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Provisioning and prey quality in Brown Pelicans (*Pelecanus occidentalis*) in Charleston Harbor, South Carolina

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PROVISIONING AND PREY QUALITY IN BROWN PELICANS (*PELECANUS
OCCIDENTALIS*) IN CHARLESTON HARBOR, SOUTH CAROLINA

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Elena Beth Sachs
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Accepted by:
Dr. Patrick G. R. Jodice, Committee Chair
Dr. William Bridges, Jr.
Ms. Felicia Sanders

ABSTRACT

I examined parent and nestling behavior during early chick rearing in Brown Pelicans (*Pelecanus occidentalis*) nesting at a colony in Charleston Harbor, South Carolina during the 2006 breeding season. There were significant differences in the frequency of feeding, attendance, and chick aggression according to chick age, although the pattern differed among behaviors. The rate of adult feeding, chick feeding and adult attendance all decreased with chick age while chick aggressive behavior peaked when chicks were ca. 21 d post-hatch. I found that nests with at least one juvenile parent had a lower average clutch size, hatch rate, and number of young that survived to 21 d than pairs with two adult parents. In addition to studying provisioning behavior, I also determined the proximate composition and energy density of seven species of marine forage fish that are potential prey items of Brown Pelicans and other seabirds on the coast of South Carolina. Some of these fish species are likely only available in the seabirds' diet as discarded bycatch from commercial shrimp operations. Proximate composition and energy density differed among the species of forage fish I examined. This suggests that piscivorous seabirds may experience differences in energy intake rates dependent upon prey availability. However, the range in energy density that I observed among species was relatively narrow and hence it appears that energy values in this region may be relatively stable among prey items during the seabird breeding season.

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CHAPTER ONE

INTRODUCTION

Most seabird species are long-lived colonial breeders with relatively low annual reproductive rates and lengthy chick rearing periods. Parent seabirds are typically central place foragers and as such, provision young with food collected at sea and delivered to the nest. In many seabirds, foraging trips often cover long distances between highly ephemeral food sources and the colony and can, therefore, present challenges to seabird parents provisioning altricial chicks. Due to the significant investment required of seabirds in rearing young and the numerous breeding opportunities over a lifetime, Stearns (1992) hypothesized long-lived species such as most seabirds should seek to optimize rather than maximize annual reproductive success. In order to balance the level of effort dedicated to brooding chicks during any one breeding attempt, seabirds may adjust provisioning rates based on environmental, behavioral and physiological variables of both adults and young. Several factors such as chick age, parent age, brood size, tide stage, and date have been shown to affect parental attendance and feeding rates in seabirds (Pinson and Drummond 1993, Meyer et al. 1997, Ploger 1997, Hedd et al. 2001).

In addition to the aforementioned factors, numerous authors have demonstrated that shifts in both prey availability and prey quality can significantly affect provisioning behavior and breeding success in seabirds (Litzow et al. 2002, Baillie and Jones 2004, Jodice et al 2006). Prey quality can be broadly defined as the proximate composition and energy density of a food item. The main prey of most seabirds is fish which are primarily comprised of water, lipid, and protein. Despite this relative simplicity, fish prey can still

present their piscivorous predators with a wide range of energy density and lipid content (Anthony et al. 2000). Two hypotheses that have been posed to describe the relationship between diet and reproductive success or individual condition are the nutritional stress hypothesis, which postulates that a decrease in quantity or quality of prey may negatively affect the condition of individuals or populations, and the junk food hypothesis, which postulates that a decrease in lipid content will negatively affect individuals and populations (Rosen and Trites 2000, Jodice et al. 2006). In order to better understand the effect that prey quality has on the diet selection and reproductive success of piscivorous predators, it is necessary to determine the proximate composition and energy density of fish consumed by seabirds during the breeding season

Here, I examine parent and nestling behavior during early chick rearing in Brown Pelicans (*Pelecanus occidentalis*) nesting at a colony in South Carolina. I also determine the proximate composition and energy density of seven species of marine forage fish that are potential prey items of Brown Pelicans and other seabirds on the coast of South Carolina. Some of these fish species are likely only available in the seabirds' diet as discarded bycatch from commercial shrimp operations. Changes in feeding rates, parental attendance, and chick behavior may occur as conditions at colonies vary in response to natural or anthropogenic stressors. Hence, a thorough understanding of factors that influence provisioning behavior and breeding biology is necessary.

The Brown Pelican is a coastal seabird that breeds along the southeastern coasts of North America to the northern coasts of South America and the Caribbean (Shields 2002). Fluctuations in Brown Pelican populations throughout the United States have

occurred within the last half century. Throughout their range, pelicans experienced severe population declines between the late 1950s and 1970s, due primarily to the effects of organochlorine pesticides. In 1970, the Brown Pelican was placed on the federal Endangered Species List and, following recovery efforts in 1985, was removed from the list in the southeastern United States. In South Carolina, pelicans have nested regularly on several of the coastal islands since at least the mid 1900s, but have recently experienced a population decline (Figure 1.1). Crab Bank, in Charleston Harbor, has provided nesting habitat for several species of seabirds, including the Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) over the last decade. Although numerous factors may be contributing to the decline in statewide breeding populations (e.g. environmental contaminants, changes in food availability or food quality, dispersal to new colony sites) human disturbance is one factor that has received substantial attention from management agencies. Prior to the 2006 breeding season, human activity was present on and around the island. In 2006, the South Carolina Department of Natural Resources (SCDNR) implemented new regulations which prohibited human access to Crab Bank during the breeding season. This provided an opportunity for studies to be conducted on breeding seabirds in the absence of human disturbance.

Chapter two of this thesis, “Provisioning behavior in Brown Pelicans in South Carolina”, examines the relationship between parent and chick behaviors at the nest and a suite of environmental and behavioral factors. I measured rates of parental attendance, parental feeding, chick feeding, chick begging, and chick aggression during the 2006 breeding season. I considered possible effects of chick age, parent age, date, tide stage

and brood size on the five aforementioned behaviors. Due to logistical constraints, my study was initiated after peak incubation and hence all results are specific to pairs that should be classified as “late nesters”.

Chapter three of this thesis, “Proximate composition and energy density of forage fish of nearshore waters of South Carolina”, examines the interspecific differences in proximate composition and energy density of forage fish that are common prey items for seabirds along the coast of the southeastern U.S. Prey quality and prey availability are both important aspects of seabird diets (Jodice et al. 2006) and few data are available on this aspect of seabird diets from temperate marine systems. Seabirds at Crab Bank, as well as other colonies in the state, also forage behind active shrimp trawlers on discarded bycatch and it appears that some of the prey items taken there are benthic or mid-water species (Jodice and Wickliffe 2007) that typically would not occur in the diet of these seabirds. I determined the proximate composition and energy density of seven species of forage fish, some of which are likely to occur in the natural diet of these seabirds and others of which are likely only available as bycatch from shrimp trawlers. Comparisons of energy density and proximate composition among species will provide insight into the possible effect that access to discarded bycatch has on seabird diets in this region.

Results of this research will contribute to our understanding of the environmental, behavioral, and physiological factors that influence provisioning behavior in seabirds and will also provide insight into constraints on reproductive parameters. In addition, this study will provide energy content values for several species of forage fish available to breeding seabirds in South Carolina. The energetic value of fish has received

considerable attention; however, most studies have been focused in high latitude, cold water regions. Collectively, information regarding provisioning behavior and diet quality will improve efforts to monitor and manage nesting colonies of Brown Pelicans, not only in the state, but throughout the southeastern U.S.

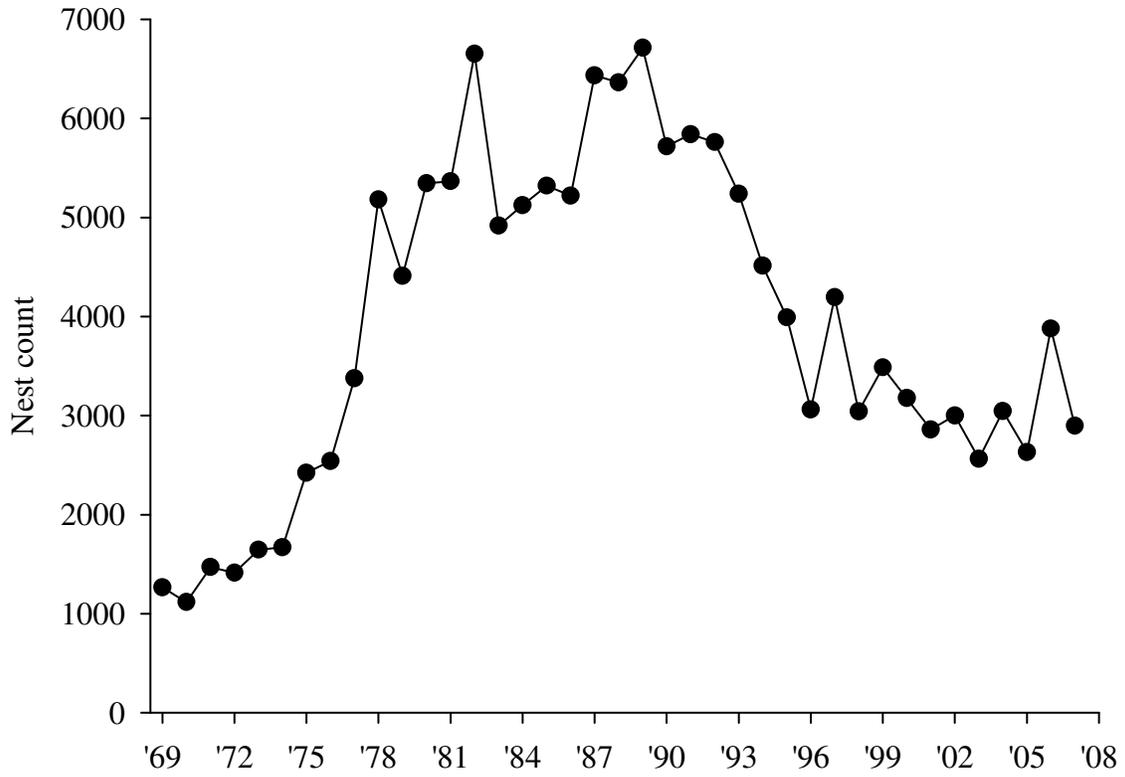
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Figure 1.1 Annual statewide nest counts of Brown Pelicans in South Carolina, 1969-2007 (updated from Jodice et al. 2007)



CHAPTER TWO

PROVISIONING BEHAVIOR IN BROWN PELICANS IN SOUTH CAROLINA

Introduction

In long-lived birds parents must balance the level of effort dedicated to raising chicks during any one breeding attempt with the long-term need to maximize lifetime reproductive success (Stearns 1992). This balance is necessary because breeding adults appear to suffer decreased annual survival when parental effort is increased (Deerenberg et al. 1995, Golet et al. 1998). In contrast, dependent young seek to maximize the delivery of resources by parents in an effort to maintain high rates of growth and development. Increased attention from parents also may serve to decrease predation at the nest as well as intraspecific aggression that may negatively affect nestlings (Schaller 1964, Anderson and Keith 1980, Lewis et al. 2004). Hence a conflict between parental effort and chick demands may develop whereby parents seek to reduce effort during the course of brood-rearing and chicks seek to maintain parental attention (Trivers 1974). This may be especially apparent in species with extended brood rearing that also rely on ephemeral and often distant food sources such as seabirds.

In order to allocate the appropriate level of parental effort, parents may adjust provisioning rates based on environmental variables or behavioral and physiological attributes of adults and young. For instance, several studies of seabirds have shown that adult provisioning behavior and chick feeding behavior vary in relation to the age of the chick, and that specifically a decrease in feeding frequency (Schaller 1964, Montevecchi et al. 1984) and nest attendance by adults (Schaller 1964, Lewis et al. 2004) often occurs

as chicks age. These trends may be attributed to developmental changes in rapidly growing chicks (Schreiber 1976). For example, in Pelecaniformes, where chicks are altricial and require extensive brood-rearing that often lasts >12 weeks, adult attendance often declines from near constant presence at the nest to less frequent attendance as chicks obtain feathers and the ability to thermoregulate (often at ca. 30 d post-hatch) (Bartholomew and Dawson 1954). Similarly, meal delivery rates by parent seabirds often decrease as the chicks age, although this decline may be compensated for by an increase in meal size (Hedd et al. 2001)

The age of the parent may also influence provisioning behavior and reproductive success in seabirds. Numerous studies have documented lower reproductive success in juvenile birds compared to mature adults (Coulson 1968, Blus and Keahy 1978, Crivelli et al. 1998, Bunce et al. 2005, Lewis et al. 2006). These differences are often attributed to underdeveloped incubation, foraging and brooding skills in juvenile parents (Orians 1969, Brandt 1984, Carroll et al. 1985, Carl 1987). This may be especially relevant in seabirds where foraging strategies are relatively complex and often involve long-distance commutes between the colony site and highly ephemeral food sources. Often, juvenile parents also nest later in the season and nest in lower quality habitat, further contributing to lower reproductive success compared to mature adult counterparts.

Numerous other factors such as brood size, tide stage, and date have been shown to affect parental attendance and feeding rates in seabirds as well (Pinson and Drummond 1993, Meyer et al. 1997, Ploger 1997, Hedd et al. 2001). While these data are relatively basic, they can have important implications for the development of management and

conservation efforts. For example, changes in feeding rates, parental attendance, and chick behavior may occur as conditions at colonies vary in response to natural or anthropogenic stressors. A thorough understanding of factors that influence provisioning behavior and breeding biology is hence necessary.

My goal was to investigate parent and nestling behavior during early chick rearing in Brown Pelicans nesting at a colony in South Carolina. Although Brown Pelicans have nested on the coastal islands of South Carolina for at least the last seventy years (Wilkinson 1982), relatively few data are available regarding their breeding biology in this region. Therefore, our understanding of provisioning strategies in Brown Pelicans is incomplete. Furthermore, although South Carolina's coastal islands have historically provided abundant nesting, roosting, and foraging habitat for wading, shore-, and seabird species, several of these species, including Royal Terns (*Sterna maxima*), Brown Pelicans, and Black Skimmers (*Rynchops niger*) have experienced declines in their breeding populations within the state during the last ca. 15 years and the causes remain unclear (Wilkinson 1997, Jodice et al 2007). Although numerous factors may have led to or may continue to contribute to the decline in statewide breeding populations (e.g. environmental contaminants, changes in food availability or food quality, dispersal to new colony sites) one that received substantial attention from management agencies is human disturbance. In an effort to reduce any negative impacts from human disturbance to breeding seabirds, SCDNR closed all islands supporting colonies to human access immediately prior to the 2006 breeding season. This management action provided an opportunity to establish baseline measures of seabird breeding biology and behavior in an

undisturbed setting and hence allow for future comparisons of any changes that might occur in these parameters if management or conditions change. My objectives, therefore, were to 1) establish baseline measures of parental and chick behavior at the nest, 2) assess the relationships among parental behavior at the nest, chick behavior at the nest, and a suite of environmental and behavioral factors, and 3) compare reproductive parameters between nesting pairs with two adult parents to those with at least one juvenile parent.

Methods

Study Species

The Brown Pelican is a long-lived marine bird that nests in colonies on offshore islands along the southeastern coasts of North America to the northern coasts of South America and the Caribbean (Shields 2002, Nelson 2005). Brown pelicans typically lay three eggs that are incubated for approximately 29-32 days. Eggs hatch asynchronously, with the second egg hatching about 24 hours after the first and the third hatching approximately 40 hours later. Pelican chicks are altricial and rely solely on adults for brooding and feeding until fledging at approximately 70 days after hatching. Both males and females share in incubation, brooding, and feeding of the chicks until fledging. There are no reports for adult care in post-fledge young (Nelson 2005). Brown Pelicans typically begin breeding at two to three years of age. In South Carolina, pelicans nest on several coastal islands that are typically free of mammalian predators (Jodice et al. 2007). Most pelicans in South Carolina are ground-nesters, although a small proportion also nests in shrubs.

Study Site

The study site was a Brown Pelican colony of approximately 400 nests located on Crab Bank Heritage Preserve in Charleston Harbor, SC, USA (32°46'N 79°53'W). Crab Bank (ca. 9 ha) is located at the mouth of Shem Creek in Charleston Harbor and is managed by SCDNR as a Heritage Preserve. Crab Bank is relatively narrow, ca. 150 m at its widest point during low tide, and thus even the interior of the colony is proximate to the edge of the island, particularly during high tide. Pelicans first nested regularly on Crab Bank in the mid- 1990s and have continued to nest there annually since. Crab Bank also supports breeding Sandwich Terns (*Sterna sandvicensis*), Royal Terns, Black Skimmers, Laughing Gulls (*Larus atricilla*) and American Oystercatchers (*Haematopus palliatus*) as well as several species of wading birds. Vegetation on the island consists mainly of Russian thistle (*Salsola* sp.), marsh hay (*Spartina patens*), camphorweed (*Heterotheca subaxillaris*), beach elder (*Iva imbricata*), beach tea (*Croton punctatus*), and dogfennel (*Eupatorium capillifolium*). Human access was permitted on the island, but not within the colony proper, prior to the 2006 breeding season. Since that time, human access has been prohibited on the entire island during the breeding season though recreational boaters and anglers still frequent the waters immediately surrounding the island year-round.

Field Procedures

The study was conducted from late May through late July 2006. In South Carolina, pelicans generally initiate nesting in mid to late April and peak incubation typically occurs in mid to late May. Annual nest surveys are usually conducted by

SCDNR in late May to correspond with peak incubation, though Brown Pelicans on Crab Bank appeared to nest earlier in 2006 and 2007 compared to recent years (i.e. greater number of older chicks observed during 2007 survey than in previous years, pers. comm. Lisa Eggert). Due to logistical constraints, my study was initiated after peak incubation and hence all results are specific to pairs that should be classified as “late nesters”.

During late May 2007 I conducted preliminary observations of incubating and brooding adult pelicans to determine the number of nests that could be observed simultaneously and the optimal distance at which observations could be conducted so as to maximize data recording while minimizing disturbance. I was able to observe behaviors of pelican parents and chicks at 13-14 nests simultaneously from a distance of < 15 m. I delineated two plots for observations with each plot representing distinct clusters of nests. Both plots consisted of nests on the edge of the colony as well as nests that were buffered from the edge by other nests. Plots were ca. 50 m apart from nearest edge to nearest edge with plot one (n = 14 nests) located on the SW side of the island and plot two (n = 13 nests) located on the NW side of the island. I used numbered flags attached to metal posts to mark each nest. Flags were placed horizontally through the nest so that the number was visible to the observer. I recorded the number of eggs in each nest in plot one on 4 June 2006 and in each nest in plot two on 5 June 2006 and used these values as the clutch size for subsequent analyses. I conducted 12 observation periods in plot one and 8 observation periods in plot two between 10 June 2006 and 22 July 2006. Each observation period lasted three hours and was conducted between either 0700-1200 hours (AM; n = 13) or 1400-1800 hours (PM; n = 7). Observations were also

equally divided between high and low tide cycles. Observations were conducted during this time because the few data available on foraging patterns of Brown Pelicans suggested that individuals foraged primarily in early morning and evening (Carroll and Cramer 1985) and on rising tides (Schnell et al 1983). Though there is limited foraging activity at night (Robert and McNeil 1989, Croll 1986), I was logistically unable to sample during those hours. In both plots, observations were conducted 50% of the time during flood tides and 50% of the time during ebb tides. I ceased observations once chicks were unable to be identified at individual nests. Statistical analyses were only conducted for AM sampling periods, because six out of seven PM sampling periods occurred in the month of June; therefore date and time of day sampled were confounded.

I recorded adult and chick behavior at each study nest within a plot during each observation period. I approached the colony slowly to minimize disturbance, and waited at least 15 minutes from the time of my arrival prior to initiating observations. I positioned myself ca. 5-15 meters from the nests on the periphery of the plot and used 8 x 42 binoculars or a spotting telescope to observe adults and chicks. Each observation period lasted three hours and I recorded behavioral data at five minute intervals (i.e., 36 intervals per nest per period). Hereafter, these are referred to as nest intervals. There were 504 nest intervals per three-hour observation period ($180 \text{ minutes} \div 5 \text{ minute intervals} * 14 \text{ nests}$) in plot one and 468 nest intervals per three-hour observation period in plot two. At the beginning of each five minute interval I would start with nest number one, count the number of adults and chicks present, and record an instantaneous behavior of any adults or chicks in that nest (behaviors described below). Typically, this

instantaneous observation required <15 s. I then systematically progressed through the remaining nests in the plot, repeating the above procedure until behavior was recorded in all nests.

I recorded five focal behaviors: adult feeds, chick feeds, adult attendance, chick begging, and chick aggression. Feeding behavior included both “indirect” feeds and “direct” feeds (terminology from Pinson and Drummond 1993). Indirect feeds occurred when adults regurgitated partially digested fish onto the nest floor (adult indirect feed) or when a chick foraged upon a regurgitated fish (chick indirect feed). I considered two indirect chick feeds distinct after a minimum 15 minute period of inactivity by the chick, prior to resuming feeding, even if upon the same previously regurgitated fish (Schaller 1964, Shields 1998). Therefore, one recorded indirect feeding bout from an adult might ultimately be recorded as >1 indirect feeding bout for a chick. Once chicks were older than ca. 21 days they were able to feed directly from an adult’s bill by reaching into the adult’s throat and intercepting the fish (Chapman 1908). I defined an event as a direct feed for both adults and chicks when I could determine that a fish had been exchanged between an adult and its’ young. It would often take several attempts by a chick thrusting its’ bill into an adult’s throat before it could successfully obtain a fish but these were all considered a single feed. I recorded a direct feed if I observed an engorged neck on a chick following the aforementioned behaviors. In all subsequent analyses, adult feeding is presented as number of actual feeds among all nests during each nest interval. Chick feeding is the number of nest intervals during which any chick in a nest was observed feeding summed across all nests. For example, whether one or three chicks were engaged

in feeding behavior within a nest during an instantaneous scan, the count for that five minute interval was “1”(i.e., observations are nest-based and account for the behavior of all chicks in the nest).

Parental attendance was defined as an adult being present in or within one meter of the nest and displaying brooding behavior and was scored as 0, 1, or 2 depending upon number of adults present. Therefore, during the 36 intervals within each observation period the highest possible attendance score was 72, which would represent both adults in attendance at the nest for the entire three-hour observation period.

Siblicide is not uncommon in Brown Pelicans (Pinson and Drummond 1993; Shields 2000), and therefore, aggressive behaviors were recorded for chicks and were defined as any hostile action or attack directed at nestmates, conspecifics, or other species. Aggressive behavior in chicks typically included pecking, biting, and pushing. For the purpose of these analyses I combined all intra- and internest aggressive behaviors.

I treated begging as a binomial variable and simply recorded whether or not it was observed at a nest during each instantaneous scan. Begging behavior by chicks was often vigorous and accompanied by loud vocalizations. Chicks attempted to peck at the mandible and gular pouch of the adult, particularly following a parent's return from a foraging trip. I did not count individual “number of begs” at each nest due to the instantaneous nature of the recording. Aggression and begging were recorded identically to chick feeding, i.e., the metric is the number of nest intervals during which the behavior was observed.

Growth Data

Growth measurements of chicks were collected to estimate their ages, which were subsequently used in age-specific analyses of behaviors. In an attempt to minimize disturbance to the colony, I only collected growth data on the day behavioral observations were conducted. I followed procedures described in Ferguson (2006). After the three hour observation period, I entered the plots and measured body mass (electronic scale if ≤ 1500 g or spring scale if > 1500 g), and culmen, tarsus and wing chord length (dial calipers ± 1 mm, wing bar ± 1 mm) for each chick in my study nests. I distinguished alpha (first hatched), beta (second hatched) and gamma (third hatched) chicks by marking their bills with non-toxic nail polish in red, blue, and green respectively early during the study. On subsequent sampling days, the largest chick was assumed to be the alpha chick if the nail polish was no longer visible (Schreiber 1976, Pinson and Drummond 1993, Ferguson 2006). Once the chicks were mobile (> 14 d), they were prone to leave the nest as I approached and were subjected to aggressive pecking from neighboring adults and chicks. Therefore, handling of chicks was discontinued when chicks were older than ca.14 d. For this same reason, it was difficult to identify the alpha, beta, and gamma chicks at each nest after ca 14 d, so subsequent analyses did not consider hatch order.

I estimated the age of all chicks using the model (age = $14.14 * \ln$ culmen length – 42.85). This model is based on a composite growth curve of 54 known age nestlings measured at two South Carolina colonies (including Crab Bank) during 2004 and 2005 (Ferguson 2006). When possible, this estimate was confirmed using known hatch dates based on observations for the chicks in this study.

Statistical Analysis

I compared the mean clutch size, hatch rate, and productivity (expressed as number of young per nest that survived to 21 d: Shields 1998) between nesting pairs with two adults compared to pairs with at least one juvenile. The age category of nesting pairs was determined by age related plumage variation in attending adults (Nelson 2005). I used one-tailed tests and predicted that each of the three reproductive variables would be lower in pairs with at least one juvenile parent compared to those with two adults.

I assessed the relationship between the five focal behaviors and a series of environmental and behavioral variables with a series of mixed models. Independent variables were chosen in part based on results and hypotheses from the literature. A preliminary review of the nest-based behavioral data suggested that both pseudoreplication and repeated measures concerns needed to be addressed both within and between days. I conducted a Durbin-Watson test on all response variables to determine if the five-minute observations were serially correlated. Results from these analyses were not significant ($D > D_L$ for all tests), indicating that the five minute interval observations showed no serial correlation (Montgomery and Peck 1982). I treated observations of nests between days, however, as a repeated measures analysis (see below).

I used a model selection approach based on the Akaike Information Criteria (Burnham and Anderson 2002) to assess the response of each of the five focal behaviors to the independent variables (Table 2.1). Data were analyzed as mixed models using a repeated measures design. An identifying nest number was included as a random

variable in each model and was also used as the subject term of the repeated measures statement. I created a set of *a priori* models (Table 2.1) for each behavior and ran each using PROC MIXED (SAS/STAT system version 9.1, Copyright 1999-2005 SAS Inc., Cary, NC). A priori models were created to test specific hypotheses about each behavior. I examined all independent variables for multicollinearity. I found that date and chick age were strongly correlated ($r = 0.81$) and so never placed these in the same model.

For each behavior I then ran each model listed in Table 2.1 and then ranked each model within each behavior based on the AICc statistic. The model with the lowest AICc value was considered the most parsimonious and plausible for the available data and the models tested. I calculated the difference in AICc between the highest ranked (i.e., most parsimonious) model and each other model under consideration (i.e., $\Delta AICc$) and also calculated the AICc weight which provides a measure of the probability that the model in question is the best model tested given the data. I used the magnitude of differences in weights between models to assess model separation. I also used these weights to compose a 95% confidence set of models, which is the set of models that would include the actual best model in 95% of all samples (Burnham and Anderson 2002). This set includes all models where the cumulative sum of the AICc weights of each model, when considered in order of lowest to highest AICc sum to approximately 0.95. The composition of 95% confidence sets and ranking of models was used to determine which independent variables were most strongly related to the focal behaviors.

To quantify the strength and direction of the effects of each independent variable on each of the five focal behaviors, I calculated unconditional estimates for coefficients

and standard error terms for each independent variable following Burnham and Anderson (2002). Model-averaged parameter estimates were then interpreted identically to any coefficient estimate from any regression analysis, i.e., the value of the coefficient estimate slope of (for continuous terms) or difference in (for categorical terms) the response behavior in relation to the independent variable being considered. Furthermore, the ratio of the coefficient estimate to the standard error estimate assesses the uncertainty associated with the coefficient estimate. Variables or interaction terms not included in any of the models comprising the 95% confidence set were regarded as unimportant and thus parameter estimates were not calculated for them (Burnham and Anderson 2002). Those variables appearing in only one model from the 95% confidence set were not suited to parameter estimation via model averaging: for these we simply used the single coefficient and standard error estimates from the appropriate model. In some cases, variables included in the top models had standard errors that were relatively large compared to the coefficient estimates and these are not discussed.

Results

There were no significant differences between the two plots on Crab Bank for clutch size per nest ($t_{25} = 0.2$, $P = 0.9$), hatch rate ($t_{25} = 1.0$, $P = 0.3$), or productivity ($t_{25} = 0.5$, $P = 0.6$). Data were therefore pooled between plots for all subsequent analyses. The mean clutch size ($n = 27$ nests) was 2.6 ± 0.1 eggs per nest. There were 17 clutches with three eggs, 9 clutches with two eggs and one clutch with one egg. The mean number of eggs that hatched per clutch was 2.0 ± 0.2 per nest, which accounted for 78% of the total number of eggs counted at the start of the study. We were not able to

determine the fate of all unhatched eggs. Some eggs remained in nests for days after appropriate incubation time while others disappeared. The mean number of young per nest that survived to 21 d was 1.6 ± 0.2 . Of the 27 nests included in the study, 4, 8, 10, and 5 nests fledged 0, 1, 2, and 3, chicks respectively.

Age Category of Parent

Seven of 27 nests had at least one juvenile parent. All other pairs consisted of mature adult parents. Clutch size, hatch rate, and productivity were all significantly lower ($P < 0.05$) in pairs with at least one juvenile compared to pairs with two adults (Table 2.2). Adult/adult pairs hatched 46 of 54 (85%) eggs and 36 of 46 (78%) young survived to 21 d. Pairs with at least one juvenile parent hatched 9 of 16 eggs (56%) and 7 of 9 (78%) young survived to 21 d.

Adult and Chick Behaviors at the Nest

For each of the five focal behaviors, the 95% confidence sets included between 1 and 5 models (Table 2.3). The highest ranked model was, on average, twice as likely to be the best model as the second ranked model and ca. 3-15 x as likely to be the best model as the third ranked model among all behaviors, suggesting good model separation (Table 2.3). Global or intercept only models never appeared in the 95% confidence set for any behavior. Each of the independent variables I measured appeared in at least one model within a 95% confidence set except date and tide stage which never appeared in any models within any 95% confidence sets. In contrast, chick age was strongly related to four of the five behaviors we analyzed and appeared in all models within the 95%

confidence set for adult feeds, chick feeds, adult attendance, and chick aggression (Table 2.3). Below I summarize which variables most strongly affected each behavior.

While adult feeds and chick feeds both decreased at similar rates with chick age and both increased at similar rates with chick begging rates (Figure 2.1, Table 2.4), adult attendance initially increased with chick age, then decreased ca. 21 d post-hatch (Figure 2.2). When chicks were younger than ca. 20 d, nest attendance rates were equivalent to having one parent on the nest 100% of the time during the three-hour observation period and an additional parent on the nest approximately 19% of the time. At ca. 21 d post-hatch and beyond attendance rates were equivalent to having one parent on the nest approximately 90% of the time but never having two adults present. Chick begging was positively related to chick aggression although this relationship was stronger for chicks with at least one juvenile parent compared to chicks with two adult parents (Table 2.4). Chick aggression was most strongly affected by an interaction of brood size and chick age. While there was no aggression in broods with only one chick there was a negative relationship between chick age and aggression in two and three chick broods with the relationship in three chick broods being more strongly negative.

Discussion

Adult and chick behavior at the nest in relation to chick age

My results clearly showed that chick age affected most of the focal behaviors I measured. In general there was a negative relationship between chick age and adult and chick behaviors although effects varied and were linear (adult and chick feeding), nonlinear (parental attendance), and interactive (aggression). There was, however, no

relationship between chick age and begging rates. Few studies have examined the relationship between chick age and parental and chick behavior in Brown Pelicans and so opportunities for intraspecific comparisons are limited. I suggest that the effects of chick age that I observed, particularly on feeding rates and parental attendance, are related to a shift in growth and development in chicks of Brown Pelicans that occurs between three and four weeks post-hatch. These may then, in turn, affect chick and adult behavioral patterns.

Schreiber (1976) observed that Brown Pelican chicks in Florida experienced maximum rates of growth during the first 3 weeks after hatching. Ferguson (2006) observed a similar trend in Brown Pelican chicks on Crab Bank and also noted that structural growth rates (e.g. culmen and tarsus length) were highest during this time. The decrease in growth rates experienced by pelican chicks ca. four weeks post-hatch may be due to developmental changes that also occur during this time (Schreiber 1976). Pelican chicks experience a sharp increase in feather growth at ca. 3 - 4 weeks post-hatch and this in turn may require chicks to partition energy away from mass and structural gain (Schreiber 1976). Furthermore, at approximately 20 d post hatch Brown Pelican chicks begin to achieve thermoregulatory abilities (Bartholomew and Dawson 1954). They also become more mobile at this age and can shade themselves in nearby vegetation rather than relying solely on adults for thermal protection (pers. obs.).

This shift in developmental stages coincides with a transition to decreasing rates of parental care and declines in feeding that I observed (although it is unclear if this relationship is causative or correlative). For example, parental attendance at the nest

prior to 21 d post-hatch during my study included two adults ca. 20% of the time but after 21 d post-hatch parental attendance was equivalent to never having two parents present. Similar patterns of decreasing adult attendance with chick age are reported in White Pelicans (Schaller 1964) and in Northern Gannets (*Morus bassanus*) (Lewis et al 1993), which also attain the ability to thermoregulate at ca. one month of age. I also observed that although feeding rates declined linearly there appeared to be a shift in these rates as chicks surpassed 21 d post-hatch. For example, chicks in my study rarely fed more than once per three hour period after 21 d post hatch while prior to that 1.5 – 2 feeds per three hours was not uncommon. Therefore parental attendance and feeding rates both appear to decline at ca. 3 – 4 weeks post-hatch as chicks experience a shift in developmental stages and gain independence.

While the eventual decline in parental attendance with chick age appears to be neatly linked to increasing independence of the chick, as well as crowding at the nest as chicks get larger, it is not entirely clear why the average number of feeds decreases as the chicks age. This trend is not uncommon within the order. White Pelicans (*Pelecanus erythrorhynchos*) and Northern Gannets (*Sula bassanus*) (Montevecchi, et al. 1984) each provision their young less frequently as chicks age and Pinson and Drummond (1993) also observed a decrease in feeding rates of brown pelican chicks with age. The decline I observed does not appear to be due to a decrease in begging rates, as that behavior did not show a negative relationship with chick age. It is possible that meal sizes increase and that this compensates for feeding frequency. For example, Hedd et al. (2001) observed that meal sizes in Shy Albatrosses (*Thalassarche cauta*) increased as feeding frequency

decreased. I was not able to measure meal size during this study but did observe that large menhaden were delivered both early and late in chick rearing and that often uneaten fish were left in the nest bowl early during chick rearing. Interestingly, Suryan et al. (2002) found that weekly variation in feeding frequency more strongly affected growth rates in Black-legged Kittiwake chicks compared to either the size of the meal or the energy density of the meal. Hence it may be that the relationship between reduced growth rates and reduced feeding frequency are tightly linked and that meal sizes or meal quality are not as important in this relationship. Nonetheless, based on these findings I would hypothesize that chicks allocate more energy to feather development during the fourth week post-hatch and this, coupled with a decrease in feeds, results in a decrease in mass gain.

Begging and aggressive behavior in chicks

In many species of seabirds begging rates appear to affect feeding rates. For example Granadeiro et al. (2000) observed a positive relationship between begging rates and provisioning in Cory's Shearwaters (*Calonectris diomedea*) and Villasenor and Drummond (2007) also reported a positive correlation between chick begging and parental feeding in Blue-footed Boobies (*Sula nebouxii*). In this study, I found that both adult and chick feeding rates were positively related to chick begging rates. I also observed that begging was subsequently related to an interaction between chick aggression and parent age. Begging was positively related to aggression for pairs with two adults and for pairs with at least one juvenile, although the relationship was stronger in the latter category. I also observed that aggression in chicks was often triggered when

a nestmate displayed begging behavior and that aggression rates in Brown Pelican chicks peaked at ca. 20 d post-hatch, coincident with the time period during which chicks undergo a maximum rate of growth (Schreiber 1976, Ferguson 2006). Unlike feeding rates, which decreased steadily with chick age, aggression rates initially increased as the chicks aged. Similar to feeding rates, however, aggression decreased after the chicks were older than ca. 25 d. Higher rates of aggression in multiple chick broods ca. 20 d post hatch might serve to provide chicks with a greater number of feeds during this important growth phase which occurs prior to a decrease in feeding and an increase in chick demand.

Interestingly, I never observed any behavior that appeared to directly lead to the death of a sibling (e.g. pecking to death) although siblicide does occur in Brown Pelicans (Pinson and Drummond 1993; Shields 2002) and is common in other Pelecaniformes (Nelson 2005). I also observed, however, a slightly higher productivity rate than in previous years despite 26% of my study nests being parented by at least one juvenile. This might indicate that more favorable conditions existed for raising young during my sampling period (i.e. higher food availability, less human disturbance, etc.) than in previous years on Crab Bank and may explain why I did not observe intense levels of aggression that resulted in siblicide. It appears therefore that during this critical growth period, when resources are in high demand to support growth, begging and aggression were at their highest levels likely to aid the chick in obtaining the maximum amount of resources. Hence it appears that feeding, aggression, begging, and attendance rates are

not fixed over time and instead reflect underlying patterns in chick growth and development.

Parental Age and Late Nesting

Variation in breeding phenology among colonies and even within colonies is well documented for *Pelecanidae* species (Chapman 1908, Schaller 1964). For example, while pairs in my study plots were still laying or were in the early stages of incubation, nests in close proximity to my study plots often contained chicks as old as ca. 10 days. Additionally, most of my study nests were at the colony edge. Edge nests in colonial seabirds often tend to be younger, less experienced nesters (Coulson 1968, Blus and Keahy 1978). For example, Dalmatian Pelicans (*Pelecanus crispus*) in late breeding units (i.e. began nesting efforts once other pairs were in advanced stages of incubating) were assumed to be young, inexperienced birds, based on the high number of nest desertions which suggested first time nesters rather than experienced pairs (Crivelli et al. 1998). Blus and Keahy (1978) also found that juvenile Brown Pelicans were more likely to nest in areas subjected to flooding (e.g., the colony edge at Crab Bank where my study was focused). This may explain, in part, the relative abundance of juvenile pairs in my study. Hence, my study nests are best categorized as late-nesting pairs on the colony edge with a moderate proportion (i.e. 26%) of nests containing at least one juvenile parent. Previous estimates of breeding pelicans in South Carolina suggest that breeding juveniles represented ca. 5-10 % of the overall nesting population each year (Blus and Keahy 1978, Wilkinson 1982).

I found that nests with at least one juvenile parent had a lower average clutch size, hatch rate, and number of young that survived to 21 d than pairs with two adult parents (n.b. I was not able to compare reproductive success between early and late nesters). Age related differences in reproductive success among colonial nesting seabirds is well documented (Blus and Keahey 1978, Bunce et al. 2005). In an early study on Brown Pelicans in South Carolina (Blus and Keahey 1978), pairs that contained immature or less experienced birds (and nested after May 1) had lower productivity compared to pairs which included primarily adults (and nested earlier). In my study productivity appeared to be lost in juvenile pairs primarily during hatching (the difference between hatch rates was greater than that between clutch sizes for juvenile compared to adult pairs). There did not appear to be a difference in attendance between parent ages (parent age was a variable in the second ranked model for attendance but the ratio of the standard error to the coefficient estimate suggests it was not an important variable). It is possible that even though attendance rates did not vary some other aspect of incubation behavior or parental quality in juvenile compared to adult pairs led to decreased hatching success.

Although a moderate proportion of nesting pairs in my study site were juveniles and although I did observe lower reproductive success for juvenile parents compared to adult parents, the mean clutch size and hatch rate in this study were still similar to results in a previous study of nesting Brown Pelicans on Crab Bank (Ferguson 2006). Additionally, productivity estimates in my study were slightly higher than values reported for Brown Pelicans in other southeastern populations (Shields 2002, Ferguson and Jodice unpubl. data). This suggests that productivity data from the current study are not atypical

despite the potential effect of studying late nesting birds. Although I did not measure prey availability in my study, there are several indicators that suggest that the prey base has been relatively stable for birds on Crab Bank and perhaps this contributed to the relatively strong productivity we observed in our late nesting birds. For example, I did not observe any sign of starvation or nutritional stress in chicks, the pelican colony appears to be growing in size on Crab Bank, and Crab Bank continues to support a diverse array of breeding seabirds and shorebirds (Jodice et al 2007). Furthermore, pelicans, terns, and gulls from this colony have been observed foraging successfully at shrimp boats in nearby waters, suggesting that additional sources of food are likely available (Jodice and Wickliffe 2007).

Human Disturbance and Colony Management

Brown pelicans nest at three locations within South Carolina (Jodice et al. 2007); Charleston Harbor (primarily on Crab Bank), Cape Romain National Wildlife Refuge (primarily on Marsh Island), and Deveaux Bank. Bird Key Stono also has supported a pelican colony in the past but currently does not. Human access has been prohibited within colonies for years but only recently has human access been prohibited on the entirety of Crab Bank, Marsh Island, and Bird Key Stono during the breeding season. Regulations differ at Deveaux Bank where limited access is permitted on the island. None of the islands currently have 'no-entry' buffer zones in the adjacent waters.

These regulations were enacted to protect nesting seabirds primarily by reducing disturbance near the edges of the colonies. In the past numerous observations of entry into colonies and resulting destruction were observed (Jodice et al. 2007). Brown

Pelicans appear to be quite sensitive to human disturbance. For example, Anderson (1988) indicated that Brown Pelicans nesting in Mexico were extremely sensitive to human disturbance, reporting detrimental effects at a distance of 600 m. Rodgers and Smith (1995) suggest that to avoid disturbing Brown Pelicans humans should not approach closer than 200 m if traveling by foot or 75 m if traveling by boat. The enactment of such a buffer at Crab Bank, for example, would require that nearshore waters also be off-limits to human presence. In contrast pelicans also appear to be able to exhibit tolerance to limited human disturbance. For example, by approaching my study plots slowly and cautiously I was able to conduct behavioral observations from ca. 5-15 m from nests without apparently disrupting regular nesting behavior. Similarly, during nest censuses Brown Pelicans are typically hesitant to leave their nests, often need to be coaxed off by researchers in order to measure clutch sizes, and typically return to their nests within approximately one minute of the researcher's departure (Bartholomew and Dawson 1954, pers. obs.).

The hesitation of adults to flush from nests when approached and apparent tolerance in some situations does not, however, indicate that nesting pelicans can be exposed to human disturbance without adverse effects. Due to their large size, Brown Pelicans may be hesitant to take flight in reaction to human disturbance because of the likely high energetic cost of take off from land. Nonetheless alarmed nest departures by Brown Pelicans can result in crushed eggs, eggs or young tossed from the nest, predation on nestlings and unattended eggs, or egg or chick mortality due to heat stress (Anderson and Keith 1980).

Brown Pelicans can, in fact, suffer reproductive losses resulting from even one event of human disturbance, particularly early in the nesting season when nest abandonment is likely to occur after disturbance (Anderson and Keith 1980). Anderson and Keith (1980) also suggest that the most detrimental effect of disturbance to chicks older than ca. 30 d is the loss of food that chicks regurgitate when startled. These observations and data suggest that, at a minimum, current management practices that restrict human access to nesting colonies are appropriate. Ongoing studies of habitat use by loafing seabirds may provide additional information that can be used to fine-tune regulations or develop location-specific regulations (Jodice and Eggert 2007).

The behavioral data collected during this study provide an improvement in our understanding of both applied and basic aspects of pelican breeding biology. I found that most of the behaviors I measured varied with the age of the chicks in the nest. Often management agencies seek to assess impacts of disturbance to colonial nesting seabirds by measuring various reproductive or behavioral traits such as parental attendance or feeding rates. My data show that, for Brown Pelicans in South Carolina, any use of adult or chick behavior at the nest as a response variable in an assessment of disturbance (or any other factor) must consider the age of the chicks and ensure that comparisons are made within relatively narrow age ranges. It is important to note, however, that I was not able to determine which variable might respond strongest to disturbance since there were no opportunities to measure disturbance. Nonetheless, my observations suggest that parental attendance and feeding rates may be the easiest of the behaviors to measure and each appear to provide sufficient variability to allow for comparisons among groups.

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Table 2.1 Models used to analyze adult and chick behaviors of Brown Pelicans nesting on Crab Bank, South Carolina June-July 2006.

Models conducted for each of the five focal behaviors^a

Chick age
 Chick age, chick age²
 Chick age, parent age
 Chick age, chick age², parent age
 Chick age, brood size
 Parent age, brood size
 Chick age, chick age², brood size
 Chick age, chick age², parent age, parent age*chick age, parent age* chick age²
 Parent age, brood size, parent age*brood size
 Chick age, chick age² brood size, chick age*brood size, chick age²* brood size
 Julian date
 Julian date, parent age
 Julian date, parent age, Julian date*parent age
 Julian date, brood size
 Tide
 Global, chick age, chick age²
 Global, Julian date
 Intercept only

Additional models conducted for measures of adult feeding

Chick begging
 Chick begging, parent age
 Chick begging, parent age, chick begging*parent age
 Chick begging, chick age
 Chick begging, chick age, chick age²
 Chick begging, brood size
 Chick begging, brood size, chick begging*brood size

Additional models conducted for measures of chick feeding

Chick begging
 Chick begging, chick age
 Chick begging, chick age, chick age²
 Chick begging, chick age, chick begging*chick age
 Chick begging, brood size
 Chick begging, brood size, chick begging*brood size

Additional models conducted for measures of chick begging

Chick aggression
 Chick aggression, brood size
 Chick aggression, parent age
 Chick aggression, brood size, chick aggression*brood size
 Chick aggression, parent age, chick aggression*parent age

Additional models conducted for measures of chick aggression

Chick begging

Chick begging, brood size

Chick begging, brood size, chick begging*brood size

^a Global models included all main variables although chick age and date were included in separate global models to avoid multicollinearity

Table 2.2. Mean (\pm SE) clutch size, hatch rate, and productivity^a of Brown Pelican pairs consisting of either two adults or at least one juvenile, Crab Bank, South Carolina, June – July 2006.

	Pairs with 2 adults (n = 20)	Pairs with < 2 adults (n = 7)	<i>t</i> -statistic, one-tailed <i>P</i> -value
Clutch size	2.7 \pm 0.2	2.3 \pm 0.1	$t_{25} = 1.71, P = 0.05$
Hatch rate	2.3 \pm 0.2	1.3 \pm 0.3	$t_{25} = 2.61, P = 0.01$
Productivity	1.8 \pm 0.2	1.0 \pm 0.2	$t_{25} = 1.98, P = 0.03$

^a Productivity measured as survival to 21 d post hatch (Shields 1998)

Table 2.3 Model selection statistics from repeated measures, mixed models for each of the five focal behaviors measured for Brown Pelicans nesting on Crab Bank, South Carolina, June – July 2006. Only models included in the 95% confidence set are presented.

<i>Response variable / 95% confidence model sets</i>	Δ AICc	AICc weight	Cumulative sum of AICc weight
<i>Adult feeds</i>			
Chick begging, chick age	0	0.61	0.61
Chick begging, chick age, chick age ²	1.5	0.29	0.89
Chick age	5.2	0.04	0.94
Chick age, chick age ²	7.2	0.02	0.95
<i>Chick feeds</i>			
Chick begging, chick age	0	0.50	0.50
Chick begging, chick age, chick begging*chick age	1.1	0.29	0.79
Chick begging, chick age, chick age ²	2.0	0.18	0.98
<i>Adult attendance</i>			
Chick age, chick age ²	0	0.51	0.51
Parent age, chick age, chick age ²	1.2	0.24	0.75
Chick age, chick age ² , brood size, chick age*brood size	2.1	0.18	0.93
<i>Chick begging</i>			
Chick aggression, parent age, chick aggression*parent age	0	0.52	0.52
Chick aggression	1.6	0.23	0.76
Chick aggression, parent age	3.0	0.12	0.87
Chick aggression, brood size	5.2	0.04	0.91
Chick aggression, brood size, chick aggression*brood size	6.9	0.02	0.93
<i>Chick aggression</i>			
Chick age, chick age ² , brood size, chick age*brood size, chick age ² *brood size	0	0.99	0.99

Table 2.4 Coefficient estimates \pm SE^a derived from model averaging approach for variables included in 95% confidence model sets for each of the five focal behaviors. Only variables occurring in models within the 95% confidence set are included in table. A “-“ indicates that the variable was not included in the 95% confidence set.

	Adult feeds	Chick feeds	Adult attendance	Chick begging	Chick aggression
Chick age	-0.04 \pm 0.01	-0.03 \pm 0.01	0.66 \pm 0.26	-	-0.11 \pm 0.05
Chick age ²	0.0004 \pm 0.0005	0.0002 \pm 0.0005	-0.02 \pm 0.005	-	0.001 \pm 0.0008
Parent age	-	-	2.05 \pm 2.5	-0.18 \pm 0.37	-
Brood size ^b 0	-	-	1.85 \pm 9.69	-	-
Brood size ^c 1	-	-	0.18 \pm 10.12	0.17 \pm 0.47	-2.93 \pm 0.72
Brood size 2	-	-	11.0 \pm 9.94	-0.15 \pm 0.46	-3.04 \pm 0.72
Chick begging	0.11 \pm 0.04	0.15 \pm 0.07	-	-	-
Chick aggression	-	-	-	-0.18 \pm 0.37	-
Chick begging*chick age	-	-0.004 \pm 0.003	-	-	-
Chick aggression*brood size	-	-	-	-0.36 \pm 0.48	-
Chick aggression*parent age	-	-	-	-2.14 \pm 0.93	-
Chick age*brood size 1	-	-	-0.24 \pm 0.72	-	0.11 \pm 0.05
Chick age*brood size 2	-	-	-0.61 \pm 0.71	-	0.21 \pm 0.05
Chick age ² *brood size 1	-	-	0.009 \pm 0.01	-	-0.001 \pm 0.001
Chick age ² *brood size 2	-	-	0.01 \pm 0.01	-	-0.003 \pm 0.001

^aCoefficient estimates and standard errors calculated via model averaging (see Methods) when variable included in > 1 model from 95% confidence set, otherwise values are as calculated from a single model.

^bBrood size 0 = incubating adult

^cThe reference level is brood size = 3, therefore the coefficient estimate is the difference between the mean for brood size = 3 and brood size = 1 or 2.

Figure 2.1 Index of A) adult feeds and B) chick feeds in relation to chick age from nests of Brown Pelicans at Crab Bank, South Carolina, June-July 2006. Values are given per three-hour observation period for chicks aged 0 to 55 days.

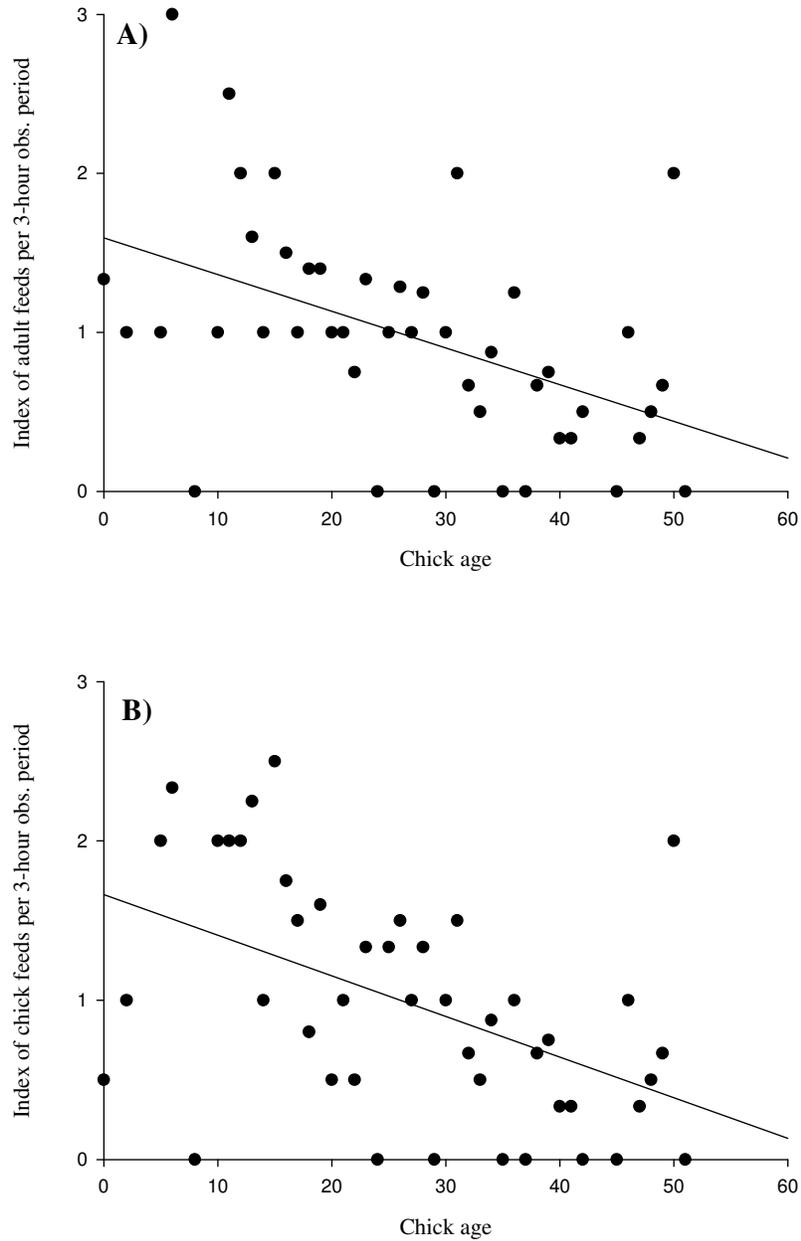
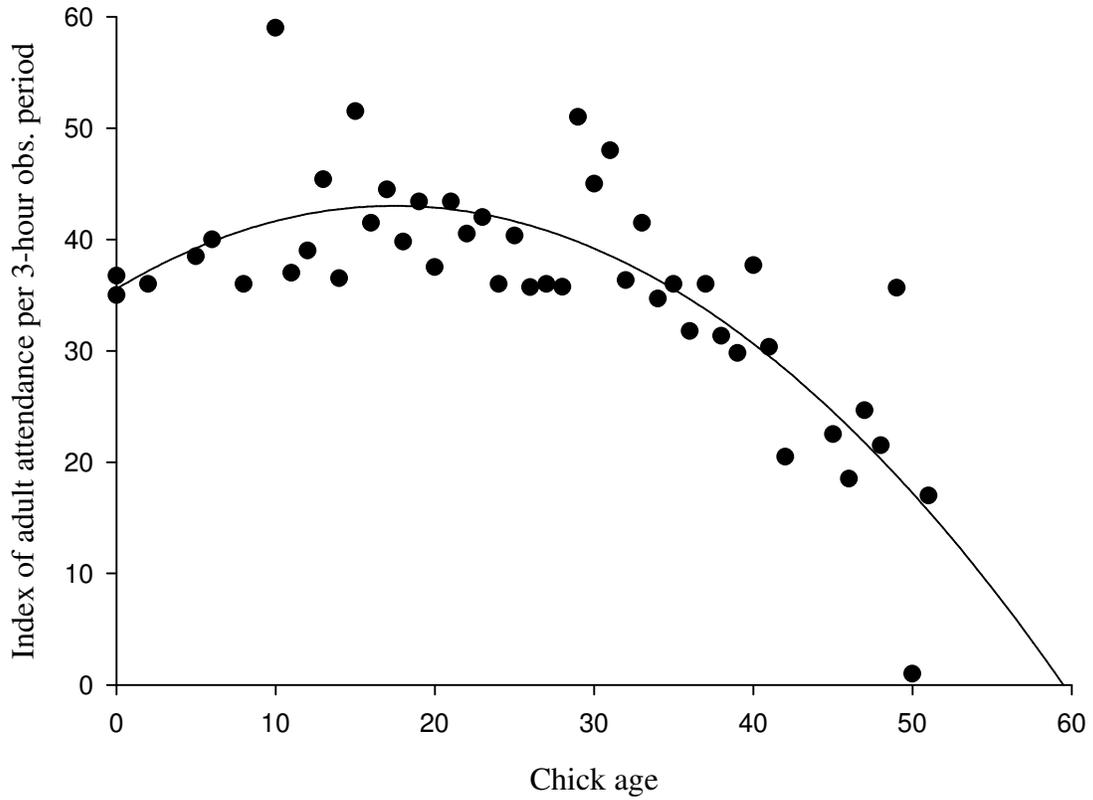


Figure 2.2 Index of adult attendance in relation to chick age from nests of Brown Pelicans at Crab Bank, South Carolina, June-July 2006. Values are given per three-hour observation period for chicks aged 0 to 55 days.



CHAPTER THREE

PROXIMATE COMPOSITION AND ENERGY DENSITY OF FORAGE FISH FROM NEARSHORE WATERS OF COASTAL SOUTH CAROLINA

Introduction

Prey quality can be broadly defined as the proximate composition and energy density of a food item. While some food items such as fruits are complex and include multiple types of carbohydrates, other items such as fish are relatively simple and contain primarily water, lipids, and proteins (Ricklefs 1996). Despite this relative simplicity piscivores may still encounter a wide range of energy density and lipid content among prey items (Anthony et al. 2000). Furthermore, fish prey are often highly ephemeral in space and time. This combination of highly variable prey quality and availability means that piscivores must integrate multiple and complex factors when selecting prey. This variability becomes particularly important to central place foragers such as breeding seabirds that often commute over substantial distances to provision dependent young for relatively long periods of time and therefore must balance high cost of food acquisition with the quality of the selected prey.

Numerous authors have demonstrated that shifts in both prey availability and prey quality can significantly affect breeding success in seabirds (Montevecchi et al. 1984, Gordon et al. 2000, Kitaysky et al 2000, Suryan et al. 2002, Litzow et al 2002, Gremillet et al. 2004, Becker and Beissinger 2005, Wanless et al. 2005, Jodice et al 2006). For example, it has been suggested that changes in the composition and distribution of forage fish communities in the northern Gulf of Alaska may have contributed to declines in seabirds and marine mammals and that this may have specifically been due to a decline in

high-lipid, pelagic schooling prey such as capelin (*Mallotus* spp.) (Anderson and Piatt 1999, Trites and Donnelly 2003). Although it remains unclear exactly what role changing prey quality may have played in these population declines, it is clear that changes in the forage fish community did occur and that the proximate composition and energy density of forage fish vary widely in that system.

Unfortunately, there has been little effort to assess the prey quality of marine piscivores outside of the Pacific Northwest specifically, and high latitude regions in general. For example, a recent analysis of population trends in breeding seabirds in South Carolina revealed that nest counts of Brown Pelicans (*Pelecanus occidentalis*), and Royal Terns (*Sterna maxima*) had declined during the past decade (Jodice et al 2007). Numerous factors may have contributed to these declines including environmental contaminants, changes in food availability or food quality, dispersal to new colony sites or human disturbance, although a combination of many factors likely underlies the trends. Due to limited data on forage fish abundance and prey quality, seabird diet, and the interaction of all of these factors in that region, however, Jodice et al. (2007) recommended that future research include assessment of seabird diet and food availability of those species, specifically in relation to interactions between seabirds and commercial fishing vessels.

Examinations of the energetic value and proximate composition of fish has received considerable attention; however, most studies have been focused in high latitude, cold water regions (Donnelly et al. 1990, Van Pelt et al. 1997, Lawson et al 1998, Payne et al. 1999, Anthony et al 2000, Eder and Lewis 2005, Ball et al 2006, Van de Putte et al

2006). Few studies are available for temperate marine waters (Stickney and Torres 1989). Differences in proximate composition and energy density between fish species in high and low latitude regions (Stickney and Torres 1989) make it difficult to simply extrapolate information for warm water species from existing data for cold water species. Similarly, data on the nutritional value of fish in the nearshore waters of the South Carolina coast is generally limited to lean mass of commercial species and is typically unavailable for whole organisms of either commercial or non-commercial species. Since seabirds typically consume whole fish, it is necessary to evaluate the energetic value of the entire fish. Along the southeastern coast, seabirds prey on a variety of pelagic and demersal fish during the breeding season, including Atlantic menhaden (*Brevoortia tyrannus*), anchovy (*Anchoa* spp.), Atlantic croaker (*Micropogonias undulatus*), mullet (*Mugil* spp.), drum (Sciaenidae), mackerel (Scombridae), and herring (Clupeidae) (Gordon et al. 2000, McGinnis and Emslie 2001, Shields 2002, Wambach and Emslie 2003, Aygen and Emslie 2006). Seabirds in this region also forage on offal and discarded bycatch from shrimp trawlers which likely expands the breadth of their diet to include mid-water and benthic species (Jodice and Wickliffe 2007). In this study, I measured the proximate composition and energy density of seven species of marine forage fish that are potential prey items of seabirds on the coast of South Carolina, some of which are likely only available in the diet as discarded bycatch from commercial shrimp operations. These data should contribute to our understanding of the effect that prey quality may have on the diet selection and reproductive success of piscivorous predators.

Methods

Samples (i.e. whole fish) for analysis were collected in June – August, 2006, from bycatch from shrimp trawlers operating offshore of Charleston and McClellenville in South Carolina (Jodice and Wickliffe 2007). Species selected for analysis (Table 3.1) were chosen based on their likelihood to appear in diets of breeding seabirds and on the frequency with which they appeared to be taken as prey during discard operations. Whole fish were collected during shrimp sorting operations, identified to species, and immediately frozen for subsequent analysis.

Laboratory Procedures

Proximate composition and energy density were determined following protocols used by Anthony et al. (2000) and Jodice et al. (2006). Fish are primarily comprised of water, lipid, and protein (Sidwell et al. 1974, Hislop et al. 1991). Carbohydrates have been shown to be a negligible component of fish (<6 %; Sidwell et al. 1974) and were therefore excluded in calculations as in other studies (Anthony et al. 2000, Romano et al. 2006, Jodice et al. 2006). Basically, three steps were conducted: 1) water content of fish was determined via drying, 2) lipid content of fish was determined via lipid extraction, and 3) protein content of fish was determined via ashing. A brief synopsis of lab procedures is described below. Results reflect whole fish measurements.

Fish were thawed prior to weighing. I then measured total standard length (± 1 mm) of each fish and determined thawed wet mass using an analytical balance (± 0.1 mg). To determine water content, I dried fish in a convection oven at 100° C. After ca. 3 days of drying, the mass of each sample was measured daily until it reached a constant mass (i.e.

± 0.005 g) for > 1 day. Most fish reached a constant dry mass in 6-10 days. Percent water content of each fish was calculated as:

$$\% \text{ water content} = \left[\frac{\text{thawed wet mass (g)} - \text{dried mass (g)}}{\text{thawed wet mass (g)}} \right] * 100$$

Once whole fish were dry, the sample was ground until homogenous using mortar and pestle. Ground samples were then placed back in the drying oven overnight to remove any moisture obtained during grinding. Samples were next placed in glass thimbles in preparation for the lipid extraction. Leaned and dried cotton balls were also placed in the thimbles to keep the samples from spilling over the top of the thimble. Again, the thimbles and samples were placed overnight in a drying oven. Lipid content of the dried fish was determined using a soxhlet apparatus. Boiling stones were used in the flasks to ensure even boiling. Total lipids were extracted using a solvent of hexane/isopropyl alcohol 7:2 (v/v) for ca. 10 hours. This solvent is non-toxic and extracts most complex lipids without extracting non-lipids (Radin 1981). Total lipids were extracted because I was interested in the nutritional value of the whole fish rather than just stored energy reserves. Following the lipid extraction, samples were allowed to sit under the hood for ca. 1 hr to allow any hexane in the samples to evaporate. Samples were then placed in the drying oven and weighed daily until they reached a constant mass. Following this step all samples were considered lean and dry. Lipid mass was calculated as:

$$\text{Lipid mass (g)} = \text{dried mass (g)} - \text{lean dry mass (g)}$$

Leaned, dry samples were then placed in glass beakers in preparation for ashing.

Samples were placed in a muffle furnace and incinerated for ca. 12 hours at 600° C,

resulting in a sample that was ash free, lean, and dry. The remaining material consisted almost exclusively of protein. Percent protein was calculated as:

$$\% \text{ protein content} = 100 - (\text{percent moisture} + \text{percent lipid} + \text{percent ash})$$

The energy density of each sample was calculated using the energy equivalents, 39.3 kJ/g and 17.8 kJ/g, for lipids and protein respectively (Schmidt-Neilson 1997). Energy density was calculated on a wet-mass basis in order to better assess the total value of each fish as obtained by seabirds.

Statistical Analysis

Statistical analyses aimed to 1) determine if proximate composition and energy density differed among species and 2) determine if proximate composition and energy density differed between species classified as demersal or pelagic. I conducted a one-way analysis of variance (ANOVA) to test for differences in water, lipid, AFLDM, and energy density among species, followed by Fisher's test for least significant differences. Because I was not able to normalize all independent variables, I also conducted a nonparametric Kruskal-Wallis ANOVA to test for differences in water, lipid, AFLDM, and energy density among species. In no case were the outcomes of the parametric and nonparametric analyses different (i.e. *P* values were always similar). Therefore, all results are reported for parametric tests. A correlation analysis was performed in order to examine the relationships among the components of proximate composition and energy density. I used a linear contrast analysis to test for differences in proximate composition and energy density between demersal and pelagic species. I classified Atlantic croaker, spot, star drum, and silver sea trout as demersal fish because they occur primarily at or

near the bottom of the water column. I classified striped anchovy, Atlantic menhaden, and Spanish mackerel as pelagic fish because they occur in schools closer to the surface.

I refer to results as significantly different when $P \leq 0.05$ and moderately significant when $0.05 < P \leq 0.10$. Results are presented as mean (\pm SE). Values for percent water, lipid, and ash free lean dry mass (AFLDM) were arcsine transformed for all statistical analyses, although raw values are presented throughout.

Results

Interspecific differences

For each fish species, the mean (\pm SE) percentage (wet mass) of water, lipid, protein, ash, and the mean energy density are presented in Table 3.2. Water content (as % wet mass) ranged only from 76.1 ± 1.1 % in Atlantic croaker to 78.2 ± 1.8 % in striped anchovy and no significant differences were observed among species ($F_{6,38} = 0.9$, $P = 0.5$). Water content was negatively correlated with both lipid content ($r^2 = -0.37$, $P = 0.01$) and energy density ($r^2 = -0.74$, $P < 0.001$).

Lipid content (as % wet mass) varied widely and ranged from 2.0 ± 0.7 % in silver sea trout to 11.8 ± 2.5 % in Atlantic croaker. There were significant differences in lipid content among species ($F_{6,38} = 11.1$, $P < 0.0001$). Lipid content was higher in Atlantic croaker, striped anchovy, and star drum compared to Atlantic menhaden, silver sea trout, Spanish mackerel, and spot.

Values for AFLMD for each species also varied widely, ranging from 68.7 ± 0.8 % in Atlantic menhaden to 83.6 ± 0.4 % in Spanish mackerel and significant differences were observed among species ($F_{6,38} = 51.92$, $P < 0.0001$). AFLDM of menhaden was

significantly lower compared to all other species. AFLDM was significantly higher in striped anchovy, silver sea trout, and Spanish mackerel compared to Atlantic croaker, spot, and star drum.

Total energy density differed among species ($F_{6,38} = 6.34, P < 0.0001$) and is presented in Figure 3.1. Standard error values ranged from 0.05-0.32 among all species. There were also significant differences between the relative contribution of lipid to energy density ($F_{6,38} = 7.81, P < 0.0001$, SE values 0.03-0.29) and the relative contribution of AFLMD to energy density ($F_{6,38} = 5.76, P = 0.0002$, SE values 0.02-0.26). Energy density was generally highest in striped anchovy, Atlantic croaker, and star drum and was least in Atlantic menhaden. Total energy density was strongly and positively correlated with lipid content ($r^2 = 0.82, P < 0.0001, n = 45$) and moderately and positively correlated with AFLDM content ($r^2 = 0.40, P = 0.007, n = 45$).

Demersal versus pelagic species

I observed some differences in proximate composition or energy density when values were compared between fish categorized as demersal or pelagic. Though there were no differences in overall energy density between these groups ($t_{38} = 1.49, P = 0.14$), Figure 3.2), percent lipid ($t_{38} = 1.98, P = 0.06$) and percent AFLDM ($t_{38} = 3.01, P = 0.005$) were both significantly to moderately significantly higher in demersal species compared to pelagic species (Figure 3.3). There were no significant differences between demersal and pelagic species for water content ($t_{38} = -1.42, P = 0.17$).

Discussion

This study describes proximate composition and energy density of nearshore marine forage fish that are important prey for piscivorous seabirds and, to the best of my knowledge, is the first to do so from the South Atlantic Bight. Proximate composition and energy density differed among the species of forage fish I examined. This suggests that piscivorous seabirds may experience differences in energy intake rates dependent upon diet and prey availability. The range in energy density that I observed was not great, however, and therefore it appears from this limited sample that energy values may not vary widely among prey items during the seabird breeding season in coastal South Carolina.

Seabirds exploit a variety of prey based on foraging strategies and food availability and seabird diets may change both within and among seasons. In North Carolina, Royal Terns (*Sterna maxima*) and Sandwich Terns (*Sterna sandvicensis*) both forage primarily on high-lipid fish, such as anchovy (*Anchoa* spp.), herring, mackerel and drum during the breeding season (McGinnis and Emslie 2001). Royal Terns in Virginia fed mostly on anchovy early in the breeding season and then switched to feeding primarily on herring late in the season (Aygen and Emslie 2006). This seasonal shift in prey selection may be due to the changing needs of the chicks. Young chicks might prefer small prey like anchovy because they are unable to consume large masses of food. Older chicks may be fed larger fish, such as herring, thereby allowing adults to increase the biomass of the food provisioned per foraging trip. This suggests that parents may trade off or select among prey sizes and prey quality depending upon chick needs.

My examination of energy density and proximate composition of potential forage fish of seabirds in South Carolina found few significant differences between demersal and pelagic species. Although I found that demersal species had slightly higher total energy density and protein values compared to pelagic species, this does not conform with patterns observed in other studies, which have indicated that pelagic species are often higher in energy density compared to demersal species (Van Pelt et al 1997, Payne et al. 1999, Anthony et al. 2000, Iverson et al. 2002) This difference may be due to the fact that the aforementioned studies were conducted in high latitude regions where the fish analyzed had higher lipid content compared to the fish in my study. In comparison, Donnelly et al. (1990) did not observe any differences in proximate composition in relation to depth of occurrence, but attributes that partially to a sample with low species diversity and minimal differences in the species' vertical distributions. The fish species in my study were simply grouped as pelagic or demersal and I did not examine the vertical distribution of these fish. This may potentially explain the limited differences I observed in proximate composition and energy density for these species. The water-column temperature may also influence proximate composition of fish (Donnelly et al. 1990) and should therefore also be measured in future research for a more complete study.

In addition to quality and availability of prey, the quantity of prey consumed is also an important aspect of a predator's diet. For example, Brown Pelicans (multi-prey loaders) may be compensating for the low quality of Atlantic menhaden (n.b. I found menhaden to be the lowest in lipid and energy density of the fish in my study) by

consuming greater amounts of a relatively large and readily available fish compared to a Royal Tern (single-prey loader) that only has the capacity to obtain one item per forage trip. Striped anchovy has a higher energy density than Atlantic menhaden, but the quantity of each may offset the differences in potential energy density per foraging trip.

Few data exist for specific comparison of the fish in my study with other studies in low latitude, warm water regions. However, I did observe similar results for energy density in striped anchovy compared to European anchovy (*Engraulis encrasicolus*) in the Adriatic Sea (Tirelli et al. 2006). In South Carolina, striped anchovy energy density values ranged from 2.89 kJ g⁻¹ (wet mass) to 4.08 kJ g⁻¹ compared to a range of 3.40 kJ g⁻¹ (wet mass) to 5.60 kJ g⁻¹ (wet mass) in the European anchovy. Tirelli et al. (2006) attribute the range in energy density to differences in season, age, size, and gender of the individual anchovy. Collectively the fish species in my study were relatively low in lipid content compared to studies based in higher latitude areas (Van Pelt 1997, Payne 1999, Anthony et al. 2000). This is fairly consistent with results from Stickney and Torres (1989) who examined proximate composition of fish from the eastern Gulf of Mexico. The authors suggested that low lipid levels are characteristic of fish in warm water regions where the food supply to fish remains relatively stable. Fish that inhabit regions with a relatively constant food source may have eliminated the need for high energy reserves (i.e. lipid). All of the species in my study showed an inverse relationship between water content and energy density, which was apparent in other studies (Hislop et al 1991, Anthony et al. 2000). The interspecific differences in proximate composition and energy density observed in my study are consistent with

results from other studies (Van Pelt 1997, Payne 1999, Anthony et al. 2000).

Due to intraspecific differences in proximate composition and energy density of fish, Hislop et al (1991) cautions that it may be difficult to ascertain the relative food values of one fish species compared to another as prey items for seabirds. Proximate composition and energy density also vary between species, seasons, age, occurrence of depth, and location (Stickney and Torres 1989, Hislop et al. 1991, Robards et al. 1999, Tirelli et al. 2006). Because I was not able to compare proximate composition and energy density values among species across these influential factors, future research should include all of them for a better understanding of the quality of the prey base for seabirds in South Carolina.

Potential implications of prey quality to seabirds

Prey quality and prey quantity are both important aspects of seabird diets (Jodice et al. 2006). Two hypotheses that have been posed to describe the relationship between diet and both reproductive success and individual condition are the nutritional stress hypothesis (NSH) and the junk-food hypothesis (JFH). The NSH posits that any decrease in quantity or quality of prey may negatively affect the condition of individuals or populations, while the JFH posits that specifically it is a decrease in prey quality that is critical (Rosen and Trites 2000, Jodice et al. 2006). Trites and Donnelly (2003) review both hypotheses in relation to Steller sea lion (*Eumetopias jubatus*) declines in Alaska and find mixed evidence for each. In contrast, Romano et al. (2006) clearly showed that Tufted Puffin (*Fratercula cirrhata*) and Black-legged Kittiwake (*Rissa tridactyla*) nestlings from Alaska fed a diet characterized by a high lipid to protein ratio experienced

higher growth rates compared to nestlings fed a diet with a lower lipid to protein ratio. An interesting assessment of the nutritional stress or junk-food hypothesis as it relates to South Carolina seabirds could be conducted by comparing the quality of natural or common prey items to the quality of prey items obtained by seabirds as they forage from shrimp trawlers and simultaneously examining diet and reproductive success of the various breeding seabirds. Though there is some overlap in fish species between the natural diet and the fish obtained from shrimp trawlers, certain demersal species such as Atlantic croaker, spot, or star drum would only be accessible to the seabirds as discarded bycatch.

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Table 3.1. Range and mean of wet mass for each species of forage fish analyzed for energy density and proximate composition and collected in nearshore waters of coastal South Carolina June - August 2006.

Scientific Name	Common Name	n	Wet Mass (g)	
			Range	Mean
<i>Anchoa hepsetus</i>	Striped anchovy	4	7.9-15.9	13.1
<i>Micropogonias undulatus</i>	Atlantic croaker	6	19.1-36.2	26.8
<i>Brevoortia tyrannus</i>	Atlantic menhaden	9	21.1-58.9	33.1
<i>Cynoscion nothus</i>	Silver seatrout	3	19.2-25.1	21.3
<i>Scomberomorus maculatus</i>	Spanish mackeral	3	34.4-41.7	37.3
<i>Leiostomus xanthurus</i>	Spot	13	18.1-44.3	30.2
<i>Stellifer lanceolatus</i>	Star Drum	7	8.6-10.2	12.5

Table 3.2. Mean \pm (SE) water content, proximate composition (% wet mass) and energy density of forage fish species collected in nearshore waters of coastal South Carolina June - August 2006.

Species	Energy Density				
	Water (%)	Lipid (%)	Protein (%)	Ash (%)	(kJg ⁻¹)
Striped anchovy	78.2 \pm 1.8	9.0 \pm 1.6	15.7 \pm 2.0	3.4 \pm 0.4	3.7 \pm 0.3
Atlantic croaker	76.1 \pm 1.1	11.8 \pm 2.5	15.1 \pm 0.6	4.4 \pm 0.2	4.1 \pm 0.3
Atlantic menhaden	77.6 \pm 0.1	2.7 \pm 0.7	11.1 \pm 1.0	6.3 \pm 0.1	2.9 \pm 0.04
Silver seatrout	77.5 \pm 0.1	2.0 \pm 0.7	13.2 \pm 3.2	4.0 \pm 0.1	3.4 \pm 0.1
Spanish mackerel	76.8 \pm 0.2	2.6 \pm 0.3	7.1 \pm 2.3	3.5 \pm 0.1	3.6 \pm 0.04
Spot	77.7 \pm 0.3	2.6 \pm 0.4	12.7 \pm 1.4	4.7 \pm 0.1	3.2 \pm 0.1
Star Drum	77.0 \pm 0.9	10.3 \pm 2.0	11.2 \pm 2.5	4.4 \pm 0.3	3.8 \pm 0.2

Figure 3.1. Mean relative contributions of lipid (black bar) and ash free lean dry mass (white bar) toward total energy density (kJg^{-1} wet mass) of forage fish collected in nearshore waters of coastal South Carolina June - August 2006. Bars with different letters are significantly different ($P < 0.05$) based on Fisher least significant differences.

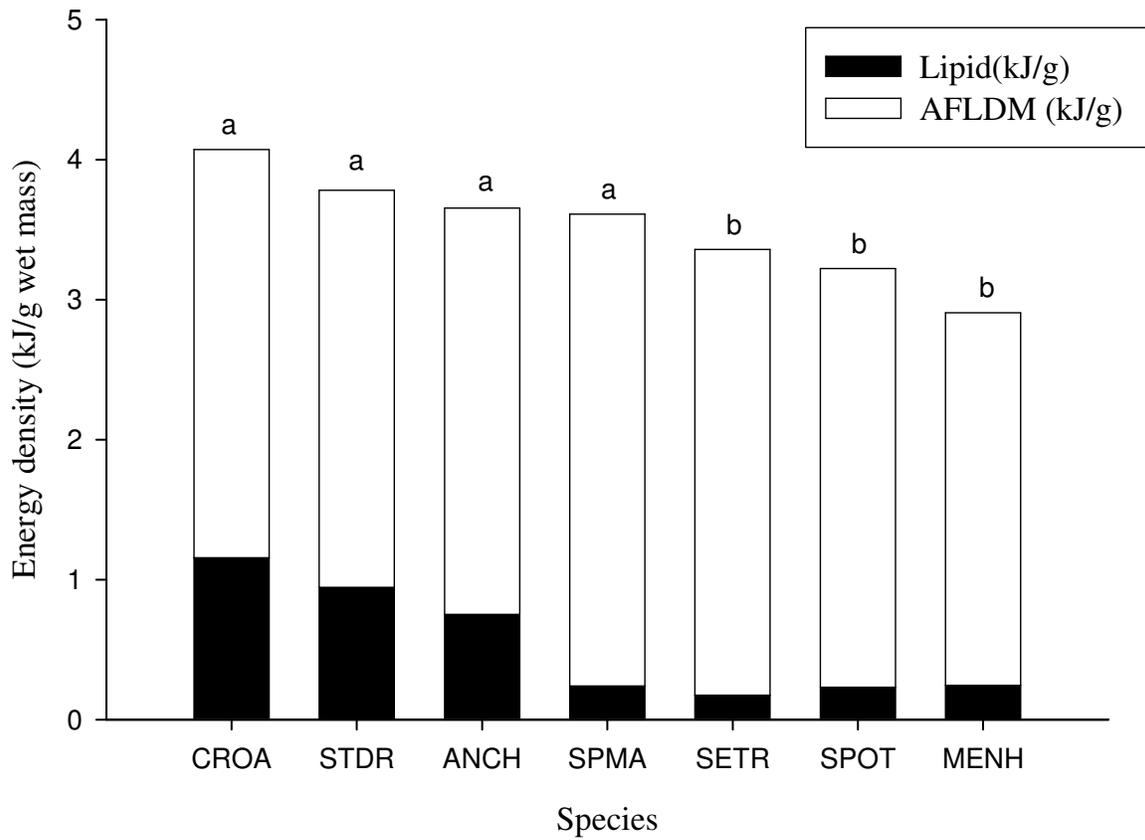


Figure 3.2 The A) energy density (kJg^{-1} wet mass) and B) percent water of demersal and pelagic forage fish species collected in nearshore waters of coastal South Carolina in June - August 2006. Bars with different letters are significantly different ($P < 0.05$) based on linear contrast estimates.

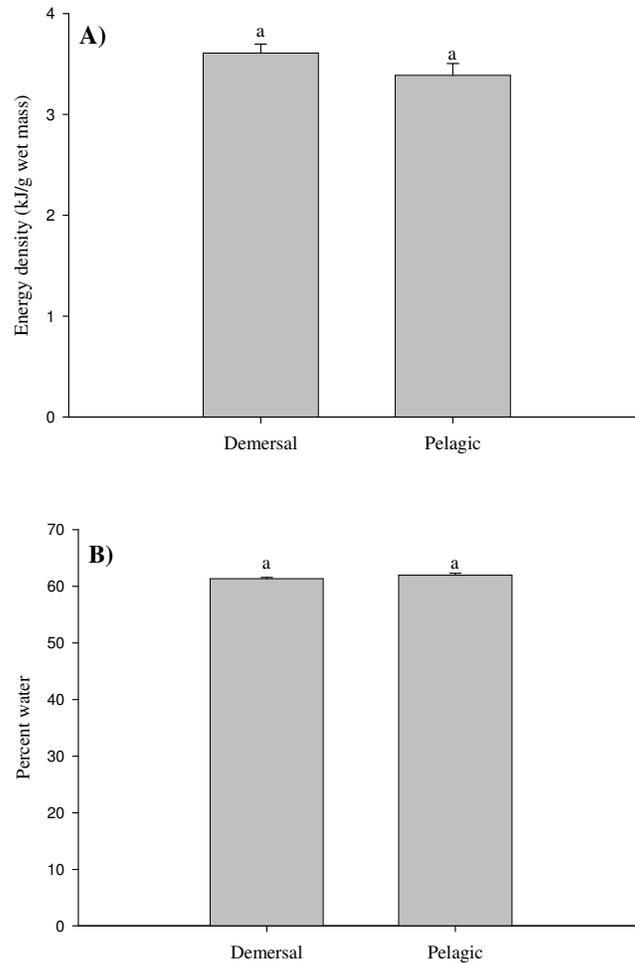
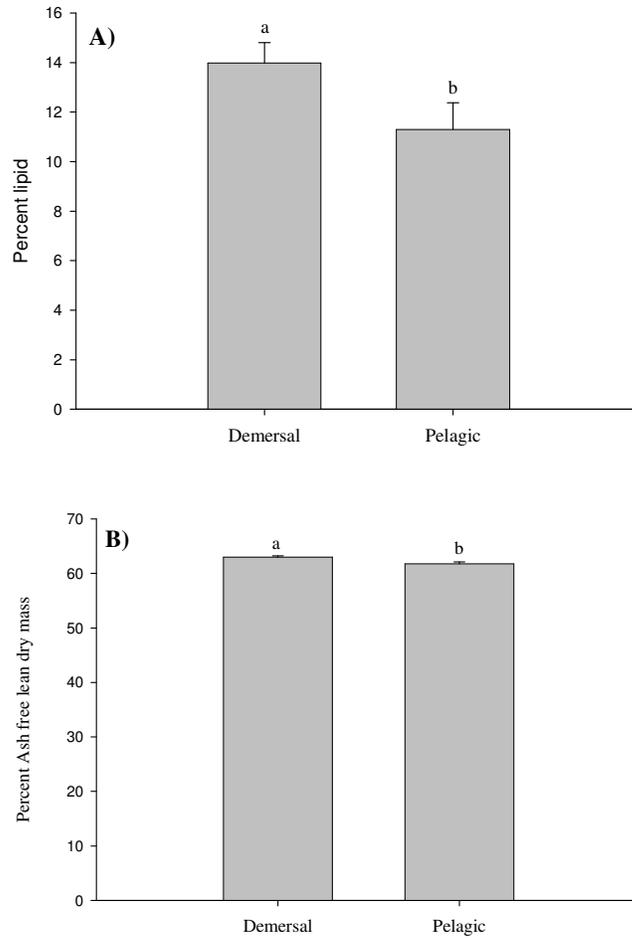


Figure 3.3 The A) percent lipid and B) percent AFLDM of demersal and pelagic forage fish species collected in nearshore waters of coastal South Carolina in June - August 2006. Bars with different letters are significantly different ($P < 0.05$) based on linear contrast estimates.



CHAPTER FOUR

CONCLUSION

Brown Pelicans nesting on the coast of South Carolina have experienced population declines within the last decade and the underlying cause remains unclear. Researchers posit that numerous factors may have led to or may continue to contribute to the decline in statewide breeding populations (e.g. environmental contaminants, changes in food availability or food quality, dispersal to new colony sites, human disturbance). In an attempt to elucidate the underlying biological, environmental and physiological mechanisms of the declines, I investigated parent and nestling behavior during early chick rearing in Brown Pelicans. I also determined the proximate composition and energy density of several marine forage fish that are common prey species for breeding seabirds in South Carolina.

The second chapter of this thesis, “Provisioning behavior in Brown Pelicans in South Carolina”, examined the relationship between parent and chick behaviors at the nest and a suite of environmental and behavioral factors. During the 2006 breeding season, I measured feeding behavior of adults and chicks, adult nest attendance, and begging and aggressive behaviors of chicks and compared these behaviors to a suite of environmental and behavioral variables. There were significant differences in the frequency of feeding, attendance, and chick aggression according to chick age, although the pattern differed among behaviors. The rate of adult feeding, chick feeding and adult attendance all decreased with chick age while chick aggressive behavior peaked when chicks were ca. 21 d post-hatch. While aggression was generally higher in multiple chick

broods compared to singletons, begging rates did not differ with brood size. There were no differences in adult or chick feeds according to brood size. However, high productivity estimates from this study suggest that more favorable conditions existed for raising young during my sampling period (i.e. higher food availability, less human disturbance, etc.) than in previous years on Crab Bank and this may explain why I did not see a difference in feeding rates according to brood size.

Because my research was initiated after peak incubation, the nests in my study were considered late nesters and contained a moderate proportion of juvenile parents. Nests with at least one juvenile parent had a lower clutch size, hatch rate, and number of young that survived to 21 d than pairs with two adult parents. However, productivity estimates from my study were comparable to values from previous studies in South Carolina, suggesting that studying late nesters may potentially underestimate the overall reproductive success for Crab Bank in 2006.

The third chapter of this thesis, “Proximate composition and energy density of forage fish of nearshore waters of South Carolina” examined the energy content of several species of fish common in the diets of seabirds. Proximate composition and energy density differed among the species of forage fish I examined. This suggests that piscivorous seabirds may experience differences in energy intake rates dependent upon prey availability. The range in energy density that I observed was not great, however, and therefore it appears from this limited sample that energy values may be relatively stable among prey items during the seabird breeding season. I found that demersal species had slightly higher total energy density and protein values compared to pelagic

species, which is inconsistent with other studies, but may be due to both a small sample size and relatively low lipid fish in my study.

Provisioning behavior in Brown Pelicans in South Carolina appears to be influenced by a combination of environmental, behavioral, and physiological variables. Productivity rates for the 2006 breeding season indicate that pelicans are successfully provisioning chicks, suggesting that food availability in the region during that year was sufficient for chick-rearing. Further research is needed to determine the primary mechanism driving the population decline of Brown Pelicans in South Carolina. Changes in reproductive parameters of seabirds can occur in conjunction with shifts in prey availability and prey quality. This study provides the first data for proximate composition and energy density of forage fish in the South Atlantic Bight which will help us to better understand any food-related limitations in breeding seabirds of South Carolina.