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Population Dynamics, Chick Diet, and Foraging Behavior of the Razorbill (*Alca torda*) at Matinicus Rock, Maine

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**POPULATION DYNAMICS, CHICK DIET, AND FORAGING BEHAVIOR OF
THE RAZORBILL (*ALCA TORDA*) AT MATINICUS ROCK, MAINE**

A Thesis Presented

by

KATHERINE E. KAUFFMAN

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

September 2012

Graduate Program in Organismic and Evolutionary Biology

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DEDICATION

To my husband and constant supporter, Jason Sears.

Thank you for supporting and assisting my endeavors throughout this graduate school journey that exceeded our expectations of time and emotional expenditure. Thank you for your presence and help as I evaluated and applied to graduate programs, moved across the country, developed my project, and collected data in the field. You were there for me when I needed encouragement, companionship, and assistance with data analysis and editing my thesis. You were patient when I was away from home for entire summers, and when I was distressed and out-of-sorts. You were excited for my small victories.

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ABSTRACT

POPULATION DYNAMICS, CHICK DIET, AND FORAGING BEHAVIOR OF THE RAZORBILL (*ALCA TORDA*) AT MATINICUS ROCK, MAINE

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During the summers of 2007-2009, I studied the population growth and reproductive and foraging ecology of the Razorbill (*Alca torda*) at Matinicus Rock (MR), Maine. This medium-sized marine bird in the family Alcidae (auks) was extirpated from the Gulf of Maine in the late 19th century by hunting, collecting, and colony disturbance. Following legislation protecting seabirds and their nesting habitats, the Razorbill has recolonized probable former nesting habitat in the Gulf of Maine during the past several decades. Six small colonies comprise the Maine population, which is listed as threatened and forms the southern extension of the species breeding distribution.

In Chapter 1, I present a population model of the MR breeding colony, based on studies of population growth and reproductive success, and supplemented with previously collected data from the National Audubon Society Seabird Restoration Program (Project Puffin), with whom I collaborated. I also describe chick diet (supplemented with Project Puffin data) and draw connections between diet and reproductive success. I found that reproductive success was too low to account for the observed population growth rate, and

conclude that the colony is a sink population supported by substantial immigration. Because annual fledging success was positively associated with prey quality, I suggest that substandard chick diet may contribute to the sink population dynamic via diet-driven depressed fledging success.

In Chapter 2, I report on the foraging behavior of chick-rearing Razorbills fitted with bird-borne data-loggers at MR in 2008-2009. I describe diving behavior including depth, duration, and profile shape of dives, as well as diel patterns. Diving activity was restricted to daylight hours, and dives were shallowest and most frequent in the evening. Though generally similar to diving behavior reported at four European and Canadian colonies, Razorbills at MR performed three times as many dives per day as at the Gannet Islands, Labrador, and the mean dive depth was greater than three of four previous studies. Deeper and more frequent dives may indicate higher foraging effort and lower prey availability. Reproductive success would suffer if parents cannot buffer chicks against the effects of low prey availability through increased foraging effort or other behavioral modifications.

Together, the pieces of our research indicate that prey availability may be negatively affecting reproduction and population growth at MR. Rapid colony growth cannot be explained by local reproductive success, and is likely the result of substantial immigration from other colonies. Chick diet is varied and includes multiple high-quality forage fish species, yet chicks also consume poor-quality prey (larval fish and euphausiids) that may signal periods of very poor prey availability. Frequency and depth of dives made by chick-provisioning adults are also suggestive of parents allocating extra effort to foraging, relative to other colonies.

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CHAPTER 1

POPULATION MODELING AND THE RELATIONSHIP BETWEEN REPRODUCTIVE SUCCESS AND CHICK DIET AT AN EXPANDING RAZORBILL COLONY IN THE GULF OF MAINE

Abstract

As central-place foragers, breeding seabirds are limited to spatially-restricted foraging grounds around the breeding colony. If foraging conditions are poor near the colony and chick-provisioning parents cannot compensate through time-budget adjustments, chicks may grow more slowly and productivity may decrease. Razorbills (*Alca torda*), piscivorous seabirds in the alcid family, reach their southern breeding distribution limit in the Gulf of Maine where they breed at a few small colonies and are listed as threatened in Maine. At the largest U.S. Razorbill colony, Matinicus Rock, wildlife managers noted the colony appeared to be growing but reproductive success seemed low. To determine if the Matinicus Rock colony is a population sink, we estimated population growth rate and productivity, then modeled population dynamics under various immigration scenarios. The Matinicus Rock colony grew at an annual rate of 12.9%, yet annual productivity was 0.48 ± 0.13 chicks per pair, a rate that, according to our model, would lead to an annual population decrease of 1.6% in the absence of net immigration. Therefore, we conclude that Matinicus Rock is a sink population supported by substantial annual immigration equal to 18-20% of the breeding population. Because chick diet has well-documented effects on productivity, and because Matinicus Rock is

located at the periphery of the species range where forage fish community composition may differ from the majority of the species range, we hypothesized that poor chick diet might be contributing to a population sink at Matinicus Rock through depressed productivity. We assessed chick diet through surveys of prey deliveries to nestlings by parents. We found support for our hypothesis that chick diet contributed to the sink through depressed productivity, in the form of associations between fledging rate and diet quality, and also low chick fledging mass. Chick diet consisted of several forage fish species, larval fish, and invertebrates. Primary prey species were lipid-rich Atlantic herring (*Clupea harengus*), sandlance (*Ammodytes* spp.), and hake (may include *Merluccius bilinearis*, *Urophycis tenuis*, *U. chuss*, and *Enchelyopus cimbrius*), and the representation of each of these species in the chick diet varied significantly between years. Fledging success was positively associated with prevalence in the chick diet of those high-quality prey items, and negatively associated with prevalence of low-quality items (larval fish and invertebrates). We were unable to assess caloric intake of chicks because we did not record feeding rates or collect prey samples to analyze energetic content. Productivity and diet composition at Matinicus Rock were similar to another Gulf of Maine colony, Machias Seal Island, which suggests that similar conditions may exist gulf-wide. Predation by gulls, kleptoparasitism, and researcher disturbance may also contribute to the low productivity observed at Matinicus Rock, and thus, to the sink.

Introduction

Central-place foragers are animals that obligately return to a central place (e.g., nest, cache, or den) between foraging trips (Orians and Pearson 1979). Marine birds are

central-place foragers during the breeding season because they must regularly return to the breeding colony to attend nests (Wakefield *et al.* 2009). Reproductive success will suffer if seabirds do not have access to prey of sufficient quantity and quality within a spatially-limited area (e.g., Hamer *et al.* 1993; Chastel *et al.* 1995; Weimerskirch 1999; Rindorf *et al.* 2000). In some species, parents are able to buffer chicks against the effects of short-term declines in food availability by allocating more time and energetic expenditure to foraging activity. However, adjustments to time and energy budgets that are large in magnitude or duration can negatively impact adult body condition (Ballard *et al.* 2010) and future survival (Royama 1966; Drent and Daan 1980) and may be unsustainable.

As central-place foragers, the population dynamics of seabirds can be intensely affected by local or regional prey conditions through the effects that foraging conditions can have on productivity, survivorship, and potentially colony fidelity. In this way, foraging conditions, interacting with seabirds' time and energy budgets, can impact population dynamics at the colony and metapopulation levels. Poor local foraging conditions that extend over multiple years could result in increased emigration from an affected colony to other colonies with more favorable conditions. However, in some cases birds might stay at a colony despite sub-optimal foraging conditions, a phenomenon that could be influenced by inherent site fidelity, absence of better conditions nearby, or saturation at nearby colonies. Alternately, it is possible for birds to be trapped into a poor situation if good foraging conditions deteriorate through the breeding season after pairs have committed to a breeding location. If, for whatever reason, birds continue to breed at a location with poor foraging conditions, it may result in a sink population (Van Horn

1983; Roughgarden and Iwasa 1986; Pulliam 1988), where local survival and reproduction are not sufficient to maintain a stable population, resulting in a declining population or one dependent on immigrants to maintain size.

Objectives

In this paper, we assess whether the Razorbill (*Alca torda*) breeding colony at Matinicus Rock (MR) is a sink population, and if so, whether chick diet could be an underlying cause. A sink population is one in which local survival and productivity rates are not sufficient to maintain a steady population size. To determine if the colony at MR is a sink population, we monitored colony size and productivity over several years, then created a population model using information gathered in this study, along with parameters gathered from the literature. We examined the forecasted population trajectory under multiple immigration scenarios. We also explore the hypothesis that chick diet is contributing to a potential sink by depressing productivity. We focused on chick diet because 1) chick diet has well-documented effects on breeding success and chick growth in seabirds, and 2) the colony we investigated is at the extreme southern periphery of the species range, where forage fish community composition and availability may differ from the rest of the species' range. We assess the potential contribution of chick diet to the sink by characterizing chick diet and chick condition at fledging. We also test hypotheses about interannual variation in reproductive success, fledging mass, and chick diet, and explore links between diet and fledging success.

Central-place Foraging

Animal foraging behavior falls into two broad categories. Mobile foragers, including many seabird species during the non-breeding season, do not necessarily return to any specific location between foraging activities, and consequently may travel widely to search for or follow mobile prey. In contrast, central-place foragers are obliged to return to a base. Because of the need to return regularly to a specific location, a central-place forager experiences a spatially-limited potential foraging ground, its size determined in part by the animal's travel speed (see Weimerskirch 1999), energy expenditure (Tamm 1989; Wakefield *et al.* 2009), and frequency with which it must return to the central place (Weimerskirch *et al.* 1994).

As central-place foragers, seabirds are highly dependent on reliable food resources within traveling distance of the breeding colony, both for self-feeding and for provisioning nestlings (Elliott *et al.* 2009; Saraux *et al.* 2011). During the breeding season, it is important that prey is available within a certain distance of the breeding colony, so that birds can complete foraging trips and still have time for activities such as courtship, socializing, offspring care, and rest. Specific factors that may limit the duration of individual foraging trips include the need to feed a chick (Weimerskirch *et al.* 1994; Weimerskirch *et al.* 2000), and the need to take over incubation or brooding duty so a mate can leave on a foraging trip (Chaurand and Weimerskirch 1994). Seabirds are able to adjust for small fluctuations in foraging conditions, but there are limits to the amount they can absorb without incurring consequences.

In some species, researchers have documented limited flexibility in the time and energy budgets of chick-rearing individuals (Burger and Piatt 1990; Monaghan *et al.*

1994; Saraux *et al.* 2011), wherein parents buffer their chicks from the effects of short-term declines in food availability by increasing the portion of time spent foraging at the expense of other activities; altering the frequency, distance, and duration of foraging trips; or adjusting time allocation during foraging trips to include more active foraging and less resting (Uttley *et al.* 1994; Dall'Antonia *et al.* 2001). However, adjustments to time and energy budgets that are large in magnitude or duration can negatively impact adult body condition (Ballard *et al.* 2010) or future survival (Royama 1966; Drent and Daan 1980) and may be unsustainable. Dall'Antonia *et al.* (2001) speculate that interannual differences in observed time budgets and dive characteristics of Razorbills breeding at Latrabjarg, Iceland represent years of more- and less-favorable foraging conditions, but nothing is known of the extent to which Maine Razorbills adjust time budgets in response to foraging conditions.

Maine Razorbill Population

The Razorbill, a seabird in the family Alcidae (alcids: i.e., auks, auklets, guillemots, murrelets, murre, puffins), is a central-place forager during the breeding season, when it is restricted to feeding near its nest sites on islands and cliffs in the North Atlantic Ocean (Gaston and Jones 1998). Approximately 500,000-700,000 breeding pairs of Razorbills nest in the boreal and sub-arctic latitudes of the North Atlantic, with 65% of the breeding pairs occurring in Iceland, and the remaining colonies extending east through the British Isles, Scandinavia, and NW Russia, and southwest to Greenland and North America (Lavers *et al.* 2009). Approximately 38,000 pairs breed in North America, with most occurring in the Atlantic Canadian provinces (Lavers *et al.* 2009), but a small

and growing U.S. population has colonized six islands in the Gulf of Maine (GOM; Allen *et al.* 2012). Despite representing less than one percent of the world Razorbill population, these GOM colonies are of particular interest because they define the southern periphery of the species range, may harbor important genetic diversity (Soulé and Wilcox 1980), and may be the first colonies to respond to global climate change if increasing temperatures result in less suitable conditions at this latitude.

At the time of European colonization of North America, Razorbills are believed to have nested in low numbers in the GOM, but by the 1890s the population was extirpated as a result of human activities that included egg collection and hunting (Drury 1973). From the 1880s, or shortly thereafter, to 1922, no Razorbills nested in Maine (Norton 1923), but following implementation of regulations protecting the birds and their breeding sites, Razorbills began returning to breed in the 1920s (Drury 1973). They gradually recolonized probable former nesting colonies in Maine over the next several decades (Podolsky 1989; Lavers *et al.* 2007), such that by 1968-1970, five pairs nested on MR, and in 1974 this increased to nine pairs (C. Buchheister, pers. comm. *in* Korschgen 1979). By 1986, there were three colonies in Maine (Podolsky 1989), and currently there are six (Allen *et al.* 2012). The largest colony (> 300 nesting pairs; Kauffman 2007) is at MR, and is managed by the U.S. Fish and Wildlife Service and the National Audubon Society Seabird Restoration Program as part of the Maine Coastal Islands National Wildlife Refuge. Since 2000, the Seabird Restoration Program has conducted censuses of Razorbill eggs on MR and estimates that the population increased from 2000 to 2007 (Kauffman 2007). Nonetheless, the Razorbill has been listed in Maine

as a state threatened species since 1997 due to its small population size and limited in-state distribution.

Despite its 300+ breeding pairs of Razorbills, MR may be a sink population as a result of its low productivity and hence dependent on immigration to maintain its population size. A sink population is one in which low adult survival, low reproduction, or both, results in a population that is not self-sustaining, but rather is dependent on an influx of immigrants from elsewhere (Van Horn 1983; Roughgarden and Iwasa 1986; Pulliam 1988). Holt (1985) and Morris (1991), have suggested that in some circumstances, local sink populations can have neutral or even positive impacts on the overall population of a species. Also, Dias (1996) suggested that source-sink systems can be temporally dynamic, with a local population's status changing over time, a phenomenon that has been documented in neotropical beetles (Johnson 2004). Nonetheless, it remains clear that in most cases, sink populations negatively affect the overall population size and viability of a species. Sink populations are especially worrisome in species of Special Concern, such as the Razorbill in Maine, because individuals recruiting to such populations are likely to live shorter lives and produce fewer offspring, resulting in lost growth opportunity for the local population and the species population as a whole. Improving conditions at sink populations or discouraging individuals from recruiting to them may prove beneficial to the overall health of the Razorbill population in the GOM, by raising the quality of the average nesting site. Naturally, one major way to improve conditions is to increase the quality and quantity of chick diet.

Importance of Chick Diet

Chick nutrition may help determine whether a population becomes a sink, because nestling provisioning rate and diet composition are major determinants of productivity through their influence on chick growth and survival. Energy and nutrient acquisition rates are affected by both the quantity and quality of food consumed. Deficiency in overall caloric and nutritive intake, whether caused by infrequent or small meals, or by low-quality food, has been linked to failure of chicks to grow (Golet *et al.* 2000; Wanless *et al.* 2005), develop properly (Barrett and Rikardsen 1992; Janssen *et al.* 2011), and thermoregulate (see Gil-Delgado *et al.* 1995; Kildaw 1999). These situations can arise if decreased food availability in the environment prevents parents from maintaining adequate provisioning rates (Anker-Nilssen 1987; Barrett and Rikardsen 1992; Rindorf *et al.* 2000; Lewis *et al.* 2001). In extreme cases, some parents may exhibit decreased chick-provisioning effort, effectively conserving their own energy reserves for future reproduction at the expense of the current year's reproductive success (Royama 1966; Drent and Daan 1980). Long intervals between parental visits can also reduce chick survival by exposing the chicks to a higher risk of predation (Martindale 1982; Houston and McNamara 1985; Sydeman *et al.* 2001), forcing them to spend more energy on temperature regulation (Ricklefs *et al.* 1980; Bech *et al.* 1984; Gabrielsen *et al.* 1992; Kildaw 1999), and increasing blood concentrations of stress hormones (Kitaysky *et al.* 2001; Buck *et al.* 2007; Quillfeldt *et al.* 2007; Brewer *et al.* 2008). Suboptimal diet may also affect post-fledging survival by causing chicks to fledge at a lower mass (Lance and Roby 1998; Österblom *et al.* 2001), or to remain in the nest for a longer time before fledging (e.g., Dentressangle *et al.* 2008), both of which can decrease the probability of

survival to age of reproduction (Perrins *et al.* 1973; Jarvis 1974, Hedgren 1981, Hatch 1983, Coulson and Porter 1985, Harris and Rothery 1985, Magrath 1991; Harris *et al.* 1992; Gaston 1997), or delay the onset of reproductive maturity (Gaston 2003; Morrison *et al.* 2009).

Prior to this investigation, Razorbill chick diet at MR had not been studied, so its composition was unknown. The diet of Razorbill chicks is well described for colonies in the boreal and sub-arctic regions of northern Europe (Harris 1970; Corkhill 1973; Bradstreet and Brown 1985; Harris and Wanless 1986; Barrett and Furness 1990; Pennington *et al.* 1990; Swann *et al.* 1991; Wagner 1997; Lyngs 2001; Birkhead and Hatchwell 2000; Birkhead and Hatchwell 2004; Harris *et al.* 2007; Anker-Nilssen *et al.* 2008; Daunt *et al.* 2008), as well as for breeding colonies in Greenland (Salomonsen 1950) and Atlantic Canada (Chapdelaine and Brousseau 1996; Lavers and Jones 2007). In the GOM, Razorbill chick diet is poorly understood, except for the population at Machias Seal Island (MSI) in the Bay of Fundy (Bowser *et al.* 2009). From this population, we know that capelin (*Mallotus villosus*), a lipid-rich forage fish that is a staple of Razorbill diets throughout the majority of the species range (e.g. Barrett and Furness 1990; Lavers and Jones 2007), is not available to Razorbills in the GOM. If Razorbill diet in the GOM consists of prey items that are less lipid-dense than capelin, the resulting lipid deficiency might negatively affect chick growth (Baillie and Jones 2004) and ultimately reproduction.

Methods

Study Location

We conducted fieldwork from 2000-2009 on MR (43°47'N, 68°51'W), a 0.12 km² treeless granite island 40 km from the mainland in outer Penobscot Bay, Maine (Fig. 1.1). Matinicus Rock, part of the Maine Coastal Islands National Wildlife Refuge, supports one of the largest and most diverse seabird colonies on the U.S. Atlantic Coast, composed of several thousand pairs of alcids, larids, storm-petrels, eiders, and shearwaters. The island is the southernmost breeding location of Razorbills and Atlantic Puffins, and is one of only two known Manx Shearwater breeding sites in North America. Human infrastructure on the island reflects its history as a U.S. Coast Guard light station: a light tower, keeper's house, foghorn, boathouse, and helicopter pad are located on the southern third of the island. Since automation of the light in 1983, there are no year-round residents on the island, but a small group of seabird researchers is present annually from May-August.

The main Razorbill colony is located on the northern third of the 700 m long, 150 m wide island, with small numbers of pairs breeding at other locations near the periphery of the island. Nesting substrate consists of cavities under boulder piles and, to a lesser extent, bedrock crevices. The site of the main Razorbill colony may be washed over by waves during winter storms, but most of the boulder substrate remains stable between years.

Data Collection

Population Size

We estimated the size of the breeding population at MR in 2000-2009 by conducting annual counts of active nest sites (those with eggs that appeared to be attended) just after peak egg laying date. We thoroughly searched all cavities and crevices within and just outside the known colony boundaries, as well as checking all known Atlantic Puffin burrows elsewhere on the island (Razorbills sometimes use nest sites previously occupied by puffins). We assumed that each active Razorbill nest site was attended by two breeding adults, and thus doubled the number of nest sites to estimate the number of individuals in the breeding population.

Reproductive Success

Monitoring Nests

To assess reproductive success, we monitored hatching success (2004-2009, sample sizes of 49-81 nests) and fledging success (2007-2009, sample sizes of 35-46 nests) at a sample of nesting burrows, and combined these estimates for each year into a measure of total annual productivity. We began monitoring nests during the week following peak laying, and when possible we selected burrows that had been monitored in the previous year. Meeting this constraint was not always feasible because nest burrows were not always reused, the boulder structure sometimes changed, or the burrow was used by more than one pair in some years. Burrows were preferentially selected for

monitoring if the nest cavity was easily visible, there was a single entrance, and the chick could be reached. Selection of nests was therefore non-random, and biased toward shallower burrows, but our selection method allowed a more accurate determination of egg and chick fates than would have been possible with randomly selected nests.

We typically inspected burrows every three to five days and recorded the nest contents (egg, abandoned egg, chick, dead chick, or empty). We avoided more frequent nest checks because entering the colony caused the majority of adults to depart for the sea, leaving eggs and chicks unattended for at least the duration of our presence. We continued checking burrows until all sampled burrows were empty.

Estimation of Hatching and Fledging Success

We defined hatching success as the proportion of eggs laid that hatched (i.e., #eggs hatched/#eggs laid), and fledging success as the proportion of chicks hatched that fledged (i.e., #chicks fledged/#chicks hatched). It can be argued that, for Razorbills and their close relatives, murrelets, nest departure does not actually represent fledging (e.g., Burger 1980) because chicks depart the nest in the company of the male parent and receive care from him at sea (Wanless and Harris 1986) for a month or more following nest departure (Hope Jones and Rees 1985), and thus do not attain, at nest departure, the independence typical of many seabirds. In this paper, however, the term *fledging* means successful departure from the nest for the sea (Hope Jones and Rees 1985). We considered chicks fledged if we found the nest burrow empty with no evidence of predation, and the chick was ≥ 18 days old, the minimum age at which Razorbill chicks commonly depart nests (Harris and Birkhead 1985; Gaston and Jones 1998).

Calculation of Productivity

We calculated productivity as the product of hatching success multiplied by fledging success. Due to the difficulty of monitoring nests (e.g., chicks that were mobile in burrow cavities containing more than one nesting pair) and uncertainty introduced by the length of time between nest-checks (e.g., ambiguous fledging status of a chick that was gone from a nest when it would have been 19 days old, but had been only 14 days old at the previous nest-check), we had to exclude from the fledging success sample some burrows that were included in the hatching success sample (Table 1.1). This resulted in a sample for fledging success that was smaller than the sample for hatching success, and necessitated making a decision about how to determine productivity: a) as a sample: from only the subset of sampled burrows in which nest fate through fledging was known with certainty, or b) as a calculation: from the smaller sample of fledging success, in combination with the larger sample of hatching success. Choosing the former method would have reduced the number of nests used to estimate productivity, and could have introduced bias to our estimate (if the burrows with uncertain chick fledging fate differed in hatching rate from burrows with certain chick fledging fate, which could have occurred if hatching success and certainty of fledging status were both related to burrow structure). Therefore, we chose the latter option, because it allowed us to include more of our sample and avoid introduction of potential bias into our estimate.

Chick Fledging Mass

We captured and weighed chicks just prior to fledging in 2005-2009. Each chick was banded with a size 5R triangular USGS stainless steel leg band and weighed with a

Pesola spring scale (a measurement hereafter referred to as fledging mass). Chicks were banded and weighed only if their legs were developed enough to prevent the band slipping off over the foot, and if, based on plumage and activity level, they appeared likely to fledge within three days. In 2009, only three chicks were banded during several visits to the colony because most chicks' legs were too small just before fledging to securely retain the bands. Due to this small sample size, 2009 was excluded from analysis of interannual variation in fledging mass.

Chick Diet

We collected diet information during the summers of 2005-2009 by observing prey items brought to burrows by chick-provisioning adults. Razorbills transport food to their chicks by carrying entire prey items crossways in their bills, thus allowing prey to be identified without disturbing the birds.

We observed prey deliveries from blinds within or near the breeding colony, using either 8- or 10-power binoculars. The number of visible burrows varied depending on observer location, but typically one or two observers could view approximately 20–40% of the colony simultaneously. We collected data throughout the chick-rearing period, generally from late June to mid-July (earliest: 21 June; latest: 29 July). We made observations throughout daylight hours, though we concentrated our effort in early to mid-morning to take advantage of this period of high delivery activity and to coordinate with other research activities. Prey deliveries were recorded opportunistically as parents returned to the colony with prey, and were not associated with specific burrows due to the difficulty of identifying the burrow to which a delivery was made. We recorded

information on a bill-load of prey only if the bill-load was seen clearly, and only after the bird landed and entered a burrow, or seemed to be approaching a burrow when it moved out of sight. We took the latter precaution in order to avoid double-counting bill-loads and to insure that the food items were being delivered to nestlings. When visual fields of two concurrent observers overlapped, we avoided duplicate recordings by subdividing the area of overlap and communicating via hand-held radios. Prey were identified to species when possible, or to species group (set of closely related species indistinguishable in the field). We estimated prey body length relative to the bill length of the Razorbill, to the nearest 0.25 bill-length.

Data Analysis

Population Model

We built a deterministic population model (using Microsoft Excel 2004 for Mac, Version 11.6.1, Microsoft, Seattle, WA) to assess population growth at the colony (2000-2009) in relation to within-colony recruitment and immigration. We parameterized the model with a combination of estimates from MR (this study) and published values for Razorbills at other colonies (Table 1.2). When published estimates of a parameter varied, we considered study protocol, similarity of colony to MR, and central concentration of values (if extant) to inform our selection of the most appropriate parameter estimate.

We defined annual age classes as follows: Age Class 0 extends from fledging until first spring (i.e., 1st year of life); Age Class 1 extends from first summer to second spring (i.e., 2nd year of life); and so on. Thus, first-time breeders returning to the colony

in the fourth summer following that of their birth would be (just entering) Age Class 4. We assumed a constant annual survival probability for immature birds (Age Classes 0-3; also referred to as pre-breeders) and a separate constant annual survival probability for mature birds (Age Classes 4-30; also referred to as breeders), except for Age Class 30, for which annual survival probability was zero. Furthermore, we assumed a constant annual productivity rate throughout an individual's breeding lifetime (Age Class 4-30). Further explanation of model assumptions and construction is provided in the Appendix.

Our population model might be strengthened by inclusion of more nuanced sub-models of immature and adult annual survival rates, and productivity across age classes. However, not enough is known about this species to support nuanced models, so we have chosen flat rates for the attributes listed above. Furthermore, we know that seabirds experience stochastic conditions, but we didn't have enough information to describe the distributions of parameters within a stochastic model. Therefore, we selected a deterministic model as most appropriate for answering our research questions.

We ran our model under two different assumptions regarding the age-distribution of immigrants:

- 1) "Young immigrants": all immigration occurs among first-time breeders, i.e. individuals in Age Class 4.
- 2) "All ages immigrants": immigration occurs among all breeding age classes, i.e. individuals in Age Classes 4-30, with the age-distribution of immigrants matching that of the population they are entering.

We chose to run our model under these two different assumptions regarding age-distribution of immigrants because they represent two extremes within the spectrum of

plausible possibilities. While they both are likely over-simplifications of actual immigration patterns, it seems likely that the actual situation at Matinicus may lie somewhere between these two assumptions. However, because we lack evidence to inform a more nuanced age-distribution expectation, we have not attempted to do so. For most seabirds, and especially for the family Alcidae, little is known about the relationship between an individual's age and their colony fidelity or propensity to switch colonies, but there is some evidence of young seabirds exhibiting, at higher rates than older seabirds, certain behaviors that are suggestive of a higher propensity to switch colonies. For example, younger seabirds may pay visits to non-natal colonies (Halley *et al.* 1995), and switch nest sites within colonies or between sub-colonies (Boekelheide and Ainley 1989), at higher rates than older birds, which in turn suggests that young birds might be more likely than older birds to immigrate to a new colony. Lavers *et al.* (2007) found support of this pattern in Razorbills at the Gannet Islands, Labrador, where philopatry was higher for older individuals (banded as adults; 97%) than for younger individuals (banded as chicks; 83%), and mean distance moved between breeding sites on the same island was higher for younger birds than older birds.

We used our model to simulate population growth of the MR colony under the “young immigrants” and “all ages immigrants” assumptions (assuming no emigration in all cases). Due to the fact that there may be some actual level of emigration from MR that is not built into our model, our immigration predictions should be thought of as *net* immigration, or the rate of immigration above the amount required to offset emigration. For this reason, our immigration estimates should be viewed as minimums, with actual colony immigration rates possibly higher depending on actual colony emigration rate.

We answered the following questions:

- 1) What would the annual population growth rate be in the absence of immigration?
- 2) What rate of immigration would be required to maintain a stable population size (i.e., 0% annual growth)
 - a. under the “young immigrants” scenario of immigrant age distribution?
 - b. under the “all ages immigrants” scenario of immigrant age distribution?
- 3) What rate of immigration would be required to maintain the population growth rate observed on MR from 2000-2009 (i.e., 12.9% annual growth)
 - a. under the “young immigrants” scenario of immigrant age distribution?
 - b. under the “all ages immigrants” scenario of immigrant age distribution?

For all scenarios, we express the immigration rate (I) as a percentage, calculated as the ratio of immigrants (i) in a given year (y), to breeders (b) in the preceding year (y-1), multiplied by 100:

$$I_y = [i_y / b_{y-1}](100)$$

In the case of simulations under the “young immigrants” assumption, we also express immigration rate (I) in terms of immigrants (i) as a percentage of the number of locally-hatched individuals (L) recruiting to the breeding population (i.e. entering Age Class 4) in the same year (y), multiplied by 100:

$$I_y = [i_y / L_y](100)$$

In other words, the immigration rate would be 23% if the number of immigrants into Age Class 4 was 23% of the number of locally-hatched recruits into Age Class 4 in the same year.

Additionally, we used the model to simulate population behavior if reproductive success rates were consistently good or poor. We modeled population growth rates at the colony under sustained conditions of high productivity (equal to largest annual productivity observed in our study) or low productivity (equal to smallest annual productivity observed in our study), assuming no net immigration. We also determined the productivity rate that would be required to attain the annual growth rate observed in this study, if no net immigration were occurring.

Reproductive Success, Fledging Mass, and Chick Diet

We analyzed various metrics of reproductive success, fledgling mass, and chick diet using ANOVA and chi-square tests. We used JMP (Versions 8.0.2 and 9.0.2, SAS Institute Inc., Cary, NC, 1989-2010) for all analyses, and all values are reported as mean \pm SE, except where identified as mean \pm SD. All α levels for statistical significance were 0.05.

Most metrics we considered are self-explanatory, but two metrics of bill-load composition in particular warrant explanation because their similar names could be confused: single- vs. multiple-item bill-loads, and single- vs. mixed-species bill-loads. In describing the number of prey items in a bill-load, deliveries of a single item are called *single-item* bill-loads, whereas deliveries with two or more items are called *multiple-item* bill-loads. In describing the number of prey types in a bill-load, deliveries that contained

only one prey type are called *single-species* bill-loads, while deliveries with two or more prey types are called *mixed-species* bill-loads. The mixed- versus single-species distinction was made only for multiple-item bill-loads. For purposes of bill-load composition, all invertebrates were pooled into a single category. Bill-loads containing unidentified items were excluded from some analyses as necessary. Finally, five unidentified prey items were included in calculations of prey length and number, but excluded from all other analyses. See Table 1.1 for summary of data excluded from various analyses.

We used 1-way ANOVA tests to assess the effect of year on mean values of bill-load size (number of items), prey length (for the three primary species), and fledging mass (2005-2008; 2009 excluded due to small sample size of $N = 3$). In the case of bill-load size and prey length, we used Welch's ANOVA, rather than standard ANOVA, to account for non-homogeneity of variances that was not improved by transformation. We followed each significant ANOVA with post-hoc pair-wise comparisons of means using the Tukey-Kramer HSD (honestly significant difference) test.

We used Pearson's chi-square test to assess the effect of year on the following metrics: proportion of single- versus multiple-item bill-loads, proportion of single- versus mixed-species bill-loads, prevalence of three primary fish species among prey items, hatching success, and fledging success. When the chi-square test was statistically significant, we used odds ratios to make comparisons between all or selected pairs of years. For pair-wise comparisons, we considered the difference statistically significant if the 95% confidence interval (CI) did not encompass one.

Results

Population Size and Modeling

The breeding population grew from 136 pairs in 2000 to 389 pairs in 2009 (Fig. 1.2), with an average annual growth rate of 12.4% (geometric mean of observed annual growth rates). Annual growth rates ranged from -10% to +37%, and eight of nine years showed positive annual growth (Table 1.3). The single year of negative growth (and extremely high growth rate the following year) is likely an artifact of the 2005 census taking place after a gale destroyed nests, but before replacement eggs were laid (Shannon 2006). For this reason, we adjusted the growth rates for 2005 and 2006 by replacing the observed annual growth rates with the mean of the two annual growth rates (i.e. we replaced both -0.10 and 0.37 with 0.14; Table 1.3). We used the average annual growth rate of 12.9% (mean of adjusted annual growth rates) in our model. Results from our model are presented here, and documented in the Appendix.

Our model predicted the following outcomes under our “young immigrants” scenario (with no emigration):

- 1) Without immigration, the MR colony would have an annual growth rate of -1.6%.
- 2) To indefinitely maintain a constant breeding population size (i.e., 0% annual growth) at the level observed in 2009 (389 breeding pairs), the MR colony would need an annual influx of immigrants equal to 2.0% of the previous year’s breeding population. This can also be expressed as annual immigration equal to 23% of the number of locally-hatched birds that return to enter the breeding population each

year. That is, among first-time breeders (Age Class 4) each year, 81% of individuals would be native to MR and 19% would be immigrants.

- 3) To indefinitely maintain the mean annual growth rate observed in 2000-2009 (12.9%), the MR colony would need an annual influx of immigrants equal to 17.7% of the previous year's breeding population. This can also be expressed as annual immigration equal to 334% of the number of locally-hatched birds that return to enter the breeding population each year. That is, among first-time breeders (Age Class 4) each year, 23% of individuals would be native to MR and 77% would be immigrants.

Our model predicted the following outcomes under our "all ages immigrants" scenario (with no emigration):

- 4) Without immigration, the MR colony would have an annual growth rate of -1.6%.
- 5) To indefinitely maintain a constant breeding population size (i.e., 0% annual growth) at the level observed in 2009 (389 breeding pairs), the MR colony would need an annual influx of immigrants equal to 2.4% of the previous year's breeding population.
- 6) To indefinitely maintain the mean annual growth rate observed in 2000-2009 (12.9%), the MR colony would need an annual influx of immigrants equal to 19.7% of the previous year's breeding population.

Our model also predicted the following outcomes, representing population growth rates under conditions of sustained high or low productivity, as well as the productivity rate required to attain the observed growth rate in the absence of immigration. The annual population growth rate at the colony, in the absence of immigration, would be

0.4% under conditions of high productivity (0.62 chicks fledged per pair; the highest annual productivity observed in our study). The annual population growth rate at the colony, in the absence of immigration, would be -3.0% under conditions of low productivity (0.39 chicks fledged per pair; the lowest annual productivity observed in our study). In order to attain the observed annual growth rate of 12.9%, if no net immigration occurred, the annual productivity rate would need to be 2.08 chicks fledged per pair. This productivity rate is outside the realm of biological possibility since Razorbills lay single-egg clutches, and the maximum possible productivity rate would therefore be 1.00 chick fledged per pair.

In addition to modeling population growth and immigration rates, we also used our model to estimate the total Razorbill population associated with MR, including pre-breeding age classes. The number of individuals in pre-breeding age classes is 46% of the number of breeders, indicating total population sizes of 400 in 2000 and 1,100 in 2009.

Reproductive Success and Relationship to Diet Composition

Mean annual productivity was 0.48 ± 0.13 SD chicks fledged per breeding pair ($N = 3$, range 0.39-0.62; Table 1.4). We could not assess statistical significance of interannual differences in productivity because this metric was calculated rather than sampled.

Hatching success for Razorbills at MR for six years was generally low, ranging from 0.43-0.87 (mean 0.72 ± 0.07 ; Table 1.4), and significantly variable between years (Pearson's chi-square test, $df = 5$, $\chi^2 = 39.2$, $p < 0.0001$). Hatching success was highest in 2006 and was significantly higher that year than 2005 and 2009; 2004 was also

significantly higher than 2005 and 2009 (see Table 1.5 for odds ratios of hatching among-year comparisons). Hatching success was lowest in 2005 and was significantly lower that year than all other years. Hatching success in 2009 was significantly lower than 2004, 2006, and 2007. Interannual variation in hatching success did not show any clear patterns in relation to chick diet.

Fledging success was also low and variable, and, unlike hatching success, showed a relationship with annual proportions of high- and low-quality prey items in chick diet (Fig. 1.3). Fledging success for three years ranged from 0.50-0.86 (mean 0.66 ± 0.10 Table 1.4), and year was a significant predictor of fledging success (Pearson's chi-square test, $df = 2$, $\chi^2 = 10.5$, $p = 0.005$). Odds of fledging were significantly higher in 2008 than in 2007 or in 2009 (see Table 1.5 for odds ratios of fledging among-year comparisons). We classified herring, hake, and sandlance as high-quality prey items, based on high lipid-densities reported in the literature for these forage fish species. We classified euphausiids and larval fish as low-quality prey items, based on the size of the items and lipid-densities reported in the literature. In 2008, the year with the highest fledging success, chick diet contained the greatest amount of high-quality prey (90%), and no low-quality prey. Conversely, in 2007, the year with the lowest fledging success, chick diet contained the smallest amount of high-quality prey items (76%), and the greatest amount of low-quality items (10%). 2009 was intermediate in fledging success and proportions of high- and low-quality prey items in the chick diet.

Chick Fledging Mass

Mean chick fledging mass for 2005-2008 was 165 ± 3 g ($N = 77$, range 100-260 g; Table 1.6). The number of chicks banded varied greatly between years (range 6-28 chicks). Mean chick fledging mass varied significantly between years (1-way ANOVA, $df = 3$, F ratio = 9.58, $p < 0.0001$) and was significantly lower in 2005, and higher in 2008, compared to 2006 and 2007 (Tukey-Kramer HSD, $q = 2.63$, $\alpha = 0.05$; Table 1.6).

Nestling Diet

Bill-loads delivered to nestlings contained one to several prey items, and average bill-load size differed between years. We recorded 760 bill-loads of prey brought to the breeding colony by chick-rearing Razorbills. Pooling bill-loads, there were 1,698 prey items, of which 1,693 were identified to species or species group. Individual bill-loads contained one to ten items ($N = 760$, mean 2.23 ± 0.05 ; Fig. 1.4), and the mean number of prey items per bill-load varied significantly between years (Welch's ANOVA, $df = 4$, F ratio = 4.94, $p = 0.001$; Fig. 1.5). Mean bill-load size was significantly lower in 2008 than in 2009 (Tukey-Kramer HSD, $q = 2.73$, $p = 0.002$). Overall, two thirds of bill-loads contained two or more items (multi-item bill-loads; 64%; $N = 760$) while one third of bill-loads contained one item (single-item bill-loads; 36%; Fig. 1.6). There was significant interannual variation in the proportion of bill-loads that were single-item (Pearson's chi-square test, $df = 4$, $\chi^2 = 46.3$, $p < 0.0001$), with 2005 bill-loads (63%; $N = 24$) significantly more likely to be single-item than 2006 (Odds ratio = 0.25, $CI = 0.10$ -0.64) or 2009 (Odds ratio = 0.13, $CI = 0.05$ -0.32). The proportion of single-item bill-

loads was lowest in 2009 at 0.18 (N = 185) and bill-loads that year were significantly less likely to be single-item than in all other years (Odds ratio tests with CIs excluding one).

In addition to variation in bill-load size, bill-loads also varied in composition, or the number of species represented among the prey items. Considering only multi-item bill-loads, the majority (83%) contained only a single species despite having several items, while a minority (17%) contained more than one species (N = 452; Fig. 1.7). The proportion of single-species bill-loads varied significantly between years (Pearson's chi-square test, $df = 4$, $\chi^2 = 13.58$, $p = 0.009$). The proportion of multi-item bill-loads that were single-species was largest in 2006 at 0.89 (N = 76) and the odds of a multi-item bill-load being single species that year were significantly greater than in 2009 (Odds ratio = 0.34, CI = 0.15-0.78). Odds of a multi-item bill-load being single-species were also significantly greater in 2008 than in 2009 (Odds ratio = 0.39, CI = 0.20-0.75). The proportion of multi-item bill-loads that were single-species was smallest in 2005 at 0.67 (N = 9) but odds of a bill-load being single-species in that year did not differ significantly from any other year (Odds ratio tests with CIs inclusive of one).

The overall composition of Razorbill chick diet was diverse and dramatically variable between years. Each year showed clear dominance of a single prey species, but the identity of this primary species was not consistent across years. Prey items brought to Razorbill chicks included seven fish species or species groups, larval fish, and invertebrates (Table 1.7). Atlantic herring (*Clupea harengus*, N = 558), sandlance (*Ammodytes* spp., N = 430), and hake (may include *Merluccius bilinearis*, *Urophycis tenuis*, *U. chuss*, and *Enchelyopus cimbrius*, N = 393) were the most common prey items overall (N = 1,693), and each predominated in at least one year. Each year a single

species represented approximately two thirds of prey items. Atlantic herring made up the majority of prey items in 2006 and 2009 (60-63%), sandlance in 2008 (70%), and hake in 2005 and 2007 (48-60%). Year was a significant predictor of the proportion of Atlantic herring in chick diet (Pearson's chi-square test, $df = 4$, $\chi^2 = 450.4$, $p < 0.0001$), as it was for sandlance (Pearson's chi-square test, $df = 4$, $\chi^2 = 808.8$, $p < 0.0001$) and hake (Pearson's chi-square test, $df = 4$, $\chi^2 = 276.0$, $p < 0.0001$; Fig. 1.8). Pairwise odds ratio tests showed that the odds of a prey item being herring varied significantly for multiple pairs of years, as did the odds of a prey item being sandlance or hake (Table 1.8).

In addition to variation in bill-load size and composition, prey items also varied in length. Mean length of prey items was 2.79 ± 0.03 bill-lengths ($N = 1,698$, range 0.5-8.0) and varied between years (Welch's ANOVA, $df = 4$, F ratio = 296.2, $p < 0.0001$; Table 1.9). Mean length of primary prey species (herring, sandlance, and hake) also varied between years (Table 1.10). Sandlance had the longest mean length and highest variation in length. Prey item lengths can be converted to metric units using the mean bill-length (exposed culmen) of 32.9 ± 1.4 mm SD (range 31.5-36.9 mm) for 14 birds we measured on MR in 2008-2009 (four males, five females, five unknown sex).

Besides post-metamorphic fish (96%), chick diet also included small amounts of invertebrates and larval fish (< 2% each, $N = 1,693$; Table 1.7), which we observed in approximately half of all years. Invertebrates were observed in three of five years, and were almost exclusively euphausiids (97%, $N = 33$; Euphausiidae, most likely *Meganyctiphanes norvegica*), with one specimen (3%) being an unidentified invertebrate. Larval fish were observed in two of five years, and were never observed in years that invertebrates were not present in the diet.

Discussion

The geographic structure of a seabird breeding distribution can be described as having an interior and a periphery. While it may sometimes be the case that a species distributional limit is demarcated by a sharp line between good and unacceptable habitat, it is probably more often the case that habitat quality declines in one or more aspects as the range boundary is approached, and the boundary marks the point at which conditions have deteriorated so much that habitat cannot support the species. In the latter case, individuals living near the distributional limit would be existing in marginal habitat, where conditions are sufficient, but not optimal, for meeting the animals' needs. Accordingly, as one moves from the interior to the periphery of a species range, one would perhaps observe survival and reproductive success declining. Examples of less desirable conditions at a breeding site are: paucity of safe habitat, uncertainty about amount or quality of food, or amount and aggression of predators or competitors; or in other words, fewer resources. The relatively less desirable conditions on the range periphery would manifest in population vital signs such as productivity. In fact, we found that the MR Razorbill colony (which is on the periphery of Razorbill distribution) is a sink population, and reproductive metrics there were weaker than those at non-peripheral breeding colonies, as reported in the literature. We also found signs that this low reproductive success was related to the quality of chick diet on an annual scale, indicating that foraging conditions at the periphery of the species range may be of poorer quality than elsewhere in the range.

Immigrant-supported Sink Population

Our population model indicated that the breeding colony of the threatened Razorbill at MR is a sink population whose recent annual growth rate could not be achieved without substantial net immigration. Specifically, our model predicted that, in the absence of all immigration, the population would decline at a rate of 1.6% annually, resulting in the eventual loss of the population. Depending on the age distribution of immigrants, low- to moderate net immigration would be necessary to maintain a constant population size, and substantial net immigration would be necessary to account for the 12.9% annual growth rate observed in this study. Nest monitoring revealed that low overall productivity, consisting of poor success at the egg and chick stages, is a component of the sink status. Our examination of chick diet suggests that inadequate nutrition may be depressing productivity by decreasing the likelihood of chick survival to fledging age. Evidence in support of this idea includes annual fledging success that correlated positively with inclusion of high-quality prey in chick diet, and negatively with low-quality prey. Additionally, chicks fledged from the colony at low masses compared to elsewhere, further supporting the idea that chicks at MR had lower caloric intake than chicks at other colonies. Chicks fledging at low weight may be less likely than heavier chicks to survive their first year (Morrison *et al.* 2009), thereby further reducing the pool of locally-hatched birds available to join the breeding population in future years.

Our model allowed us to estimate the immigration rates required for certain hypothetical population growth rates. It predicted that to maintain a steady-state population, the number of annual immigrants would need to equal 2.0-2.4% (depending on the immigrants' age distribution) of the previous year's breeding population. This

estimate was made under the assumption that no birds were leaving the MR population through emigration; if emigration were occurring, immigration rates would need to be higher than our reported estimates. Under the “young immigrants” scenario, approximately five out of six first-time breeders each year would be native to MR, while one out of six would be immigrants. This shows that MR is a sink.

But it is a sink that is experiencing rapid growth. In order to maintain the 12.9% annual growth rate we observed at MR, the number of annual immigrants would need to equal 18-20% of the previous year’s breeding population. Under the “young immigrants” scenario, this immigration rate translates to approximately three quarters of the first-time breeders being immigrants, and only one quarter being native to MR. This would be a startlingly high representation of immigrants among most animal populations, and especially so for a seabird that has been considered highly philopatric.

If foraging conditions were consistently good near the colony, our model indicates that the colony could maintain size or grow slowly, even in the absence of immigration. If the colony had consistent annual productivity equal to the highest annual rate observed in this study, which occurred during the year with the highest-quality chick diet, the colony would be expected to grow at a rate of 0.4% per year based solely on recruitment of locally-hatched individuals.

It is unclear where the source population(s) for the MR immigrants might be. The paucity of banded individuals and lack of systematic resighting effort in the western North Atlantic region precludes a clear understanding of the source of immigrants to MR. However, MSI, the nearest colony (161 km) of significant size to MR, may be a primary source of immigrants to the colony, as several individuals banded at MSI were seen at

MR between 1995-2006 (Lavers *et al.* 2007). Additionally, a single individual banded in Newfoundland as a chick was observed on MR in 2011 (Banfield and Poli 2011).

Total Population Size

In addition to facilitating predictions of colony growth and immigration rates, our model allowed us to model the total population of Razorbills associated with the MR colony, including pre-breeding age classes which have not previously been counted due to the fact that they do not usually return to the breeding colony during their first few years of life. Estimating total population is an important outcome because total population size is a useful metric for conservation planning, and can help improve estimates of the number of birds using oceanic habitat, as opposed to merely those that are using breeding colony habitat. Knowledge of total (versus breeding) population numbers would be useful, for example, in calculating seabird consumption of forage fish for consideration in fisheries regulations or ecosystem food-web modeling, or estimating numbers of birds exposed to oil spills. Using our model, we estimated that the number of pre-breeders in the population is approximately 46% of the number of breeders. Based on this work, we estimate that the *total* Razorbill population associated with the MR breeding colony increased from approximately 400 individuals in 2000 to over 1,100 individuals in 2009.

Low Reproductive Success

Reproduction at MR was low and variable for all the metrics we examined: productivity, hatching success, and fledging success. First, the overall productivity at MR

of 48% was much lower than the typical range of 65-75% reported for the species, as summarized by Lavers *et al.* (2009). Those chicks that survived to fledging age left the colony in poorer average condition than elsewhere, as indicated by the low average mass of fledglings. At 165 g, the fledgling mass of chicks at MR was lower than typical for North American colonies (195-205 g; Lavers *et al.* 2009). This suggests chicks received inadequate nutrition, which could be due to poor foraging conditions. A further indication of unusually small chicks came in 2009, when only a small portion of the chicks we attempted to band had legs large enough to hold a band by the time they fledged. 2009 was a year with moderate fledging success following low hatching success, and some inclusion of poor-quality food (larval fish and euphausiids) in the chick diet.

Next, the 72% hatching rate was near the low end of the published range (85% of studies reporting $\geq 70\%$ success; Lavers *et al.* 2009) and was not consistent across the six years of our study. Nest failures during the incubation stage in our sample included eggs that were cracked, abandoned, showed signs of predator damage, or were missing and presumed eaten by predators. We speculate the interannual variability in hatching rate could be related to variable weather events and predation level in the colony, while prey availability could also play a role.

With regard to fledging rate, the 66% fledging rate observed at MR was much lower than the published range as summarized by Lavers *et al.* (usually 85-95%; 2008), and was quite variable over the three years of our study. In fact, Lavers *et al.* (2008) state that “fledge success is invariably higher than hatch success,” which was not the case at MR, where mean annual fledging rate (N = 3) was lower than mean annual hatching rate (N = 6), and fledging rate was lower than hatching rate in two of the three years when

both metrics were recorded. A fledging rate similar to MR was recorded in 2004-2006 at Gannet Islands, Canada (63%; Lavers and Jones 2007). In the Gannet Islands study, 43% of chick mortalities occurred among late-stage chicks that appeared emaciated, and the authors suspected starvation due to inadequate nutrition, coinciding with both a decreased prevalence of adult capelin in the diet, and the appearance for the first time of larval capelin (Lavers and Jones 2007). At MSI, fledging rates were not reported per hatched chick so direct comparison to our results is not possible, but fledging rates per nest were very low from 1995-2008 (see discussion below; Bowser *et al.* 2009). Failure during the nestling stage in our sample included many chicks that disappeared (presumed killed by predators), some chicks that died in nests possibly from starvation or hypothermia, and one chick that was found inside its burrow with superficial and neurological damage, possibly inflicted by a nest intruder such as a predator or a prospecting Razorbill or Atlantic Puffin. We speculate the interannual variability of fledging rate could be related to weather events and predation level in the colony, in addition to chick diet.

Fledging Success Linked to Chick Diet

For the three years of our fledging study, the annual fledging rates were positively correlated with the amounts of high-quality food (lipid-dense forage fish), and negatively correlated with the amounts of poor-quality food (larval fish and invertebrates) in the chick diet. Specifically, the highest fledging rate was attained in 2008 when the chick diet contained no poor-quality food and a very high proportion of high-quality food, particularly sandlance. Conversely, the lowest fledging rate occurred in 2007, when poor-

quality food was most prevalent in the diet, and high-quality food the least prevalent. In 2009, the inclusion of both food types were intermediate, as was fledging success.

Our sample size for fledging success was small (three years), as was one of the between-year differences in prevalence of poor-quality prey items in the chick diet (0% versus 1%). However, we suggest that any inclusion of poor-quality prey items in the chick diet, no matter how small the amount, may signal that high-quality prey is scarce, and even chicks that are not fed the low-quality items may be experiencing lower caloric intake due to less frequent meal delivery, lower meal mass, or prey of lower energy-density. Our data does not allow us to address these hypotheses but they would be interesting to examine in the future, along with measures of parental foraging effort. Likewise, we could not calculate chick caloric intake because our study did not assess chick feeding rates or sample prey items to determine actual energy density, which can vary greatly within and between years (Hislop *et al.* 1991; Diamond and Devlin 2003; Wanless *et al.* 2005; Schrimpf 2011).

There is more than one possible explanation for poor nutritional intake by chicks at MR. Contributing factors could include poor availability or quality of prey in the environment, or poor foraging skills of chick-provisioning adults. For example, Davoren and Montevecchi (2003) found that in eastern Canada, Common Murre (*Uria aalge*) chicks at an island distant from foraging grounds experienced lower provisioning rates (due to increased foraging trip length), leading to slower growth and poorer condition at fledging when compared to chicks at a colony close to foraging grounds.

Diet Compositional Quality

Our observations of chick diet at MR indicate that the prey conditions around the island may be quite variable, with frequent availability of at least one high-quality forage fish species, but also periodic declines in high-quality food availability during the chick-rearing season to the point that low-quality food is substituted in the chick diet. Chick diet generally showed high inclusion of nutritious, lipid-dense forage fish species, which suggests that chicks may be receiving adequate nutrition despite the absence in the diet of capelin, a nutrient-dense species that is a staple in chick diet at many other colonies. However, chick diet also showed high interannual variation in composition, and the inclusion of larval fish and euphausiids in the diet was notable because these are poor-quality chick foods that have been associated with decreased reproductive success.

Each of the primary prey species, Atlantic herring, sandlance, and hake, made up $\geq 23\%$ of overall prey items by number, and comprised $\geq 60\%$ of prey items in at least one year. Other observed prey, in order of decreasing prevalence, included euphausiids, butterfish (*Peprilus triacanthus*), Atlantic pollock (*Pollachius virens*), larval fish (unknown species), Atlantic saury (*Scomberesox saurus*), and rock eel (*Pholis gunnellus*). Atlantic saury was first documented in the diet of seabird chicks at MR in 2006 (S. Kress, unpub. data), and its continued representation in chick diet through the end of this study may indicate an increased presence of this fish in the GOM during the seabird chick-rearing season, possibly due to a change in saury distribution or timing of movements.

The three main items in chick diet are lipid-dense species with generally high energy contents. Herring is quite lipid-dense, giving it high energetic contents and

making it good food for vertebrate predators (Lawson *et al.* 1998) such as young piscivorous auks. Sandlance is also considered a high-quality diet item for seabirds (Anthony and Roby 1997; Russell 1999; Anthony *et al.* 2000; Baillie and Jones 2003; Wanless *et al.* 2005) and has been hypothesized to be a preferred food for Razorbills (Gaston and Woo 2008) but, unexpectedly, Lawson *et al.* (1998) found its lipid-content to be among the lowest of twelve Northwest Atlantic prey species. We found very little information on the energy content of forage-size hake, but Russell (1999) reported its energy density was similar to that of herring, and slightly lower than that of sandlance, in samples of Atlantic Puffin chick diet collected at multiple colonies in Newfoundland.

The larval fish and invertebrates found in chick diet at MR are uncommon in chick diet elsewhere, most likely because they are poor quality food. The only published cases, to the best of our knowledge, are at Hornøya, Barents Sea (larval capelin and unidentified fish, 17% by number; Barrett 2003), MSI (euphausiid shrimp and larval fish; Diamond and Devlin 2003; Bowser *et al.* 2009) and in very small amounts at the Gannet Islands (squid and larval capelin; Lavers and Jones 2007). Occurrence of these items in chick meals tended to be clustered in time, and might represent prey-switching when favored prey was not available. These items are probably less nutritious than post-metamorphic fish due to small size and, especially in the case of larval fish, low lipid density (e.g., Van Pelt *et al.* 1997). Inclusion of these items in chick diet among other alcid species has sometimes been correlated with decreased chick growth (Massias and Becker 1990; Baillie and Jones 2004), reproductive success (Baird 1990; but see Baillie and Jones 2004), and availability of usual prey (Baillie and Jones 2004). We would like to note that euphausiids are a regular part of *adult* diet, especially in winter (Lavers *et al.*

2009; Lilliendahl 2009), which suggests that they are sufficient quality as Razorbill prey. Nevertheless, their infrequent presence in chick diet still suggests that they are poor chick food, perhaps due to the inefficiency of transporting them to the nest in large enough numbers to feed a chick.

The chick diet at MR is more similar to other North American colonies than it is to European colonies, though there is some overlap with the prey species found at colonies throughout Europe including Iceland, British Isles, and the Baltic Sea (Lavers *et al.* 2009). Herring and sandlance are common in the diet of Razorbill chicks at North American colonies (Lavers *et al.* 2009). Hake is less common than herring and sandlance in the diet of North American auks, although it is a staple of Atlantic Puffin diet in the GOM and Nova Scotia (Lowther *et al.* 2002) and has been reported in Razorbill diet at MSI (Bowser *et al.* 2009). Hake represented a larger proportion of the diet at MR (31% mean annual proportion; 60% and 48% of items in two years) than at MSI (16% mean annual proportion; 40% largest annual proportion; Bowser *et al.* 2009). Of the three primary prey species in the chick diet at MR, sandlance was the most variable, having usually low inclusion but spiking dramatically in 2008. Again, this is similar to the pattern observed at MSI (see discussion below; Bowser *et al.* 2009) in 1995-2008, though the peak years did not overlap. The amount of sandlance in the diet of Atlantic Puffin chicks at another North American colony also fluctuated considerably (Burke and Montevecchi 2008). These patterns of extreme sandlance fluctuation in chick diet may reflect highly variable sandlance recruitment and large fluctuations in abundance that occur every few years (Robards *et al.* 1999).

At MR, prey lengths were similar to those reported for other colonies, although the observed lengths of Atlantic herring may indicate exploitation of older age classes than reported elsewhere. Prey lengths varied from shorter than the adult's bill to several times the length of the bill (0.5-8.0 bill-lengths, or 1.6-26.0 cm, converted using mean adult culmen length of 32.9 mm, N = 14; Kauffman unpub. data), with the shortest items being larval fish and euphausiids, and the longest items being mature sandlance and herring. The mean observed length of herring correlates to the 1-group (post-metamorphic juvenile) age class, while the minimum and maximum observed lengths of herring correlate to 0-group (larval) and 3-group (first-year mature) age classes (Reid *et al.* 1999). This is a broader exploitation of herring than reported by Diamond and Devlin (2003), who stated that the age group generally eaten by seabirds is 0-group juveniles. The mean observed length of sandlance indicates those prey were most likely 1- and 2-group (late juvenile and early mature) with the range of observed lengths correlating to a broad range of ages from 0-group (larval and post-metamorphic juvenile) to mature individuals near the maximum age of ten to twelve years (Nelson and Ross 1991). Hake was probably 0- and 1-group individuals (Koeller *et al.* 1989; Russell 1999; Lock and Packer 2004).

Bill-load characteristics were similar to values reported at other colonies, in terms of number and size of items, and tendency for all items in a bill-load to be of a single species. Bill-loads delivered to chicks contained one to ten items with approximately one third of all bill-loads containing a single item, another third containing two items, and 85% containing three or fewer items. Bill-loads with seven to ten items represented less

than one percent of all bill-loads. This is similar to reports of Razorbill bill-load size distribution elsewhere (Gaston and Jones 1998; Paredes *et al.* 2006; Lavers *et al.* 2009).

Interannual Diet Variation

The single dominant prey species of Razorbill chicks on MR was not consistent between years, but three species (herring, sandlance, and hake) were consistently major diet components. In four of five years, one of these major prey species represented $\geq 60\%$ of diet by numbers, with the dominant species varying by year. Herring dominated in 2006 and 2009 (60% and 63% of items, respectively) but represented only 6-16% of prey items in other years. Similarly, hake was the dominant prey species in 2005 and 2007 (60% and 48%, respectively) but represented 9-27% of prey items in other years. Likewise, sandlance dominated in 2008 (70%) but was otherwise a minor component of diet, representing twelve percent of items in 2007 and two percent or less in the remaining three years.

The variety of prey items present in Razorbill chick diet at MR, along with the interannual variation in dominant prey species, indicates that Razorbills are capable of harvesting a broad range of prey items, and that they are capable of behavioral flexibility to exploit a changing prey base or differing environmental conditions. However, the overall low reproductive success at MR, when considered in context of the observed correlation between reproductive success and diet quality, suggests that foraging conditions may have a negative effect on the colony despite the ability of chick-provisioning adults to exploit a varied and changing prey base. It may be the case that chicks are not receiving adequate nutrition, despite the presence of high-quality forage

fish in the diet. This could be occurring if feeding rates are low, or if the energy densities of the local herring, sandlance, and hake are lower than what is usually found for those prey species. We did not examine feeding rates, nor sample prey items for determination of energy content, so we cannot assess caloric intake of chicks.

Gulf-wide Conditions?

Prevailing conditions for Razorbills in the GOM may be worse than conditions found farther north, as indicated by similarity of our results to those of the only other GOM Razorbill colony at which the same factors have been studied. The diet and reproductive success of MR Razorbills closely reflect those reported at MSI, located in the Bay of Fundy at the north end of the GOM. This similarity holds true at least in terms of chick diet composition and recent reproductive success that is low, but highly variable between years. The similarity of the two colonies in diet and reproductive metrics suggests that there may be common factors affecting both colonies, and perhaps also smaller GOM colonies. Gulf-wide conditions that are unfavorable to Razorbills could be long-term and reflective of the location at the periphery of the Razorbill's range being on the edge of suitable conditions. On the other hand, the unfavorable conditions could reflect relatively recent changes in Gulf-wide conditions, possibly in response to commercial fishing activities and changes in climate and oceanic patterns (Harris and Tyrrell 2001, Nye *et al.* 2009, Lucey and Nye 2010, Nye 2010). Since information on historic distribution of Razorbills is sparse, and nothing is known of reproductive success or diet in the GOM before recent decades, we are not able to distinguish which of these possible explanations is more likely. However, it does seem that further research is called

for, to establish whether Razorbills are indeed experiencing low reproductive success throughout the GOM, and further explore the relationship that chick diet and prey availability may have to productivity.

The similarity in chick diet between MR and MSI consisted of considerable overlap in prey species and similar interannual changes in primary prey species identity (see Bowser *et al.* 2009). Furthermore, chicks at MR and MSI both consumed larval fish and in addition to the typical Razorbill chick diet of post-larval forage fish. Larval fish and are unusual (though not unheard of) in Razorbill chick diet (e.g., Barrett 2003; Lavers and Jones 2007; Bowser *et al.* 2009). However, the euphausiids observed in Razorbill chick diet at MR have previously only been reported at MSI (Bowser *et al.* 2009). Capelin, a subarctic fish that visits the Gulf of Maine only occasionally (Klein-MacPhee 2002), is a common component of chick diet at many North American and European colonies, but was absent from the diet at both MR and MSI.

With regard to productivity, low productivity similar to MR has been reported in the last two decades at other North American breeding sites, namely MSI and the Gannet Islands. MSI had mean productivity of 56% from 1995-2008, including a low of ten percent in 2007 (Bowser *et al.* 2009), and productivity at the Gannet Islands from 2004-2006 was only 39%, attributed partly to high kleptoparasitism (Lavers and Jones 2007).

Due to the similarity in diet of chicks at MR and MSI, we believe that diet is a factor in the low reproductive success observed at both colonies. However, it is possible that other gulf-wide conditions also have a role in the low reproductive success at these two colonies. For example, reproductive rates at both MR and MSI colonies could be

negatively affected by predation, kleptoparasitism, human disturbance, or possible high rates of immigration of young, inexperienced breeders.

Other Factors: Predation, Kleptoparasitism, and Disturbance

Predation by gulls, and possibly by corvids, occurred in the Razorbill colony throughout the breeding season. We frequently observed evidence of predation (damaged and displaced eggs, missing chicks), and on several occasions we observed Herring Gulls (*Larus argentatus*) hunting within the Razorbill colony. From 2006-2009, we observed three Herring Gulls and one Great Black-backed Gull carrying Razorbill chicks from the colony. Additionally, a fledgling-size Razorbill chick was found in one of seven Great Black-backed Gull stomachs that were examined in 2010 (Banfield and Poli 2010). Laughing Gulls nesting on the island are regular nest predators of terns, but do not nest near the main Razorbill colony and are unlikely to be predators of this species. We did not observe depredation by corvids, but Common Ravens (*Corvus corax*) and American Crows (*Corvus brachyrhynchos*) sometimes spent time near the Razorbill colony in pairs or alone, and may have been nest predators.

Another factor that could be negatively affecting reproductive success at MR is kleptoparasitism. Kleptoparasitism may occur at higher rates when prey is more limited in the environment, and can result in decreased prey delivery to chicks, affecting productivity. For example, Lavers and Jones (2007) suggested that depressed reproductive success at the Gannet Islands, Canada, may be attributable to an unsustainably high level of intraspecific kleptoparasitism, with repeated attacks on individual adults possibly hurting chick survival. On MR, we observed numerous

incidents of kleptoparasitism on Razorbills by gulls. Herring Gulls attempted to kleptoparasitize Razorbills as they returned to the colony with bill-loads of prey for chicks, and they were sometimes successful. Razorbills themselves infrequently exhibited kleptoparasitism, sometimes on other Razorbills and sometimes on Atlantic Puffins that nested among the Razorbills. Lavers and Jones (2007) suggested that intraspecific kleptoparasitism by Razorbills at the Gannet Islands may be a response to low prey availability. Furness (1987) also presented that opportunistic kleptoparasitism is more common when food is scarce, and furthermore suggested that opportunist (versus specialist) kleptoparasites, which include gulls and alcids, can sometimes rob hosts at rates that deprive the hosts of a significant proportion of prey, and may not be stable over evolutionary time. Gulls at MR may be robbing Razorbills of prey deliveries at a rate that impacts chick growth or survival.

Our presence in the Razorbill colony may have had negative impacts on Razorbill reproductive success, by decreasing parental nest attendance and feeding rates. Negative effects from researcher presence on reproductive success at alcid colonies have been documented (Pierce and Simons 1986; Rodway *et al.* 1996), including evidence that more frequent visits to the colony have more negative impact (Pierce and Simons 1986). However, other studies have found no significant negative effect of researcher activity on alcid reproductive success (Ashcroft 1979; Shearler and Haverland 2000). For Razorbills specifically, regular disturbance at breeding sites has been shown to reduce breeding success (Birkhead and Nettleship 1983; Lyngs 1994), yet Lavers and Jones (2007) reported significantly higher reproductive success in moderate-disturbance plots than in low-disturbance plots. While this body of literature is inconclusive regarding the presence

and magnitude of a researcher effect on alcid breeding success, we selected a nest-visitation frequency that was as infrequent as possible while maintaining accuracy. Additionally, our presence in the colony may have negatively affected reproductive success by increasing exposure of eggs and chicks to predation following flushing of adults.

A recent meta-analysis found, for birds in general, found no significant increased risk of nest predation due to researcher disturbance (Ibáñez-Álamo *et al.* 2012). However, the meta-analysis authors noted that their results varied by taxon. Alcids, among birds, may be particularly susceptible to disturbance (Götmark 1992; Rodway *et al.* 1996), with entire colonies departing en masse when large avian or mammalian predators appear (Parish *et al.* 2001; Ainley *et al.* 2002). Razorbills are very sensitive to disturbance, and also relatively vulnerable to nest predation due to burrow structures that are generally more open than other burrow-nesting auks (e.g., puffins, auklets), though generally more enclosed than the most closely related auks, the murre. Predators can inflict large losses at alcid colonies in a short amount of time following departure of adults (e.g., Parrish 1995). Adult Razorbills at the MR colony did flush from the Razorbill colony at the approach of researchers. However, we took measures to minimize our impact, including entering observation blinds before dawn, and restricting activities outside the blinds to limited time periods on non-consecutive days, and most adults returned to the colony within five to fifteen minutes after we entered observation blinds or left the colony.

Conclusions

In summary, our research indicated that Razorbills had limited success breeding on MR, resulting in an immigration-dependent sink population. The colony experienced low and variable reproductive success at the egg and chick stages, and chicks fledged at lower masses than elsewhere. Poor foraging conditions likely contributed to the low reproductive success and low fledging masses, as annual fledging success was correlated with the quality of the chick diet. We documented a positive relationship between chick fledging rates and the prevalence of high-quality forage fish in the diet. We also documented the larval fish and euphausiids among the prey delivered to chicks, and an inverse relationship between the prevalence of these low-quality prey items and chick fledging rates. Further research is needed to further elucidate the extent to which diet quality is affecting the population. It would be interesting to study whether meal sizes and delivery rates vary inversely with inclusion of larval fish and invertebrates in the chick diet. In other words, when faced with decreased availability of preferred prey, do some chick-provisioning adults switch to poor-quality prey, while others continue to forage for high-quality prey but deliver smaller and less frequent meals? Further study to clarify the relationship between diet and productivity at MR would facilitate effective management of this species, especially in the threatened Maine population. Specifically, knowledge on feeding rate and energy density of delivered prey items on a short time scale would be useful to confirm the link we found between prey quality and fledging success, and further elucidate the role that chick diet may play in the population dynamics of the colony. Examining these factors on a nest-specific level would be especially useful, since individual chick-provisioning parents may be differently skilled

at foraging, or exhibit differing foraging strategies. Casual observations during our study also indicated sustained and possibly high levels of nest predation by gulls, which may further contribute to the low reproductive success rates and sink population dynamics at this colony.

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Table 1.1. Summary of data excluded from specific diet and reproductive success analyses.

Analysis	Excluded	Reason
Single- vs. mixed-species bill-loads	Bill-loads containing only 1 prey item	Single-item bill-loads were, by definition, single-species, but their inclusion masked interannual differences in composition of multiple-item bill-loads.
Single- vs. mixed-species bill-loads	Bill-loads containing ≥ 1 fish of unidentified species, which did not also contain ≥ 2 identified species	Not possible to classify these bill-loads, since it was unknown whether the unidentified fish were of the same species as each other, or, where appropriate, the same species as the single identified prey species.
All diet analyses except prey length and number per bill-load	5 items of unidentified species	Presence and length of prey item recorded, but species identity was not recorded.
Fledging success, 2007	38 nests	Unknown fledging outcome
Fledging Success, 2008	24 nests	Unknown fledging outcome
Fledging success, 2009	35 nests	Unknown fledging outcome

Table 1.2. Population model parameters and source of information.

Parameter	Value	Source
Age at first breeding	4 years	P. Lyngs pers. comm. in Hipfner and Chapdelaine 2002, Lavers <i>et al.</i> 2008
Annual survival rate, pre-breeders	81% (annualized from 44% survival to 4 years)	Lyngs 1994
Annual survival rate, breeders	90%	Lavers <i>et al.</i> 2009
Maximum longevity (i.e. age of oldest breeders)	30 years	Subjective decision based on breeder age records in the literature (see text); also, the age at which < 3% of individuals survive under our model's annual survival probabilities.
Annual population size	range: 272-778 pairs	this study
Annual productivity	0.48 chicks per pair	this study
Annual recruitment to breeding population of native-born birds	Annual productivity rate ¹ multiplied by survival rate to 4 years ²	¹ this study; ² Lyngs 1994

Table 1.3. Annual changes in the number of breeding pairs of Razorbills at Matinicus Rock, Maine, 2000-2009. The adjusted annual growth rates consist of replacing the observed annual growth rates for 2005 and 2006 with a mean value of those 2 years. We made this adjustment because the breeding population census in 2005 probably undercounted the actual population, due to the census taking place after a gale that destroyed nests, but prior to probable relaying by pairs that lost eggs in the storm (Shannon 2006).

Year	Breeding pairs	Annual growth rate	Adjusted annual growth rate
2000	136	-	-
2001	159	0.17	0.17
2002	168	0.06	0.06
2003	211	0.26	0.26
2004	236	0.12	0.12
2005	212	-0.10	0.14
2006	291	0.37	0.14
2007	312	0.07	0.07
2008	343	0.10	0.10
2009	389	0.13	0.13
Geometric mean		0.124	0.129

Table 1.4. Hatching and fledging success and total productivity of Razorbills breeding on Matinicus Rock, Maine, 2004-2009. Year pairs that do not share the same letter in the significance column have significantly different odds of success for the reproduction metric (Odds ratio tests; Table 1.5). Sample sizes are smaller for fledging success than hatching success due partially to uncertain fledging outcomes at some nests, which were excluded from fledging calculations while being retained for hatching calculations.

Year	Hatching success (N)	Signif?	Fledging success (N)	Signif?	Productivity*
2004	0.85 (60)	a	—	—	—
2005	0.43 (49)	b	—	—	—
2006	0.87 (55)	a	—	—	—
2007	0.82 (74)	a	0.50 (36)	a	0.41
2008	0.73 (59)	a,c	0.86 (35)	b	0.62
2009	0.64 (81)	c	0.61 (46)	a	0.39
Mean	0.72		0.66		0.48
Standard error	0.07		0.10		0.13 SD

*Productivity = (Hatching success)(Fledging success)

Table 1.5. Odds ratio comparisons for Razorbill hatching success and fledging success across years at Matinicus Rock, Maine, 2004-2009. These results underlie significance information shown in Table 1.4.

Years compared	Hatching success				Fledging success			
	Odds ratio	Lower 95%	Upper 95%	Signif?	Odds ratio	Lower 95%	Upper 95%	Signif?
2004, 2005	7.56	3.05	18.71	yes	—	—	—	—
2004, 2006	0.83	0.29	2.39	no	—	—	—	—
2004, 2007	1.21	0.48	3.05	no	—	—	—	—
2004, 2008	2.11	0.85	5.25	no	—	—	—	—
2004, 2009	3.16	1.36	7.33	yes	—	—	—	—
2005, 2006	0.11	0.04	0.29	yes	—	—	—	—
2005, 2007	0.16	0.07	0.36	yes	—	—	—	—
2005, 2008	0.28	0.12	0.62	yes	—	—	—	—
2005, 2009	0.42	0.2	0.86	yes	—	—	—	—
2006, 2007	1.46	0.54	3.95	no	—	—	—	—
2006, 2008	2.55	0.96	6.79	no	—	—	—	—
2006, 2009	3.82	1.53	9.54	yes	—	—	—	—
2007, 2008	1.75	0.76	4	no	0.17	0.05	0.53	yes
2007, 2009	2.62	1.23	5.55	yes	0.64	0.27	1.55	no
2008, 2009	1.5	0.72	3.12	no	3.86	1.26	11.78	yes

Table 1.6. Mean mass at fledging for Razorbill chicks at Matinicus Rock, Maine, 2005-2008. Year pairs that do not share the same lower-case letter have significantly different means (Tukey-Kramer HSD test).

Year	N	Mass (g)			Standard error	Signif?
		Minimum	Maximum	Mean		
2005	6	100	145	129	8	c
2006	28	100	200	165	4	b
2007	25	119	190	159	4	b
2008	18	133	260	184	7	a
Total	80	100	260	165	3	

Table 1.7. Percentage of food items (N = 1,693) in each prey species category for Razorbills nesting on Matinicus Rock, Maine, 2005-2009.

Year	Atlantic herring	Hake	Sandlance	Butterfish	Atlantic pollock	Atlantic saury	Rock eel	Unidentified fish	Larval fish	Invertebrate (97% krill)	Total
2005	5.8	59.6	0	0	3.8	0	0	3.8	0	26.9	100
2006	59.7	26.5	1.3	4.6	5.0	1.7	0.8	0.4	0	0	100
2007	16.2	47.8	12.3	0.7	3.1	1.9	0	7.7	6.0	4.1	100
2008	10.8	8.7	69.6	0.4	0.9	0	0	9.6	0	0	100
2009	62.8	12.0	1.7	15.9	0.2	0.9	0	5.2	0.9	0.4	100
Mean annual %	31.0	30.9	17.0	4.3	2.6	0.9	0.2	5.4	1.4	6.3	100
Standard error	12.4	10	13.3	3.0	0.9	0.4	0.2	1.6	1.2	5.2	
Overall %	33.0	23.2	25.4	5.3	1.9	0.9	0.1	6.5	1.7	1.9	100

Table 1.8. An odds ratio comparison of the frequency of Atlantic herring, sandlance, and hake in the diet of Razorbills across years at Matinicus Rock, Maine, 2005-2009.

Years compared	Atlantic herring				Sandlance				Hake			
	Odds ratio	Lower 95%	Upper 95%	Signif?	Odds ratio	Lower 95%	Upper 95%	Signif?	Odds ratio	Lower 95%	Upper 95%	Signif?
2005, 2006	0.04	0.01	0.14	yes	—	—	—	—	4.1	2.2	7.66	yes
2005, 2007	0.32	0.1	1.05	no	—	—	—	—	1.61	0.9	2.9	no
2005, 2008	0.51	0.15	1.68	no	—	—	—	—	15.5	8.25	29.14	yes
2005, 2009	0.04	0.01	0.12	yes	—	—	—	—	10.87	5.84	20.24	yes
2006, 2007	7.66	5.3	11.07	yes	11.01	3.4	35.67	yes	0.39	0.28	0.56	yes
2006, 2008	12.25	8.4	17.87	yes	179.05	56.48	567.59	yes	3.78	2.49	5.74	yes
2006, 2009	0.88	0.64	1.21	no	1.39	0.36	5.27	no	2.65	1.77	3.97	yes
2007, 2008	1.6	1.09	2.34	yes	16.27	11.5	23.01	yes	9.63	6.72	13.78	yes
2007, 2009	0.11	0.08	0.16	yes	0.13	0.06	0.27	yes	6.75	4.8	9.5	yes
2008, 2009	0.07	0.05	0.1	yes	0.01	0	0.02	yes	0.7	0.46	1.06	no

Table 1.9. Length of prey items by year, relative to adult bill length, delivered by chick-rearing adult Razorbills at Matinicus Rock, Maine, 2005-2009. Year pairs that do not share the same lower-case letter have significantly different means (Tukey-Kramer HSD test). Prey item lengths can be converted to metric units using the mean bill-length of 32.9 ± 1.4 mm SD (range 31.5-36.9 mm; exposed culmen) for 14 adults we measured on Matinicus Rock in 2008-2009 (4 male, 5 female, 5 unknown sex).

Year	N	Length (bill-lengths)			Standard error	Signif?
		Minimum	Maximum	Mean		
2005	52	0.5	2.5	1.36	0.08	c
2006	240	0.75	3.5	1.72	0.03	c
2007	415	0.5	5	2.36	0.06	b
2008	530	0.5	7	3.97	0.06	a
2009	461	1	8	2.53	0.04	b
Total	1,698*	0.5	8	2.79	0.03	

*Includes 5 items recorded as "unidentified"

Table 1.10. Length of prey items by species, relative to adult bill length, delivered by chick-rearing adult Razorbills at Matinicus Rock, Maine, 2005-2009. Prey item lengths can be converted to metric units using the mean bill-length of 32.9 ± 1.4 mm SD (range 31.5-36.9 mm; exposed culmen) for 14 adults we measured on Matinicus Rock in 2008-2009 (4 male, 5 female, 5 unknown sex).

Prey species	N	Item length (bill-lengths)				Interannual variation (Welch's ANOVA)		
		Mean	Standard error	Minimum	Maximum	df	F Ratio	p-value
All	1,698	2.79	0.03	0.5	8.0	4	296.2	< 0.0001
Atlantic herring	558	2.56	0.04	0.75	8.0	4	62	< 0.0001
Sandlance	430	4.13	0.07	0.75	8.0	3	78.2	< 0.0001
Hake	393	2.16	0.05	0.5	5.5	4	59.3	< 0.0001

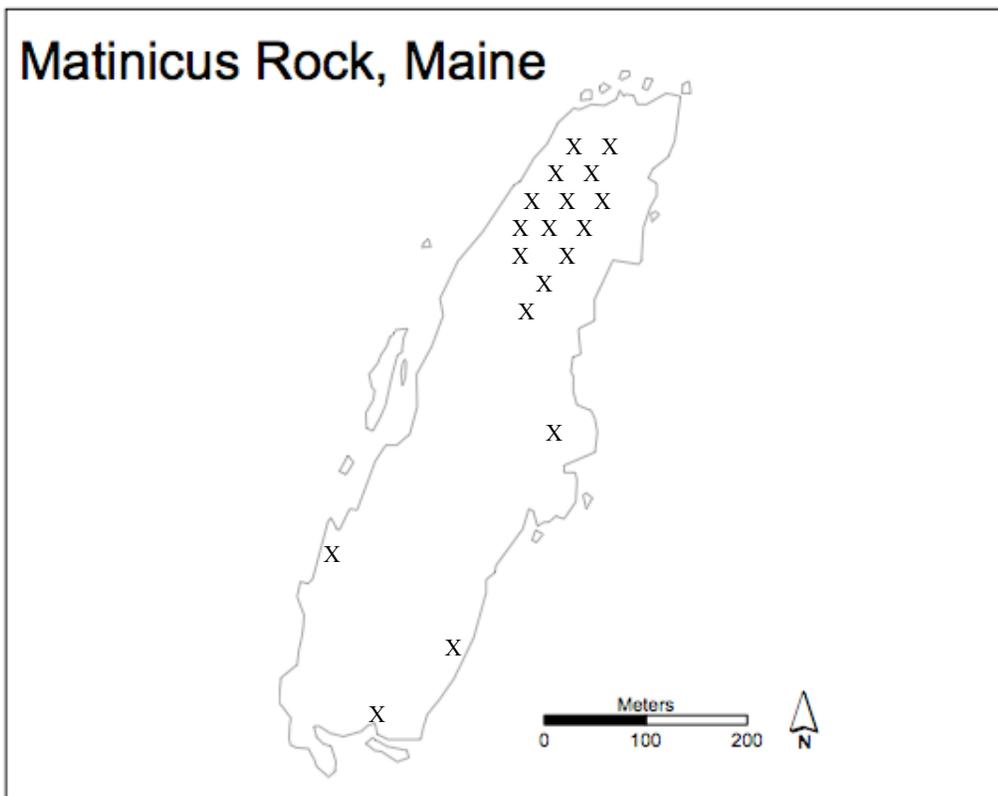
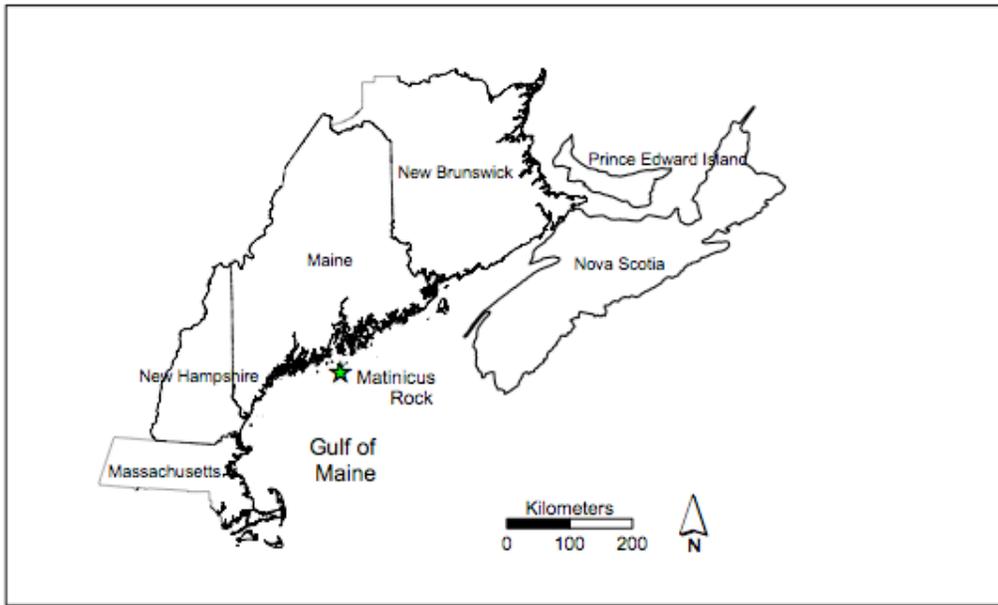


Figure 1.1. Map of Matinicus Rock, Maine, showing approximate locations of Razorbill nesting areas as of 2009 (marked with “X”). This island in outer Penobscot Bay, Gulf of Maine, supports a diverse seabird breeding colony including the largest U.S. Razorbill colony.

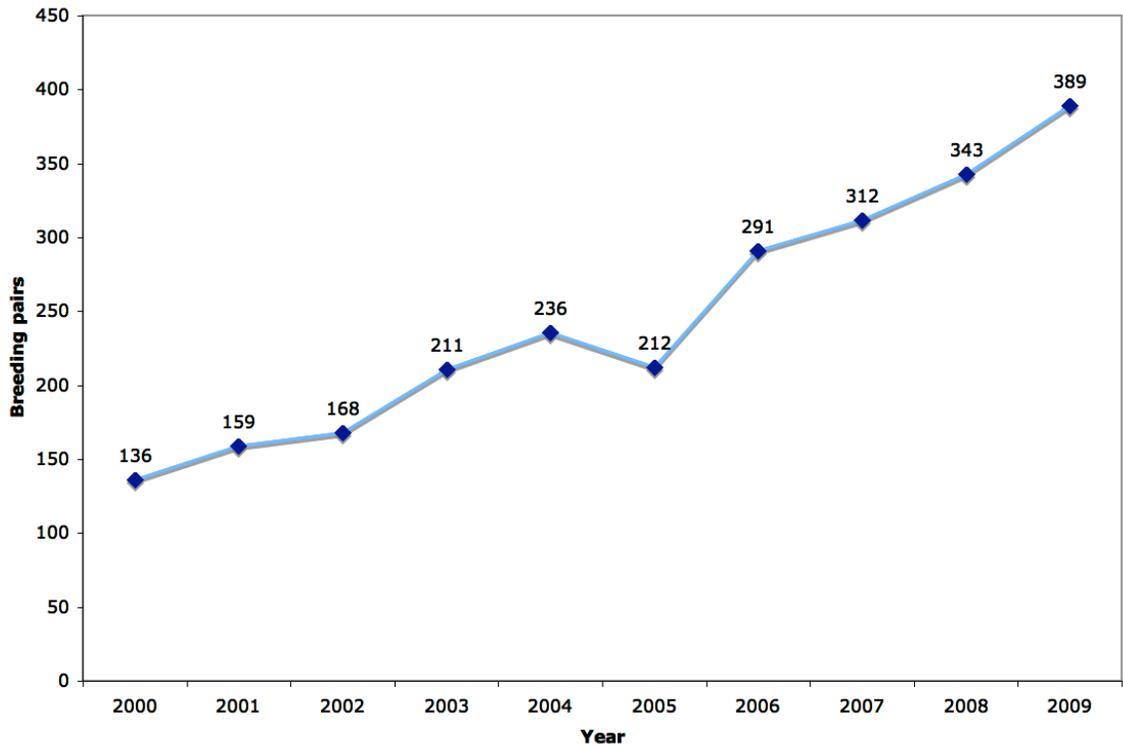


Figure 1.2. The breeding population of Razorbills showed a 12% mean annual growth rate from 2000-2009 on Matinicus Rock, Maine. The dip in 2005 is likely an artifact of the census occurring soon after a gale destroyed nests, rather than reflecting a true reduction in pairs nesting at the island that year.

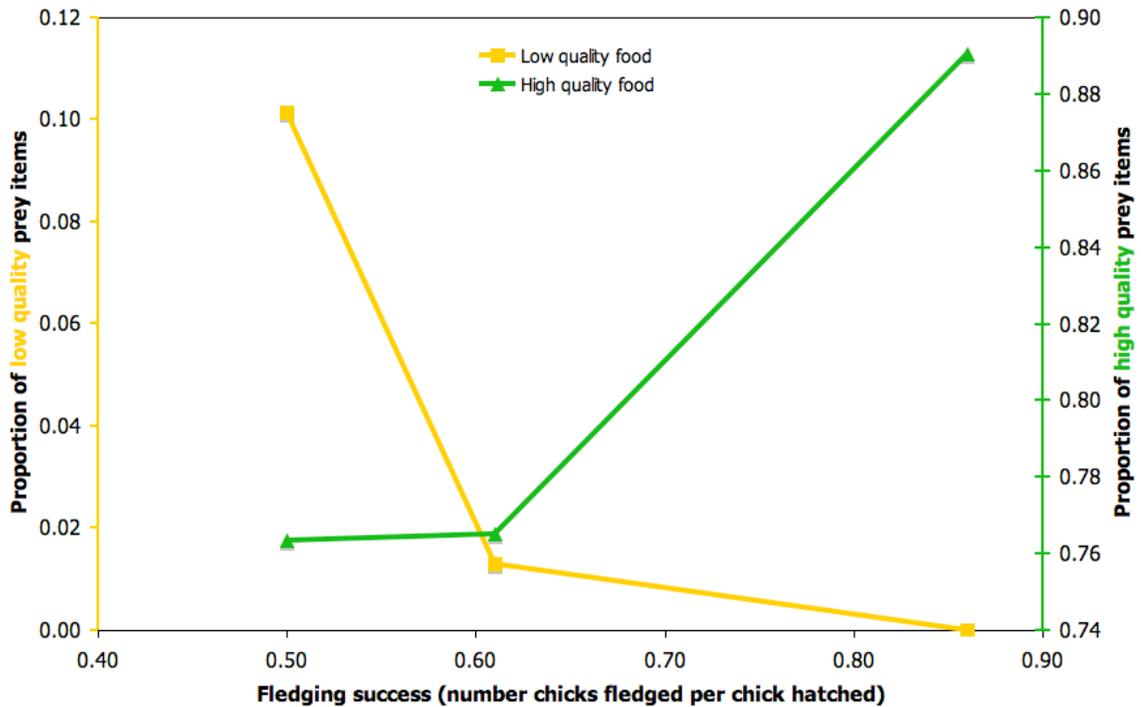


Figure 1.3. The annual fledging success rate of Razorbill chicks was correlated with the annual proportions of high quality prey items (herring, hake, sandlance) and low quality prey items (euphausiids, larval fish) in the chick diet at Matinicus Rock, Maine during 2007-2009. Herring, hake, and sandlance were classified as high quality prey due to high lipid content of these forage fish species. Larval fish and euphausiids were classified as low quality prey due to the low energy content of a bill-load of these prey items. Classification decisions were based on prey size, and on energy density values reported in the literature.

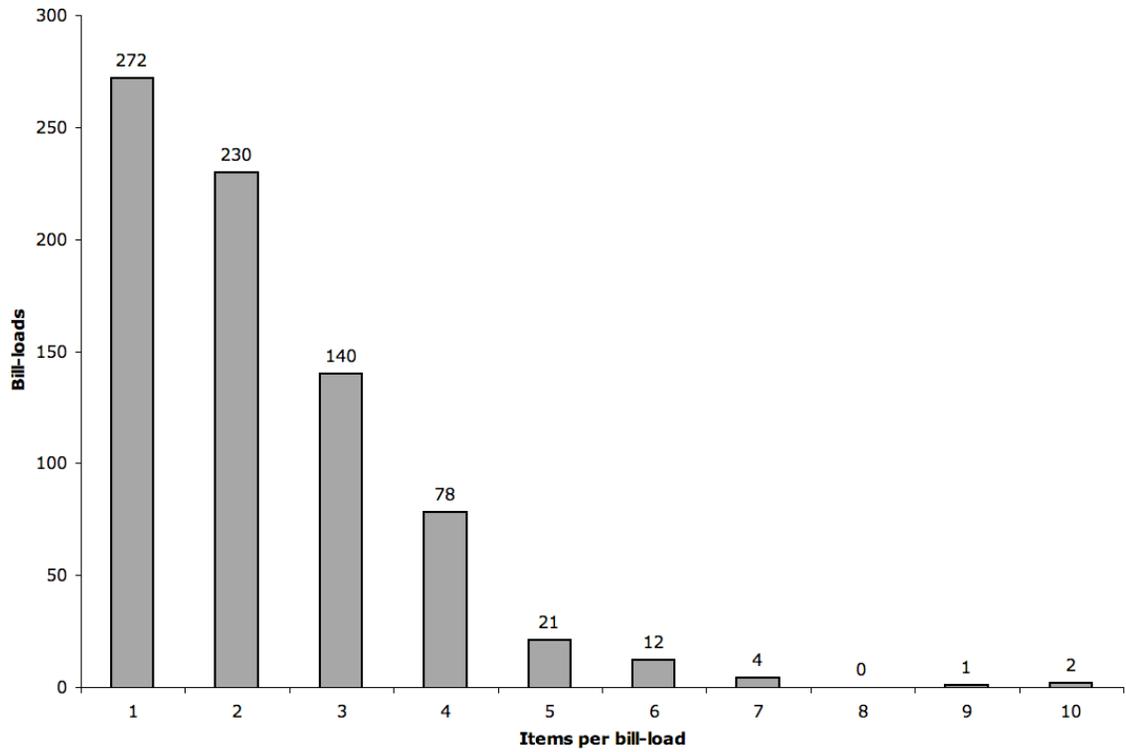


Figure 1.4. Number of prey items per bill-load (N = 760) for adult Razorbills feeding chicks at Matinicus Rock, Maine, 2005-2009.

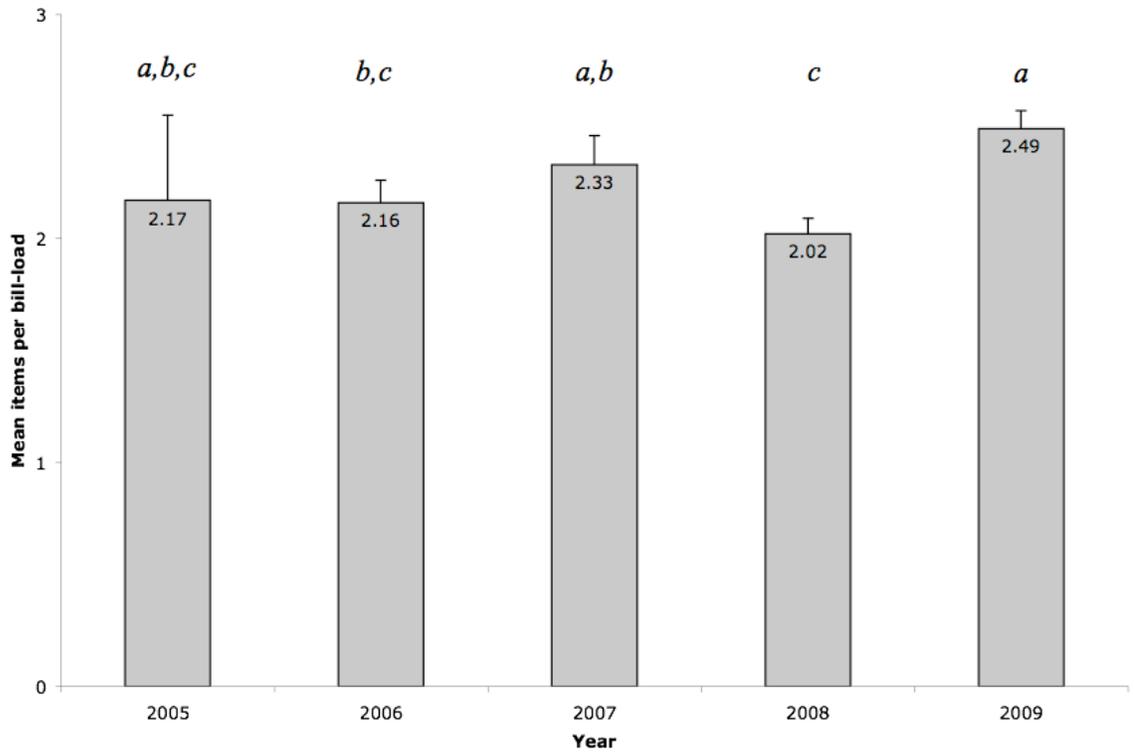


Figure 1.5. Mean number of prey items per bill-load in each of five years (N = 760) for Razorbills nesting on Matinicus Rock, Maine, 2005-2009. Year pairs that do not share the same lower-case letter have significantly different means (Tukey-Kramer HSD test).

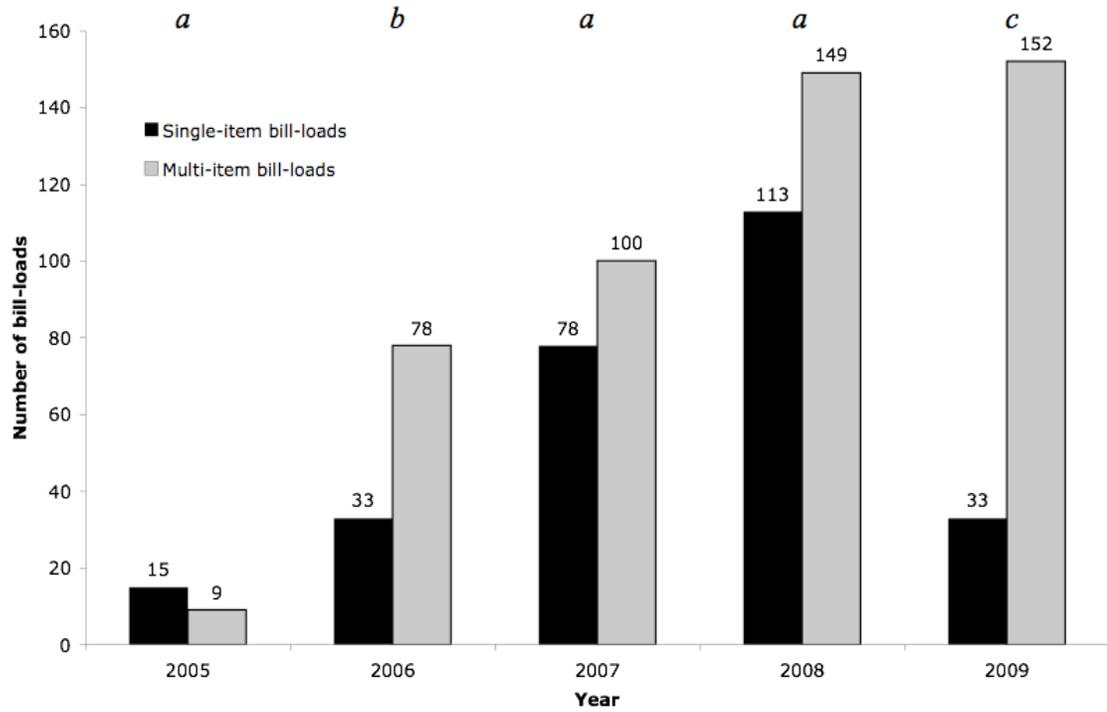


Figure 1.6. The effect of year on proportion of bill-loads (N = 760) containing a single prey item (versus more than one prey item) for Razorbills nesting on Matinicus Rock, Maine, 2005-2009. Year pairs that do not share the same lower-case letter have significantly different odds of a bill-load containing a single item (Odds ratio tests).

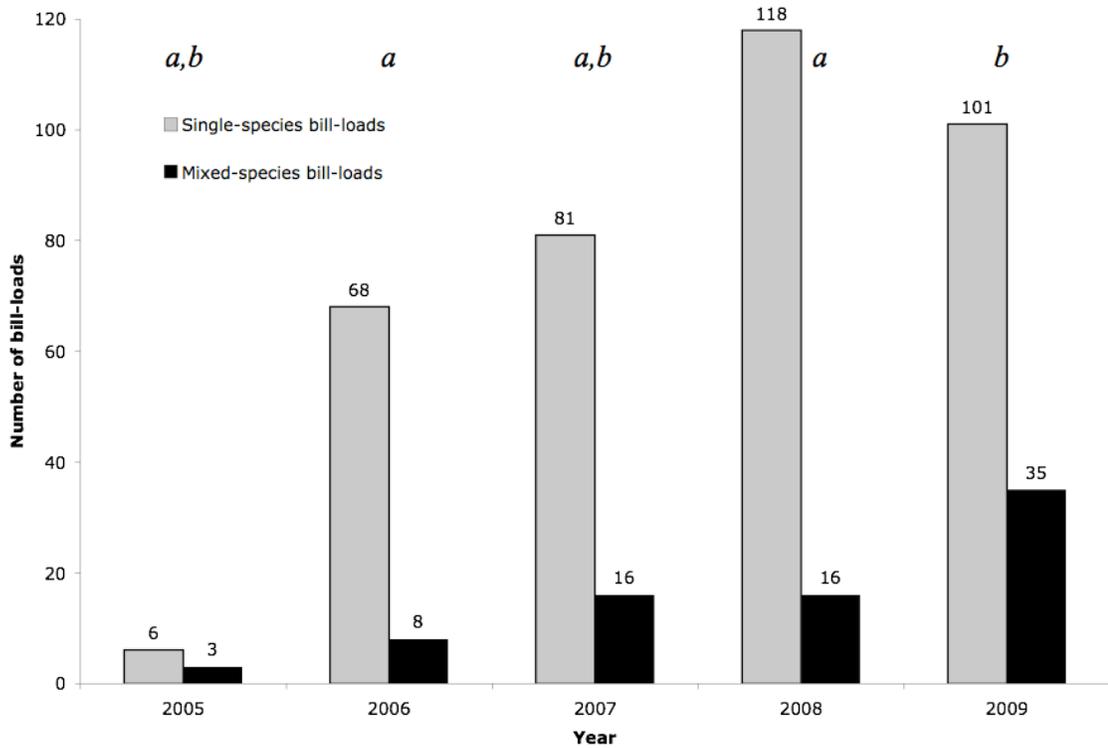


Figure 1.7. The effect of year on proportion of bill-loads containing single species of prey item (versus mixed species; multi-item bill-loads only) for Razorbills nesting on Matinicus Rock, Maine, 2005-2009. Year pairs that do not share the same lower-case letter have significantly different odds of a bill-load containing multiple species (Odds ratio tests).

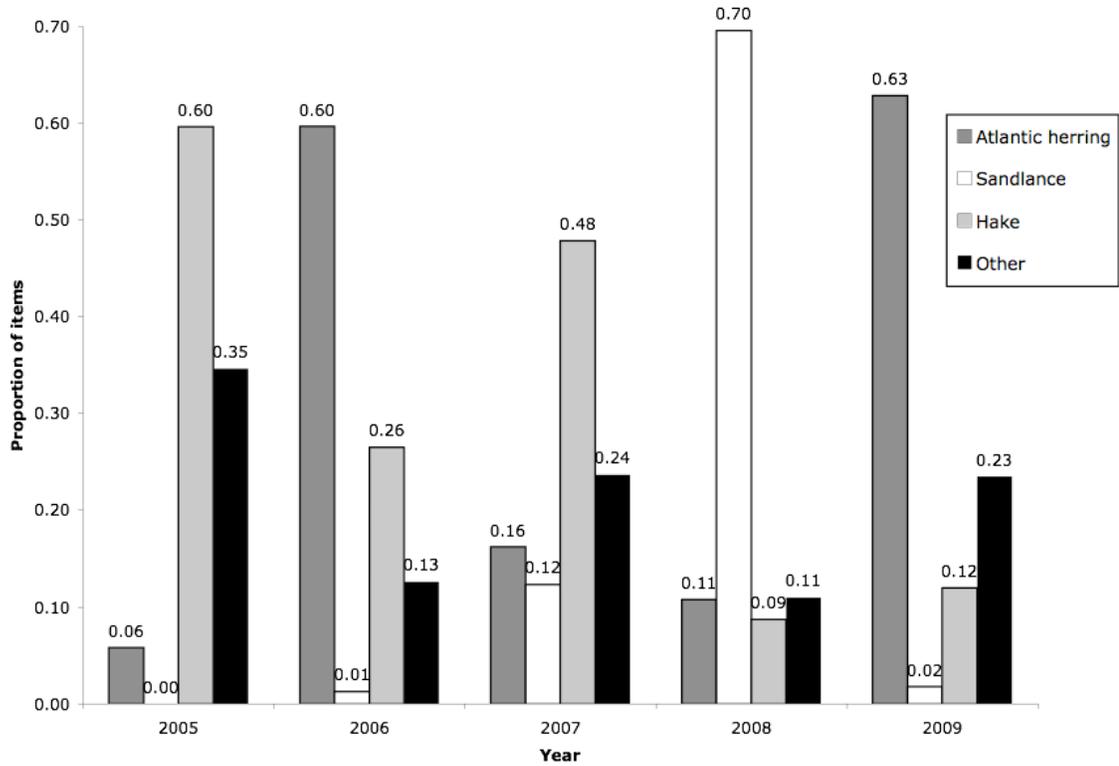


Figure 1.8. Variation in proportions of three fish prey species across years for Razorbills nesting on Matinicus Rock, Maine, 2005-2009.

CHAPTER 2

DIVING BEHAVIOR OF CHICK-REARING RAZORBILLS AT MATINICUS ROCK, MAINE

Abstract

Foraging behavior is a major component of the daily activities of seabirds. Foraging success and effort are closely linked to reproductive success and population dynamics through chick growth and survival. Recent technological advances are fueling a renaissance in research on the at-sea behaviors of marine animals, including seabirds. Such studies have revealed influences and constraints on seabird foraging behavior that include physiological limits, prey type and environment, energy cost-gain trade-offs, and the challenges of transporting food to chicks at the nest.

However, much remains to be learned about the foraging behaviors of many diving seabird species because observing birds at sea and under the ocean surface is difficult. Foraging behavior of the Razorbill (*Alca torda*), a mid-sized Atlantic auk, has not been studied in the southern portion of the species range, where day-length is shorter and the prey community may be different than that in the north. We used bird-borne electronic data-loggers to document foraging behavior of 4 chick-rearing Razorbills at the species' southernmost breeding colony at Matinicus Rock, Maine in 2008 and 2009.

We recorded 3 full days of diving behavior for each individual. Individuals performed 141.3 ± 42.5 dives per day, grouped into 17.9 ± 4.5 diving bouts per day. Dives had maximum depth of 36.1 m, maximum duration of 92.0 s, and the majority had

U-shaped dive profiles. Dives were not uniformly distributed through the day; dives occurred only during daylight hours and were most frequent in the evening, possibly indicating increased prey availability at that time. Dives were deeper during maximum light at mid-day, and shallower at twilight.

Dive characteristics were generally similar to those previously reported at 4 European and Canadian colonies. However, the mean number of dives per day was 3 times greater than at the Canadian colony, and mean dive depth was deeper than 3 of 4 previous studies. Deeper and more frequent dives could indicate reduced quality of foraging conditions for Razorbills in the Gulf of Maine, compared to more northern latitudes, leading to decreased chick survival and reproductive success.

Introduction

Foraging is a major component of the daily activities of seabirds. Foraging effort and success are intimately linked to other aspects of seabird biology and ecology, such as energetics, reproductive success, population dynamics, and food-web interactions. Yet, foraging behavior of many seabird species remains poorly understood because of the difficulty of observing animals at sea and under the sea surface. However, recent technological advances in data-loggers and remote sensing are facilitating a renaissance in the field of at-sea animal behavior, including the foraging activities of seabirds. Over the last few decades, animal-borne technologies such as time-depth recorders (TDRs), accelerometers, geo-locators, and cameras have been employed to document at-sea animal behaviors, including foraging. However, despite a burgeoning body of knowledge revealed by these recent at-sea animal behavior studies, such as migration routes,

foraging hot spots, and wintering regions, the basic behaviors of many species remain unknown or poorly described when they are not on land to breed. This represents a significant realm of missing knowledge because seabirds, like pinnipeds and turtles, spend the majority of their lives at sea, and are fundamentally creatures of the open ocean. Thus the focus in scientific literature on the land-based activities of marine animals paints an incomplete picture of the way they interact with, and have been shaped by, the oceanic environments they inhabit and exploit. While a thorough understanding of species-specific behaviors remains to be developed for most marine birds, studies over the last few decades have identified several factors that are likely to influence and constrain foraging behavior.

Factors Influencing Foraging Behavior

Studies of multiple seabird taxa have found evidence that foraging and diving behaviors are affected by the following factors: physiological limits (oxygen storage capacity; e.g. Burke & Montevecchi 2008), foraging style (benthic versus pelagic; e.g. Elliott *et al.* 2008a, b), prey type (activity level, agility, schooling tendency; Garthe *et al.* 2000, Tremblay *et al.* 2005, Elliott *et al.* 2008a, b), energetic cost-gain ratio (costs of capture versus nutritional payoff; e.g. Elliott *et al.* 2008a, 2009), and constraints of transporting prey to nestlings (increased flight costs due to mass or drag of prey, limited storage space in bill or crop; e.g. Burke & Montevecchi 2009). Diving marine birds modulate their prey capture strategies dependent on these factors. Foraging behavior and prey selection interface to have impacts on chick growth and survival, and ultimately on population growth.

Response to Declines in Foraging Conditions

Because food is limited, individuals adjust foraging behavior in order to maximize foraging success under changing conditions (Monaghan *et al.* 1994). For example, certain aspects of foraging behavior in populations of breeding seabirds have been observed to change in predictable ways in response to prey shortages or other changes in prey availability in the environment. These changes include shifts in daily time activity budgets (e.g. spending more time on foraging trips and less time at the colony; Cairns *et al.* 1987, Harding *et al.* 2007), shifts in time budget within foraging trips (e.g. more time spent underwater, and less spent resting at the surface; Monaghan *et al.* 1994), and possibly changes in dive characteristics (e.g. deeper dives, more dives per bout or day; Dall'Antonia *et al.* 2001). Also, in response to a decline in foraging conditions, the foraging trips of chick-provisioning adults may become longer (Monaghan *et al.* 1994, Uttley *et al.* 1994) as individuals search more locations before encountering prey, fly further from the colony to access alternate reliable food sources, or remain longer at the foraging grounds to capture an amount of prey that could previously be captured in a shorter amount of time. Furthermore, a decline in foraging conditions may be indicated by changes in chick meals: fewer meal deliveries per day (Uttley *et al.* 1994, Harding *et al.* 2007), or meals that contain fewer or smaller prey items (Jakubas *et al.* 2007), or less nutritious items (Wanless *et al.* 2005) compared to what is typically delivered when foraging conditions are good. Thus, studies of foraging behavior, often in tandem with an examination of chick diet, can indicate the relative quality of the local foraging conditions available to individuals in a region.

Chick-provisioning parents of many species, including alcids, are capable of behavioral plasticity in foraging, such that by changing aspects of their foraging behavior, they may avoid or lessen the negative impacts on their chicks when prey conditions decline (Uttley *et al.* 1994, Harding *et al.* 2007). However, this buffering may come at a cost of declining parental condition and possible consequences for future survival and reproductive potential (Wanless *et al.* 2005, Harding *et al.* 2007). Also, when declines are extreme, or when they last for extended periods of time, parents are unable to mitigate the negative effects on their chicks through behavioral changes (Burger & Piatt 1990, Monaghan *et al.* 1994, Uttley *et al.* 1994). In these cases of extreme declines, chicks may show decreased growth and survival rates once parents reach the limits of their behavioral modifications, or when sufficient prey is unavailable despite increased foraging effort and modified foraging behavior by parents.

Razorbills in Maine

The Razorbill is a marine bird that breeds in colonies on rocky islands and cliffs in the North Atlantic Ocean. Razorbills capture prey on wing-propelled pursuit dives and parental pairs provision solitary chicks by holding prey items crossways in the bill for transport and delivery to the chick at the nest. Razorbill adults consume forage fish and invertebrates, while the diet of chicks consists largely of forage fish.

Until recently, knowledge of the foraging behavior of the Razorbill, a marine bird in the family Alcidae, was non-existent. In the last decade, TDRs have been used to describe the foraging behavior of a small number of Razorbills in northern Europe and Labrador, Canada (Benvenuti *et al.* 2001, Dall'Antonia *et al.* 2001, Paredes *et al.* 2008,

Thaxter *et al.* 2010). These studies sampled Razorbills breeding at northern and central latitudes within the species range. Prior to this study, the foraging behavior of this mid-sized Atlantic auk had not been described for individuals breeding in the southern portion of the species range. Because foraging behavior could be affected by latitudinal differences in day length, or regional differences in prey base composition, it is important to investigate how these marine predators forage at the southern edge of their distribution, in the Gulf of Maine (GOM).

In Maine, where 6 small colonies represent the southern range limit for Razorbills, the species is listed as threatened due to its small population size and high spatial concentration. Despite the threatened status of the population, nothing is known of the foraging behavior of this species in the GOM. We investigated the foraging behavior of Razorbills breeding at Matinicus Rock (MR), the largest U.S. colony, in order to describe the foraging activities and evaluate them in comparison to other colonies that have been previously studied at more northern latitudes of the species range, and evaluate the possibility that foraging conditions in the GOM differ from conditions elsewhere in the range, possibly posing special challenges to Razorbills rearing chicks in the GOM. Understanding the foraging behavior of Razorbills will provide the groundwork for more advanced studies of these birds in the future, as it is a necessary building block for studies of energetics, cost-benefit analysis of prey selection, and the effect of prey availability on chick fate and population dynamics.

Because the parents must return to the colony regularly to feed their chicks, the availability of prey near the colony is essential to raising a healthy chick. The period of time when the chicks are in the nest is compressed for this species; chicks depart the

colony when they are approximately one third of adult size, a strategy that, among seabirds, is unique to Razorbills and their closest extant relatives, the Common Murre and Thick-billed Murre. The shortness of the nestling period (~18 days; Lavers *et al.* 2009) adds intensity to the need to regularly provide enough food for the chicks. For the Atlantic Puffins that also breed at MR, the chicks are in the nest for ~40 days (Lowther *et al.* 2002), so if food is scarce for a week, there is enough time for the parents to compensate once the food supply improves. For Razorbills, however, a week of food scarcity could be much more detrimental, because there is not enough time to compensate after a period of reduced provisioning. Thus, a week of poor food availability for puffins can be overcome, but it could have a severe effect on a colony of Razorbills, especially if it occurs during the time when many chicks are in their last week before fledging. Chicks that fledge at lower weights are less likely to survive the first winter at sea (e.g. Morrison *et al.* 2009), and may begin breeding at a later age compared to heavier fledglings (Gaston 2003, Morrison *et al.* 2009).

Objectives

In this study we used TDRs to record the foraging behavior of Razorbills on MR in the GOM. We explore the diving behavior of chick-rearing Razorbills, including: frequency, depth, and shape of dives; dive bouts; diel patterns; and inter-annual variation in diving behavior. We test the hypotheses that dive frequency and dive depth will vary with time of day, and that dives will be more frequent and shallower at dawn and dusk due to lower ambient light and possible differences in prey behavior and type. We discuss our findings in the context of prey that were delivered to chicks during the study period,

and implications for reproductive success and colony growth. We compare our results to those of previous studies of Razorbill foraging behavior at more northerly colonies.

Methods

Study Location

Fieldwork was conducted in late June and early July of 2008 and 2009 on Matinicus Rock (43°47'N, 68°51'W), a 0.12 km² treeless granite island 40 km from the mainland in outer Penobscot Bay, Maine (Fig. 2.1). MR, part of the Maine Coastal Islands National Wildlife Refuge, is the furthest offshore island in Maine. It supports one of the largest and most diverse seabird colonies on the U.S. Atlantic Coast, composed of alcids, terns, gulls, storm-petrels, eiders, and shearwaters. The island is the southernmost breeding location of the Razorbill and the Atlantic Puffin, and is one of only two known Manx Shearwater breeding sites in North America. Human infrastructure on the island reflects its history as a U.S. Coast Guard light station: a light tower, keeper's house, foghorn, boathouse, and helicopter pad are located on the southern third of the island. Since automation of the light in 1983, there have been no year-round residents on the island, but a small group of seabird researchers is present annually from May-August.

The main Razorbill colony is located on the northern third of the 700 m long, 150 m wide island, with small numbers of pairs breeding at other locations near the periphery of the island. Nesting substrate consists of cavities under boulder jumbles and, to a lesser extent, bedrock crevices. Winter storm waves sometimes wash over the colony location, which limits vegetation growth but usually does not move the boulders.

Data Collection

We collected data during the summers of 2008 and 2009. Breeding adult Razorbills were selected for TDR deployment based on a combination of nest chamber accessibility, nest site suitability for trap placement, and nest entrance visibility from observation blinds. Birds were captured using noose-mats at the burrow entrance, or by hand from the nest chamber (2008: $n = 6$; 2009: $n = 5$). We tagged each bird with a steel USFWS leg band, then measured mass with a Pesola spring scale, wing chord with a wing rule, and head and bill with a vernier caliper. We attached a TDR to each bird using a plastic leg band (details below) and made a color-mark on the breast feathers with a Sharpie® pen or petroleum-based dye (see Donehower & Bird 2005) to allow recognition at distance. We collected a single drop of blood from the tarsal vein for DNA sex analysis (details below). Birds were held for 12-18 min and released either into their nest chambers, on prominent rocks, or at the shoreline. We began recapture effort 3-7 d after TDR deployment. Upon recapture, each bird was held for 5-15 min while we removed the TDR, re-weighed the bird, and then released it into its nest chamber or on a prominent rock. To minimize negative effects on reproductive success of individual pairs, we tagged only one member of a pair, and did not tag birds from the same nest site in more than one year.

After retrieval, we downloaded data from the TDRs to a laptop computer using TagTalk software (Version 1.743, Lotek Wireless Inc., St. John's, Newfoundland, Canada, 2008).

Archival Tags

The TDRs (LAT 1500, Lotek Wireless Inc.; Fig. 2.2) had 512 kB of memory and weighed 4.5 g including a leg-mount cradle (3.5 g alone). Assuming a Razorbill mass of 505-890 g (Lavers *et al.* 2009), the mass of the device was 0.5-0.9% of the bird's mass. The TDRs were cylindrical with one rounded end, one flexible blunt end (housing the pressure sensor) with two protruding wire loops (conductivity circuit), and an internal temperature sensor. The streamlined shape may minimize increased drag which could negatively affect foraging performance (Wilson *et al.* 1986). Length was 32 mm and width was 8 mm. The manufacturer-specified accuracies were $\pm 1\%$ for pressure (dbar) and $\pm 0.2\text{ }^{\circ}\text{C}$ for temperature. Elliott and Gaston (2009) attached pairs of Lotek TDRs to individual birds ($n = 18$) and found that the variation of pressure readings from two TDRs attached to the same individual differed by amounts equating to depth differences of less than 4.0 m, and usually less than 1.0 m; these amounts were in agreement with the manufacturer's specifications. We programmed the TDRs to record into two different logs: one when the unit was wet, and one when the unit was dry. The wet log recorded pressure (precision 0.025 dbar) at 2-s intervals, and temperature (precision 0.1 $^{\circ}\text{C}$) at 5-s intervals. The dry log recorded pressure and temperature at 30-s intervals.

Each archival tag was factory-glued to a plastic cradle, which we mounted on a plastic color coil band using black tesa[®] tape (Fig. 2.2). After placing the band around a bird's leg, we taped around the TDR/band apparatus such that the band was fully covered by black tape. We mounted the TDRs with the sensitive end (pressure sensor, wet-dry sensor loops) facing anteriorly to prevent damage from contact with rocks. We placed the

TDR proximal to a metal service band on the same leg, to ensure that the TDR remained high enough on the leg to minimize interference with landing and walking.

Sex Determination

Blood samples were collected from TDR-carrying birds for DNA sex determination. We used PermaCode™ Blood Collection & Transport System cards provided by Avian Biotech International (Tallahassee, Florida). A single drop of blood was collected from the tarsal vein of each bird by pricking the leg with a single-use, sterile hollow needle and lightly touching the absorbent collection card to the blood bead that formed on the skin surface. The cards were marked with individually identifying numbers, allowed to dry for one minute, and inserted into plastic zip-top sleeves. The cards were stored at ambient temperature until August, then shipped to Avian Biotech International for sex analysis.

Data Analysis

We converted pressure data (dbar) recorded by the TDRs to depths (m) using Fofonoff & Millard's (1983) equations for the pressure-depth relationship in salt water. We offset time-stamps on our temperature data by 20-23 s (constant value within each TDR) to compensate for lag time due to temperature sensor inertia. We determined the magnitude of the time-shift subjectively to attain the best match of peaks and troughs between depth and temperature data. We then processed depth and temperature data to identify and characterize dives, using Multitrace Dive and its accessory program FillGap (Jensen Software Systems, Laboe, Germany). We wrote a custom macro (Microsoft

Excel 2004 for Mac, Version 11.6.1, Microsoft Corp., Seattle, WA) to identify and characterize dive bouts. Statistical analyses were performed using JMP (Version 10.0.0, SAS Institute Inc., Cary, NC, 1989-2012) and Microsoft Excel 2004. Statistical analyses included chi-square tests followed by Tukey-Kramer Highly Significant Differenced (HSD) tests of pairwise differences, ANOVA and Welch's ANOVA, t-tests, and linear correlation and regression. Values are reported as mean \pm 1 SD, unless otherwise stated.

We defined a dive as a series of consecutive data points at depths > 0 m below the sea surface. Dives with maximum depth < 2 m were not counted or included in analyses because they were unlikely to be foraging dives, and may have been self-maintenance or social interaction behaviors. Excluding dives less than a certain depth (usually 1-5 m) is standard in seabird data-logger studies (e.g. 2 m criterion used by Falk *et al.* 2000, Tremblay *et al.* 2003).

Each dive was divided into three phases: descent, bottom, and ascent. Bottom phase was defined as the portion of a dive at or below 75% of the maximum depth of that dive (Tremblay *et al.* 2003, Paredes *et al.* 2008), and bottom time was the duration of the bottom phase. Descent phase was the period between leaving the surface and reaching the bottom phase, while ascent phase was the period between the bottom phase and re-attaining the surface. Descent and ascent phases usually consisted of steady continuous motion downward or upward, respectively, in the water column, and only occasionally included small vertical zig-zags or shelves. Descent and ascent rates were calculated as the absolute value of vertical change in depth over time, and were not necessarily equivalent to swimming speed because they did not incorporate simultaneous travel in the horizontal plane.

Dives were classified by Multitrace Dive into profile shape categories as follows: U (descent, vertical deceleration, flattened bottom profile, vertical acceleration, ascent), V (descent followed immediately by ascent with no flattened bottom time, nor periods of vertical deceleration or acceleration), u (descent followed immediately by ascent, with no flattened bottom time, but with vertical deceleration and acceleration around maximum depth inflection point, such that profile resembles a parabola), W (multiple inflection points resulting in multiple ascent and descent segments, sandwiched between initial descent and final ascent, usually but not always with sharp inflection points), and Y (central deep extension to maximum depth, with a flattened shoulder on one or both sides). Biological significance of profile shape is addressed in the discussion. See Fig. 2.3 for illustration.

A foraging bout was defined as one dive, or a series of consecutive dives, within which no dives were separated by > 60 s of surface time. Dives were therefore classified as belonging to the same bout as the preceding dive, or to a new bout, based on a bout-ending criterion (BEC) of a 60-s inter-dive surface interval, following a modified version of the Mori *et al.* (2001) sequential differences analysis method.

Results

We deployed eleven TDRs (six in 2008 and five in 2009) on chick-rearing Razorbills. We recaptured four birds (2008: $n = 2$; 2009: $n = 2$) after 4-7 d and retrieved their TDRs. The remaining seven birds were not recaptured for the following reasons: evaded traps ($n = 2$); ceased burrow attendance following chick fledging ($n = 1$); chick

died ($n = 1$); abandoned nest near time of chick being taken by predator ($n = 2$); or ceased nest attendance although a chick successfully fledged ($n = 1$).

The response of adults following TDR deployment was variable (Table 2.1), with the majority (73%) continuing to attend nests, and the others divided equally between probable (9%) and possible (9%) abandonment, and desertion following chick death (9%). Of the four birds from which we recovered TDRs, all continued attending nests, and two of four (50%) were resighted in the colony in subsequent year(s) through 2011. Of the seven birds from which we did not recover TDRs, five (71%) were resighted in the colony in the subsequent year(s) through 2011, including two at nest sites used in the capture year. Altogether, seven of eleven study birds (64%) were resighted in later years at the colony. The four birds that were not resighted in later years (through 2011) included one male and one female that continued nest attendance and fledged chicks in the capture year, one (unknown sex) that continued nest attendance following TDR deployment but stopped several days later after its chick died from injuries unrelated to this study, and one male that may have abandoned its nest after TDR deployment.

All resighted birds had lost their TDRs by the beginning of the breeding season in the year following deployment. TDR loss probably resulted from abrasion and failure of tape attaching them to leg bands; abrasion occurred rapidly on recovered TDRs, with significant tape wear after a few days of deployment.

The four recovered TDRs each contained between 86-109 h of pressure and temperature information after deployments of 4-7 d. We recorded 2,368 dives (413-851 per bird) in 302 bouts (65-82 per bird). For twelve bird-days we had complete 24-hour records (00:00-23:59; 3 days each for 4 birds), which included 1,694 dives (314-558 per

bird) and 215 bouts (38-69 per bird). Among our analyses, those that characterize dives and bouts are based on all recorded data, while those pertaining to diel patterns are based on data only from entire days.

On average, individual birds performed 141.3 ± 42.5 dives per day ($n = 4$, range 104.7-186.3), grouped into 17.9 ± 4.5 bouts per day ($n = 4$, range 12.7-23.0). Diving Razorbills remained underwater for 3.8 - 92.0 s per dive (45.8 ± 19.5 , $n = 2,368$) and maximum depth of individual dives varied from 2.0 - 36.1 m (mean 13.1 ± 7.8 , $n = 2,368$; Fig. 2.4). Maximum depths reached by four individuals were 25.9 m, 33.8 m, 34.6 m, and 36.1 m. Nearly half of dives had maximum depths of ≤ 10 m, and 79% were ≤ 20 m. When considering all time spent underwater during dives, the proportion of time spent at a given depth was inversely related to depth (5-m depth bins; Table 2.2). Thirty-seven percent of underwater time was spent at ≤ 5 m, and three quarters of underwater time was spent at depths ≤ 15 m. Only one percent of time was spent at > 30 m.

All individuals exhibited several dive profile shapes; most dives were U-shaped (69%), with the remainder being W- (13%), V- (11%), Y- (4%), and u-shaped (3%). Mean bottom time of dives was 19.4 ± 10.7 s ($n = 2,368$, range 1.7-60.0), and bottom time as a proportion of total dive duration was 0.41 ± 0.11 ($n = 2,368$, range 0.11-0.99). The mean vertical travel rates of the ascent and descent periods were both less than 1 m/s, with ascent (0.83 ± 0.36 m/s, $n = 2,368$) slightly faster than descent (0.71 ± 0.24 m/s, $n = 2,368$). To assess the relationship between vertical travel rates and dive depth, we calculated an average vertical travel rate (mean of descent and ascent rates) because descent and ascent rates were positively associated ($r^2 = 0.27$, $p < 0.0001$; Fig. 2.5).

Vertical travel rate showed a positive linear relationship with dive depth ($r^2 = 0.54$, $p = 0.0001$; Fig. 2.6).

Birds began diving in the morning, and ceased diving at times varying from late morning to dusk. The earliest dive began at 04:23 and the latest dive ended at 21:07 (Table 2.3). These times are within ten minutes of civil dawn and dusk (04:20 and 20:57, respectively; Fig. 2.7). The latest time to start diving was 08:11, and each of the four individuals began by 04:29 on at least one day. The earliest time to cease diving was 10:00, and each of the individuals continued diving until 20:27 or later on at least one day. On 67% of the bird-days, the first dive was before sunrise ($n = 15$), and on 56% of bird-days, the last dive was after sunset ($n = 16$).

Diel distribution of dive frequency varied between individuals (1-hour bins, Likelihood Ratio, $df = 48$, $\chi^2 = 595.7$, $p < 0.0001$), and by day within individuals (Likelihood Ratios shown in Table 2.4). Despite this high variation in timing of dives, we pooled data across individuals to provide an overall description of diel distribution. Dives occurred throughout daylight hours, but were not distributed uniformly across the day (3-hour bins, Pearson's chi-squared test, $df = 5$, $\chi^2 = 235.7$, $p < 0.0001$). Peaks in diving frequency occurred in late evening (19:00 – 21:00, 24% of dives) and, to a lesser degree, in early afternoon (12:00-14:00, 16% of dives; Fig. 2.8). Additionally, birds consistently dove at a moderate frequency in the first three hours of daylight (04:00-07:00, 18% of dives). Together, the aforementioned seven hours comprised approximately 44% of daylight hours available for diving, but contained 58% of dives. Diving frequency was very low for all individuals from 14:00-15:00 (2% of dives). No dives occurred during

hours of darkness (with the exception of a single dive each by two birds to < 5 m at 01:04 and 03:54, which probably did not represent foraging and were excluded from analysis).

Depth of dives varied throughout the day, with a general trend toward deeper dives near mid-day. For this comparison we analyzed the mean dive depth per bout, rather than depths of all dives, because dive depth was not independent of bout (Welch's ANOVA, $df = 180$, $F = 75.3$, $p < 0.0001$). We compared dive depth during five periods of the day (early morning 4:00-5:59, morning 6:00-9:59, mid-day 10:00-13:59, afternoon 14:00-17:59, and evening 18:00-20:59; Table 2.5), and found that mean dive depth varied by period of day (Welch's ANOVA, $df = 4$, F ratio = 14.1, $p < 0.0001$). Evening dives were shallower than dives during the rest of the day, and this difference was significant compared to all periods except early morning (Tukey HSD test, $q = 2.75$, all p -values < 0.01 except $p = 0.07$ against early morning; Table 2.6). Also, we specifically compared dive depths during periods of minimal light (nautical twilight: dawn 03:33-04:56, and dusk 20:21-21:44) and maximal light (noon-time: 11:00-13:00). Dives were significantly deeper during maximal light conditions ($15.3 \text{ m} \pm 1.3 \text{ SE}$, $n = 28$) than during minimal light conditions ($9.7 \text{ m} \pm 1.7 \text{ SE}$, $n = 17$; Student's t -test, 1-tailed, $df = 43$, $t = 2.66$, $p = 0.006$).

Razorbills showed considerable variation in the number and duration of dives and bouts performed per day, and also in the length of time between dives and bouts. This variation existed both between individuals and within individuals (between days). Individuals performed 3-36 bouts per day (mean 17.9 ± 12.0 , $n = 12$). Bouts lasted between 4 s and 104 min (mean $491 \text{ s} \pm 806$, $n = 302$, Fig. 2.9) and contained 1-129 dives (mean 7.8 ± 12.1 , $n = 302$, Fig. 2.10). Seventy-five percent of bouts contained ≤ 10 dives

and 95% contained ≤ 30 dives. Within bouts, the mean interdive surface interval was 18.2 ± 14.1 (n = 2,069, range 0-60). Mean time separating bouts was 64.2 ± 161.4 min (n = 297, range 60 s-18.8 h; Fig. 2.11). Each inter-bout period included one or more of the following activities: sea surface rest or travel, flight, and colony attendance; however, examining time-budget among these activities is beyond the scope of this paper.

The frequency of most, but not all, dive profile shapes varied with dive depth. U-shapes (Pearson's chi-squared test, $df = 1$, $\chi^2 = 28.7$, $p < 0.0001$) and u-shapes (Pearson's chi-squared test, $df = 1$, $\chi^2 = 74.4$, $p < 0.0001$) were more common among deep dives (≥ 15 m) than shallow dives (< 15 m). Conversely, V-shapes (Pearson's chi-squared test, $df = 1$, $\chi^2 = 102.0$, $p < 0.0001$) and Y-shapes (Pearson's chi-squared test, $df = 1$, $\chi^2 = 19.8$, $p < 0.0001$) were more common among shallow than deep dives. W-shaped dives were unaffected by depth (Pearson's chi-squared test, $df = 1$, $\chi^2 = 0.1$, $p = 0.75$).

The distribution of dives among profile shape categories was not consistent throughout the day (Fig. 2.12). U-shaped dives, as a proportion of all dives, decreased steadily from early morning through afternoon, then rose again in the evening. The opposite pattern existed for V-shaped dives, the proportion of which increased steadily through the day until afternoon, then decreased slightly in the evening. Y- and u-shaped dives were proportionately highest in mid-day, while W-shaped dives maintained a consistent proportion from early morning through afternoon, then declined in the evening.

Dive shape frequency also varied by year, although it is not possible to separate this from an individual effect. U- and W-shape dives were more common in 2009 (Fisher's exact tests, 2-tailed, $p < 0.0001$ and $p = 0.03$), when Atlantic herring (*Clupea*

harengus) was the dominant prey item during TDR deployment period. The remaining three dive shapes were more common in 2008 (Fisher's exact tests, 2-tailed, all p-values ≤ 0.0005), when sandlance (*Ammodytes* sp.) predominated. Fig. 2.13 shows the prey items delivered to chicks during the TDR deployment periods in 2008 and 2009.

Razorbills dove in water that ranged in temperature from 7.4-15.0 °C and the temperatures at the deepest part of dives were generally cooler than temperatures at the surface. Temperatures were warmer in 2008 than 2009, both at the surface (by 0.9 °C) and at depth (by 0.5 °C, Table 2.7), and within-dive temperature differential was greater in 2008. Sea surface temperatures encountered by Razorbills at their foraging locations ranged between 8.5-15.0 °C (mean 9.8 ± 0.9 , n = 2,256). Water temperatures recorded at the maximum depth of dives ranged between 7.4-13.4 °C (mean 9.4 ± 0.9 , n = 2,256). Actual temperatures at maximum foraging depth may have been slightly colder than recorded temperatures reported here, due to inertia of the temperature loggers. The temperature differential within dives (i.e. the difference between temperature at the surface and maximum depth) ranged between -0.1-3.6 °C (mean 0.4 ± 0.6 , n = 2,256).

Discussion

In contrast to its larger relatives, the murrelets, the Razorbill's foraging behavior remains less well understood. Our study contributes to the understanding of how the Razorbill uses the marine environment throughout its range to exploit prey resources during the chick-rearing season. Furthermore, the Razorbill is listed as a threatened species in Maine, yet its foraging ecology remains poorly understood in the GOM. This

study is the first to describe the diving behavior of Razorbills in the GOM, at the southern limit of the species distribution.

Comparison with Other Colonies

The dive attributes of Razorbills at MR had many similarities to those of Razorbills at other colonies in Europe and Canada. For example, mean and maximum dive depths, and mean dive duration were all within the ranges documented at other locations (Table 2.8). Likewise, ascent and descent rates were within the range of values reported for Razorbills elsewhere, and followed the previously documented pattern of ascents being slightly faster than descents (Table 2.8). Also, we observed a positive relationship between dive depth and mean vertical travel rate, which is in concordance with the positive association between dive depth and mean descent rate found previously for Razorbills (Benvenuti *et al.* 2001, Thaxter *et al.* 2010), and may signal that Razorbills anticipate the depth to which they will swim on individual dives and adjust their swim speed accordingly.

Although Razorbill diving behavior at MR was similar overall to that found by previous studies at other colonies, it did differ in several aspects. Notably, the number of dives per day was approximately three times greater than at the Gannet Islands, Labrador (Paredes *et al.* 2008), with the increase apparent in both the number of dives per bout, and the number of bouts per day (Table 2.8). Also, the mean dive depth at MR was greater than that found by three of four previous studies (Table 2.8). Because Razorbills at MR are performing dives of similar duration as elsewhere, but are diving much more

frequently, and to greater average depth, they are likely using more energy for diving activity than Razorbills elsewhere. This could be an indication of prey scarcity.

Biological Significance of Dive Profile Shape

Prey Type and Location

Dive profile shape can offer insight into the type of prey being hunted, and also the location at which the bird is hunting, relative to the sea floor. For example, different dive profile shapes have been commonly associated with capture by alcids of pelagic prey (V-shaped; Elliott *et al.* 2008b), benthic prey (U-shaped; Elliott *et al.* 2008b) and pelagic invertebrates (W-shaped; Paredes *et al.* 2008). Associations have been made usually by assuming that an observed chick meal was caught during the last dive of the foraging trip preceding chick meal delivery, so the delivered prey type is associated with the profile shape of the last dive (e.g. Elliott *et al.* 2009). Some species, including sandlance, have not been associated with a particular dive profile and are caught on dives of varied profile shapes (Elliott *et al.* 2008b, 2009). Interestingly, the predominant profile shape observed for Razorbills in this study was not the V-shape dive that was the most common shape in three previous studies reporting on Razorbill profile shape (Benvenuti *et al.* 2001, Dall'Antonia *et al.* 2001, Paredes *et al.* 2008), but rather U-shape.

The predominance of U-shaped, rather than V-shaped, dives among Razorbills at MR could indicate that they are feeding differently than Razorbills at the previously studied colonies, perhaps on prey with different behavior or spatial distribution in the foraging area. U-shaped dives have often been interpreted as indicative of benthic

foraging, however, the bottom phase of the U-shaped dives performed in this study was not as wide as U-shaped dives reported for species that commonly feed benthically (e.g. Thick-billed Murres; Croll *et al.* 1992). It may be, rather, that the Razorbills are making U-shaped dives into the mid-water column. It is possible that Razorbills at MR make a more leisurely change of direction at the bottom of their U-shaped dives, relative to the V-shaped dives documented elsewhere, because they are approaching prey from a different angle, or because local schools of prey differ in characteristics such as size or density. While there is a lack of standardization across studies in methods of categorizing dive profile shapes, the magnitude of the difference in U- and V-shaped dives between this and previous studies (69% U-shaped in this study, versus, e.g., 76-81% V-shaped in Dall'Antonia *et al.* (2001)) makes it unlikely that the difference is an artifact of differences in categorization method.

Paredes *et al.* (2008) suggested that V-shaped dives for Razorbills may represent a specific foraging strategy for exploiting sandlance schools, which form tight balls when attacked underwater. The authors of that study posit that Razorbills may make use of positive buoyancy to enhance acceleration when attacking sandlance on the way back to the surface during V-shaped dives. However, Elliott *et al.* (2008b) found that sandlance were frequently captured on shallow U-shaped dives, as well as on V-shaped dives. We did find that V-shaped dives were more common in 2008 when sandlance was the dominant prey type delivered to chicks during the study period (Fig. 2.13), which would support the hypothesis of Paredes *et al.* (2008). Conversely, we observed a greater proportion of U-shaped dives in 2009, when herring was the dominant prey type, which could indicate that Razorbills attack herring schools horizontally, or from above but at a

slower vertical velocity than they use for sandlance. Additionally, a sizeable portion of 2009 chick diet at MR was made up of hake (may include *Merluccius bilinearis*, *Urophycis tenuis*, *U. chuss*, and *Enchelyopus cimbrius*) and butterfish (*Peprilus triacanthus*), which are uncommon at other colonies where Razorbill diving behavior has been studied, and may also be targeted during U-shaped dives.

We found variation in the way that dive profiles were distributed by depth. One profile shape (W) occurred evenly across depths, while the remaining profile shapes were more common in either shallow (V, Y) or deep (U, u) dives. This may represent an interplay between prey-specific hunting strategies, and differing locations of prey types in the water column, with U- and u-shaped dives being effective for hunting prey that uses deeper habitat, while V- and Y-shaped dives are effective for hunting prey that uses habitat near the surface.

We also observed variation in the way that dive profiles were distributed by time of day, and they were sometimes inconsistent with our expectations based on daily patterns of dive depth, and mean depths of the various dive profile shapes. U-shaped dives were more prevalent in early morning and evening hours, while V-, Y-, and u-shaped dives were most prevalent in mid-day or afternoon hours. This finding was surprising because U-shaped dives tended to be deeper than other dives, yet they occurred in the greatest proportions during times of the day when average dive depths were relatively shallow. The diel pattern of V-shaped dives was similarly surprising, because V-shaped dives tended to be shallow dives, and while they occurred frequently in evening, when dives were shallowest, their most frequent occurrence was in afternoon hours, when dives were of moderate depth. W-shaped dives, which were evenly

distributed between deep and shallow depths, were also evenly distributed throughout the day. These incongruent patterns demonstrate that a complex interplay of factors is influencing diving behavior, and diel patterns may be based not only on ambient light levels, but also on changing prey location and behavior throughout the day.

V-shaped dives have sometimes been suggested to represent ‘scouting’ dives, or dives on which the predator was searching for prey but not actively attempting capture. However, for some species, including Razorbills, V-shaped dives regularly comprise large proportions of total diving activity, strongly indicating that V-shaped dives can represent hunting as well as scouting. Because TDRs only indicate depth, and do not record presence or absence of travel in a horizontal plane, it is not possible to know whether a bird at the bottom of U-shaped dive is slowing down in absolute speed, but only that it is slowing down in *vertical* travel rate. It is possible that birds travel at the same swim speed through the water during the bottom phases of V- and U-shaped dives, despite the decreased vertical velocity at the bottom of U-shaped dives that is not present in V-shaped dives. This could occur if a bird reaching the bottom of a U-shaped dive maintained the swim speed of the descent phase, but changed its body angle relative to the sea floor, such that the rate of travel in the horizontal plane increased as the vertical rate of travel decreased. It is not possible to deduce, from information gathered with TDRs, the rate of horizontal travel during a dive, so we do not whether Razorbills in U-shaped dives decreased their swim speed at the bottom of the dive, or merely shifted the direction of travel while maintaining constant swim speed. If the latter is the case, then it is possible that V-shaped and U-shaped dives are not as different as they might seem. Rather than representing a difference in the speed at which prey is approached (more

slowly in U-shaped and more quickly in V-shaped), the difference may instead represent the angle at which prey is approached: from the side (U-shaped), or from above or below (V-shaped).

Relationship of Vertical Travel Rate and Dive Depth

The positive relationship between vertical travel rate and dive depth became more tightly coupled at deep depths (> 20 m). This may be because deep depths were only achieved on dives where travel to a deep depth was anticipated, thus the birds transited rapidly to near the maximum depth in order to minimize travel time and maximize bottom time (see Elliott *et al.* 2008b). Shallow dives, in comparison, could be achieved whether or not vertical travel was rapid, and thus have more variation in the vertical travel rate. It may be that the majority of shallow dives were anticipated as such (accounting for the majority of shallow dives having relatively slow vertical travel rates), while a smaller number of shallow dives were, in essence, ‘aborted’ deep dives, where the bird descended rapidly toward a deep targeted depth, but then remained shallow instead, perhaps after encountering prey. Interestingly, the highest individual rates of vertical travel are for relatively shallow dives (Fig. 2.6), which could possibly be explained by considering how the bird’s buoyancy changes with depth. Buoyancy of a diving bird is greatest at shallow depth, resulting in rapid travel during the entirety of the ascent phase on shallow dives, whereas birds would have to work against negative buoyancy during part of the ascent phase on dives reaching > 20 m (see Lovvorn *et al.* 2004), resulting in a slower average ascent rate.

Time of Day Affects Diving Activity

Our hypothesis regarding diel patterns of dive frequency was supported, and diving activity was not randomly distributed over the day. Dives were most frequent around sunset, with smaller peaks of frequency in mid-day and early morning. There were two lulls in diving activity during the day between these peaks, one in mid-morning and one in mid-afternoon. This activity pattern mirrors that found by Benvenuti *et al.* (2001) for Razorbills in Græsholmen, Denmark, although on a condensed time-scale owing to the shorter duration of daylight at MR.

Our hypothesis regarding diel patterns of dive depth was also supported. Birds dove deeper during mid-day (high illumination) than twilight (low illumination), in agreement with the pattern found for Razorbills in Labrador (Paredes *et al.* 2008) and Europe (Dall'Antonia *et al.* 2001). As at other colonies, birds did not perform foraging dives during hours of darkness, but did dive with more frequency and at shallower depths during hours of low illumination. However, because MR is at the most southern latitude in the species range, birds at this colony experience shorter days than conspecifics at other colonies, in some cases by more than seven hours. Whereas birds at far northern latitudes (e.g. Latrabjarg, northwest Iceland; Dall'Antonia *et al.* 2001) are able to forage throughout 24 hours per day during the breeding season because the sun only dips below the horizon for 2.5 hours per day, birds at the southern range limit in the GOM have less than 17 hours of daylight available for foraging activity. This difference in potential foraging day length could cause Razorbills at the southern range limit to be more sensitive to declines in foraging conditions than Razorbills at more northerly colonies, because southern breeding birds have less time available during which they could

increase foraging effort to compensate for lower prey encounter rates and buffer chicks against the effects of decreased food intake.

Foraging Conditions, Foraging Effort, and Reproductive Success

Seabirds are capable of adjusting their activity time budgets to increase foraging effort in the face of poor foraging conditions, enabling them to buffer their chicks against negative effects of declines in foraging conditions. However, this strategy works well only during minor to moderate declines (Burger & Piatt 1990), and may be insufficient to avoid negative effects on chick growth and fledging success when declines in conditions are large or last for an extended period (Harding *et al.* 2007, Ronconi & Burger 2008, Wilhelm *et al.* 2008).

Researchers have proposed that alcids facing poor foraging conditions exhibit observable characteristic responses, including shifts in time activity budgets, and changes in diving patterns (Monaghan *et al.* 1994, Dall'Antonia *et al.* 2001). Conditions that may indicate birds are under foraging stress include those that involve increases in time and energy devoted to foraging activity. For example, birds may spend a larger proportion of their time on foraging trips (Harding *et al.* 2007), or they may spend a greater proportion of the foraging trip in travel and diving activity, and less time resting at sea (Monaghan *et al.* 1994). Also, diving to deeper depths could indicate the need to travel farther in the vertical direction to encounter food, an activity that would incur additional energetic and time costs for each prey encounter, relative to shallower dives. We are unable to determine conclusively from our study whether chick-rearing Razorbills at MR show a pattern of foraging behavior that is consistent with response to poor foraging conditions.

They do have some characteristics that are possibly indicative of increased foraging effort. For example, the mean dive depth is near the top of the range of published values (Table 2.8). Compared to the Gannet Islands, Labrador (Paredes *et al.* 2008), the number of dives per day at MR is substantially greater, despite similar dive duration and greater average depth of dives, which together indicate much more time and energy devoted to diving at MR than at the Gannet Islands.

We are missing several important pieces of the puzzle that would be necessary to determine with reasonable confidence whether Razorbills at MR are encountering poor foraging conditions. Additional information on time activity budget, foraging trip length, distance to foraging area, and number of daily meals per chick would be needed to clarify the quality of foraging conditions for MR Razorbills.

Conclusions

We conclude that chick-rearing Razorbills at the southern range limit perform foraging dives and bouts that are generally similar to those of conspecifics in Labrador and Europe, as documented in previously published studies. However, individuals at MR may be diving deeper and more frequently, on average, than Razorbills at some other breeding colonies. This could indicate poor foraging conditions and might manifest in poor chick condition and fledging rate. Investigation of additional factors not addressed in this study, including foraging trip length, chick feeding rate, and adult time activity budgets, would support a more complete assessment of the foraging effort of this threatened bird in the GOM.

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Table 2.1. Nest and colony attendance behavior of eleven chick-rearing Razorbills fitted with TDRs at Matinicus Rock, Maine, 2008-2009.

Bird	Year	Sex	TDR recovered?	Abandoned nest?	Fledged chick?	Observed after TDR attachment		
						at nest, same year	at colony, same year	later years (to 2011) ^e
65	2008	F	yes	no	yes	yes	yes	yes
241	2008	F	yes	no	yes	yes	yes	yes
313	2009	F	yes	no	yes	yes	yes	no
265	2009	M	yes	no	yes	yes	yes	no
287	2008	unk.	no	maybe	yes	no	maybe	yes
456	2008	unk.	no	no	no ^a	yes	yes	no
219	2008	F	no	no	yes	yes	yes	yes
315	2008	M	no	maybe	no ^b	no	no	no
291	2009	F	no	maybe	no ^c	no	yes	yes
289	2009	M	no	no	yes	yes	yes	yes
212	2009	M	no	no	maybe ^d	yes	yes	yes

^a chick died in burrow from injuries unrelated to this study

^b chick disappeared; may have died before or after TDR parent, but not mate, abandoned nest

^c chick disappeared; may have been killed by a predator or abandoned

^d chick disappeared before typical fledging size, but was late season chick and may have fledged

^e Resighting effort was not exhaustive; birds not observed in subsequent years may have been present

Table 2.2. Underwater dive time of chick-rearing Razorbills at Matinicus Rock, Maine, as shown by pressure readings (n = 40,172) collected at two-second intervals from four TDR-carrying individuals, over a time-period of three days each in 2008-2009.

Depth (m)	Portion of time at depth by individual				Mean	Cumulative total of mean
	Bird 65	Bird 241	Bird 313	Bird 265		
0 – 5	0.35	0.42	0.40	0.32	0.37	0.37
>5 – 10	0.20	0.23	0.21	0.24	0.22	0.59
>10 – 15	0.17	0.11	0.16	0.22	0.17	0.76
>15 – 20	0.09	0.11	0.14	0.18	0.13	0.89
>20 – 25	0.09	0.08	0.06	0.04	0.07	0.96
>25 – 30	0.07	0.04	0.01	0.00	0.03	0.99
>30 – 35	0.03	0.01	0.00	0.00	0.01	1.00
>35 – 40	< 0.01	0.00	0.00	0.00	0.00	1.00

Table 2.3. Timing of onset and end of daily diving activity for four chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009.

Individual	Day	Time of diving activity	
		Start	End
65	1	-	15:24
	2	5:53	20:41
	3	4:23	14:20
	4	5:50	20:27
	5	4:29	-
241	1	-	18:15
	2	6:04	20:10
	3	4:58	13:25
	4	8:11	20:27
	5	4:29	-
313	1	-	20:12
	2	4:27	21:00
	3	4:26	20:32
	4	4:38	10:00
265	1	-	21:07
	2	4:52	20:31
	3	4:24	20:47
	4	4:29	20:40
	5	4:34	-

Table 2.4. Results of Likelihood Ratio tests comparing diel distribution of dive frequency between days (post-hoc pairwise comparisons), within individuals, for chick-provisioning Razorbills carrying TDRs at Matinicus Rock, Maine, 2008-2009. For analysis, dives were binned into three-hour periods (starting with 03:00-05:59, and ending with 18:00-20:59).

Individual	No. days compared	N	df	χ^2	p
65	2 ^a	308	5	18.9	0.002*
241	3	506	10	281.3	<0.0001*
313	2 ^a	266	3	102.3	<0.0001*
265	3	558	10	293.0	<0.0001*

^aThe day with fewest dives (out of three) was excluded from this analysis for individuals 65 and 313, to avoid a negative effect on test reliability due to large numbers of contingency table cells with small expected values.

Table 2.5. Average depths of foraging dives made during different periods of the day by four chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. Because maximum depths of multiple dives within a bout (group of dives clustered in time) are correlated, we averaged the maximum depths of all dives within each bout, and used this average bout value of depth as our unit of comparison. Periods of the day that do not share the same letter in the far right column have significantly different means (Tukey-Kramer HSD test) and specific comparisons are detailed in Table 2.6.

Period of day	Hours	N	Mean depth (m)	Standard error	Significance
Early morning	4:00-5:59	18	11.7	1.2	a,b
Morning	6:00-9:59	36	13.1	1.2	a
Mid-day	10:00-13:59	55	13.4	1.1	a
Afternoon	14:00-17:59	66	11.3	1.1	a
Evening	18:00-20:59	39	6.3	0.6	b

Table 2.6. Results of Tukey-Kramer HSD tests for post-hoc pairwise comparisons of average dive depth during five periods of the day, for four chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. See Table 2.5 for hours included in each time period.

Period 1	Period 2	Difference in dive depth (m)*	Standard error	p
Mid-day	Evening	7.1	1.5	<0.0001*
Morning	Evening	6.8	1.7	0.0008*
Early morning	Evening	5.4	2.1	0.07
Afternoon	Evening	5.0	1.5	0.007*
Mid-day	Afternoon	2.1	1.3	0.53
Morning	Afternoon	1.8	1.5	0.77
Mid-day	Early Morning	1.7	2.0	0.92
Morning	Early Morning	1.4	2.1	0.97
Early morning	Afternoon	0.4	1.9	0.99
Mid-day	Morning	0.3	1.6	0.99

*Difference in dive depth (m) = (value_{Period 1}) - (value_{Period 2})

Table 2.7. Water temperatures recorded during dives of four TDR-carrying Razorbills near Matinicus Rock, Maine, 2008-2009.

		Individual				Year		Total
		65	241	313	265	2008 (Birds 65, 241)	2009 (Birds 313, 265)	
n		413	590	514	739	1003	1253	2256
Surface temperature, °C	Mean	10.4	10.3	9.3	9.4	10.3	9.4	9.8
	SD	1.0	0.7	0.7	0.7	0.8	0.7	0.9
	Max.	15.0	13.1	12.8	14.1	14.0	14.1	15.0
	Min.	8.6	8.8	8.6	8.5	8.6	8.5	8.5
Bottom temperature, °C	Mean	9.7	9.7	9.2	9.2	9.7	9.2	9.4
	SD	1.3	1.0	0.6	0.6	1.1	0.6	0.9
	Max.	13.4	12.4	10.8	11.6	13.4	11.6	13.4
	Min.	7.6	7.4	8.3	8.1	7.4	8.1	7.4
Within-dive temperature differential, °C	Mean	0.7	0.6	0.1	0.2	0.6	0.2	0.4
	SD	0.8	0.8	0.2	0.3	0.8	0.3	0.6
	Max.	3.6	3.2	2.1	3.3	3.6	3.3	3.6
	Min.	-0.1	-0.1	0.0	0.0	-0.1	0.0	-0.1

Table 2.8. Comparison of characteristics of dives and diving bouts for Razorbills at Matinicus Rock, Maine, 2008-2009, and previously published studies at Razorbill colonies in Europe and Canada.

Mean dive depth (m)	Max. dive depth (m)	Mean dive duration (s)	Mean descent rate (m/s)	Mean ascent rate (m/s)	Mean # dives per day	Mean # dives per bout	Mean # bouts per day	Location	Source
13.1	36	46	0.71	0.83	141	7.8	17.9	Matinicus Rock, Maine	this study
6.5	32	23	0.64	0.64	-	-	-	Isle of May, Scotland	Thaxter <i>et al.</i> 2010
10	36	50	0.54	0.63	43 (M), 55 (F)	3.0 (M), 3.3 (F)	13 (M), 17 (F)	Gannet Islands, Labrador	Paredes <i>et al.</i> 2008
19 ^a	43	47	0.77	0.90	-	8.1	-	Græsholmen, Denmark	Benvenuti <i>et al.</i> 2001
11 ^b	41	-	1	1	-	-	-	Latrabjarg, Iceland	Dall'Antonia <i>et al.</i> 2001
-	31	-	-	-	-	-	-	Svalvard, Norway	Watanuki <i>et al.</i> 2006
-	38	-	-	-	-	-	-	Hornøy, Norway	Barrett and Furness 1990
-	32	-	-	-	-	-	-	Isle of May, Scotland	Harris <i>et al.</i> 1990

^aMean dive depth value estimated from dive depth histogram. Paper stated that > 50% of dives were shallower than 15 m.

^bMean dive depth value estimated from dive depth histogram. Paper stated that > 70% of dives were shallower than 15 m.

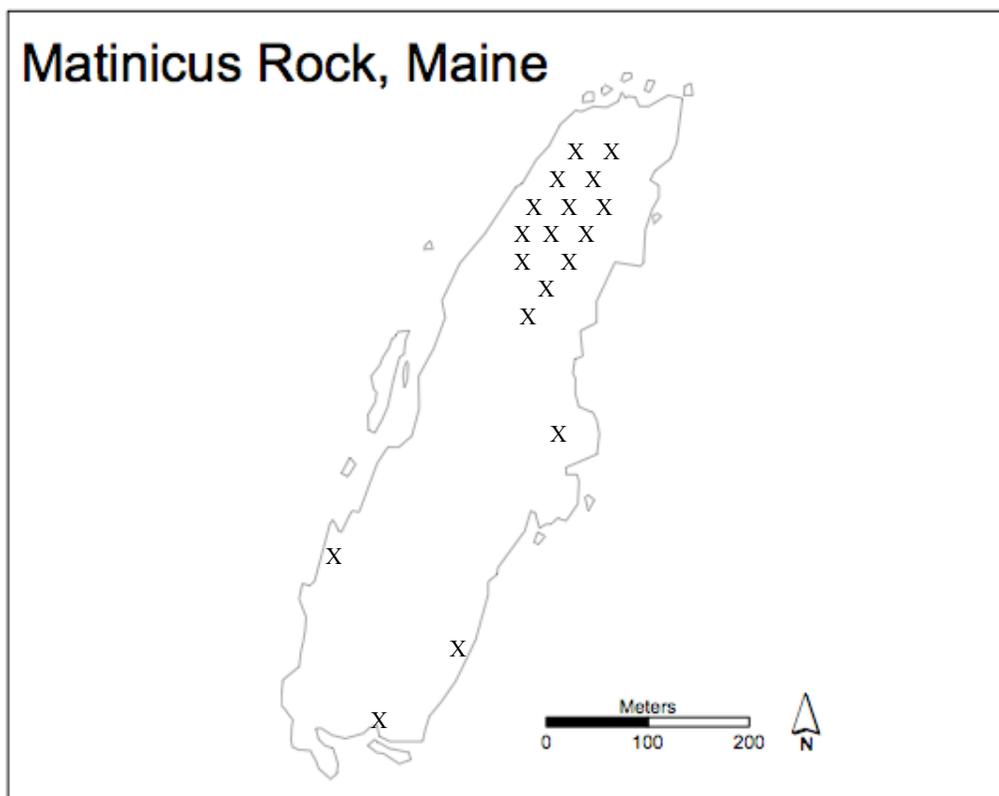
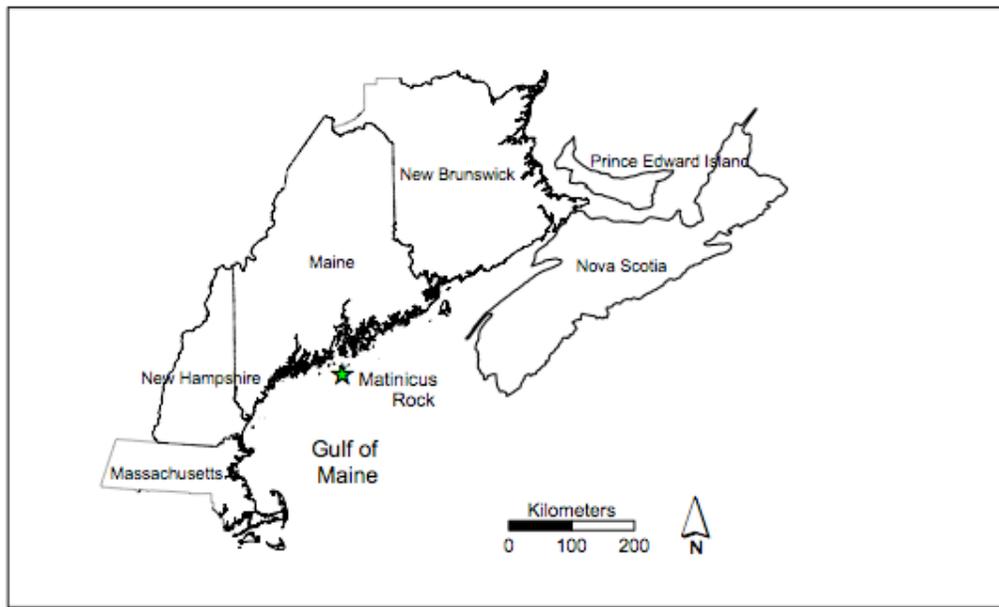


Figure 2.1. Map of Matinicus Rock, Maine, showing approximate locations of Razorbill nesting areas as of 2009 (marked with “X”). This island in outer Penobscot Bay, Gulf of Maine, supports a diverse seabird breeding colony including the largest U.S. Razorbill colony.



Figure 2.2. Electronic data loggers (Lotek LAT 1500 temperature-depth recorder (TDR)) were attached to plastic coil leg-bands using plastic mounting brackets and black tesa[®] tape, for deployment on Razorbills at Matinicus Rock, Maine, 2008-2009. A TDR is shown before deployment, during attachment, and after a deployment of several days.

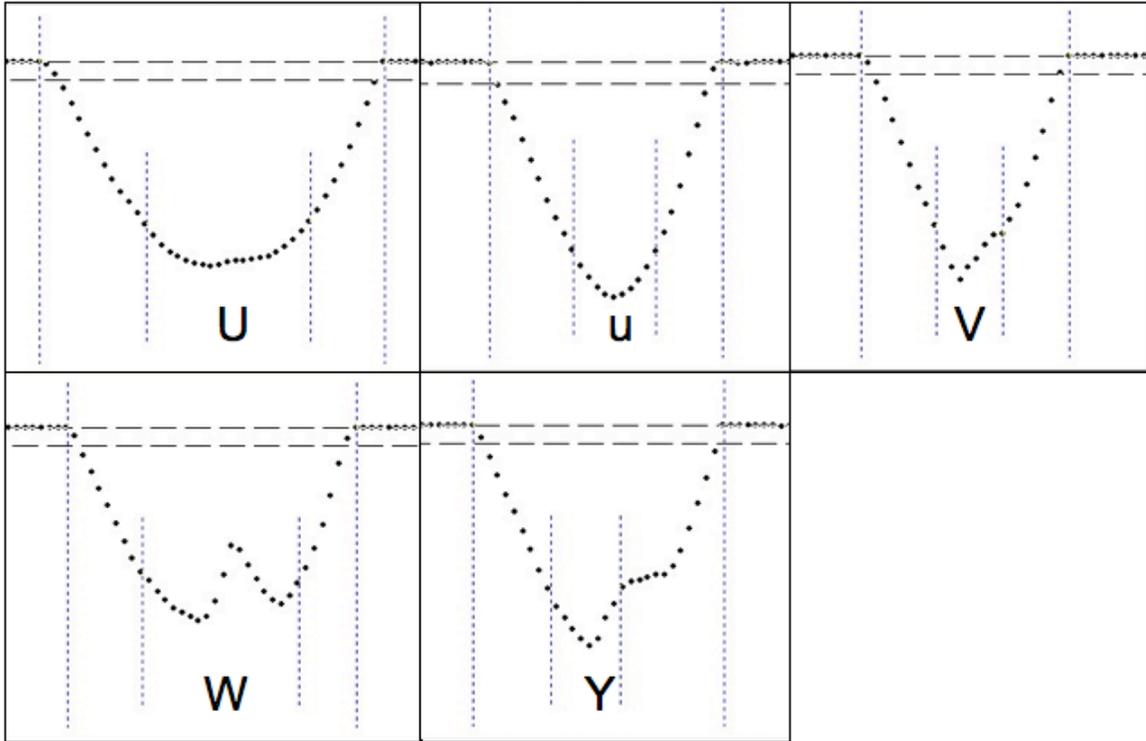


Figure 2.3. Dive profile shape categories for Razorbills at Matinicus Rock, Maine, 2008-2009: U (flattened bottom), u (parabolic), V (sharp inflection point), W (multiple inflection points), and Y (shelf during descent or ascent). The horizontal axis is time, and the vertical axis is depth below sea surface. Horizontal dashed lines are at 0 m (sea surface) and 2 m depth. Vertical dashed lines indicate the start and end of the dive (outer pair) and the bottom phase (inner pair; the portion of each dive at $\geq 75\%$ of the maximum depth for that dive). The dive portions to the left and right of the bottom phase are the descent and ascent phases, respectively. Each dot represents a depth reading, which were recorded at two-second intervals.

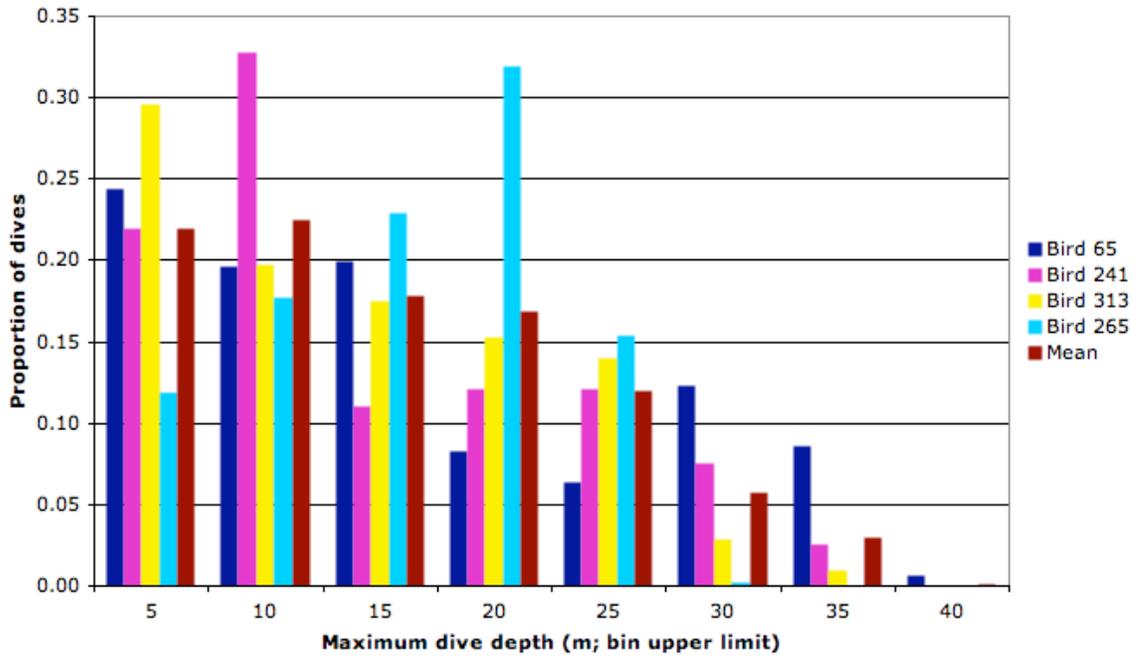


Figure 2.4. Distribution of maximum depths reached on foraging dives made by chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. Maximum depth was 36.1 m, but 79% of dives had maximum depths ≤ 20 m.

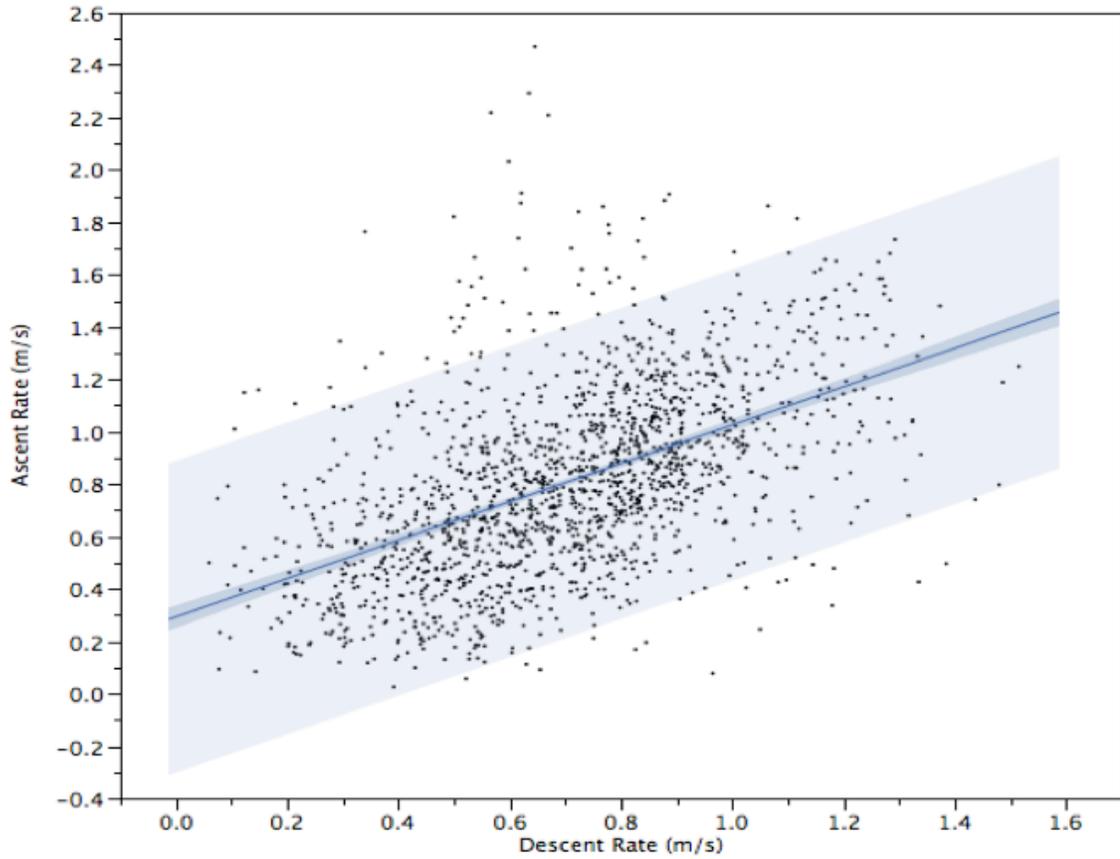


Figure 2.5. Dive descent rate and ascent rate were positively correlated for Razorbills diving near Matinicus Rock, Maine, 2008-2009. Linear regression line: Ascent rate = $0.29 + (0.73)(\text{Descent rate})$.

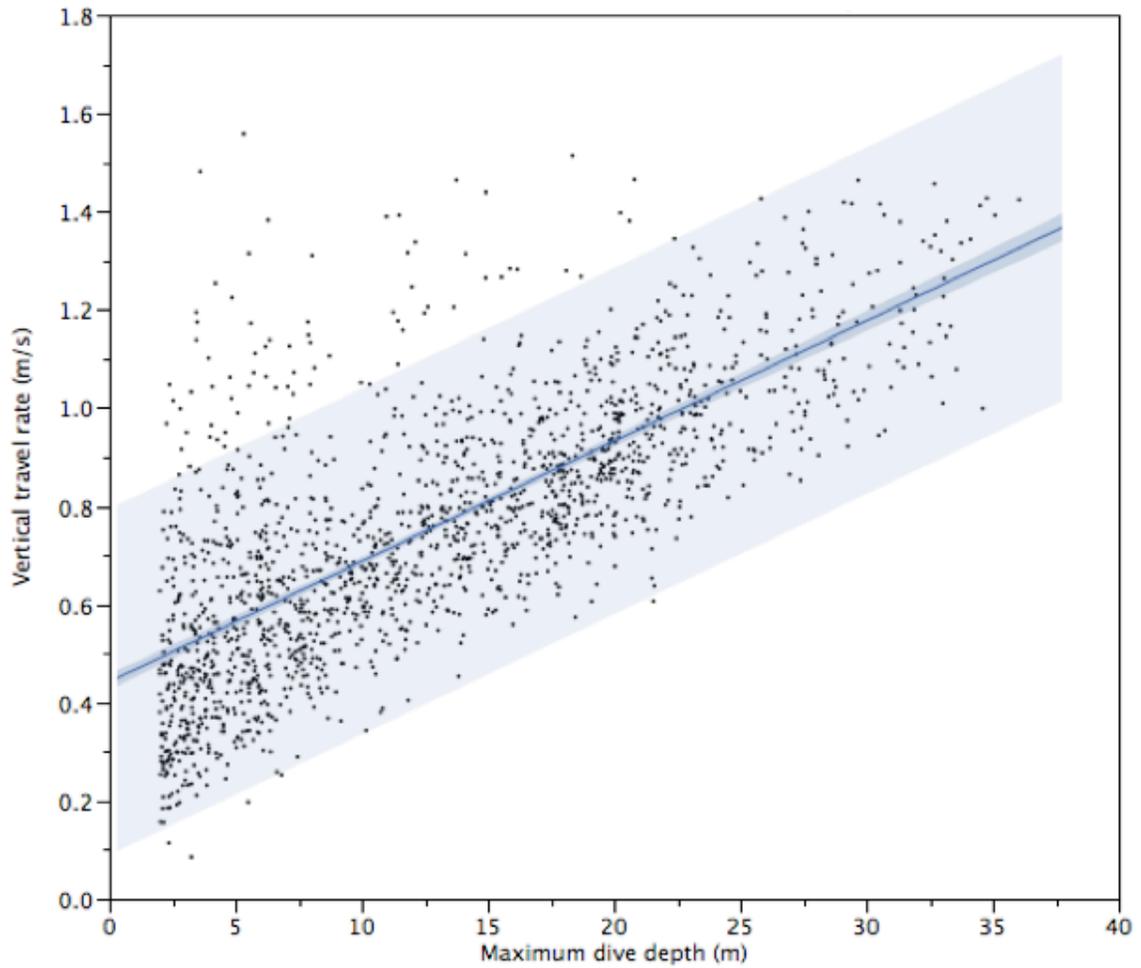


Figure 2.6. Vertical travel rate of a dive was positively correlated with maximum depth reached for Razorbills diving near Matinicus Rock, Maine, 2008-2009 (where vertical travel rate is the average of the descent and ascent rates). Linear regression line: Vertical travel rate = $0.44 + 0.025(\text{Maximum dive depth})$.

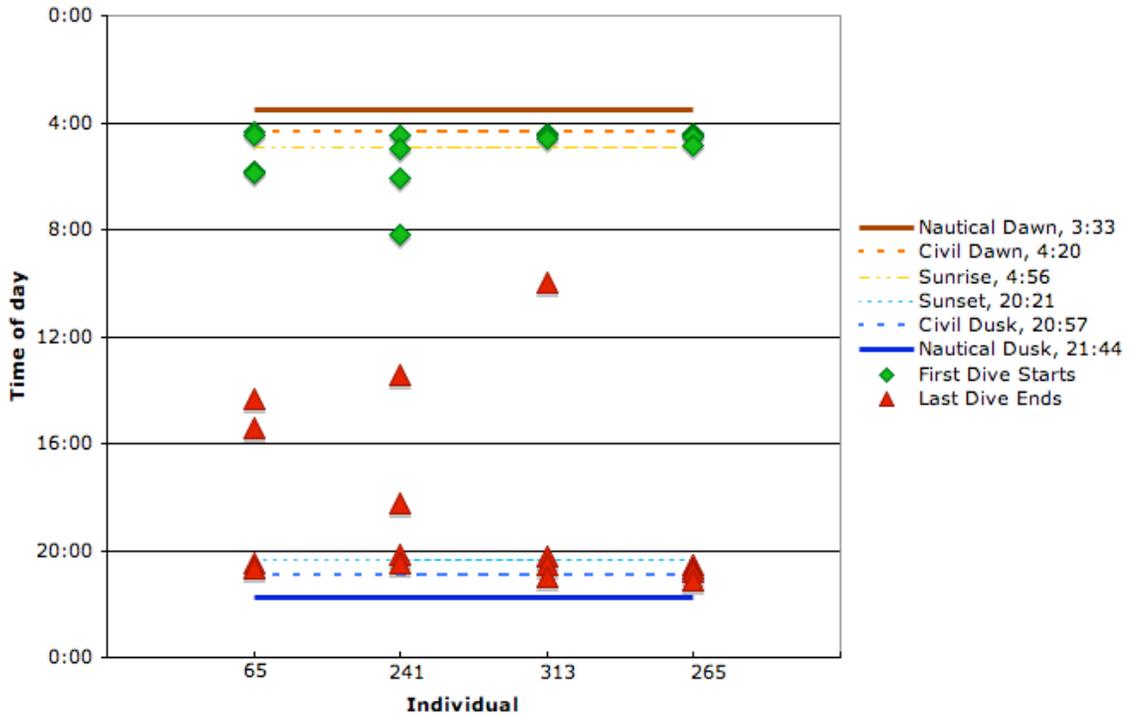


Figure 2.7. Razorbills at Matinicus Rock, Maine in 2008-2009 ($n = 4$) usually began diving between civil dawn and sunrise, and stopped diving between sunset and nautical dusk. Each symbol represents the start or end time of diving activity for the indicated bird on one day. Individual 313 has fewer start times (3) than the other birds (4 each) due to timing of data-logger deployment. Individual 265 was male and the other three were female.

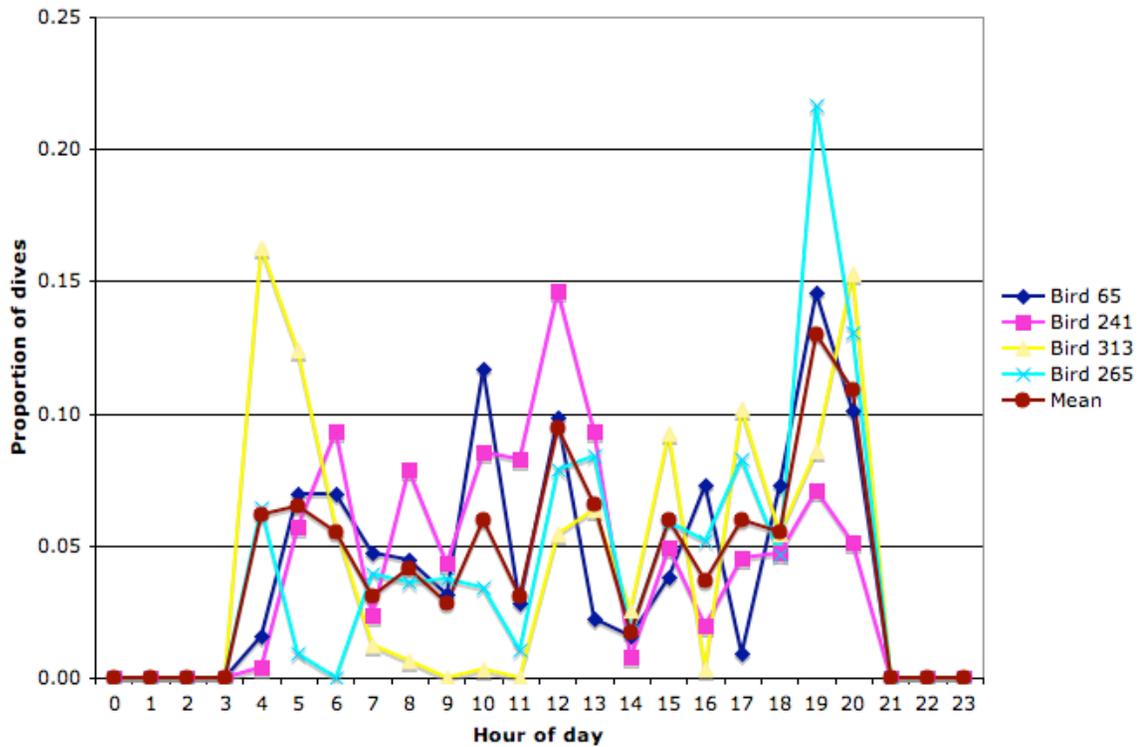


Figure 2.8. Proportion of dives varied by hour of day for chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009 (n = 1,694 dives; proportion of dives are for each individual over three days). Peaks of diving activity occurred in the evening, mid-day, and, to a lesser extent, early morning hours.

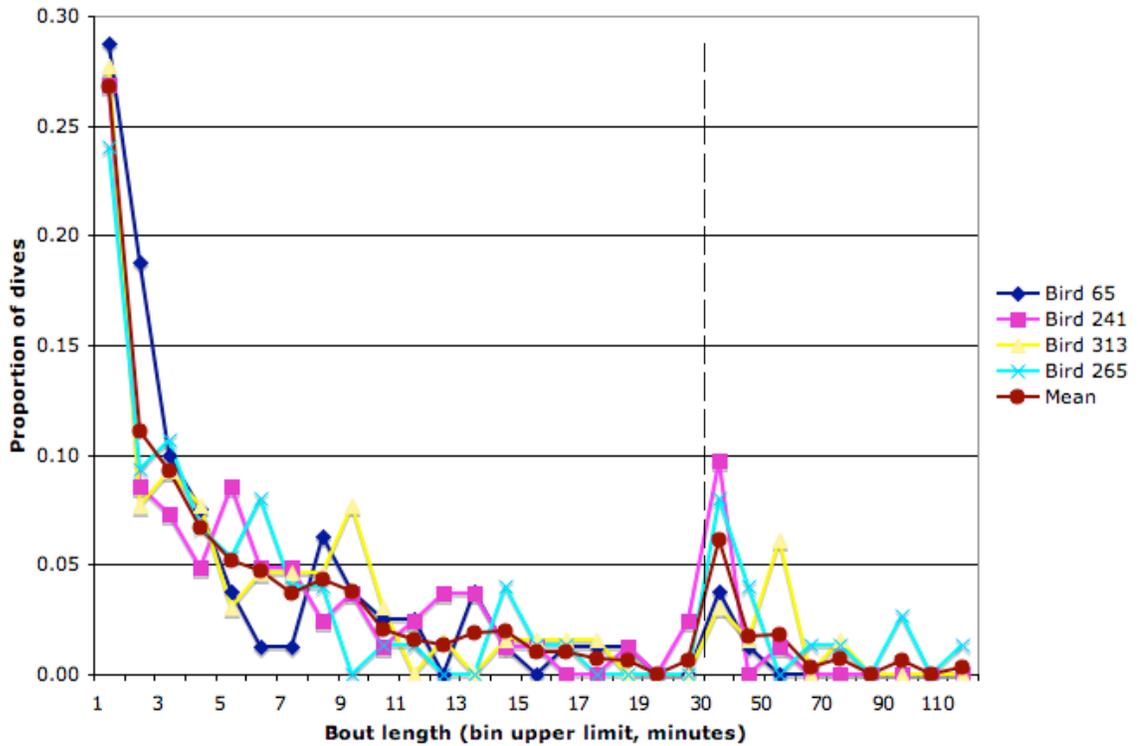


Figure 2.9. Foraging dives were clustered into bouts of varying length for chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. A bout is one dive or a series of consecutive dives, within which no dives were separated by > 60 seconds of surface time. Dives occurred in bouts lasting between 4 s and 104 min (n = 302). The peak seen at the 30-min bout length bin is an artifact of the change in displayed bin intervals (from 1-min bins left of the dashed line, to 10-min bins right of the dashed line).

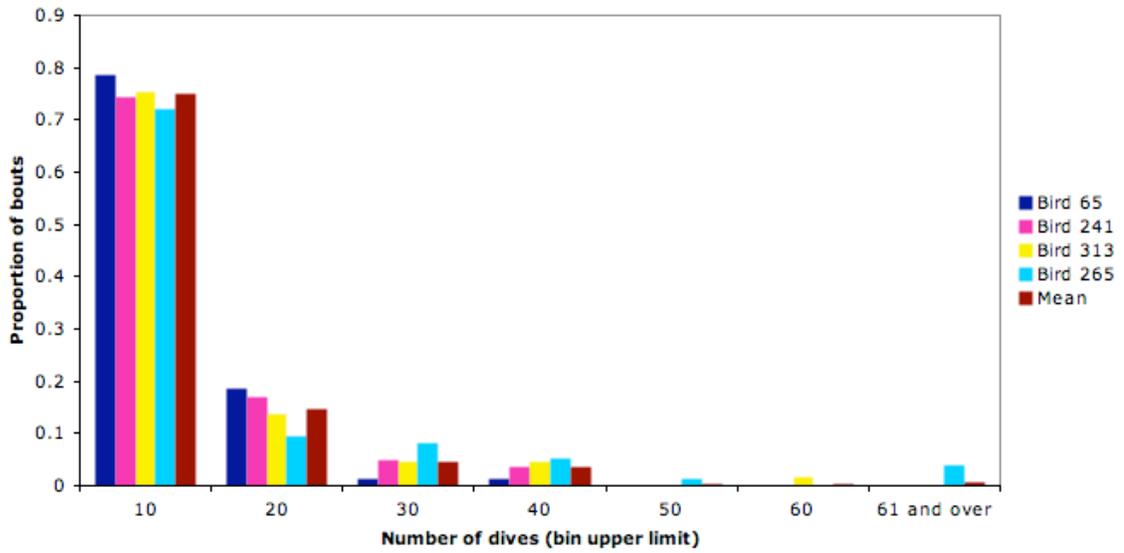


Figure 2.10. Distribution of diving bouts by number of dives per bout for four chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009 (n = 302). Seventy-five percent of foraging bouts contained ≤ 10 dives and 99% contained ≤ 60 dives.

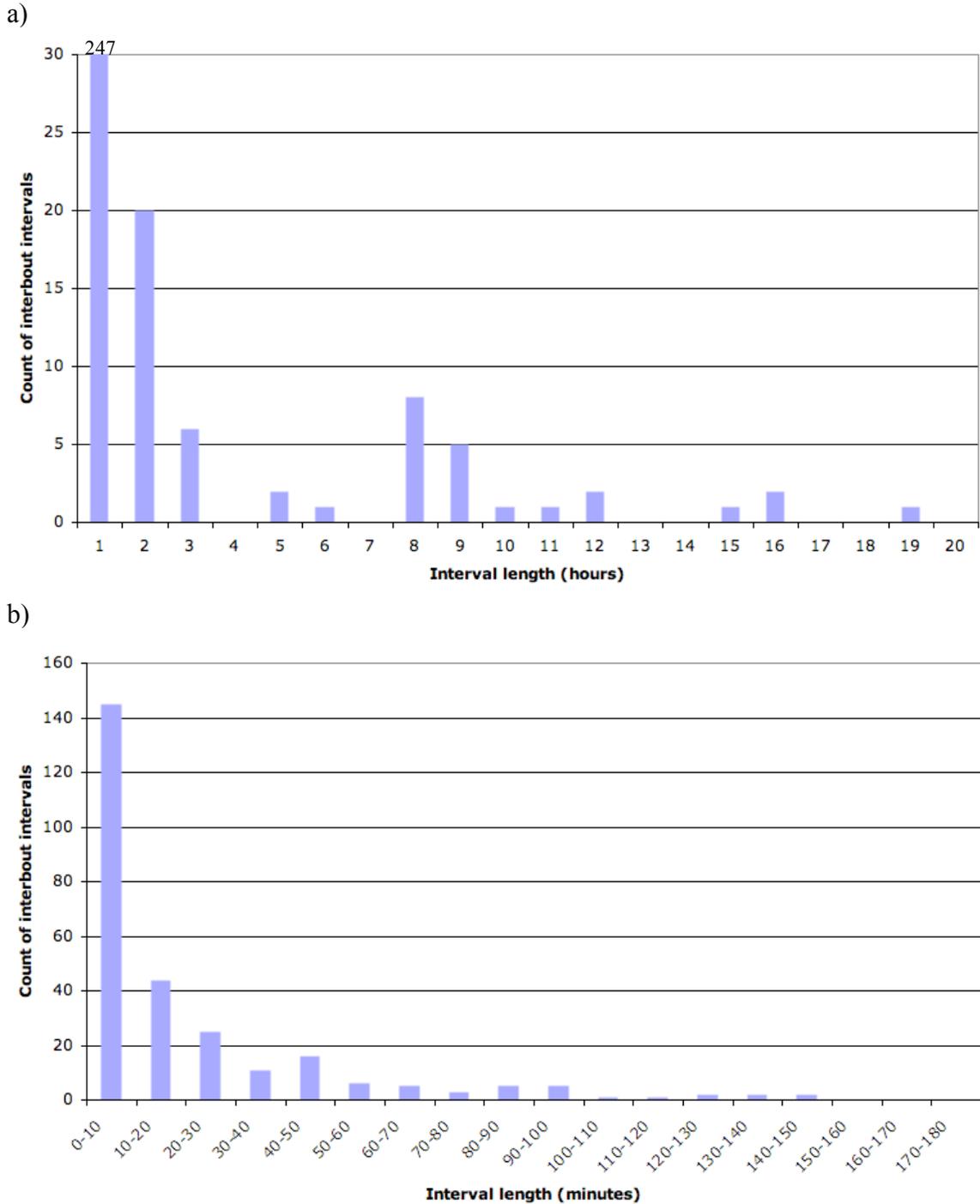


Figure 2.11. The length distribution of interbout intervals (the period of time between bouts of diving; $n = 297$) is shown for (a) all interbout intervals, and (b) interbout intervals under three hours in length, for chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. Most intervals in the eight- and nine-hour categories were overnight periods, as were many of the longer intervals. In section (a), the vertical axis scale is truncated to better view small values, resulting in the top of the 1-hour category bar being truncated; there were 247 interbout intervals with lengths of one hour or less.

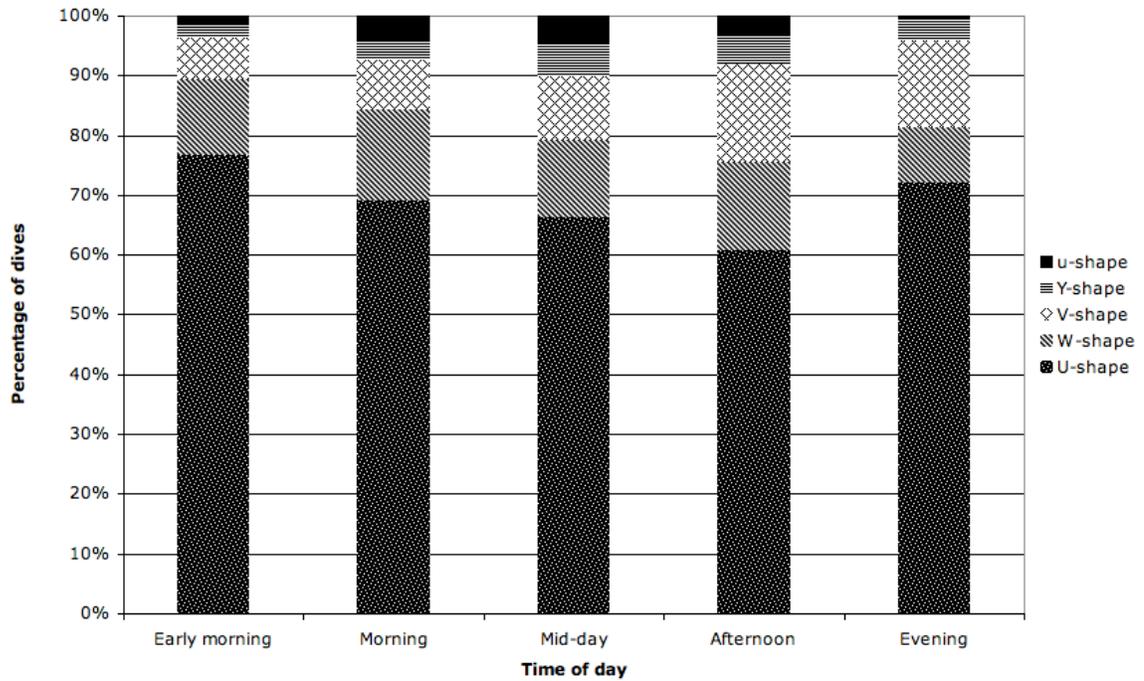


Figure 2.12. Proportion of dives (n = 1,994) in five profile shape categories by time of day, for chick-rearing Razorbills at Matinicus Rock, Maine, 2008-2009. Time of day categories are: early morning 4:00-5:59, morning 6:00-9:59, mid-day 10:00-13:59, afternoon 14:00-17:59, and evening 18:00-20:59.

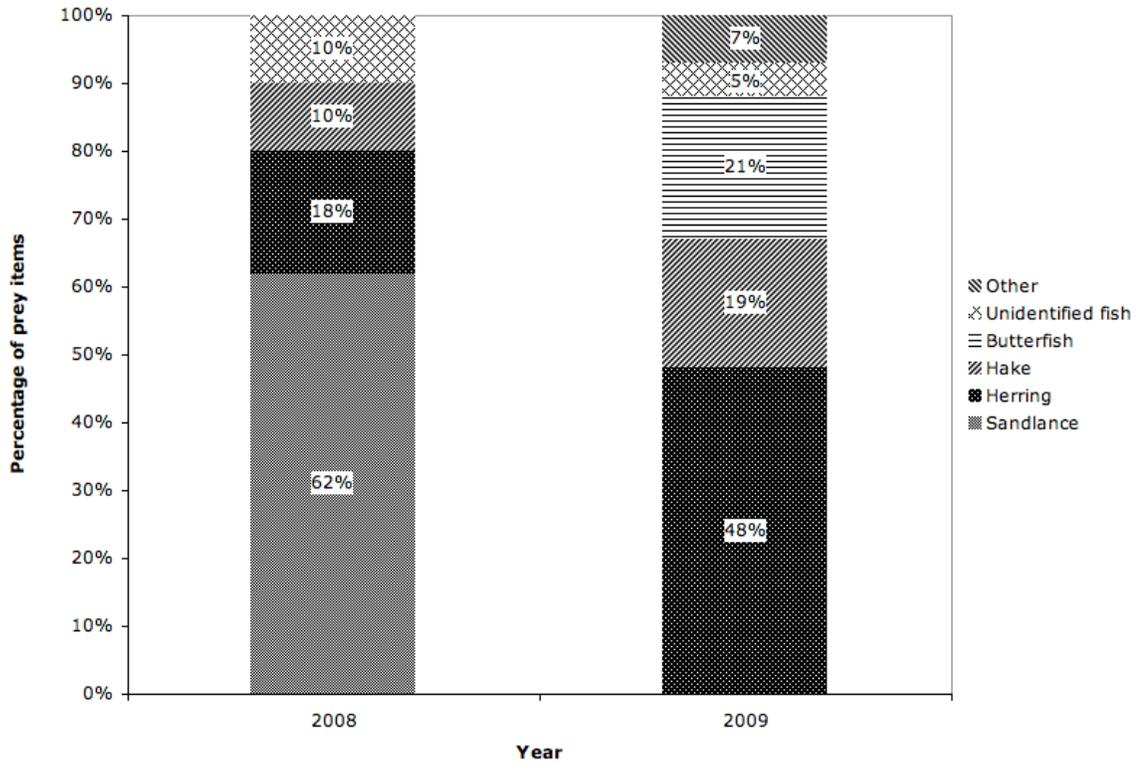


Figure 2.13. Prey items delivered by chick-provisioning adults at Matinicus Rock, Maine during the TDR deployment periods of 26 June-1 July 2008 (n = 135) and 28 June-2 July 2009 (n = 177). This is a colony-wide sample, and is not specific to the TDR study individuals. The “Other” category included Atlantic saury, larval fish, euphausiid, and unidentified invertebrate.

APPENDIX

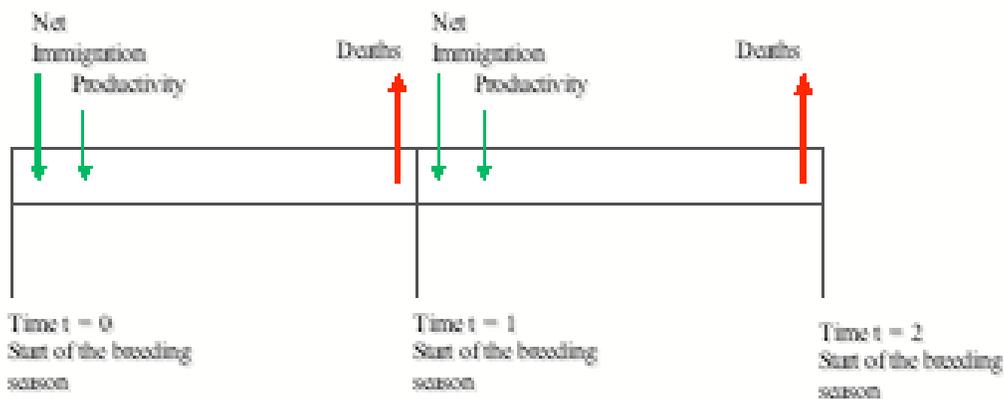
DOCUMENTATION OF POPULATION MODEL ASSUMPTIONS, CONSTRUCTION, CALCULATIONS, AND RESULTS

Define Variables

- A = age ($A = \{0, 1, 2, \dots, 30\}$)
- Y = year ($Y = \{0, 1, 2, \dots, 28\}$)
- M = Maturity rate. The maturity rate is the proportion of birds of the given age that have reached sexual maturity and can produce offspring.
- I = Annual net immigration rate
- S = Annual survival rate
- P = Annual productivity rate (per individual)
- X = Quantity of individuals
- M, I, S, P and X are able to take on different values depending on the specified age. Let $\alpha \in A$ and $y \in Y$. Then,
- M_α is the maturity rate that applies to birds age a .
- I_α is the annual net immigration rate that applies at age a .
- I_A is solved for by use of the population model.
- S_α is the annual survival rate that applies to birds age a .
- S_A is estimated from the literature.
- P_α is the annual productivity rate (per individual) that applies to birds of age a .
- P_A is estimated from data collected from this study. Also, this variable can be solved for by use of the population model.
- $X_{y,\alpha}$ is the quantity of individuals in year y , that are age a .
- $X_{0,A}$ is the initial age distribution function. It is estimated through a combination of data from this study and the model structure.
- $X_{y \neq 0,A}$ are the calculated values for the quantity of individuals in year $y \neq 0$, that are age a .

Method

- All population decrements occur at the end of the year (i.e. just before a new breeding season begins) and all population increments occur at the beginning of the year (i.e. at the beginning of a new breeding season).

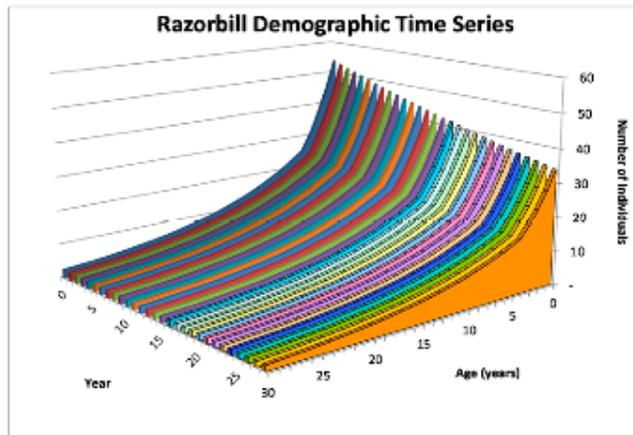


- b_y is the breeding population in year y .
 - $b_y = \sum_{a=4}^{30} X_{y,a}$
- B_y is the total population in year y .
 - $B_y = \sum_{a=0}^{30} X_{y,a}$
- g_y is the breeding population growth rate.
 - $g_y = b_y / b_{y-1}$ for $y = 1, 2, \dots, 28$
- G_y is the total population growth rate.
 - $G_y = B_y / B_{y-1}$ for $y = 1, 2, \dots, 28$
- \bar{g} is the average breeding population growth rate.
 - $\bar{g} = \frac{1}{28} \sum_{y=1}^{28} g_y$
- \bar{G} is the average total population growth rate.
 - $\bar{G} = \frac{1}{28} \sum_{y=1}^{28} G_y$
- The quantity of birds of age 1 or older is a result of the net annual immigration rate, the annual survival rate, and the prior year quantity.
 - $X_{y+1,a+1} = X_{y+1,a+1} \times (1 + I_a) \times S_a$ for $1 \leq y \leq 27$ and $a \geq 1$.
- The quantity of birds of age 0 is a result of the number of birds of breeding age the previous season, the productivity of the previous season, and the annual survival of age class 0 birds, so,
 - $X_{y,0} = [\sum_{a=1}^{30} M_a \times P_a \times X_a]$ for $0 \leq y \leq 28$ and $a = 0$.
- The following parameters are only defined when there is at least one year in which immigration is positive.
- δ is the number of immigrants as a percent of the previous year breeding population. This is equal to (total breeding population – the quantity of returning breeders) ÷ the quantity of immigrants.
 - $\delta_y = \frac{\sum_{a=4}^{30} X_{y,a} - \sum_{a=3}^{30} X_{y,a} \times S_a}{\sum_{a=4}^{30} X_{y,a}}$
- μ_y is the number of immigrants as a percent of the current year native recruits (this only applies to the ‘Young’ immigrant scenarios), so $I_a = 0$ for all a except $a = 4$.
 - $\delta_y = \frac{\sum_{a=4}^{30} X_{y,a} - \sum_{a=3}^{30} X_{y,a} \times S_a}{\sum_{a=3}^{30} X_{y,a} \times S_a}$

Growth Rate, given 0.24 Productivity Rate and 0% Immigration Rate

			Total																									
Average Growth			Population	439	431	424	417	410	404	397	390	384	378	372	365	359	353	348	342	...	276							
-1.6%			Growth %	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	...	-1.6%							
			Breeding																									
Average Growth			Population	272	268	263	259	255	250	246	242	238	234	230	227	223	219	216	212	...	171							
-1.6%			Growth %	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	-1.6%	...	-1.6%							
			Year																									
			Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28							
-	0.81	-	0	54	53	52	51	51	50	49	48	47	47	46	45	44	44	43	42	...	34							
-	0.81	-	1	45	44	43	43	42	41	41	40	39	39	38	37	37	36	35	35	...	28							
-	0.81	-	2	37	36	36	35	35	34	34	33	32	32	31	31	30	30	29	29	...	23							
-	0.81	-	3	31	30	30	29	29	28	28	27	27	26	26	26	25	25	24	24	...	19							
-	0.90	0.24	4	25	25	25	24	24	23	23	23	22	22	22	21	21	20	20	20	...	16							
-	0.90	0.24	5	23	23	22	22	22	21	21	21	20	20	20	19	19	19	18	18	...	15							
-	0.90	0.24	6	21	21	21	20	20	20	19	19	19	18	18	18	17	17	17	17	...	13							
-	0.90	0.24	7	19	19	19	19	18	18	18	17	17	17	16	16	16	16	15	15	...	12							
-	0.90	0.24	8	18	18	17	17	17	16	16	16	16	15	15	15	15	14	14	14	...	11							
-	0.90	0.24	9	16	16	16	16	15	15	15	15	14	14	14	14	13	13	13	13	...	10							
-	0.90	0.24	10	15	15	14	14	14	14	14	13	13	13	13	12	12	12	12	12	...	9							
-	0.90	0.24	11	14	13	13	13	13	13	12	12	12	12	12	11	11	11	11	11	...	9							
-	0.90	0.24	12	12	12	12	12	12	11	11	11	11	11	11	10	10	10	10	10	...	8							
-	0.90	0.24	13	11	11	11	11	11	11	10	10	10	10	10	9	9	9	9	9	...	7							
-	0.90	0.24	14	10	10	10	10	10	10	9	9	9	9	9	9	8	8	8	8	...	7							
-	0.90	0.24	15	10	9	9	9	9	9	9	9	8	8	8	8	8	8	8	7	...	6							
-	0.90	0.24	16	9	9	8	8	8	8	8	8	8	8	7	7	7	7	7	7	...	6							
-	0.90	0.24	17	8	8	8	8	8	7	7	7	7	7	7	7	6	6	6	6	...	5							
-	0.90	0.24	18	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	...	5							
-	0.90	0.24	19	7	7	6	6	6	6	6	6	6	6	6	6	6	5	5	5	...	4							
-	0.90	0.24	20	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	...	4							
-	0.90	0.24	21	6	6	5	5	5	5	5	5	5	5	5	5	5	5	4	4	...	4							
-	0.90	0.24	22	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	...	3							
-	0.90	0.24	23	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	...	3							
-	0.90	0.24	24	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	3	...	3							
-	0.90	0.24	25	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	...	2							
-	0.90	0.24	26	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	2							
-	0.90	0.24	27	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	2							
-	0.90	0.24	28	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	...	2							
-	0.90	0.24	29	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	...	2							
-	-	0.24	30	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2							

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)

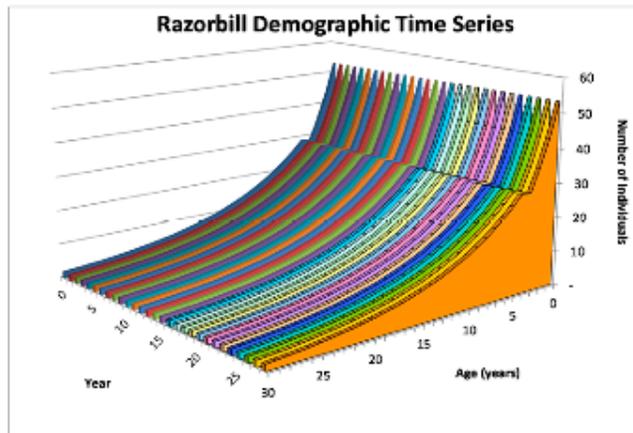


Immigration Rate, given 0.24 Productivity Rate, 0% Growth Rate, and 'Young' immigrant age distribution

			Total																									
Average Growth			Population	432	432	432	432	432	432	432	432	432	432	432	432	432	432	432	432	...	432							
0.0%			Growth %	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	...	0.0%							
			Breeding																									
Average Growth			Population	272	272	272	272	272	272	272	272	272	272	272	272	272	272	272	272	...	272							
0.0%			Growth %	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	...	0.0%							
			Year																									
			Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28							
-	0.81	-	0	53	53	53	53	53	53	53	53	53	53	53	53	53	53	53	53	...	53							
-	0.81	-	1	43	43	43	43	43	43	43	43	43	43	43	43	43	43	43	43	43	...	43						
-	0.81	-	2	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	...	35						
-	0.81	-	3	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	...	29						
0.234	0.90	0.24	4	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	...	29						
-	0.90	0.24	5	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	26	...	26						
-	0.90	0.24	6	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	...	23						
-	0.90	0.24	7	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	21	...	21						
-	0.90	0.24	8	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	...	19						
-	0.90	0.24	9	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	...	17						
-	0.90	0.24	10	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	...	15						
-	0.90	0.24	11	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	...	14						
-	0.90	0.24	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	...	12						
-	0.90	0.24	13	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	...	11						
-	0.90	0.24	14	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	...	10						
-	0.90	0.24	15	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	...	9						
-	0.90	0.24	16	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	...	8						
-	0.90	0.24	17	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	...	7						
-	0.90	0.24	18	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	...	7						
-	0.90	0.24	19	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	...	6						
-	0.90	0.24	20	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	5						
-	0.90	0.24	21	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	5						
-	0.90	0.24	22	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4						
-	0.90	0.24	23	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4						
-	0.90	0.24	24	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4						
-	0.90	0.24	25	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3						
-	0.90	0.24	26	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3						
-	0.90	0.24	27	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3						
-	0.90	0.24	28	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2						
-	0.90	0.24	29	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2						
-	-	0.24	30	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2						

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)

Immigrants as % of previous year breeding population	2.0%
Immigrants as % of current year native recruits	23%

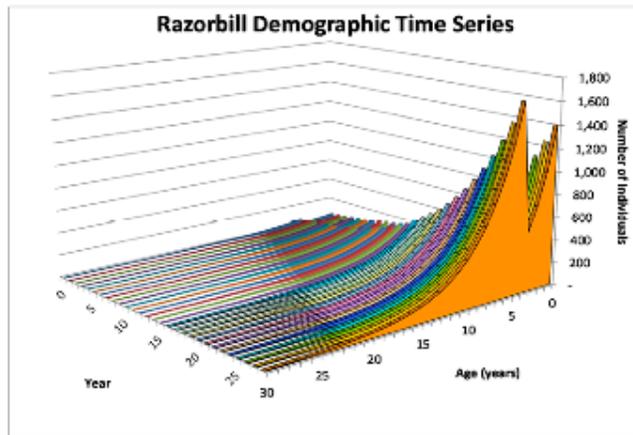


Immigration Rate, *given* 0.24 Productivity Rate, 12.9% Growth Rate, and 'Young' immigrant age distribution

			Total																			
Average Growth			Population	395	446	504	569	642	725	819	924	1043	1178	1330	1501	1695	1914	2161	2439	...	11811	
12.9%			Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%
			Breeding																			
Average Growth			Population	272	307	347	391	442	499	563	636	718	811	915	1033	1167	1317	1487	1679	...	8128	
12.9%			Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%
			Year																			
I	S	P	Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28	
-	0.81	-	0	47	53	60	68	77	86	98	110	124	140	158	179	202	228	257	291	...	1407	
-	0.81	-	1	34	38	43	49	55	62	70	79	90	101	114	129	146	164	186	210	...	1015	
-	0.81	-	2	25	28	31	35	40	45	51	57	65	73	82	93	105	119	134	151	...	732	
-	0.81	-	3	18	20	23	25	29	32	37	41	47	53	59	67	76	86	97	109	...	528	
3.335	0.90	0.24	4	55	62	70	80	90	101	115	129	146	165	186	210	237	268	302	341	...	1652	
-	0.90	0.24	5	44	50	56	63	72	81	91	103	116	131	148	167	189	213	241	272	...	1317	
-	0.90	0.24	6	35	40	45	51	57	64	73	82	93	105	118	133	151	170	192	217	...	1050	
-	0.90	0.24	7	28	32	36	40	46	51	58	65	74	83	94	106	120	136	153	173	...	837	
-	0.90	0.24	8	22	25	28	32	36	41	46	52	59	67	75	85	96	108	122	138	...	667	
-	0.90	0.24	9	18	20	23	26	29	33	37	42	47	53	60	68	76	86	97	110	...	532	
-	0.90	0.24	10	14	16	18	20	23	26	29	33	37	42	48	54	61	69	78	88	...	424	
-	0.90	0.24	11	11	13	14	16	18	21	23	26	30	34	38	43	49	55	62	70	...	338	
-	0.90	0.24	12	9	10	11	13	15	17	19	21	24	27	30	34	39	44	49	56	...	269	
-	0.90	0.24	13	7	8	9	10	12	13	15	17	19	21	24	27	31	35	39	44	...	215	
-	0.90	0.24	14	6	6	7	8	9	11	12	13	15	17	19	22	25	28	31	35	...	171	
-	0.90	0.24	15	5	5	6	7	7	8	9	11	12	14	15	17	20	22	25	28	...	136	
-	0.90	0.24	16	4	4	5	5	6	7	8	9	10	11	12	14	16	18	20	22	...	109	
-	0.90	0.24	17	3	3	4	4	5	5	6	7	8	9	10	11	12	14	16	18	...	87	
-	0.90	0.24	18	2	3	3	3	4	4	5	5	6	7	8	9	10	11	13	14	...	69	
-	0.90	0.24	19	2	2	2	3	3	3	4	4	5	5	6	7	8	9	10	11	...	55	
-	0.90	0.24	20	1	2	2	2	2	3	3	3	4	4	5	6	6	7	8	9	...	44	
-	0.90	0.24	21	1	1	1	2	2	2	2	3	3	3	4	4	5	6	6	7	...	35	
-	0.90	0.24	22	1	1	1	1	2	2	2	2	2	3	3	4	4	5	5	6	...	28	
-	0.90	0.24	23	1	1	1	1	1	1	2	2	2	2	3	3	4	4	5	...	22		
-	0.90	0.24	24	1	1	1	1	1	1	1	1	2	2	2	2	3	3	3	4	...	18	
-	0.90	0.24	25	0	1	1	1	1	1	1	1	1	1	2	2	2	2	3	3	...	14	
-	0.90	0.24	26	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	2	...	11	
-	0.90	0.24	27	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	...	9	
-	0.90	0.24	28	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	...	7	
-	0.90	0.24	29	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	...	6	
-	-	0.24	30	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	...	5	

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)

Immigrants as % of previous year breeding population	17.7%
Immigrants as % of current year native recruits	334%

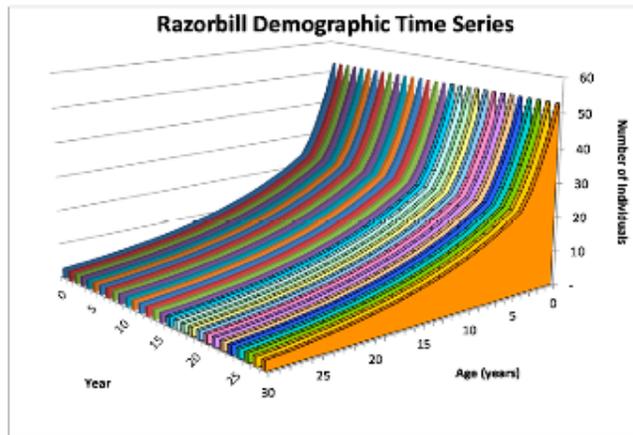


Immigration Rate, given 0.24 Productivity Rate, 0% Growth Rate, and 'All Ages' immigrant age distribution

			Total																									
Average Growth			Population	432	432	432	432	432	432	432	432	432	432	432	432	432	432	432	432	...	432							
0.0%			Growth %	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	...	0.0%							
			Breeding																									
Average Growth			Population	272	272	272	272	272	272	272	272	272	272	272	272	272	272	272	272	...	272							
0.0%			Growth %	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	...	0.0%							
			Year																									
			Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28							
-	0.81	-	0	53	53	53	53	53	53	53	53	53	53	53	53	53	53	53	53	...	53							
-	0.81	-	1	43	43	43	43	43	43	43	43	43	43	43	43	43	43	43	43	...	43							
-	0.81	-	2	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	35	...	35							
-	0.81	-	3	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	29	...	29							
0.024	0.90	0.24	4	24	24	24	24	24	24	24	24	24	24	24	24	24	24	24	24	...	24							
0.024	0.90	0.24	5	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	...	22							
0.024	0.90	0.24	6	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20	...	20							
0.024	0.90	0.24	7	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	19	...	19							
0.024	0.90	0.24	8	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	17	...	17							
0.024	0.90	0.24	9	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	...	16							
0.024	0.90	0.24	10	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	15	...	15							
0.024	0.90	0.24	11	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	...	14							
0.024	0.90	0.24	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	12	...	12							
0.024	0.90	0.24	13	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	...	11							
0.024	0.90	0.24	14	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	...	11							
0.024	0.90	0.24	15	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	...	10							
0.024	0.90	0.24	16	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	...	9							
0.024	0.90	0.24	17	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	...	8							
0.024	0.90	0.24	18	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	...	8							
0.024	0.90	0.24	19	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	...	7							
0.024	0.90	0.24	20	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	...	6							
0.024	0.90	0.24	21	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	...	6							
0.024	0.90	0.24	22	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	...	6							
0.024	0.90	0.24	23	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	5							
0.024	0.90	0.24	24	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	5							
0.024	0.90	0.24	25	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4							
0.024	0.90	0.24	26	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4							
0.024	0.90	0.24	27	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4							
0.024	0.90	0.24	28	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3							
0.024	0.90	0.24	29	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3							
0.024	-	0.24	30	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3							

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)

Immigrants as % of previous year breeding population
 2.4%

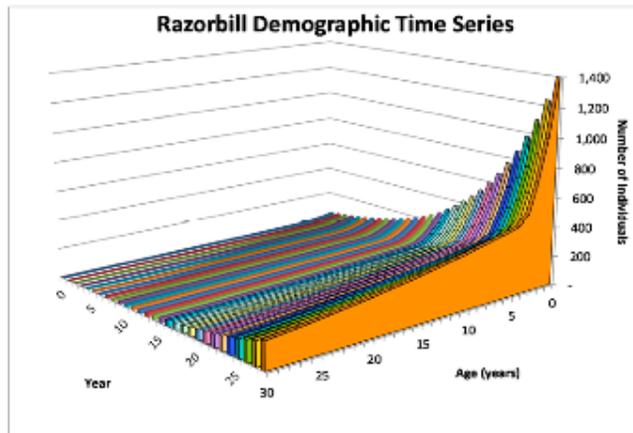


Immigration Rate, given 0.24 Productivity Rate, 12.9% Growth Rate, and 'All Ages' immigrant age distribution

		Total																											
Average Growth		Population	395	446	504	569	642	725	819	924	1043	1178	1330	1501	1695	1914	2161	2439	...	11811									
12.9%		Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%								
		Breeding																											
Average Growth		Population	272	307	347	391	442	499	563	636	718	811	915	1033	1167	1317	1487	1679	...	8128									
12.9%		Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%								
		Year																											
		Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28									
I	S	P	0	47	53	60	68	77	86	98	110	124	140	158	179	202	228	257	291	...	1407								
-	0.81	-	1	34	38	43	49	55	62	70	79	90	101	114	129	146	164	186	210	...	1015								
-	0.81	-	2	25	28	31	35	40	45	51	57	65	73	82	93	105	119	134	151	...	732								
-	0.81	-	3	18	20	23	25	29	32	37	41	47	53	59	67	76	86	97	109	...	528								
0.210	0.90	0.24	4	15	17	20	22	25	28	32	36	41	46	52	59	66	75	84	95	...	461								
0.210	0.90	0.24	5	15	17	19	21	24	27	31	35	39	44	50	57	64	72	81	92	...	445								
0.210	0.90	0.24	6	14	16	18	21	23	26	30	34	38	43	48	55	62	70	79	89	...	429								
0.210	0.90	0.24	7	14	16	18	20	23	25	29	32	37	41	47	53	59	67	76	86	...	414								
0.210	0.90	0.24	8	13	15	17	19	22	25	28	31	35	40	45	51	57	65	73	83	...	400								
0.210	0.90	0.24	9	13	15	16	19	21	24	27	30	34	38	43	49	55	62	71	80	...	386								
0.210	0.90	0.24	10	12	14	16	18	20	23	26	29	33	37	42	47	53	60	68	77	...	372								
0.210	0.90	0.24	11	12	14	15	17	20	22	25	28	32	36	40	46	52	58	66	74	...	359								
0.210	0.90	0.24	12	12	13	15	17	19	21	24	27	31	35	39	44	50	56	63	72	...	346								
0.210	0.90	0.24	13	11	13	14	16	18	21	23	26	30	33	38	42	48	54	61	69	...	334								
0.210	0.90	0.24	14	11	12	14	16	18	20	22	25	28	32	36	41	46	52	59	67	...	322								
0.210	0.90	0.24	15	10	12	13	15	17	19	22	24	27	31	35	40	45	50	57	64	...	311								
0.210	0.90	0.24	16	10	11	13	14	16	18	21	23	27	30	34	38	43	49	55	62	...	300								
0.210	0.90	0.24	17	10	11	12	14	16	18	20	23	26	29	33	37	42	47	53	60	...	290								
0.210	0.90	0.24	18	9	11	12	13	15	17	19	22	25	28	31	36	40	45	51	58	...	279								
0.210	0.90	0.24	19	9	10	12	13	15	17	19	21	24	27	30	34	39	44	49	56	...	270								
0.210	0.90	0.24	20	9	10	11	13	14	16	18	20	23	26	29	33	37	42	48	54	...	260								
0.210	0.90	0.24	21	8	9	11	12	14	15	17	20	22	25	28	32	36	41	46	52	...	251								
0.210	0.90	0.24	22	8	9	10	12	13	15	17	19	21	24	27	31	35	39	44	50	...	242								
0.210	0.90	0.24	23	8	9	10	11	13	14	16	18	21	23	26	30	34	38	43	48	...	234								
0.210	0.90	0.24	24	8	9	10	11	12	14	16	18	20	22	25	29	32	37	41	47	...	225								
0.210	0.90	0.24	25	7	8	9	10	12	13	15	17	19	22	24	28	31	35	40	45	...	218								
0.210	0.90	0.24	26	7	8	9	10	11	13	15	16	19	21	24	27	30	34	38	43	...	210								
0.210	0.90	0.24	27	7	8	9	10	11	12	14	16	18	20	23	26	29	33	37	42	...	203								
0.210	0.90	0.24	28	7	7	8	9	11	12	14	15	17	19	22	25	28	32	36	40	...	195								
0.210	0.90	0.24	29	6	7	8	9	10	12	13	15	17	19	21	24	27	31	34	39	...	189								
0.210	-	0.24	30	6	7	8	9	10	11	13	14	16	18	20	23	26	29	33	38	...	182								

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)

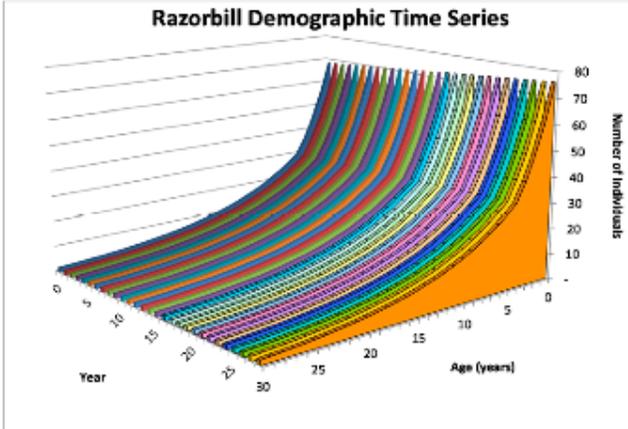
Immigrants as % of previous year breeding population
 19.7%



Growth Rate, given high (0.31) Productivity Rate and 0% Immigration Rate

			Total																											
Average Growth			Population																											
0.4%			Growth %																											
			Breeding																											
Average Growth			Population																											
0.4%			Growth %																											
			Year																											
I	S	P	Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28									
-	0.81	-	0	68	69	69	69	69	70	70	70	70	71	71	71	72	72	72	72	72	...	76								
-	0.81	-	1	56	56	56	56	56	57	57	57	57	57	58	58	58	58	58	58	59	...	62								
-	0.81	-	2	45	45	45	46	46	46	46	46	46	47	47	47	47	47	47	48	...	50									
-	0.81	-	3	37	37	37	37	37	37	37	38	38	38	38	38	38	38	38	39	...	41									
-	0.90	0.31	4	30	30	30	30	30	30	30	30	31	31	31	31	31	31	31	31	...	33									
-	0.90	0.31	5	27	27	27	27	27	27	27	27	27	28	28	28	28	28	28	28	...	29									
-	0.90	0.31	6	24	24	24	24	24	24	24	24	25	25	25	25	25	25	25	25	...	26									
-	0.90	0.31	7	21	21	22	22	22	22	22	22	22	22	22	22	22	22	23	23	...	24									
-	0.90	0.31	8	19	19	19	19	19	20	20	20	20	20	20	20	20	20	20	20	...	21									
-	0.90	0.31	9	17	17	17	17	17	18	18	18	18	18	18	18	18	18	18	18	...	19									
-	0.90	0.31	10	15	15	16	16	16	16	16	16	16	16	16	16	16	16	16	16	...	17									
-	0.90	0.31	11	14	14	14	14	14	14	14	14	14	14	14	14	14	15	15	15	...	15									
-	0.90	0.31	12	12	12	13	13	13	13	13	13	13	13	13	13	13	13	13	13	...	14									
-	0.90	0.31	13	11	11	11	11	11	11	11	11	11	11	12	12	12	12	12	12	...	12									
-	0.90	0.31	14	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	11	...	11									
-	0.90	0.31	15	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	9	...	10									
-	0.90	0.31	16	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	...	9									
-	0.90	0.31	17	7	7	7	7	7	7	7	7	7	7	7	7	7	8	8	8	...	8									
-	0.90	0.31	18	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	7	...	7									
-	0.90	0.31	19	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	...	6									
-	0.90	0.31	20	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	6									
-	0.90	0.31	21	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	...	5									
-	0.90	0.31	22	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	5									
-	0.90	0.31	23	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	...	4									
-	0.90	0.31	24	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	...	4									
-	0.90	0.31	25	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3									
-	0.90	0.31	26	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	...	3									
-	0.90	0.31	27	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	...	3									
-	0.90	0.31	28	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2									
-	0.90	0.31	29	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2									
-	-	0.31	30	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	...	2									

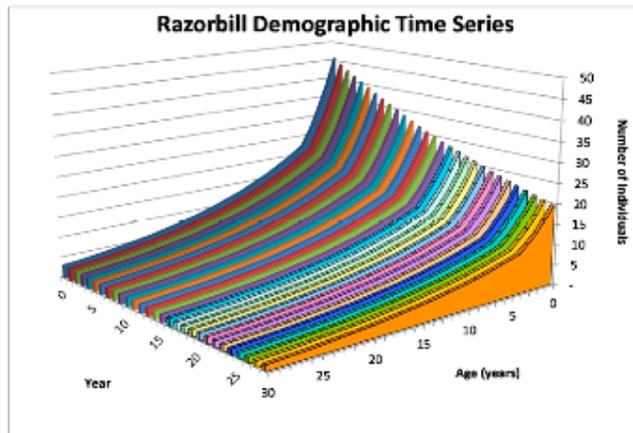
I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)



Growth Rate, given low (0.20) Productivity Rate and 0% Immigration Rate

			Total																												
Average Growth			Population	415	403	391	379	368	357	346	336	326	316	307	298	289	280	272	264	...	178	Breeding									
-3.0%			Growth %	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	...	-3.0%									
Average Growth			Population	272	264	256	248	241	234	227	220	214	207	201	195	189	184	178	173	...	117	Breeding									
-3.0%			Growth %	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	-3.0%	...	-3.0%									
			Year																												
			Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28										
-	0.81	-	0	46	44	43	42	40	39	38	37	36	35	34	33	32	31	30	29	29	...	20									
-	0.81	-	1	38	37	36	35	34	33	32	31	30	29	28	27	27	26	25	24	23	22	...	16								
-	0.81	-	2	32	31	30	29	29	28	27	26	25	25	24	23	22	22	21	20	20	...	14									
-	0.81	-	3	27	26	25	25	24	23	23	22	21	21	20	19	19	18	18	17	17	...	12									
-	0.90	0.20	4	23	22	21	21	20	19	19	18	18	17	17	16	16	15	15	14	14	...	10									
-	0.90	0.20	5	21	20	20	19	19	18	18	17	17	16	16	15	15	14	14	13	13	...	9									
-	0.90	0.20	6	20	19	18	18	17	17	16	16	15	15	14	14	14	13	13	12	12	...	8									
-	0.90	0.20	7	18	18	17	17	16	16	15	15	14	14	13	13	13	12	12	12	12	...	8									
-	0.90	0.20	8	17	16	16	15	15	14	14	14	13	13	12	12	11	11	11	11	11	...	7									
-	0.90	0.20	9	16	15	15	14	14	13	13	13	12	12	12	11	11	11	10	10	10	...	7									
-	0.90	0.20	10	14	14	14	13	13	12	12	12	11	11	11	10	10	10	9	9	9	...	6									
-	0.90	0.20	11	13	13	13	12	12	12	11	11	11	10	10	10	9	9	9	9	9	...	6									
-	0.90	0.20	12	12	12	12	11	11	11	10	10	10	9	9	9	9	8	8	8	8	...	5									
-	0.90	0.20	13	12	11	11	11	10	10	10	9	9	9	9	8	8	8	8	7	7	...	5									
-	0.90	0.20	14	11	10	10	10	9	9	9	9	8	8	8	8	7	7	7	7	7	...	5									
-	0.90	0.20	15	10	10	9	9	9	9	8	8	8	8	7	7	7	6	6	6	6	...	4									
-	0.90	0.20	16	9	9	9	8	8	8	8	7	7	7	7	6	6	6	6	6	6	...	4									
-	0.90	0.20	17	9	8	8	8	8	7	7	7	7	6	6	6	6	5	5	5	5	...	4									
-	0.90	0.20	18	8	8	7	7	7	7	6	6	6	6	6	5	5	5	5	5	5	...	3									
-	0.90	0.20	19	7	7	7	7	7	6	6	6	6	6	5	5	5	5	5	5	5	...	3									
-	0.90	0.20	20	7	7	6	6	6	6	6	5	5	5	5	5	5	4	4	4	4	...	3									
-	0.90	0.20	21	6	6	6	6	6	5	5	5	5	5	5	5	4	4	4	4	4	...	3									
-	0.90	0.20	22	6	6	6	5	5	5	5	5	5	4	4	4	4	4	4	4	4	...	3									
-	0.90	0.20	23	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	3	...	2									
-	0.90	0.20	24	5	5	5	5	4	4	4	4	4	4	4	4	4	3	3	3	3	...	2									
-	0.90	0.20	25	5	5	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	...	2									
-	0.90	0.20	26	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	...	2									
-	0.90	0.20	27	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	...	2									
-	0.90	0.20	28	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	2	2	...	2									
-	0.90	0.20	29	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	...	1									
-	-	0.20	30	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	...	1									

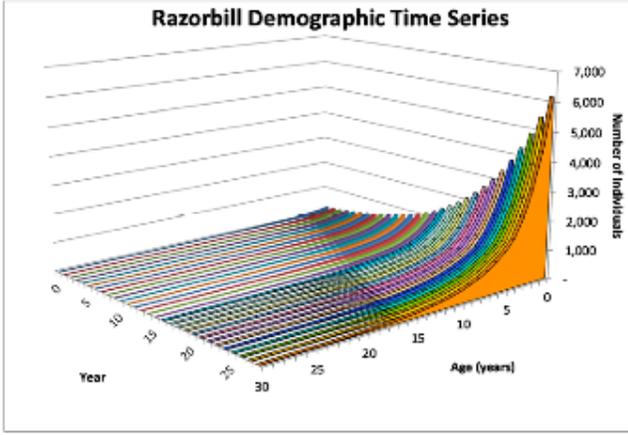
I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)



Productivity Rate, given 12.9% Growth Rate and 0% Immigration Rate

		Total																			
Average Growth		Population	806	910	1028	1160	1310	1479	1669	1885	2128	2402	2712	3062	3457	3903	4406	4974	...	24079	
12.9%		Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%
		Breeding																			
Average Growth		Population	272	307	347	391	442	499	563	636	718	810	915	1033	1166	1317	1486	1678	...	8123	
12.9%		Growth %	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	12.9%	...	12.9%
		Year																			
I	S	P	Age	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	...	28
-	0.81	-	0	204	230	260	294	332	374	423	477	539	608	687	775	875	988	1116	1259	...	6096
-	0.81	-	1	147	166	188	212	239	270	305	344	389	439	495	559	631	713	805	909	...	4398
-	0.81	-	2	106	120	135	153	173	195	220	248	280	317	357	403	455	514	581	655	...	3173
-	0.81	-	3	77	87	98	110	125	141	159	179	202	228	258	291	329	371	419	473	...	2289
-	0.90	1.04	4	55	62	70	80	90	101	114	129	146	165	186	210	237	268	302	341	...	1651
-	0.90	1.04	5	44	50	56	63	72	81	91	103	116	131	148	167	189	213	241	272	...	1316
-	0.90	1.04	6	35	40	45	51	57	64	73	82	93	105	118	133	151	170	192	217	...	1049
-	0.90	1.04	7	28	32	36	40	46	51	58	65	74	83	94	106	120	136	153	173	...	836
-	0.90	1.04	8	22	25	28	32	36	41	46	52	59	67	75	85	96	108	122	138	...	667
-	0.90	1.04	9	18	20	23	26	29	33	37	42	47	53	60	68	76	86	97	110	...	532
-	0.90	1.04	10	14	16	18	20	23	26	29	33	37	42	48	54	61	69	78	88	...	424
-	0.90	1.04	11	11	13	14	16	18	21	23	26	30	34	38	43	49	55	62	70	...	338
-	0.90	1.04	12	9	10	11	13	15	17	19	21	24	27	30	34	39	44	49	56	...	269
-	0.90	1.04	13	7	8	9	10	12	13	15	17	19	21	24	27	31	35	39	44	...	215
-	0.90	1.04	14	6	6	7	8	9	11	12	13	15	17	19	22	25	28	31	35	...	171
-	0.90	1.04	15	5	5	6	7	7	8	9	11	12	14	15	17	20	22	25	28	...	136
-	0.90	1.04	16	4	4	5	5	6	7	8	9	10	11	12	14	16	18	20	22	...	109
-	0.90	1.04	17	3	3	4	4	5	5	6	7	8	9	10	11	12	14	16	18	...	87
-	0.90	1.04	18	2	3	3	3	4	4	5	5	6	7	8	9	10	11	13	14	...	69
-	0.90	1.04	19	2	2	2	3	3	3	4	4	5	5	6	7	8	9	10	11	...	55
-	0.90	1.04	20	1	2	2	2	2	3	3	3	4	4	5	6	6	7	8	9	...	44
-	0.90	1.04	21	1	1	1	2	2	2	2	3	3	3	4	4	5	6	6	7	...	35
-	0.90	1.04	22	1	1	1	1	2	2	2	2	2	3	3	4	4	5	5	6	...	28
-	0.90	1.04	23	1	1	1	1	1	1	2	2	2	2	3	3	4	4	5	...	22	
-	0.90	1.04	24	1	1	1	1	1	1	1	2	2	2	2	3	3	3	4	...	18	
-	0.90	1.04	25	0	1	1	1	1	1	1	1	1	2	2	2	2	3	3	...	14	
-	0.90	1.04	26	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	...	11	
-	0.90	1.04	27	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	...	9	
-	0.90	1.04	28	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	...	7	
-	0.90	1.04	29	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	...	6	
-	-	1.04	30	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	...	5	

I = Annual Net Immigration Rate
 S = Annual Survival Rate
 P = Annual Productivity Rate (per individual)



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