Plenum Press, New York.
- and E.F. Martinez. 1982. A review of Western Sandpiper migration in interior North America. *Southwest. Nat.* 27: 149-159.
- , G.C. West, and D.W. Norton. 1981. The spring migration of Western Sandpipers and Dunlins in south central Alaska: numbers, timing, and sex ratios. *J. Field Ornithol.* 52: 271-284.
- Smit, C.J. 1981. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea. Pp. 290-301 in: C.J. Smit and W.J. Wolff (eds.). *Birds of the Wadden Sea*. Balkema, Rotterdam.
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. W.H. Freeman and Company, New York. 859 pp.
- Spaans, A.L. 1978. Status and numerical fluctuations of some North American waders along the Surinam coast. *Wilson Bull.* 90: 60-83.
- Strauch, J., Jr., and L.G. Abele. 1979. Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. Pp. 217-230 in: F.A. Pitelka (ed.). *Shorebirds in marine environments. Studies in avian biology, No. 2*.
- Summers, R.W. 1977. Distribution, abundance, and energy relationships of waders (Aves: Charadrii) at Langebaan Lagoon. *Trans. R. Soc. S. Afr.* 42: 483-495.
- Swennen, C.P. Duiven, and A.L. Spaans. 1982. Numerical density and biomass of macrobenthic animals living in the intertidal zone of Surinam, South America. *Netherlands J. Sea. Res.* 15: 406-418.

- Thomas, B.T. 1987. Spring shorebird migration through central Venezuela. *Wilson Bull.* 99(4): 571-578.
- Wetmore, A. 1916. Birds of Porto Rico. U.S. Dept. of Agriculture. Bulletin No. 326. 140 pp.
- Williams, R.W. 1957. Observations on the breeding habitats of some Heleidae of the Bermuda Islands (Diptera). *Proc. Entomol. Soc. Wash.* 59: 61-66.
- Wilson, W.H. 1989. Predation and the mediation of intraspecific competition in an infaunal community in the Bay of Fundy. *J. Exp. Mar. Biol. Ecol.* 132: 221-245.
- . 1990. Relationship between prey abundance and foraging site selection by Semipalmated Sandpipers on a Bay of Fundy mudflat. *J. Field Ornithol.* 61: 9-19.
- Wirth, W.W. and F.S. Blanton. 1974. The West Indian sandflies of the genus *Culicoides* (Diptera: Ceratopogonidae). U.S. Dept. Agric. Tech. Bull. No. 1474: 1-98.
- Wirth, W.W., N.C. Ratanaworabhan, and D.H. Messersmith. 1977. Natural history of Plummers Island, Maryland. XXII. Biting midges (Diptera: Ceratopogonidae). 1. Introduction and key to genera. *Proc. Biol. Soc. Wash.* 90: 615-647.
- Wolff, W.J. 1969. Distribution of non-breeding waders in an estuarine area in relation to the distribution of their food organisms. *Ardea* 57: 1-28.
- ., A.M.M. van Haperen, A.J.J. Sandee, H.J.M. Baptist, and H.L.F. Saeys. 1976. The trophic role of birds in the Grevelingen estuary, the Netherlands, as compared to their role in the saline Lake Grevelingen. Pp. 673-689 in: G. Persoone and E. Jaspers (eds.). *Proc. 10th Europ. Biol. Symp., Vol 2.* Universa Press, Wetteren.
- Wunderle, J.M. Jr, R.B. Waide, and J. Fernandez. 1989. Seasonal abundance of shorebirds in the Jobos Bay Estuary in southern Puerto Rico. *J. Field Ornithol.* 60: 95-105.