

POPULATION DYNAMICS OF THE AMERICAN OYSTERCATCHER
(*HAEMATOPUS PALLIATUS*) NEAR THE NORTHERN LIMIT OF ITS RANGE

By

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ABSTRACT

POPULATION DYNAMICS OF THE AMERICAN OYSTERCATCHERS
(*HAEMATOPUS PALLIATUS*) NEAR THE NORTHERN LIMIT OF ITS RANGE

By Sean P. Murphy

Adviser: Dr. Richard R. Veit

American Oystercatchers (*Haematopus palliatus*) expanded their range north along the Atlantic Coast, reaching Massachusetts 40 years ago. Concurrent to northward range expansion, oystercatchers have declined in the core part of their range, and have been designated a “Species of High Concern” by the U.S. Shorebird Plan. I examined the demographics of a migratory population of American Oystercatchers in Nantucket, Massachusetts to explore factors influencing local populations. I estimated fecundity (0.20 females fledged per female), annual survival, and dispersal using a variety of field and statistical techniques. I analyzed data from four nesting seasons for oystercatchers in Nantucket and examined temporal patterns in reproductive success. All my measures of reproduction were higher than those from other Atlantic Coast populations. I hypothesized that island populations experience higher reproductive success due to the absence of mammalian predators, and these populations may be sustaining mainland populations. Furthermore, I found that egg survival was exceptionally high but chick survival was low. Therefore, identification of chick loss should be a priority in

conservation efforts. I used advanced mark-recapture techniques to estimate annual adult survival and breeding-site fidelity for American Oystercatchers. My results revealed a high rate of true annual survival (0.94) and a strong, but variable, degree of breeding-site fidelity (0.93). Additionally, I used mark-recapture data to estimate juvenile annual survival (0.51) and subadult transition probability (0.18). Using perturbation analyses, I found adult survival and breeding-site fidelity had the greatest impact on local population growth. My modeling also indicated that current reproductive success is sufficient to maintain the population ($\lambda = 0.970$, 95% CI: 0.90 – 1.02), but not sufficient to predict the recent increase. Using reverse encounter histories, I estimated movement parameters and found approximately 7% of the population permanently emigrates while 16% of the population is likely comprised of adults immigrating into Nantucket. Demographic analyses confirmed that high immigration rates are responsible for the observed growth ($\lambda = 1.08$, 95% CI: 0.99 – 1.16). My dissertation provides a foundation for continued examination of shorebird population demographics, a model for demographic analyses of a species of conservation concern, and a preliminary work illuminating the advantages of dispersal and the relationship between breeding-site fidelity and reproductive success.

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DEDICATION

This dissertation is dedicated to my best friend, Ashley Ringling Murphy.

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CHAPTER 1

Introduction

The U.S. Shorebird Conservation Plan (Brown et al. 2001) designated the Atlantic population of American Oystercatchers (*Haematopus palliatus*) a “Species of High Concern” due to its small population size, habitat loss, and threats. The coastal population of 11,000 individuals (Brown et al. 2005) is limited to the narrow band of barrier beaches and coastal marshes along the Atlantic Coast which are under increasing pressure from growth and development. Additionally, oystercatchers face increasing threats during the breeding and nonbreeding seasons including human recreational disturbance, predators, and prey contamination. There are important gaps in our understanding of what limits a population of oystercatchers that must be addressed before effective conservation and management is instituted for this species. In 2003, the American Oystercatcher Working Group (AOWG) began an ambitious species-wide color banding study throughout the Atlantic Coast. This assemblage of researchers encourages the partnership of state organizations to better understand the biology of oystercatchers. Currently, ongoing AOWG projects occur in Massachusetts, New Jersey, Virginia, North and South Carolina, Georgia, and Florida.

ORGANIZATION OF DISSERTATION

My objective in this dissertation was to investigate the population dynamics of American Oystercatchers (*H. palliatus*) in Massachusetts (Fig. 1.1) near the northern limit of their range (Fig. 1.2). American Oystercatchers are large, conspicuous black, brown, and white shorebirds that use their red-orange, laterally compressed bill to feed on bivalves, molluscs, and marine worms (Nol and Humphrey 1994). These striking shorebirds occur only in coastal zones where intertidal prey abundant.

There are two races of American Oystercatcher that breed in North America: the eastern, *H. p. palliatus*, which is found along the Atlantic and Gulf Coasts, and the western race, *H. p. frazeri*, found from Southern California into Western Mexico (Nol and Humphrey 1994). My study focused on the eastern population of *H. p. palliatus*. Oystercatchers are excellent shorebirds for studying population biology because collecting extensive mark-recapture data and measures of reproductive success are relatively easy. In this dissertation, I carried out parameter estimation of critical life-history characteristics that influence fitness including reproduction, survival, and dispersal. Secondly, I synthesized estimates of demographic parameters to a matrix model to explore the dynamics of a local population of oystercatchers. My central question was to identify what demographic parameters are driving the growth of the Massachusetts population.

I color banded and collected data on American Oystercatchers in a four-year study during the breeding seasons from 2005 – 2008 in Nantucket, Massachusetts. The islands of Nantucket are located approximately 40 kilometers south of Cape Cod, Massachusetts and include: Nantucket (41.28° N, 70.10° W), Tuckernuck (41.30° N, 70.25° W), and Muskeget (41.33° N, 70.30° W) (Fig. 1.1). The islands are formed of glacial moraine and outwash plain and contain extensive salt marshes and shorelines of sandy beaches and sand dunes, which serve as primary habitat for American Oystercatchers (Lauro and Burger 1989, Humphrey 1990). Nantucket supports one of the largest breeding populations of oystercatchers in Massachusetts. In 2006, the largest concentrations of Massachusetts oystercatchers were on Cape Cod and the islands to the south (Melvin 2007), and 29% (60/202) of the birds were in Nantucket (Fig 1.3).

*Chapter 2: Reproductive success of a migratory population of American Oystercatchers
in Massachusetts, USA*

Reproductive output is one of the most common demographic parameters used to evaluate the fitness of avian populations. In Chapter 2, I studied the breeding biology of a northern oystercatcher population to better understand local production and identify potential threats to reproductive success. I found that productivity in Nantucket was low. More importantly, my data suggest that Nantucket oystercatcher eggs have a strong probability of surviving to hatching, but that low chick survival is maintaining low overall productivity. I suspect that high egg survival resulted from a lack of mammalian predators, and the low chick survival due to avian predators, including two *Larus spp.* I recommend that future investigations identify causes of chick mortality. I suggest that island populations, such as Nantucket, have relatively high productivity and may support mainland sites. To maintain or increase reproductive success of oystercatchers, efforts must maintain the mammalian predator-free islands located in Massachusetts.

*Chapter 3: Disentangling the demographics of an increasing population of shorebirds
(Haematopus palliatus): the roles of survival and movement*

Annual survival is often the demographic parameter that has the largest influence on the growth of a population of a long-lived species. I investigated the relationship between survival and movement and how each parameter influences the apparent (local) survival of adult oystercatchers. Using model techniques incorporating multiple information sources, I estimated true survival and breeding-site fidelity from four years

of mark-recapture data. My results suggest that adult oystercatchers exhibit exceptionally high annual survival with the probability of encounter also being high. Adults were strongly faithful to breeding sites. If adults emigrated from Nantucket, they never returned. More importantly, my results identify breeding-site fidelity as a demographic parameter that is highly variable among years and significantly influences observed levels of apparent survival. Therefore, understanding breeding-site fidelity is critical to understanding the dynamics of the global population of American Oystercatchers.

*Chapter 4: Identifying causes of an increasing population of American Oystercatchers
(Haematopus palliatus) in Massachusetts, USA*

While American Oystercatcher abundance has declined in southern breeding areas, Massachusetts oystercatchers have increased. Using parameter estimates from Chapters 2 and 3, I designed a stage-structured demographic model to explore how the aforementioned demographic parameters influence the local population growth (λ). In addition to adult survival, breeding-site fidelity, and fecundity, I estimated immigration and juvenile and subadult survival from the mark-recapture data. Using the parameters estimated in this study, I show that current fecundity rates are insufficient to explain the recent observed population growth. I demonstrate that including the estimated immigration rate in the demographic model tightly predicts the recent growth in Nantucket. My work suggests that despite higher reproductive success, the continued growth in Massachusetts is most likely a result of adults immigrating into the population. I also found that adult survival, breeding-site fidelity, and fecundity greatly influence local population dynamics, and I suggest that all three parameters need careful

examination during the design and implementation of conservation strategies. In particular, I hypothesize that increasing reproductive success will increase site faithfulness, and in turn, increase local population growth.

TABLES

TABLE 1.1 – Number of breeding pairs of American Oystercatchers recorded in Massachusetts from 1969 – 2007; number of breeding pairs in Nantucket, Massachusetts found in parentheses.

Year	No. of pairs	Source
1969	1	Finch (1970), Veit and Petersen (1993)
1970	2	Finch (1971), Veit and Petersen (1993)
1972	3	Veit and Petersen (1993)
1974	11	Humphrey (1990)
1979	18	Veit and Petersen (1993)
1984	40	Myers et al. (1998), Humphrey (1990)
1985	36	Myers et al. (1998), Humphrey (1990)
1986	36	Myers et al. (1998), Humphrey (1990)
1987	40	Myers et al. (1998), Humphrey (1990)
1992	77	Myers et al. (1998), Humphrey (1990)
2002	153 (49)	Melvin (2003)
2003	184 (49)	Melvin (2004)
2004	193 (57)	Melvin (2005)
2005	185 (57)	Melvin (2006)
2006	191 (64)	Melvin (2007)
2007	201 (65)	Melvin (unpublished data)
2008	197 (66)	Melvin (unpublished data)

FIGURES

FIGURE 1.1 – Breeding (blue), year-round (green), and nonbreeding (orange) distribution of the American Oystercatcher; dashed lines indicates year-round population with only local distribution (*taken and adapted from Nol and Humphrey 1994; distribution map courtesy of Birds of North America Online (<http://bna.birds.cornell.edu>) and the Cornell Lab of Ornithology*).



FIGURE 1.2 – Study area. Nantucket County, Massachusetts includes the islands of Nantucket, Tuckernuck, and Muskeget.

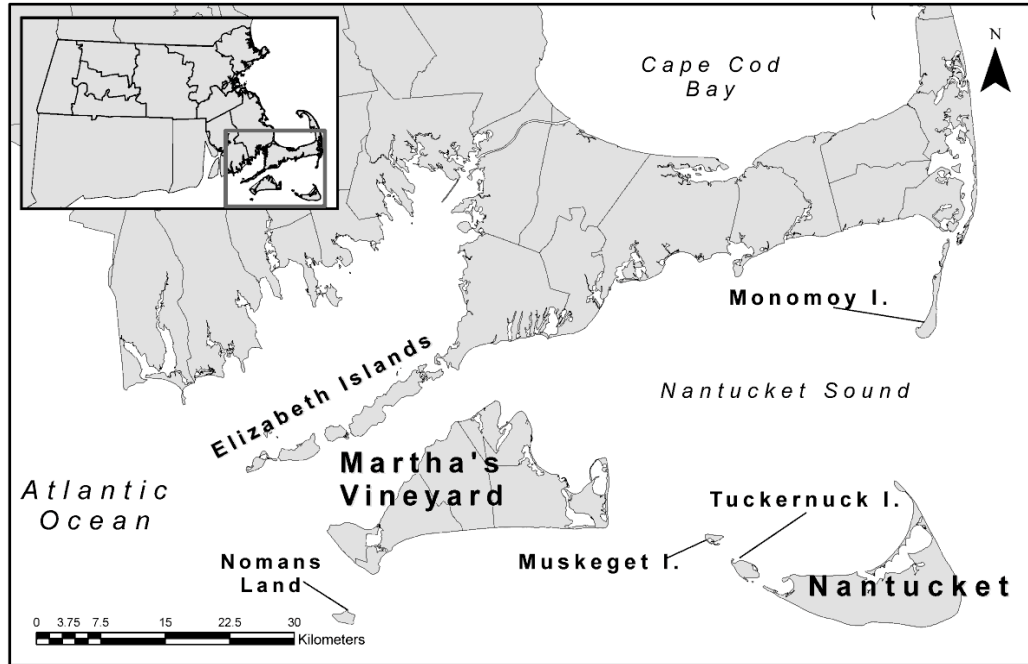
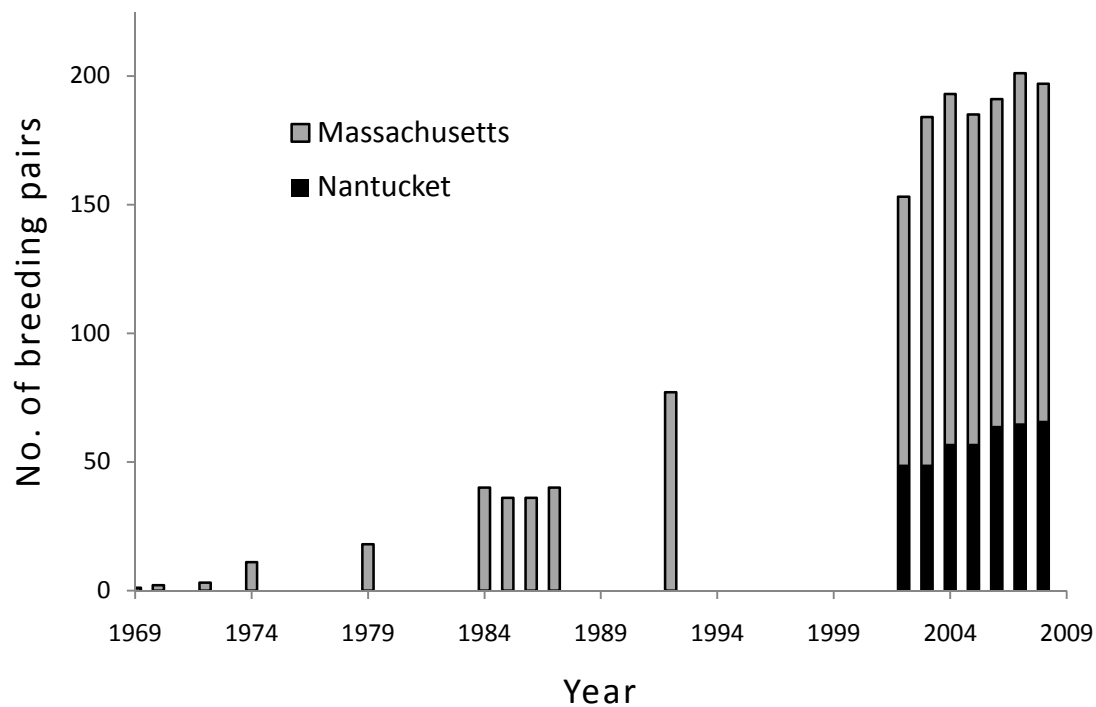


FIGURE 1.3 – Number of breeding pairs of American Oystercatchers recorded in Massachusetts from 1969 – 2008; gray bars represent statewide surveys that were intermittent until annual breeding census and monitoring efforts began in 2002; black bars represent annual census counts in Nantucket, Massachusetts from 2002 – 2008 (for source of data, see Table 1.1).



CHAPTER 2

Reproductive success of a migratory population of American Oystercatchers

(Haematopus palliatus) in Massachusetts, USA

INTRODUCTION

In the early 1800s, American Oystercatchers (*Haematopus palliatus*) nested on coastal beaches and salt marshes along the entire Atlantic Coast of North America, possibly as far north as Labrador (Audubon 1835, Bent 1929). Specimens document the species breeding in Maine (Forbush 1912, 1925, Bent 1929), but by the early twentieth century, hunting and egging pressure pushed the northern limit of the range south to Virginia where they nested in small numbers (American Ornithologists' Union 1910, Post and Raynor 1964). After the passage of the Migratory Bird Treaty Act in 1918, oystercatchers began to recover and expanded north. During the past 70 years, oystercatchers have re-colonized the Atlantic Coast north to Cape Sable Island, Nova Scotia (Myers et al. 1998, Mawhinney et al. 1999).

Oystercatchers are large, conspicuous shorebirds that rarely go unnoticed and, therefore, comprehensive records document their arrival to new sites. The first recent nest north of Virginia was found on Assateague Island, Maryland (1939, Stewart and Robbins 1958) followed by another at Little Beach Island, New Jersey (1947, Kramer 1948), then Long Island, New York (1957, Post and Raynor 1964), and Massachusetts (1969, Finch 1970, Veit and Petersen 1993). The current breeding range extends north to Boston Harbor, Massachusetts (Veit and Petersen 1993, Nol and Humphrey 1994), but small numbers have reached Green and Stratton Islands, Maine and Cape Sable Island, Nova Scotia (1997, Myers et al. 1998, Mawhinney et al. 1999). The winter distribution of the Atlantic population occurs from Ocean County, New Jersey south to the Gulf Coast with major concentrations in Virginia and the Carolinas (Nol and Humphrey 1994).

During the recovery period, the first oystercatchers observed in Massachusetts were in 1969 on Martha's Vineyard (Finch 1970, Veit and Petersen 1993). The following year, breeding pairs were observed on Tuckernuck and Monomoy Islands (Fig. 1.2, Veit and Petersen 1993). Not only has the species expanded its range, but its abundance has increased dramatically in the northern portion of its range. Long Island, New York (New York Department of Environmental Conservation, unpublished report) and Massachusetts (Melvin 2007) each contain approximately 400 breeding individuals (Table 1.1). Since being added as a species of concern to the Massachusetts Division of Fisheries and Wildlife - Natural Heritage and Endangered Species Program (MDFW), the Massachusetts breeding population has shown significant growth over the past seven years (Table 1.1, Fig. 1.3). MDFW efforts documented approximately a 6% annual increase in breeding pairs in the state from 2003 to 2008 (Melvin 2007).

As American Oystercatchers continue to expand their range and abundance in the northeastern U.S., recent evidence shows they are declining in the core Mid-Atlantic breeding areas including Virginia, South Carolina, and Florida (Mawhinney and Benedict 1999, Davis et al. 2001). Population numbers before 1989 are unknown. Recent surveys in Cape Romain, South Carolina suggest a 21% decline since 1986 (Sanders et al. 2004). Wilke et al. (2005) reported a 47% population decline on the barrier islands of Virginia from 1984 – 2003. These two states combined hold approximately 20% of the coastal population (Schulte et al. 2007). American Oystercatchers were recently named as a “Species of High Concern” in the U.S. Shorebird Conservation Plan (Brown et al. 2001) due to a restricted range, small population size, widespread habitat loss, and threats during the breeding and nonbreeding seasons (Brown et al. 2001). As coastal

development continues, oystercatchers may serve as helpful indicators of coastal conservation and management.

North of New Jersey, American Oystercatchers depart their breeding range during the winter, and oystercatchers breeding within the winter range are primarily residents (Terres 1980, Sanders *pers. comm.* 2009). Many studies have been conducted on southern breeding populations of American Oystercatchers (Table 2.1). I studied dispersal, reproduction, and survival of a northern breeding population of American Oystercatchers with the goal of learning how these processes interact to impact population growth. I measured reproductive success of these birds and compared this to reproductive success estimates from southern, less migratory populations.

STUDY AREA AND METHODS

From 2005 – 2008, I conducted an annual standardized count of breeding American Oystercatchers during a two week period occurring between mid-May to early-June. Nests were located by walking suitable habitat and observing incubating adults, active scrapes, or nests. Breeding birds typically leave and enter the nest on the ground, so nests were often located by following tracks left in the substrate. I visited all nest sites every two to four days until the nest failed or young fledged. If a nest failed prior to hatching, I tried to determine the cause of nest failure. If a nest hatched, the status and number of young were monitored every two to four days until fledging or loss of chicks.

Analytical approach

I used four variables: date of clutch initiation, average clutch laid, apparent nesting success, and fledging success, along with their associated standard errors (SE), to provide baseline measures of nesting ecology of oystercatchers in Massachusetts, and to compare with other studies of American Oystercatchers throughout the breeding range. When appropriate, I used Z statistics to determine if there was a significant difference between estimates from this study and previous research on breeding oystercatchers of the Atlantic Coast. Additionally, a single factor analysis of variance was used to detect significant differences between years of the study for normally distributed parameters. If a significant difference was identified among years, I employed a Tukey post-hoc multiple comparison analysis to determine which means were different (Zar 1984) and included actual p-value estimate.

I selected a subset of the study area to estimate nest survival of American Oystercatchers nests ($n = 28$) on Tuckernuck from 2005 – 2007 (Fig 2.1). I estimated daily nest survival rates (S) using the nest survival model (Dinsmore et al. 2002, Rotella et al. 2004) in Program MARK (White and Burnham 1999). Assumptions of the survival models include (Dinsmore et al. 2002): 1) the fate of a nest was correctly determined, and 2) monitoring did not impact nest survival. These assumptions were most likely met in this study. If either of these assumptions was violated, my estimate of daily nest survival would be negatively biased. I found that determining the success or failure of a nest was relatively easy by behavior of the parents. I was often able to detect successful hatches by the observation of chicks or adults carrying food into the nest territory on subsequent nest checks. I documented failed nest attempts by the presence of shell fragments or

other egg material in or around the nest bowl. Upon a successful hatch, adult oystercatchers carry shell fragments approximately 50 m from the nest (Nol and Humphrey 1994). Therefore, the presence of shell fragments in a nest is strong indication of a depredation event. After confirmation of nest presence, I checked nests two ways to minimize the level of disturbance. First, I assessed nest presence by observing an adult either incubating or displaying aggressively toward a predator. Second, I observed many nests by walking the tide line. If either of these low-disturbance techniques was not effective, only then would I approach the nest to determine its status.

I constructed encounter histories for analysis of nest survival using the following information collected from nest monitoring (Table 2.2): the day the nest was found (k), the last day the nest was observed with eggs (l), the last day the nest was checked (m), the nest fate (f , 0 = success, 1 = failed), and the frequency of this encounter history (n). I transformed the dates into a standardized format for Program MARK (Cooch and White 2009) by determining the earliest date a clutch was initiated, and assigned it as day one of the nesting season (25 March, $k = 1$), then all other dates were formatted relative to $k = 1$. I used a midpoint rule to designate the time of hatch for nests that successfully hatched between nest visits. I developed a set of 12 candidate models in Program MARK to address variation in the probability of nest survival of American Oystercatchers in Massachusetts and used model notations following Dinsmore et al. (2002) with the following subscripts: ‘ T ’, time-dependent variation as a linear function across the nesting season; ‘ TT ’, time-dependent variation as a quadratic function across the nesting season; ‘year’, annual variation; ‘clutch’, effect of clutch size; and ‘.’ constant model (Table 2.3).

I assessed the fit of competing models using an information-theoretic approach (Burnham and Anderson 2002). I selected the best fit model using Akaike's Information Criterion corrected for small sample size (AIC_c ; Lebreton et al. 1992) which calculates the log-likelihood of the observed encounter history given the model (i) and the number of parameters (K). I considered all models within 2 units ($AIC_c < 2$) from the model that minimized AIC_c (Burnham and Anderson 2002, Cooch and White 2009).

In addition, I compared two techniques for measuring reproductive success. The first, a synthetic estimate (Sandercock et al. 2005), is an estimate of fecundity per female (F_n) estimated as a function of breeding propensity, reneating, egg survival, and chick survival (Tables 2.4 and 2.5). This estimate requires more information, and thus more frequent nest checks. The advantage to a synthetic estimate is that it controls for nest exposure time prior to discovery. The second technique I used is "annual productivity". I estimated "annual productivity" by dividing total young fledged by total number of breeding pairs. The advantage of "annual productivity" is that it minimizes observer disturbance. By comparing these two estimates, I hoped to guide future conservation and monitoring.

I used the following demographic parameters collected during the nesting seasons to produce a synthetic estimate of fecundity per breeding female that accounts for variation in nest exposure (F_n , Sandercock et al. 2005):

$$F_A = [(BP \cdot TCL_1 \cdot NEST_1) + ((1 - NEST_1) \cdot RENEST_1 \cdot TCL_2 \cdot NEST_2) + ((1 - NEST_1) \cdot RENEST_1 \cdot (1 - NEST_2) \cdot RENEST_2 \cdot TCL_3 \cdot NEST_2)] \cdot (C/E \cdot FLED \cdot F/C \cdot 0.5)$$

where,

BP = proportion of females in the total population that are breeding

TCL_i = mean number of eggs laid per nest

$NEST_i$ = probability of a nest surviving to successfully hatch

$RENEST_i$ = probability of renesting after the loss of the previous clutch

C/E = proportion of eggs per nest that hatched to produce chicks (conditional on nest survival)

FLED = probability of at least one chick survives to fledge

F/C = proportion of chicks per nest that produce fledged young (conditional on nest survival)

and subscripts 1, 2, and 3 identify with which nesting attempt the parameter is associated. I used parametric bootstrapping to estimate confidence intervals for the fecundity calculation. I performed all modeling efforts in Program MATLAB Version 7.5 (MathWorks 2007). “Total clutch laid” (TCL) was randomly selected from a normal distribution. The remaining reproductive parameters were randomly selected from beta distributions because the probabilities are bounded between 0 and 1. From these distributions, I randomly drew each parameter and repeated this process 10,000 times to estimate fecundity.

I identified “breeding propensity” (BP) as the proportion of adults that are breeding. Adults were confirmed as “breeding” through the observation of a pair at nest. Nonbreeding adult oystercatchers are often observed during the breeding season and may possibly defend a territory and even create nest scrapes (Nol and Humphrey 1994). I distinguished subadult birds from adult nonbreeding birds by observing behavior.

Subadult birds remain on foraging grounds throughout the breeding season and are found in groups of more than two birds (Nol and Humphrey 1994).

“Total clutch laid” (TCL) was the number of eggs laid in each nest. I included nests that were known to have reached completion, thus reducing the bias of nests with partial clutch loss or lost during egg-laying.

“Nest success” (NEST) was the probability of a nest successfully surviving from the start of incubation to the hatching of at least one egg. I calculated hatching success by using the product of the daily nest survival (S) over the incubation period ($S_1 \cdot S_2 \cdot \dots \cdot S_i$). I assumed an incubation period of 27 days (Bent 1929, Palmer 1967, Nol and Humphrey 1994). I estimated the average day of incubation initiation (2 May) using the average clutch initiation date (29 April) for this study and the number of days from initiation to onset of incubation (+2.5 days, Nol and Humphrey 1994). I pooled information to produce a single estimate of nest success across initial nest and subsequent renests. An estimate of variance could not be taken directly from the distribution of NEST, so I calculated variance using the following formula:

$$Var(p) = p(1 - p)/N,$$

where, p represents the probability of nest survival and N is the sample size.

The “probability of renesting” after the loss of the initial clutch (RENEST) was the proportion of breeding pairs that failed on the initial nesting attempt and attempted a second clutch. Renesting is possible if nests are destroyed or young depredated soon after hatching (Nol and Humphrey 1994). Birds rarely renested more than once, and never after 1 July.

C/E was the mean proportion of eggs per nest that hatched into chicks. A C/E < 1 indicated partial clutch loss, which was rare, or inviable eggs that did not hatch.

FLED was the probability that at least one chick from a nest survived to fledging which occurred at 35 – 45 days. I recorded successfully fledged chicks when young were observed flying farther than 50 m. When parents lost an entire brood, they exhibited pronounced differences in parental behavior including a reduction in territoriality and chick provisioning. From hatching to fledging, adult American Oystercatchers carry whole food back to the young approximately twice per hour depending on the brood size (Nol 1989). Observing either of these behaviors or observing young indicated that a brood remained active.

F/C was the mean proportion of young per nest that successfully fledged (observed in flight > 50 m). I estimated this parameter using only successfully hatched nests, so F/C < 1 was the result of partial brood loss. The function is multiplied by a factor of 0.5 in order to estimate fecundity of the female population, assuming a 1:1 sex ratio at hatching.

I estimated “annual productivity” (P) by measuring the number of young fledged per breeding pair. This parameter requires the fewest assumptions about population size, within season site fidelity, and annual territory retention of breeding adults. It requires that the number of breeding pairs does not change throughout a single breeding season and that each breeding pair retains its territory. Violations of these assumptions could result in overestimation of “annual productivity”. Observations of the marked birds in this study support these assumptions (Chapter 3) as do other studies of American Oystercatchers (McGowan 2004, Nol and Humphrey 1994).

RESULTS

Clutch initiation

I monitored 168 American Oystercatcher nests in a four-year period from 2005 – 2008 (2005: 42 nests, 2006: 40 nests, 2007: 46 nests, 2008: 40 nests) in Nantucket, Massachusetts, and Tables 2.4 and 2.5 summarize the nesting parameters estimated. The initiation of first nests occurred between 25 March and 10 April of each year, and the last chick that fledged or failed ranged from 13 – 20 August. The average duration of nest activity (from initiation of first nest until the last chick fledges or fails) was 133 days.

The birds initiated clutches from 25 March (day 83) to 1 July (day 182). The mean date of clutch initiation for known first nests ($INIT_1$) from 2005 – 2008 was Julian day 119 (29 April, 95% CI: 116 – 122, median = 119, $n = 100$ nests). The average laying date of known replacement clutches was day 150 ($INIT_2 = 29$ May, 95% CI: 142 – 158, median = 153, $n = 18$ nests). Using five pairs with known dates for first nest loss and reinitiation, reinitiation attempts were initiated 19 days (95% CI: 13 – 26, range = 8 – 27 days, $n = 5$) after the loss of the first nest.

Nesting propensity

Of the 168 pairs monitored, I confirmed nesting for nearly all (166 pairs, 98.8%). As a result the probability of a breeding pair initiating a nest (BP) was 0.99 (SE 0.008). The two pairs that were monitored but apparently never laid eggs were located on Tuckernuck in 2005 and 2006. These pairs were located in similar territory

sites each year, observed defending a territory, and monitored throughout the entire season, but a nest was never located.

Fifty-four percent of the oystercatcher pairs laid a second nest following the loss of the initial clutch ($RENEST_1 = 0.540$, SE 0.07, $n = 50$ pairs). Due to the challenge of quickly determining whether a nest has been destroyed or hatched, I was unable to measure the relationship between the probability of renesting and timing of first nest loss. Six pairs successfully incubated a first nest to hatching, lost chicks within 1 – 2 days, and laid a second clutch. These observations support renesting following chick loss (Nol and Humphrey 1994). Of six breeding pairs that renested after a successful hatch, two renests successfully hatched (Table 2.6). Over the course of this study, five of 15 breeding pairs laid a subsequent nest after losing the second nest ($RENEST_2 = 0.313$, SE 0.12, $n = 16$). Of these five third clutch nests, two successfully hatched, and each clutch produced a single fledged young.

Clutch size

Mean clutch size of first nests (TCL_1) was 2.82 eggs (SE 0.043, range = 4, mode = 3, $n = 142$ nests). The mean clutch size of second nests (TCL_2) was 2.39 eggs (SE 0.14, range = 1, mode = 3, $n = 23$ nests), and the mean clutch size of third nests (TCL_3) was 2.00 eggs (SE 0.00, mode = 2, $n = 5$ nests). Total clutch size differed significantly across the three nest types ($F_{2,168} = 11.00$, $p < 0.0001$). Tukey post-hoc comparisons of the three nest types suggested that the total clutch size of first nests (2.82) was significantly larger the total clutch size of third nests (2.00, $p < 0.01$) but not different from second nests (2.39).

Nest survival and success

I modeled nest survival from 28 nests from 2005 – 2007 on Tuckernuck. The top four models have a combined Akaike weight of 0.72 with $AIC_c < 2$ (Table 2.4). There was little support for the remaining models. The absence of annual variation should be considered with some caution because it may be a function of a small sample size. Due to the sparseness of the data used to analyze the survival of a nest and no method to evaluate the goodness of fit (Dinsmore et al. 2002), only the top two candidate models were evaluated for their predictions. The best fit model of nest survival included a linear effect during the nesting season (S_T , Table 2.4) which predicted daily survival to decline through the nesting season (Fig. 2.1a, $\beta = -0.04$, SE = 0.029, 95% CI: $-0.093 - 0.022$). The predicted survival rates throughout the season ranged from 0.999 (SE 0.003) to 0.647 (SE 0.738). A high level of daily nest survival (≥ 0.99) is maintained until day 140 (20 May) (Fig 2.3). The probability of a nest surviving from the mean start of incubation (2 May) to hatching was 0.814 with a 95% confidence interval of 0.487 to 0.940 (Fig. 2.2a). Figure 2.3a shows the declining probability of a nest surviving to successfully hatch through the nesting season determined by the first day of incubation.

Other models that fit included a quadratic effect (S_{TT}) which estimated a curvilinear response through the nesting season ($\beta = -0.02$, SE = 0.137, 95% CI: $-0.047 - 0.063$) with high daily survival predicted between 20 April to 5 June (Fig. 2.1b). The quadratic model predicted a higher survival to hatching (0.897, CI: 0.526 – 0.981) than the linear model (Fig. 2.2b). S_{TT} predicted lower levels of nests surviving to

hatch both early and late in the nesting season than in mid-season (Fig. 2.3b). Under the constant model (S), daily nest survival throughout the entire season was 0.988 (SE 0.005) and predicted 0.728 (95% CI: 0.487 – 0.870) nests to survive to hatching over a 27-day exposure period.

Chick survival

I estimated chick survival only from nests that successfully hatched (Table 2.5). There was no difference between years of the number of oystercatcher chicks produced per egg from successful nests ($C/E = 0.916$, SE 0.020) which reveals a low frequency for partial clutch loss. Therefore, if a clutch was lost, most likely to overwash or depredation, then the full clutch was taken. FLED, the probability that one chick fledged, was 0.463 (SE 0.046), and the proportion of young hatched that fledged (F/C) was 0.377 (SE 0.035). There was no difference in FLED between years, but F/C differed significantly across years ($F_{3,187} = 4.42$, $P < 0.01$) with the only significant difference between 2005 (0.240) and 2008 (0.563).

Adult oystercatchers provision food to their precocial young (Nol and Humphrey 1994) which made chick location difficult for the majority of pairs. Chick mobility also made it difficult to identify a source of mortality when a chick was lost. However, because young were often observed on foraging territories with adults during late pre- and post-fledging, I was able to determine when young fledged.

Estimate of fecundity

I employed two techniques to investigate fecundity. The synthetic estimate ranged from 0.129 (in 2005, SE 0.037) to 0.428 (in 2008, SE 0.104) female young produced per breeding female with no annual variation. The estimate pooled across years was 0.195 (SE 0.029) (Table 2.5). Over the course of this study, the direct measure of “annual productivity” ranged from 0.188 (in 2006, SE 0.050) to 0.263 (in 2008, SE 0.059) females fledged per breeding pair and a mean productivity of 0.223 (SE 0.023). I detected no difference between “annual productivity” and the synthetic estimate for each year (Table 2.7) or across the study period ($Z = 0.699$, $P = 0.48$).

DISCUSSION

Reproductive success of American Oystercatchers was low in my four-year study from 2005 – 2008. Egg survival was exceptionally high but chick survival was lower. This pattern is similar to other areas where the breeding biology of oystercatchers has been studied (Hockey 1996). American Oystercatchers have lived at least 17 years (Nol and Humphrey 1994), and Eurasian Oystercatchers (*Haematopus ostralegus*) to 40 years (Ens et al. 1996). With annual adult survival comparable to the Eurasian Oystercatcher (Chapter 3), low fecundity levels can be adequate to maintain a stable population (Davis 1999). For most oystercatchers, low productivity is a direct consequence of egg loss (Hockey 1996), contrary to what I found in Nantucket where low reproductive success was a product of high chick mortality. Nantucket oystercatcher egg, nest, and chick survival were higher than those from other Atlantic Coast populations (Table 2.1).

The precision of the two fecundity estimation techniques (Table 2.7) suggests that efforts to locate and monitor breeding American Oystercatchers were comprehensive. With multiple management partners continuing to collect nesting data in Nantucket, the relative straightforwardness of estimating “annual productivity” will facilitate the use of these measures in future demographic analyses. On the other hand, if the identification of the demographic mechanics of reproductive success is sought, then the collection of detailed nesting information is best.

In this study, one four-egg clutch and two five-egg clutches were found. Although four eggs can be attributed to a single female (Nol and Humphrey 1994), five eggs or more may be the result of communal nesting (Lauro et al. 1992). Both five-egg clutches were observed in 2008 on the same beach approximately 30 m away from each other. In 2009, two six-egg clutches were found in Nantucket, and both were confirmed communal associations through the observation of three different banded oystercatchers incubating (E. Ray and N. Ernst, *pers. comm.*). Lauro et al. (1992) found that communal nesting in New York was a direct consequence of high nest densities. Additionally, if communal nesting occurs, it usually originates on territories of superior quality (Emlen 1982). Lauro et al. (1992) reported that all communal associations in New York occurred on sandy beaches and none on wrack or grass. The four communal nests found in Nantucket were on sandy substrate. These communal nests suggest that regions within Nantucket are reaching carrying capacity for breeding American Oystercatchers. The frequency of clutches with five or more eggs may serve as a gauge to measure the densities of specific sites. Communal nesting is interesting because 1) it will positively bias any reproductive parameters that are proportions of the total breeding pairs (e.g.

annual productivity) and 2) individual reproductive success may change as communal nesting increases.

Apparent nest success, the proportion of observed clutches that successfully hatched (0.67), was 1.6 – 5.1 greater than all other previous studies (Table 2.1). Oystercatcher nests are often exposed to various native mammalian predators capable of nests depredation such as: raccoon (*Procyon lotor*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), Virginia opossum (*Didelphis virginiana*), and striped skunk (*Mephitis mephitis*). In North Carolina, mammalian predators were documented as the most common cause of egg loss (Davis et al. 2001, McGowan 2004). Furthermore, McGowan et al. (2005b) found that the absence of mammalian predators increased nest survival. Nantucket lacks native mammalian predators (Cardoza et al. 2009) that account for the majority of American Oystercatcher nest losses. In order to maintain these elevated levels of nest survival, it is important for local management strategies to prevent introductions of mammalian predators.

Chick loss was the major source of reproductive failure in Nantucket although few mortality events were observed. It was suspected that many mortality events occurred soon after hatching. Early mortality was documented for African Black Oystercatchers (*H. moquini*) in which 87% of chick mortality occurred within seven days after hatching. Following the initial seven days, mortality was greatly reduced (30%) (Hockey 1983). Since native mammalian predators are absent from Nantucket, all suspected predators were avian species. Over the course of the study, I documented chick loss resulting from the attack and killing by a Great Black-backed Gull (*Larus marinus*), and suspected Herring Gull (*Larus argentatus*), American Crow (*Corvus*

brachyrhynchos), and Northern Harrier (*Circus cyaneus*). With most nests surviving to hatch, management efforts aimed to improve the reproductive success of oystercatchers in Massachusetts will need to focus on identifying sources of chick loss and reducing threats from avian predation, human disturbance. It is hypothesized that islands free of mammalian predators may serve as source populations to oystercatchers nesting on mainland sites (Hockey 1996). On coastal islands in Virginia, a reduction in mammalian predator abundance increased oystercatcher productivity, even reaching greater than one chick per breeding pair (Wilke et al. 2008). My data suggest that island populations of Nantucket may serve as source populations that play a critical role in maintaining species abundance. Sixty percent of Massachusetts oystercatchers nest on islands (Melvin 2007) and may likely be supporting mainland populations on Cape Cod and, possibly Long Island, New York.

Oystercatcher populations appear to be declining south of Virginia (Davis et al. 2001), and recent studies reported low reproductive success and found that mammalian predation and human disturbance were driving high rates of nest failure (McGowan 2004, Sabine et al. 2008). The only exception is Cumberland Island National Seashore where low predator abundance on the island resulted in higher production (Sabine et al. 2006). The contrary may be occurring from Virginia and north (this study, Wilke et al. 2008). Elevated production has been found in populations that are thought to be growing. Further studies need to be conducted to understand if the observed reproductive success is sufficient to drive the opposing observed population trends in the northern and southern regions of the American Oystercatcher distribution.

American Oystercatchers began breeding in Massachusetts 50 years ago and have established a breeding population of approximately 400 individuals. Although my study does not identify factors that may be influencing high levels of reproductive success, a number of potential sources can be identified including the lack of native mammalian predators, low levels of human disturbance, or the likelihood that the local population has not reached capacity. It will be the responsibility of future research to quantify what impact these factors have on the nesting ecology in Nantucket. An additional factor that may contribute to heightened reproductive success is the influence that migratory distance may have on reproductive output. Seasonal migration to breeding areas often occurs when exploitation of a resource elevates reproductive output and this outweighs a decreased survival due to the cost of migration (Pérez-Tris and Tellería 2002). Migration costs include exposure to predators and energetic costs that may lower survival of the organism (Alerstam 1991). Thus, oystercatchers nesting in the northeastern U.S. may trade decreased survival for improved fecundity. Due to the complexities of studying this relationship, little empirical data exists. Continued oystercatcher research may illuminate this important evolutionary ecology system in shorebirds.

TABLES

TABLE 2.1 – Comparison of reproductive success of American Oystercatchers along the Atlantic Coast.

Parameter	Estimate	State	Years	Source
Clutch initiation date	19 April	MA	2005-2008	This study
	21 April	VA	1981-1983	Nol 1989
Mean clutch size (renew)	2.8 (2.4)	MA	2005-2008	This study
	2.5 (n/a)	GA	2003-2004	Sabine et al. 2005 ^a
	2.8 (2.4)	VA	1981-1983	Nol 1989
Apparent nest success	0.67	MA	2005-2008	This study
	0.13	NC	1997-1999	Davis et al. 1999
	0.24	NC	1995-2003	McGowan 2004
	0.38	GA	2003-2004	Sabine et al. 2005
	0.14	VA	1981-1983	Nol 1989
Daily survival rate (nest success)	0.99 (0.73)	MA	2005-2008	This study
	0.928 (0.13)	NC	1997-1999	Davis et al. 1999
	0.94 (0.20)	NC	1995-2003	McGowan 2004
	0.973 (0.48)	GA	2003-2004	Sabine et al. 2005
Fledging success	0.32	MA	2005-2008	This study
	0.05	NC	1997-1999	Davis et al. 1999
	0.28	GA	2003-2004	Sabine et al. 2005
Productivity	0.22	MA	2005-2008	This study
	0.059	NC	1997-1999	Davis et al. 1999
	0.06	NC	2003-2004	McGowan et al. 2005b
	0.71	GA	2003-2004	Sabine et al. 2006
	0.18	VA	1981-1983	Nol 1989
	0.35	MD	2003	Traut et al. 2006
	0.63-0	VA	2003-2007	Wilke et al. 2007

^a reneating clutches not identified

TABLE 2.2 – Encounter history of 28 American Oystercatcher nests on Tuckernuck Island, Massachusetts from 2005 - 2007 for nest survival analysis in Program MARK with the following nest information: k = day a nest is found, l = last day a nest was observed alive, m = last day a nest was checked, f = nest fate (0 = hatched, 1 = failed), and the number of eggs in the clutch.

Year	Nest	k	l	m	f	1-egg	2-egg	3-egg
2005	1	35	35	37	1	0	1	0
	2	33	65	65	0	0	0	1
	3	33	55	55	0	0	1	0
	4	33	47	72	1	1	0	0
	5	38	67	76	1	0	0	1
	6	48	77	77	0	0	0	1
2006	1	25	28	28	0	0	0	1
	2	1	30	30	0	0	0	1
	3	25	41	41	0	0	0	1
	4	1	1	25	1	0	0	1
	5	46	63	63	0	0	1	0
	6	2	26	26	0	0	0	1
	7	2	25	150	1	0	0	1
	8	26	40	40	0	0	1	0
	9	2	26	26	0	0	0	1
	10	25	54	54	0	0	0	1
	11	23	24	24	0	0	0	1
2007	1	15	16	17	0	0	0	1
	2	18	27	28	0	0	0	1
	3	19	26	27	0	0	0	1
	4	19	22	23	0	0	0	1
	5	19	24	25	0	0	0	1
	6	19	35	36	0	0	0	1
	7	19	41	155	1	1	0	0
	8	19	26	27	0	0	0	1
	9	19	26	27	0	0	0	1
	10	20	23	24	0	0	0	1
	11	20	24	25	0	0	0	1

TABLE 2.3 – The 12 candidate models developed for estimating nest survival probabilities from 28 American Oystercatchers nests on Tuckernuck Island, Massachusetts (2005 – 2007). For each model the following information is given: model notation, a description of the model, Akaike’s Information Criterion (AIC_c), differences in AIC_c values from the best fit model (ΔAIC_c), AIC_c weights (w_i), Model likelihood, the number of parameters (K), and deviance (Dev). Description of the characteristics for each parameter are the subscripts: ‘.’ constant, ‘ T ’ linear trend over the course of the nesting season, ‘ TT ’ quadratic trend over the course of the nesting season, ‘clutch’ effect of clutch size, and ‘year’ effect of annual variation.

Model notation	Model description	AIC_c	ΔAIC_c	w_i	Model likelihood	K	Dev
S_T	Linear trend	29.17	0.00	0.21	1.00	2	25.14
S_{TT}	Quadratic trend	29.32	0.15	0.19	0.93	3	23.26
$S_{clutch + TT}$	Effect of clutch size with a quadratic trend	29.51	0.34	0.18	0.84	5	19.36
$S_{.}$	Constant rate	29.97	0.80	0.14	0.67	1	27.96
$S_{year + T}$	Effect of year, linear trend	31.45	2.28	0.07	0.32	2	27.42
$S_{clutch + T}$	Effect of clutch size, linear trend	32.40	3.23	0.04	0.20	4	24.30
$S_{year + TT}$	Effect of year, quadratic trend	32.42	3.25	0.04	0.20	3	26.36
S_{clutch}	Effect of clutch size	32.66	3.49	0.04	0.17	3	26.60
$S_{year + clutch}$	Effect of year, clutch size	32.66	3.49	0.04	0.17	3	26.60
S_{year}	Effect of year	32.70	3.53	0.04	0.17	3	26.64
$S_{clutch + year + T}$	Effect of clutch size, year, linear trend	33.82	4.65	0.02	0.10	4	25.72
$S_{clutch + year + TT}$	Effect of clutch size, year, quadratic trend	387.65	358.48	0.00	0.00	6	375.44

TABLE 2.4 – Egg production for American Oystercatchers in Nantucket, Massachusetts during four breeding seasons from 2005 – 2008 (SE); includes: breeding propensity (BP), clutch initiation (INIT₁, INIT₂) clutch size (TCL₁, TCL₂, TCL₃) and probability of reneesting (RENEST₁, RENEST₂).

Parameter	Notation	<i>n</i>	2005	2006	2007	2008	Total
Breeding Propensity	BP	168	0.98 (0.02)	0.98 (0.03)	1.00 (0.00)	1.00 (0.00)	0.99 (0.01)
Date of first clutch initiation	INIT ₁	100	111 (2.0)	124 (3.0)	119 (1.6)	120 (4.1)	119 (1.4)
Date of second clutch initiation	INIT ₂	18	153 (3.5)	161 (0.0)	136 (6.5)	157 (9.1)	150 (4.1)
Total clutch laid (first)	TCL ₁	142	2.52 (0.12)	2.87 (0.06)	2.90 (0.06)	2.97 (0.08)	2.82 (0.04)
Total clutch laid (second)	TCL ₂	23	2.25 (0.25)	2 (0.00)	2.5 (0.34)	2.67 (0.21)	2.39 (0.14)
Total clutch laid (third)	TCL ₃	5	2.00 (0.00)	2.00 (0.00)	2.00 (0.00)	2.00 (0.00)	2.00 (0.00)
Probability of first reneest	RENEST ₁	50	0.60 (0.16)	0.33 (0.17)	0.57 (0.14)	0.59 (0.12)	0.54 (0.07)
Probability of second reneest	RENEST ₂	16	0.25 (0.25)	0.00 (0.00)	0.33 (0.33)	0.43 (0.20)	0.31 (0.12)

TABLE 2.5 – Chick production for American Oystercatchers in Nantucket, Massachusetts in four breeding seasons from 2005 – 2008; includes: chick survival (C/E, FLED, F/C) and fecundity (P, *F*) with associated standard errors in parentheses.

Parameter	Notation	<i>n</i>	2005	2006	2007	2008	Total
Chicks produced per egg	C/E	203	0.948 (0.025)	0.833 (0.063)	0.897 (0.040)	0.970 (0.029)	0.916 (0.020)
Probability of fledging	FLED	121	0.50 (0.09)	0.39 (0.09)	0.40 (0.08)	0.60 (0.10)	0.46 (0.046)
Fledged young produced per chick	F/C	191	0.240 (0.049)	0.500 (0.093)	0.389 (0.067)	0.563 (0.089)	0.377 (0.035)
Fledged female young per breeding female	P	168	0.214 (0.052)	0.188 (0.050)	0.228 (0.060)	0.263 (0.059)	0.223 (0.028)
Synthetic estimate of fecundity ^a	<i>F</i>	-	0.129 (0.037)	0.186 (0.060)	0.180 (0.051)	0.428 (0.104)	0.195 (0.029)

^a Mean synthetic estimates and corresponding standard error were generated using bootstrap resampling (10,000 replications).

TABLE 2.6 – Nest fates of six American Oystercatcher breeding pairs that attempted to renest following loss of chicks in Nantucket, Massachusetts from 2005 – 2008. HD = chicks were only observed on hatch day; n/d = no data.

Nest no.	Year	First nest				Second nest		
		No. of Eggs	Clutch initiation day	Hatch day	Chicks last observed	No. of eggs	Renest initiation days	Nest fate
1	2005	2	103	132	HD	2	157	hatched
2	2005	3	106	137	10 days	2	159	failed
3	2006	3	120	151	n/d	2	n/d	failed
4	2006	3	120	151	n/d	2	n/d	failed
5	2007	3	112	143	HD	n/d	n/d	hatched ^a
6	2008	3	122	153	n/d	2	n/d	failed

^a fledged one chick.

TABLE 2.7 – Z statistics of observed and synthetic estimates of fecundity by year and pooled across the study period for American Oystercatchers breeding in Nantucket, Massachusetts from 2005 – 2008.

Year	Observed (SE)	Simulated (SE)	Z	P
2005	0.214 (0.052)	0.1287 (0.037)	- 0.287	0.774
2006	0.188 (0.050)	0.1861 (0.060)	- 0.006	0.995
2007	0.228 (0.060)	0.1797 (0.051)	0.362	0.718
2008	0.263 (0.060)	0.4282 (0.104)	0.410	0.683
Pooled	0.223 (0.028)	0.1945 (0.029)	0.699	0.485

FIGURES

FIGURE 2.1 – Predicted daily survival rates of American Oystercatcher nests ($n = 28$) on Tuckernuck Island, Massachusetts from 2005 – 2007; survival is illustrated for the (a) linear model (S_T) and (b) quadratic model (S_{TT}) predicting a negative effect of time with associated 95% confidence interval.

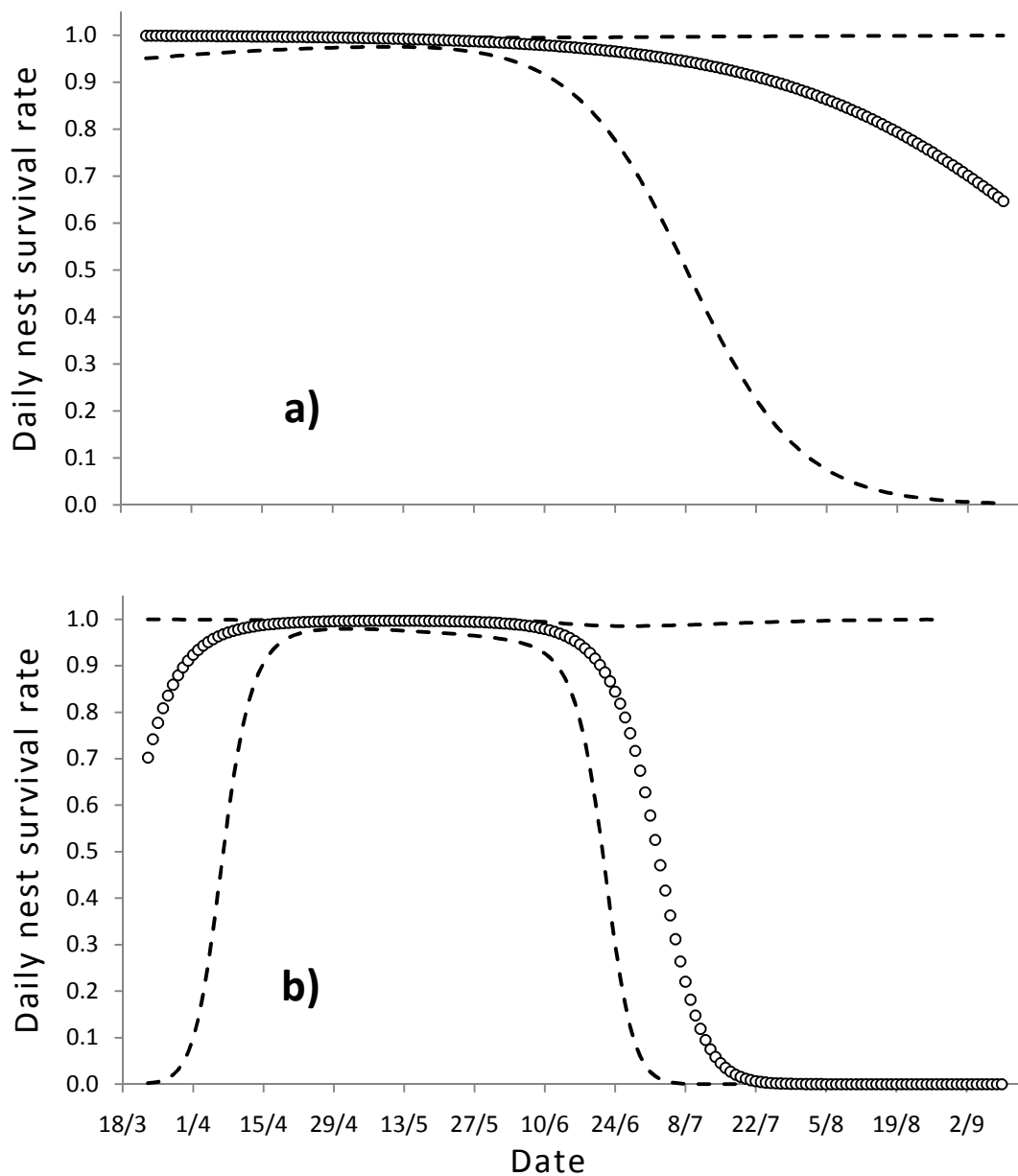
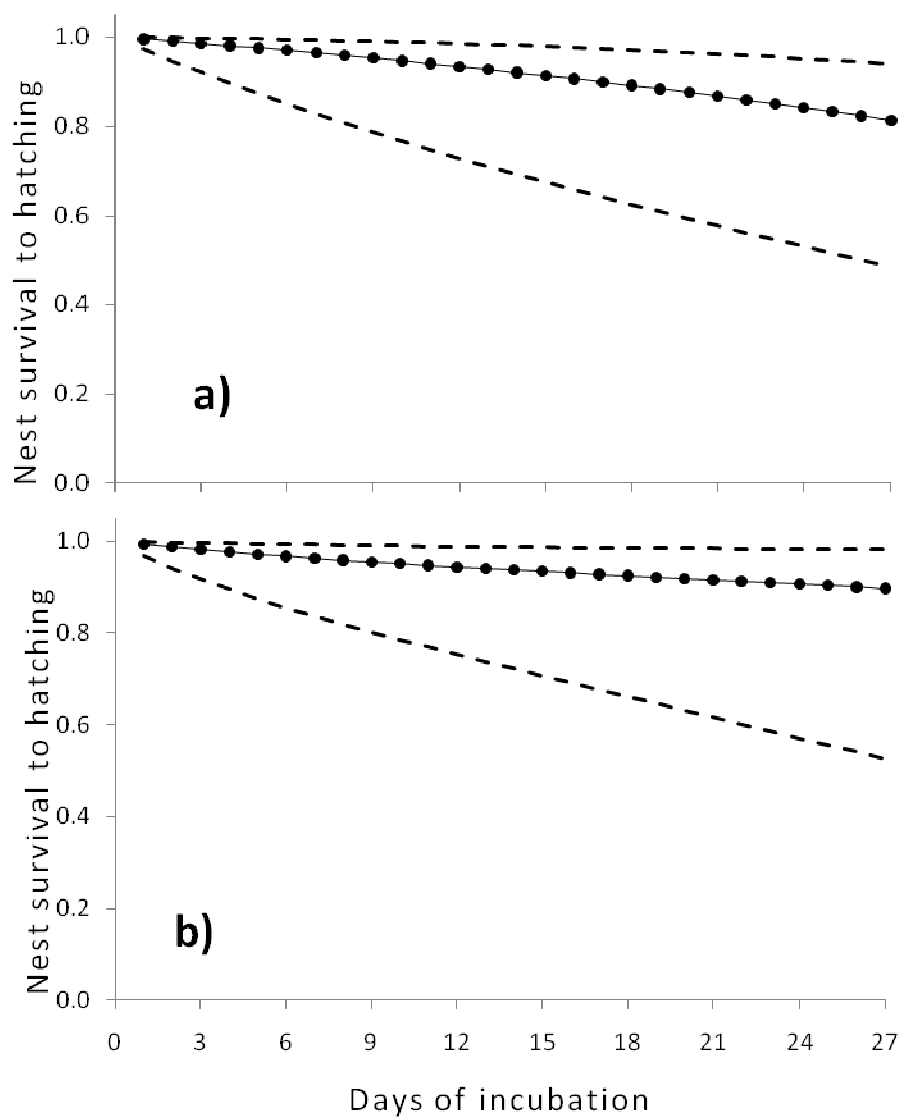


FIGURE 2.2 – Predicted nest success from the onset of incubation to successful hatch and the associated confidence interval for American Oystercatchers nests () on Tuckernuck Island, Massachusetts from 2005 – 2007; survival is illustrated for the (a) linear model () and (b) quadratic model () with the associated confidence interval (dashed lines) for a nest that begins incubation on 2 May and continued for days.



CHAPTER 3

Disentangling the demographics of an increasing population of oystercatchers

(Haematopus palliatus): the roles of survival and movement

INTRODUCTION

Individual fitness depends on fecundity and survival. Therefore measurement of these quantities is critical to the design and implementation of management and conservation efforts for wildlife populations. Fecundity is often used to measure fitness, may be because of the relative ease by which reproductive success can be measured in vagile animals (Crone 2001, Sandercock 2006). Recent studies have revealed that estimates of annual survival are more influential in long-lived species (Crone 2001). For shorebirds, survivorship may be the single most challenging parameter to accurately estimate under field conditions because individuals must be marked and followed for many years (Lebreton et al. 1992). I provide the first estimates of adult survival rates for American Oystercatchers based on new estimation methods that allow for the use of multiple information sources. Traditional mark-recapture methods have been based upon a single type of information to construct models and estimate survival. The mark-recapture model I used takes advantage of three sources of information: 1) Resightings of birds during the capture period, 2) Resightings of birds during the interval between capture periods, and 3) Recoveries of dead birds. Table 3.1 provides suggested notations and definitions of commonly used demographic estimates associated with mark-recapture models.

The most commonly reported measure of survival for shorebirds is return rates (rr , the proportion of marked individuals that are recaptured either in the following or some future year). Although this estimate is the most accessible measure to calculate, it is confounded because it is a composite of true survival (S , the probability that a bird survives between two sampling periods); site fidelity (η , the probability that a bird returns

to the same sampling area and does not permanently emigrate, if it survives); site propensity (γ^* , the probability that a bird returns to the same sampling area the next year without skipping a year, if it survives and returns to the same area); and detection rates (p^* , the probability that an observer detects the bird, if it survives, returns to the same area the next year and is available for capture).

$$rr = S \eta \gamma^* p^*$$

As the product of these four probabilities, return rates can be a highly biased indicator of survival because rr could reflect any of these probabilities or a combination (Sandercock 2003).

Recent advancements in the collection and analyses of live encounter data, researchers have produced more accurate estimates of survival by separating the apparent survival,

$$\phi = S \eta$$

from the probability of recapture have been made,

$$p = \gamma^* p^*.$$

The apparent survival provides a more accurate estimate of survival because the variation in γ^* and p^* have been removed in mark-recapture models (CJS models) developed by Cormack (1964), Jolly (1965), and Seber (1965). Although CJS models adjust for recapture probability, the apparent, or local, survival still depends on the probability that an individual returns to the study area and is available for capture. This probability, η , is also known as site fidelity. For a species that shows signs of low adult site fidelity or high natal site dispersal, η will bias estimates of apparent survival negatively.

Recently developed methods for analyzing mark-recapture data allow for a variety of encounter information taken from a large geographic region to be included. The addition of extra parameters increases degrees of freedom, but also improves estimates of true survival. Increasing the complexity of a model also requires an increased sampling effort. The Barker (1997) model, for example, includes live recaptures, dead recoveries, and resighting between capture periods. To date, few studies have disentangled true survival and fidelity in a nongame avian system. The Barker model has been used in systems that involved South Island Oystercatchers (*Haematopus finschi*, Sagar et al. 2002), Peregrine Falcons (*Falco peregrinus*, Kauffmann et al. 2003), marine mammals (Hall et al. 2001, Mizroch et al. 2004), and several game species (reviewed by Sandercock 2006). I used the Barker model to analyze mark-recapture data from an American Oystercatcher population in Massachusetts and to estimate true survival and site fidelity. Joint-analysis models are an invaluable addition to mark-recapture analyses of migratory shorebirds because they allow for the inclusion of multiple years of resighting data collected during migration and on the wintering grounds.

American Oystercatchers (*Haematopus palliatus*) nest on coastal beaches and salt marshes from Texas to Nova Scotia (Nol and Humphrey 1994). The Atlantic Coast population was recently estimated at 10,971 (\pm 298) individuals (Brown et al. 2005). Knowledge about the breeding biology of the American Oystercatcher in North America is dominated by studies in core southern populations along the U.S. Atlantic Coast (Nol 1989, Davis et al. 2001, McGowan et al. 2005, Wilke 2007, Sanders 2008). Within the last 70 years, the American Oystercatcher has expanded its breeding range north to include most of the northeastern U.S. (Davis 1999, Mawhinney and Benedict 1999, Nol

et al. 2000, Davis et al. 2001). Northward extension may be a recolonization of formerly occupied habitat (Audubon 1835, Forbush 1912, Bent 1929). As American Oystercatchers continue to move north in the northeastern U.S. (Fig. 1.3), recent evidence shows they are declining overall (Mawhinney and Benedict 1999, Nol et al. 2000, Davis et al. 2001) and have recently been listed as a “Species of High Concern” in the U.S. Shorebird Conservation Plan (Brown et al. 2001). No quantitative estimates of survival have been published for American Oystercatchers, but Davis (1999) used unpublished mark-recapture data from Nol (1985) to estimate apparent annual survival of breeding American Oystercatchers in Virginia using a CJS model. That analysis estimated annual survival as 0.949 for the Virginia population. However, they probably underestimated survival because they could not distinguish permanent emigration from mortality.

I studied annual survival of American Oystercatchers breeding in Nantucket County, Massachusetts. Using models of Barker (1997) and Program MARK (White and Burnham 1999), I analyzed four years of mark-recapture data for 97 American Oystercatchers breeding in Massachusetts. I had two objectives: 1) To estimate true survival (S) using the Barker model and compare these results to estimates of apparent survival from oystercatchers in Virginia (Davis 1999), and 2) To ask how emigration in the population impacted apparent survival. I also examined the relative impact that movement has on the true survival of a long-lived shorebird.

STUDY AREA AND METHODS

I color banded American Oystercatchers from 2005 – 2008 on the Nantucket Islands. During the nesting season (approximately 15 March – 1 August), I identified

breeding pairs by searching potential nesting areas for adult oystercatchers. Once a pair of adults was located, attempts to determine the nesting status were made from a distance to minimize disturbance to the pair. I observed each pair and recorded copulation, incubation, aggressive displays toward conspecifics, or defense of territory from potential predators. If nesting status could not be determined from a distance, the nesting area would be approached to check for the presence of a nest scrape or nest. Breeding pairs were not trapped during the egg laying stage or the egg hatching stage (McGowan and Simons 2005). In all years but 2008, I captured breeding adults with decoys, playbacks, and leg-hold noose mats (McGowan and Simons 2005). Later, I tried other methods, including self-releasing box traps (Mills and Ryder 1979), walk-in traps (Bub 1991), and drop (Bub 1991) and small whoosh nets (Fig. 3.1, Doherty unpublished) that used decoys as well. Although others have experienced high trapping efficiency of oystercatchers with drop nets in Virginia (Doherty, pers. comm.) and self-releasing box-traps in South Carolina (Sanders, pers. comm.), no oystercatchers were successfully trapped in Massachusetts using techniques other than noose mats and the whoosh net.

I fitted each bird with a U.S. Geological Survey #5 metal band (USGS, U.S. Bird Banding Laboratory, Laurel, MD, USA) on the right tarsometatarsus and a pair of American Oystercatcher Working Group (AOWG) coded Darvic color bands (Haggie Engraving, Inc; #6; Fig. 3.2) were affixed to each tibiotarsus. Yellow bands with black engraving identify birds banded in Massachusetts. Each band was engraved with a two character code (Fig. 3.2, color band [39]). I used a pair of identical bands, one on each leg, both to enhance readability and also to quantify band loss. Although American Oystercatchers exhibit sexual dimorphism, there was sufficient overlap in the

morphometric characters to preclude separating males and females by body size (Nol and Humphrey 1994). Consequently, I pooled sexes together.

I calculated survival and fidelity based on resights of 97 color banded adult oystercatchers using two types of observations: population surveys and opportunistic sightings. As Massachusetts Division of Fisheries and Wildlife - Natural Heritage and Endangered Species Program (MDFW) coordinated shorebird monitors conduct nest surveys within the study area. Shorebird monitors checked breeding pairs every 2 – 4 days throughout the extent of the nesting season (early March – late August), and noted the presence of banded individuals. These observations were later classified as breeding or nonbreeding. All other resights occurred outside of the study area and outside of the nesting season. These opportunistic observations were collected by volunteers and submitted to the AOWG or by fellow AOWG biologists during nonbreeding surveys along the Atlantic and Gulf Coasts.

Analytical approach

I used a recently developed mark-recapture method for the joint-analysis of simultaneous information from live resightings, live recaptures, and dead recoveries (Barker 1997). These encounter categories were defined as:

1. *Local resights*. These were banded birds that were captured or resighted within Nantucket County during the breeding season (March 15 – August 1).
2. *Distant resights*. These were banded birds that were resighted outside of Massachusetts during the open interval (August 1 – March 15).
3. *Dead recoveries*. These were bands or banded carcasses collected.

I chose to use the Barker model specifically because it can use multiple types of encounter data simultaneously. Using Program MARK, the model obtains parameter estimates by maximizing the likelihood function constructed by the probabilities of each unique encounter history (White and Burnham 1999). The Barker model (1997) estimates seven parameters. The parameters and their definitions are described according to Barker and White (2001) as follows:

True survival (S_i) = probability that a bird survives at i and at $i + 1$.

Encounter probability (p_i) = probability of detecting a bird, alive at i .

Recovery probability (r_i) = probability that a bird dies between i and $i + 1$, is reported.

Resighting probability (R_i) = probability that a bird alive between i and $i + 1$, is resighted.

Resighting' probability (R'_i) = probability that a bird dies between i and $i + 1$, is resighted before it died.

Site fidelity (η_i) = probability that a bird at risk of capture at i , is at risk of capture at $i + 1$.

Temporary emigration (η'_i) = probability that a bird not at risk of capture at i , is at risk of capture at $i + 1$.

I compiled encounter history records for adult birds ($n = 97$) captured from 2005 through 2008 in Nantucket (Table 3.2). The marked birds can be encountered as alive or dead during the sampling period (L) or during the interval between sampling periods (D);

therefore, the encounter history is formatted LDLD. A '1' in the 'D' element means that the bird was reported dead during the interval, and a '2' in the 'D' element means the bird was resighted alive during the interval; A '1' in the 'L' element means animal resighted alive during sampling period, and a '0' in either element ('D' or 'L') indicates that the bird was not encountered. The recapture period was defined to include the breeding season (15 March – 1 August). This was when my capture and resight effort were most intense. Marked adults observed throughout the remainder of the year (1 August – 15 March) outside of Massachusetts were classified as interval resights. During the early months of the interval (1 August – 13 October), oystercatchers were consistently observed in post-breeding flocks at Monomoy Island – South Beach Complex (MISB). Because MISB is approximately 20 km north of Nantucket (Fig. 1.2), these resightings were not included because I wanted to estimate winter resighting probability using R , and these post-breeding resights occurred prior to a southern directed migration and wintering season. Not including these data has the potential to negatively bias some of the Barker parameter estimates, but I am confident this is not the case because there were no cases of adult oystercatchers not resighted in the study area but observed at MISB.

I used a set of models incorporating constraints on different parameters and used model notations of Lebreton et al. (1992) with the subscripts ' t ' and '.' representing temporal variation and the absence of variation over time, respectively. The Barker model allows for the inclusion of three distinct types of animal movement: random temporary emigration, permanent emigration, and Markov emigration. Random temporary emigration ($\eta = \eta'$) is when a bird can leave the population and later return. Permanent emigration ($\eta' = 0$) means that if a bird leaves the study area, it never returns

to the population. This is an assumption in CJS models. The third type of movement, Markov emigration, is when a bird's risk of capture is dependent of its risk of capture in the preceding capture period. Markov movement models assume no constraints on η_t and η'_t .

I assessed the fit of these competing models using an information-theoretic approach (Burnham and Anderson 2002). Selection of the best fit model model was done using Akaike's Information Criterion corrected for a small sample size (AIC_c ; Lebreton et al. 1992) which calculates the log-likelihood of the observed encounter history given the model (i) and the number of parameters (K). I also used the model selection strategy recommended by Burnham and Anderson (2002) for selecting the best model from a set of candidate models. This approach recommends considering all models that are within 2 units ($\Delta AIC_c < 2$) from the model that minimized AIC_c .

I calculated the goodness-of-fit (GOF) for these models using a parametric bootstrap procedure (White and Burnham 1999). The bootstrap GOF test assesses the amount of variation in data and can be used to estimate a variation inflation factor, \hat{c} . This GOF test was applied to the global model and compares the observed deviance to randomly generated values obtained from the fitted model. If a small proportion (< 5%) of the bootstrapped simulated values are larger than the observed values, then the GOF test provides evidence that the model fits the data poorly. The \hat{c} values can be calculated by dividing the observed deviance of the global model by the mean deviance estimated from the bootstrap replications. After the bootstrap procedure, the models were adjusted for overdispersion and the quasi-likelihood AIC ($QAIC_c$) values were reported.

Since apparent survival (ϕ) is the product of survival (S) and site fidelity (η), I calculated apparent survival of Nantucket oystercatchers using ($\phi = S \eta$). I used parametric bootstrap resampling to estimate a 95% confidence interval (MathWorks 2007). The mean and confidence interval for adult survival (S) and site fidelity (η) were randomly selected from a beta distribution which bounds the distribution between 0 and 1. From these distributions, I randomly drew each parameter to fill the formula and repeated this process for 10,000 iterations.

RESULTS

I captured and marked a total of 97 (65 Nantucket, 24 Tuckernuck, 8 Muskeget) breeding American Oystercatchers from 2005 to 2008 in Nantucket, Massachusetts (Table 3.1), and established a marked population (Fig. 3.3). In addition, 121 interval sightings of the 97 marked birds from Nantucket (Fig. 3.4) were included in the analysis. Table 3.3 (and Fig. 3.5) shows the spatial distribution of interval resighting events that occurred outside of the study area from 2005 – 2008. No dead recoveries from outside the study area or observation of missing color bands were reported. However, two recoveries occurred during capture periods. Currently, Program MARK cannot include recoveries during capture period, so these two events were entered as recoveries in the interval following the capture period. Since this was relatively infrequent, I expect it not to bias my estimates.

Model selection

The parametric bootstrap GOF test indicated good fit for the most general, time-dependent model ($S_t p_t r_t R_t R'_t \eta_t \eta'_t$). The data were corrected for small sample size and overdispersion using the estimated variance inflation factor (\hat{c}) of 1.76. The Akaike weights in Table 3.4 provide evidence in favor of a particular model being the best fit of the candidate models. The two top models have a combined Akaike weight of 0.62 (Table 3.4). There was little support for the remaining models, which suggests there is no annual variation in survival (S), capture probability (p), or immigration (η').

The model that minimized QAIC_c was the “time fidelity” model ($S.p.r.R.R'.\eta_t \eta'$) (Table 3.5). This model included site fidelity as a function of time but held all other parameters constant (Table 3.5). The next best model was the “constant fidelity” model ($S.p.r.R.R'.\eta.\eta'$) which is identical to the best fit model except that annual variation was removed from site fidelity (Table 3.4). Among the top seven models, there was no evidence for annual variation in true survival and encounter probability. Although these parameter values are constant in the top two models, the estimates reported are different (Table 3.5). The parameter estimates considered are derived from the “constant fidelity” model because it represents the best compromise between model complexity and data fit. The ΔQAIC_c was less than 2.0 (0.46) and there were two fewer parameters estimated by the model ($K = 7$). There was no evidence of temporal variation in true survival. The “time fidelity” and “constant fidelity” models estimates of true annual survival for adult oystercatchers nesting in Nantucket County, MA were 0.940 (SE 0.029) and 0.932 (SE 0.035), respectively, and both estimated an

encounter probability of 1.000 (SE 0.000). The probability of live resightings occurring during the open interval was high ($R = 0.49$, $SE = 0.046$) which indicates that a marked oystercatcher has a 49% (CI 95% = 39.8 – 57.9) chance of being resighted outside of Massachusetts during the nonbreeding season. Conversely, the probability of resighted birds later dying during the same open interval was low ($R' = 0.048$, $SE = 0.255$).

Disentangling oystercatcher movements

Site fidelity is the probability that a marked oystercatcher returned to breed in Nantucket County the following year. From the best fit model (“time fidelity”), site fidelity was estimated with annual variation included and ranged from 0.885 to 1.000 (Table 3.5). The geometric mean was used to obtain a single probability estimate for site fidelity (0.929, SE 0.049). The model predicts that approximately 93% of the breeding population returns during the subsequent breeding season. The mean site fidelity estimated using the time-dependent model is not different from the constant model (Fig. 3.6). The complement to site fidelity is permanent emigration ($1 - \eta$). Therefore, this estimate indicates that approximately 7.1% of breeding oystercatchers in Nantucket permanently emigrated from the study area to regions where they are no longer detectable. Relative to the estimated population size in 2007, this equates to approximately 9 individuals permanently emigrating from Nantucket County each year.

The model predicted no immigration into the study population ($\eta' = 0.000$). In the Barker model, $\eta' = 0.000$ means that marked birds in the population are likely to be recaptured in the study area year after year. If a marked bird is not resighted during any capture period, then it is unlikely that they will be subsequently resighted again. If a

parameter is estimated to be zero, the estimate is valid but the associated standard error is not. These results, coupled with a high detection probability, suggest that adult oystercatchers that emigrate never return to nest in Nantucket. The candidate models that included temporary random emigration ($\eta' = \eta$) and Markov movement (η' and η are not constrained) offered no significant improvement (Table 3.4).

Comparison to Virginia study

Comparable estimates of American Oystercatcher survival are from a mark-recapture study in Virginia. Nol (1985) estimated adult return rates ($rr = 0.85$) and Davis (1999) later analyzed the same data to estimate apparent annual survival rates ($\phi = 0.949$). Davis (1999) did not correct the model to account for a small sample size ($n = 59$). To arrive at a single estimate for apparent survival, Davis (1999) removed any ϕ with a standard error less than 0.05. This process inflated apparent survival (0.949).

Using CJS models, I re-analyzed the Virginia data generated from Nol (1984, 1985, 1989) and examined (Davis 1999) again adhering to the protocol outlined in this study (Table 3.6). An annual apparent survival estimate was computed for oystercatchers nesting in Virginia from 1978 – 1983. Of the four candidate models, the best fit ($\Delta\text{QAIC}_c < 2$) were the global model ($\phi_t p_t$) and time-dependent model ($\phi_t p$). The model, $\phi_t p$ ($\Delta\text{QAIC}_c = 0.06$, $K = 6$), was reported (Table 3.7).

The recapture probability was ($p = 0.982$, SE 0.013) and apparent survival ($\phi_\mu = 0.886$, SE 0.040) ranged from 0.74 to 0.97 (Table 3.8). Model results are similar to my Barker model estimation of apparent survival ($\phi = 0.88$ SE 0.053) in our study, with results reporting a high rate of survival and an encounter probability close to one.

Without disentangling true survival from site fidelity, the Virginia estimates of apparent survival underestimate true survival.

DISCUSSION

Using an unusually detailed set of mark-recapture data on American Oystercatchers breeding in Massachusetts, I found that oystercatchers exhibited high survival, strong, yet variable breeding-site fidelity, and emigrate permanently. More importantly, my results suggest that breeding-site fidelity is a demographic parameter required to understand the dynamics of this long-lived shorebird.

Adults were strongly and consistently faithful to breeding sites with η ranging from 88.5 to 100%. The variation may be due to sexual differences. Sagar et al. (2002) detected high levels of adult survival (0.892, SE 0.034) from a 13-year study of South Island Oystercatchers (*H. finschi*) nesting in farmlands in Canterbury, New Zealand and then wintering along the New Zealand Coast. The results presented are similar to those reported for South Island Oystercatcher, including constant true survival and variable measures of site fidelity. New Zealand oystercatcher survival was independent of sex, site fidelity was sex-dependent with males have a greater probability to return to the study site (0.982, SE 0.009) while females had a greater tendency to emigrate (0.905, SE 0.017). Sex differences may be one of the reasons for high levels of variation in site fidelity in American Oystercatchers. Pooling the encounter histories probably did not impact survival estimates because many studies have reported oystercatcher survival to be sex-independent (Sagar et al. 2002, Nol 1985, Safriel et al. 1984). In fact, Ens et al. (1993) found that the probability of *H. ostralegus* changing territories was far greater in

females than in males, and Sagar et al. (2002) hypothesized that *H. finschi* males are more likely than females to return to a breeding territory after mate loss due to divorce or mortality based on η' being greater in females. My data did not support this theory because the best fit models estimated $\eta' < 0.000$. The potential difference among sexes in American Oystercatchers deserves further study.

American Oystercatchers have nested in the study area for 40 years, and have continued to increase. One potential hypothesis for continued growth of the northern breeding populations may be due to a northward dispersal of juveniles and displaced adults. Assuming the movement parameters presented in this study, η and η' , are similar to those estimated in southern populations, my findings from Nantucket suggest that displaced adults from southern populations are likely not be driving the continued growth of northern populations. It will be important to collect similar data in core southern populations to ultimately identify the parameter or parameters driving the observed population growth before one can develop effective conservation and management. Continued work at Nantucket is needed to diagnose these demographic processes and their relative influence on population growth.

Birds banded at Nantucket were resighted outside of Massachusetts with a probability of nearly 50%. This is an exceptionally high frequency for a migratory bird. During the winter season, nonbreeding oystercatchers congregate into large flocks along the Atlantic Coast from New Jersey to Florida. These winter flocks have a patchy distribution because the flocks occur within close proximity to major shellfish beds. The majority of these winter roosts are regularly surveyed as part of this study. The

resighting probability reported provides evidence that the winter roost surveys conducted throughout the major traditional sites in the southeastern U.S. have good coverage.

Comparison of survival rates with other studies

I found high adult survivorship for oystercatchers at Nantucket (0.943). American Oystercatchers re-colonized Nantucket approximately 40 years ago and has now reached 130 individuals. During the same period, oystercatchers have declined substantially in the southern, core areas of the breeding range. Recent surveys suggest a 21% decline since 1986 in South Carolina (Sanders et al. 2008) and 47% decline in Virginia from 1984 – 2003 (Wilke et al. 2005). Could different rates of adult survival be driving these two contrasting population trajectories, or are subadult and adults being displaced from the southern regions and dispersing north? I was not able to identify the reason or reasons for population growth. However, with exceptionally high survival, my data suggests that the observed growth in Nantucket is more influenced by the variability in breeding-site fidelity than survival.

The similar survival rates estimated from growing and declining populations support the hypothesis that variation in adult survival is not a demographic rate influencing current population changes. Estimated true survival for Nantucket oystercatchers was higher than any other Atlantic Coast estimate. This is not surprising because neither of these studies accounted for permanent emigration and only estimated apparent survival. Then again, apparent survival calculated from S and η are strikingly similar to the Virginia estimate (0.87) from Davis (1999) ($Z = 1.96$, $p = 0.976$). The wide range of η_t (0.89 – 1.00) may be the demographic rate influencing the range of

local, or apparent, survival. However, all other values were not assessed using robust methods, like the Barker model, and these comparisons should be considered with some prudence because the former studies were unable to distinguish survival and movement.

Annual survival of Massachusetts oystercatchers was at the high end of the range of values of oystercatchers in general. The only higher survivorship is for a 10-year study of Eurasian Oystercatchers (*H. ostralegus*) breeding on the island of Schiermonnikoog in the Netherlands estimated annual adult survival rates of 0.950 (Hulscher 1989). Other estimates of annual survival include 0.902 from a 14-year period of a breeding population in Skokholm, Wales (Safriel et al. 1984), 0.891 for oystercatchers during the nonbreeding season on the Exe Estuary in England (Durrell et al. 2003), and 0.919 for a breeding population that was studied on the Isle of May, Scotland (Harris and Wanless 1997). Additionally, a true survival of 0.892 was found for the South Island Oystercatcher of New Zealand (*H. finschi*, Sagar et al. 2002). Unlike American Oystercatchers, all these populations breed on gravel-bed rivers or in agricultural fields and then migrate to the coast for the nonbreeding season. Because *H. palliatus* spends its annual cycle on coastal beaches and marshes, comparisons made to the survival rates of other oystercatcher species may be revealing about the impact a change in life history may have on survival. Other oystercatcher species have recently expanded their breeding inland (reviewed by Goss-Custard et al. 1996). It is hypothesized that the shift has been directed by a number of factors including the degradation of suitable coastal habitat, increased density of coastal breeding oystercatchers, and a drastic change in behavior (Heppleston 1972).

Dispersal into new breeding areas may be favored if resources newly acquired by this dispersal outweigh the cost of seasonal migration (Pérez-Tris and Tellería 2002). Oystercatcher species that have dispersed inland to take advantage of available agricultural land have also incurred a decrease in life expectancy (Ens et al. 1996). This trend can be identified in the direct relationship of fecundity and indirect relationship of survival to migratoriness. Due to a lack of data, it is unclear if this relationship is present in the Eurasian Oystercatcher. Furthermore, American Oystercatchers breeding in Massachusetts would be expected to invest more effort in fecundity and have a lower annual survival relative to birds breeding and wintering in the southern regions of the species distribution. A more southern, resident population would be expected to have a survival rate greater than 0.94. Additional research is needed to determine if the relationship of survival, fecundity, and migratoriness exists in this species. In particular, survival and fidelity should be estimated using the Barker model for a southern population that is known to remain within close proximity of its breeding sites (e.g. South Carolina).

TABLES

TABLE 3.1 – Parameters, notation, and definitions of demographic parameters associated with mark-recapture models (Return rate, Cormack-Jolly-Seber, and Barker models).

Parameter	Notation	Definition
Return rate	rr	proportion of marked birds that are recaptured (or resighted) in the following or some future year.
Survival (apparent)	ϕ	probability that a bird survives between sampling periods and returns to the sampling area.
Site propensity	γ^*	probability that a bird returns to the sampling area in the subsequent sampling period.
Detection rate	p^*	probability that an observer detects the bird, if it survives, returns to the sampling area, and is available for capture.
Recapture probability	p	probability that a bird returns to the sampling area in the subsequent period and is detected.
Survival (true)	S	probability that a bird survives between sampling periods.
Site fidelity	η	probability that a bird returns to the sampling area, if it survives.

TABLE 3.2 – Encounter history matrix for American Oystercatchers breeding in Nantucket, Massachusetts from 2005 – 2008 ($n = 97$).

Encounter history	No. of individuals	Encounter history	No. of individuals
12121212	1	10000000	2
12121202	1	00121212	3
12121000	1	00121210	5
12101012	1	00121202	1
12101010	2	00121200	1
12101000	1	00121012	2
12100000	1	00121010	1
12010000	1	00101210	6
10121212	5	00101200	1
10121210	1	00101010	10
10121010	2	00101000	2
10101212	1	00001212	12
10101202	1	00001210	4
10101200	1	00001010	7
10101010	2	00001000	3
10100000	1	00000012	7
10010000	1	00000010	6

^a The marked birds can be encountered as alive or dead during the sampling period (L) or during the interval between sampling periods (D); therefore, the encounter history is formatted LDLDLDL. D = 1: reported dead during the interval; D = 2: resighted alive during the interval; L = 1: animal resighted alive during sampling period; L or D = 0: animal not encountered.

TABLE 3.3 – Summary of encounter histories by location for 97 breeding American Oystercatchers captured from 2005 – 2008 in Nantucket, Massachusetts and recapture events during subsequent breeding seasons and nonbreeding seasons along the Atlantic and Gulf Coasts.

Period	Location	Number re-encountered each year ^a									
		2005		2006		2007		2008		Total	
		Mark	Obs	Mark	Obs	Mark	Obs	Mark	Obs	Mark	Obs
Recapture	Nantucket	7	-	24	12 ^c	22	55	12	51	65	118
	Tuckernuck	14	-	6	11	2	14	2	13	24	38
	Muskeget	4	-	2	4 ^c	2	7	0	5	8	16
Open interval	New York	-	0	-	1	-	1	-	-	-	2
	New Jersey	-	2	-	1	-	5	-	-	-	8
	Virginia	-	1	-	6	-	11	-	11	-	29
	North Carolina	-	2	-	0	-	0	-	-	-	2
	South Carolina	-	3	-	5	-	5	-	4	-	17
	Georgia / NE Florida	-	1	-	4	-	3	-	1	-	9
	Gulf Coast	-	0 ^b	-	9	-	25	-	20	-	54
	<i>n</i> encounters	25	9	32	53	26	126	14	105	97	293

^a Mark: oystercatchers that were captured and color banded; Obs: oystercatchers that were observed either during the recapture period or the subsequent interval.

^b The Gulf Coast winter surveys were not conducted in 2005.

^c A single event was the recovery of a marked bird.

TABLE 3.4 – The 13 candidate models developed for estimating survival probabilities from 96 breeding American Oystercatchers in Nantucket County, Massachusetts. For each model the following information is given: corrected quasi-likelihood Akaike’s Information Criterion (QAIC_c), differences in QAIC_c values from the best fit model (Δ QAIC_c), QAIC_c weights (w_i), Model Likelihood, the number of parameters (K), and QDeviance (QDev). Description of the characteristics of the model for each parameter are the subscripts: ‘.’ constant through time, ‘t’ time dependence in each year, ‘0’ parameter constrained at 0, and ‘1’ parameter constrained at 1.

No.	Model description	QAIC _c ^a	Δ QAIC _c	w_i	Model Likelihood	K	QDev
1	$S.p.r.R.R'.\eta_t \eta'$	286.61	0.00	0.28	1.00	9	65.48
2	$S.p.r.R.R'.\eta.\eta'$	287.06	0.46	0.22	0.80	7	70.15
3	$S.p.r.R.R'.\eta. = \eta'$ ^b	288.37	1.77	0.12	0.41	5	75.61
4	$S.p.r.R.R'.\eta_1 \eta'_0$ ^c	288.37	1.77	0.12	0.41	5	75.61
5	$S.p.r.R.R'.\eta_t \eta'_t$	288.73	2.12	0.10	0.35	10	65.48
6	$S.p_t r.R.R'.\eta.\eta'$	289.35	2.74	0.07	0.25	9	68.22
7	$S.p.r.R.R'.\eta.\eta'_1$	290.45	3.84	0.04	0.15	6	75.61
8	$S_t p.r.R.R'.\eta.\eta'$	291.36	4.75	0.03	0.09	10	68.11
9	$S.p.r_t R.R'.\eta.\eta'$	292.79	6.18	0.01	0.05	10	69.54
10	$S.p.r.R_t R'_t \eta.\eta'$	294.28	7.67	0.01	0.02	12	66.75
11	$S.p.r.R_t R'_t \eta.\eta'_t$	296.44	9.83	0.00	0.01	13	66.75
12	$S_t p_t r_t R.R'.\eta.\eta'$	299.97	13.36	0.00	0.00	15	65.92
13	$S_t p_t r_t R_t R'_t \eta_t \eta'_t$	308.57	21.96	0.00	0.00	21	61.12

^a Akaike’s Information Criterion adjustment (QAIC_c) where $\hat{c} = 1.76$.

^b The constraint $\eta = \eta'$ represents temporary random emigration.

^c The constraint $\eta' = 0$ is arbitrary as η' does not contribute to the likelihood function if $\eta = 1$.

TABLE 3.5 – Parameter estimates under the two best fit models in Table 3.4: time-dependent fidelity ($S, p, r, R, R', \eta_t, \eta'$) and constant fidelity ($S, p, r, R, R', \eta, \eta'$) for breeding American Oystercatchers in Nantucket County, Massachusetts. Parameters are as follows: S = true survival, p = capture probability, r = reporting rate, R = live resightings, R' = resighting before mortality, η = site fidelity, and η' = immigration.

Fidelity	Parameter	Estimate	SE	LCL	UCL
Time-dependent	S	0.940	0.029	0.852	0.977
	p	1.000	0.000	1.000	1.000
	r	0.133	0.125	0.018	0.561
	R	0.484	0.046	0.396	0.573
	R'	0.000	0.000	0.000	0.000
	η_{2006}	0.905	0.083	0.587	0.985
	η_{2007}	1.000	0.000	1.000	1.000
	η_{2008}	0.889	0.054	0.731	0.959
	η_{μ}^a	0.930	0.048	0.837	1.000
	η'	0.000	0.000	0.000	0.000
Constant	S	0.932	0.035	0.822	0.976
	p	1.000	0.000	1.000	1.000
	r	0.118	0.114	0.015	0.534
	R	0.487	0.046	0.398	0.576
	R'	0.064	0.267	0.000	0.998
	η	0.938	0.035	0.822	0.980
	η'	0.000	0.000	0.000	0.000

^a η_{μ} is the geometric mean calculated from η_t .

^b SE (η_{μ}) was estimated using the coefficient of variation.

TABLE 3.6 – Encounter history matrix for adult American Oystercatchers breeding in Virginia from 1978 – 1983 (Nol, unpublished data).

Encounter history ^a	No. of individuals
111111	14
111110	2
111100	3
111000	1
110000	8
101110	1
101100	1
100000	1
011111	5
011110	3
011000	1
010000	3
001111	2
001110	1
000111	10
000110	3

^a Each element represents each sampling period; 1 = Capture or resighting event; 0 = no capture or resighting.

TABLE 3.7 – The four candidate models developed by Davis (1999) for estimating survival probabilities from 59 breeding American Oystercatchers in Virginia from 1978-1983 (Nol, unpublished data). For each model the following information is given: corrected quasi-likelihood Akaike’s Information Criterion (QAIC_c), differences in QAIC_c values from the best fit model (Δ QAIC_c), QAIC_c weights (w_i), Model Likelihood, the number of parameters (K), and QDeviance (QDev). Description of the characteristics of the model for each parameter are the subscripts: ‘.’ constant through time and ‘t’ time dependence in each year.

No.	Model	QAIC _c ^a	Δ QAIC _c	w_i	Model Likelihood	K	QDev
1	$\phi_t p_t$	177.34	0.00	0.48	1.00	9	34.02
2	$\phi_t p.$	177.41	0.06	0.47	0.97	6	40.62
3	$\phi. p_t$	183.18	5.83	0.03	0.05	6	46.39
4	$\phi. p.$	183.21	5.87	0.03	0.05	2	54.82

^a Akaike’s Information Criterion adjustment (QAIC_c) where $\hat{c} = 1.23$.

TABLE 3.8 – Estimates of apparent survival (transitions) and encounter probabilities (occasions), standard error (SE), lower 95% confidence limit (LCL), and upper 95% confidence limit (UCL) for breeding American Oystercatchers in Virginia from 1978-1983 under the best fit model in Table 3.7.

Parameter	Estimate	SE	LCL	UCL
Apparent survival				
1978 – 1979	0.992	0.038	0.009	1.000
1979 – 1980	0.725	0.071	0.568	0.841
1980 – 1981	0.941	0.040	0.793	0.985
1981 – 1982	0.911	0.042	0.786	0.966
Average ^a	0.886	0.050 ^b	0.789	0.984
Encounter probability				
Constant	0.982	0.013	0.931	0.996

^a Geometric mean.

^b SE for average was estimated using the coefficient of variation.

FIGURES

FIGURE 3.1 – Side view of whoosh net and rigging (image reproduced with permission of P. Doherty).

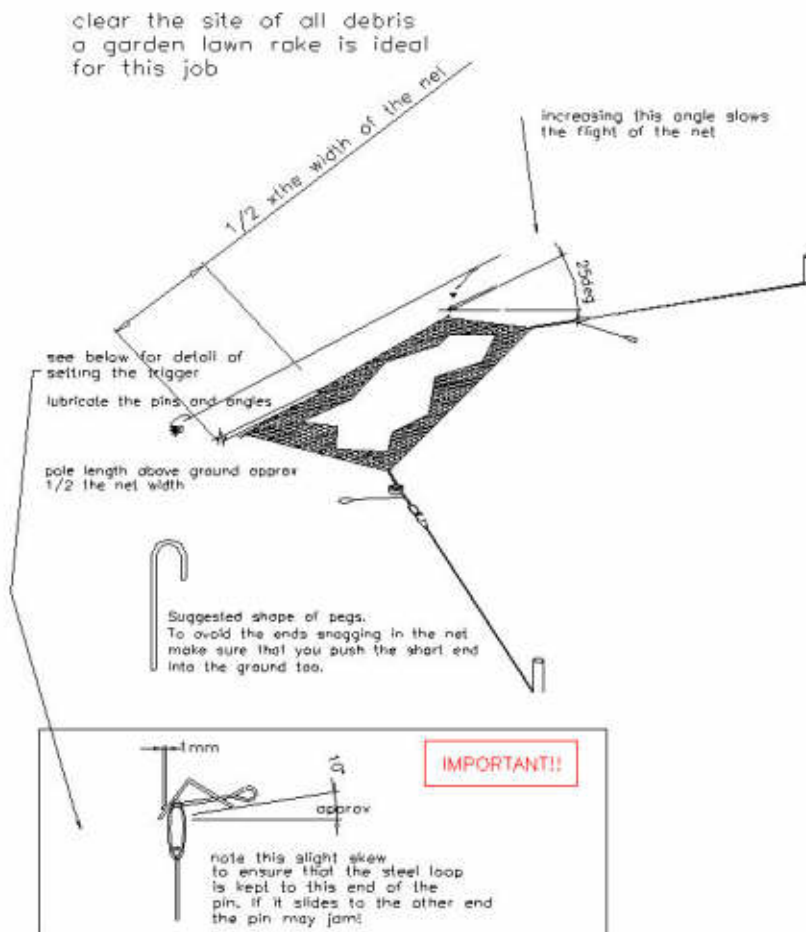


FIGURE 3.2 – An adult color banded American Oystercatcher (*Haematopus palliatus*) fitted with two identical color coded Darvic wraparound bands on each tibia; the yellow color band identifies this bird as being banded in Massachusetts; the two-character code (39) is repeated on each band and separated by a single dot delimiter (visible on band fitted to the right tibia of this bird); code repetition and double bands help ensure proper identification and monitor band loss; additionally, a U.S. Geological Survey band has been fitted to the right tarsus.



FIGURE 3.3 – Total number of American Oystercatchers nesting in Nantucket, Massachusetts from 2002 – 2008; total oystercatchers banded, newly banded, and resightings during the open interval outside of the study area from 2005 – 2008.

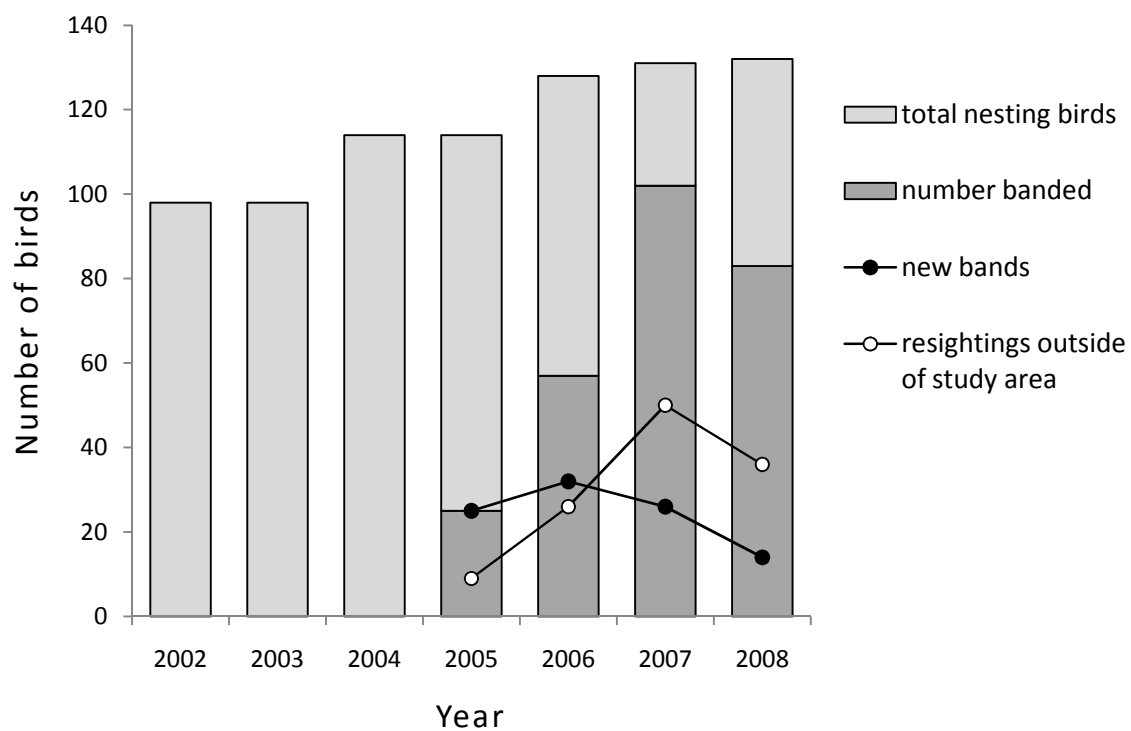


FIGURE 3.4 – Location of capture (circles) and resighting (triangles) events of color banded adult American Oystercatchers breeding in Nantucket, Massachusetts during the capture period (15 March – 1 August).

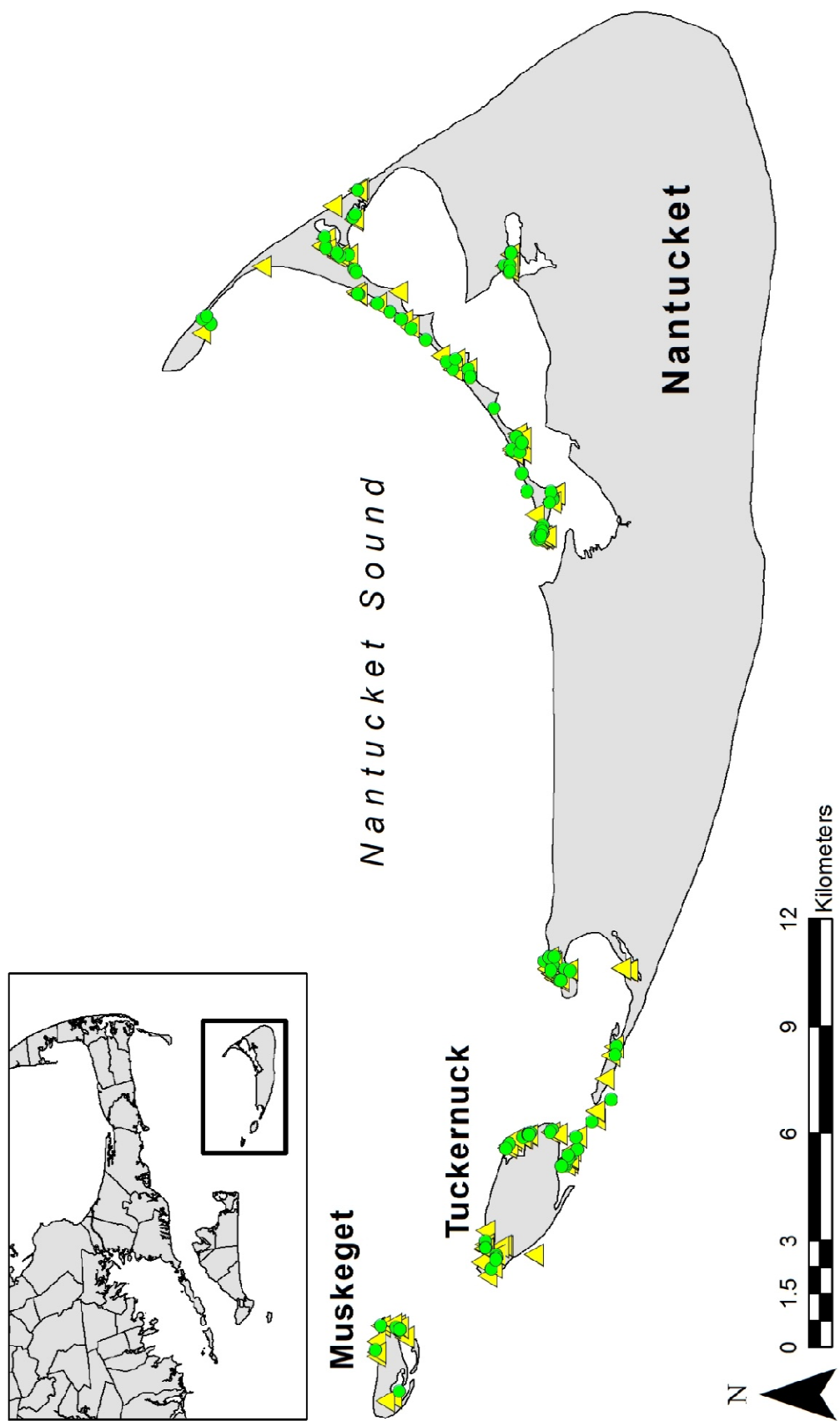


FIGURE 3.5 – Location of resighting events along the U.S. Atlantic and Gulf Coasts of adult American Oystercatchers color banded during the nesting season in Nantucket, Massachusetts, and later observed during the nonbreeding interval (1 August – 15 March) of a) 2005-06, b) 2006-07, c) 2007-08, and d) 2008-09.

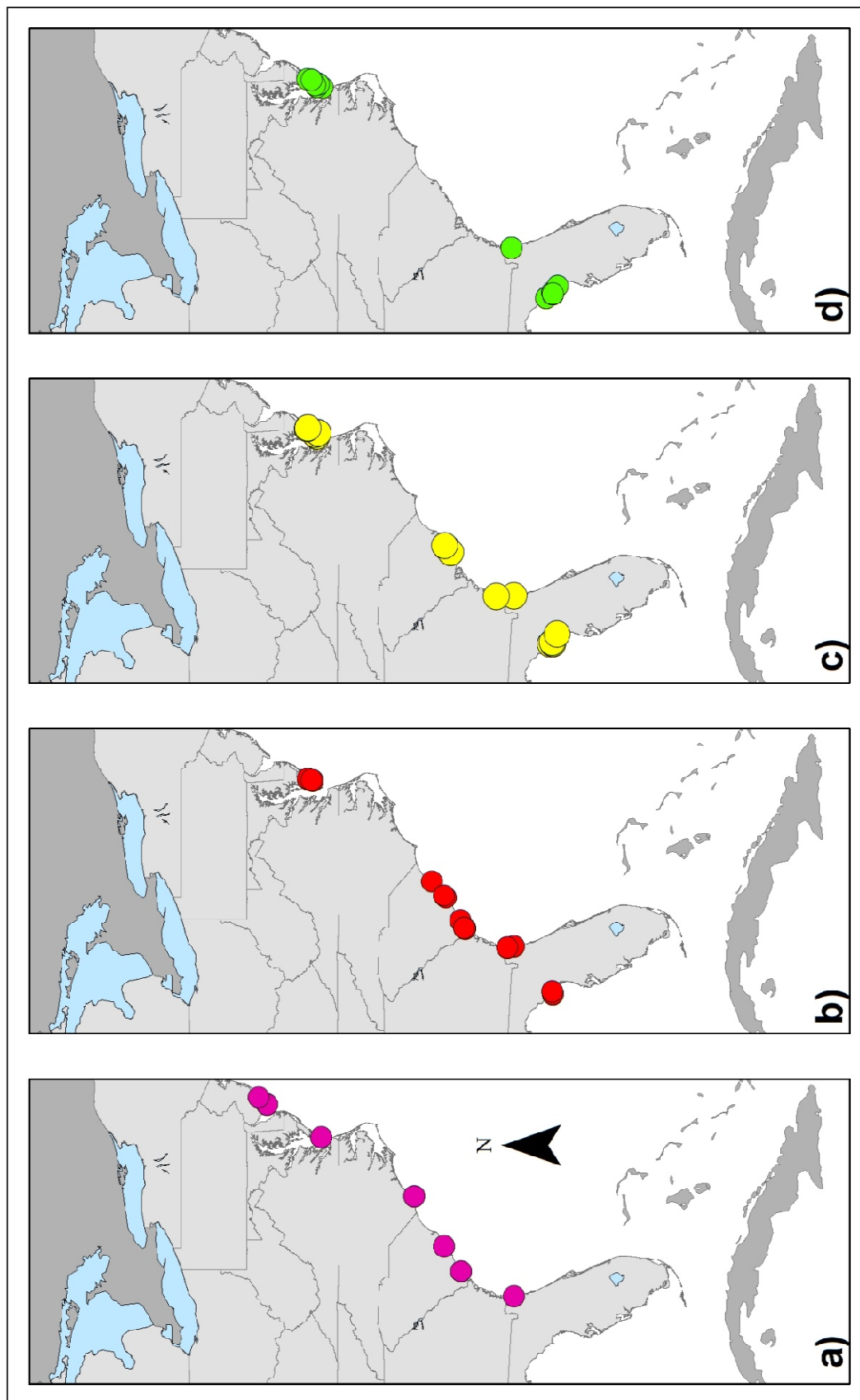
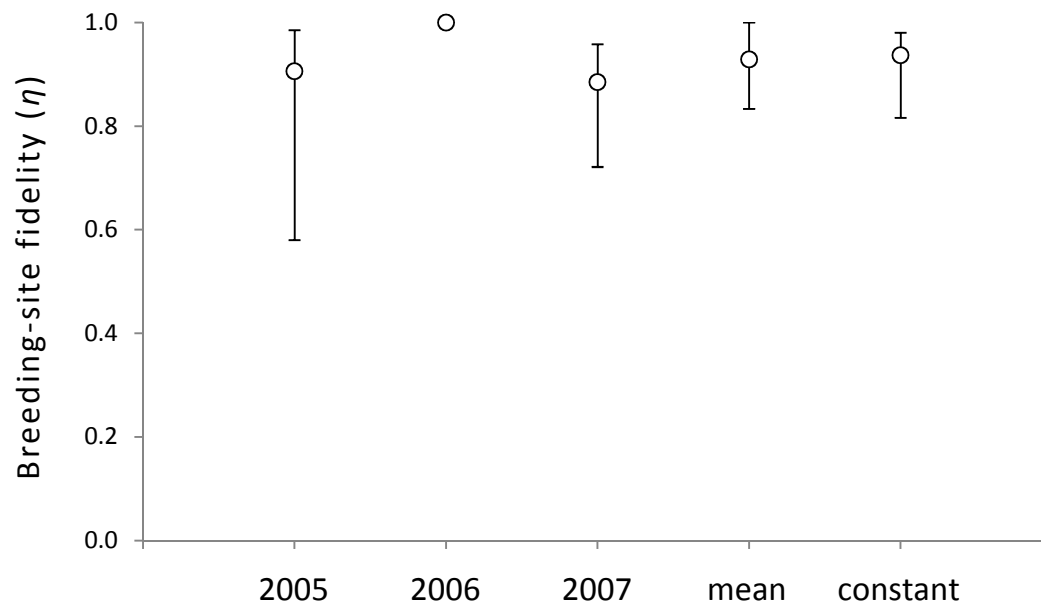


FIGURE 3.6 – Breeding-site fidelity (η) estimates with the associated 95% confidence intervals obtained from the time-dependent model (2005, 2006, 2007, and mean) and the time-independent model (constant) for adult American Oystercatchers breeding in Nantucket, Massachusetts.



CHAPTER 4

Identifying causes of an increasing population of American Oystercatchers

(Haematopus palliatus) in Massachusetts, USA

INTRODUCTION

In many cases, management decisions are implemented using limited data with little knowledge regarding the demographic factors that may be limiting a population or species. The recent surge of interest in endangered and threatened species has rejuvenated research in the demographics of populations at a local level (Kaufmann et al. 2003). Species recovery plans are often implemented in a hasty manner in order for management to take action. Even after recovery plans are drafted and implementation begins, the collection of critical information on the life history of the species with respect to spatially distinct populations is imperative.

Since the initial application of age- and stage-structured population models to conservation and management, the necessity for these analyses has increased for endangered and threatened species. Incorporating demographic data collected from a population, matrix based models allow one to explore the dynamics of a study population (Leslie 1945, 1948). Stage-structured population models rely on parameter estimation of key life history characteristics such as reproduction, annual survival, and transition probabilities. Using perturbation analyses, the potential for change in the population growth rate relative to change in each model parameter can be evaluated.

American Oystercatchers (*Haematopus palliatus*) of the Atlantic Coast have declined over much of their range and the reasons for this decline are unclear (Davis et al. 2001, Wilke et al. 2005, Sanders et al. 2008). I constructed a demographic model and used it to explore factors influencing this decline. In the early 1800s, the American Oystercatcher nested along the entire Atlantic Coast, possibly as far north as Labrador, Canada (Audubon 1835, Bent 1929). By the early twentieth century, hunting and egging

pressure dramatically reduced the northern limit of the range to Virginia where the bird had become a rare nesting species (American Ornithologists' Union 1910, Post and Raynor 1964). After the passing of the Migratory Bird Treaty Act (1918), the species began to recover and to expand its range to the north. Over the past 70 years, the oystercatcher has re-colonized northern breeding areas north to Cape Sable Island, Nova Scotia (Nol and Humphrey 1994). Concurrent to northward range expansion, oystercatchers have declined in the core part of their range south of Virginia (Davis et al. 2001). Notably, the population nesting on Virginia barrier islands declined by more than 50% over the past 20 years (Wilke et al. 2005), and recent surveys in Cape Romain, South Carolina suggest a 21% decline in breeding pairs since 1986 (Sanders et al. 2008).

In 2001, the U.S. Shorebird Conservation Plan designated the Atlantic Coast population of the American Oystercatcher as a "Species of High Concern" because of a small population (~11,000 individuals, Brown et al. 2005), loss of habitat, and increasing threats during the breeding and non-breeding seasons (Brown et al. 2001). Although the management plan lists this species as a priority (Brown et al. 2001), trends of the entire population are unknown, and the majority of studies conducted on breeding and non-breeding populations of American Oystercatchers focus on reporting abundance and reproduction rates for local populations (Nol 1989, Davis et al. 2001, McGowan 2004, McGowan et al. 2005b, Traut et al. 2006, Wilke et al. 2007, Sanders et al. 2008, Thibault 2008). These data are important measures of local production (or fecundity) and can be used to draw comparisons to subsequent years for the study population and/or geographically different populations. However, no analyses have been conducted to evaluate the influence key demographic parameters, such as fecundity, may have on the

growth (or decline) on the global population of American Oystercatchers. Demographic models require an extensive suite of vital rates, many of which have yet to be estimated for American Oystercatchers.

For this study, I designed a stage-structured matrix model to investigate the dynamics of American Oystercatchers using recently derived parameter estimates (Chapters 2 and 3) for a population of breeding birds in Nantucket County, Massachusetts from 2005 – 2008. Since 2003, the Nantucket breeding population increased from 49 to 66 pairs (Fig. 3.3) with an observed population growth rate ($\lambda = N_{t+1}/N_t$) that ranged from 1.000 to 1.163 with an average of 1.063. I produced predictions of population growth rate using Monte Carlo simulations, an assumed stable age distribution, and reproductive values from my study, and performed a perturbation analysis of survivorship, fecundity, and dispersal. I also extended the use of the model to estimate critical levels of key demographic parameters and identify management strategies that target specific demographic parameters and increase λ . Finally, I explored how the model could be used to investigate other American Oystercatcher populations along the Atlantic Coast.

STUDY AREA AND METHODS

In a four-year study, I worked during the nesting seasons from 2005 – 2008 on the three islands within Nantucket, Massachusetts. During the nesting season (15 March – 1 August), I searched for breeding pairs in all suitable habitat. Once I located a pair of adults, attempts to determine the nesting status were made from a distance to minimize disturbance. In all years but 2008, I captured breeding adults on the territory using

decoy, playback, and leg-hold noose mats (McGowan and Simons 2005) or decoy, whoosh net systems (P. Doherty, unpublished). I fitted each bird with a U.S. Geological Survey #5 metal band (USGS, U.S. Bird Banding Laboratory, Laurel, MD, USA) on the right tarsometatarsus. I also put two coded Darvic wraparound color bands (Haggie Engraving, Inc; #6; Fig. 3.2) on each tibiotarsus. Yellow bands with black engraving are unique for every bird banded in Massachusetts and approved by the American Oystercatcher Working Group (AOWG). From 2006 – 2008, I captured nestling oystercatchers by hand to ensure the safety of the young birds. I captured all young and color banded them once they reached age 21 days. Over the course of regular nest checks, monitors were able to confirm the successful fledging of banded young. Breeding oystercatchers typically remain near their breeding territory until late July, thus facilitating the observation of adults associated with a specific banded fledgling.

I calculated survival and breeding-site fidelity based on the encounter history of 97 color banded adult oystercatchers and 39 fledged young using two types of observation: census and opportunistic sightings. As shorebird monitors from Massachusetts Division of Fisheries and Wildlife (MDFW) conducted nest surveys every 2– 3 days within the study area, they also noted the presence of banded individuals. These observations were later classified as breeding bird or non-breeding bird. All other resights occurred outside of the study area and outside of the nesting season. These opportunistic observations were collected by volunteers and submitted to the AOWG or by fellow AOWG biologists during non-breeding winter roost surveys. There were 293 encounters of adult oystercatchers with 170 occurring during the capture period, 121

reported during the open interval between capture periods, and two marked birds were found dead in April 2006 in Nantucket.

From 2005 – 2008, I monitored 168 breeding pairs (2005: 42 nests, 2006: 40 nests, 2007: 46 nests, 2008: 40 nests) to estimate fecundity. After locating an oystercatcher nest, I visited all nest sites every two to four days until the nest failed or young fledged. If a nest failed prior to hatching, I tried to determine the cause of nest failure. If a nest hatched, the status and number of young was monitored every 2 – 4 days until fledging or loss of chicks. I used a synthetic estimate of annual fecundity to account for nests that failed prior to discovery or unobserved nests (F_n , Sandercock et al. 2005). For a more detailed account of this technique, see Chapter 2.

For my demographic model, I estimated annual survival for each stage class, the probability that a breeding bird will return to the study area the subsequent year, the proportion of adults breeding, the rate of immigration of adult oystercatchers into the study population, and the number of female chicks fledged per breeding female in each stage class.

Estimation of survival parameters

Of the 39 fledglings that were banded over the course of this study, four returned to the study area during the breeding season in a subsequent year (Table 4.1). In 2009, preliminary reports documented two marked birds of known age attempting to nest in the study area. American Oystercatchers are thought to not breed until their third or fourth year (Nol and Humphrey 1994), but there are few supporting data for this estimate. Similar to many shorebird species, non-breeding oystercatchers have a tendency to

remain near their wintering grounds until reaching sexual maturity (Nol and Humphrey 1994). This proclivity more than likely contributed to the small number of banded young encountered in subsequent breeding seasons. Sparse data also limited my ability to estimate juvenile and subadult survival. In addition to the encounter histories of locally returning birds of known age, AOWG compiled a more extensive encounter history of these 39 individuals throughout the annual cycle (Table 4.2). In order to collect estimates for these critical probabilities, I employed two approaches. First, I calculated point estimates of the parameters, and second, I extracted estimates of age at maturity from literature from other species of oystercatchers.

Chapter 3 reports estimates of adult annual survival calculated from the encounter history of 97 oystercatchers breeding in Massachusetts from 2005 – 2008. The analyses were conducted in Program MARK (White and Burnham 1999) using the Barker model (Barker 1997, Barker and White 2001) and estimated seven parameters including the probability that an adult bird survives (S_A), the proportion of breeding birds that return to the study area (η_A), the proportion of adults permanently emigrating from the study area ($1 - \eta_A$), the probability that an animal not at risk of capture is at risk of capture in the next year (η'_A), and the probability of detection of adults both during the capture period (p_A) and the open interval (R_A). The Barker model facilitates the inclusion of multiple sources of information which allows for the estimation of survival separate from breeding-site fidelity. Therefore, in this study, adult survival refers to the probability that a bird survives independently of returning to the study area, and local survival (ϕ_A), the probability that a breeding bird survives and returns to the study site, is a product of the two aforementioned parameters ($\phi_A = S_A \eta_A$).

Estimation of local production

I used the following demographic parameters collected during the nesting seasons to produce a synthetic estimate of fecundity (per breeding female) that accounts for variation in nest exposure (F_n , Sandercock et al. 2005) from 188 breeding pairs in Nantucket, Massachusetts from 2005 – 2008:

$$F_A = [(BP \cdot TCL_1 \cdot NEST_1) + ((1 - NEST_1) \cdot RENEST_1 \cdot TCL_2 \cdot NEST_2) + ((1 - NEST_1) \cdot RENEST_1 \cdot (1 - NEST_2) \cdot RENEST_2 \cdot TCL_3 \cdot NEST_2))] \cdot (C/E \cdot FLED \cdot F/C \cdot 0.5)$$

where,

BP = proportion of adults in the total population that are breeding

TCL_i = mean number of eggs laid per nest

$NEST_i$ = probability of a nest surviving to successfully hatch

$RENEST_i$ = probability of renesting after the loss of the previous clutch

C/E = proportion of eggs that hatched to produce chicks

FLED = probability that at least one chick survives to fledge

F/C = proportion of chicks that become fledged young

and subscripts 1, 2, and 3 identify with which nesting attempt the parameter is associated. To estimate confidence intervals for the fecundity calculation, I used parametric bootstrapping. A detailed account of these estimation techniques and the results of this study are found in Chapter 2.

Estimation of immigration

Since the re-colonization of Massachusetts was well documented over that past 50 years, immigration into the state played a role in the population dynamics and may continue to be a critical factor in the local dynamics. A per-capita immigration rate, I_t , quantifying the proportion of new birds entering the study population and birds leaving the study population was added to the projection equation. For this model, immigrants were defined as the proportion of oystercatchers that are breeding on an island that did not hatch within the study site ($I_t > 0$), and emigration were the individuals leaving the local population ($I_t < 0$).

I estimated immigration rates (I_t) from the mark-resight encounter history of adult oystercatchers banded in Nantucket County, Massachusetts from 2005 – 2008. I analyzed the reverse order of the encounter history for a Cormack-Jolly-Seber (CJS) mark-recapture model to estimate the probability (ι_t) that a bird breeding in the study area at year t had also been breeding in the study area at year $t - 1$. In this case, the complement, $1 - \iota_t$, is the rate of adult birds immigrating into the study population. I used a set of candidate models incorporating temporal and constant effects on ι and p (encounter rate), and used model notations of Lebreton et al. (1992) with the subscripts ‘ t ’ and ‘.’ representing temporal variation and the absence of variation over time, respectively.

I assessed the fit of these competing models using an information-theoretic approach (Burnham and Anderson 2002). Selection of the best fit model was done using corrected Akaike’s Information Criterion (AIC_c ; Lebreton et al. 1992) which calculates the number of parameters (K) and the log-likelihood of the observed encounter history

given the model (*i*). I also used the model selection strategy recommended by Burnham and Anderson (2002) for selecting the best model from a set of candidate models. This approach advises considering all models that are within 2 units ($\Delta AIC_c < 2$) from the model that minimized AIC_c .

The goodness-of-fit (GOF) for these models was conducted using a parametric bootstrap procedure in Program MARK (White and Burnham 1999). The bootstrap GOF test can detect overdispersion in the data and can be used to estimate a variation inflation factor, \hat{c} . This GOF test was applied to the global model and compares the observed deviance to randomly generated values obtained from the fitted model. If a small proportion of the bootstrapped simulated values are larger than the observed, then the GOF test provides evidence that the model fits the data poorly. The \hat{c} values can be calculated by dividing the observed deviance of the global model by the mean deviance estimated from the bootstrap replications.

I estimated ι_t from the best fit model and calculated the immigration rate as,

$$I_t = (1 - \iota_t)N_t$$

where the number of adult female birds immigrating into the study population is equal to the product of the immigration rate ($1 - \iota$) and the number of breeding females in the population (N_t).

Estimation of population growth rate

I used series of demographic models to explore the following: (1) projected population trajectory and the potential reasons for the observed increase in breeding pairs in Massachusetts, (2) the relative effect each parameter has on the trajectory of the

population, and (3) the effect of dispersal (i.e. immigration and emigration) on the local population. I used a stage-structured Leslie matrix model and estimated matrix elements from the compilation of fecundity rates (Chapter 2) and mark-resight data (Chapter 3) for the study population.

The post-breeding model describes the dynamics of the female population. To estimate the intrinsic growth rate (λ), I constructed a stage-structured matrix model with a corresponding life-cycle (Fig. 4.1). Shorebirds typically have low fecundity, delayed maturity, and high survival. The population was divided into three stages (Table 4.3): fledged juvenile (1, hatch-year to next calendar year); subadult (2, after hatch-year until reaching adult stage); and adult (3+, breeding adult). The matrix population model (Leslie 1945) is represented as the equation and follows that notation suggested by Hitchcock and Gratto-Trevor (1997) including an additive immigration matrix to the adult stage-class:

$$\mathbf{N}_{t+1} = \mathbf{A} \mathbf{N}_t$$

where

$$\mathbf{A} = \begin{bmatrix} 0 & F_2 & F_{3+} \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_{3+} + I_{3+} \end{bmatrix}$$

and

$$\mathbf{N}_t = \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_{3+}(t) \end{bmatrix}$$

\mathbf{N}_t is a population vector that represents the number of individuals found in each stage i at time t . The Leslie transition matrix, \mathbf{A} , with the elements a_{ij} illustrates the population

dynamics including demographic parameters estimating fecundity (F_i), survival (P_i), survival with transition (G_i), and immigration (I_i).

In the model, the subadult stage was divided into two separate elements: G_2 and P_2 as,

$$G_2 = S_S \tau_S, \text{ and } P_2 = S_S(1 - \tau_S)$$

where survival with successful advance of the subadult to the adult stage (G_2) is the composite of subadult survival (S_S) and the probability of transition (τ_S), and survival without advance to the adult stage (P_2) is equal to subadult survival (S_S) and the complement to the probability of transition ($1 - \tau_S$).

Adult fecundity, F_{3+} , was measured as:

$$F_{3+} = S_A \eta_A F_A$$

where the adult contribution to annual production is a product of the proportion of adults surviving (S_A), the probability the bird returns to the study area to breed (η_A), and the synthetic estimate of annual fecundity (F_A). This is a post-breeding model, and therefore, the proportion of subadult oystercatchers that successfully transition to the adult stage-class (τ_S) will contribute to the local production (F_2) as:

$$F_2 = (S_S \tau_S \eta_S) F_A$$

where the proportion of the subadults contribution to the local production is represented as $S_S \tau_S \eta_S$.

I used the demographic parameter values in matrix **A** to estimate the population growth rate, stable age distribution, and reproductive values (Caswell 2001). The population growth rate, λ , is the dominant eigenvalue from the transition matrix **A** with

$\lambda > 1$ predicting population growth, $\lambda < 1$ population declines, and $\lambda = 1$ a stationary population. The right and left eigenvectors represent the stable stage distribution (w) and reproductive value (v), respectively. If a population is at a stable stage distribution, then all stages will adhere to the proportions predicted from the eigenvector regardless of the population trajectory. The stable reproductive value is an estimate of the each stage's contribution to the subsequent first stage.

Estimation of confidence limits for λ

I used Monte Carlo sampling to estimate confidence limits for the predicted rate of population growth. These techniques resample from the distributions of each demographic parameter to generate random estimates which are then used in the transition matrix \mathbf{A} to calculate λ . The sampling variance and confidence intervals were then estimated from the distribution of λ produced from 10,000 random draws. All demographic parameters that are represented as probabilities were sampled from a beta distribution because this continuous distribution is defined between the interval $[0, 1]$. Fecundity was sampled from a normal distribution. I reported all lambda values with upper and lower 95% confidence intervals and used these data to determine if model estimates were significantly different from a stable population ($\lambda = 1$) and the observed annual population growth rate ($\lambda = 1.063$) from 2003 – 2008 in Nantucket, Massachusetts.

Sensitivity analysis

The sensitivity of λ to small changes in the demographic parameters shows which of the parameters have the potential to have the largest impact on the growth rate (Lande 1988). Sensitivity shows the effects of absolute change while elasticities show the proportional change relative to the parameter with the largest impact. Sensitivities of λ were calculated according to (Caswell 2001):

$$\frac{\delta\lambda}{\delta a_{ij}} = \frac{\mathbf{v}_i \mathbf{w}_j}{\langle \mathbf{w}, \mathbf{v} \rangle}.$$

where \mathbf{v} and \mathbf{w} are the left and right eigenvectors of matrix \mathbf{A} , and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of the vectors. Elasticities (e_{ij}) measure the proportional change in the multiplication rate of the population, assuming that all other demographic parameters that were used to construct the matrix are held constant (Doak et al. 1994), and were calculated as:

$$e_{ij} = \frac{a_{ij}}{\lambda} \left(\frac{\delta\lambda}{\delta a_{ij}} \right).$$

I used elasticities to identify demographic parameters of the oystercatcher life history that should be the focus of management effort, or those that contribute most to fitness. I completed all matrix modeling efforts using MATLAB version 7.5 (MathWorks 2007).

RESULTS

Juvenile survival

Juvenile survival and subadult survival estimates were not estimated using maximum likelihood techniques in Program MARK. Despite being the first data, the

sparseness of the data (Tables 4.1 and 4.2) produced unrealistic estimates. In order to estimate these important parameters, I used the proportion of birds resighted in each stage-class. For juvenile birds, this was equal to the number of birds observed at any time during the year following the hatch year. Of the 39 fledged young banded between 2005 and 2008, 20 oystercatchers were observed during a later year, and thus, known to be alive ($S_j = 0.513$). This estimate of juvenile survival is a conservative estimate that is biased low because it does not account for marked birds that were never observed. Therefore, the estimate assumes that if a bird is not observed at a later time, then the bird has died. Eurasian Oystercatchers (*H. ostralegus*) have estimated S_j ranging from 0.43 – 0.88 (Hockey 1996, Van de Pol et al. 2006). In addition to using survival estimated from this study, I sampled from this set of values to examine the potential effects of an elevated level of juvenile survival (Table 4.4).

My estimation of subadult survival and transition probability are likely sufficient for the model for two reasons. First, Eurasian Oystercatcher mortality does not appear to be influenced by territory acquisition but winter severity (Ens et al. 1996). Winter elements that impact mortality equally affect non-breeding subadults and breeding adults. Secondly, if this population has yet to reach capacity, then non-breeding birds may acquire territories quickly. Thus experiencing the high survival rates associated with breeding adults.

Age at maturity

To date, only a single bird that was banded as a fledgling later returned to breed in Massachusetts, and no fledglings have been observed breeding anywhere along the

Atlantic Coast. This is likely due to the short duration of this study and because birds banded as young are too young breed. Similar methods were used to facilitate estimates of the two elements that account for subadult life history parameters. Van de Pol et al. (2006) documented high survival (0.94 – 0.98) of Eurasian Oystercatchers during their third year. In my model, the second year is the first year of the subadult stage-class. The oystercatcher family, Haematopodidae, exhibits high levels of survival with delayed maturity (Hockey 1996). Based on this information, the model presented assumes that subadult survival (S_S) is equal to adult survival (S_A). The differentiation introduced to the model is the probability of a subadult becoming a breeding adult which is dependent on the duration of that stage-class. It is thought that American Oystercatchers begin breeding between years three and four (Nol and Humphrey 1994), but this estimate was derived from circumstantial data (Cadman 1980, Johnsgard 1981). Age of first reproduction has been extensively studied for Eurasian Oystercatchers and varies among individuals, normally occurring between years 3 – 10 with variation being dependent on territory availability (Ens et al. 1995, Van de Pol 2005). Since it is unlikely that all American Oystercatchers begin breeding at age three, I calculated the transition probability for subadults (τ_S) with an age of first reproduction occurring, on average, at 6.6 years using the following:

$$\tau_S = \frac{1}{\text{Dur}_S}$$

where Dur_S is 5.6 years (6.6 years – 1 year, Van de Pol et al. 2006) and is the average duration of the subadult stage-class ($\tau_S = 0.179$). I also calculated the probability that a subadult bird will survive but remain in the subadult stage-class ($1 - \tau_S = 0.821$). These estimates of subadult transition are similar to probabilities found by Ens et al. (1995) for

non-breeding adult Eurasian Oystercatchers becoming breeding adults in the Netherlands. Therefore, subadult survival with successful transition ($S_S\tau_S$) is 0.168 and without transition, $S_S(1 - \tau_S)$, is 0.772. These estimates are summarized in Table 4.4.

Adult survival

The analyses (Chapter 3) estimated the probability of survival (S_A) and the probability an oystercatcher will return to the study area in the following year (η_A). For breeding oystercatchers in this study, annual survival and site fidelity remained relatively constant at 0.93 (SE 0.029) and 0.94 (SE 0.048), respectively. Parameter estimation techniques revealed that $\eta'_A = 0$ which means that emigration from the study population ($1 - \eta_A$) is permanent. From these demographic estimates, local annual survival (ϕ) was 0.88. For a detailed explanation of the estimation of adult survival (S_A) and site fidelity (η_A) see Murphy (Chapter 3).

Fecundity

Due to small sample size, I pooled nest data from 2005 – 2008 to determine the best model for estimating fecundity. The function included a daily nest survival that decreased over the course of the nesting season, assumed a 1:1 sex ratio, and was 0.195 (SE 0.029) female young fledged per breeding female.

Model results

According to the projection matrix that accounted for adults that permanently emigrated, the predicted growth rate of American Oystercatchers breeding in Nantucket,

Massachusetts was 0.9659 (Table 4.5) with lower and upper 95% confidence limits 0.900 and 1.020, respectively (Fig. 4.2). Therefore, the model predicts a declining population (-3% annually), but my estimate of λ is not significantly different from a stable population ($\lambda = 1$). The annual population surveys conducted in the study area indicate a 6.3% annual increase in the size of the population between 2003 and 2008 (Fig. 4.2). My estimate ($\lambda = 0.9659$) is significantly lower than the observed population trend ($\lambda = 1.063$) and does not predict the observed trend (Fig. 4.3a). The stable stage distribution (w) is dominated by breeding adults followed by subadults and juveniles (0.53 adults, 0.36 subadults, and 0.11 juveniles). The reproductive values (v) also follow the same trend (2.21 adults, 1.91 subadults, and 1.00 juveniles).

Immigration rates of adult oystercatchers into the study population were estimated using encounter histories of 93 breeding American Oystercatchers from 2006 – 2008 in reverse order (Table 4.6). To calculate the rate of immigration ($1 - \iota_t$), I used a Cormack-Jolly-Seber (CJS) modeling approach outlined in Chapter 3 to estimate the probability that a bird breeding in the study area was also breeding in the previous year (ι_t). Of the four candidate models, the best fit ($\Delta AIC_c < 2$) included the global model ($\iota_t p_t$), $\iota_t p.$, and $\iota. p_t$ (Table 4.7). Estimates of ι ranged from 0.679 – 0.835 (Table 4.8). In order to employ this estimate in the demographic model, model averaging was conducted to calculate a single estimate ($\iota = 0.831$, SE 0.045). The complement of ι is the immigration rate, $I_t = 0.169$.

When the immigration rate was incorporated into the adult stage-class in transition matrix **A**, the predicted growth rate of the population of American Oystercatcher breeding in Nantucket, Massachusetts was 1.079 (Table 4.5) with lower

and upper 95% confidence limits 0.985 and 1.163, respectively (Fig. 4.2). The inclusion of an immigration matrix into the model predicts an increasing population ($\sim 8\%$ annually), but again my estimate of λ is again not significantly different from a stable population ($\lambda = 1$). My estimate ($\lambda = 1.079$) is not significantly different than the observed population trend ($\lambda = 1.063$), and the annual population simulated from the immigration model closely mimics the observed growth over the course of this study (Fig. 4.3b).

Sensitivity analysis

The sensitivity analyses estimate the impact of demographic parameters, both in absolute terms (sensitivity) and relative terms (elasticity), have on the population growth. The analyses indicate changes to site fidelity would have the largest impact on λ followed by adult and subadult survival (Table 4.9). An increase of 6.5% (from 0.93 to 0.99) in fidelity and 6.4% (from 0.94 to 1.00) in adult survival would result in a stable population. If subadult survival is assumed to change with adult survival, then a stable population would be predicted with an increment of 4.3% (from 0.94 to 0.98). Whereas a 79.5% increase (from 0.20 to 0.35) in fecundity would be needed to reach a stable population. Juvenile survival, which was estimated from sparse data, a 71.1% increase (from 0.52 to 0.89) to achieve a stable population.

DISCUSSION

With inclusion of an immigration rate, my model predicts the observed population growth from 2002 to 2008. Furthermore, my model indicates that elevated levels of local

production alone could not explain the recent population growth in Nantucket, Massachusetts. This is critical information for conservation and management efforts for the American Oystercatcher because the model reveals that one of the few Atlantic Coast populations that was thought to be stable may be behaving more like a pseudo-sink population sustained by the positive effect of immigrants. Watkinson and Sutherland (1995) suggested that a pseudo-sink occurs when high rates of immigration result in apparent, elevated mortality that exceed local production. Although this type of population is challenging to diagnose in wild populations, the movement dynamics presented in my study of Nantucket oystercatchers supports the pseudo-sink hypothesis. Listed by the U.S. Shorebird Conservation Plan as a “Species of High Concern” (Brown et al. 2001), it was believed that northern, smaller populations may be less imperiled than those in the core areas of the species breeding distribution. These general surveys of northern populations have been interpreted as encouraging evidence that the Atlantic Coast population may still be stable. My model supports the theory that populations are declining due to low production. Furthermore, one reason that a marked decline has recently occurred in the southern areas is that adult breeding oystercatchers are permanently emigrating from the southern breeding range and entering northern populations. When the immigration model is projected since 1987 (when MDFW began an American Oystercatcher breeding census), the model adequately explains the population trends throughout Massachusetts (Fig. 4.4) and supports this emigration hypothesis.

The Massachusetts population of oystercatchers has been growing since the first breeding pair was observed in 1969. Recently, management has been unsure whether

continued growth was a result of sufficient local productivity or immigration. My study suggests that current growth in the Nantucket, Massachusetts population is likely due to adult American Oystercatchers immigrating into the population or immigration and heightened productivity.

According to the sensitivity analyses, the demographic parameters that are realistic candidates for influencing the dramatic population growth documented in Nantucket, Massachusetts and amenable to conservation and management plans are breeding-site fidelity and adult survival. My modeling explorations reveal that large adjustments to reproductive success result in only moderate changes to the population growth rate. The two parameters associated with the adult stage-class as the most influential on population size are similar to those identified for other long-lived iteroparous birds (Sæther and Bakke 2000). Small changes in adult survival and fidelity rates can shift the trajectory of a population which, in combination with immigrating adults, can conceal low levels of breeding productivity. For these reasons, to appropriately evaluate population status will not only require collecting counts of breeding American Oystercatchers but measures of annual reproductive success, survival, and movement as well.

If we target parameters for management effort, success will hinge on whether those parameters can realistically improve. There are data on adult survival of American Oystercatchers in a stable population. Although fecundity has a smaller influence on population growth, current annual productivity in our population is not near its potential upper limit (Chapter 2). Therefore, management efforts may still be directed at productivity despite the model simulation predicting little impact (Hiraldo et al.1996).

Heightened fecundity ($F = 0.35$ females fledged per breeding female) that would result in a stable population is within the range of values recorded for American Oystercatchers in Massachusetts and elsewhere along the U.S. Atlantic Coast (Chapter 2). Studies of oystercatcher populations with high fecundity ($F = 0.35$) have many reasons that contribute to higher reproduction, including nest-site selection (McGowan et al. 2005b), overwash (Traut et al. 2006, Thibault 2008), and human disturbance (McGowan 2004, Sabine et al. 2006). Additionally, these studies identified mammalian predators as one of, if not, the major threat to reproductive success of oystercatchers. Oystercatcher populations not impacted by mammalian predators, like those in Nantucket, may potentially achieve exceptionally high levels of fecundity (0.63 in Virginia, Wilke et al. 2007). According to the elasticity analyses, a management strategy that would effectively increase fecundity would target the number of chicks that successfully hatch and nestling mortality (Table 4.9).

Apparent survival has been reported on a declining population of American Oystercatchers breeding in Virginia ($\phi = 0.88$, Davis 1999). My estimate of survival ($S = 0.94$) is similar or higher than estimates reported for other species of oystercatcher that are not declining (0.89: South Island Oystercatcher *H. finschi*, Sagar et al. 2002; 0.90 (Safriel et al. 1984), 0.89 (Durrell et al. 2003), 0.92 (Harris and Wanless 1997): Eurasian Oystercatcher *H. ostralegus*). These survival estimates suggest that adult survival for Nantucket American Oystercatchers is near a theoretical maximum, and therefore, management effort to reduce adult mortality is unlikely to succeed.

Based on the sensitivity analyses, the probability that an adult breeding bird returns to breed in subsequent years has the largest impact on the local population.

Emigration, the complement of fidelity, predicts that ~7% of the breeding population will not return for the next breeding season. Although few studies have simultaneously estimated survival and fidelity, my estimate ($\eta = 0.93$) was similar to an estimate for South Island Oystercatchers ($\eta_{males} = 0.98$, $\eta_{females} = 0.90$, Sagar et al. 2002). The best fit model of fidelity varied the estimate by year ranging from 0.89 to 1.00 (Chapter 3). Although the estimates for this demographic parameter will become clearer as the encounter histories continue to accrue across capture periods, this model documents breeding American Oystercatchers exhibiting a range of high fidelity rates that are similar to other oystercatcher species (*H. ostralegus*: Ens et al. 1996, Van de Pol et al. 2005; *H. bachmani*: Hazlitt and Butler 2001; *H. finschi*: Sagar et al. 2002) and can approach $\eta = 1.00$. My model demonstrates that a 6% increase in fidelity would result in a stable population. This suggests that conservation and management strategies should be applied to breeding American Oystercatchers to elevate their degree of site faithfulness. In other words, efforts of local conservation organizations may be best applied to identifying causes of adult oystercatchers permanently emigrating from Nantucket, Massachusetts.

The study population exhibited high level of breeding-site fidelity with high variability. Evolutionary advantages that could promote strong fidelity rates include familiarity with resources like foraging areas and knowledge of local threats (Pärt 1994). Interannual breeding dispersal leads to three potential outcomes for the individual: 1) locate a higher-quality site or mate and improving reproductive success, 2) locate a lower-quality site or mate and reducing reproductive success, or 3) failing to locate a site and/or mate resulting in a loss of all reproductive success (Johnson and Walters 2008).

To correctly detect factors affecting permanent emigration, further research of American Oystercatcher demography is required. Although this study did not identify variables, or a combination of variables, that influence adult fidelity rates, current shorebird literature provides background to suggest that human disturbance may have the potential to negatively impact site faithfulness in the American Oystercatcher. For instance, human recreational disturbance may greatly affect nest site selection of American Oystercatchers (Schulz and Stock 1991, Davis 1999). Davis (1999) documented that American Oystercatchers avoid nesting in suitable areas that are near areas of high human activity. Human disturbance influencing nesting shorebird distribution have been discovered in other species. Schulz and Stock (1991) found that Kentish Plovers (*Charadrius alexandrinus*) avoided nesting in suitable habitat that was also used by tourists. Specifically, 'resting' tourists had a greater influence on nesting distribution than 'beach-walking' tourists (Schulz and Stock 1991). If human disturbance events occur in areas containing suitable nest habitat during the nesting season, this would decrease the amount of nesting habitat in the study area which could lead to an increase in adult emigration. As human recreational activities increase along coastal environments in the U.S. (Boyle and Sampson 1985), the probability of human disturbance events in nesting habitat may increase.

It has been shown that oystercatchers that successfully fledge young tend to be more site faithful (Safriel et al. 1984, Harris et al. 1987, Ens et al. 1992, Hazlitt and Butler 2001, Morse et al. 2006) as do successful individuals in many other bird species (Greenwood 1980). Over time, high nest success is a mechanism influencing the spatial distribution of a population (Newton 1998), which undoubtedly affects Nantucket

oystercatchers. Factors that negatively impact local reproduction would also negatively impact fidelity rates. Human recreational disturbance has been shown to influence population dynamics by affecting nest survival, hatching success, and fledging success of shorebirds (see references in Ruhlen et al. 2003). In other species of oystercatchers, human disturbance has been shown to decrease fledging success (*H. ostralegus*, Verhulst et al. 2001) and nesting success (*H. moquini*, Leseberg et al. 2000), and increase egg and chick loss (*H. moquini*, Tjørve and Underhill 2008) through direct disturbance and increasing potential predator pressure. McGowan (2004) determined that low levels of human disturbance on American Oystercatcher nests along the Outer Banks of North Carolina were directly correlated with hatching success.

Although the direct causes for the observed range of fidelity rates during this study are unknown, varying levels of human recreation may contribute to the probability that oystercatchers return to nest in the study area. More information is needed to understand the degree of human disturbance that potentially impacts nest-site selection and reproductive success. Based on the sensitivity analyses, management may want to consider regulating human recreation near traditional and potential nesting habitat during the breeding season.

Assuming the dynamic relationship of emigration and immigration in my model, demographic simulations account for the recent population growth through an incursion of immigrants greater than the number of breeding adults lost to emigration. The model estimates approximately 16% and 7% of the local population immigrate and permanently emigrate, respectively. With extensive color banding and resighting efforts taking place in a number of states, one would expect to observe marked Nantucket oystercatchers that

permanently emigrated or immigrated. To date, no observations such as this have occurred, but similar movement has been documented through natal dispersal of oystercatchers in South Carolina (Sanders, *pers. comm.*). Although I am unsure of why these dispersal events have not been observed in Massachusetts, there are two probable reasons for the presence of movement without observations. First, natal dispersal may be the primary reason for immigration. Although preliminary studies document evidence of natal philopatry in American Oystercatchers (McGowan et al. 2005a), the marked individuals were part of a more resident population in Cape Lookout and Cape Hatteras, North Carolina, and none of the observed birds were observed breeding. As oystercatchers reach sexual maturity and acquire a mate and suitable nesting territory, they may disperse from their natal site. If this is the case, the duration of my study, spanning four years, would be insufficient to detect natal dispersal because fledglings banded over the course of this study have yet to successfully enter the breeding stage-class.

The second reason for an absence of marked individuals observed breeding outside of the study area may be the lack of a banded population adjacent to the study population. The largest concentration of American Oystercatchers occurring outside of Massachusetts is on Long Island, New York. The Long Island population was most recently estimated to hold 201 breeding pairs (New York Department of Environmental Conservation, unpublished data). To date, no mark-recapture studies have occurred on Long Island, leaving a large population neighboring the study area unmarked. If oystercatchers are entering the study population from nearby locations (i.e. Long Island), they would arrive into the study population without color bands regardless of whether

immigrants result from natal dispersal or permanent emigration. These scenarios would explain the presence of a positive immigration rate despite lack of observed dispersal events. In order to better understand the role movement plays in American Oystercatcher populations along the Atlantic Coast, it is critical to continue this mark-recapture study (especially the marking of juveniles) as well as begin a concurrent study on Long Island, New York.

Predictions on the population dynamics of American Oystercatchers in Nantucket, Massachusetts generated from modeling exercises assume that a number of life history characteristics are similar to other oystercatcher species. Further work needs to be conducted to refine estimates of parameters into the model, especially juvenile survival, subadult survival, and subadult transition probabilities. Efforts need to continue monitoring reproductive success. It is evident that this critical demographic parameter is variable and can have a tremendous effect on populations even if it is not predicted to influence the growth rate. An investigation into the dynamics in fidelity rates is essential to understanding how local American Oystercatcher populations fluctuate, and ultimately, to what degree movement at the local scale influences the Atlantic Coast population. Concurrent color banding studies along the Atlantic Coast will facilitate and refine the use of this model and eventual demographic analysis of multiple populations across the breeding distribution of this species.

TABLES

TABLE 4.1 – Encounter history matrix for American Oystercatchers banded as young in Nantucket, Massachusetts during the breeding season from 2005 – 2008.

Encounter history ^a	No. of individuals
1001	1
0101	2
0100	13
0011	1
0010	22
0001	5

^a Each element represents each sampling period (breeding season); 1 = Capture or resighting event; 0 = no capture or resighting.

TABLE 4.2 – Encounter history matrix for fledged American Oystercatchers in Nantucket, Massachusetts throughout the annual cycle from 2005 – 2008 that were resighted along the Atlantic Coast.

Encounter history ^a	No. of individuals
1001	1
0111	3
0110	3
0101	4
0100	4
0011	9
0010	15
0001	5

^a Each element represents each sampling period (year); 1 = Capture or resighting event; 0 = no capture or resighting.

TABLE 4.3 – Three stage-classes, notations, and definitions assigned to the post-breeding life-cycle (Fig. 4.1) of American Oystercatchers.

Stage-class	Notation	Definition
Juvenile	1	From fledgling (hatch-year) to next year
Subadult	2	Nonbreeding; from 2nd year until breeding
Adult	3+	Breeding

TABLE 4.4 – Demographic parameter estimates used in the three stage-class structured population model for female American Oystercatchers breeding in Nantucket, Massachusetts.

Stage-class	Parameter	Notation	Mean	SE ^b
			0.513	n/a
Juvenile (1)	Juvenile survival	S_J ^a	0.650	n/a
			0.750	n/a
			0.880	n/a
			0.940	n/a
Subadult (2)	Subadult survival	S_S	0.940	0.290
	Subadult transition	τ_S	0.168	n/a
Adult (3+)	Breeding-site fidelity	η_A	0.930	0.048
	Adult survival	S_A	0.940	0.290
	Immigration complement	ι_A	0.831	0.045
	Fecundity	F_A	0.195	0.029

^a Juvenile survival (0.513) was calculated from a point estimate; therefore, alternative parameter estimates were used from current Eurasian Oystercatcher literature.

^b n/a: estimation technique did not include variance.

TABLE 4.5 – Summary of simulated population growth rates (λ) with lower (LCL) and upper (UCL) 95% confidence intervals generated using parametric bootstrap resampling (1,000 replications) for different models; juvenile survival and immigration varied while all other parameters were held constant according to Table 4.3.

Juvenile survival (S_j)	Immigration (I_t)	λ	LCL	UCL
0.51	0.000	0.967	0.904	1.024
0.51	0.169	1.079	0.985	1.163
0.65	0.000	0.981	0.914	1.038
0.75	0.000	0.989	0.917	1.048
0.88	0.000	1.002	0.936	1.059
0.94	0.000	1.005	0.930	1.065

TABLE 4.6 – Reverse encounter history matrix for color banded breeding American Oystercatchers breeding in Nantucket, Massachusetts from 2006 – 2008.

Encounter history ^a	No. of individuals
111	44
110	22
100	13
011	9
010	3
001	2

^a Each element represents each sampling period; 1 = capture or resighting event; 0 = no capture or resighting.

Table 4.7 – The four candidate models developed for estimating immigration rates from 97 breeding American Oystercatchers in Nantucket, Massachusetts from 2006-2008. For each model the following information is given: Akaike’s Information Criterion (AIC_c), differences in AIC_c values from the best fit model (ΔAIC_c), AIC_c weights (w_i), Model Likelihood, the number of parameters (K), and Deviance (Dev). Description of the characteristics of the model for each parameter are the subscripts: ‘.’ constant through time and ‘t’ time dependence in each year.

No.	Model notation	AIC_c	ΔAIC_c	w_i	Model Likelihood	K	Dev
1	$\iota . p_t$	174.66	0.00	0.31	1.00	3	0.34
2	$\iota_t p.$	174.66	0.00	0.31	1.00	3	0.34
3	$\iota_t p_t$	174.66	0.00	0.31	1.00	3	0.34
4	$\iota . p.$	177.85	3.19	0.06	0.20	2	5.61

TABLE 4.8 – Estimates of the probability a breeding bird was breeding the previous year (ι) and encounter probabilities (p), standard error (SE), lower (LCL) and upper (UCL) 95% confidence limit of breeding American Oystercatchers in Nantucket, Massachusetts from 2006 – 2008 under the three best fit models in Table 4.7.

Model	Parameter	Estimate	SE (\leq)	LCL	UCL
1	ι	0.835	0.042	0.737	0.902
	p_{2008}	1.000	0.001	1.000	1.000
	p_{2007}	0.813	0.075	0.623	0.920
2	ι_{2008}	0.835	0.042	0.737	0.902
	ι_{2007}	0.679	0.053	0.569	0.773
	p	1.000	0.001	1.000	1.000
3	ι_{2008}	0.835	0.042	0.737	0.902
	ι_{2007}	0.824	0.001	0.824	0.824
	p_{2008}	1.000	0.001	1.000	1.000
	p_{2007}	0.824	0.001	0.824	0.824

TABLE 4.9 – Lower-level elasticity and sensitivity analyses of λ to the different demographic parameters (π , see Tables 2.4 and 2.5 for definitions) when $S_J = 0.51$.

Parameter	Elasticity	Sensitivity ($\partial\lambda/\partial\pi$)
C/E	0.0601	0.0632
F/C	0.0601	0.1536
FLED	0.0601	0.1258
TCL ₁	0.0558	0.0191
BP	0.0558	0.0543
NST	0.0370	0.0438
RENEST ₁	0.0043	0.0076
TCL ₂	0.0039	0.0016
NST ₂	0.0036	0.0052
TCL ₃	0.0003	0.0002
RENEST ₂	0.0003	0.0010
F	0.3413	0.4754
η_A	0.5969	0.6187
S_A	0.3480	0.3568
S_S	0.3480	0.5505
τ_S	0.0086	0.0550
S_J	0.0601	0.1129

FIGURES

FIGURE 4.1 – The post-breeding stage-structured life-cycle illustration of American Oystercatchers (= juvenile, = subadult, and + = adult) with corresponding demographic parameters: fledgling survival with transition to subadult (), subadult survival without transition (), survival with transition to subadult (), adult survival (), subadult fecundity (), and adult fecundity (). Transition matrix model corresponding to a post-breeding census for American Oystercatchers. Elements are determined by stage-specific survival rates (), site fidelity (), transition probabilities (), immigration rate (), and fecundity ().

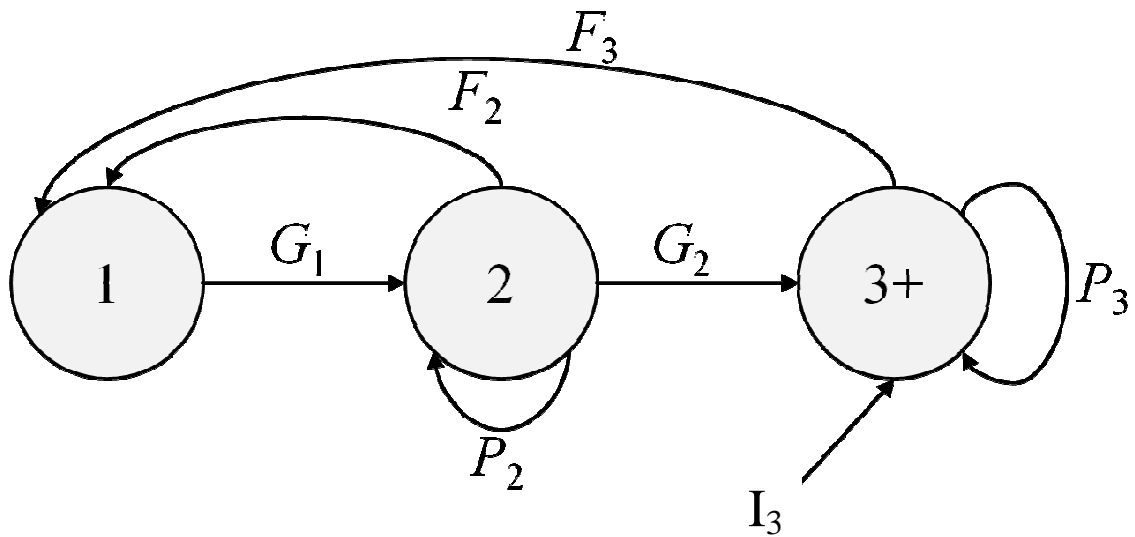


FIGURE 4.2 – Frequency within the 95% confidence intervals and mean (\dagger) for the population growth rate (λ) of American Oystercatchers breeding in Nantucket, Massachusetts ($\lambda = 0.966$, shaded bars) and including an immigration matrix (\mathbf{I}_t , $\lambda = 1.079$, filled bars) generated using parametric bootstrap replicates ($n = 10,000$).

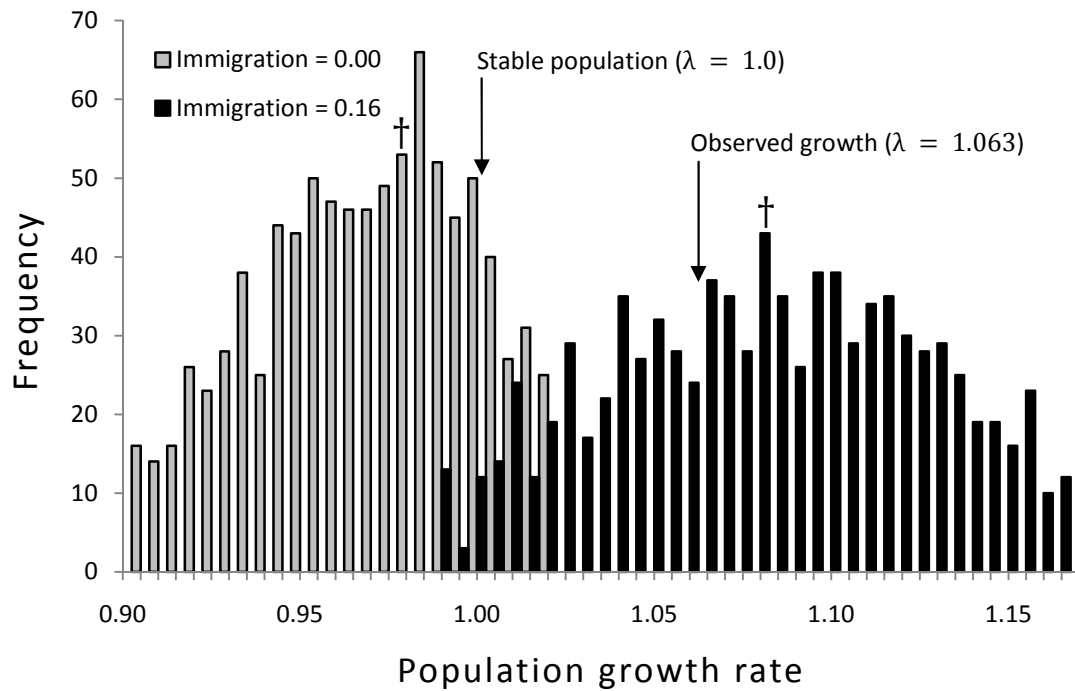


FIGURE 4.3 – Observed population trend (filled circles) from 2002 – 2008 for an American Oystercatcher population in Nantucket, Massachusetts, and population projections (empty circles) using basic model (a) ($\lambda = 0.966$), immigration model (b) ($\lambda = 1.079$) and their lower and upper 95% confidence limits (dashed lines).

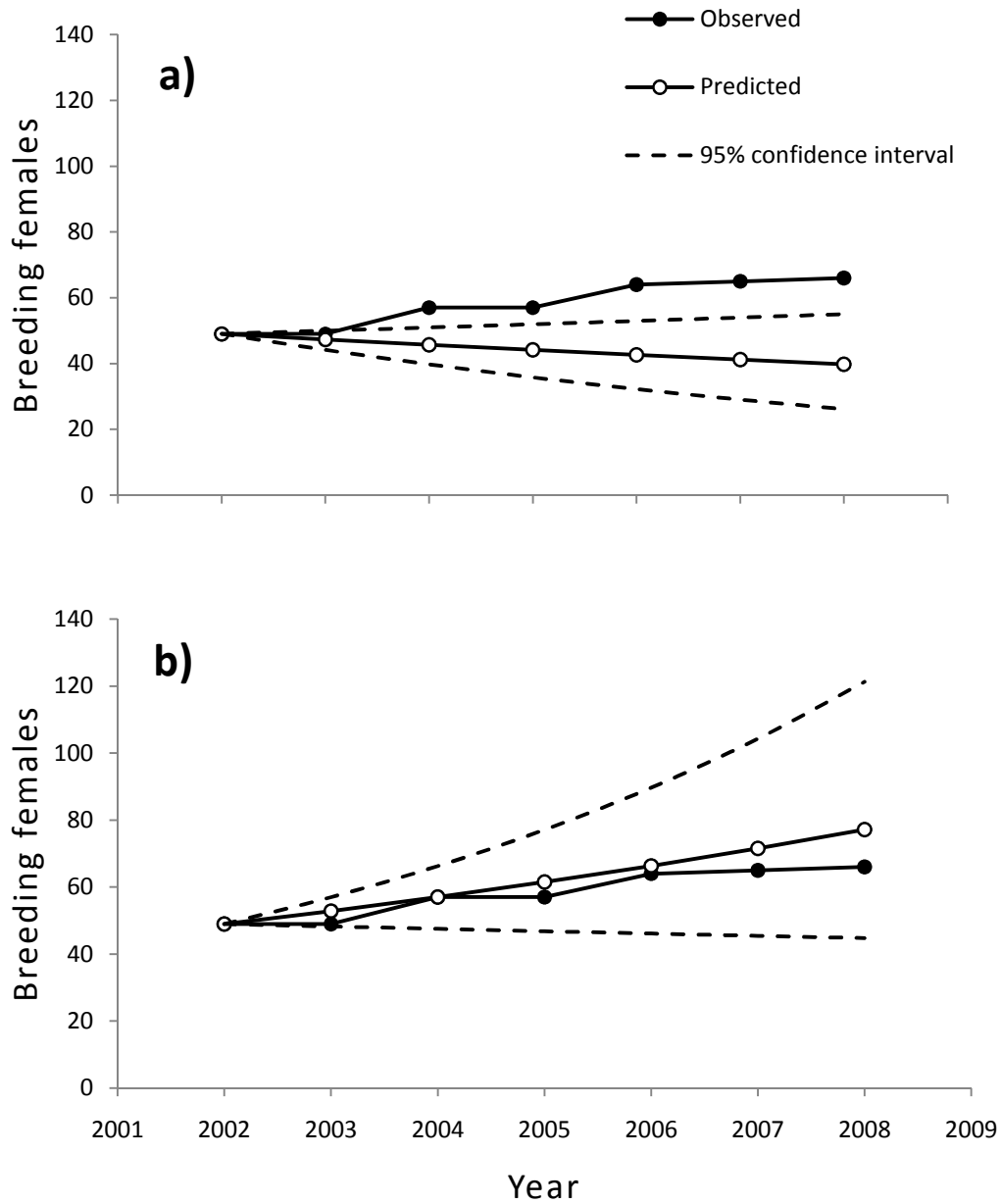
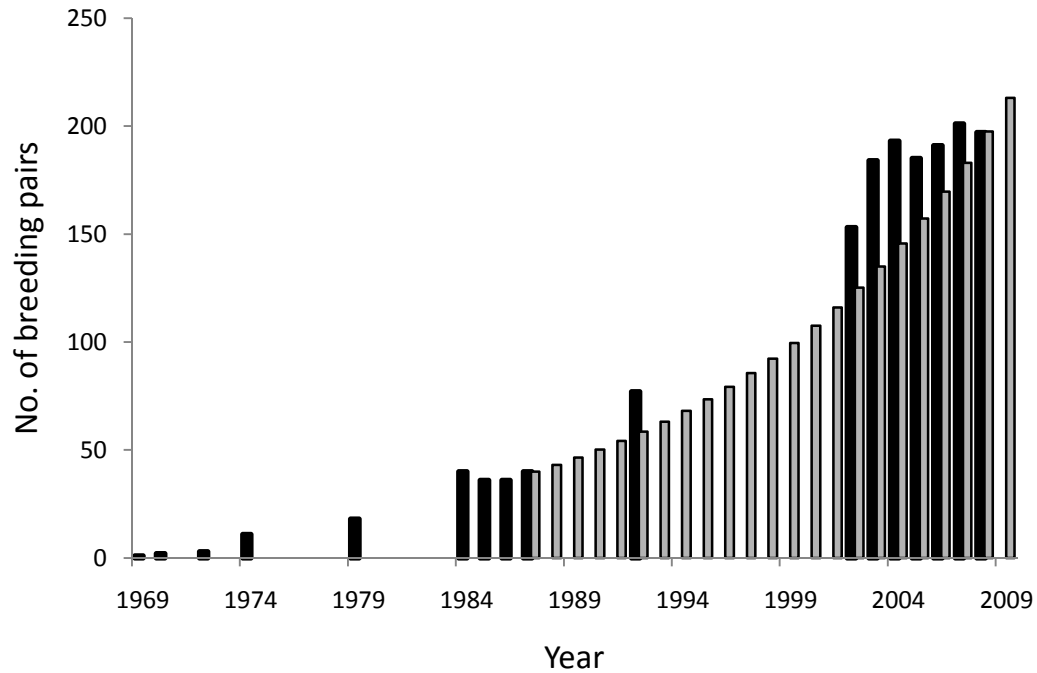


FIGURE 4.4 – Number of breeding pairs of American Oystercatchers recorded in Massachusetts from 1969 – 2007; filled bars represent statewide surveys that were intermittent until annual breeding census and monitoring efforts began in 2002, and the shaded bars represent population size predictions using the demographic model that includes an immigration probability (0.16) starting after the first series of annual statewide breeding censuses (1984 – 1987).



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