TIDEPOOL VALUE AS FORAGING PATCHES FOR BREEDING AND MIGRATING BIRDS IN TIDAL SALT MARSHES IN THE LOWER CHESAPEAKE BAY

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirement for the Degree of

Master of Arts

by

Amanda Susan Allen

1995

October 30, 1995

Dear Dr. Byrd:

Greetings from Indiana. I have finally finished up a draft of my thesis and wanted to send the final product on to you. I hope there is room on your shelf for it (although with Dana always borrowing books I am sure there are a few holes that it might fill!). Things at Purdue are hectic with classes, teaching and trying to come up with a project. Needless to say, I don't have too many things to distract me here as I am not on any major flyways and miss the raptors coming through like on the coast. However, the greater sandhill cranes do come by in tremendous numbers and stopover at one of the USFW areas north of me.

I am sure that you are spending much of your time over on the shore trapping. Catch a peregrine for me please. I am planning to come to Virginia at Christmas time so hope to see you then. Perhaps I can time my trip to coincide with the Cape Charles Christmas Bird Count.

Thank you for everything and talk to you soon.

Amanda

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

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This work is dedicated to Dr. Mitchell A. Byrd,
for his unwavering mentorship and especially, for showing me falcons.

TABLE OF CONTENTS

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LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES continued

ABSTRACT

Tidepools serve as patches of avian foraging habitat within the tidal salt marsh landscape. Natural tidepools (N=303) in 4 tidal salt marshes along the lower Chesapeake Bay were characterized for a variety of physical and biological components including: area, water depth, profile type, vegetation, prey, and benthic macrofauna. Tidepools were surveyed for bird use to determine the abundance and diversity of avian species using tidepools and to investigate relationships between avian use and various intrinsic and landscape-level tidepool components.

Overall, 6,475 birds of 54 species were observed associated with tidepools over a 6 month period. Less than half of all tidepools (46.53%) had birds associated with them and distribution of birds was not normal with 4 pools having 48% of all bird observations. Birds utilized pools mainly as foraging patches although use of pools varied with a species' resource needs.

Tidepool area and water depth were highly significant in determining bird distribution and abundance. Tidepools >0.02 ha were much more attractive to all species of birds. Pools with both shallow (<2 cm) and deep (>10 cm) water were used more often than purely shallow or deep pools. Pools with water >20 cm deep and steep, vertical sides, similar to those pools often constructed by wetland managers, were used significantly less than expected.

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INTRODUCTION

Of all the salt marsh communities, avian systems remain one of the most apparent yet unstudied components of the marsh ecosystem. While coastal and estuarine wetlands comprise only a small percentage of total land mass in the eastern United States, they support disproportionately high densities of birds with considerable species richness (Bildstein et al. 1991) especially, herons, waterfowl, shorebirds, and a variety of passerines. A host of residents, including herons and passerines, breed and forage throughout the entire habitat spectrum from the intertidal to the marsh-upland transition zone. Nonetheless, few studies have documented bird abundance or investigated the patterns and relationships between bird communities and various marsh components.

In 1992, Watts studied avian community dynamics within tidal salt marshes along the lower Chesapeake Bay. Marshes were split into various landscape components (sloughs, tideguts, open water, etc.) and surveyed for bird use. While marsh physiognomy varied greatly due to tidal inundation and vegetational zonation (due in part to salt and hydric regimes), Watts' study showed that of all the different marsh components, tidepools appeared to be preferred habitat for many resident and transient species. Over one-third of all birds and nearly 40% of all species detected were associated with tidepools. Ninety-five percent of transient shorebirds were observed foraging in tidepools. Relative bird abundance in tidepools was considerably greater than in any other marsh component and many species, including Snowy Egrets and small shorebirds, were nearly exclusive tidepool users.

Like the marshes they are found in, tidepools are diverse and relatively unstudied systems. Origin of tidepools is circumspect and documentation often vague; although they appear to predominately be an Atlantic Coast phenomenon. It has been hypothesized that tidepools form from the damming of tidal creeks by vegetation or shifting sediments (Mitsch and Gosselink 1986) or due to the gradual erosion of shallow, vegetated depressions in the marsh. Tidepools are most abundant in the low marsh zone where they are inundated during high tides. Frequent inundation replenishes pools and enables them to support a variety of fauna, including juvenile fish (especially *Fundulus* spp.), blue crabs (*Callinectes sapidus*), fiddler crabs (*Uca* spp.) and a diversity of aquatic and benthic invertebrates. A smaller number of pools form in the high marsh but are often stagnant, full of algal mats and devoid of fish and other fauna as in healthier pools (pers. obs.); perhaps a consequence of decreased inundation rates.

Besides Watts (1992), mention of bird use of natural tidepools is sparse. Master (1989) extensively documented foraging patterns and prey resources of Snowy Egrets in tidepools in a New Jersey marsh. Along with Snowy Egrets, Master described large aggregations of Glossy Ibis, Great Egrets, Tricolored and Little Blue Herons, Laughing Gulls and Forster's Terns foraging in pools. In his investigation of community structure and production in a Virginia marsh, Robblee (1973) noted the use of tidepools by foraging Great Egrets and Great Blue Herons.

The lack of information about natural tidepools is countered with a wide exploration of avian use of manmade pools. In recent decades, wetland managers have recognized the value of constructing marsh pools in lieu of the historical practice of ditching to control for mosquitoes (Meridith et al. 1985). Pools constructed under this system of Open Marsh Water Management (OMWM) are typically pothole in nature and serve as refuges for fish (which feed on mosquito larvae) and subsequently, as attractive foraging sites for a wide spectrum of marsh birds especially herons, shorebirds, gulls and waterfowl (see Burger et al. 1982, Erwin 1986, Erwin et al. 1991, Erwin et al. 1994). Clarke et al. (1984) reported higher numbers of shorebirds, herons, terns and aerial insectivores in marshes with poorly maintained ditches and extensive pool systems than in marshes with well-maintained ditches and few pools. Species from all guilds foraged extensively in and around pools. In a follow up study, Brush et al. (1986) documented OMWM pool use by herons and ibis, shorebirds, terns and kingfishers and showed that relative use of study sites was dependent on pool abundance.

Tidepools serve as patches of key avian foraging habitat within the tidal salt marsh landscape; however, which tidepools and the way in which they are utilized depends upon the resource needs of individual bird species countered by resource availability and accessibility within the tidepool. An understanding of the ecology of bird use of tidepools is integral to the understanding of avian resource needs and the development of resource-conscious management decisions concerning coastal wetlands.

This research aims to investigate the relatively unknown field of bird - tidepool interactions. The primary objectives of this study were:

1) To determine the abundance and diversity of avian species using tidepools throughout migration and the breeding season.

2) To describe the physical and biological components of tidepools found within tidal salt marshes in the lower Chesapeake Bay.

3) To reveal patterns of avian use of tidepools and describe the relationships between avian use and various intrinsic and/or landscape level pool components.

4) To present management recommendations concerning tidepools in natural and managed wetlands.

MATERIALS AND METHODS

Study Area

This study was conducted in four tidal salt marshes on the western shore of the lower Chesapeake Bay (see Figure 1) from Robins Neck (Gloucester Co., VA) along Mobjack Bay, south to Messick (City of Poquoson, VA). Sites are coastal wetlands within the extensive wetland region along the lower Chesapeake Bay and support a large, but relatively undocumented avian community. Sites include Four Point (37° 20' N, 76° 25' W), Seafood (37° 17' N, 76° 24' W), Maryus (37° 17' N, 76° 23' W), and Messick (37° 8' N, 76° 20' W) marshes (see Figure 2). All marshes are tidally influenced on approximately 6 hour cycles with mean and spring tidal ranges at approximately 0.73 m and 0.88 m, respectively (Tide Graphs and Tidal Difference Table for Hampton Roads, Virginia). Salinities range from mesohaline to polyhaline, depending on temperature, rainfall, and location on the river system. Marshes range in size from 8.95 ha to 80.18 ha (see Table 1) and are surrounded by relatively rural upland areas.

Marshes were chosen based on vegetational composition, tidepool abundance and ease of access (either by canoe or on foot). Because vegetation type is a factor in determining bird use of a marsh, vegetational composition was controlled for during marsh selection. Dominant vegetation of each marsh consisted of smooth cordgrass

Figure 1: Map of lower Chesapeake Bay region. Darkened regions indicate location of study marshes

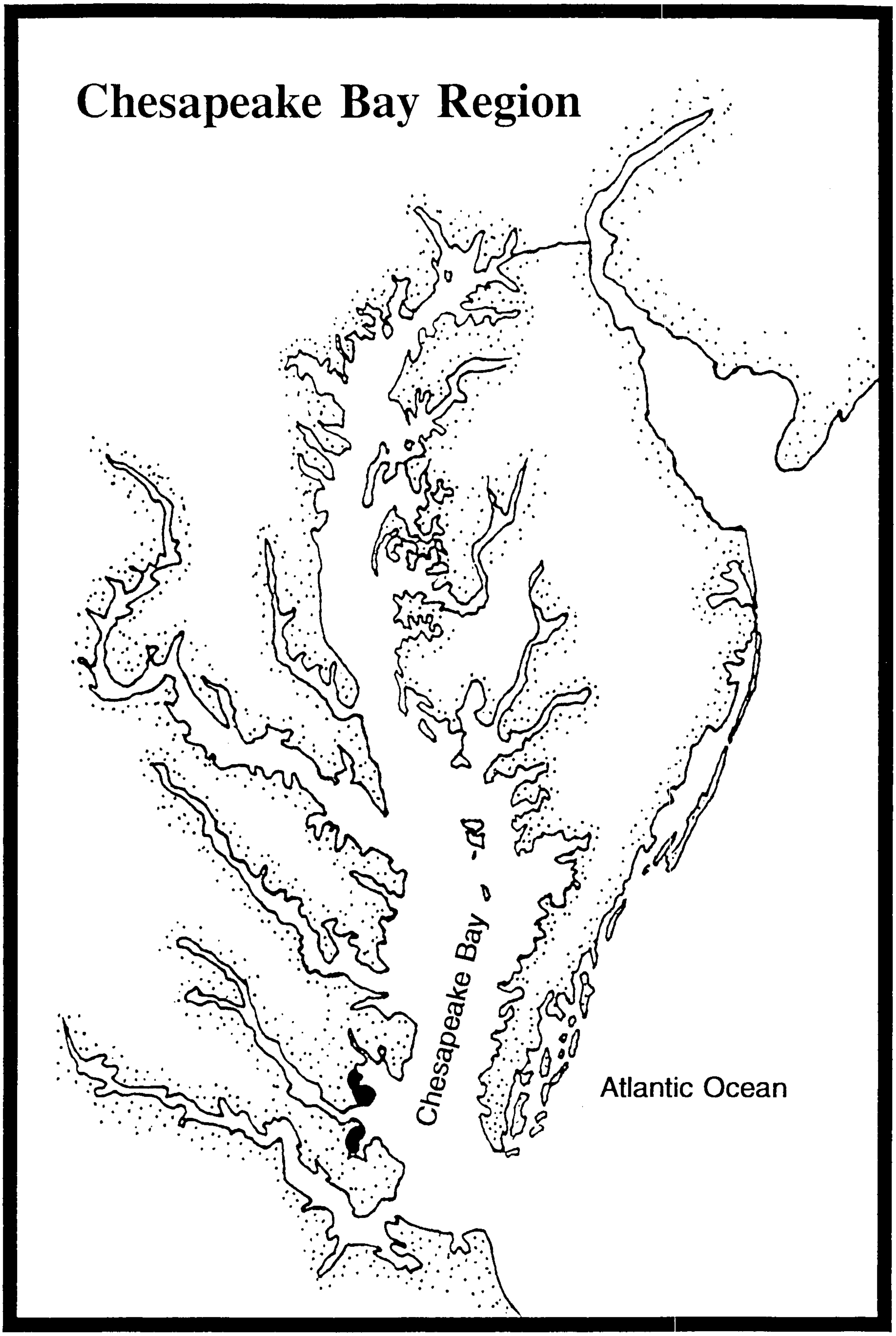
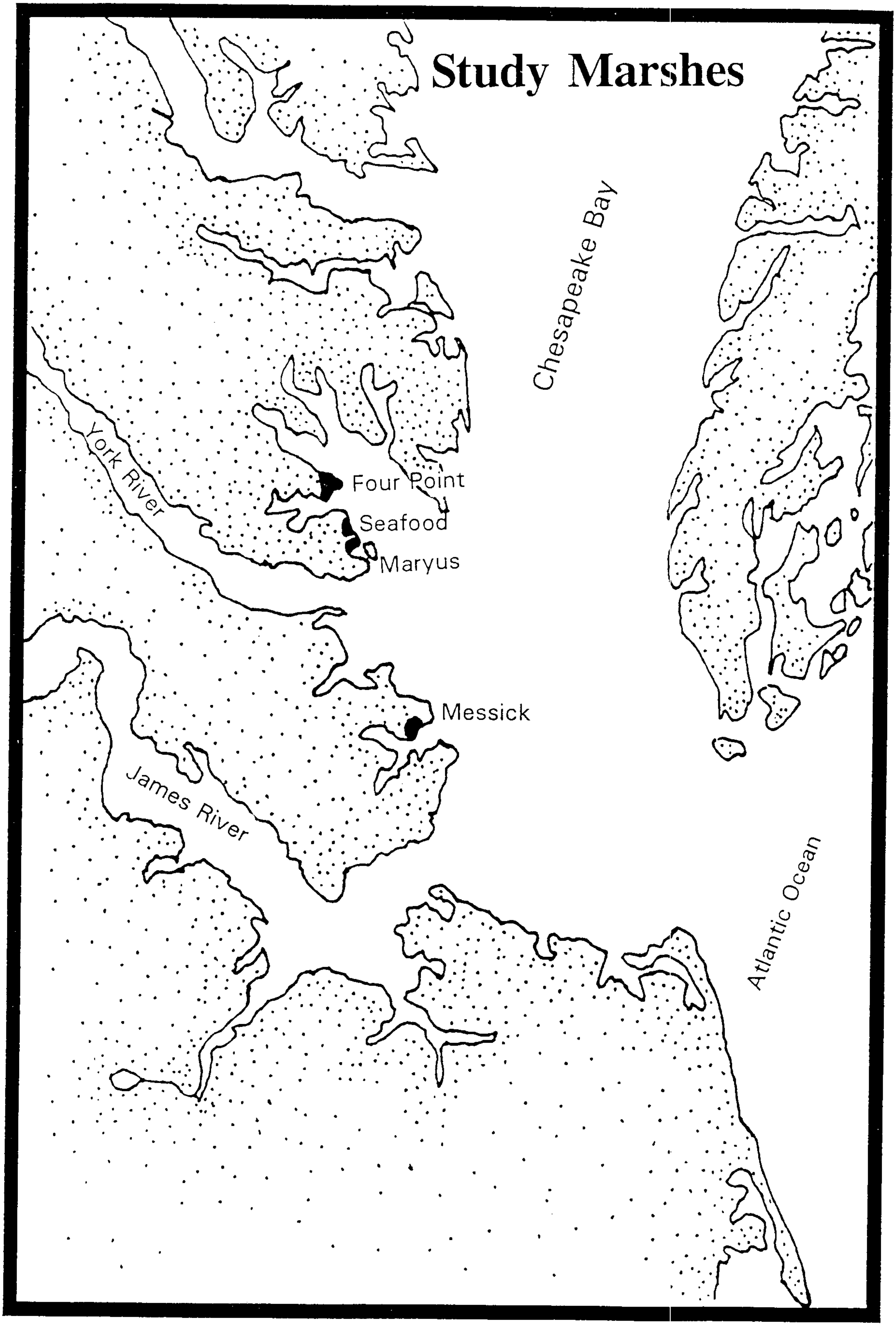


Figure 1

Figure 2: Map of study marshes within lower Chesapeake Bay region.



Study Marshes
Chesapeake Bay
York River
Four Point
Seafood
Maryus
Messick
James River
Atlantic Ocean

Figure 2

Table 1. Area (x 10^{-2} ha) and number (N) of pool types for study marshes.

Marsh	Marsh Area	Pool Types (x 10^{-2} ha)				Total Pool Area	Pool/Marsh Area Ratio
		Shallow	Graded	Pothole	Intermediate		
Four Point	8018	14.08(50)	7.66(30)	23.95(72)	23.19(13)	66.70(165)	0.008
Maryus	6756	2.81(39)	2.46(7)	2.17(42)	25.48(7)	32.90(95)	0.005
Seafood	895	7.46(9)	6.21(6)	2.11(11)	0.54(2)	16.30(28)	0.018
Messick	2035	13.98(7)	0.45(1)	22.63(7)	0(0)	37.00(15)	0.018
Totals	17704	38.33(105)	16.79(44)	50.87(132)	49.21(22)	152.90(303)	0.009

(*Spartina alterniflora*) $\geq$30%, black needlerush (*Juncus roemerianus*) $\geq$20%, saltgrass (*Distichlis spicata*), saltmeadow hay (*Spartina patens*) $\geq$15% and salt bush (*Iva frutescens* or *Baccharis halimifolia*) $\geq$10%. Wetland inventory maps and summaries were used to determine physical characters of possible study sites (Moore 1976, Silberhorn 1981). Vegetational zonation of all sites is characteristic of tidal salt marshes found on the southern Atlantic Coast (Mitsch and Gosselink 1986).

A subset of marshes that met vegetational criteria were visited to determine accessibility and tidepool density. In general, tidepool abundance appears to vary with marsh area (the larger the marsh the more tidepools it supported) with small isolated marshes usually devoid of pools (Watts 1993). Tidepool abundance for chosen sites ranged from 15 to 166 pools and the ratio of pool/marsh surface area from 0.5 x 10^{-2} to 1.80 x 10^{-2} (see Table 1).

Tidepools

Tidepools are natural, permanent depressions in the marsh that are intertidal and isolated from other bodies of water during low tides when they retain water (Mitsch and Gosselink 1986, Watts 1993). They are devoid of emergent vegetation due to their continued standing water although edge vegetation is characteristic of the surrounding low marsh. Pool shape varies, although most are somewhat circular. Larger pools tend to be irregular and may have small meandering fingers. Likewise, larger pools have small, often vegetated, islands or hummocks scattered throughout them. Pool bottoms vary in consistency from extremely soft and muddy to hard bottomed.

Pool physiognomy varies both within and between marshes although they are characteristically flat bottomed and range in depth from <1 cm to >30 cm and in area from $<1 \times 10^{-4}$ ha (1 m^2) to >5.5 ha (55,000 m^2) (Master 1989, pers. obs.). I defined three pool types according to profile type and relative depths. Types include: 1) shallow, 2) graded, and 3) pothole. Shallow pools are flat bottomed with shallow water (<10 cm) throughout. Graded pools are shallow edged and slope gradually towards deeper water (>10 cm) in the center. Pothole pools have steep, vertical sides and deep water (>10 cm) often greater than that of the graded pools. Pothole pools may have an overhanging edge (see Figure 3) which serves as a refuge area for fish and crabs (Master 1989, pers. obs.). Variations on these three main profiles do exist and it is common to find intermediate pools which are a combination of two or all three pool types; especially with expansive pools.

It has been suggested that edge profiles may be a limiting factor to bird use of pools (eg. pools with steep, vertical sides do not permit easy access to prey by predators) (Brush et al. 1986, Erwin et al. 1994). In order to examine the importance of profile type, I placed pools into 4 categories based on dominant ($\geq$75%) edge type. Pools which had no dominant edge profile (<75% edge of one of the three main profiles types) were placed into an intermediate category. The most common intermediate type consisted of graded and pothole edges. Figure 3 illustrates the pool categories used. Overall, breakdown of the 303 pools was: 105 shallow, 44 graded, 132 pothole and 22 intermediate pools. Of the intermediate pools, 19 of these were Graded-Pothole pools and 3 were a combination of all three. The distribution and total

Figure 3: Illustration of the three main and one intermediate pool profile types.

Tidepool Profiles

A. Shallow:

B. Graded:

C. Intermediate:

D. Pothole:

Non-overhang

Overhang

Figure 3

area of pool types among study marshes is given in Table 1.

Pools are often located in complexes of many small pools or a large pool surrounded by many smaller pools. Each pool was considered unique if it had no common water connection with any other pool at low tide.

Site Establishment

Study sites were visited 2 - 5 times at low tide for set up. Since pools are not easily seen from the ground, the entire marsh area was walked and every tidepool located, marked with a survey flag and numbered for individual identification. Only pools which were inaccessible due to tideguts or mud were not used. Tidepools were mapped on enlarged 7.5 minute U.S.G.S. topographic maps to ensure relocation of pools in case flags were lost during high tides. After all the tidepools were located, census routes were devised to ensure complete detection of birds in association with each tidepool. Final routes were often dictated by hydrology and physical characteristics of the marsh itself. Four Point and Maryus marshes were set up in February and March of 1993 while Messick and Seafood marshes were set up in the first week of May, after these 2 marshes were added to increase pool replicates.

Bird Surveys

Ninety surveys were completed from 25 April through 23 October 1993. Four Point and Maryus were surveyed a total of 24 times while Messick and Seafood were surveyed 19 times. All marshes were censused weekly. The order of surveys within weeks was determined randomly with the exception of Four Point which, due to waterfowl hunting on the property, was surveyed on Sundays during the Fall hunting season.

Because I wanted to cover the entire spectrum of migrants and residents using the marshes, surveys were begun during the beginning of Spring migration in April and continued through the peak of Fall migration in October. In order to investigate seasonal abundance patterns for the various species and guilds, I grouped surveys into three time blocks: Spring (25 April - 7 June), Summer (16 June - 15 August), and Fall (20 August - 23 October). Time blocks were set to approximate general breakpoints in local migration and breeding patterns. Six sets of surveys were made during the Spring, 8 during the Summer and 9 during the Fall.

A variety of abiotic factors are known to affect bird activity patterns including time of day and tidal cycles. Bird activity cycles are highest in the period right after dawn, with diminished activity in the afternoon when temperature normally reaches its peak. Likewise, tidal cycles may drive species abundance and diversity patterns for birds using intertidal habitats (eg. Recher 1966, Burger et. al. 1977, Burger 1984, Colwell 1993). In order to increase the samples of birds, I chose to survey marshes in the morning despite tide cycles. The effects of tide on bird abundance and diversity were later examined to determine the magnitude of any bias.

To assess the effect of tide on bird groups, tidal charts were used to determine the tide cycle for each survey day. Cycles were split into 6 hour blocks of high and low tide and then each of these was subsequently subdivided for a total of four 3-hour tide ranges. Tidal ranges used included: Incoming High, Outgoing High, Outgoing Low or Incoming Low. Field observations of tide range were taken at the start of each survey and this, along with the starting time of the surveys, was later used to place each survey into 1 of the 4 categories. Approximately even numbers of surveys occurred during each of the 4 cycles (see Table 2).

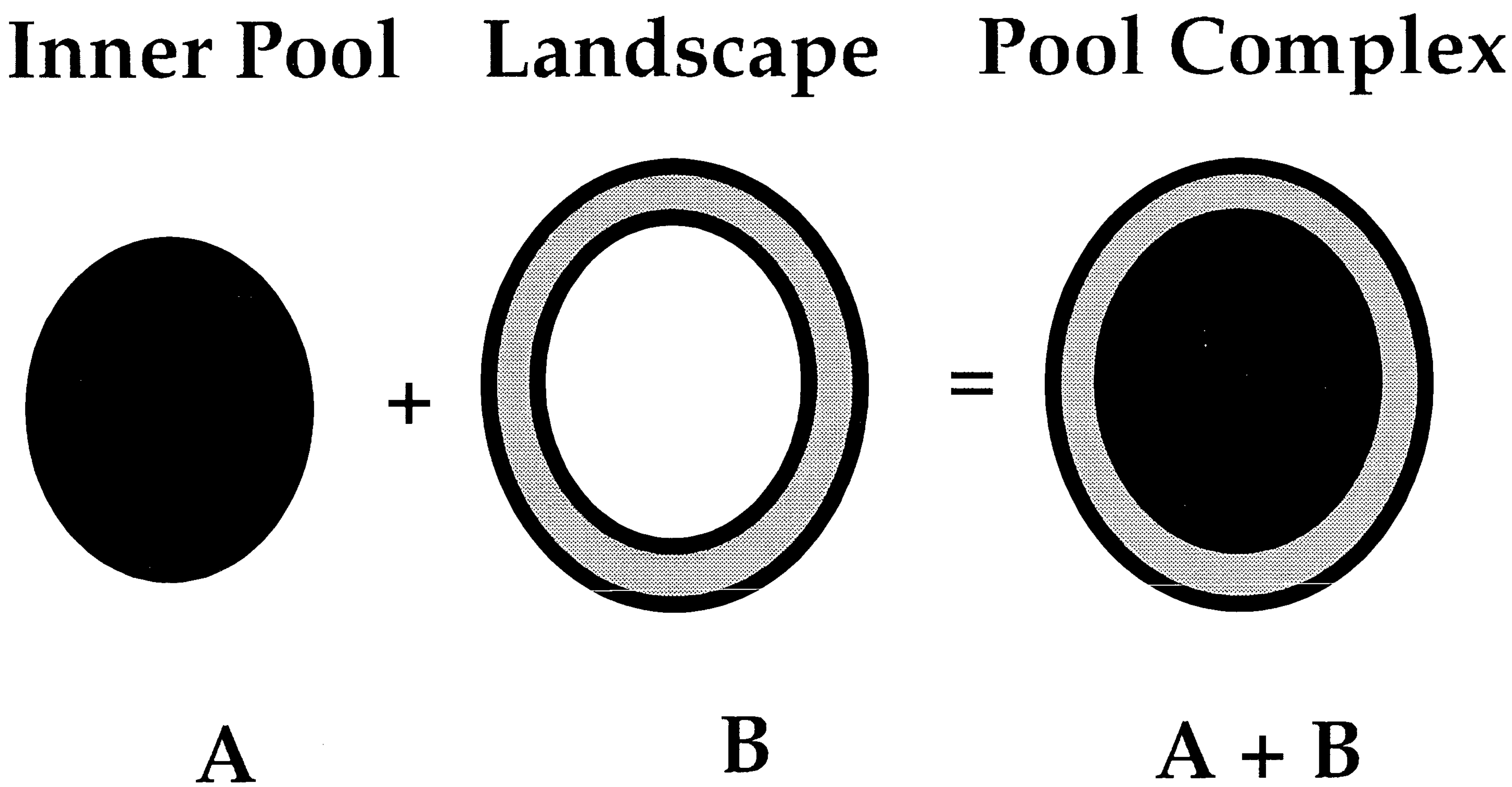
Surveys were begun at or as close to sunrise as possible and never begun after 10:00 hrs. Length of surveys varied with number of birds present, number of pools and marsh size and ranged from 25 to 305 min. ($X \pm SD = 109.5 \pm 67.08$). Routes were walked slowly while scanning each pool from a distance to prevent early disturbance and flushing of individuals. I would then approach the pool and walk the perimeter, locating birds visually and \ or aurally. No standard time was spent at each pool and I moved on to the next pool only when certain that I had located all birds. Despite precautions to reduce disturbance, 23% of birds detected were flushed from pools. Birds flushed from pools typically moved to an area of the same tidepool away from me. Birds which moved to another tidepool were noted and not recounted in that new tidepool.

Information was recorded only for individuals in association with the tidepools which I defined as those birds actively using or located within 1 m of the pool edge. Birds flying over the pool were counted only if they were actively working the pool. For example, a tern hovering over a pool looking for fish or a sparrow perched 0.5 m from the edge would both be recorded while a Barn Swallow flying 3 m above the pool would not be.

Table 2. Breakdown of tide stages for bird surveys (N).

Marsh	Incoming high (N)	Outgoing high (N)	Incoming low (N)	Outgoing low (N)
Four Point	7	9	5	5
Maryus	7	6	7	6
Seafood	6	3	6	4
Messick	4	7	3	5
Totals	24	25	21	20

Figure 4: Representation of tidepool complex with inner pool and surrounding landscape.


Inner Pool
Landscape
Pool Complex
+
=
A
B
A + B

The area of study is actually a pool complex encompassing the intrinsic body of water of the tidepool along with the surrounding landscape in which the pool is located (see Figure 4). Birds were recorded as associated with the pool itself (A), with the pools' landscape (B), or both (A + B) since birds may be utilizing resources from either one or both features of the tidepool complex. Based on location and substrate association information, species were then categorized into 2 distinct user groups: Pool Users and Pool Associates. Pool Users include species actively using the pool as a resource patch. Pool Associates include species passively associated with the pool, rarely using pool resources more than other habitats within the marsh. Within the pool complex, Pool Associates are normally found within the surrounding edge landscape while Pool Users are associated with the intrinsic characters of the pool or a combination of the intrinsic pool and landscape features (see Figure 5).

Since birds are rarely stationary, I recorded information on the first detected location and behavior of birds. Any bird which flew into the pool area while I was surveying that site was included unless they had previously been counted elsewhere. Bias due to recounting of birds was thought to be low due to easy tracking of the movements of flushed individuals across the marsh.

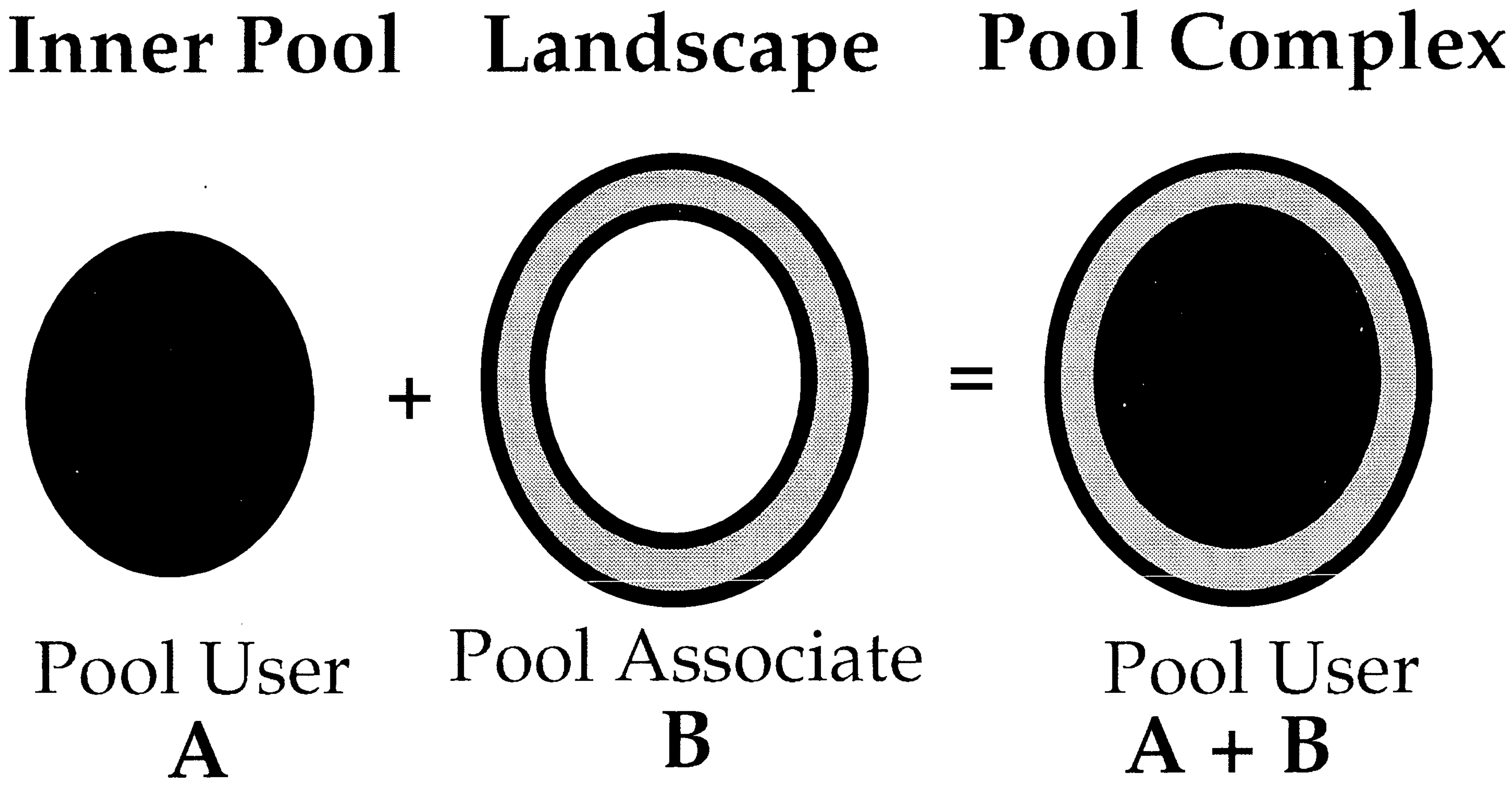
Data Collected

The following information was recorded for each individual bird:

Pool: Pool identification number

Species: The majority (99.71%) of birds were identified to species either visually or aurally. Individuals that could not be positively identified to species were placed in groups as possible.

Figure 5: Relationship of bird user groups (Pool User and Pool Associate) to the tidepool complex.



Inner Pool
Landscape
Pool Complex
+
=
Pool User
A
Pool Associate
B
Pool User
A + B

<u>Location</u>: Birds were classified as being in or out of the pool

a. In: Standing in direct contact with the water

b. Out: On the pool edge, standing on a hummock, or flying over the pool

<u>Substrate</u>: Substrate associated with each bird was categorized as follows:

a. Unvegetated: Mud, water, or manmade object (eg. duck blinds)

b. Vegetated: Vegetation in which birds were found were categorized as follows:

1. Marsh Cordgrass: all forms of *Spartina alterniflora*
    a. Short Cordgrass: *Spartina alterniflora* short form found in less hydric conditions
    b. Tall Cordgrass: *Spartina alterniflora* tall form found in hydric conditions
    c. Cordgrass shoots: *Spartina* shoots in mud and shallows of tidepool edges
2. Saltmeadow Hay: *Spartina patens*
3. Black Needlerush: *Juncus roemerianus*
4. Saltbush: *Iva frutescens* or *Baccharis halimifolia*

<u>Behavior</u>:

a. Foraging: Actively searching for, catching or eating prey item

b. Not foraging:

1. Flushed
2. Vocalizing, not seen
3. Perched
4. Standing, Resting, Preening

In addition to bird data and tide range (Incoming High, Outgoing High, Outgoing Low, Incoming Low), a number of environmental parameters which are not included in the analysis were also recorded at the beginning of each survey.

Pool Components

In order to describe the general characteristics of salt marsh tidepools and to investigate how they might influence bird abundance and distribution within them a set of physical and biological pool components was measured. Collection of pool component information was begun after the completion of bird surveys in the Fall and, due to the onset of cold weather and the large sample size, completed in the Spring of 1994. Seasonal differences in collection date should not affect vegetation information due to the stability and low decomposition rate of salt marsh vegetation across seasons. A complete listing and description of pool components is found in Table 3.

Pool Component Data Collection

Physical Components

Profile (PR) was based on the 4 main pool types described above. Percentage of each edge type was visually estimated to the nearest 5% for each pool and then each pool was categorized into a main profile type based on dominant ($\geq$75%) edge. Pools with no dominant edge type were placed into the intermediate type. Pool shape was examined using aerial photography (year: 1988; scale: 1 cm = 120.03 m). Typically this could be done only with expansive pools due to poor resolution of the photographs and therefore, when possible, pools were mapped in the field. In the field, pools were mapped by measuring the distances (using either a meter tape or by pacing) from the approximate center of the pool out to the edges in the 4 cardinal directions (N,S,E,W). The remaining outline of the pool was then approximated by walking the perimeter of the pool and sketching it in on graph paper at a known scale (eg. scale used for small pools (Area <150 m^2): 16 mm^2 = 1 m^2; large pools (Area >150 m^2): 1 mm^2 = 1 m^2). Area (AR) was then determined in the lab using an electromagnetic digitizer and SigmaScan software. Since pools are often convoluted, I measured length of pool edge (PE) from the field sketches using the digitizer.

Table 3. Descriptions of pool components.

Type	Name/Code	Component Description

Physical Components

Area (AR): Total pool area (m^2)
Perimeter (PE): Total length of pool edge (m)
Depth: Percent cover and area (m^2) of each of the following four depth ranges:
- 0-2 cm. (DA)
- 2-10 cm. (DB)
- 10-20 cm. (DC)
- $>$20 cm. (DD)

Profile: Dominant ($\geq$75%) edge type
- Shallow (PS)
- Graded (PG)
- Intermediate (PI)
- Pothole (PP)

Biological Components

Vegetation: Percent cover and area within 1 m band surrounding the pool
- Tall Cordgrass (TC): Tall form of *Spartina alterniflora* found around high inundation zones; especially around tideguts and channels
- Short Cordgrass (SC): Short form of *Spartina alterniflora* found in less hydric and higher elevated areas
- Cordgrass Shoots (CS): Small *Spartina* shoots in shallow and muddy areas
- Saltmeadow Hay (SH): *Spartina patens*
- Black Needlerush (BN): *Juncus roemerianus*
- Saltbush (SB): *Iva frutescens* or *Baccharis halimifolia*

Prey: Presence/absence information
- Fish (FI): Primarily *Fundulus* spp.
- Blue Crab (BC): *Callinectes sapidus*
- Fiddler Crab (FC): *Uca* spp.
- Benthic invertebrates (BI): Variety of benthic macrofauna in pool sediments

Visual approximations of the percent coverage of each of the four depth categories were made during low tide and then converted into area (Pool area x percent cover of depth category). Depth (DE) categories were based on approximate morphological breakpoints for core species groups (peeps, large shorebirds, waders). While birds often walk through deep water many do not forage in water greater than 'knee'-depth, perhaps due to difficulty in locating and catching prey. Thus, breakpoints are based on average tarsus lengths of the three core groups according to measurements taken from study skins in the bird collection at the College of William and Mary and from the literature (Hayman et. al. 1986). A meter stick marked with the four depth categories was used to ensure accuracy in depth measurements.

Biological Components

Percent cover of the vegetation along the 1 m boundary of the pool edge were visually approximated to the nearest 5%. The presence of submerged aquatic vegetation (SAV's) and Cordgrass shoots within pools was noted.

Beginning the first week of July, I began surveying pools for a variety of prey species. Surveys were conducted in conjunction with weekly bird surveys and covered the wide spectrum of prey taken by bird groups including fish, crabs, and benthic macrofauna. Due to the logistical difficulty in quantifying exact numbers of fish and crabs within all pools, I instead recorded information as presence / absence only.

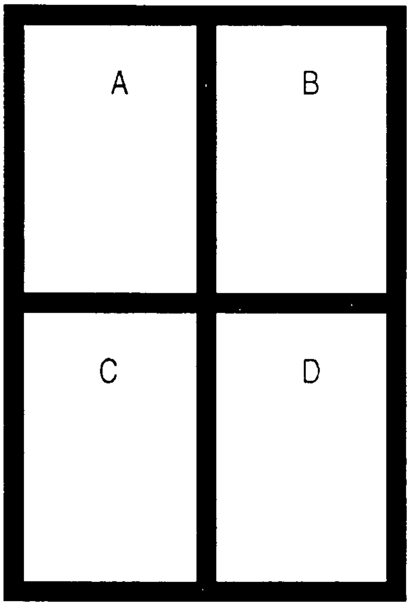
Benthic sampling

In an attempt to describe distribution patterns of invertebrate species within and between pool types, benthic macrofauna (organisms retained on a 500 um mesh sieve) were sampled monthly from May through October 1993 in a subsample of tidepools at Four Point and Maryus marshes. While 6 months of data were collected, only May samples were analyzed for this study due to the time intensity of picking and sorting invertebrates from the cores (extraction of invertebrates from vegetated cores often took from 4 to 6 h/sample). A subset of 12 tidepools (four replicates of each pool type: shallow, graded, and pothole) were sampled. Five 10.5 cm x 4 cm sediment cores were extracted per pool with the exception of the graded pools where 10 samples were taken. See Figure 6 for sampling design. Samples in graded pools were split evenly between shallow (depth <2 cm) and deep (depth >10 cm) areas. Since the presence of *Spartina* culms has been shown to have a substantial impact on distribution and abundance patterns of macrofauna (Rader 1984), cores were also taken in the short cordgrass along the edges of shallow and graded pools.

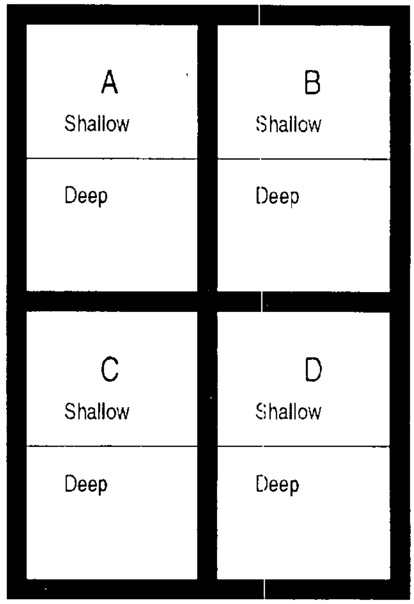
Because benthic sampling is labor intensive, marshes were sampled over a 3 day period between 12 May and 17 May, 1993. Forty man-hours were required to collect samples over this period. All samples were collected in the morning during low tide to reduce potential biases related to temperature and tide. Pool water temperature and salinity, measured with a refractometer, were recorded for each pool and are summarized in Table 4. Sediment cores for analysis of grain size were taken in each pool and frozen for future analysis.

Figure 6: Illustration of the sampling design for benthic macrofauna.

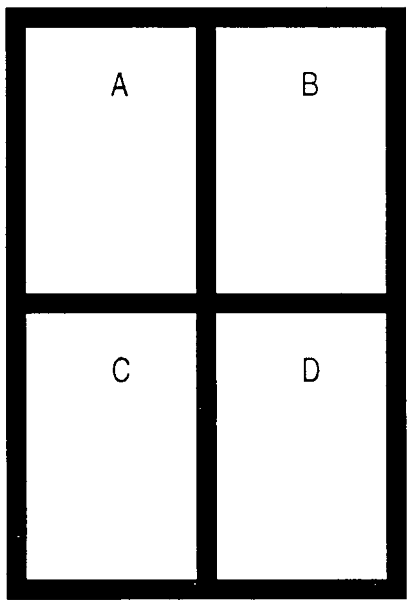
Benthic Sampling Design



Shallow



Graded



Deep

Table 4. Temperature, salinity and sampling date of pools used for benthic sampling.

Marsh	Pool	Profile/ Replicate	Date Sampled	Temperature(C)	Salinity (ppt)
Maryus					
	28	Shallow A	12 May 1993	22	17
	25	Shallow B	12 May 1993	23	16
	21	Graded A	12 May 1993	28	17
	57	Graded B	12 May 1993	19	19
Four Point					
	105	Shallow C	14 May 1993	18	10 *
	96	Shallow D	17 May 1993	24	17
	23	Graded C	14 May 1993	16	10
	92	Graded D	17 May 1993	24	14
	2	Pothole A	14 May 1993	17	12
	30	Pothole B	14 May 1993	20	15
	80	Pothole C	17 May 1993	20	14
	107	Pothole D	17 May 1993	17	10

*Heavy rains before sampling on 14 May 1993 may have lowered salinity.

A total of 96 cores (for May sampling) were extracted using 10.5 cm x 4 cm PVC corers with a sharpened lower edge. Cores in shallow pools and the shallow sections of graded pools were always taken in < 10 cm of water while pothole cores and the deep sections of graded pools were always taken in > 10 cm of water. Control for water depth allowed for the assessment of potential relationships between invertebrate populations and depth. Pools were visually split into 5 approximately equal areas and one PVC corer was pushed into the sediment in one of each of the 5 areas to ensure sampling of the entire pool area. When possible, the sampler took the core while leaning over the pool edge in order to reduce sediment disturbance. Cores were sunk into the bottom such that the top layer of sediment was even with the top of the core and then the PVC corer with the sediment was carefully removed. Care was taken not to lose the top portion of sediment which often consisted of a watery flocculent. Sediment cores were extracted from the PVC corer using an extractor and fractioned at 2 cm from the top into a top and bottom section. A hacksaw was used to split sections which were matted with *Spartina* roots.

Since the majority of infaunal marsh invertebrates are known to live in the top 1 - 4 cm of sediment associated with higher redox potentials (Wieser and Kanwisher 1961, Bell et al. 1978, Coull and Bell 1979), fractioning permitted the analysis of macrofaunal vertical distribution. Fractioning also allowed for the assessibility of invertebrates by different bird groups (based on bill length). Upon extraction, samples were immediately placed into plastic collection bags labeled by pool, replicate, and core section (top or bottom) and stored in a cooler of ice to reduce mortality and decomposition until they could be sieved and preserved. Samples were then taken back to the Virginia Institute of Marine Science and immediately hand sieved with salt water on 500 um sieves to remove most of the mud from the sections. Microfauna (organisms not retained on a 500 um sieve) were not sampled. Sieving took 5 - 15 min/sample. Sieved samples were then preserved in a mixture of 10% formalin and Rose Bengal vital stain and stored until they could be sorted.

Before being picked, samples were washed and refixed into a solution of ethanol. Samples were hand picked during the Summer of 1993. However, due to the labor involved only 116 of the 192 fractioned samples were completed. From August 1993 - March 1994, samples were sorted, identified and all the invertebrates recovered were counted. Species were identified to the lowest possible taxonomic level and stored in vials filled with 2% formalin.

Data Analysis

To assess relationships between pool components and various bird user groups, only the most abundant individual species detected were chosen for analysis. Species were also categorized into guilds based on phylogeny, morphology and diet. A listing of the species within each guild can be found in Appendix I. A list of all dependent variables is found in Table 5.

Table 5. Dependent variables used for analysis of bird data.

Bird abundance	
Species richness	
Species	
	Great Egret
	Snowy Egret
	Green-backed Heron
	Clapper Rail
	Greater Yellowlegs
	Willet
	Semipalmated Sandpiper
	Laughing Gull
	Marsh Wren
	Seaside Sparrow
	Boat-tailed Grackle
Guilds	
	Waders
	Gulls, Terns, and Skimmers
	Shorebirds - large
	Peeps
	Waterfowl
	Sparrows

RESULTS

Over a six month period, 303 tidepools were surveyed. A total of 6,475 birds representing 54 different species were detected in association with tidepools. A full species list of the birds detected is given with associated scientific names in Appendix II. The total number of birds detected per survey ranged from 3 to 601 ($X \pm SD = 71.9 \pm 47.27$). Species richness varied from 10 to 28 species per weekly round (see Appendix III). Laughing Gulls, Boat-tailed Grackles and Seaside Sparrows were the most prevalent species recorded representing 14.4%, 13.0% and 11.2% of all observations, respectivel. Of the guilds, waders were the most predominant (>20% of all birds), with Great and Snowy Egrets, each comprising 7% of total observations. See Appendix IV for weekly guild abundances.

Seasonal Patterns

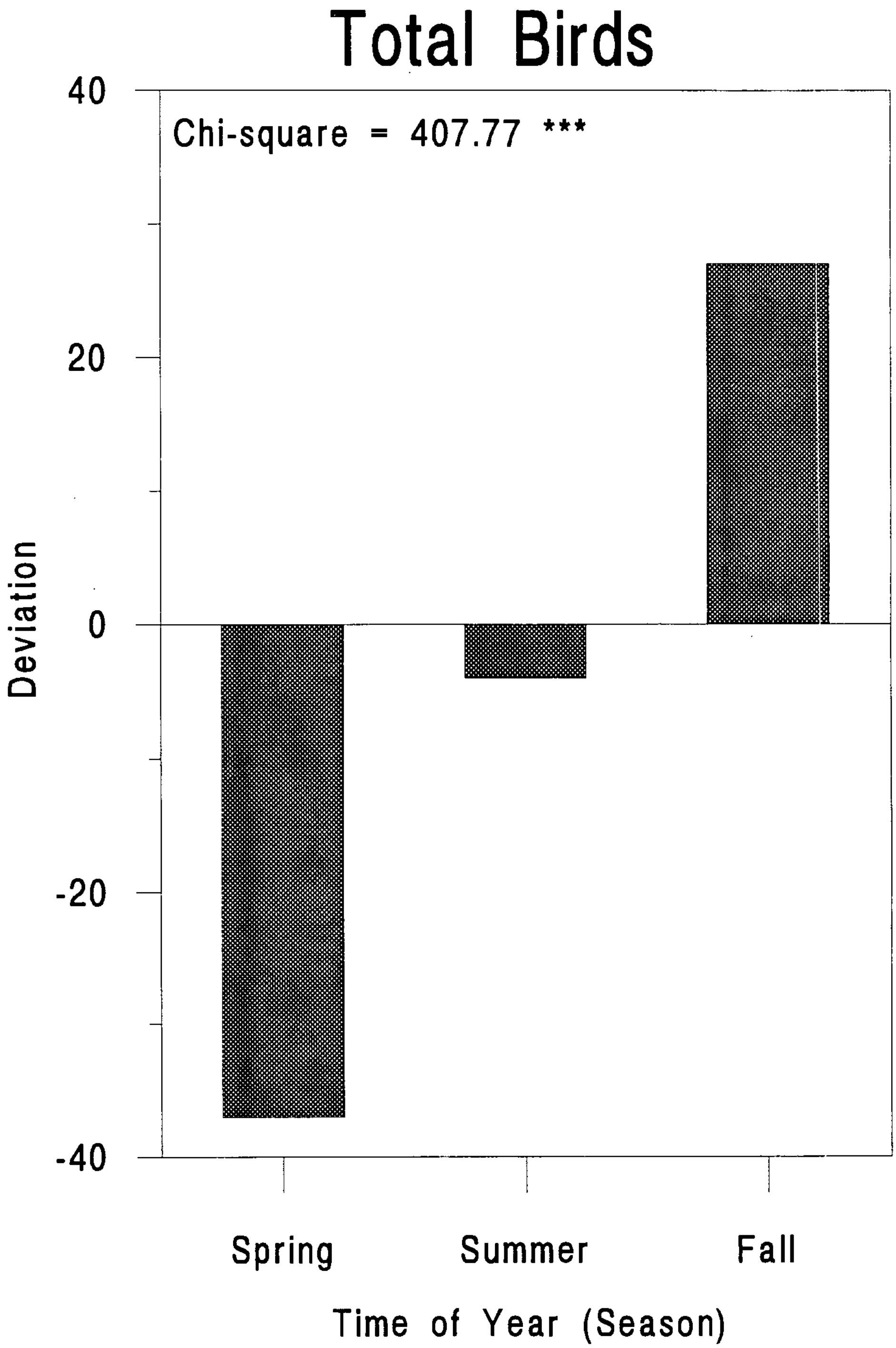
Totals (standardized for survey effort) (see Appendix II) revealed an increase in bird abundance throughout the three seasonal periods, doubling from Spring (451.2) to Fall (911.4). Species richness remained relatively stable (Spring: 37 species; Summer: 42 Fall: 38 species); however, the abundance of individual species varied between seasons with many using the marsh only during particular windows of time. The most prevalent species per season were: Spring - Semipalmated Sandpiper (29.68% of total observations), Summer - Seaside Sparrow (22.50%) and Laughing Gull (15.27%) and

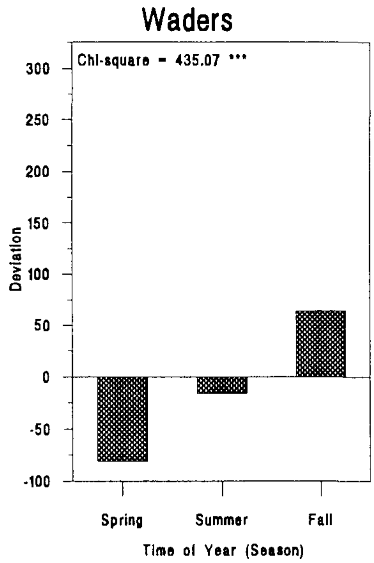
Fall - Boat-tailed Grackle (18.26%) and Laughing Gull (17.37%). Individual species often drove abundance patterns for specific guilds as reflected in the most prevalent guilds per season: Spring - peeps (33.60% of total observations), Summer - large shorebirds (19.41%) and sparrows (19.14%) and Fall - waders (26.12%). See Figure 7 for relative abundance patterns.

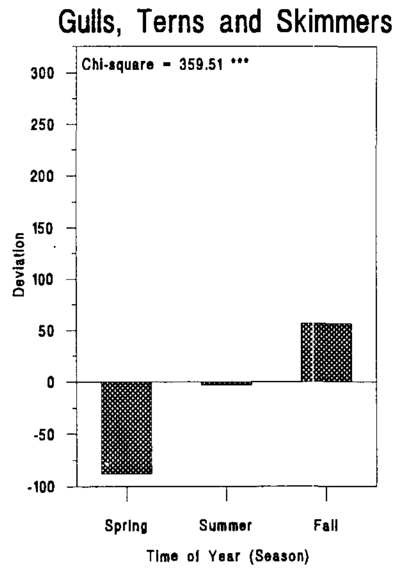
Frequency analysis (Chi-square) was run on abundance values and indicated significant seasonal effects ($\chi^2 > 18.21$, $p < 0.001$) for all guilds and species with the exception of Marsh Wrens ($\chi^2 = 2.92$, $p > 0.05$). Chi-square statistics and significance values are presented in Figure 7.

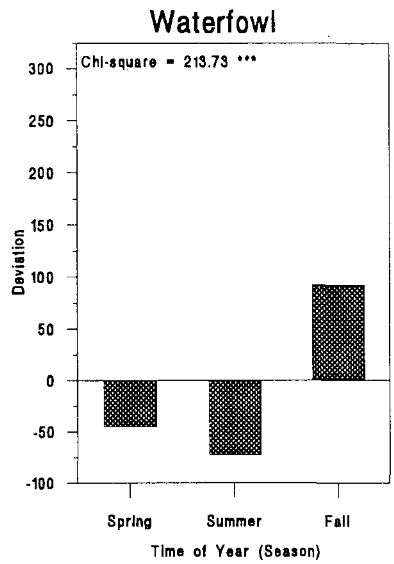
Species were also placed into 1 of 3 user groups based on their residency patterns within the Coastal Plain of Virginia (see Appendix I for a list of species placements). User groups include: 1) Transients - species which do not breed in Virginia but use the marsh during migration 2) Residents - species that breed locally outside the marsh but use the marsh as a foraging area and 3) Resident breeders - species which breed and forage within the marsh. Transients, migrating through in the Spring and early Summer, dropped out completely by the third week of June increasing again as they passed on their southward migration in late Summer and early Fall. Resident breeders, such as the Seaside Sparrow and Willet, peaked in early Summer gradually dropping off in relative occurrence with increasing numbers of residents using the marsh. Chi-square analysis revealed significant seasonal effects on the presence of all three resident groups within tidepools (Transients: $\chi^2 = 302.69$, $p < 0.001$; Residents: $\chi^2 = 343.90$, $p < 0.001$; Resident Breeders: $\chi^2 = 742.30$,

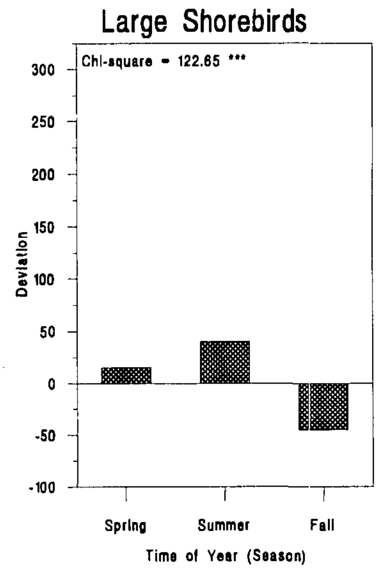
Figure 7. Relative abundance patterns across seasons of total observed birds, guilds and target species. Values indicate % deviation from an expected even distribution. Negative distribution implies less than average occurrence for specific season. Positive deviation implies overrepresentation for specific season. (*** = $p < 0.001$).

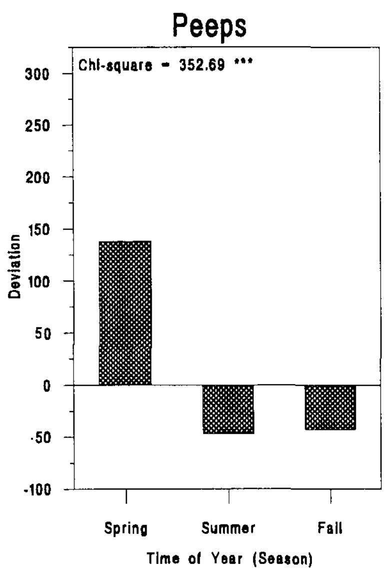

Total Birds
Chi-square = 407.77 ***
40
20
0
-20
-40
Deviation
Spring
Summer
Fall
Time of Year (Season)

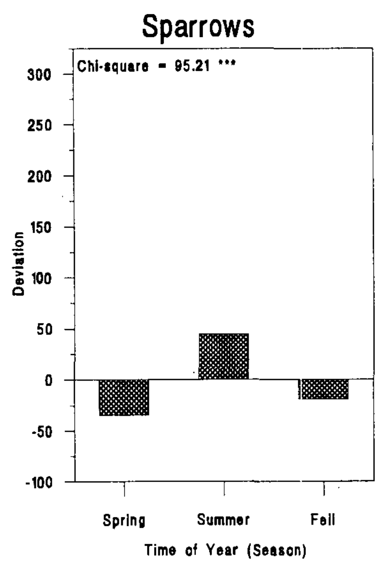

Waders
Chi-square = 435.07 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

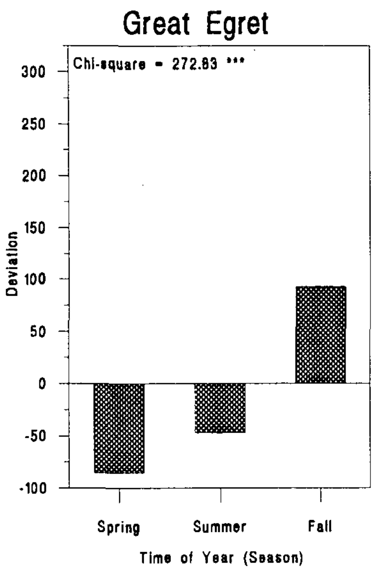

Gulls, Terns and Skimmers
Chi-square = 359.51 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

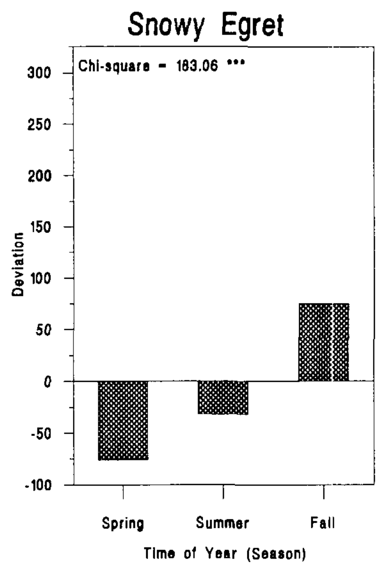

Waterfowl
Chi-square = 213.73 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

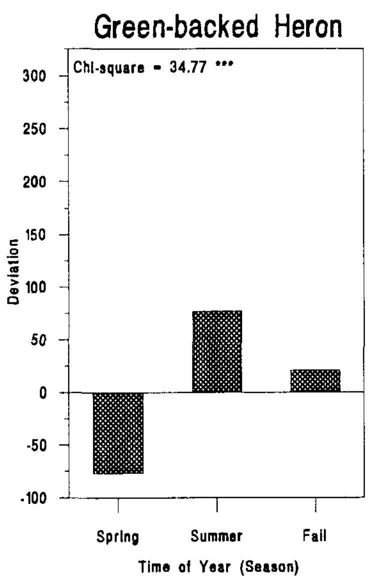

Large Shorebirds
Chi-square = 122.65 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

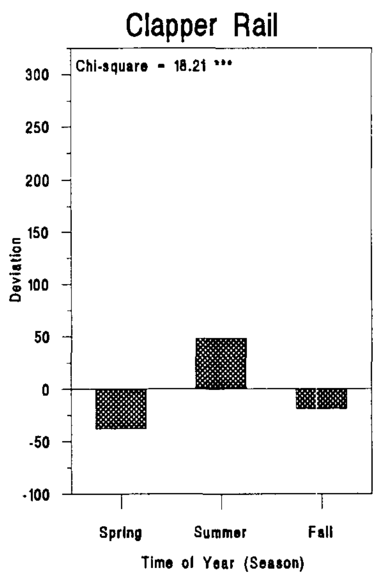

Peeps
Chi-square = 352.69 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

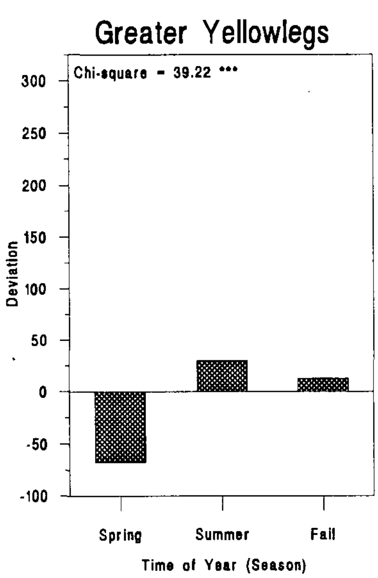

Sparrows
Chi-square = 95.21 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

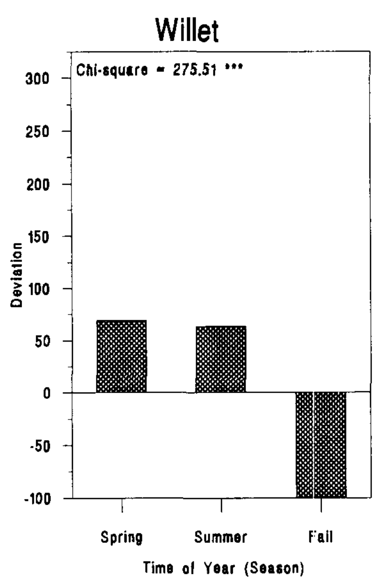

Great Egret
Chi-square = 272.83 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)

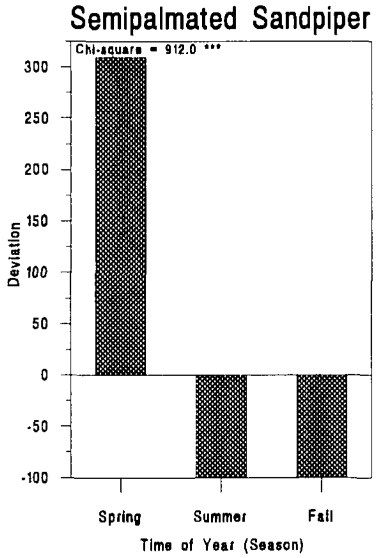

Snowy Egret
Chi-square = 183.06 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)

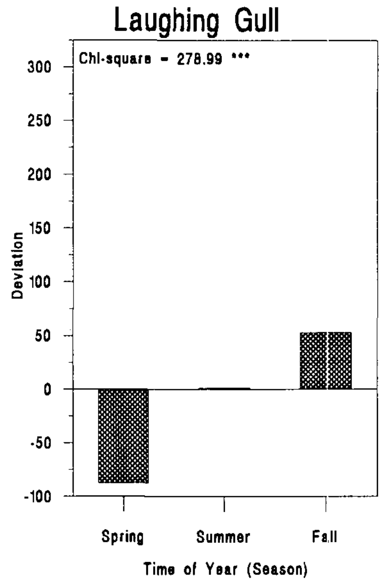

Green-backed Heron
Chi-square = 34.77 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)

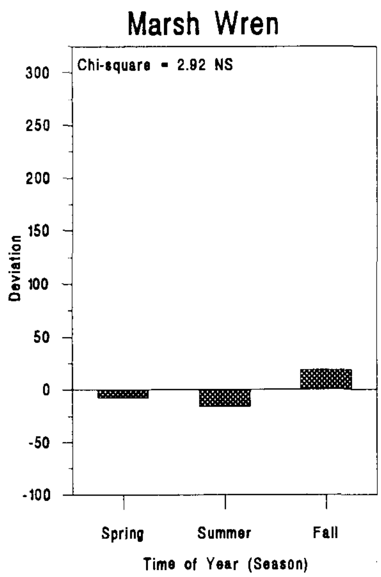

Clapper Rail
Chi-square = 18.21 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)

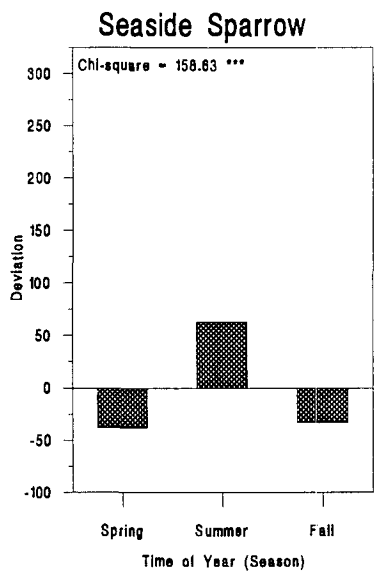

Greater Yellowlegs
Chi-square = 39.22 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)

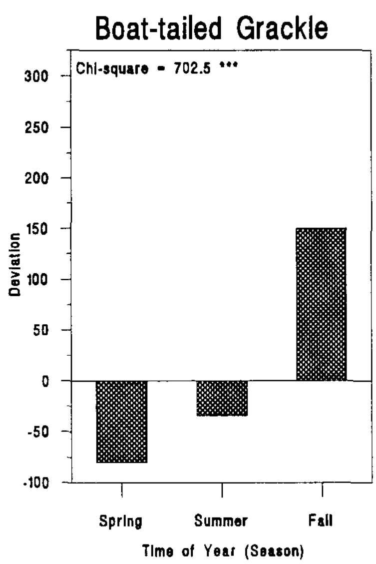

Willet
Chi-square = 275.51 ***
300
250
200
150
100
50
0
-50
-100
Deviation
Spring
Summer
Fall
Time of Year (Season)


Semipalmated Sandpiper
Chi-square = 912.0 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)


Laughing Gull
Chi-square = 278.99 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)


Marsh Wren
Chi-square = 2.92 NS
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)


Seaside Sparrow
Chi-square = 158.63 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)


Boat-tailed Grackle
Chi-square = 702.5 ***
Deviation
300
250
200
150
100
50
0
-50
-100
Spring
Summer
Fall
Time of Year (Season)

$p < 0.001$). See Figure 8 for seasonal abundance for all three groups. All three groups had considerably more individuals than expected in the Fall; with Resident Breeders the only group present more than expected during the Summer.

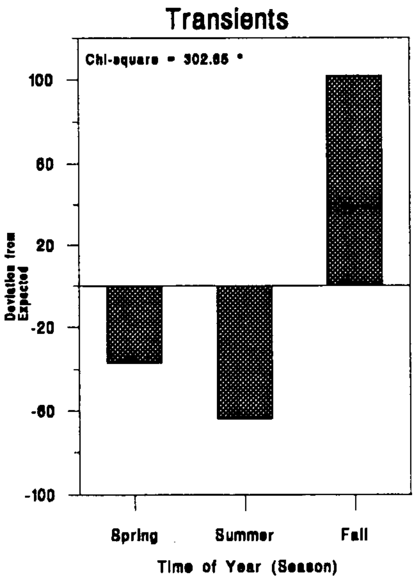
Dramatic increases in bird numbers occurred during the Fall when many waders and blackbirds flock together and often forage in large aggregations. During the Fall, I had repeated counts of mixed flocks with over 100 individuals each of Great and Snowy Egrets accompanied by hundreds of Boat-tailed Grackles and a scattering of shorebirds, waterfowl and other waders in one or more pools during a survey. One large flock of approximately 200 individuals each of Great and Snowy Egrets foraged in tidepools at Maryus and Seafood marshes for almost 2 months. The flock was identified by the presence of a Snowy Egret which had been banded and color dyed on the Eastern Shore of Virginia earlier that season (Erwin pers. comm.) and was seen in one of the two marshes with the flock nearly each week from 6 August until 25 September.

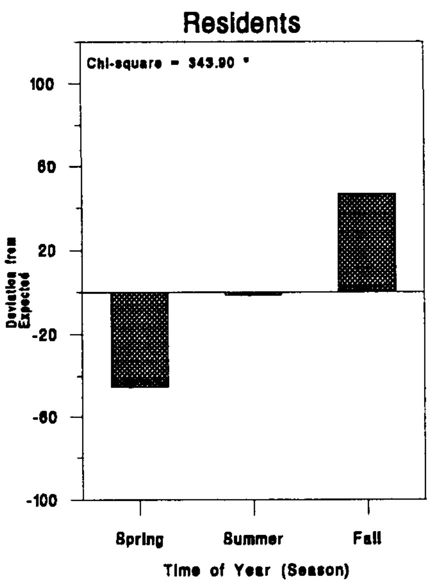
Tidal Patterns

Although tide was not controlled for, it was influential in dictating when birds were in the marsh and thus, the tidepools. Chi-square analysis (presented in Figure 9) revealed significant tidal effects on the use of tidepools by all bird groups and species with the exception of large shorebirds and Greater Yellowlegs.

Outgoing low tide was the only range used more than expected for Total Birds. Fish eaters, such as the Great Egret, Snowy Egret, Green-backed Heron and Willet were most prevalent during outgoing low tides. Boat-tailed Grackles, which were often

Figure 8. Relative abundance patterns across seasons of residency user groups. Values indicated % deviation from an expected even distribution. Negative distribution implies less than average occurrence for specific season. Positive deviation implies overrepresentation for specific season (* = p < 0.001).


Transients
Chi-square = 302.65 *
100
60
20
-20
-60
-100
Deviation from Expected
Spring
Summer
Fall
Time of Year (Season)


Residents
Chi-square = 343.90 *
100
60
20
-20
-60
-100
Deviation from Expected
Spring
Summer
Fall
Time of Year (Season)

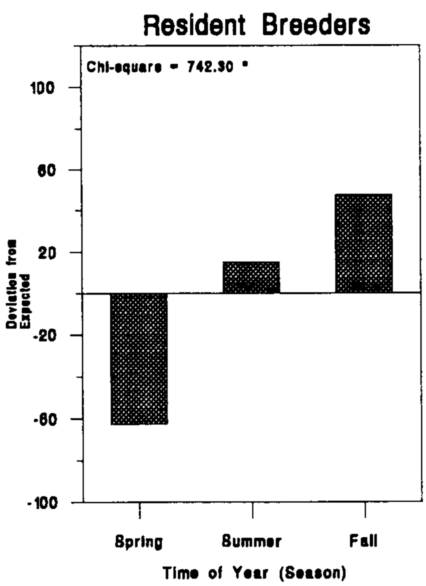
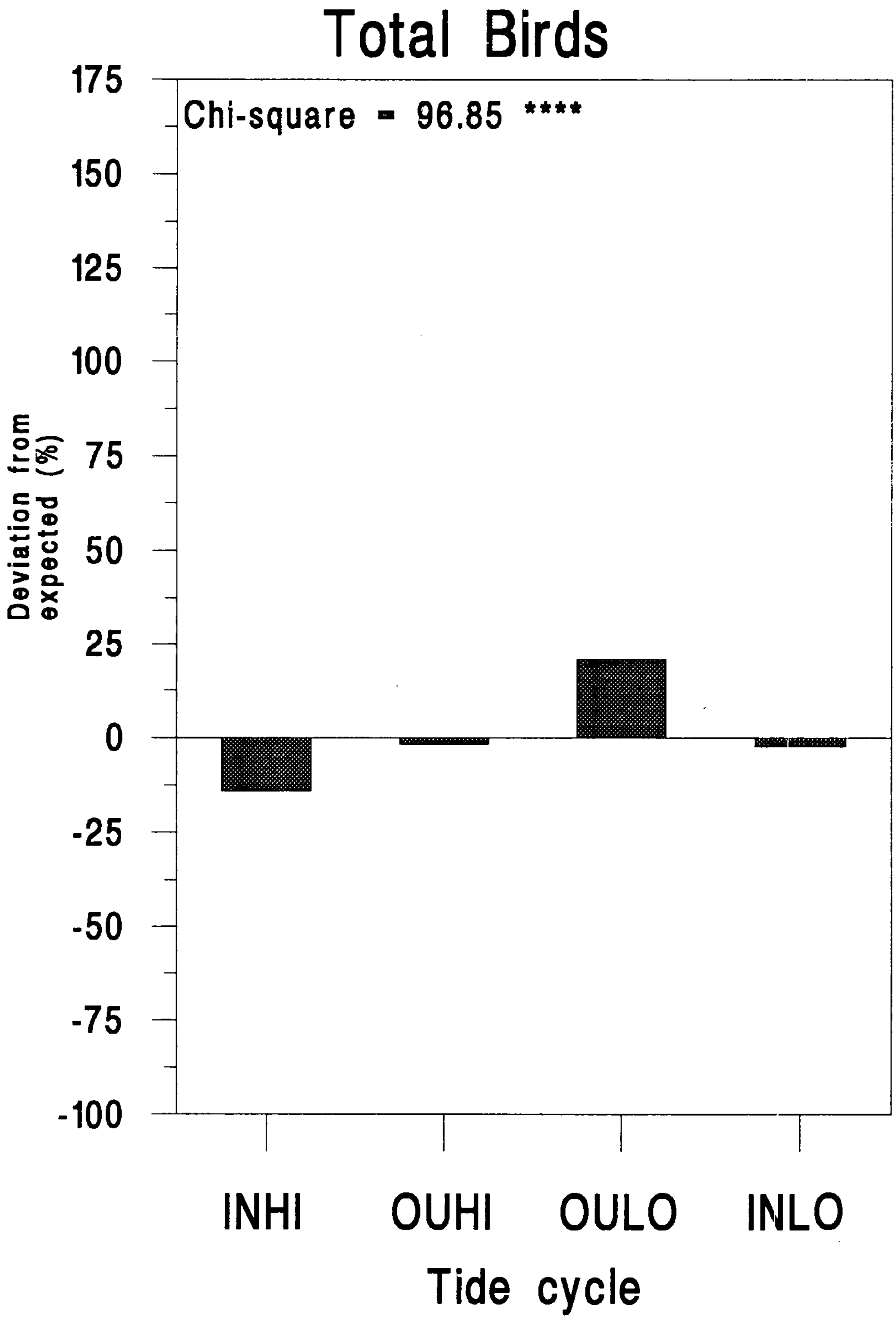
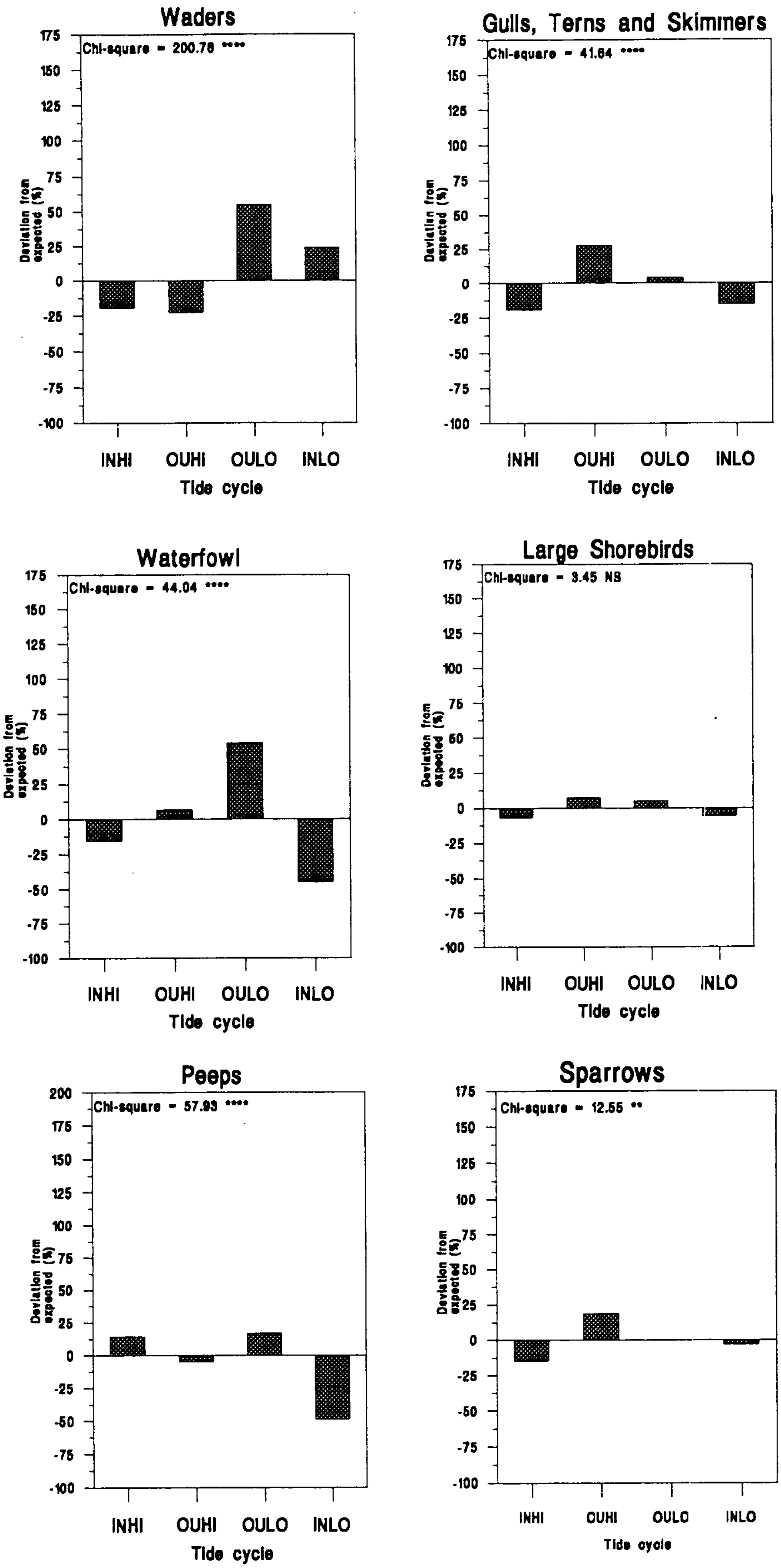
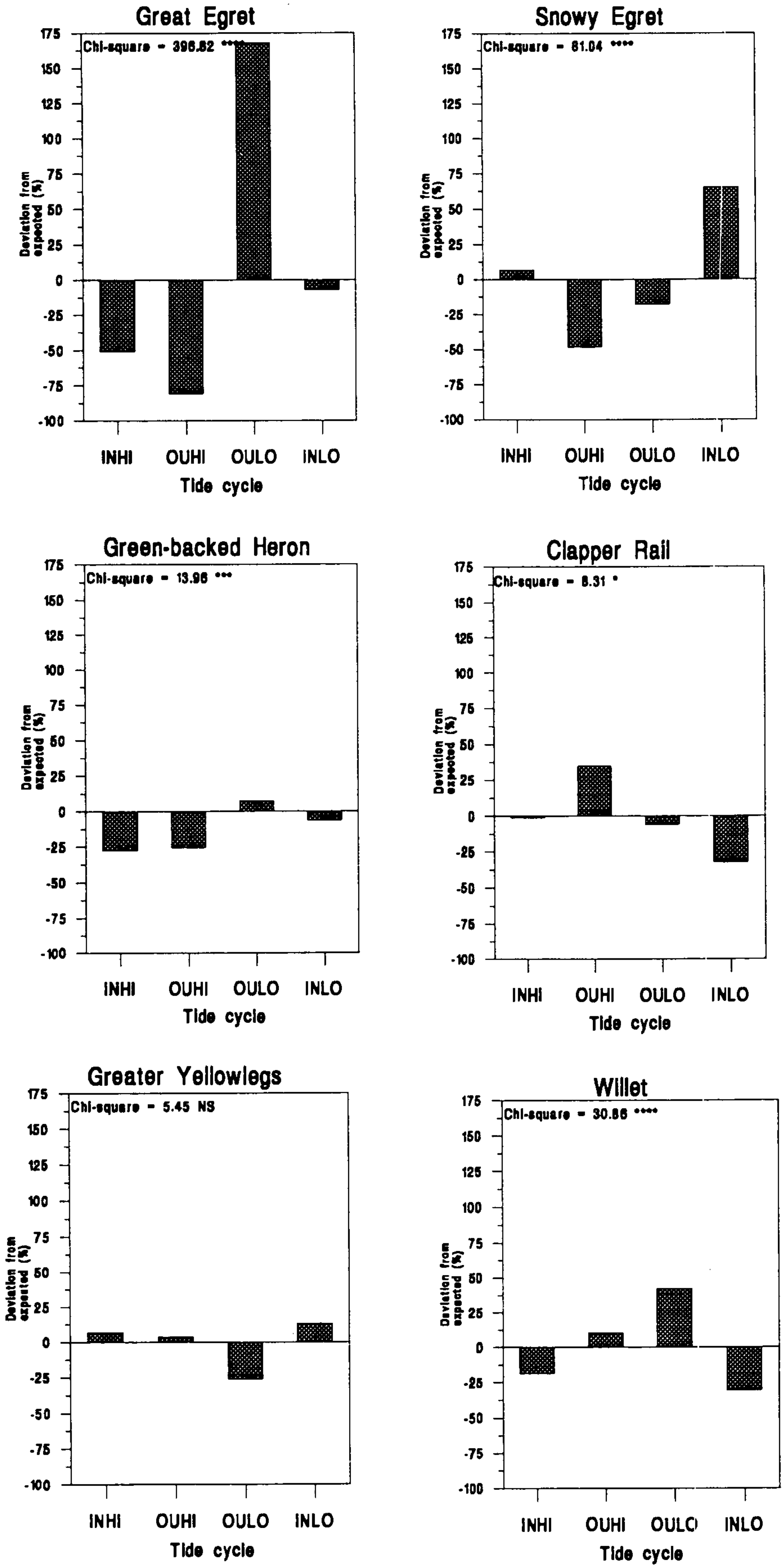
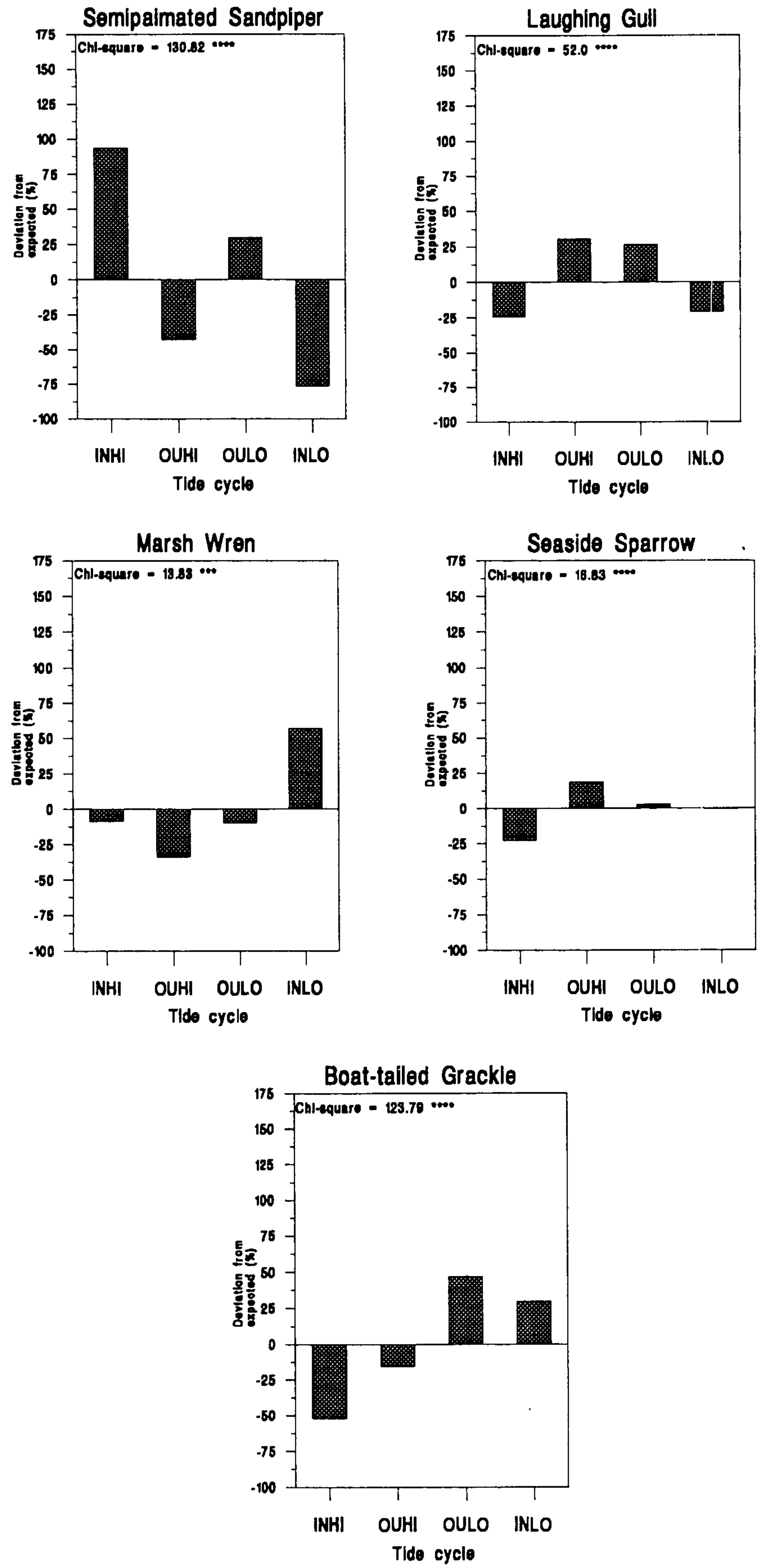

Resident Breeders
Chi-square = 742.30 *
100
60
20
-20
-60
-100
Deviation from Expected
Spring
Summer
Fall
Time of Year (Season)

Figure 9. Relative abundance patterns across tides for total observed birds, guilds and target species. Values indicate % deviation from an expected even distribution. Negative distribution implies less than average occurrence for specific tide cycle. Positive deviation implies overrepresentation for specific tide cycle. (*** = $p < 0.001$).


Total Birds
Chi-square = 96.85 ****
Deviation from expected (%)
175
150
125
100
75
50
25
0
-25
-50
-75
-100
INHI
OUHI
OULO
INLO
Tide cycle


Waders
Chi-square = 200.78 ****
Gulls, Terns and Skimmers
Chi-square = 41.64 ****
Waterfowl
Chi-square = 44.04 ****
Large Shorebirds
Chi-square = 3.45 NS
Peeps
Chi-square = 57.93 ****
Sparrows
Chi-square = 12.55 **
Deviation from expected (%)
INHI
OUHI
OULO
INLO
Tide cycle


Great Egret
Chi-square = 396.82 ****
Snowy Egret
Chi-square = 81.04 ****
Green-backed Heron
Chi-square = 13.96 ***
Clapper Rail
Chi-square = 8.31 *
Greater Yellowlegs
Chi-square = 5.45 NS
Willet
Chi-square = 30.86 ****
Deviation from expected (%)
175
150
125
100
75
50
25
0
-25
-50
-75
-100
INHI
OUHI
OULO
INLO
Tide cycle


Semipalmated Sandpiper
Chi-square = 130.82 ****
Laughing Gull
Chi-square = 52.0 ****
Marsh Wren
Chi-square = 13.83 ***
Seaside Sparrow
Chi-square = 16.83 ****
Boat-tailed Grackle
Chi-square = 123.79 ****
Deviation from expected (%)
175
150
125
100
75
50
25
0
-25
-50
-75
-100
INHI
OUHI
OULO
INLO
Tide cycle

associated with mixed heron flocks, mimic waders. Likewise, gulls, waterfowl and rails were more prevalent during low tides. Semipalmated Sandpipers were the only species to use incoming high tides more than expected.

POOL CHARACTERISTICS

Physical Components

Descriptive results for components organized by pool profile type are presented in Appendix V. Pool areas ranged from <1 m^2 to >2300 m^2. Over 68% of all pools were ≤ 10 m^2; however, these small pools comprised $<0.01\%$ of total pool area. Large pools were rare. However, each marsh had 1 or 2 expansive pools (>400 m^2) which dominated the landscape and had complexes of smaller pools bordering them. Pool area for all marshes totalled 1.53 ha of open water ($<0.01\%$ of total marsh area). In order to reduce the number of variables for analysis, depth was reorganized into 3 categories: 1) Shallow: pools <10 cm deep 2) deep: pools >10 cm deep and 3) shallow/deep: pools with both depths. Although tidepool water levels fluctuated greatly with tidal inundation, all of the pools could be categorized into 1 of these 3 categories at low tide: Shallow: 59.4%; Deep: 27.4%; Shallow/Deep: 13.2%. Pothole and shallow profiled pools were the most abundant profile type. See Table 1 for distribution of pools and area of different profile types.

Relationship of physical components

Overall, relationships between different physical pool components are apparent. Profile types (with intermediate pools left out of the analysis) were significantly different with respect to area of water depths and area of black needlerush (see

Appendix V). Principal Components Analysis (varimax rotation) on all tidepools grouped together revealed that pool area and water depth were the primary sources of variability within tidepools (see Appendix V). The first principal component explained 61.5% of the variability.

Pearson correlation coefficients also reveal component relationships (see Table 6). Pool area, profile and water depths appear correlated. Typically, pools < .10m^2 are pothole in nature with larger, perhaps more eroded, pools graded or intermediate in structure. Edge type is often related to tidepool water depth. Consistently, shallow pools were exclusively (100%) <10 cm deep while pothole pools contained deeper waters.

Biological Components

Area of vegetation surrounding various pool types is presented in Appendix V. The dominant vegetation surrounding pool perimeters was short cordgrass, typical of the less hydric low marsh landscape, with 94% of all pools having at least some short cordgrass. Cordgrass was typically mixed with spikegrass (*Distichlis spicata*) and sea lavender (*Limonium carolinianum*). Cordgrass shoots were present in 126 (41.6%) of the pools over half of which were shallow pools; since shoots were often scattered throughout the pool shallows and edges no attempt was made to quantify area. See Figure 10 for the percent cover of substrate types.

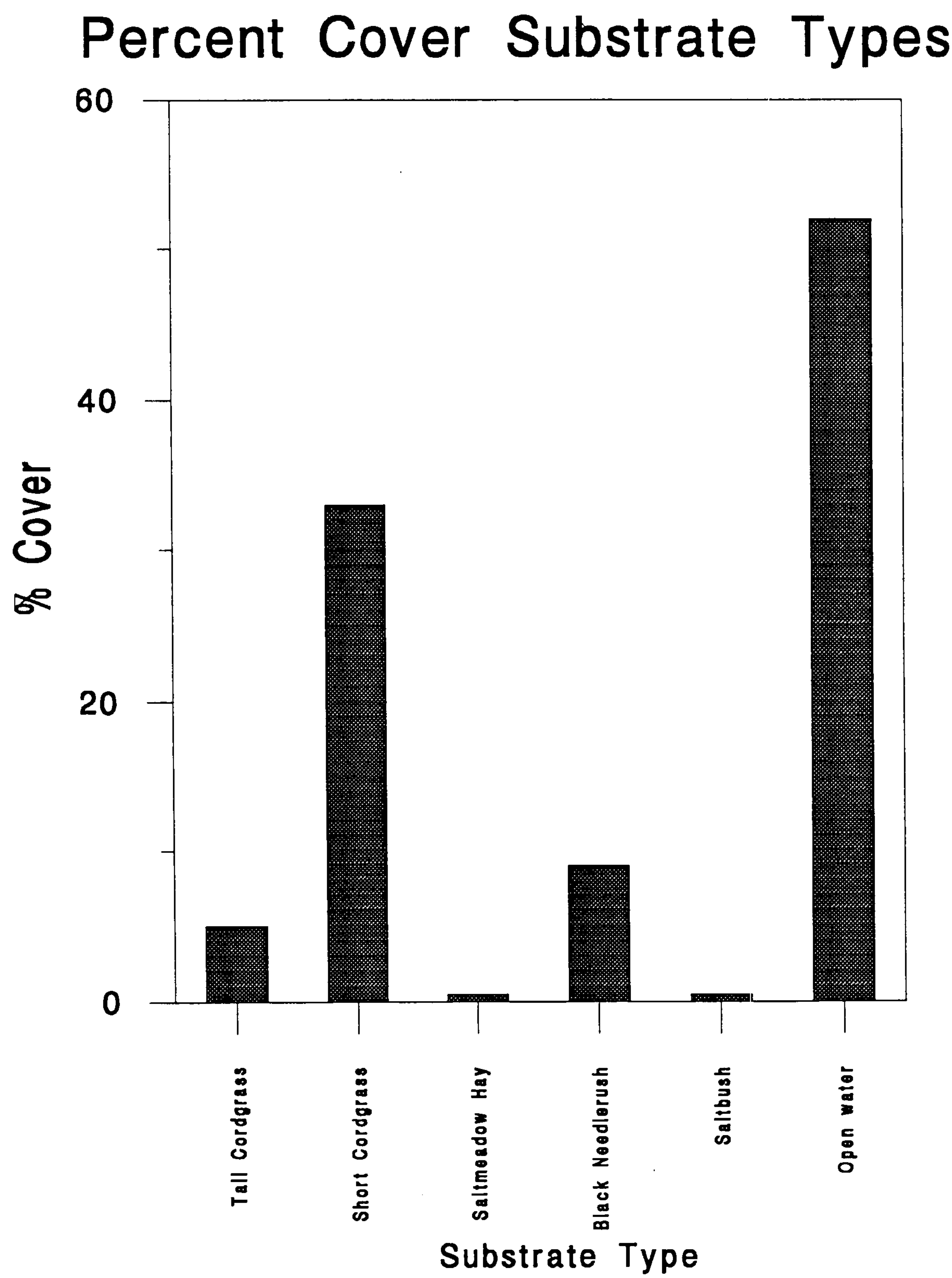
Widgeon grass (*Ruppia maritima*), a submerged aquatic vegetation (SAV) and frequent food item of waterfowl, was present in 5.9% of the pools.

Table 6: Pearson correlation coefficients (r) between physical components* measured for all 303 tidepools.

Variables	AR	SB	BN	SH	SC	TC	DA	DB	DC	DD	PE
AR	1										
SB	0.34	1									
BN	0.83	0.33	1								
SH	0.36	0.00	0.12	1							
SC	0.89	0.44	0.64	0.25	1						
TC	0.18	0.02	0.05	0.17	0.01	1					
DA	0.70	0.14	0.64	0.40	0.54	0.48	1				
DB	0.82	0.29	0.88	0.24	0.66	0.22	0.70	1			
DC	0.82	0.04	0.70	0.18	0.61	0.01	0.50	0.60	1		
DD	0.61	0.34	0.23	.040	0.67	0.07	.019	0.21	0.30	1	
PE	0.94	0.45	0.84	0.27	0.93	0.23	0.71	0.83	0.69	0.56	1

*AR = Tidepool area, SB = Area Saltbush, BN = Area Black Needlerush, SH = Area Saltmeadow hay, SC = Area Short Cordgrass, TC = Area Tall Cordgrass, DA = Area 0-2 cm depth, DB = Area 2-10 cm depth, DC = Area 10-20 cm depth, DD = Area >20 cm depth, PE = Distance of edge.

Figure 10. Percent cover of substrate categories (total substrate type area/total tidepool area + total vegetation area).


Percent Cover Substrate Types
60
40
20
0
% Cover
Tall Cordgrass
Short Cordgrass
Saltmeadow Hay
Black Needlerush
Saltbush
Open water
Substrate Type

Prey

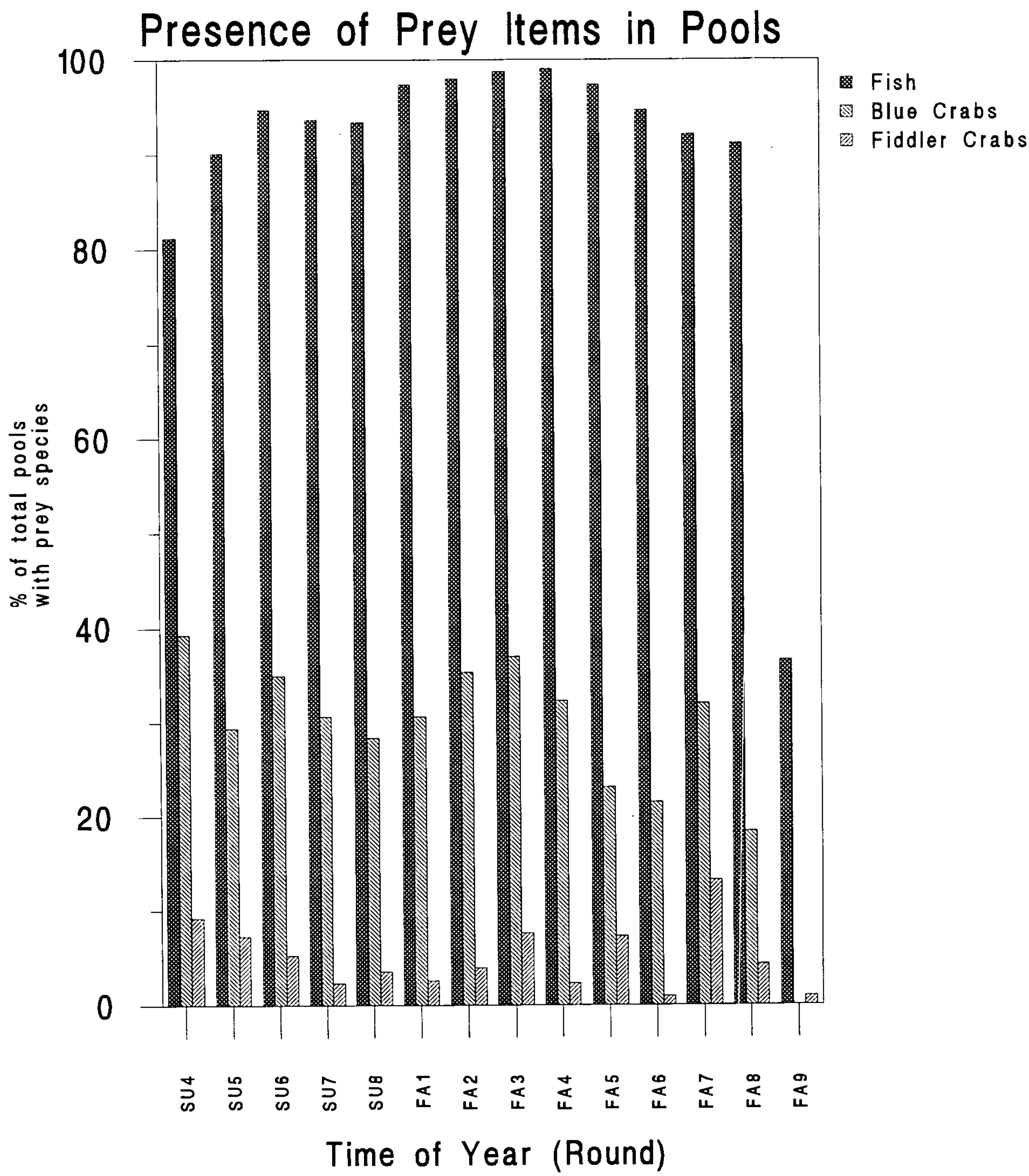
A summary of prey occurrence within pools (% pools with prey items present/ survey round) is found in Figure 11. Fish (*Fundulus spp.)* were the most abundant prey item in tidepools (92% of all pools had fish $\geq$ 75% of surveys). Blue crabs were present at least once in 72% of all pools while fiddler crabs were rare (present less than a third of the time in 98% of the pools). This low percentage is probably unrepresentative of actual fiddler crab presence. Most pools had evidence of burrows which crabs may have entered at my approach or to escape inundation at high tides. Scattered piles of fiddler crab claws were frequently found around pool edges, left by Clapper Rails who feed almost exclusively on these crustaceans. While no surveys were conducted for other possible prey species, marsh crabs (*Sesarma*), ribbed mussels (*Modiolus*), marsh snails (*Melampus*) and the marsh periwinkle (*Littorina*) were frequently found in and around tidepools.

Colder temperatures in late Fall led to sharp declines in prey. By mid-October, blue crabs had disappeared completely from pools and fish were present in less than half of their former pools. Both species burrow into the mud to overwinter.

Benthic macrofauna

A total of 115 cores were sorted and 3,523 individuals of 16 different taxa of macrofauna found and identified. A full species list is given in Appendix VI. Annelid worms were the most abundant taxa group represented strongly by oligochaetes (61% of total individuals) and the polychaetes *Asabellides oculata* (11%) and Capitellidae spp. (8%). Midge larvae (Chironomidae) were the most prevalent non-annelid (7%).

Figure 11. Presence of prey species in pools during weekly rounds (% total pools with prey species present).



Presence of Prey Items in Pools
100
80
60
40
20
0
% of total pools
with prey species
Fish
Blue Crabs
Fiddler Crabs
SU4
SU5
SU6
SU7
SU8
FA1
FA2
FA3
FA4
FA5
FA6
FA7
FA8
FA9
Time of Year (Round)

G-tests were run on different pool treatments to test possible patterns in benthic macrofauna distribution between pool depths (Shallow vs. Deep), pool types (Pure Depth vs. Graded), vegetation types (Vegetated vs. Unvegetated) and within cores (Top vs. Bottom).

Results are presented in Tables 7 - 13 and reveal significant differences between the total number of macrofauna found between pool depths and core depths in all treatments. Core tops had significantly more individuals than core bottoms in all treatments. In addition, vegetated cores had significantly higher numbers of macrofauna than unvegetated cores (G-statistic = 1692.5, $p < 0.001$). Tests of abundance differences between depth variations in both pure (G-statistic = 80.5, $p < 0.001$) and graded pools (G-statistic = 265.5, $p < 0.001$) were highly significant with shallow depths having greater numbers of individuals.

POOL USE BY BIRDS

Bird behavior and substrate associations are presented in Figure 12. In general, pools were used as foraging patches. Over 47% of all birds were seen actively pursuing, catching or eating prey (Foraging). Another 23% of birds were observed after being flushed; many likely foraging before being disturbed. Transients were more likely to be foraging than residents or resident breeders (72.05% transients; 58.11% residents; 25.67% resident breeders) although all groups foraged significantly more than expected (Transients: $\chi^2 = 1297.7$, $p < 0.001$; Residents: $\chi^2 = 63.16$, $p < 0.001$; Resident Breeders: $\chi^2 = 825.1$, $p < 0.001$). Over 63% of all birds were located within the waters of the tidepool (In) with remaining birds located either on the

Table 7. Mean(S.E.) total of macrofauna individuals for pool depth and core depth treatments. Vegetation cores not included in analysis. Pool depth: Shallow $\leq$ 10 cm, Deep $\geq$ 10 cm. Core depth: Top = top 2 cm of core, Bottom = Bottom 8 cm of core. ST = Shallow, top, SB = Shallow, bottom, DT = Deep, top, DB = Deep, bottom.

	Pool Treatments			
Pool Type	ST	SB	DT	DB
<u>Pure Shallow and Deep Pools</u>				
Total individuals	32.2(6.5)	19.5(5.1)	15.7(4.1)	11.1(2.7)
#Cores (N)	6	13	9	15
<u>Graded Pools</u>				
Total individuals	13.7(7.3)	37.6(10.7)	3.4(1.1)	12.1(2.3)
#Cores (N)	9	15	9	16

Table 8. G-test for treatment effects of Pool depth and Core depth on macrofauna abundance.

	Pool Depth Shallow vs. Deep		Core Depth Top vs. Bottom		Association	
Pool Type	G-stat[a]	P	G-stat	P	G-stat	P
Pure Shallow and Deep Pools	80.5	<0.001***	25.7	<0.001***	0.1	>0.05
Graded Pools	265.5	<0.001***	178.0	<0.001***	0.1	>0.05

[a] - calculated with Williams' correction (Sokal and Rohlf 1981).

Table 9. Mean(S.E.) total of macrofauna individuals for pool type and core depth within similiar pool depth categories. Pool type: Shallow, Graded Shallow. Core depth: Top = top 2cm of core, Bottom = Bottom 8cm of core. ST = Shallow, top. SB = Shallow, bottom. GT = Graded shallow, top. GB = Graded Shallow, bottom.

	Pool Treatments			
	ST	SB	GT	GB
Total individuals	32.2(6.5)	19.5(5.1)	13.7(7.3)	37.6(10.7)
#Cores (N)	6	13	9	15

Table 10. Mean(S.E.) total of macrofauna individuals for pool type and core depth within similiar pool depth categories. Pool type: Deep, Graded Deep. Core depth: Top = top 2cm of core, Bottom = Bottom 8cm of core. DT = Deep, top. DB = Deep, bottom. GT = Graded deep, top. GB = Graded Deep, bottom.

	Pool Treatments			
	DT	DB	GT	GB
Total individuals	15.7(4.1)	11.1(2.7)	3.4(1.1)	12.1(2.3)
#Cores (N)	9	15	9	16

Table 11. G-test for treatment effects of Pool type and Core depth on macrofauna abundance within similar pool depths (shallow or deep).

	Pool Type Pure vs. Graded		Core Depth Top vs. Bottom		Association	
Pool Type	G-stat[a]	P	G-stat	P	G-stat	P
Shallow and Graded Shallow						
Total individuals	10.5	<0.005**	26.3	<0.001***	2.2	>0.05
Deep and Graded Deep						
Total individuals	16.6	<0.001***	4.4	<0.05*	4.1	<0.05*

[a] - calculated with Williams' correction (Sokal and Rohlf 1981).

Table 12. Mean(S.E.) total of macrofauna individuals for vegetation type and core depth treatments. Core depth: Top = top 2 cm of core, Bottom = Bottom 8 cm of core. VT = Vegetation, top, VB = Vegetation, bottom, UT = Unvegetated, top, UB = Unvegetated, bottom.

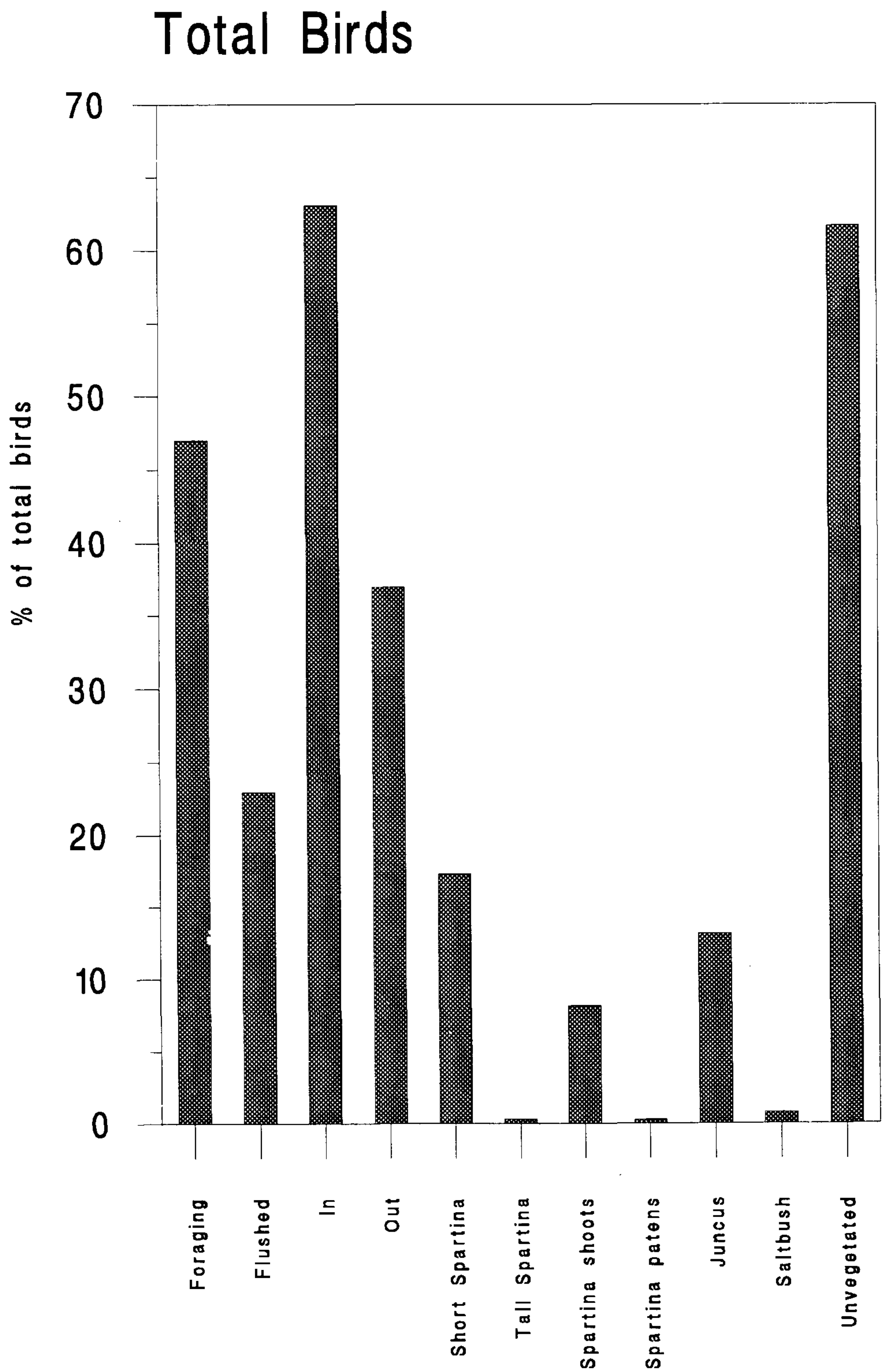
	Pool Treatments			
	VT	VB	UT	UB
Total individuals	115.9(33.7)	38.1(11.8)	14.8(3.0)	19.8(3.2)
#Cores (N)	12	12	33	59

Table 13. G-test for treatment effects of Vegetation type and Core depth on macrofauna abundance.

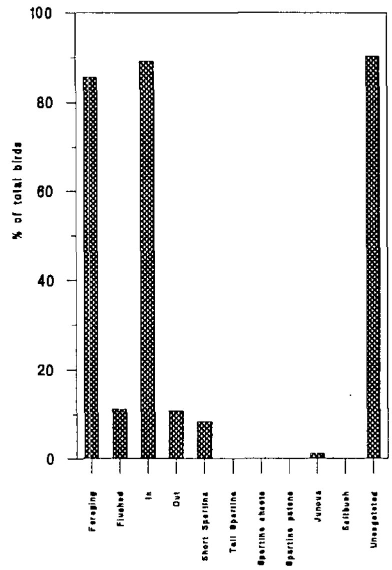
	Vegetation Type		Core Depth		Association	
	G-stat[a]	P	G-stat	P	G-stat	P
Total individuals	1692.5	<0.001***	300.9	<0.001***	12.9	<0.001***

[a] - calculated with Williams' correction (Sokal and Rohlf 1981).

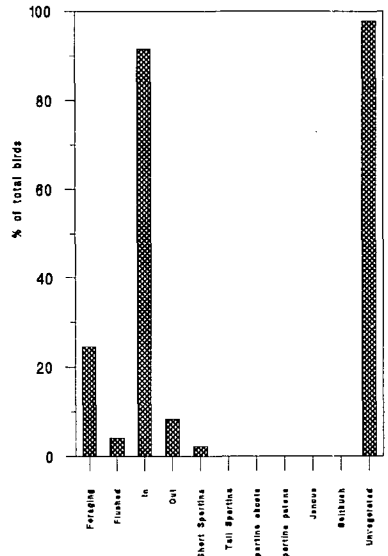
Figure 12. Behavior and substrate associations of birds observed utilizing tidepools.


Total Birds
70
60
50
40
30
20
10
0
% of total birds
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated

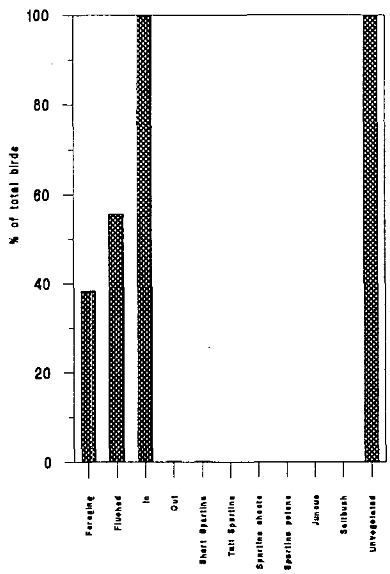
Waders



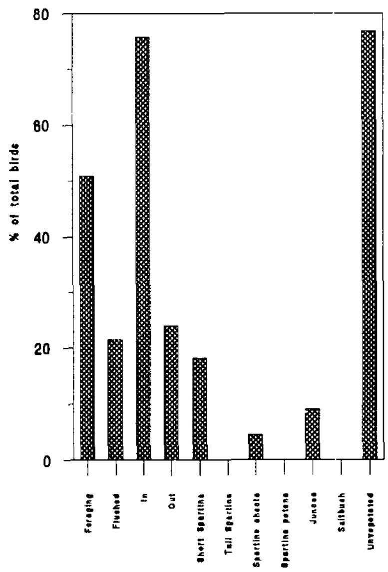
Gulls, terns and skimmers



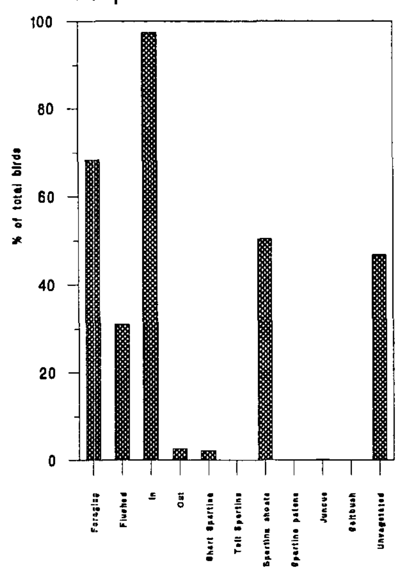
Waterfowl



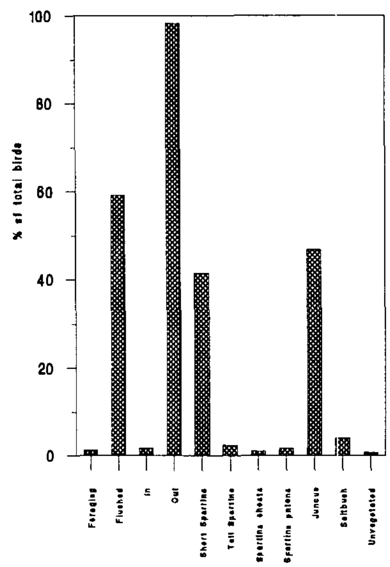
Large shorebirds



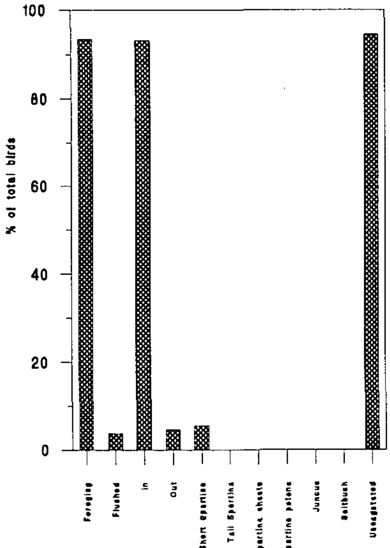
Peeps



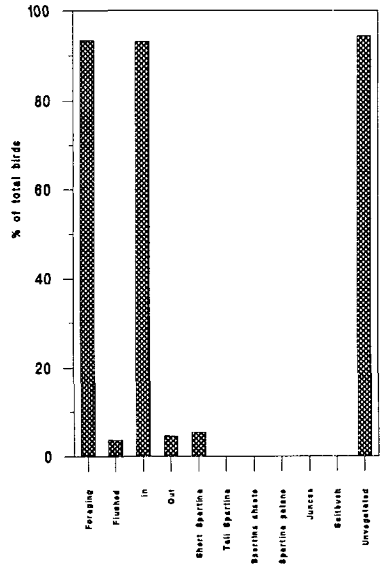
Sparrows



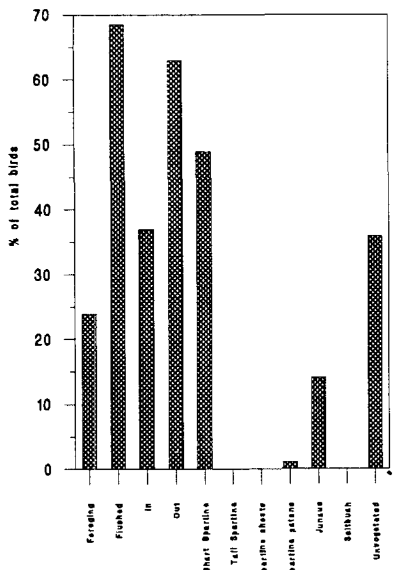
Great egret



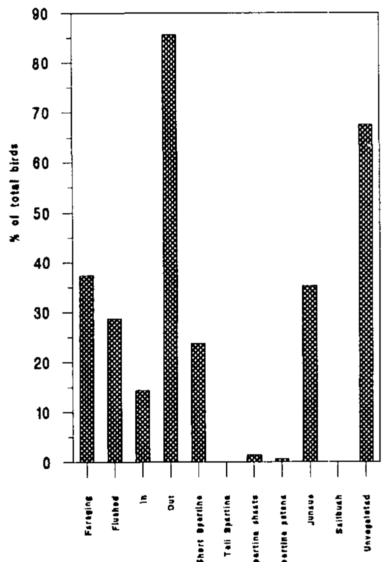
Snowy egret



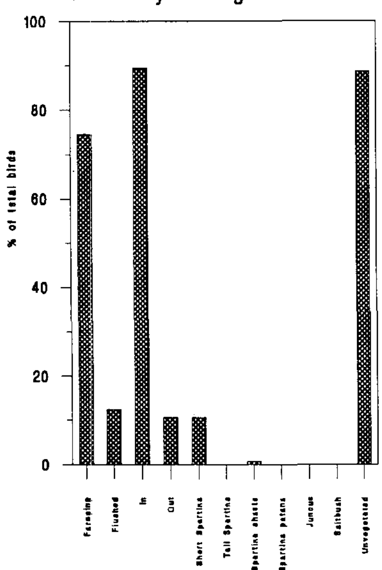
Green-backed heron



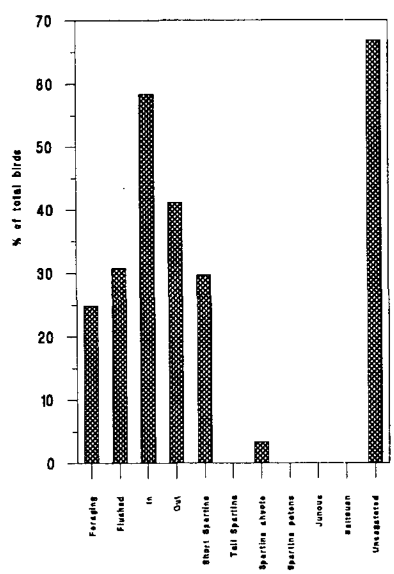
Clapper rail

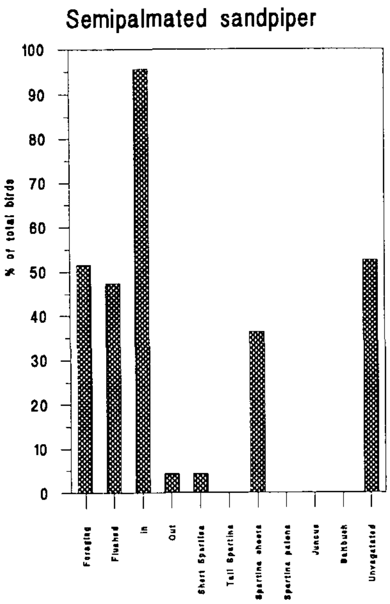


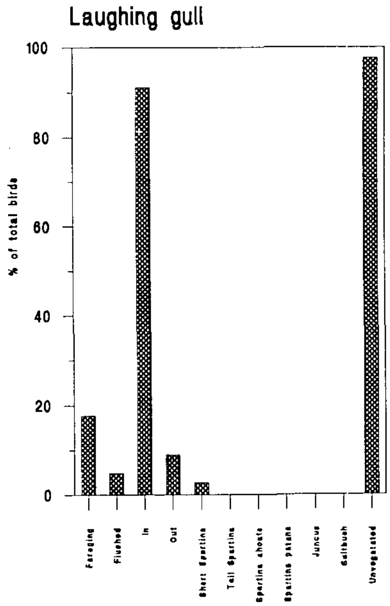
Greater yellowlegs

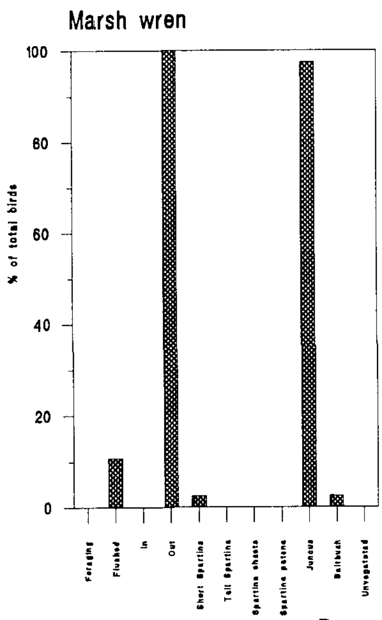


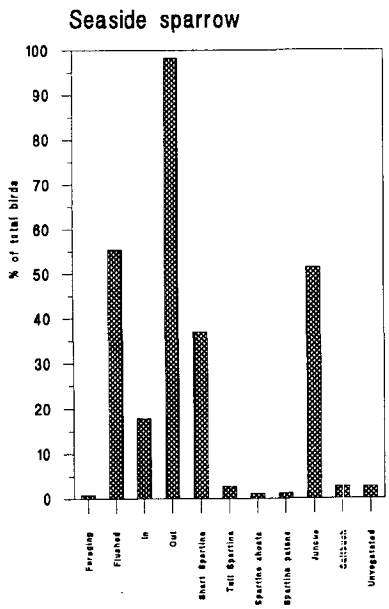
Willet

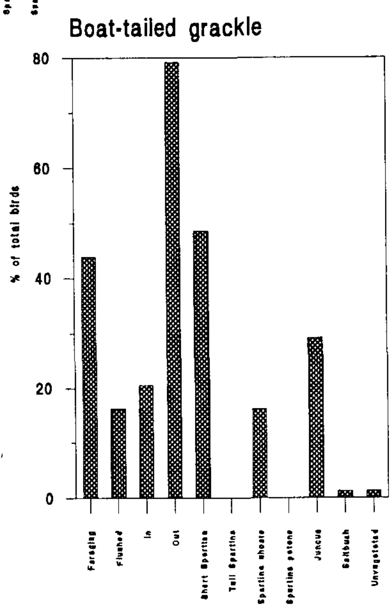



Semipalmated sandpiper
% of total birds
100
90
80
70
60
50
40
30
20
10
0
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated


Laughing gull
% of total birds
100
80
60
40
20
0
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated


Marsh wren
% of total birds
100
80
60
40
20
0
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated


Seaside sparrow
% of total birds
100
90
80
70
60
50
40
30
20
10
0
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated


Boat-tailed grackle
% of total birds
80
60
40
20
0
Foraging
Flushed
In
Out
Short Spartina
Tall Spartina
Spartina shoots
Spartina patens
Juncus
Saltbush
Unvegetated

outer edge of on a hummock (Out) (see Appendix VII for a summary of individual species locations and chi-square statistics). Transients and residents were more likely than resident breeders to be found in pools (83.6% of all transients; 85.81% of all residents; 32.38% of all resident breeders). As expected, as the inner portion of the tidepool comprised the greatest area of study, all three groups were found in the pool a significantly more than out (Transients: $\chi^2 = 45.16$, $p < 0.001$; Residents: $\chi^2 = 51.29$, $p < 0.001$; Resident Breeder: $\chi^2 = 12.40$, $p < 0.001$). Passerine breeders were almost always outside the pool proper.

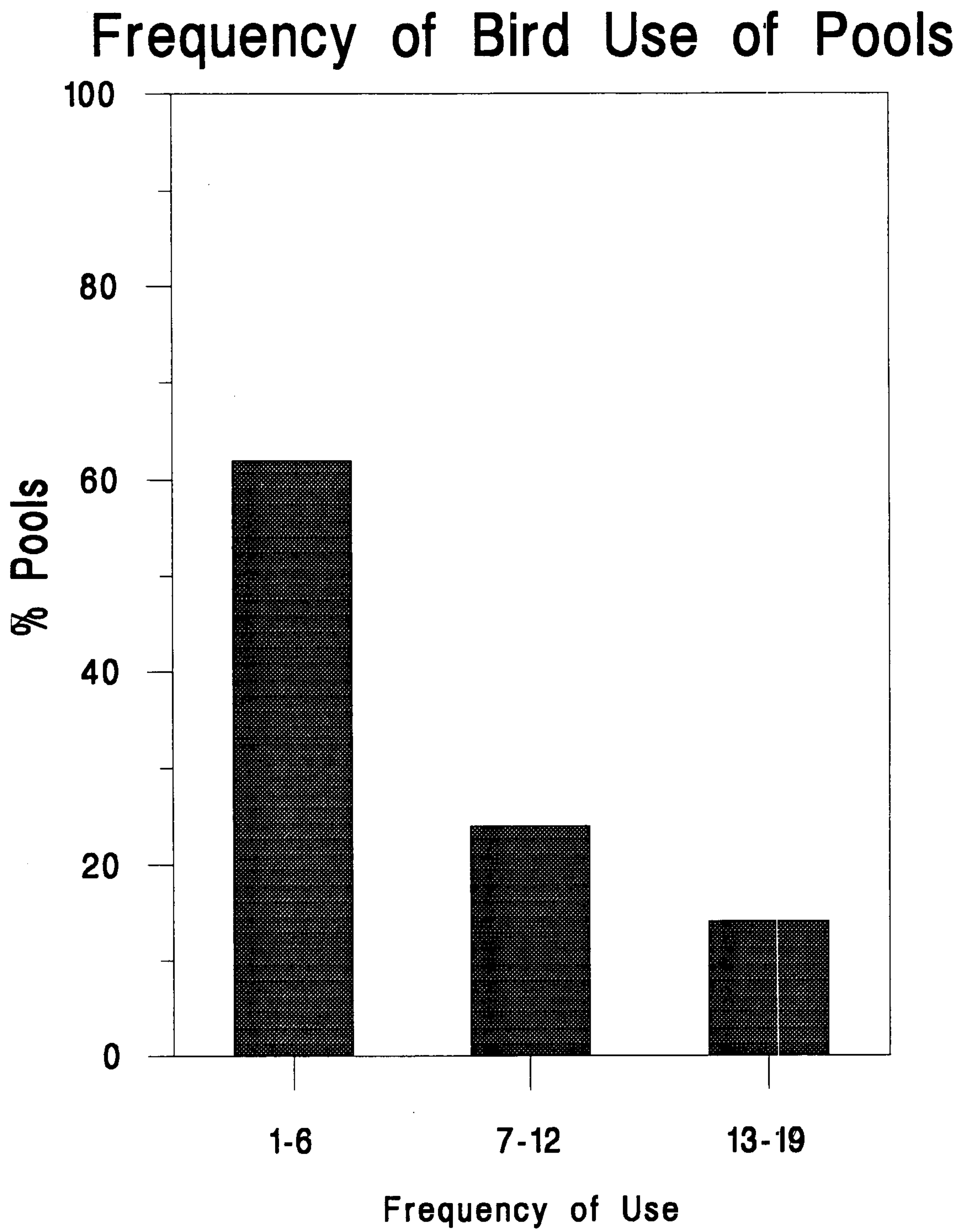
Throughout the surveys, 141 pools (46.53% of all pools) had birds observed in association with them. The highest percentage of pool use occurred during the Summer (Spring - 27.06% pools used; Summer - 35.31%; Fall - 30.36%). Distribution of birds across pools was not normal with 4 pools having 48% of all birds.

Frequency of pool use (the number of times a pool was occupied by birds) was determined for the last 19 surveys (to standardize for varying survey effort between marshes). Only 4% of pools had birds in all 19 surveys while 30% were used only once. See Figure 13 for frequency of pool use.

Effects of Pool Components on Bird Abundance, Richness and Frequency

Pool area had a significant effect on bird distribution and abundance. Although the majority of tidepools were ≤ 10 m^2, these pools accounted for 1.4% of bird observations (see Figure 14 for bird abundance over area ranges). Chi-square analysis between pools $\leq$ and >50 m^2 revealed significant effects of area on bird distribution for all guilds and species with the exception of Green-backed Herons (see Table 14 for

Figure 13. Frequency of bird use of tidepools (% pools occupied by birds per survey round).



Frequency of Bird Use of Pools
100
80
60
40
20
0
% Pools
1-6
7-12
13-19
Frequency of Use

Figure 14. Abundance of birds across range of tidepool areas (% individuals/total tidepools per area range).

Influence of Pool Area on Bird Abundance

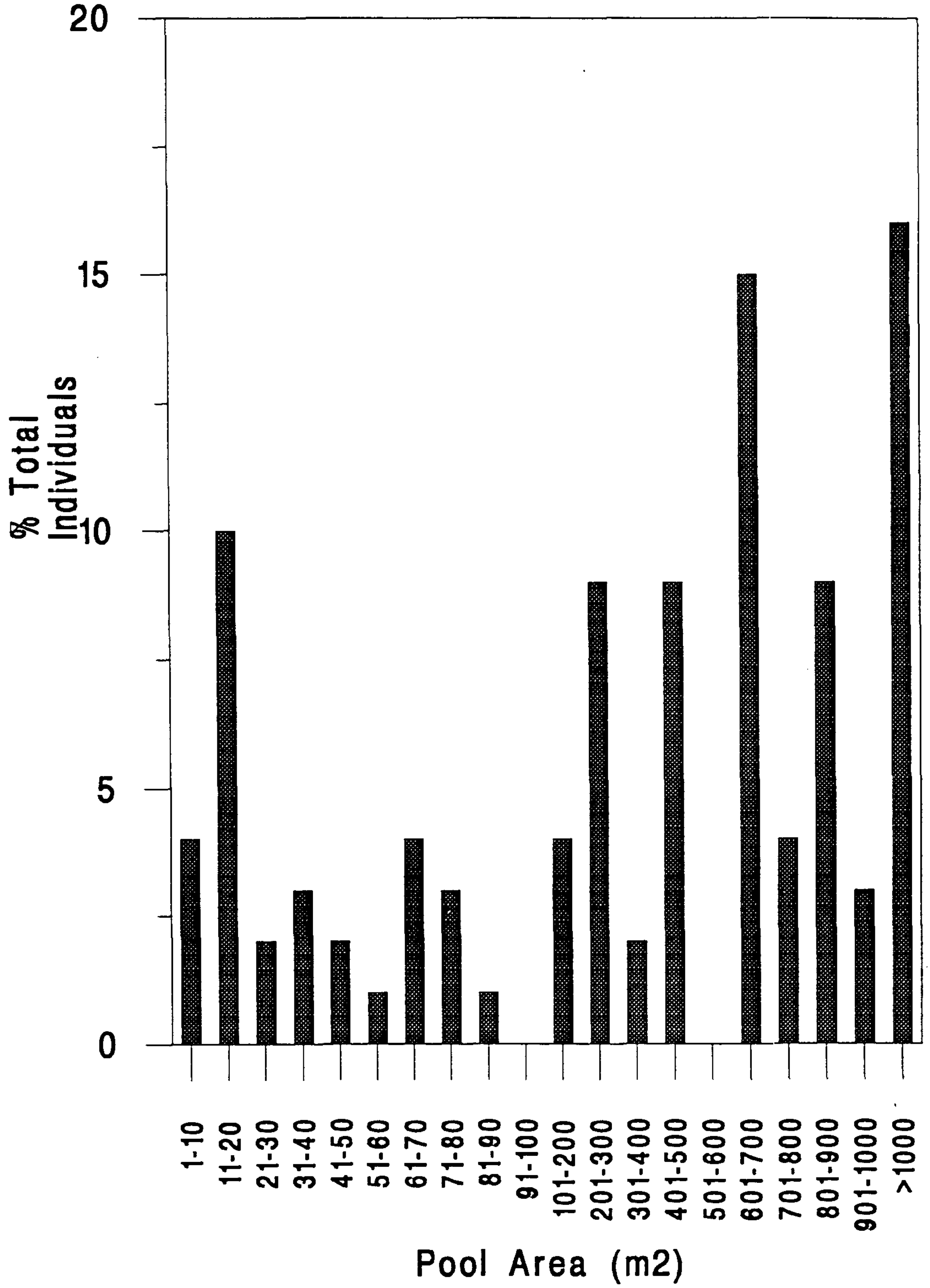


Table 14. Results of Chi-square analysis on tidepool area ($\leq$ 50 m^2 vs. >50 m^2).

Dependent Variable	χ^2	P
Total Birds	1161.36	<0.001
Guilds		
Waders	169.72	<0.001
Gulls, Terns and Skimmers	311.96	<0.001
Waterfowl	60.09	<0.001
Large Shorebirds	177.18	<0.001
Peeps	143.0	<0.001
Sparrows	114.96	<0.001
Species		
Great Egret	14.95	<0.001
Snowy Egret	108.91	<0.001
Green-backed Heron	3.92	NS
Clapper Rail	6.58	<0.05
Greater Yellowlegs	65.39	<0.001
Willet	49.34	<0.001
Semipalmated Sandpiper	174.82	<0.001
Laughing Gull	248.68	<0.001
Marsh Wren	31.13	<0.001
Seaside Sparrow	101.99	<0.001
Boat-tailed Grackle	81.93	<0.001

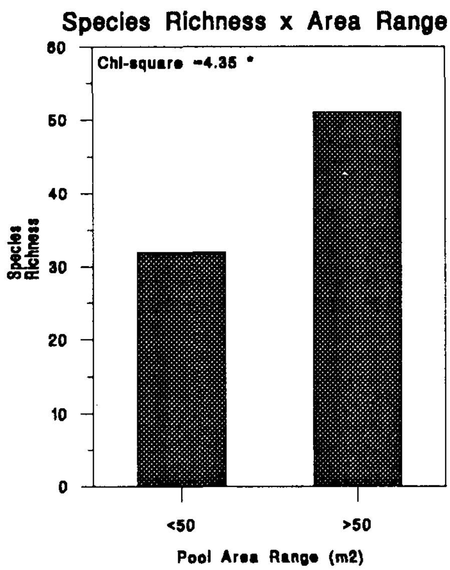
chi-squared statistics and significance values). Species richness was greater in pools $>50\ m^2$ than compared to $<50\ m^2$ (see Figure 15) while frequency of use was positively related to pool area (see Figure 16).

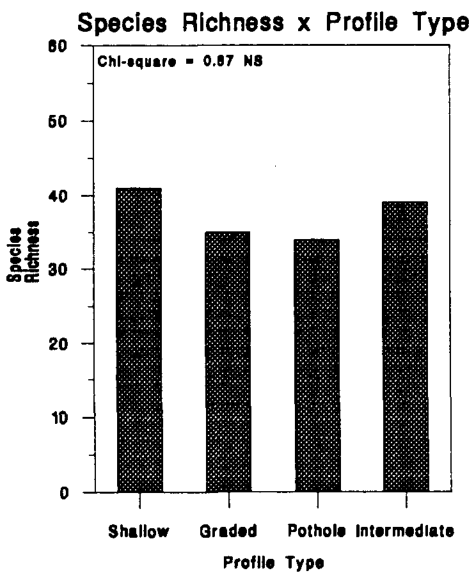
The percentage of shallow/deep pools used by birds was greater than all other depth types (46% shallow pools used, 68% shallow/deep, 40% deep) and these pools had 58% of all bird observations. Chi-square analysis revealed significant differences in use between pool depths for all treatments (see Figure 17) with deep pools used less than expected for all guilds and species. Likewise, species richness within deep pools was less than half of shallow and shallow/deep pools. Frequency of use was greatest among shallow/deep pools (see Figure 16).

Not only were deep pools used by fewer birds (4% of total observations) but they were also used differently. The majority of birds associated with deep pools were located on the pool perimeter rather than within the water (Chi-square statistics and significance values are presented in Figure 18). This contrasts with shallow pools with more birds in than out ($\chi^2 = 5.76$, $p < 0.02$) and shallow/deep pools which birds did not use significantly different.

Chi-square analysis of the three main profile types showed significant effects of profile type on bird use (see Figure 19 for Chi-square statistics and significance values). Shallow and graded pools were used considerably more than expected unlike pothole pools. Profile type had no detectable influence on the frequency of pool use (see Figure 16).

Figure 15. Relationship between species richness and physical pool characteristics (Area, Water Depth, Profile).


Species Richness x Area Range
Chi-square =4.35 *
Species Richness
0
10
20
30
40
50
60
<50
>50
Pool Area Range (m2)


Species Richness x Profile Type
Chi-square = 0.87 NS
Species Richness
0
10
20
30
40
50
60
Shallow
Graded
Pothole
Intermediate
Profile Type

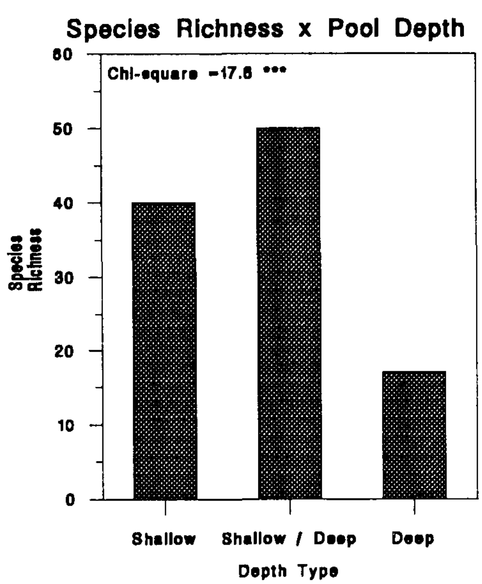
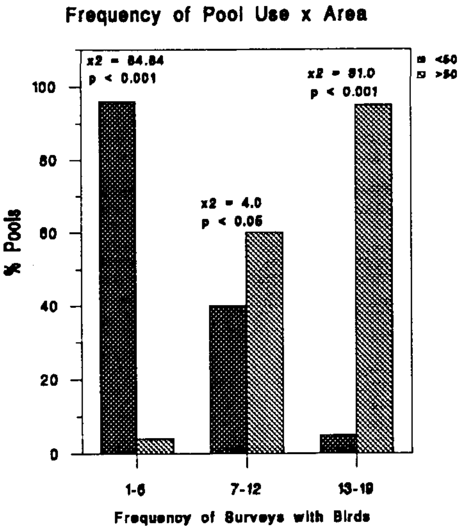
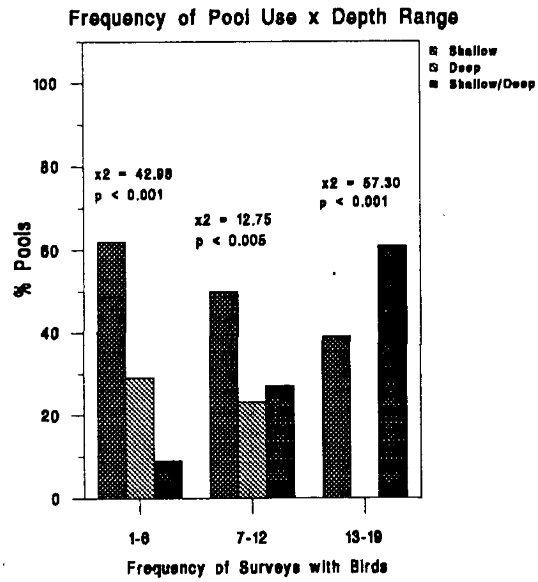

Species Richness x Pool Depth
Chi-square =17.6 ***
Species Richness
0
10
20
30
40
50
60
Shallow
Shallow / Deep
Deep
Depth Type

Figure 16. Frequency of use of tidepools by total birds for different component ranges (Area, Water Depth, Profile).


Frequency of Pool Use x Area
x2 = 84.84
p < 0.001
x2 = 4.0
p < 0.05
x2 = 91.0
p < 0.001
<50
>50
% Pools
0
20
40
60
80
100
1-6
7-12
13-19
Frequency of Surveys with Birds


Frequency of Pool Use x Depth Range
Shallow
Deep
Shallow/Deep
x2 = 42.98
p < 0.001
x2 = 12.75
p < 0.005
x2 = 57.30
p < 0.001
% Pools
0
20
40
60
80
100
1-6
7-12
13-19
Frequency of Surveys with Birds

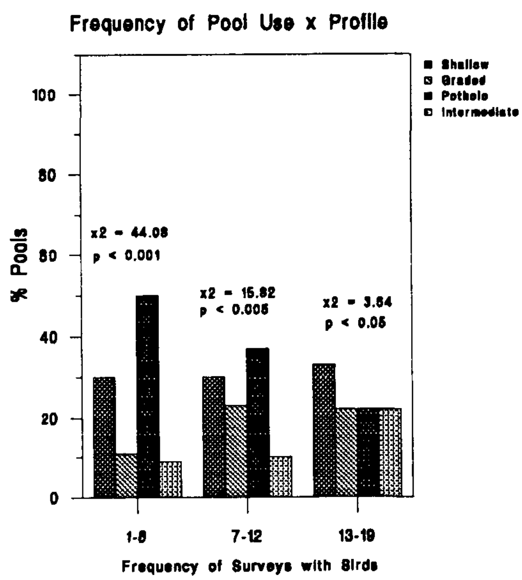
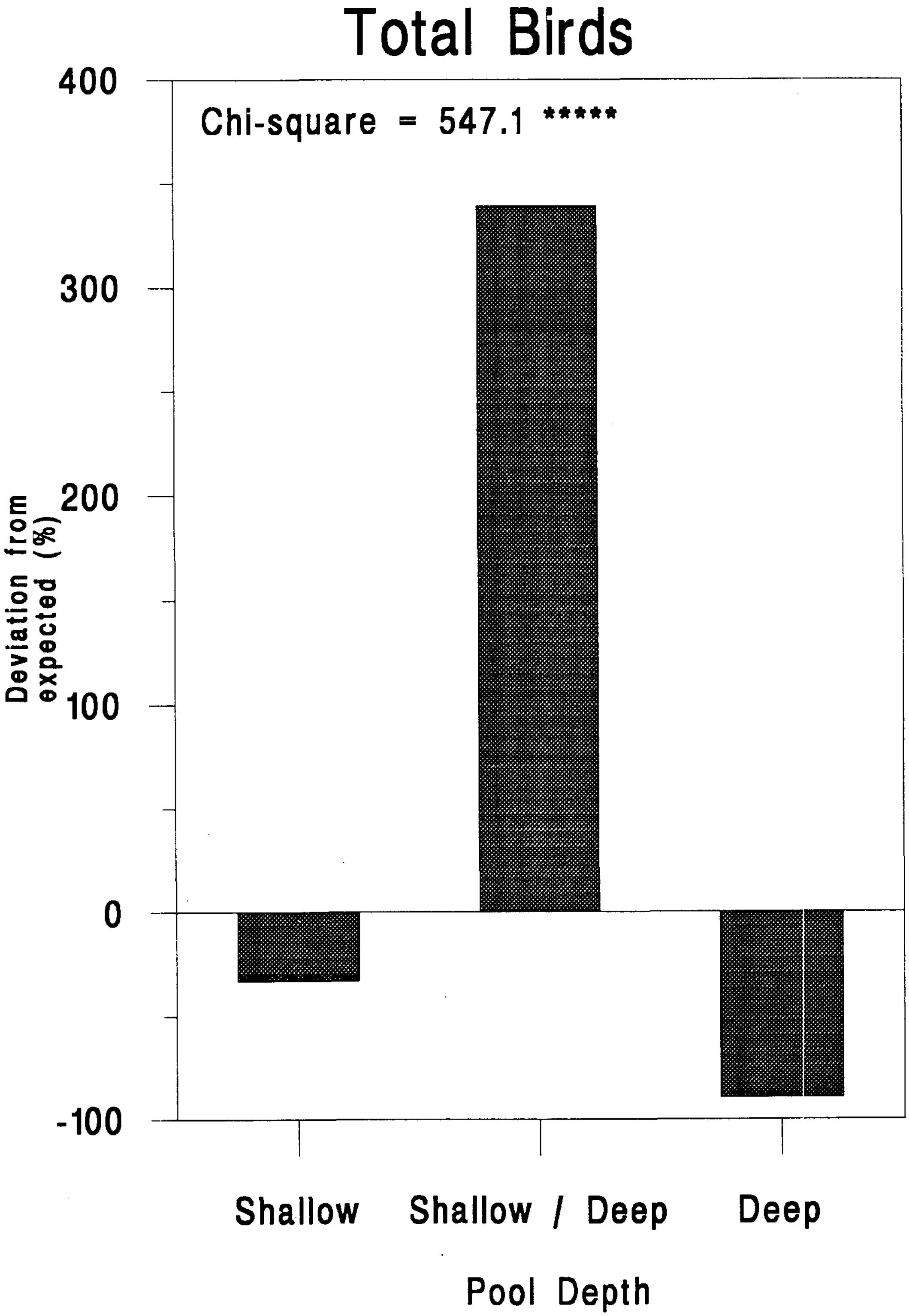
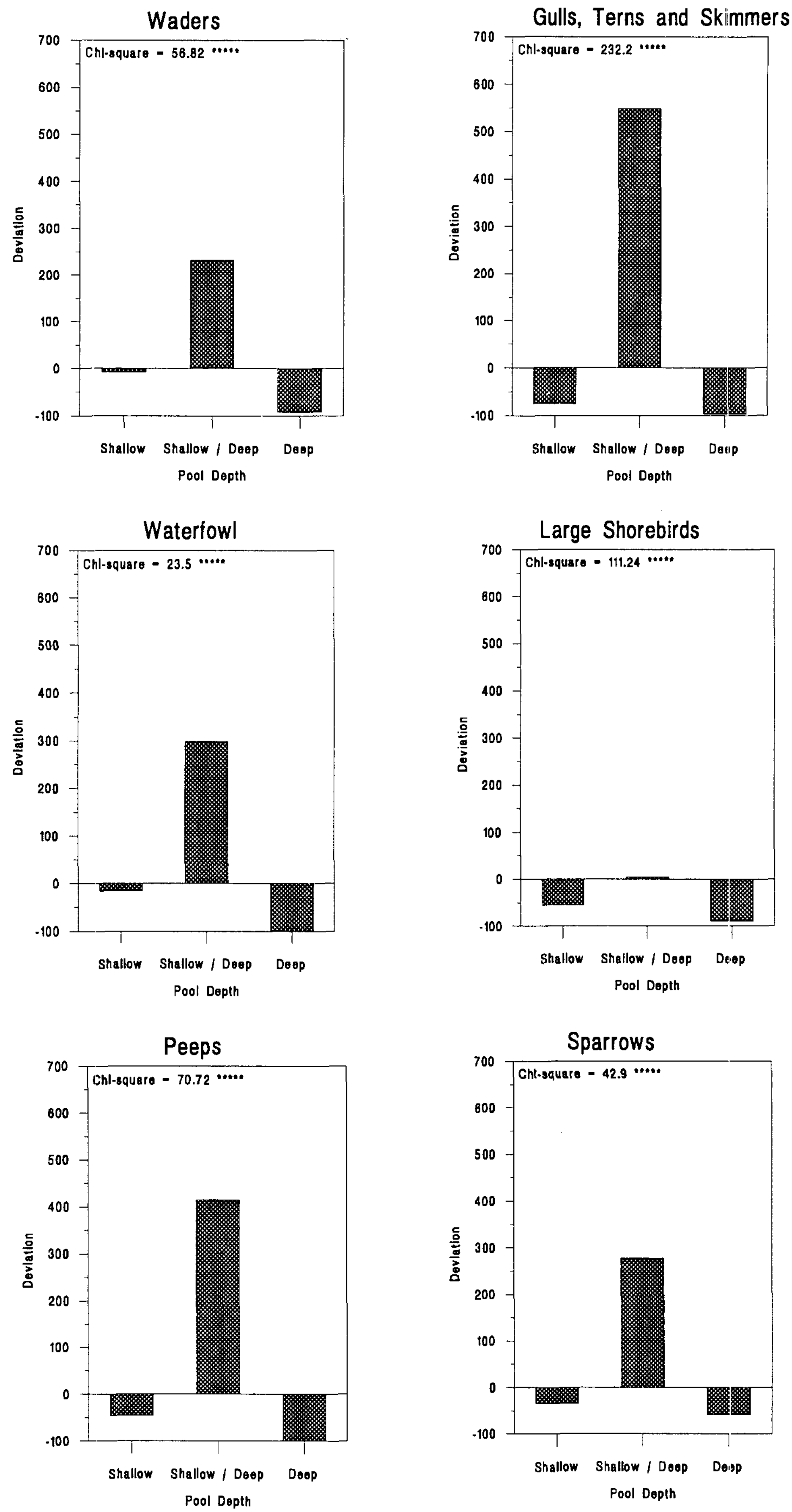
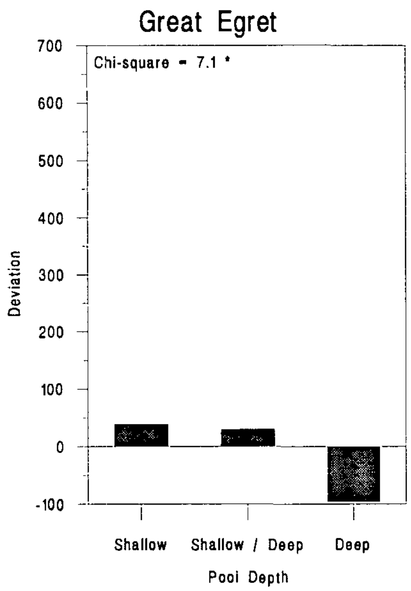
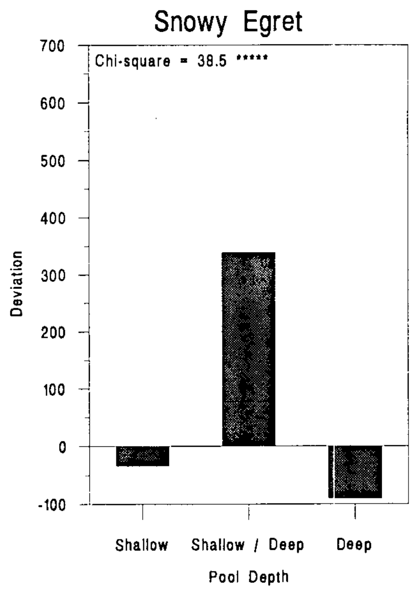

Frequency of Pool Use x Profile
Shallow
Graded
Pothole
Intermediate
x2 = 44.08
p < 0.001
x2 = 15.82
p < 0.005
x2 = 3.64
p < 0.05
% Pools
0
20
40
60
80
100
1-6
7-12
13-19
Frequency of Surveys with Birds

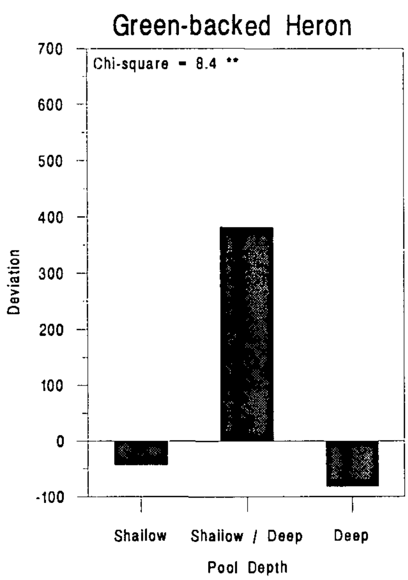
Figure 17. Effect of pool water depth on relative pool use (% deviation from expected based on total pool area per depth category) by total observed birds, guilds and target species. Chi-square statistics and significance values included. (***** = $p < 0.001$; **** = $p < 0.005$; *** = $p < 0.01$; ** = $p < 0.025$; * = $p < 0.05$).

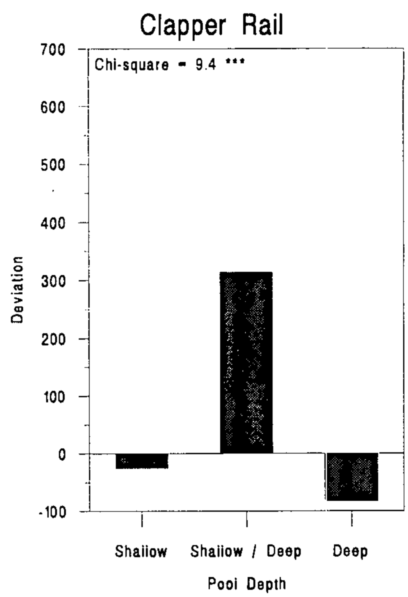

Total Birds
Chi-square = 547.1 *****
400
300
200
100
0
-100
Deviation from expected (%)
Shallow
Shallow / Deep
Deep
Pool Depth

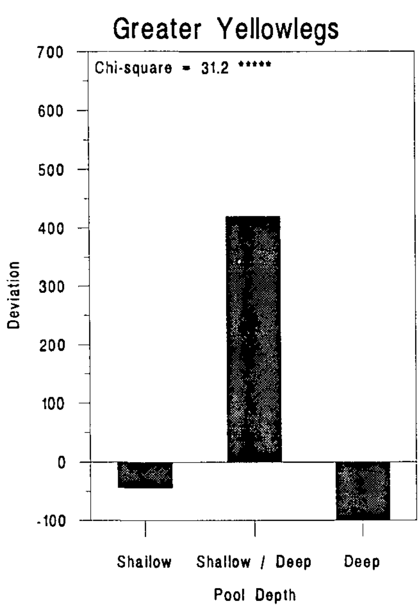

Waders
Chi-square = 56.82 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth
Gulls, Terns and Skimmers
Chi-square = 232.2 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth
Waterfowl
Chi-square = 23.5 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth
Large Shorebirds
Chi-square = 111.24 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth
Peeps
Chi-square = 70.72 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth
Sparrows
Chi-square = 42.9 *****
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth

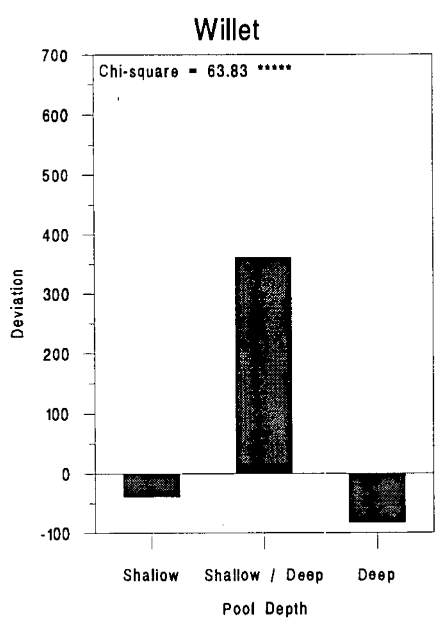

Great Egret
Chi-square = 7.1 *
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth


Snowy Egret
Chi-square = 38.5 *****
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth


Green-backed Heron
Chi-square = 8.4 **
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth


Clapper Rail
Chi-square = 9.4 ***
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth


Greater Yellowlegs
Chi-square = 31.2 *****
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth


Willet
Chi-square = 63.83 *****
700
600
500
400
300
200
100
0
-100
Deviation
Shallow
Shallow / Deep
Deep
Pool Depth

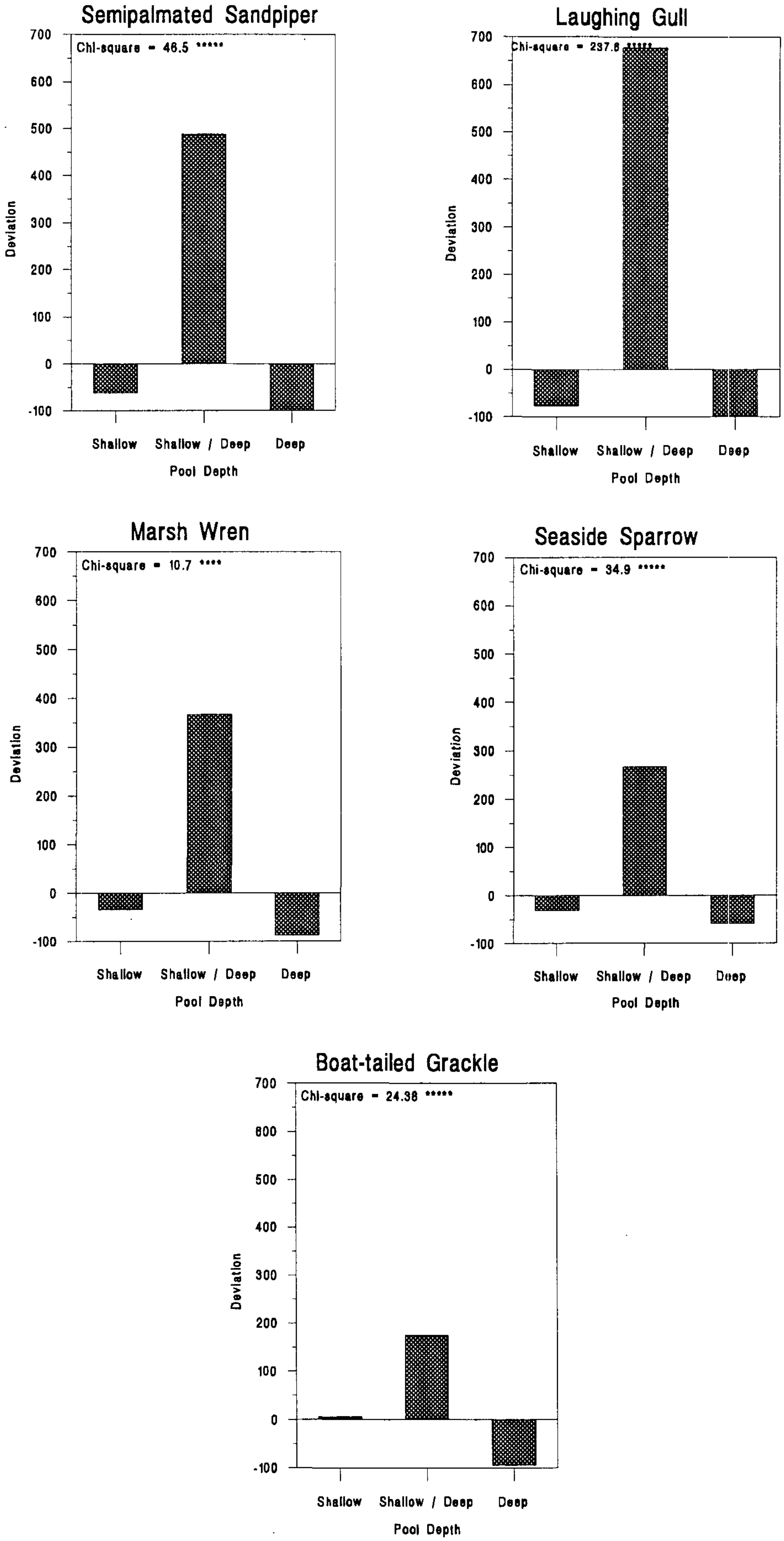

Semipalmated Sandpiper
Chi-square = 46.5 *****
Laughing Gull
Chi-square = 237.6 *****
Marsh Wren
Chi-square = 10.7 ****
Seaside Sparrow
Chi-square = 34.9 *****
Boat-tailed Grackle
Chi-square = 24.38 *****
Deviation
700
600
500
400
300
200
100
0
-100
Shallow
Shallow / Deep
Deep
Pool Depth

Figure 18. Location of birds within "pool complex" as a function of pool type. Chi-square results assume equal probability (Out vs. In).

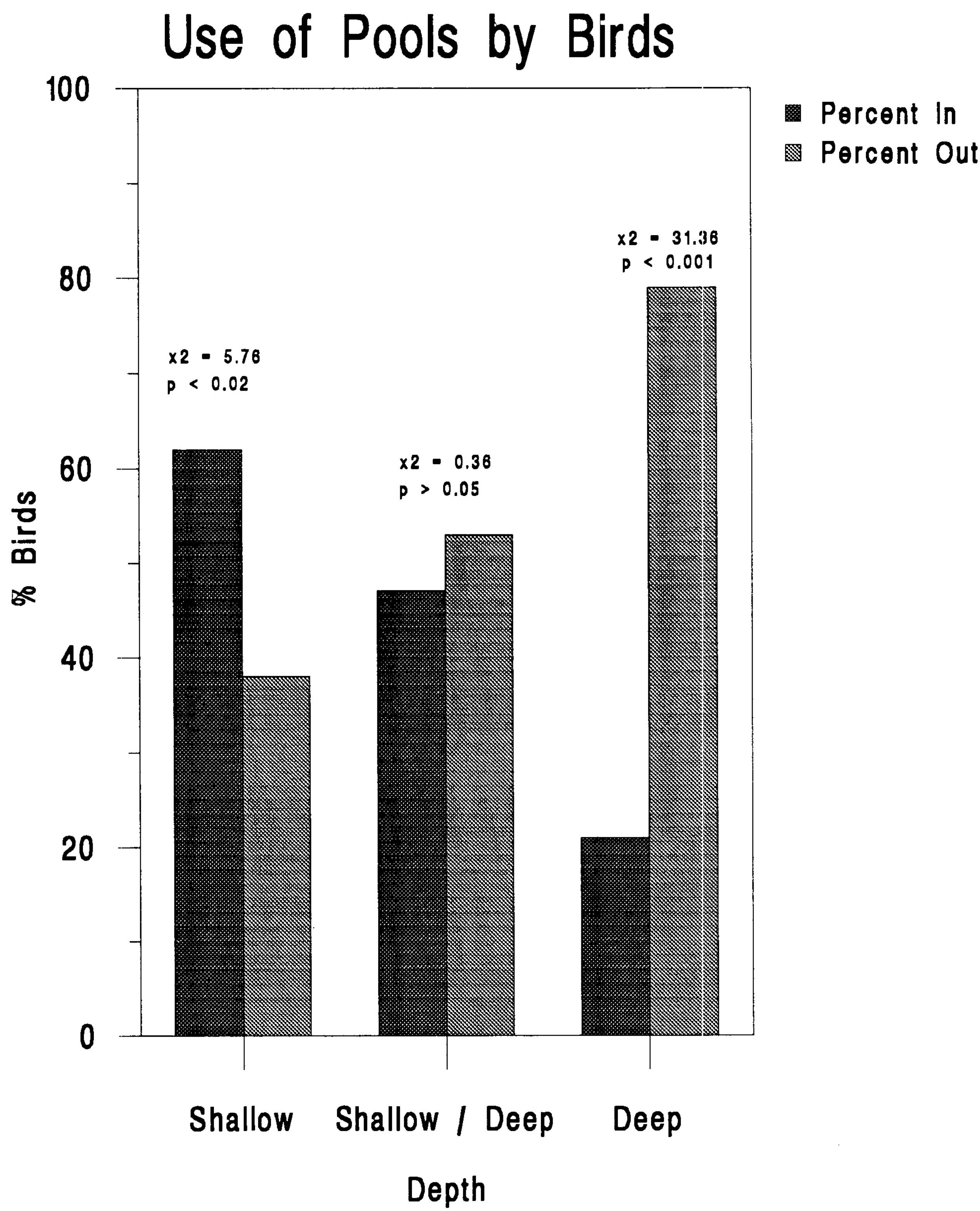
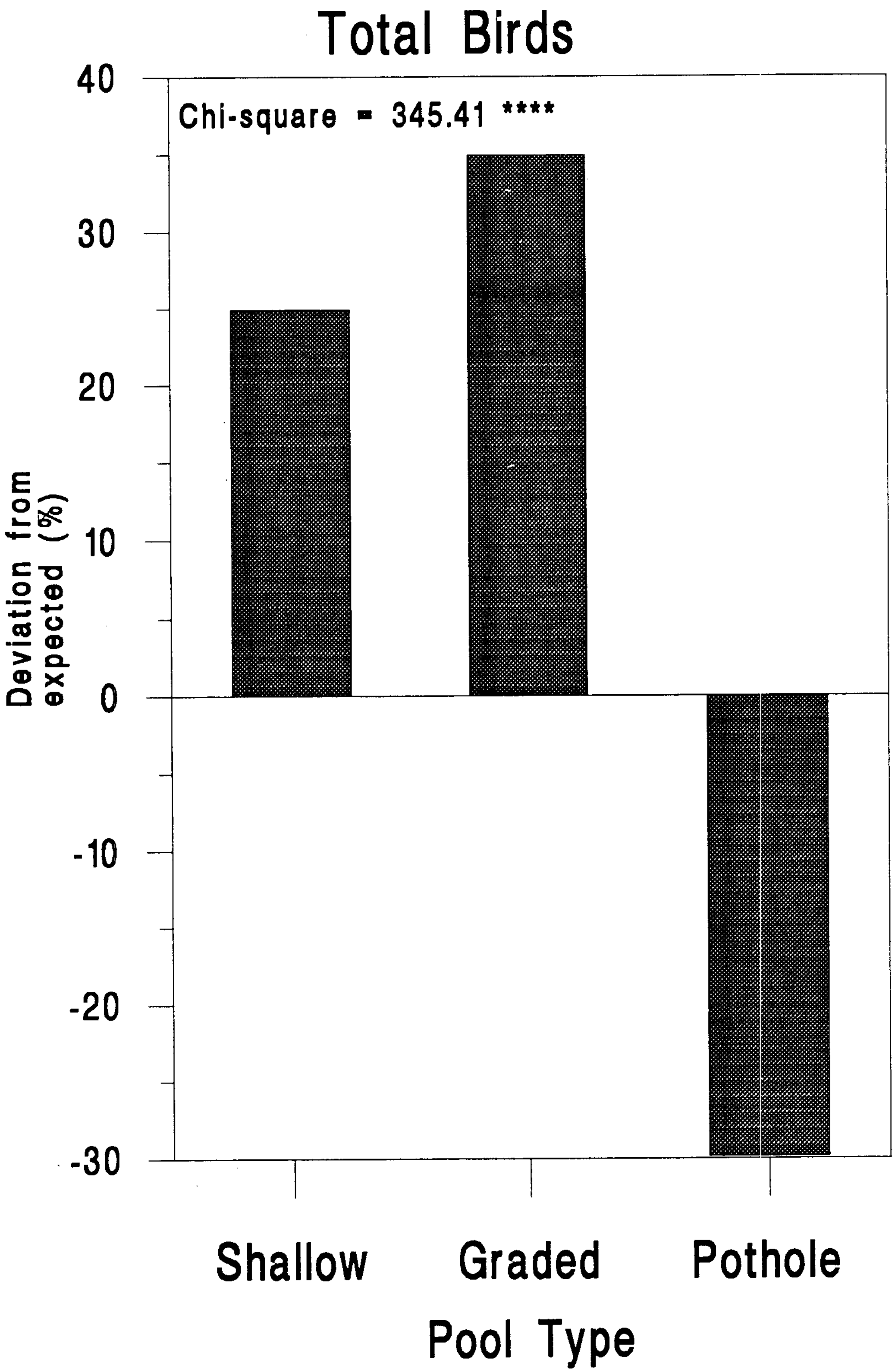
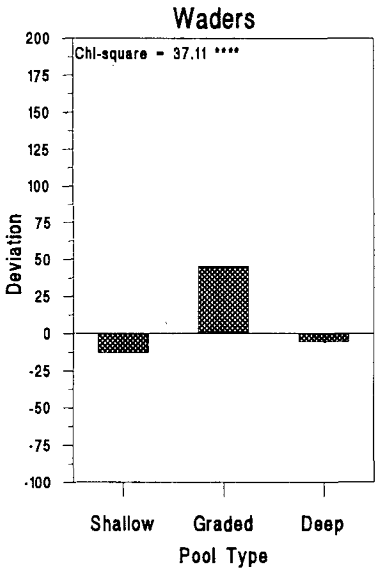
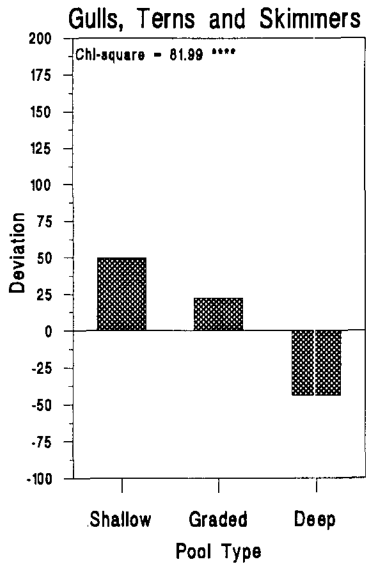
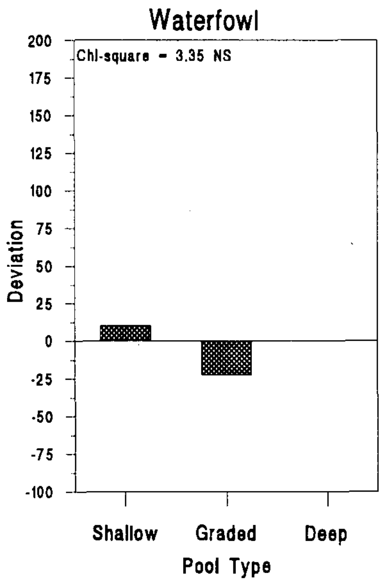

Use of Pools by Birds
Percent In
Percent Out
x2 = 5.76
p < 0.02
x2 = 0.36
p > 0.05
x2 = 31.36
p < 0.001
100
80
60
40
20
0
% Birds
Shallow
Shallow / Deep
Deep
Depth

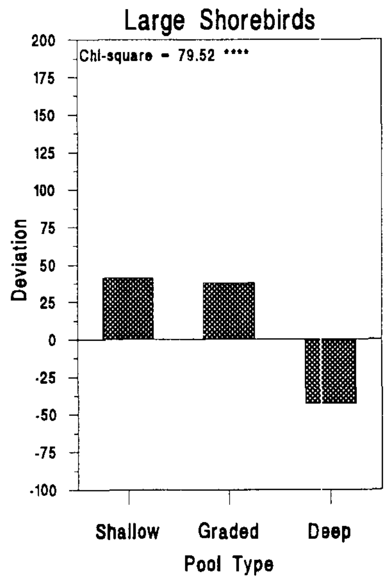
Figure 19. Abundance patterns (deviation from expected assuming equal probability within profile types) within profile types (Shallow, Graded, Pothole) of total observed birds, guilds and target species. Chi-square statistics and significance values given. (**** = p <0.001; *** = p <0.01).

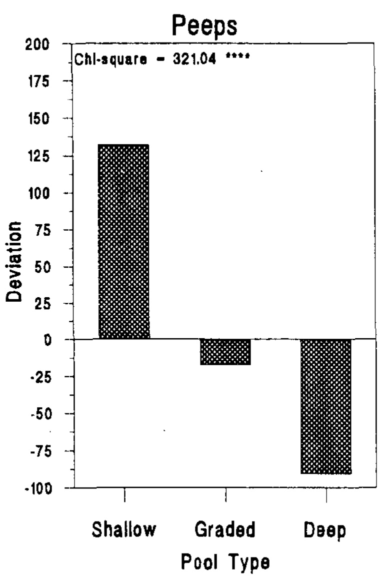

Total Birds
Chi-square = 345.41 ****
Deviation from expected (%)
40
30
20
10
0
-10
-20
-30
Shallow
Graded
Pothole
Pool Type

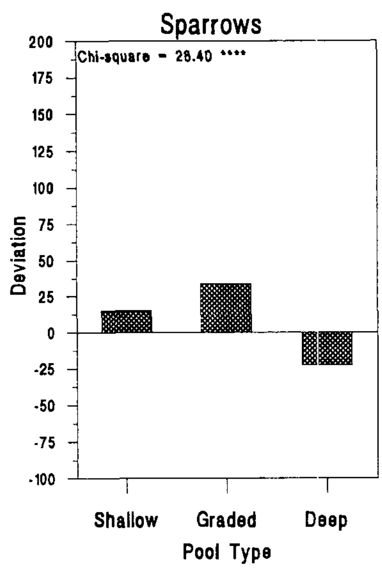

Waders
Chi-square = 37.11 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type

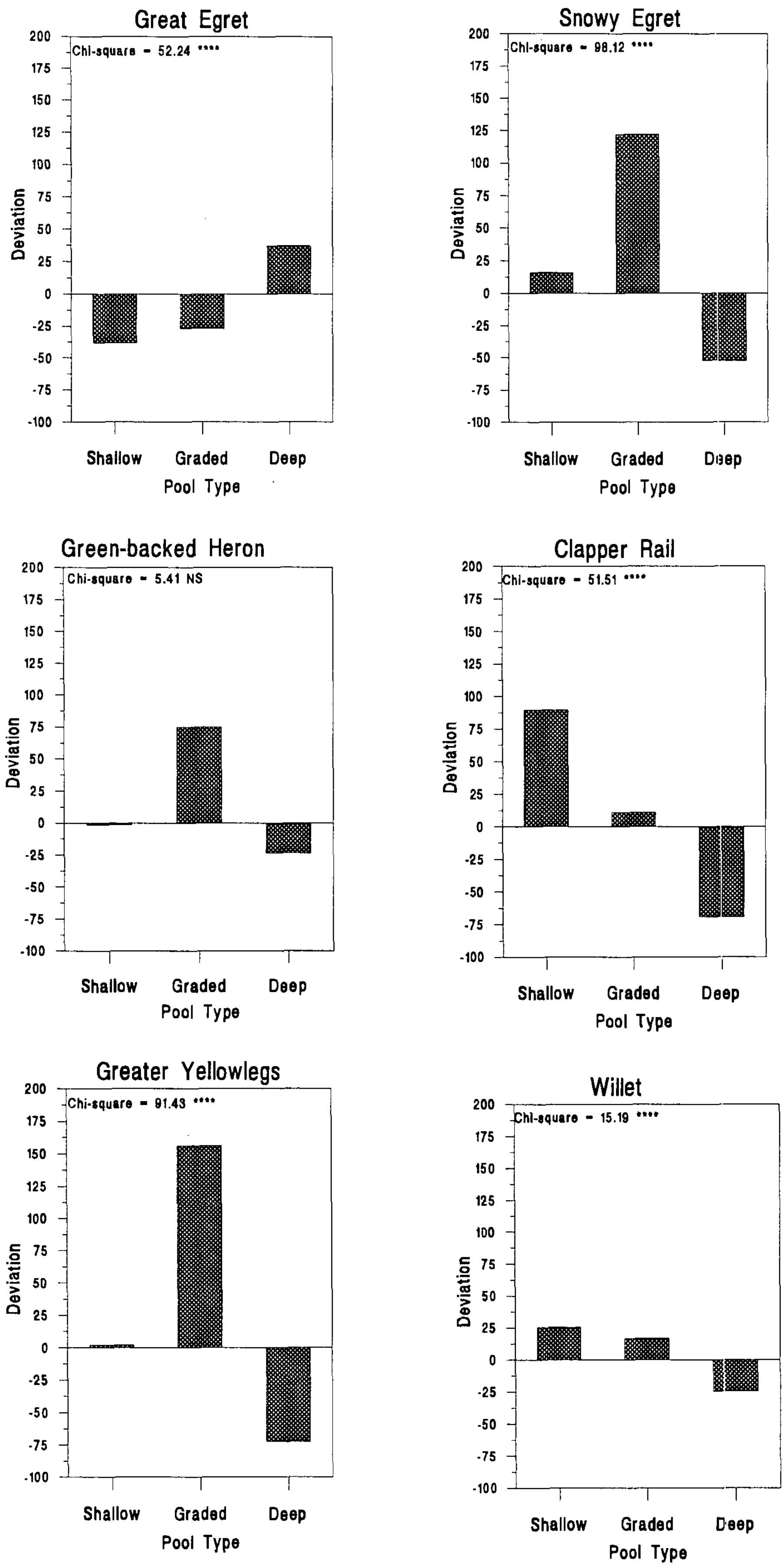

Gulls, Terns and Skimmers
Chi-square = 81.99 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type

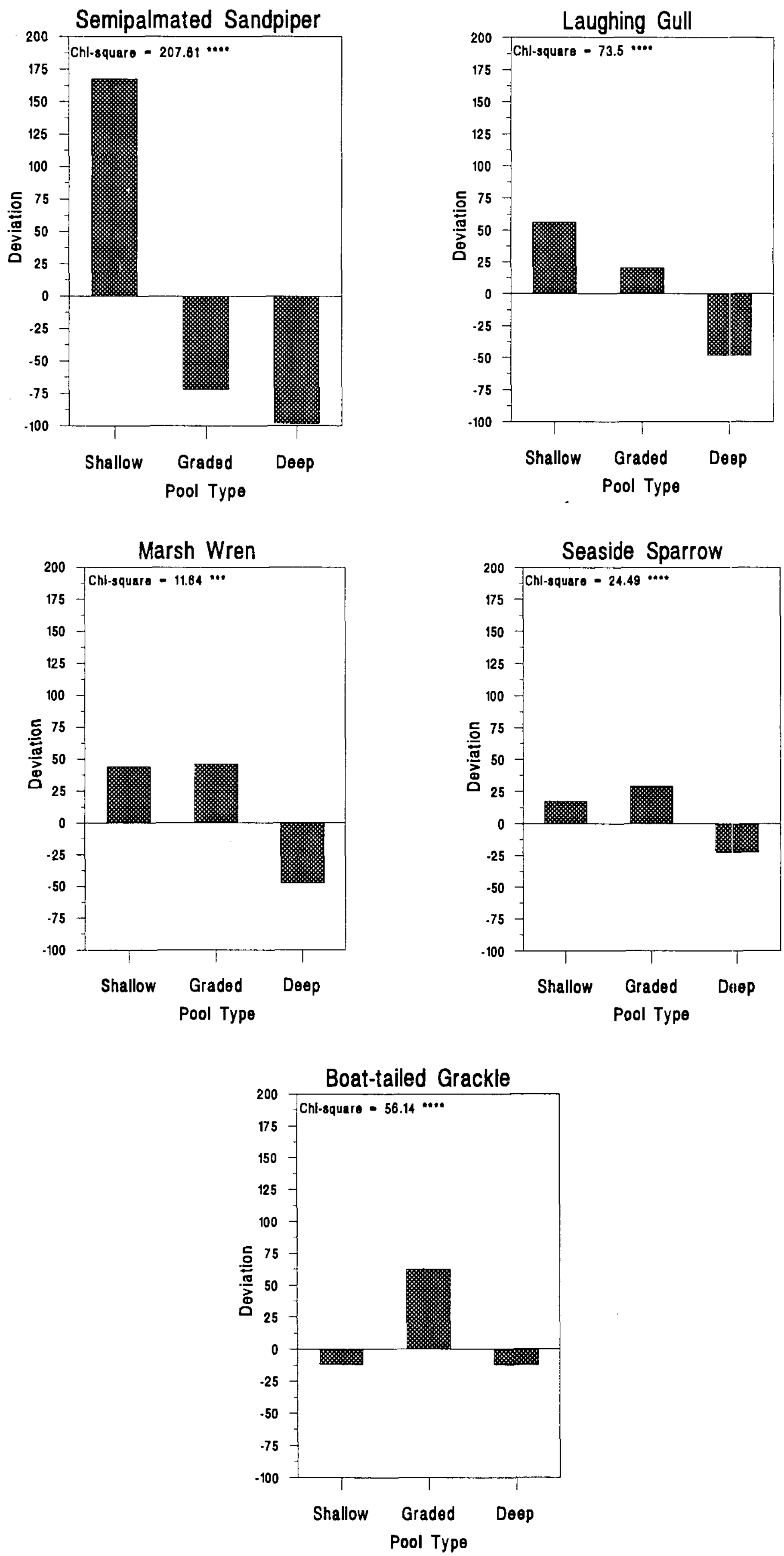

Waterfowl
Chi-square = 3.35 NS
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type


Large Shorebirds
Chi-square = 79.52 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type


Peeps
Chi-square = 321.04 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type


Sparrows
Chi-square = 26.40 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type


Great Egret
Chi-square = 52.24 ****
Snowy Egret
Chi-square = 98.12 ****
Green-backed Heron
Chi-square = 5.41 NS
Clapper Rail
Chi-square = 51.51 ****
Greater Yellowlegs
Chi-square = 91.43 ****
Willet
Chi-square = 15.19 ****
Deviation
Shallow
Graded
Deep
Pool Type
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100


Semipalmated Sandpiper
Chi-square = 207.81 ****
Laughing Gull
Chi-square = 73.5 ****
Marsh Wren
Chi-square = 11.64 ***
Seaside Sparrow
Chi-square = 24.49 ****
Boat-tailed Grackle
Chi-square = 56.14 ****
Deviation
200
175
150
125
100
75
50
25
0
-25
-50
-75
-100
Shallow
Graded
Deep
Pool Type

Intermediate pools, which were left out of the analysis due to compounding effects of having more than one profile type, accounted for over 37% of all bird observations and were used more often than other profile types (68% of intermediate pools used by birds).

Vegetation

Birds were found in unvegetated areas 61.6% of the time. The majority of birds within vegetated areas were passively associated with short cordgrass, which is prevalent around pool edges. See Figure 12 for substrate association of individual species and guilds.

Pool Associates were more likely to be associated with tidepools due to surrounding vegetation rather than inner pool characteristics. Marsh passerines were especially associated with the presence and area of black needlerush along pool edges. Marsh Wrens were found in black needlerush >95% of all observations and 75% of the wrens were located in pools with >100 m^2 of black needlerush (6 of 8 pools with >100 m^2 black needlerush had wrens as compared with 10 of 94 pools with <100 m^2). Seaside Sparrows were also dependent on edge vegetation. Singing males and perched individuals were found in black needlerush >51% of all observations while another 36% were found on the ground among short cordgrass.

Peeps were the only Pool Users highly associated with vegetation with >68% of all individuals foraging among cordgrass shoots.

DISCUSSION

Tidepools are attractive resource patches for a suite of birds within the tidal salt marsh landscape. Over a 6 month time period I found 6,475 birds of 54 different species associated with tidepools. Of the 303 tidepools surveyed, less than half (46.53%) were used and distribution of birds across tidepools was not normal. A small contingency of just four tidepools were used by 48% of all birds. Frequency of use (#surveys birds found at a tidepool) varied considerably with only 4% of tidepools having birds during all survey rounds. Tidepools were utilized primarily as foraging patches, especially by transient and resident species, such as Semipalmated Sandpipers and Snowy Egrets, which come into the marsh to find food. Results suggest that tidepools are not equal and that birds non-randomly choose tidepools based on some criteria of profitability dependent on the availability and accessibility of resources.

Two distinct categories of avian tidepool users were distinguished based on their behavior and location within the tidepool complex: 1) Pool Associates and 2) Pool Users. Pool Users included species actively using the pool as a resource patch (i.e. as a prey source). Pool Associates included species passively associated with the tidepool, rarely using pool resources more than other marsh habitat. Within the pool complex, Pool Associates were found within the surrounding edge landscape while Pool Users were associated with the intrinsic pool characters or a combination of the intrinsic pool and landscape features (see

Figure 5).

Use of tidepools by individual species varied seasonally (see Figure 7); however, tidepools were occupied throughout the entire study period with different species present during different windows of time. Tidal cycles also influenced bird use of tidepools with the majority of birds present during outgoing low tides. It is likely that prey abundance increased on outgoing tides as fish and crabs are replenished and trapped in the tidepools with the receding tides. Tidepool accessibility also increased as high tide water levels dropped, allowing birds to forage more easily in shallower water. Semipalmated Sandpipers were the only species to use incoming high tides more than expected. Many peeps are known habitat shifters, moving from their preferred mudflat foraging areas which are covered at high tides to higher elevated, exposed upper beaches or marshes where they can continue foraging during high tides (Burger et al. 1977, Connors et al. 1991).

Prey

Tidepools appeared to be viable patches of prey for possible avian predators and bird choice of certain tidepools may reflect the availability of prey resources. Blue crabs, fiddler crabs and fish were all prevalent in and around tidepools with fish the most abundant. Unlike more ephemeral foraging patches, tidepools were replenished twice daily, trapping fish during receding tides. Such non-ephemeral patches may prove more profitable to species, especially waders who are known to return to a previously used patch as long as patch resources are renewed sufficiently (Kushlan 1981).

Juvenile fish, especially *Fundulus* spp., were present in 92% of all tidepools, regardless of area or water depth, during $\geq$75% of surveys. Even the smallest of tidepools often had relatively large schools of fish within them and fish activity may have been an important factor in attracting birds to tidepools as noted by Master (1989). While I did not quantify fish abundance between pool types, Master (1989) found that deep pools had more fish than shallow pools.

Benthic Macrofauna

Core samples from tidepools revealed a wide variety of invertebrates, all documented prey of shorebirds and waders foraging within salt marshes (see Baker 1977, Baldassarre et al., Quammen 1984, Wenner and Beatty 1988). A total of 3,523 individuals of 16 taxa groups were found in benthic cores (N = 115) and tidepool infauna was dominated by a few species, especially annelid worms including Oligochaetes, *Asabellides oculata* and Capitellidae spp. Chironomidae larvae were the most abundant non-annelid. Similar taxa were found in salt marsh cores taken by Moy and Levin (1991) with 93% of all samples dominated by annelids, including oligochaetes, *Streblospio benedicti* and Capitellidae spp.

Significantly more individuals were present in the top 2 cm of substrate. This finding correlates with the habitat requirements of macrofauna which are typically found in the less anoxic layer of sediment (Wieser and Kanwisher 1961, Bell et al. 1978, Coull and Bell 1979). R. Raible (unpublished data in Moy and Levin 1991) found >85% of total infauna of salt marsh cores within the top 2 cm of the sediment water interface while McCann and

Levin (1989) found 87% of all oligochaetes in the top 4 cm. Macrofauna within these depths would be accessible to foraging shorebirds, especially in shallow waters.

The presence of *Spartina* culms had a substantial impact on macrofaunal distribution and abundance. Vegetated cores taken from the inner edges of pool with shallow water had significantly more macrofauna than unvegetated cores (G-statistic = 1692.5, $p < 0.001$). Rader (1984) showed that macrofaunal densities in cores with *Spartina* culms varied 3 to 90 times that of bare sediment. Many species, especially oligochaetes, take refuge in decaying *Spartina* stems as root mats may cause looser packing of sediment and thus, easier burrowing.

G-tests revealed significant effects of water depth on macrofaunal abundance in all treatments (see Tables 8 and 11), although species diversity was similar. Significantly more individuals were found in shallow water (either in pure shallow or graded tidepools) than deep water (deep or the deep areas of graded tidepools). However, significance may be an artifact of the increased amount of vegetation (cordgrass culms) in the substrate of many shallow tidepools, even though shoots were not present above the surface.

Relative abundance of macrofauna may also be correlated to predation by shorebirds, benthic feeding fish or crabs (all present in tidepools) which may affect the spatial distribution and density of some infauna (Kneib and Stiven 1978, Kneib and Stiven 1982, Quammen 1984).

Overall, tidepools are patches of prey for fish and invertebrate predators which are continually renewed with the exception of tidepools found in the less inundated, high marsh. Such stagnant pools were rarely visited by birds.

Area

Area proved to be a strong determinant of bird abundance within tidepools. Despite the large number of small tidepools (<50 m^2), they had significantly fewer birds than those >50 m^2. Tidepools >150 m^2 were the most attractive to all species and the four tidepools >400 m^2 accumulated approximately 48% of all observations. Frequency of use was directly related to pool area (see Figure 15) and along with abundance patterns suggest that birds key in to tidepool area.

Area of open water has long been targeted as a prime source of bird choice of patches. Baker et al. (1992) showed that bird abundance and diversity were related to area of open water of vernal pools. Both Erwin et al. (1994) and Burger et al. (1982) indicated that bird abundance was correlated with area of manmade pools, even though density may not be higher. Erwin et al (1994) showed that different bird groups were segregated in size preferences. Pools 0.03 to 0.06 ha were most attractive to waterfowl and pools >0.10 ha were best for shorebirds. My results showed that pools >0.02 ha were attractive to all species (which may be an artifact resulting from the small number of tidepools attracting a majority of birds) and gave a clear indication that small tidepools were considerably less desirable.

Speculation for the preference for large areas of open water suggest that larger area pools allow for better surveillance for predators or for enhanced feeding (Erwin et al. 1994). However, Master (1989) showed that while visitation rate of Snowy Egrets to tidepools in New Jersey increased with area, efficiency of prey capture remained the same. Larger areas do permit access for more birds to use tidepools and large mixed flock aggregations often gathered. Flocking effects may have affected use of tidepools as also noted by Master (1989, 1992).

Due to the large percentage of individuals present in such a few large tidepools, area had an overriding effect on other components affecting both Pool Associate and Pool User choice of tidepools (i.e. due to the large number of birds within a small number of tidepools it was difficult to flesh out variation between other tidepool components affecting bird choice of pools).

Vegetation

Since Pool Associates were found in the edge of the tidepool 98.5% of the time, they did not appear to benefit directly from tidepool prey resources (although association with tidepools may in some way be profitable), this group may be linked to tidepools because of landscape characteristics. Species associated with tidepool edges (i.e. Pool Associates) relied on vegetation as substrate for cover, perch sites during territorial defense, mate attraction and for building nests. The best examples of vegetational effects on bird abundance are the resident marsh passerines. Presence of both Seaside Sparrows and Marsh Wrens were directly related to the presence and area of edge vegetation.

While a small proportion of sparrows were seen walking on the mud edge of shallow pools, over 98% were located in the surrounding vegetation. I frequently flushed them (>55% total observations) from the ground where they foraged for seeds or small insects among short cordgrass (>36% total observations). Singing males and perched individuals were found in black needlerush (>51% total observations), which is often the highest point of vegetation in the marsh and may serve as a prime perching spot, especially for territorial males.

Marsh wrens were always found along the pool edge where they are near exclusive associates (>95%) of black needlerush in which they find cover and build their secretive nests. Observations of wrens were restricted to marshes with extensive black needlerush. Four Point, the largest study marsh, had little black needlerush and just 2 wrens. Sixteen of the 103 tidepools with black needlerush had wrens associated with them (2 pools had wrens and no black needlerush but, were within close proximity of pools with expansive black needlerush). The majority of wrens (75%) were located in pools with >100 m^2 black needlerush (6 of 8 pools with >100 m^2 black needlerush had wrens as compared with 10 of 94 with <100 m^2).

For species actively foraging in tidepools (Pool Users) vegetation served as both a prey base and mode of cover. Invertebrate predators were linked to patches of short cordgrass shoots within the shallow edges of tidepools where, as noted by benthic macrofauna results, invertebrate densities are significantly higher than in bare sediment. The majority of all peeps were associated with cordgrass shoots in shallow water where they probed the mud around the shoots or gleaned stalks for invertebrates.

Depth

Relative abundance, richness and frequency of use by bird species and guilds of deep pools was significantly less than in shallow or shallow/deep tidepools; with multi-depth tidepools having more birds and being used more frequently than all others. Birds that were associated with deep tidepools were more likely to be found on the edge of the tidepool rather than in the pool waters (i.e. Pool Associates such as Seaside Sparrows); contrasting with the other pool types (see Figure 18).

Morphological limitations of water depth appear to be a stringent limiter of the habitat a bird can access while foraging within a body of water. Depth that a species will exploit varies with both size and foraging guild of the species. Small birds, especially peeps, and other invertebrate foragers frequented shallow (usually <2 cm deep) portions of the graded depth pools where they can access bottom dwelling invertebrates along the mud interface. Small shorebirds were almost never found in purely deep water pools. Likewise, Laughing Gulls and Waterfowl chose to forage in the shallow waters of shallow or shallow/deep pools. Dabbling ducks were observed sieving mud from the pool bottom for invertebrates, often in association with small patches of *Ruppia maritima*, which they could only access in shallow waters, especially at low tides (see also Burger et el. 1984 and

Erwin et al. 1994).

Although capable of accessing deeper (10-20 cm) waters, larger waders and fish predators also shunned deep (>20 cm) pools, preferring to frequent shallow/deep pools. It has been suggested that species which forage by wading, may have difficulty wading in water deeper than tarsus length where they may not only be unable to access prey, but may be less likely to accurately assess prey resources. Even species such as Green-backed Herons which forage from the edge of pools, thus not limited morphologically by depth, use deep pools significantly less than other pool types.

Master (1989) showed that visitation rates of Snowy Egrets to tidepools decreased with increasing pool depth. In Erwin et al (1994), depth affected only a few bird groups using manmade pools; however, all study pools had depths > 15 cm and had little available shallow edge. Such deep pools appeared to attract many more waterfowl and large waders than shorebirds and the authors point out that pools with shallow areas would be more attractive to a wider diversity of species.

Profile

Tidepools with steep, vertical pothole edges were used by significantly fewer birds than those with shallow or graded edges. Shallow water along edges attracted smaller shorebirds, passerines, waterfowl and, especially, other invertebrate foragers which could access the mud bottom or vegetation for macrofauna. Steep, vertical sided pools were unsuitable for use by smaller birds, as also noted by Brush et al. (1986) and pothole edges may also deter larger waders. Master (1989) showed that Snowy Egrets were more efficient in pannes with gradually sloping sides rather than steep vertical sides.

Summary

Both my results and those of Watts (1992) highlight natural tidepools as integral components of the salt marsh landscape for avian species. Studies by Clarke et al. (1984) and Brush et al. (1986) indicate that marsh profitability for birds is increased by the addition of manmade tidepools within the marsh.

Tidepools >0.02 ha with a variety of water depths, some portion of shallow or graded sides with cordgrass shoots present, and edge vegetation including large patches of black needlerush and short cordgrass comprise the most attractive setting for the widest diversity and abundance of birds. Intermediate tidepools drew an overwhelming proportion of the bird observations throughout the entire study. All of these intermediate pools were >150 m^2 and had a variety of water depth and edge types, perhaps a result of the gradual erosion and expansion of the tidepool over time.

Management

In the past, salt marsh ponds have been constructed in wetland management and are typically pothole in nature with deep water and steep, vertical sides. Natural tidepools are much more variable in physiognomy and complex pools with a variety of water depths, ranging from open mud and shallow <2 cm water to areas of deep water, and graded edges appear much more conducive to attracting more and a higher diversity of species which can access needed resources.

I suggest, as have others (including Brush et al. 1986, Erwin et al. 1994), that instead of small, pothole pools, that large (>0.02 ha) tidepools with graded edges and a variety of depths be formed. These pools, when surrounded by a variety of natural low marsh vegetation, including black needlerush and short cordgrass may serve as more attractive resource patches within managed marshes.

This study showed that tidepools are integral patches of prey for foraging transient and resident birds and likewise, attract a wide diversity of associated species found along the pool edge suggesting that the tidepool complex is an integral part of the landscape within the tidal salt marshes of the lower Chesapeake Bay

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Appendix I: Listing of bird species observed during surveys categorized into guilds.

Guild/Species	Guild/Species
Waders	Waterfowl
Least Bittern	Black Duck
Great blue Heron	Mallard
Great Egret	Blue-winged Teal
Snowy Egret	Red-breasted Merganser
Tricolored Heron	
Green-backed Heron	Sparrows
Little blue Heron	Sharp-tailed Sparrow
Glossy Ibis	Seaside Sparrow
White Ibis	Song Sparrow
Yellow-crowned Night-Heron	Unidentified sparrows
Gulls, Terns, and Skimmers	
Laughing Gull	
Herring Gull	
Ring-billed Gull	
Common Tern	
Forsters Tern	
Least Tern	
Royal Tern	
Black Skimmer	
Shorebirds-Large	
Greater Yellowlegs	
Lesser Yellowlegs	
Stilt Sandpiper	
Black-necked Stilt	
Whimbrel	
Willet	
Killdeer	
Spotted Sandpiper	
American Oystercatcher	
Short-billed Dowitcher	
Peeps	
Semipalmated Sandpiper	
Western Sandpiper	
Least Sandpiper	
Unidentified peeps	

Appendix II: List of scientific names and guild designations for species detected. Prey represents most commonly taken prey according to Bent and Ehrlich et al. 1988.

Common Name	Scientific Name	Guild[a]	User Group[b]	Prey[c]
Least Bittern	*Ixobrychus exilis*	WD	R	F,AI,I
Great Blue Heron	*Ardea herodias*	WD	R	F,AI
Great Egret	*Casmerodius albus*	WD	R	F,AI
Snowy Egret	*Egretta thula*	WD	R	F,AI,I
Little Blue Heron	*Florida caerulea*	WD	R	F,AI
Tricolored Heron	*Hydranassa tricolor*	WD	R	F,AI
Green-backed Heron	*Butorides striatus*	WD	R	F,AI,W
Yellow-crowned Night-heron	*Nyctanassa violacea*	WD	R	C
White Ibis	*Eudocimus albus*	WD	T	F,C,AI
Glossy Ibis	*Plegadis falcinellus*	WD	T	AI,I
American Black Duck	*Anas rubripes*	WF	RB	V,AI
Mallard	*Anas platyrhynchos*	WF	RB	V,AI,I
Blue-winged Teal	*Anas discors*	WF	T	V,AI
Red-breasted Merganser	*Mergus serrator*	WF	T	F
Osprey	*Pandion haliaetus*		R	F
Northern Harrier	*Circus cyaneaus*		RB	SM
Clapper Rail	*Rallus longirostris*		RB	C,AI,I
Virginia Rail	*Rallus limicola*		RB	I,AI,V
Sora	*Porzana carolina*		RB	V,AI,I
Killdeer	*Charadrius vociferus*	SH	R	I,AI
American Oystercatcher	*Haematopus palliatus*	SH	R	C,AI
Black-necked Stilt	*Himantopus mexicanus*	SH	T	AI,I
Greater Yellowlegs	*Tringa malanoleuca*	SH	T	F,AI,I
Lesser Yellowlegs	*Tringa flavipes*	SH	T	I,C,F
Willet	*Catoptrophorus semipalmatus*	SH	RB	F,AI,W
Spotted Sandpiper	*Actitis macularia*	SH	T	I,AI
Whimbrel	*Numenius phaeopus*	SH	T	AI,I
Semipamated Sandpiper	*Calidris pusilla*	PE	T	W,I,AI
Western Sandpiper	*Calidris mauri*	PE	T	W,I,AI
Least Sandpiper	*Calidris minutilla*	PE	T	W,I,AI
Stilt Sandpiper	*Micropalama himantopus*	SH	T	AI
Short-billed Dowitcher	*Limnodromus griseus*	SH	T	AI,I
Laughing Gull	*Larus atricilla*	GU	R	F,C,AI
Ring-billed Gull	*Larus delawarensis*	GU	T	F,I
Herring Gull	*Larus argentatus*	GU	R	F,C
Royal Tern	*Sterna maxima*	GU	R	F
Common Tern	*Sterna hirundo*	GU	R	F,AI,I
Forsters Tern	*Sterna forsteri*	GU	R	F,AI,I
Least Tern	*Sterna albifrons*	GU	R	F,AI

Appendix II: continued

Black Skimmer	*Rhynchops niger*	GU	R	F
Belted Kingfisher	*Megaceryle alcyon*		R	F
Eastern Kingbird	*Tyrannus tyrannus*		RB	I
Purple Martin	*Iridoprocne subis*		R	I
Tree Swallow	*Tachycineta bicolor*		T	I
Barn Swallow	*Hirundo rustica*		R	I
Marsh Wren	*Cistothorus palustris*		RB	I
Sharp-tailed Sparrow	*Ammospiza caudacutus*	SP	T	I,V
Seaside Sparrow	*Ammospiza maritima*	SP	RB	I,V
Song Sparrow	*Melospiza melodia*	SP	RB	I,V
Red-winged Blackbird	*Agelaius phoeniceus*		RB	I,V
Boat-tailed Grackle	*Quiscalus quisqula*		RB	F,I,V
Common Grackle	*Quiscalus major*		R	F,I,V
Brown-headed Cowbird	*Molothrus ater*		R	I,AI,V

[a] Guilds: WD = Waders, WF = Waterfowl, SH = Large shorebirds, PE = Peeps, GU = Gulls, terns, and skimmers, SP = Sparrows.
[b] Prey: AI = Aquatic Invertebrates, W = Benthic worms, C = Crustaceans, F = Fish, I = Invertebrates, SM = Small mammals, V = Vegetation/Seeds.
[c] User Groups: R = Residents, RB = Resident Breeders, T = Transients.

Appendix III: Weekly, seasonal and total summaries of bird species detected. Species designated by AOU code. Standardized totals (total birds/total surveys) are in parentheses.

AOU	Spring							Summer								
Code	1	2	3	4	5	6	Total	1	2	3	4	5	6	7	8	Total
LEBI	0	0	0	2(.5)	0	0	2 (.09)	1(.25)	0	0	2(.5)	0	1(.25)	0	0	4(.18)
GTBH	1(.25)	0	1(.25)	2(.2)	1(.25)	4(1)	9 (.41)	4(1)	3(.75)	1(.25)	20(5)	10(2.5)	6(1.5)	1(.25)	3(.75)	48(1.5)
GREG	14(3.5)	0	0	0	2(.5)	1(.25)	17(.77)	7(1.75)	2(.5)	0	8(2)	41(10.25)	23(5.75)	3(.75)	2(.5)	86(2.69)
SNEG	10(2.5)	0	10(2.5)	5(1.25)	2(.5)	0	27(1.23)	6(1.5)	4(1)	1(.25)	9	48(12)	18(4.5)	11(2.75)	13(3.25)	110(3.44)
LBHE	0	0	0	0	0	0	0	0	0	0	0	0	1(.25)	0	0	1(.03)
TRHE	0	0	1(.25)	0	0	0	1(.05)	0	0	0	1(.25)	6(1.5)	21(5.25)	11(2.75)	16(4)	55(1.72)
GNBH	1(.25)	0	1(.25)	1(.25)	1(.25)	1(.25)	5(.23)	5(1.25)	9(2.25)	16(4)	8(2)	7(1.75)	2(.5)	7(1.75)	4(1)	58(1.81)
YCNH	0	0	0	0	0	0	0	0	2(.5)	0	0	0	0	0	1(.25)	3(.09)
WHIB	0	0	0	0	0	0	0	0	0	0	4(1)	4(1)	0	0	14(3.5)	22(.69)
GLIB	0	0	0	0	0	0	0	0	0	0	1(.25)	1(.24)	0	0	0	2(.06)
ABDU	3(.75)	0	2(.5)	5(1.25)	13(3.25)	4(1)	27(1.23)	1(.25)	2(.5)	0	0	0	0	3(.75)	3(.75)	9(.28)
MALL	2(.5)	0	2(.5)	2(.5)	5(1.25)	5(1.25)	16(.07)	3(.75)	0	1(.25)	1(.25)	7(1.75)	0	4(1)	10(2.5)	26(.81)
BWTE	0	0	0	1(.25)	0	2(.5)	3(.14)	1(.25)	0	0	0	0	0	0	0	1(.03)
RBME	4(1)	0	0	0	0	0	4(.18)	0	0	0	0	0	0	0	0	0
OSPR	0	0	0	0	0	0	0	0	1(.25)	0	0	0	0	0	0	1(.03)
NOHA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CLRA	6(1.5)	2(1)	1(.25)	6(1.5)	2(.5)	4(1)	21(.96)	13(3.25)	11(2.75)	5(1.25)	11(2.75)	4(1)	3(.75)	10(2.5)	16(4)	73(2.28)
VIRA	1(.25)	0	0	0	0	0	1(.05)	0	0	0	0	0	0	0	0	0
SORA	1(.25)	0	0	0	0	0	1(.05)	0	0	0	0	0	0	0	0	0
KILL	0	0	0	0	0	1(.25)	1(.05)	2(.5)	12(3)	3(.75)	1(.25)	1(.25)	1(.25)	1(.25)	4(1)	25(.78)
AMOY	0	0	0	0	0	3(.75)	3(.14)	0	0	0	0	0	4(1)	4(1)	0	8(.25)
BNST	0	0	0	0	0	0	0	0	0	0	0	1(.25)	0	0	0	1(.03)
GRYE	19(4.75)	1(.5)	2(.5)	0	0	0	22(1)	0	0	7(1.75)	24(6)	20(5)	35(8.75)	17(4.25)	16(4)	119(3.72)
LEYE	3(.75)	0	0	0	0	0	3(.14)	0	0	0	0	0	1(.25)	0	1(.25)	2(.06)
WILL	39(9.75)	8(4)	26(6.5)	40(10)	18(4.5)	42(10.5)	173(7.86)	42(10.5)	55(13.75)	44(11)	46(11.5)	10(2.5)	28(7)	14(3.5)	5(1.25)	244(7.63)
SPSA	0	0	0	2(.5)	0	0	2(.09)	0	0	0	0	0	0	0	0	0
WHIM	3(.75)	0	0	0	0	0	3(.14)	0	0	0	0	0	0	0	0	0
SESA	7(1.75)	2(1)	70(17.5)	93(23.25)	100(25)	23(5.75)	295(13.41)	0	0	0	0	0	0	0	0	0
WESA	0	0	0	0	0	0	0	0	0	0	1(.75)	0	0	0	0	1(.03)
LESA	34(9.75)	1(.5)	1(.25)	1(.25)	0	0	37(1.68)	0	0	3(.75)	8(2)	19(4.75)	8(2)	14(3.5)	51(12.75)	103(3.22)
STSA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SBDO	16(4)	0	5(1.25)	8(2)	4(1)	0	33(1.5)	0	0	0	2(.5)	3(.75)	8(2)	6(1.5)	9(2.25)	28(.88)
LAGU	10(2.5)	5(2.5)	1(.25)	4(1)	5(1.25)	3(.75)	28(1.27)	15(3.75)	15(3.75)	42(10.5)	20(5)	40(10)	68(17)	38(9.5)	98(24.5)	336(10.5)
RBGU	1(.25)	0	0	0	0	0	1(.05)	0	0	0	0	0	0	0	0	0
HERG	0	0	0	0	0	0	0	2(.5)	0	0	0	0	3(.75)	0	0	5(.16)
ROYT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
COTE	0	0	0	0	0	0	0	0	0	0	0	4(1)	16(4)	4(1)	6(1.5)	30(.94)
FOTE	2(.5)	0	0	0	0	1(.25)	3(.14)	0	0	0	4(1)	1(.25)	0	0	2(.5)	7(.22)
LETE	0	0	0	0	0	1(.25)	1(.05)	1(.25)	1(.25)	0	0	0	0	0	0	2(.06)

Appendix III: Continued

AOU				Spring				Summer								
Code	1	2	3	4	5	6	Total	1	2	3	4	5	6	7	8	Total
BLSK	0	0	0	0	0	0	0	0	2(.5)	0	0	0	0	0	4(1)	6(.19)
BEKI	0	0	0	0	0	0	0	0	0	0	1(.25)	0	0	0	0	1(.03)
EAKI	0	0	0	0	0	1(.25)	1(.05)	0	0	0	0	0	0	0	2(.5)	2(.06)
PUMA	0	0	0	0	0	0	0	0	1(.25)	0	0	0	0	0	0	1(.03)
TRES	4(1)	0	3(.75)	0	0	0	7(.32)	0	0	0	0	0	0	0	0	0
BARS	1(.25)	0	6(1.5)	3(.75)	5(1.25)	11(2.75)	26(1.18)	2(.5)	11(2.75)	1(.25)	8(2)	6(1.5)	10(2.5)	12(3)	12(3)	62(1.94)
MAWR	7(1.75)	6(3)	5(1.25)	6(1.5)	0	3(.75)	27(1.23)	6(1.5)	11(2.75)	4(1)	4(1)	3(.75)	3(.75)	4(1)	1(.25)	36(1.13)
STSP	4(1)	0	1(.25)	5(1.25)	1(.25)	0	11(.5)	0	0	0	0	0	0	0	0	0
SESP	13(3.25)	5(2.5)	13(3.25)	23(5.75)	24(6)	32(8)	110(5)	24(6)	49(12.25)	56(14)	43(10.75)	55(13.75)	62(15.5)	59(14.75)	72(18)	420(13.13)
SOSP	0	0	0	0	0	0	0	0	1(.25)	0	0	0	0	0	0	1(.03)
RWBL	2(.5)	0	3(.75)	8(2)	3(.75)	4(1)	20(.9)	9(2.25)	6(1.5)	6(1.5)	2(.5)	25(6.25)	5(1.25)	0	0	53(1.66)
BTGR	2(.5)	1(.5)	5(1.25)	20(5)	11(2.75)	3(.75)	42(1.91)	9(2.25)	80(20)	11(2.75)	17(4.25)	23(5.75)	20(5)	8(2)	30(7.5)	198(6.19)
COGR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BHCO	0	0	0	0	0	0	0	0	0	0	4(1)	0	0	0	0	4(.18)
CROW?	0	0	0	0	0	0	0	0	1(.25)	0	0	0	0	0	0	1(.03)
PEEP?	0	1(.5)	0	0	0	1(.25)	2(.09)	0	0	0	2(.5)	0	1(.25)	0	2(.5)	5(.16)
SPARROW	9(2.25)	0	0	0	0	0	9(.41)	0	0	0	0	0	0	0	0	0
Total	**219 (54.75)**	**32 (16)**	**159 (39.75)**	**237 (59.25)**	**197 (49.25)**	**150 (37.5)**	**994 (45.18)**	**153 (38.25)**	**279 (69.75)**	**201 (50.25)**	**252 (63)**	**339 (84.75)**	**348 (87)**	**231 (57.75)**	**397 (99.25)**	**2200 (68.75)**
Species Richness	**27**	**10**	**20**	**20**	**16**	**21**	**37**	**19**	**21**	**15**	**26**	**23**	**24**	**20**	**26**	**42**

Appendix III: Continued

AOU				Fall							
Code	1	2	3	4	5	6	7	8	9	Total	Total for all Seasons
LEBI	0	0	0	0	0	0	0	0	0	0	6
GTBH	7(2.75)	1(.25)	10(2.5)	3(.75)	6(1.5)	13(3.25)	1(.25)	0	1(.25)	42(1.17)	99
GREG	39(9.75)	9(2.5)	22(5.5)	1(.25)	10(2.5)	267(66.75)	1(.25)	0	2(.5)	351(9.75)	454
SNEG	89(22.25)	25(6.25)	100(5)	5(1.25)	48(12)	46(11.5)	0	2(.5)	4(1)	319(8.86)	456
LBHE	2(.5)	0	0	0	1(.25)	1(.25)	0	0	0	4(.11)	5
TRHE	12(3)	11(2.75)	10(2.5)	5(1.25)	6(1.5)	12(3)	2(.5)	0	0	58(1.61)	114
GNBH	9(2.25)	3(.75)	3(.75)	2(.5)	4(1)	4(1)	3(.75)	0	1(.25)	29(.81)	92
YCNH	0	0	0	0	0	1(.25)	0	0	0	1(.03)	4
WHIB	1(.25)	0	11(2.75)	0	0	0	0	0	0	12(.33)	34
GLIB	13(3.25)	4(1)	9(2.25)	0	5(1.25)	10(2.5)	0	0	0	41(1.14)	43
ABDU	0	0	3(.75)	26(6.5)	64(16)	111(27.75)	10(2.5)	20(5)	32(8)	266(7.39)	302
MALL	1(.25)	1(.25)	1(.75)	0	4(1)	3(.75)	2(.5)	2(.5)	5(1.25)	19(.53)	61
BWTE	0	0	0	0	0	0	0	0	0	0	4
RBME	0	0	0	0	0	0	0	0	0	0	4
OSPR	1(.25)	0	1(.25)	0	0	0	0	0	0	2 (.06)	3
NOHA	0	0	0	0	0	0	0	0	1(.25)	1(.03)	1
CLRA	5(1.25)	5(1.25)	7(1.75)	3(.75)	5(1.25)	5(1.25)	5(1.25)	3(.75)	7(1.75)	45(1.26)	139
VIRA	0	0	0	0	0	0	0	0	0	0	1
SORA	0	0	0	0	0	0	0	0	0	0	1
KILL	0	1(.25)	0	0	0	0	1(.5)	0	0	2(.06)	28
AMOY	0	0	0	0	0	0	0	0	0	0	11
BNST	0	0	0	0	0	0	0	0	0	0	1
GRYE	16(4)	25(6.25)	28(7)	7(1.75)	7(1.75)	17(4.25)	14(3.5)	2(.5)	0	116(3.22)	257
LEYE	0	1(.25)	3(.75)	0	0	0	0	0	0	4(.11)	9
WILL	0	0	0	0	1(.25)	0	0	0	0	1(.03)	418
SPSA	0	0	0	0	0	0	0	0	0	0	2
WHIM	0	0	0	0	0	0	0	0	0	0	3
SESA	0	0	0	0	0	0	0	0	0	0	295
WESA	1(.25)	0	0	0	0	0	0	0	0	1(.03)	2
LESA	19(4.75)	36(9)	37(18.25)	8(2)	12(3)	5(1.25)	8(2)	3(.75)	1(.75)	129(3.58)	269
STSA	0	0	0	0	0	1(.75)	0	0	0	1(.03)	1
SBDO	15(3.75)	13(3.25)	24(6)	1(.25)	1(.25)	4(1)	6(1.5)	0	1(.75)	65(1.81)	126
LAGU	47(11.75)	91(22.75)	70(17.5)	63(15.75)	40(10)	175(43.75)	51(12.75)	13(3.25)	20(5)	570(15.83)	934
RBGU	0	0	0	0	0	0	0	0	0	0	1
HERG	0	4(1)	7(1.75)	9(2.25)	9(2.25)	18(4.5)	11(2.75)	18(4.5)	10(2.5)	86(2.39)	91
ROYT	0	0	1(.25)	2(.5)	0	2(.5)	1(.25)	0	0	6(.17)	6
COTE	16(4)	3(.75)	6(1.5)	3(.75)	1(.25)	4(1)	0	1(.25)	2(.75)	36(1)	66
FOTE	0	2(.5)	1(.25)	0	0	2(.5)	0	0	0	5(.14)	15
LETE	0	0	0	0	0	2(.5)	1(.25)	0	0	3(.08)	6
BLSK	0	2(.5)	0	0	0	0	0	0	0	2(.06)	8

Appendix III: Continued

AOU Code				Fall							
	1	2	3	4	5	6	7	8	9	Total	Total for all Seasons
BEKI	0	0	0	0	0	0	1(.25)	0	0	1(.03)	2
EAKI	0	0	0	0	0	0	0	0	0	0	3
PUMA	0	0	0	0	0	0	0	0	0	0	1
TRES	0	0	2(.5)	0	0	0	71((17.75)	0	0	73(2.03)	80
BARS	3(.75)	4(1)	4(1)	0	0	0	0	0	0	11(.31)	99
MAWR	5(1.25)	3(.75)	5(1.25)	5(1.25)	6(1.5)	5(1.25)	13(3.25)	7(1.75)	8(2)	57(1.58)	120
STSP	0	0	0	0	10(2.5)	11(2.75)	19(4.75)	19(4.75)	12(3)	71(1.97)	82
SESP	42(10.5)	41(10.25)	34(8.5)	21(5.25)	21(5.25)	13(3.25)	13(3.25)	7(1.75)	3(.75)	195(5.42)	725
SOSP	0	0	0	0	0	0	0	0	0	0	1
RWBL	0	0	0	0	0	0	0	0	0	0	73
BTGR	64(16)	10(2.5)	26(6.5)	27(6.75)	97(24.25)	266(66.5)	18(4.5)	26(6.5)	65(16.25)	599(16.64)	839
COGR	1(.25)	0	0	0	5(1.25)	14(3.5)	0	35(8.75)	0	55(1.53)	55
BHCO	0	0	0	0	0	0	0	0	0	0	4
CROW?	0	0	0	0	0	0	0	0	0	0	1
PEEP?	0	0	0	0	0	0	0	0	2(.5)	2(.06)	9
SPARROW?	0	0	0	0	0	0	0	0	0	0	9
Total	**408 (102)**	**295 (73.75)**	**425 (106.25)**	**191 (48)**	**363 (90.75)**	**1012 (253)**	**252 (63)**	**158 (39.5)**	**177 (44.25)**	**3281 (91.14)**	**6475**
Species Richness	**22**	**22**	**25**	**17**	**22**	**26**	**21**	**14**	**18**	**38**	**54**

Appendix III: Continued

AOU Code	1	2	3	Fall 4	5	6	7	8	9	Total	Total for all Seasons
BEKI	0	0	0	0	0	0	1(.25)	0	0	1(.03)	2
EAKI	0	0	0	0	0	0	0	0	0	0	3
PUMA	0	0	0	0	0	0	0	0	0	0	1
TRES	0	0	2(.5)	0	0	0	71((17.75)	0	0	73(2.03)	80
BARS	3(.75)	4(1)	4(1)	0	0	0	0	0	0	11(.31)	99
MAWR	5(1.25)	3(.75)	5(1.25)	5(1.25)	6(1.5)	5(1.25)	13(3.25)	7(1.75)	8(2)	57(1.58)	120
STSP	0	0	0	0	10(2.5)	11(2.75)	19(4.75)	19(4.75)	12(3)	71(1.97)	82
SESP	42(10.5)	41(10.25)	34(8.5)	21(5.25)	21(5.25)	13(3.25)	13(3.25)	7(1.75)	3(.75)	195(5.42)	725
SOSP	0	0	0	0	0	0	0	0	0	0	1
RWBL	0	0	0	0	0	0	0	0	0	0	73
BTGR	64(16)	10(2.5)	26(6.5)	27(6.75)	97(24.25)	266(66.5)	18(4.5)	26(6.5)	65(16.25)	599(16.64)	839
COGR	1(.25)	0	0	0	5(1.25)	14(3.5)	0	35(8.75)	0	55(1.53)	55
BHCO	0	0	0	0	0	0	0	0	0	0	4
CROW?	0	0	0	0	0	0	0	0	0	0	1
PEEP?	0	0	0	0	0	0	0	0	2(.5)	2(.06)	9
SPARROW?	0	0	0	0	0	0	0	0	0	0	9
Total	**408 (102)**	**295 (73.75)**	**425 (106.25)**	**191 (48)**	**363 (90.75)**	**1012 (253)**	**252 (63)**	**158 (39.5)**	**177 (44.25)**	**3281 (91.14)**	**6475**
Species Richness	**22**	**22**	**25**	**17**	**22**	**26**	**21**	**14**	**18**	**38**	**54**

Appendix IV: Total observed birds per weekly round and season for selected guilds. Standardized numbers (total birds/total surveys) are in parantheses.

Guild[a]	Spring 1	Spring 2	Spring 3	Spring 4	Spring 5	Spring 6	Spring Total	Summer 1	Summer 2	Summer 3	Summer 4	Summer 5	Summer 6	Summer 7	Summer 8	Summer Total
WD	26(6.5)	0	13(3.25)	10(2.5)	6(1.5)	6(1.5)	61(27.73)	23(5.75)	20(5)	18(4.5)	53(13.25)	117(29.25)	72(18)	33(8.25)	53(13.25)	389(121.56)
GU	13(3.25)	5(2.5)	1(.25)	4(1)	5(1.25)	5(1.25)	33(15)	19(4.75)	18(4.5)	42(10.5)	24(6)	45(11.25)	87(21.75)	45(11.25)	109(27.25)	386(120.63)
WF	9(2.25)	0	4(1)	8(2)	18(4.5)	11(2.75)	50(22.73)	5(1.25)	2(.5)	1(.25)	0	7(1.75)	0	7(1.75)	13(3.25)	36(11.25)
SH	80(20)	9(4.5)	33(8.25)	50(12.5)	22(5.5)	46(11.5)	240(109.09)	44(11)	67(16.75)	54(13.5)	73(18.25)	35(8.75)	77(19.25)	42(10.5)	35(8.75)	427(133.44)
PE	41(10.25)	4(2)	71(17.75)	94(23.5)	100(25)	24(6)	334(151.82)	0	0	3(.75)	11(2.75)	19(4.75)	9(2.25)	14(3.5)	53(13.25)	109(34.06)
SP	26(6.5)	5(2.5)	14(3.5)	28(7)	25(6.25)	32(8)	130(59.09)	24(6)	50(12.5)	56(14)	43(10.75)	55(13.75)	62(15.5)	59(14.75)	72(18)	421(131.56)

Guild	Fall 1	Fall 2	Fall 3	Fall 4	Fall 5	Fall 6	Fall 7	Fall 8	Fall 9	Fall Total	Total for all seasons
WD	172(43)	53(13.25)	465(116.25)	16(4)	80(20)	354(88.5)	7(1.75)	2(.5)	8(2)	857(238.06)	1307
GU	63(15.75)	102(25.5)	85(21.25)	77(19.25)	50(12.5)	203(50.75)	64(16)	32(8)	32(8)	708(196.67)	1130
WF	1(.25)	1(.25)	4(1)	26(6.5)	68(17)	114(28.5)	12(3)	22(5.5)	37(9.25)	285(79.17)	371
SH	31(7.75)	40(10)	55(13.75)	8(2)	9(2.25)	22(5.5)	21(5.25)	2(.5)	1(.25)	189(52.50)	856
PE	20(5)	36(9)	37(9.25)	8(2)	12(3)	5(1.25)	8(2)	3(.75)	3(.75)	132(36.67)	575
SP	42(10.5)	41(10.25)	34(8.5)	21(2.25)	31(7.75)	23(5.75)	22(5.5)	26(6.5)	15(3.75)	266(73.89)	817

[a] Guilds: WD = Waders, WF = Waterfowl, SH = Shorebirds, PE = Peeps, GU = Gulls, terns and skimmers, SP = Sparrows.

Appendix V. Physical and biological components (Mean (S.E.)) and Kruskal - Wallis and Principal Components Analysis statistics for 303 tidepools.

Components	Pool Type				Kruskal-Wallis[1]		Principal Components Analysis[2]	
	Shallow	Graded	Pothole	Intermediate	G	P	Factor 1	Factor 2
Physical								
Area (m^2)	37(11.2)	39(10.5)	38(10.7)	224(114.3)	2.547	NS	0.89	0.31
Edge (m)	47(10.8)	38(8.6)	37(8.2)	123(54.7)	2.509	NS	0.91	0.37
Water Depth[3](cm^2)								
0-2	14(3.2)	6(2.0)	0(0.3)	30(13.1)	155.837	<0.05	0.94	-0.30
2-10	20(6.9)	26(8.4)	6(1.6)	68(34.4)	46.789	<0.05	0.94	-0.30
10-20	0 (2.9)	4(1.8)	14(4.8)	79(53.0)	63.803	<0.05	0.94	-0.30
>20	0(0)	2(1.1)	19(7.6)	50(31.2)	42.445	<0.05	0.94	-0.30
Biological								
Vegetation[4](m^2)								
Tall Cordgrass	9(3.5)	2(0.6)	2(0.7)	8(5.8)	0.158	NS	0.40	-0.59
Short Cordgrass	28(6.1)	27(6.3)	30(7.1)	72(28.3)	4.495	NS	0.76	0.50
Saltmeadow Hay	0(0.1)	0(0.5)	0(0.1)	4(2.3)	5.890	NS	0.42	-0.27
Black Needlerush	10(4.6)	8(3.2)	4(1.8)	41(26.3)	6.663	<0.05	0.79	0.35
Saltbush	0(0.4)	0(0.2)	1(0.3)	0(0.4)	2.186	<0.05	0.32	0.59

[1] = Kruskal - Wallis statistics run on pools split by profile type (Shallow, Graded and Pothole); Intermediate profile types not included.
[2] = Principal Components Analysis of all pools combined.
[3] =Area of water falling within depth range.
[4]= Area of vegetation along edge of pools.

Appendix VI: Mean x 10^{-2} (S.E.) total of macrofauna found in benthic cores (N) during May 1993.

Species	Shallow		Graded Shallow		Graded Deep		Deep		Vegetation		Total
	Top (6)	Bottom (13)	Top (9)	Bottom (15)	Top (9)	Bottom(16)	Top (9)	Bottom(15)	Top(12)	Bottom(12)	
Cnidaria											
Edwardsia elegans	100(0.5)	70(0.7)	200(1.6)	7(0.07)	0	6(0.06)	480(2.9)	50(0.2)	380(2.0)	70(0.5)	138
Platyhelminthes											
Turbellaria	370(1.6)	70(0.7)	0	10(0.09)	10(0.11)	10(0.13)	20(0.2)	30(0.3)	20(0.2)	20(0.2)	49
Mollusca											
Gastropoda	20(0.2)	0	0	0	0	0	0	7(0.07)	20(0.2)	8(0.08)	5
Annelida											
Asabellides oculata	430(2.6)	140(1.0)	130(0.8)	130(1)	70(0.4)	6(0.06)	440(2.9)	0	2310(21.2)	100(0.9)	401
Capitellidae spp.	0	210(0.7)	40(0.3)	410(1.1)	10(0.1)	330(0.7)	0	250(0.7)	330(1.5)	280(1)	271
Eteone heteropoda	0	0	10(0.1)	20(0.1)	20(0.2)	10(0.09)	0	0	20(0.1)	0	10
Glycinde solitaria	0	0	0	0	0	0	0	0	7(0.07)	0	1
Nereis solitaria	0	40(0.4)	0	30(0.3)	0	20(0.1)	0	0	20(0.2)	20(0.2)	17
Polydora ligni	0	10(0.1)	60(0.4)	0	0	20(0.1)	0	20(0.1)	120(0.7)	50(0.20)	33
Streblospio benedicti	20(0.2)	20(0.1)	60(0.2)	30(0.2)	30(0.2)	20(0.1)	670(0.55)	10(0.1)	80(0.4)	20(0.2)	40
Oligochaetes	2250(7.3)	1340(4.8)	710(6.2)	3090(9.4)	110(0.5)	730(1.7)	410(1.4)	650(2.2)	6180(20.8)	2650(10.2)	2158
Arthropoda											
Amphipoda	0	0	0	0	0	0	10(0.1)	0	20(0.2)	8(0.08)	4
Crustacea spp.	0	8(0.08)	0	10(0.09)	10(0.1)	10(0.1)	0	7(0.07)	0	30(0.2)	13
Leptochelia savigny	20(0.2)	0	60(0.3)	10(0.13)	10(0.1)	0	10(0.1)	0	670(3.9)	120(0.6)	105
Insecta spp.	0	0	0	0	0	0	0	0	20(0.2)	0	3
Chironomidae	20(0.2)	50(0.4)	110(0.6)	10(0.09)	70(0.3)	30(0.2)	120(0.8)	70(0.6)	1300(5.6)	420(1.5)	263
Total Individuals	3220(6.5)	1950(5.1)	1370(7.3)	3760(10.7)	340(1.1)	1210(2.3)	1570(4.1)	1110(2.7)	11590(33.7)	3810(11.8)	3523

Appendix VII. Results of Chi-square analysis on locations (In vs. Out) of species and guilds within the tidepool complex.

Dependent Variable	χ^2	P
Guilds		
Waders	800.6	<0.001
Gulls, Terns and Skimmers	436.1	<0.001
Waterfowl	228.2	<0.001
Large Shorebirds	516.6	<0.001
Peeps	367.0	<0.001
Sparrows	761.9	<0.001
Species		
Great Egret	426.4	<0.001
Snowy Egret	452.0	<0.001
Green-backed Heron	6.26	<0.025
Clapper Rail	3.17	NS
Greater Yellowlegs	160.3	<0.001
Willet	11.7	<0.001
Semipalmated Sandpiper	245.3	<0.001
Laughing Gull	651.4	<0.001
Marsh Wren	120.0	<0.001
Seaside Sparrow	673.9	<0.001
Boat-tailed Grackle	292.0	<0.001

VITA

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