Broad Spatial Trends in Osprey Provisioning, Reproductive Success, and Population
Growth within Lower Chesapeake Bay

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ABSTRACT PAGE

Since the banning of DDT in 1972, the Chesapeake Bay osprey (*Pandion haliaetus*) population has recovered remarkably. However, spatial variation in the population growth rate was revealed by a Bay-wide survey conducted in 1995 and 1996. Generally, the highest rates had occurred in the upper estuarine areas while the slowest rates had occurred in the lower estuarine areas. Indications of food stress have been previously documented along the Bay proper, and reduced reproductive success has been recently observed in the same locale. To what extent food availability might be influencing population dynamics on a broad scale in the Bay is currently unknown.

We hypothesized that the spatial variation in the population growth rate of ospreys in Chesapeake Bay reflected, in large part, differences in reproductive success mediated through the ability of parents to provision young. To address this, we assessed reproductive success, diet composition, and provisioning rates in both upper and lower estuarine sites in lower Chesapeake Bay during the 2006 and 2007 breeding seasons. In addition to commonly measured reproductive parameters, we characterized reproductive success by calculating nestling growth rates. Diet composition and provisioning rates were determined by installing micro-video monitors at selected nests. Our results were analyzed using a linear mixed-effects model that incorporated random effects.

We found significant differences in osprey diet composition between salinity zones. Atlantic menhaden (*Brevoortia tyrannus*) and spotted seatrout (*Cynoscion* spp.) dominated the diet in the lower estuarine sites, while gizzard shad (*Dorosoma cepedianum*) and catfish (Ictaluridae) dominated the diet in the upper estuarine sites. Temporal comparisons indicated that the contribution of Atlantic menhaden to diet composition in the lower estuary has decreased markedly during the past two decades.

We also found significant differences in osprey productivity, nestling growth rates, and provisioning rates between salinity zones. All parameters were highest in the upper estuarine sites. More importantly, these parameters were positively correlated, and differences in productivity were primarily due to the extent of brood reduction. Our data therefore indicate that broad scale food availability and its subsequent impact on reproductive success is contributing to spatial variation in the growth rate of the Chesapeake Bay osprey population. Given the availability of nesting substrate in the lower estuary, these findings are particularly interesting in light of the emphasis that has historically been placed on nesting substrate as perhaps the primary natural limiting factor for osprey populations.

The cause(s) for reduced food availability along the Bay proper has important implications. Food resources may simply becoming naturally restricted through density dependent feedback mechanisms. Though, an arguably much more plausible explanation is the overharvesting of preferred prey such as Atlantic menhaden. Thus, ospreys may once again be serving as a valuable bioindicator of ecosystem health in Chesapeake Bay.

To my golden family and wonderful friends, who inspire me every day

And to the Center for Conservation Biology staff, who untiringly work to protect those resources that truly allow us to look both within and beyond ourselves

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General Introduction

Ospreys (*Pandion haliaetus*) received an incredible amount of attention from researchers during the latter half of last century. Their persistence in many parts of the world, particularly the United States, was threatened by the pesticide DDT. Through bioaccumulation of this toxin, ospreys collectively suffered catastrophic reproductive failure, and subsequent population collapses occurred on an unprecedented scale (Ames and Mersereau 1964, Wiemeyer et al. 1975, Spitzer et al. 1978, Wiemeyer et al. 1978, Westall 1990, Poole et al. 2002).

Osprey populations, however, have generally recovered since the banning of DDT in 1972. The Chesapeake Bay population, for example, had more than doubled by 1996 (Watts et.al. 2004). This population was of particular concern given that it has historically been considered to be the largest concentration of breeding ospreys in the world (Henny et al. 1974, Spitzer and Poole 1980). Interestingly, the survey that documented the recovery also revealed a striking spatial pattern in population growth rates. The slowest rates had occurred in the lower estuarine areas along the Bay proper while the fastest rates had occurred in the upper estuarine areas of the main tributaries (Watts et al. 2004).

Such spatial variation within a single population provides us with an excellent opportunity to learn more about osprey population regulation. This variation is especially interesting given that nesting substrate is still apparently plentiful in the lower estuarine areas (Watts and Byrd pers. comm.). Researchers in the past have believed nesting substrate availability to be the primary natural variable limiting population growth (Poole 1989). Food availability, on the other hand, has generally been assumed to far surpass

population needs (Meyburg and Chancellor 2002, Poole et al. 2002). However, indications of food stress have been previously documented along the Bay proper (McLean and Byrd 1991), and anecdotal evidence suggests that reproductive success in this locale has declined in recent years (Watts and Byrd pers. comm.). To what extent food stress might be contributing to the spatial pattern of population growth in the Bay is currently unknown.

The goal of this thesis was to acquire an understanding of how the availability of food resources might be influencing the dynamics of the Chesapeake Bay osprey population. We hypothesized that the spatial variation in the population growth rate of ospreys in Chesapeake Bay reflected, in large part, differences in reproductive success mediated through provisioning rate. To address this we implemented a two-fold objective. We assessed both reproductive success and provisioning along a salinity gradient. Specifically, we categorized sites as either "lower estuarine" or "upper estuarine." Measures of reproductive success included all common reproductive parameters. Nestling growth rates were additionally calculated to further characterize reproductive success. Diet composition and provisioning rates were determined by installing micro-video monitors at selected nests. The completion of these objectives facilitates an investigation into the role of food availability in osprey population regulation. Furthermore, these data mark some of the first obtained from ospreys in the upper estuarine areas of the Bay, where the fastest growing portion of one of the world's largest populations is found.

Chapter 1 presents our research into osprey diet composition. All identified taxa recorded in provisioning events were summarized by number of individuals, biomass,

and energy content for both upper and lower estuarine sites. We discuss current spatial differences in diet composition quality. We also compare our findings from the lower estuarine sites to those of previous researchers who worked in the same locale, and consider the implications of the dissimilarities.

Chapter 2 presents our research into osprey reproductive success and provisioning rates. All parameters are summarized for both upper and lower estuarine sites for both years. We again compare our data collected in the lower estuarine sites with earlier studies in the same area, and discuss potential important implications. More importantly, by considering both spatial and temporal analyses, we discuss whether osprey provisioning rates and population growth may be related.

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Chapter One
Comparison of Osprey Diet Composition Between Upper and Lower Estuarine Areas

Introduction

Despite unique taxonomic classification as the only member of its family, the osprey (*Pandion haliaetus*) is perhaps one of the most widely distributed raptors in the world today (Poole 1989). It is found on every continent except Antarctica. One of the main factors contributing to the worldwide distribution of ospreys is the abundance of suitable ecosystems it can inhabit. Though restricted to a diet composed almost entirely of live fish, ospreys can opportunistically consume a wide array of species and can therefore occur in an amazing diversity of habitats (Poole et al. 2002). Prey bases of coastlines, estuaries, marshes, lagoons, rivers, lakes, and reservoirs can all adequately support osprey populations. The only primary additional habitat requirements exist during the breeding season, and include nearby exposed nesting substrate inaccessible to predators and warm temperatures of sufficient duration to fledge young. In the United States alone, breeding ospreys have been documented in all but four states (Poole et al. 2002). Ospreys' worldwide distribution is also partly due to the vast migratory distances they travel each year between breeding and wintering ranges. In the Americas, for example, ospreys breed in the United States and Canada and winter approximately 4,000 km away in South America (Poole 1989).

As piscivorous top predators, ospreys are not only integral components of their communities, but they are particularly susceptible to threats such as biomagnification, which makes them very valuable indicators of environmental contamination (Wiemeyer et al. 1975, Spitzer et al. 1978, Wiemeyer et al.1978, Westall 1990). This became acutely

apparent when breeding osprey populations throughout the United States began experiencing significant declines in the middle part of last century (Henny and Ogden 1970, Henny 1975, Henny et al. 1977, Reese 1975, Spitzer and Poole 1980). This was attributed to decreased productivity, defined as the number of chicks produced per active nest (Poole et al. 2002). Productivity was documented to be between 60% and 95% below that required for population maintenance in some populations, the lowest of which occurred in the Northeast (Ames and Mersereau 1964).

Environmental contamination of the pesticide DDT (Dichloro-Diphenyl-Trichloroethane) was implicated as the cause for the historic delince in osprey numbers. Ames and Mersereau (1964) documented high concentrations of DDT in eggshell fragments collected from failed nests in Connecticut. They determined that DDT was causing the shells to be formed much thinner than normal, and consequently break during incubation (Ames and Mersereau 1964). Thinner egg shells were also implicated in water loss and reduced gas exchange. This was a classic example of biomagnification, whereby a contaminant in the environment accumulates in increasing concentrations in organisms as it ascends to higher trophic levels. The threatened persistence of ospreys in the region served as the impetus for the modern environmental movement, and resulted in a pioneering lawsuit in 1966 that succeeded in banning the use of DDT within New York State. In 1972, the Environmental Protection Agency (EPA) followed suit and implemented a nationwide ban on DDT (Gessner 2001).

The nation-wide ban on DDT led to a recovery in reproductive rates and contributed to a general interest in Osprey ecology and management. Ospreys became the subject of numerous research efforts as scientists aimed to learn as much as possible

about their ecology. Given its direct relatedness to the problem of biomagnification, the foraging ecology of the osprey particularly received considerable attention.

To capture fish, ospreys dive as deep as one meter into the water after extending their legs forward just before breaking the surface (Poole et al. 2002). Reversible outer digits, unique foot scales, and sealable nostrils each contribute greatly to their ability to successfully forage (Poole 1989). Ospreys have been documented hunting over open water as well as from perches. When hunting over open water, ospreys flap or glide approximately 10 to 35 meters above the water until they locate a prey item, at which time they then briefly hover and quickly dive (Vana-Miller 1987). Hunting from perches is much rarer, particularly during breeding season, when high energy demands likely preclude this method because prey are less frequently encountered (Poole et al. 2002).

Many variables have been shown to influence osprey prey selection and ultimately dive success. For example, the size of targeted fish is extremely important, as ospreys must be able to regain flight with their prey after entering the water. Therefore, fish typically fall within a narrow size class. Prey items generally range between 10 and 35 cm in length (Swenson 1978, Van Daele and Van Daele 1982), which corresponds to approximately 10 to 30% of osprey body mass (Poole et al. 2002). The ecology of fish can also critically affect dive success. Benthic-feeding fish, for instance, are more easily captured than are piscivorous fish (Swenson 1979). This is likely explained by the difference in foraging behavior of each. Benthic-feeders are heavily focused on the substrate, while piscivorous fish are more aware of their entire surroundings (Swenson 1979). Finally, environmental conditions such as wind speed can substantially affect dive success. Studies conducted by Grubb (1977) and Machmer and Ydenburg (1990) both

showed that increased wind speed, and subsequent poorer water surface conditions, reduce osprey foraging efficiency.

The above factors notwithstanding, the osprey is an incredibly opportunistic forager. Over 80 species of both freshwater and saltwater fish have been identified in the diet of this opportunistic species in North America alone (Poole et al. 2002). Individuals, though, commonly focus hunting efforts on a small proportion of the total fish species available in a given area. A review of the diets of ospreys breeding near rivers and lakes throughout the West indicated that only one to three species dominated the diet at any given location (Vana-Miller 1987). For example, cutthroat trout (*Salmo clarki*) comprised 93% of the diet at Yellowstone Lake, Wyoming (Swenson 1978), largescale sucker (*Cactostomus macrocheilus*) comprised 59% of the diet at Flathead Lake, Montana (MacCarter 1972), common carp (*Cyprinus carpio*) comprised 67% of the diet in western Oregon (Hughes 1983), and black bullhead (*Ictalurus melas*) comprised 83% of the diet in southeast British Columbia (Flook and Forbes 1983). Studies of coastal populations in the East have revealed similar findings. At Newnan's Lake, Florida, a resident population fed almost exclusively on sunfish (*Lepomis* spp.), shad (*Dorosoma* spp.), and largemouth bass (*Micropterus salmoides*) (Edwards 1988). Further north in Cow Bay estuary, Nova Scotia, more than 90% of the osprey diet consisted of winter flounder (*Pseudopleuronectes americanus*), pollock (*Pollachius virens*), alewife (*Clupeus harengus*) and smelt (*Osmerus mordax*) (Greene 1987). At nearby rivers, white sucker (*Catostomus commersonei*), alewife, and blueback herring (*Alosa aestivalis*) were primarily documented in the diet (Jamieson et al. 1982). One highly important fish species for ospreys along the East Coast is Atlantic menhaden (*Brevoortia tyrannus*).

Atlantic menhaden have historically been documented as one of the primary prey items of ospreys from New England (Poole 1989), to Gardiner's Island, New York (Spitzer and Poole 1980), to Delaware Bay, New Jersey (Steidl et al. 1991), to lower Chesapeake Bay, Virginia (McLean and Byrd 1991).

Outside of resident Florida populations, though, only two quantitative analyses of the osprey diet are known to have been conducted along the East Coast. One was completed on Long and Gardiner's Islands in New York (Poole 1984), and the other was completed in southwestern Chesapeake Bay (McLean and Byrd 1991). This strikingly small number of descriptive diet analyses along the East Coast is quite surprising given the many intensive research efforts focused on ospreys in the region as well as the incredibly large numbers of ospreys that annually breed here.

The importance of populations in the mid-Atlantic and northeastern United States cannot be overestimated. Of particular note is the Chesapeake Bay population, which has historically been considered to have the largest concentration of breeding ospreys in the world since the 1800s (Henny et al. 1974, Spitzer and Poole 1980). Factors contributing to this large concentration include both the estuary's shallow depth, which exposes the bottom to light, maintaining a vast food web, and sinuous coastline, which serves as prime foraging habitat.

Though heavily impacted by DDT, this population recovered remarkably following its banning. A Bay-wide survey conducted in 1995 and 1996 revealed that the breeding population had more than doubled since 1973 (Watts et al. 2004). In addition to the population recovery, this survey documented considerable geographic variation in the growth rate of the population. Mean doubling times were recorded to range from 4.3

years to more than 40 years, with the lowest doubling times occurring in the tidal fresh and lower salinity areas and some of the highest doubling times occurring along the higher salinity Bay proper (Watts et al. 2004). Such a pattern is somewhat surprising given that historical records, most of which are from the DDT years, reveal that ospreys have primarily been concentrated along the Bay proper rather than the upper tidal fresh reaches (Watts et al. 2004). A 1973 breeding survey documented a clear decrease in nest density as distance from the Bay proper increased and a near absence of nests in the upper 60-70% length of most of the rivers (Henny et al. 1974).

Clearly, the dynamics of this highly important population are changing which warrants a more thorough examination of its foraging ecology. Diet characterization is a fundamental component of any wildlife ecological study at the population level, as food supply is one of the strongest factors influencing dynamics. The only diet composition study that has focused on ospreys in Chesapeake Bay was conducted over twenty years ago in 1985 and was geographically localized (McLean 1986). The purpose of our study was to quantitatively describe the diet of provisioning adults during the 2006 and 2007 breeding seasons on a much broader spatial scale. We incorporated both higher and lower saline areas while still utilizing the site used in the previous study, thus allowing for both temporal and spatial comparisons of diet within the Bay.

Implementing a study design that facilitated a more thorough spatial analysis of osprey diet was particularly desirable because no ecological data have ever been collected from ospreys in the lower saline areas of the Bay. The absence of these data precludes an understanding of possible causes for the rapid population growth that is now occurring there. Studies have shown that salinity gradients, such as along the Bay's river systems,

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can profoundly influence their associated ecosystems. The distribution of fish populations, for example, can often be directly related to salinity (Boesch 1977, Murdy et al. 1997, Jung 2002). Thus, prey availability, and ultimately foraging behavior, in the lower saline areas may differ markedly from the higher saline areas. Better understanding the osprey's niche in these unique lower saline estuarine ecosystems will fill a much needed knowledge gap. Expanding our knowledge of the interconnectedness of organisms, particularly bioindicators at higher trophic levels such as raptors, within their ecosystems is becoming increasingly important as humans continue to impact the environment.

Methods

Locations of study sites for the 2006 and 2007 breeding seasons were chosen by referencing the Chesapeake Bay Program analytical segmentation scheme, which delineates salinity zones within the Bay (DAWG 1997). The four salinity zones defined by this scheme, in order of decreasing salinity, are the following: polyhaline (>18 ppt), mesohaline (5-18 ppt), oligohaline (0.5-5 ppt), and tidal fresh (<0.5 ppt). We restricted research efforts to the more extreme ends of the salinity spectrum.

Since the vast majority of osprey nests in the Bay are either over open water or immediately adjacent to the shoreline, work was conducted via piloting a small boat. Therefore, the site selection was based, in part, on the availability of boat ramps and was not completely randomized. For the purposes of this study, tidal fresh and oligohaline sites were categorized as "upper estuarine," and polyhaline sites were categorized as "lower estuarine." A total of nine study sites were divided between the upper and lower

ends of the gradient (Figure 1.1).   In 2006, unforeseen circumstances and logistical difficulties precluded a balanced sampling regime from being implemented.   The three sites identified within the polyhaline zone included the Ware River and the mouths of the James and York Rivers.   In the lower saline reaches, the three sites identified within the oligohaline zone included Jamestown Island on the James River, West Point on the York River, and Tappahannock on the Rappahannock River.   The two sites identified within the tidal fresh zone included the Chickahominy River and Hopewell on the James River. Thus, five upper estuarine sites and three lower estuarine sites were sampled.   In 2007, the geographic scope was reduced to ensure a more balanced data set.   The upper estuarine sites were limited to the Chickahominy River and Hopewell on the James River, and the lower estuarine sites included the North and Ware Rivers.   Also, to encourage nesting at more humanly accessible locations along the Chickahominy, Ware, and North Rivers in 2007, artificial platforms were erected in appropriate areas early in the season. Approximately two of these were utilized by breeding ospreys at each of the three sites. It is possible that, instead of encouraging a shift in utilized nesting substrate within these sites, we encouraged immigration to these sites.   This may have increased population size and possibly reduced provisioning rates.   However, given the small number of ospreys that used these structures relative to the total number of ospreys within the sites, we believe the potential effects of such manipulation would have been negligible.

The specific aspect of osprey foraging ecology that was analyzed in this study was provisioning, or the delivery of food to young.   The parameters that were assessed included taxonomy, length, mass, and energy content of provisioned prey items.   Micro-video monitoring was the primary technique employed to collect the provisioning data.

The camera unit consisted of a portable Digital Video Recorder (DVR) connected to a 10-cm color bullet camera, both of which were powered by a 12V deep-cycle marine battery. Digital data were stored on a 2GB (gigabite) Scan Disk memory cards. The bullet camera was secured approximately 1 m from the nest to obtain the highest resolution image of provisioning behavior. Following the installation of the camera unit, the nest was observed closely to ensure that the female returned and resumed normal behavior, which occurred in all cases.

In 2006, limited equipment availability precluded the installment of more than one camera at each site at any given time. But in 2007, the reduced geographic scope of the study allowed two cameras to be simultaneously installed at each of the four sites utilized. Nests were randomly selected for monitoring to the maximum extent practicable, but choices were usually restricted because some of the nesting substrate could not adequately support the camera unit.

Additionally, studies have indicated that ospreys conduct foraging during all daylight hours, but may preferentially feed during certain periods of the day such as dawn (MacCarter 1972, Stinson 1978, Van Daele and Van Daele 1982). Therefore, to avoid biases that could potentially result from sampling during a shorter time period, filming was completed continuously between 05:30 and 21:00 hours. However, occasional heavy accumulation of condensation on the camera lens was later noted during some of the footage review which precluded all of the data from being analyzed.

In 2006, a total of 442 hours of footage were recorded in the upper estuarine sites and a total of 194 hours were recorded in the lower estuarine sites. Two nests per site were surveyed for approximately 41 hours each, averaging 106 hours per site. In 2007, a

total of 485 hours of footage were recorded in the upper estuarine sites while 667 hours were recorded in the lower estuarine sites. Three to five nests per site were surveyed for approximately 82 hours each, averaging 288 hours per site.

Prey items observed during review of the video footage were usually identified to species. However, due to the lack of strong morphological distinctions between some species, compounded by a poor angle of view and/or a low video image resolution, most of the catfish and some of the shad were identified only to genus or family. Fish lengths were estimated to the nearest cm using multiples of either the adult's bill or claw length. Since the adults were not handled, average adult bill (male mean ± standard deviation [SD] = 32.5 ± 12 mm, n = 49; female mean ± SD = 34.6 ± 13 mm, n = 47) and claw (male mean ± SD = 28.9 ± 10 mm, n = 49; female mean ± SD = 30.5 ± 12 mm, n = 47) lengths identified in published literature were used (Poole et al. 2002). In cases where the whole fish could not be seen, total fish length was extrapolated using published morphometric data including standard length, fork length, pre-anal length, pre-dorsal length, pre-pectoral length, and pre-pelvic length (Crozier and Hecht 1913, Lagler and Van Meter 1951, Muncy 1959, Muncy 1960, Mansueti 1961, June and Nicholson 1964, Carlander 1969, St. Pierre and Davis 1972, Wilk et al. 1978, Bykov 1983, Chavance et al. 1984, Crawford 1993, Claro and Garcia-Arteaga 1994, Frimodt 1995, Madenjian et al. 2003). Fish mass was then estimated using total length by referencing published length-weight conversion equations (Appendix 1.1) (Crozier and Hecht 1913, Lagler and Van Meter 1951, Muncy 1959, Muncy 1960, Mansueti 1961, June and Nicholson 1964, Carlander 1969, St. Pierre and Davis 1972, Wilk et al. 1978, Bykov 1983, Chavance et al. 1984, Crawford 1993, Claro and Garcia-Arteaga 1994, Frimodt 1995, Madenjian et al.

2003). Finally, since energy content per unit mass varies among species, the total kilocalories delivered per prey item were calculated using published energy density data (Appendix 1.2) (Watt and Merrill 1975, Frimodt 1995). In the few cases where length-weight conversion equations or energy density data were unavailable for identified species, values were calculated by using representative species that were closely related. Mass and energy content for prey items that were identified only to family or genus were calculated in a similar manner by averaging the published values of closely related species. Consistent with previous osprey diet studies, all fish delivered to nests were considered to be entirely edible and therefore wholly consumed (e.g., Stinson 1977, Poole 1982, Van Daele and Van Daele 1982, McLean and Byrd 1991, Steeger et al. 1992). Catfish (Ictaluridae) greater than 31 cm in total length were an exception and assumed to be only 90% consumable (Dykstra 1995 and Markham 2004).

Several methods were used to analyze the data. All identified taxa recorded in provisioning events were summarized by number of individuals, biomass, and energy content for both lower and higher saline sites. Chi-square tests were conducted for each taxon to assess whether its frequency of occurrence in the higher and lower saline reaches deviated significantly from that which was expected. Since the sampling efforts for the upper estuarine (926.9 hours) and lower estuarine (880.4 hours) treatments were not equal, the expected values were standardized by calculating a correction factor that reflected this difference.

Since all nests were not surveyed equally, more rigorous comparisons of diet compositions included only those nests that approached asymptote for diet breadth. The asymptotic number of species consumed at each nest was determined by fitting each

distribution to the following negative exponential function: accumulated no. species = b0*(1-exp(-b1*accumulated no. observations)), where b0 = asymptote (Miller and Wiegert 1989). None of the nests sampled at the mouth of the York River approached this value, and were therefore eliminated from additional analyses. Analyses incorporating this more limited sample pool included frequency distributions of prey length, mass, and energy content as well as species diversity indices (Simpson's 1-D: Simpson 1949). This pool was additionally used to assess the uniformity of diet composition among sites within each of the two treatments, as well as between years for each treatment. Since sampling efforts among sites both within treatments and between years were unequal, valid conclusions regarding spatial and temporal variation of diet were difficult to make. To allow for the most meaningful analyses, we characterized the contributions of major fish taxa by delivery rates (g/hr).

Results

During the 2006 and 2007 osprey breeding seasons, a total of 1,807 hours of provisioning behavior were recorded via micro-video monitoring. The upper and lower estuarine treatments were represented by 926.9 hours and 880.4 hours, respectively. We positively identified a total of 589 prey items during review of this footage. The upper and lower estuarine treatments were represented by 382 and 207 prey items, respectively. While ospreys have been anecdotally observed preying on non-fish species (Poole et al. 2002), all prey identified in our study were fish.

In total, fifteen taxa were identified to species. Additionally, one taxon was identified to genus and two taxa were identified to family since conclusive distinguishing

characteristics were not apparent during video footage review. The genus was *Cynoscion*, and was represented by either spotted seatrout (*Cynoscion nebulosus*) or weakfish (*Cynoscion regalis*). The two families were Ictaluridae and Clupeidae. Given the shape of the caudal fins, though, the Ictaluridae were likely represented by either channel catfish (*Ictalurus punctatus*), blue catfish (*Ictalurus furcatus*), or white catfish (*Ameirus catus*). The Clupeidae could often be identified to species, but when not they were likely represented by gizzard shad (*Dorosoma cepedianum*), American shad (*Alosa sapidissima*), hickory shad (*Alosa mediocris*), or alewife (*Alosa pseudoharengus*).

By frequency of occurrence, catfish and gizzard shad were overwhelmingly the greatest percentage (80%) of total prey items provisioned in the upper estuarine sites. *Cynoscion* spp., Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker (*Micropogonias undulates*), and spot (*Leiostomus xanthurus*) comprised the major percentage (74%) of fish provisioned in the lower estuarine sites (Table 1.1). Excluding Atlantic croaker, Chi-square tests revealed that the frequency of occurrence of each of these dominant species differed significantly between salinity zones. Though comprising an obviously much smaller proportion of diet composition, Chi-square tests also revealed that the occurrences of Atlantic thread herring (*Opisthonema oglimum*), unidentified Clupeidae, round herring (*Etrumeus teres*), and summer flounder (*Paralichthys dentatus*) differed significantly between salinity zones (Table 1.1).

Similar patterns were observed for prey items represented as percentages of total energy delivered to nests (Table 1.1). Again, Ictaluridae and gizzard shad were the dominant species in the upper estuarine sites, representing 77.2% of the total energy

provisioned to nestlings. In the lower estuarine sites, *Cynoscion* spp., Atlantic menhaden, and gizzard shad dominated this aspect of the diet composition.

Utilizing only those nests that approached an asymptotic value for diet breadth, descriptive statistics were used to characterize lengths, masses, and energy contents of provisioned fish. Fish length ranged from 10.2 – 42.9 cm with a mean ± SD (standard deviation) of 23.7 ± 7.0 cm in the upper estuarine sites, and ranged from 12.7 – 42.0 cm with a mean ± SD of 22.2 ± 5.0 cm in the lower estuarine sites (Figure 1.2). Fish biomass ranged from 10.2 – 850.0 g with a mean ± SD of 239.8 ± 194.9 g in the upper estuarine sites, and ranged from 18.1 – 850.0 g with a mean ± SD of 157.8 ± 112.8 g in the lower estuarine sites (Figure 1.3). Energy content of fish ranged from 16.6 – 1411.2 kcal with a mean ± SD of 356.5 ± 352.7 kcal in the upper estuarine sites, and ranged from 19.9 – 1410.0 kcal with a mean ± SD of 215.0 ± 192.9 kcal in the lower estuarine sites (Figure 1.4). Kolmogorov-Smirnov tests revealed that lengths ($D=0.203$, $p<0.005$), masses ($D=0.305$, $p<0.001$), and energy contents ($D=0.247$, $p<0.001$) of consumed fish differed significantly between salinity zones.

We used this same pool to assess the uniformity of diet composition among sites within each of the two treatments, as well as between years for each treatment. Contributions of major fish taxa were characterized by delivery rates (g/hr) (Table 1.2). Chi-square tests revealed that observed site values differed significantly from expected site values within treatments for all taxa. Significant temporal differences for each treatment were noted only for gizzard shad in the upper estuarine sites (Table 1.2).

Finally, Simpson's Index of Diversity (1-D) was also calculated for nests that approached an asymptotic value for diet breadth (Simpson's 1-D: Simpson 1949).

Simpson's 1-D ranged from 0.236-0.823 with a mean ± SD of 0.526 ± 0.163 in the upper estuarine sites, and ranged from 0.549-0.844 with a mean ± SD of 0.696 ± 0.119 in the lower estuarine sites. A linear mixed-effects model, however, revealed that the differences between salinity zones were not significant (p=0.4032).

Discussion

Only two known studies, both of which were conducted over 20 years ago, have quantitatively described the diet composition of breeding ospreys in the mid-Atlantic and northeastern United States. Poole (1984) documented 210 hours of provisioning at 14 nests on Long Island in New York, and McLean (1986) observed provisioning at seven nests in southwestern Chesapeake Bay for 642 hours. The lack of additional quantitative diet studies in the region is striking given the extremely large number of ospreys that breed here. With over 1,800 observational hours at 28 nests, our study easily represents the most comprehensive analysis of osprey diet composition in the Chesapeake Bay, as well as throughout the coastal northeastern United States, to date.

McLean's study site was located in lower estuarine Mobjack Bay within lower Chesapeake Bay. By direct observation, he identified a total of 15 fish species in the diet composition of ospreys he observed. He summarized the contribution of each species to the diet as the percentage of total biomass delivered to nests. Atlantic menhaden, which constituted 75% of the diet, was clearly the dominant prey item consumed. White perch (*Morone americana*), the second most abundant species, accounted for 7% of the diet. Other important species included Atlantic croaker (*Micropogonias undulates*), oyster toadfish (*Opsanus tau*), and American eel (*Anguilla rostrata*), which each accounted for

approximately 3% of the diet. Although separate broods did vary somewhat in their diet composition, McLean noted that all of them received over 50% Atlantic menhaden (McLean and Byrd 1991).

Though covering an overall broader geographic region, our study within the higher saline areas included sites within Mobjack Bay such as the Ware and North Rivers, thus allowing for a more meaningful comparison to McLean's study. We positively identified a total of 14 taxa. After similarly summarizing the contribution of each to the diet as a percentage of the total biomass delivered to nests, we noted marked temporal differences in diet composition. Atlantic menhaden still remained the dominant prey item consumed, but its contribution to the diet was much lower at 32% of the total biomass delivered. Nearly as dominant was *Cynoscion* spp., which accounted for 27% of the diet. In order of decreasing abundance, gizzard shad, Atlantic croaker, striped bass (*Morone saxatilis*), and spot (*Leiostomus xanthurus*) comprised a total of 29% of the diet. The remaining eight species, including white perch, each accounted for less than 2% of the diet.

Clearly, the osprey diet compositions quantified in the two studies differ greatly, despite being conducted in the same general locale. Perhaps the most notable difference is the large decrease in the proportion of the diet comprised of Atlantic menhaden. The average percentage of the total biomass delivered for this species dropped by nearly 45%. Such a sharp reduction in the delivery rate of this species is surprising given that it has almost twice the energy content per unit mass as *Cynoscion* spp., the second most dominant species in the diet. Though constituting only 24% of the diet by frequency of

occurrence, Atlantic menhaden provided 44% of the total kilocalories provisioned to broods in the lower estuarine sites.

Due in large part to their high lipid content relative to other species, Atlantic menhaden have historically been shown to be a choice prey item for ospreys breeding throughout the coastal waters of the mid-Atlantic and northeastern United States (Spitzer and Poole 1980, Poole 1989, McLean and Byrd 1991, Steidl et al. 1991). The schooling behavior exhibited by Atlantic menhaden is also believed to greatly contribute to their preference by ospreys (Poole 1989). They form large compact schools very near the water surface, often breaking it with their dorsal and caudal fins (Munroe 2000). This makes them relatively easy to locate and capture. Ospreys have actually been observed capturing two Atlantic menhaden simultaneously, an event undocumented for other fish species (McLean and Byrd 1991, pers. obs.)

Osprey diet has been shown to reflect local prey availability (Greene et al. 1983, Edwards 1988). Therefore, the reduced proportion of Atlantic menhaden we documented in the diet of Chesapeake Bay ospreys may indicate that this species is currently less available than it has been historically. Interestingly, many researchers have become increasingly concerned that Atlantic menhaden are suffering from over-harvesting by humans (e.g., Powell 1994, Franklin 2001, Uphoff 2003). The large quantity of fish oil contained within these fish has become the center of a massive and highly mechanized fishing industry. The annual catch of Atlantic menhaden is larger than the catch of any other species in the United States (Murdy et al. 1997). It composes approximately half of the total fishery harvest on the East Coast (Peters and Schaaf 1991). As might be expected, population analyses have revealed a constant decline in Atlantic menhaden

numbers. Just between 1992 and 1998, the Atlantic States Marine Fisheries Commission (ASFMC) estimated a drop in numbers along the Atlantic Coast from 10 and 15×10^9 to a historic low of 3.7×10^9 (Uphoff 2003). More localized population estimates, though, have been notoriously difficult to produce. The Chesapeake Bay has particularly received a great deal of attention because this estuary serves as the primary nursery ground for the species (Hildebrand and Schroeder 1928). Recent findings do suggest that intense localized depletion may be occurring in the Chesapeake Bay (Gottlieb 1998, Latour pers. comm.). Also, an outbreak of skin lesions on striped bass in Chesapeake Bay has been linked to a decline in the abundance of Atlantic menhaden, their preferred prey (Uphoff 2003). Diet composition analyses have revealed a steady decline in the contribution of this species to the diet of striped bass in the Bay (Uphoff 2003). The percentage of total biomass comprised of Atlantic menhaden dropped from 66% in 1992 to 43% in 1997 to 21% in 1998 (Atlantic Menhaden Advisory Committee [AMAC] 1999). Striped bass were instead increasingly relying on less nutritional invertebrates such as polychaete worms (Uphoff 2003). This likely lowered their nutritional state, and negatively impacted their immune system rendering them more vulnerable to infections such as lesions (Uphoff 2003).

If the diet composition of ospreys is a reflection of prey availability, as indicated by other studies, then the reduced contribution of Atlantic menhaden to the diets of ospreys in our study may be yet another sign that this species is becoming overexploited. If so, the loss of such an energy rich resource could have dire consequences for ospreys in the region if not replaced by prey that provide an equivalent net gain in energy. In recent years, there has been a nearly 50% reduction in the number of active osprey nests

on Gardiner's Island in New York, perhaps one of the largest colonies in the Northeast (Franklin 2001). Productivity has dropped to 0.5 chick per nest (Franklin 2001), reminiscent of the DDT effects. Though no intensive research has been conducted to address this concern, a decline in the local Atlantic menhaden population has been implicated as the cause for the reduction (Franklin 2001, Poole et al. 2002). Whether such a drastic numerical response is occurring in our study region, where ospreys appear to be consuming considerably less Atlantic menhaden than in the past, is currently unknown.

At the least, a functional response in diet composition of ospreys in lower Chesapeake Bay seems to have occurred. Much of the osprey diet once filled by Atlantic menhaden now appears to be largely replaced by *Cynoscion* spp. This taxon accounted for nearly 25% more of the total biomass delivered in our study than it did in McLean's (1986). While not definitively known due to inadequate digital image resolution, this genus appeared to be represented primarily by spotted seatrout (*Cynoscion nebulosus*). This concurs with McLean and Byrd's study (1991) as well as with the opinions of local recreational anglers (pers. comm.), who routinely fished for this species throughout the lower estuarine sites. In biomass, spotted seatrout are the second largest catch annually landed by the saltwater fishing industry in the Southeast, and the recreational catch is believed to be greater than the commercial catch (Murdy et al. 1997). While found throughout the Bay in a wide range of salinities, spotted seatrout predominantly occur in the higher saline waters of the lower Bay (Murdy et al. 1997). They frequent shallow waters with sandy bottoms, making them accessible to ospreys (Murdy et al. 1997).

The spatial differences we documented in osprey diet composition within lower Chesapeake Bay, however, were even more pronounced than the temporal differences. Fish taxa targeted by ospreys in the upper and lower estuarine sites varied in both frequency of occurrence and percentage of total energy content delivered to broods. The Atlantic menhaden and *Cynsoscion* spp. that dominated the lower estuarine diet were virtually absent from the upper estuarine diet. Only six Atlantic menhaden were documented, and no *Cynoscion* spp. were observed. Instead, gizzard shad and catfiish dominated the diet in the upper estuarine sites. Although gizzard shad occurred only half as frequently as Ictaluridae, gizzard shad and Ictaluridae constituted 46% and 33%, respectively, of the total energy delivered to broods. Though somewhat counterintuitive, this is explained by both the larger mass and higher energy content per unit mass of gizzard shad.

The dominance of these taxa in the upper estuarine diet is not surprising. They are abundant in these waters, while forage-size Atlantic menhaden and *Cynoscion* spp. are preferentially found in higher saline waters (Murdy et al. 1997). Though the gizzard shad can occur in salinities as high as 22 ppt within Chesapeake Bay, it is not anadromous and primarily occurs in the tidal fresh and upper estuarine waters where it spawns from March to August (Munroe 2000). This species is therefore an ideal prey item for ospreys breeding in these areas because, unlike anadromous clupeids that either die or return to the sea after spawning, it is available throughout the breeding season (Murdy et al. 1997). Gizzard shad also school between 0.3-1.6 m below the surface (Jenkins and Burkhead 1994) making them easy targets for diving ospreys. Their availability to ospreys is further increased by a rapid growth rate which quickly precludes

consumption by most piscivorous fish (Jenkins and Burkhead 1994). Furthermore, a large size associated with a very high energy content per unit mass guarantees that gizzard shad provide a relatively substantial net gain in energy for foraging ospreys.

Like gizzard shad, catfish can also be found in a wide range of salinities, but occur most frequently in fresher water (Murdy et al. 1997). Within the main river systems of lower Chesapeake Bay, Virginia Institute of Marine Science (VIMS) trawl surveys revealed that the upper estuarine waters were preferentially inhabited by the Ictaluridae (VIMS unpubl. data). Several species of catfish are well established throughout the lower saline reaches of Chesapeake Bay (Murdy et al. 1997), and their localized spawning ensures their presence through the duration of the osprey breeding season (Jenkins and Burkhead 1994). The foraging ecology of catfish likely also contributes greatly to their large presence in the diet composition of ospreys within the lower saline sites. Catfish primarily feed on benthic organisms (Murdy et al. 1997), and bottom-feeders have been shown to be more vulnerable to osprey attacks than limnetic-feeders (Swenson 1979). Bottom-feeders, such as catfish, may have their visual sensory predominantly focused on the underlying substrate, and are therefore less aware of potential attacks from above (Swenson 1979). Also, benthic fish are often drawn to shallower waters to forage (Haywood and Ohmart 1986), thus further increasing their vulnerability to depredation. Finally, although catfish possess substantially less energy per unit mass than gizzard shad, they grow rapidly and can quickly attain a large size (Graham 1999). The blue catfish, for example, is larger than all but three of the freshwater fish in the United States (Graham 1999). Given the above, the prevalence of catfish in the diet of ospreys in the upper estuarine reaches is not surprising.

Our study marks the first assessment of osprey diet composition in the tidal fresh and upper estuarine waters of Chesapeake Bay. Gizzard shad, which dominated the composition by percentage of total energy delivered, has only been documented in the osprey diet within the resident population of southern Florida (Collopy 1984, Edwards 1988). By frequency of occurrence, catfish represented a striking 52% of the diet in the upper estuarine sites. Ictaluridae was strongly believed to be represented by channel catfish, blue catfish, or white catfish as suggested by the deeply forked caudal fins noted. We are currently utilizing pectoral fin spines in an attempt to more accurately estimate the representation of each of these species in the diet. To our knowledge, only bullhead catfish have been documented in the osprey diet thus far (Van Daele and Van Daele 1982, Collopy 1984, Vana-Miller 1987, Poole 1989, Steeger et al. 1992). The importance of gizzard shad and catfish to breeding ospreys cannot be overstated. These taxa comprise the vast majority of the diet composition of individuals within the fastest growing portion of the Bay.

Gizzard shad and catfish have also been shown to be important prey items for bald eagles (*Haliaeetus leucocephalus*) breeding in the upper estuarine areas of the Chesapeake Bay. Clupeidae and Ictaluridae comprise over 50% of the diet by percentage of total individuals, biomass, and energy (Markham 2004). As ospreys and bald eagle populations both continue to expand in these rapidly growing areas of the Bay, competition for these resources is certain to escalate. Exploitive or interference competition would subsequently impact population dynamics. While bald eagles are believed to displace ospreys when territories overlap strongly, some have suggested that the dominance may be reversed if ospreys greatly outnumber bald eagles (Ogden 1975).

However, intense competition may perhaps be alleviated, or at least delayed, through resource partitioning (e.g., targeting different size distributions of prey). The co-occurrence of ospreys and bald eagles in the Bay provides a great opportunity to learn how competition for limited resources influences the foraging behavior and distributions of these respective populations.

We also described prey items using standard morphological characteristics such as length and biomass, which ultimately influence the energy content, or quality, of prey. As all foragers do, ospreys must carefully target prey items that will maximize energy gained per unit effort (Stephens and Krebs 1986). Fish that are too small do not provide enough energy to offset the metabolic cost incurred during foraging, whereas fish that are too large may be too heavy and possibly cause injury. Additionally, since ospreys eat only live fish, prey that are too massive may spoil before they can be entirely consumed (Poole 1989, pers. obs.), thus resulting in wasted energy. Consistent with foraging theory, ospreys typically target fish within a narrow size range (Swenson 1978, Van Daele and Van Daele 1982, Poole 1989). Interestingly, therefore, statistical analyses revealed that the average length, biomass, and energy content of consumed fish all differed significantly between the lower and higher salinity zones. Differing 1.5 cm in length on average, the lower estuarine fish were 6.3% smaller than their upper estuarine counterparts. While significant, such a small difference in length alone would not likely affect prey biomass intraspecifically. However, we found average prey biomass to differ by 82 g between salinity zones, rendering the lower estuarine fish 34.2% smaller than the upper estuarine fish. This is due to the different species that comprise the diets in the two zones because each species has a unique length-weight conversion factor. Identical fish

length frequency distributions could have very different biomass distributions depending on the relative numbers and lengths of each species they represent. We found an even greater difference in the energy content of fish delivered to the two zones. With an average difference of 141.5 kilocalories per fish, broods in the lower estuarine sites received nearly 40% less energy per fish delivered. While certainly largely reflective of biomass, the relative proportions of species again undoubtedly contributed to this difference since each has a unique mass-energy conversion factor.

As can be seen, length, biomass, and energy per unit mass of fish are all interrelated parameters. They determine the energy content of each fish consumed, and ultimately the quality of the diet composition. Although spatial differences in diet composition within treatments did exist, our results strongly indicate that ospreys breeding in the upper estuarine sites enjoy a higher quality diet composition than those in the lower estuarine sites. Given the broad spatial scale of our study, extrapolation of our findings to the broader region seem valid. We therefore conclude that diet quality may be pivotally influencing the dynamics of the Chesapeake Bay osprey population.

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Table 1.1. Relative contributions (No. = number of individuals) of all prey taxa identified in the osprey diet within the lower and upper estuarine sites in lower Chesapeake Bay during the 2006 and 2007 breeding seasons. Associated Chi-square tests were conducted to detect significant differences in frequencies of occurrence between treatments.

	Lower		Upper		Lower		Upper		Obs vs. Exp Frequency	
Species	No.	% Total	No.	%Total	Kcals	%Total	Kcals	%Total	Chi-Square	p value
alewife (*Alosa pseudoharengus*)	0	0.00%	1	0.25%	0.00	0.00%	767.64	0.43%	0.9498	0.3298
Atlantic croaker (*Micropogonias undulatus*)	27	12.33%	26	6.62%	3642.03	5.49%	6901.39	3.89%	0.1055	0.7454
Atlantic menhaden (*Brevoortia tyrannus*)	53	24.20%	6	1.53%	29613.13	44.67%	7899.39	4.46%	39.9246	<0.0001
Atlantic thread herring (*Opisthonema oglimum*)	5	2.28%	0	0.00%	628.63	0.95%	0.00	0.00%	5.2641	0.0218
bluefish (*Pomatomus saltatrix*)	1	0.46%	0	0.00%	133.93	0.20%	0.00	0.00%	0.9498	0.3298
Clupeidae (unidentified)	0	0.00%	15	3.82%	0.00	0.00%	7139.28	4.03%	14.2475	0.0002
gizzard shad (*Dorosoma cepedianum*)	9	4.11%	110	27.99%	8811.69	13.29%	81548.24	46.00%	80.6578	<0.0001
hickory shad (*Alosa mediocris*)	0	0.00%	3	0.76%	0.00	0.00%	5110.26	2.88%	2.8495	0.0914
hogchoker (*Trinectes maculatus*)	1	0.46%	0	0.00%	94.23	0.14%	0.00	0.00%	0.9498	0.3298
Ictaluridae	0	0.00%	203	51.65%	0.00	0.00%	58567.28	33.04%	192.8164	<0.0001
largemouth bass (*Micropterus salmoides*)	0	0.00%	1	0.25%	0.00	0.00%	381.40	0.22%	0.9498	0.3298
round herring (*Etrumeus teres*)	4	1.83%	0	0.00%	1318.47	1.99%	0.00	0.00%	4.2113	0.0402
spot (*Leiostomus xanthurus*)	19	8.68%	0	0.00%	2421.81	3.65%	0.00	0.00%	20.0035	<0.0001
spotted seatrout/ weakfish (*Cynoscion* sp.)	63	28.77%	0	0.00%	11995.12	18.10%	0.00	0.00%	66.3273	<0.0001
striped bass (*Morone saxatilis*)	10	4.57%	5	1.27%	2905.44	4.38%	3202.57	1.81%	1.9352	0.1642
summer flounder (*Paralichthys dentatus*)	12	5.48%	0	0.00%	1291.35	1.95%	0.00	0.00%	12.6338	0.0004
threadfin shad (*Dorosoma petenense*)	1	0.46%	4	1.02%	36.12	0.05%	638.13	0.36%	1.6500	0.1990
white perch (*Morone americana*)	2	0.91%	8	2.04%	548.53	0.83%	1157.38	0.65%	3.3001	0.0693
unknown	12	5.48%	11	2.80%	2847.28	4.30%	3964.19	2.24%		
Total	**219**		**393**		**66287.76**		**177277.14**			

Table 1.2. Spatial and temporal comparisons of provisioning rates (g/hr) for major taxa (mean ± SD) identified in the osprey diet during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Associated Chi-sqaure tests were conducted to detect significant differences.

Upper Estuarine Zone

Species	Site Mean ± SD	Obs vs. Exp Frequency Chi-Square	p value	Annual Mean ± SD	Obs vs. Exp Frequency Chi-Square	p value
Atlantic croaker (*Micropogonias undulatus*)	12.12 ± 13.98	64.481	<0.0001	1.39 ± 1.51	1.635	0.2011
gizzard shad (*Dorosoma cepedianum*)	78.48 ± 41.79	88.990	<0.0001	93.94 ± 57.12	34.727	<0.0001
Ictaluridae	55.60 ± 26.06	48.844	<0.0001	66.25 ± 7.02	0.743	0.3887

Lower Estuarine Zone

Species	Site Mean ± SD	Obs vs. Exp Frequency Chi-Square	p value	Annual Mean ± SD	Obs vs. Exp Frequency Chi-Square	p value
Atlantic croaker (*Micropogonias undulatus*)	7.91 ± 5.62	13.077	0.0014	4.06 ± 1.77	0.769	0.3807
Atlantic menhaden (*Brevoortia tyrannus*)	25.09 ± 30.49	63.017	<0.0001	9.09 ± 4.47	2.197	0.1383
spotted seatrout/ weakfish (*Cynoscion* sp.)	11.04 ± 10.59	20.317	<0.0001	22.97 ± 5.69	1.407	0.2356

Figure 1.1. Study sites utilized within southwestern Chesapeake Bay during the 2006 and 2007 field seasons.
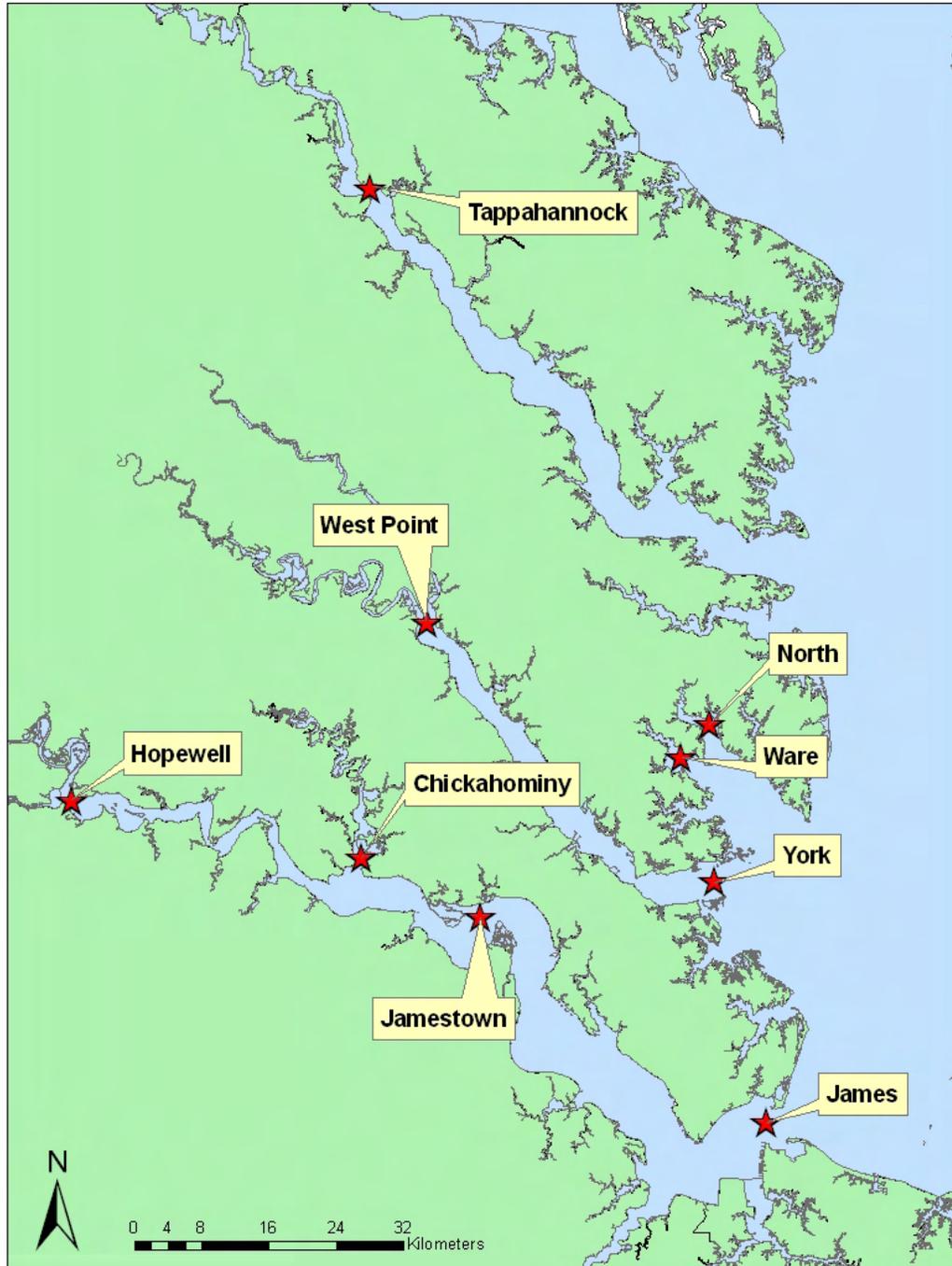
Figure 1.2. Frequency distributions of individual fish lengths identified in the osprey diet within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay..

**Size Distribution of Consumed Fish
within Upper and Lower Estuarine Sites**
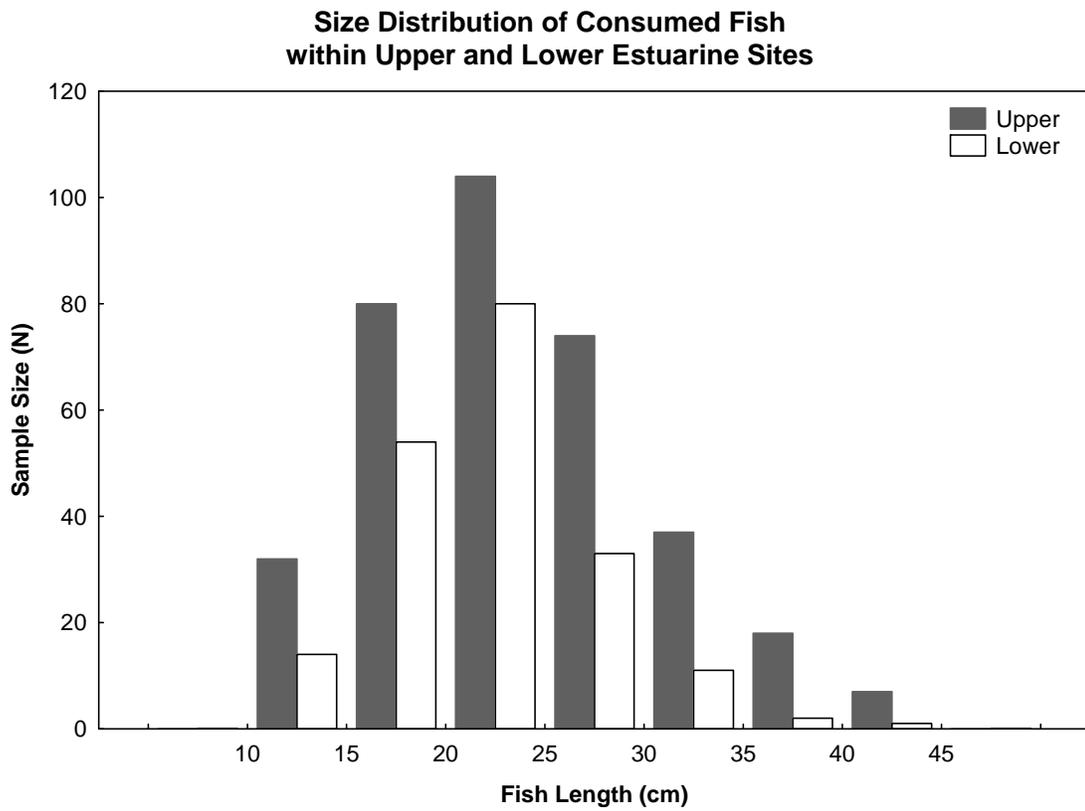
Figure 1.3. Frequency distributions of individual fish biomass identified in the osprey diet within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

Biomass Distribution of Consumed Fish within Upper and Lower Estuarine Sites
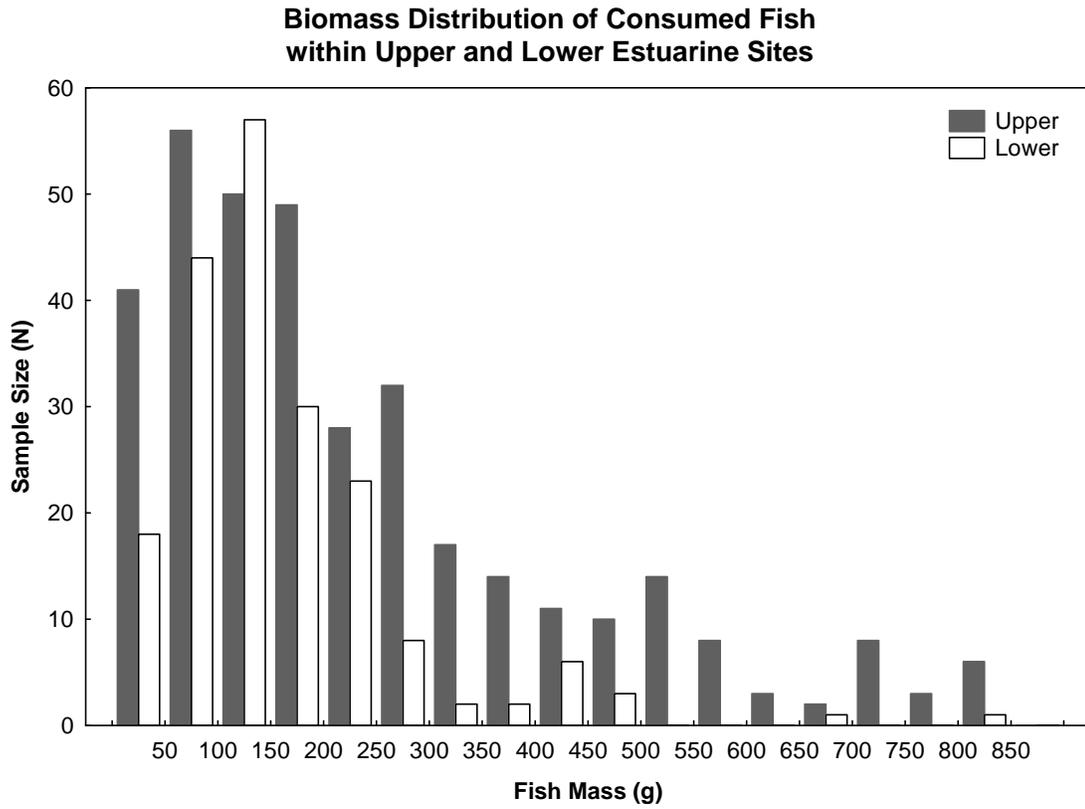
Figure 1.4. Frequency distributions of individual fish energy contents identified in the osprey diet within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

Energy Content Distributions of Consumed Fish within Upper and Lower Estuarine Sites
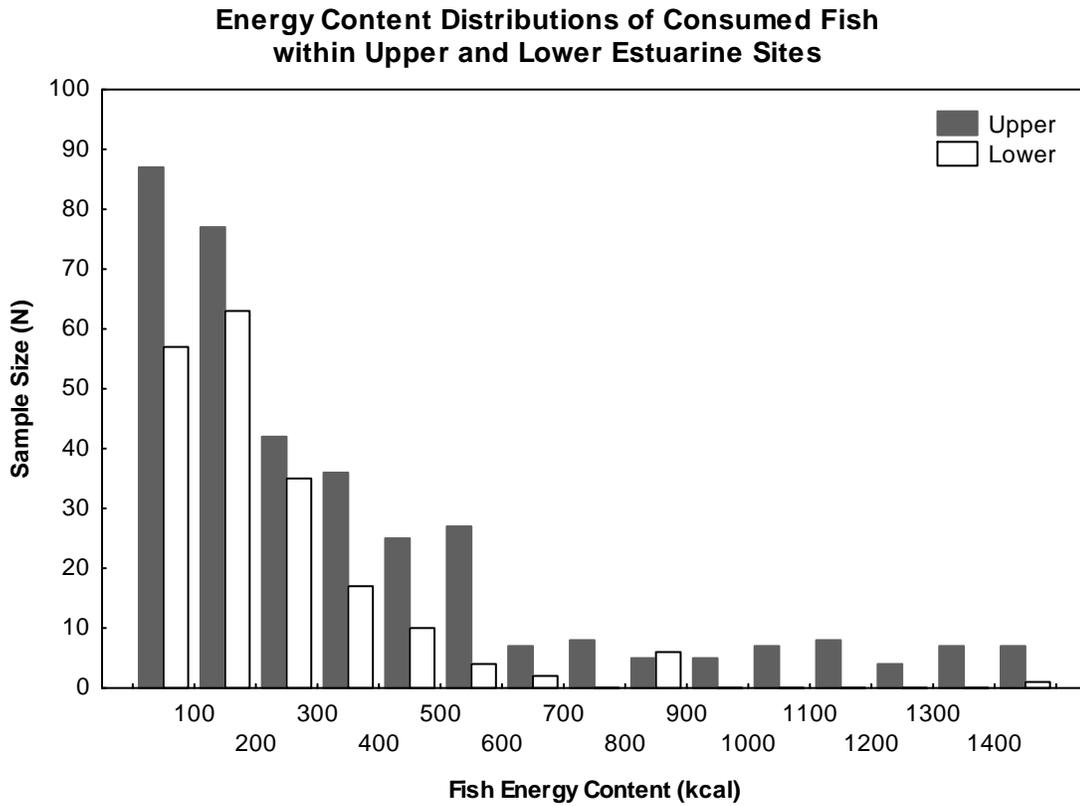
Appendix 1.1. Length-weight conversion equations for all taxa identified in the osprey diet during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

Species	Biomass Conversion	Reference
alewife (*Alosa pseudoharengus*)	M = 0.0085*L3.000	Madenjian et al. 2003
American shad (*Alosa sapidissima*)	M = 0.0065*L2.959	Muncy 1960
Atlantic croaker (*Micropogonias undulatus*)	M = 0.0052*L3.148	Wilk et al. 1978
Atlantic herring (*Clupea harengus*)	M = 0.0075*L3.030	Hubold 1978
Atlantic menhaden (*Brevoortia tyrannus*)	M = 0.0161*L3.000	June and Nicholson 1964
Atlantic thread herring (*Opisthonema oglimum*)	M = 0.0186*L2.92	Claro and Garcia-Arteaga 1994
banded rudderfish (*Seriola zonata*)	M = 0.0259*L2.908	Bohnsack and Harper 1988
black crappie (*Pomoxis nigromaculatus*)	M = 0.0096*L3.075	Vanderpuye and Carlander 1971
blue catfish (*Ictalurus furcatus*)	M = 0.0185*L3.000	Crawford 1993
channel catfish (*Ictalurus punctatus*)	M = 0.0041*L3.407	Muncy 1959
clearnose skate (*Raja eglanteria*)	M = 0.0022*L3.295	Sulikowski et al. 2003
gizzard shad (*Dorosoma cepedianum*)	M = 0.0182*L2.89	Lagler and Van Meter 1951
hickory shad (*Alosa mediocris*)	used American shad	
hogchoker (*Trinectes maculatus*)	M = 0.0199*L3.001	Dawson 1965
largemouth bass (*Micropterus salmoides*)	M = 0.0158*L2.960	Swingle 1965
round herring (*Etrumeus teres*)	M = 0.0059*L3.158	Sanders et al. 1984
spot (*Leiostomus xanthurus*)	M = 0.0092*L3.072	Dawson 1965
spotted seatrout (*Cynoscion nebulosus*)	M = 0.0131*L3.000	Crawford 1993
striped bass (*Morone saxatilis*)	M = 0.0061*L3.153	Mansueti 1961
summer flounder (*Paralichthys dentatus*)	M = 0.0102*L2.994	Smith and Daiber 1977
threadfin shad (*Dorosoma petenense*)	M = 0.0035*L3.774	Carlander 1969
weakfish (*Cynoscion regalis*)	M = 0.0088*L3.000	Crozier and Hecht 1913
white perch (*Morone americana*)	M = 0.0125*L3.020	St. Pierre and Davis 1972

Appendix 1.2. Mass energy conversion equations for all taxa identified in the osprey diet during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

Species	Biomass Conversion	Reference
alewife (*Alosa pseudoharengus*)	E = 185*(M/100)	Frimodt 1995
American shad (*Alosa sapidissima*)	E = 192*(M/100)	Watt and Merrill 1975
Atlantic croaker (*Micropogonias undulatus*)	E = 100*(M/100)	Frimodt 1995
Atlantic herring (*Clupea harengus*)	E = 190*(M/190)	Frimodt 1995
Atlantic menhaden (*Brevoortia tyrannus*)	E = 189*(M/100)	Frimodt 1995
Atlantic thread herring (*Opisthonema oglimum*)	used Atlantic herring	
banded rudderfish (*Seriola zonata*)	used white perch	
black crappie (*Pomoxis nigromaculatus*)	used white perch	
blue catfish (*Ictalurus furcatus*)	E = 103*(M/100)	Frimodt 1995
channel catfish (*Ictalurus punctatus*)	E = 112*(M/100)	Frimodt 1995
clearnose skate (*Raja eglanteria*)	used summer flounder	
gizzard shad (*Dorosoma cepedianum*)	E = 200*(M/100)	Watt and Merrill 1975
hickory shad (*Alosa mediocris*)	used American shad	
hogchoker (*Trinectes maculatus*)	used summer flounder	
largemouth bass (*Micropterus salmoides*)	used white perch	
round herring (*Etrumeus teres*)	used Atlantic herring	
spot (*Leiostomus xanthurus*)	used Atlantic croaker	
spotted seatrout (*Cynoscion nebulosus*)	E = 99*(M/100)	Frimodt 1995
striped bass (*Morone saxatilis*)	E = 92*(M/100)	Frimodt 1995
summer flounder (*Paralichthys dentatus*)	E = 84*(M/100)	Frimodt 1995
threadfin shad (*Dorosoma petenense*)	used gizzard shad	
weakfish (*Cynoscion regalis*)	E = 99*(M/100)	Frimodt 1995
white perch (*Morone americana*)	E = 118*(M/100)	Watt and Merrill 1975

Chapter Two
Comparison of Osprey Provisioning and Nestling Growth Rates Between Upper and Lower Estuarine Areas

Introduction

As piscivorous top predators, ospreys (*Pandion haliaetus*) are not only integral components of their communities, but they are particularly susceptible to threats such as biomagnification, which makes them very valuable indicators of environmental contamination (Wiemeyer et al. 1975, Spitzer et al. 1978, Wiemeyer et al.1978, Westall 1990). This became acutely apparent when osprey populations in the coastal northeastern United States began experiencing significant declines in the middle part of last century (Henny and Ogden 1970, Henny 1975, Henny et al. 1977, Reese 1975, Spitzer and Poole 1980). This was attributed to decreased productivity, which is defined as the number of chicks produced per active nest (Poole et al. 2002). Productivity was documented to be between 60% and 95% below normal in some populations (Ames and Mersereau 1964).

Environmental contamination of the pesticide DDT (Dichloro-Diphenyl-Trichloroethane) was implicated as the cause for the historic decline in osprey numbers. DDT was proven to be effective abroad during World War II, and was subsequently used domestically following the conclusion of the war. Research biologists Ames and Mersereau (1964) documented high concentrations of DDT in eggshell fragments collected from failed nests. They determined that DDT was causing the shells to be formed much thinner than normal, and consequently break during incubation. Thinner egg shells were also implicated in water loss and reduced

gas exchange (Ames and Mersereau 1964). This was a classic example of biomagnification, whereby a contaminant in the environment accumulates in increasing concentrations in organisms as it ascends to higher trophic levels. The threatened persistence of ospreys in the region resulted in a pioneering lawsuit in 1966 that succeeded in banning the use of DDT within New York State (Gessner 2001). In 1972, the Environmental Protection Agency (EPA) followed suit and implemented a nationwide ban of DDT (Gessner 2001).

Of particular concern was the Chesapeake Bay region, which has historically been considered to have the largest concentration of breeding ospreys in the world since the 1800's (Henny et al. 1974, Spitzer and Poole 1980). Factors contributing to this large concentration include both the estuary's average depth of only 8.4 m, which exposes the bottom to light ultimately maintaining a vast food web, and approximately 13,000 km of sinuous coastline, which serves as prime foraging habitat (United States Department of Commerce 1991).

The Chesapeake Bay population recovered remarkably following the banning of DDT. A Bay-wide survey conducted in 1995 and 1996 revealed that the breeding population had more than doubled since 1973 (Watts et al. 2004). However, considerable geographic variation in the growth rate of the population was noted. Mean doubling times were recorded to range from 4.3 years to more than 40 years, with the lowest doubling times generally occurring in the tidal fresh and upper estuarine areas and some of the highest doubling times occurring in the higher saline areas along the Bay proper (Watts et.al. 2004). Such a pattern is somewhat surprising

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given that historical records, most of which are from the DDT years, reveal that ospreys have primarily been concentrated along the Bay proper rather than the upper tidal fresh reaches (Watts et al. 2004). A 1973 breeding survey, for example, documented a clear decrease in nest density as distance from the Bay proper increased and a near absence of nests in the upper 60-70% length of most of the rivers (Henny et al. 1974).

Such slow growth in the higher salinity areas of the Bay in recent years may indicate that this portion of the population may be nearing carrying capacity. In 1986, McLean suggested that such a limit was possibly being approached in southwestern Chesapeake Bay, after he documented occurrences of sibling aggression in Mobjack Bay (McLean 1986). Interestingly, Stinson (1977) specifically stated that he observed no such behavior in his earlier study that had focused on the same geographic location. Sibling aggression is widely believed to be an indication of food stress in ospreys. Hatching asynchrony facilitates the establishment of a nestling hierarchy resulting in sequential feeding of nestlings. Only after dominant nestlings are no longer hungry do they permit subordinates to engage in feeding. Thus, reduced provisioning rates are associated with increased aggression and may ultimately lead to siblicide (Poole 1979, Poole 1982, Jamieson et al. 1983, Eriksson 1986, Hagan 1986, Forbes 1991). McLean's prediction regarding his study site was supported ten years later by the data obtained during the 1995 and 1996 breeding survey, which revealed that it had remained relative stability and had exhibited little to no growth (Watts et.al. 2004). Interestingly, recent anecdotal evidence suggests

that the population in the Bay proper may currently even be experiencing reduced productivity and be in decline (Watts and Byrd pers. comm.). The number of nestlings in this area available for hacking projects seems to have decreased during the past several years, and some of the chicks produced have been underdeveloped (Watts and Byrd pers. comm.). However, McLean's sample was both geographically localized and small in size (approximately 13 breeding pairs), and little direct research has been focused on the Chesapeake Bay osprey population since this time. Consequently, nothing is currently known about the prevalence of food stress throughout the areas of the Bay exhibiting relatively negligible growth rates, or its potential significance as a factor in influencing current population dynamics.

Focusing research efforts on osprey productivity in the Bay and the variables that may be influencing it is essential to better understand the proximate cause(s) for the observed population trends. This would ultimately provide valuable insight into the factors that will contribute to the capacity of this important population, as well as the response of ospreys to reaching capacity. Furthermore, no ecological data have ever been collected from the ospreys in the lower salinity areas of the Bay, where historic rapid population growth is now occurring. Better understanding the osprey's niche in these unique upper estuarine ecosystems will fill a much needed knowledge gap. Expanding our knowledge of the interconnectedness of wildife within their ecosystems is becoming increasingly important as humans continue to impact the environment. The success of potential future conservation measures aimed at individual species will undoubtedly hinge on our understanding of their ecology.

As top predators, ospreys are particularly susceptible to bottom-up effects caused by human mediated disturbances in their ecosystems. While populations in many parts of the country are considered stable, ospreys are still protected in many areas. For example, in the United States alone the osprey is listed as Endangered in Vermont, Pennsylvania, Indiana, and Ohio, and is listed as Threatened in New Hampshire, New Jersey, Tennessee, Michigan, and Wisconsin (Poole et al. 2002). Additionally, the osprey is listed as a Species of Special Concern in Rhode Island, New York, Utah, California, and Monroe County in Florida, and is listed as a Rare Species of Conservation Concern in Delaware (Poole et al. 2002). Thus, acquiring data that are instrumental in elucidating factors that contribute to osprey population growth and regulation is particularly important.

An especially important research need that has yet to be addressed is acquiring a better understanding of how food availability contributes to osprey population regulation (Meyburg and Chancellor 1989, Poole et al. 2002). While some studies have addressed the effect of foraging efficiency on individual breeding success (e.g., Koplin et al. 1977, Collopy 1984), few studies have addressed the importance of food availability as a potential limiting factor on a broad spatial scale (Meyburg and Chancellor 1989, Poole et al. 2002). Sample sizes have generally been small and the growth trends of the populations have typically been either unknown or unreported (Steeger et al. 1992, Poole 1982, Van Daele and Van Daele 1982, Jamieson et al. 1983, Eriksson 1986, Hagan 1986, McLean and Byrd 1991, Saurola 1997). One known exception is a study of the resident Florida Bay population, where the number

of occupied nests decreased 60% between 1973 and 1980 (Kushlan and Bass 1983). Researchers suggested that increased food stress and subsequent reproductive failure may have contributed to this declining population trend (Poole 1982 and Kushlan and Bass 1983). However, temporal comparisons of reproductive success were conflicting, and temporal comparisons of provisioning rates were not conducted. Provisioning rates were instead compared spatially to those of colonies in the northeastern United States (Poole 1982). Unlike prior studies, the spatial variation in growth rate exhibited by the Chesapeake Bay osprey population since the middle 1970s provides an incredibly unique opportunity to increase our knowledge of this species' reproductive and foraging ecology at the population level.

One of the main resources that can limit reproductive success of raptor populations is nesting substrate availability, which has generally been believed to be the primary factor regulating osprey population growth (Poole 1989b). This belief was supported by patterns of post-DDT population recoveries, which typically occurred fastest in populations that had the greatest amount of available substrate (Meyburg and Chancellor 1989, Poole 1989b, Poole et al. 2002). The pivotal role of nest site availability in population regulation has been evidenced in other ways as well. First, ospreys nesting on substrates that are the most stable and least vulnerable to depredation commonly fledge the most young, and thus contribute the most to population growth (Reese 1969, Henny et al. 1974, Meyburg and Chancellor 1989). Second, ospreys have been observed nesting the most densely in areas with the highest quality nest sites, seemingly at the expense of foraging efficiency (Meyburg

and Chancellor 1989). Third, studies in both New England and Sweden have shown that sites with the greatest nesting availability are associated with shorter natal dispersal distances and younger ages at first breeding.   (Meyburg and Chancellor 1989, Poole 1989b, Postupalsky 1989).

Nesting substrate saturation, however, does not likely account for the decreased productivity recently documented anecdotally in the Bay proper. As nesting sites become saturated and raptor populations subsequently expand, the oldest and newest territories are typically characterized by the highest and lowest quality habitats, respectively, as measured by productivity (Ferrer and Donazar 1996, Lohmus 2001). Therefore, higher productivity, rather than lower, would be expected to occur in the Bay proper, where nesting has been documented for the longest period of time. Additionally, a decrease in the number of active nests has been anecdotally documented in some of the lower estuarine areas of the Bay in recent years, thus indicating that all of the available nesting substrate is not being utilized (Byrd pers. comm.).

Food availability has been shown both experimentally and circumstantially to be another main resource that can strongly influence carrying capacity of raptor populations (Newton 1979). As food availability decreases, birds become less efficient in obtaining the energy requirements needed to maintain basal metabolic rates, provision young, or conduct other daily activities. Provided food availability continues to remain below the necessary threshold, populations then either stabilize or decline (Newton 1980). Evidence that raptor populations are regulated by food

includes the following: larger raptor species typically breed at lower densities, spatial differences in breeding density within species are often associated with spatial differences in food availability, and temporal fluctuations in breeding density within species are often associated with temporal fluctuations in food availability (Newton 1979).

Data have shown that raptor body-weight and territory size are closely correlated, with larger raptors occupying larger territories (Newton 1980). For example, Africa's largest eagle, the African Martial eagle (*Dolemaetus bellicosus*), breeds at some of the lowest densities recorded for any bird. It has bred at densities as low as one pair per 125 km^2 in the Embu District of Kenya, one pair per 182 km^2 in South Africa's Kruger Park, and even one pair per 300 km^2 in Kenya's Tsavo Park (Newton 1979). Other eagle species typically breed at densities of one pair per 30-190 km^2, while smaller hawks breed at densities between 1-8 km^2 and the smallest raptors, falcons and kites, commonly breed at densities of one pair per 1-3 km^2 (Newton 1979). This trend is believed to be exhibited because larger raptors tend to feed on larger prey than smaller raptors. Since larger prey occupy larger home ranges and live at lower densities than smaller prey, raptors that feed on them are required to defend larger territories.

Many studies have also shown that spatial variation in breeding density is often explained by spatial variation in prey availability. For example, spatial variation in densities of European sparrowhawks (*Accipiter nisus*), Peregrine falcons (*Falco peregrinus*), and common buzzards (*Buteo buteo*) in Britain have all been

positively correlated with spatial variation in prey biomass (Newton 1979). Similarly, black eagle (*Ictinaetus malayensis*) densities in Rhodesia were found to correlate with abundance of hyraxes (*Procavia capensis*), and unusually high black kite and Egyptian vulture densities in Delhi were attributed to the inordinate amount of garbage and animal carcasses within the city (Newton 1979). Also, European kestrel, Tengmalm's owl, short-eared owl, and long-eared owl densities have been shown to reflect prey densities in Finland, and red-tailed hawk, northern harrier, and American kestrel densities have been correlated with prey abundance in Kansas (Norrdahl and Korpimaki 1996, Williams et al. 2000). Ospreys have been noted to occur at higher densities in areas characterized by shallow coastal areas that are more accessible to prey (Newton 1976). This is clearly exemplified by the uniquely large size of the population in Chesapeake Bay, which encompasses a vast area of shallow coastline.

Studies have shown that temporal variations in raptor population sizes are often correlated with prey availability. Scarcity of rabbits, for example, has been recently implicated in the disappearance of Bonelli's eagles (*Hieraaetus fasciatus*) in many of the most threatened areas of its range (e.g., northern Spain) (Ontiveros et al. 2005). The hen harrier (*Circus cyaneus*) population on the Orkney Islands of Scotland has also been in decline during recent years due to a reduction in the number of breeding adults (Amar et al. 2003). The number of non-breeding adults has apparently increased because many males have been unable to adequately provide females with a food supply necessary to initiate production of a clutch (Amar et al.

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2003). Additional studies have shown that breeding density, clutch size, and fledging success in other hen harrier populations are positively correlated with the vole cycle as well (Hamerstrom 1979, Redpath et al. 2002).   Finally, Montagu's harrier (*Circus pygargus*), Gyr falcon (*Falco rusticolus*), Aplomado falcon (*Falco femoralis*), and Imperial eagle (*Aquila heliaca*) populations have also all been shown to respond numerically to fluctuations in prey abundance (Salamolard et al. 2000, Macias-Duarte 2004, Katzner 2005, Nystrom 2005).

The contribution of food availability to osprey breeding population regulation, however, is currently unknown. Food supply has been believed to play a much smaller role than nesting substrate in influencing population dynamics, as it has been generally assumed to far surpass demand in previous osprey population studies (Meyburg and Chancellor 2002, Poole et al. 2002). There are indications, though, that food availability may play a more important role in osprey population regulation than has been previously thought. For example, as mentioned above, a downward population trend in Florida Bay between 1973 and 1980 was attributed to a reduced food supply, though this was not conclusively determined (Kushlan and Bass 1983). In the 1980s, the number of ospreys at Martha's Vineyard nearly doubled every four years, but then stabilized and even declined in the 1990s despite the presence of empty nesting platforms (Poole et al. 2002). Also, in recent years, there has been a nearly 50% reduction in the number of active osprey nests on Gardiner's Island in New York, perhaps one of the largest colonies in the Northeast (Franklin 2001). Productivity has dropped to 0.5 fledgling per active nest, reminiscent of the DDT

effects (Franklin 2001). Though no intensive research has been conducted to address this concern, a decline in the local Atlantic menhaden population (*Brevoortia tyrannus*) has been implicated as the cause for the decline (Poole in Franklin 2001, P. Spitzer in Poole et al. 2002). The Atlantic menhaden has a high lipid content relative to other fish species, and has historically been shown to be a preferred choice of prey for ospreys throughout the mid-Atlantic and northeastern United States (Spitzer and Poole 1980, Poole 1989a, Steidl et al. 1991, McLean and Byrd 1991).

As shown by some of the predator and prey interactions for other raptors described above, factors that affect the distribution and availability of fish throughout the Bay could significantly influence osprey foraging behavior and ultimately reproductive success. Given all of the above, we hypothesized that the spatial variation in the population growth rate of ospreys along the salinity gradient in Chesapeake Bay reflects, in large part, differences in reproductive success mediated through provisioning rate. Specifically, our null hypothesis was that ospreys along a salinity gradient exhibit no significant differences in provisioning rate or subsequent reproductive success.

Methods

To address this hypothesis, a two-fold objective was implemented. Both reproductive success and provisioning rate were assessed along a salinity gradient. Locations of study sites for the 2006 and 2007 breeding seasons were chosen by referencing the Chesapeake Bay Program analytical segmentation scheme, which

delineates salinity zones within the Bay (DAWG 1997). The four salinity zones defined by this scheme, in order of decreasing salinity, are the following: polyhaline (>18 ppt), mesohaline (5-18 ppt), oligohaline (0.5-5 ppt), and tidal fresh (<0.5 ppt). We restricted research efforts to the more extreme ends of the salinity spectrum, and ultimately the correlative population growth rate spectrum. This allowed us to more efficiently achieve our objective of characterizing osprey reproductive success and provisioning rate spatially within the Bay.

A total of 12 study sites were divided between the upper and lower ends of the gradient (Figure 2.1). The seven sites identified within the polyhaline zone included the Ware River, North River, mouth of the York River, Poquoson River, Back River, mouth of the James River, and Lynnhaven River. In the upper estuarine reaches, the two sites identified within the tidal fresh zone included the Chickahominy River and Hopewell on the James River, and the three sites identified within the oligohaline zone included Jamestown Island on the James River, West Point on the York River, and Tappahannock on the Rappahannock River.

Since the vast majority of osprey nests in the Bay are either over open water or immediately adjacent to the shoreline, work was conducted via piloting a small boat. Therefore, the site selection was based, in part, on the availability of boat ramps and was not completely randomized. For the purposes of this study, tidal fresh and oligohaline sites were categorized as "upper estuarine," and polyhaline sites were categorized as "lower estuarine."

All sites were thoroughly surveyed in late April and early May of 2006 and 2007 to map occupied nests. A Global Positioning System (GPS) unit was utilized to accurately record locations. Nests were considered "active" only if they had ospreys on or immediately near them or if they exhibited signs of recent breeding activity such as egg laying or nest building. Since adults begin arriving at nests in early March and peak laying occurs in April, all occupied nests for the breeding season were likely identified (Reese 1977). It is conceivable the number of breeding pairs was over estimated since researchers have documented that in some populations approximately 5-10 percent of pairs associated with nests are nonbreeders (Henny and VanVelzen 1972, Henny et al. 1974). Though, virtually all of the pairs observed at active nests in this study exhibited clear signs of breeding activity.

The reproductive parameters assessed in this study are all known to be potentially reflective of local food availability in avian populations (Newton 1980). Where feasible, clutch sizes were documented concurrently with nest mapping activities. Most of the nests were on channel markers, duck blinds, or platforms and nest contents could therefore be observed either directly or via a mirror pole. Clutch sizes for many of the tree nests, though, could not be documented. The number of fledglings produced per active nest was later assessed by visiting all of the previously documented nests near the end of the breeding season, specifically during the first half of July. Unlike in the initial clutch survey, most of the tree nests could be included because nearly fledged nestlings were readily observed from a distance. If the number of active nests was potentially overestimated as described above, then the

number of fledglings produced per occupied nest may be slightly underestimated. Though, a similar rate of error would be expected across all sites and would therefore not bias analyses.

More labor intensive reproductive data were collected from fewer nests. These parameters included laying date, number of hatchlings, nestling growth rate, and extent of brood reduction. In 2006, this sample pool was limited to 5-10 nests per site, and not all of the sites were included in the sampling regime. Regular visits to the Lynnhaven and Back Rivers were not logistically feasible, and most of the nests on the North River were not directly accessible because they were on open water platforms with no ladders. The nests that were sampled within each site were randomly selected from a pool of sequentially numbered nests that had been identified as workable. In 2007, the sampling regime was altered to obtain a more complete data set. Excluding the Lynnhaven and Back Rivers, all nests with clutches that could be feasibly observed were regularly visited early in the season to record the dates of first hatched eggs and the numbers of hatchlings. This enabled a more highly representative estimate of hatching success and ultimately brood reduction to be made. Additionally, nestlings were measured at only the Chickahominy River, Hopewell on the James River, North River, and Ware River. These two upper estuarine and two lower estuarine sites respectively highlighted sites with high and low productivity in 2006. The reduction in geographic scope was deemed critical to more feasibly elucidate the causes for differences in productivity. Also, to encourage nesting at more humanly accessible locations along the Chickahominy, Ware, and

North Rivers in 2007, artificial platforms were erected in appropriate areas early in the season. Approximately two of these were utilized by breeding ospreys at each of the three sites. It is possible that, instead of encouraging a shift in utilized nesting substrate within these sites, we encouraged immigration to these sites. This may have increased population size and possibly reduced provisioning rates. However, given the small number of ospreys that used these structures relative to the total number of ospreys within the sites, the potential effects of such manipulation would have been negligible.

Evaluating the reproductive parameters was generally straightforward with the exception of hatching success. Occasionally, the number of eggs that successfully hatched was not readily identifiable because the initial brood size was smaller than the clutch size, despite the absence of unhatched eggs. In these cases, eggs were considered to have hatched and nestlings to have died due to subsequent brood reduction. This was considered a reasonable assumption for several reasons. Addled eggs appear to remain in nests throughout most of the duration of the breeding season and often throughout its entirety (pers. observ.). Likewise, failed hatchings caused by exposure to contaminants such as DDT are typically apparent because they result in broken eggshell fragments that remain in the nest long for long periods of time (Reese 1975, Wiemeyer et al. 1975, Reese 1977). On the contrary, fragments of successfully hatched eggs are promptly removed from the nest (pers. observ.). Depredation of hatchlings is also not believed to be a very plausible explanation for the smaller than expected initial brood sizes occasionally noted because the nests are over open water

and are therefore only vulnerable to attacks from avian predators such as bald eagles (*Haleaetus leucocephalus*) and great horned owls (*Bubo virginianus*), which are rare but occasionally documented (Poole 1989a, Spitzer 1989, Flemming and Bancroft 1990, Liston 1997). Also, depredation by such predators would likely involve older nestlings and result in whole brood losses unlike in these instances. Finally, and perhaps most convincingly, nestlings that die by fratricide are often removed from nests (Steidl and Griffin 1991).

Laying date was back-calculated from the hatching date of the oldest nestlings using the average incubation period of 39 days for New England ospreys (Poole 1989a). When nest visits did not coincide with actual hatching events, nestling ages were estimated. Previous research has shown that the osprey culmen grows linearly, and is therefore a good predictor of age (Poole 1982, Steeger et al. 1992, Schaadt and Bird 1993, Poole et al. 2002). Therefore, the following culmen length – age regression was calculated using nestlings with known hatch dates to estimate nestling ages: age = (1.536*culmen length(mm))-14.5; $r^2 = 0.906$. Culmen length was defined as the length from the tip of the upper mandible to the proximal end of the cere.

After nestlings hatched, body mass and lengths of culmen, tarsus, wing chord, and tail were measured during visits using Pesola spring scales, dial calipers, and a ruler. To distinguish nestlings from one another, they were uniquely marked with fingernail polish on their talons after hatching and were later banded with standard USFWS aluminum bands at approximately four weeks of age. When applicable, measurements were taken from the same side of the body to avoid potential biases

caused by asymmetries. These data were collected in repeated measures on a weekly basis to the maximum extent practicable. Since osprey nestlings require approximately seven weeks to develop into fledglings, this temporal resolution was deemed adequate to accurately project growth curves (Steeger 1992).

Nestling growth curves were projected using nonlinear regression analyses. The data and associated ages were fit to logistic curves, which have been shown to best describe osprey nestling growth (Steidl and Griffin 1991, Schaadt and Bird 1993). The logistic equation may be expressed as the following: $x(t) = a/[1+(1/x_0-1)e^{-Kt}]$, where $x(t)$ is the value of the growth parameter at time t, x_0 = the value of the growth parameter at time 0, and *K* is the growth rate constant. To generate a more robust curve for body mass, perhaps the growth parameter to be most likely impacted by food availability, the published average osprey hatching weight of 50.3 g was used for all nestlings (Steidl and Griffin 1991). This was justified because hatching weight varies remarkably little from this value while asymptotic range is relatively great (Poole et al. 2002). The best fit curves were then used to calculate *K*, asymptotic weight, and the time lapse between 10-90% of asymptotic weight ($t_{10} - t_{90}$). The estimated asymptotic weights were ultimately used to sex the osprey nestlings since distinct ranges have been well defined for this sexually dimorphic species (MacNamara 1977). In cases where a projected asymptote did not fall within either of the two ranges, the respective nestling was considered to belong to the sex of the nearest range.

In large raptors such as ospreys, crop mass can be relatively great and thus account for a substantial portion of the individual's total weight (Schaadt and Bird 1993). Therefore, depending upon the fullness of the crop at the time of measurement, a nestling's mass can vary greatly leading to inaccurate estimations of growth parameters if not considered. To ensure that the most accurate growth curves were projected, crop mass was subtracted from each mass measurement. Crop volume was calculated at each visit by utilizing the following formula for the volume of a spherical cap: $V = (\pi/6)(3r+h)h$, where V = volume, r = radius, and h = height. A standard fish meat density was then applied to each calculated volume to ultimately determine crop mass. The standard fish meat density was estimated using samples of locally caught gizzard shad (*Dorosoma cepedianum*). Both large and small specimens were incorporated into the analysis to generate the most representative density, which was calculated to be 0.8396 g/cm^3 (standard deviation [SD] = 0.0423 g/cm^3, n = 10).

The second objective implemented in this study was an analysis of provisioning rate. This included an assessment of the taxonomy, length, mass, energy content, and delivery rate of each provisioned prey item. Micro-video monitoring was the primary technique employed to collect provisioning data. The camera unit consisted of a portable Digital Video Recorder (DVR) connected to a 10 cm color bullet camera, both of which were powered by a 12V deep-cycle marine battery. Digital data were stored on a 2 gigabite (GB) Scan Disk memory card. The bullet camera was secured approximately 1 m from the nest to obtain the highest

resolution image of provisioning behavior. Following the installation of the camera unit, the nest was observed closely to ensure that the female returned and resumed normal behavior, which occurred in all cases.

In 2006, unforeseen circumstances and logistical difficulties precluded a balanced sampling regime from being implemented. Only eight of the study sites were utilized. The three lower estuarine sites included the Ware River and the mouths of the James and York Rivers, and the five upper estuarine sites included Jamestown Island on the James River, West Point on the York River, Tappahannock on the Rappahannock River, the Chickahominy River, and Hopewell on the James River. Limited equipment availability precluded the installment of more than one camera at each site at any given time. In 2007, the geographic scope was reduced to ensure a more balanced data set. As with the collection of the nestling morphometric data described above, the collection of provisioning data was limited to the Chickahominy River, Hopewell on the James River, North River, and Ware River. Unlike during 2006, the reduced spatial coverage allowed two cameras to be simultaneously installed at each of the four sites utilized.

Nests were randomly selected for monitoring to the maximum extent practicable, but choices were usually restricted because some of the nesting substrate could not adequately support the camera unit. Another factor that influenced nest selection was brood size. Only nests with broods of two or three nestlings were sampled to minimize potentially confounding variables associated with different provisioning rates for different brood sizes. Studies have shown that while significant

differences in provisioning rates exist between one and three chick broods, none exist between two and three chick broods (Stinson 1978, Jamieson et al. 1983, Green and Ydenburg 1994). The age of nestlings was an additional factor that was considered. Osprey nestlings typically enter the steepest phase of their growth curve at approximately two and one-half weeks of age. That this age marks the beginning of a period of extremely high energy demand is supported by the concurrence of brood reduction at this age more than any other (Hagan 1986). As might be expected, studies have shown that provisioning rates reflect the logistic growth curve early in nestling development, but rates plateau soon after nestlings reach approximately two weeks of age (Green and Ydenburg 1994). Therefore, micro-video monitoring was restricted to nests with first-hatched nestlings that were at least 14 days old.

Some studies have indicated that ospreys conduct foraging during all daylight hours, but may preferentially feed during certain periods of the day such as dawn (MacCarter 1972, Stinson 1978, Van Daele and Van Daele 1982). To avoid biases that could potentially result from sampling during a shorter time period, filming was completed continuously between 05:30 and 21:00 hours. However, occasional heavy accumulation of condensation on the camera lenses was later noted during some of the footage review which precluded all of the data from being analyzed.

In 2006, a cumulative total of 442 hours of footage were recorded in the upper estuarine sites and a total of 194 hours were recorded in the lower estuarine sites. Two nests per site were surveyed for approximately 41 hours each, averaging 106 hours per site. In 2007, a total of 485 hours of footage were recorded in the upper

estuarine sites while 667 hours were recorded in the lower estuarine sites. Three to

five nests per site were surveyed for approximately 82 hours each, averaging 288

hours per site.

Analysis of provisioning rates, however, necessitated a sub-sampling of the

data set since only prey items delivered within known time intervals could be used.

The first prey item delivered after initiation of each video recording, for example, was

eliminated from this sample pool because the amount of time that had transpired

during its capture was not known. Also, since all nests were not surveyed equally,

provisioning rate analyses included only those nests that approached asymptote for

diet breadth. The asymptotic number of species consumed at each nest was

determined by fitting each distribution to the following negative exponential function:

accumulated no. species = b0*(1-exp(-b1*accumulated no. observations)), where b0

= asymptote (Miller and Wiegert 1989). None of the nests sampled at the mouth of

the York River in 2006 approached this value, and were therefore eliminated from the

sample pool. In 2006, a total of 434 hours were subsampled, with an average of 54

hours per site and 39 hours per nest. In 2007, a total of 983 hours were subsampled,

with an average of 245 hours per site and 70 hours per nest.

Prey items observed during review of the video footage were usually

identified to species. However, due to the lack of strong morphological distinctions

between some species, compounded by a poor angle of view and/or a low video

image resolution, most of the catfish and some of the shad were identified only to

genus or family. Fish lengths were estimated to the nearest cm using multiples of

either the adult's bill or claw length. Since the adults were not handled, average adult

bill (male mean ± SD = 32.5 ± 12 mm, n = 49; female mean ± SD = 34.6 ± 13 mm, n

= 47) and claw (male mean ± SD = 28.9 ± 10 mm, n = 49; female mean ± SD = 30.5

± 12 mm, n = 47) lengths identified in published literature were used (Prevost 1983).

In cases where the whole fish could not be seen, total fish length was extrapolated

using published morphometric data including standard length, fork length, pre-anal

length, pre-dorsal length, pre-pectoral length, and pre-pelvic length (Crozier and

Hecht 1913, Lagler and Van Meter 1951, Muncy 1959, Muncy 1960, Mansueti 1961,

June and Nicholson 1964, Carlander 1969, St. Pierre and Davis 1972, Wilk et al.

1978, Bykov 1983, Chavance et al. 1984, Crawford 1993, Claro and Garcia-Arteaga

1994, Frimodt 1995, Madenjian et al. 2003). Fish mass was then estimated using

total length by referencing published length-weight conversion equations (Appendix

2.1) (Crozier and Hecht 1913, Lagler and Van Meter 1951, Muncy 1959, Muncy

1960, Mansueti 1961, June and Nicholson 1964, Carlander 1969, St. Pierre and Davis

1972, Wilk et al. 1978, Bykov 1983, Chavance et al. 1984, Crawford 1993, Claro and

Garcia-Arteaga 1994, Frimodt 1995, Madenjian et al. 2003). Finally, since energy

content per unit mass varies among species, the total kilocalories delivered per prey

item were calculated using published energy density data (Appendix 2.2) (Watt and

Merrill 1975, Frimodt 1995). In the few cases where length-weight conversion

equations or energy density data were unavailable for identified species, values were

calculated by using representative species that were closely related. Mass and energy

content for prey items that were identified only to family or genus were calculated in

a similar manner by averaging the published values of closely related species. Consistent with previous osprey diet studies, all fish delivered to nests were considered to be entirely edible and therefore wholly consumed (e.g., Stinson 1977, Poole 1982, Van Daele and Van Daele 1982, McLean and Byrd 1991, Steeger et al. 1992). Catfish (Ictaluridae) greater than 31 cm in total length were an exception and assumed to be only 90% consumable (Dykstra 1995, Markham 2004).

A variety of statistical tests were utilized to analyze the data. A linear mixed-effects model was the primary test implemented since all nest samples within each salinity zone were not independent from one another. Instead, they were clustered within sites which were often separated by long distances and characterized by somewhat unique environmental conditions. Mixed models account for the effects of such spatial clustering by incorporating random-effects terms (Fox 2002). When comparing parameters that had one value per nest among salinity treatments, salinity was designated as a fixed variable, and both site and year were designated as random variables, and sites were nested within years. Parameters evaluated as such included laying date, clutch size, hatching success, brood reduction, number of chicks fledged, and provisioning rate. Comparisons of nestling growth rates were similarly conducted, but sex was specified as an additional fixed variable ranked above salinity, and nest was treated as a random variable within site. Descriptive statistics were used for more basic data summarization and analysis.

Results

A total of 458 occupied osprey nests were mapped during the 2006 and 2007 breeding seasons (Appendix 2.3-2.13). The Chickahominy River (n = 75), West Point on the York River (N = 32), Hopewell on the James River (N = 60), Jamestown Island on the James River (N = 39), and Tappahannock on the Rappahannock River included 245 nests within the upper estuarine sites. The Ware River (N = 25), Back River (n = 43), Lynnhaven River (N = 21), mouth of the James River (N = 15), mouth of the York River (N = 27), North River (N = 43), and Poquoson River (N = 39) included 213 nests within the lower estuarine sites.

Laying dates were characterized numerically relative to the first lay date (March 21=0). In 2006, mean laying date $\pm$ SD was 18.5 $\pm$ 11.6 days for the upper estuarine sites (N = 41) and was 24.2 $\pm$ 15.3 days for the lower estuarine sites (N = 29). In 2007, mean laying date $\pm$ SD was 15.3 $\pm$ 13.3 days for the upper estuarine sites (N = 31) and was 26.9 $\pm$ 4.4 days for the lower estuarine sites (N = 25) (Table 2.1, Figure 2.2). Differences between salinity zones were significant (lme model, $F_{(1, 15)}$ = 12.691, p = 0.003).

In 2006, mean clutch size $\pm$ SD was 2.8 $\pm$ 0.1 eggs for the upper estuarine sites (N = 132) and 2.7 $\pm$ 0.2 eggs for the lower estuarine sites (N = 158). In 2007, mean clutch size $\pm$ SD was 2.5 $\pm$ 0.1 eggs for the upper estuarine sites (N = 125) and was 2.6 $\pm$ 0.2 eggs for the lower estuarine sites (N = 158) (Table 2.1, Figure 2.3). Differences between salinity zones were not significant (lme model, $F_{(1, 22)}$ = 0.028, p = 0.869).

In 2006, 118 (89%) of the eggs (N = 132) in the upper estuarine nests (n = 46) successfully hatched, and 82 (91%) of the eggs (N = 90) in the lower estuarine nests (N = 30) successfully hatched. In 2007, 234 (87%) of the eggs (N = 270) in the upper estuarine nests (N = 102) successfully hatched, and 299 (95%) of the eggs (N = 315) in the lower estuarine nests (N = 127) successfully hatched. The mean number of hatchlings ± SD per nest was 2.6 ± 0.2 hatchlings in the upper estuarine sites and was 2.8 ± 0.2 hatchlings in the lower estuarine sites during 2006. In 2007, the mean number of hatchlings ± SD per nest was 2.3 ± 0.1 hatchlings in the upper estuarine sites and was 2.4 ± 0.3 hatchlings in the lower estuarine sites (Table 2.1, Figure 2.4). No significant differences were noted between salinity zones (lme model, $F_{(1, 18)}$ = 0.809, p = 0.381).

In 2006, 82 (82%) of the hatchlings (N = 100) in upper estuarine nests (N = 37) successfully fledged, and 57 (63%) of the hatchlings (N = 90) in lower estuarine nests (N = 34) successfully fledged. In 2007, 138 (53%) of the hatchlings (N = 206) in upper estuarine nests (N = 89) successfully fledged, and 131 (47%) of the hatchlings (N = 279) in lower estuarine nests (N = 119) successfully fledged. The mean number of nestlings that did not fledge ± SD per nest was 0.5 ± 0.1 nestlings in the upper estuarine sites and was 1.1 ± 0.7 nestlings in the lower estuarine sites during 2006. In 2007, the mean number of nestlings that did not fledge ± SD per nest was 0.8 ± 0.3 nestlings in the upper estuarine sites and was 1.4 ± 0.3 nestlings in the lower estuarine sites (Table 2.1, Figure 2.5). Significant differences in the number of

nestlings that did not fledge, presumably due to brood reduction, existed between salinity zones (lme model, $F_{(1, 17)} = 10.168$, p = 0.006).

In 2006, the mean number of fledglings produced per active nest ± SD was 1.8 ± 0.1 fledglings for the upper estuarine nests (N = 120) and was 1.2 ± 0.4 fledglings for the lower estuarine nests (N = 168). In 2007, the mean ± SD was 1.6 ± 0.3 fledglings for the upper estuarine nests (N = 97) and was 1.1 ± 0.3 fledglings for the lower estuarine nests (N = 160) (Table 2.1, Figure 2.6). Differences in productivity between salinity zones were highly significant (lme model, $F_{(1, 22)} = 16.658$, p < 0.001).

A Kolmogorov-Smirnov test revealed significant differences in the growth rate of body mass between sexes (D = 0.000, p < 0.001), with a mean male growth rate constant K ± SD of 0.17 ± 0.03 (N = 81) and a mean female K ± SD of 0.15 ± 0.03 (N = 84). Differences between salinity zones were just short of significant (lme model, $F_{(1, 24)} = 3.905$, p = 0.076). In 2006, mean male K ± SD was 0.17 ± 0.01 (N = 16) and 0.19 ± 0.01 (n = 18) in the lower and upper estuarine sites, respectively. Mean female K ± SD was 0.14 ± 0.02 (N = 17) and 0.16 ± 0.01 (N = 24) in the lower and upper estuarine sites, respectively. In 2007, mean male K ± SD was 0.17 ± 0.01 (N = 10) and 0.17 ± <0.01 (N = 13) in the lower and upper estuarine sites, respectively. Mean female K ± SD was 0.16 ± 0.01 (N = 5) and 0.16 ± 0.01 (N = 13) in the lower and upper estuarine sites, respectively (Table 2.2, Figure 2.7).

A Kolmogorov-Smirnov test also revealed significant differences in body mass t_{10}-t_{90} between sexes (D = 0.238, p < 0 .025). The mean male t_{10}-t_{90} ± SD was

26.6 ± 5.5 days and the mean female t_{10}-t_{90} ± SD was 27.9 ± 4.0 days. Significant differences between salinity zones, however, were not detected (lme model, $F_{(1, 24)}$ = 0.022, p = 0.885). In 2006, mean male t_{10}-t_{90} ± SD was 28.3 ± 4.7 days and 28.5 ± 2.5 days in the lower and upper estuarine sites, respectively. Mean female t_{10}-t_{90} ± SD was 27.9 ± 0.05 days and 27.7 ± 1.6 days in the lower and upper estuarine sites, respectively. In 2007, mean male t_{10}-t_{90} ± SD was 24.0 ± 2.7 days and 25.5 ± 0.5 days in the lower and upper estuarine sites, respectively. Mean female t_{10}-t_{90} ± SD was 25.8 ± 3.2 days and 27.5 ± 1.1 days in the lower and upper estuarine sites, respectively (Table 2.2).

Unlike the previous two parameters, differences in asymptotic body mass between salinity zones were found to be significant (lme model, $F_{(1, 24)}$ = 5.755, p = 0.037). In 2006, the mean asymptotic mass ± SD was 1457.7 ± 67.2 grams and 1468.3 ± 59.6 grams for males in the lower and upper estuarine sites, respectively. The mean asymptotic mass ± SD for females was 1728.0 ± 30.8 grams and 1790.0 ± 44.0 grams for the lower and upper estuarine sites, respectively. In 2007, the mean asymptotic mass ± SD was 1301.1 ± 12.2 grams and 1399.4 ± 56.2 grams for males in the lower and upper estuarine sites, respectively. The mean asymptotic mass ± SD for females was 1607.8 ± 31.7 grams and 1724.1 ± 78.0 grams for the lower and upper estuarine sites, respectively (Table 2.2, Figure 2.8).

A Kolmogorov-Smirnov test revealed that no significant differences in tarsus K existed between sexes (D = 0.148, p > 0.10). Mean male K ± SD was 0.14 ± 0.03, and mean female K ± SD was 0.14 ± 0.03. Similarly, no differences were found

between salinity zones (lme model, $F_{(1, 24)} < 0.001$, p = 0.984). In 2006, the mean K ± SD was 0.14 ± 0.05 and 0.14 ± 0.04 in the lower and upper estuarine sites, respectively. In 2007, the mean K ± SD was 0.14 ± 0.01 and 0.14 ± 0.02 in the lower and upper estuarine sites, respectively (Table 2.2, Figure 2.9).

A Kolmogorov-Smirnov test revealed no significant differences between sexes in asymptotic length of tarsus either (D = 0.138, p > 0.10). Mean male asymptote ± SD was 65.7 ± 5.2 mm, and mean female asymptote was 65.6 ± 4.7 mm. Again, no differences were found between salinity zones (lme model, $F_{(1, 24)} = 2.1629$, p = 0.1721). In 2006, the mean asymptote ± SD was 62.4 ± 3.0 mm and 64.3 ± 5.7 mm in the lower estuarine and upper estuarine sites, respectively. In 2007, the mean asymptote ± SD was 67.9 ± 2.8 mm and 69.5 ± 2.7 mm in the lower estuarine and upper estuarine sites, respectively (Table 2.2, Figure 2.10).

A Kolmogorov-Smirnov test revealed that no significant differences in wing chord K existed between sexes (D = 0.028, p > 0.10). Mean male wing chord K ± SD was 0.12 ± 0.02, and mean female wing chord K ± SD was 0.12 ± 0.02. Similarly, no differences were found between salinity zones (lme model, $F_{(1, 24)} = 2.236$, p = 0.139). In 2006, the mean K ± SD was 0.13 ± 0.01 and 0.13 ± 0.01 in the lower and upper estuarine sites, respectively. In 2007, the mean K ± SD was 0.11 ± <0.01 and 0.12 ± <0.01 in the lower and upper estuarine sites, respectively (Table 2.2, Figure 2.11).

A Kolmogorov-Smirnov test revealed no significant differences between sexes in asymptotic length of wing chord either (D = 0.206, p <0.10). Mean male

asymptote $\pm$ SD was 397.2 $\pm$ 53.9 mm, and mean female asymptote was 383.3 $\pm$ 32.5 mm. Again, no differences were found between salinity zones (lme model, $F_{(1, 24)}$ = 0.975, p = 0.326). In 2006, the mean asymptote $\pm$ SD was 370.6 $\pm$ 14.4 mm and 379.2 $\pm$ 36.9 mm in the lower estuarine and upper estuarine sites, respectively. In 2007, the mean asymptote $\pm$ SD was 403.0 $\pm$ 8.1 mm and 400.5 $\pm$ 6.7 mm in the lower estuarine and upper estuarine sites, respectively (Table 2.2, Figure 2.12).

The sex ratios of fledglings within the study sites were determined and subsequently analyzed with Chi-Square tests. The results indicate that observed sex ratios did not differ from those expected within either lower or upper estuarine sites during the 2006 and 2007 breeding seasons (Table 2.3). Nestlings that did not survive late enough into development to allow projection of asymptotes could not be sexed, and were thus excluded from these analyses. To assess how brood reduction may have potentially affected fledgling sex ratios, we combined all broods that underwent reduction and conducted an additional Chi-Square test. The observed sex ratio was not significantly different from that which was expected (Table 2.4).

During the 2006 and 2007 osprey breeding seasons, a total of 1,415.1 hours of provisioning behavior were recorded via micro-video monitoring. The upper and lower estuarine treatments were represented by 748.2 hours and 667 hours, respectively. We positively identified a total of 529 prey items, and their respective delivery times, during review of this footage. The upper and lower estuarine treatments were represented by 351 and 178 prey items, respectively. While ospreys

have been anecdotally observed preying on non-fish species (Poole 2002), all prey identified in our study were fish.

The provisioning rates of prey items were measured in units of biomass, energy, and number of individuals. To eliminate potentially confounding factors associated with different brood sizes, per capita provisioning rates were calculated. However, to better understand how provisioning rates influenced brood reduction and nestling growth rates, per capita values were calculated using both the total number of nestlings (Table 2.5) and the number of fledglings (Table 2.6) per nest. Per capita values for the total number of nestlings for all parameters varied greatly between upper and lower estuarine sites. Differences in provisioning rates of biomass were highly significant between salinity zones (lme model, $F_{(1, 9)} = 19.906$, p = 0.002). The mean biomass delivery rate $\pm$ SD was 14.8 $\pm$ 5.5 g/hr and 30.1 $\pm$ 7.9 g/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 15.8 $\pm$ 6.0 g/hr and 61.8 $\pm$ 12.1 g/hr, respectively (Figure 2.13). Differences in provisioning rates of energy were likewise highly significant between salinity zones (lme model, $F_{(1, 9)} = 25.949$, p < 0.001). The mean energy delivery rate $\pm$ SD was 20.5 $\pm$ 4.2 kcals/hr and 44.0 $\pm$ 14.8 kcals/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 21.9 $\pm$ 8.6 kcals/hr and 92.0 $\pm$ 10.2 kcals/hr, respectively (Figure 2.14). The differences in provisioning rates of individual prey items were significant between salinity zones (lme model, $F_{(1, 9)} = 10.384$, p = 0.012). The mean delivery rate of individuals $\pm$ SD was 0.08 $\pm$ 0.01

prey/hr and 0.16 ± 0.09 prey/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 0.10 ± 0.04 prey/hr and 0.23 ± 0.06 prey/hr, respectively (Figure 2.15).

Fledgling per capita values for all parameters also varied greatly between upper and lower estuarine sites. Differences in provisioning rates of biomass were highly significant between salinity zones (lme model, $F_{(1, 9)} = 14.634$, p = 0.005). The mean biomass delivery rate $\pm$ SD was 22.2 ± 8.2 g/hr and 37.6 ± 14.4 g/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 24.2 ± 2.2 g/hr and 69.4 ± 14.3 g/hr, respectively (Figure 2.16). Differences in provisioning rates of energy were likewise highly significant between salinity zones (lme model, $F_{(1, 9)} = 14.821$, p = 0.005). The mean energy delivery rate $\pm$ SD was 30.7 ± 6.3 kcals/hr and 56.2 ± 27.9 kcals/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 34.0 ± 0.7 kcals/hr and 101.0 ± 6.5 kcals/hr, respectively (Figure 2.17). The differences in provisioning rates of individual prey items approached significance between salinity zones (lme model, $F_{(1, 9)} = 4.305$, p = 0.072). The mean delivery rate of individuals $\pm$ SD was 0.12 ± 0.01 prey/hr and 0.17 ± 0.06 prey/hr in the lower and upper estuarine sites, respectively, during 2006. In 2007, the mean $\pm$ SD for the lower and upper estuarine sites were 0.16 ± 0.1 prey/hr and 0.26 ± 0.06 prey/hr, respectively (Figure 2.18).

Further analyses revealed differences just short of significance between salinity zones in both biomass per prey item (lme model, $F_{(1, 9)} = 5.104$, p = 0.054)

and energy content per prey item (lme model, $F_{(1, 9)} = 5.001$, $p = 0.056$). In 2006, average biomass of consumed fish was 188.2 ± 45.7 g and 245.3 ± 97.0 g in the lower and upper estuarine sites respectively. Average biomass of consumed fish in 2007 was 156.5 ± 22.4 g and 263.9 ± 15.9 g in the lower and upper estuarine sites, respectively (Figure 2.19). In 2006, average energy content of consumed fish was 263.5 ± 19.6 kclas and 373.3 ± 178.2 kcals in the lower and upper estuarine sites respectively. Average biomass of consumed fish in 2007 was 218.9 ± 19.2 kcals and 395.1 ± 77.5 kclas in the lower and upper estuarine sites, respectively (Figure 2.20).

Discussion

We found highly significant differences in productivity between the upper and lower estuarine sites. Combining years, the upper and lower estuarine sites produced an average of 1.70 and 1.15 fledglings, respectively, per active nest. Provided that these values are not temporally atypical, such disparity would be reflected by commensurable population growth in the respective regions. Osprey population growth is primarily determined by local mortality and reproductive rates since ospreys exhibit both high natal and annual site fidelity (Henny and Wight 1969, Spitzer et al. 1983).

Numerous studies have focused on osprey breeding rates within the Bay. While some date back to as early as 1936, when Tyrell's data indicated productivity to be 1.60 young per active nest at Smith Point, Virginia, most were conducted in response to concerns regarding the negative effects of DDT. Widespread use of this

pesticide reduced the average number of fledglings produced per active nest in the Chesapeake Bay population to 0.46 on the Potomac River in 1965 (Schmidt 1977), 0.69 within the southern portion in 1971 (Kennedy 1977), 1.08 within the northeast portion in the early 1970s (Reese 1977), and 1.17 within the southwest portion and 0.86 along the Eastern Shore in 1975 (Stinson and Byrd 1976). Following population recovery, however, little attention has been focused on the productivity of the Chesapeake Bay population.

With the exception of Kennedy who summarized breeding rates for the Chickahominy River in 1971, our study marks the first known attempt to document breeding rates specifically in the upper estuarine areas of the Bay. These areas were virtually uninhabited by ospreys during the DDT era, as ospreys were predominantly concentrated along the Bay proper (Henny et al. 1974). While Kennedy determined that 0.5 young were produced per active nest on the Chickahominy River, we found that productivity had increased to 1.85 young per active nest. Such high productivity was characteristic of all the upper estuarine sites we surveyed, which produced 1.50-2.0 fledglings per active nest during both seasons. West Point on the York River was the sole exception in 2007 when it produced only 1.06 young per active nest. Cause(s) for this anomaly are unknown. These values are among the highest known to have ever been reported for ospreys. Rates we documented in the lower estuarine sites, however, were substantially lower at only 1.15 young per active nest compared to 0.69 (Kennedy 1977) and 1.17 (Stinson and Byrd 1976) documented in the same locale during the DDT era. Considerable spatial variation was also noted in this

salinity zone as the productivity ranged 0.60-1.56 fledglings per active nest during both years. Surprisingly, the lower end of this range is comparable with the historically low rates caused by the DDT contamination. Whether this portion of the population is stable is an obvious question.

While raptor studies have substantiated the correlation between the number of young successfully fledged and the number of individuals recruited in the following years (Newton 1979, Postupalsky 1989), the specific breeding rate required to maintain osprey population stability has understandably been a subject of much interest. Henny and Wight (1969) used band recoveries in the eastern U.S. to estimate mortality rates, and determined that an annual breeding rate of 0.95-1.30 young produced per active nest was required to maintain population stability. The many variables that can influence band recoveries warrants caution with the use of this estimate, though. Spitzer et al. (1983) used a more straightforward approach by simultaneously documenting productivity and population size during a 12 year study between New York City and Boston. They estimated that a minimal breeding rate of 0.8 young per active nest was needed to prevent population decline. However, since the minimal breeding rate is strongly influenced by factors such as age at first breeding, it is population specific. For example, the breeding rate needed for stability of the Chesapeake Bay population, where ospreys don't start breeding until approximately 5.7 years of age, is calculated to be 1.15 young per active nest (Poole 1989a). Some of the post-DDT data collected in the Bay, however, suggest that the minimum required breeding rate may be less than this (Byrd unpubl. Data, Watts

pers. comm.). If the published estimate is accurate, our data indicate that the osprey population along the Bay proper is stable, but has ceased to grow. The spatial variation in breeding rates we noted within this region, though, do suggest that both population growth and decline are occurring on a more localized scale within the lower estuarine areas. The upper estuarine sites, on the contrary, appear to be collectively growing quite rapidly. These deductions concur with the results of the 1995 and 1996 Bay wide breeding survey.

The clear differences in reproductive success between the upper and lower estuarine sites could potentially be explained by a number of factors. Laying date, clutch size, hatching success, and brood reduction can either individually or interactively influence the number of fledglings produced at a given nest. For instance, laying date can directly influence reproductive success because ospreys that breed earlier typically produce both more and longer-lived young (Poole 1984 and Poole 1989). Late breeding attempts are often characterized by both lower hatching success and brood survival due to nest abandonment by adults (Poole 1989). Interestingly, ospreys in the lower estuarine sites laid eggs an average of 8.5 days later than their upper estuarine counterparts. This delay may have been sufficient to impact reproductive success to some extent, but it was likely not enough to completely account for the substantial disparity in productivity between salinity zones (Poole 1989). Several hypotheses have been proposed to explain the reduced breeding effort by late breeders, but none have been conclusive. Perhaps an equally legitimate concern is the cause for breeding late. Research in other raptor species has

shown that the date of egg laying can be indicative of food availability. Eurasian kestrels (*Falco tinnunculus*), for example, have been found to lay later in years when adults experienced poor nutritional condition than in years when adults had optimal energy levels (Korpimaki and Wiehn 1998). That limited food availability may have caused the delayed breeding in the lower estuarine sites is therefore at least plausible.

Clutch size has been shown to reflect nutritional condition in many avian species (Newton 1998). It has also been related to food availability in ospreys, but results have been conflicting. Postupalsky (1989) noted smaller clutches in freshwater populations than saltwater populations, and attributed it to respective differences in available food resources. However, Poole (1984) argued that since the ratio of egg mass to adult female mass is very small in ospreys relative to smaller species, less energy is required to produce eggs, and clutch size may not be an adaptive trait that strongly reflects environmental conditions (Poole 1984). Clutches we identified in our study were comparable in size to those identified by others in the region (Wiemeyer 1971, Kennedy 1977, Reese 1977), and we observed no significant differences in clutch sizes between salinity zones.

Hatching success in ospreys has received a substantial amount of attention because the reduced reproductive success caused by DDT was largely mediated through this parameter (Ames and Mersereau 1964, Wiemeyer 1971, Wiemeyer et al. 1975). DDT is responsible for nearly all of the documented instances of reduced reproductive success caused by organochlorines, but it has been banned since 1972 (Wiemeyer et al. 1988). However, polychlorinated biphenyls (PCBs), heptachlor,

dioxins, dieldrin, chlorodanes, lead, and mercury include other contaminants that have been found in osprey eggs in recent years (Wiemeyer et al. 1988, Elliott et al. 2000). A recent study in Delaware Bay, revealed that concentrations of p,p'-DDE, heptachlor epoxide, chlordane and metabolites, and total PCBs were predictors of hatching success (Toschik et al. 2005). Logistic regression analyses in a recent study within Chesapeake Bay, though, yielded different results, finding no relationship between concentrations of these contaminants and osprey hatching success (Rattner et al. 2004). This apparent discrepancy may have been due to the excessively high contaminant concentrations in Delaware Bay (Toschik et al. 2005), which is generally considered to be one of the most highly polluted aquatic systems in the northeastern United States. Regardless, we documented a high rate of hatching success in both the upper (88%) and lower (93%) estuarine sites with no significant differences between salinity zones.

The reproductive parameter that appeared to be most responsible for the spatial disparity in reproductive success was brood reduction. Differences in the extent of brood reduction were highly significant, with approximately 45% of the nestlings dying in the lower estuarine sites and only 33% dying in the upper estuarine sites. Given that the extent and intensity of brood reduction is generally considered to be a function of food availability (Poole 1979, Poole 1982, Jamieson et al. 1983, Eriksson 1986, Hagan 1986, Forbes 1991), these data suggest that ospreys in the lower estuarine sites are experiencing a much greater degree of food stress than those in the upper estuarine sites.

Just as brood size can be adjusted to meet prevailing environmental conditions, thus maximizing reproductive success, nestling growth rates can be adjusted to environmental conditions to increase probability of survival. Developmental plasticity of growth processes allows normal maturation to occur under a suite of dynamic environmental variables such as food availability (Starck and Ricklefs 1998). By slowing growth rate when food is limited, for example, nestlings can better ensure that morphological traits fully develop without permanent abnormalities (Starck and Ricklefs 1998).

Osprey nestling growth has been characterized in several studies. Steidl and Griffin (1991) calculated K to be 0.17 for body mass increase, and they found no significant correlation between growth rate and brood size. Schaadt and Bird (1993) reported a similar growth rate constant of 0.18, and they found no significant differences between sexes. Their study is the only known attempt to account for potential differences between sexes. Our significant differences between sexes for body mass K, however, indicate that sexually dimorphic growth rates can occur. Males and females had an average K of 0.17 and 0.15, respectively. We found no sexual dimorphism in wing chord and tarsus growth rates, though, which were comparable to those calculated by Steidl and Griffin. The discrepancy between the studies is hard to explain. The methodology used to sex the ospreys was the same, but the sample sizes did differ. Steidl and Griffin sampled 20 males and 12 females, and we sampled 81 males and 84 females. Perhaps variance precluded detection of sexual dimorphism in the smaller sample pool. Additionally, Steidl and Griffin only

sampled a total of 26 individuals older than 32 days of age and seven individuals older than 48 days. All of our nestlings were measured past 45 days of age, as those that did not survive to fledging were eliminated from the sample pool. Thus, their asymptotic estimates may have been less accurate, which can lead to subsequent inaccuracies in estimation of growth rates (Ricklefs et al. 1986). Another potential factor that may have resulted in the differences is the temporal resolution utilized. They aimed for two day resolution while we aimed for weekly resolution. Our accuracy in projecting growth curves did not appear to be compromised, however, because our curve fitting was very successful ($R = >0.99$). An intriguing thought is that the differences may be explained by the geographic locations of the two studies. Their research was conducted in Nova Scotia and ours was conducted in southern Chesapeake Bay. Whether latitudinal variation in osprey nestling growth rates may exist is unknown, but other reproductive parameters such as laying date and clutch size have exhibited latitudinal trends (Poole 1989). While a discussion of the significance of sexually dimorphic growth rates in ospreys is outside the scope of our study, our data indicate that sexually dimorphic growth rates do occur in some populations, and we encourage a revisiting of this topic.

More pointedly, differences just short of significance in body mass K existed between salinity zones. Both males and females averaged higher growth rates in the upper estuarine sites than the lower estuarine sites. This was driven by the 2006 breeding season, though, as virtually no difference was noted in the 2007 breeding season. Surprisingly, this pattern was not reflected by *t10-t90*, which is considered to

be an inverse of *K* (Ricklefs 1968). Asymptotic mass, however, was found to differ significantly between salinity zones, with both sexes fledging at a larger mass in the upper estuarine sites. While this pattern was noted during both seasons, the disparity between salinity zones was far greater during the 2007 season. This may account for the lack of difference in *K* during this year. Rather than minimize growth rate when resources are limited, an individual may maintain growth rate and instead reduce asymptotic mass. Adopting this strategy is likely less desirable and indicative of more intense food stress because mass at fledging can have a direct bearing on an individual's probability of surviving to breeding age. For numerous species, intraspecific variation in fledgling mass has been shown to positively correlate with survival and subsequent recruitment into the breeding population (Both et al. 1999, Green and Cockburn 2001, Monros et al. 2002). Even a slight reduction in fledging mass may have catastrophic consequences for ospreys, which have a greater than 50% chance of dying before their first breeding attempt (Poole 1989a).

The remaining growth parameters for tarsus and wing chord exhibited no significant differences between salinity zones. Some studies have shown that the development of more important structures may be hierarchically protected from the negative effects of lower energy reserves (Starcks and Ricklefs 1998). The tarsus and wing are central to two of the most important activities engaged in by ospreys, hunting and flight, and may indeed be protected in this way.

McLean and Byrd (1991) calculated body mass growth rates for nestlings in Mobjack Bay in 1985 and compared them to Stinson's 1975 data from the same

locale in an effort to assess how apparent food stress might have been influencing growth of the young. The growth rates calculated in 1985 ($K = 0.13$) and 1975 ($K = 0.12$), are among the slowest ever reported for ospreys (Schaadt and Bird 1993), and are actually slower than all falconiform species summarized by Ricklefs (1968) except the golden eagle (*Aquila chrysaetos*). While comparing our growth parameters to those of McLean and Byrd would be highly desirable, such a comparison is not valid because, unlike them, we distinguished between sexes and accounted for crop mass. Given that fledging mass is distinctly sexually dimorphic and crop contents can account for a large percentage of overall body mass, excluding these variables may lead to inaccurately projected growth curves.

Like increased brood reduction and reduced growth rates, manipulation of sex ratios has been thought to serve as a potential mechanism whereby adults can adjust reproductive effort to limited food availability. In sexually dimorphic species, the larger sex is assumed to be more costly to produce than the smaller one (Fiala and Congdon 1983, Slavsgold et al. 1986). Thus, more of the smaller sex, usually the male, might be produced when conditions are unfavorable and vice versa. Studies have documented such correlative shifts in sex ratio in the red-winged blackbird (*Agetaius phoeniceus*) (Fiala 1981), common grackle (*Quiscalus quiscula*) (Howe 1977), Seychelles warbler (*Acrocephalus seychellensis*) (Komdeur et al. 2002), American kestrel (*Falco sparverius*) (Wiebe and Bortolotti 1992), and golden eagle (Edwards et al. 1988). While biases may occur hormonally during egg laying in some species, they may occur through nestling mortality in others. Despite the prevalence

of sexual dimorphism in birds, though, documented deviances from unity in sex ratio are surprisingly rare (Clutton-Brock 1986, Breitwisch 1989). We found that osprey fledgling sex ratios did not differ significantly from 1:1 in either the upper or lower estuarine sites. If brood reduction was resulting in a male bias, we might have expected a deviance specifically in broods that were reduced. However, analysis of this sub-sample did not reveal a bias either. Arguably, our sample size may have been too small to detect potential differences in sex ratios (Bortolotti 1989).

The differences in reproductive success and growth parameters between salinity zones discussed above suggest the existence of a spatial correlation with provisioning behavior. Indeed, our data indicated that upper and lower estuarine sites exhibited highly significant differences in provisioning rate for all parameters measured. On average, ospreys in upper estuarine sites provisioned at more than twice the rate of ospreys in lower estuarine sites. While this spatial disparity occurred during both years, it was substantially greater during the 2007 breeding season. Given the reduced geographic scope in 2007, this may be a function of localized variation within salinity zones. Interestingly, the disparity between salinity zones in per capita provisioning rates was only slightly less when calculated using the number of nestlings that fledged than when using the total number of nestlings. Clearly, and coincidentally, little brood reduction occurred in the nests that were filmed. This might lead one to conclude that ospreys in the upper estuarine sites were provisioning at a much higher rate than was necessary to successfully raise their young. Such inefficient use of energy, though, rebuts well established reproductive and foraging

theories (Stephens and Krebs 1986). Instead, it appears that modification of growth parameters such as body mass K and asymptote may perhaps be dominant mechanisms to brood reduction in adjusting reproductive effort to resource availability. The existence of such a hierarchy in ospreys has not been previously proposed, and may warrant further examination as it would provide valuable insight into the reproductive strategy of ospreys with respect to trade offs like quality and number of young. Attempting to correlate provisioning rates with specific growth parameters, however, was outside the scope of our study given the much larger sample size of provisioning data likely required to conduct such a test as well as the interactive nature of the growth parameters.

Comparing our study with those conducted in Mobjack Bay in 1975 and 1985 yielded interesting findings. The delivery rate per nest dropped 33% from 0.527 fish/hr in 1975 to 0.351 fish/hr in 1985 (McLean and Byrd 1991). Our delivery rate dropped an additional 27% to 0.258 fish/hr. The average biomass of prey items has also fluctuated over time. The 1975, 1985, and 2007 studies reported mean biomasses of 237.1, 156.9, and 172.3 g, respectively. These values indicate that the average daily provisioning rate of biomass has dropped from 1936.8 g in 1975 to 853.6 g in 1985 to 687.9 g in 2007. This represents a startling total decrease of nearly 65%. But caution should be used when comparing provisioning parameters since estimation of osprey prey length is known to vary among individual observers (Cars and Godfrey 1996), and videography provides more accurate results than direct observation (Lewis et al. 2004). Nonetheless, these data suggest that provisioning

rates along the Bay proper have substantially decreased during the past 30 years. On the contrary, provisioning rates in the upper estuarine sites, which averaged 1,689.2 g/day per nest in 2007, were comparable to those calculated by Stinson in 1975 in Mobjack Bay.

Reasons for the observed temporal and spatial differences in provisioning rates are unknown. The two most probable causes are either increased interference or a depleted prey base in the higher salinity zone. If in large enough numbers, conspecifics might interfere with one another's ability to efficiently capture prey. For example, search time might be increased if more than one osprey routinely targeted the same prey item. Also, while ospreys do not defend foraging grounds, they do defend nest sites (Poole et al. 2002). Thus, they could potentially become preoccupied with defending their nests at the expense of provisioning. Preliminary analyses, however, did not indicate that nearest neighbor distances between nests were significantly shorter in the lower estuarine sites than in the upper estuarine sites. Furthermore, some have indicated that dense nesting may actually lead to higher provisioning rates via transfer of foraging information among individuals (Ward and Zahavi 1973, Greene 1987). Interference can also occur interspecifically, though. For instance, bald eagles (*Haliaeetus leucocephalus*) are known to engage in piracy and steal captured prey from ospreys (Bent 1937, Ogden 1975). However, no such occurrences were documented during our study. But as ospreys and bald eagle populations both continue to expand in the Bay, competition for resources is certain to escalate.

Perhaps the more plausible explanation for the reduced provisioning rates we observed in the lower estuarine sites is a depleted prey base. Atlantic menhaden (*Brevoortia tyrannus*) have historically been shown to be a choice prey item for ospreys breeding throughout the coastal waters of the mid-Atlantic and northeastern United States (Spitzer and Poole 1980, Poole 1989, McLean and Byrd 1991, Steidl et al. 1991). Both the high energy content and schooling behavior of Atlantic menhaden contribute to this preference. This species accounted for nearly 75% of the diet composition of breeding ospreys in lower Chesapeake Bay in 1985 (McLean and Byrd 1991). Surprisingly, recent research (Chapter 1) indicates that Atlantic menhaden now comprise only 32% of the osprey diet in the same locale.

Given that the osprey diet has been shown to reflect local prey availability (Greene et al. 1983, Edwards 1988), the reduced proportion of Atlantic menhaden recently documented in the diet of Chesapeake Bay ospreys may indicate that this species is currently less available than it has been historically. Interestingly, many researchers have become increasingly concerned that Atlantic menhaden are suffering from over-harvesting by humans (e.g., Powell 1994, Franklin 2001, Uphoff 2003). The large quantity of fish oil contained within these fish has become the center of a massive and highly mechanized fishing industry. The annual catch of Atlantic menhaden is larger than the catch of any other species in the United States (Murdy et al. 1997). It composes approximately half of the total fishery harvest on the East Coast (Peters and Schaaf 1991). As might be expected, virtual population analyses have revealed a constant decline in Atlantic menhaden numbers. Just between 1992

and 1998, the Atlantic States Marine Fisheries Commission (ASFMC) estimated a drop in numbers along the Atlantic Coast from 10 and 15×10^9 to a historic low of 3.7×10^9 (Uphoff 2003). More localized population estimates, though, have been notoriously difficult to produce. The Chesapeake Bay has particularly received a great deal of attention because this estuary serves as the primary nursery ground for the species (Hildebrand and Schroeder 1928). Recent findings do suggest that intense localized depletion may be occurring in the Chesapeake Bay (Gottlieb 1998, Latour pers. comm.). Also, an outbreak of skin lesions on striped bass in Chesapeake Bay has been linked to a decline in the abundance of Atlantic menhaden, their preferred prey (Uphoff 2003). Diet composition analyses have revealed a steady decline in the contribution of this species to the diet of striped bass in the Bay (Uphoff 2003). The percentage of total biomass comprised of Atlantic menhaden dropped from 66% in 1992 to 43% in 1997 to 21% in 1998 (Atlantic Menhaden Advisory Committee [AMAC] 1999). Striped bass were instead increasingly relying on less nutritional invertebrates such as polychaete worms (Uphoff 2003). This likely lowered their nutritional state, and negatively impacted their immune system, rendering them more vulnerable to infections such as lesions (Uphoff 2003).

If the diet composition of ospreys is a reflection of prey availability, as indicated by other studies, then the reduced contribution of Atlantic menhaden to the diets of ospreys recently documented may be yet another sign that this species is becoming overexploited. If not replaced by prey that provide an equivalent net gain in energy, provisioning rates would be negatively impacted, perhaps much like we

observed. Again, though, we can conclude only that provisioning rates are lower in the lower estuarine sites. Explanations as to the potential cause(s) for the lower rates are purely speculative.

Nonetheless, our study provides valuable insight into osprey population dynamics by revealing a strong positive correlation between provisioning rates and population growth. Provisioning rates, growth parameter estimates, and productivity were all significantly less in the lower estuarine sites than in the upper estuarine sites, where population growth has been the slowest and fastest, respectively. This is the first known documented direct link between food availability, which we assume to be reflected by provisioning rates, and osprey population growth. While others have implied such a relationship, none have been able to draw the spatial and temporal comparisons within a single population that we did. Our study, though, was somewhat temporally restricted, and did not account for potential annual fluctuations in fish populations. Unfortunately, we could not address this because fish population estimates on a spatial scale equivalent to our own are virtually nonexistent. However, we feel that our conclusions are still highly relevant, particularly in light of the two previously published studies, the anecdotal evidence discussed, and the recent concern regarding the status of Atlantic menhaden in the Bay.

Poole et al. (2002) were correct in their suggestion that our understanding of osprey population regulation may need to be modified. Researchers in the past have considered nesting substrate availability to be the primary variable influencing population growth (Poole 1989b). Our data, however, strongly suggest that food

availability can also affect osprey breeding distribution on a broad spatial scale. We do concede that nesting substrate availability is certainly still influencing osprey distribution within the Bay, as indicated by the occupancy of relatively new platforms in sites characterized by low provisioning rates. But broad scale food availability and its subsequent impact on reproductive success is undoubtedly playing a significant role in influencing the dynamics of the Chesapeake Bay osprey population. Food availability may likewise explain the intriguing dynamics of other populations around the world that cannot seem to be explained by nesting substrate availability (Poole et al. 2002).

Obviously, the cause(s) for reduced food availability has important implications. If due to intraspecific interference, this might indicate the existence of a density dependent feedback mechanism that is mediated through foraging ecology. If due to interspecific exploitive or interference competition with bald eagles, potential negative impacts to either or both species are sure to escalate as their populations continue to expand within the Bay. While bald eagles are generally believed to displace ospreys when territories overlap strongly, some have suggested that the dominance may be reversed if ospreys greatly outnumber bald eagles (Ogden 1975). Intense competition, though, may perhaps be alleviated, or at least delayed, through resource partitioning (e.g., targeting different size distributions of prey). The co-occurrence of ospreys and bald eagles in the Bay provides a great opportunity to learn how competition for limited resources influences the foraging behavior and distributions of these respective species. If the reduction in food availability is

instead due to a decreased prey base, though, more serious consequences might be implicated. This could suggest overexploitation of fish by humans along the Bay proper. If continued, osprey breeding rates could decline sufficiently enough to jeopardize population stability, and perhaps even lead to a population collapse. The persistence of numerous other wildlife species would undoubtedly be eventually compromised as well.

Ospreys may simply be approaching the natural capacity of the Bay proper, or they, more likely, may be serving as a valuable harbinger of ecosystem health once again. At any rate, our data indicate that food availability is likely playing a pivotal role in the dynamics of the Chesapeake Bay osprey population. The myriad questions that arise from this finding should serve as an impetus to focus additional research efforts not only on this important population, but on other osprey populations around the world as well.

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Table 2.1. Values (mean ± SD) for reproductive parameters assessed for ospreys breeding within upper and lower estuarine sites during the 2006 and 2007 seasons in lower Chesapeake Bay. Laying dates were characterized numerically relative to the first lay date (March 21=0). Significant differences between treatments, as indicated by the lme model, are noted by an asterisk (*).

Reproductive Parameter	2006		2007	
	Upper	Lower	Upper	Lower
Lay Date*	18.5 ± 11.6	24.2 ± 15.3	15.3 ± 13.3	26.9 ± 4.4
Clutch Size	2.8 ± 0.1	2.7 ± 0.2	2.5 ± 0.1	2.6 ± 0.2
Hatchlings	2.6 ± 0.2	2.8 ± 0.2	2.3 ± 0.1	2.4 ± 0.3
Unfledged Nestlings*	0.5 ± 0.1	1.1 ± 0.7	0.8 ± 0.3	1.4 ± 0.3
Fledglings*	1.8 ± 0.1	1.2 ± 0.4	1.6 ± 0.3	1.1 ± 0.3

Table 2.2. Growth measurements (mean $\pm$ SD) for osprey nestlings within upper and lower estuarine sites during the 2006 and 2007 seasons in lower Chesapeake Bay. *T10-t90* units are in days. Significant differences between treatments, as indicated by the lme model, are noted by an asterisk (*). Annual values were not tested independently.

2006

Growth Parameter	Upper (m)	Lower (m)	Upper (f)	Lower (f)
Body mass growth rate (K)	0.19 ± 0.01	0.17 ± 0.01	0.16 ± 0.01	0.14 ± 0.02
Body mass growth rate (t_{10}-t_{90})	28.5 ± 2.5	28.3 ± 4.7	27.7 ± 1.6	27.9 ± 0.05
Asymptotic body mass (g)*	1468.3 ± 59.6	1457.7 ± 67.2	1790 ± 44	1728 ± 30.8
Tarsus growth rate (K)	0.14 ± 0.05	0.15 ± 0.06	0.14 ± 0.02	0.14 ± 0.01
Asymptotic tarsus length (mm)	64.1 ± 7.8	61.4 ± 3.3	63.8 ± 1.7	62.4 ± 1.2
Wing chord growth rate (K)	$0.14 \pm {<}0.01$	0.13 ± 0.01	$0.13 \pm {<}0.01$	0.12 ± 0.01
Asymptotic wing chord length (mm)	350.5 ± 23.8	362.3 ± 13.2	402.1 ± 28.5	381 ± 7.8

2007

Growth Parameter	Upper (m)	Lower (m)	Upper (f)	Lower (f)
Body mass growth rate (K)	$0.17 \pm {<}0.01$	0.17 ± 0.01	0.16 ± 0.01	0.16 ± 0.01
Body mass growth rate (t_{10}-t_{90})	25.5 ± 0.5	24.0 ± 2.7	27.5 ± 1.1	25.8 ± 3.2
Asymptotic body mass (g)*	1399.4 ± 56.2	1301.1 ± 12.2	1724.1 ± 78	1607.8 ± 31.7
Tarsus growth rate (K)	0.15 ± 0.01	0.14 ± 0.01	$0.14 \pm {<}0.01$	0.15 ± 0.01
Asymptotic tarsus length (mm)	67.9 ± 0.2	68.2 ± 2.1	71.3 ± 0.1	68.8 ± 1.9
Wing chord growth rate (K)	$0.12 \pm {<}0.01$	$0.11 \pm {<}0.01$	$0.12 \pm {<}0.01$	$0.11 \pm {<}0.01$
Asymptotic wing chord length (mm)	396.6 ± 0.6	396.7 ± 5.7	404.4 ± 8.5	409.4 ± 1.5

Table 2.3. Observed (O) and expected (E) sex ratios with associated Chi-square tests for osprey nestlings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

2006 and 2007 Breeding Seasons

Zone	Male O	Male E	Female O	Female E	N	Chi-Square	DF	p
Upper	44.0	50.5	57.0	50.5	101.0	1.6733	1	0.1958
Lower	37.0	32.0	27.0	32.0	64.0	1.5625	1	0.2113

Table 2.4. Observed (O) and expected (E) sex ratios of osprey broods that experienced brood reduction within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

2006 and 2007 Breeding Seasons

Male O	Male E	Female O	Female E	N	Chi-Square	DF	p
40.0	34.0	28.0	34.0	68.0	2.1176	1	0.1456

Table 2.5. Per capita hourly provisioning rates for osprey nestlings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Significant differences between treatments, as indicated by the lme model, are noted by an asterisk (*).

Measure of Provisioning	2006		2007	
	Upper	Lower	Upper	Lower
Biomass (g)*	30.1 ± 7.9	14.8 ± 5.5	61.8 ± 12.1	15.8 ± 6.0
Energy (kcals)*	44.0 ± 14.8	20.5 ± 4.2	92.0 ± 10.2	21.9 ± 8.6
Prey items*	0.16 ± 0.09	0.08 ± 0.01	0.23 ± 0.06	0.10 ± 0.04

Table 2.6. Per capita hourly provisioning rates for osprey nestlings that successfully fledged within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Significant differences between treatments, as indicated by the lme model, are noted by an asterisk (*).

Measure of Provisioning	2006		2007	
	Upper	Lower	Upper	Lower
Biomass (g)*	37.6 ± 14.4	22.2 ± 8.2	69.4 ± 14.3	24.2 ± 2.2
Energy (kcals)*	56.2 ± 27.9	30.7 ± 6.3	101.0 ± 6.5	34.0 ± 0.7
Prey items	0.17 ± 0.06	0.12 ± 0.01	0.26 ± 0.06	0.16 ± 0.10

Figure 2.1. Study sites utilized within southwestern Chesapeake Bay during the 2006 and 2007 field seasons.
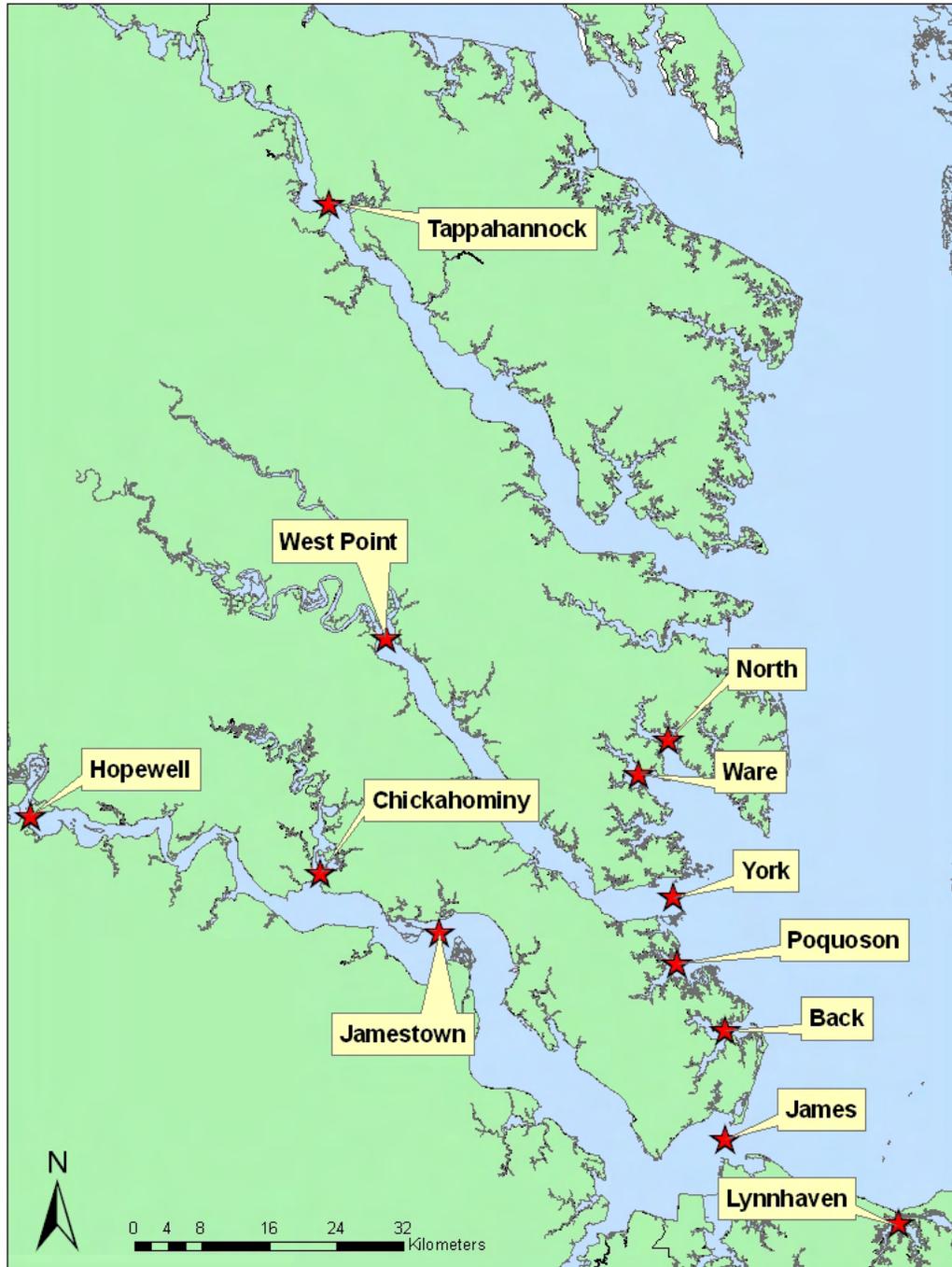
Figure 2.2. Egg laying date of female ospreys within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Laying dates were characterized numerically relative to the first lay date (March 21=0). The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 5)}$=12.691, p=0.003).

Laying Date within Upper and Lower Estuarine Sites
Day 0 = March 21
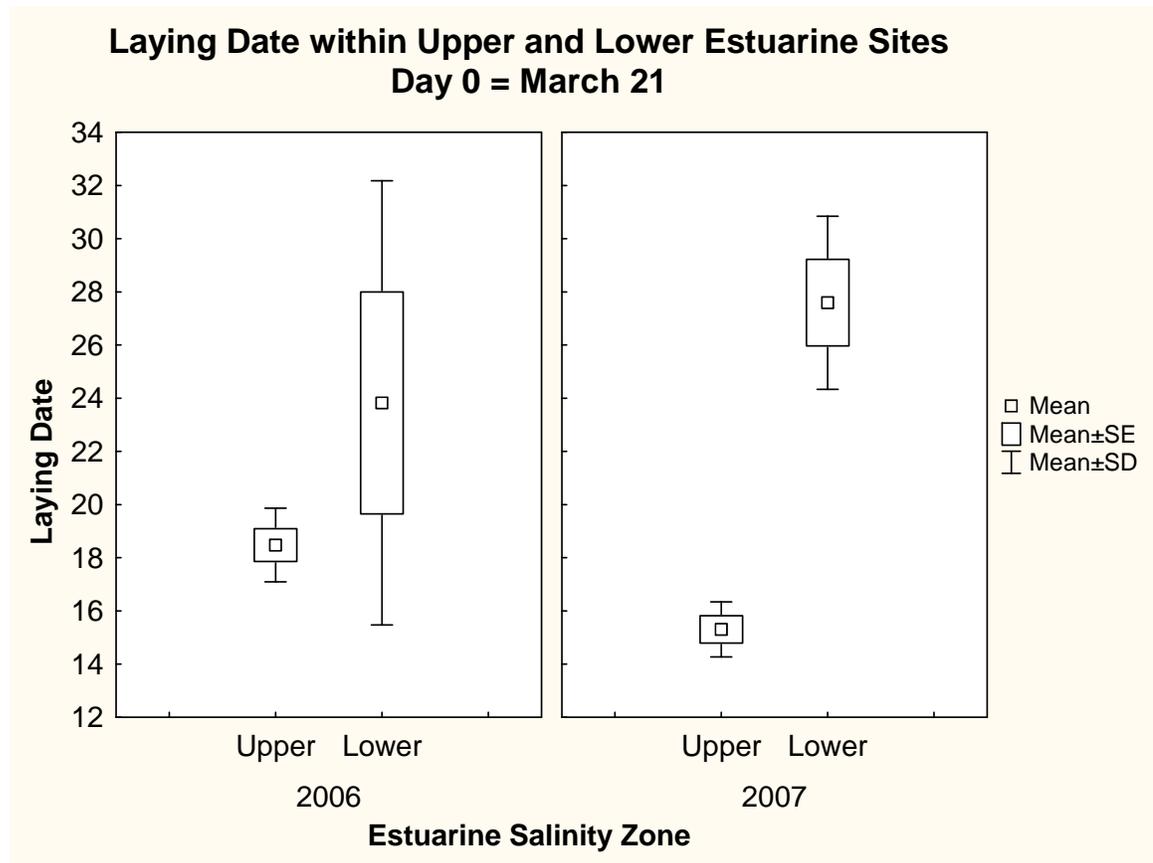
Figure 2.3. Clutch size of ospreys within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1,22)}$=0.028, p=0.869).

**Clutch Size
within Upper and Lower Estuarine Sites**
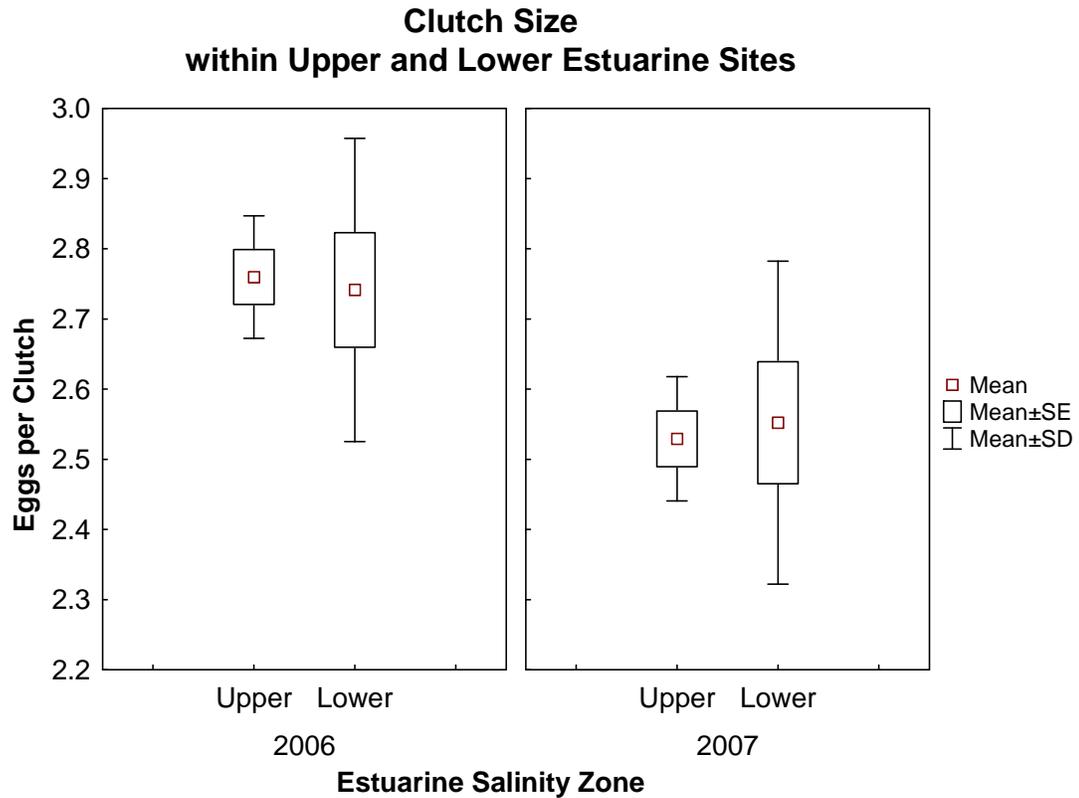
Figure 2.4. Hatching success of ospreys within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 18)}$=.809, p=0.381).
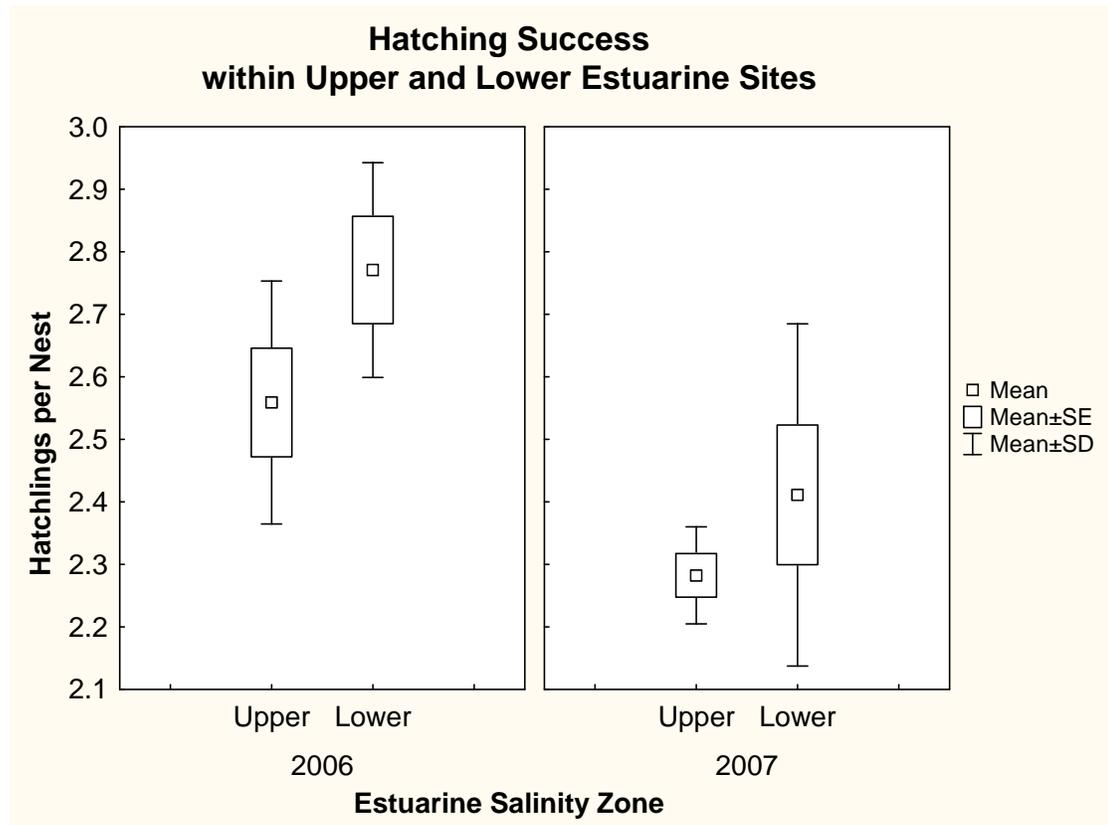
Figure 2.5. Extent of osprey brood reduction within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 17)}$=10.168, p=0.006).
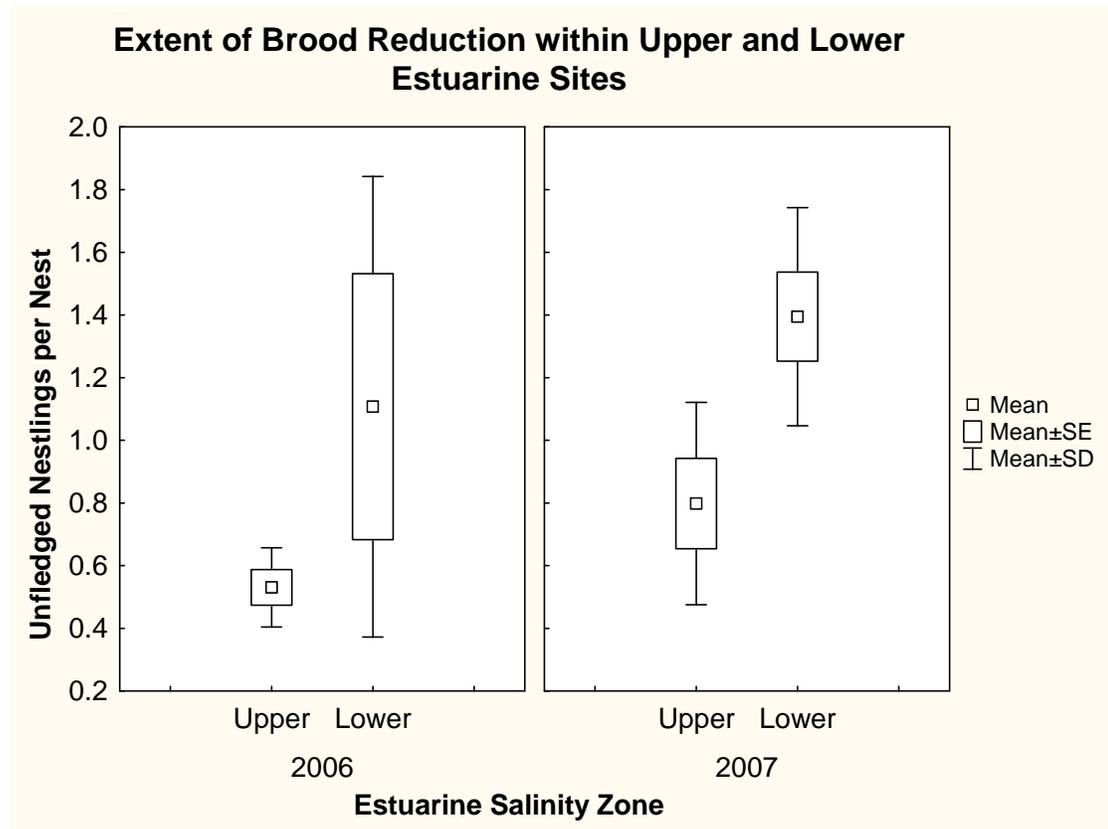
Figure 2.6. Osprey productivity within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 22)}$=16.658, p<0.001).

Fledging Success within Upper and Lower Estuarine Sites

Figure 2.7. Body mass growth rates (*K*) of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 24)}$=3.905, p=0.076).

Body Mass Growth Rates of Nestlings within Upper and Lower Estuarine Sites

Figure 2.8. Asymptotic body masses of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 24)}$=5.755, p=0.037).
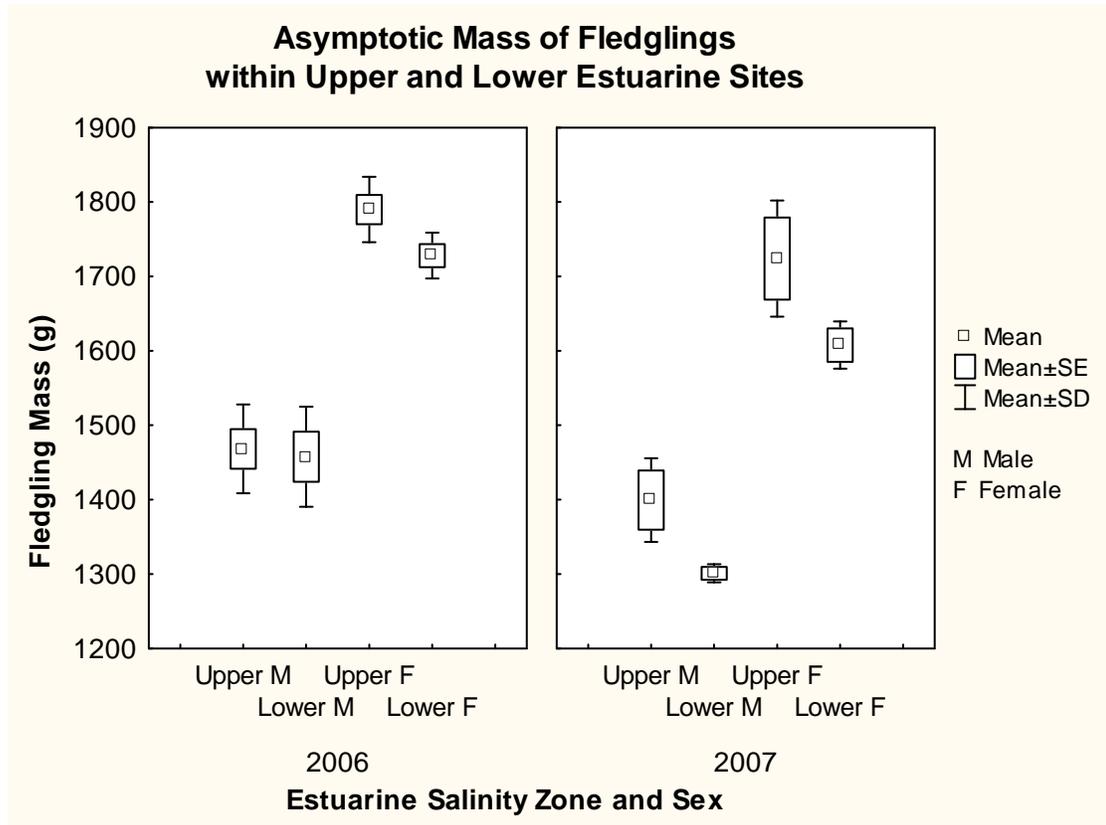
Figure 2.9. Tarsus growth rates (*K*) of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 24)}$=<0.001, p=0.984).

Growth Rates of Nestling Tarsi within Upper and Lower Estuarine Sites
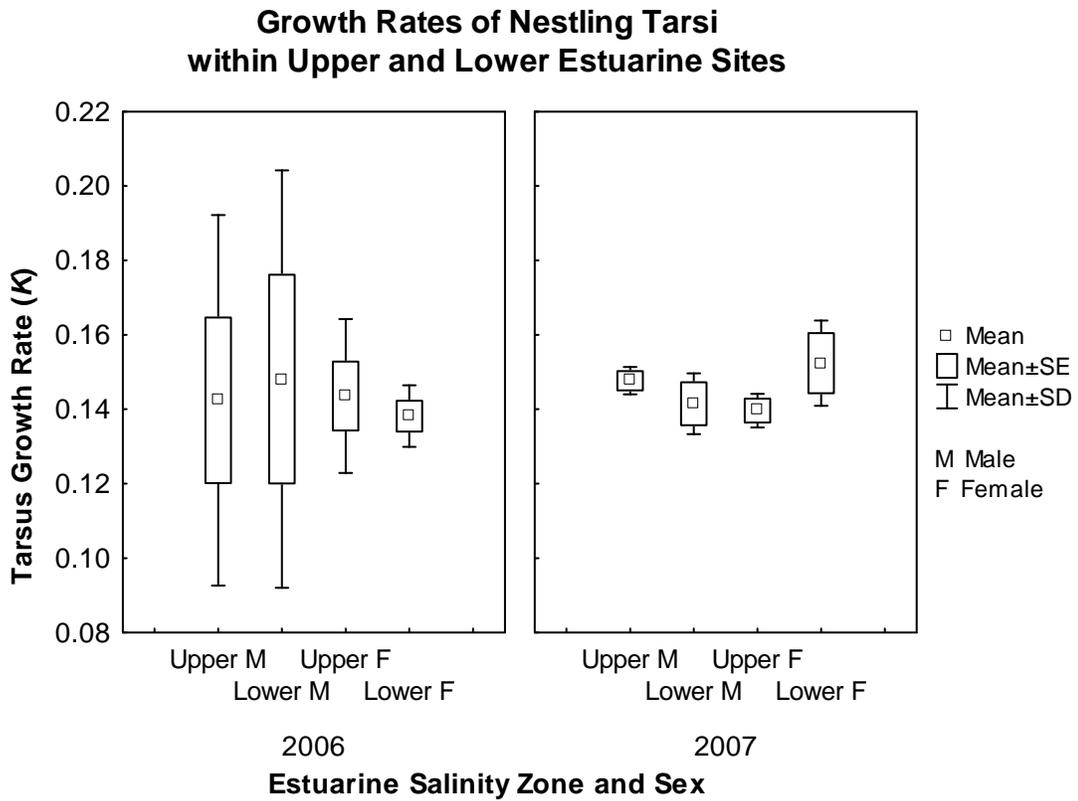
Figure 2.10. Asymptotic tarsus lengths of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 24)}$=2.163, p=0.172).
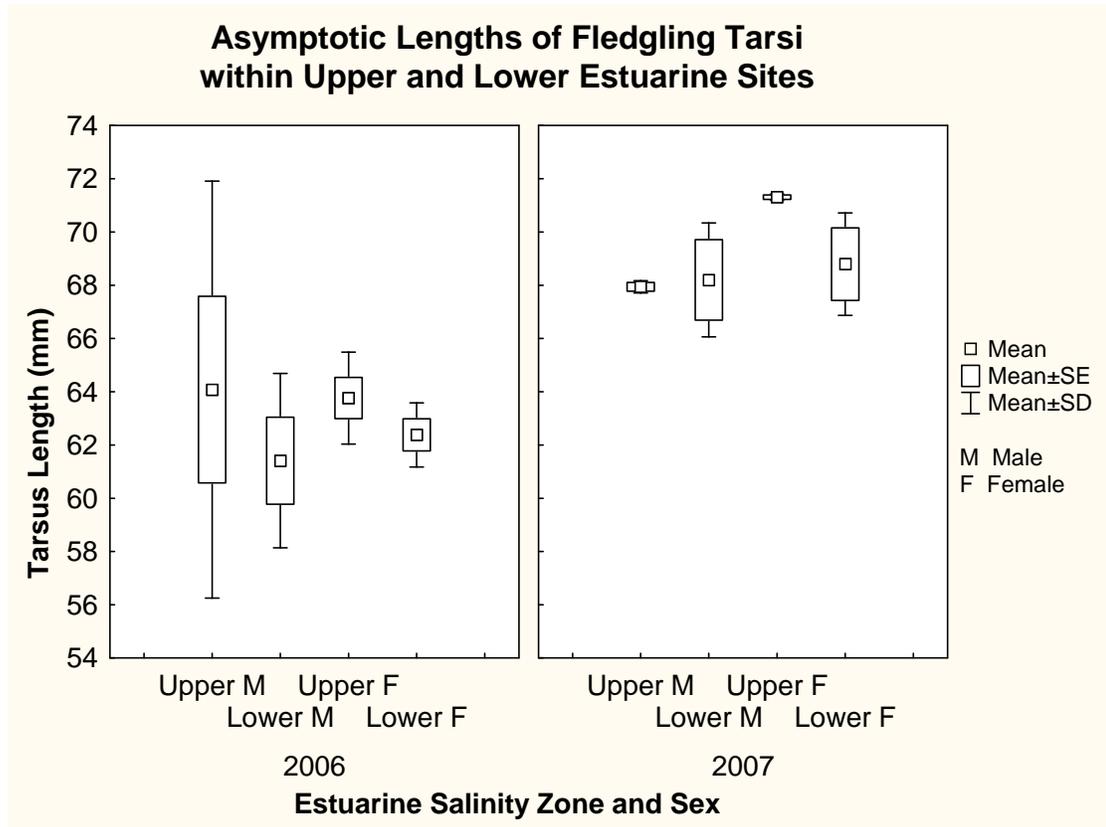
Figure 2.11. Wing chord growth rates (K) of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 24)}$=2.236, p=0.139).
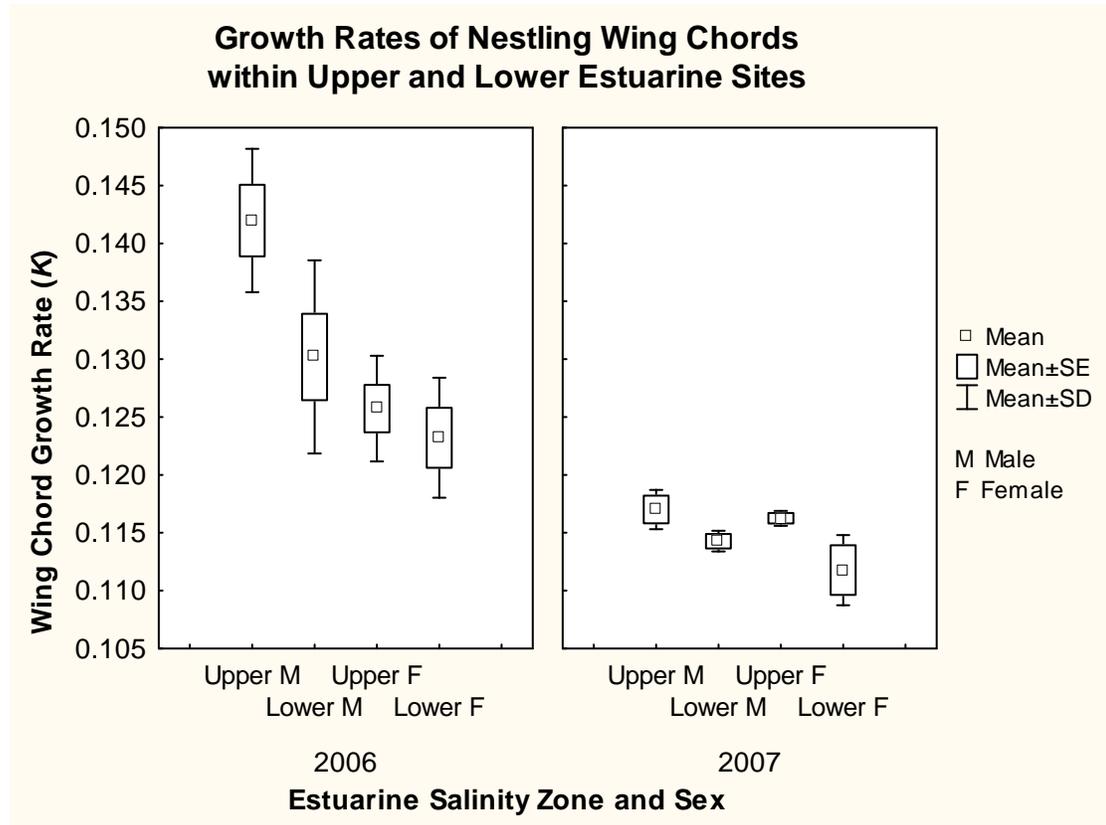
Figure 2.12. Asymptotic wing chord lengths of male and female osprey fledglings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1,24)}$=0.975, p=0.326).
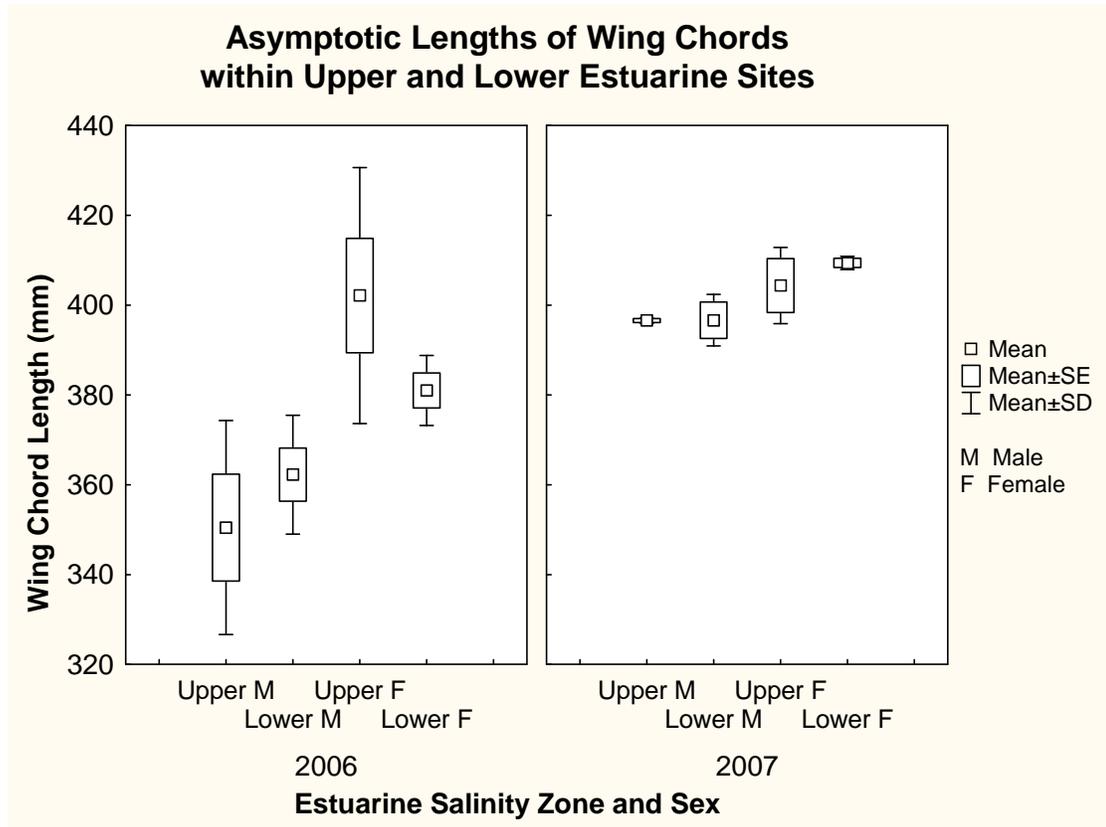
Figure 2.13.   Per capita rate of biomass provisioning for osprey nestlings that successfully hatched within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=19.906, p=0.002).

Hourly Provisioning Rate
Biomass Delivered per Nestling
within Upper and Lower Estuarine Sites
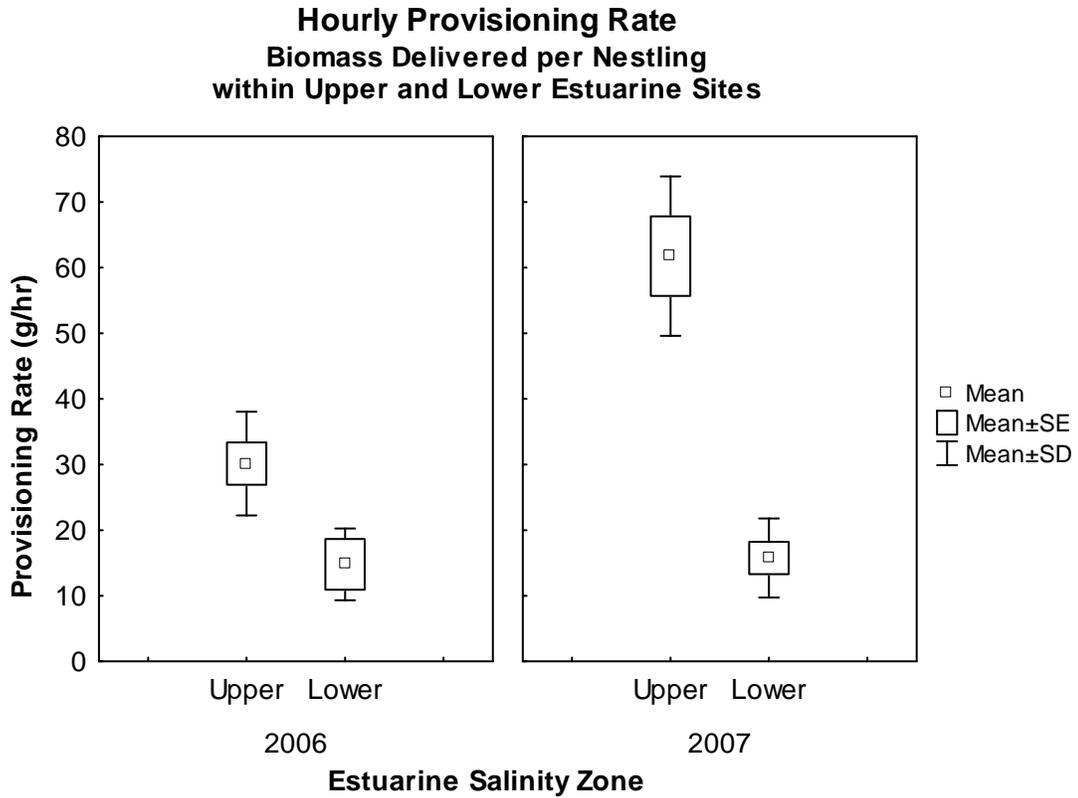
Figure 2.14. Per capita rate of energy provisioning for osprey nestlings that successfully hatched within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}=25.949$, $p<0.001$).
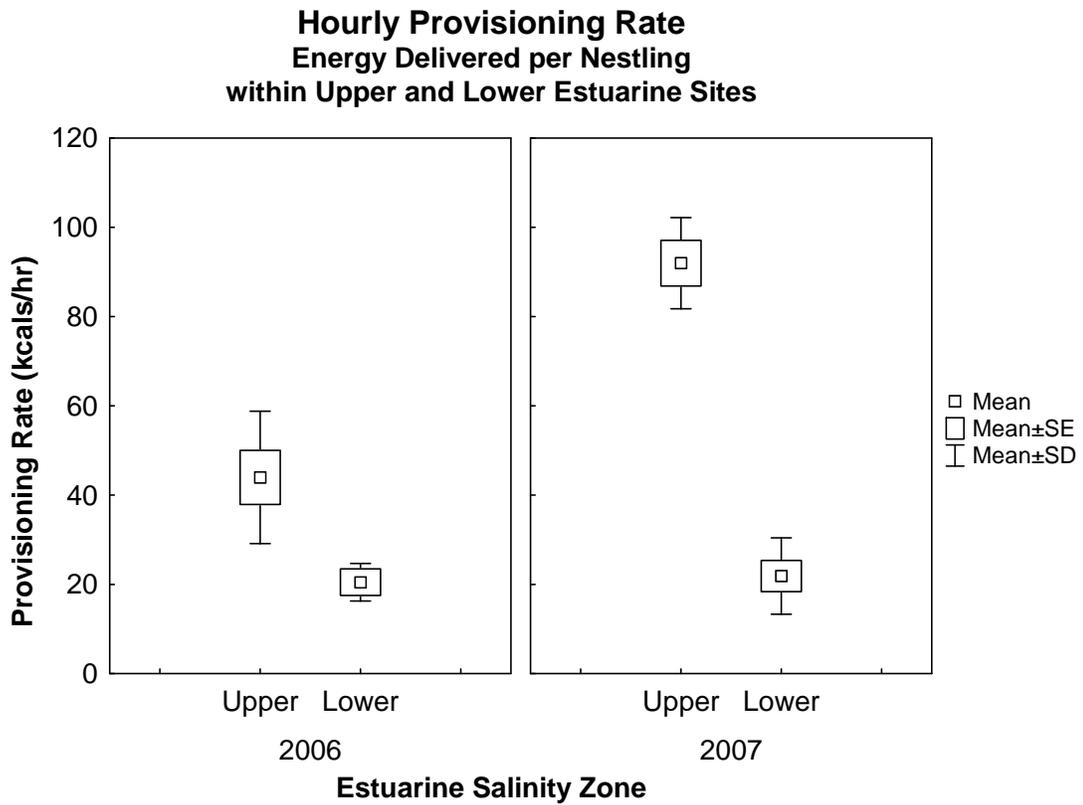
Figure 2.15.   Per capita rate of prey provisioning for osprey nestlings that successfully hatched within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=10.384, p=0.012).

Hourly Provisioning Rate
Fish Delivered per Nestling
within Upper and Lower Estuarine Sites
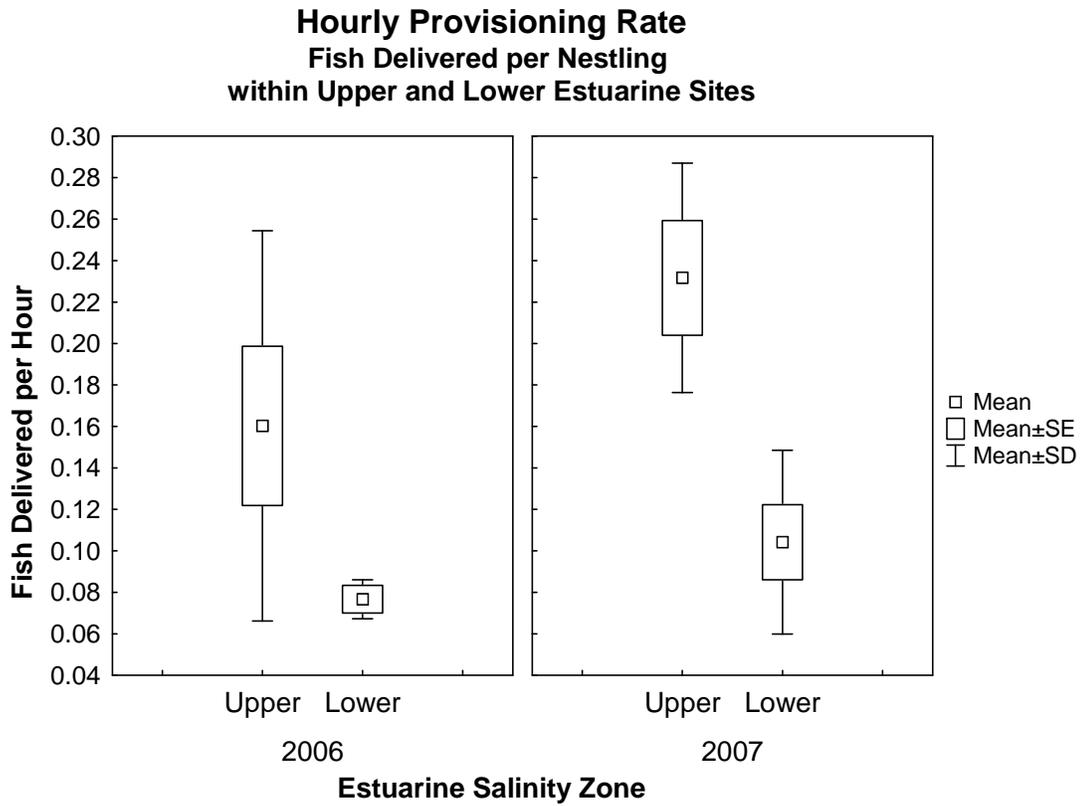
Figure 2.16.   Per capita rate of biomass provisioning for osprey nestlings that successfully fledged within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=14.634, p=0.005).

Hourly Provisioning Rate
Biomass Delivered per Fledgling
within Upper and Lower Estuarine Sites
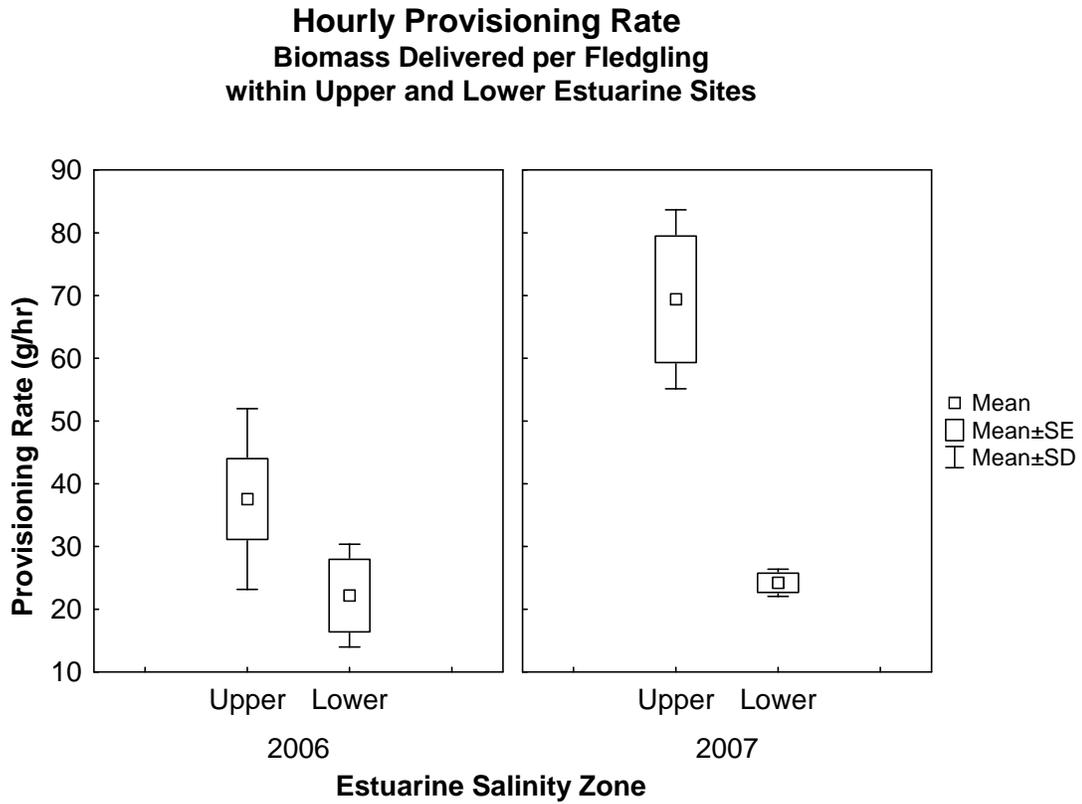
Figure 2.17. Per capita rate of energy provisioning for osprey nestlings that successfully fledged within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=14.821, p=0.005).

Hourly Provisioning Rate
Energy Delivered per Fledgling
within Upper and Lower Estuarine Sites
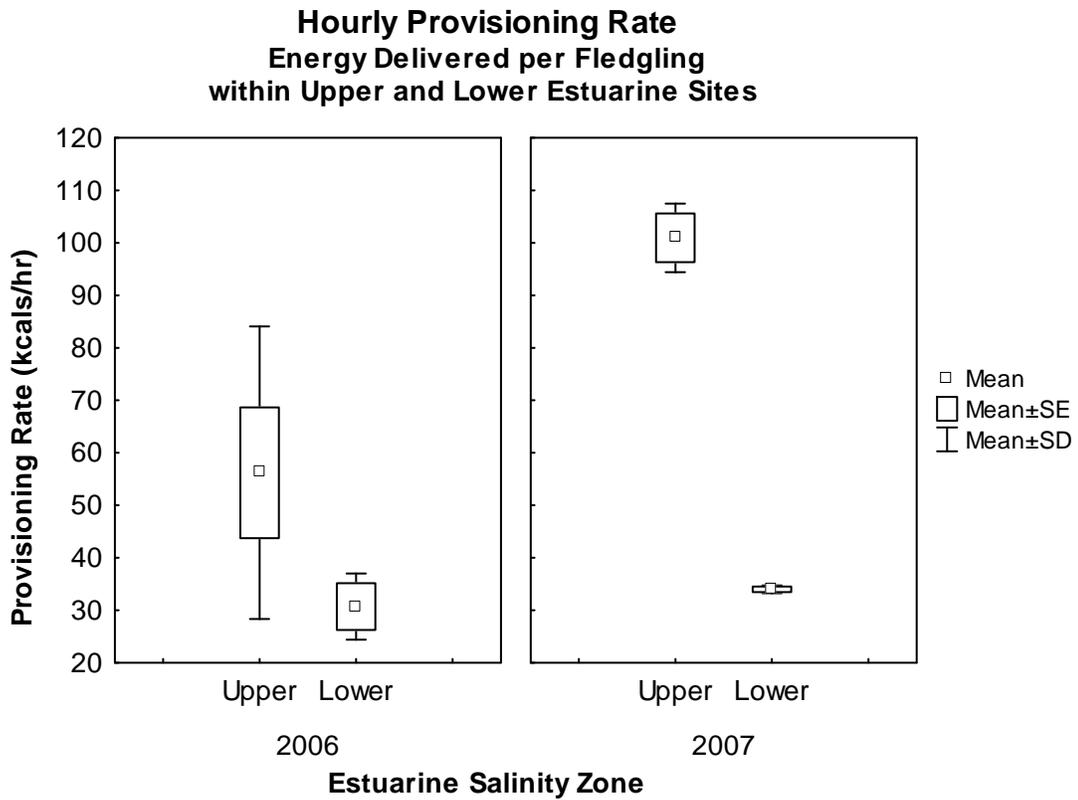
Figure 2.18.   Per capita rate of prey provisioning for osprey nestlings that successfully fledged within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites did not exist ($F_{(1, 9)}$=4.305, p=0.072).

Hourly Provisioning Rate
Fish Delivered per Fledgling
within Upper and Lower Estuarine Sites
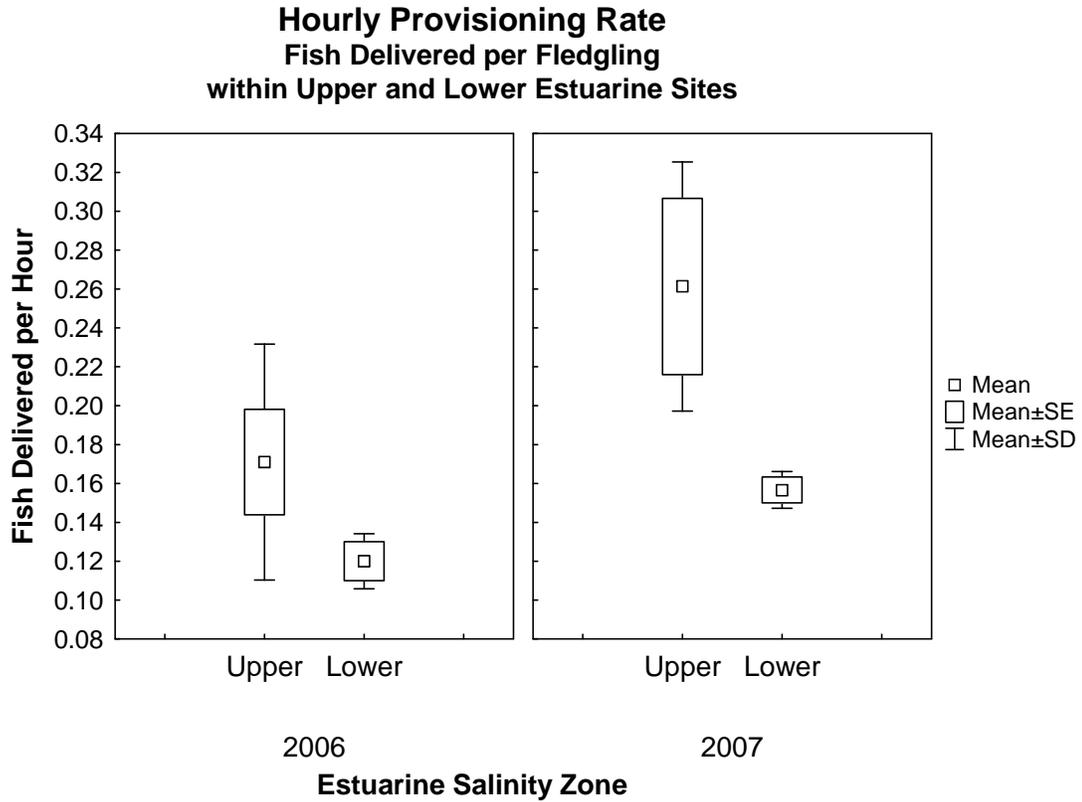
Figure 2.19. Biomass of individual fish delivered to osprey nestlings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=5.104, p=0.054).

**Biomass of Fish Delivered
within Upper and Lower Estuarine Sites**
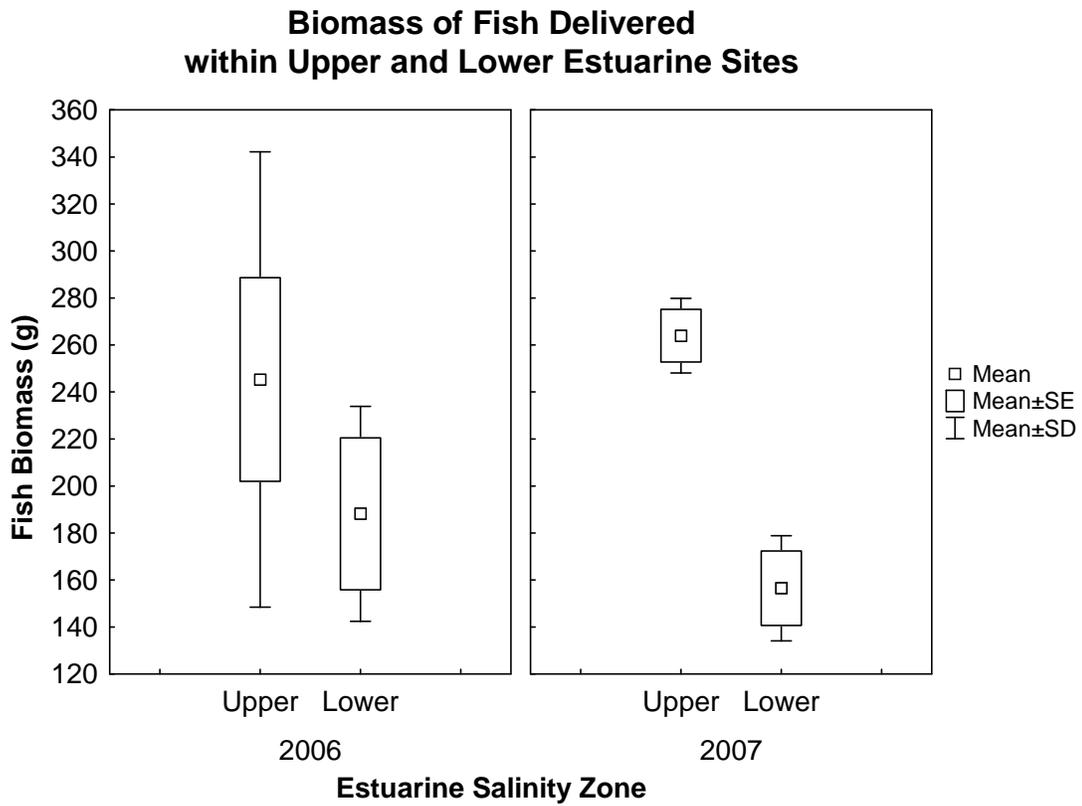
Figure 2.20. Energy content of individual fish delivered to osprey nestlings within upper and lower estuarine sites during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. The lme model indicated that significant differences between upper and lower estuarine sites existed ($F_{(1, 9)}$=5.001, p=0.056).

Energy Content of Fish Delivered within Upper and Lower Estuarine Sites
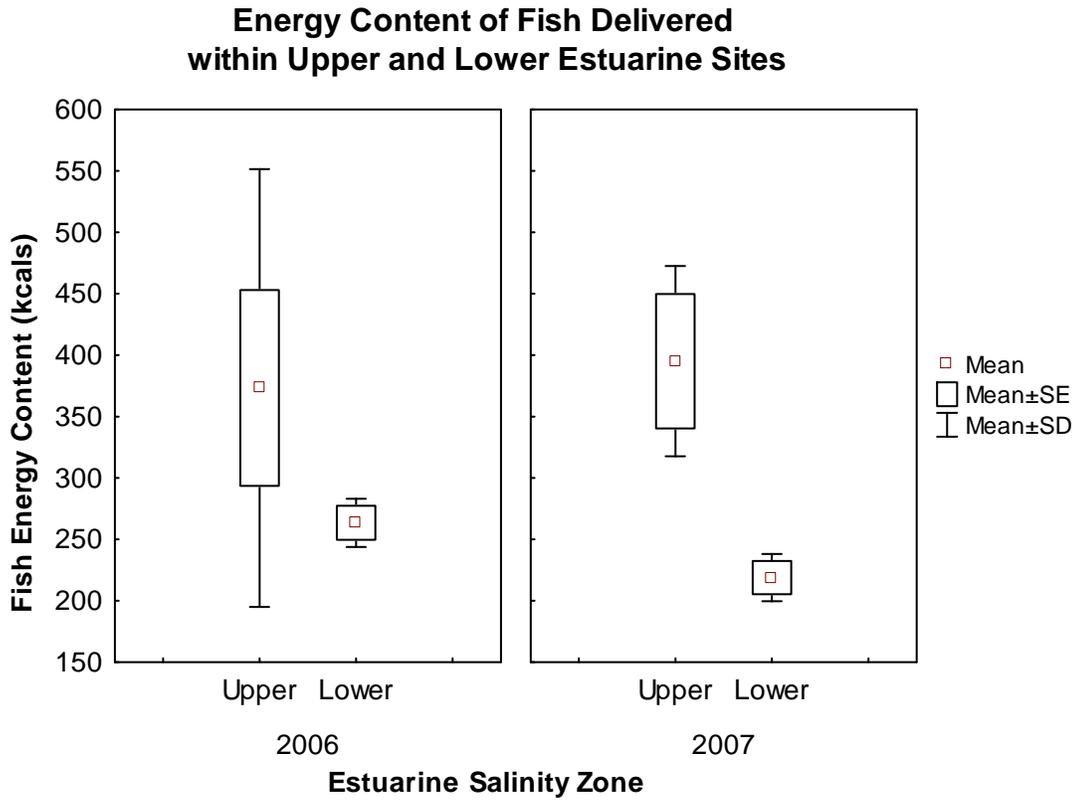
Appendix 2.1. Length-weight conversion equations for all taxa identified in the osprey diet during the 2006 and 2007 breeding Seasons in lower Chesapeake Bay.

Species	Biomass Conversion	Reference
alewife (*Alosa pseudoharengus*)	M = 0.0085*L3.000	Madenjian et al. 2003
American shad (*Alosa sapidissima*)	M = 0.0065*L2.959	Muncy 1960
Atlantic croaker (*Micropogonias undulatus*)	M = 0.0052*L3.148	Wilk et al. 1978
Atlantic herring (*Clupea harengus*)	M = 0.0075*L3.030	Hubold 1978
Atlantic menhaden (*Brevoortia tyrannus*)	M = 0.0161*L3.000	June and Nicholson 1964
Atlantic thread herring (*Opisthonema oglimum*)	M = 0.0186*L2.92	Claro and Garcia-Arteaga 1994
banded rudderfish (*Seriola zonata*)	M = 0.0259*L2.908	Bohnsack and Harper 1988
black crappie (*Pomoxis nigromaculatus*)	M = 0.0096*L3.075	Vanderpuye and Carlander 1971
blue catfish (*Ictalurus furcatus*)	M = 0.0185*L3.000	Crawford 1993
channel catfish (*Ictalurus punctatus*)	M = 0.0041*L3.407	Muncy 1959
clearnose skate (*Raja eglanteria*)	M = 0.0022*L3.295	Sulikowski et al. 2003
gizzard shad (*Dorosoma cepedianum*)	M = 0.0182*L2.89	Lagler and Van Meter 1951
hickory shad (*Alosa mediocris*)	used American shad	
hogchoker (*Trinectes maculatus*)	M = 0.0199*L3.001	Dawson 1965
largemouth bass (*Micropterus salmoides*)	M = 0.0158*L2.960	Swingle 1965
round herring (*Etrumeus teres*)	M = 0.0059*L3.158	Sanders et al. 1984
spot (*Leiostomus xanthurus*)	M = 0.0092*L3.072	Dawson 1965
spotted seatrout (*Cynoscion nebulosus*)	M = 0.0131*L3.000	Crawford 1993
striped bass (*Morone saxatilis*)	M = 0.0061*L3.153	Mansueti 1961
summer flounder (*Paralichthys dentatus*)	M = 0.0102*L2.994	Smith and Daiber 1977
threadfin shad (*Dorosoma petenense*)	M = 0.0035*L3.774	Carlander 1969
weakfish (*Cynoscion regalis*)	M = 0.0088*L3.000	Crozier and Hecht 1913
white perch (*Morone americana*)	M = 0.0125*L3.020	St. Pierre and Davis 1972

Appendix 2.2. Mass energy conversion equations for all taxa identified in the osprey diet during the 2006 and 2007 breeding seasons in lower Chesapeake Bay.

Species	Biomass Conversion	Reference
alewife (*Alosa pseudoharengus*)	E = 185*(M/100)	Frimodt 1995
American shad (*Alosa sapidissima*)	E = 192*(M/100)	Watt and Merrill 1975
Atlantic croaker (*Micropogonias undulatus*)	E = 100*(M/100)	Frimodt 1995
Atlantic herring (*Clupea harengus*)	E = 190*(M/190)	Frimodt 1995
Atlantic menhaden (*Brevoortia tyrannus*)	E = 189*(M/100)	Frimodt 1995
Atlantic thread herring (*Opisthonema oglimum*)	used Atlantic herring	
banded rudderfish (*Seriola zonata*)	used white perch	
black crappie (*Pomoxis nigromaculatus*)	used white perch	
blue catfish (*Ictalurus furcatus*)	E = 103*(M/100)	Frimodt 1995
channel catfish (*Ictalurus punctatus*)	E = 112*(M/100)	Frimodt 1995
clearnose skate (*Raja eglanteria*)	used summer flounder	
gizzard shad (*Dorosoma cepedianum*)	E = 200*(M/100)	Watt and Merrill 1975
hickory shad (*Alosa mediocris*)	used American shad	
hogchoker (*Trinectes maculatus*)	used summer flounder	
largemouth bass (*Micropterus salmoides*)	used white perch	
round herring (*Etrumeus teres*)	used Atlantic herring	
spot (*Leiostomus xanthurus*)	used Atlantic croaker	
spotted seatrout (*Cynoscion nebulosus*)	E = 99*(M/100)	Frimodt 1995
striped bass (*Morone saxatilis*)	E = 92*(M/100)	Frimodt 1995
summer flounder (*Paralichthys dentatus*)	E = 84*(M/100)	Frimodt 1995
threadfin shad (*Dorosoma petenense*)	used gizzard shad	
weakfish (*Cynoscion regalis*)	E = 99*(M/100)	Frimodt 1995
white perch (*Morone americana*)	E = 118*(M/100)	Watt and Merrill 1975

Appendix 2.3. Lower estuarine Lynnhaven River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
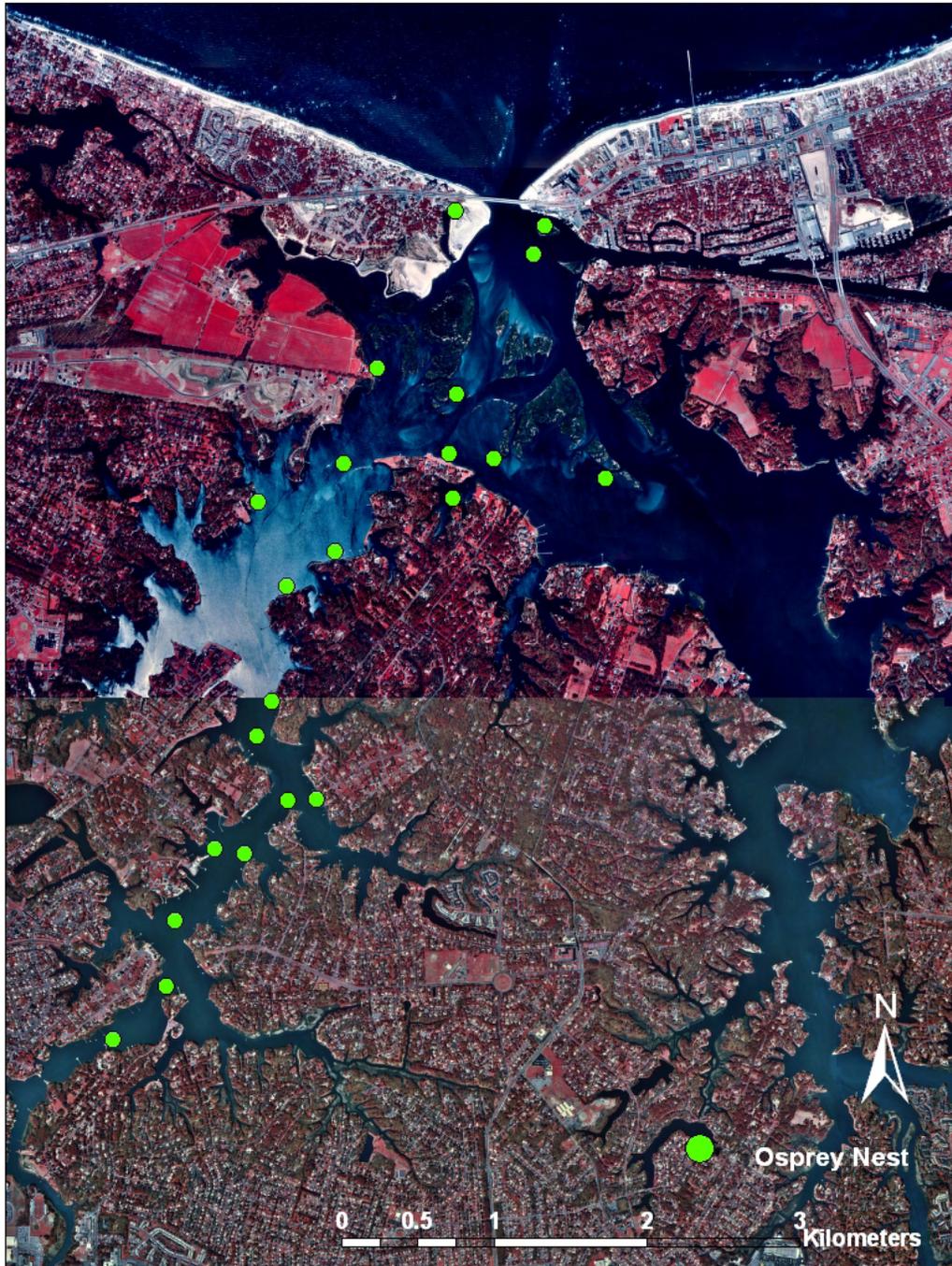
Appendix 2.4. Lower estuarine mouth of James River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.

Appendix 2.5. Lower estuarine Ware River and North Rivers sites utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
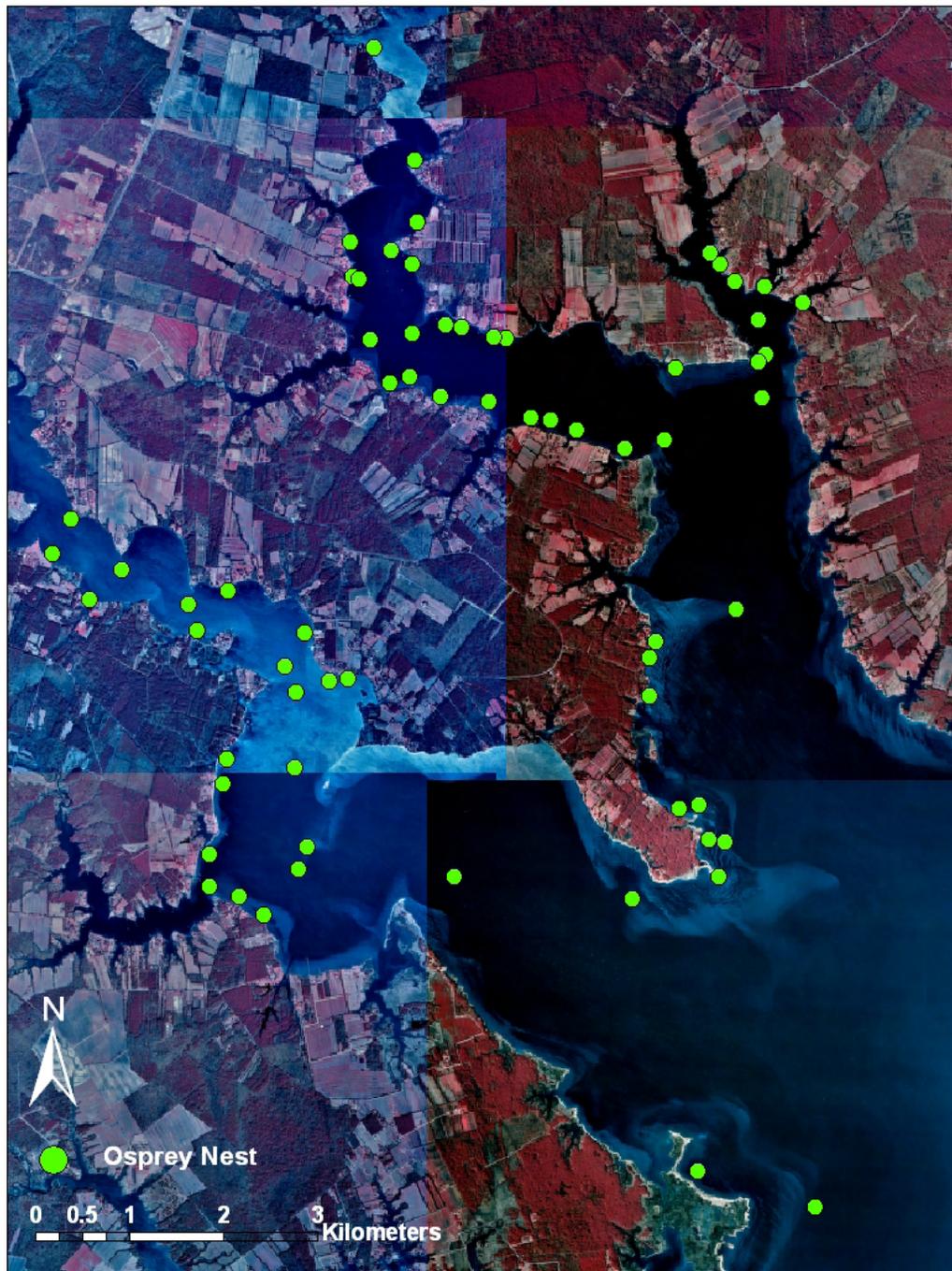
Appendix 2.6. Lower estuarine Poquoson River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.

Appendix 2.7. Lower estuarine mouth of York River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
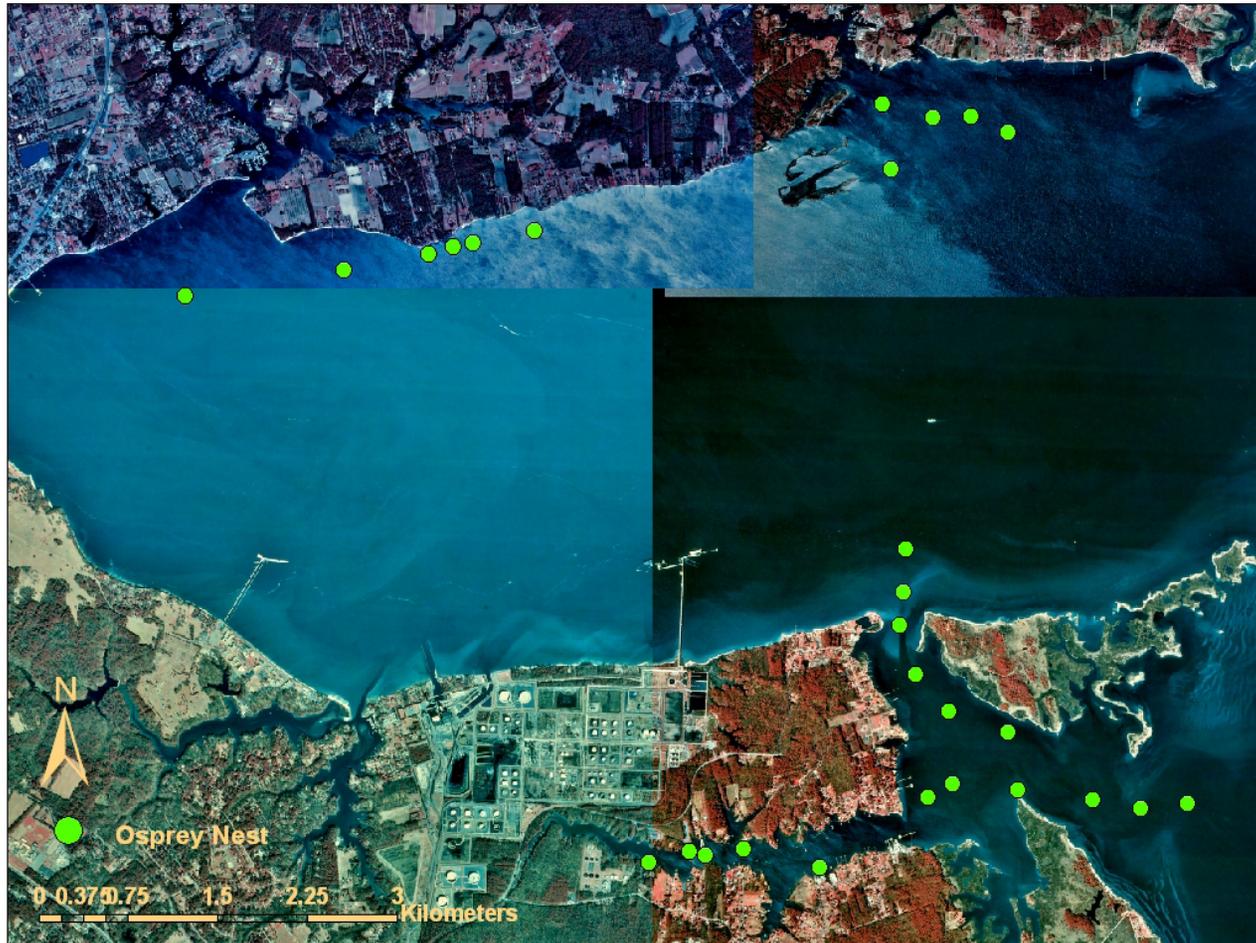
Appendix 2.8. Lower estuarine Back River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.

Appendix 2.9. Upper estuarine Hopewell site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
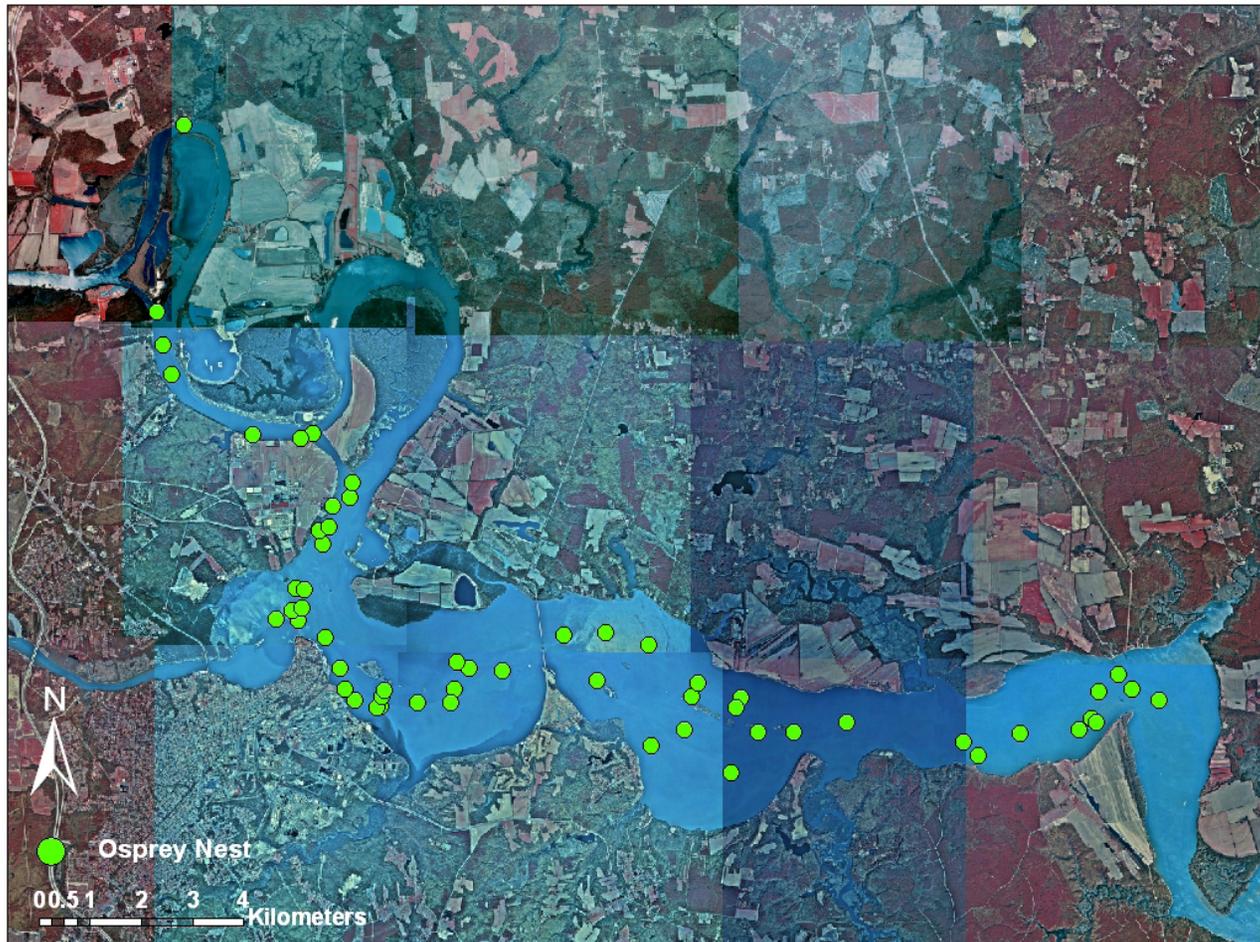
Appendix 2.10.   Upper estuarine Jamestown Island site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
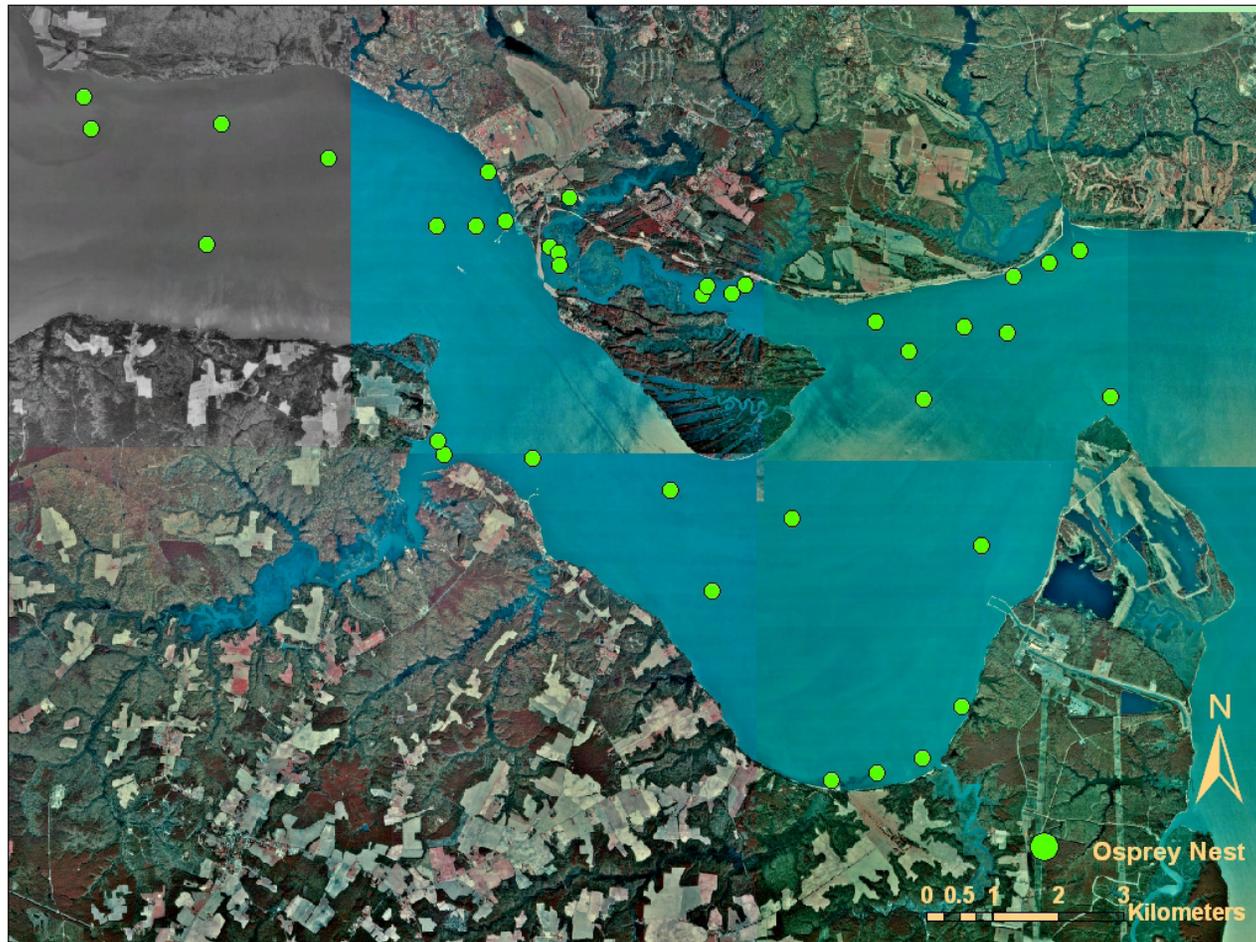
Appendix 2.11. Upper estuarine Chickahominy River site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
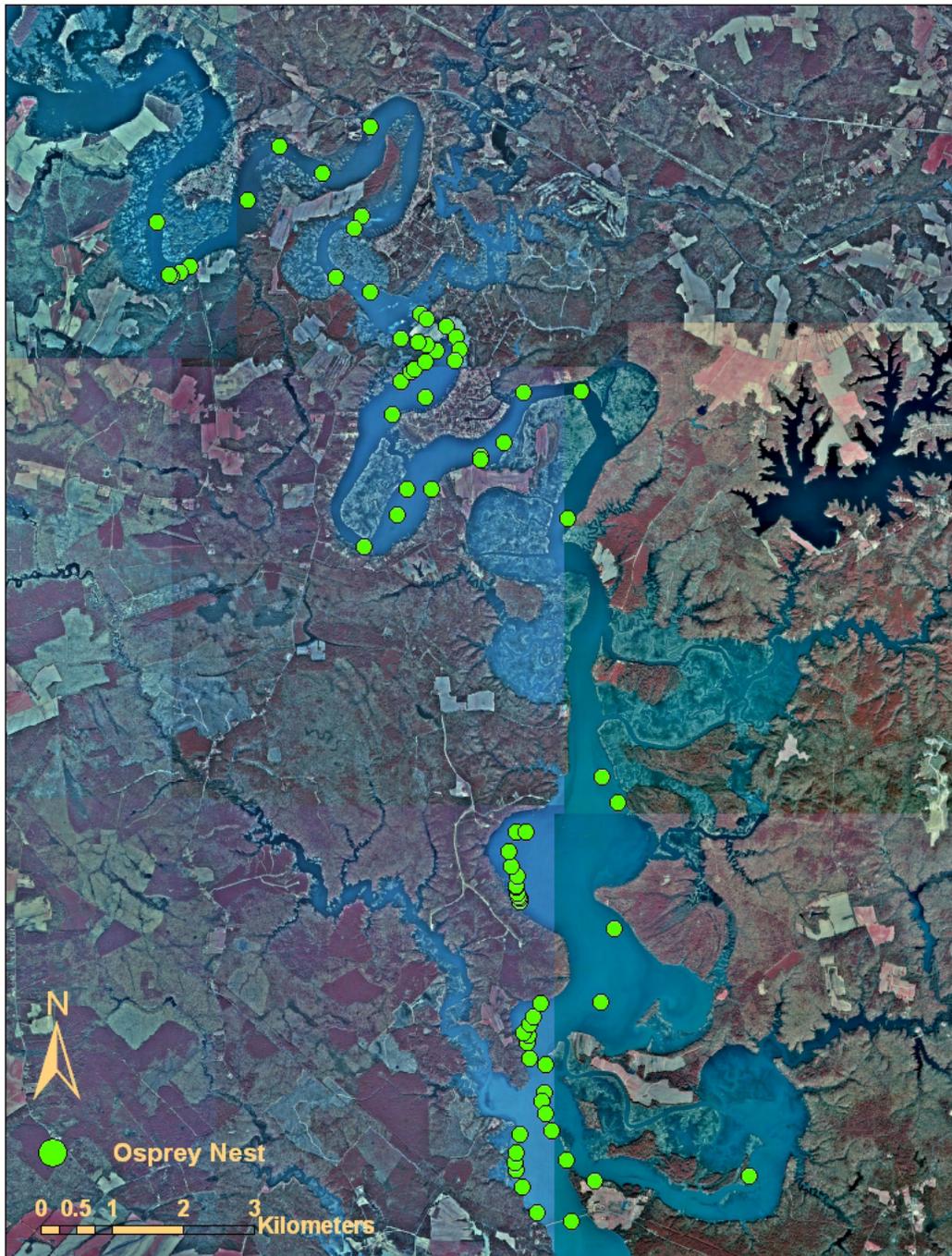
Appendix 2.12. Upper estuarine West Point site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
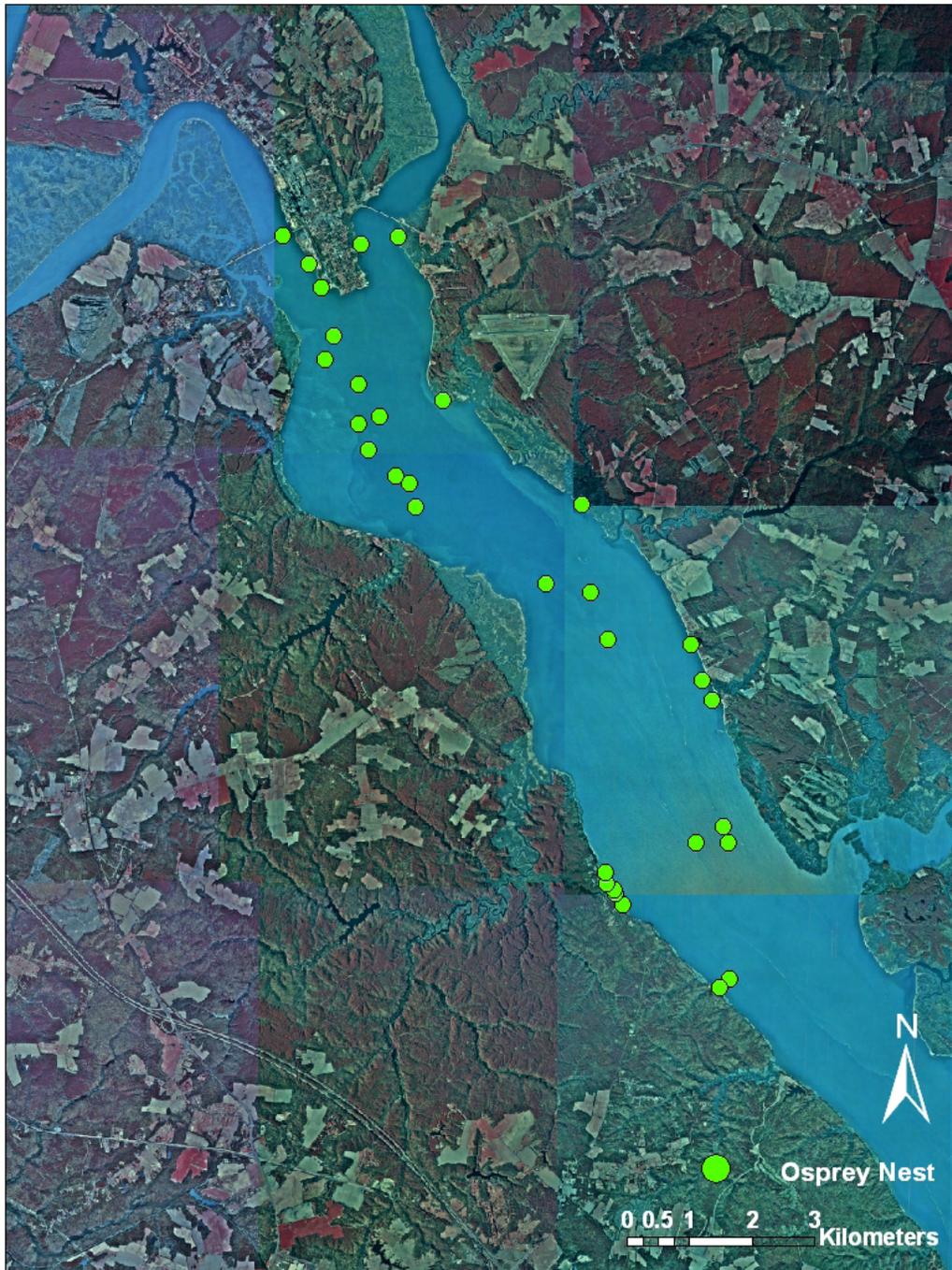
Appendix 2.13. Upper estuarine Tappahannock site utilized during the 2006 and 2007 breeding seasons in lower Chesapeake Bay. Active osprey nests are indicated.
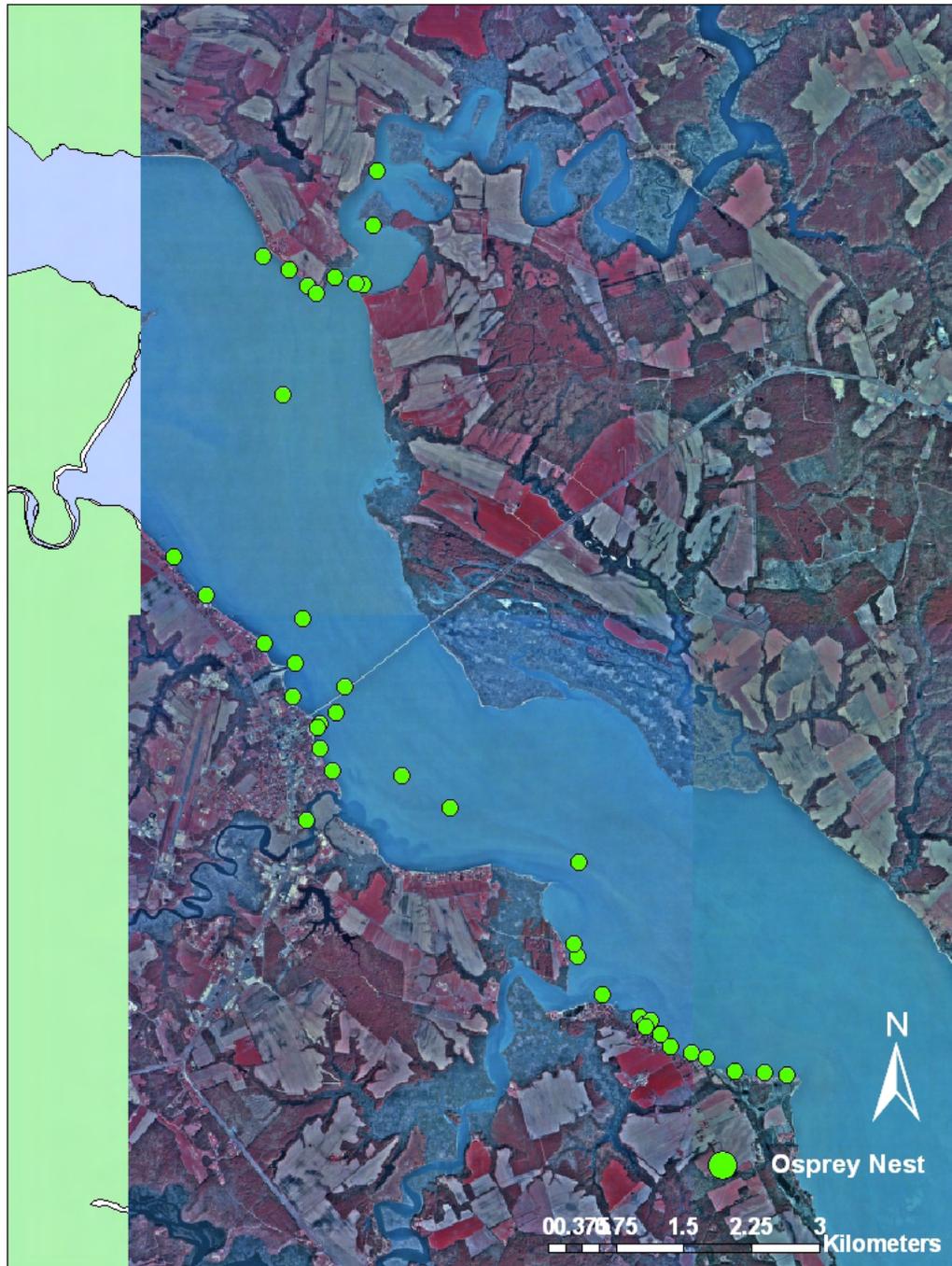
VITA

Kenneth Andrew Glass

Kenneth Andrew Glass received his B.S. in Biology from Berry College in 2000. Upon graduation he conducted summer work at Cape Hatteras National Seashore where he collected life history information and implemented management procedures to protect sea turtles and shorebirds. He then worked until December with the National Marine Fisheries Service collecting biological data aboard commercial fishing vessels in the Bering Sea.

In early 2001, he joined the private sector and worked as a biologist in California's environmental consulting industry until the middle of 2004. His primary responsibilities included conducting biological resource assessments, researching and surveying for special status species, ensuring project compliance with environmental regulations, and preparing technical reports.

During the fall of 2004, he traveled to Spain where he completed an approximately 600 mile hike along the historic Camino de Santiago. Upon returning, he worked as a research assistant with Dartmouth College on an NSF project in San Diego through the spring and summer of 2005. The project assessed the impacts of habitat fragmentation on avian population dynamics.

Finally, in the fall of 2005 he began graduate studies in the Department of Biology at the College of William and Mary. He defended the work presented in this thesis in September of 2007.