BLUE CRAB POPULATION ECOLOGY AND USE BY FORAGING WHOOPING CRANES ON THE TEXAS GULF COAST

A Dissertation

by

DANIELLE MARIE GREER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2010

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	R. Douglas Slack
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ABSTRACT

Blue Crab Population Ecology and Use by Foraging Whooping Cranes on the Texas Gulf Coast. (December 2010)

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Chair of Advisory Committee: Dr. R. Douglas Slack

In 2002, a proposal was submitted to divert water from the confluence of the Guadalupe and San Antonio Rivers to San Antonio, Texas. To investigate the potential impacts of diverting water from the Guadalupe Estuary, my research focused on the foraging ecology of the crane and population ecology of the blue crab, a documented crane food.

During winters 2004-2005 and 2005-2006, I examined diets and optimal foraging patterns of territorial adult cranes at Aransas National Wildlife Refuge, Texas. To identify foods of greatest benefit to cranes, I used currencies of optimization to evaluate foraging gain, cost, and efficiency. Foraging benefit differed among foods, depending on the foraging currency used and resource targeted (e.g., energy). Wolfberry fruit, snails, and insects were consumed in the highest quantities, required the least foraging effort, and were generally associated with the highest foraging efficiency. Blue crabs and clams were important sources of protein and biomass.

During September 2003-October 2005, I used novel artificial settlement substrates and modified methods of standard deployment to investigate the spatio-temporal patterns of blue crab terminal settlement and recruitment rates. Monitoring rates in shallow bay habitat and ponds of the interior salt-marsh revealed megalopal crabs were developmentally advanced when arriving to study sites and the extent to which young crabs infiltrated the salt-marsh increased with age. Such findings suggested sites represented optimal terminal settlement habitat and consequently critical nursery habitat. Model selection indicated water temperature before and during embryonic development was the best predictor of megalopal settlement, whereas juvenile recruitment was most influenced by recent precipitation.

I studied the size-specific abundance patterns of blue crabs in and around mature salt-marsh. Using drop-trapping and throw-trapping methods, I collected monthly samples in several habitats during October 2004-March 2006. Interior-marsh habitats contained fewer but larger crabs than bay habitat. Crabs contributing greatest to biomass were smallest (11-30 mm carapace-width) in bay habitat, larger (31-80 mm) along interior-marsh pond edges, and largest (41-130 mm) in interior-marsh open water. Model selection revealed crab density was most influenced by micro-site characteristics (habitat, water column structure type and structural complexity). Overall, shallow bay provided important nursery habitat for young blue crabs and interior marsh ponds were important for dispersing juvenile and adult crabs.

DEDICATION

I dedicate this work to the world's greatest mother, my mom – Colleen Hungelmann. I also dedicate this dissertation to three men who made this research possible, as well as meaningful: my husband and very best friend, Andy Greer II; my good friend, Dennis Pridgen (January 1959-October 2008); and my field technician, Erick "Rick" Rogers Jr. (April 1981-February 2005).

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My research was only a small part of a larger effort, but, despite the project's relative size, the successes achieved since commencement in 2003 have been enormous. Project design, development of field and lab materials and methods, data collection, analysis, and synthesis, presentation of research findings, completion of this dissertation, and, most importantly, personal lessons learned have occurred only because of the selfless contributions of many, many people. I cannot possibly list all of the people that have benefited this project or myself, but I am genuinely grateful for their gifts of kindness, humor, loyalty, and hard work.

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Above all, I thank God, with whom all things have been possible.

NOMENCLATURE

AICc	Akaike's Information Criteria for small sample sizes
ANOVA	Analysis of variance
ANWR	Aransas National Wildlife Refuge (Texas)
AWB	Aransas-Wood Buffalo (whooping crane population)
BJ	Blackjack (crane territory, study site)
BR	Boat Ramp (crane territory, study site)
CBL	Crane bill length
COW	Connected, open water (habitat type)
CP	Connected pond (habitat type)
CPE	Connected pond edge (habitat type)
CW	Carapace-width
DM	Dry mass
ESV	Emergent salt-marsh vegetation
ETT	Ebb-tide transport (generally referred to as STST)
FTT	Flood-tide transport (generally referred to as STST)
GBRA	Guadalupe-Blanco River Authority
GIS	Geographic Information System
GIWW	Gulf Intracoastal Waterway
GLIMMIX	SAS procedure appropriate for GLMMs
GLMM	Generalized linear mixed model

J1	Juvenile instar 1
J2	Juvenile instar 2
J3	Juvenile instar 3
J4	Juvenile instar 4
MB	Mustang Bay (reference study site)
NOAA	National Oceanic and Atmospheric Administration
PC	Pump Canal (crane territory, study site)
PL	Pipeline (crane territory, study site)
ppt	Parts per thousand (unit of measure for salinity)
SAS	Statistical computer software
SAV	Submerged aquatic vegetation
SD	Standard deviation
SE	Standard error
STST	Selective tidal-stream transport (comprises both ETT and FTT)
TC	Tidal creek (habitat type)
UOW	Unconnected, open water (habitat type)
UP	Unconnected pond (habitat type)
UPE	Unconnected pond edge (habitat type)
WM	Wet mass

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CHAPTER I

INTRODUCTION

In response to increasing human demand for water resources, several major rivers supplying freshwater to estuaries on the Texas Coast have become the target of proposed or implemented water diversion projects. In 2002, a proposal was submitted to the Texas Commission on Environmental Quality to divert water from the confluence of the Guadalupe and San Antonio Rivers to the city of San Antonio, Texas. In compliance with Section 7 of the Endangered Species Act, sound scientific data were needed to effectively assess the impacts of freshwater diversion on the endangered whooping crane (*Grus americana*) and its critical wintering habitat in the Guadalupe Estuary. This need was fulfilled by a team of Texas A&M University scientists, which collected empirical data and used mathematical models to examine the underlying relationship between freshwater inflows and whooping crane energetics (Slack et al. 2009). Central to this effort, research for my dissertation focused on the foraging ecology of the crane and population ecology of the blue crab (*Callinectes sapidus*), a food previously perceived to be of great value to whooping cranes (Hunt and Slack 1989; Chavez-Ramirez 1996; Pugesek et al. 2008).

The only self-sustaining, wild population of whooping cranes in existence today winters in and around Aransas National Wildlife Refuge, Texas in the Guadalupe Estuary and breeds in Wood-Buffalo National Park of the Northwest Territories and

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This dissertation follows the style of *Estuaries and Coasts*.

Alberta, Canada. Following decades of unregulated harvest and extensive habitat loss throughout its migratory range, the Aransas-Wood Buffalo (AWB) population reached a low of 15 individuals and became the species' foundation for recovery by 1941 (Allen 1952). Since that time, conservation measures have included federal protection in Canada and the United States, protection of critical habitats (e.g., coastal salt-marsh), and research and monitoring programs revealing the life-history, population dynamics, behavior, food habits, and habitat-use patterns of cranes. Response has been marked, as the AWB population has grown exponentially (approx. 4.5% yr^{-1}; Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005) and currently comprises over 250 individuals and 70 reproductive pairs (Stehn 2009). Moreover, captive breeding efforts have demonstrated increasing success for over 30 years, and reintroduction attempts have provided invaluable lessons on imprinting, release techniques, crane vulnerability to predation and stochastic weather events, and habitat suitability.

Despite high rates of population growth observed for AWB whooping cranes, down-listing of this species from endangered to threatened status and eventual recovery of the species will likely require that future reintroduction efforts lead to successful establishment of one or two additional self-sustaining, wild populations (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005). The AWB flock must also increase its numbers but, as cranes approach carrying capacity of their current wintering area, range expansion and continued population growth will ultimately depend on availability of suitable habitat in adjacent areas of the Texas coast.

A recent survey of salt-marsh habitat within the crane's current Texas range and in unoccupied areas north and south of the Guadalupe Estuary suggests that areal coverage is adequate to support 1,004 individuals (Stehn and Prieto 2010), a population size sufficient for down-listing the crane to threatened status (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005). However, as factors influencing territory quality and selection by cranes are not fully understood, the survey did not account for possible measures of quality, such as habitat configuration within salt-marsh, proximity to other important habitats (e.g., uplands, shallow bay), winter patterns of food availability, or disturbance regime. Rather, calculation of carrying capacity within "apparently suitable salt-marsh" was based on an estimate of minimum crane territory size (202 ha) and assumptions that (1) unoccupied salt-marsh is, on average, of comparable quality to currently occupied salt-marsh, (2) habitat quality of occupied salt-marsh will remain unaffected by coastal developments or alterations in the future, and (3) unoccupied salt-marsh will remain unaffected by coastal developments or alterations and still available for crane use (Stehn and Prieto 2010). The survey emphasized the importance of protecting salt-marsh and other critical habitats on the Texas coast but also revealed the need for development of criteria to effectively assess habitat suitability.

Mated whooping crane pairs may defend territories each winter for a variety of reasons, including maintenance of pair-bonds, access to foods and foraging, loafing and roost sites, and decreased risks of interference competition, predation, and human disturbance (Fretwell and Lucus 1969). Moreover, assurance of these advantages for young-of-the-year birds, who stay with parents until spring migration, may be of particular importance (Allen 1952; Ohsako 1989; Alonso et al. 2004). Collectively, these resources and opportunities associated with territoriality determine the quality or economic defendability of territories (Krebs and Davies 1993:110-118).

Extreme variability observed among crane territories in size, shape, and habitat composition (Stehn and Johnson 1987; Stehn and Prieto 2010) suggests territory quality is most influenced by food resources. However, quality may still differ among territories even when overall abundance or biomass of food perceivably does not. As a result of spatio-temporal patterns in food abundance (Nolet and Drent 1998; Nolet et al. 2001; Moore and Black 2006), factors influencing food availability (Charnov et al. 1976; Gill 1996; Sutherland 1996:52-60; Gawlik 2002), costs associated with search and handling of food (Beissinger et al. 1994; O'Brien et al. 2005; Halsey et al. 2007), and food mass, nutrient content, and digestibility (Nelson et al. 1996, 1997; Richman and Lovvorn 2003), the optimality of foraging for food can differ significantly among food types. Consequently, knowledge of which foods provide the greatest benefits to cranes may substantially improve evaluations of habitat suitability at currently unoccupied sites.

Previous studies examining the whooping crane diet have consistently described the crane as omnivorous, feeding largely on blue crabs and clams in salt-marsh and shallow bay habitats and acorns (*Quercus* spp.) in adjacent upland habitat. Less commonly, cranes have consumed wolfberry fruit (*Lycium carolinianum*), snails, insects, crayfish, fish, shrimp, fiddler crabs (*Uca* spp.), other crabs, snakes, tubers, and other plant material. Data collection has relied on incidental observation and circumstantial evidence (e.g., empty, discarded clam shells; Stevenson and Griffith 1946), analysis of fecal droppings (Stevenson and Griffith 1946; Allen 1952; Hunt and Slack 1989), stomach contents of dead cranes (Allen 1954; Uhler and Locke 1970; Hunt and Slack 1987), and focal observation (Chavez-Ramirez 1996). While temporal or spatial variability was accounted for in some earlier studies, most did not follow a priori sampling designs intended to account for either source of variation. Furthermore, estimates of relative use (e.g., percent aggregate volume; Hunt and Slack 1989), nutritional value (Nelson et al. 1996), and captive crane preference (Nelson et al. 1997) of foods have led to some foods being identified as important to cranes, but no study has yet accounted for costs associated with foraging or fully considered the optimality of cranes foraging for foods.

In addition to being regarded as the dominant and perhaps most important food consumed by wintering whooping cranes (Allen 1952; Chavez-Ramirez 1996), the blue crab supports a major commercial fishery in the United States (Guillory et al. 2001) and functions ecologically as both food and predator of countless marine and estuarine fishes, shrimps, crabs, and other invertebrates throughout the western Atlantic (Guillory et al. 2001; Guillory and Elliot 2001; Guillory and Prejean 2001). Its complex life cycle involves offshore dispersal and development of larvae, estuarine invasion and settlement of postlarvae (megalopae), and juvenile dependence on shallow, structurally-distinct nursery habitats within estuaries. Decades of research on the recruitment dynamics of blue crabs and other estuarine-marine species reveal that a suite of physical (e.g., wind-driven currents; Goodrich et al. 1989), chemical (e.g., water salinity; King 1971), and biological (e.g., density-dependent predation; Pile et al. 1996) factors regulate the transport, growth and survival of individuals in early development and ultimately influence recruitment to adult-form populations.

Likely due to the challenges of sampling (Connolly 1999), however, few studies have investigated the contributions of interior salt-marsh habitats to settler, recruit, or adult blue crab populations (e.g., Peterson and Turner 1994; Rozas and Zimmerman 2000; Rozas and Minello 2010) and most studies have occurred only during high-recruitment (August-October) or high-water (spring, autumn) periods of the year. Tidal creeks, tidally-connected ponds, and isolated ponds in the interior salt-marsh commonly comprise the same structured habitats (e.g., seagrass) as found in shallow embayments and along the salt-marsh periphery, where most studies are performed (Minello et al. 2003). However, spatio-temporal patterns in crab settlement, recruitment, and juvenile and adult abundance may contrast markedly between inside and outside the marsh due to inherent differences in geomorphology, inundation regime, effects of tides and weather events, nutrient load, and resident community structure. For these reasons, I intensively studied the patterns in which blue crab megalopae, juveniles, and adults used shallow bay and salt-marsh habitats on the central Texas coast.

As part of a greater collaborative venture investigating the potential impacts of freshwater diversion on whooping cranes, my primary research goal was to quantify relationships existing among whooping cranes, their foods (principally blue crabs), and environmental attributes of Aransas National Wildlife Refuge, Texas. Three stand-alone yet companionable studies were conducted to attain this goal and are discussed in detail in Chapters II-IV. In Chapter II, I explore the terminal settlement and recruitment patterns of blue crabs in the same shallow bay and interior salt-marsh habitats used by cranes and devote considerable effort to identifying factors influencing these patterns. In Chapter III, I examine the size-specific abundance patterns of juvenile and adult blue crabs and again investigate the complexity of small- and large-scale factors regulating such patterns. In Chapter IV, I report on temporal patterns in the diet and foraging behavior of whooping cranes during winter and use several possible currencies of optimal foraging to compare the values of crane foods. Patterns described for variables of interest in each empirical chapter depended heavily on sampling across both spatial and temporal gradients, which incorporated multiple crane territories, shallow bay and interior salt-marsh habitats, and yearly cycles. Lastly, Chapter V summarizes the findings of earlier chapters and discusses implications of these findings for maintenance of ecological integrity in the Guadalupe Estuary, future recovery of the whooping crane, and conservation of critical habitats for estuarine-marine nekton, such as the blue crab.

Objectives

In Chapter II, the study objectives were to:

1. Develop methodology enabling collection of megalopal settlement and juvenile recruitment data for blue crabs in shallow intertidal and subtidal habitats.
2. Document fine-scale temporal patterns in settlement and recruitment rates to evaluate the potential biases of using new methodology.
3. Document long-term patterns in settlement and recruitment rates at several shallow subtidal bay locations immediately adjacent to salt-marsh.

4. Investigate the effects of stochasticity and environmental conditions on settlement and recruitment rates of blue crabs in shallow subtidal bay habitat.
5. Investigate spatial patterns of megalopal settlement and juvenile recruitment in intertidal and subtidal habitats of the interior salt-marsh.

In Chapter III, the study objectives were to:

1. Develop field methodology and sampling gear appropriate for quantitative measure of crab abundance within and adjacent to salt-marsh.
2. Identify temporal and spatial patterns in blue crab abundance and size-class structure within and adjacent to salt-marsh, accounting for the effect of spatial scale.
3. Investigate the effects of small- and large-scale environmental and stochastic variation on blue crab abundance and size-class structure.

In Chapter IV, the study objectives were to:

1. Document temporal (within and across winters) and spatial (within and across crane territories) variability in proportional use of foods by cranes.
2. Document temporal and spatial variability in foraging rewards, represented by numeric, dry mass, lipid, energy, and protein intake rates.
3. Quantify the effort required to search for and handle foods (e.g., steps, probes, food manipulations), representing the costs of foraging.
4. Quantify the optimality of foraging for foods by calculating indices of foraging efficiency (i.e., ratios of reward:cost).

CHAPTER II

BLUE CRAB SETTLEMENT AND RECRUITMENT PATTERNS IN SHALLOW HABITATS OF THE GUADALUPE ESTUARY, TEXAS

Synopsis

During September 2003-October 2005, I investigated the spatio-temporal patterns of blue crab terminal settlement and juvenile recruitment rates in shallow estuarine habitats. I collected data at three replicate study sites within Aransas National Wildlife Refuge, Texas using artificial settlement substrates (collectors). To sample in shallow (14-103 cm) habitats, the dimensions and floating orientation of collectors were highly modified from standard protocol. Furthermore, collectors were deployed fortnightly for entire semi-lunar collection periods rather than daily for 24-h periods due to intensity of data collection. Continuous monitoring of settlement and recruitment rates in bay habitat revealed that settlement and recruitment events occurred throughout most of the year but were of highest frequency and magnitude in spring (March-June) and autumn (August-October). Also, megalopal crabs were developmentally advanced when arriving at study sites, suggesting sites represented optimal terminal settlement habitat. Of all settlers collected, 27-93% were recruits (i.e., recently metamorphosed juvenile crabs), with the percentage representative of recruits increasing with distance (51-59 km) from the nearest coastal water or larval supply. Using an information theoretic approach to explore sources of variability in megalopal settlement and juvenile recruitment rates, I determined water temperature before and during embryonic

development was the best predictor of settlement, whereas recruitment was most influenced by recent levels of precipitation. The best approximating model of settlement rate also included the effects of wind speed and direction, river discharge, and water level, while the best model of recruitment also included water level and wind speed and direction. To investigate the spatial extent to which megalopae settled in the salt-marsh and were recruited into the crab population, I additionally deployed collectors within each of three possible interior salt-marsh habitats (tidal creek, connected pond, unconnected pond) per study site during five non-adjacent semi-lunar periods. Results indicated that the extent to which crabs infiltrated the salt-marsh increased with age or mobility associated with advancements in development. In this study, progress was made in identifying environmental conditions and habitats important to terminally settling and metamorphosing megalopal blue crabs. Highly effective methods for monitoring settlement of nekton in extremely shallow environments were also demonstrated.

Introduction

Populations of transient estuarine-marine nekton are widely viewed as recruitment limited. Consequently, the recruitment dynamics of commercially valuable species, such as the blue crab (*Callinectes sapidus*), have received considerable attention. Research reveals that a suite of physical (e.g., wind-driven currents; Goodrich et al. 1989), chemical (e.g., salinity; King 1971), and biological (e.g., predation; Pile et al. 1996) factors regulate the transport, growth and survival of individuals in early development. Moreover, recruitment to juvenile or adult-form populations occurs following a lengthy sequence of life-history events (e.g., embryonic development, hatching, larval export from estuary, etc.), wherein factors uniquely associated with each event either limit or promote individuals passing to the next event (Pineda 2000). Factors operating early in development are generally associated with larger spatial and temporal scales and greater numbers of eggs, larvae, or post-larvae than those operating later, but recent studies suggest recruitment and adult population size may be limited most by post-settlement processes, such as interference competition for space, density-dependent growth and dispersal, and habitat-specific predation mortality (Moksnes et al. 1998; Heck et al. 2001; Moksnes 2004; Pardo et al. 2007).

Predation mortality within estuaries, especially through cannibalism (Hines and Ruiz 1995; Moksnes et al. 1997), strongly influences juvenile recruitment in blue crabs. While the relative contribution of offshore predation to total cohort loss is unclear, field experiments with planktonic larvae suggest rates of predator encounter and subsequent predation in the neuston are extremely low (<1% d^{-1}; Johnson and Shanks 2003). In contrast, constricted water columns and diverse and abundant food and shelter markedly increase predator densities and encounter rates within coastal bays and marshes, where post-larval crabs (megalopae) intermittently and then permanently settle and adopt a benthic existence. Field experiments conducted within bays reveal loss rates of freely developing Dungeness crab (*Cancer magister*) post-larvae are significantly (12-28 times) greater on or near benthos than in the plankton (Allen and McAlister 2007). Likewise, mortality rates of invading Caribbean spiny lobster (*Panulirus argus*) post-larvae are almost 60% d^{-1} over bottom substrate but <15% d^{-1} near the water's surface (Acosta and Butler 1999).

Following terminal settlement, blue crab megalopae and young juveniles incur predation rates of up to 70-100% d^{-1} (Heck and Coen 1995; Pile et al. 1996; Heck et al. 2001; Spitzer et al. 2003; Mosknes and Heck 2006). However, partial refuge from predation may be attained by inhabiting the shallow, structurally-complex habitats of estuaries (e.g., seagrass, algae, oysters), as opposed to bare sediment (Pile et al. 1996; Moksnes et al. 1998). Increasing body size also provides refuge, as demonstrated by planktonic sand dollar larvae (*Dendraster excentricus*; Allen 2008), small juvenile shore crabs (*Carcinus maenas*; Moksnes et al. 1998), and early-instar juvenile blue crabs (Pile et al. 1996). Crabs in the earliest stages of life, consequently, should benefit from rapid up-estuary transport and conditions promoting growth. In agreement, estuary-invading blue crab megalopae use a host of physical and chemical cues to enter tidally flooding waters, stimulate swimming, and orient toward structurally-complex, predator-free habitats (Olmi 1994; Forward et al. 2003a, 2003b).

Identification of terminal settlement habitat or sites actively used by terminally settling or metamorphosing megalopal blue crabs has not been a principle focus of most recruitment studies, but several field and laboratory studies have provided insight into the probable characteristics of optimal settlement habitats. For example, megalopae have shown to selectively settle in structurally-complex habitats versus nonvegetated bottoms, sometimes without obvious preference for any particular structure (e.g., *Ruppia maritima*, *Zostera marina*, artificial eelgrass, oyster shell; Morgan et al. 1996; Pardieck et al. 1999; van Montfrans et al. 2003; Moksnes and Heck 2006). Also, increases in structural complexity have generally supported greater densities, lower predation rates, and higher growth rates of post-larval and newly-recruited juvenile nekton (Perkins-Visser et al. 1996; Pile et al. 1996; Hedvall et al. 1998; Moksnes et al. 1998; Orth and van Montfrans 2002; Stunz et al. 2002). These findings, along with those indicating that stimuli for blue crab terminal settlement and metamorphosis originate from estuarine vegetation (e.g., *Zostera marina*, *Spartina alterniflora*) and other marsh cues (Wolcott and De Vries 1994; Forward et al. 1996, 2003a), support the presumption that terminal settlement of megalopae takes place at least as far up-estuary as shallow, subtidal habitat adjacent to salt-marsh. However, whether terminally settling or metamorphosing megalopae are capable of infiltrating similar habitats of the interior salt-marsh or benefit from doing so is unknown.

A growing body of literature suggests blue crabs may undergo ontogenetic shifts in habitat use following terminal settlement and metamorphosis to the juvenile lifestage. Habitats of lesser complexity, such as nonvegetated sediment and vegetative structures with broad blades or low stem density, and areas of lower salinity have shown to be increasingly utilized by young juveniles as they increase in size (Orth and van Montfrans 1987; Moksnes and Heck 2006). Less clear, however, are the size or age at which changes in juvenile ontogeny occur and the significance of differences in spatial distribution between terminally settling megalopae and successive juvenile molt-stages. For instance, following metamorphosis, juveniles may immediately redistribute themselves among settlement habitats, disperse to habitats directly adjacent to settlement areas, or disperse farther upstream and away from terminal settlement habitat (e.g., Hedvall et al. 1998; Pardo et al. 2007). Alternatively, newly-recruited juveniles may inhabit the same habitats as megalopae and undergo changes in dietary, space, or refuge requirements at later stages in development (e.g., J4; Pardieck et al. 1999; Moksnes and Heck 2006). To my knowledge, only one study has presented early-instar juvenile abundance from passive collectors used to monitor megalopal settlement (7 August-23 September 1997; Rakocinski et al. 2003) and none have comparatively monitored megalopa and juvenile recruit abundances at known terminal settlement sites. By documenting in parallel the spatial distributions of megalopal and early-instar juvenile blue crabs, habitat conservation priorities for estuarine nekton may be implicitly supported or, alternatively, results may indicate the need to reevaluate priorities to ensure habitats for both recruitment and dispersing, young juveniles are protected.

A multitude of studies have examined relationships between megalopal or juvenile blue crab abundance within estuaries and environmental conditions. These studies most often have related abundance with conditions or processes specific to the recruitment step in which abundance was measured (e.g., tidal amplitude) and lesser often have related abundance with conditions or processes operating earlier or outside the estuary (e.g., oceanographic patterns). To my knowledge, no studies have predicted numbers of settling megalopae or newly-metamorphosed juveniles based on conditions or processes occurring during the earliest stages of development (e.g., embryogenesis) nor have models been developed wherein numbers are predicted based on all previous developmental stages and environmental processes. Failure to account for early life-history events may provide explanation to studies where settlement events corresponded with seemingly optimal tide or wind patterns but optimal conditions often were not followed by settlement events (e.g., Hasek and Rabalais 2001; Queiroga et al. 2006; see also Pineda 2000). Such findings suggest that a linkage between steps earlier in the recruitment process was broken and, despite favorable within-estuary conditions, no megalopae were available to settle (Pineda 2000). Although processes involved in recruitment are generally understood, effects of environmental conditions (e.g., water level, river discharge, precipitation) and stochasticity on full development in situ, eventual use of shallow habitats, and probability of recruitment are not yet well defined.

My overall goal for this research was to investigate the terminal settlement and recruitment patterns of blue crabs on the central Texas Coast, with terminal settlement defined as the final act of falling out of the water column to permanently adopt a benthic existence and recruitment defined as the addition of individuals to the adult-form (juvenile plus adult) population. Studies examining the recruitment dynamics of blue crabs have been conducted at several locations along the Atlantic and Gulf coasts but rarely so in Texas. My efforts were directed to shallow intertidal and subtidal habitats found in and adjacent to salt-marsh, as these habitats were the most probable locations for terminal settlement and metamorphosis of megalopal crabs because (1) destination habitat of estuarine-invading megalopae is likely the same as that containing stimuli for metamorphosis (e.g., *Spartina alterniflora*; Forward et al. 1996, 2003a), (2) within-estuary, these are the most structurally-complex habitats and megalopae and young juveniles select for structural complexity (Mosknes and Heck 2006), (3) advanced development (e.g., post-larval pre-molt) and readiness-to-settle are most prevalent upriver (Lipcius et al. 1990) or near intertidal habitats (in Terrebone Bay; Rabalais et al. 1995), (4) abundance of recently-metamorphosed juvenile blue crabs is generally greater in up-estuary than down-estuary habitats (Mense and Wenner 1989), and (5) survival of juvenile crabs increases with shallower water (Dittel et al. 1995; Hines and Ruiz 1995; Lipcius et al. 2005) and increased prevalence of submerged vegetation (Pile et al. 1996) or salt-marsh fringe (Posey et al. 2005).

Specific objectives for this research were to (1) develop methodology enabling collection of megalopal settlement and juvenile recruitment data for blue crabs in shallow intertidal and subtidal habitats within and adjacent to salt-marsh, (2) document fine-scale temporal patterns in settlement and recruitment rates to evaluate the potential biases of using new methodology (i.e., two-week sampling interval), (3) document long-term patterns in settlement and recruitment rates at several shallow bay locations immediately adjacent to salt-marsh, (4) investigate the effects of stochasticity and environmental conditions (e.g., freshwater discharge, water temperature, wind speed) on settlement and recruitment rates of blue crabs in shallow subtidal bay habitat, and (5) investigate spatial patterns of megalopal settlement and juvenile recruitment in intertidal and subtidal habitats of the interior salt-marsh.

Background: Early Life-stages of the Blue Crab

The blue crab is one of countless estuarine-dependent species with a dispersive larval phase that develops offshore. Following mating in low-salinity habitats within estuaries, newly-inseminated females migrate toward higher salinity areas at or beyond estuary inlets to spawn (Tankersley et al. 1998). During migration, several hundred-thousand to a few million eggs per brood are fertilized (Hsueh et al. 1993; Pereira et al. 2009), extruded into a cohesive mass or "sponge" under the female's abdomen (i.e., oviposition), and incubated through embryonic development (8-11 d; Amsler and George 1984a). Migrating females maximize travel efficiency using ebb-tide transport (ETT), which involves rising into the water column during ebb tides and maintaining position or moving along the bottom during flood tides (Tankersley 1998; Forward 2003b; Carr et al. 2004; Forward et al. 2005). Following female release of newly-hatched larvae, seaward currents (e.g., ebb tides) quickly export larvae offshore (Tankersley et al. 1998; Forward et al. 2003b), where they develop through seven or eight successive zoeal stages (31-49 d) and metamorphose into post-larvae (i.e., the megalopa (6-20 d); Costlow and Bookhout 1959).

While offshore, larval crabs maintain a position within or just below the neuston (Johnson 1985). In the upper reaches of the water column, they are least vulnerable to predation but highly susceptible to wind-driven currents, which have shown to be a significant transport mechanism for nekton in the early stages of life (Goodrich et al. 1989; Blanton et al. 1999; Queiroga et al. 2006). These currents, along with internal waves, deep residual currents, and tides, function to disperse larvae farther off-shore, aggregate larvae and post-larvae outside the estuary mouth (i.e., form the larval pool), and eventually promote ingress of megalopae to estuarine waters (i.e., constitute the post-larval or megalopal supply; Shanks 1983; Goodrich et al. 1989; Epifanio 1995; Mense et al. 1995; Morgan et al. 1996; Queiroga et al. 2006, 2007).

During estuary invasion, blue crab megalopae are no longer transported as passive particles but instead utilize a suite of strategies or behaviors to avoid predation, expedite up-estuary transport, and ensure terminal settlement in suitable habitat for the onset of benthic existence (Olmi 1994; Epifanio 1995; Forward et al. 2003b). A pattern of tidally-timed vertical migrations called flood-tide transport (FTT) is used in which megalopae enter the water column during flood tide and settle to the bottom during ebb tide (Forward 2003b). Their rise into the water column occurs as increasing salinity during flood tide stimulates the onset of swimming behavior. Swimming activity continues in response to turbulence caused by tidal flow but discontinues at or shortly after slack tide, when decreases in salinity stimulate megalopae to settle. Megalopal blue crabs are also negatively phototaxic within estuaries (Luckenbach and Orth 1992), causing them to swim closer to the water's surface during night than day flood tides (Olmi 1994; Lochman et al. 1995). Continued throughout up-estuary travel, FTT promotes rapid up-estuary transport during in-flowing currents while also allowing individuals to maintain horizontal position within estuaries during out-flowing currents.

In addition to using FTT, estuary-invading megalopae use cues to determine orientation of travel and ultimately reach terminal settlement habitat. Readiness to terminally settle (i.e., cease FTT and permanently adopt a benthic existence) and time until metamorphosis to first-instar juvenile increases and decreases, respectively, in response to low salinity water and chemicals that originate from the structural components of shallow estuarine habitats (e.g., *Zostera marina*, *Spartina alterniflora*; Wolcott and De Vries 1994; Forward et al. 1996). Chemical cues are also used to orient away from predators and toxins (Forward et al. 2003a). In combination, these cues signify the nearby presence or absence of suitable settlement habitat and cause megalopae to orient toward or away from cue origin. The need for such cues in addition to structural complexity of habitat ensures up-estuary transport continues until invading megalopae reach favorable conditions for metamorphosis, growth, and survival.

In summary, recruitment may be viewed as sequentially encompassing: (1) egg production, (2) egg fertilization, oviposition, and embryonic development during or after migration of the parent female to the estuary mouth, (3) hatching, larval release, and advection of larvae from the parent estuary, (4) offshore dispersal and development of larvae (zoeae), (5) aggregation of larvae outside the estuary mouth (i.e., larval pooling) and development of post-larvae (megalopae), (6) ingress of megalopae to estuarine waters (i.e., post-larval supply), (7) invasion of nearshore habitats and continued megalopal development (i.e., readiness for settlement), (8) active terminal settlement by megalopae in shallow, nursery habitat, and (9) metamorphosis to first-instar juvenile crab (i.e., recruitment into the juvenile or adult-form population).

Materials and Methods

Study Location

The study area was located on and immediately adjacent to the Aransas National Wildlife Refuge (ANWR) in Aransas and Calhoun counties, Texas (Fig. 2-1). The refuge is situated almost entirely on the Blackjack Peninsula, which is bounded by two major bays (San Antonio and Copano-Aransas), the smaller St. Charles and Mesquite Bays, and the Gulf Intracoastal Waterway (GIWW). The Guadalupe, Aransas, and Mission Rivers drain into these surrounding bays, though the study area lies largely within the Guadalupe Estuary.

Presence and movement of water within the estuary is influenced by tides, meteorological events (e.g., rainfall, wind, hurricanes), and fresh and coastal waters entering the estuary. Diurnal tides (one high, one low) along this portion of the coast exhibit a narrow daily tidal range of approximately 9-13 cm (Texas A&M University-Corpus Christi, Division of Nearshore Research, Station 031, Seadrift). Fortnightly tides influence the tidal range minimally, but tidal range in fall and spring can be considerably larger (≤30 cm) and water typically reaches high marsh. Water exchange also occurs during strong wind events. North winds in winter and southeast winds in summer force waters out of and into the salt-marsh, respectively. North and southeast winds also increase and decrease, respectively, the ease (or speed) at which southward-flowing

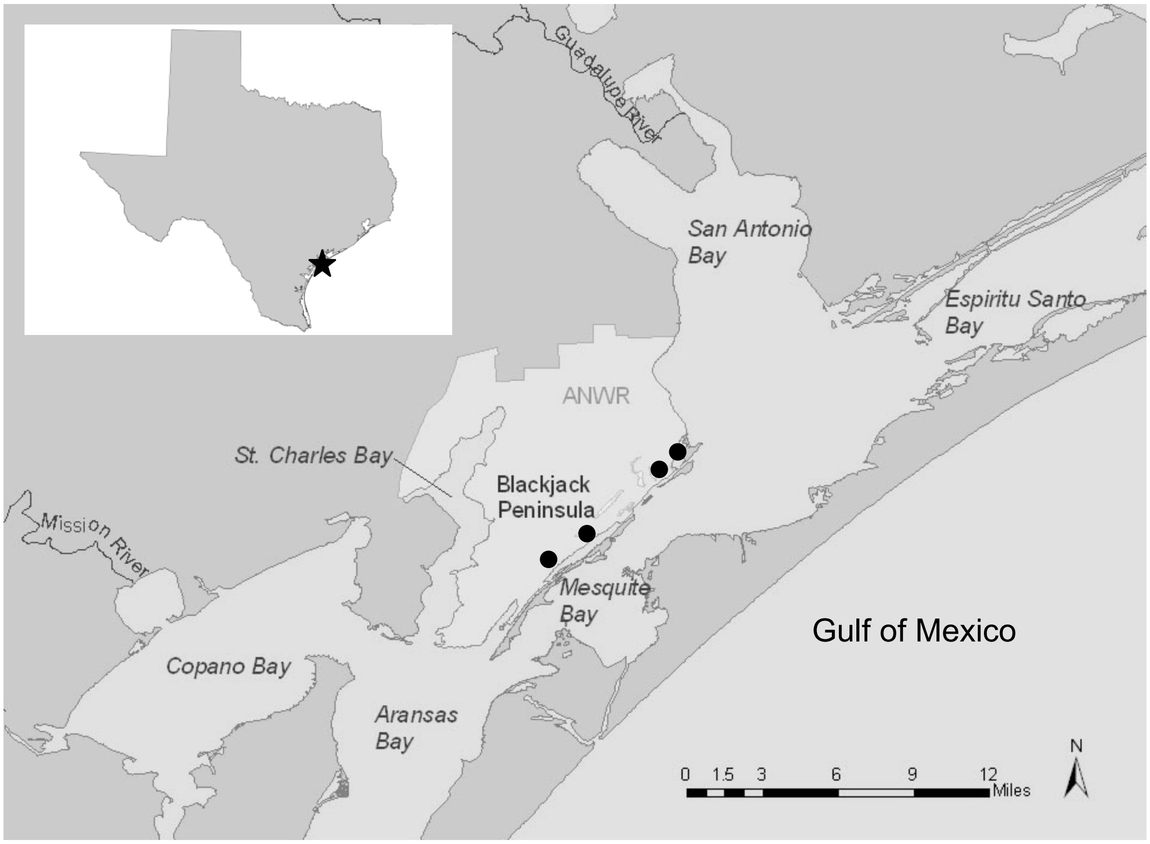

Fig. 2-1. Map depicting the locations of study sites (dots) on the central Texas coast (star) and eastern perimeter of Aransas National Wildlife Refuge (ANWR). From northeast to southwest, study sites included Mustang Bay, Boat Ramp, Pump Canal, and Pipeline.

waters in the GIWW are transported. The Blackjack Peninsula receives higher quantities of freshwater discharge from the Guadalupe River than any other nearby river, but the southern tip of the peninsula is also influenced by water flow into the Copano-Aransas Bay system. Exchange between nearshore and off-shore waters occurs at Pass Cavallo, located at the north end of the estuary. Cedar Bayou, a much smaller source of exchange into Mesquite Bay, was closed by siltation during the study. During high freshwater inflow, salinities are lowest at the northern-most extent of the peninsula and increase progressively southward. All estuarine habitats within the study area annually experience a wide range of salinities (1-30 ppt).

The general climate of the area is sub-tropical. Normal annual rainfall is 103.7 cm, 45% (46.4 cm) of which falls during May-June (22.0 cm) and September-October (24.4 cm). Normal monthly minimum and maximum temperatures are 17.4°C and 24.9°C, respectively, during March-May, 25.1°C and 31.8°C during June-August, 18.0°C and 26.6°C during September-November, and 8.0°C and 17.8°C during December-February (NOAA, National Climatic Data Center 1971-2000, Aransas Wildlife Refuge, Texas weather station).

Estuarine habitats used by blue crabs of all life-history stages include shallow bays and salt-marsh. Bays are primarily subtidal and consist of open-water, nonvegetated (mud or sand) bottoms and beds of submerged aquatic vegetation (SAV; e.g., *Ruppia maritima*), algae, and oysters. The salt-marsh is primarily intertidal and contains mixed emergent vegetation, connected and isolated ponds, and occasional small-scale tidal creeks. Approximately 15-50% of the marsh is made up of ponds (table on page 104), which typically are nonvegetated but seasonally contain SAV and algae. Islands of slightly-elevated ground support the emergent growth of highly salt-tolerant but intermediately flood-tolerant plant species (e.g., *Borrichea frutescens, Batis maritima, Salicornia virginica, S. bigelovii, Lycium carolinianum*), while shallow depressions and edges of ponds and tidal creeks support species of both high salt and flood tolerance (e.g., *Distichlis spicata, Spartina alterniflora*; Stutzenbaker 1999).

Study Design

This study was conducted in association with efforts to examine the diet and foraging behavior of whooping cranes during winter. To facilitate both the crane and crab portions of this greater study, three of the 19 winter territories of whooping cranes located within ANWR were used as replicate study sites, including those named Boat Ramp (BR), Pump Canal (PC), and Pipeline (PL; Fig. 2-2). Territories (hereafter, study sites) differed considerably in habitat composition and connectivity of bay to interior salt-marsh waters. Distances to each the Guadalupe River and Pass Cavallo, respectively, increased from BR (29 km, 51 km) to PC (35 km, 56 km) to PL (38 km, 59 km). All sites were considered fully representative of the contiguous salt-marsh and adjacent bay habitat in which they were located, and inferences from study results were intended to be applied to the population of sites represented by those sampled. Sampling also occurred within a fourth site not specifically associated with any crane territory. The site, named Mustang Bay (MB), was situated along the southern end of Mustang Bay, immediately north of the ANWR boat ramp canal (Fig. 2-2).

Fig. 2-2. Satellite imagery and habitat overlays for each of four sites located along the eastern perimeter of Aransas National Wildlife Refuge, Texas and studied during September 2003-October 2005. Study sites included Mustang Bay (the reference site) and Boat Ramp (top), Pump Canal (middle), and Pipeline (bottom). All sites except Mustang Bay were based on the winter territories of whooping cranes and included multiple shallow-water habitats.

Area within each study site was categorized by habitat and included one or more of (1) bay-marsh interface (shallow bay within 50 m of emergent salt-marsh vegetation; bay), (2) tidal creek (connection between bay and interior salt-marsh waters; TC), (3) connected pond (water within salt-marsh interior, seldom disconnected from bay; CP), (4) unconnected pond (isolated water in salt-marsh interior, intermittently connected; UP), and (5) emergent salt-marsh vegetation (Fig. 2-2). Habitats were not represented at every study site. Bay habitat was not represented within boundaries of the BR crane territory, because salt-marsh at this site was enveloped by large, reinforced levees designed to protect the marsh surface from intense wave-action in the adjacent boat ramp canal and GIWW. However, shallow open water situated along the NW (landward) side of the GIWW and south of the territory was used as surrogate bay habitat at the site. Tidal creek habitat provided the connection between the ponds of PL and the bay, but the main tidal channel was located outside site boundaries and thus not included in sampling efforts. MB comprised bay habitat only, and PC contained all habitats.

Sampling efforts associated with each study objective differed by design. To examine fine-scale temporal trends in rates of megalopal settlement and juvenile recruitment in bay habitat and subsequently evaluate biases associated with using a semi-lunar sampling interval at BR, PC, and PL, I sampled continuously at four locations at MB during two distinct semi-lunar periods of time (objective 2). To quantify and further investigate long-term trends in settlement and recruitment rates, I used repeated measures of a one-level nested design structure and sampled continuously at four locations within the bay habitat of each BR, PC, and PL during September 2003-

October 2005 (objectives 3-4). To determine the spatial extent to which megalopae settled in the salt-marsh and individuals were recruited into the crab population (newly-metamorphosed juveniles), I used an incomplete block design with sub-sampling (objective 5). Sampling for this last objective occurred at four locations within each of one to three fixed habitats (TC, CP, UP) per site or block (BR, PC, PL) during five distinct semi-lunar periods of time. For each objective, the mean relative abundances of megalopal and juvenile blue crabs were computed per experimental unit (habitat study site^{-1} sampling period^{-1}) using data acquired from the four sampling locations therein. Thus, samples collected per experimental unit were considered sub-samples in all cases, and computed response variables are herein referred to as rates (e.g., megalopal settlement rate).

Data Collection

During the past 30 yr, onshore transport and settlement patterns of post-larval crabs have been investigated at several locations along the Atlantic and Gulf Coasts using artificial settlement substrates or collectors (e.g., Shanks 1983; Lipcius et al. 1990; van Montfrans et al. 1990; Rabalais et al. 1995). Following some experimentation, standard methods of collector construction and deployment were devised (Metcalf et al. 1995). Protocol subsequently includes collectors constructed of 16-cm-diameter x 38-cm-height PVC piping wrapped in blue hogs-hair furnace filter material. When deployed, collectors float vertically in the water column by means of a flotation device on top and small weight on the bottom. Typically, collectors have been deployed along coastal docking structures or piers where water depths ranged 2-4 m. Daily collection intervals (i.e., length of time between collector deployment and retrieval) have been used due to immense temporal variability and highly episodic patterns observed in settlement. Periods of collector deployment have coincided with high-water periods of the year and/or months believed to represent the principal period(s) of megalopal settlement (e.g., Wrona et al. 1995).

My objectives for this research were to estimate rates of terminal megalopa settlement and juvenile recruitment throughout the annual cycle and at several replicate sites to capture both temporal and spatial variability. Objectives also included examining natural settlement and recruitment patterns in shallow habitats within and adjacent to the salt-marsh, as opposed to patterns along nearby piers. Consequently, as water depths in bay habitat during low-water periods of the year and in interior-marsh habitats throughout the year were too low for vertically-oriented collectors, my objectives precluded the use of standard protocol in its entirety, and modification of the dimensions and floating orientation of collectors was essential. Moreover, the collection interval was increased due to the overall high intensity of data collection.

Collectors used in this study were constructed by wrapping ca. 0.38 m^2 of blue hogs-hair furnace filter material (two halves of one 50-cm x 76-cm filter) length-wise around PVC piping (3.8-cm (1.5-in) diameter x 1.5-m (5-ft) length) and securing it with cable-ties. Four permanent stands, or collector stations, were installed in each habitat and site sampled (Fig. 2-3). Collectors were secured to stands with rope and floated horizontally in the water column within 5-20 cm of the water's surface by attaching crab

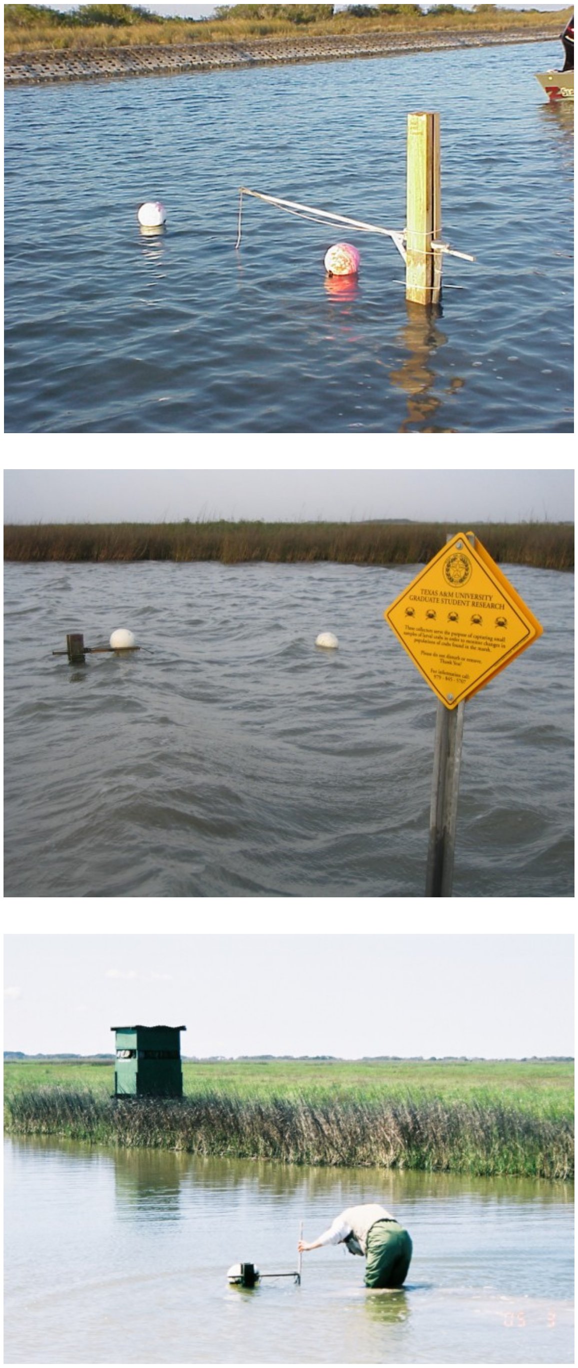

Fig. 2-3. Collector stations in the bay habitat of Boat Ramp (top), Pump Canal (middle), and Pipeline (bottom). Bay stations included reinforced wooden or galvanized steel stands, rope, the collector (i.e., artificial habitat), and two crab-pot buoys. Stations in interior salt-marsh habitats did not require reinforcement and used only small stringer floats.

pot buoys to the ends of collectors. Collectors were deployed at the start of sampling or collection periods, which, for objectives 3-5, began during the new or full moon and lasted one-half the lunar cycle (14-16 d). Sampling for objective 2 comprised a series of 14 daily collection periods during each of two non-adjacent semi-lunar periods, beginning with the full and new moon, respectively. At the end of each collection period, which, in the cases of objectives 2-4, was also the start of the following period, previously-deployed collectors were retrieved and new ones secured in their place. Data used for objectives 3-4, consequently, were collected during a series of 50 semi-lunar collection periods. Retrieved collectors were placed in modified wallpaper trays, covered, and taken to land, where they were carefully disassembled and thoroughly washed with fresh water to remove all settled organisms and debris (Fig. 2-4). All matter removed from collectors was preserved in formalin (10% formaldehyde) and taken to the lab for processing.

In the lab, megalopae and juveniles of *Callinectes sapidus* and *C. similis* were identified by life-stage and enumerated per sample. All data were later combined under *Callinectes* spp., because no megalopae and few juveniles were collected for *C. similis.* Juvenile crabs were measured for carapace width (CW) in millimeters and classified as either class 1 (1-5 mm) or class 2 (>5 mm). In agreement with Pardo et al. (2007), crab recruitment was defined as the addition of individuals to the estuary’s adult-form (juvenile) population through successful megalopa-to-juvenile metamorphosis. Consequently, class-1 juveniles were considered recruits and are herein described as newly-metamorphosed or newly-recruited.

Fig. 2-4. Megalopal settlement collectors post-deployment. Upon retrieval, collectors were placed into trays and transported to land (top and middle). Filters were removed, placed in buckets filled with freshwater, and thoroughly washed to remove all organisms (bottom).

At times of collector deployment and/or retrieval, several environmental variables were measured per collector station, including water temperature, salinity, and depth. In addition, data for several other parameters were obtained from remote sources in San Antonio Bay, on the Guadalupe River, and at ANWR and included water temperature (°C), primary water level (m above reference datum), wind speed (km hr^{-1}) and direction (0-359°; Texas A&M University-Corpus Christi, Division of Nearshore Research, station 031, Seadrift), river discharge (cu ft sec^{-1}; US Geological Survey, Guadalupe Rv nr Tivoli, TX, station 08188800), and precipitation (cm; NOAA, National Climatic Data Center 1971-2000, Aransas Wildlife Refuge, Texas weather station).

Statistical Analysis

For all objectives, I calculated mean rates of megalopal settlement (number of megalopae $collector^{-1}$) and juvenile recruitment (number of class-1 juveniles $collector^{-1}$) per experimental unit (habitat study $site^{-1}$ sampling $period^{-1}$). I also calculated mean collection rate of larger juveniles (number of class-2 juveniles $collector^{-1}$) per experimental unit for comparative purposes. Examination of fine-scale patterns at MB required only visual inspection of mean rates across each series of 14 collection periods (objective 2). To examine long-term patterns at BR, PC, and PL (objective 3), I used mean rates per experimental unit to additionally calculate overall means by study site (all periods combined) and period (all sites combined). To examine spatial patterns or use of interior salt-marsh habitats by megalopal and juvenile crabs (objective 5), I used mean rates per experimental unit to calculate overall means by site and habitat for each of the five collection periods. Presence or absence of megalopae and juveniles in any habitat clearly implied use or no use of the habitat; statistical tests were not needed to identify differences in use of habitats across sites.

I used an information theoretic approach to investigate causes of variability in mean rates of settlement and recruitment (objective 4). I developed a priori biological hypotheses concerning the variability in rates and used these hypotheses as the basis for subsequent development of several generalized linear mixed models modeling settlement and recruitment as functions of environmental and random effects.

Sources of variation in models of settlement corresponded to two broad steps in the overall recruitment process: (1) embryonic development (Period E) and (2) larval development (Period L). Period E incorporated life history events ranging from egg production to release of newly-hatched zoeae in coastal waters. As embryogenesis lasts at least 8-11 d (Amsler and George 1984a) and hatching to first juvenile instar takes at least 37-55 d (Costlow and Bookout 1959), Period E was represented by the string of 7-28 d ending 28-49 d prior to the date of collector retrieval (i.e., potential date of terminal settlement). Period L accounted for larval and post-larval development as well as all concurrent processes, including offshore dispersal, larval pooling, estuary ingress, up-estuary movement (invasion), and terminal settlement. Consequently, Period L was simply represented in analyses by the 35 d immediately prior to and including the date of collector retrieval. Six hypothetical sources of variation in megalopal settlement were identified, including:

1. *Water temperature*. Field studies have yet to identify water temperature as a significant regulator of post-larval settlement by blue crabs (but see Wenner et al. 2005 for reinvading post-larval shrimp). However, laboratory studies of blue crabs demonstrate that eggs fail to hatch when temperatures are outside the range of 19-29°C (Sandoz and Rogers 1944) and larvae fail to develop past the first zoeal stage when held at 20°C (versus 25°C or 30°C; Costlow and Bookhout 1959). Generally, larval and post-larval rates of survival and growth increase with temperature for blue crabs (Costlow and Bookhout 1959; Costlow 1967) and other decapods (Templeman 1936; Costlow et al. 1960; Ong and Costlow 1970; Li and Hong 2007), but an upper limit to the benefits of warm water has been observed around 30°C (Costlow and Bookhout 1959). I hypothesized settlement rate would positively relate to water temperature during both embryonic and larval development. However, I also believed these relationships would be evident only when spawning was probable (i.e., temperature was optimal for embryonic development).
2. *Water salinity*. Laboratory studies have provided insight concerning the effects of salinity on development of estuarine decapods. For example, the eggs of blue crabs are more likely to hatch with increasing salinity through 32 ppt (Sandoz and Rogers 1944) but have failed to hatch in experimental salinities of 10.5 and 15.6 ppt (Costlow and Bookhout 1959). For American lobster (*Homarus americanus*) and Kuruma prawn (*Marsupenaeus japonicus*), tolerance to low salinity decreases through the larval stages, reaches minimum during metamorphosis to post-larva, and increases through the post-larval stages (Charmantier et al. 1988). For several crab

species, including blue crab, low salinities have shown to produce especially high mortality rates, decrease the likelihoods of complete zoeal development and metamorphosis to post-larva, and markedly reduce growth rates (Costlow and Bookhout 1959; Costlow et al. 1960; Costlow 1967; Ong and Costlow 1970; Roberts 1971). Consequently, the likelihoods of spawning and completing larval development should each increase with salinity and thereby increase the rate of post-larval settlement. Furthermore, as estuarine decapods in early development are commonly more sensitive to low salinity when temperature is also low (Costlow et al. 1960; Ong and Costlow 1970), I believed salinity and temperature would synergistically affect settlement rate, i.e., the effect of decreasing salinity is greater in low than high temperatures.

3. *Water level*. To my knowledge, the effect of discrete water levels on post-larval settlement is uninvestigated (but see Rabalais et al. 1995), but changes in water level and directional water flow during daily and fortnightly tides have been shown to affect advection of larval crabs from estuaries, as well as eventual invasion and settlement of post-larvae (Olmi 1994; Tankersley et al. 1998; Forward et al. 2003b). More individuals seem to be transported with selective tidal-stream transport (STST) during the new and full moons (spring tides) than other periods of the lunar cycle, demonstrating the increasing utility of STST with tidal amplitude (Mense et al. 1995; Metcalf et al. 1995; González-Gordillo et al. 2003; Queiroga et al. 2006). I did not sample megalopa abundance on a daily scale but believed the effects of ebb tides (when larvae are advected offshore) and flood tides (when post-larvae invade

estuaries) would be greatest during tropic or seasonal (spring and autumn) tides, when tidal amplitude and overall mean water levels are highest. I also postulated that the effect of water level would interact with the effects of temperature and salinity. Specifically, the effect of water level should be evident only when spawning is probable (i.e., temperature is optimal for embryonic development) and should increase with salinity (as low salinities negatively affect survival).

4. *Wind.* I believed the rate of blue crab megalopal settlement would increase with wind speed from the period of larval development. Studies have shown through empirical data collection and mathematical simulation that wind stress is a major driver in both offshore and nearshore water circulation patterns and, as a result, is a significant mechanism of transport for dispersed larval and post-larval decapods (Goodrich et al. 1989; Blanton et al. 1999; Queiroga et al. 2006). Within estuaries, winds also may function similar to tides (see Forward et al. 2003b) by altering water salinity and turbulence levels and consequently influencing megalopa swimming behavior and ascent into the water column. Moreover, turbidity (or low light transmissivity) associated with wind stress may inhibit predation (Minello et al. 1987; Macia et al. 2003) and result in greater numbers of invading megalopae (King 1971). While I believed increasing wind speed would enhance settlement rate, I also believed that the effect of wind speed would differ by wind direction (Blanton et al. 1999; Queiroga et al. 2006; Gimenez and Dick 2007) and winds promoting estuary ingress and invasion would be more effective in transporting individuals when water level was high (e.g., due to tropic tides) than low (Hasek and Rabalais 2001).

5. *Previous measures of settlement*. Study sites were repeatedly sampled, and residual error surrounding mean rate of megalopal settlement during collection period x was potentially correlated with that of sample period $x + 1$. This followed the notion that megalopal settlement rates of consecutive periods were not independent. This would be the case, for example, if individuals arriving to a site during one collection period were still present in megalopal form during the next period. Settlement during the latter period would depend on settlement during the first period and not factors influencing the initial settlement event. The probability of this occurring, however, would depend on stage of individual development upon arrival and conditions experienced at the site influencing further development, mortality, or emigration. Due to the short period of the megalopa life-stage (6-20 d; Costlow and Bookhout 1959) and long collection interval (14-16 d), I hypothesized correlation of errors would be possible but unlikely.
6. *Study site*. I believed stochastic variability among study sites would contribute to uncertainty surrounding the true mean rate of megalopal settlement. Unmeasured or unpredictable differences in characteristics associated with each site (e.g., bottom substrate, vegetative cover, predator abundance) and transport to each site (e.g., current flow, susceptibility to wind, distance) likely contributed to random error. Thus, the random effect of study site was incorporated into all models.

Sources of variation in models of recruitment corresponded to the 14 d prior to and including the date of collector retrieval and included processes occurring immediately prior to and following metamorphosis from megalopa to juvenile crab. Hypothetical sources of variation in juvenile recruitment included:

1. *Water temperature*. For megalopal blue crabs, rates of survival and progression through development generally increase with increasing water temperature. In an experiment designed to examine the effects of water temperature and salinity, megalopae held at 15°C demonstrated highly prolonged (30-67 d) or incomplete development and high rates of mortality (57.9-100%), particularly in the salinity category of 10 ppt (versus 20, 30, 35, and 40 ppt; Costlow 1967). When held at 20°C in 10-40 ppt, megalopae metamorphosed to first-instar juvenile at higher rates (70.0-95.0%) and spent less time in development (12-26 d), but 100% of individuals in 5 ppt failed to reach or successfully complete metamorphosis. In contrast, complete development was evidenced in all salinity categories when megalopae were held at 25°C and 30°C. Moreover, 78.9-100% of individuals metamorphosed in 10-40 ppt, 22.2-40.9% metamorphosed in 5 ppt, and the length of time spent in development was the shortest observed (5-13 d). Because probability of juvenile recruitment (i.e., metamorphosis to juvenile crab) is higher in warm than cold water, I hypothesized recruitment rate would increase with mean temperature from the preceding 14 d. However, I also believed the effect of increasing temperature on recruitment rate would be evident only when conditions were optimal (e.g., mean temperature >15°C or 20°C).
2. *Water salinity*. The effects of water salinity on the survival and development of blue crab megalopae are less clear than those of temperature. For instance, Costlow

(1967) found that megalopa survival and probability of metamorphosis to first-instar juvenile generally increased with increasing water salinity in all experimental water temperatures from 15-30°C. Costlow (1967) also observed that probabilities of metamorphosis in the highest salinity (40 ppt) of the two lowest temperatures tested (15°C and 20°C) were lower rather than higher than the probabilities observed in 35 ppt. In addition, time spent in the megalopal life-stage decreased with increasing salinity in the highest temperatures examined but increased with increasing salinity in the coldest temperatures examined. These patterns demonstrate elevated effects of salinity at low temperatures (and vice versa) but also represent possible physiological strategies by which survival is ensured during long periods in cold conditions. I hypothesized that recruitment rate would decrease with salinity during the preceding 14 d but discounted the effects of salinity at 40 ppt, because salinities >30 ppt rarely occur in shallow portions of the Guadalupe Estuary. I also acknowledged the compounding effect of temperature and believed that decreases in recruitment rate resulting from decreased salinity would be increasingly pronounced as temperature during the preceding 14 d also decreases.

3. *Water level*. Within estuarine habitat, Rakocinski et al. (2003) found crabs <6 mm CW were greater associated with deep (90 cm) than shallow (30 cm, 60 cm) waters and postulated that such distribution may result from the greater refuge afforded by greater water volume. Similar in function, increasing water levels in this study may reduce predation mortality of terminally-settled megalopae and newly-recruited juveniles by decreasing their overall densities and increasing the water volume to be

searched by predators. I believed increased survival of settled megalopae would increase the probability of transition to juvenile crab and subsequently lead to higher observed recruitment rates.

4. *Wind*. Wind-generated currents are an important mechanism of water transport and may significantly aid dispersal of young blue crabs within the estuary immediately prior to terminal settlement or following metamorphosis to first-instar juvenile crab. For individuals in deep estuarine waters or other unsuitable settlement habitat, wind may augment movement to the more protective, structurally-complex habitats of shallow bay and salt-marsh. For individuals having already reached these habitats, increasing wind stress may increase water turbidity, thereby reducing the searching capabilities of predators and increasing individual survival (Minello et al. 1987; Macia et al. 2003). I believed increased survival during the final steps of the recruitment process would subsequently lead to higher observed recruitment rates. However, I also believed this relationship would differ by wind direction, with higher numbers of recruits occurring in shallow bay habitat when wind was blowing toward shore (e.g., east to northeast winds).
5. *Megalopal settlement rate*. Megalopal blue crabs metamorphose into the adult life-form (i.e., undergo juvenile recruitment) following terminal settlement in suitable nursery habitat (see Introduction and Background). If individuals arrive to study sites and settle as megalopae, rate of juvenile recruitment may closely correlate with megalopal settlement rate as long as dispersal and mortality rates following settlement are minimal or at least consistent among sampling periods. I theorized

this would be the case and further suspected the concurrent rate of settlement would be more predictive of recruitment rate than that of the previous period.

6. *Previous measures of recruitment*. Rates of juvenile recruitment associated with collection period *x* were potentially correlated with those of collection period *x*+1, depending on the developmental stage of individuals present during period *x* and conditions promoting growth and survival thereafter. Newly-recruited juveniles likely outgrow the class size of 1-5 mm CW in less time than one collection interval and also likely have more control of movement (dispersal) than megalopae. Therefore, I hypothesized that correlation of juvenile recruitment estimates between successive sample periods would be possible but very unlikely.
7. *Study site*. I believed stochastic variability among study sites would contribute to uncertainty surrounding the true mean rate of juvenile recruitment. Unmeasured or unpredictable differences in characteristics associated with each site (e.g., bottom substrate, vegetative cover, predator abundance) likely contributed to random error.

Hypothetically, the effects of water temperature, salinity and other environmental attributes could be represented by a multitude of variables. For this reason, I incorporated two to three variables in analyses for each water temperature, water salinity, water level, and wind (Tables 2-1 and 2-2). To explore the timing of effects on settlement rate, I restructured remotely collected data into several forms, consisting of (1) descriptive measures (mean, mode, sum, or an index of variability (var = (max-min)/mean) for the 7, 14, 21, and 28 consecutive days ending 28, 35, 42, and 49 d prior

Table 2-1. Fixed effects and representative explanatory variables included in models of blue crab megalopal settlement rate. Explanatory data corresponded to the periods of embryonic (E) or larval (L) development. Period E was represented by the string of *y*=7, 14, 21, or 28 d ending *z*=28, 35, 42, or 49 d ago. Period L was the *y*=1, 7, 14, 21, 28, or 35 d immediately prior to and including the date of collector retrieval.

Effect/Variable	Description
Water temperature	
wtm	Mean water temperature (°C) recorded per experimental unit.
wt*y*.*z*[1]	Mean water temperature during E.
wt*y*[1]	Mean water temperature during L.
wt15.*y*.*z*[1] wt20.*y*.*z*[1]	Mean water temperature during E, noted as ≤ or > (0 or 1) the lower threshold of optimal water temperature (15°C or 20°C).
wt15.*y*[1] wt20.*y*[1]	Mean water temperature during L, noted as ≤ or > (0 or 1) the lower threshold of optimal water temperature (15°C or 20°C).
Water salinity	
sm	Mean water salinity (ppt) recorded per experimental unit.
rd*y*.*z*[2]	Mean river discharge (cu ft sec^{-1}) during E.
rdm*y*[2]	Mean river discharge during L.
rdv*y*[2]	Variability in river discharge ((maximum-minimum)/mean) during L.
p*y*[3]	Total precipitation (cm) during L.
Water level	
wpm	Mean water depth (cm) recorded per experimental unit.
wl*y*.*z*[1]	Mean water level (m above reference datum) during E.
wlm*y*[1]	Mean water level during L.
wlv*y*[1]	Variability in water level ((maximum-minimum)/mean) during L.
Wind	
ws*y*[1]	Mean wind speed (km hr^{-1}) during L.
wg*y*[1]	Mean gust speed (km hr^{-1}) during L.
wd*y*[1]	Modal wind direction (N, NE, E, SE, S, SW, W, NW) during L.

[1] Data recorded at station 031 (Seadrift) by Division of Nearshore Research, Texas A&M, Corpus Christi.
[2] Data recorded at station 08188800 (Guadulupe River near Tivoli) by the U.S. Geological Survey.
[3] Data recorded at Aransas National Wildlife Refuge as part of the National Weather Service, NOAA.

Table 2-2. Fixed effects and representative explanatory variables included in models of blue crab juvenile recruitment rate. Explanatory data corresponded to the *y*=1, 7, or 14 d consecutively preceding and including the date of collector retrieval, representing the period of time occurring immediately prior to and following metamorphosis from megalopa to juvenile crab (M).

Effect/Variable	Description
Water temperature	
wtm	Mean water temperature (°C) recorded per experimental unit.
wt*y*[1]	Mean water temperature during M.
wt15.*y*[1] wt20.*y*[1]	Mean water temperature during M, noted as ≤ or > (0 or 1) the lower threshold of optimal water temperature (15°C or 20°C).
Water salinity	
sm	Mean water salinity (ppt) recorded per experimental unit.
rdm*y*[2]	Mean river discharge (cu ft sec^{-1}) during M.
rdv*y*[2]	Variability in river discharge ((maximum-minimum)/mean) during M.
p*y*[3]	Total precipitation (cm) during M.
Water level	
wpm	Mean water depth (cm) recorded per experimental unit.
wlm*y*[1]	Mean water level (m above reference datum) during M.
wlv*y*[1]	Variability in water level ((maximum-minimum)/mean) during M.
Wind	
ws*y*[1]	Mean wind speed (km hr^{-1}) during M.
wg*y*[1]	Mean gust speed (km hr^{-1}) during M.
wd*y*[1]	Modal wind direction (N, NE, E, SE, S, SW, W, NW) during M.
Megalopal settlement	
meg meglag	Megalopal settlement rate (number of megalopae collector^{-1}) during the current collection period or previous collection period (lag).

[1] Data recorded at station 031 (Seadrift) by Division of Nearshore Research, Texas A&M, Corpus Christi.
[2] Data recorded at station 08188800 (Guadulupe River near Tivoli) by the U.S. Geological Survey.
[3] Data recorded at Aransas National Wildlife Refuge as part of the National Weather Service, NOAA.

to collector retrieval, and (2) descriptive measures (mean, mode, sum, or var) for the 1, 7, 14, 21, 28, and 35 consecutive day(s) immediately prior to and including dates collectors were retrieved (Table 2-1). The first set of measures represented effects during Period E, whereas the second set represented effects during Period L. To explore the timing of effects on recruitment rate, explanatory data were limited to descriptive measures (mean, mode, sum, or var) for the 1, 7, and 14 consecutive day(s) immediately prior to and including dates collectors were retrieved (Table 2-2). That is, I constrained potential sources of variation to conditions presumably occurring immediately prior to and following metamorphosis from megalopa to juvenile crab. In total, the hypothesized sources of variation for each settlement and recruitment rate were represented, respectively, by 163 and 38 different variables. Not all variables were included in model-building procedures, however, because preliminary examination revealed that most variable forms were not useful in predicting settlement or recruitment rate.

All models, whether preliminary or otherwise, were generalized linear mixed models (GLMMs) and examined using the GLIMMIX procedure in SAS (version 9.1.3; SAS 2006). This was so, because variation surrounding the mean response of settlement or recruitment rate was explained by one or more fixed effects and a random G-side effect (study site). Correlations of residual error (R-side random effects) resulting from repeated measures of the response through time were also examined, but analysis indicated errors were minimally correlated ($AR \leq 0.14$) and inclusion of R-side random effects were unnecessary.

As is common in studies with count data, distributions of the response variables were non-normal (heavily right-skewed) and zero-inflated. The Poisson distribution with canonical link function (log) was assumed appropriate for the response data, but some problems with overdispersion caused by excess zeros were evident. To minimize overdispersion, a value of one was added to each observed response. The expected conditional mean response then took the form:

$g(\mathrm{E}[(\mathrm{Y} + 1)|\mathrm{u}]) = \mathrm{X}\beta + \mathrm{Zu} + \mathrm{e}$

where

g is the link function (in this case, natural log),

X is the matrix of constants determined by fixed effects (covariates),

β is the matrix of fixed effect parameters,

Z is the matrix of constants determined by random G-side effects,

u is the matrix of random model effects, and

e represents residual errors, which in this model are not correlated.

Full models, or those incorporated into model-building procedures, contained all six or seven effects identified a priori but only one variable per effect and period (i.e., Period E (28-49 d ago) or Period L (preceding 1-35 d)), because variables representing the same effect and period were presumed correlated. The only exceptions to this rule were variables of inherently different form. For example, variability of river discharge was included with mean river discharge, variability of water level was included with mean water level, and wind direction was included in models with wind speed. Also, the bivariate form of water temperature was included in an interaction with the continuous form of water temperature. Numerous other two-way and three-way interactions, based on a priori hypotheses (see above), were also included in full models. In total, I examined about 70 full models of megalopal settlement rate and 30 full models of juvenile recruitment rate.

For each model of settlement or recruitment, I used a manual stepwise selection procedure to identify the most important predictive variables. Decisions to remove or keep variables were based on model fit and cautiously guided by changes in Pseudo-AICc values (Akaike 1973; Burnham and Anderson 2002). Caution was heeded because likelihoods (and subsequently AICc values) associated with GLMMs are derived using a doubly iterative model-fitting process and based on pseudo-data, not original data (Littell et al. 2006: 752-754; SAS 2006:151,163). Model dispersion ($\hat{c} = \chi^2/\mathrm{df}$) was an important indicator of model fit. Values of $\hat{c} = 1$ were considered optimal (good model fit), whereas $1 < \hat{c} \leq 4$ indicated slight overdispersion with adequate model structure and $\hat{c} > 4$ indicated poor model structure (inadequate fit; Burnham and Anderson 2002: 67-69). The best fitting model of each settlement rate and recruitment rate, along with hierarchical sub-models, were compiled for comparison.

Results

Data Collection

Settlement collectors were deployed and successfully retrieved in bay habitat at BR, PC, and PL for 46 of 50 semi-lunar collection periods during 25 September 2003-1 October 2005. Collectors were also deployed at MB during two of these periods (7-21

March and 14-28 October 2004) using a daily collection interval, for a total of 28 collection periods. Collectors in interior salt-marsh habitats were deployed during five semi-lunar periods: 25 September-10 October 2003, 18 May-2 June 2004, 26 September-13 October 2004, 13-27 October 2004, and 17 September-1 October 2005. Of the 727 total samples collected during the study, 621 samples were collected in bay habitat (*n*=157 BR, 176 PC, 176 PL, 112 MB) and 106 samples were collected in tidal creek (*n*=15 BR, 14 PC), connected pond (*n*=9 BR, 8 PC, 12 PL), and unconnected pond (*n*=12 BR, 16 PC, 20 PL) habitats combined.

Environmental Conditions

Hydrologic variables (water temperature, salinity, depth) measured at collector stations in bay habitat differed little among study sites (Fig. 2-5). The only exception was water depth, which proved consistently deeper (by >10 cm) at BR than all other sites. Water characteristics measured at collector stations in interior salt-marsh habitats were similar among the five periods sampled (Fig. 2-6). Typically, values ranged 25-30°C for water temperature, 10-15 ppt for salinity, and 25-35 cm for water depth. Deviations occurred during 25 September-10 October 2003, when water was about 20 cm deeper than during other periods, and 18 May-2 June 2004, when water was noticeably fresher at about 5 ppt. Additionally, BR was always deeper in tidal creek and shallower in unconnected pond habitat than other sites.

In attempts to explain variability surrounding mean rates of settlement and recruitment, several environmental variables were remotely recorded. Patterns in water

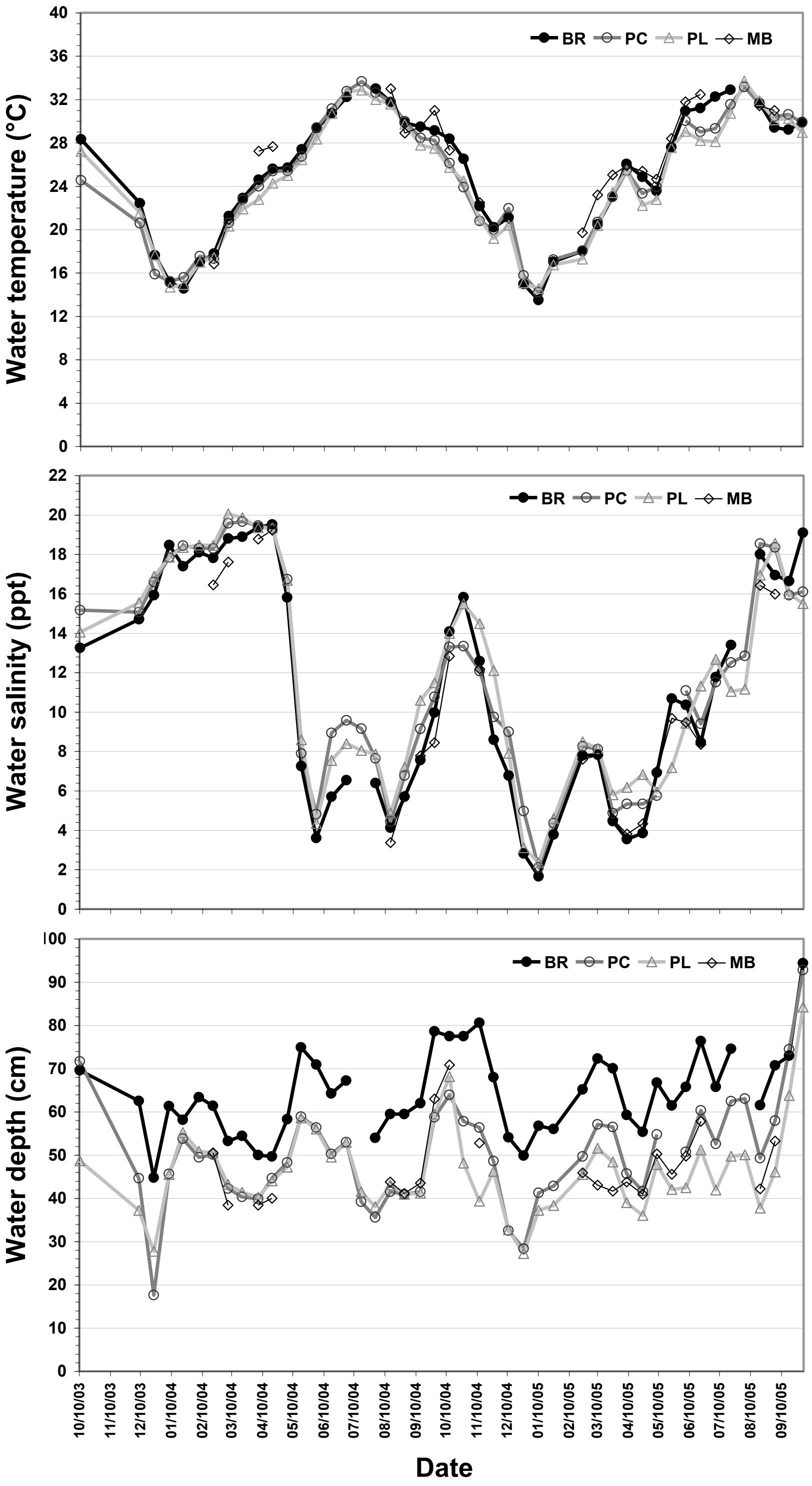

Fig. 2-5. Mean water temperature, salinity, and depth at collector stations located in bay habitat by date and study site. Study sites included Boat Ramp (BR), Pump Canal (PC), Pipeline (PL), and Mustang Bay (MB).

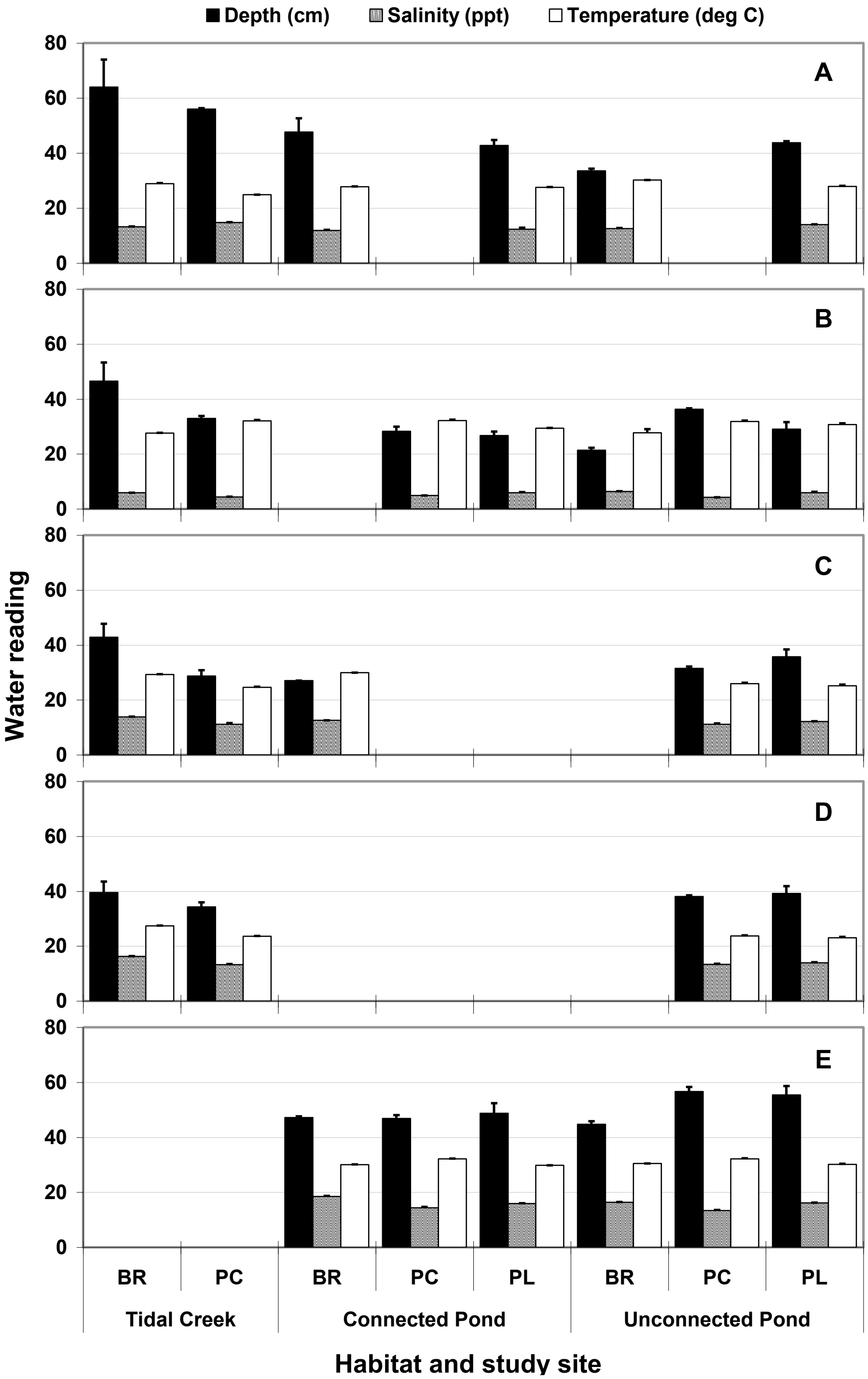

Fig. 2-6. Mean water depth, salinity, and temperature at collector stations in interior salt-marsh habitats by habitat and study site. Collection periods included (A) 25 September-10 October 2003, (B) 18 May-2 June 2004, (C) 28 September-13 October 2004, (D) 13-27 October 2004, and (E) 17 September-1 October 2005.

temperature recorded remotely (Fig. 2-7) closely followed patterns observed at collector stations. Precipitation (pp; Fig. 2-8) and river discharge (rd; Fig. 2-9) were correlated with measures of salinity recorded at collector stations (smn) during five broad periods of time in the study. Periods included: (1) October 2003-March 2004 (low pp, low rd, high smn), (2) April-June 2004 (high pp, high rd, low smn), (3) August-September 2004 (low pp, low rd, high smn), (4) October 2004-March 2005 (high pp, high rd, low smn), and (5) April-October 2005 (low pp, low rd, high smn). Low levels of precipitation were rarely evident in patterns of water level in San Antonio Bay (Fig. 2-10) or water depth recorded at collector stations, likely due to the effects of seasonal (spring and autumn) tides. Low precipitation and water levels coincided during the natural drought periods of August 2003, 2004, and 2005. Wind speed followed a normal seasonal pattern of high(er) speeds in spring and low(er) speeds in autumn (Fig. 2-11). Wind direction was also normal with north winds in autumn-spring and southeast winds in summer, but southeast winds were less prevalent during year 2 than year 1.

Fine-scale Temporal Patterns in Settlement and Recruitment

Two fine-scale patterns of settlement and recruitment were observed at MB when collectors were exchanged daily during two series of 14 collection periods (7-21 March and 14-28 October 2004; Fig. 2-12). During the first series (March), settlement of megalopae occurred on days 13 and 14 only, with the number of settlers collected on day 14 alone comprising over 90% of the total for the series. Patterns of this type typically qualify as episodic (infrequent or random, high levels). In contrast, settlement of

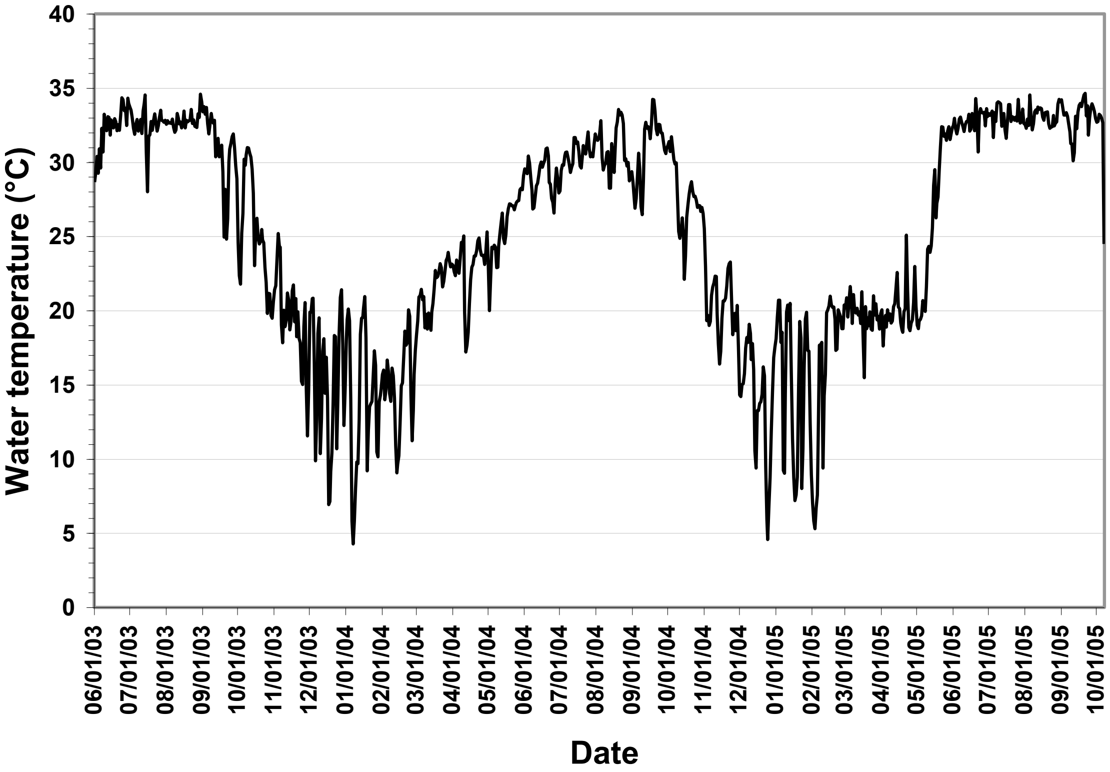

Fig. 2-7. Mean daily water temperature during June 2003-October 2005 in San Antonio Bay, Texas. Data were recorded at the Seadrift water and meteorological monitoring station 031 by the Division of Nearshore Research, Texas A&M University, Corpus Christi.

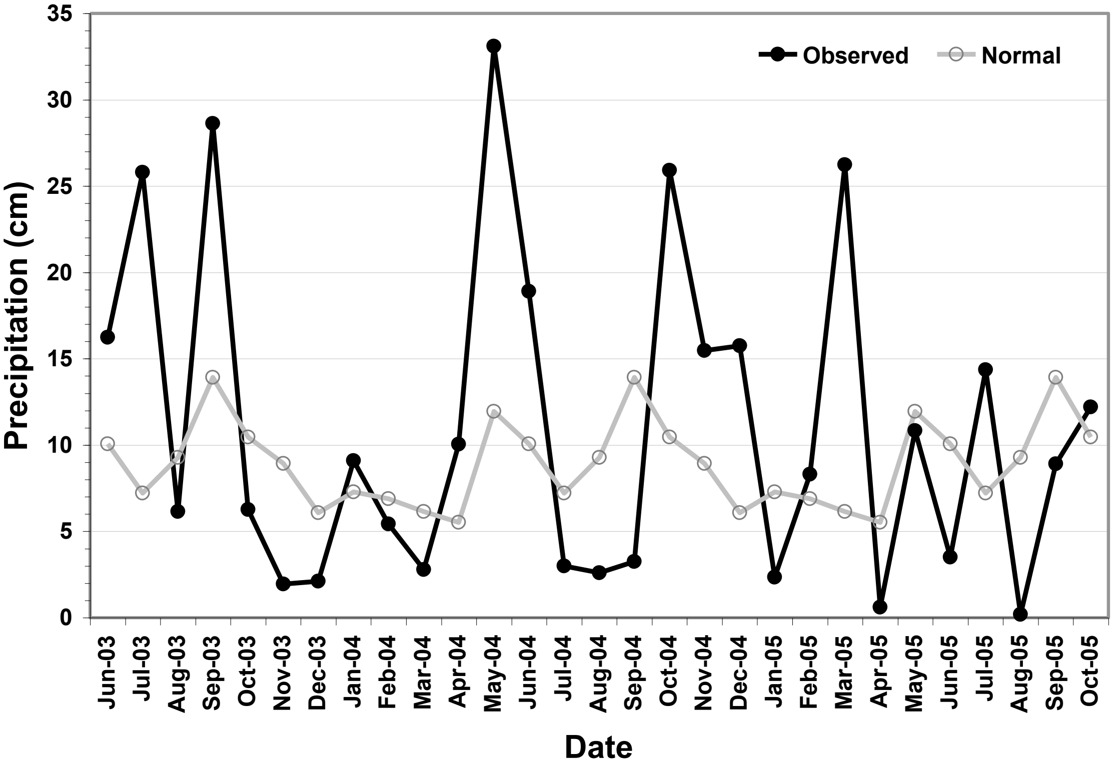

Fig. 2-8. Monthly precipitation observed during June 2003-October 2005 versus normal levels observed during 1971-2000 at Aransas National Wildlife Refuge, Texas (National Weather Service monitoring program, National Oceanic and Atmospheric Administration).

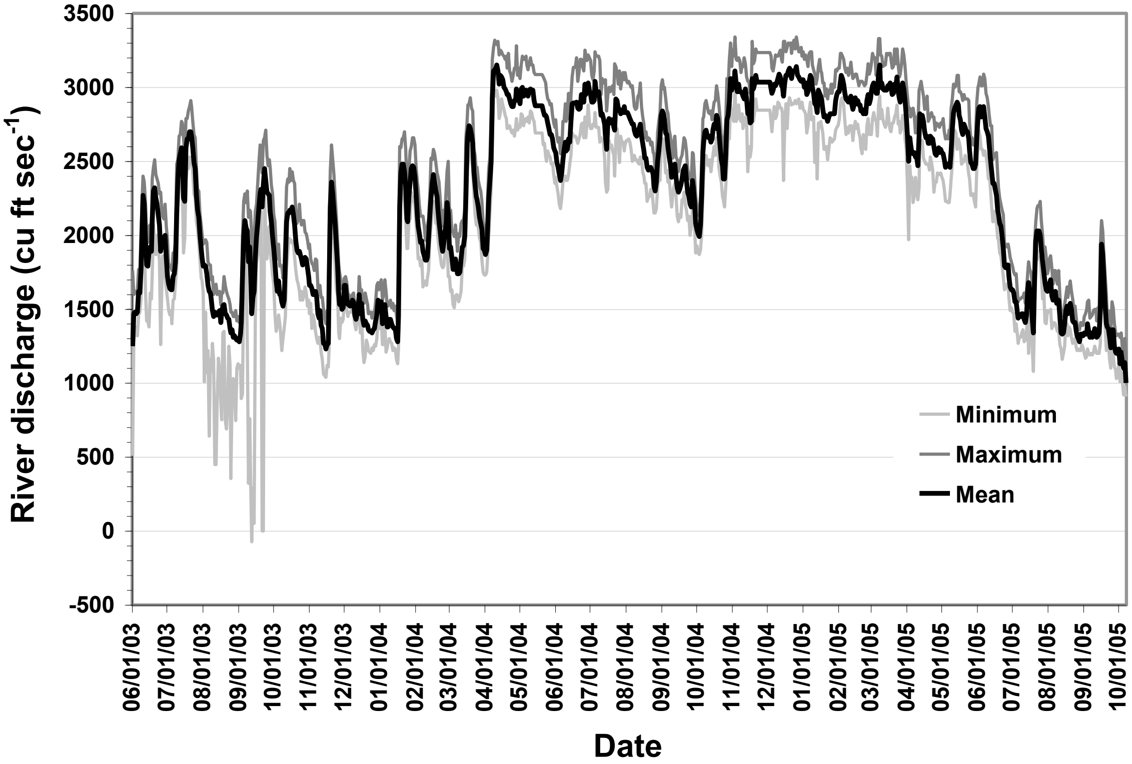

Fig. 2-9. River discharge during June 2003-October 2005 on the Guadalupe River near Tivoli, Texas. Data were recorded at station 08188800 by the U.S. Geological Survey.

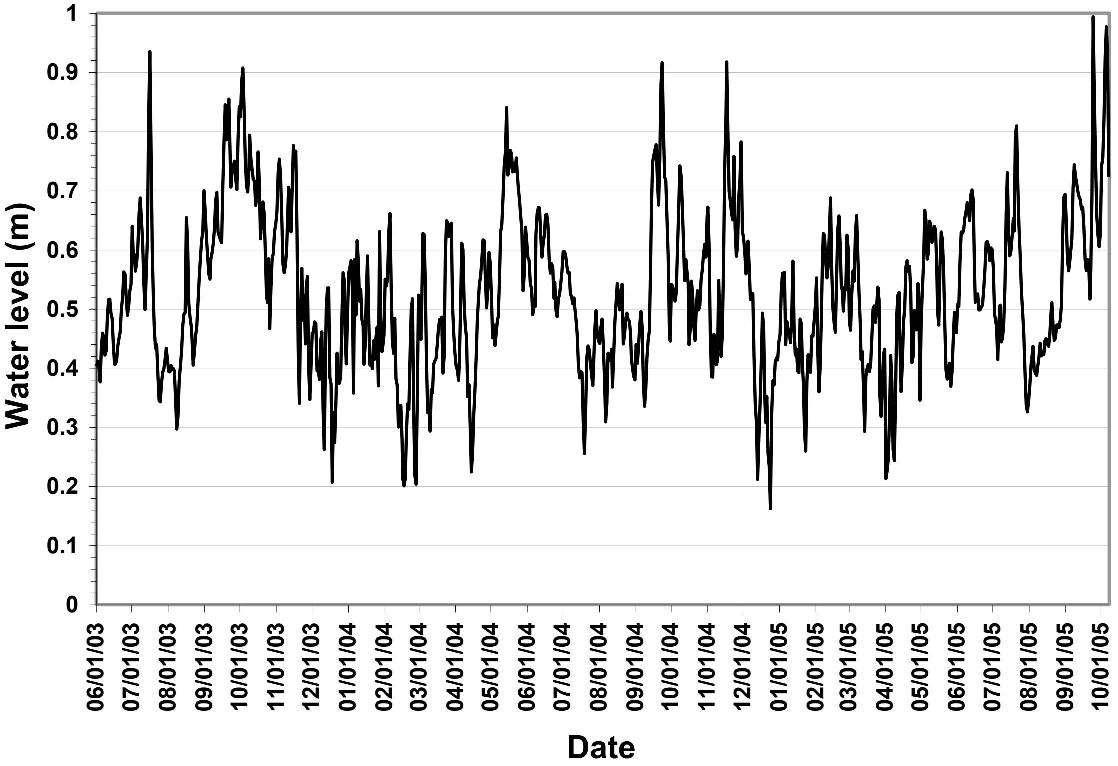

Fig. 2-10. Mean daily primary water level (m above reference datum) during June 2003-October 2005 in San Antonio Bay, Texas. Data were recorded at the Seadrift water and meteorological monitoring station 031 by the Division of Nearshore Research, Texas A&M University, Corpus Christi.

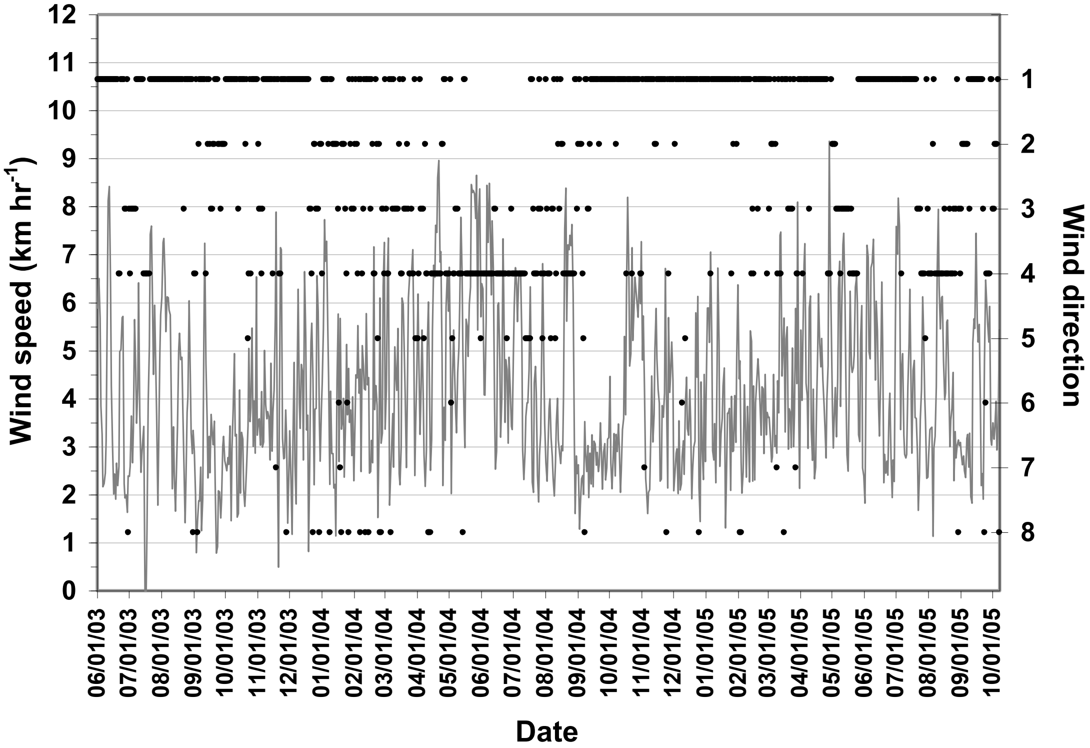

Fig. 2-11. Mean daily wind speed (gray line) and direction (black dots) during June 2003-October 2005 in San Antonio Bay, Texas. Data were recorded at the Seadrift water and meteorological monitoring station 031 by the Division of Nearshore Research, Texas A&M University, Corpus Christi. Wind direction was divided into eight categories: (1) north (≥337.5° or <22.5°), (2) northeast (≥22.5° and <67.5°), (3) east (≥67.5° and <112.5°), (4) southeast (≥112.5° and <157.5°), (5) south (≥157.5° and <202.5°), (6) southwest (≥202.5° and <247.5°), (7) west (≥247.5° and <292.5°), and (8) northwest (≥292.5° and <337.5°).

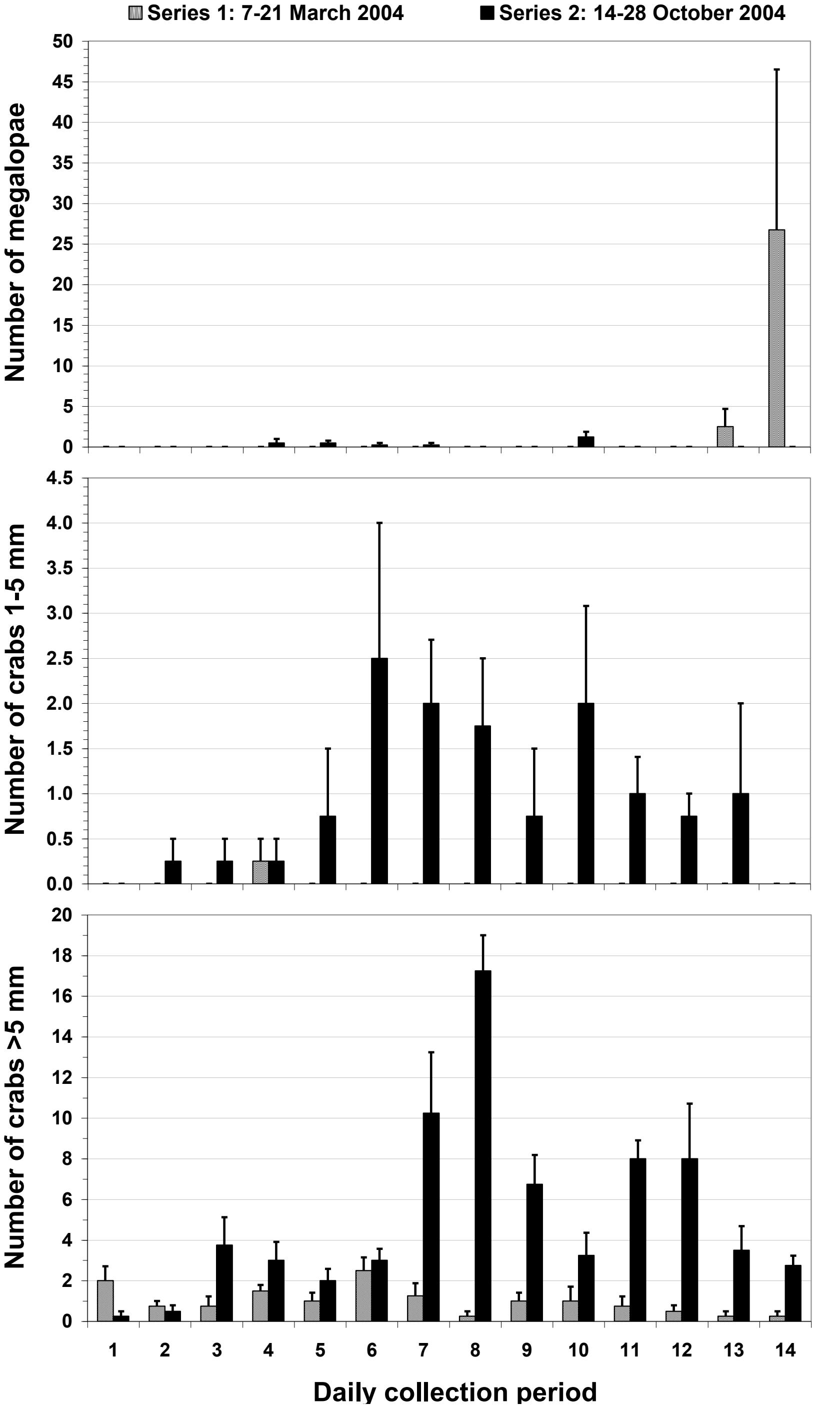

Fig. 2-12. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) collected daily at Mustang Bay during two 14-d series.

megalopae during the second series (October) occurred more frequently (during 5 of 14 d) and at much lower levels than observed during March. Mean settlement (±1 SD) during days of occurrence only was 14.63 ± 17.15 megalopae collector^{-1} in March and 0.55 ± 0.41 megalopae collector^{-1} in October. Recruitment patterns were similar to those of settlement in that frequency of recruitment events was far less in March (1 of 14 d) than October (12 of 14 d). However, the single recruitment event of March was not associated with a high number of individuals (0.25 class-1 juveniles collector^{-1}) and recruitment during days of occurrence was considerably higher in October (1.10 ± 0.77 class-1 juveniles collector^{-1}). Collection of class-2 juveniles occurred during all 14 daily collection periods and was non-episodic for both series, but collection patterns differed slightly. Numbers of class-2 juveniles collected in March (0.98 ± 0.66) were lower and more evenly distributed across days than those of October (5.16 ± 4.56).

Long-term Patterns in Settlement and Recruitment

Over the course of the study, megalopal settlement occurred in all months during March-November (Fig. 2-13). Mean settlement rates (number of megalopae collector^{-1}) were highly variable among semi-lunar collection periods and ranged 0-19.25 megalopae collector^{-1} when data were averaged across sites. Peak settlement rates occurred exclusively in March-June and August-October with magnitude of settlement dependent on study site. Mean settlement rate, variability surrounding mean settlement rate, and frequency of settlement events all decreased from the northern-most site (BR) to the southern-most site (PL; Figs. 2-14 and 2-15). Specifically, the range of mean settlement

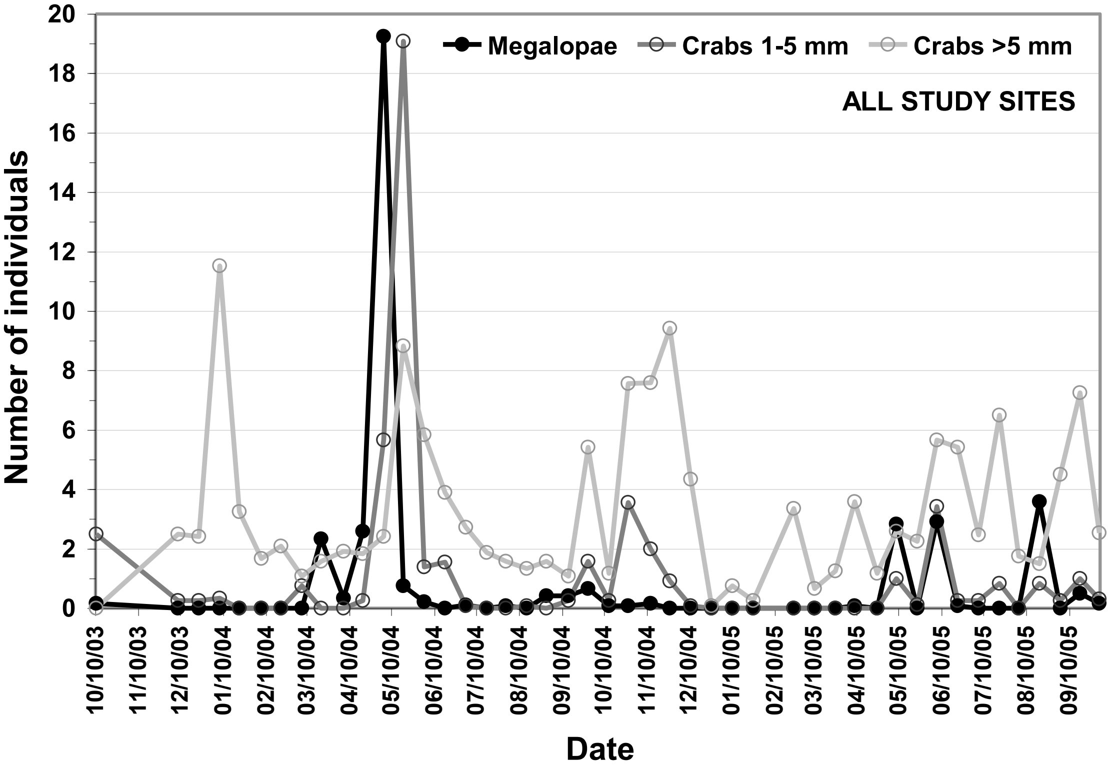

Fig. 2-13. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) per collector in bay habitat during September 2003-October 2005 (all study sites combined). Collectors were deployed for settlement 2 wk prior to retrieval.

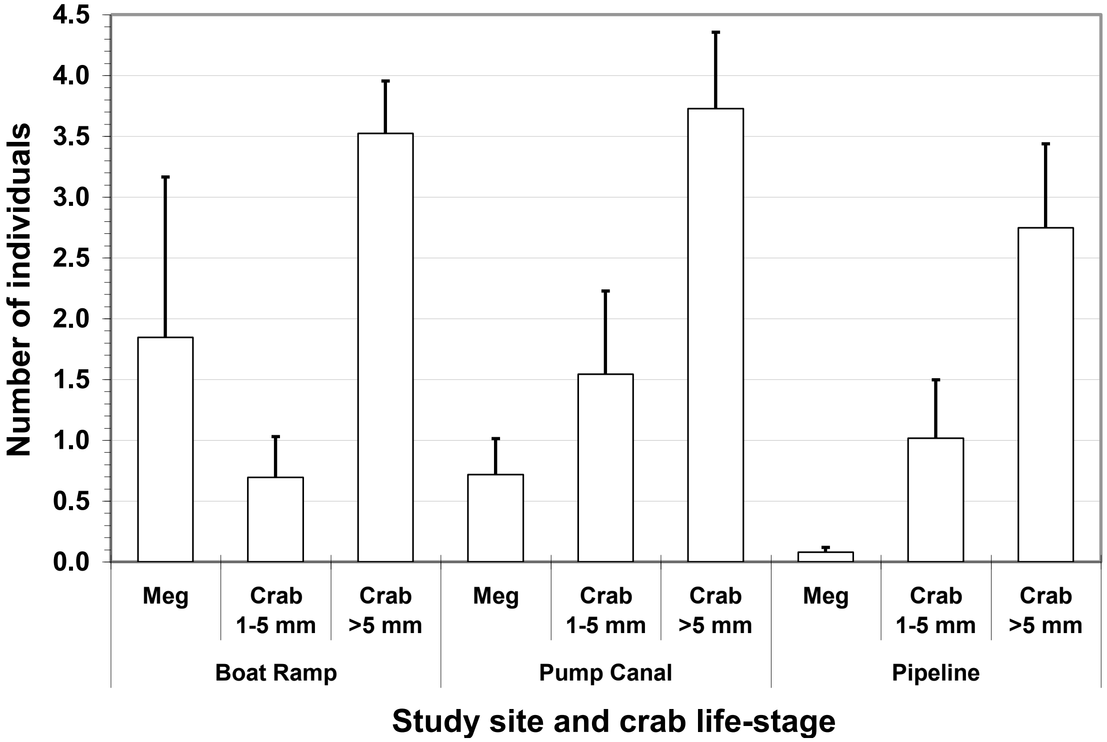

Fig. 2-14. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) per collector in the bay habitat of each study site for all collection periods combined (September 2003-October 2005).

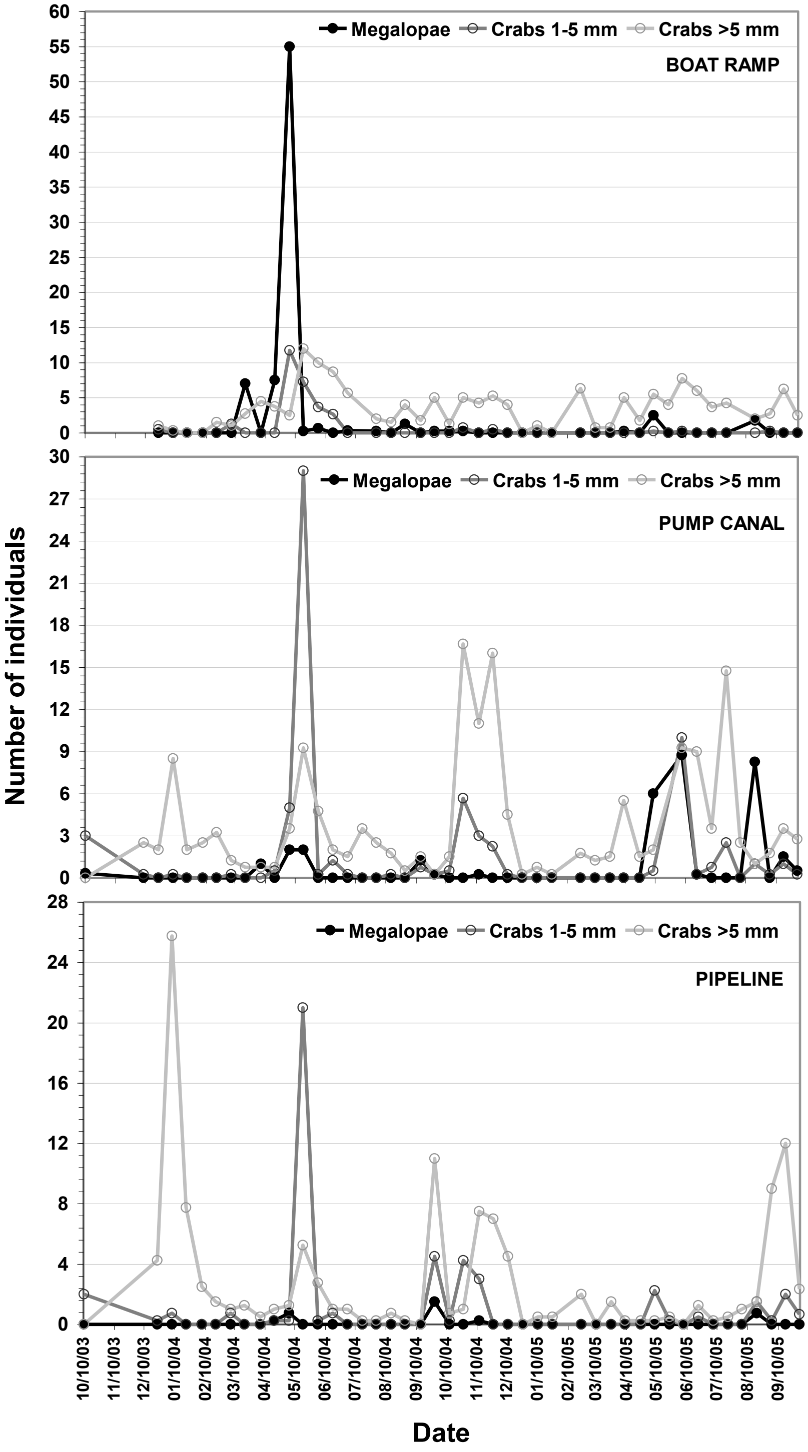

Fig. 2-15. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) per collector in the bay habitat of each study site during September 2003-October 2005. Collectors were deployed for settlement 2 wk prior to retrieval.

rates among collection periods decreased from BR (0-55) to PC (0-8.75) to PL (0-1.5), and the percentage of all sampling periods resulting in one or more megalopae collected also decreased from BR (33.3%) to PC (28.9%) to PL (11.1%; Fig. 2-15).

Juvenile recruitment, evident by presence of class-1 juveniles (1-5 mm), occurred throughout most of the year, though infrequently so in January and March and never in February (Fig. 2-13). Mean recruitment rates (number of class-1 juveniles collector^{-1}) were highly variable among collection periods, ranging 0-19.08 juveniles collector^{-1} when data were averaged across sites. Peak recruitment rates occurred around the same time as or immediately following peaks in settlement. Differences in recruitment rates among sites were evident, but did not follow the same pattern as for settlement. Mean recruitment rate, variability surrounding the mean, and frequency of recruitment events were again higher at PC than PL but were instead lowest at BR (Figs. 2-14 and 2-15). Specifically, range of mean recruitment rates among collection periods decreased from PC (0-29) to PL (0-21) to BR (0-11.75), and frequency of recruitment events decreased from 56.8% at PC to 43.2% at PL to 26.8% at BR (Fig. 2-15).

Class-2 juveniles ranged 6-60 mm CW and were collected during all periods of the study but the first (25 September-10 October 2003). Mean collection rates (number of class-2 juveniles collector^{-1}) as averaged across study sites were variable among collection periods and ranged 0-11.53 juveniles collector^{-1} (Fig. 2-13). Collection in 2004 was marked by major peaks in January, May, and September-December, whereas collection in 2005 revealed frequent, regularly-spaced peaks of lesser magnitude. Mean collection rates varied minimally across sites (Fig. 2-14), but variability in collection among periods increased (i.e., higher peak rates) from BR (0-12) to PC (0-16.67) to PL (0-25.75; Fig. 2-15).

Prediction of Settlement and Recruitment Rates

Megalopal settlement rate

Results of GLMM analyses indicated that the best approximating model of megalopal settlement rate included effects of water temperature, wind speed, wind direction, river discharge, and water level (Model 5, Table 2-3). This was the best model due to its parsimonious nature. A better fit to the data was achieved by adding several terms which accounted for water level variability and the interactions among it, mean water level, and water temperature (Model 6, Table 2-3). However, improvement to model fit was minimal compared to the substantial increase in model complexity. Several nested models, inherently less complex than the best approximating model, also fit the observed data well, as indicated by dispersion parameter values near one and high correlation coefficients for observed versus predicted responses (Models 2-4, Table 2-3). All of these models demonstrated that effects acting on embryonic and larval development (Periods E and L) were both important in determining settlement rate.

The most important predictor of settlement rate was water temperature. Using a model containing only the fixed effect of water temperature and random effect of site (Model 1, Table 2-3), strength of linear association between observed and predicted values of settlement rate was over 46% (r=0.467-0.575). In the best approximating model, water temperature (28-d mean) during the Period E (42 d prior to collector

Table 2-3. Best approximating model (Model 6) of megalopal settlement rate plus hierarchical submodels in order of increasing model fit. Indices of model fit include (1) Pseudo-Akaike's Information Criteria values for small sample sizes (PAIC$_c$), (2) dispersion parameter $\widehat{c}$ estimated by χ^2/df, (3) Pearson's product-moment correlation factor (r) describing the linear association between observed and predicted values of megalopal settlement, and (4) Pearson's product-moment correlation factor (r_{ave}) describing the linear association between observed and predicted values of megalopal settlement as averaged across study sites per period. Model 5 was identified as the most parsimonious approximating model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
PAIC$_c$	572.50	411.53	399.62	382.33	366.90	345.77
$\widehat{c}$	2.75	1.45	1.22	1.16	1.10	1.03
r	0.467	0.765	0.798	0.821	0.825	0.824
r_{ave}	0.575	0.922	0.964	0.979	0.985	0.992
Fixed Effects	wt28.42 wt20.28.49 wt28.42* wt20.28.49	wt28.42 wt20.28.49 wt28.42* wt20.28.49 ws35 wd35 ws35*wd35	wt28.42 wt20.28.49 wt28.42* wt20.28.49 ws35 wd35 ws35*wd35 rd07.35	wt28.42 wt20.28.49 wt28.42* wt20.28.49 ws35 wd35 ws35*wd35 rd07.35 wl07.35 wl07.35* wt20.28.49	wt28.42 wt20.28.49 wt28.42* wt20.28.49 ws35 wd35 ws35*wd35 rd07.35 wl07.35 wl07.35* wt20.28.49 wlm21 wlm21* wt20.28.49	wt28.42 wt20.28.49 wt28.42* wt20.28.49 ws35 wd35 ws35*wd35 rd07.35 wl07.35 wl07.35* wt20.28.49 wlm21 wlm21* wt20.28.49 wlv21 wlm21*wlv21 wlv21* wt20.28.49 wlm21*wlv21* wt20.28.49

retrieval) showed a positive relationship with settlement rate, but the exact nature of the relationship depended on whether temperature (28-d mean, 49 d prior) was ≤20°C or >20°C (Table 2-4). Temperature had a greater effect on settlement when ≤20°C than when >20°C, with an untransformed regression slope 12 times greater for the former than latter. Also, across collection periods, mean settlement rate (±1 SE) was greater following temperatures ≤20°C (1.78 ± 1.13 megalopae collector^{-1}, *n*=17) than >20°C (0.25 ± 0.12 megalopae collector^{-1}, *n*=29). Settlement events, however, occurred more frequently following temperatures >20°C (51.7%, *n*=15) than ≤20°C (41.2%, *n*=7).

Wind speed averaged across the 35 d prior to collector retrieval had a positive effect on settlement rate across all wind directions (Table 2-4), but the addition of wind direction (35-d mode) and the wind speed*direction interaction substantially improved model prediction. Although experimental units (*n*=132; study site collection period^{-1}) were more frequently associated with N (59.8%, *n*=79) than SE (28.8%, *n*=38) winds, mean settlement rate, frequency of settlement events, and the effect of increasing wind speed were greater following SE (2.16 ± 1.13 megalopae collector^{-1}; 39.5%, *n*=15) than N (0.29 ± 0.14 megalopae collector^{-1}; 19.0%, *n*=15) winds (see also Table 2-4). Few experimental units were linked with NE (*n*=6) and E (*n*=9) winds, so effects of increasing wind speed from either direction were unclear. Moreover, no experimental units were associated with the 35-d modes of S, SW, W, and NW winds.

Several other effects were incorporated into the best approximating model of settlement rate. River discharge (7-d mean, 35 d prior to collector retrieval) was the only model effect not involved in an interaction. Results indicated that reduced flows of

Table 2-4. Effect estimates and significance values associated with the most parsimonious model of megalopal settlement rate (Model 5, Table 2-3). Values are on the (natural) log scale.

	Effect Solutions			Type III
Effect	Estimate	SE[1]	Prob. >|t|	Prob. >F
Intercept	0.3360	1.8310	0.8713	
wt28.42	0.0299	0.0380	0.4333	<0.0001
wt20.28.49 (≤20°C)	-7.8266	1.8062	<0.0001	<0.0001
wt20.28.49 (>20°C)	0			
wt28.42*wt20.28.49 (≤20°C)	0.2169	0.06125	0.0006	0.0006
wt28.42*wt20.28.49 (>20°C)	0			
ws35	0.2662	0.3419	0.4378	0.8153
wd35 (N)	0.6647	1.9272	0.7308	0.0002
wd35 (NE)	-7.5943	29.9108	0.8000	
wd35 (E)	17.4314	4.0074	<0.0001	
wd35 (SE)	0			
ws35*wd35 (N)	-0.2661	0.3958	0.5028	0.0001
ws35*wd35 (NE)	1.5134	7.3165	0.8365	
ws35*wd35 (E)	-4.0250	0.8759	<0.0001	
ws35*wd35 (SE)	0			
rd07.35	-0.00051	0.000152	0.0010	0.0010
wl07.35	-0.2407	1.1767	0.8383	0.0372
wl07.35*wt20.28.49 (≤20°C)	4.5301	1.9321	0.0208	0.0208
wl07.35*wt20.28.49 (>20°C)	0			
wlm21	-1.0969	1.8542	0.5553	0.1358
wlm21*wt20.28.49 (≤20°C)	6.6334	2.9335	0.0256	0.0256
wlm21*wt20.28.49 (>20°C)	0			
Site BR (random)	1.2140	0.8704	0.0964	
Site PC (random)	0.3835	0.8737	0.8914	
Site PL (random)	-1.5975	0.9081	0.1309	
Covariance (site)	0.2489	0.2628		

[1] Standard errors for random effects are predicted.

freshwater into the Guadalupe Estuary during Period E ultimately increased megalopal settlement rates (Table 2-4). Water levels during this same period (7-d mean, 35 d prior), as well as Period L (mean during preceding 21 d), were also important predictors of settlement rate (Table 2-4). The effects of both measures of water level depended on water temperature during Period E (28-d mean, 49 d ago), demonstrating positive effects (increasing slopes) on settlement rate when mean water temperature was ≤20°C but no significant effect when water temperature was >20°C. The random effect of site in the model accounted for random differences in magnitude of settlement rate among sites (BR, PC, and PL; Table 2-4) and supported results of descriptive statistics, which indicated mean megalopal settlement rate progressively decreased from BR to PC to PL.

The best approximating model of megalopal settlement rate predicted settlement rates at BR extremely well, but model fit was less for PC and PL (Fig. 2-16). When both observed and predicted values of settlement rate were averaged across sites, model fit improved markedly, as evidenced by an increase in strength of linear association between mean observed and predicted values of settlement rate from r=0.825 to 0.985 (Table 2-3, Fig. 2-17).

Juvenile recruitment rate

The most predictive model of juvenile recruitment included the effects of precipitation, water level, wind direction and speed, and megalopal settlement rate (Model 6, Table 2-5). However, this model and the next most predictive model (Model 5, Table 2-5) were minimally user-friendly due to the inclusion of megalopal settlement

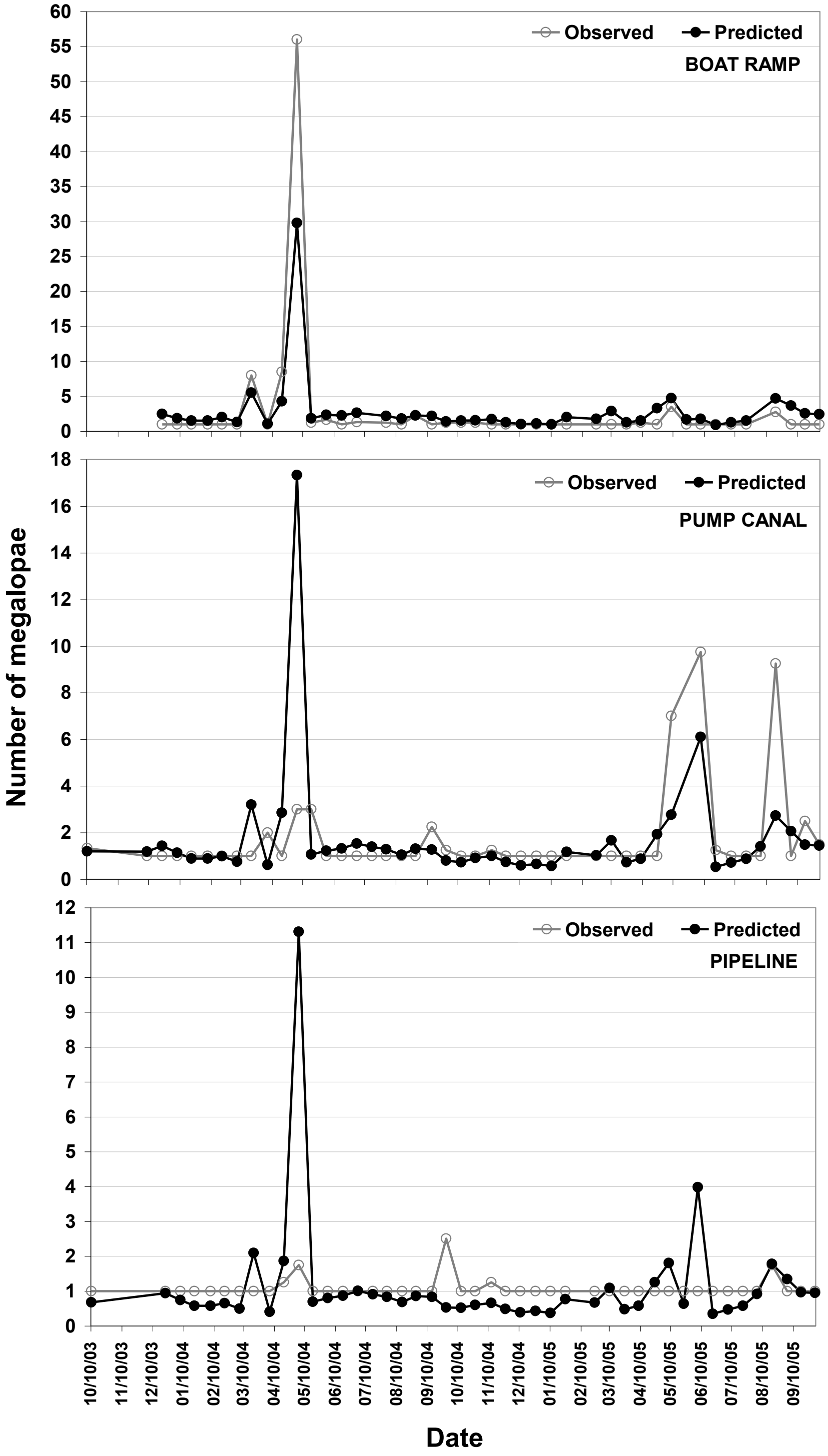

Fig. 2-16. Overlay of predicted and observed values of blue crab megalopal settlement rate (number of megalopae per collector) by date for each study site as derived by the most parsimonious model (Model 5, Table 2-3).

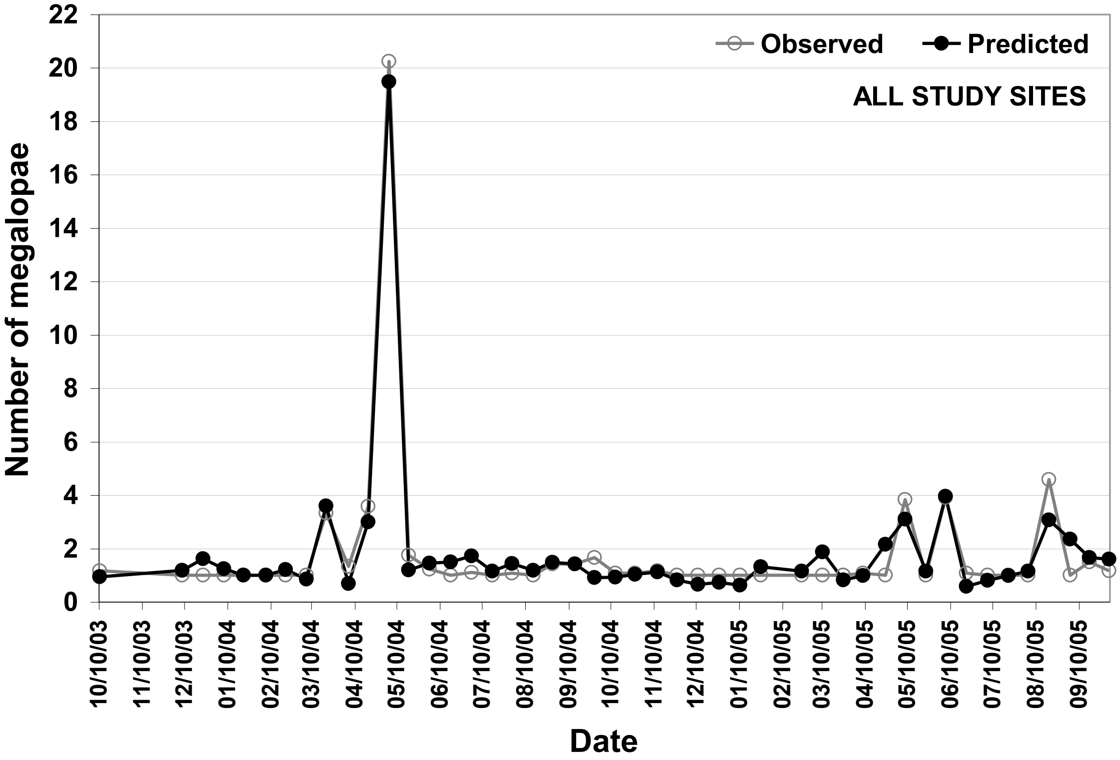

Fig. 2-17. Overlay of predicted and observed values of blue crab megalopal settlement rate (number of megalopae per collector) by date as derived by the most parsimonious model (Model 5, Table 2-3) and averaged across study sites.

Table 2-5. Best approximating model (Model 6) of juvenile recruitment rate plus hierarchical submodels in order of increasing model fit. Indices of model fit include (1) Pseudo-Akaike's Information Criteria values for small sample sizes (PAIC$_c$), (2) dispersion parameter $\hat{c}$ estimated by χ^2/df, (3) Pearson's product-moment correlation factor (r) describing the linear association between observed and predicted values of juvenile recruitment per experimental unit, and (4) Pearson's product-moment correlation factor (r_{ave}) describing the linear association between observed and predicted values of juvenile recruitment as averaged across study sites per period. Model 4 was identified as the most parsimonious approximating model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
PAIC$_c$	409.48	386.27	334.47	328.00	303.10	300.62
$\hat{c}$	1.75	1.53	1.15	1.06	0.78	0.72
r	0.557	0.694	0.837	0.855	0.883	0.902
r_{ave}	0.557	0.728	0.881	0.898	0.903	0.924
Fixed Effects	p14	p14 wlm14	p14 wlm14 wd1	p14 wlm14 wd1 ws1 ws1*wd1	p14 wlm14 wd1 meg	p14 wlm14 wd1 ws1 ws1*wd1 meg

and overly complex, as revealed by a dispersion parameter ($\hat{c}$) <1.00. Consequently, I considered Model 4 to be the best approximating model of juvenile recruitment, because model fit was excellent and predictability of recruitment rate was only slightly less than achieved with Models 5 and 6 (Table 2-5).

The most important predictor of juvenile recruitment rate was precipitation (14-d mean), as it demonstrated the lowest PAICc value and highest model fit of any single-fixed effect model (Model 1, Table 2-5). Moreover, correlation of observed and predicted values of recruitment rate revealed a strength of linear association approaching 56% (r=0.557). Contrary to my hypothesis, juvenile recruitment rate was positively related to precipitation (Table 2-6), which was included in analyses to represent the inverse of salinity.

Other important predictors in the best approximating model of recruitment rate included water level (14-d mean), wind direction (1-d mean), wind speed (1-d mean), and the interaction of wind direction and speed (Model 4, Table 2-5). Recruitment rate was positively and significantly related to water level, whereas all effects of wind were less clear due to statistical insignificance (Table 2-6). The interaction term of wind direction and speed, however, suggested that the effects of wind speed differed among wind directions. Wind speed was positively related to recruitment rate for N, NE and E winds, but increasing wind speed had little to no obvious effect for SE, S, SW, W, and NW winds. Moreover, both mean recruitment rate (number of class-1 juveniles collector^{-1} ± 1 SE) and frequency of recruitment events (%) were highest corresponding to SE winds (2.50 ± 1.02, n=36 experimental units; 58.3%, n=21 of 36 units), at

Table 2-6. Effect estimates and significance values associated with the most parsimonious model of juvenile recruitment rate (Model 4, Table 2-5). Values are on the (natural) log scale.

	Effect Solutions			Type III
Effect	Estimate	SE[1]	Prob. >|t|	Prob. >F
Intercept	0.9305	6.7298	0.9027	
p14	0.1815	0.02118	<0.0001	<0.0001
wlm14	2.3078	0.6495	0.0006	0.0006
ws1	-0.4983	1.4025	0.7230	0.9266
wd1 (N)	-2.7145	6.7785	0.6896	0.3125
wd1 (NE)	-2.2412	6.8490	0.7441	
wd1 (E)	-2.6191	6.7934	0.7006	
wd1 (SE)	-1.5840	6.7699	0.8154	
wd1 (S)	-2.1885	7.0275	0.7560	
wd1 (SW)	-0.3701	1.7801	0.8357	
wd1 (W)	-2.7538	2.8323	0.3330	
wd1 (NW)	0			
ws1*wd1 (N)	0.6780	1.4045	0.6302	0.4277
ws1*wd1 (NE)	0.5446	1.4488	0.7077	
ws1*wd1 (E)	0.6537	1.4082	0.6434	
ws1*wd1 (SE)	0.4804	1.4015	0.7324	
ws1*wd1 (S)	0.4951	1.4534	0.7340	
ws1*wd1 (SW)	0			
ws1*wd1 (W)	0			
ws1*wd1 (NW)	0			
Site BR (random)	-0.1017	0.1217	0.4896	
Site PC (random)	0.1547	0.1178	0.2015	
Site PL (random)	-0.05305	0.1189	0.5738	
Covariance (site)	0.02665	0.03762		

[1] Standard errors for random effects are predicted.

intermediate levels for N (0.83 ± 0.25, *n*=52; 44.2%, *n*=23), NE (0.19 ± 0.07, *n*=13; 46.2%, *n*=6) and E (0.52 ± 0.22, *n*=16; 43.8%, *n*=7) winds, and lowest for S (0.05 ± 0.05, *n*=5; 20%, *n*=1), SW, W and NW (0, *n*=3-4; 0%, *n*=0) winds. As with models of settlement, random effect estimates for each site mirrored descriptive results presented earlier, which indicated recruitment rate decreased from PC to PL to BR (Table 2-6).

Model fit for the best approximating model of juvenile recruitment rate was quite good at PC, but poorer at PL and poorest at BR (Fig. 2-18). However, overall model fit was relatively high ($\hat{c} \approx 1.00$), and the strength of linear association between observed and predicted recruitment rates ranged from 86% (*r*=0.855) when correlated using values per experimental unit (Table 2-5, Fig. 2-18) to 90% (*r*=0.898) when values were averaged across study sites (Table 2-5, Fig. 2-19).

Spatial Patterns in Settlement and Recruitment

The spatial extent to which crabs were found in salt-marsh was distinctly related to stage of development (Fig. 2-20). Megalopal crabs were collected in tidal creek habitat during two of four collection periods and were never found in either connected or unconnected pond habitats. Collection of class-1 juveniles (recruits) occurred in tidal creek habitat during all four periods sampled and in connected pond habitat during two of four sample periods, but were never found in unconnected ponds. Class-2 juveniles were collected in nearly every habitat and period combination sampled. Thus, the extent to which young crabs infiltrated the salt-marsh increased with age or mobility associated with advancements in development.

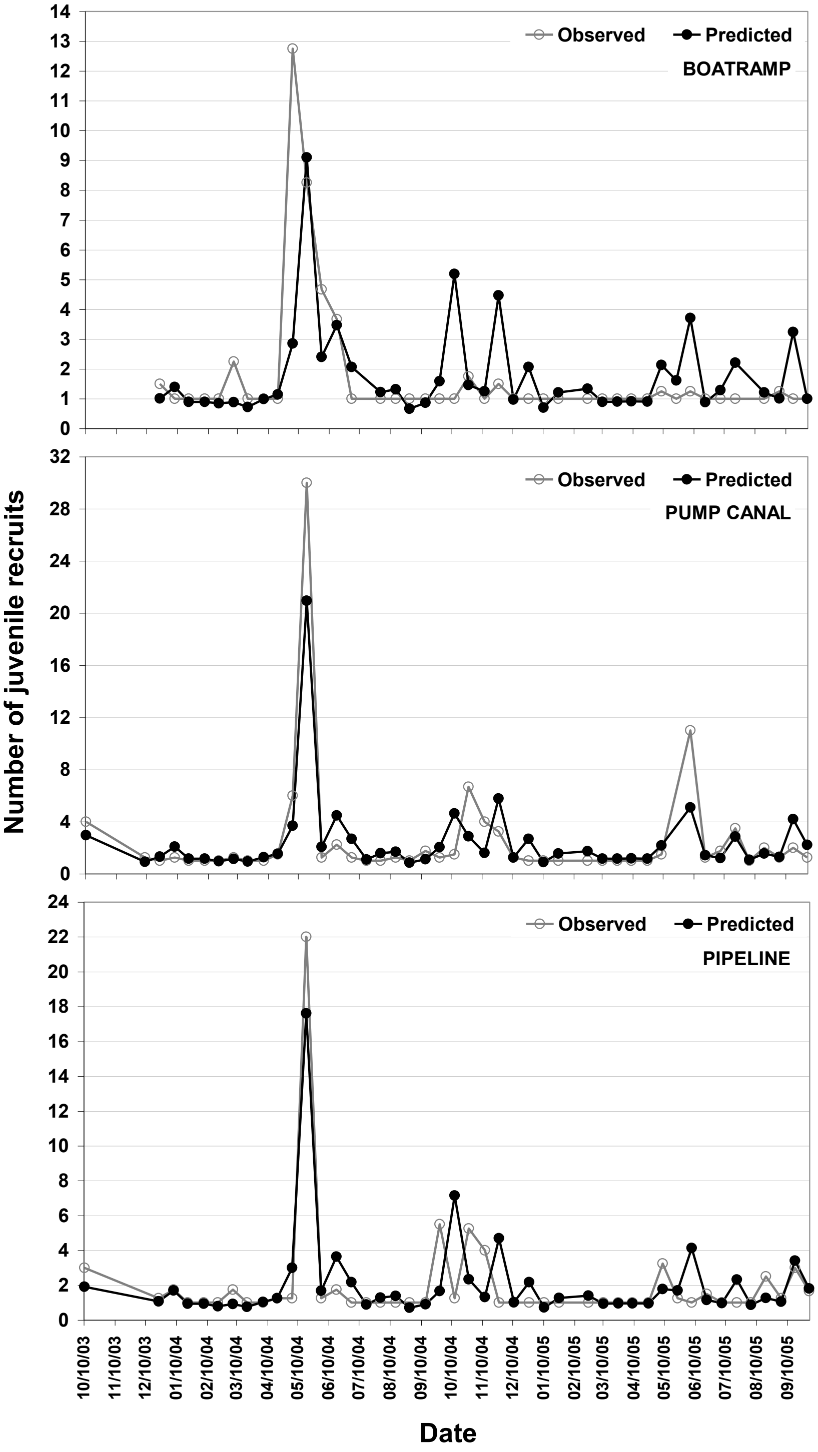

Fig. 2-18. Overlay of predicted and observed values of blue crab juvenile recruitment rate (number of juvenile recruits per collector) by date for each study site as derived by the most parsimonious model (Model 4, Table 2-5). Juvenile recruits are represented by class-1 blue crabs (1-5 mm in carapace-width).

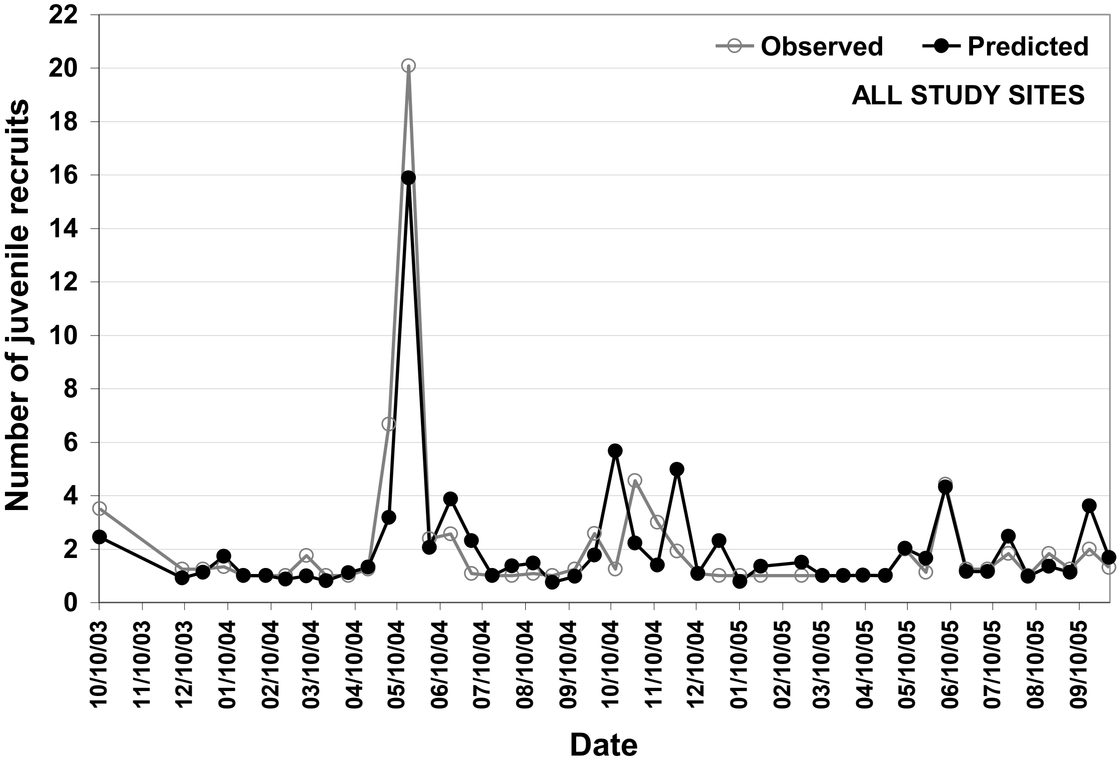

Fig. 2-19. Overlay of predicted and observed values of blue crab juvenile recruitment rate (number of juvenile recruits per collector) by date as derived by the most parsimonious model (Model 4, Table 2-5) and averaged across study sites. Juvenile recruits are represented by class-1 blue crabs (1-5 mm in carapace-width).

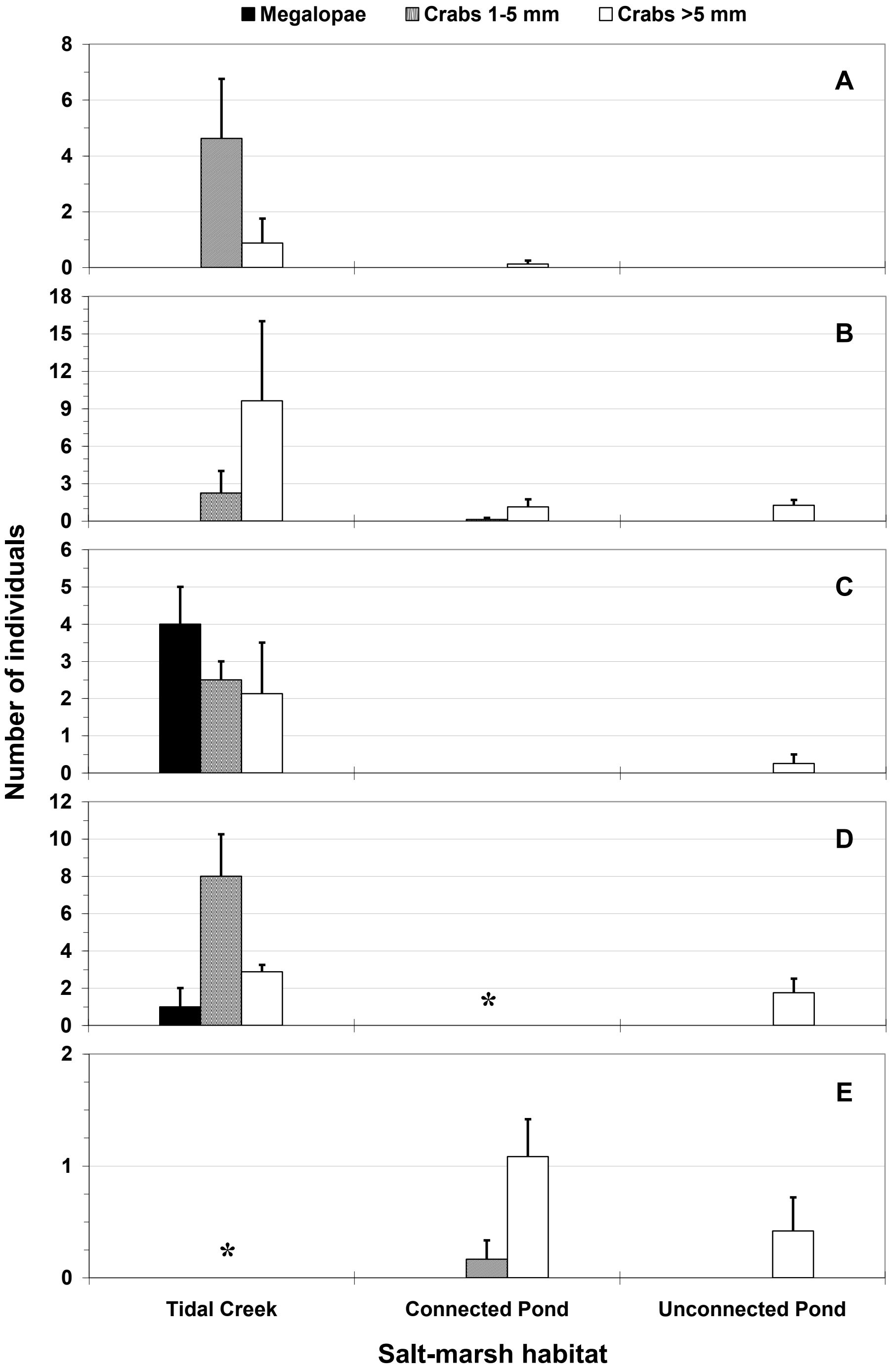

Fig. 2-20. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) per collector in each salt-marsh habitat sampled for all study sites combined (* = not sampled). Collection periods were (A) 25 September-10 October 2003, (B) 18 May-2 June 2004, (C) 28 September-13 October 2004, (D) 13-27 October 2004, and (E) 17 September-1 October 2005.

The numbers of megalopae and juvenile recruits collected in the salt-marsh differed among sites (Fig. 2-21). In tidal creek habitat, rates of settlement and recruitment at BR were always equal to or greater than those at PC. In connected ponds, recruitment occurred at PC only. Megalopal and newly-recruited juvenile crabs were never collected at PL in interior salt-marsh. Class-2 juveniles, however, were collected in all habitats and sites during most collection periods.

Discussion

Development of Field Materials and Methods

Standard methods for monitoring the settlement rate of megalopal blue crabs include use of artificial settlement substrates or collectors (16 cm x 38 cm; van Montfrans et al. 1990; Metcalf et al. 1995), which orient vertically in the water column when deployed and, for sake of convenience, are usually deployed along coastal piers where water depth ranges 2-4 m. Adhering to protocol can be difficult, if not impossible, when targeting patterns of terminal settlement in natural, undisturbed settings, such as shallow bay and salt-marsh. Along the central Texas coast, open water bodies within salt-marsh are shallowly flooded, experience a limited tidal range (<30 cm), and can be almost entirely drained or dry for lengthy periods of time (days to weeks) due to natural droughts and seasonally low tides. Consequently, to investigate natural patterns of settlement and recruitment, I deployed collectors of similar surface area but markedly different dimensions and floating orientation to standard collectors (see Materials and Methods; Figs. 2-3 and 2-4). Horizontal orientation and shallow draft

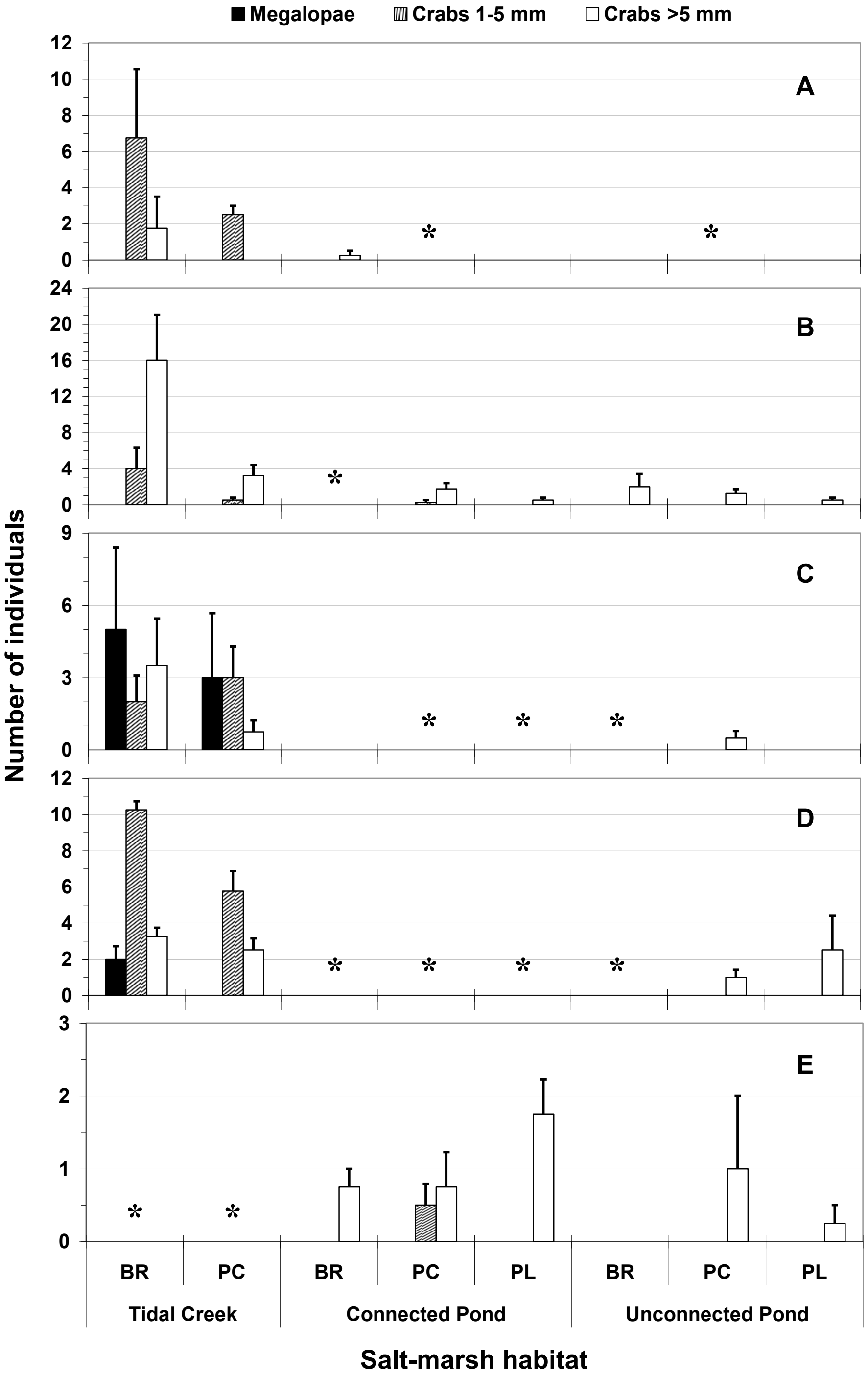

Fig. 2-21. Mean number of blue crab megalopae, class-1 juveniles (1-5 mm in carapace-width), and class-2 juveniles (>5 mm in carapace-width) per collector in each interior salt-marsh habitat and study site sampled (* = not sampled). Collection periods were (A) 25 September-10 October 2003, (B) 18 May-2 June 2004, (C) 28 September-13 October 2004, (D) 13-27 October 2004, and (E) 17 September-1 October 2005.

of these collectors consequently allowed for flotation in all observed water depths (14-103 cm) and resulted in successful deployment and retrieval of collectors in all habitats and periods sampled.

Standard procedures for monitoring settlement also incorporate a daily collection interval to account for highly variable patterns through time (e.g., van Montfrans et al. 1995; Morgan et al. 1996; Spitzer et al. 2003). I chose to use a much longer collection interval (semi-lunar (14-16 d)) to minimize intensity of sample collection and disturbance to whooping cranes but recognized that several factors may confound study results. For instance, some evidence suggests that postlarvae settling on collectors deployed for long periods may not accumulate completely or in direct proportion to time of collector deployment due to density-dependent emigration (i.e., space limitation; Pineda 2000), cannibalism (Moksnes et al. 1998), or use of collectors as temporary settlement habitat (Moksnes and Wennhage 2001). While predation and saturation of collectors by larval and juvenile forms of crabs, shrimps and fishes likely influenced settlement and recruitment rates in this study, the magnitudes of their effects are unknown. Conversely, high rates of recruitment suggest megalopae were in advanced stages of development at all sites and temporary use of collectors was increasingly improbable from north (BR) to south (PL). An additional source of settler loss from collectors may simply be that a long deployment period provides adequate time for outgrowth of settler or recruit categories. In this case, loss of settlers would be implied but not actually occur, because young crabs would still inhabit collectors upon retrieval. This is supported by studies demonstrating strong similarity between habitat selection of settling megalopal crabs and subsequent distributions of early-instar (J1-J3) juveniles (Pardieck et al. 1999; van Montfrans et al. 2003; Moksnes and Heck 2006).

In a short field experiment in July 2005, deployment of collectors at MB for variable periods of time prior to the end of a typical semi-lunar collection period (15-d) revealed mud crab (*Eurypanopeus depressus*) megalopae accumulated in great numbers (maximum 250) on all collectors. However, mean daily rate of accumulation decreased with increasing duration of collector deployment, and percent loss was considerable (up to 57%) for megalopae settling >6 d prior to collector retrieval. This loss represented 34% of the estimated total number of settlers from the entire semi-lunar period. Though comparable data were not recorded for *Callinectes* spp. due to low settlement rates (0-1.5 megalopae collector^{-1}) and effects of post-settlement processes on the distributional patterns of *E. depressus* are not well understood, results of this experiment suggest that settlers redistributing among habitats several days after settlement may be sampled effectively using a one-week (one-quarter lunar cycle) rather than two-week (this study) collection period. However, to adequately assess settler losses associated with long collection periods, replication of the experiment across both temporal and spatial gradients is needed.

Fine-scale Temporal Patterns in Settlement and Recruitment

Examination of fine-scale settlement patterns of blue crab megalopae provided further insight into the potential error caused by using a collection period longer than fully represented by samples. Two types of settlement patterns were observed in this study: episodic and evenly-distributed. Episodic settlement events were characterized by distinct, infrequent, and seemingly unpredictable episodes of high-magnitude settlement, whereas evenly-distributed settlement events were frequent, seemingly-predictable, and of low magnitude. Supposing settlement during all collection periods was of even distribution, failure to account for crabs having settled and then emigrated during the first week of collection would simply instill bias or a regular adjustment to the true mean rate of settlement. Despite reduced accuracy, biased estimates of settlement rate might still exhibit similar patterns to unbiased estimates.

On the other hand, if megalopal settlement was purely episodic, incomplete collection of settlers from the first week of the period could mean that all or only some of the settlers are accounted for, depending on timing of settlement events. Results of many studies of brachyuran settlement suggest timing and frequency of settlement events, as well as magnitude of settlement rates, are partly driven by water movement associated with the lunar cycle. Studies disagree as to whether settlement events co-occur more frequently with the minimum amplitude tides of quarter-moons (neap tides) or maximum amplitude tides of new and full moons (spring tides), but settlement patterns regularly exhibit semilunar periodicity (Metcalf et al. 1995; van Montfrans et al. 1995; Morgan et al. 1996; Hasek and Rabalais 2001; González-Gordillo et al. 2003; Amaral et al. 2007). In this study, long-term patterns in settlement and recruitment were monitored by retrieving collectors during new and full moons. Therefore, if settlement events were in fact associated with specific days of the lunar cycle, then settler loss due to incomplete collection of settlers in the first week of the collection period was likely consistent among periods and possibly minimal in magnitude.

Long-term Patterns in Settlement and Recruitment

The climate of the central Texas coast is subtropical, consequently allowing for nearly year-around breeding by numerous estuarine-marine species inhabiting the region. In this study, megalopal settlement of *Callinectes* spp. was observed during most of the year (March-November), with peaks in settlement rate occurring in both spring (March-June) and autumn (August-October). Autumnal peaks in settlement have commonly been observed elsewhere along the Gulf and Atlantic coasts. However, comparable spring settlement data are few, because most previous studies confined within-year sampling (i.e., collector deployment) to portions of summer and autumn only (e.g., Mense et al. 1995; Rabalais et al. 1995; van Montfrans et al. 1995; Morgan et al. 1996; Spitzer et al. 2003). When sampling did occur as early in the year as February (Rabalais et al. 1995), April (Wrona et al. 1995), and March (Perry et al. 1995) or occurred throughout the year (Boylan and Wenner 1993), blue crab megalopae were observed in extremely low numbers and spring was not identified as a principal period of settlement. In this study, neither spring nor autumn was determined as more important, because inter-annual variability surrounding settlement rates and a relatively short period of study (2 yr) prevented such. However, peaks in settlement rate 4-23 times the overall study mean occurred during both seasons at all three study sites.

Dramatic differences in magnitude of blue crab settlement rates were evident between this and other studies conducted along the Gulf Coast. I observed peak semilunar settlement rates of <60 megalopae collector^{-1}, but daily rates of several hundred to >7,000 megalopae collector^{-1} have been recorded elsewhere (Rabalais et al. 1995). As invading megalopae are influenced by high rates of predation mortality and dispersal throughout their journey to suitable terminal settlement habitat, differences in settlement rates may be explained by dissimilar intra-estuary placement of settlement collectors. In studies where megalopal settlement was monitored at multiple sites differing in distance from a single coastal inlet, numbers of settlers progressively decreased with movement shoreward (in Mobile Bay; Rabalais et al. 1995; Morgan et al. 1996). In this study, artificial substrates were located 51-59 km from the nearest coastal water source (i.e., post-larval supply). In contrast, distances from collectors to the Gulf of Mexico were 0-50 km in Mobile Bay, Alabama (Rabalais et al. 1995; Morgan et al. 1996; Spitzer et al. 2003), 16 km in Mississippi Sound, Alabama (Morgan et al. 1996; Spitzer et al. 2003), 13 km in Mississippi Sound, Mississippi (Perry et al. 1995; Rabalais et al. 1995), 22 km in Terrebone Bay, Louisiana (Rabalais et al. 1995; Hasek and Rabalais 2001), and 5 km in Galveston Bay, Texas (Rabalais et al. 1995). Consequently, comparisons of settlement patterns among most studies are likely not appropriate due to the inherent loss of individuals with up-estuary distance. When considering only similarly-situated sites, however, relative abundance of megalopae in the Guadalupe Estuary (this study) was comparable to abundance levels in Mobile Bay, Alabama (Morgan et al. 1996).

Juvenile recruitment of blue crabs in shallow bay habitat occurred throughout most of the year and generally peaked during the same periods of the year as settlement (i.e., spring and autumn). To my knowledge, only one other settlement study using passive collectors has reported juvenile abundance (Rakocinski et al. 2003), but sampling intensity (7 August-23 September 1997) was not sufficient for seasonal comparisons with this study. However, juvenile crab abundance has also been estimated in nursery habitats (e.g., seagrass and salt-marsh fringe) of shallow embayments using alternative methods of sampling (e.g., suction-sampling). In Virginia, juveniles (<4.25 mm CW) were found extremely abundant in autumn, persisted in low numbers through early winter, but were entirely absent during the remainder of the year (Orth and van Montfrans 1987). Limited duration of the recruitment period, as compared to the present study, was likely due to the colder climate and limited spawning season (April-October; Williams 1984). In Texas, trends in juvenile abundance were similar to this study in that juveniles (principally <40 mm CW) were found throughout most of the year (Thomas et al. 1990; see also Chapter III). However, peak abundance occurred during late summer-autumn and not during spring. This suggests juveniles recruiting in spring may subsequently experience high mortality rates or disperse to alternative habitats not previously sampled. Persistence in shallow water during much or all of winter was also observed consistently among Texas studies and may result from the limited ability of small crabs to disperse or migrate great distance in short periods of time, particularly in cold temperatures. It also plausibly represents a strategy to reduce mortality by remaining in habitat with greater availability of food resources and shelter and subsequently less risk of predation than less structured habitat in deeper water.

Differences in blue crab settlement and recruitment rates among study sites were pronounced but unsurprising. From north to south, sites were progressively farther from coastal water exchange (post-larval supply) and increasingly separated from residual and wind-induced currents. Combined numbers of megalopal crabs and newly-recruited juveniles decreased by nearly 60% along the southward gradient, probably resulting from continuous mortality loss and dispersal of individuals. In addition, the proportion of settling individuals having recently metamorphosed from megalopa to juvenile increased from 27% to 93% within a distance of only 8 km, suggesting megalopae were developmentally advanced by the time they reached study sites, particularly PL. Similar patterns were observed in other studies where multiple sites were sampled using either artificial substrates or plankton tows and late-molt stage megalopae and/or early-instar juveniles were more prevalent at shoreward than seaward sites (Mense and Wenner 1989; Rabalais et al. 1995; Morgan et al. 1996). Consequently, findings suggest that sample sites used in this study, which were 51-59 km from Pass Cavallo and situated in shallow bay adjacent to salt-marsh, were representative of terminal settlement habitat and optimal for metamorphosis of megalopa to juvenile.

These data provide added evidence that inter-estuary comparisons in settlement patterns among sites differing significantly in proximity to coastal water may not be entirely meaningful. Many studies have reported settlement rates for megalopal blue crabs near the mouths of estuaries. However, megalopae are thigmotactic (i.e., strongly tend to cling to structures) throughout development, and temporary settlement occurs repeatedly throughout estuary invasion as part of a strategy to expedite up-estuary transport and reduce predation (see Introduction and Background). Consequently, settlement data obtained from artificial substrates placed near an estuary's mouth may prematurely measure terminal settlement abundance and instead best represent post-larval supply. Although absolute abundance may be low, greater relative abundance of premolt megalopae and early-instar (J1-J2) juveniles at sites of considerable distance up-estuary and near contiguous salt-marsh indicates these sites provide better estimates of terminal settlement and juvenile recruitment rates. Notably, standard procedures for construction of artificial settlement substrates have been devised (Metcalf et al. 1995), but selection of intra-estuary deployment locations has received little attention.

Prediction of Settlement and Recruitment Rates

To adequately investigate the timing of environmental effects on the early development and subsequent megalopal settlement of blue crabs, explanatory data used in model analyses were structured in several forms. Development from hatching to metamorphosis of megalopae to first-instar juveniles has shown to take 37-55 d (at 26.7 ppt and 25°C; Costlow and Bookhout 1959), but the full recruitment process begins long before this period with adult mating, seaward migration of females, development and fertilization of eggs, and embryogenesis. I tried to account for these steps by examining models with explanatory data (e.g., water temperature) originating up to eleven weeks prior to collector retrieval. Although I did not account for the much longer period of development that would occur if females mated prior to winter and delayed spawning until late winter or early spring, model-building procedures resulted in highly accurate prediction of megalopal settlement rates throughout the study. In addition, analyses revealed environmental conditions occurring throughout early development were important in determining terminal settlement. As most previous studies have related megalopal abundance to concurrent abiotic conditions or focused on a limited period of development, this study made significant strides toward comprehensive investigation of processes leading to terminal megalopal settlement in natural conditions.

Water temperature occurring before and during embryonic development (28-d period ending 42-49 d prior to settlement) was the most important abiotic determinant of terminal settlement rate. Its positive relationship with settlement rate depended on whether mean temperature was ≤20°C or >20°C but was supported by early laboratory studies of blue crab development, demonstrating rates of survival and progression through development generally increased with temperature. During embryogenesis, respiration was shown to be depressed, particularly in the gastrula stage, and overall duration was significantly prolonged in 16°C (versus 26°C; Amsler and George 1984a). Studies also revealed failure of eggs to hatch outside the range of 19-29°C and of larvae to develop past the first zoeal stage when held at 20°C (versus 25°C or 30°C; Sandoz and Rogers 1944; Costlow and Bookhout 1959). However, contrary to my belief and suggestions from earlier studies that temperatures ≤20°C would altogether inhibit development and eliminate opportunity for settlement, the effect of increasing water temperature during the earliest stages of life was significantly greater for suboptimal

(≤20°C) than for optimal (>20°C) temperatures. The nature of water level effects originating from around the time of hatching (7-d period, 35 d before settlement) and during larval development (preceding 21-d period) was similarly influenced by bivariate temperature. That is, water level related positively to settlement rate when initial conditions were colder than optimum but had little to no observable effect on individuals developed in optimal conditions. These relationships strongly suggest that individuals associated with suboptimal conditions during the critical periods of egg production and embryogenesis either achieve greater benefit per unit increase in water temperature (or water level) due to inherent physiological disadvantages or utilize dissimilar strategies (physiological, behavioral or otherwise) for maximizing survival, growth, or transport.

The notion that blue crab larval and megalopal performance depends on conditions preceding larval development was further substantiated by the greater overall mean settlement rate observed for water temperatures ≤20°C than >20°C. Previous studies support this finding, revealing that physiological stress experienced during the earliest stages of development, including oogenesis, holds both immediate and long-term consequences for individual growth, body size, and tolerance to environmental stressors (Giménez 2006). Although some variability in initial size of oviposited eggs may be attributed to size of the parent female (Stella et al. 1996; Fischer et al. 2009), investigations of latitudinal and seasonal patterns in egg traits of estuarine and nearshore marine crabs commonly illustrate a pattern of increasing egg size (i.e., parental investment per egg) with decreasing temperature (Shirley et al. 1987; Brante et al. 2003; Arruda Leme 2006; Fischer et al. 2009). Similarly, Amsler and George (1984b) found greater initial content and overall use of lipids in blue crab eggs spawned early in the reproductive season (16°C) than spawned later (26°C). As a result of suboptimal pre-hatching conditions or larger than average embryo size, individuals may be prone to a longer developmental pathway involving not only slower incremental growth but also larger size and higher survival in subsequent larval, post-larval and juvenile life-stages (Shirley et al. 1987; Giménez et al. 2004; Giménez 2006; Hamasaki et al. 2006). I did not record megalopa body size in this study, but I distinctly observed both small and large megalopal blue crabs within samples and documented greater settlement rates following lower temperatures. Moreover, Mense and Wenner (1989) found notably larger blue crab megalopae settling in spring (following cold temperatures) than fall (following warm temperatures), and Robinson and Tully (2000) discovered megalopa body size at settlement for the porcelain crab (*Pisidia longicornis*) was positively associated with both temperature during larval development and probability of survival. These data suggest that life-history strategies for dealing with suboptimal temperatures in early development may strongly influence the recruitment potential and population dynamics of a species.

As was predicted, reductions in freshwater inflow ultimately led to increased megalopal settlement rates for blue crabs. River discharge around the time of hatching (7-d period ending 35 d prior to settlement) presumably entered the best approximating model of megalopal settlement rate for the same reasons that recently-mated females begin migration to higher salinities prior to or immediately following oviposition (Forward et al. 2005; Goldman 2007; Ramach et al. 2009). As tolerance to low salinity (i.e., high river discharge or inflow) is especially low for blue crabs during embryogenesis, hatching, and subsequent larval development (Sandoz and Rogers 1944; Costlow and Bookhout 1959; Costlow 1967), incubation of embryos and release of newly-hatched larvae in saline waters increases probability of hatching and larva and post-larva survival due to ambient conditions.

Inclusion of river discharge as a negative effect in the best model of settlement rate was in sharp contrast to public intuition that, as an estuarine-dependent species, blue crabs should increase in number with increasing freshwater inflow. However, models examined in this study only incorporated variables that either directly or immediately could have influenced the development, survival or transport of early-stage crabs. Effects that acted on a larger spatial or temporal scale to indirectly influence individual persistence or population dynamics were beyond the scope of the data and analyses used. Therefore, model results supported earlier studies indicating that blue crab embryos, larvae and post-larvae achieve maximum developmental and survival rates in salinities higher than typical of estuaries, but the models did not account for the seemingly intuitive fact that blue crabs of all stages indirectly depend on a salinity regime which incorporates at least periodic occurrence of high freshwater inflow. That is, while blue crabs directly rely on biotic (e.g., primary production) and abiotic (e.g., nutrient loading) processes for the provisions of food and shelter, these processes directly depend on a variable but largely predictable pattern of river discharge. Moreover, data collected during 2003-2005 were likely representative of normal seasonal variation in discharge within the Guadalupe Estuary, but they certainly could not have accounted for the estuary's large-scale disturbance regime as defined by extremes in freshwater inflow (e.g., severe or long-term drought or flooding). Consequently, low river discharge (i.e., high salinity) proved to be favorable for blue crabs in early development, but an inflow regime including both low and high discharge is ultimately needed for maintenance of ecological functions and persistence of local to regional populations.

Wind-generated currents are a significant mechanism of transport for larval and post-larval decapods, particularly in offshore waters (Goodrich et al. 1989; Blanton et al. 1999; Queiroga et al. 2006). In this study, inclusion of wind speed and direction in the best approximating model of blue crab megalopal settlement rate suggested wind patterns during zoeal and megalopal development (35-d period preceding collector retrieval) were important determinants of terminal settlement patterns. Settlement rate increased with wind speed from all observed wind directions (principally N and SE), but mean settlement rate, frequency of settlement events, and the effect of increasing wind speed were all greatest following SE winds. Blanton et al. (1999) provided a possible explanation for these settlement patterns. They used numerical models to demonstrate that winds of different and even opposing directionality may ultimately promote larval pooling and estuary ingress, but winds pointed directly toward the inlet mouth were most effective in concentrating (or pooling) offshore plankton near the mouth and transporting individuals through the inlet. Results of the present study support these earlier findings, as orientation of coastline adjacent to the study area is northeast-southwest and SE winds lend perfectly to larval pooling and transport into the estuary.

Tidal flux is another important transport mechanism for early-stage blue crabs, especially within estuaries where megalopae utilize a pattern of tidally-timed vertical migrations to reach terminal settlement sites (see Background). However, Lochman et al. (1995), who studied post-larval supply within the Matagorda Ship Channel (adjacent to Pass Cavallo, Texas), suggested that megalopae may not respond effectively to environmental cues necessary for FTT (e.g., changes in water salinity and turbulence) when invading well-mixed estuaries. With little tidal influence and a tidal range of <30 cm all year, the Guadalupe Estuary represents a well-mixed estuary. Consequently, along the central Texas coast, settlement patterns may be wind-driven both offshore (resulting in dispersal, larval pooling and ingress) and nearshore (resulting in estuary invasion and settlement). However, because the best model of settlement rate incorporated wind data from a period of 35 d preceding and including the day of collector retrieval, I cannot be certain of the timing of influence or specific function of wind during that time. Inclusion of wind effects from the 35-d period as opposed to the 1, 7, 14, 21, or 28-d periods implies wind was important early in larval development, presumably for transport, but implies nothing about the influence or function of wind thereafter. If wind stress was a key mechanism for megalopal transport in the Guadalupe Estuary, N winds may have expedited estuary invasion by enhancing the southward-flowing waters of the GIWW. Conversely, SE winds would have either slowed the progression of southward-invading megalopae, possibly reducing the episodic nature of settlement events, or transported megalopae westward from the GIWW to the shallow bays and marshes of the mainland (i.e., to the study sites). As key drivers in patterns of settlement rate, wind stress and direction on the Texas coast should be more thoroughly investigated.

Precipitation was incorporated into model-building procedures to explain variability in the rate of juvenile recruitment by representing the inverse effect of salinity. Contrary to my hypothesis, recruitment rate dramatically increased with precipitation (14-d total), which unarguably was the most important explanatory variable examined. To my knowledge, no other study has identified precipitation as an important driving variable of crab abundance at any early life-stage, but both megalopal (King 1971) and early-instar juvenile blue crabs (<6 mm CW; Rakocinski et al. 2003) have shown greater association with high than low salinity waters in natural settings. The lack of concurrence between this and earlier studies suggests the response of settlers to rainfall was not a result of physiological tolerance to salinity. Rather, recruitment may have increased with precipitation because freshwater (rainfall) mixing with water from shallow estuarine habitats acted as a stimulus for terminally-settling megalopae to metamorphose. Similarly, Wolcott and De Vries (1994) experimentally found that the amount of time to metamorphosis decreased as invading megalopae encountered estuarine cues, such as marsh and low-salinity water. Alternatively, precipitation may have improved the quality of terminal settlement (recruitment) habitat by increasing turbidity and impairing the visual searching capabilities of predators, thereby reducing predation risk (Minello et al. 1987; Macia et al. 2003). King (1971) supports this last explanation for precipitation influence, as he found blue crab megalopae most frequently invaded the Guadalupe Estuary in low light transmissive waters (i.e., high turbidity).

Hence, it seems probable in this study that increasing precipitation enhanced conditions for development and survival of settling megalopae and newly-recruited juvenile crabs, leading to higher observed rates of recruitment.

The best approximating model of juvenile recruitment rate also included the effects of water level (14-d mean), wind speed (1-d mean) and wind direction (1-d mode). These effects possibly functioned in a similar manner as did precipitation. By essentially diluting overall recruit densities and increasing water turbidity (King 1971; Minello et al. 1987; Macia et al. 2003), increased water level and wind speed, respectively, may have reduced predation pressure. Alternatively, mean recruitment rate and frequency of recruitment events were highest co-occurring with SE winds and an increasing influence of wind speed was observed for N, NE and E winds, suggesting that higher water levels and N to SE winds enhanced recruitment by facilitating transport of megalopae to terminal settlement sites in shallow bays and adjacent salt-marsh (i.e., to the study sites). Although precise functions are speculative, analyses of settlement and recruitment rates indeed indicate that water level and wind play important roles in the larval and post-larval transport and survival of blue crabs both offshore and nearshore.

Spatial Patterns in Settlement and Recruitment

To my knowledge, few field studies have simultaneously examined use of shallow estuarine habitats by either megalopal or newly-metamorphosed juvenile blue crabs (e.g., Orth and van Montfrans 1987; Mense and Wenner 1989; Pardieck et al. 1999). In some cases, these studies and others using passive collectors to document settlement (e.g., Rabalais et al. 1995) were generally described as being situated in salt-marsh. However, sampling nearly always occurred in shallow embayments adjacent to salt-marsh or along major rivers, channels or tidal creeks, and collectors were typically deployed from piers or docks. In this study, I deployed passive collectors in multiple interior salt-marsh habitats (tidal creeks, connected ponds, unconnected ponds) and sites. All habitats sampled were either too narrow or shallow for piers or associated structures and were integrated into entirely natural surroundings. As waters around piers and in navigable channels may be void of suitable settlement habitat and demonstrate accelerated velocity or high turbulence due to anthropogenic effects, this study was my attempt to uncover naturally-occurring spatial patterns in blue crab settlement and recruitment while minimizing potential biases (Pineda 2000).

Previous observations of ontogenetic shifts in habitat use by both early-instar and larger juvenile blue crabs reveal the marked influence of structural complexity at a fine spatial-scale. While megalopae selectively settle in structurally-complex habitats (e.g., seagrass, algae, oyster shell; Morgan et al. 1996; van Montfrans et al. 2003; Moknes and Heck 2006), habitats of lesser complexity (e.g., vegetation with broad blades or low stem density, nonvegetated sediment) are increasingly used by juveniles as they increase in size (Orth and van Montfrans 1987; Pile et al. 1996; Rozas and Minello 1998; Pardieck et al. 1999; Moksnes and Heck 2006; see also Chapter III). This study did not directly assess the selection or switching of micro-habitats by blue crabs in early development (as all settled on passive collectors), but the spatial ranges in which crabs of different early life-stages used habitats corresponded well with patterns in habitat characteristics observed at the meso-scale. Specifically, the extent to which early-stage crabs infiltrated the salt-marsh increased with advancements in development. Megalopal settlement was limited to tidal creeks, but class-1 juveniles (≤5 mm CW) minimally reached connected ponds and class-2 juveniles (>5 mm to ≤40 mm CW) were abundant in all habitats of the salt-marsh. Moreover, from shallow bay habitat to increasingly disconnected water bodies of the interior salt-marsh, coverage of SAV decreased while prevalence of non-vegetated bottoms and density of emergent vegetation edge increased (see Chapter III).

The over-lapping distributions of crabs in different life-stages revealed shifts in habitat use were not complete and suggested changes in juvenile ontogeny might not be distinctive during J1-J3 (up to around 5 mm CW). Rather, newly-metamorphosed juveniles may inhabit the same habitats as megalopae and undergo changes in dietary, space, or refuge requirements gradually or at later stages in development (e.g., ≥J4; Pardieck et al. 1999; Moksnes and Heck 2006). Because all juveniles >5 mm CW were combined in summaries, gradual or marked changes in habitat use by crabs within this size group were not evident. However, study results clearly demonstrated the notable pattern of increasing spatial distribution with crab age, size, or mobility and affirmed the gradual use and importance of interior salt-marsh for dispersing early-instar juveniles.

An important note is that I sampled habitats of the interior salt-marsh during May-June and September-October, which in normal years exhibit high water levels throughout the estuary and extensive inundation of salt-marsh. Sampling during these times, when most interior habitats were linked to adjacent bay, presumably increased probability that, if indeed blue crab megalopae and early-instar juveniles used salt-marsh, their presence would be observed. However, during all collection periods sampled, submerged aquatic vegetation and algae were highly abundant throughout shallow waters. Consequently, structural complexity in the water column of bay habitat may have offset the positive influence of increasing water level either by physically preventing some individuals from moving into the marsh or by providing sufficient refuge for settlers and new recruits and eliminating the need for additional upstream movement. Although a clear spatial pattern was observed in use of salt-marsh habitat with age, size, or mobility of crabs, water level and structural complexity, as well as other factors (e.g., density-dependence competition; Moksnes 2004), likely influenced the magnitude of use by crabs. To determine the abiotic and biotic factors governing movement of early-stage blue crabs into the salt-marsh, further study with more extensive sampling and diverse sample period conditions would be needed.

CHAPTER III

BLUE CRAB ABUNDANCE PATTERNS IN SHALLOW BAY AND SALT-MARSH HABITATS OF THE TEXAS GULF COAST

Synopsis

Coastal salt-marshes are widely recognized as important nursery habitats of estuarine-marine nekton. However, contributions of interior salt-marsh to blue crab (*Callinectes sapidus*) populations have received little attention, and studies of crab use of salt-marsh have occurred almost exclusively in young, *Spartina*-dominated marshes or peripheral *S. alterniflora* fringe. In this study, I examined the size-specific abundance patterns of blue crabs in shallow habitats of the Guadalupe Estuary, Texas, where salt-marsh is mature and dominated by high-marsh halophytes (e.g., *Batis maritima*, *Salicornia* spp., *Monanthochloa littoralis*, *Borrichea frutescens*). Habitat types included shallow bay within 50 m of salt-marsh and the edges and open water of connected and isolated interior-marsh ponds. During October 2004-March 2006, monthly crab samples were collected in bay waters using novel methods of drop-trapping and in interior-marsh pond habitats using a throw-trap. Descriptive summaries of crab abundance revealed that interior-marsh habitats comprised fewer but larger crabs than bay habitat. Mean crab density was ten times greater in bay (9.5 ± 2.2 crabs m^{-2}) than any interior-marsh

(0.6-1.0 crabs m^{-2}) habitat, but mean biomass was comparable across habitats (2.4-3.3 g m^{-2}). Extreme right-skewness was prevalent in the size-class distribution of crabs in all habitats but most pronounced in shallow bay, where crabs were typically ≤10 mm CW. Crabs contributing greatest to biomass were smallest (11-30 mm CW) in bay habitat, larger (31-80 mm) along interior-marsh pond edges, and largest (41-130 mm) in interior-marsh open water. At a larger spatial-scale, total crab number was most influenced by crab abundance in bay habitat. Conversely, the open water of connected inner-marsh ponds contributed more to standing stock biomass than all other habitats, reflecting its proportionally larger area and average crab size. Using an information-theoretic approach to investigate potential sources of variation in crab density, I determined the best predictors of density for crabs 1-10 mm and 11-30 mm in size were micro-site characteristics, including habitat type, water column structure type, and structural complexity. Overall, findings suggested that shallow bay provided nursery habitat for young blue crabs and interior-marsh ponds were important habitats for dispersing juvenile and adult crabs.

Introduction

As transitional zones created by the mixing of fresh and coastal waters, estuaries are among the world's most biologically diverse and ecologically complex systems. Extremely high secondary productivity, particularly of transient estuarine-marine fishes and invertebrates, occurs within a variety of estuarine biotopes (e.g., seagrass beds, salt marshes, mangrove forests) and has led to the widespread appreciation of these structurally-distinct communities as nursery habitats for juvenile nekton (Beck et al. 2001). While rapid rates of human population growth and coastal development threaten the productivity of these systems (Kennish 2002), guidelines for identifying juvenile nursery habitats continue to aid in the prioritization of nurseries for protection and restoration (Beck et al. 2001; e.g., Essential Fish Habitat – see Minello 1999). Juvenile nursery habitat is defined as that which, on average, contributes greater juvenile biomass to adult populations (i.e., production) than other habitats in which juveniles occur (Beck et al. 2001). Growth, survival, and movement to adult habitats are key factors regulating production and important considerations for comparing quality among juvenile habitat types and later identifying essential nurseries (Beck et al. 2001; Minello et al. 2003).

Field experiments and quantitative sampling efforts used to study life-history variation and density patterns of nekton have most commonly occurred in shallow embayments, along the salt-marsh periphery, or in large tidal creeks. Within these areas, comparisons made among structurally distinct biotopes or habitat types, such as submerged aquatic vegetation (SAV), algae, non-vegetated bottom, oysters, and *Spartina alterniflora* marsh edge, have revealed differences in habitat quality (e.g., faunal density in SAV > density in *S. alterniflora*; Minello 1999). Other micro-habitat characteristics, including water depth (Hines and Ruiz 1995), substrate type (Lipcius et al. 2005), vegetation shoot density or structural complexity (Heck and Wetstone 1977; Wilson et al. 1987; Leber 1985; Hovel and Fonseca 2005; Moksnes and Heck 2006), and distance to emergent marsh edge (Micheli and Peterson 1999; Minello et al. 2008), have also shown to influence nekton growth, mortality, and density.

Recent studies suggest that nekton should also be examined at larger spatial scales, which account for the composition and spatial heterogeneity of habitats (Peterson et al. 2000; Partyka and Peterson 2008). Significant relationships have been identified between nekton diversity, density or mortality and density of marsh edge or tidal creeks (Kneib 2003; Larkin et al. 2008), degree of water connectivity (Layman et al. 2004; Larkin et al. 2008), presence of habitat corridors (Micheli and Peterson 1999), habitat patch size (Hovel and Fonseca 2005), patchiness of habitats (Hovel and Fonseca 2005), and patch shape and orientation (Tanner 2003). These relationships, combined with evidence of ontogenetic changes in habitat use by nekton (Orth and van Montfrans 1987; Pile et al. 1996; Rozas and Minello 1998; Mosknes and Heck 2006), suggest the fundamental criteria outlined by Beck et al. (2001) may be most effectively applied only after fully accounting for habitat complexity at multiple spatial scales.

Few studies (e.g., Peterson and Turner 1994; Rozas and Zimmerman 2000; Kneib 2003; Rozas and Minello 2010) have investigated the contributions of interior salt-marsh habitats to estuarine nekton populations (Minello 1999; Minello et al. 2003), likely due to the challenges of sampling (Connolly 1999). Although tidal creeks, tidally-connected ponds, and isolated ponds commonly contain the same biotopes also found in shallow embayments and along the marsh periphery, patterns in nekton growth, mortality, dispersal, and density have been thoroughly described only outside the salt-marsh and may not be entirely applicable to the marsh interior. Patterns inside and outside the marsh may contrast markedly due to inherent differences in geomorphology, inundation regime, effects of tides and weather events, nutrient load, and resident community structure. Despite these uncertainties, nekton diversity, density, and production have been positively correlated with tidal creek density and proportional coverage of emergent vegetation in the salt-marsh (Kneib 2003; Minello et al. 2008), suggesting that various components of the interior marsh may play uniquely important roles in regulating nekton populations and comparisons between inside and outside the marsh deserve additional attention.

Temporal variability should also be considered when estimating population size or secondary production or comparing the relative contributions of habitats to production at various sites. Patterns in nekton density, mortality, growth, and movement to adult habitats may depend on gradual physical changes (e.g., sediment deposition, scouring, oxidation), predictable seasonal changes (e.g., plant growth and senescence, marsh inundation, water temperature), or ontogenetic changes (e.g., dietary requirements, physical constraints, social behavior). Moreover, density-dependent factors (e.g., predation mortality, access to food, dispersal among habitats) may cause organisms to exhibit unique behaviors or respond more sensitively to environmental change at certain levels of abundance. During periods of peak recruitment, for example, saturation of some habitats may cause young juveniles to use other (suboptimal) habitats in greater proportion than alternative times of the year (Moksnes 2004). Consequently, by sampling only during the high-water periods of the year or seasons of highest recruitment, some previous studies may not have fully or accurately quantified the ecological relationships of interest.

In this study, I focused on the blue crab (*Callinectes sapidus*), one of our nation's most important commercial fishery species and a key ecological component of estuarine ecosystems throughout the western Atlantic (Guillory et al. 2001). While the blue crab is important as both food and predator of marine and estuarine fishes, shrimps, crabs, and other invertebrates (Guillory and Elliot 2001; Guillory and Prejean 2001; Guillory et al. 2001), adults and large juveniles (>30 mm) in the current study area are also a principle food of the endangered whooping crane during winter (October-April; Hunt and Slack 1989; Chavez-Ramirez 1996). Current recovery planning (Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005) and annual updates by the U.S. Fish and Wildlife Service (e.g., Stehn 2009) emphasize the importance of blue crabs as a food resource for the winter survival and subsequent breeding success of cranes and further speculate on the capacity of freshwater inflows to determine winter patterns of blue crab availability for foraging cranes.

My overall goal for this research was to examine the size-specific abundance patterns of blue crabs in shallow (<1 m deep) estuarine habitats of the central Texas Gulf Coast. These habitats incorporated creeks and ponds of the interior salt-marsh, which, along this portion of the coast, is characterized by complex geomorphology, highly reticulated marsh edge, and dominance of mixed, high-marsh halophytes (e.g., *Batis maritima*, *Salicornia* spp., *Monanthochloa littoralis*, *Borrichea frutescens*). To capture both temporal and spatial variability, I sampled at multiple sites and across all months of the year and used randomization within biotopes (e.g., shallow bay, connected marsh ponds, isolated marsh ponds) to adequately sample the structural components present (e.g., SAV, algal bed, non-vegetated bottom) in proportion to their area coverage. I did not examine the mortality or growth of crabs or explicitly measure movement of juveniles to adult size-classes or habitat, as suggested by Beck et al. (2001). However, I did use novel sampling methods to (1) estimate crab density, total population number, and standing-stock biomass, (2) document habitat-specific size-class structure, and (3) gather evidence of ontogenetic changes in habitat use.

Specific objectives for this research were to (1) develop field methodology and sampling gear appropriate for quantitative measure of crab abundance within and adjacent to salt-marsh, (2) identify temporal and spatial patterns in blue crab abundance and size-class structure within and adjacent to salt-marsh, accounting for the effect of spatial scale, and (3) further investigate the effects of small- (e.g., vegetation structure) and large-scale (e.g., freshwater discharge) environmental variation and stochasticity on blue crab abundance and size-class structure.

Materials and Methods

Study Location

The study area was located on and immediately adjacent to the Aransas National Wildlife Refuge (ANWR) in Aransas and Calhoun counties, Texas (Fig. 3-1). The refuge is situated almost entirely on the Blackjack Peninsula, which is bounded by two major bays (San Antonio and Copano-Aransas), the smaller St. Charles and Mesquite bays, and the Gulf Intracoastal Waterway (GIWW). The Guadalupe, Aransas, and Mission Rivers drain into these surrounding bays, though the study area lies largely within the Guadalupe Estuary.

Presence and movement of water within the estuary is influenced by tides, meteorological events (e.g., rainfall, wind, hurricanes), and fresh and coastal waters entering the estuary. Diurnal tides (one high, one low) along this portion of the coast exhibit a narrow daily tidal range of approximately 9-13 cm (Texas A&M University-Corpus Christi, Division of Nearshore Research, station 031, Seadrift). Fortnightly tides influence the tidal range minimally, but tidal range in fall and spring can be considerably larger (≤30 cm) and water typically reaches high marsh. Water exchange also occurs during strong wind events. North winds in winter and southeast winds in summer force waters out of and into the salt-marsh, respectively. North and southeast winds also increase and decrease, respectively, the ease (or speed) at which southward-flowing waters in the GIWW are transported. The Blackjack Peninsula receives higher quantities of freshwater discharge from the Guadalupe River than any other nearby river, but the southern tip of the peninsula is also influenced by water flow into the Copano-Aransas

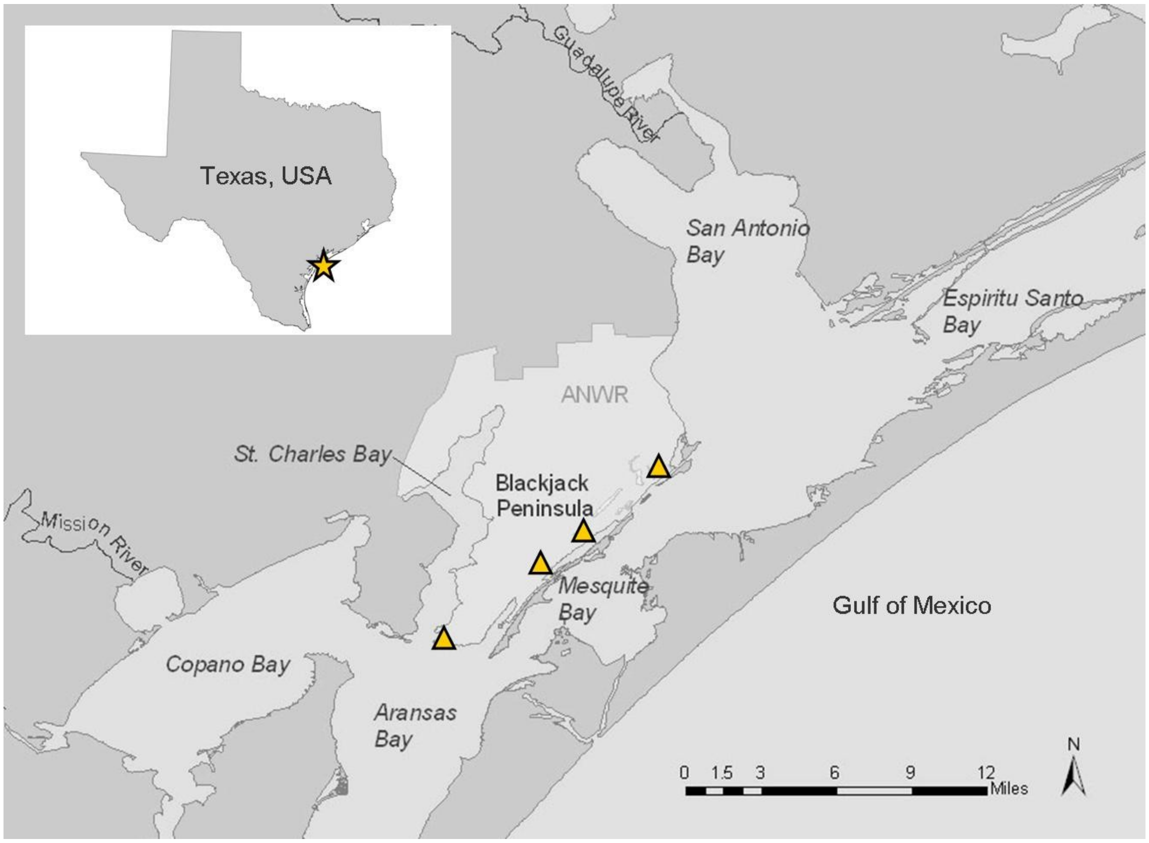

Fig. 3-1. Map depicting the locations of four study sites (triangles) on the central Texas coast (star) and eastern perimeter of Aransas National Wildlife Refuge (ANWR). From northeast to southwest, study sites were Boat Ramp, Pump Canal, Pipeline, and Blackjack.

Bay system. Exchange between nearshore and offshore waters occurs at Pass Cavallo and Aransas Pass, located at the north and south ends of the estuary, respectively. Cedar Bayou, a much smaller source of exchange into Mesquite Bay, was closed by siltation during the study. During high freshwater inflow, salinities are lowest at the northern-most extent of the peninsula and increase progressively southward. All estuarine habitats within the study area annually experience a wide range of salinities (1-30 ppt).

The general climate of the area is sub-tropical. Normal annual rainfall is 103.7 cm, 45% (46.4 cm) of which falls during May-June (22.0 cm) and September-October (24.4 cm). Normal monthly minimum and maximum temperatures are 17.4°C and 24.9°C, respectively, during March-May, 25.1°C and 31.8°C during June-August, 18.0°C and 26.6°C during September-November, and 8.0°C and 17.8°C during December-February (NOAA, National Climatic Data Center 1971-2000, Aransas Wildlife Refuge, Texas weather station).

Estuarine habitats used by blue crabs include shallow bays and salt-marsh. Bays are primarily subtidal and consist of open-water, nonvegetated (mud or sand) bottoms and beds of submerged aquatic vegetation (SAV; e.g., *Ruppia maritima*), algae, and oysters. The salt-marsh is primarily intertidal and contains mixed emergent vegetation, connected and isolated ponds, and occasional small-scale tidal creeks. Approximately 15-50% of the marsh is made up of ponds, which typically are nonvegetated but seasonally contain SAV and algae. Islands of slightly-elevated ground support the emergent growth of highly salt-tolerant but intermediately flood-tolerant plant species (e.g., *Borrichea frutescens, Batis maritima, Salicornia virginica, S. bigelovii, Lycium* *carolinianum*), while shallow depressions and edges of ponds and tidal creeks support species of both high salt and flood tolerance (e.g., *Distichlis spicata, Spartina alterniflora*; Stutzenbaker 1999).

All navigable waters adjacent to and within the salt-marsh are under the governance of the State of Texas and open to the public throughout the year. The most common uses of public waters include recreational rod-and-reel fishing, commercial fishing (e.g., crabbing with crabpots, shrimping with trawls, dredging for oysters), recreational boating (e.g., sailing), barge transport, and wildlife viewing via tour boat.

Study Design

This study was conducted in association with efforts to examine the diet and foraging behavior of whooping cranes during winter. To facilitate both crane and crab studies, four of the nineteen winter territories of whooping cranes located within ANWR were used as replicate study sites, including those named Boat Ramp (BR), Pump Canal (PC), Pipeline (PL), and Blackjack (BJ). Territories (hereafter, study sites) differed considerably in habitat composition and connectivity of bay to interior salt-marsh waters (Fig. 3-2), as well as distances to each the Guadalupe River (freshwater source) and Pass Cavallo (northern offshore water source; Fig. 3-1). All sites were considered fully representative of the contiguous salt-marsh and adjacent shallow bay, and inference from study results was intended to be applied to the population of sites represented by those sampled.

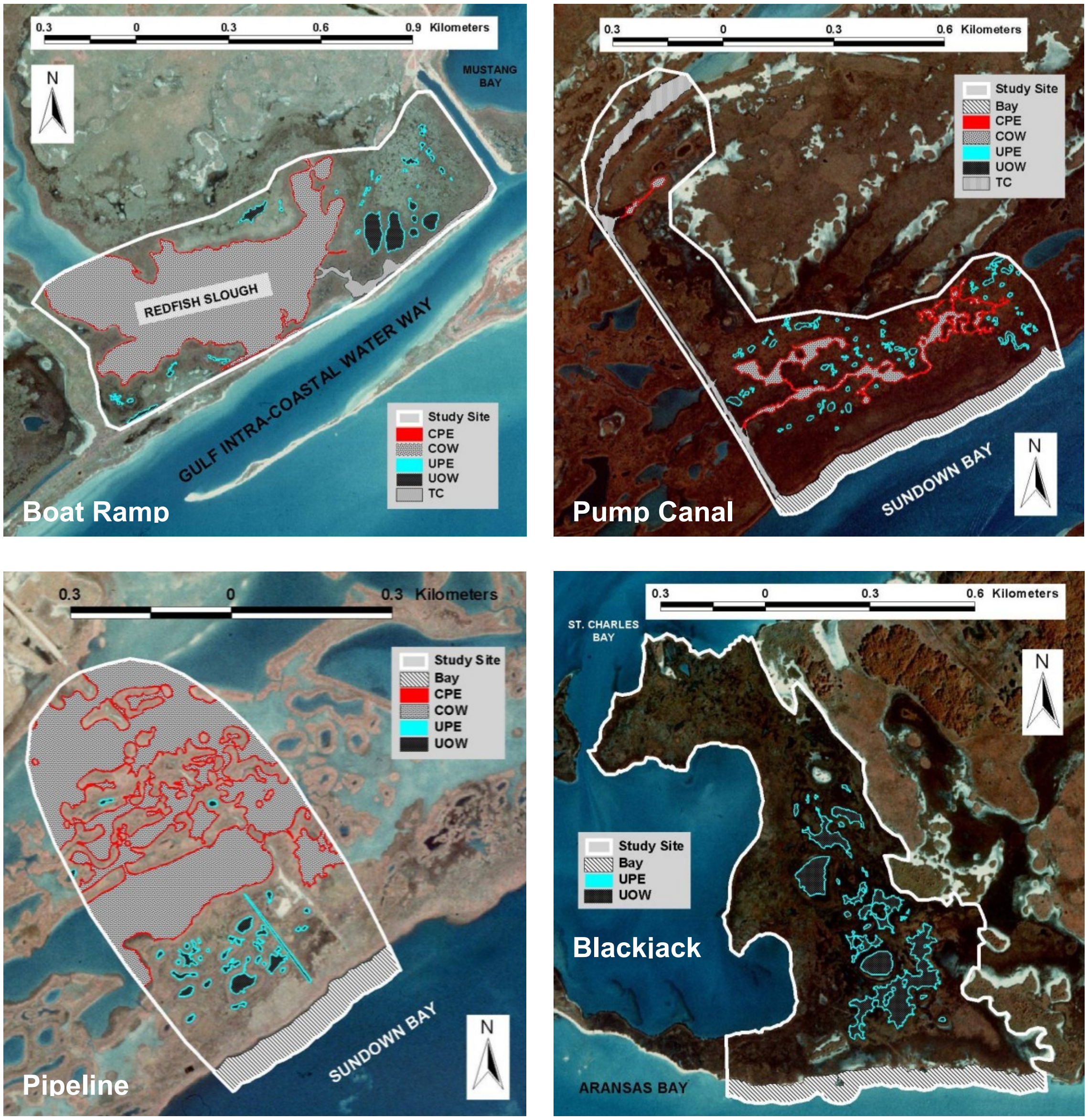

Fig. 3-2. Satellite imagery and habitat overlays for each of four study sites located at Aransas National Wildlife Refuge, Texas and studied during October 2004-March 2006. Boundaries of all sites were based on the winter territories of whooping cranes, and delineated habitats included bay-marsh interface (Bay), tidal creek (TC), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), unconnected pond edge (UPE), and emergent salt-marsh vegetation (no color or pattern).

Area within each study site was categorized by habitat and included three or more of (1) bay-marsh interface (shallow bay within 50 m of emergent salt-marsh vegetation; bay), (2) tidal creek (connection between interior salt-marsh water and bay), (3) connected pond (interior salt-marsh water, seldom disconnected from bay), (4) unconnected pond (isolated water in salt-marsh interior, infrequently connected), and (5) emergent salt-marsh vegetation (ESV). Connected and unconnected ponds were each further classified as either open water (>1 m from emergent vegetation) or pond edge (2-m wide strip straddling the water-emergent vegetation interface), thereby creating connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE) habitats for a total of seven habitats. Habitats were not inherently represented at every study site; only PC contained all habitats (Table 3-1). Bay habitat was absent from BR, because the site was separated from the GIWW by a large levee covered with rip-rap. Tidal creek habitat provided a connection between the ponds and bay of PL, but the main tidal channel was located outside site boundaries and consequently not sampled. Tidal creek and connected pond habitats were not represented at BJ, because no direct connection existed between the bay and salt-marsh.

To investigate patterns in blue crab abundance, I collected samples using an incomplete-blocks design with repeated (monthly) measures. Under this design, habitats represented treatments that were incompletely replicated across study sites (blocks), and experimental units were all combinations of habitat x study site x monthly sampling period. Prior to each sampling period, four trapping locations per experimental unit

Table 3-1. Areal coverage of habitats within study sites. Total area (ha) at each site was divided into seven major habitats: bay-marsh interface (Bay), tidal creek (TC), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), unconnected pond edge (UPE), and emergent salt-marsh vegetation (ESV). Only Pump Canal (PC) contained all habitats.

				Salt-marsh Interior											
		Bay		TC		COW		CPE		UOW		UPE		ESV	
Site	Total Area	Area	%	Area	%	Area	%	Area	%	Area	%	Area	%	Area	%
Actual Area															
BR	67.61	0.00	0.00	1.48	2.19	27.52	40.70	0.95	1.40	1.94	2.87	0.68	1.01	35.04	51.83
PC	55.35	4.45	8.03	2.58	4.65	2.07	3.73	1.13	2.03	0.58	1.05	0.75	1.36	43.81	79.14
PL	31.77	2.01	6.32	0.00	0.00	12.19	38.39	1.74	5.49	0.51	1.60	0.49	1.53	14.83	46.67
BJ	71.42	5.13	7.19	0.00	0.00	0.00	0.00	0.00	0.00	4.31	6.03	1.18	1.66	60.79	85.13
Sampled Area															
BR	31.09	0.00	0.00	0.00	0.00	27.52	88.50	0.95	3.05	1.94	6.25	0.68	2.20	0.00	0.00
PC	8.97	4.45	49.57	0.00	0.00	2.07	23.02	1.13	12.55	0.58	6.47	0.75	8.38	0.00	0.00
PL	16.94	2.01	11.85	0.00	0.00	12.19	71.99	1.74	10.29	0.51	3.00	0.49	2.87	0.00	0.00
BJ	10.62	5.13	48.31	0.00	0.00	0.00	0.00	0.00	0.00	4.31	40.53	1.18	11.16	0.00	0.00

were randomly selected using a random point generator in ArcView GIS (version 3.3). Samples collected at these locations were thus considered sub-samples. Regular monthly sampling occurred during October 2004-March 2006 in bay and connected and unconnected pond habitats. Samples were inconsistently collected in tidal creeks, and ESV was never sampled (other than that incorporated in pond edge habitats); therefore, neither habitat was included in investigations.

Development and Use of Sampling Gear

Standard drop-trapping protocol, otherwise known as suction-sampling, was not an option for quantitative measure of crab abundance in this study. Use of this method has been limited to shallow bays and deep tidal creeks where water depth ranged 50-110 cm (e.g., Zimmerman et al. 1984; Rozas and Minello 1998; Minello and Rozas 2002). Trapping in interior salt-marsh habitats, such as those identified in this study, is virtually impossible using standard methods, because water depth is most often too low (0-50 cm) for boat travel and unconnected or temporarily disconnected ponds are inaccessible via water (Rozas and Minello 1997).

To facilitate sampling for blue crabs in connected waters ≥30 cm deep, I designed and constructed multiple large, three-dimensional frames called booms (one for each study site) and a pair of large, portable styrofoam floats (<30 lbs (13.6 kg) each) to be used at each site (Fig. 3-3). Multiple cylindrical, stainless steel (20-gauge) drop-traps (approximately 30 lbs (13.6 kg), 1-m diameter x 75-cm height) were also constructed (one for each site). When combined, the boom assembly (boom, trap, and floats)

Fig. 3-3. Drop-trapping for blue crabs in bay habitat. The drop-trap was part of an assembly, which included a boom (the frame), two floats, and an anchor also used as a counter-balance to the trap (top). Crabs were retrieved from within the trap by sweeping inside the trap with a large dip net (middle) and sorting through the vegetation, debris, and sediment obtained (bottom).

functioned much like a smaller, more versatile version of a standard drop-trapping system. To assemble, the boom was set atop the floats as if skis, and the drop-trap was attached to a rope threaded through a pulley. While in transit from one sampling location to another, the trap was lifted to maximum height (≥1 m from trap bottom to water's surface) using an anchor crank. The boom assembly was pushed through contiguous waters and strategically guided to each predetermined sample location using wind force and a push (if needed). Release of the trap from the front arm of the boom was triggered by pulling a long rope extending from a pin positioned in the back of the boom. A cinder-block (approximately 25-30 lbs (11.3-13.6 kg)) was attached by a rope to the back of the boom and functioned both as a counter-balance to the trap during transit and as an anchor following the release of the trap. Booms and traps were stored on platforms situated at the edge of the marsh.

I used throw trapping methodology to sample blue crab abundance in unconnected habitats and water <30 cm in depth. The throw-trap used was similar to the drop-trap but shorter (1-m diameter x 40-cm height) and made of 18-gauge steel to maintain the 30-lb (13.6 kg) weight (Fig. 3-4). The trap had handles and was carried by two persons over the vegetated marsh to sample locations. When throwing the trap, we always stood out of the water so as to minimize disturbance to crabs in ponds. For pond edge samples, we stood as far away as we knew we could throw and either (1) stood on and threw along the emergent vegetated pond edge or (2) stood far away from and threw to the pond edge. One major difference between typical throw-trapping methods and those used in this study was the way in which the trap was thrown. Rather than throwing

Fig. 3-4. Throw-trapping for blue crabs in the interior salt-marsh. The throw-trap was always thrown by two people from elevated ground that supported emergent salt-marsh vegetation and never from within flooded ponds (top). Throw-traps were used in open water (middle) and pond edge (bottom) habitats, and only occasionally in bay habitat when water was <30 cm in depth.

the trap like a saucer, we together threw the trap up and out at an angle that ensured the trap would fall vertically and the entire bottom of the trap would hit ground at the same time. For locations predetermined to be farther than we could throw (some COW and UOW locations), we simply threw as far as possible (maximum 5 m) in the direction of the predetermined location and considered the location where the trap landed to be our sample location. I assumed all samples collected in COW and UOW were representative of their respective habitats.

Data Collection

At each trapping location, several environmental attributes were measured inside the trap, including minimum and maximum water depth (cm), surface water salinity (ppt), surface water temperature (°C), bottom substrate (mud or sand, mud or sand with debris, mud or sand with debris and/or algae, blocky clay, blocky clay with matte algae, blocky clay with matte algae and/or debris, shell or oyster), and water column structure type (none, SAV, algae, SAV/algae) and complexity (i.e., density; none, low, medium, high). In the water column, algae included both filamentous and plant-like (branching) forms, and SAV was predominantly *Ruppia maritima*. Levels of structural complexity were based on percent coverage of the volume of water inside the trap. I also recorded date, time, shortest distance to pond or bay edge (i.e., distance to nearest ESV; m), dominant edge ESV (*Spartina alterniflora*, *Batis maritima*, *Distichlis spicata*, mixed high-marsh vegetation, or other), and geographic location (latitude and longitude).

Data for several other parameters were obtained from remote sources within San Antonio Bay, on the Guadalupe River, and at ANWR. Parameters included primary water level (m above reference datum) and wind speed (km hr^{-1}; Texas A&M University-Corpus Christi, Division of Nearshore Research, Station 031, Seadrift), water temperature (°C) and salinity (ppt; Texas A&M University-Corpus Christi, Division of Nearshore Research, station 127, GBRA#2), river discharge (cu ft sec^{-1}; US Geological Survey, Guadalupe River near Tivoli, Texas, station 08188800), and precipitation (cm; NOAA, National Climatic Data Center 1971-2000, Aransas Wildlife Refuge, Texas weather station).

Blue crabs (*Callinectes sapidus* and *C. similis*) captured within the trap were collected by sweeping inside the trap in a circular motion with a 40-cm x 40-cm baitwell net (0.48-cm mesh). The sweeping action slowly wore away bottom sediment and stirred up crabs that had burrowed. Sweeping continued until at least two consecutive sweeps resulted in no crabs or other organisms captured. Crabs were placed in formalin and taken to the lab for processing.

In the lab, preserved crabs in each sample were identified by species, measured for carapace-width (CW; mm), and enumerated for 10-mm size-classes: (1) 1-10 mm, (2) 11-20 mm, (3) 21-30 mm, (4) 31-40 mm, (5) 41-50 mm, (6) 51-60 mm, (7) 61-70 mm, (8) 71-80 mm, (9) 81-90 mm, (10) 91-100 mm, (11) 101-110 mm, (12) 111-120 mm, and (13) 121-130 mm. No crabs >130 mm were captured during the study. A subset of samples was randomly selected to also record crab biomass (wet weight to the nearest 0.01 g). From these data, I developed a regression equation relating crab biomass to size and predicted biomass of crabs not weighed. All subsequent analyses were performed for *C. sapidus* and *C. similis* combined due to extremely low capture rates of *C. similis*.

Statistical Analysis

Crab abundance and size-class structure

To investigate spatio-temporal patterns in crab abundance at a fine spatial scale, I first computed mean crab density (number m^{-2}) and biomass (g m^{-2}) values per experimental unit (habitat x study site x monthly sampling period). Spatial patterns were further examined by calculating density and biomass means per habitat and per habitat within study site. Temporal patterns were investigated by averaging across sites per habitat within month. Patterns in mean crab size and distribution of densities and biomasses among size-classes were similarly explored.

To investigate the availability of crabs to foraging whooping cranes, crabs were combined across size-classes to form three broader size categories relevant to cranes, and densities were again computed per experimental unit. Size categories were in relation to crane bill length (CBL) and included (1) small (CW ≤25% of CBL (≤37 mm)), best represented by size-classes 1-4, (2) medium (CW >25% and ≤50% of CBL (38-73 mm)), best represented by size-classes 5-7, and (3) large (CW >50% of CBL (≥74 mm)), represented by size-classes 8-13. Temporal patterns in small, medium and large crab densities were then examined by habitat (bay, connected ponds, unconnected ponds) and study site for November 2004-March 2005 (winter 1) and November 2005-March 2006 (winter 2).

I investigated large spatial scale patterns in crab abundance by accounting for the proportional area of habitats within study sites. Total number (number ha^{-1}; *N*) and standing stock biomass (g ha^{-1}; *B*) of crabs in each experimental unit were computed, respectively, as:

$$N_{hsm} = d_{hsm} \times cf \times w_{h(s)}$$

$$B_{hsm} = b_{hsm} \times cf \times w_{h(s)},$$

where

h represents habitat type h_i (i = Bay, COW, CPE, UOW, UPE),

s represents study site s_j (j = BR, PC, PL, BJ),

m represents monthly sampling period m_k (k = 10/2004, 11/2004, 12/2004,… 03/2006),

d is crab density (number m^{-2}) estimated within the experimental unit of interest,

b is crab biomass (g m^{-2}) estimated within the experimental unit of interest,

cf is the conversion factor of 10,000 used to convert area from meter-squared to ha,

$w_{h(s)}$ is the weight of h_i within s_j as computed by $a_{h(s)} \div a_s$, and

a is actual area in ha of some defined space.

Monthly estimates of total crab number and standing stock per study site were simply computed by summing values of N_{hsm} or B_{hsm} across all habitats within a particular site and month. Total number and standing stock were summarized similar to fine-scale measures, but mean crab size and size-class structure were not examined, because patterns within and among habitats or sites mirrored those observed at the finer spatial-scale. Monthly estimates of total crab number were also computed per site for each of the three size categories relevant to whooping cranes during winters 1 and 2.

Sources of variation in crab density

I took an information theoretic approach to investigate causes of variability in crab abundance at the fine spatial scale. I developed a priori biological hypotheses concerning variability in crab density (number m^{-2}) and used these hypotheses as the basis for subsequent development of several generalized linear mixed models that modeled density as a function of environmental and random effects. Fourteen hypothetical sources of variation in crab density were identified, including:

1. *Bottom substrate.* Prior research found blue crabs 23-36 mm in size more readily buried in mud than sand (Barshaw and Able 1990). Consequently, crabs in sandy substrate environments should incur higher predation risk (Lipcius et al. 2005) and experience lower foraging efficiency than crabs in muddy bottom environments (Lipcius and Hines 1986). I did not differentiate between mud and sand at each trapping location but applied the concept of readiness to bury (or potential for concealment) to a broader range of substrate categories. Specifically, I hypothesized potential for concealment and, subsequently, crab density would decrease across substrates in the order of (1) mud or sand, (2) shell or oyster, and (3) blocky clay.
2. *Water column structural complexity.* Macroinvertebrate diversity and abundance increase with structural complexity in the water column (Heck and Wetstone 1977;

Heck and Orth 1980; Heck and Thoman 1984; Leber 1985; Mosknes and Heck 2006). Increases in structural complexity or surface area of submerged vegetation not only provide more space for habitation (i.e., increase carrying capacity) but also increase the structure's value as refuge from predation (Heck and Wetstone 1977; Leber 1985). I hypothesized blue crab density would increase with structural complexity in the water column from category "none" to "high." I also recognized that the relationship between abundance and complexity might differ among crabs of different size classes. Ontogenetic shifts in habitat use or utilization of increasingly more spacious habitat with increases in size have commonly been observed for crabs (Beck 1995; Bertini and Fransozo 2000; Mosknes and Heck 2006; Pardo et al. 2007).

3. *Water column structure type.* Despite anoxic conditions and toxic exudates widely associated with algae, I hypothesized locations comprising both SAV and algae would support the highest densities of blue crab. Nekton abundance and survival in each SAV (e.g., seagrass; Wilson et al. 1987; Pile et al. 1996) and macroalgae (Wilson et al. 1990) have proven greater than in adjacent non-vegetated bottoms. Moreover, the mesograzers (e.g., amphipods) that feed on macroalgae (Dittel et al. 2006) and the epiphytic algae of SAV (Valentine and Duffy 2006; Douglass et al. 2007) are both important foods for blue crabs.
4. *Distance to the ESV edge.* Previous research findings demonstrate patterns of decreasing prevalence of decapods with increasing distance from interior salt-marsh vegetation (Minello et al. 2008) or removal of plant cover (i.e., shade; Whitcraft and Levin 2007). Presuming these patterns represent a mixed strategy used by crabs to

both avoid predation and maximize food acquisition, I hypothesized results from my study would be consistent with those of earlier findings, and crab density would decrease with distance to ESV edge.

5. *Dominant edge ESV.* Several studies have compared blue crab use of *Spartina alterniflora* marsh edge to that of adjacent habitats, such as SAV and non-vegetated substrates (e.g., Thomas et al. 1990; Rozas and Minello 1998; Rozas et al. 2007). Little attention, however, has been given to crab use of pond edges dominated by middle- and high-marsh halophytes (see Minello 1999). In the salt-marsh of this study, these species are found on islands of elevated ground. Plant stems hang over steep, abruptly sloped pond edges, providing concealment to crabs from terrestrial and aerial predators, but are not often found in the water column. Conversely, *S. alterniflora* fringes the salt-marsh where elevational change is gradual; stems hang over the water but also provide refuge and a source of food to crabs within the water column. Therefore, I hypothesized crab density would be higher near bay or pond edges dominated by *S. alterniflora* than edges dominated by mixed, higher-marsh species. Because crabs would exhibit a stronger affinity for *S. alterniflora*, I also believed the effect of distance to edge would be greater with *S. alterniflora*.
6. *Presence of water.* Decapods can survive out of water for extended periods (18 h-3 d) in cool, humid conditions (Spicer et al. 1990; Samet et al. 1996; Lorenzon et al. 2007), but emersion dramatically elevates physiological stress (Spicer et al. 1990; Ridgway et al. 2006; Giomi et al. 2008) and likely increases vulnerability to terrestrial and aerial predators. I hypothesized the effect of water presence/absence

on crab density would solely be evident through interactions with other variables. That is, no crabs should be found on exposed sediment flats, and crab density should depend on other environmental variables when water is present.

7. *Water depth.* Crabs may be influenced by water depth for several reasons, which led me to believe that generally more crabs would be found in deep than shallow water. Crabs may select deeper water to avoid predation from foraging wading birds or other terrestrial or aerial predators that experience limited visibility or mobility in deep versus shallow waters. Also, the volume of water available to crabs per unit area increases with depth, causing a dilution effect and decreasing risk of predation by aquatic predators. The effect of water depth may also interact with other variables, such as water temperature and structural complexity in the water column. Crabs may be buffered against extreme hot or cold surface water temperatures when water depth is high versus low, and increasing structural complexity may decrease the need for crabs to seek shelter in deeper waters.
8. *Variability in water depth.* As temporal variability in water depth (i.e., probability of exposure and predation) increases, blue crabs may increasingly exhibit risk-adverse behavior. Accordingly, they may move into deeper water, position themselves closer to pond edges, inhabit SAV or algal beds of greater complexity, or maintain contact with bottom substrates of little burrowing difficulty. The effect of variability in water depth should then be seen through interactions with other effects, such as water depth, distance to ESV, structural complexity, and bottom substrate type.

9. *Water temperature*. Water temperature is an important determinant of crab growth. Whether measured as an increase in dry weight per ecdysis or 24-hr period or as an increase in CW per ecdysis, growth rate has generally shown to increase from 13-15°C to 30-34°C (Leffler 1972; Cadman and Weinstein 1988). I hypothesized crab density would increase with temperature but also believed the effect of temperature would be more pronounced in shallow than deep water because of greater vulnerability of crabs in shallow water to extreme cold temperatures, which limit mobility. While I recognized the potential lethal effects of low dissolved oxygen levels at extremely high temperatures, I believed such temperatures would infrequently be of concern in the study area and thus disregarded their effects.
10. *Water salinity*. Blue crabs are able to tolerate a wide range of salinities, but, as euryhaline species hyperosmoregulating in salinities below 27 ppt, they incur increasingly higher metabolic demands and osmoregulatory stress with decreasing salinity (Cadman and Weinstein 1988). In laboratory studies, salinity alone has shown to have little effect on crab growth and instead influences growth through an interaction with temperature. Specifically, osmoregulatory stress is highest and growth rate is lowest in conditions of both low salinity and temperature (Cadman and Weinstein 1988). I hypothesized crab density would positively relate to potential for growth, being lowest in conditions of low salinity and temperature.
11. *Water turbidity*. Although the effect of turbidity on nekton density and survival differs among species and depends on predator behaviors (Macia et al. 2003), I predicted increasing mechanisms for turbulence (e.g., wind) would increase water

turbidity and subsequently increase concealment (or survival) of blue crabs in the water column (see Minello et al. 1987). I believed crabs in turbid conditions would be less prone to hide from predators and, therefore, less dependent on other variables regulating concealment or predation risk. For instance, they should be less tied to pond edges, soft bottom substrate, high structural complexity in the water column, shallow water depths, and so on. If true, wind speed (a proxy for turbidity) and variables describing the micro-environment should interact to explain crab density.

12. *Recruitment rate*. No study has yet quantified a significant recruit-adult relationship. This is likely so because numerous factors or processes combine to determine the survival, growth, and dispersal of blue crabs in each stage of the lifecycle, and processes involved act as filters so that the proportion of individuals moving from one stage to another is successively smaller (Pineda 2000). Furthermore, as earlier life-stages are associated with larger spatial and temporal scales, small changes in the proportion of individuals passing from one stage to the next can cause considerable spatial and temporal variability in resultant population numbers. The rate of blue crab recruitment, however, is a logical source of variation in adult-form crab density. I hypothesized crab density would increase with increasing rates of megalopal settlement and juvenile recruitment (see Chapter II).
13. *Habitat type*. Known or potential differences in characteristics among habitat types in this study included connectivity to coastal waters, subsequent distance and difficulty of travel for immigrating crabs, diversity and abundance of crab predators and prey, inundation regime (including timing, frequency, duration), and effects of

wind and tides. I hypothesized crab density would decrease from bay to connected ponds to unconnected ponds and from edge to open-water pond habitat.

14. *Study site*. The random effect of study site was incorporated into all predictive models, because I believed unmeasured or unpredictable differences (stochastic variability) among sites significantly contributed to overall variation in mean crab density.

Hypothetically, the effects of water depth, temperature, and so on could be represented by a multitude of variables. For this reason, I incorporated two to four variables in analyses for each water depth, temperature, salinity, and turbidity (Table 3-2). Variables recorded at trapping locations (e.g., bottom substrate) were presumed to represent small-scale effects regulating micro-habitat selection by crabs. Conversely, variables recorded remotely (e.g., wind speed) represented large-scale phenomena affecting the entire estuary and overall abundance of blue crabs. To explore the timing of effects on crab density, I restructured remotely collected data into several forms consisting of computed means for the 1, 7, 14, 21, and 28-d periods including and preceding the day of trapping (Table 3-2). In total, 63 different explanatory variables represented the 14 hypothesized sources of variation in crab density. Not all variables were included in model-building procedures, because preliminary examination revealed that most variable forms were not useful in predicting crab density.

All evaluated models, whether preliminary or otherwise, were generalized linear mixed models (GLMMs), because variation surrounding the mean response of crab

Table 3-2. Fixed effects and representative explanatory variables included in models of blue crab density (number per meter-squared). Explanatory data were collected at trapping locations or remotely recorded in San Antonio Bay, on the Guadalupe River, or at Aransas National Wildlife Refuge. Model analyses were performed separately for crabs 1-10 mm, 11-30 mm, 31-50 mm, and 51-130 mm.

Effect	Variable	Description of data
Bottom substrate	bsub	Bottom substrate (mud, clay, or shell) at trapping location.
Structure type	stype	Structure type (none, SAV, algae, SAV/algae) within water column at trapping location.
Structural complexity	scomp	Structural complexity (none, low, medium, high) within water column at trapping location.
Distance to ESV	dist	Shortest distance (m) from trapping location to ESV along pond or bay edge.
Dominant ESV	dom	Dominant ESV (*Spartina alterniflora*, *Batis maritima*, *Distichlis spicata*, mixed high-marsh vegetation, or other) along nearest pond or bay edge.
Presence of water	wpres	Presence or absence (0 or 1) of water at trapping location.
Water depth	wdm	Mean ([maximum + minimum]/2) water depth (cm) at trapping location.
	wlm*x*[1]	Mean water level (m above reference datum) during preceding *x*=1, 7, 14, 21, or 28 d.
Water depth variability	wlv*x*[1]	Water level variability ([maximum-minimum]/mean) during preceding *x*=1, 7, 14, 21, or 28 d.
Water temperature	wts	Surface water temperature (°C) at trapping location.
	wtm*x*[2]	Mean water temperature (°C) during preceding *x*=1, 7, 14, 21, or 28 d.
	wt15*x*[2] wt20*x*[2]	Mean water temperature during preceding *x*=1, 7, 14, 21, or 28 d, noted as above or below (0 or 1) the lower threshold of optimal water temperature (15°C or 20°C).

Table 3-2 continued.

Effect	Variable	Description of data
Water salinity	sal	Water salinity (ppt) at trapping location.
	sm$x$[2]	Mean daily salinity (ppt) during preceding x=1, 7, 14, 21, or 28 d.
	rdm$x$[3]	Mean daily river discharge (cu ft per sec) during preceding x=1, 7, 14, 21, or 28 d; represents inverse effect of water salinity.
	px[4]	Total precipitation (cm) during preceding x=1, 7, 14, 21, or 28 d.
Water turbidity	ws$x$[1]	Mean daily wind speed (km per hr) during preceding x=1, 7, 14, 21, or 28 d; positively relates to water turbidity.
	wg$x$[1]	Mean daily speed (km per hr) of wind gusts during preceding x =1, 7, 14, 21, or 28 d; positively relates to water turbidity.
Recruitment abundance	meg[5] juv[5]	Relative abundance of crabs during the period of terminal megalopal settlement or post-metamorphosis to the juvenile life-stage.
Habitat type	habitat	Habitat type (bay, connected pond, unconnected pond) at trapping location; the full range of original habitat categories (bay, connected open water, connected pond edge, unconnected open water, unconnected pond edge) was also considered by omitting the effect of distance to ESV.

[1] Water and meteorological monitoring station 031 (Seadrift), Division of Nearshore Research, Texas A&M, Corpus Christi.

[2] Water and meteorological monitoring station 127 (GBRA#2), Division of Nearshore Research, Texas A&M, Corpus Christi.

[3] National Water Information System station 08188800 (Guadalupe River near Tivoli), U.S. Geological Survey.

[4] Aransas National Wildlife Refuge weather station, National Weather Service, National Oceanic and Atmospheric Administration.

[5] Empirical data from intensive study of megalopal settlement and juvenile recruitment patterns (see Chapter II).

density was explained by one or more fixed effects and a random G-side effect (study site). Models were examined for each of four size groups of crabs (1-10 mm, 11-30 mm, 31-50 mm, 51-130 mm) using the GLIMMIX procedure (2006) in SAS (version 9.1.3). Correlations of residual error (R-side random effects) resulting from repeated measures of the response were not accounted for due to the unbalanced nature of the data.

As is common in studies with count data, distributions of the response variables were non-normal (heavily right-skewed) and zero-inflated. The Poisson distribution with canonical link function (log) was assumed appropriate for the response data, but some problems with overdispersion caused by excess zeros were evident. To minimize overdispersion, a value of one was added to each observed response. The expected conditional mean response then took the form:

$$g(\mathrm{E}[(\mathrm{Y} + 1)|\mathrm{u}]) = \mathrm{X}\beta + \mathrm{Zu} + \mathrm{e}$$

where

g is the link function (in this case, natural log),

X is the matrix of constants determined by fixed effects (covariates),

β is the matrix of fixed effect parameters,

Z is the matrix of constants determined by random G-side effects,

u is the matrix of random model effects, and

e represents residual errors, which in this model are not correlated.

Full models, or those incorporated into model-building procedures, contained all 14 effects identified a priori but only one variable per effect, because variables representing the same effect were presumed correlated. The only exception was bivariate water temperature, which was included in an interaction with the continuous form of water temperature. Numerous other two- and three-way interactions were also included in full models and were based on a priori hypotheses (see above). In total, I examined 40-50 full models of blue crab density for each size group.

I used a manual stepwise selection procedure to identify the most important predictive variables of crab density. Decisions to remove or keep variables in each model were based on model fit and cautiously guided by changes in Pseudo-AICc values (Akaike 1973; Burnham and Anderson 2002). Caution was heeded because likelihoods (and subsequently AICc values) associated with GLMMs are derived using a doubly iterative model-fitting process and based on pseudo-data, not original data (Littell et al. 2006: 752-75; SAS 2006:151,163). Model dispersion ($\hat{c} = \chi^2/\text{df}$) was an important indicator of model fit. Values of $\hat{c} = 1$ were considered optimal (good model fit), whereas $1 < \hat{c} \leq 4$ indicated slight overdispersion with adequate model structure and $\hat{c} > 4$ indicated poor model structure (inadequate fit; Burnham and Anderson 2002: 67-69). The best fitting model of crab density for each crab size group, along with the hierarchical sub-models of each, were compiled for comparison.

Results

Data Collection

I collected samples for 17 of the 18 months during October 2004-March 2006. Of the 913 total samples collected, 153 samples were from bay habitat (*n*=60 (PC), 62 (PL), 31 (BJ)), 178 were from COW (*n*=54 (BR), 62 (PC), 62 (PL)), 177 were from CPE (*n*=52 (BR), 62 (PC), 63 (PL)), 203 were from UOW (*n*=51 (BR), 55 (PC), 58 (PL), 39 (BJ)), and 202 were from UPE (*n*=51 (BR), 55 (PC), 57 (PL), 39 (BJ)). The relationship between crab size and biomass was quantified by measuring 230 crabs of varying sizes (2.7-125.5 mm) from 100 samples. The resulting regression equation was used to predict the biomass of over 1,600 other crabs captured during the study (Fig. 3-5).

Environmental Conditions

Precipitation was well above normal during October 2004-March 2005 and generally lower than normal thereafter (April 2005-March 2006; Fig. 3-6). The effect of this pattern was evident in several aspects of the environment. Freshwater discharge from the Guadalupe River was greater than normal during October 2004-October 2005 but much less than normal thereafter (Fig. 3-7). Salinity measured at trapping locations and in San Antonio Bay was markedly lower early than late in the study (Fig. 3-8). Mean water depth at trapping locations and primary water level in San Antonio Bay were noticeably higher during the first than second half of the study (Fig. 3-9). Correspondingly, the marsh was more completely inundated early than late in the study (Fig. 3-10). Finally, though structural complexity within the water column was generally highest during summer, an overall decrease in complexity and increase in algal contribution was noticeable during the study (Fig. 3-11).

Marsh attributes remaining consistent throughout the study included bottom substrate and dominant edge ESV. Substrate was predominantly mud or sand in all habitats, but debris and algal mattes were found more often in pond edge than open

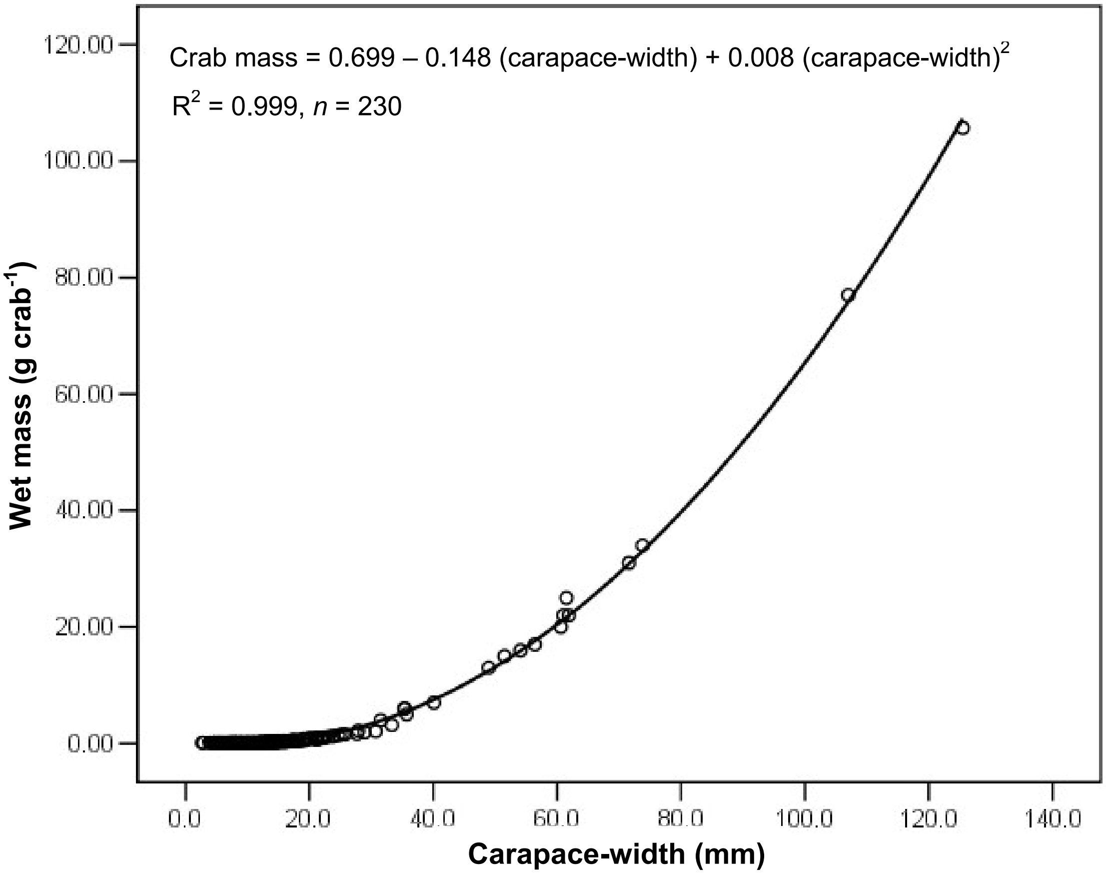

Fig. 3-5. Regression equation quantifying the relationship between individual blue crab size (carapace-width) and wet mass. A subset (n=100) of the total 913 crab-trap samples collected was used to measure 230 crabs of varying sizes (2.7-125.5 mm).

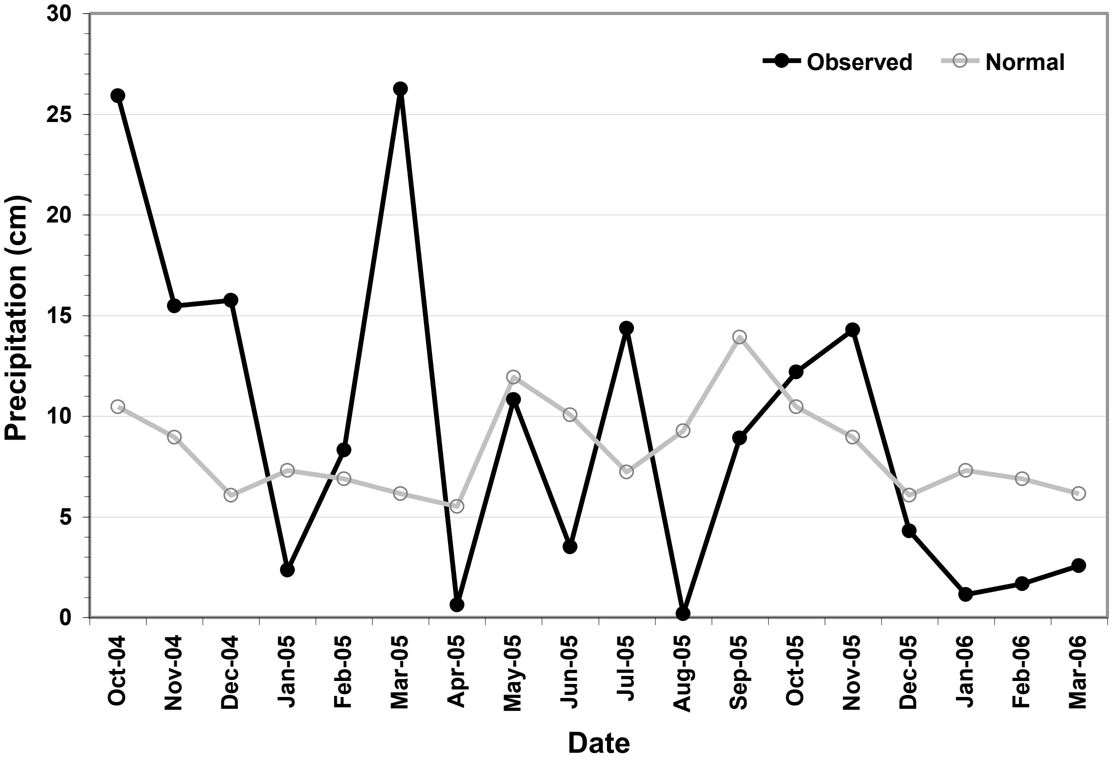

Fig. 3-6. Monthly precipitation observed during October 2004-March 2006 versus normal levels observed during 1971-2000 at Aransas National Wildlife Refuge, Texas (National Weather Service monitoring program, National Oceanic and Atmospheric Administration).

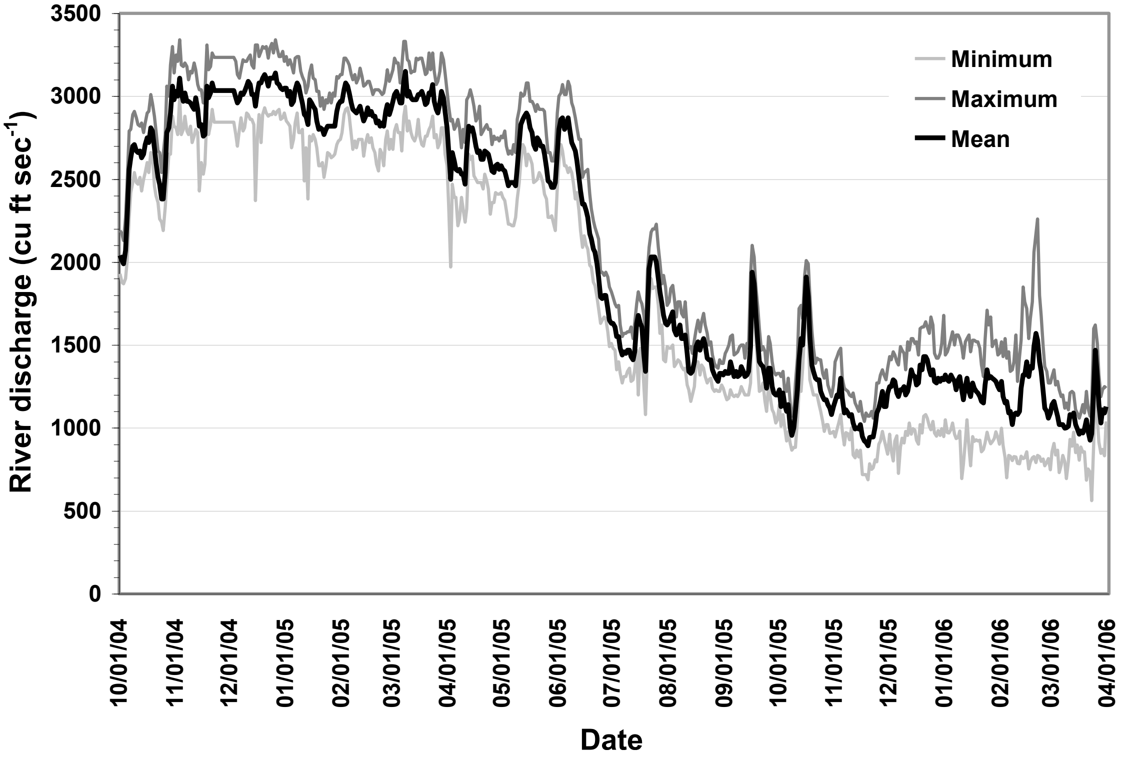

Fig. 3-7. River discharge recorded during October 2004-March 2006 on the Guadalupe River near Tivoli, Texas (station 08188800) by the U.S. Geological Survey.

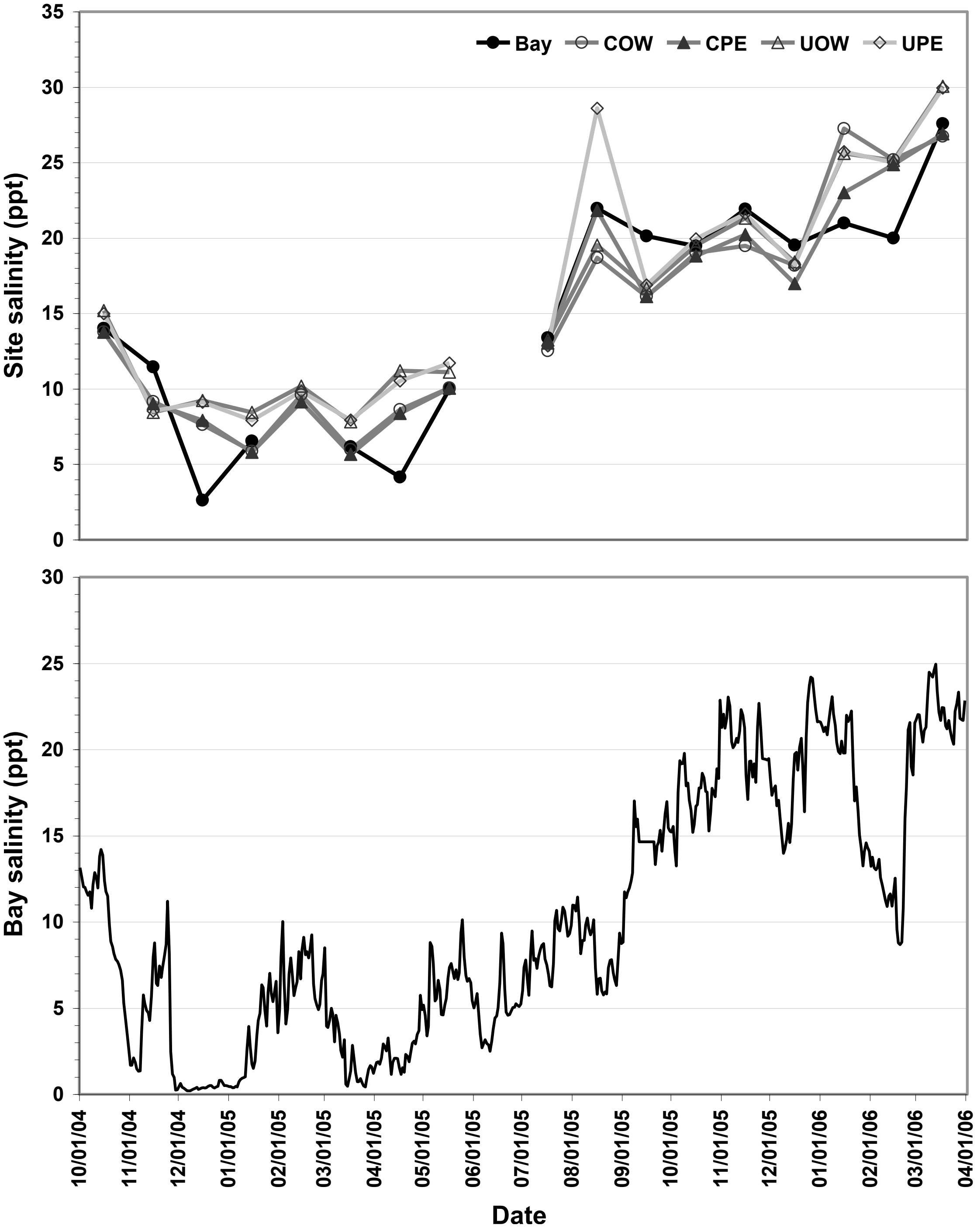

Fig. 3-8. Mean water salinity at trapping locations in five study habitats (top) and in San Antonio Bay (bottom) during October 2004-March 2006. Study habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE).

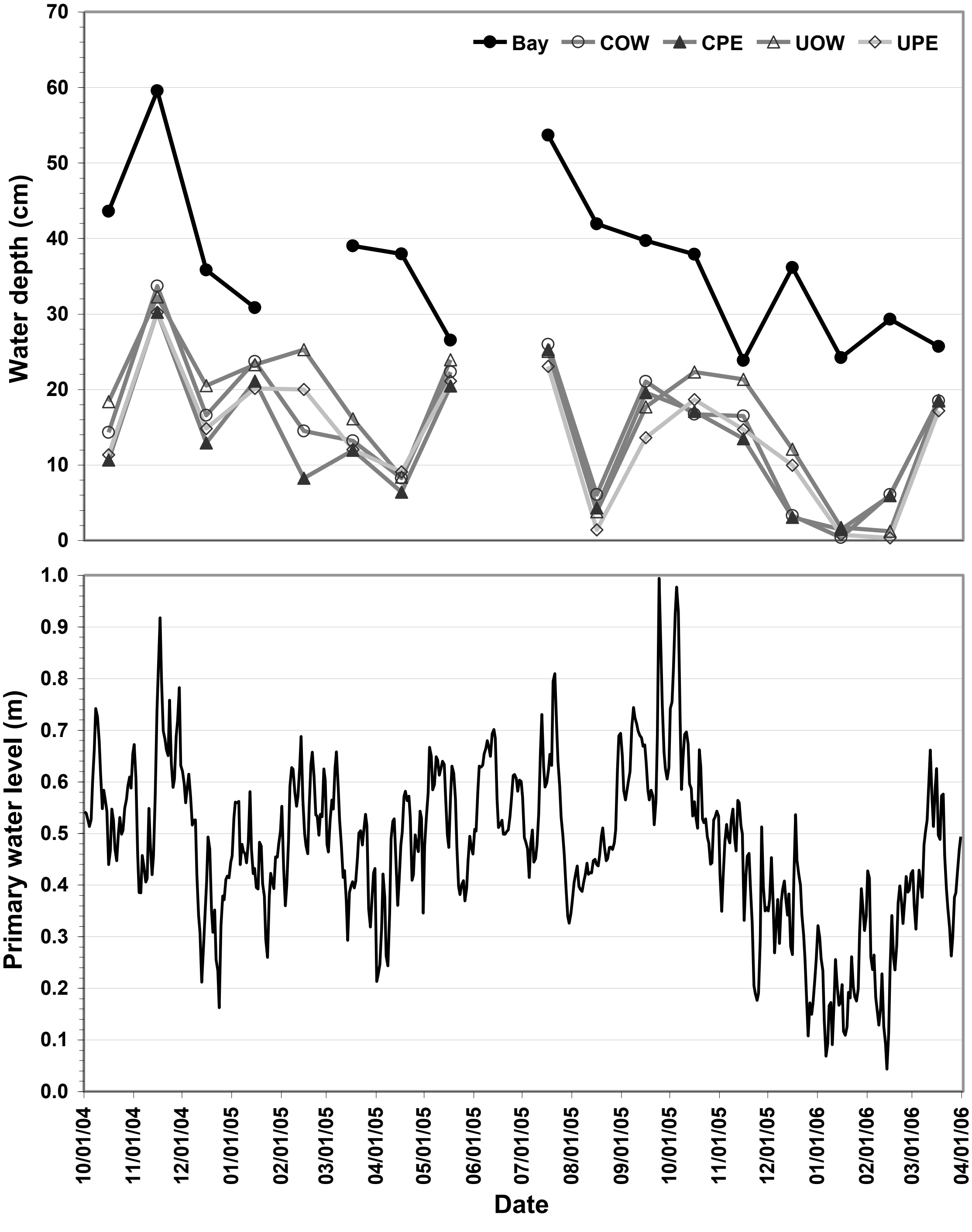

Fig. 3-9. Mean water depth at trapping locations in five habitats (top) and primary water level in San Antonio Bay (bottom) during October 2004-March 2006. Study habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE).

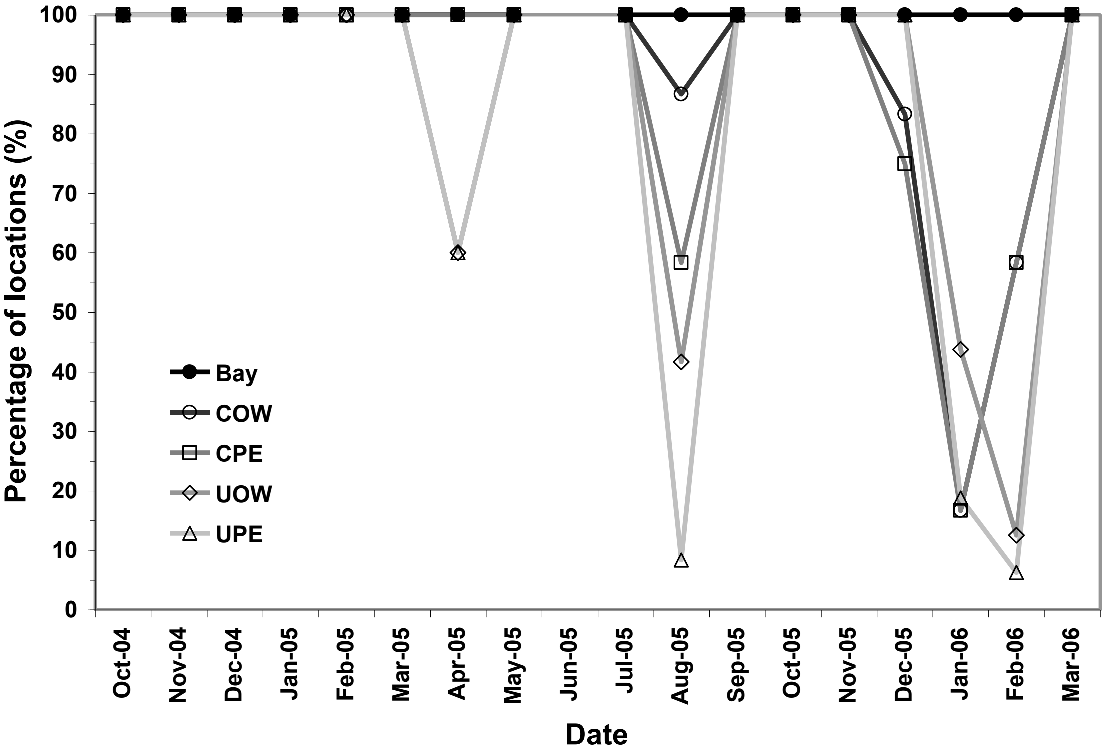

Fig. 3-10. Percentage of trapping locations inundated (with standing water) in each of five study habitats during October 2004-March 2006. Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE).

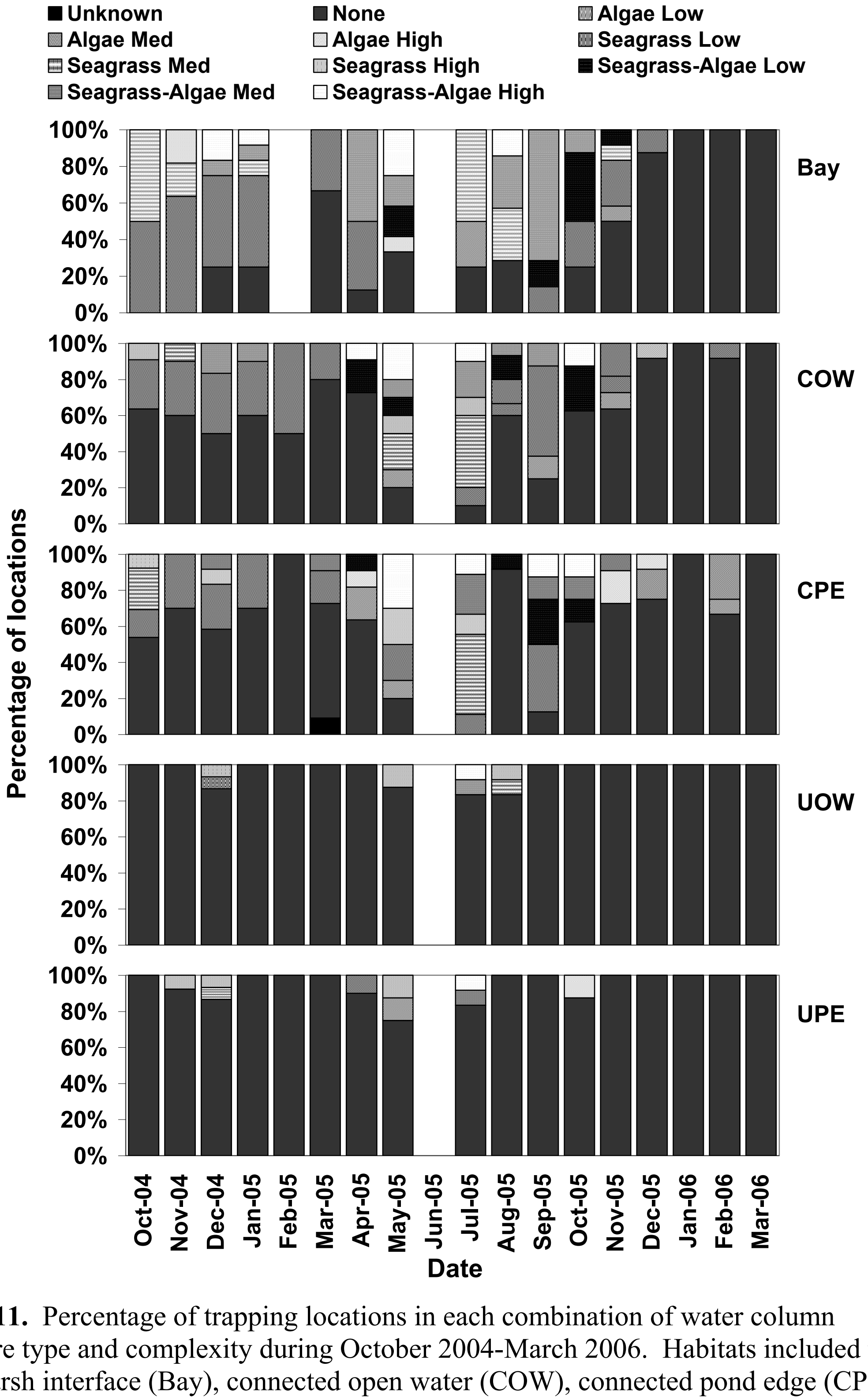

Fig. 3-11. Percentage of trapping locations in each combination of water column structure type and complexity during October 2004-March 2006. Habitats included the bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE).

water habitats and blocky clay sediment was found only in unconnected ponds (Table 3-3). Differences in dominant edge ESV occurred almost exclusively between the bay and interior salt-marsh. Bay habitat was 97% bounded by *Spartina alterniflora* fringe, whereas ESV adjacent to connected and unconnected ponds comprised primarily mixed high-marsh vegetation (51-81%), *Distichlis spicata* (12-28%), *Spartina alterniflora* (5-18%), and *Batis maritima* (<6%).

Fine Spatial Scale Estimates of Crab Density and Biomass

Averaged across monthly sampling periods, overall densities of blue crabs differed markedly between bay and interior-marsh habitats (Fig. 3-12). Densities in the interior-marsh appeared similar, but density in bay habitat was about ten times that of any interior-marsh habitat. Among study sites, patterns in crab density across habitats were similar and mirrored the pattern observed overall (Fig. 3-13). The only minor divergence was that interior-marsh densities were noticeably lower at PL and BJ than BR and PC. In contrast to crab density, overall estimates of crab biomass were consistent across habitats (Fig. 3-12), and inter-habitat patterns were highly variable among study sites (Fig. 3-14). At both BR and BJ, biomass was generally higher in edge than open water pond habitats. Biomass at PC was higher in unconnected than connected ponds, and biomass at PL was higher in open water than edge habitats.

Mean crab size explained the disparity between patterns in overall density and biomass across habitats. Density was highest in bay habitat though biomasses were

Table 3-3. Percentage of sampled area in each bottom substrate category for habitats studied during October 2004-March 2006. Habitats included the bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE) habitats.

	Habitat				
Substrate	Bay	COW	CPE	UOW	UPE
Mud or sand	97.53	95.11	89.83	89.16	83.66
Mud or sand with debris	1.23	4.35	9.04	3.45	6.44
Mud or sand with debris and/or algae	0.00	0.54	1.13	0.00	0.00
Blocky clay	0.00	0.00	0.00	0.00	0.50
Blocky clay with algae	0.00	0.00	0.00	7.39	8.42
Blocky clay with algae and/or debris	0.00	0.00	0.00	0.00	0.99
Shell or oyster	1.23	0.00	0.00	0.00	0.00

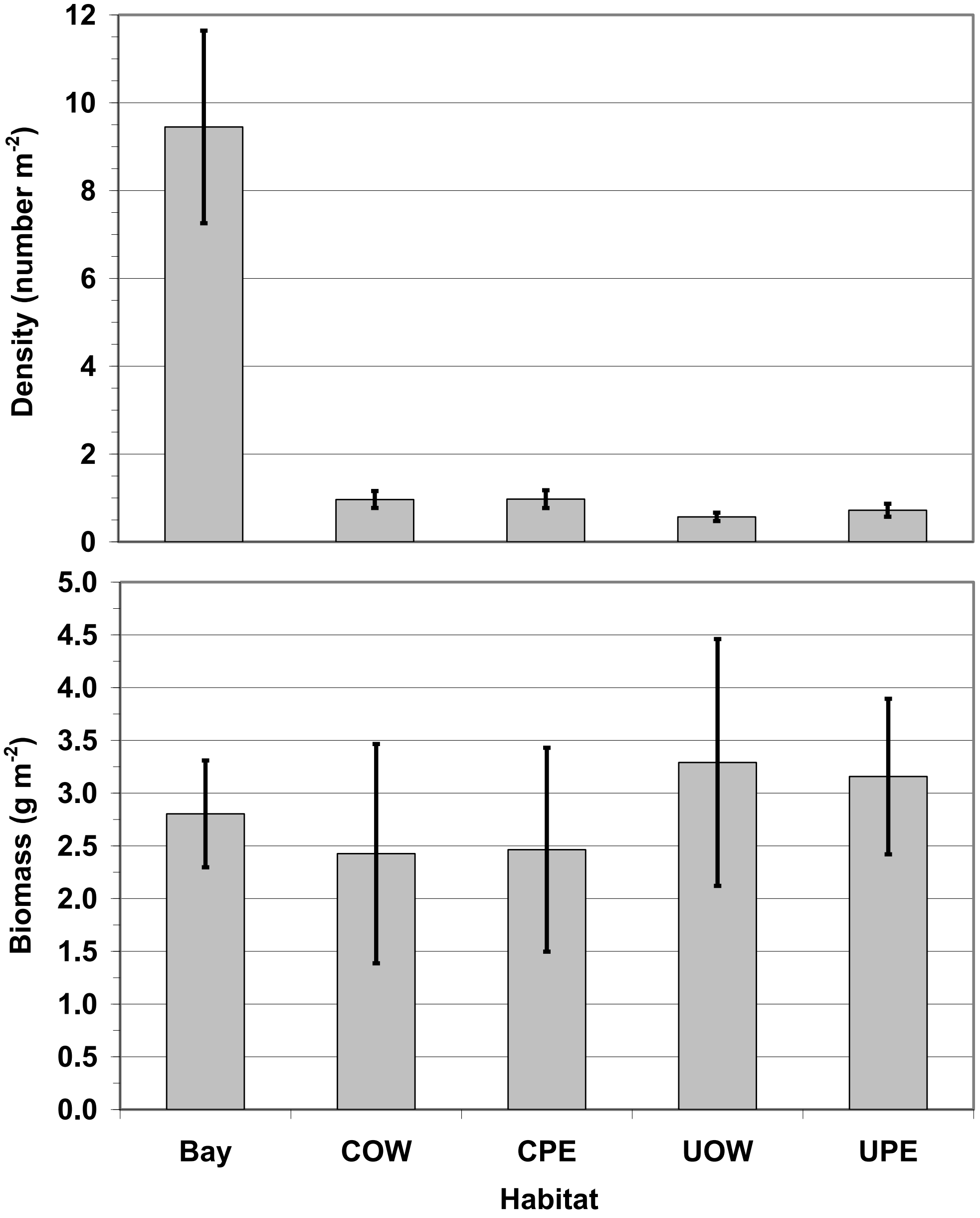

Fig. 3-12. Mean blue crab density (number per meter-squared; top) and biomass (g per meter-squared; bottom) by habitat during October 2004-March 2006 (all study sites and months combined). Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE).

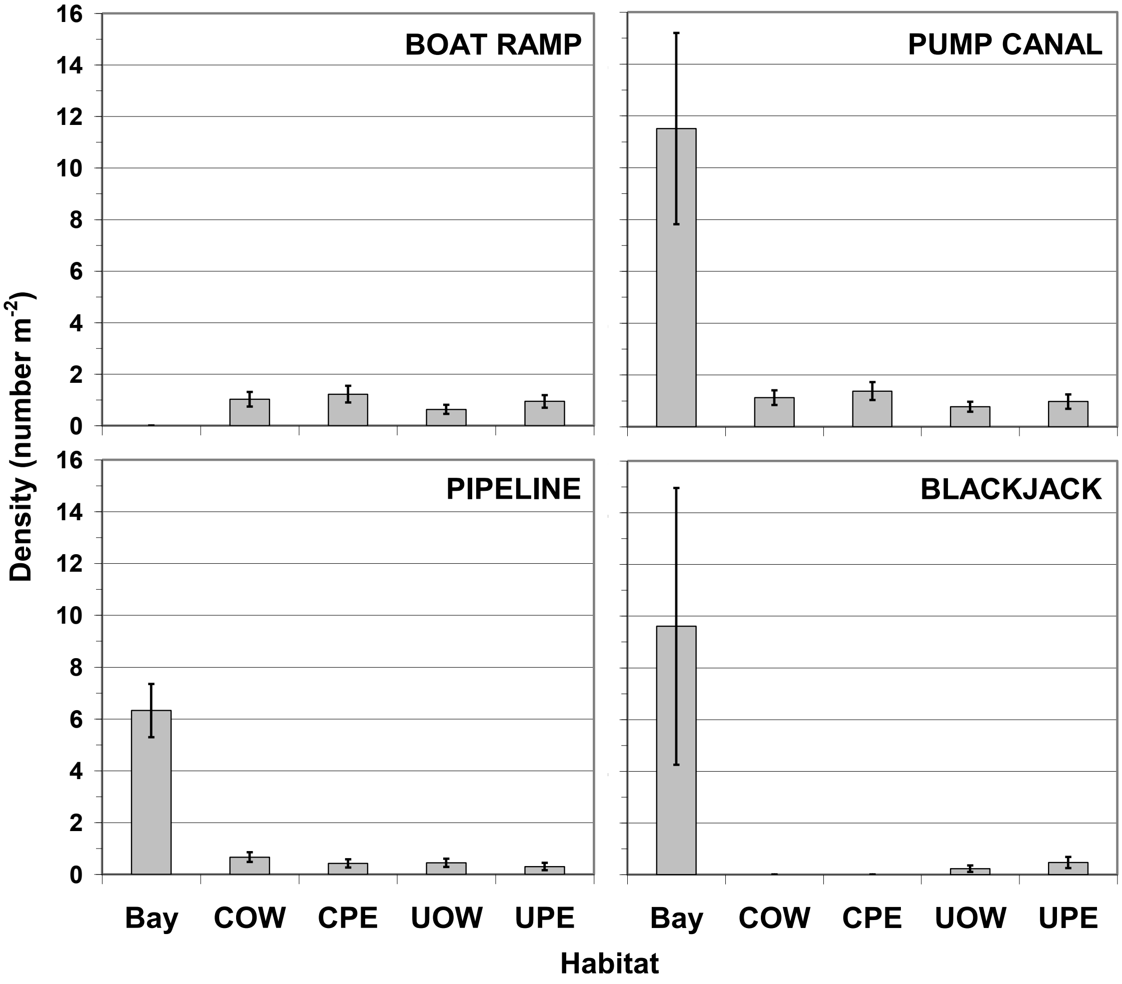

Fig. 3-13. Mean blue crab density (number per meter-squared) by habitat and study site, averaged over all months sampled during October 2004-March 2006. Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE). Bay habitat and connected ponds were absent from BR and BJ, respectively.

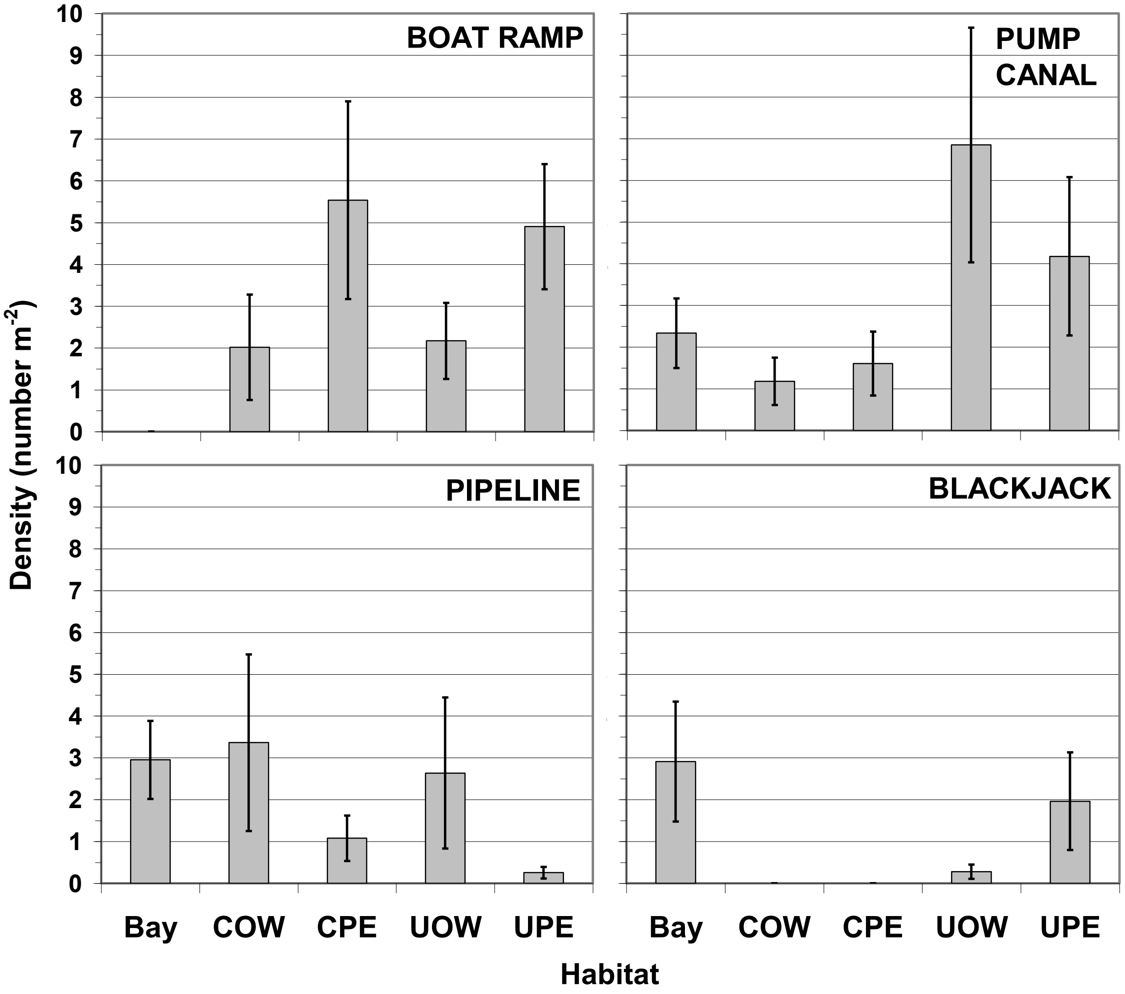

Fig. 3-14. Mean blue crab biomass (g per meter-squared) by habitat and study site, averaged over all months sampled during October 2004-March 2006. Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE). Bay habitat and connected ponds were absent from BR and BJ, respectively.

similar among habitats, because interior-marsh habitats generally comprised fewer but larger crabs than shallow bay (Fig. 3-15). This held true at all study sites (Fig. 3-16).

Comparisons of crab densities among size-classes reaffirmed the size discrepancy between bay and interior-marsh (Fig. 3-17). Size-class distributions were highly right-skewed in all habitats, but skewness was more pronounced in bay than any other habitat. In bay habitat, nearly all crabs were ≤30 mm in size, and density per size-class was highest for crabs in the smallest class (1-10 mm). In all interior-marsh habitats, crab densities were highest in the second smallest size-class (11-20 mm). Also, crabs in the interior-marsh were distributed throughout the full range of sizes (1-130 mm) in open water habitats and up to 90 mm in pond edge habitats.

Distributions of biomasses among size-classes were strikingly different than those of density (Fig. 3-18). In bay habitat, the distribution of biomasses was only slightly right-skewed. Distributions in pond edge habitats were nearly normal and in open water habitats were skewed to the left. Not surprisingly, crab size at maximum contribution to biomass differed by habitat. Crabs contributing greatest to biomass (range of sizes encompassing all biomass estimates ≥75th percentile) were of smallest size (11-30 mm) in bay habitat, slightly larger (31-80 mm) in interior pond edge habitats, and largest (41-130 mm) in interior open water habitats.

Crab density was generally highest in fall in bay habitat and in both spring and fall in interior-marsh habitats (Fig. 3-19). Densities in fall 2004 were lower than those of fall 2005, but subsequent densities in winter 2004-2005 were substantially higher than in winter 2005-2006. Biomass followed similar temporal patterns, except that an

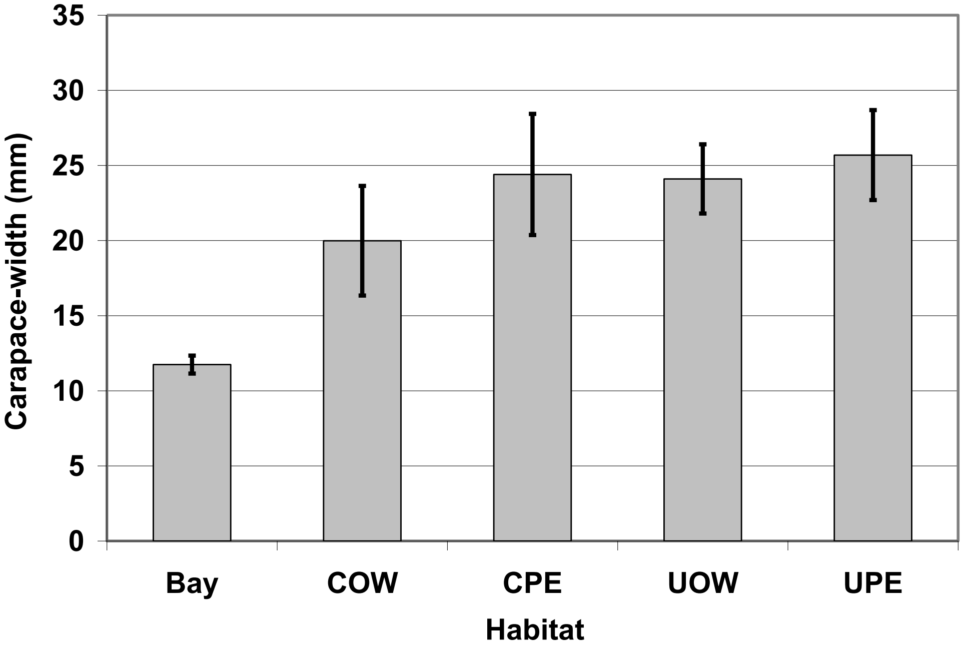

Fig. 3-15. Mean blue crab size (carapace-width) by habitat, averaged over all study sites and months sampled during October 2004-March 2006. Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE).

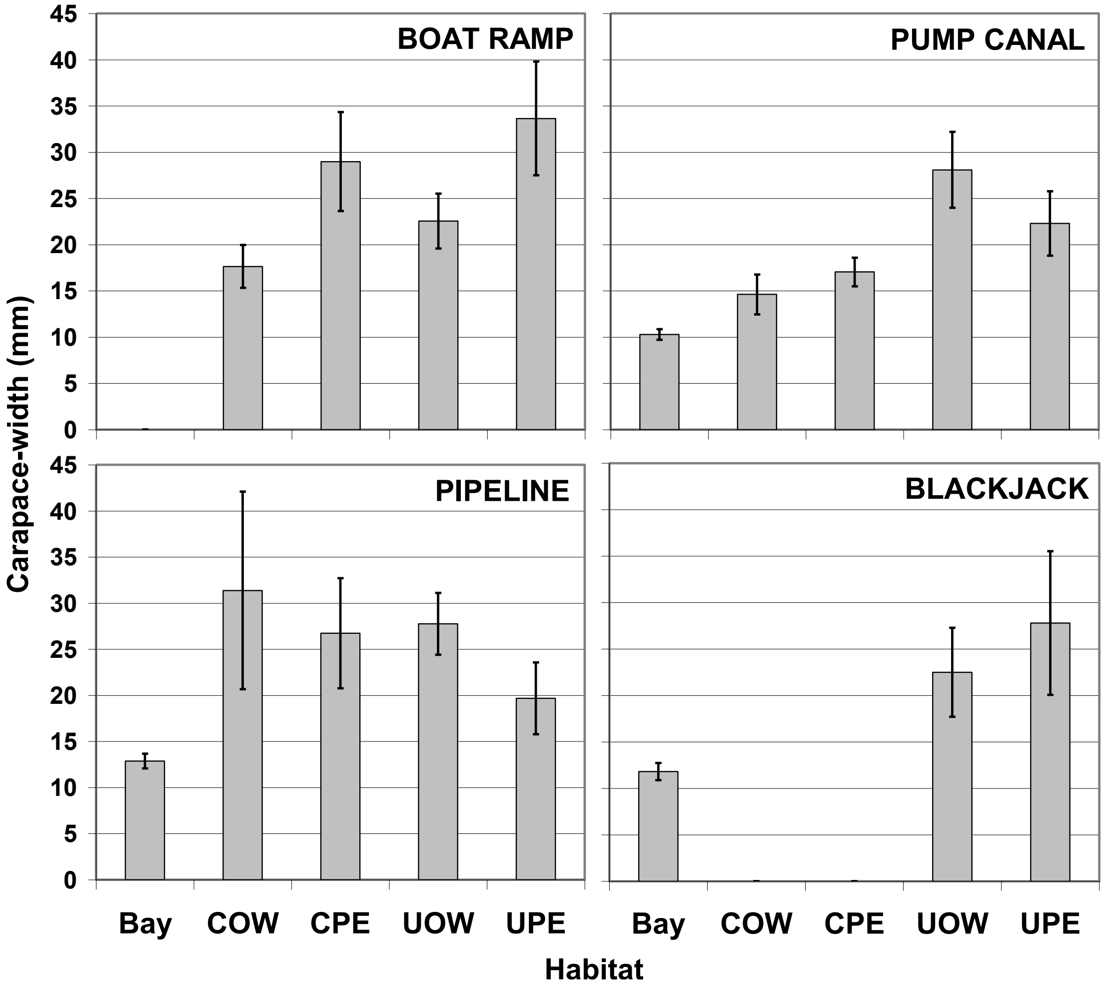

Fig. 3-16. Mean blue crab size (carapace-width) by habitat and study site for all months (October 2004-March 2006) combined. Habitats included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE). Bay habitat and connected ponds were absent from BR and BJ, respectively.

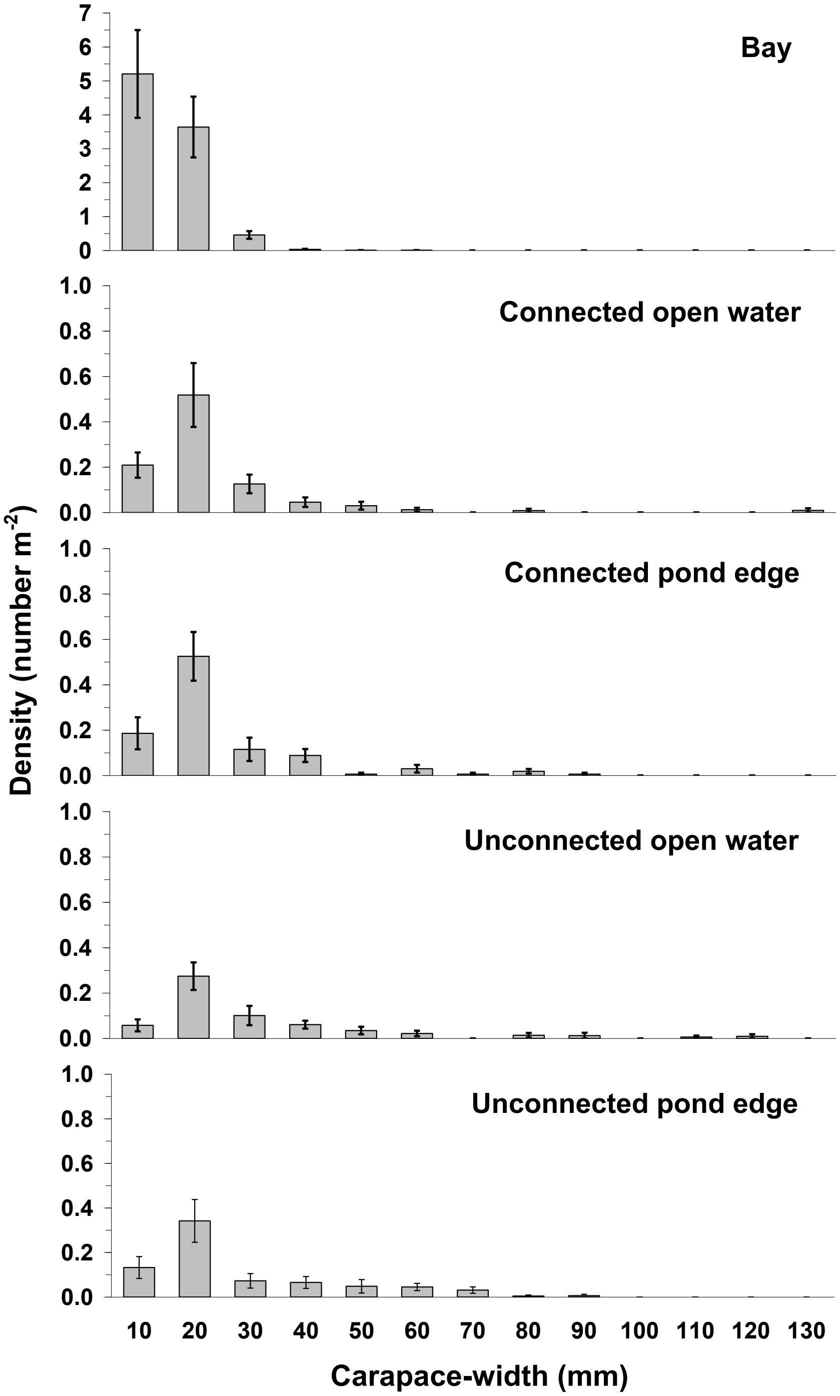

Fig. 3-17. Mean density (number per meter-squared) of blue crabs by carapace-width for each habitat sampled during October 2004-March 2006 (all months combined). Upper bounds of 10-mm size classes are listed on the x-axis. Notice the difference in y-axis scale between the bay and remaining habitats. Error bars represent variability in densities among months (±1 SE).

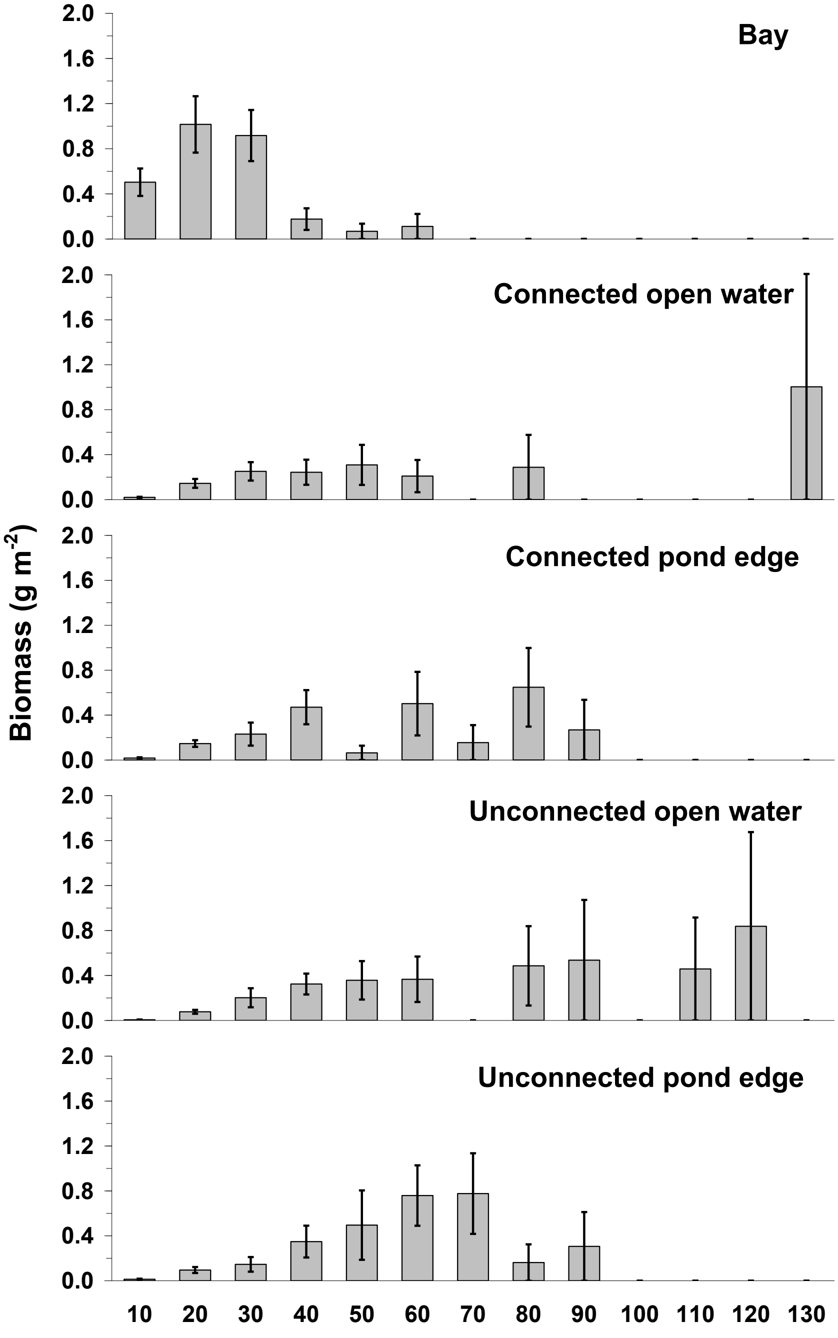

Fig. 3-18. Mean biomass (g per meter-squared) of blue crabs by carapace-width for each habitat sampled during October 2004-March 2006 (all months combined). Upper bounds of 10-mm size classes are listed on the x-axis. Error bars represent variability in densities among months (±1 SE).

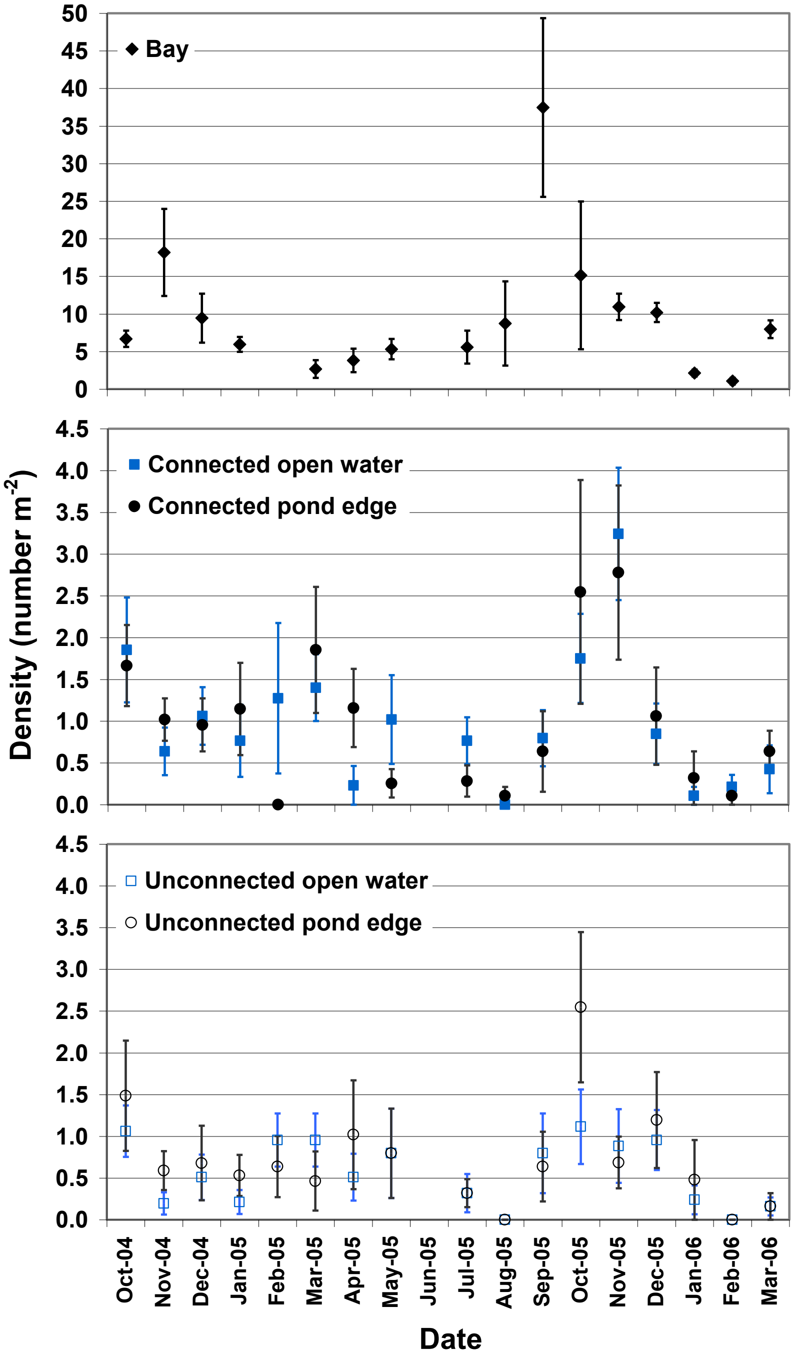

Fig. 3-19. Temporal patterns in blue crab density (number per meter-squared) by habitat during October 2004-March 2006. Habitats included bay (top), connected open water and pond edge (middle), and unconnected open water and pond edge (bottom). Error bars represent variability in densities among sites (±1 SE).

additional peak was observed in bay habitat in spring (Fig. 3-20). Mean size in bay habitat was consistent throughout the study, whereas mean sizes in interior-marsh habitats were extremely variable and lowest when low temperatures coincided with low water levels (e.g., December 2005-February 2006; Fig. 3-21). Moreover, mean size was highest when high temperatures coincided with low water levels (e.g., August 2005).

Examination of crab densities in each of the three size categories relevant to foraging cranes revealed that small crabs were always more abundant than medium and large crabs and medium crab abundance was similar to or only slightly greater than large crabs throughout winter (Fig. 3-22). While small crab density was consistent across winter 2004-2005 in connected and unconnected ponds, the significantly higher densities of bay habitat showed a marked decline from November to March. Small crab density during winter 2005-2006 was distinctly highest in November-December and lowest in January-February, with replenishment to bay habitat evident in March. Medium and large crabs were abundant in the marsh during November-December of both winters but entirely absent from the marsh in January-February 2005 and January-March 2006. Replenishment of medium and large crabs to the marsh was evident in March of 2005 but not 2006.

Large Spatial Scale Estimates of Total Crab Number and Standing Stock Biomass

Examination of the total number and standing stock of blue crabs at the spatial resolution of the shallow estuarine complex (salt-marsh plus 50-m-wide strip of adjacent bay) revealed 9,646 individuals ha^{-1} and 11,580 g ha^{-1} when averaged across sites and

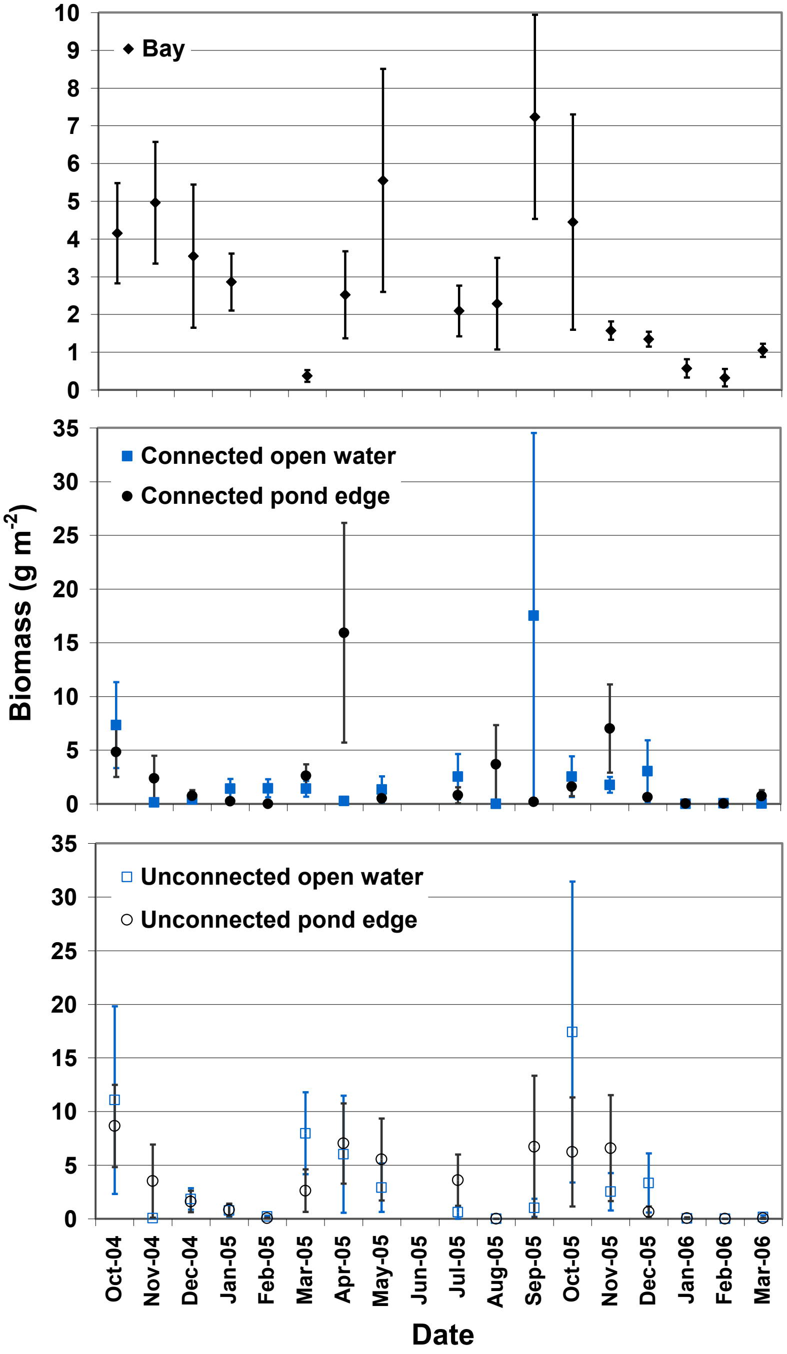

Fig. 3-20. Temporal patterns in blue crab biomass (g per meter-squared) by habitat during October 2004-March 2006. Habitats included bay (top), connected open water and pond edge (middle), and unconnected open water and pond edge (bottom). Error bars represent variability in densities among sites (±1 SE).

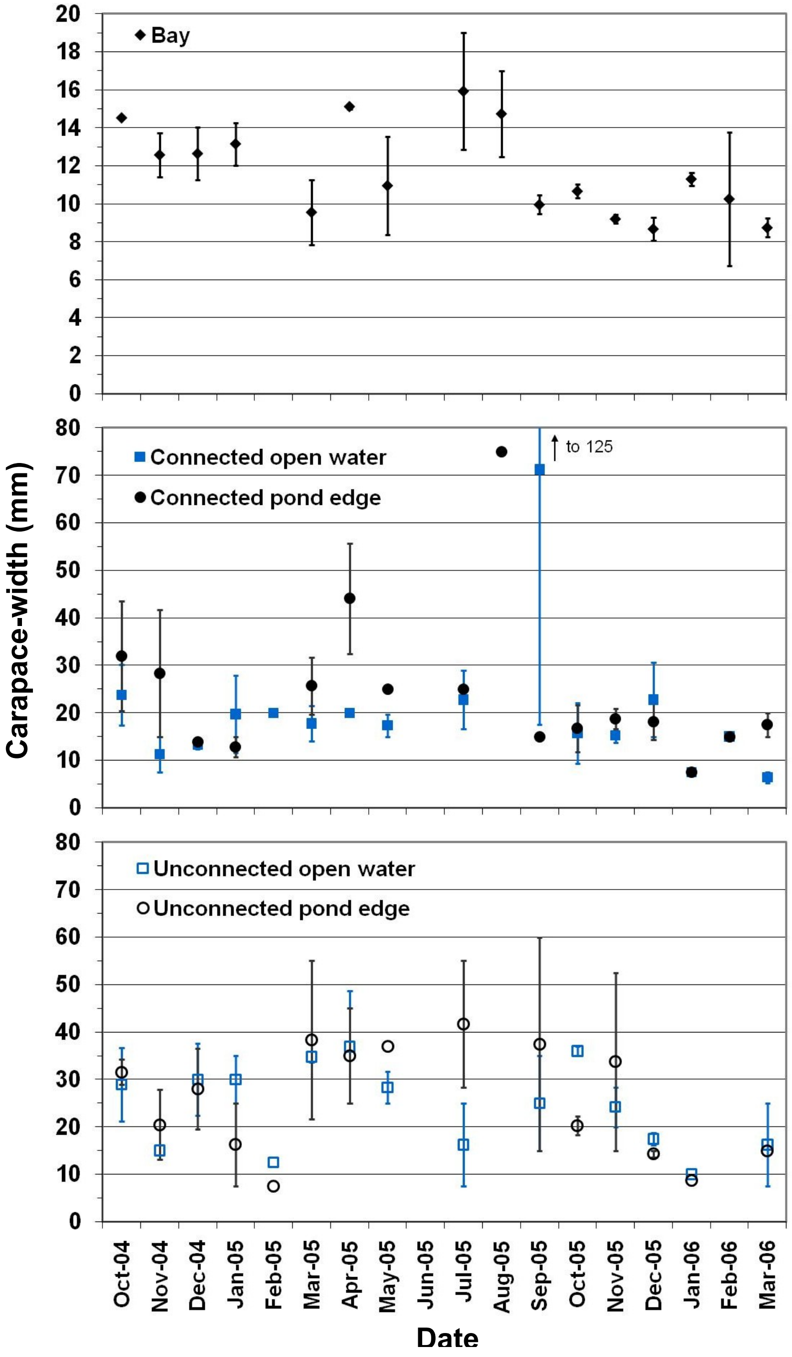

Fig. 3-21. Temporal patterns in mean blue crab size (carapace-width) by habitat during October 2004-March 2006. Habitats included bay (top), connected open water and pond edge (middle), and unconnected open water and pond edge (bottom). Error bars represent variability in mean crab sizes among sites (±1 SE).

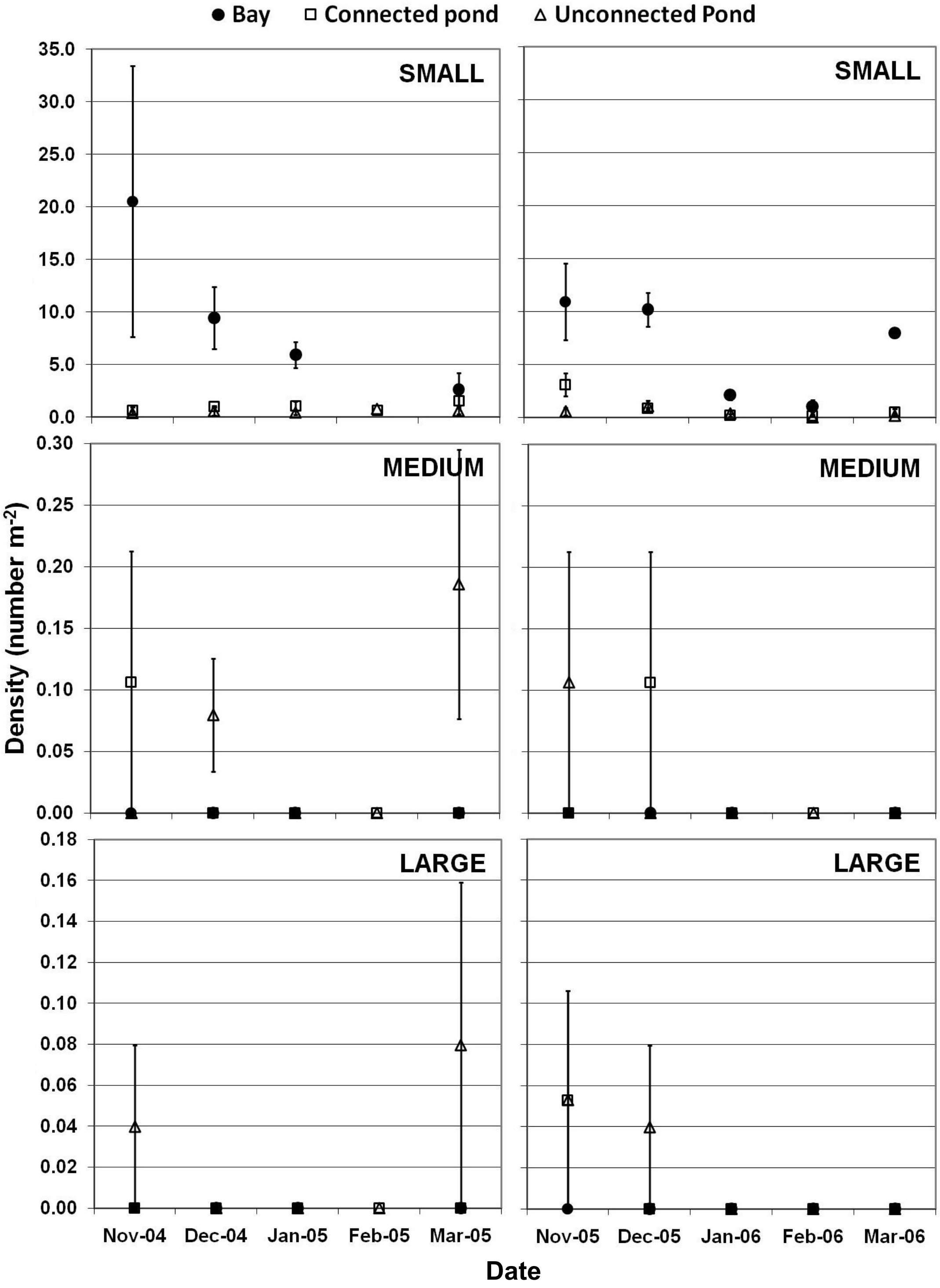

Fig. 3-22. Temporal patterns in blue crab density (number per meter-squared) by habitat for each of three size categories (small, medium, large) of crabs during winters 2004-2005 (left) and 2005-2006 (right). Error bars represent variability among sites (±1 SE).

sampling periods. Bay habitat (6,890 ± 1,604 crabs ha^{-1}) contributed more to the total number of blue crabs than any other habitat, but connected open water (2,319 ± 524 crabs ha^{-1}) held the second largest total number, which was greater than any other interior-marsh habitat (≤225 crabs ha^{-1}). Examining the total number of blue crabs per study site revealed that numbers were highest in bay habitat at all study sites except BR, where adjacent shallow bay was absent (Fig. 3-23). In addition, at PL only, the number of crabs in connected open water closely followed that estimated for bay habitat. Across monthly sampling periods, the percent contribution of bay habitat to total crab number ranged from 38% to >99%, with the highest levels of contribution occurring when water levels were lowest (i.e., other habitats were least available) and highest (i.e., juvenile recruitment was greatest; Fig. 3-24).

Contribution to standing stock was greater for connected open water (8,130 ± 1,604 g ha^{-1}) than any other habitat (≤1,981 g ha^{-1}), reflecting both its large proportional area in the marsh and the large average size of inhabiting crabs. Per study site, standing stock was pronounced in connected open water at BR and PL but was generally quite low at PC and BJ, where connected open water habitat comprised only 0-2% of site area (Fig. 3-23). Percent contribution of connected open water habitat to standing stock fluctuated greatly throughout the study (<1% to 92%) without a clear pattern (Fig. 3-24).

Averaged across study sites (or crane territories), the total numbers of small, medium, and large crabs potentially available to whooping cranes differed somewhat between winters (Fig. 3-25). Small and medium crabs were noticeably less and more abundant, respectively, in November 2004 than 2005, and large crabs were abundant in

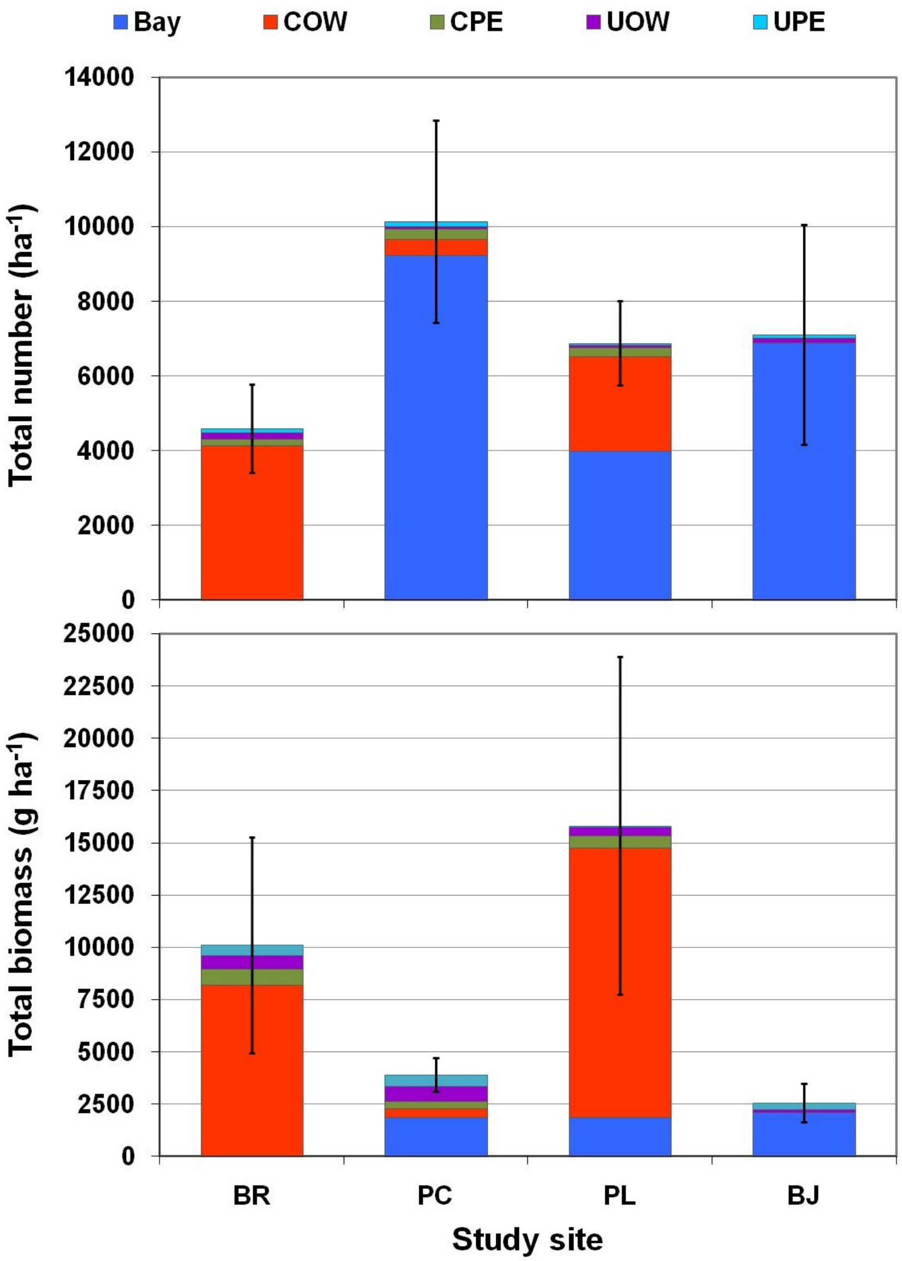

Fig. 3-23. Total number (top) and biomass (bottom) of blue crabs per ha of the shallow estuarine zone sampled in this study by study site for all months (October 2004-March 2006) combined. Habitats contributing to the totals included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability among monthly sampling periods (±1 SE).

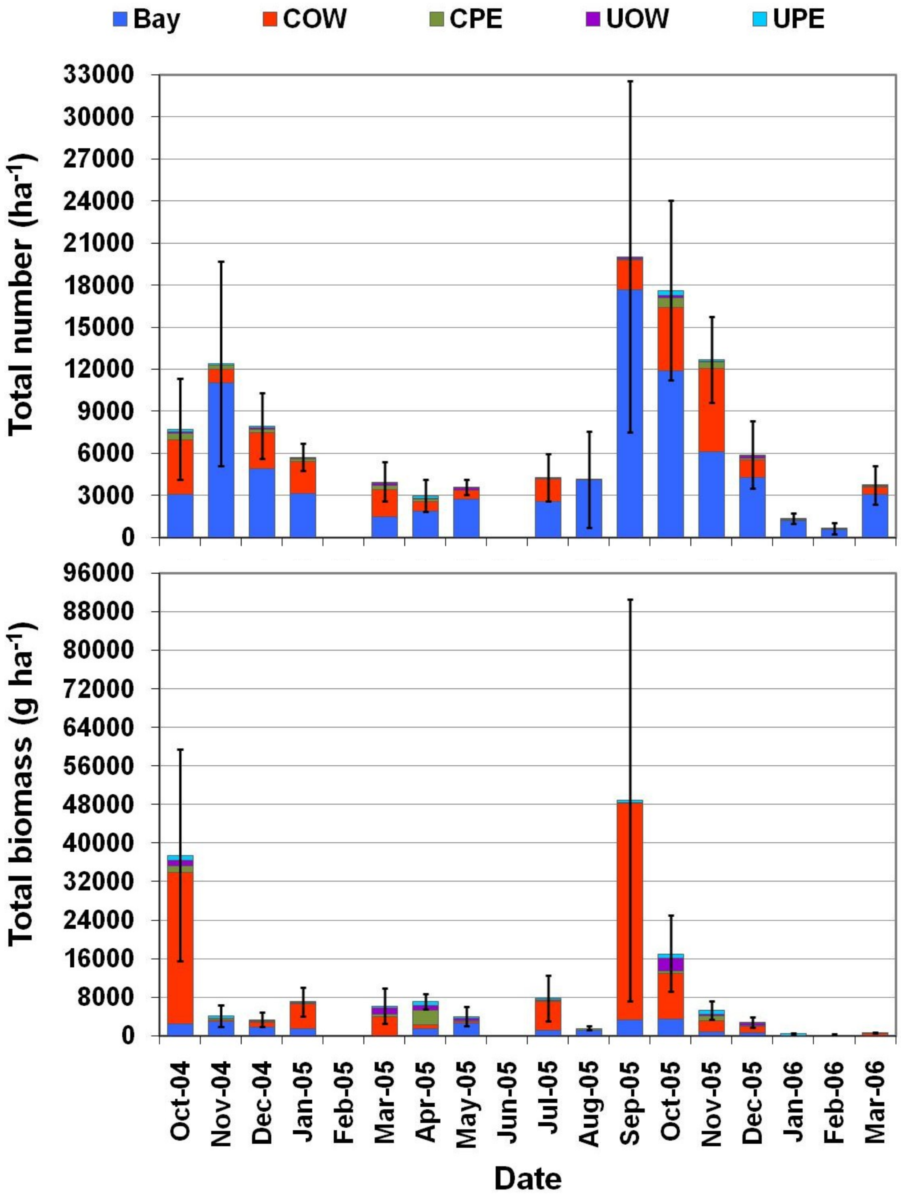

Fig. 3-24. Temporal patterns in total number (top) and biomass (bottom) of blue crabs per ha of shallow estuarine habitat during October 2004-March 2006 for all study sites combined. Habitats contributing to the totals included bay-marsh interface (Bay), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), and unconnected pond edge (UPE). Error bars represent variability in total number or biomass among sites (±1 SE).

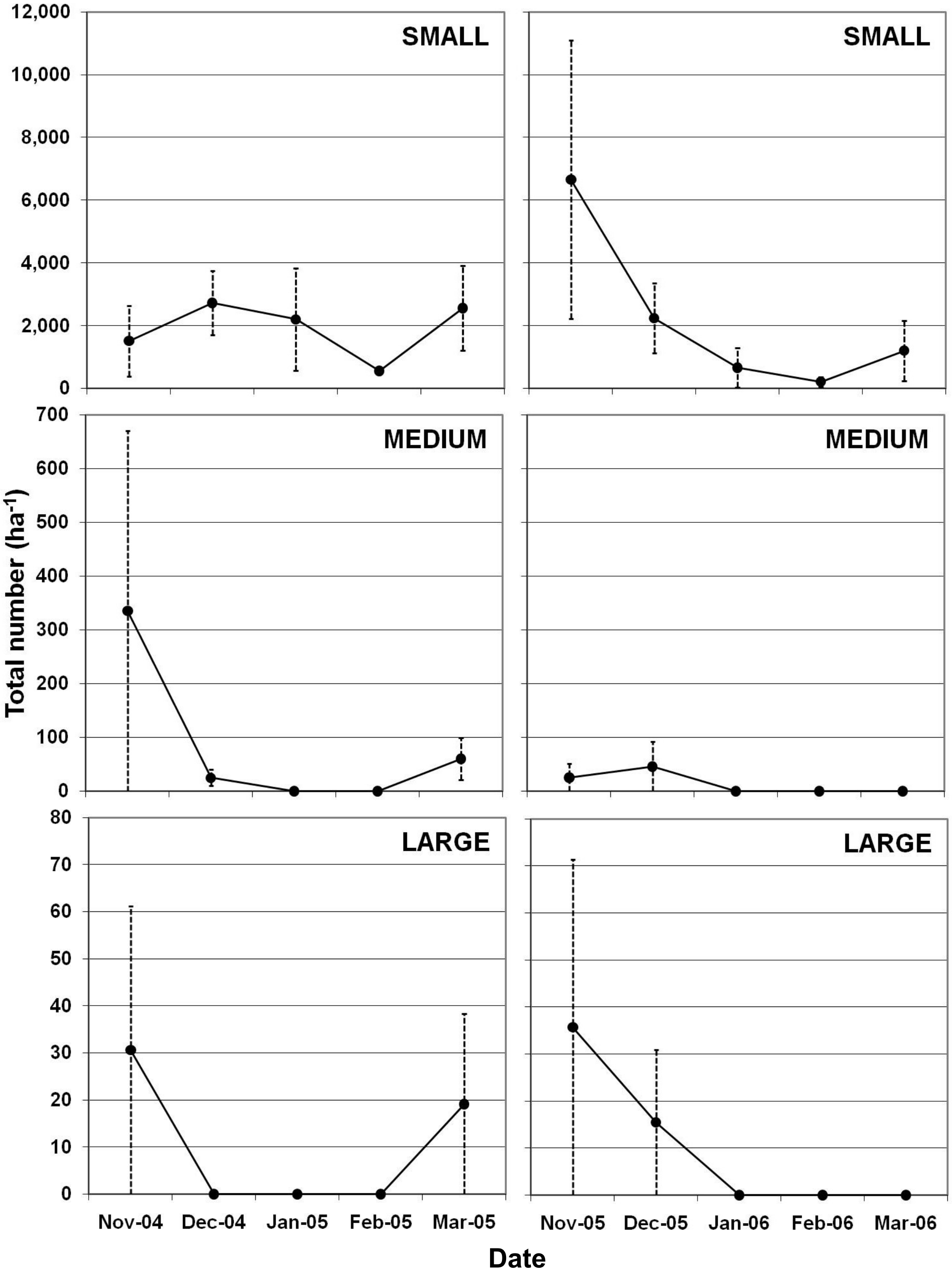

Fig. 3-25. Total number of small, medium and large blue crabs per ha of shallow estuarine habitat during November-March of winters 2004-2005 (left) and 2005-2006 (right), as averaged across study sites. Error bars represent variability among sites (±1 SE).

December 2005 but not 2004. Patterns in total crab number among size categories were consistent with those for crab density, demonstrating small crabs were significantly more abundant than medium and large crabs, and total numbers of medium crabs were either similar to or greater than total large crab numbers. Winter patterns in total crab number at the level of study sites, however, demonstrated some variability in crab abundance across the shallow estuarine complex (Fig. 3-26).

Sources of Variation in Crab Density

Crabs 1-10 mm CW

The best approximating model of density for crabs 1-10 mm CW included the effects of habitat type, water column structure type, and structural complexity at the trapping location, water salinity, water level, water temperature, and wind speed in San Antonio Bay, and interactions between structure type and complexity, water level and wind speed, and water salinity and temperature (Model 7, Table 3-4). The model fit the observed data extraordinarily well, with a dispersion parameter only slightly below one and a linear association of observed and predicted values at nearly 87% (r=0.868). Correlation of observed and predicted values, as averaged across study sites per monthly sampling period, revealed a linear association of about 96% (r=0.959).

The best approximating model, however, was unnecessarily complex, and a more parsimonious and user-friendly model of density was attained by simply removing the latter two interactions listed above (Model 5, Table 3-4). This new model fit the observed responses nearly identically to the best approximating model. Both models

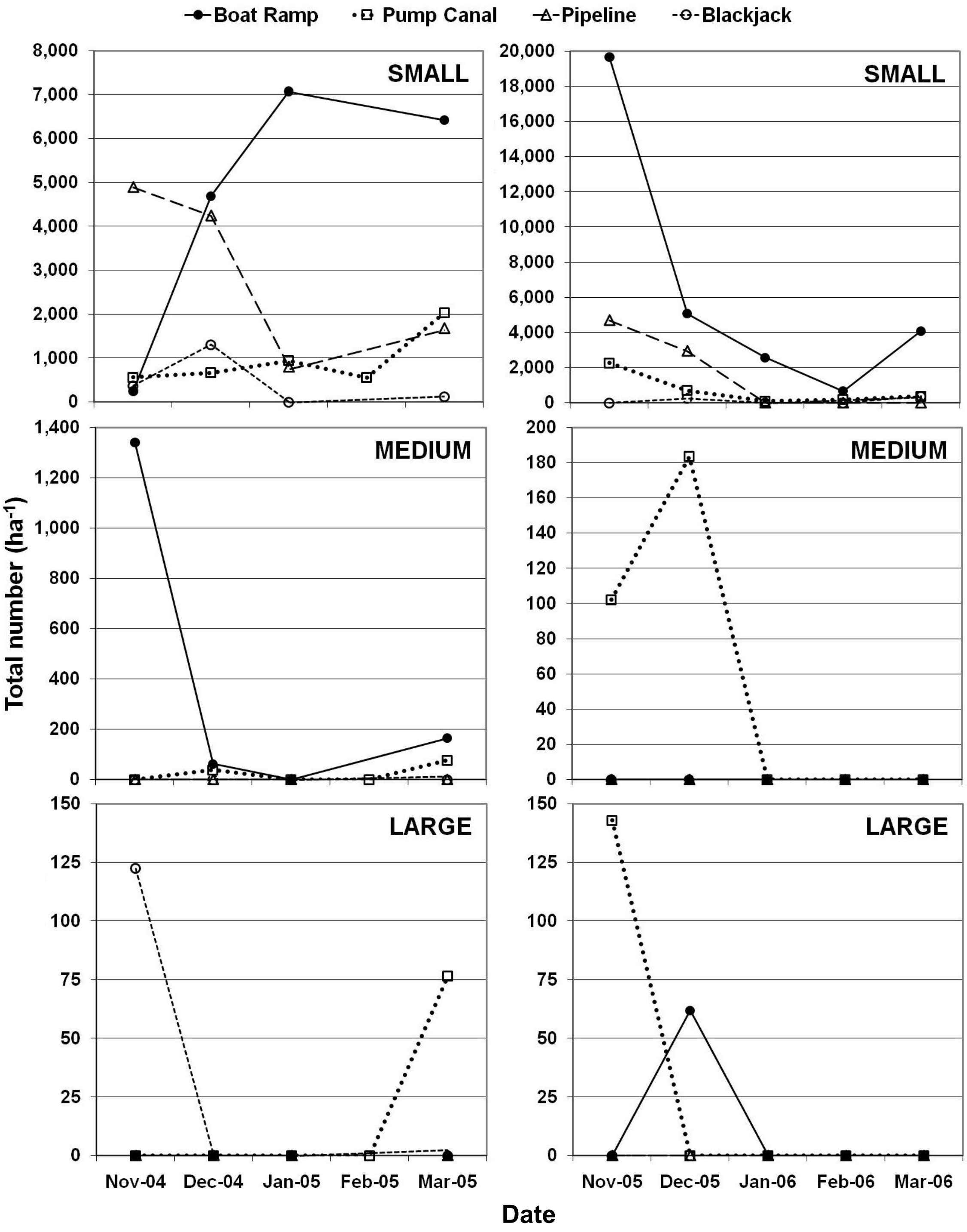

Fig. 3-26. Total number of small, medium and large blue crabs per ha of shallow estuarine habitat during November-March of winters 2004-2005 (left) and 2005-2006 (right) in each of four study sites.

Table 3-4. Best approximating model (Model 7) of density for blue crabs 1-10 mm in carapace-width plus hierarchical submodels in order of increasing model fit. Indices of model fit include (1) Pseudo-Akaike's Information Criteria values for small sample sizes ($PAIC_c$), (2) dispersion parameter $\widehat{c}$ estimated by χ^2/df, (3) Pearson's product-moment correlation factor (r) describing the linear association between observed and predicted values of crab density, and (4) Pearson's product-moment correlation factor (r_{ave}) describing the linear association between observed and predicted values of crab density averaged across study sites per period. Model 5 was identified as the most parsimonious approximating model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6	Model 7
$PAIC_c$	2004.14	1922.42	1906.21	1875.64	1854.11	1849.91	1854.62
$\widehat{c}$	0.97	0.83	0.80	0.74	0.71	0.70	0.69
r	0.718	0.807	0.838	0.854	0.861	0.865	0.868
r_{ave}	0.785	0.888	0.924	0.935	0.940	0.952	0.959
Fixed Effects	habitat stype scomp stype*scomp	habitat stype scomp stype*scomp sm14	habitat stype scomp stype*scomp sm14 wlm28	habitat stype scomp stype*scomp sm14 wlm28 wtm14	habitat stype scomp stype*scomp sm14 wlm28 wtm14 ws28	habitat stype scomp stype*scomp sm14 wlm28 wtm14 ws28 wlm28*ws28	habitat stype scomp stype*scomp sm14 wlm28 wtm14 ws28 wlm28*ws28 sm14*wtm14

noticeably achieved the best fit for data originating from PC and bay habitat, where crabs 1-10 mm CW were most frequently captured (Fig. 3-27). Predictability of crab density markedly decreased from bay to salt-marsh interior habitats. However, when observed and predicted values were each averaged across sites, densities were better approximated (Fig. 3-28). This improvement was expected, as the study was designed to estimate crab densities by incorporating data from replicate sites.

The most important predictors of crab density were habitat, water column structure type, and structural complexity. Observed and predicted responses of this simple model demonstrated a linear association of 72% (r=0.718), but, when averaged across sites, responses demonstrated an association over 78% (r=0.785; Model 1, Table 3-4). These three variables were the only ones appearing in the best approximating models that were specific to trapping locations and likely represented the factors most influencing micro-site selection by young juvenile crabs. Other variables included in the best models (salinity, water level, water temperature, wind speed) probably generally described conditions within the estuary influencing dispersal into/out of the salt-marsh, physiological function (e.g., osmoregulation, respiration), and overall predation risk. In other words, these latter predictors likely determined whether or not young crabs were present in and around the salt-marsh, whereas micro-site characteristics (per meter-squared) influenced variability in magnitude of use by crabs.

Model 5 highlighted several relationships between crab density and environmental variables that were both statistically and biologically meaningful (Table 3-5). Higher densities of crabs occurred in bay than all other habitats, and no difference

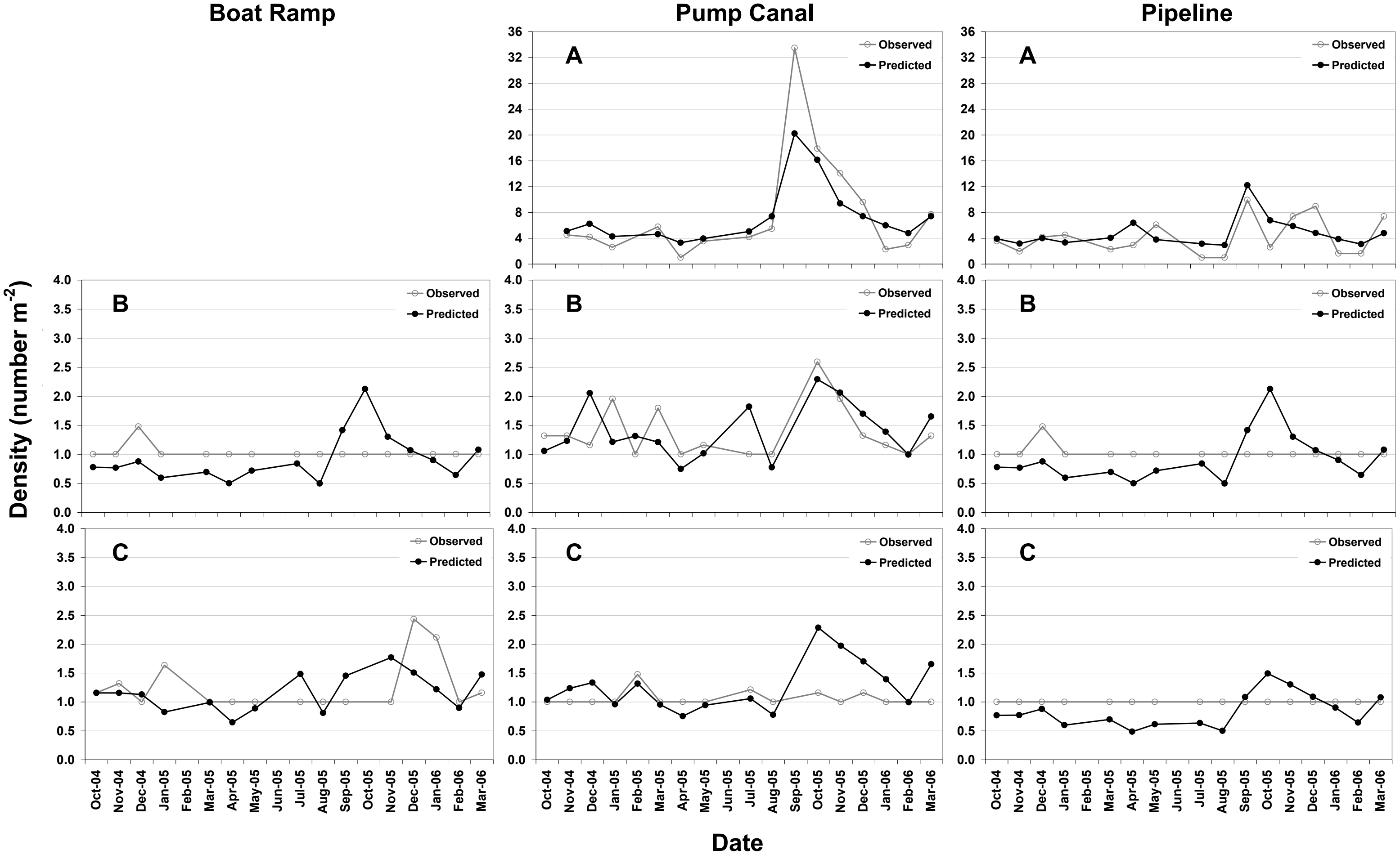

Fig. 3-27. Overlay of mean predicted and observed values of density (number per meter-squared) for blue crabs 1-10 mm in carapace-width in each study site and habitat during October 2004-March 2006. Predicted values were derived using the most parsimonious model of density (Model 5, Table 3-4). Habitats included bay (A) and connected (B) and unconnected (C) ponds.

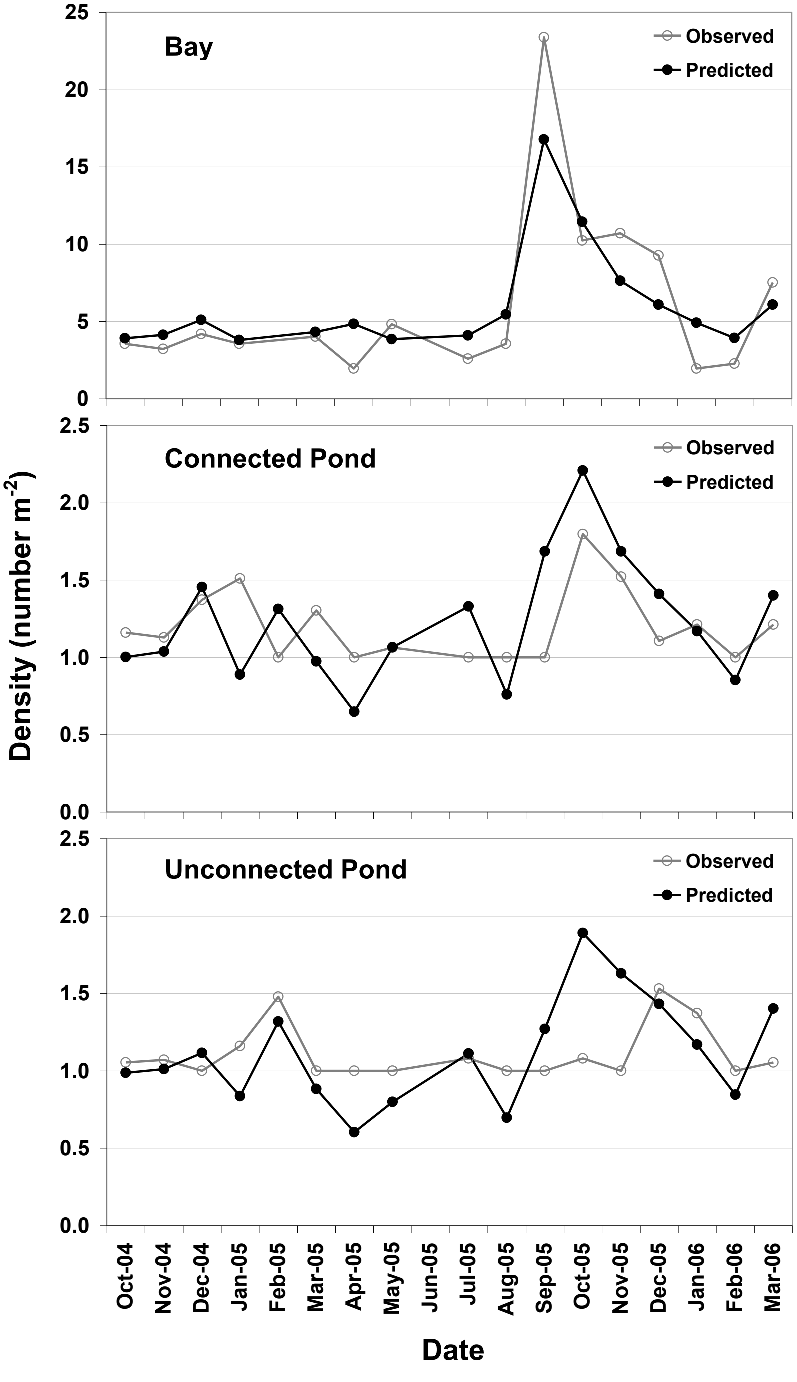

Fig. 3-28. Overlay of mean predicted and observed values of density (number per meter-squared) for blue crabs 1-10 mm in carapace-width in each habitat during October 2004-March 2006 (study sites combined). Predicted values were derived using the most parsimonious model of density (Model 5, Table 3-4). Habitats included bay (A) and connected (B) and unconnected (C) ponds.

Table 3-5. Effect estimates and significance values associated with Model 5 (Table 3-4), the most parsimonious model of density for blue crabs 1-10 mm in carapace-width. Values are on the (natural) log scale.

	Effect Solutions			Type III
Effect	Estimate	SE[1]	Prob. >|t|	Prob. >F
Intercept	0.2492	0.4424	0.6300	
habitat (bay)	1.5122	0.07997	<0.0001	<0.0001
habitat (connected pond)	-0.00148	0.07572	0.9844	
habitat (unconnected pond)	0			
stype (none)	-0.00752	0.2817	0.9787	0.0004
stype (algae)	0.1158	0.4678	0.8046	
stype (savalgae)	0.4735	0.3255	0.1462	
stype (sav)	0			
scomp (none)	0			0.0903
scomp (low)	-0.01748	0.2896	0.9519	
scomp (med)	0.1303	0.3094	0.6738	
scomp (high)	0			
stype*scomp (none, none)	0			<0.0001
stype*scomp (algae, low)	0.4442	0.5261	0.3988	
stype*scomp (algae, med)	-0.05697	0.5887	0.9229	
stype*scomp (algae, high)	0			
stype*scomp (savalgae, low)	-0.4967	0.3625	0.1710	
stype*scomp (savalgae, med)	0.5432	0.3597	0.1314	
stype*scomp (savalgae, high)	0			
stype*scomp (sav, low)	0			
stype*scomp (sav, med)	0			
stype*scomp (sav, high)	0			
sm14	0.04012	0.004100	<0.0001	<0.0001
wlm28	1.5642	0.2807	<0.0001	<0.0001
wtm14	-0.02712	0.006954	0.0001	0.0001
ws28	-0.1920	0.05697	0.0008	0.0008
Site BR (random)	0.06719	0.1426	0.6375	
Site PC (random)	0.1838	0.1385	0.1848	
Site PL (random)	-0.2510	0.1390	0.0713	
Covariance (site)	0.05339	0.05534		

[1] Standard errors for random effects are predicted.

was detected between the effects of connected and unconnected interior ponds. Density was generally higher in the water column structure type of SAV/algae than either SAV or algae, but mean crab density within each type depended differently on structural complexity. Crab density was highest when complexity was low in algae and medium in SAV/algae but did not vary by complexity level in SAV. Density was positively related to salinity and water level and negatively related to water temperature and wind speed. The random effect of study site accounted for random differences in magnitude of crab density among sites (BR, PC, and PL; Table 3-5) and supported results of descriptive statistics, which indicated crab densities were highest at PC.

Crabs 11-30 mm CW

Model results for crabs 11-30 mm CW were very similar to those for crabs 1-10 mm CW. The best approximating model of density included the effects of habitat type, water column structure type, structural complexity, and distance to ESV at the trapping location, water level, water salinity, and wind speed in San Antonio Bay, and interactions between structure type and complexity, and water level and wind speed (Model 6, Table 3-6). A slightly simpler, more user-friendly model was attained by removing the latter interaction (Model 5, Table 3-6). Both models demonstrated good model fit, with dispersion parameters only slightly above one and linear associations of observed and predicted values at 73% (r=0.731; Table 3-6). Correlations of observed and predicted values, averaged across study sites per monthly sampling period, revealed even stronger associations of 94% (r=0.943-0.947; Table 3-6). Graphics of mean

Table 3-6. Best approximating model (Model 6) of density for blue crabs 11-30 mm in carapace-width plus hierarchical submodels in order of increasing model fit. Indices of model fit include (1) Pseudo-Akaike's Information Criteria values for small sample sizes ($PAIC_c$), (2) dispersion parameter $\widehat{c}$ estimated by χ^2/df, (3) Pearson's product-moment correlation factor (r) describing the linear association between observed and predicted values of crab density, and (4) Pearson's product-moment correlation factor (r_{ave}) describing the linear association between observed and predicted values of crab density averaged across study sites per period. Model 5 was identified as the most parsimonious approximating model.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
$PAIC_c$	2174.81	2077.00	2048.57	2009.81	2004.10	1995.92
$\widehat{c}$	1.37	1.23	1.18	1.12	1.11	1.10
r	0.658	0.690	0.710	0.728	0.731	0.731
r_{ave}	0.859	0.915	0.930	0.942	0.943	0.947
Fixed Effects	habitat stype scomp stype*scomp	habitat stype scomp stype*scomp wlm28	habitat stype scomp stype*scomp wlm28 sm28	habitat stype scomp stype*scomp wlm28 sm28 dist	habitat stype scomp stype*scomp wlm28 sm28 dist ws28	habitat stype scomp stype*scomp wlm28 sm28 dist ws28 wlm28*ws28

predicted and observed values per monthly sampling period did not reveal any obvious differences in model fit by site or habitat (Fig. 3-29), but model fit was noticeably better for bay than connected or unconnected habitat when values were averaged across sites (Fig. 3-30).

Model analyses again revealed important relationships between crab density and the environment (Table 3-7). Crab density was higher in bay than all other habitats, and no difference was detected between the effects of connected and unconnected interior ponds. Crab density was also highest in SAV versus other water column structure types. Though density did not depend on complexity of SAV, density in each algae and SAV/algae was highest in medium complexity. Density was positively related to salinity and water level and negatively related to wind speed and distance to ESV. The random effect of site accounted for random differences in crab density among sites (Table 3-7), which again were consistent with results of descriptive statistics.

Crabs >30 mm CW

I was unsuccessful in developing models to predict densities of crabs >30 mm CW, as model selection procedures used to explore patterns in density resulted in non-convergence or excessively large dispersion estimates, presumably due to zero-inflation.

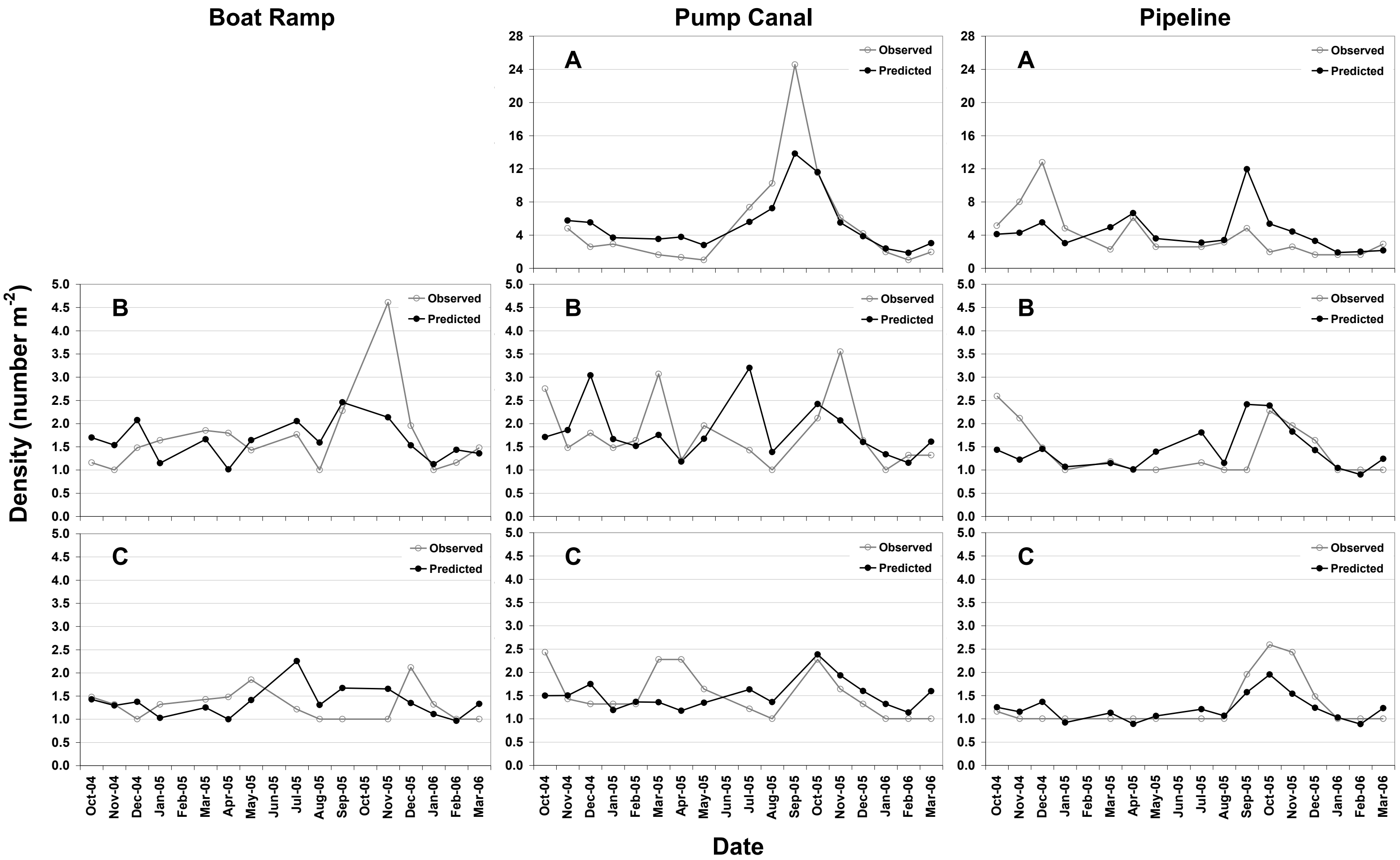

Fig. 3-29. Overlay of mean predicted and observed values of density (number per meter-squared) for blue crabs 11-30 mm in carapace width in each study site and habitat during October 2004-March 2006. Predicted values were derived by the most parsimonious density model (Model 5, Table 3-6). Habitats included bay (A) and connected (B) and unconnected (C) ponds.

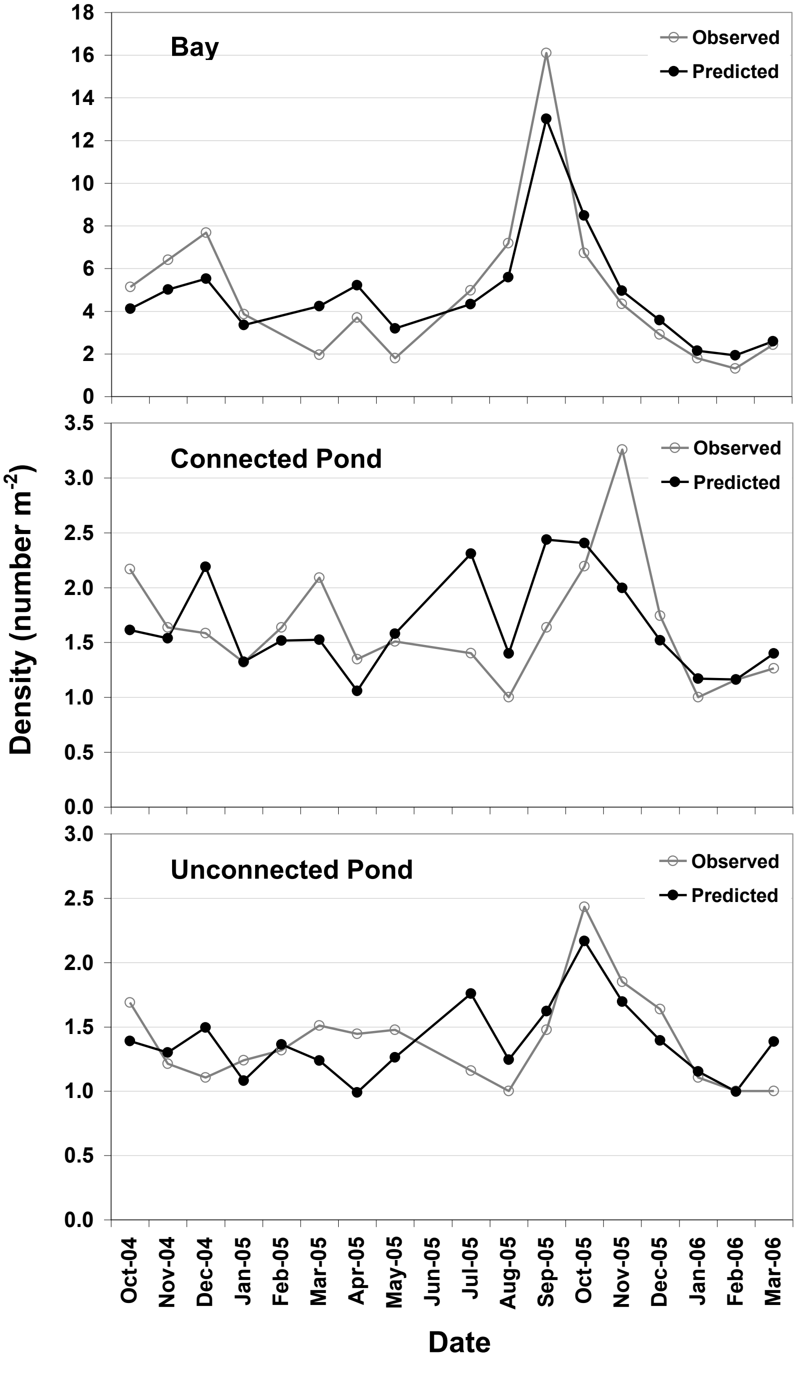

Fig. 3-30. Overlay of mean predicted and observed values of density (number per meter-squared) for blue crabs 11-30 mm in carapace-width in each habitat during October 2004-March 2006 (study sites combined). Predicted values were derived using the most parsimonious model of density (Model 5, Table 3-6). Habitats included bay (A) and connected (B) and unconnected (C) ponds.

Table 3-7. Effect estimates and significance values associated with Model 5 (Table 3-6), the most parsimonious model of density for blue crabs 11-30 mm in carapace-width. Values are on the (natural) log scale.

	Effect Solutions			Type III
Effect	Estimate	SE[1]	Prob. >|t|	Prob. >F
Intercept	0.5159	0.4022	0.3282	
habitat (bay)	1.1047	0.08899	<0.0001	<0.0001
habitat (connected pond)	0.01501	0.06852	0.8267	
habitat (unconnected pond)	0			
stype (none)	0			0.5870
stype (algae)	-0.00007	0.3525	0.9998	
stype (savalgae)	-0.2797	0.2724	0.3047	
stype (sav)	0			
scomp (none)	-0.3436	0.2044	0.0931	0.0022
scomp (low)	0.02120	0.2117	0.9203	
scomp (med)	-0.1751	0.2394	0.4646	
scomp (high)	0			
stype*scomp (none, none)	0			<0.0001
stype*scomp (algae, low)	0.04349	0.4076	0.9150	
stype*scomp (algae, med)	0.4159	0.4386	0.3434	
stype*scomp (algae, high)	0			
stype*scomp (savalgae, low)	-0.1736	0.3212	0.5891	
stype*scomp (savalgae, med)	1.2810	0.3112	<0.0001	
stype*scomp (savalgae, high)	0			
stype*scomp (sav, low)	0			
stype*scomp (sav, med)	0			
stype*scomp (sav, high)	0			
wlm28	1.1998	0.2406	<0.0001	<0.0001
sm28	0.01846	0.004230	<0.0001	<0.0001
dist	-0.02461	0.005803	<0.0001	<0.0001
ws28	-0.1500	0.05758	0.0094	0.0094
Site BR (random)	-0.02851	0.08874	0.7481	
Site PC (random)	0.1383	0.08502	0.1041	
Site PL (random)	-0.1098	0.08527	0.1982	
Covariance (site)	0.01813	0.01983		

[1] Standard errors for random effects are predicted.

Discussion

Development and Use of Sampling Gear

Although standard methods of drop-trapping have proven highly effective for quantitative sampling of nekton, such methods were not entirely appropriate or feasible in this study. Standard methods of drop-trapping incorporate use of a shallow-draft boat and have been employed previously in shallow bays and deep tidal creeks where water depth ranged 50-110 cm (e.g., Zimmerman et al. 1984; Rozas and Minello 1998; Minello and Rozas 2002). Objectives for this research were to examine the abundance patterns of blue crabs in extremely shallow habitats within and adjacent to mixed emergent salt-marsh. However, trapping in interior salt-marsh habitats was virtually impossible using standard drop-trapping methods, because water depth was typically too low (0-50 cm) for boat travel and unconnected or temporarily disconnected ponds were inaccessible via water travel (see Rozas and Minello 1997).

Throw-trapping was an alternative considered for this research, because portability of the trap within and among study sites was essential. Several types of throw-traps were experimentally tested for use in this study. These included round and square traps constructed of two parallel frames adjoined by fine-mesh fabric and square traps constructed entirely of heavy, non-collapsible material (e.g., stainless steel). None of the models, however, were perfectly suited for the salt-marsh in this study, as the marsh was dominated by mixed high-marsh emergent vegetation and characterized by abrupt changes in elevation. Even slight changes in elevation resulted in openings under the dual-framed models, and the protruding square corners of the non-collapsible models often got hung-up on woody, thick-stemmed vegetation or firm, uneven ground, allowing crabs and other nekton to escape. In attempts to combine the best attributes of all models, I used a smaller (0.79 m^2 versus 1.00 m^2), round, non-collapsible, and extremely sharp-bottomed throw trap. At 30 lbs (13.6 kg), this trap was conveniently carried by two people and heavy enough to cut into substrate, generally unaffected by elevational changes. Moreover, when the edge of a pond comprised a vertical wall of sediment and emergent plant roots (which was the majority of cases), the trap was thrown in a manner that allowed it to land perfectly next to “the wall” or nearly so. This was not viewed as a bias to the study, because, in most cases, “the wall” and elevated emergent marsh remained nonflooded.

The combination of trapping methods used in this study allowed for great versatility within the habitats sampled. The boom assembly was relatively light-weight (approximately 200 lbs (90.7 kg)) and small (base 2.6 m x 1.5 m), allowing it to float in water as shallow as 30 cm and be maneuvered by a single person wading through bay and small tidal creeks waters. Because the drop-trap was 75 cm tall, trapping was possible in water as deep as 65-70 cm, depending on the bottom sediment type. The throw-trap was ideal for water depths ≤35 cm and conveniently used at all unconnected pond and most connected pond locations when waters were of this depth. Also, the throw-trap was used when bay water depth fell below 30 cm, and drop-trapping was implemented in connected ponds deeper than 35 cm.

The drop- and throw-trapping methods used in this study allowed for capture of blue crabs 2-127 mm CW. However, I suspect that trap avoidance increased with crab size and that crabs >127.0 mm were simply able to avoid being trapped. When drop-trapping, the floats of the boom-assembly sank only up to 30 cm into the water column, and the next closest disturbance to crabs was me, walking in the water approximately 15-20 m behind the front of the boom assembly. When throw-trapping, we always threw from elevated ground outside the target pond and stood at a distance approximately 3-5 m from the ultimate landing location of the trap. Also, by throwing the trap at the angle we did, we likely minimized disturbance to crabs in the pond by elevating the trap far from the water's surface during the throw and increasing the probability of a clean, secure landing. Consequently, trap avoidance was probably minimal to non-existent for crabs of all sizes in pond edge habitats of the interior-marsh, but small gaps in the size-class distributions of crabs in bay habitat and open water habitats of the interior-marsh suggest that trap avoidance may have increased as a function of size for crabs >60 mm in these habitats. This makes sense, because large crabs inhabited open water more often than edge habitats and, though possibly more conspicuous to predators, they are more mobile than small crabs.

Patterns in Crab Abundance

To my knowledge, this was the first study to document size-specific patterns of habitat use by blue crabs in mature salt-marsh dominated by mixed, high-marsh vegetation. While intensive sampling efforts throughout adjacent bay habitat reaffirmed the importance of shallow embayments and fringing *Spartina alterniflora* for recently-recruited juvenile blue crabs, sampling in the interior salt-marsh revealed the importance of marsh ponds for dispersing juvenile and adult blue crabs. Moreover, calculations of total population number and standing stock (biomass), as well as estimation of crab production (see below), allowed for comparison between mature salt-marsh of the central Texas Coast (this study) and younger marshes on the Gulf and Atlantic Coasts of the southern U.S. Overall, this research contributes to understanding the capacity of mature salt-marshes to support productive blue crab populations.

In efforts to identify critical nursery habitats for juvenile blue crabs, crab densities have most often been estimated for structurally-distinct habitats, such as seagrass or SAV (e.g., *Ruppia, Halodule, Zostera, Halophila, Potamogeton*), marsh edge or salt-marsh (e.g., *Spartina alterniflora*), macroalgae (e.g., *Ulva*), and shallow nonvegetated bottom or bare mud/sand (Minello 1999; Minello et al. 2003). These habitats generally have corresponded to areas within salt-marsh fringe or neighboring embayments that were differentiated at a micro-scale. In contrast, habitats in this study were defined at a larger spatial scale based on connectivity to bay water and included the bay-marsh interface (within *Spartina alterniflora* fringe and up to 50 m from salt-marsh) and open water and edge zones of connected and unconnected ponds in the salt-marsh interior. Each habitat alone encompassed a diversity of water column structure and substrate types and, because several trapping locations were randomly selected per experimental unit (monthly sampling period x study site x habitat), density estimates were influenced by all structures present (e.g., *Spartina* fringe, SAV, macroalgae, nonvegetated bottom) in proportion to their areal coverage.

Estimates of crab density for bay habitat in this study were comparable to those of studies situated in similar bay complexes of the southern U.S. In fact, overall crab density in bay habitat (9.45 ± 2.19 crabs m^{-2}) proved well within the broad range of earlier estimates, which varied from 0.1-5.6 crabs m^{-2} over nonvegetated substrate (i.e., mud or sand; Mense and Wenner 1989; Thomas et al. 1990; Rozas and Minello 1998; Sheridan et al. 2003) to 2.2-13.0 crabs m^{-2} in natural fringing salt-marsh cordgrass (*Spartina alterniflora*; Mense and Wenner 1989; Thomas et al. 1990; Rozas and Minello 1998; Zeug et al. 2007) to 2.5-50.6 crabs m^{-2} in SAV (e.g., *Ruppia maritima*, *Holodule wrightii*; Thomas et al. 1990; Rozas and Minello 1998; Sheridan et al. 2003). Particularly relevant were the similar magnitudes of crab density observed between this and other studies conducted in the Guadalupe Estuary, as crab populations targeted within the bay were alike and some sample sites were possibly within meters of one another (see Rozas and Minello 1998; Zeug et al. 2007).

Due to considerable variability in timing of sample collection among studies, examination of temporal patterns in crab density more clearly revealed the consistencies existing between this and other studies. Accounting for temporal effects was important, because, while some prior studies sampled monthly throughout the annual cycle, most studies sampled only once within each of one to three seasons (e.g., spring, summer, autumn). Sampling in this study occurred throughout the year to include periods of low water levels, low crab recruitment, and limited crab use of shallow estuarine habitat. As a result, crab densities should have been lower in this study than others, if at all different. For instance, when averaging across three years of spring (April or May), summer (June or July), and autumn (September or October) data, Sheridan et al. (2003) found 24 crabs m^{-2} in natural seagrass habitat, an overall level of abundance greater than two and one-half times the bay habitat estimate in this study. At the temporal resolution of season, however, densities from this study and Sheridan et al. (2003) did not appear to differ during spring (4.1-5.3 versus 1.8-11.4 crabs m^{-2}) or autumn (6.7-37.5 versus 32.2-33.9 crabs m^{-2}), and only estimates derived for summer (3.6-5.6 versus 20.1-41.4 crabs m^{-2}) suggested fewer crabs used the Guadalupe Estuary (this study) than Galveston Bay (Sheridan et al. 2003).

During this and other studies situated in shallow estuarine bay habitats, a single, relatively distinct peak in blue crab abundance was documented in autumn (Rozas et al. 2007), concurrent with or immediately following the major autumnal influx of newly-recruited juvenile crabs (see Chapter II). Although investigations of crab density patterns have been limited within salt-marsh, a handful of studies, recording relative levels of crab abundance in the marsh, revealed temporal patterns mirroring those observed in this study (Peterson and Turner 1994). In contrast to the single peak observed for bay habitat, periods of peak crab abundance within salt-marsh instead occurred during both spring and autumn. The additional spring peak in abundance might be explained by the movement of returning or newly-inhabiting crabs into the marsh, unhindered by the structure lacking within the bay's water column. Alternatively, while bay densities that were elevated during autumn may be the result of crabs moving into the area (i.e., inputs to the bay-marsh population), fluctuations in density within the salt-marsh may be a consequence of crabs moving out of the marsh and shifting to deeper waters due to temperature extremes and low water levels during winter and summer.

In this study, crabs captured in the bay were significantly smaller (principally ≤20 mm CW) but ten times more numerous than crabs of the interior salt-marsh (>30 mm, 0.1 crabs m^{-2}). Moreover, crab size-distributions in interior-marsh habitats were less skewed and three to four times more encompassing than that in bay habitat. The most obvious explanation for this pattern was that the increasing mobility and environmental tolerance afforded with increasing crab size or age allowed crabs to increasingly infiltrate shallow habitats farther up-estuary. Losses of individuals due to mortality and dilution effects (i.e., dispersal) were likely in part responsible for the coupled patterns of decreasing number and increasing size, as similar trends have been observed for megalopal and newly-metamorphosed blue crabs during invasion, terminal settlement, and initial redistribution within estuaries (Orth and Heck 1987, Moksnes 1989; see also Chapter II).

I did not directly assess the habitat preference or movement patterns of blue crabs, but the spatial ranges in which crabs of different sizes used habitats corresponded well with observed patterns of plant structure within habitats, suggesting possible ontogenetic shifts in microhabitat. From shallow bay habitat to increasingly disconnected water bodies of the interior salt-marsh, coverage of SAV decreased while prevalence of nonvegetated bottoms and density of emergent vegetation edge increased. In addition, small crabs (≤30 mm CW) were most abundant in SAV and algae-dominated bay waters while slightly larger crabs (31-80 mm CW) contributed proportionally more to biomass in pond edge habitats and the largest crabs (41-130 mm CW) utilized predominantly open water pond habitats of the interior-marsh.

Size-specific habitat use patterns observed for crabs in this study were in agreement with an earlier study, which suggested that blue crabs incur increasing independence from cover, such as seagrass or *Spartina*, due to natural refuge attained by increasing size (Hines and Ruiz 1995). From a simple habitat use perspective, crabs have been shown to inhabit structurally-complex microhabitats (e.g., seagrass, algae, oyster shell) as new recruits and increasingly inhabit habitats of lesser complexity (e.g., broad-blade or low-density vegetation, nonvegetated sediment) with increasing size (Orth and van Montfrans 1987, Pile et al. 1996, Pardieck et al. 1999, Morgan et al. 2003, van Montfrans et al. 2003, Moksnes and Heck 2006; see also Chapter II). Moreover, crabs in non-vegetated mud habitats were found to be larger in size than those in adjacent *Spartina* salt-marsh fringe, which in turn were shown to be larger than those in adjacent seagrass beds (Thomas et al. 1990, Rozas and Minello 1998). In the current study, small crabs likely benefited most from the structurally-complex cover present in bay habitat, whereas larger juveniles and adults incurred benefit from the diverse composition of microhabitats available in the interior marsh.

Whereas fine spatial-scale summaries of crab abundance (number or g m^{-2}) revealed how crabs used resources within salt-marsh and adjacent bay habitats, larger spatial-scale estimates of crab abundance (total number or kg ha of marsh-bay complex^{-1}) provided valuable information on the current study area’s capacity to support a transient population of crabs. Contributions of specific habitats to total abundance, patterns of contribution among study sites, and total abundance supported per study site were key findings in this study, because, while numerous studies have recognized structurally-distinct micro-habitats as essential for estuarine nekton (Minello 1999), far fewer have investigated landscape level effects, such as habitat composition (Micheli and Peterson 1999). In this study, small crabs were numerically dominant within the population and had the greatest potential for affecting patterns in total crab number. Large crabs, on the other hand, were infrequently observed but had great influence on patterns in biomass. As might be expected, the habitat that contributed most to total crab number was bay habitat, the same habitat where young crabs were in densities up to forty times those in other habitats. Connected open water habitat contributed substantially more to standing stock (total biomass) than any other habitat and also contained significantly larger crabs than the bay, demonstrated a broader range of crab sizes than all other habitats, and comprised an average of 20% of all crabs in the bay-marsh complex as compared to <5% for all other habitats.

Although not initially identified as an objective for this study, I was interested in how blue crab production within the salt-marsh and surrounding shallow bay habitats of the Guadalupe Estuary compared to that of a bay-marsh complex containing younger, *Spartina alterniflora*-dominated salt-marsh. Production estimates for blue crabs in Galveston Bay, Texas provided the opportunity for such a comparison (Minello et al. 2008). Recognizing crab production within the bay-marsh complex as equivalent to the rate of total crab biomass (kg ha^{-1}) produced in the complex over a specified interval, I calculated annual production using monthly size-specific crab densities computed for

April-November 2005, a growth rate of 0.5 mm d^{-1} (Minello et al. 2008), and the crab size-wet biomass relationship defined earlier. No data were collected during June 2005; therefore, production for this month was determined by averaging estimates from May and July. Production in the Guadalupe Estuary (201 kg ha^{-1}) was very similar to the regions studied in Galveston Bay (126-202 kg ha^{-1}), as well as to all regions combined (170 kg ha^{-1}). Despite some differences in methodology (e.g., no sampling occurred within ESV in this study), results strongly suggested that the capacity for mature marshes to support blue crab populations was not significantly different than younger, more frequently inundated marshes.

Sources of Variation in Crab Density

Effects included in the best generalized linear mixed models of crab density were not surprising, as all variables initially included in the full models were hypothesized beforehand to be important sources of variation in crab density. However, differences in the relative importance of effects were extremely informative and suggested environmental conditions distinguished at a fine scale (i.e., trapping location) played a greater role in determining crab density than variables representing estuary-wide conditions. Habitat type (bay, connected pond, unconnected pond), structure type (e.g., none, SAV, algae, SAV/algae), and structural complexity (low, intermediate, high) were by far the most important predictors of small crab density, as strengths of linear association between observed and predicted densities using this simple model were 0.72-0.79 for crabs 1-10 mm CW and 0.69-0.86 for crabs 11-30 mm CW. In contrast, all other variables included in the best models of crab density, including mean salinity, water level, water temperature, and wind speed for the preceding 2-4 wk in San Antonio Bay, minimally improved model fit.

Effect estimates for the model variables of habitat type, structure type, and structural complexity strongly supported the size-specific patterns of habitat use observed for crabs in this and earlier studies. For both crabs 1-10 mm and 11-30 mm CW, the best models predicted markedly greater crab densities in bay habitat than interior-marsh ponds. Moreover, crabs were tied closely to structures in the water column, as opposed to inhabiting nonvegetated, sand, mud, or clay bottoms. Crabs 11-30 mm CW were most concentrated in SAV, but densities of crabs 1-10 mm CW were highest when algae was additionally present (i.e., in SAV/algae). As the form of most algae encountered at trapping locations was filamentous and, therefore, inherently more complex than SAV, this latter finding provided additional evidence of crabs switching to less complex habitats with increasing size.

Crabs 1-10 mm and 11-30 mm CW were very similarly influenced by mean water level, salinity, and wind speed, with slight differences likely reflecting different stages of development. For both size categories, density increased with the 28-d mean of San Antonio Bay water level, possibly because increasing water depths within the estuary facilitated crab movement into the most shallow, densely-vegetated habitats or, alternatively, because increases in total water volume reduced predation pressure. Crab density was also found to increase with the 14-d mean of salinity for crabs 1-10 mm CW and 28-d mean of salinity for crabs 11-30 mm CW. Salinity effects suggested that crabs entered the Guadalupe Estuary during or immediately following periods of high salinity, possibly due to their still developing tolerance of freshwater. In contrast to water level and salinity, the effect of the 28-d mean of wind speed was negative for all crabs ≤30 mm CW. One probable explanation was that wind enhanced the turbidity of water, which then provided refuge to crabs and lessened crab dependence on physical structures used for refuge. Alternatively, crabs may have dispersed not because they were released from the pressures of predation, but because dispersion itself represented a strategy for avoiding tactile (nonvisual) predators still active in turbid waters.

The development of predictive models for larger juvenile and adult crab (>30 mm CW) densities was not feasible in this study using methods described for smaller crabs. However, the problem of low predictability of large crabs, as well as zero-inflation associated with crabs of all sizes (particularly those inside the salt-marsh), may be overcome to some degree by simply increasing sample size (number of trapping locations). Moreover, given the inherently low levels of large crab abundance within the bay-marsh complex (as compared to young juveniles) and low predictability of micro-habitat use, temporal models of large crab abundance might be more feasibly developed using data summarized at a larger spatial-scale.

CHAPTER IV

WHOOPING CRANE FORAGING ECOLOGY: THE REWARDS, COSTS, AND EFFICIENCY OF FORAGING DURING WINTER

Synopsis

Recovery planning for the endangered whooping crane (*Grus americana*) incorporates the reintroduction of captive cranes into the wild and also acknowledges the importance of available habitat for wild cranes expanding their winter range in coastal Texas. Evaluations of habitat suitability at potential reintroduction sites and sites adjacent to the crane's present range in Texas currently rely on information gathered from previous empirical studies, which suggest certain foods as important but do not fully depict use of foods on temporal and spatial scales or evaluate optimality of foraging for foods. To satisfy these needs and determine the foods of greatest value to cranes, I intensively observed 4 of 19 total pairs of territorial adult cranes at Aransas National Wildlife Refuge, Texas during November-March of winters 2004-2005 and 2005-2006. I quantified the proportional use of foods by cranes (defined as the percentage of dry mass in the crane's diet comprised by each food type), as well as the rewards, costs, and efficiencies of foraging for these foods during winter. Foraging rewards were represented by rates of numeric (number min^{-1}), dry mass (g min^{-1}), lipid (mg min^{-1}), energy (kJ min^{-1}), and protein (mg min^{-1}) intake. Foraging costs were quantified using surrogates of foraging effort, which included rates of stepping (number of steps min^{-1}), probing (number of probes min^{-1}), handling (number of food manipulations min^{-1}), and total foraging movements (number of steps, probes, and manipulations min^{-1}). Foraging efficiency was defined as the ratio of foraging rewards to costs and examined using indices of numeric, dry mass, lipid, energy, and protein efficiency (i.e., intake:total movements). The crane diet included wolfberry fruit (*Lycium carolinianum*), blue crab (*Callinectes* spp.), clams (*Tagelus* spp.), snails (e.g., *Littorina* spp.), insects (e.g., grasshoppers), fiddler crabs (*Uca* spp.), snake (e.g., *Nerodia clarkia*), and fish (*Myrophis punctatus*). Overall benefit achieved from foraging differed among foods, depending on the foraging currency used (intake rate, effort, efficiency), resource gained or conserved (number of food items, biomass, lipids, energy, protein), and temporal patterns of food availability during winter. Wolfberry fruit, snails, and insects were consumed in the highest quantities, required the least effort during foraging, and generally were associated with the most efficient foraging behavior. However, blue crab was the most optimal food when foraging for protein, and clam was a significant source of biomass. Findings from this study provide guidance for future crane recovery efforts by identifying foods with the greatest potential for influencing suitability of winter habitat.

Introduction

Determining the contribution or value of foods to forager diet is often a key element in the recovery of endangered and threatened species. Data describing the food habits and foraging patterns of species at risk have proven integral in understanding the susceptibility of species to contamination (e.g., sea otter – Johnson et al. 2009; burrowing owl – Woodin et al. 2007), degree of diet specialization and vulnerability to habitat loss or degradation (e.g., Karner blue butterfly – U.S. Fish and Wildlife Service 2003; roseate tern – Rock et al. 2007; snail kite – Beissinger et al. 1994), and influence of food limitations on carrying capacity thresholds (e.g., black rhino – Reid et al. 2007). For the endangered whooping crane, guidelines used to evaluate habitat suitability at potential reintroduction sites and at sites adjacent to the crane's present range in Texas could be improved with knowledge of which foods provide the greatest benefit to foragers. Currently, evaluations rely on information gathered from earlier studies (e.g., Allen 1952; Blankinship 1976; Chavez-Ramirez 1996), which suggest certain foods as important to cranes but do not fully depict use of foods on temporal or spatial scales or consider optimality of foraging for foods.

While wintering on the Texas Gulf Coast, whooping cranes feed primarily in salt-marsh and lesser often in adjacent shallow bay and upland habitats. Previous studies examining the crane diet describe the bird as omnivorous, feeding largely on blue crab, clam, and acorn (an upland food), and less commonly on wolfberry fruit, snail, insect, crayfish, fish, shrimp, fiddler crab, other crab, snake, nutgrass tuber, and other plant material. Early efforts to describe the assemblage of foods in the crane diet were qualitative and relied principally on incidental observation and circumstantial evidence (e.g., empty, discarded clam shells; Stevenson and Griffith 1946). Later studies identified food composition and quantitatively (though relatively) measured food use through analysis of fecal droppings (Stevenson and Griffith 1946; Allen 1952; Hunt and Slack 1989) and stomach contents of dead cranes (Allen 1954; Uhler and Locke 1970; Hunt and Slack 1987). Focal-bird observation has also been used to compute absolute measures of intake but only for some foods targeted by cranes (Chavez-Ramirez 1996).

As collection of food habit data during most previous studies has been opportunistic (i.e., via fecal droppings or dead cranes), little emphasis has been given to a priori sampling designs intended to account for temporal or spatial variability. Hunt and Slack (1989), revealing the importance of a temporal component in studies, showed winter patterns in relative use of foods by cranes (i.e., percent aggregate volume and frequency of occurrence) were masked when considering only mean use across winter or per any one period (early, mid-, late) during winter. During both years of their study, use of clam increased from early to late winter and wolfberry fruit was consumed in early but not late winter. Moreover, crane use of blue crab decreased during the first but not second winter. Because overwinter changes in diet may indicate ontogenetic or seasonal changes in forager nutrient requirements, variability in food abundance and/or availability, or differential profitability of foraging for foods (Euliss and Harris 1987; Sekiya et al. 2000; Schummer et al. 2008; Hedd et al. 2010), winter patterns in crane diet deserve further attention.

To my knowledge, no study has controlled for sources of spatial or intraspecific (among-crane) variability when describing the whooping crane diet. Intraspecific variability can arise from (1) differences in the search and handling abilities of cranes due to social group (territorial mated pairs vs. non-territorial, flocking subadults) and age (or level of experience) within each group (Rutz et al. 2006; Avilés and Bednekoff 2007), (2) habitat or territory quality, as influenced by resource availability or predation risk (Krebs and Davies 1993), and (3) random (unpredictable) differences among individuals. Examination of adults foraging on winter territories, consequently, may provide insight into factors driving population dynamics, as differences in nutrient intake or energy expenditure among territorial pairs may lead to variation in winter survival and subsequent breeding productivity. Furthermore, differences in survival and reproductive probabilities among individuals may be attributable to conditions present across an entire winter or, alternatively, may depend chiefly on conditions during a discrete time period of winter.

Estimates of relative use (e.g., percent aggregate volume; Hunt and Slack 1989), nutritional value (Nelson et al. 1996), and captive crane preference (Nelson et al. 1997) of foods suggest certain foods are important to cranes, but not yet clear are the rewards and costs of foraging for foods by cranes in the wild. These very uncertainties lie at the heart of optimal foraging theory, which asks ‘What are the behavioral strategies used by foragers to achieve the delicate balance of reward and cost leading to maximal fitness?’ (Pyke et al. 1977). Decades of study indicate that foragers use currencies of reward and cost, which are based on behavioral or physiological constraints imposed at the individual level, to guide foraging decisions and thus optimize foraging behavior. Using mathematical models of achievable rewards, costs, or both, behavioral ecologists have examined optimal prey selection (i.e., the optimal diet; Berec et al. 2003; O'Brien et al. 2005), optimal patch choice (Fretwell and Lucus 1969; Gill 1996), optimal allocation of time to patches or habitats (Alonso et al. 1995; Nolet et al. 2006), and optimal foraging modes and movement patterns (Guillemain et al. 2000; Nolet and Mooij 2002). It follows then that, by examining the overall benefits of foraging for foods in light of the possible currencies used by cranes, foods could be ranked optimally and knowledge could be attained regarding important habitat elements to be considered in future conservation and management plans.

My overall goal for this research was to determine the winter foods of greatest value to adult whooping cranes at Aransas National Wildlife Refuge (ANWR), Texas. My approach was to quantify the contribution of foods to the crane's diet, as well as the rewards, costs, and overall benefits achieved by cranes when foraging for foods. Specific objectives were to (1) document temporal (within and across winters) and spatial (within and across crane territories) variability in proportional use of foods by cranes, (2) document temporal and spatial variability in foraging rewards, represented by numeric, dry mass, lipid, energy, and protein intake rates, (3) quantify some of the costs of foraging, including the effort required to search for and handle foods (e.g., steps, probes, food manipulations), and (4) further quantify the optimality of foraging for foods by calculating indices of foraging efficiency (i.e., ratios of reward:cost).

Materials and Methods

Study Location

The study area was located within and immediately adjacent to the Aransas National Wildlife Refuge (ANWR) in Aransas and Calhoun counties, Texas (Fig. 4-1). The refuge is situated almost entirely on the Blackjack Peninsula, which is bounded by two major bays (San Antonio and Copano-Aransas), two smaller bays (St. Charles and Mesquite), and the Gulf Intracoastal Waterway (GIWW). During both years of the study, Blackjack Peninsula supported 19 territorial adult pairs of whooping cranes (19 winter territories) out of 62 total pairs in the flock (62 winter territories). The remaining 43 crane pairs defended territories on Welder Flats (n=6), Lamar Peninsula (n=2), Matagorda Island National Wildlife Refuge (n=20), and San Jose Island (n=15).

Estuarine habitats used by whooping cranes include salt-marsh and shallow bays. Bays are primarily subtidal and consist of open-water, non-vegetated (mud or sand) bottoms, seagrass beds, algal blooms, and oyster reefs. The salt-marsh is primarily intertidal and is a complex of mixed emergent vegetation, interrupted by scattered potholes and flushed with coastal waters through a network of tidal creeks. Roughly 10-50% of the marsh is non-vegetated, open water, but these waters seasonally contain submerged vegetation (e.g., *Ruppia maritima*) and algae. Islands of elevated ground support the emergent growth of highly salt-tolerant but intermediately flood-tolerant plant species (e.g., *Borrichea frutescens, Batis maritima, Salicornia virginica, S. bigelovii, Lycium carolinianum*), while shallow depressions and edges of ponds and tidal

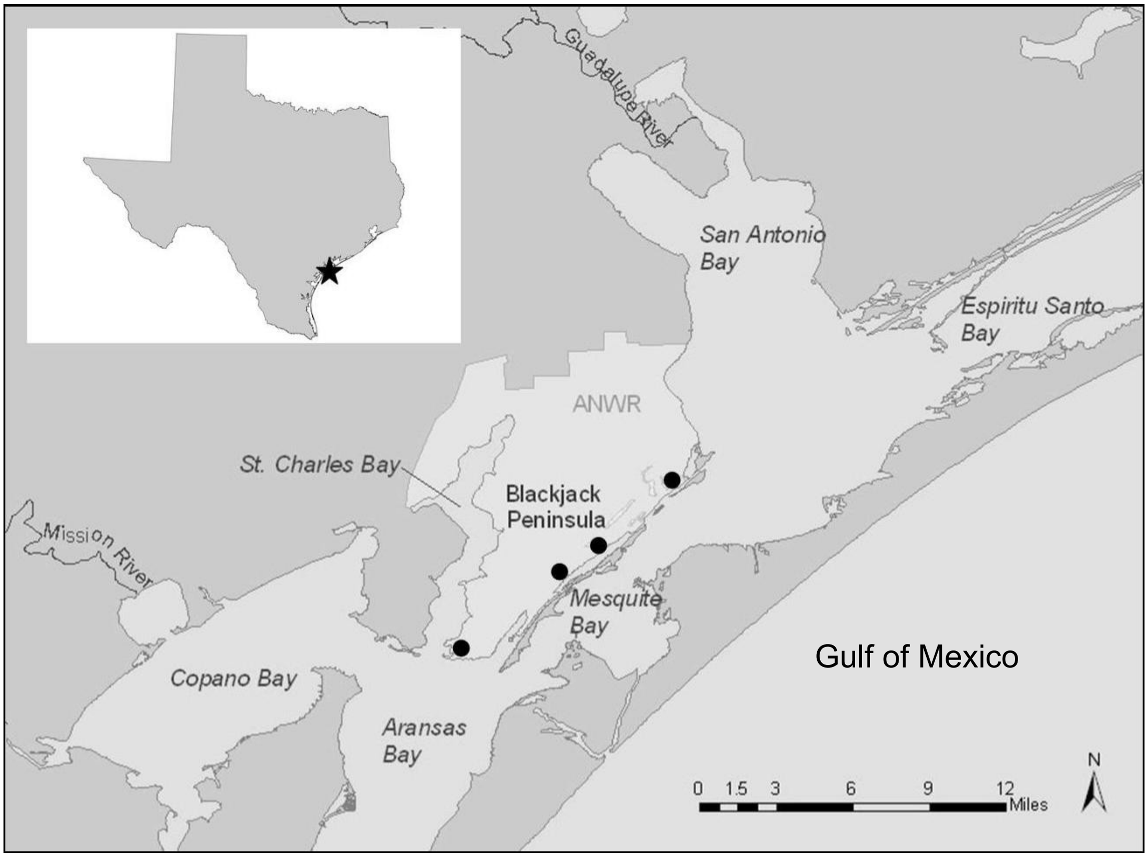

Fig. 4-1. Map depicting the locations of four whooping crane territories (dots) studied during November-March of winters 2004-2005 and 2005-2006. Crane territories were located at Aransas National Wildlife Refuge (ANWR) along the central Texas coast. From northeast to southwest, territories included those named Boat Ramp, Pump Canal, Pipeline, and Blackjack.

creeks support species of both high salt and flood tolerance (e.g., *Distichlis spicata, Spartina alterniflora*; Stutzenbaker 1999).

Navigable waters integrated within the salt-marsh of Blackjack Peninsula are closed to the public every winter (15 October-15 April) to limit disturbance to wintering whooping cranes. However, navigable waters adjacent to the peninsula are under the governance of the State of Texas and open to the public throughout the year. The most common uses of these waters include recreational rod-and-reel fishing, commercial fishing (e.g., crabbing with crabpots, shrimping with trawls, dredging for oysters), recreational boating (e.g., sailing), and barge transport. Wildlife-viewing via tour boat is also popular during winter, particularly for view of whooping cranes, but disturbance to cranes caused by tour boats is considered negligible (LaFever 2006). Hunting likely had little influence on wintering cranes, because the activity is not permitted within a 152-m (500-ft) buffer of refuge-owned lands (including the emergent salt-marsh).

The general climate of the area is sub-tropical. Normal minimum and maximum temperatures during the crane's wintering season (November-March) range from 6.9 to 12.8°C and 16.6 to 22.0°C, respectively (NOAA, National Climatic Data Center 1971-2000, Aransas Wildlife Refuge, Texas weather station). Normal annual rainfall is 103.7 cm, 34% (35.3 cm) of which falls during the wintering season. All estuarine habitats within the study area annually experience a wide range of salinities (1-30 ppt). Diurnal tides (one high, one low) are seemingly insignificant along this portion of the coast with a tidal range of about 9-13 cm (Texas A&M University-Corpus Christi, Division of Nearshore Research, Station 031, Seadrift).

Study Design

Four of the 19 winter territories of whooping cranes located on Blackjack Peninsula were selected for intensive study, including those named Boat Ramp (BR), Pump Canal (PC), Pipeline (PL), and Blackjack (BJ; Fig. 4-2). Three territories (BR, PC, and PL) were selected based on ease of inland access (e.g., paved or unpaved road, mowed levee or pathway) to ensure that sites could be visited when boating conditions were sub-optimal. The fourth territory (BJ) was located on the east side of St. Charles Bay, immediately across from the boat ramp at Goose Island State Park and was most easily accessed by boat, but it was specifically selected to increase spatial distribution of study sites across Blackjack Peninsula. Selection of territories, therefore, was not strictly random but likely was functionally so. Selection criteria probably had little to no effect on the outcome of physical characteristics and behavior respectively describing the territories and cranes chosen for study. Such characteristics were not acknowledged until after territories were chosen for study, at which time territories were discovered to differ considerably in size, shape, habitat composition, connectivity to adjacent bay waters, proximity to major freshwater inflows, and proximity to offshore waters (Fig. 4-2). All sites were considered fully representative of the contiguous salt-marsh and adjacent bay habitat in which they were located, and inference from study results was intended to be applied to the population of territories (*n*=19) represented by those sampled.

Within each territory, I used intensive focal-bird observation to collect data on the rewards (food consumption) and costs (risks, effort) of foraging by whooping cranes.

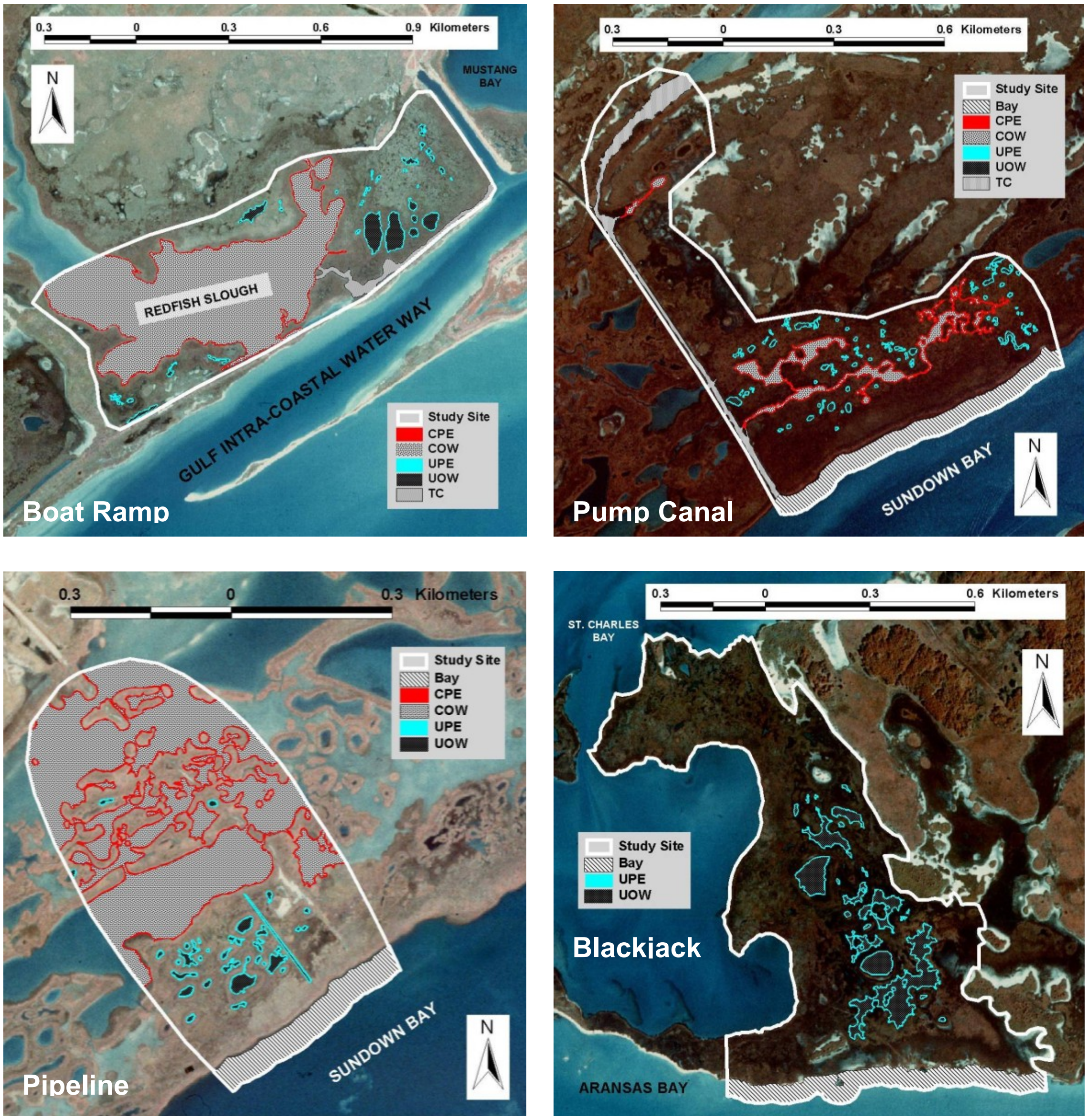

Fig. 4-2. Satellite imagery and habitat overlays for whooping crane territories located at Aransas National Wildlife Refuge, Texas and studied during November-March of winters 2004-2005 and 2005-2006. Territories were named Boat Ramp (top left), Pump Canal (top right), Pipeline (bottom left), and Blackjack (bottom right), and delineated habitats within territories included bay-marsh interface (Bay), tidal creek (TC), connected open water (COW), connected pond edge (CPE), unconnected open water (UOW), unconnected pond edge (UPE), and emergent salt-marsh vegetation (no color or pattern).

To facilitate observation and limit disturbance to territorial adult cranes, two 1.22-m x 1.52-m x 1.83-m (4-ft x 5-ft x 6-ft; width x length x height) observation blinds were built along the perimeter of salt-marsh habitat within the boundaries of each territory (Figs. 4-2 and 4-3). Blinds were constructed along the edges of large shrub patches when possible and elevated in height by a maximum of 1.22 m (4 ft), for a total blind height of 3.05 m (10 ft). I observed cranes in each territory during November-March of two consecutive winters (2004-2005 and 2005-2006). During each month within winter, observations were conducted during as many days as possible in attempts to collect data within each of 11 daylight hour-blocks (0700, 0800, 0900,… 1700) per territory. Data obtained from observation sessions within each combination of winter, month, and territory were compiled to define experimental units.

Data Collection

To increase accuracy of collected data, I video-recorded cranes in situ for a target duration of 25 min or more of foraging behavior and later watched videos ex situ to transcribe data. Recordings were made using a digital camcorder, but close-up view of the cranes was made possible with attachment of a 2,000-mm telescope lens (Fig. 4-3). Such magnification was necessary, because cranes were typically 200-1,200 m away from the observation blind and food items were often as small in size as 1 cm (e.g., wolfberry fruit). When cranes were close to the blind (<200 m away) or when wind speed was high or heat-waves prevalent, the camcorder was used alone.

Fig. 4-3. Observation blinds at Pump Canal (top) and Boat Ramp (middle) and video-recording system (bottom) used to collect diet and behavior data from whooping cranes during winters 2004-2005 and 2005-2006.

During the video-recording of each observation session, my intent was to track only one crane. The focal crane of each session was selected by identifying the adult farthest right in the field view and observable. Only adult cranes were selected for observation, despite the presence of juvenile cranes on two of four territories during each winter. When the original focal crane disappeared from view for an extended period of time and the amount of foraging behavior recorded during the hour-block was minimal, I tracked the crane's mate (when possible) in attempts to achieve the targeted 25 min of foraging behavior. Sessions were less than 25 min when both adult birds either walked or flew out of view for the remainder of the hour-block.

When watching videos, I recorded values for several random variables. Variables included total length of time spent foraging by the focal crane, total number of items consumed for each observed food type, and total numbers of steps, probes, and food manipulations (e.g., jabs, violent head-jerks, ripping) per observation session. Because blue crab was a food previously identified as important to whooping cranes, I identified apriori three categories within which to tally the number of blue crabs consumed: (1) small blue crab, i.e., crab with carapace width (CW) ≤25% of the crane's bill length, (2) medium blue crab, i.e., crab with CW >25% and ≤50% of the crane's bill length, and (3) large blue crab, i.e., crab with CW >50% of the crane's bill length. When food items were not identifiable by sight, food type was either inferred from crane behavior (seen previously with confirmed foods) or deemed unknown.

Typically, when a family group rather than adult pair alone was present on a territory, one parent (usually the smaller individual or female; Canadian Wildlife Service and U.S. Fish and Wildlife Service 2005) fed the young crane(s) while feeding herself, and the other parent (usually the larger individual or male) fed himself while remaining more vigilant. In the case that the focal adult crane was feeding a young crane (<10% of observations), each food item captured by the adult and subsequently consumed by either adult or young was classified as (1) processed (handled) and eaten by the adult, (2) given to a juvenile to be processed and eaten, or (3) shared between the adult and juvenile (i.e., adult processed food item and some or all edible matter was passed on to a juvenile). Summaries in this report combine all such data as though foraging adults consumed all food items, because few observations included an adult feeding young, the composition of foods consumed by adults versus fed to young was similar within any given observation session, and nearly 100% of all foods given to young were entirely processed by the adult.

In addition, several assumptions were made, which supported uniting data from adult-feeding and adult-and-young-feeding observations. First, I assumed frequency and duration of vigilant behavior were similar between parenting and non-parenting territorial adults. I further assumed that feeding of young did not alter the rate at which food items were encountered or captured by the adult. Rather, maximum encounter and capture rates should have been achieved regardless of whether foods were consumed strictly by the adult or by both adult and young. Feeding of young may cause parents (versus non-parenting adults) to feed for longer periods each day, thus altering daily time-activity patterns, but capture rates and effort exhibited while foraging should be similar among adults. I also assumed the feeding of young did not influence the diet patterns of parents through winter. Although foods may be exhausted at slightly earlier points in time during winter for territories with than without young (i.e., three versus two cranes exploiting resources), the effect of adults feeding young on the successive use of foods would have been difficult to quantify due to small sample size (number of territories) and the plausible influences of overall territory quality, age, experience and physical abilities of adults, and natural tendencies of juveniles toward independence.

Statistical Analysis

To examine the assemblage and proportional use of foods in the diet of cranes, I calculated per observation session the percentage of total dry mass in the diet comprised by each food type (hereafter, proportional use or percent diet). To examine the rewards achieved by foraging cranes, I calculated the rate of numeric intake (number of items min^{-1}) per food type. Dry mass (g min^{-1}), energy (kJ min^{-1}), protein (mg min^{-1}), and lipid (mg min^{-1}) intake rates were then derived using numeric intake, conversion factors for dry mass (DM; g item^{-1}), conversion factors for gross energy (kJ g^{-1}), crude protein (% DM), and lipid (% DM) contents, and coefficients for metabolizable energy, digestible protein, and digestible lipid (Table 4-1). Rates of total numeric, dry mass, energy, protein, and lipid intake were calculated by combining food types. To examine the costs of foraging, I computed indices of foraging effort, including rates of stepping (number of steps min^{-1}), probing (number of probes min^{-1}), and handling (number of food manipulations min^{-1}).

Table 4-1. Mass and nutritional values of foods in the whooping crane diet. Amounts of energy, protein and lipids available (Avail) to cranes from each food are computed by multiplying content by appropriate metabolizable energy (MEC) and digestible protein (DPC) and lipid (DLC) coefficients.

Food type	Wet mass (WM)	Dry mass (DM)		Energy			Protein			Lipid		
		%WM	g item^{-1}	Content kJ g^{-1}	MEC	Avail kJ g^{-1}	Content %DM	DPC	Avail %DM	Content %DM	DLC	Avail %DM
Wolfberry fruit[1] *Lycium carolinianum*	0.46	23.72	0.11	21.430	0.448	9.60	19.46	0.534	10.39	13.38	0.600	8.03
Blue crab[2] *Callinectes sapidus* (small, medium, large)	6.175 32.527 81.219	27.04	1.67 8.80 21.96	11.947	0.341	4.07	41.89	0.752	31.50	5.28	0.671	3.54
Clam[3], e.g., stout razor clam, *Tagelus plebius*			5.48	4.397	0.750	3.30	14.34	0.694	9.95	1.74	0.753	1.31
Blue crab or clam[4]			3.57			3.69			20.73			2.43
Snail, e.g., periwinkle, *Littorina* spp.			3.83[5]			2.51[6]	9.4[7]	0.694[8]	6.52	0.6[7]	0.753[8]	0.45
Insect, e.g., salt-marsh grasshopper species	4.0[9]	31.0[10]	1.24	22.609[10]	0.72[11]	16.28	64.9[12]	0.752[13]	48.81	13.8[12]	0.671[13]	9.26
Snail or insect[14]			2.53			9.39			27.66			4.86
Fiddler crab[15] e.g., *Uca* spp.			1.67			4.07			31.50			3.54
Blue or fiddler crab[15]			1.67			4.07			31.50			3.54
Snake, e.g., Gulf salt-marsh, *Nerodia clarkii*	150.0[16]	32.0[17]	48.00	18.333[18]	0.866[19]	15.88	65.5[20]	0.752[13]	49.26	27.88[21]	0.671[13]	18.70
Fish, e.g., whip eel, *Myrophis punctatus*	23.0[22]	25.0[23]	5.75	20.515[24]	0.866[19]	17.77	21.59[25]	0.752[13]	16.24	18.32[25]	0.671[13]	12.29
Unknown[26]			2.07			6.64			23.11			4.36

Table 4-1 continued.

[1] All values from Nelson et al. 1996, except wet mass from Chavez-Ramirez 1996.

[2] All values from Nelson et al. 1996, except wet mass from this study (see Chapter III); small crab=37 mm, medium crab=73 mm, large crab=110 mm.

[3] All values from Nelson et al. 1996, except dry mass derived using multiple sources. Dry body mass (without shell) of average-sized (70-mm) *T. plebius* clams during winter is about 1.6 g (Holland and Dean 1977). Jorde and Owen (1988) found calcium carbonate (as % of dry mass) in shelled organisms made up 6.1-9.4% less than ash. Adjusting the ash portion of *T. plebius* (78.55%; Nelson et al. 1996) by 7.75%, the shell equals about 70.8% of dry mass or 3.88 g, and total dry mass=3.88 g +1.6 g.

[4] Average of small blue crab and clam.

[5] Dry mass (3.5-g shell, 0.325-g body) for median-size (approximately 24.9 mm) *Littorina littorea* from Stefaniak et al. 2005.

[6] True metabolizable energy for gastropoda from Ballard et al. 2004.

[7] For *Littorina* spp. from Jorde and Owen 1988.

[8] For *Rangia cuneata* from Nelson et al. 1996.

[9] Estimate based on species of large grasshoppers from Greenlee et al. 2007.

[10] For grasshoppers/crickets (U.S. Environmental Protection Agency 1993; Bernard and Allen 1997); gross energy content=5.4 kcal x 4.1868 kJ kcal^{-1}.

[11] Assimilation efficiency for birds feeding on terrestrial insects (U.S. Environmental Protection Agency 1993).

[12] For domestic crickets *Acheta domestica* (Bernard and Allen1997).

[13] For blue crab *Callinectes sapidus* from Nelson et al. 1996.

[14] Average of snail and insect.

[15] All values same as those for small blue crab.

[16] Estimate based on body weight of similar-sized sea snake *Lapemis curtus* (60-80 cm, 150-200 g wet mass; Westhoff et al. 2005).

[17] Average of values from Vitt 1978 (28.0%, various desert snakes), Koplin et al. 1980 (34.0%, garter *Thamnophis sirtalis*), and Secor and Nagy 2003 (34.9%, diamondback *Nerodia rhombifer*).

[18] Average of values from Vitt 1978 (4.657 kcal=(5.613 kcal x % ash-free dry mass)/100) and Koplin et al. 1980 (4.10 kcal); gross energy content=4.379 kcal x 4.1868 kJ kcal^{-1}.

[19] For great blue herons feeding on various fish from Bennett et al. 1995.

[20] Average of values for bearded dragon *Pogona vitteceps* and green anole *Anolis carolinensis* from Cosgrove et al. 2002.

[21] Average for sea snake *Lapemis curtus* <80 cm total length (Secor and Nagy 2003).

[22] Value for a whip eel of 34 cm total length measured in this study.

[23] Average of values for bony fishes (U.S. Environmental Protection Agency 1993), salmon/trout (Bennett et al. 1995), channel catfish (Brugger 1993), sandeel (Massias and Becker 1990).

[24] For bony fishes (U.S. Environmental Protection Agency 1993; gross energy content=4.9 kcal x 4.1868 kJ kcal^{-1}); supported by resources in footnote 23.

[25] For sandeel from Massias and Becker 1990.

[26] Average of values for wolfberry fruit, small blue crab, clam, snail, insect, and fiddler crab.

Using values derived per session, I summarized each computed variable per month (within winter) and per winter. Monthly means (±1 SE) were calculated per territory (mean across sessions within each month x territory combination; equivalent to the experimental unit) and overall (mean across territories for each month), and winter means (±1 SE) for each territory and overall were simply determined by averaging across respective monthly means. Only sessions containing ≥4 min of foraging behavior and of which I was confident of observing ≥50% of all feeding events were incorporated into summaries. Data acquired at BJ were not included in overall means or corresponding statistical analyses because few observations were conducted in comparison to other territories.

Temporal variability in diet within winters was examined using the Pearson chi-square statistic. Controlling for winter, the odds of cranes consuming a target food type (e.g., wolfberry fruit) versus all other foods combined were compared between months for all pairs of months. Compared values were overall monthly means of percent diet per food type. Inter-annual variability was examined using the Breslow-Day test of homogeneity of odds ratios to compare odds ratios for defined pairs of months between winters (e.g., winter 1 versus 2 for November:December). The Pearson chi-square statistic was also used to examine spatial variability. Within each month that proportional use of a target food was >0% for any territory (including BJ), the odds of consuming that food were compared between territories for all pairs of territories. Compared values were monthly means of percent diet by territory and food type (2 x 2 table). Intake rates and measures of foraging effort did not undergo statistical testing.

Findings related to the rewards and costs of foraging were integrated to explore the efficiency of crane foraging. Several indices of foraging efficiency were used, namely numeric, dry mass, energy, protein, and lipid. Efficiency was defined as the ratio of mean total numeric, dry mass, energy, protein, or lipid intake rate to total foraging effort (total number of foraging movements min^{-1}). Because I was not always able to count steps, probes, and food manipulations within the same observation session (at the sub-sample level), total foraging effort was determined by adding together the mean rates of stepping, probing, and handling at the level of the experimental unit (winter x month x territory). Efficiency was then derived per experimental unit and summarized by winter, month within winter, and territory within winter.

Comparisons of efficiency among food types were possible by first identifying the principal foods contributing to total intake at the level of experimental unit. Principal foods were defined as those foods contributing most to intake that, when combined, accounted for 80% of mean total intake. Depending on level of contribution to intake, principal foods fell into one of four categories: (1) sole principal food, (2) dominant food, (3) co-dominant food, and (4) lesser principal food. Sole principal foods were those that alone accounted for ≥80% of total intake (i.e., were the only principal food). Dominant foods were those that contributed at least twice as much to intake as any other food in the crane diet but were not the only principal food (i.e., alone comprised <80% of total intake). Co-dominant foods were one of two dominant foods in the crane diet, contributing to intake more than one-half but less than two times as much as their co-dominant partner food and at least twice as much as all other foods. Only in rare cases did the contribution to intake of a co-dominant food for one winter x month x territory diet exceed that of a dominant food in another diet. Lesser principal foods were simply those of which were compliments to dominant or co-dominant foods or were in mixed diets where, of three or more principal foods, no one food contributed twice as much to intake as any other.

Efficiency associated with each food type was examined by computing mean, minimum, and maximum efficiency values for each index x food type x minimum level of contribution to intake. For example, when examining wolfberry fruit at the level of *lesser principal food*, mean numeric efficiency of foraging encompassed the efficiency values from all experimental units where wolfberry fruit was at least a principal food (i.e., sole principal food, dominant food, co-dominant food, or lesser principal food). Additionally, when snails-and-insects represented the *sole principal food*, mean energy efficiency accounted for only those experimental units where snails and insects comprised ≥80% of energy intake. These calculations allowed for comparisons among foods, but also demonstrated the effect of successively adding foods to a monotypic diet.

For each index of efficiency x minimum level of contribution to intake, foods were ranked in descending order of computed efficiency. Efficiencies were ln(x+1)-transformed due to non-normal distributions and then analyzed using one-way ANOVA to determine if they differed by food type. Multiple comparisons were performed using the Waller-Duncan method (alpha=0.05) to identify differences among foods.

Results

Environmental Conditions

Minimum temperatures fluctuated around normal during both winter 1 (2004-2005) and winter 2 (2005-2006; Table 4-2). Only temperatures during February differed between winters. Total cumulative precipitation was nearly twice normal during winter 1 and only two-thirds normal in winter 2. Rainfall levels were well above normal during November of both winters, but, during winter 2, monthly levels quickly fell and stayed below normal for the remainder of the season. Consequently, the salt-marsh was fully inundated during winter 1 (i.e., 100% of pond, creek, and adjacent shallow bay habitat remained covered with water) but minimally inundated, disconnected, and in great part dry (unsaturated) during December-February of winter 2.

Data Collection

During winters 1 and 2, respectively, 105 and 120 observation sessions were successfully conducted from over 300 and 400 hours attempted. Observations were limited at BJ and occurred during November-January of winter 1 (*n*=5) and December of winter 2 (*n*=2) only, because cranes were infrequently present and did not actively defend the site during this study. Unforeseen circumstances prevented observations from being formally conducted at any territory during February 2005. In some cases, the numbers of observations used in data summary and analysis were less than the total conducted, because inclement conditions (e.g., high wind speed and/or prevalence of heat waves) made data retrieval from videos difficult (see Table 4-3).

Table 4-2. Mean minimum temperature, cumulative precipitation, and percent area of salt-marsh inundated during November-March of winters 2004-2005 (winter 1) and 2005-2006 (winter 2). Normal minimum temperature and cumulative precipitation values are based on data from 1971-2000. Inundation within salt-marsh is listed for connected pond open water (CPO) and edge (CPE) and unconnected pond open water (UPO) and edge (UPE) habitats.

	Minimum Temperature (°C)[1]			Cumulative Precipitation (cm)[1]			Area Inundated (%)[2]							
							Winter 1				Winter 2			
Month	Winter 1	Winter 2	Normal	Winter 1	Winter 2	Normal	CPO	CPE	UPO	UPE	CPO	CPE	UPO	UPE
November	13.9	13.3	12.7	15.5	14.3	8.9	100	100	100	100	100	100	100	100
December	6.8	6.2	8.2	15.7	4.3	6.1	100	100	100	100	83	75	100	100
January	9.6	9.1	6.9	2.3	1.1	7.3	100	100	100	100	17	17	44	19
February	11.6	7.8	8.9	8.3	1.7	6.9	100	100	100	100	58	58	13	6
March	13.1	15.8	12.8	26.2	2.6	6.1	100	100	100	100	100	100	100	100
Total				68.1	24.0	35.3								

[1] Data from Aransas National Wildlife Refuge weather station, National Weather Service, National Oceanic and Atmospheric Administration.

[2] Based on data collected for Chapter II; % area inundated = number of sample locations with standing water / total number of random sample locations.

Table 4-3. Numbers of observations (i.e., samples sizes) used to summarize response variables for each combination of winter, month, and territory.

		Winter 2004-2005						Winter 2005-2006					
Variable	Territory	Nov	Dec	Jan	Feb	Mar	Total	Nov	Dec	Jan	Feb	Mar	Total
Percent diet, Intake rates	BR	4	8	5	0	9	26	2	9	8	3	9	31
	PC	0	6	2	0	9	17	5	6	3	6	6	26
	PL	0	10	3	0	9	22	5	5	7	4	1	22
	BJ	3	1	1	0	0	5	0	2	0	0	0	2
	Total	7	25	11	0	27	70	12	22	18	13	16	81
Stepping rate	BR	4	8	7	0	12	31	3	9	9	3	12	36
	PC	0	6	3	0	12	21	6	6	3	6	9	30
	PL	1	11	5	0	9	26	5	5	8	4	4	26
	BJ	3	1	1	0	0	5	0	2	0	0	1	3
	Total	8	26	16	0	33	83	14	22	20	13	26	95
Probing rate	BR	4	8	7	0	9	28	2	9	9	2	6	28
	PC	0	4	1	0	5	10	6	4	3	3	6	22
	PL	0	6	2	0	8	16	3	5	8	4	1	21
	BJ	2	1	1	0	0	4	0	0	0	0	0	0
	Total	6	19	11	0	22	58	11	18	20	9	13	71
Handling rate	BR	4	8	5	0	9	26	1	9	9	2	6	27
	PC	0	6	1	0	5	12	6	5	3	3	6	23
	PL	1	8	2	0	8	19	4	5	8	4	1	22
	BJ	2	1	1	0	2	4	0	0	0	0	0	0
	Total	7	23	9	0	22	61	11	19	20	9	13	72

Proportional Use of Foods

The whooping crane diet comprised wolfberry fruit (*Lycium carolinianum*), blue crab (*Callinectes* spp.), clam (*Tagelus* spp.), snails (e.g., marsh periwinkle, *Littorina* spp.), insects (e.g., grasshoppers), and fiddler crab (*Uca* spp.) during both winter 1 and 2 (Figs. 4-4 and 4-5). Snake (e.g., Gulf salt-marsh snake, *Nerodia clarkia*) and fish (whip eel, *Myrophis punctatus*) were observed in the diet on one occasion each during the first and second winter, respectively. With the exception of wolfberry fruit, the overall mean proportional use of foods (percent of dry mass) in the diet differed considerably between winters (Fig. 4-4). Percent of the diet containing blue crab (all sizes combined) declined by over 80%, clam and blue crab-or-clam combined nearly doubled, and snail, insect and snail-or-insect combined (hereafter, snail-and-insect) tripled from winter 1 to 2. Percent diet of all other foods combined remained consistent between winters at <2%.

Wolfberry fruit was the single-targeted food of territorial cranes in November of winter 1 (100%; Fig. 4-5). During winter 2, the fruit was a principal food in November (47%) and the dominant food of December (90%). The odds of cranes consuming wolfberry fruit differed for all pairs of months during both winters, except for those pairs exclusively incorporating January, February and March when fruit was not consumed (Table 4-4). Only the November:December odds ratio differed between winters, as peak proportional use occurred in November of winter 1 but December of winter 2.

During winter 1, blue crab was the sole principal food of December (90%), a co-dominant food in January (56%), and one of few principal foods in March (28.1%; Fig. 4-5). Medium blue crab made up 50-91% of all blue crab consumed. During winter 2,

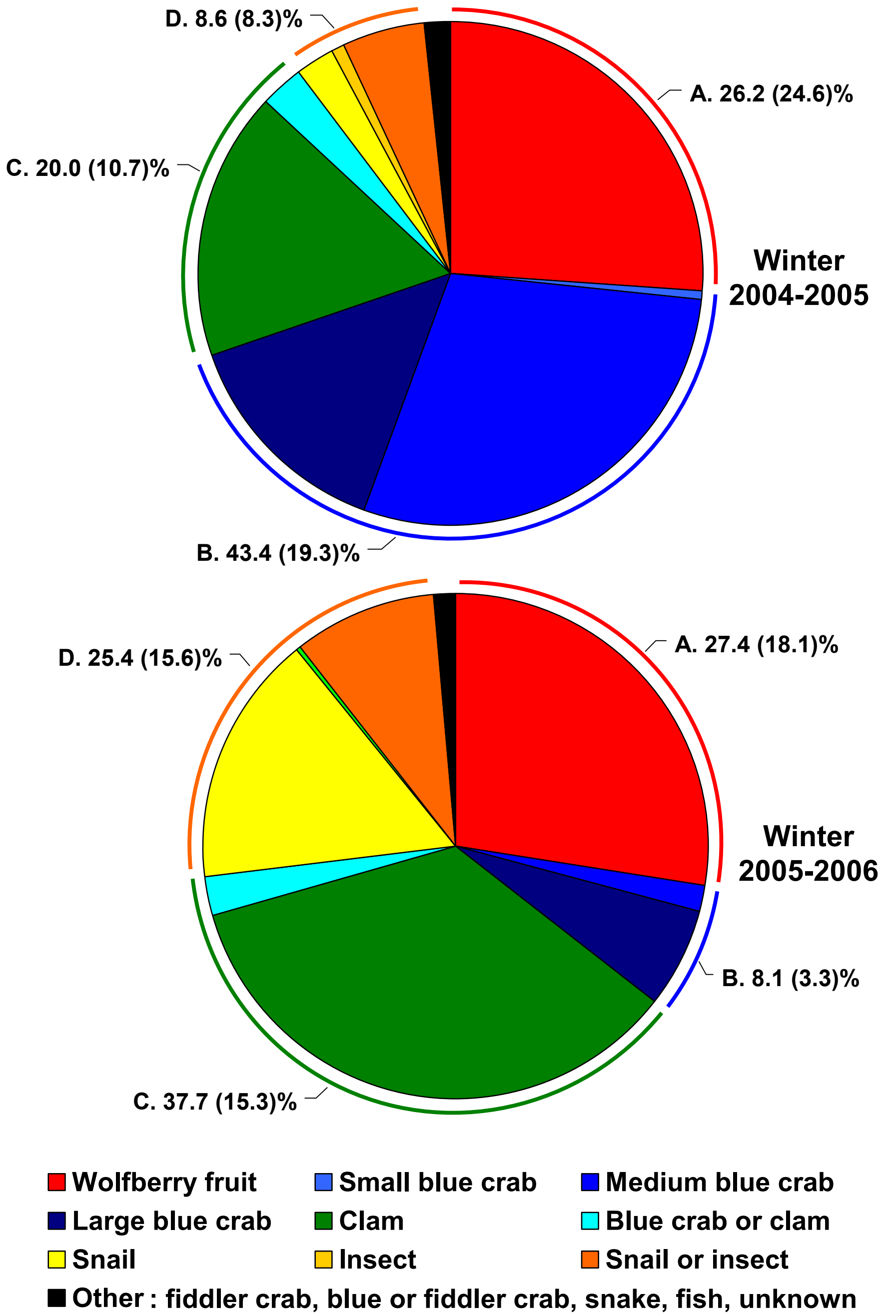

Fig. 4-4. Mean percent dry mass in whooping crane diet comprised by each food type during winter 2004-2005 (*n*=4 mon; top) and 2005-2006 (*n*=5 mon; bottom). Mean percent (±1 SE) is also identified above for each of four major groups of foods, including (A) wolfberry fruit, (B) all blue crabs combined, (C) clam and blue crab-or-clam combined, and (D) snail, insect and snail-or-insect combined. Standard errors represent variability among months. Data from BJ are not incorporated in above summaries.

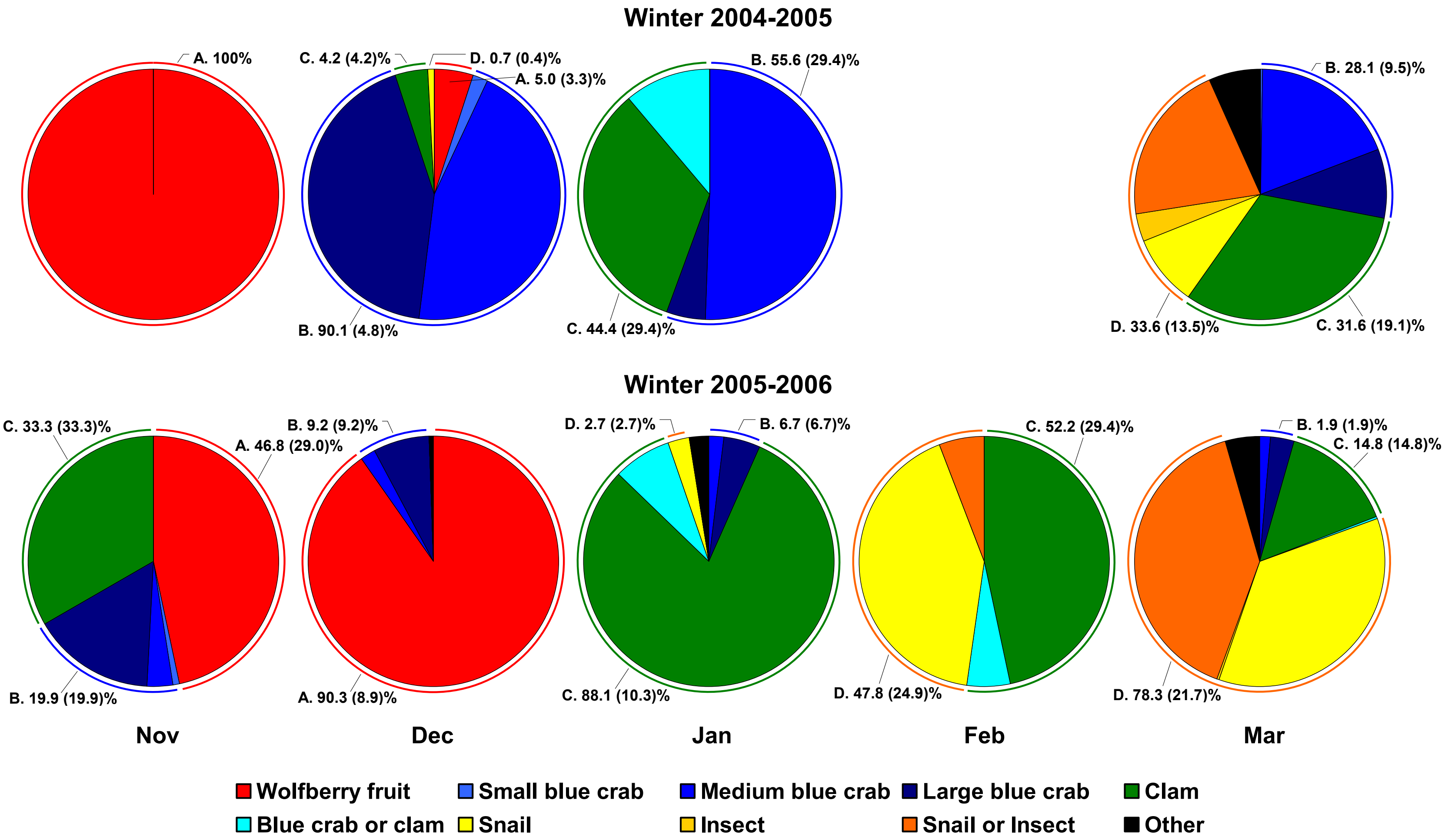

Fig. 4-5. Mean percent dry mass in the whooping crane diet per food type during November-March of winters 2004-2005 (top) and 2005-2006 (bottom). Mean percent (±1 SE) is listed for (A) wolfberry fruit, (B) all blue crabs combined, (C) clam and blue crab-or-clam combined, and (D) snail, insect and snail-or-insect combined. Standard errors represent variability among territories (*n*=3 for all months, except *n*=1 in November 2004). No data were collected during February 2005.

Table 4-4. Results of tests examining differences in percent diet between months and winters for all territories (except BJ) combined. Chi-square values (*p*-values, below) are shown for Pearson's chi-square test of association for winter 1 (2004-2005) and winter 2 (2005-2006) and for the Breslow-Day test of homogeneity of odds ratios for comparing association patterns between winters. Values are significant when *p*-value <0.05 (*), <0.01 (**), <0.001 (***), or <0.0001 (****). Statistical significance within winters indicates the odds of cranes consuming the target food item (e.g., wolfberry fruits) versus all other foods combined were significantly different between the two months being compared. Comparison of association patterns between winters results in statistical significance when the odds ratios for the two winters differ significantly.

	Test statistics for association								Test statistics for homogeneity of odds ratios winter 1 vs. 2			
Food/	Winter 1				Winter 2							
Month	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb
Wolfberry fruit												
Dec	**181.00** ****				**43.83** ****				**207.48** ****			
Jan	**199.98** ****	**5.1068** ****			**61.08** ****	**164.53** ****			0.3685 0.5438	0.0237 0.8777		
Feb	–	–	–		**61.08** ****	**164.53** ****	0.000 1.000		–	–	–	
Mar	**199.98** ****	**5.1068** ****	0.000 1.000	–	**61.08** ****	**164.53** ****	0.000 1.000	0.000 1.000	0.3685 0.5438	0.0237 0.8777	0.000 1.000	–
Blue crab - small												
Dec	1.8507 0.1737				0.5760 0.4479				2.4129 0.1203			
Jan	0.000 1.000	1.8506 0.1737			0.5760 0.4479	0.000 1.000			0.1445 0.7038	0.4632 0.4961		
Feb	–	–	–		0.5761 0.4479	0.000 1.000	0.000 1.000		–	–	–	
Mar	0.1511 0.6975	1.4367 0.2307	0.1511 0.6975		0.5760 0.4479	0.000 1.000	0.000 1.000	0.000 1.000	0.7220 0.3955	0.0051 0.9432	0.0383 0.8449	–

Table 4-4 continued.

	Test statistics for association								Test statistics for homogeneity of odds ratios winter 1 vs. 2			
	Winter 1				Winter 2							
Month	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb
Blue crab - medium												
Dec	**58.501** ****				0.3770 0.5392				**32.379** ****			
Jan	**67.570** ****	0.5511 0.4579			0.4083 0.5228	0.0007 0.9794			**36.497** ****	0.0495 0.8239		
Feb	–	–	–		3.4066 0.0649	1.9730 0.1601	1.9218 0.1657		–	–	–	
Mar	**21.153** ****	**15.639** ****	**21.688** ****	–	0.9200 0.3375	0.1317 0.7166	0.1139 0.7357	1.3120 0.2520	**16.488** ****	0.5273 0.4677	0.8832 0.3473	–
Blue crab - large												
Dec	**54.814** ****				3.7369 0.0532				**45.447** ****			
Jan	**5.1749** *	**39.496** ****			**6.7398** **	0.5293 0.4669			**10.919** ***	**9.0148** **		
Feb	–	–	–		**17.324** ****	**7.4659** **	**4.8734** *		–	–	–	
Mar	**9.2384** **	**30.434** ****	1.1097 0.2922	–	**9.2651** **	1.5641 0.2111	0.2916 0.5892	3.3131 0.0687	**18.236** ****	2.4778 0.1155	1.1594 0.2816	–
Clam and blue crab/clam combined												
Dec	**4.2525** *				**39.997** ****				**38.632** ****			
Jan	**57.140** ****	**44.087** ****			**62.788** ****	**157.35** ****			**5.3566** *	**15.544** ****		

Table 4-4 continued.

	Test statistics for association								Test statistics for homogeneity of odds ratios winter 1 vs. 2			
	Winter 1				Winter 2							
Month	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb	Nov	Dec	Jan	Feb
Clam and blue crab/clam combined continued.												
Feb	–	–	–		**7.2552** **	**70.594** ****	**30.736** ****		–	–	–	
Mar	**37.478** ****	**25.578** ****	3.5196 0.0606	–	**9.3808** **	**15.997** ****	**107.40** ****	**31.335** ****	**45.067** ****	1.6379 0.2006	**42.039** ****	–
Snail, insect, and snail/insect combined												
Dec	0.7280 0.3935				0.0000 1.0000				0.1825 0.6692			
Jan	0.0000 1.0000	0.7279 0.3936			2.7757 0.0957	2.7757 0.0957			0.6944 0.4047	3.4727 0.0624		
Feb	–	–	–		**62.840** ****	**62.841** ****	**53.788** ****		–	–	–	
Mar	**40.335** ****	**37.952** ****	**40.335** ****	–	**123.20** ****	**123.20** ****	**113.04** ****	**17.150** ****	0.0018 0.9658	2.5229 0.1122	0.6293 0.4276	–
Other												
Dec	0.0000 1.0000				0.5691 0.4506				1.1428 0.7055			
Jan	0.0000 1.0000	0.0000 1.0000			2.5557 0.1099	1.2548 0.2626			0.6394 0.4239	0.0014 0.9705		
Feb	–	–	–		0.0000 1.0000	0.5691 0.4506	2.5557 0.1099		–	–	–	
Mar	**6.9828** **	**6.9825** **	**6.9827** **	–	**4.4706** *	3.0018 0.0832	0.5132 0.4737	**4.4707** *	0.0001 0.9918	0.8233 0.3642	3.0729 0.0796	–

blue crab made up 20% of the diet in November but was minimally used during the remainder of the season (0-7%). Of all blue crab consumed in winter 2, 71-80% comprised large crab. The odds of cranes consuming small blue crab during either winter were near or equal to zero and statistically similar among all winter months (Table 4-4). The odds of cranes consuming medium blue crab were similar between December and January but significantly different between all other pairs of months during winter 1; odds during winter 2 were similar among all months. Proportional use of large blue crab during winter 1 was variable with the odds of consumption different for all pairs of months except January:March. During winter 2, the odds of cranes consuming large blue crab generally (though slightly) declined from November to February and then increased subtly in March.

Proportional use of clam by whooping cranes was greatest in January (33%) and March (32%) in winter 1 (Fig. 4-5). In January, a sizeable portion of the diet (11%) was made up of food items that were either blue crab or clam. These items were swallowed whole by cranes when actively foraging for clam and were likely clam. As a result, up to 44% of the January diet comprised clam. During winter 2, clam and blue crab-or-clam combined (hereafter, clam) were a significant food (15-88%) for cranes in all months except December. The odds of clam being consumed differed among all months except January:March in winter 1 and among all months in winter 2 (Table 4-4). However, differences evident in winter 2 were more pronounced than those in winter 1.

During both winters, the discontinuation of wolfberry fruit and gradual decrease of each blue crab and clam in the crane diet was offset by a marked increase in use of snail-and-insect (winter 1, maximum 34%; winter 2, maximum 78%). The odds of cranes consuming snail-and-insect were greater in March than all previous months during both winters.

The winter diets of whooping cranes observed in this study were somewhat distinctive among territories (Figs. 4-6, 4-7, and 4-8; Table 4-5). For instance, clam was consumed in greater proportion and more consistently across months at BR than any other territory during both winters. At BR, only one month during each winter (no more than two months total) was wholly allotted to each wolfberry fruit and blue crab. Further, during both winters, snail-and-insect made up only a moderate fraction of the crane diet and was less consistently used at BR than any other territory studied.

Proportional use of wolfberry fruit at each PC and PL was as much as or more than use at either BR or BJ. This was evident during winter 2 (Fig. 4-7) but not formally so during winter 1 (Fig. 4-6), because cranes were rarely seen at PC and PL in November 2004 and foods were not recorded (Fig. 4-8). Cranes at PC were seen on two occasions in November while I sampled blue crab (see Chapters II-III) but not when formal observations were attempted. However, use of emergent salt-marsh vegetation and steady searching behavior by cranes during incidental observations circumstantially suggested cranes were feeding on wolfberry fruit. At PL, cranes were formally observed only once. During the observation, cranes foraged in mixed, emergent salt-marsh and repeatedly “probed” into vegetation, but any foods that were obtained were not visible. Probes into vegetation were likely feeding events associated with wolfberry fruit, demonstrating 100% proportional use of fruit and an intake rate of 8.32 fruits min^{-1}.

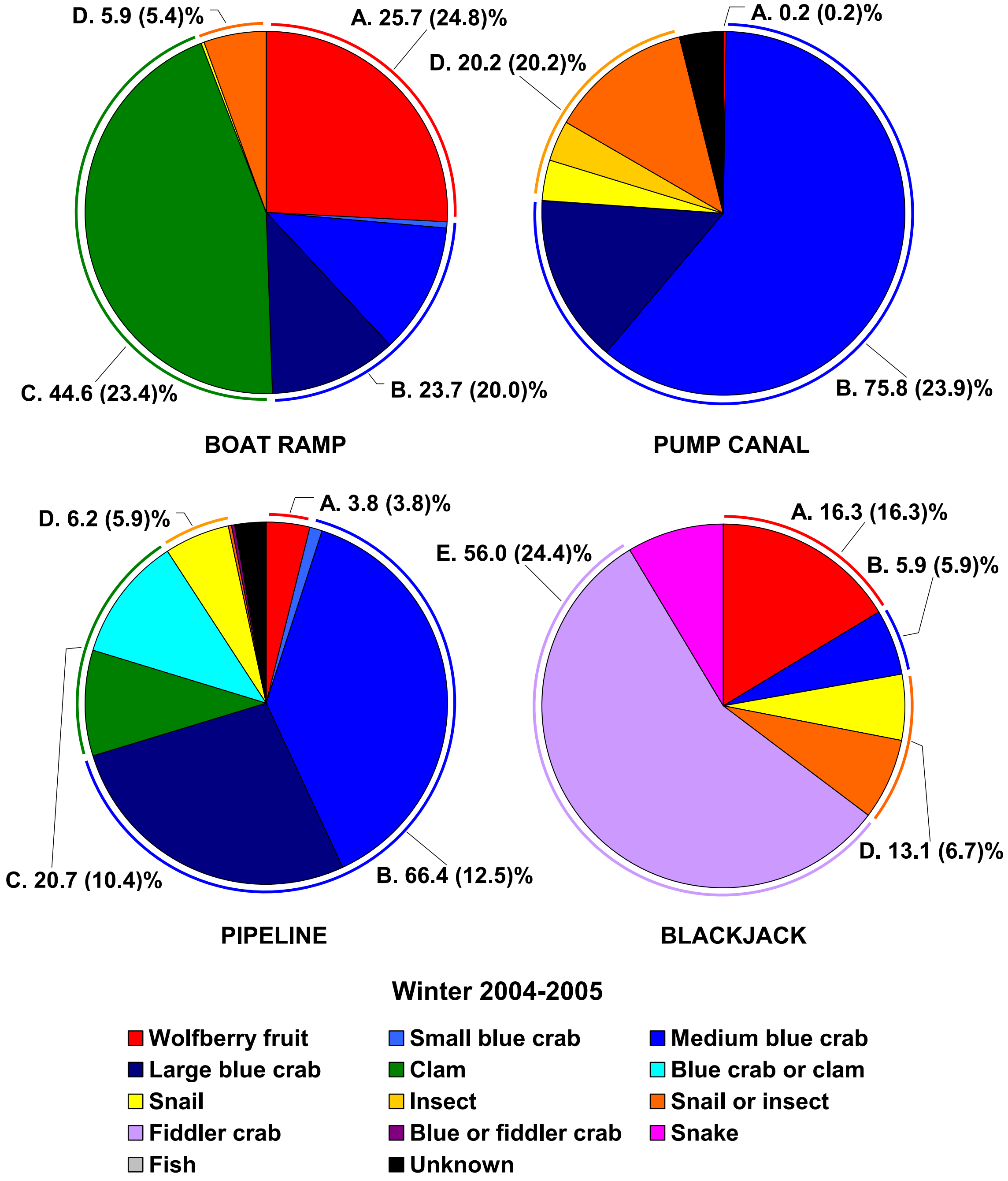

Fig. 4-6. Mean percent dry mass in whooping crane diet comprised by each food type during winter 2004-2005 for four crane territories. Mean percent (±1 SE) is also identified for each of five major groups of foods, including (A) wolfberry fruit, (B) all blue crabs combined, (C) clam and blue crab-or-clam combined, (D) snail, insect and snail-or-insect combined, and (E) fiddler crabs. Standard errors represent variability among months (*n*=4 mon for BR and *n*=3 mon for each PC, PL, and BJ).

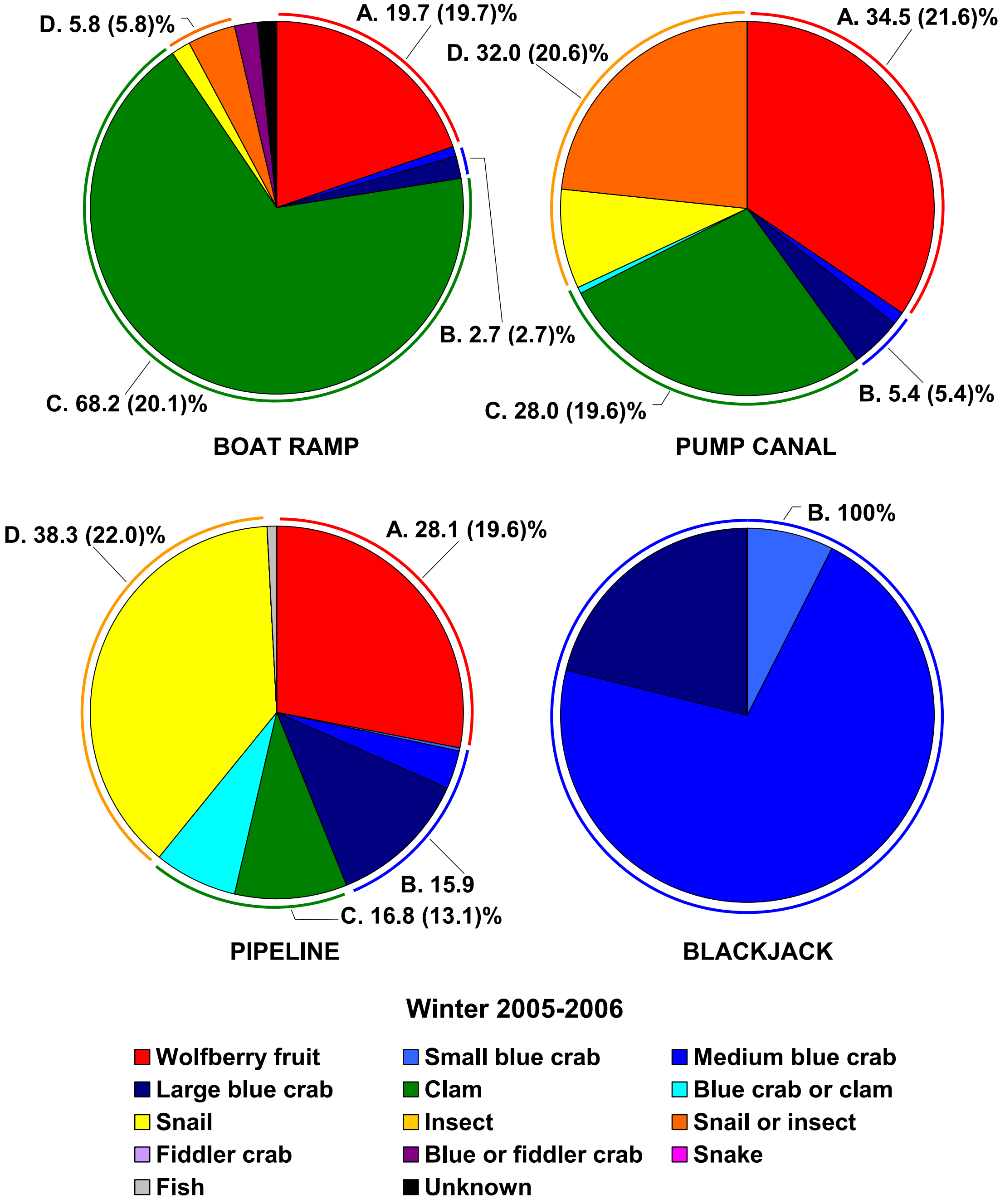

Fig. 4-7. Mean percent dry mass in whooping crane diet comprised by each food type during winter 2005-2006 for four crane territories. Mean percent (±1 SE) is also identified for each of four major groups of foods, including (A) wolfberry fruit, (B) all blue crabs combined, (C) clam and blue crab-or-clam combined, and (D) snail, insect and snail-or-insect combined. Standard errors represent variability among months (*n*=5 mon for all territories, except *n*=1 mon for BJ).

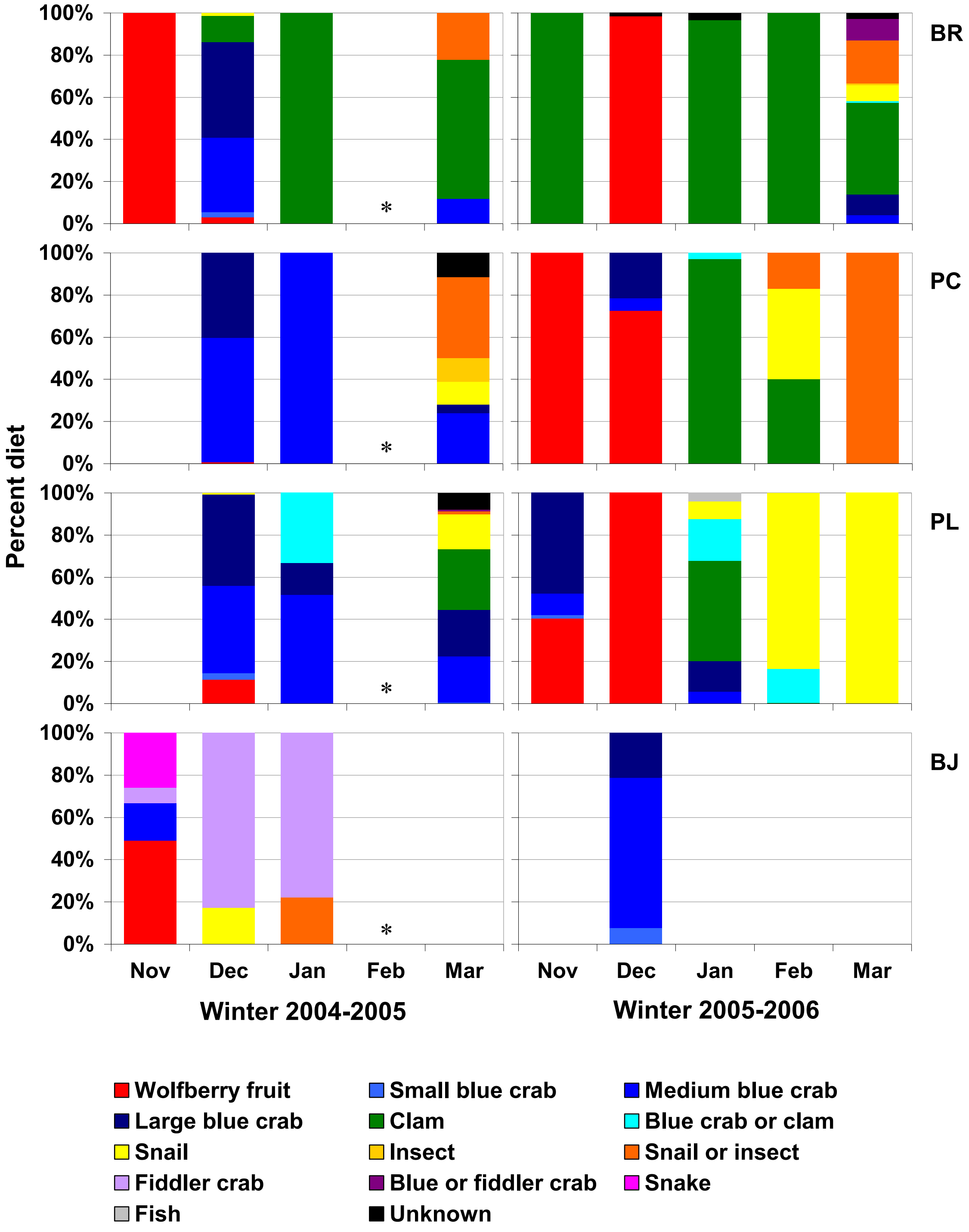

Fig. 4-8. Mean percent dry mass of foods in the whooping crane diet during November-March of winters 2004-2005 (left) and 2005-2006 (right) for each of four crane territories. Territories included Boat Ramp (BR), Pump Canal (PC), Pipeline (PL), and Blackjack (BJ). No data were collected in February 2005 (*).

Table 4-5. Comparisons of percent total dry mass among territories for foods in the whooping crane diet during November-March of winters 2004-2005 and 2005-2006. For each food type x winter x month combination, territories are listed in decreasing order of percent diet and, using Pearson's chi-square test of association, are considered significantly different when the odds of cranes consuming the target food item (e.g., wolfberry fruits) versus all other foods combined were statistically different (alpha=0.05) between each pair of territories being compared. Statistical differences are indicated by differences in letters. The food type *Clam* includes both clam and blue crab-or-clam categories, *Snail and insect* includes snail, insect, and snail-or-insect categories, and *Other* includes fiddler crab, blue-or-fiddler crab, snake, fish, and unknown. No data were collected in February 2005.

	Winter 2004-2005				Winter 2005-2006				
Food type	Nov	Dec	Jan	Mar	Nov	Dec	Jan	Feb	Mar
Wolfberry fruit	BR a	PL a			PC a	PL a			
	BJ b	BR b			PL b	BR a			
		PC b			BR c	PC b			
		BJ b				BJ c			
Blue crab small		PL a		PL a	PL a	BJ a			
		BR a		BR a	BR a	BR b			
		PC a		PC a	PC a	PC b			
		BJ a				PL b			
Blue crab medium	BJ a	PC a	PC a	PC a	PL a	BJ a	PL a		BR a
	BR b	PL b	PL b	PL ab	BR b	PC b	BR b		PC b
		BR b	BR c	BR b	PC b	BR c	PC b		PL b
		BJ c	BJ c			PL c			
Blue crab large		BR a	PL a	PL a	PL a	PC a	PL a		BR a
		PL a	BR b	PC b	BR b	BJ a	BR b		PC b
		PC a	PC b	BR c	PC b	BR b	PC b		PL b
		BJ b	BJ b			PL b			
Clam		BR a	BR a	BR a	BR a		PC a	BR a	BR a
		PC b	PL b	PL b	PC b		BR a	PC b	PC b
		PL b	PC c	PC c	PL b		PL b	PL c	PL b
		BJ b	BJ c						
Snail and insect		BJ a	BJ a	PC a			PL a	PL a	PL a
		BR b	BR b	BR b			BR b	PC b	PC a
		PL b	PC b	PL b			PC b	BR c	BR b
		PC b	PL b						
Other	BJ a	BJ a	BJ a	PC a		BR a	PL a	BR a	BR a
	BR b	BR b	BR b	PL a		PC a	BR ab	PC a	PC b
		PC b	PC b	BR b		PL a	PC b	PL a	PL b
		PL b	PL b			BJ a			

Subtle differences were observed between the crane diets of PC and PL (Figs. 4-6, 4-7, and 4-8; Table 4-5). Proportional use of wolfberry fruit was somewhat greater and peaked earlier at PC than PL during winter 2. Additionally, the percent of medium blue crab in the diet was greater at PC than PL during winter 1, but use of large blue crab was greater and occurred more consistently at PL during both winters. Lastly, insect consumption was observed at PC but not at PL during either winter.

In both winters, when cranes used the BJ territory, proportional use of wolfberry fruit, blue crab, and clam was significantly less than that observed at other territories (Figs. 4-6, 4-7, and 4-8; Table 4-5). Fiddler crab was the dominant and most consistently used food during winter 1, and blue crab was the only food consumed during winter 2. Use of feeding habitat at BJ, however, occurred during an extremely brief period of time (<1 month) in winter 2.

Foraging Rewards

Foraging rewards incurred by whooping cranes, as measured by numeric, dry mass, energy, protein, and lipid intake rates, were over twice as much in winter 2 as winter 1 (Table 4-6). Intake of wolfberry fruit increased nearly fourfold from winter 1 to 2, despite concurrent findings of equivalent proportional use. Dry mass intake of blue crab (all sizes combined) declined 70%, and medium and large blue crab decreased 90% and 43%, respectively, from winter 1 to 2. Consumption of blue crab was predominantly of medium crab during winter 1 (1.5 times that of large crab) and large crab during winter 2 (over four times that of medium crab). Small blue crab was rarely consumed

Table 4-6. Mean (±1 SE) numeric, dry mass, energy, protein, and lipid intake rates for whooping cranes per food type during winters 2004-2005 (winter 1; *n*=4 mon) and 2005-2006 (winter 2; *n*=5 mon). The food type *Other* includes fiddler crab, blue-or-fiddler crab, snake, fish, and unknown. Standard errors represent variability among months within winter, and trace values (tr) are those <0.01. Data from BJ are not incorporated.

	Intake rate									
	Numeric (number min^{-1})		Dry mass (g min^{-1})		Energy (kJ min^{-1})		Protein (mg min^{-1})		Lipid (mg min^{-1})	
Food type	Winter 1	Winter 2	Winter 1	Winter 2	Winter 1	Winter 2	Winter 1	Winter 2	Winter 1	Winter 2
Wolfberry fruit	1.38 ± 1.28	5.11 ± 3.47	0.15 ± 0.14	0.56 ± 0.38	1.45 ± 1.34	5.35 ± 3.64	15.69 ± 14.54	57.96 ± 39.37	12.12 ± 11.23	44.77 ± 30.42
Blue crab small	0.01 ± 0.01	tr tr	0.01 ± 0.01	tr tr	0.04 ± 0.03	0.02 ± 0.02	2.89 ± 2.57	1.41 ± 1.41	0.32 ± 0.29	0.16 ± 0.16
Blue crab medium	0.06 ± 0.03	0.01 tr	0.55 ± 0.26	0.05 ± 0.03	2.25 ± 1.07	0.22 ± 0.10	173.64 ± 82.46	16.71 ± 8.01	19.53 ± 9.27	1.88 ± 0.90
Blue crab large	0.02 ± 0.01	0.01 ± 0.01	0.38 ± 0.28	0.22 ± 0.13	1.55 ± 1.16	0.89 ± 0.51	119.91 ± 89.64	68.52 ± 39.70	13.49 ± 10.08	7.71 ± 4.46
Clam	0.19 ± 0.10	0.19 ± 0.08	1.05 ± 0.52	1.06 ± 0.42	3.47 ± 1.72	3.51 ± 1.39	104.85 ± 51.81	105.84 ± 42.03	13.80 ± 6.82	13.93 ± 5.53
Blue crab or clam	0.01 ± 0.01	tr tr	0.04 ± 0.04	0.02 ± 0.01	0.14 ± 0.14	0.06 ± 0.03	7.72 ± 7.72	3.36 ± 1.94	0.90 ± 0.90	0.39 ± 0.23
Snail	0.05 ± 0.05	1.18 ± 0.77	0.19 ± 0.18	4.50 ± 2.96	0.47 ± 0.45	11.29 ± 7.43	12.18 ± 11.81	293.47 ± 193.07	0.84 ± 0.82	20.32 ± 13.37
Insect	0.28 ± 0.28	tr tr	0.35 ± 0.35	tr tr	5.64 ± 5.64	0.01 ± 0.01	169.11 ± 169.11	0.20 ± 0.20	32.09 ± 32.09	0.04 ± 0.04
Snail or insect	0.17 ± 0.17	1.50 ± 1.48	0.44 ± 0.44	3.79 ± 3.74	4.14 ± 4.14	35.60 ± 35.18	121.93 ± 121.93	1048.49 ± 1035.88	21.40 ± 21.40	184.04 ± 181.82
Other	0.01 ± 0.01	0.01 ± 0.01	0.02 ± 0.02	0.02 ± 0.01	0.13 ± 0.13	0.16 ± 0.10	4.76 ± 4.76	5.64 ± 3.28	0.86 ± 0.86	1.10 ± 0.67
Total (all foods)	2.18 ± 1.10	8.01 ± 2.87	3.18 ± 1.14	10.22 ± 4.98	19.27 ± 9.98	57.10 ± 35.74	732.67 ± 306.60	1601.60 ± 1060.90	115.35 ± 48.46	274.35 ± 172.45

and comprised less than 2% of all blue crab consumed during either winter. Intake of clam was consistent between winters. Snail-and-insect was consumed in quantities 8.5 times greater during winter 2 than 1, and all other foods combined comprised less than 1% of total intake.

Numeric intake rate

Wolfberry fruit was consumed by whooping cranes at an overall mean rate of numeric intake greater than any other food consumed during both winters (Table 4-6). The next most frequently consumed foods were snail-and-insect at intake rates 35-52% that of wolfberry fruit and clam at rates 4-15% that of wolfberry fruit. Monthly numeric intake was highest during early winter (November-December) when wolfberry fruit was actively consumed, followed by late winter when snail-and-insect was the major food group targeted (Fig. 4-8). The lowest numeric intake occurred in January, when food items consumed by cranes were principally clam. These patterns were also seen at the level of a crane territory, where cranes achieved higher overall intake rates by incorporating more wolfberry fruit and snail-and-insect and less blue crab into their diet (Table 4-7). Alternatively, cranes at BJ in winter 1 attained a relatively high rate of numeric intake by targeting both wolfberry fruit and fiddler crab.

Dry mass intake rate

Cranes achieved the highest overall mean rates of dry mass intake by feeding for clam and snail-and-insect (Table 4-6). The overall mean intake of blue crab (all sizes

Table 4-7. Mean (±1 SE) total numeric intake rates (number of food items min^{-1}) for whooping cranes of each territory during the winter months of 2004-2005 and 2005-2006. For each combination of winter, month, and territory, principal foods and their percent contribution to total intake rate (in parentheses) are also listed. Foods included wolfberry fruit (wb), small (sbc), medium (mbc), and large (lbc) blue crab, clam and blue crab-or-clam combined (clam), snail, insect, and snail-or-insect combined (si), and fiddler crab (fc). No data were collected in February 2005.

	Numeric intake rate (no. of items min^{-1})							
	Winter 2004-2005				Winter 2005-2006			
Month	Boat Ramp	Pump Canal	Pipeline	Blackjack	Boat Ramp	Pump Canal	Pipeline	Blackjack
November	5.22 ± 0.40 wb (100)			6.84 ± 3.12 wb (96)	0.63 ± 0.16 clam (100)	19.99 ± 3.07 wb (100)	4.27 ± 2.88 wb (96)	
December	1.05 ± 0.46 wb (62) clam (18)	0.35 ± 0.12 wb (44) mbc (44)	0.33 ± 0.09 mbc/wb/lbc (38/37/17)	0.53 (*n*=1) fc (92)	20.09 ± 2.60 wb (99+)	15.45 ± 4.68 wb (99+)	17.12 ± 2.94 wb (100)	0.15 ± 0.01 mbc (59) sbc (33)
January	1.16 ± 0.25 clam (100)	0.21 ± 0.05 mbc (100)	0.23 ± 0.07 clam (54) mbc (39)	1.88 (*n*=1) fc (84)	0.93 ± 0.12 clam (92)	0.40 ± 0.04 clam (100)	0.20 ± 0.10 clam (83)	
February					0.47 ± 0.04 clam (100)	0.49 ± 0.22 si (75) clam (25)	11.42 ± 4.31 si (99+)	
March	2.25 ± 0.80 si (63) clam (37)	4.41 ± 3.23 si (98)	0.55 ± 0.23 si/clam/mbc (54/24/7)		0.59 ± 0.10 clam (50) si (36)	22.06 ± 5.46 si (99+)	6.09 (*n*=1) si (100)	
Mean	2.42 ± 0.97	1.66 ± 1.38	0.37 ± 0.09	3.08 ± 1.92	4.54 ± 3.89	11.68 ± 4.71	7.82 ± 2.94	0.15 (*n*=1)

combined) was also high in winter 1 and closely followed that of snail-and-insect. However, in winter 2, blue crab was consumed at an extremely low rate of numeric intake that was not offset by high body mass, and, consequently, it was the least profitable food for cranes in terms of dry mass intake. Monthly rates of dry mass intake generally increased from November to March, as the crane diet increasingly incorporated more clam and snail-and-insect (Fig. 4-9). Though blue crab and wolfberry fruit contributed little to the overall mean rate of total dry mass intake, they were the major contributors to intake in December of both winters. Among territories, cranes achieved higher overall rates of total dry mass intake by consuming more clam (e.g., at BR in winter 1) and snail-and-insect (e.g., at PC in winter 2; Table 4-8).

Energy and lipid intake rates

Patterns of energy and lipid intake rates were similar during this study. In both winters, snail-and-insect was consumed by cranes at overall mean rates of energy and lipid intake equal to or greater than all other foods combined (Table 4-6). Monthly intake rates were highest in March of both winters when cranes fed primarily on snail-and-insect (Fig. 4-10). In winter 1, intake rates were also relatively high during December-January when blue crab and clam were the dominant foods consumed and were lowest in November when cranes fed on wolfberry fruit. In winter 2, intake rates were moderately high during November-December, when wolfberry fruit was the chief source of acquired energy and lipids, and lowest in January, when clam was the principal food consumed. At the level of a crane territory, cranes achieved higher overall rates of

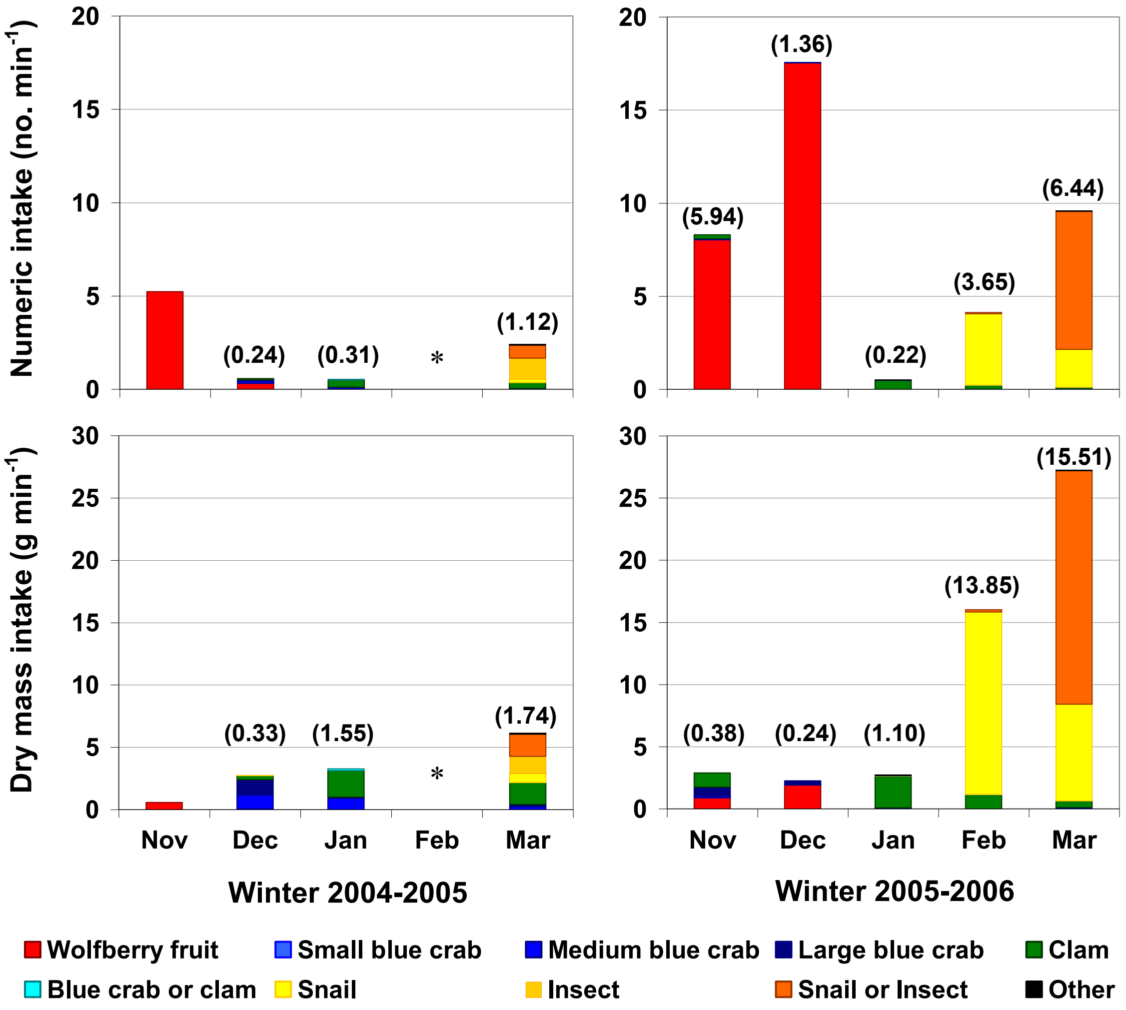

Fig. 4-9. Contribution of foods to mean numeric and dry mass intake rates for whooping cranes during each month of winters 2004-2005 and 2005-2006. Standard errors (in parentheses) represent variability among territories (*n*=3 for all months, except *n*=1 in November 2004). No data were collected in February 2005 (*), and data from BJ are not included.

Table 4-8. Mean (±1 SE) total dry mass intake rates (g min^{-1}) for whooping cranes of each territory during the winter months of 2004-2005 and 2005-2006. For each combination of winter, month, and territory, principal foods and their percent contribution to total intake rate (in parentheses) are also listed. Foods included wolfberry fruit (wb), small (sbc), medium (mbc), and large (lbc) blue crab, clam and blue crab-or-clam combined (clam), snail, insect, and snail-or-insect combined (si), and fiddler crab (fc). No data were collected in February 2005.

	Dry mass intake rate (g min^{-1})							
	Winter 2004-2005				Winter 2005-2006			
Month	Boat Ramp	Pump Canal	Pipeline	Blackjack	Boat Ramp	Pump Canal	Pipeline	Blackjack
November	0.57 ± 0.04 wb (100)			2.49 ± 0.90 snake (56) wb (29)	3.46 ± 0.88 clam (100)	2.18 ± 0.34 wb (100)	3.01 ± 0.84 lbc/wb/mbc (69/15/14)	
December	3.40 ± 0.70 lbc/clam/mbc (38/30/28)	2.45 ± 0.42 mbc (50) lbc (49)	2.37 ± 0.44 lbc (50) mbc (47)	0.99 (*n*=1) fc (83)	2.20 ± 0.28 wb (99)	2.69 ± 0.46 wb (62) lbc (30)	1.87 ± 0.32 wb (100)	1.16 ± 0.12 mbc (69) lbc (23)
January	6.37 ± 1.35 clam (100)	1.89 ± 0.41 mbc (100)	1.57 ± 0.31 mbc/clam/lbc (50/28/21)	3.40 (*n*=1) fc (78) si (22)	4.85 ± 0.63 clam (97)	2.14 ± 0.25 clam (100)	1.18 ± 0.53 clam (73) lbc (14)	
February					2.56 ± 0.19 clam (100)	1.78 ± 0.63 si (63) clam (37)	43.71 ± 16.49 si (99+)	
March	8.20 ± 1.69 clam (55) si (43)	7.50 ± 3.87 si (93)	2.66 ± 0.84 si/cl/lbc/mbc (41/27/14/12)		2.56 ± 0.52 clam (62) si (21)	55.86 ± 13.83 si (99+)	23.30 (*n*=1) si (100)	
Mean	4.63 ± 1.68	3.95 ± 1.75	2.20 ± 0.33	2.29 ± 0.70	3.13 ± 0.48	12.93 ± 10.73	14.61 ± 8.37	1.16 (*n*=1)

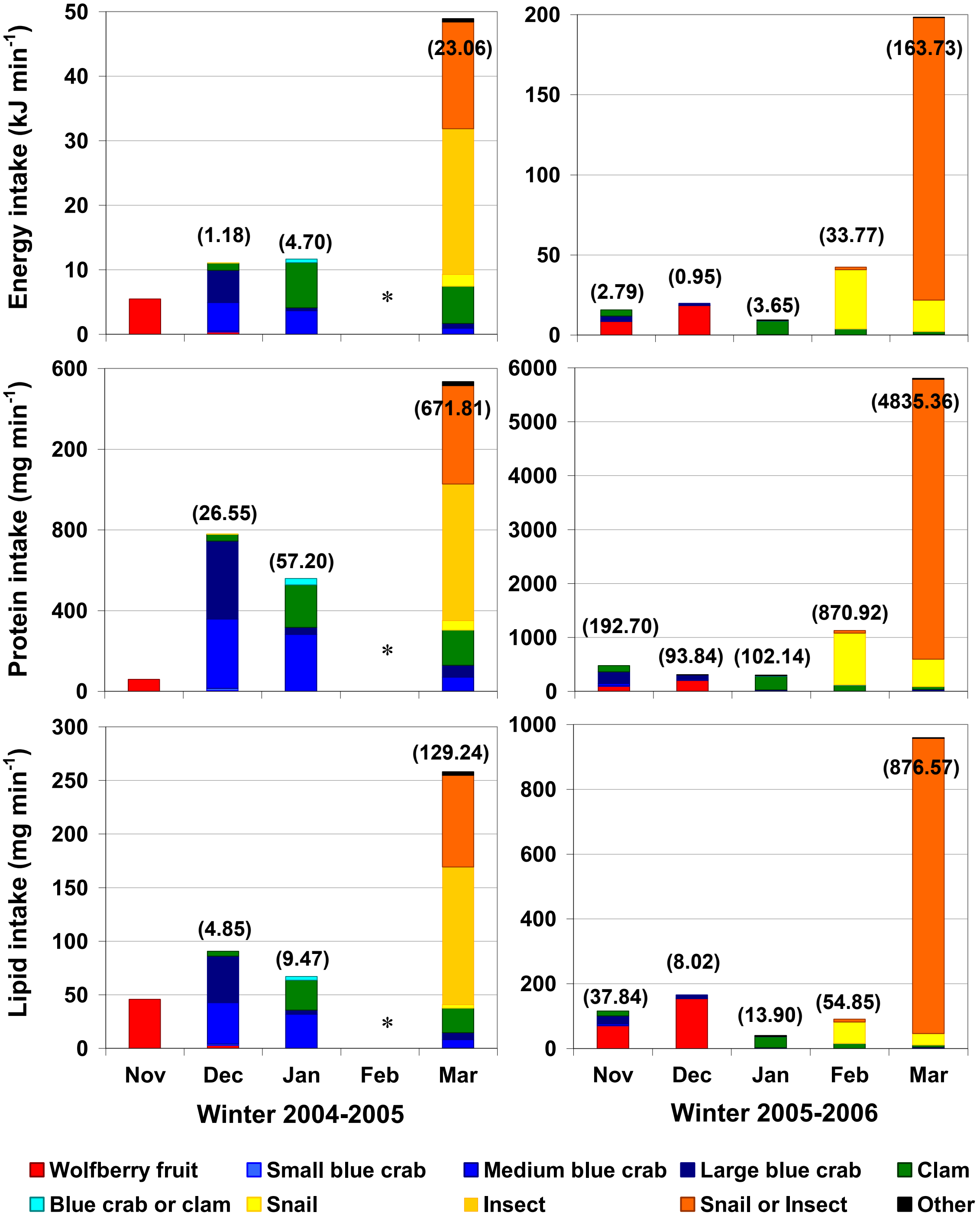

Fig. 4-10. Contribution of foods to mean energy, protein, and lipid intake rates for whooping cranes during each month of winters 2004-2005 and 2005-2006. Standard errors (in parentheses) represent variability among territories (*n*=3 for all months, except *n*=1 in November 2004). No data were collected in February 2005 (*), and data from BJ are not included. Note the large differences in y-axis scales between winters.

total intake by incorporating more snail-and-insect into their diet in winter 1 and by feeding more on snail-and-insect and wolfberry fruit in winter 2 (Tables 4-9 and 4-10). The benefits of opportunistic feeding were apparent in November of winter 1 at BJ when the observed adult crane fed on a snake (see Tables 4-9 and 4-10).

Protein intake rate

Overall mean rates of protein intake for snail-and-insect and blue crab were similar to each other and 2.5 times greater than clam in winter 1 (Table 4-6). In winter 2, intake of snail-and-insect contributed 84% to the total rate of protein intake and was 12, 15, and 23 times that of clam, blue crab (all sizes combined), and wolfberry fruit, respectively. Protein intake from consuming wolfberry fruit was minimal (2-4% of mean overall rate of total protein intake) in both winters 1 and 2, as was also shown by overall low rates of protein intake during November 2004 and December 2005 (Fig. 4-10; Table 4-6). During both winters, total protein intake was highest in late winter (February-March) when snail-and-insect was the primary source of protein consumed (Fig. 4-10). Total protein intake was also high during December-January of winter 1 when the monthly diet principally comprised blue crab. Intake rates during December-January of winter 2, however, were considerably lower than those of winter 1, as blue crab was a minimal part of the diet. It was also obvious within territories that cranes consuming more snail-and-insect and blue crab attained higher rates of protein intake (Table 4-11).

Table 4-9. Mean (±1 SE) total energy intake rates (kJ min^{-1}) for whooping cranes of each territory during the winter months of 2004-2005 and 2005-2006. For each combination of winter, month, and territory, principal foods and their percent contribution to total intake rate (in parentheses) are also listed. Foods included wolfberry fruit (wb), medium (mbc) and large (lbc) blue crab, clam and blue crab-or-clam combined (clam, cl), snail, insect, and snail-or-insect combined (si), fiddler crab (fc), and snake. No data were collected in February 2005.

	Energy intake rate (kJ min^{-1})							
	Winter 2004-2005				Winter 2005-2006			
Month	Boat Ramp	Pump Canal	Pipeline	Blackjack	Boat Ramp	Pump Canal	Pipeline	Blackjack
November	5.47 ± 0.42 wb (100)			27.06 ± 14.52 snake (64) wb (26)	11.43 ± 2.89 clam (100)	20.94 ± 3.22 wb (100)	14.73 ± 2.70 lbc (57) wb (29)	
December	13.41 ± 2.05 lbc/mbc/clam (39/28/25)	10.09 ± 1.74 mbc (50) lbc (49)	9.69 ± 1.75 lbc (50) mbc (46)	3.75 (*n*=1) fc (87)	21.11 ± 2.68 wb (99+)	20.23 ± 3.28 wb (80)	17.94 ± 3.08 wb (100)	4.71 ± 0.47 mbc (69) lbc (23)
January	21.00 ± 4.44 clam (100)	7.70 ± 1.67 mbc (100)	6.22 ± 1.35 mbc/clam/lbc (52/26/22)	17.84 (*n*=1) fc (60) si (40)	16.50 ± 2.07 clam (94)	7.09 ± 0.80 clam (100)	4.48 ± 1.79 clam (64) lbc (21)	
February					8.46 ± 0.63 clam (100)	8.77 ± 4.93 si (75) clam (25)	109.92 ± 41.33 si (99)	
March	48.84 ± 19.66 si (69) clam (31)	88.89 ± 65.23 si (97)	9.02 ± 2.00 si/cl/lbc/mbc (33/26/17/15)		11.81 ± 2.48 clam (44) si (41)	524.66 ± 129.81 si (99+)	58.48 (*n*=1) si (100)	
Mean	22.18 ± 9.43	35.56 ± 26.67	8.31 ± 1.06	16.22 ± 6.78	13.86 ± 2.22	116.34 ± 102.12	41.11 ± 19.51	4.71 (*n*=1)

Table 4-10. Mean (±1 SE) total lipid intake rates (mg min^{-1}) for whooping cranes of each territory during the winter months of 2004-2005 and 2005-2006. For each combination of winter, month, and territory, principal foods and their percent contribution to total intake rate (in parentheses) are also listed. Foods included wolfberry fruit (wb), medium (mbc) and large (lbc) blue crab, clam and blue crab-or-clam combined (clam, cl), snail, insect, and snail-or-insect combined (si), fiddler crab (fc), snake, and fish. No data were collected in February 2005.

	Lipid intake rate (mg min^{-1})							
	Winter 2004-2005				Winter 2005-2006			
Month	Boat Ramp	Pump Canal	Pipeline	Blackjack	Boat Ramp	Pump Canal	Pipeline	Blackjack
November	45.76 ± 3.47 wb (100)			286.78 ± 181.14 snake (72) wb (20)	45.40 ± 11.49 clam (100)	175.08 ± 26.90 wb (100)	126.70 ± 23.67 lbc (58) wb (28)	
December	99.98 ± 6.64 lbc/mbc/clam (45/33/13)	87.67 ± 15.15 mbc (50) lbc (49)	83.91 ± 15.23 lbc (50) mbc (46)	29.69 (*n*=1) fc (97)	176.45 ± 22.48 wb (99+)	170.55 ± 27.20 wb (79) lbc (17)	150.00 ± 25.71 wb (100)	40.98 ± 4.09 mbc (69) lbc (23)
January	83.43 ± 17.64 clam (100)	66.98 ± 14.48 mbc (100)	50.62 ± 13.71 mbc/lbc/clam (55/23/21)	130.24 (*n*=1) fc (72) si (28)	68.03 ± 8.84 clam (91)	28.68 ± 2.98 clam (100)	24.35 ± 9.21 clam/lbc/fish (50/24/15)	
February					33.60 ± 2.52 clam (100)	37.87 ± 25.57 si (77) clam (23)	200.26 ± 73.31 si (98)	
March	235.84 ± 104.35 si (73) clam (25)	492.27 ± 372.43 si (96)	46.25 ± 5.29 lbc/mbc/cl/si (29/25/20/14)		60.59 ± 14.28 si/clam/lbc (40/34/13)	2712.36 ± 671.36 si (99+)	105.26 (*n*=1) si (100)	
Mean	116.25 ± 41.44	215.64 ± 138.44	60.26 ± 11.89	148.90 ± 74.80	76.81 ± 25.61	624.91 ± 522.80	121.31 ± 28.93	40.98 (*n*=1)

Table 4-11. Mean (±1 SE) total protein intake rates (mg min^{-1}) for whooping cranes of each territory during the winter months of 2004-2005 and 2005-2006. For each combination of winter, month, and territory, principal foods and their percent contribution to total intake rate (in parentheses) are also listed. Foods included wolfberry fruit (wb), medium (mbc) and large (lbc) blue crab, clam and blue crab-or-clam combined (clam, cl), snail, insect, and snail-or-insect combined (si), fiddler crab (fc), and snake. No data were collected in February 2005.

	Protein intake rate (mg min^{-1})							
	Winter 2004-2005				Winter 2005-2006			
Month	Boat Ramp	Pump Canal	Pipeline	Blackjack	Boat Ramp	Pump Canal	Pipeline	Blackjack
November	59.24 ± 4.49 wb (100)			826.89 ± 550.07 snake/mbc/fc (65/14/12)	344.81 ± 87.29 clam (100)	226.63 ± 34.82 wb (100)	854.69 ± 311.92 lbc (76) mbc (16)	
December	828.95 ± 65.10 lbc (49) mbc (36)	769.33 ± 133.29 mbc (51) lbc (49)	738.47 ± 138.76 lbc (51) mbc (47)	268.24 (*n*=1) fc (96)	230.54 ± 27.69 wb (99)	492.09 ± 187.34 lbc (52) wb (35)	194.17 ± 33.28 wb (100)	364.35 ± 36.39 mbc (69) lbc (23)
January	633.74 ± 133.95 clam (100)	595.59 ± 128.76 mbc (100)	446.26 ± 124.44 mbc/lbc/clam (56/23/21)	1041.34 (*n*=1) fc (80)	502.27 ± 63.17 clam (93)	219.10 ± 22.31 clam (100)	176.98 ± 76.03 clam (54) lbc (30)	
February					255.25 ± 19.16 clam (100)	254.75 ± 145.19 si (74) clam (26)	2867.77 ± 1066.52 si (99)	
March	1466.78 ± 573.23 si (67) clam (31)	2729.73 ± 1946.61 si (94)	405.43 ± 58.61 lbc/mbc/si/cl (29/26/19/18)		433.13 ± 93.38 clam/si/lbc (37/32/17)	15452.00 ± 3824.14 si (99+)	1519.85 (*n*=1) si (100)	
Mean	747.18 ± 290.21	1364.88 ± 684.26	530.05 ± 104.87	712.15 ± 230.43	353.20 ± 51.63	3328.91 ± 3031.20	1122.69 ± 501.57	364.35 (*n*=1)

Foraging Costs

Mean overall foraging effort was higher in winter 1 than 2. Specifically, cranes probed and manipulated foods (e.g., jabbed) more frequently during winter 1, when blue crab was a major component the diet (Table 4-12).

In winter 1, total foraging effort gradually increased from November to January and then remained constant through March (Table 4-12). Rates of stepping, probing, and handling were all lowest in November when wolfberry fruit was the principal food consumed. Stepping rate subsequently increased in December to a level observed through the remainder of winter. Probing rate increased slightly in December when blue crab was the primary food consumed and then was dramatically higher during January-March when clam was a dominant food in the diet. Rate of handling was additionally low when cranes actively consumed snail-and-insect in March and was highest in December when cranes fed principally on blue crab, followed by January when both clam and blue crab were principal foods in the diet.

In winter 2, total foraging effort was significantly lower in December when cranes fed on wolfberry fruit than all other months during winter (Table 4-12). Rate of stepping was variable across winter but highest in January when cranes primarily fed on clam. No probing was used in December when cranes foraged for wolfberry fruit, but rates of probing were consistently higher in all other months when blue crab, clam, and snail-and-insect were consumed. Rate of handling was low throughout winter but was highest in November when crabs were actively targeted at PL.

Table 4-12. Foraging effort exhibited by whooping cranes in each territory during the winter months of 2004-2005 and 2005-2006. Indices of foraging effort included mean (±1 SE) rates of stepping (number of steps min^{-1}; S), probing (number of probes min^{-1}; P), handling (number of food manipulations min^{-1}; H), and total effort (total number of foraging movements (steps, probes, and food manipulations) min^{-1}; T), shown in bold. No data were collected in February 2005, and data from BJ are not included in overall monthly and winter means.

Winter / Month	Index	Territory				
		Boat Ramp	Pump Canal	Pipeline	Blackjack	Mean
Winter 2004-2005						
November	S	8.86 ± 1.22		11.21 (*n*=1)	12.44 ± 6.56	10.03 ± 1.17
	P	2.14 ± 0.26			1.17 ± 1.17	2.14 (*n*=1)
	H	0.00 ± 0.00		0.00 (*n*=1)	1.51 ± 1.51	0.00 ± 0.00
	T	**11.00**		**11.21**[*]	**15.12**	**12.17**
December	S	22.70 ± 3.94	21.75 ± 2.22	20.54 ± 2.69	40.44 (*n*=1)	21.66 ± 0.62
	P	9.53 ± 7.18	4.88 ± 2.79	11.44 ± 3.05	13.33 (*n*=1)	8.62 ± 1.95
	H	11.34 ± 2.01	18.62 ± 3.57	12.63 ± 3.09	5.33 (*n*=1)	14.20 ± 2.24
	T	**43.56**	**45.26**	**44.61**	**59.11**	**44.48**
January	S	9.85 ± 0.92	21.62 ± 2.71	26.68 ± 3.27	20.99 (*n*=1)	19.38 ± 4.99
	P	88.37 ± 2.91	4.04 (*n*=1)	29.90 ± 28.68	3.47 (*n*=1)	40.77 ± 24.94
	H	1.43 ± 0.76	14.49 (*n*=1)	9.65 ± 8.90	57.92 (*n*=1)	8.52 ± 3.81
	T	**99.65**	**40.15**	**66.23**	**82.38**	**68.68**
March	S	19.47 ± 2.47	21.12 ± 1.75	21.27 ± 2.42		20.62 ± 0.58
	P	60.56 ± 14.82	17.56 ± 8.72	61.53 ± 11.54		46.55 ± 14.50
	H	0.52 ± 0.23	1.20 ± 1.08	2.88 ± 0.85		1.54 ± 0.70
	T	**80.56**	**39.98**	**85.69**		**68.71**
Mean	S	15.22 ± 3.46	21.50 ± 0.19	19.93 ± 3.21	24.63 ± 8.28	17.92 ± 2.67
	P	40.15 ± 20.66	8.83 ± 4.37	34.29 ± 14.63	5.99 ± 3.73	24.52 ± 11.19
	H	3.32 ± 2.69	11.44 ± 5.26	6.29 ± 2.93	21.59 ± 18.20	6.06 ± 3.29
	T	**58.69**	**41.76**	**60.51**	**52.20**	**48.51**
Winter 2005-2006						
November	S	14.73 ± 0.41	21.97 ± 1.65	20.61 ± 3.53		19.10 ± 2.22
	P	73.60 ± 19.67	0.16 ± 0.10	2.61 ± 2.30		25.46 ± 24.08
	H	1.95 (*n*=1)	0.00 ± 0.00	18.98 ± 7.22		6.98 ± 6.03
	T	**90.29**	**22.13**	**42.20**		**51.54**
December	S	11.99 ± 1.36	17.33 ± 2.24	17.40 ± 3.44	14.27 ± 0.70	15.57 ± 1.79
	P	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00		0.00 ± 0.00
	H	0.01 ± 0.01	3.31 ± 3.31	0.00 ± 0.00		1.11 ± 1.10
	T	**11.99**	**20.64**	**17.40**	**14.27**[*]	**16.68**
January	S	15.06 ± 2.55	22.32 ± 0.44	34.49 ± 2.33		23.96 ± 5.67
	P	27.24 ± 5.01	37.80 ± 4.37	11.81 ± 3.97		25.62 ± 7.55
	H	8.21 ± 2.44	1.41 ± 0.35	2.60 ± 1.89		4.07 ± 2.10
	T	**50.51**	**61.53**	**48.90**		**53.65**

Table 4-12 continued.

Winter / Month	Index	Territory				
		Boat Ramp	Pump Canal	Pipeline	Blackjack	Mean
Winter 2005-2006 continued						
February	S	12.35 ± 1.91	14.56 ± 3.28	30.77 ± 6.06		19.23 ± 5.81
	P	41.77 ± 0.68	21.72 ± 9.80	4.19 ± 1.55		22.56 ± 10.86
	H	1.09 ± 0.18	0.37 ± 0.37	0.07 ± 0.04		0.51 ± 0.30
	T	**55.21**	**36.66**	**35.02**		**42.30**
March	S	13.00 ± 1.61	14.76 ± 2.67	21.45 ± 2.24	9.64 (*n*=1)	16.40 ± 2.57
	P	56.08 ± 15.51	0.06 ± 0.06	14.77 (*n*=1)		23.64 ± 16.77
	H	2.19 ± 0.85	0.00 ± 0.00	0.00 (*n*=1)		0.73 ± 0.73
	T	**71.27**	**14.82**	**36.22**	**9.64***	**40.77**
Mean	S	13.43 ± 0.62	18.19 ± 1.69	24.94 ± 3.26	11.95 ± 2.31	18.85 ± 1.47
	P	39.74 ± 12.56	11.95 ± 7.70	6.68 ± 2.82		19.45 ± 4.90
	H	2.69 ± 1.43	1.02 ± 0.63	4.33 ± 3.70		2.68 ± 1.25
	T	**55.85**	**31.15**	**35.95**	**11.95***	**40.98**

*Rate of total movements does not incorporate probes and/or handling (food manipulations).

Cranes exhibited relatively distinct levels of foraging effort for specific food types (Table 4-13). Effort required to forage for wolfberry fruit was less than any other food in the crane’s diet and involved only stepping. Snail-and-insect required slightly more effort, principally through stepping and low levels of probing. Blue crab was the next most “expensive” food, requiring relatively high levels of stepping, low levels of probing, and high levels of handling. When foraging for clam, cranes stepped and handled food relatively infrequently but probed at higher and more variable rates than for any other food type. Effort required to search for, capture, and consume fiddler crab was somewhat similar to that for blue crab, only more variable and costly in each component of foraging (stepping, probing, handling).

Foraging Efficiency

Whooping cranes foraged three to seven times more efficiently during winter 2 than 1, as determined by all five indices of foraging efficiency (Table 4-14). During both winters, efficiency was highest in early (November and/or December) and late (February and/or March) winter and lowest in January. Early winter peaks in efficiency corresponded with peak use of wolfberry fruit in all cases, except for indices relating to dry mass and protein in winter 1. No clear peak in efficiency of foraging for dry mass was evident early in winter 1, and a distinct peak in efficiency of foraging for protein occurred instead in December when blue crab proportionally comprised 90% of the diet and accounted for 95% of the mean rate of total protein intake. Late winter peaks in

Table 4-13. Foraging effort exhibited by whooping cranes per food type and index of foraging effort during winters 2004-2005 and 2005-2006. Indices of foraging effort included rates of stepping (number of steps min^{-1}), probing (number of probes min^{-1}), handling (number of food manipulations min^{-1}), and total effort (total number of foraging movements (steps, probes, and food manipulations) min^{-1}).

	Index of foraging effort			
Food type	Stepping rate	Probing rate	Handling rate	Total effort
Wolfberry fruit	10-15	0	0	10-15
Snail-and-insect	15-30	0-15	0	15-40
Blue crab	20-23	3-11	11-19	40-45
Clam	10-22	27-88	1-8	50-100
Fiddler crab	21-40	3-13	5-58	59-82

Table 4-14. Mean foraging efficiency (±1 SE) exhibited by whooping cranes during the winter months of 2004-2005 and 2005-2006. Indices of foraging efficiency (reward:cost) included numeric (number of food items foraging movement^{-1}), dry mass (g foraging movement^{-1}), energy (kJ foraging movement^{-1}), protein (mg foraging movement^{-1}) and lipid (mg foraging movement^{-1}) efficiencies. The cost of foraging was defined by total foraging effort and included all movements (steps, probes, jabs, head jerks, etc.) made while foraging. No data were collected in February 2005, and data from BJ are not included.

	Index of foraging efficiency				
Winter / Month	Numeric	Dry mass	Energy	Protein	Lipid
Winter 2004-2005					
November	0.475 (*n*=1)	0.052 (*n*=1)	0.498 (*n*=1)	5.39 (*n*=1)	4.17 (*n*=1)
December	0.014 ± 0.006	0.062 ± 0.009	0.250 ± 0.030	17.53 ± 0.77	2.04 ± 0.13
January	0.007 ± 0.003	0.045 ± 0.012	0.166 ± 0.037	9.33 ± 2.79	1.10 ± 0.30
March	0.049 ± 0.032	0.107 ± 0.046	0.981 ± 0.641	30.47 ± 19.39	5.28 ± 3.61
Mean	0.136 ± 0.114	0.067 ± 0.014	0.474 ± 0.184	15.68 ± 5.54	3.15 ± 0.96
Winter 2005-2006					
November	0.338 ± 0.285	0.070 ± 0.018	0.475 ± 0.245	11.44 ± 4.79	3.81 ± 2.18
December	1.136 ± 0.278	0.141 ± 0.023	1.258 ± 0.253	18.08 ± 3.71	10.54 ± 2.10
January	0.010 ± 0.005	0.052 ± 0.023	0.178 ± 0.075	5.71 ± 2.12	0.78 ± 0.29
February	0.116 ± 0.106	0.448 ± 0.401	1.177 ± 0.982	31.16 ± 25.38	2.46 ± 1.64
March	0.556 ± 0.470	1.484 ± 1.157	12.397 ± 11.515	363.65 ± 339.79	62.28 ± 60.40
Mean	0.431 ± 0.200	0.439 ± 0.271	3.097 ± 2.335	86.01 ± 69.54	15.97 ± 11.70

efficiency coincided with peak consumption of snail-and-insect, while low efficiency in January paralleled use of clam.

Foraging efficiency varied among cranes of different territories (Table 4-15). Cranes at PC exhibited the highest levels of efficiency during both winters, whereas cranes from PL and BR experienced the lowest levels of efficiency during winters 1 and 2, respectively. While overall means of numeric, energy, and lipid efficiencies in winter 2 were actually calculated as lowest for cranes at BJ, means for BJ incorporated data from only one month (December) and, thus, were not comparable to values for other territories, all of which incorporated five months (November-March) of data.

Values of efficiency experienced by cranes in November of winter 1 were not computed and, therefore, not accounted for in overall winter 1 means of efficiency for PC and PL. By lacking data from November, when cranes principally fed on wolfberry fruit, the overall winter estimates of numeric, energy, and lipid efficiency were possibly biased low for these territories. Numeric efficiency in November was similar between BR (0.475 food items foraging movement^{-1}) and BJ (0.452 food items foraging movement^{-1}). Therefore, to examine the potential biases associated with PC and PL, I recalculated the overall winter mean of numeric efficiency for each territory by using the average obtained from BR and BJ (0.464 food items foraging movement^{-1}) as the level of efficiency experienced in November. Overall winter means of numeric efficiency for PC (0.147 food items foraging movement^{-1}) and PL (0.120 food items foraging movement^{-1}) were then similar to those for BR and BJ (see Table 4-15). However, the

Table 4-15. Mean foraging efficiency (±1 SE) exhibited by whooping cranes in each territory during winters 2004-2005 and 2005-2006. Indices of foraging efficiency (reward:cost) included numeric (number of food items foraging movement^{-1}), dry mass (g foraging movement^{-1}), energy (kJ foraging movement^{-1}), protein (mg foraging movement^{-1}) and lipid (mg foraging movement^{-1}) efficiencies. The cost of foraging was defined by total foraging effort and included all movements (steps, probes, jabs, head jerks, etc.) made while foraging.

	Index of foraging efficiency				
Winter / Territory	Numeric	Dry mass	Energy	Protein	Lipid
Winter 2004-2005					
Boat Ramp	0.135 ± 0.114	0.074 ± 0.011	0.406 ± 0.090	12.25 ± 3.69	2.56 ± 0.70
Pump Canal	0.042 ± 0.035	0.097 ± 0.046	0.882 ± 0.674	33.45 ± 17.52	5.32 ± 3.52
Pipeline	0.006 ± 0.002	0.036 ± 0.009	0.139 ± 0.040	9.35 ± 3.66	1.07 ± 0.42
Blackjack	0.162 ± 0.146	0.075 ± 0.046	0.690 ± 0.552	23.96 ± 15.55	7.02 ± 5.99
Winter 2005-2006					
Boat Ramp	0.344 ± 0.333	0.081 ± 0.029	0.507 ± 0.316	8.74 ± 2.83	3.61 ± 2.79
Pump Canal	0.633 ± 0.283	0.817 ± 0.739	7.539 ± 6.971	217.50 ± 206.38	40.15 ± 35.77
Pipeline	0.317 ± 0.175	0.419 ± 0.236	1.245 ± 0.544	31.78 ± 14.09	4.15 ± 1.40
Blackjack	0.011 (*n*=1)	0.082 (*n*=1)	0.331 (*n*=1)	25.54 (*n*=1)	2.88 (*n*=1)

trend among territories did not change, as numeric efficiency was highest at BJ and lowest at PL.

Several important discoveries were made by comparing foods within each of five indices of foraging efficiency and four levels of contribution to total intake (Table 4-16). First, the most optimal foods for whooping cranes varied among indices of foraging efficiency and depended on the specific resource gained (number of food items, energy, protein, etc.). Wolfberry fruit and snail-and-insect were the most optimal foods according to indices of numeric, lipid and energy efficiency, but cranes foraging for mass were most efficient when feeding on snail-and-insect and clam. In addition, optimal foraging for protein was achieved when cranes targeted snail-and-insect and large blue crab.

Secondly, by examining diets that differed in the level at which a food contributed to total intake, patterns were revealed which related foraging efficiency to heterogeneity of diet. As would be expected, foraging efficiency corresponding to diets that initially contained solely the most optimal foods decreased as other foods (inherently less optimal) were added (Table 4-16). Conversely, efficiency increased as foods (inherently more optimal) were added to diets of solely the least optimal foods.

Lastly, this examination provided opportunities to quantify the optimality of foraging for blue crabs of different size. Foraging for small blue crab was shown to be more efficient than foraging for either medium or large blue crab when number of food items consumed mattered (Table 4-16). However, small blue crab never significantly contributed to dry mass, energy, protein, or lipid intake and, consequently, was assumed

Table 4-16. Efficiency of foraging by whooping cranes during winters 2004-2005 and 2005-2006 for each food type and level of contribution to total intake. Indices of foraging efficiency were defined by ratios of numeric (number of food items min^{-1}), dry mass (g min^{-1}), energy (kJ min^{-1}), protein (mg min^{-1}), or lipid (mg min^{-1}) intake to total foraging effort (total number of foraging movements (steps, probes, and food manipulations) min^{-1}). Mean, minimum (min), and maximum (max) ratios were computed across n-combinations of winter x month x territory. Level of contribution increased from principal food (one of one to several foods together comprising ≥80% of total intake) to co-dominant food (one of two dominant foods) to dominant food (principal food contributing at least twice as much to total intake as all other foods) to sole principal food (see text for more detailed definitions). For each index of efficiency, foods were ranked according to ratio means; assigned ranks differ statistically when letters differ (alpha=0.05). Foods with *n*<3 were not included in Waller-Duncan multiple comparison testing.

	Level of food contribution to total intake											
	Sole principal food			Dominant food			Co-dominant food			Principal food		
Index of efficiency / Food type	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*
Numeric efficiency (numeric intake:total foraging effort)												
Wolfberry fruit	1^{a}	0.763 (0.101, 1.675)	7	1^{a}	0.670 (0.024, 1.675)	8	1^{a}	0.597 (0.008, 1.675)	9	1^{a}	0.538 (0.007, 1.675)	10
Blue crab (small)			0			0	3	0.011 (0.011, 0.011)	1	5	0.011 (0.011, 0.011)	1
Blue crab (med)	5	0.005 (0.005, 0.005)	1	5	0.005 (0.005, 0.005)	1	6^{b}	0.007 (0.003, 0.011)	4	6^{b}	0.007 (0.003, 0.011)	7
Blue crab (large)			0			0			0	7	0.007 (0.007, 0.007)	1
Clam	4^{b}	0.009 (0.004, 0.018)	6	4^{b}	0.009 (0.004, 0.018)	6	4^{b}	0.011 (0.003, 0.028)	9	4^{b}	0.012 (0.003, 0.028)	12
Snail/Insect	2^{ab}	0.523 (0.110, 1.489)	4	2^{ab}	0.352 (0.006, 1.489)	6	2^{ab}	0.269 (0.006, 1.489)	8	2^{ab}	0.269 (0.006, 1.489)	8
Fiddler crab	3	0.016 (0.009, 0.023)	2	3	0.016 (0.009, 0.023)	2	5	0.016 (0.009, 0.023)	2	3	0.016 (0.009, 0.023)	2

Table 4-16 continued.

Index of efficiency / Food type	Level of food contribution to total intake											
	Sole principal food			Dominant food			Co-dominant food			Principal food		
	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*
Dry mass efficiency (dry mass intake:total foraging effort)												
Wolfberry fruit	4^{b}	1.706 (0.570, 2.204)	4	5^{b}	1.902 (0.570, 2.688)	5	6^{b}	2.000 (0.570, 2.688)	6	7^{b}	2.144 (0.570, 3.012)	7
Blue crab (med)	3	1.891 (1.891, 1.891)	1	6	1.524 (1.157, 1.891)	2	7^{b}	1.967 (1.157, 2.453)	4	4^{b}	2.314 (1.157, 3.402)	8
Blue crab (large)			0	3	3.012 (3.012, 3.012)	1	3^{b}	2.611 (2.367, 3.012)	3	5^{b}	2.276 (1.157, 3.402)	9
Clam	2^{b}	3.879 (2.143, 6.368)	5	2^{b}	3.304 (1.179, 6.368)	7	2^{b}	3.678 (1.179, 8.197)	9	2^{b}	3.395 (1.179, 8.197)	12
Snail/Insect	1^{a}	32.594 (7.504, 55.863)	4	1^{a}	32.594 (7.504, 55.863)	4	1^{a}	23.392 (1.780, 55.863)	6	1^{a}	16.552 (1.780, 55.863)	9
Fiddler crab	5	0.986 (0.986, 0.986)	1	4	2.192 (0.986, 3.397)	2	5	2.192 (0.986, 3.397)	2	6	2.192 (0.986, 3.397)	2
Snake			0			0	4	2.488 (2.488, 2.488)	1	3	2.488 (2.488, 2.488)	1
Energy efficiency (energy intake:total foraging effort)												
Wolfberry fruit	2^{b}	1.043 (0.498, 1.761)	5	3^{ab}	1.043 (0.498, 1.761)	5	3^{a}	0.928 (0.349, 1.761)	6	3^{ab}	1.051 (0.349, 1.790)	7
Blue crab (med)	3	0.193 (0.193, 0.193)	1	4^{b}	0.206 (0.094, 0.330)	3	5^{a}	0.211 (0.094, 0.330)	5	6^{b}	0.210 (0.094, 0.330)	7
Blue crab (large)			0			0	4^{a}	0.263 (0.217, 0.349)	3	4^{b}	0.215 (0.092, 0.349)	8

Table 4-16 continued.

Index of efficiency / Food type	Level of food contribution to total intake: Sole principal food			Dominant food			Co-dominant food			Principal food		
	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*
Energy efficiency (energy intake:total foraging effort) continued												
Clam	4^{b}	0.186 (0.115, 0.327)	5	5^{b}	0.171 (0.092, 0.327)	6	6^{a}	0.170 (0.092, 0.327)	7	5^{b}	0.212 (0.092, 0.606)	12
Snail/Insect	1^{a}	10.598 (1.615, 35.410)	4	1^{a}	7.206 (0.239, 35.410)	6	1^{a}	5.452 (0.166, 35.410)	8	1^{a}	4.858 (0.105, 35.410)	9
Fiddler crab	5	0.063 (0.063, 0.063)	1	6	0.063 (0.063, 0.063)	1	7	0.140 (0.063, 0.217)	2	7	0.140 (0.063, 0.217)	2
Snake			0	2	1.790 (1.790, 1.790)	1	2	1.790 (1.790, 1.790)	1	2	1.790 (1.790, 1.790)	1
Protein efficiency (protein intake:total foraging effort)												
Wolfberry fruit	3^{b}	11.50 (5.39, 19.22)	4	5^{ab}	11.50 (5.39, 19.22)	4	5^{b}	13.97 (5.39, 23.84)	5	6^{ab}	13.97 (5.39, 23.84)	5
Blue crab (med)	2	14.89 (14.89, 14.89)	1	4^{ab}	15.72 (6.74, 25.54)	3	4^{b}	16.62 (6.74, 25.54)	6	4^{ab}	19.94 (4.73, 54.69)	9
Blue crab (large)			0	3	20.25 (20.25, 20.25)	1	3^{b}	16.72 (3.62, 23.84)	6	5^{ab}	14.34 (3.62, 25.54)	10
Clam	5^{b}	5.66 (3.56, 9.94)	5	7^{b}	5.66 (3.56, 9.94)	5	7^{b}	5.32 (3.56, 9.94)	6	7^{b}	6.78 (3.56, 18.21)	11
Snail/Insect	1^{a}	308.79 (41.96, 1042.89)	4	1^{a}	210.06 (6.95, 1042.89)	6	1^{a}	210.06 (6.95, 1042.89)	6	1^{a}	158.89 (4.73, 1042.89)	8
Fiddler crab	4	8.59 (4.54, 12.64)	2	6	8.59 (4.54, 12.64)	2	6	8.59 (4.54, 12.64)	2	3^{ab}	23.96 (4.54, 54.69)	3

Table 4-16 continued.

Index of efficiency / Food type	Level of food contribution to total intake											
	Sole principal food			Dominant food			Co-dominant food			Principal food		
	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*	Rank	Mean (min, max)	*n*
Protein efficiency (protein intake:total foraging effort) continued												
Snake			0	2	54.69 (54.69, 54.69)	1	2	54.69 (54.69, 54.69)	1	2	54.69 (54.69, 54.69)	1
Lipid efficiency (lipid intake:total foraging effort)												
Wolfberry fruit	2^{a}	8.85 (4.16, 14.71)	4	3^{a}	8.73 (4.16, 14.71)	5	3^{a}	8.73 (4.16, 14.71)	5	3^{a}	9.38 (3.00, 18.97)	7
Blue crab (med)	3	1.67 (1.67, 1.67)	1	5^{ab}	1.77 (0.76, 2.87)	3	5^{bc}	1.83 (0.76, 2.87)	5	5^{b}	1.71 (0.54, 2.87)	7
Blue crab (large)			0	4	3.00 (3.00, 3.00)	1	4^{abc}	2.27 (1.88, 3.00)	3	4^{b}	2.29 (0.50, 8.26)	10
Clam	4^{b}	0.75 (0.47, 1.35)	5	7^{b}	0.71 (0.47, 1.35)	6	7^{c}	0.71 (0.47, 1.35)	6	6^{b}	1.06 (0.47, 2.93)	12
Snail/Insect	1^{a}	51.01 (2.91, 183.06)	4	1^{a}	34.67 (1.03, 183.06)	6	1^{ab}	34.67 (1.03, 183.06)	6	1^{a}	26.30 (0.85, 183.06)	8
Fiddler crab	5	0.50 (0.50, 0.50)	1	6	1.04 (0.50, 1.58)	2	6	1.04 (0.50, 1.58)	2	7	1.04 (0.50, 1.58)	2
Snake			0	2	18.97 (18.97, 18.97)	1	2	18.97 (18.97, 18.97)	1	2	18.97 (18.97, 18.97)	1

to be the least optimal of the three size groups examined. In all cases other than for numeric efficiency, foraging for large blue crab was more efficient than foraging for medium blue crab.

Discussion

Focal-bird observation indicated that territorial whooping cranes, when feeding in salt-marsh, fed on an assemblage of foods comprising 73% animal and 27% plant matter during both study winters. Previous studies similarly found cranes to consume mostly animal matter (e.g., 82-98% of diet; Hunt and Slack 1989) but emphasized blue crabs or both blue crabs and clams as the most important foods for cranes based on dry mass, numeric or volumetric contribution to diet (Stevenson and Griffith 1946; Allen 1952; Blankinship 1976, 1983; Hunt and Slack 1989). In this study, blue crabs and clams were, in fact, used more consistently across winter (3-4 mon winter^{-1}) than other foods (2-3 mon winter^{-1}), but thorough examination of food habits across temporal and spatial scales revealed that several other foods (e.g., wolfberry fruits, snails, insects) significantly contributed to and even dominated the crane's diet at various points in time during winter and at locations (territories) within the study area.

As wolfberry fruit was the dominant food consumed by whooping cranes during November and December (up to 90-100% of the diet), the amount of plant food consumed by cranes in this study was greater than expected. When averaged across each winter, numeric intake rates of wolfberry fruits (1.38-5.11 fruits min^{-1} (83-307 fruits hr^{-1})) were similar to estimates computed for winters 1993-1994 (135 fruits hr^{-1}) and 1994-

1995 (231 fruits hr^{-1}; Chavez-Ramirez 1996). However, analysis of fecal droppings during winters 1983-1984 and 1984-1985 revealed that fruit made up a mere 0.8% and 13.7% of total fecal volume, respectively, and <7.6% and 29-34% of the diet when considering exclusively early to mid winter (Hunt and Slack 1989). Blankinship (1983) also mentioned inclusion of wolfberry fruit in the crane's diet but minimized its importance, emphasizing the contributions of blue crab and clam to the diet. In addition, the earliest studies of whooping cranes did not at all recognize the fruit as an important food for cranes (Stevenson and Griffith 1946; Allen 1952). Rather, through observation of crane feeding behavior, circumstantial evidence at feeding sites (e.g., shell remains of blue crab and razor clam), and examination of fecal droppings, "vegetable foods" altogether were thought to be only incidentally ingested and considered of little significance.

Several explanations are plausible for the seemingly marked increase in crane consumption of wolfberry fruit during the last 60 yr. First, wolfberry plants may have been less abundant or more locally distributed historically than today; alternatively, other foods may have been more abundant or widely distributed. Secondly, significant increases in the crane's population size and subsequent foraging pressure on commonly targeted foods may have led to a more diverse crane diet (Svanbäck and Bolnick 2007). Thirdly, in studies using fecal analyses to determine diet (i.e., most previous field studies of crane diet), methodological biases based on differential digestibility and size of prey may have resulted in overestimated contribution by large, skeleton-supported animals but underestimated contribution by plants and small, soft-bodied animals (Barrett et al.

2007; Pincheira-Donoso 2008). Extremely small sample sizes (i.e., few fecal samples collected) also may have influenced prior results by reducing the probability of detection for small or less frequently consumed prey items versus larger or more frequently consumed items (Swanson et al. 1974; Trites and Joy 2005).

Increase of wolfberry fruit in the crane diet, as well as other notable disparities between this and earlier studies, may also have resulted from dissimilar study designs or methodologies. For instance, up until this study, behavioral observations had not yet been used to document patterns of consumption for all foods contributing to the crane diet within any single winter season. Either only a few select foods were targeted for study (Chavez-Ramirez 1996) or methods other than observation were used to gather data (e.g., Stevenson and Griffith 1946; Allen 1952; Hunt and Slack 1989). Also, most earlier studies were not designed to account for both temporal and spatial (or intra-specific) variability in feeding patterns. As demonstrated in this study and by Hunt and Slack (1989), both inter- and intra-seasonal patterns in crane diet are typical, and quantitative descriptions of food use from a specific point or period of time (e.g., early winter) may differ greatly from an overall winter average. Moreover, this study focused on adult cranes that had exclusive access to large quantities of fruit (and other foods) through territorial defense, but most or possibly all previous field studies incorporated both subadult and adult cranes into the study's target population. Because dependable food resources are neither defended by nor readily accessible to subadults, these non-territorial cranes likely have a more diverse (less homogenous) and less temporally-distinct diet than territorial adult cranes. Studies described above, as well as those that collected data from an unidentified sample population, a single sample site, or an unrepresentative sample of territories or feeding locations, inherently can offer only insufficiently comparable results to those of this study.

Comparisons between this and earlier studies were also somewhat difficult, because nearly all previous studies summarized findings using relative measures (e.g., percent aggregate dry mass) rather than discrete (absolute) measures (e.g., intake rate in g min^{-1}) of consumption. I collected data with the intent of computing discrete food intake rates but also summarized findings using relative measures for comparative purposes. By computing both discrete and relative measures of food intake, this study revealed the potential biases associated with comparing relative values among different time periods or localities. For instance, in this study, both overall winter and monthly means of proportional food use suggested that cranes used wolfberry fruit equally between winters, when in fact fruit was consumed during winter 2 (5.11 fruits min^{-1}) at levels nearly four times that of winter 1 (1.38 fruits min^{-1}). Similarly, proportional use of clam suggested its importance during winter 2 (38%) was nearly twice that of winter 1 (20%), when in fact clam was consumed at nearly identical rates of intake (1.05-1.06 g min^{-1}). Comparisons of relative measures, therefore, may be misleading and generally inappropriate when investigating the importance or optimality of foods for foragers.

This was the first study to take an optimal foraging approach in determining the importance or value of foods for wintering whooping cranes. All previous field studies of the crane's diet (e.g., Stevenson and Griffith 1946; Allen 1952; Uhler and Locke 1970; Hunt and Slack 1989), as well as countless other studies of waterbird diets (e.g., Jorde et al. 1983; Niethammer and Kaiser 1983; Duffy and Jackson 1986), have more traditionally apportioned value based on frequency of occurrence or the percent contribution of foods to total biomass, volume, energy, or number of food items consumed. More recently, the Index of Relative Importance (IRI), which incorporates the frequency of occurrence (FO), numeric percent (N), and percent by weight (W) of prey items, has also become a common means for quantifying food values within the diet (IRI = %FO x (%N + %W); e.g., York et al. 2000; Ahula et al. 2006; Burke and Montevecchi 2008). However, unlike examining the optimality of foraging for specific foods, these methods evaluate each food consumed based solely on the amount consumed (i.e., gain of food biomass, energy, volume, or items) and in relation to all other foods in the diet rather than relative to forager constraints, differential benefits achieved by foraging, or risks (or other costs) incurred while foraging. In fact, the maximum overall benefit achieved by foraging for a food can be somewhat or even entirely independent of its proportional contribution to diet.

Using cranes born and raised in captivity, other prior attempts to evaluate crane foods have studied the nutrient content and digestibility of foods (Nelson et al. 1996) and experimentally examined the preference of cranes for pelleted foods made of various natural ingredients (Nelson et al. 1997). Research revealed that wolfberry fruits were generally avoided by cranes when included in food pellets but contained more available energy and digestible lipids on a dry-weight basis than several other principle foods (e.g., acorns, *Rangia* clams, blue crabs). Cranes were found to maximize protein gain by selecting pellets of blue crab or stout razor clam, which were shown to have three to five times more digestible crude protein per unit capture than wolfberry fruit, and pellets containing clams were preferred above all other types. Since these studies, both energy-budget (Chavez-Ramirez 1996) and optimal foraging (this study) analyses have relied on the computed nutritive values of foods, but neither the examination of nutritive values nor the tests of crane preference for pellet type fully described the benefits attained by wild cranes when foraging for foods. As neither study accounted for the risks (e.g., injury, predation, territory intrusion), challenges (e.g., physical manipulation of shells), constraints (e.g., time), or other costs (e.g., energy expenditure) associated with searching for, handling, and digesting whole (ungrounded) or only partly broken foods, the preferences and digestive efficiencies demonstrated by captive birds might not accurately represent the behavioral or physiological responses of cranes in the wild.

Examination of whooping crane feeding behavior from the perspective of optimal foraging theory shed light on the probable strategies used by cranes to attain the optimal winter diet. Extensive daily travel across one's territory coupled with distinctive patterns of food-switching and consumption across winter suggested cranes were learner-driven and adept at sampling their environment. Continual tracking of the environment, in addition to family-based territorial defense and strong territory fidelity, are especially advantageous in areas that are highly variable but rich in resources, such as the salt-marsh (Pyke et al. 1977; Caraco 1981). Though regular sampling may reduce time spent foraging in the highest quality patches (e.g., Alonso et al. 1995), foragers can gain information about the probability distributions of encountering various prey types and develop expectation rules for when and where to find prey, when to return to a food patch, and whether or not to consume a prey item when encountered (Charnov 1976; Charnov et al. 1976; Pyke et al. 1977; Clark and Mangel 1984; Krebs and Davies 1993). Moreover, by improving predictability of encounter rates and learning the optimal rankings of foods, cranes can reduce the time required for finding the most profitable resources, minimize the total amount and variability of daily time spent foraging, and reduce the likelihood of competition (i.e., territory intruders). Together, the optimizing strategies used by cranes supported the maximization of long-term resource gain rather than short-term gain and increased the likelihood that resources would be secured during subsequent days, weeks and winters (Pyke et al. 1977; see also van Baalen et al. 2001).

During both winters of this study, cranes consumed foods within relatively distinct periods of time, exhibiting both sequential feeding and gradual food-switching behavior. Generally, cranes first targeted wolfberry fruit for 1-2 mon, followed by blue crabs, stout razor clams, and large terrestrial insects (e.g., grasshoppers) or periwinkle snails, each for multiple weeks to months. The order in which foods were used across winter, however, did not wholly correspond to patterns in food abundance or the order that foods were optimally ranked by foraging efficiency. Rather, patterns of food consumption appeared to relate closely with food availability, i.e., the amount or number of food items potentially consumable as determined by forager constraints (e.g., water depth). In some cases, consumption of a particular food occurred when it was presumably most available (see the clam, snail and insect discussions below). In other cases, consumption of one food type, despite its own availability, may have been limited by the high availability and consumption of a more optimal food type (Charnov 1976).

For instance, in conjunction with this study, quantitative sampling for wolfberry fruits (see also Butzler 2005) and blue crabs (see Chapter II) provided evidence that both food types reached peak abundance within or adjacent to the salt-marsh during November-December. However, cranes first targeted wolfberry fruit and then only increasingly incorporated blue crabs into their diet as fruit abundance was depressed. One explanation for the successive feeding of fruit and crab may be that, despite similar timing of peak abundance, blue crabs actually became increasingly more available from early to mid-winter as water levels in the marsh receded and shallow water increased accessibility of encountered crabs (Maheswaran and Rahmani 2001). Consequently, the order in which foods were consumed would also have been the order in which foods became maximally available during winter, with blue crabs most available to cranes in December (i.e., following exploitation of wolfberry fruit).

Results of this research certainly do not discount the plausibility of shallower waters leading to greater blue crab availability, but they do provide significant support to the explanation that greater inherent optimality of foraging for wolfberry fruit than blue crab led cranes to select fruits first and crabs later, if at all. In November 2004, both blue crab (medium and large-sized; 365 crabs ha^{-1}) and wolfberry fruit (0.43 fruits m^{-2}) were at peak abundance, but cranes solely targeted fruit. Blue crabs (25 crabs ha^{-1}) were then consumed throughout December, following the near depletion of fruits (0.04 fruits m^{-2}). In 2005, blue crab abundance was similar between November and December (60 crabs ha^{-1}), and water depth throughout early to mid-winter was notably shallower than in 2004 (see Chapter II). Therefore, conditions in December 2005 should have been more favorable for feeding on blue crabs than those of December 2004, when cranes consumed almost entirely blue crab. However, in 2005, peak fruit density in November (3.44 fruits m^{-2}) was eight times that of 2004, and fruits were abundant well into December at levels (0.37 fruits m^{-2}) only slightly less than the maximum of the 2004. Consequently, in 2005, cranes targeted fruits throughout most or all of November and December and only minimally consumed blue crabs in late December, when ponds of the interior salt-marsh began to go dry.

Several possible explanations exist for why cranes consumed clams during mid-winter and may have benefited most from feeding on clams at that time. First, as foods generally associated with greater maximum foraging efficiency than clams (e.g., wolfberry fruit, snails, and insects) were exploited by cranes and peaked in availability during periods other than mid-winter, razor clams may have been the most inherently optimal food of all foods available in mid-winter. Secondly, though clam densities were presumably higher earlier in winter (i.e., before loss to predation mortality), clams are of largest average size in mid- to late winter, just prior to recruitment of young into the population (Holland and Dean 1977). Therefore, for the amount of effort associated with foraging for clams, cranes may have attained the greatest net reward by foraging for clams at lower density but greater average size (e.g., Sutherland 1982).

Alternatively, mid-winter may have been the period of highest clam availability (i.e., density of potentially consumable clams) due to factors influencing forager search efficiency or encounterability of clams. During both winters, water depths along the coast were lowest in January and February, with water depths in winter 2005-2006 being so low that most ponds of the interior salt-marsh were entirely drained and only the centers of large mudflats within the marsh and the adjacent bays held shallow water. Moreover, mid-winter of both seasons represented a period of sparse structure within the water column (i.e., low densities of algae and submerged aquatic vegetation). Although acquisition of benthic prey depends in large part on tactile abilities (Kushlan 1978; Kelly et al. 2003) and, theoretically, should be little influenced by water depth or column clarity, the overall availability of clams to cranes may be influenced by the increasing predation risk associated with foraging in deeper water (Fritz et al. 2002) or the additional energetic costs or challenges of finding clam burrows without visual cues. Crane behavior, in fact, did suggest that the challenges of foraging increased with water depth, for foraging effort expended by cranes at the BR territory (the site of greatest clam consumption) was twice as much in January 2005 (100 movements min^{-1}) as in January 2006 (51 movements min^{-1}) even though consumption rates were similar (1.16 versus 0.95 clams min^{-1}, respectively).

Previous studies on the abundance patterns of snails and insects provide insight on the potential availability of these organisms to cranes foraging during winter. Strong trophic interactions documented between blue crabs and *Littoraria* periwinkle snails have reflected the capacity of predatory blue crabs to regulate or limit snail populations in the salt-marsh (Silliman and Bertness 2002; Moody and Aronson 2007). It follows then that snail abundance within the marsh should be lowest in the presence of blue crabs but highest after an extended period without predation pressure (i.e., in the absence of crabs; Silliman and Bertness 2002). Consistent with this pattern, crabs were present in the marsh of this study at greater densities during winter 2004-2005 than 2005-2006, and cranes consumed snails during winter 2005-2006 at numeric intake rates 10-24 times that recorded in 2004-2005. Earlier studies of marsh insects were less informative relevant to the late winter consumption patterns observed for cranes. However, some evidence has suggested that certain insects may be more accessible to cranes during late than early winter. Specifically, the standing crops (g m^{-2}) of both *Spartina* and *Salicornia* were shown to reach yearly lows during January-April, providing minimal refuge for prey, and predacious insects were observed within the *Salicornia* community during February-March but not earlier in winter (Cameron 1972).

This was the first study to consider prey-size selection when examining patterns of blue crab consumption by whooping cranes. Comparisons of optimality among foods suggested cranes foraged more efficiently (i.e., gained more of a resource per unit of effort expended) when targeting large than medium or small blue crabs. Consistent with this finding, winter patterns of intake rate and proportional use of foods (by dry mass) revealed that small crabs were almost never consumed by cranes despite exhibiting the highest densities of all size-classes (see Chapter II). However, contrary to this finding, patterns of consumption revealed that large crabs were never a sole principle food in the crane’s diet, rarely a dominant food, and only consumed at intake rates greater than for medium crabs during winter 2005-2006, when medium crab density was less than or similar to that of large crab.

Size-specific selection of foods is not unusual, as numerous studies have documented suboptimal use of foods by foragers. Factors believed to contribute to sizedefinitive patterns of consumption include those that limit intake rate or reduce the true availability of foods, such as the depth of clam burrows. Burrowing clams have shown to maintain increasingly deeper burrows with size (or age), thereby decreasing the number of avian predators with long enough bills to reach them (Kober 2004). Other factors limit the benefit achieved by consuming foods. For example, oystercatchers select for smaller than energetically-optimal mussels to reduce bill damage, which can reduce long-term foraging efficiency (Rutten et al. 2006). Prey-size selection is also influenced by risks of predator and competitor interactions (Nilsson and Brönmark 1999; Nilsson et al. 2000) which, as shown by limpets feeding on apple snails (Tanaka et al. 2006), can be reduced by selecting smaller prey and thus minimizing handling time.

In this study, cranes may have incorporated more medium than large crab into their diet simply because large crabs were rarely encountered at rates sufficient to support both specialization and maximization of foraging efficiency. Following the classic optimization model for prey selection (Charnov 1976; Kreb and Davies 1993), cranes would have always attempted to capture and consume large crabs (the more profitable food) when encountered but would have only consumed less profitable foods (e.g., medium crabs) upon being encountered when large crabs were minimally available. Thus, the decision to specialize (targeting only large crab) versus incorporate additional prey types into the diet would depend solely on availability of large crabs within the marsh, and patterns of selection based on prey size would not differ from patterns based on energetic or nutritional optimality.

Alternatively, cranes may have actually selected for medium crabs over large crabs due to risks or constraints associated with feeding on large crabs that were unaccounted for in optimality analyses. Though not yet documented, cranes may incur greater bill wear or risk of bill, nare, or eye injury when feeding on large crabs. The major physical defense of large crabs is a pair of large, powerful chelipeds (claws or pinchers), which are also used to secure and crack open clam shells and capture rapidly retreating prey. As both medium and large crabs are first subdued by cranes using no more than a few jabs and then carried from open water to a nearby pond bank, large crabs may still be alive and pose threat during transport. Moreover, time spent digesting medium versus large crabs was not incorporated in analyses, but cranes exhibited comfort behavior (e.g., preening) for long periods immediately following consumption of every large crab. In contrast, multiple medium crabs or a single medium crab plus several other food items were always consumed before comfort behavior was observed.

Despite great diversity in the study designs and methods used to investigate the winter diet and foraging patterns of whooping cranes, the combined findings of this and earlier studies (e.g., Hunt and Slack 1989) notably highlight that a handful of foods (wolfberry fruits, blue crabs, clams, snails, and insects) are predictably available to and consumed by cranes at some level during most years. As cranes are surrounded by seemingly countless potential food sources in the salt-marsh, consistent consumption of foods across years demonstrates initial but significant selection of the most inherently optimal of all available foods (Pyke et al. 1977). In addition, numerous other foods, such as fiddler crabs, crayfish, and other arthropods and molluscs, may be less predictably available across years but are opportunistically consumed by cranes when encountered in high abundance. Thorough documentation of the whooping crane diet, consequently, has provided evidence of the crane's ecological role as a generalist species, dependent not on one or only a few prey species but on a diversity of food types derived from (and contributing to) the highly dynamic salt-marsh of the Texas coast.

CHAPTER V

CONCLUSIONS

This dissertation research was in direct response to a 2002 proposal for diverting freshwater from the confluence of the Guadalupe and San Antonio Rivers to the city of San Antonio, Texas. To comply with Section 7 of the Endangered Species Act, sound scientific data were needed to effectively assess impacts of diversion on the endangered whooping crane and its critical wintering habitat in the Guadalupe Estuary. Concerns also arose in the general public regarding the diversion project due to logical reasoning that reduced freshwater inflows would lead to increased salinity levels, loss of estuarine species diversity (especially fisheries species; e.g., blue crab), loss of commercial fishing opportunities, and economic instability for coastal towns and industries dependent on fresh catch. Probable outcomes of diversion were also thought to include significant reductions in food availability for whooping cranes, as the blue crab was perceived to be the dominant food of cranes during winter (Chavez-Ramirez 1996; Pugesek et al. 2008).

My investigative contribution to understanding the impacts of diversion focused on both the whooping crane and the blue crab. I studied the settlement, recruitment, abundance, and distribution patterns of blue crabs in relation to factors of the estuarine environment, and examined the food habits and optimal foraging patterns of cranes in attempts to better understand their winter foraging ecology. The crab portion of my study revealed that settlement of megalopal crabs into shallow habitats of the Guadalupe Estuary was negatively related to freshwater discharge occurring during the earliest stages of development, whereas juvenile and adult crab densities displayed distinct patterns in and around the salt-marsh relating to micro-habitat characteristics (e.g., habitat type, water column structure type and structural complexity). Recruitment of individuals into the adult-form population was most prevalent around 59 km from the estuary's coastal water source, and the extent to which young crabs infiltrated the salt-marsh increased with age. Overall, shallow bay provided important nursery habitat for young blue crabs, while interior marsh ponds were important for dispersing juvenile and adult crabs. Most notably, however, this study included the most comprehensive examination yet conducted of the whooping crane diet and dispelled the general belief that cranes wintering on the Texas coast depend on blue crabs for survival during winter.

Despite great diversity in the study designs and methods used to investigate the winter diet and foraging patterns of whooping cranes, the combined findings of this and earlier studies (e.g., Hunt and Slack 1989) highlight that a handful of foods (wolfberry fruits, blue crabs, clams, snails, and insects) are predictably available to and consumed by cranes at some level during most years. As cranes are surrounded by seemingly countless potential food sources in the salt-marsh, consistent consumption of foods across years demonstrates initial but significant selection of the most inherently optimal of all available foods (Pyke et al. 1977). In addition, numerous other foods, such as fiddler crabs, crayfish, and other arthropods and molluscs, may be less predictably available across years but are opportunistically consumed by cranes when encountered in high abundance. Thorough documentation of the whooping crane diet in this study, consequently, provided evidence of the crane's ecological role as a generalist species, dependent not on one or only a few prey species but on a diversity of food types.

Blue crabs are, undeniably, a very important food source for wintering whooping cranes, and this study confirms such. However, prior notions that cranes depend on crabs for survival and experience deteriorated body condition during periods of low crab availability are simply not well-founded. In fact, this study suggests that, while crabs are a valuable food source for cranes when available, they are not the most optimal food in terms of foraging reward (e.g., numeric, dry mass, or energetic intake), cost (i.e., foraging effort), or efficiency (i.e., ratio of reward:cost). Moreover, as long as foods of greater optimality (e.g., less cost) were available in this study, blue crabs were rarely or not at all consumed by cranes. For instance, despite maximum levels of crab abundance in early winter, foraging cranes first targeted wolfberry fruit and then only increasingly incorporated blue crabs into their diet as fruit abundance was depressed. Perhaps the most convincing piece of evidence, however, was that cranes achieved greater reward and expended less effort during the second winter of this study, when crab abundance in the salt-marsh was lowest. If whooping cranes were a specialist forager of blue crabs, such a pattern, no matter how infrequent, would not be possible.

Data describing the foraging ecology of whooping cranes and population ecology of blue crabs were significant in and of themselves, but this study also provided a unique perspective on the value of scientific inquiry versus the potential biases of casual observation. Wildlife- (and, specifically, whooping crane-) viewing via private boat tours has become a popular activity along the Texas coast, and observations made by tour-boat captains and passengers on the numbers and foraging activities of cranes have regularly contributed to monthly and annual whooping crane updates written by the U.S. Fish and Wildlife Service. However, while these casual observers quite easily notice when a crane has captured a blue crab, they likely do not notice when the same crane has plucked a berry or snail from a plant or gulped a clam newly-removed from its burrow. Behavioral observations conducted in this study documented that both blue crabs themselves and the handling behavior of crab-feeding cranes are highly conspicuous. Small crabs (<30 mm CW), which may be difficult to spot by the casual observer, were nearly never consumed during the two years of this study, but medium to large crabs were consumed during both winters. In contrast to smaller, less motile, or less aggressive prey, these larger crabs were chased, violently jabbed, carried to nearby elevated ground, and literally beaten to pieces before being consumed by cranes. Therefore, as is evident in the previous predator-prey example, unbiased documentation of some ecological relationships might only be possible through scientific study.

The down-listing of the whooping crane from endangered to threatened status and eventual recovery of the species will require a much greater increase in population size than yet realized. However, as the Aransas-Wood Buffalo cranes approach carrying capacity of their current wintering area, range expansion and continued population growth will depend highly on availability of suitable habitat in adjacent areas of the Texas coast. Though criteria have not yet been developed to effectively assess habitat suitability, estimate carrying capacity, or identify high priority areas for conservation of whooping cranes, this study suggests that the development of such criteria may benefit most from studies on the abundance and distribution patterns of crane foods not previously examined (e.g., snails, insects, clams).

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