THE EFFECT OF PHYSICAL AND BIOLOGICAL PARAMETERS ON THE
BREEDING SUCCESS OF RAZORBILLS (*ALCA TORDA* L. 1758) ON MACHIAS
SEAL ISLAND, NB IN 2000 AND 2001

by

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A Thesis Submitted in Partial Fulfilment of
the Requirements for the Degree of

Master of Science

in the Graduate Academic Unit of Biology

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THE UNIVERSITY OF NEW BRUNSWICK

Fredericton, New Brunswick, Canada

December, 2004

ABSTRACT

The influence of various physical and biological parameters on the breeding biology of Razorbills (*Alca torda*) on Machias Seal Island (MSI) was studied in 2000 and 2001. The major predators (gulls) on seabird eggs and chicks on MSI are controlled, providing an unusual opportunity to study breeding biology in the virtual absence of predation. The timing of egg-laying was right skewed in both years. A complete survey 10-14 June 2000 of all Razorbill breeding habitat on MSI was combined with radio telemetry to estimate the total number of inaccessible breeding sites that may not have been counted. A corrected breeding pair estimate for MSI is 592 ± 17 pairs.

Overall breeding success was 55% in 2000 and 59% in 2001. Most chicks that hatched also departed the island, so differences in breeding success were due chiefly to differences in hatching success. Adults breeding in burrows were more successful than adults in crevice and open nest sites. Nesting sites that included vegetation as part of substrate material were more successful than nest sites whose substrate did not include any vegetation. Nest site temperature was not related to breeding success. Large eggs, and those laid early in the season were more successful then smaller eggs laid later.

Egg size (measured by 'volume index', *i.e.* length times breadth squared) declined with increasing laying date in both seasons; chick growth (of mass but not wing-length), and breeding success followed the same trend. The relationship between seasonal decline in egg size and breeding success may be related to adult female characteristics, or another parameter that was not measured. Razorbill chicks on MSI appear to trade wing growth for mass growth, giving priority to mass.

PREFACE

This thesis is written in traditional format. The appendix has been published. My project was part of long-term seabird monitoring and research on a small, offshore island in the Bay of Fundy, New Brunswick, Canada. After receiving the initial question and project description from Dr. A.W. Diamond, the principle investigator at this location, I was part of the further development of the study, in which I collected and analyzed the data. My co-supervisor and committee member provided technical input at the development stage and at the technical/statistical writing stage. Both of my supervisors were extremely helpful with field techniques and each spent some time in the field helping to collect data.

program, I received special travel grants from the School of Graduate Studies to attend

conferences in Newfoundland, Massachusetts and Washington.

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1 INTRODUCTION

1.1 RAZORBILL NATURAL HISTORY

The Razorbill (*Alca torda*) Linnaeus (1758) is a member of the family Alcidae (auks), Order Charadriiformes (Strauch 1985). Razorbills are stocky, robust, long-lived seabirds widely distributed in North America throughout boreal and low Arctic waters (Chapdelaine *et al.* 2001), with the population centered in southern Labrador and lower North Shore of the Gulf of St. Lawrence, Québec. North American population levels represent a fraction of the world population (~9%) (Gaston and Jones 1998) and they have the lowest population of any seabird breeding in eastern North America (Nettleship and Evans 1985).

Two subspecies of Razorbill are recognized, based on size. The larger, *A. t. torda* Linnaeus (1758), breeds in eastern North America, western Greenland, Jan Mayen, the Baltic Sea area, southwest and northern Norway, and northwest Russia (Gaston and Jones 1998). Within the southern range of *A. t. torda* in North America, little variation in size exists (Gulf of Maine to southern Labrador, see Table 1-1). The smaller *A. t. islandica* C.L. Brehm (1831) breeds in Iceland, Faeroe Islands, British Isles, and in very small groups in Brittany, France, and at Helgoland, Germany (Cramp 1985). It is thought that only *A. t. torda* over winters off eastern North America (Brown 1985).

Razorbills exhibit many traits that are typical of animals that are *K*-selected (Krebs 1985). Razorbills are long-lived, have high inter-annual survival, and have low annual reproductive output (Harris and Wanless 1989). Razorbills have a ~90% annual adult survival rate in both the British Isles (Lloyd 1974, Mead 1974, Lloyd and Perrins 1977, Harris and Wanless 1989) and North America (Chapdelaine 1997). Razorbills

defer breeding until 4-5 years of age, and lay a single egg (Cramp 1985). The pressures of *K*-selection push organisms to use resources efficiently, and to compete for any available resources both within and between species (Krebs 1985).

Razorbills (*Alca torda*) breed in heterogeneous habitat that includes crevices, holes and burrows (Hudson 1982, Gaston and Jones 1998, Rowe and Jones 2000). Most Razorbill colonies have a diversity of habitat that offers both crevice (covered) and ledge (no cover) breeding site types (Hudson 1982, Rowe and Jones 2000). Ledge sites are often easier to count than crevice sites and thus colonies with many ledge breeders generate population estimates with smaller confidence intervals than colonies with more crevice breeders (Cairns 1979). Razorbills usually nest in scattered pairs or in mixed numbers with other alcids and in a variety of habitats where nests cannot be counted from a distance. In these situations, a count of eggs or chicks may be the only feasible census method (Nettleship 1976).

1.2 ESTIMATING POPULATIONS OF RAZORBILLS

Censusing has two main objectives - to obtain an estimate of the breeding population in an area or colony and to determine the status or trend of that particular population (Birkhead and Nettleship 1980). It is important to account for as many breeding birds as possible when surveying populations of colonial waterbirds. Conditions are not always favorable when a survey crew arrives at a colony and time spent in the colony needs to be minimized. Sometimes conditions are rugged, and accurate counting is difficult. Typically, some sites are missed. When habitat makes counting difficult, it is important to be able to estimate the number of sites missed due to inaccessibility.

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Standard survey methods use a correction factor, or k-ratio ($k = N_p/N_i$, where N_p is the number of sites counted in a measured area plot and N_i is the number of adults seen to associate with that same plot) (Nettleship 1976, Birkhead and Nettleship 1980) to estimate the number of breeding pairs at a colony when absolute counts of adults or sites are not possible (Chapdelaine *et al.* 2001). There are several ways to estimate the k-ratio: one method is to count adult razorbills roosting on the water (N_i) in front of their respective breeding areas while simultaneously counting sites in that breeding area (N_p); another is to count all the breeding sites (eggs or chicks (N_p) in a given plot and then later count the adults seen within that plot (N_i); (Chapdelaine *et al.* 2001). The k-ratio is then multiplied by counts of adults to determine the number of sites and give the breeding pair estimate for the colony. In some situations, counts of individuals may be taken to represent pairs (Chapdelaine *et al.* 2001).

Current survey techniques, such as aerial photography or k-ratios generate population estimates with broad confidence intervals (Chapdelaine *et al.* 2001). Applying any correction to counts of adults is confounded by variation in numbers of adult Razorbills counted (N_p) due to time of day, season, and weather conditions (Chapdelaine *et al.* 2001). K-ratios can be highly variable; for example, at the Saint-Marie Islands in 1999, k-ratios ranged from 0.23 to 2.35 (n=16) and at the Gannet Islands 1.10 to 9.25 (Chapdelaine *et al.* 2001). The range of an order of magnitude in k-ratio generates such large confidence intervals around estimates of breeding pairs that it is impossible to detect population trends.

MSI is a small Razorbill colony near the southern extreme of this species' range in North America (Chapdelaine *et al.* 2001). It has very little ledge breeding habitat but

many boulder piles provide crevices in which Razorbills breed (Charette *et al.* 2004). A fundamental goal of continuing seabird research on this colony is to assess trends in the breeding population of Razorbills, so it is necessary to develop techniques that can cope with crevice sites.

Razorbills on MSI have been counted twice daily on and around the island from an 18m light tower using the same counting protocols each year from 1995 to 2000 (Charette *et al.* 2004). These counts were continued from early May through to August. These 'tower' counts, however, may include prospecting birds, immatures, and non-breeding birds that are indistinguishable from breeding birds, introducing considerable error in estimates of the number of breeding Razorbills. No attempt has previously been made to census the Razorbill breeding population on MSI. Without any means of correcting counts, it would be difficult to ascertain which time of day and season to use as a correction for the number of breeding pairs on the island. To use counts of adults alone may lead to an over- or underestimation of the number of breeding birds.

1.3 RAZORBILL BREEDING BIOLOGY

Razorbill breeding biology was described in North America by Bédard (1969), but has recently been reviewed by Hipfner and Chapdelaine (2002). Razorbills have a life-history strategy that is typical of marine birds: socially monogamous, with strong mate and nest-site fidelity (Harris and Wanless 1989). Razorbills breed only in marine, coastal and continental shelf waters, where summer sea-surface temperatures range from 4-15°C (Hipfner and Chapdelaine 2002). Razorbills breed on rocky islands and steep, mainland cliffs where a variety of nesting habitat is used (Hudson 1982, Gaston and Jones 1998). Established Razorbill pairs generally re-use old nest sites (Harris and

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Wanless 1989). Intra-specific competition for nest sites may be relatively unimportant for Razorbills (Birkhead 1978).

In North America, breeding begins in mid-May at Machias Seal Island (Charette *et al.* 2004), late May-early June at Is. Ste.-Marie (Bédard 1969, Chapdelaine and Brousseau 1996) and mid-late June at Gannet Is. (Hipfner and Bryant 1999, Rowe and Jones 2000). The majority of older experienced females lay earlier and more synchronously than young, inexperienced females (Lloyd 1979).

The Razorbill life history includes an incomplete chick development in that the chick leaves the site/colony while not yet fully-grown (Cramp 1985, Gaston and Jones 1998). A Razorbill chick leaves the breeding site around fourteen days of age and follows the adult(s) to sea where the rest of its development takes place (Harris and Wanless 1989). The chick is usually one-third the size and mass of an adult and leaves the island fully feathered, but without tail and primary flight feathers (Hipfner and Bryant 1999). This 'intermediate' development strategy suggests a trade-off between safety in the nest, and higher growth attainable at sea (Ydenberg 1989).   This 'intermediate' fledging strategy among Alcids is unique to Razorbills and murres (*Uria* spp.) (Ydenberg 1989).

1.3.1 Breeding success

An adult Razorbill's annual breeding success cannot be measured, as the fate of chicks that leave the colony is unknown (Gaston and Jones 1998, Chapdelaine *et al.* 2001). Field investigations usually measure breeding success as the number of eggs that hatch and chicks that survive at the nest site for a certain length of time, usually 14

(Rowe and Jones 2000) or 15 (Hipfner and Bryant 1999) days. In this work, "survive to 14 days in a nest" constitutes breeding success, unless otherwise stated.

Unfortunately, most techniques used for recording annual breeding success at Razorbill colonies include nest visitation, and the effects of this disturbance can be negative (Lyngs 1994, Hipfner and Bryant 1999, Rowe and Jones 2000). Abandonment or the opportunistic predation of eggs or chicks may result from disturbance created by a survey crew, therefore the actual breeding success may be lower than in a natural setting.

Breeding success can be divided into three parts - hatching, nestling, and reproductive success. Hatching success has been recorded as low as 36%, but it usually ranges higher, up to 86% (Chapdelaine *et al.* 2001). Egg loss is reported as the major cause of low breeding success (Hipfner and Chapdelaine 2002). However, nestling success (or the number of chicks that hatch and survive to 14 days of age in the nest site) is higher, ranging from 85-95% (Keighley and Lockley 1948, Plumb 1965, Ingold 1974, Lloyd 1979, Barrett 1984, Harris and Wanless 1989, Lyngs 1994, Hipfner and Bryant 1999). Reproductive success (the proportion of eggs that hatch and survive to 14 days) usually ranges between 65-75% (Bédard 1969, Birkhead and Nettleship 1986, Chapdelaine and Brousseau 1996, Hipfner and Bryant 1999). A large portion of unsuccessful breeding is related to the non-hatching of eggs (Hipfner and Bryant 1999) and predation (Hudson 1982, Rowe and Jones 2000).

For a Razorbill chick, surviving to departure from the colony is affected by two main factors. First, characteristics of nest sites may be important (Hudson 1982); nest sites may vary in the amount of shelter provided for eggs and adults from weather, or from moisture in the nest site (Bédard 1969), predation (Hudson 1982), and likelihood of

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accidentally rolling away (Olsthoorn and Nelson 1990). Second, parental quality and effort are related to breeding success. For example, Razorbill breeding success increases with parental age/experience (Lloyd 1979).

1.3.2 The importance of the nest site to breeding success

Nest sites are resources that seabirds partition among species (Wallace *et al.* 1992). Nettleship and Birkhead (1985) describe the nest site as 'a small partition of space that is valuable to a pair of Razorbills for success'. This idea suggests that a study of nest site characteristics may demonstrate which nest characteristics may be important to predict nesting success. Although some Razorbills use nesting materials (Hipfner and Dussurreault 2001), most use little or none (Gaston and Jones 1998, VDG *pers. obs.*), so the term 'nest' is more accurately described as a breeding or nesting site. An important first step in determining the influence of nest site characteristics on breeding biology is to examine differences at the nest site level, before considering the breeding history of individual Razorbills.

Established Razorbill pairs generally re-use old nest sites (Harris and Wanless 1989). Adults moving away from previously used nest sites tend to be females (Lloyd 1976), which suggests that males own nest sites (Harris and Birkhead 1985).

Throughout their range, Razorbills lay their eggs on cliffs and offshore islands (Gaston and Jones 1998), where habitat available for breeding varies from ledges to boulder piles (Hipfner and Chapdelaine 2002). Within these heterogeneous habitats, Razorbill nest sites are prone to different levels of predation and environmental exposure, including temperature and moisture variability (Tschanz *et al.* 1989). However, there has

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been little investigation into the effects of physical nest site characteristics on breeding success.

Nest sites can be found in open spaces between boulders, in caves, deep vertical cracks and fissures on cliffs, on narrow ledges of cliffs with overhangs or even (rarely) on steep grassy slopes (Hudson 1982, Cramp 1985, Gaston and Jones 1998). Most nest sites have some amount of overhead cover, but open-topped sites are also used (Hudson 1982). Razorbills will sometimes use burrows excavated by other species such as Atlantic Puffins (*Fratercula arctica*) (Plumb 1965), or even a puffin nest (VDG, pers. obs.). In the White Sea area, some Razorbills nest under driftwood on beaches (Barrett *et al.* 2000). This variety of breeding habitat is problematic for surveys that use nest counts as an estimate of the number of breeding pairs, because some nests may not be visible (Cairns 1979).

Nest site substrate may include rock or mixed rock and earth, and can often be covered with small rocks or other debris (Tschanz *et al.* 1989, Hipfner and Dussurreault 2001). A nest site may be constructed by scraping together loose stones or other debris, or by carrying material (pebbles, stones, grass, shell or bones) into a small pile (Williams 1971). The availability of nesting materials varies between colonies as do the substrates, and if a nest structure can not be constructed, eggs will be laid on bare rock. Nest sites on bare granite may be the least used nest structure (Bédard 1969).

Physical nest site characteristics such as cover may affect a Razorbill pair's ability to raise a chick. Cover provides protection to shelter eggs and young from poor weather and predation. Nest site characteristics have been shown to alter the microclimate within a nest site (Tschanz *et al.* 1989).

Nest site characteristics may (Hudson 1982), or may not (Rowe and Jones 2000) affect breeding success, depending on the nesting site type and degree of predation experienced at the colony. During initiation of egg laying on the Gannet Islands, Razorbills did not use crevice or ledge nests in any particular order when each was in abundance (Rowe and Jones 2000), implying that each breeding site type offered similar advantages.

Birkhead (1978) noted that intraspecific competition for nest sites may be relatively unimportant for Razorbills. However, as Hudson (1982) reported, Razorbills bred more successfully in enclosed nest sites, and it could be expected that competition would exist at colonies where these nest types were limited and/or where there was predation.

Where suitable sites may be limiting at a colony, inter- and intraspecific competition for available nest sites could arise (Lack 1968). Therefore, the study of nest-site selection is important on both theoretical and applied conservation grounds (Ramos 1998). Conservation policies for any species may include policies to protect physical nesting habitat necessary for breeding success (Quintana 2001). A site's physical attributes may allow birds to minimize the adverse effects of predation, inclement weather, or conspecific aggression, all possible influences on breeding success (Ramos 1998).

1.3.3 The relationship of laying date and egg size with breeding success

In general, most birds invest heavily in breeding. In waterfowl, energy reserves have been shown to influence breeding performance (Mawhinny 1999). Female pre-breeding condition has been positively correlated with hatching success and recruitment,

and negatively correlated to brood abandonment. Female body condition has also been shown to influence laying date and incubation duration (Mawhinny 1999).

Razorbill egg size increases with age/experience over a female's first few breeding attempts but then remains relatively constant between years (Lloyd 1979). The levels of energy reserves available for breeding may affect the size (constituent yolk/protein components) of eggs and be the primary reason that egg size declines with laying date within a season (Lloyd 1979, Rowe and Jones 2000). Egg size varies little within a colony between years but can be different between colonies (Hipfner and Chapdelaine 2002).

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The extent to which breeding success is influenced by any one particular characteristic or trait may be difficult to separate. Female age and condition is related to egg size, laying date, and the ability to provision. The relative contribution of these parameters, and others, to breeding success varies between years and will depend on some parameters that cannot be measured in space or time, *i.e.* genetic makeup.

1.4 CURRENT STUDY

Since the 1980s Razorbills have been a species of interest to the Canadian Wildlife Service (Nettleship and Evans 1985). Due to occasional oil spills in the 1970s and reported widespread low breeding success, there was a decrease in North American numbers (to ca. 15,000 pairs) by the mid 1980s (Brown 1985). Another source of mortality was the Newfoundland murre hunt in which young razorbills were taken incidentally (Chardine *et al.* 1999). Elliott *et al.* (1991) and Chardine *et al.* (1999) examined the impact of this hunt on Razorbills.

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The effective conservation of Razorbills will include knowledge of which factors of their natural history affect breeding success (Rowe and Jones 2000). In order to accomplish this goal, the present breeding population on MSI must first be censused, and then the physical and biological parameters associated with breeding success of Razorbills on MSI must be investigated.

A Razorbill population estimate for MSI was the first priority for this study after recognizing the limited applicability for counting adult Razorbills only. A novel method for counting Razorbills on MSI was developed to account for those breeding in unseen sites. The availability and use of Razorbill nest sites on MSI was examined before any attempt to describe how nest site characteristics may be related to breeding success. The study addressed these questions: *How many Razorbills' nests were not counted in the survey? In comparison to other Razorbill population estimation methods, did this method and result seem reasonable?*

A second major component of this study was a description and analysis of physical characteristics of Razorbill nest sites. Breeding success was examined based on these characteristics. The following questions regarding breeding success of Razorbills at MSI in 2000 and 2001 were addressed: *Were there differences in nest site characteristics among breeding sites? Were there any differences in microclimate among breeding sites? Did breeding success vary among breeding sites? Was there any pattern of how adults of varying quality (as indicated by egg laying date) distributed themselves among breeding sites?*

The third major component of the thesis involves an analysis of Razorbill breeding biology on MSI. The biological parameters investigated include egg size, chick

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growth and breeding success. Differences in these variables among years, laying date and among breeding sites was studied. Questions that were addressed included: *Was laying date influenced by year? Did egg size differ among years, laying date or within breeding sites? Did chick growth differ with year, laying date, or between breeding sites? Was breeding success associated with year, size of egg, laying date?*

A brief concluding section summarizes the major findings of this study. A series of models and their classification successes are presented combining physical nest site and biological parameters that predicted breeding success. The summary presents some ideas about *What characteristics of Razorbill biology on MSI can be used to assess breeding success?*

2 METHODS

2.1 STUDY SITE: MACHIAS SEAL ISLAND

MSI (44°30'N, 67°06'W) lies about 20 km SW of Southwest Head on Grand Manan, New Brunswick, between the Bay of Fundy and the Gulf of Maine (Figure 1). Diamond and Devlin (2003) describe the island, its environs, and the context of the research. MSI is a Migratory Bird Sanctuary in which visitors to the island are regulated and breeding of large gulls is eliminated. MSI has permanent logistical support (shelter, regular boat traffic, communication, etc.) that enables researchers to remain on the island throughout the breeding season. This combination of factors makes MSI a valuable research and monitoring station for seabirds.

MSI is composed of granite bedrock with a large central patch of herbaceous vegetation surrounded in most areas by scattered boulders and large rocks (Diamond and

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Devlin 2003). Breeding is not uniform over the entire island but the three main habitats are available for breeding - the vegetated center (Veg), boulder shore (Boulder), or on the bare, exposed granite (Granite) nearest the ocean.

MSI hosts a multi-species seabird colony that includes Arctic Tern *Sterna paradisaea*, Common Tern *Sterna hirundo*, Razorbills, Atlantic Puffin, Leach's Storm-Petrel *Oceanodroma leucorhoa*, and Common Eider *Somateria mollissima*. Herring Gulls *Larus argentatus* and Great Black-backed Gulls, *L. marinus*, do not breed on MSI, but immature and non-breeding adults loaf on the outer periphery and on nearby Gull Rock. There are no known mammalian predators that visit MSI and humans directly prohibit all breeding attempts by large gulls. Therefore, this island presents a unique opportunity to study the breeding biology of Razorbills without ground or aerial predators, which have been shown to reduce breeding success elsewhere (Hudson 1982, Lyngs 1994, Rowe and Jones 2000).

Razorbills use nests that have complete, some or no overhead cover throughout the breeding habitat on MSI. MSI has little vertical relief (~11 m above sea level) so there are no cliff-nesting Razorbills as in most other Razorbill colonies (Rowe and Jones 2000, Chapdelaine *et al.* 2001).

Razorbills breed in loose aggregations in which nests are fairly widely separated, so disturbance when collecting data is limited to the birds being studied. Further, because of the virtual absence of predators, disturbance caused by researchers during this study did not lead to losses from predation.

2.2 DATA COLLECTION

2.2.1 Daily Razorbill counts

Razorbills were counted on land, and on water, in each of four zones (A-D) around the island (Figure 2) daily at 0700 and 0730 and at 1900 and 1930, between May and August 2000 except when fog reduced visibility. The number of Razorbills standing within each zone was a separate tally from the number of birds sitting on the water adjacent to each zone.

2.2.2 Census

A Razorbill breeding site survey was completed between peak lay and peak hatch (10-14 June, 2000) and Razorbills were counted from the 18 m tower from May to August. The survey was conducted throughout Razorbill breeding habitat using a 2m x 2m quadrat within the 30 m grid square system (Charette *et al.* 2004); therefore, each site was located within an area of roughly 4 m^2. The quadrat was moved systematically along grid lines so that no 2 m x 2 m grid squares were counted twice. Breeding sites were defined by the presence of an egg or chick. One observer (VDG) completed the whole survey. Data were recorded on field sheets with the following information for each site: habitat (Veg, Boulder, or Granite), location (South, Southwest, West), and amount of cover (Burrow, Crevice and Open). Disturbance was minimized by not handling site contents. Nothing was left in the site to indicate that it had been counted in the survey.

2.2.3 Telemetry

One hundred and eighteen (118) adult Razorbills were captured in 2000 with leg nooses or in a drop-box, and of these, 24 breeding Razorbills were used in this study. Adults were identified as breeders by the presence of a well-developed brood patch.

The birds were fitted with a 3.7-g radio transmitter custom-built by ATS (Advanced Telemetry Systems, Inc.). The design used had the battery, transmitter, and a coiled internal antenna packaged together within an epoxy coating (Figure 4). The transmitter was glued with epoxy to a celluloid band before being placed around the tarsus on the leg opposite to a Bird Banding Lab (BBL) band. The transmitter mass was below the recommended 5% body mass (Gaunt and Oring 1997).

Once the radio-tagged bird was considered to be still active in the colony (recorded daily for 2-4 days post attachment), its nesting site was found through a combination of observation from blinds and walking to the burrow with a hand-held Yagi antenna and receiver. Once the site was found, it was scored according to whether or not it had been counted in the survey. The same observer who recorded breeding sites in the survey scored the 'radio-tagged' birds breeding site. A correction factor was generated based on the number of sites that were not counted in the survey (N_p) out of the total number of radios released (N_t).

Radio transmitters were deployed on Razorbills in three of the four main breeding areas on the island, excluding the northeast. The small sample size of radio-marked birds, and the similar proportion of breeding site types among the three release areas, justified using a single correction factor for all areas except the northeast where no radios were deployed. The correction factor was one plus the ratio of sites used by radio-tagged

birds that were not scored on the survey (N_p) to the number of radios released on the island (N_i). The number of nest sites counted during the survey was multiplied by ($1 + N_p / N_i$) to obtain a corrected number of sites. The estimate of total sites (breeding pairs) on the island was derived from a single correction factor so a margin of error around this estimate could not be calculated. Instead, an interval of $N_p \pm 1$, and ± 2 radios, was calculated for the corrected number of sites to give an estimation of the effect of scoring one or more radio sites or not scoring one or more radio sites in the N_p value. The corrected number of sites is the Razorbill breeding pair estimate for MSI.

2.2.4 Cover at nest site

Razorbill nesting sites were classified into three types according to the amount of overhead cover: burrow (complete overhead cover), crevice (partial overhead cover), and open (no cover)(Figure 3). Other studies that have investigated nest sites have divided breeding sites into two categories, crevice (any overhead cover) and ledge (open) (Hudson 1982, Rowe and Jones 2000).

2.2.5 Habitat

Each site was categorised based on the dominant habitat within a 2 m radius of the nest site. Sites were classified as vegetation (central herbaceous vegetation of the island), granite (nest sites on bare, exposed rock), or boulder (among the tumbled beach boulder piles between the central vegetation and peripheral bare rock).

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2.2.6 Location

The location of each breeding site was categorised based on the geographic region of the island: south, southwest, or west (Figure 2). A fourth region in the northeast part of the island was not sampled.

2.2.7 Substrate

Razorbill breeding site substrate was categorised by the primary material underneath the egg. Six general types of substrate were recorded: vegetation, rocks, granite, granite and vegetation, granite and rocks, and rocks and vegetation. "Rocks" was defined as a substrate made of pieces of granite smaller than 8 cm in diameter. Substrate was considered independent of habitat in that all nesting site substrates were possible in each habitat category.

2.2.8 Number of walls

Walls were counted if they were taller than the width of an egg. The number of walls ranged from zero to four and for the purposes of the analyses sites were grouped into those having <2, 2 or >2 walls. This definition was based on the normal distribution of the number of walls (N = 520, mean = 2, SD = 0.86). (<2 → N = 118, 2 → N = 294, >2 → N = 108).

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2.2.9 Roof height

The variable "roof height" was a measure of the perpendicular distance from an egg to the overhead cover in a breeding site. A value was recorded for burrow and crevice nesting sites only, as open sites have no roof. The values of roof height were

categorised into High (> 25 cm, N = 281), Low (< 25 cm, N = 170), and None (N = 79). This definition was also based on the distribution of roof heights.

2.2.10 Temperature amplitude

In 2001, three HOBO ProSeries Temperature Loggers (Onset Computer Corp.) were deployed to record temperature in nesting sites throughout the breeding season in a 3-7 day period. Each logger had four separate probes so twelve sites could be logged at the same time. Temperature was logged for 13 periods throughout the incubation and early chick rearing period between 26 May and 18 July 2001. Each breeding site was used only once during the season. The difference between daily maximum and minimum temperatures (amplitude) for each nest site was calculated over the period and recorded as the mean nest site amplitude (AMP). Mean temperature amplitude for each site was standardized to remove the effect of a natural seasonal increase in ambient temperature, by subtracting the mean period amplitude. AMP was negative when a site's amplitude was below the mean for that period and positive when a site's amplitude was above the mean for that period. For an example of how AMP was calculated, see Appendix 1.

In the case of any instrument malfunction (e.g., dead battery) or when a Razorbill interacted with the temperature probe in the nest site, that site was removed from the analyses.

2.2.11 Laying date

In 2000, but more so in 2001, systematic, alternate-day searches through the colony for new Razorbill eggs were conducted; new-found eggs were assumed to have been laid on the day previous to the search. Only known laying dates were used in

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Comment [DG11]: DH-Could you state this more clearly? I think it makes sense but it's hard to follow. Same with next paragraph. Also how did you come up with the measurements? Are there references for the methods?

calculations and tests requiring laying date. Data from re-laying attempts were not used in any analysis; all egg characteristics are from first-laid eggs.

To remove the effect of year on laying date, a relative laying date was calculated by subtracting the observed laying date from the peak (modal) laying date. For each year, the values for relative laying date are negative if an egg was laid before peak laying date of that year and positive if it was laid after the peak. Relative laying date was used in all analyses as a continuous variable except where laying date was used in an ANOVA test. For all ANOVA style tests, laying date was converted to three categories. Eggs laid more than one day before the peak were called Early, eggs laid within a day of the peak were called Middle and eggs laid more than a day from the peak were called Late (following Rowe and Jones 2000).

2.2.12 Egg size

Razorbill egg length and maximum width (± 0.1 mm, measured with dial calipers) were measured. In Razorbills, fresh egg mass has a strong linear relationship with egg volume index (length x width^2) (Nettleship and Birkhead 1984) so egg volume index (cm^3) was used as a measure of egg size. Eggs in crevices or burrows were removed, and then replaced, with rubber-coated tongs when they could not be reached by hand. In both years, eggs were labeled twice (on either side of the wide end) with a black permanent ink marker and given a nest site code to 1) aid in identifying nesting sites, and 2) reveal re-laying attempts (not used in any analysis).

2.2.13 Chick growth

Razorbill breeding sites were scheduled for visit on the predicted hatching date. If the egg was still present it was quickly checked for incubation status (warmth in hand),

evidence of pipping, and a new hatching visit scheduled. A newly hatched chick was not

handled if it was wet. Chicks were subsequently measured every 3-4 days, so the whole

colony was not visited on any one day. Mass ($\pm$ 1 g) was measured with a 200 g

electronic balance, and wing length ($\pm$ 1 mm, the maximum flattened chord excluding the

downy tips - Hipfner and Bryant 1999), was measured with a 100 mm stopped ruler. All

chicks were banded, usually on the second or third visit. Mass gain or wing gain was

defined as the total increase in chick mass or wing length between 2-14 days of age.

Growth parameters were calculated according to Hipfner (2000).

2.2.14 Breeding success

Breeding was recorded as successful if a chick was found in a site 14 days post

hatch.   Success was investigated on two levels, hatching (HS) and reproductive (RS)

success. Hatching success is the ratio of eggs that hatch to the number of eggs laid.

Reproductive success is the proportion of chicks that reached 14 days out of the number

of eggs laid.

The probable fates of 151 eggs that did not hatch in 2000 and 2001 combined

were recorded according to the evidence present at the breeding site. "Died While

Hatching" was recorded for eggs that failed to hatch when the chick did not emerge after

the egg was starred or pipped. Eggs found submerged in breeding site and subsequently

failed to hatch were considered "Drowned". Eggs that developed holes or cracks between

visits to the site and subsequently did not hatch were called "Hole/Cracked".

Significantly undersized eggs were called "Mini". Any eggs that went missing from the

nest site before scheduled hatch date and there was no sign of hatching, or predation,

were called "Predated/Missing". If an egg rolled sufficiently under an adjacent rock, or

out of a nest site so that it could not be incubated, the egg was considered "Roll From Nest". The term "Abandonment" was used for eggs that were not incubated (egg never was warm to the hand). Eggs that did not hatch even though they continued to be incubated (warm to the hand) well past the scheduled hatch date were called "Present".

2.3 DATA ANALYSIS

Data were analyzed using SPSS v. 10 (SPSS 1999). Parametric statistics were used as residuals fit the assumptions of normality and homogeneity of variances. A significance level of $\alpha = 0.05$ was used for all statistical tests except Bonferroni post-hoc tests which use an adjusted alpha (alpha / # of categories). All reported probability values are two-tailed.

Razorbill tower count data were graphed to show the mean morning and evening counts. Chi-squared analysis was used to compare the number of nest sites in the three radio-transmitter deployment locations to results from the survey.

Chi-Square analyses were used to test for differences in the number of breeding sites within cover, by habitat, location, substrate, roof height and number of walls. General Linear Models (ANOVAs) were used to test for the effect of cover, habitat, location, substrate, roof height and number of walls on temperature in the nesting site. Bonferroni post-hoc tests, significant at the correctly adjusted alpha value, were used to make pair-wise, multiple comparisons following significant ANOVAs.

Logistic regressions were used to compare the number of successful to unsuccessful nest sites among cover, habitat, location, substrate, roof height and number of walls. The reported P values are based on the Wald Statistic which examines the ratios

of the fitted coefficients over their standard errors and evaluates these as normal deviates (Sokal and Rohlf 1995).

Egg size, mass gain, wing gain, and breeding success were tested for effects of year, laying date and cover in the nesting site. All parameters were gathered from the same chicks and thus the response variables are non-independent. Therefore, to look for responses within these Razorbill chicks, a Multivariate Analysis of Variance (MANOVA) was used to test for differences among year, laying date and cover at the nest site and to identify which variables contribute most to the multivariate response, considering correlations among variables. MANOVA assumes that covariance between dependent variables must be the same in all groups. The MANOVA is followed by a canonical analysis, producing standardized canonical variates for each response variable. The canonical analysis defines model explanatory strength while standardized variates give the direction of correlation between each response variable and the contribution to the overall multivariate result. Pillai's Trace, a conservative multivariate test statistic, is recorded for the multivariate test. Assumptions about homogeneity of covariance in the response variables were checked with Box's Test for Equality of Covariances and Levene's Test of Equality of Variance (SPSS 1999). Box's Test tests the assumption of homogeneity of covariance matrices. Levene's Test is used to evaluate the variance of k samples across groups. An ANOVA is presented for a response variable with a significant multivariate result. I used Bonferroni-corrected post-hoc pair-wise comparisons following a significant ANOVA result.

Mass and wing gain data were evaluated for their correlation with egg size. A locally weighted regression fit mass gain data better than a linear relationship. Mass gain

data were corrected by the mean residual (0.276) between the fitted and locally weighted

regressions (Sokal and Rohlf 1996). This correction removed the effect of egg size on

mass gain. Corrected mass gain data were used in all models. Wing gain was not

correlated to egg size so no correction was made to these data. The effect of egg size on

mass gain and wing gain was evaluated with linear regressions.

Logistic regressions were used to compare proportions of breeding success among

year, laying date, and egg size. The reported P values are based on the Wald Statistic

which examines the ratios of the fitted coefficients over their standard errors and

evaluates these as normal deviates (Sokal and Rohlf 1995).

3 RESULTS

**3.1 THE RELATIONSHIP BETWEEN VISUAL COUNTS OF RAZORBILLS
AND THE BREEDING PAIR ESTIMATE**

Razorbills were counted in 65 of the possible 98 count periods in 2000. Figure 4

shows the mean number (each point N = 2) of Razorbills recorded on tower counts

around MSI throughout the breeding season (12 May to 18 Aug 2000). Razorbill

numbers remained stable from mid-May to mid-July, after which they declined steeply.

Table 1 shows a variety of tower count summaries for the 2000 breeding season,

illustrating the complexity in using these data as an estimate of the number of breeding

pairs on MSI.

A complete census of Razorbill habitat was completed between 10-14 June 2000.

Four hundred nineteen nest sites that had either an egg or a chick were counted (Table 2).

Fifty-one other sites were added to the total from the northwestern and northeastern part

of the island where radio deployment was not feasible. These sites were added to the total from a direct count of 25 sites from the extreme northwest part of the island, and a visual estimate of 20 in the northeast where observations were made from blinds to estimate the number of pairs there. Six additional sites were subsequently found in a small rock outcrop south of the old tramway (see Figure 2).

3.2 THE EFFECT OF USING TELEMETRY ON THE BREEDING PAIR ESTIMATE

All 24 transmitters functioned properly after attachment, and no abandonment by radio tagged birds was recorded. All 24 radio-tagged birds were later found to occupy burrow sites and did not have a radio-tagged mate. Seven of the 24 radios were found in burrows not counted in the breeding site survey. Two burrows took 10 days to find; the others averaged 7 days (range 6-9 days).

The proportions of breeding site types in the three deployment areas did not differ statistically from the number in the island-wide survey ($\chi^2_{0.05,4}$ = 2.497, P = 0.232). Therefore, the correction factor of 7/24 = 0.292 was applied to all areas where radio transmitters were deployed. Table 3 shows the sensitivity of the population estimate to one or more radios being scored as 'uncounted'. The estimate ranges from 20.8 – 37.5% more sites than counted. Thus, the total estimate of Razorbill breeding pairs for the island is 592 ± 17 (Table 3).

3.3 BREEDING SITE CHARACTERISTICS

Razorbill breeding sites were classified based on their structure (Hudson 1982). The amount of overhead cover at a breeding site was used to classify every nesting site

Comment [DG12]: What does this mean? Did you go in just stepwise analysis> If you decided what was "primary" then you have to support this. Why do you have a "primary" variable?

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for analyses during both years of the study (N = 520). Burrow sites were most common (59%, n = 307) and had complete overhead cover, followed by crevice (26%, n = 134) with partial overhead cover and open nesting sites (15%, n = 79). The number of nests in each cover was not different between years so site characteristic data from 2000 and 2001 were combined. The number of nest sites in each cover category varies due to missing characteristic data for some sites.

The effect on the number of burrow, crevice and open nesting sites within location, habitat, substrate, roof height and number of walls is shown in Table 4. Location, habitat, and substrate did not affect the number of nests in each cover type but roof height and the number of walls varied within cover (Table 5). The percentages of burrow nests with high roofs (178/303 = 59%) and burrow nests with low roofs (125/303 = 41%) was different than the percentages of crevice nests with high roofs (100/132 = 76%) and crevice nests with low roofs (32/132 = 24%). The number of walls in burrow, crevice and open nests was different. Burrow nests had 32% (N = 98), 53% (N = 163) and 15% (N = 45) respectively. Crevice nests had 10% (N = 13), 63% (N = 85) and 27% (N = 36) respectively while open nests had 9% (N = 7), 59% (N = 47), and 32% (N = 25).

There was no evidence of a pattern of nest site usage by birds of varying quality (as indicated by laying date), based on cover, habitat, substrate, roof or walls, however there was an effect of location, however, Bonferroni multiple pair-wise comparisons were not significant at P = 0.017.

3.4 THE EFFECT OF PHYSICAL NEST SITE CHARACTERISTICS ON TEMPERATURE IN THE NEST SITE

Figure 6 and Table 6 shows the mean period amplitude calculated for 13 time periods between 26 May – 18 July 2001 on MSI. The number of nest sites sampled in each period varies due to battery failure in some data loggers, and the occasional removal of temperature probes by breeding Razorbills.

Overall, the mean period amplitude declined slightly as the season progressed (adj $r^2 = 0.044$, F = 6.08, 1, 110, P = 0.015), and the temperature increased throughout the season (minimum nest site temperature - adj $r^2 = 0.529$, F = 145.88, 1, 128, P < 0.0001). AMP was not related to this seasonal temperature increase (adj $r^2 = -0.009$, F = 0.000, 1, 110, P = 1.0).

Table 7 is a summary of the effects of physical nest site characteristics on AMP. Habitat was removed from the analysis due to its highly unequal sample sizes. A difference in AMP was detected among roof height only, but the differences are small (Table 8). The mean amplitude of a nesting site without a roof was 3.4 ^{o}C greater than a nest site with a full roof (significant pair-wise comparisons that resulted from Bonferroni post-hoc tests significant at P = 0.017; Table 7, Figure 7).

3.5 THE EFFECT OF PHYSICAL CHARACTERISTICS ON BREEDING SUCCESS

> **Comment [DG13]:** DH_ Is this data from Table 4??

Breeding success (or the number of eggs laid that produced chicks and survived to 14 days of age) differed only among cover and substrate (Table 9). Tables 10 and 11 are the breakdown of eggs laid, hatching success, nestling and breeding success for Razorbills in 2000 (N = 194) and 2001 (N = 326).

The pattern of Razorbill breeding success within cover is the same in 2000 and 2001 (Figure 8). When both years were combined the number of successful burrow nests is 66%, 20% greater than crevice nests and 22% greater than open nest sites (Figure 9).

Figure 10 shows the proportion of nest sites within substrate where a chick was successfully raised. The proportion of successful nest sites ranged from 47 to 74%. Nest sites that included any vegetation underneath the egg, as part of substrate, had higher proportions of chicks surviving to 14 days than nest sites without vegetation (Figure 10). Similar letters denote groups of substrate where the SE overlaps.

3.6 BREEDING BIOLOGY CHARACTERISTICS

The peak laying date for sites with known laying dates in 2000 and 2001 was 17 May (N = 39) and 22 May (N = 244), respectively. Peak hatch dates for 2000 were 21 June (N = 29) and 24 June (N = 173) for 2001 (Table 12). The mean ± 1 SE incubation period is 35.7 ± 0.5 days (N = 29) in 2000 and 36.1 ± 0.3 days (N = 173) in 2001 and are not different at $\alpha = 0.05$ ($F = 0.21$, $df_1 = 1$, $df_2 = 200$, $P = 0.65$). Peak laying and hatching dates for 2000 are the earliest recorded for MSI while the same dates for 2001 are similar to the average at MSI since 1995 (Table 12).

Although the sample size of known laying dates was smaller in 2000, in both years laying showed a right skewed distribution (Figure 11) with over 80% of all sites in 2000 initiated within 8 to 10 days from the peak and within 4 to 6 days from the peak in 2001. One new breeding attempt was recorded more than 20 days after peak laying in 2000 and 8 were recorded ≥ 20 days after peak laying in 2001.

Mean relative laying date did not differ among years ($F = 1.54$, $df_1 = 1$, $df_2 = 267$, $P = 0.22$), nor did I detect a difference in laying date by cover at the nest site ($F = 1.223$,

$df_1 = 1$, $df_2 = 267$, $P = 0.27$). There was no significant interaction between year of study and cover at nest site.

Fresh egg mass and egg volume were highly correlated (adj $r^2 = 0.84$, $F = 1517.3$, $df_1 = 1$, $df_2 = 285$, $P < 0.0001$) so egg volume index (length*breadth^2) (cm^3) was used as egg size (Nettleship and Birkhead 1984). Razorbill eggs from MSI fell within the size range of Razorbill eggs from other colonies in North America (Table 13). There was an obvious decrease in egg size through the season (adj $r^2 = 0.124$, $F = 34.68$, $df_1 = 1$, $df_2 = 238$, $P < 0.0001$) (Figure 12).

Sixty chicks in 2000 and 136 chicks in 2001 were measured every 3-4 days throughout the nestling period. In 2000 the mean mass gain $\pm$ SE (corrected for egg size) was 26.4 ± 0.9 (N = 60) and mean wing gain was 33.6 ± 1.3 mm (N = 59) while in 2001 mean mass gain was 26.2 ± 0.6 g and mean wing gain was 35.2 ± 0.6 mm (N = 135).

3.7 MULTIVARIATE RESULTS FOR SIZE, MASS GAIN, AND WING GAIN

Results of the MANOVA are found in Table 14. The observed covariance matrices across the dependent variables are similar (Box's Test of Equality of Covariance Matrices, $F = 0.522$, $df_1 = 66$, $df_2 = 325$, $P = 0.999$). The error variance of each dependent variable is similar across groups (Levene's Test of Equality of Variance). This means that homogeneity of variance assumptions about the MANOVA tests are not violated and parametric tests can proceed.

The results of the MANOVA show that there is a significant overall multivariate effect (Pillai's Trace = 0.312, $df_1 = 9$, $df_{err} = 405$, $P = <0.0001$), however the significant response is seen as an effect only of laying date and not year or cover (Table 14). The MANOVA model including year, laying date and cover explained 29% of the variation in

Comment [TD14]: New pint, new paragraph. Rewrite to condense; don't repeat data in Tables/Figures, summarise them here. Comparison between hatched and unhatched eggs is potentially confounded by differences in lay-date, which must be controlled for first.

Comment [TD15]: Why not?

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the multivariate response. The standardized coefficients for the dependent loading generated in the canonical analysis were: egg size -0.544, mass gain -0.705, and wing gain 0.384. These results indicate that egg size and mass gain are positively correlated and they will respond similarly to an effector, such as laying date. The effect of laying date is not significant for wing gain (Table 14), however, any effect on wing gain would have been opposite from the response of egg size and mass gain. Mass gain and egg size contribute the most to the multivariate result while wing gain contributes least.

Mass gain declined with declining egg size ($F = 4.17$, 1, 138, $P = 0.043$) but wing gain was not affected by egg size ($F = 0.55$, 1, 137, $P = 0.459$).

3.8 THE EFFECT OF LAYING DATE ON SIZE AND MASS GAIN

Eggs laid late were significantly smaller than those laid early or mid-season ($F = 11.62$, $df_1 = 2$, $df_2 = 138$, $P < 0.0001$) (significant Bonferroni post-hoc tests with alpha = 0.017). Early eggs had a mean size $\pm$ SE of 186.3 ± 2.7 cm^3 (N = 30), middle eggs 183.3 ± 2.3 cm^3 (N = 32), and late eggs 174.6 ± 1.4 cm^3 (N = 79). Late eggs were 12.3 ± 2.8 cm^3 smaller than early eggs and 6.1 ± 1.1 cm^3 smaller than middle eggs.

There was an effect of laying date on chick mass gain ($F = 20.72$ $df_1 = 2$, $df_2 = 192$, $P < 0.0001$). Late chicks gained less mass than those from early or mid-season eggs (significant Bonferroni post-hoc tests with adjusted alpha). Razorbill chicks from early and middle eggs increased in mass similarly, 29.2 ± 0.8 g (N = 44) and 29.7 ± 0.7 g (N = 44) respectively. Chicks that hatched from the latest eggs gained the least amount of mass, 23.7 ± 0.7 g (N = 107) during the 2-14 day nestling period. Chicks from late eggs gained 5.5 ± 1.1 g less than early eggs and 6.1 ± 1.1 g fewer than chicks from mid-season eggs during the same nestling growth stage.

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3.9 THE EFFECT OF BIOLOGICAL PARAMETERS ON BREEDING SUCCESS

Breeding success was measured as a binomial variable of positive or negative survival to 14 days old in a nest site. Logistic regressions testing for the effect of biological parameters on breeding success are shown in Table 15. Laying date and egg size had an effect on breeding success. The effect of laying date and egg size on breeding success is shown in Table 16 as a comparison between the laying date and egg size of eggs that hatched to those that did not (HS) and comparing the laying date and size of eggs that produced chicks that survived to those that did not (RS). The probable fate of eggs that did not hatch is displayed in Table 17. It is difficult to say that 'abandoned' and 'present' are different categories, but an effort was made to separate these egg fates. 'Abandoned' eggs were cold before the end of their calculated incubation period, whereas 'present' eggs continued to be incubated long after the expected hatch date.

3.10 THE EFFECT OF YEAR ON BREEDING SUCCESS

No effect of year on breeding success was detected (Table 15). Year did not interact with laying date (Figure 11) or egg size. Therefore, all subsequent analyses of breeding success are for both years combined.

3.11 THE EFFECT OF LAYING DATE ON BREEDING SUCCESS

There was an effect of laying date on breeding success (Table 15). Eggs laid early hatched and fledged more chicks (Table 16). The mean laying date of an egg that hatched was 2.0 ± 0.4 days (N = 198) compared to 5.8 ± 0.8 days (N = 85) for eggs that did not hatch. The mean laying date of a chick that departed from the island was 1.4 ± 0.4 days (N = 162) compared to 5.6 ± 0.7 (N = 121) for eggs that did not hatch, or chicks

that did not survive to depart the island. Eggs that did not hatch were laid 3.8 days later than eggs that did. Razorbill chicks that left the island were hatched from eggs laid 4.2 days earlier.

3.12 THE EFFECT OF EGG SIZE ON BREEDING SUCCESS

An effect of Razorbill egg size on breeding success was detected (Table 15). Differences in size were evident in hatching and reproductive success (Table 16). Larger eggs had higher hatching and reproductive success. The mean egg size of an egg that hatched was 179.3 ± 1.1 cm^3 (N = 165) compared to 171.6 ± 1.7 cm^3 (N = 75) for an egg that did not hatch. The mean egg size of a chick that departed from the island was 179.7 ± 1.3 cm^3 (N = 135) compared to 173.2 ± 1.4 cm^3 (N = 105) for eggs that did not hatch, or hatched and chicks did not survive to depart the island. Eggs that did not hatch were 7.7 cm^3 smaller than eggs that did. Razorbill chicks that left the island were hatched from eggs that were 6.5 cm^3 larger. There was no interaction between egg size and either laying date or cover.

4 DISCUSSION

4.1 BREEDING PAIR CENSUS

Current survey techniques that generate 'K-ratios' or correction factors to estimate the number of breeding pairs usually have broad confidence intervals (Chapdelaine *et al.* 2001). A small range in correction factor applied over time of day or season (Nettleship 1976) may generate such large confidence intervals that it is impossible to detect population trends. A fundamental goal of seabird research is to assess trends in populations, so it is necessary to develop a technique that can cope with

nesting sites that are not visible (Nettleship 1976, Cairns 1979). This study showed that there is a reliable method to count breeding sites that are not apparent in visual surveys.

4.1.1 The relationship between visual counts and the breeding pair estimate

Tower counts of adult Razorbills on MSI during 2000 likely included prospecting birds, immature or non-breeding birds that were indistinguishable from breeding birds. If counts of Razorbills around the island (Table 2-1) were the only means of obtaining an estimate of breeding pairs, there would be considerable bias in the estimate of breeding Razorbills on MSI. In some cases, counts of adults are taken as a 1:1 correction (Nettleship 1976, Chapdelaine *et al.* 2001). Using this correction, the Razorbill breeding population would range from no pairs to 1282 pairs (Table 2-1). Neither is likely to be a good estimate of the breeding population. The estimate becomes 176 to 1282 pairs when zero counts are eliminated. This estimate is more reasonable, but still too large to estimate trends in successive years. As Table 2-1 demonstrates, count data alone leave the researcher with uncertainty about the appropriate estimate.

4.1.2 The effect of using telemetry on the breeding pair estimate

Direct counts of eggs/chicks are preferable when censusing alcids (Nettleship 1976). Direct counts of eggs/chicks remove the variability introduced from counting non-breeding adults. However, in colonies such as MSI where Razorbills nest under boulders, direct counts of eggs/chicks are not possible and the use of a correction factor is necessary (Nettleship 1976).

The habitat being used by Razorbills for breeding was similar in structure to those encountered in the survey, and the probability of counting a breeding site in the survey

would be similar throughout the whole island. This was an important test to show that the areas into which the radio-transmitters were released did not differ in the proportion of breeding site types. If the proportion of breeding site types were different, the results may have been biased by that difference. For example, if one area had no burrow habitat, then all the radio-tagged birds would have been using nesting sites other than burrows, *i.e.* sites that were more readily counted in the survey.

So few radio-tagged birds (7) were in undetected sites that the differences in the number of undetected sites in different parts of the island could not be assumed to represent real differences in detectability of sites, therefore, the same correction factor was applied to the whole colony.

A correction of nearly 30% (Table 3) suggests that some Razorbill sites were not easily found anywhere on the island. This method proved to be extremely useful in obtaining the first estimate of the number of Razorbill breeding pairs on MSI.

This correction factor substantially reduces variability in breeding pair estimates. The 'margin of error' on the correction factor was low in comparison to some Razorbill surveys where k-ratios have ranged from 0.23 to 2.35 (Chapdelaine *et al.* 2001). As Table 3 shows, the error that would result if one more radio marked bird was in a site that could or could not be counted was 3 %. The change in the corrected number of nests was 5.8 % when two radio marked Razorbills could or could not have been counted.

The potential existed that the capture and handling of Razorbills would affect natural behaviour. Some concerns included colony abandonment, lack of pair-bond behaviour, lack of incubation or colony attendance, and chick provisioning. However, all radio-marked Razorbills were present on the colony shortly after being captured, and

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remained in the colony throughout the tracking period. Radio-marked Razorbills were seen participating in social and courtship behaviors within the colony and during the nestling stage they were observed carrying fish to chicks (VDG). It was assumed then, that the attachment of the radio transmitter did not have an adverse affect on Razorbill behaviour. In a study of foraging location and behaviour, Wanless *et al.* (1988) showed that Razorbills did not change their regular schedule once a radio transmitter was attached and their foraging trip duration did not change. Therefore, the correction factor is thought to be without biological bias.

4.1.3 The application of this correction to other Razorbill colonies

North American Razorbill colonies in other locations may not be similar in overall habitat structure to MSI, however this method of correcting counts of breeding pairs could be useful for the parts of those colonies that do have inaccessible sites. The Gannet Islands off the coast of Labrador and the islands of the Gulf of St. Lawrence have greater diversity of breeding habitat than MSI (Bédard 1969, Nettleship and Birkhead 1985, Gaston and Jones 1998) but these breeding locations do have deep crevices and cracks where observation of sites is impossible. Also, where breeding habitat is heterogeneous, this method may be useful for correcting survey counts of species with similar breeding habits, *eg*. Black Guillemot (*Cepphus grylle*).

4.2 THE EFFECTS OF PHYSICAL NEST SITE CHARACTERISTICS ON BREEDING SUCCESS

For Razorbills, the breeding site is an important component of breeding success (Nettleship and Birkhead 1985). While some studies have linked breeding success to the

probability of predation at nest sites with varying characteristics (Gilchrist and Gaston 1997, Rowe and Jones 2000, Massaro *et al.* 2001), this study could analyze breeding success in relation to nest site characteristics without the impact of predation.

4.2.1 Breeding site characteristics

The analysis of nest site characteristics did not reveal any difference in the number of burrow, crevice and open nest sites partitioned among habitats, locations, and substrates on MSI in 2000 and 2001. This suggests that each breeding site type had similar proportions of nests in the different locations, habitats, and on the different substrates. This knowledge may be important in the future for predicting Razorbill breeding success using the same physical nest site characters. Any portion of the colony that includes a representative sample of all nest cover types would be useful for estimating breeding success on MSI. This would eliminate the need to collect Razorbill breeding information from the whole island.

The differences in the number of burrow, crevice and open nest sites among roof and number of walls were probably not biologically important. In this study, 76 % of crevice nest sites had a high roof ($>$ 25 cm) compared to only 59 % of burrow nests. This structural difference did not affect the nest site temperature or breeding success. The mechanism by which burrow nests are more successful is not clear. These results may be spurious and not important indicators of good nest sites on MSI.

Rowe and Jones (2000) included roof height and the number of walls within the main structural definition of each Razorbill nest site. These characteristics may be more important on islands where there is predation. Open sites have no roof, and the majority

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of sites used in the study had two walls. Eggs or chicks in open sites, and sites with fewer walls, may be more visible to potential predators.

Burrow sites are used most commonly throughout the island (Table 3-1), but based on timing of breeding, there is no evidence of a preference for burrows over nests with less cover, even though this study and others have reported higher breeding success in burrows (Hudson 1982). This finding coincides with Rowe and Jones (2000) and suggests that all sites on MSI during 2000 and 2001 either a) provided sufficient resources and were not the subject of competition, and/or b) the quality of adults (as indicated by laying date) was similar (Rowe and Jones 2000).

Birkhead (1978) pointed out that intraspecific competition for nest sites may be unimportant in Razorbills, and there were many suitable but un-occupied burrow sites on MSI (VDG). It may be expected that if the population of Razorbills continues to grow on MSI, intraspecific competition for nest sites may arise. Further, if predation were to become a factor on MSI, then competition for burrow nests may become prevalent (Hudson 1982).

4.2.2 The effect of nest site characteristics on nest site temperature

As expected, ambient temperature increased throughout the 2001 season on MSI. Relative temperature amplitude (AMP), calculated from the difference of mean period amplitude from an individual site's amplitude during the same period, eliminated this effect of season. Using the AMP calculation, each period of temperature logging was independent of the seasonal trend in temperature.

Habitat and roof had an effect on AMP in Razorbill breeding sites on MSI. Open sites (those with no roof) had no protective barrier from either heating or cooling. It

follows that open nests would have the highest temperature amplitudes throughout the season.

The direct effect of ambient nest site temperature on eggs or chicks is not known, as adults (incubating and brooding) would ameliorate most temperature fluxes that might influence an egg/chick. This study failed to detect a difference in breeding success in relation to ambient nest site temperature. Eberl and Picman (1993) reported that microclimatic conditions at the nest site influenced reproductive success during one year of a Red-throated Loon (*Gavia stellata*) study. While temperature values were not given, nests that warmed earlier in the season had lower success.

4.2.3 The effect of nest site characteristics on breeding success

The major reason for decreased breeding success in Razorbills, aside from predation, is attributed to non-hatching of eggs (Hipfner and Chapdelaine 2002, VDG). Although temperature did not predict breeding success on MSI in 2001, high temperature extremes in nest sites may require the incubating adults to spend more time at the site, preventing excessive heat loss or gain.

Other major colonies of Razorbills in North America have predation pressure that directly affects survival of eggs, chicks or adults (Rowe and Jones 2000). Where avian predators take Razorbill eggs and unguarded chicks (Lloyd 1979, Lyngs 1994, Rowe and Jones 2000) nest sites that have adequate overhead protection will be preferred, and competition could arise for these nest sites (Rowe and Jones 2000). In colonies where a ground predator exists, ledge nests may be preferred and competed for where there is not an abundant supply (Rowe and Jones 2000).

The cover at a nest site and the nest site substrate had an effect on breeding success. In both years of the study, a higher proportion of burrow nests had chicks surviving to 14 days than either crevice or open nests. This result was contrary to Rowe and Jones (2000) who found no difference in breeding success between crevice and ledge nesters, but consistent with Hudson (1982) who reported higher breeding success in nest sites that had overhead cover. Razorbills at the Gannet Islands and at MSI may be genetically similar, based on head and bill size (Grecian *et al.* 2003), so a difference in breeding success based on population structure is not likely. Crevice nests in this study are nest sites with partial cover, while crevice nests in Rowe and Jones (2000) and Hudson (1982) are all nests with any overhead cover. The observed pattern of breeding success on MSI did not change if the definition of nest site structural classification of Hudson (1982) was used.

The highest number of chicks surviving to 14 days occurred in nest sites that contained some vegetation. This is not related to temperature regulation, because there was no effect of substrate on nest site temperature. Alternatively, vegetation may offer protection against inadvertent egg damage. However, the major reason for low breeding success in this study is eggs failing to hatch, not damaged or broken eggs, even within nest sites with only granite or rock for substrate.

Nest site characteristics have been linked to reproductive success in other species of birds. Decreased nesting success and fewer 2 chick broods in nests further from the ocean were observed in one year of a study of Red-throated Loons (Eberl and Picman 1993). As well, higher probability of raising at least one chick from a nest with vegetative cover was demonstrated in Kelp Gulls (Yorio *et al.* 1995). Increased nesting

success in Magellanic Penguins was observed where nests had more cover (Stokes and Boersma 1998). Increased breeding success was found in Black-legged Kittiwakes nesting on narrower ledges (Massaro *et al.* 2001). The reasons for differences in breeding success were attributed to the risk of predation in a variety of nest site types, and/or the heterogeneity of nest sites provided some sites with more protection from physical factors such as insolation and cooling.

4.3 THE EFFECTS OF BIOLOGICAL PARAMETERS ON BREEDING SUCCESS

Results of this study indicated that laying date influenced biological parameters of Razorbills breeding at MSI during 2000 and 2001. The timing of breeding on MSI was similar in all breeding site types and not different between years of this study, however laying date predicted egg size, mass gain, and breeding success. In this study, laying date produced responses in egg size and mass gain that are positively correlated with each other and both declined with increasing date. Wing gain was unrelated to egg size but mass gain increased with increasing egg size.

Differences in Razorbill biological parameters (egg size, mass gain, and breeding success) were consistent in both years. The environmental conditions at MSI (not included in analysis) can be assumed to be similar between years of the study, or at least during the breeding season. for breeding Razorbills. There was no change in the percent of herring *Clupea harrengus*, in the diet of breeding Razorbills on MSI, between the two years (Charette *et al.* 2004).

4.3.1 The impact of laying date on biological parameters egg size, mass gain, and breeding success

In this study, early eggs were larger, and chicks from early eggs gained more mass (corrected for egg size) than chicks that hatched from late eggs. Declining egg size, fledging mass and breeding success with date of laying has been recorded in a wide range of marine bird species (de Forest and Gaston 1996), including Razorbills (Lloyd 1979). Young or inexperienced birds differ from older birds in that they lay later in the season and have diminished reproductive capabilities, including the ability to provision (de Forest and Gaston 1996).

If one were to assume that on MSI the pattern of older birds breeding earlier was repeated, this would explain why egg size and mass gain responded in the way they did. Unfortunately, no other criteria are available to describe other reproductive measures of adult Razorbills breeding on MSI. For example, the age of a breeder could be used as a co-variate in analyses looking for cues to explain variation in breeding success. A logical progression of this work would be to continue banding as many chicks as possible and follow the same individuals from year to year to provide breeding histories of adults, especially females.

In this study, only 24 % of the variation in hatchling mass was explained by egg size in 2001 (N = 42); however, chick mass gain, increased with increasing egg size. From research on Coates Island, in the Canadian arctic, Hipfner (2000) wrote that egg size explained 71% of the variation in Razorbill hatchling mass, a result that was similar to other bird species (Williams 1971). It seems reasonable that a chick that hatched from a large egg has more yolk reserves and may be able to gain mass at a faster rate. He

found, however, that any early differences in nestling mass due to egg size were quickly erased as the chick aged (Hipfner 2000).

The significance of my finding is unclear but may be related to a wide range of issues that are different between these colonies, such as the availability of food items, environmental conditions, the presence of predators, and large-scale differences in the breeding habitat. Colder temperatures in the Arctic breeding season may increase thermal-regulatory activity and use cause chicks to use energy stores that chicks in the Bay of Fundy can convert directly to mass. The age structure and physiological condition of breeding adults, on each colony may be different as well. Potentially, there may be different physiological constraints for Razorbills breeding in the Arctic compared to the Bay of Fundy. Adults that arrive at northern colonies may not be in the same condition prior to breeding, and less able to provision chicks during nestling. There might be a difference in the yolk component of eggs in Arctic compared to eggs in the Bay of Fundy. Other questions to be answered include: Do Arctic Razorbills invest more in reproductive output (eggs - Yolk:Albumen ratio) in lieu of fewer resources? and Are there any trade-offs between breeding condition and reproductive output occurring between the geographic extremes of the Razorbill range in North America?

Egg size and mass gain decreased with increasing laying date but wing gain was unaffected. I had expected the response of wing gain to be similar in direction to that of mass gain. A lower contribution to the multivariate result may be evidence that wing growth is not so strongly affected by laying date or it may be related to a parameter that was not tested. Hipfner (2000) found wing growth to be positively correlated with egg size, and suggested that chicks from larger eggs had an advantage over other chicks

because their longer wing coverts would be more beneficial in helping chicks "float/glide" down to the sea when departing the colony (Gaston and Jones 1998). However this study does not support Hipfner's (2000) findings in which chicks from larger eggs had longer wings at departure time. MSI does not have great cliffs like the Razorbill colony at Coates Island, Nunavut, and wing growth is not predicted by egg size. This may suggest that Razorbills in the Bay of Fundy convert food energy primarily into mass growth, chicks have different physiological responses between the Arctic and Bay of Fundy, large wings are not an advantage on MSI, and/or food supply is higher in the Bay of Fundy and Razorbills' physiology reacts accordingly.

In this study, breeding success declined with increasing laying date and decreasing egg size. My results are consistent with those of Lloyd (1979), who also showed that breeding success declined with date. Conversely, Hipfner and Bryant (1999) did not record a seasonal decline in breeding success of Razorbills at the Gannet Islands.

de Forest and Gaston (1996) list several hypotheses relating declining reproductive success and laying date: 1) the risk of predation on later laid eggs and chicks is increased, referred to as 'late predation hypothesis' 2) the risk of predation is greatest for birds out of synchrony with rest of colony, referred to as 'synchrony hypothesis' 3) a seasonal decline in prey availability would favour early breeders, referred to as 'prey availability hypothesis' and 4) young or inexperienced birds have lower success than older birds, referred to as the 'age/experience hypothesis'. The Razorbill colony on MSI suffers very little predation and the period in which adults are feeding the young is short. It is probable that the food being delivered does not vary significantly. Unfortunately, the age/experience hypothesis (Hedgren 1980) could not be adequately tested in this study

but the data did support the hypothesis in explaining the observations of declining egg size, mass gain, and breeding success on MSI. There may be another parameter, not yet tested, that would explain, more than laying date, the response in Razorbill growth parameters on MSI.

4.4 OVERALL MODEL FOR PREDICTING BREEDING SUCCESS

The model was composed of a number of physical and biological characteristics that predicted breeding success. The results of various logistic models included cover, substrate, laying date and egg size (Appendix 2).

Cover, substrate, laying date and egg size predict breeding success. A maximum classification success of 68 % was obtained when all these parameters were combined. That means that these parameters would successfully classify 68 % of nest sites, identifying that a particular nest would be successful (almost 20 percent greater than guessing!). Laying date alone classifies a successful nest site at 63%. The other parameters do not add much more classification ability. This model has a limited use because the classification success is so low. Laying date is variable with season and geographic location, but in similar colonies, especially those with similar habitats and no predation, a researcher may rightly classify the breeding success of a Razorbill nest site 68% of the time if the laying dates are known. It may allow an estimate where no estimate of breeding success is obtainable.

4.5 SUMMARY OF FINDINGS

Were there differences in nest site characteristics among breeding areas? The analysis of nest site characteristics did not reveal any difference in the number of burrow,

crevice and open nest sites partitioned among habitats, locations, and substrates on MSI in 2000 and 2001. However, the number of burrow, crevice, and open sites were different among roof height and number of walls. I do not believe this effect is significant to the biology of Razorbills, but more of a spurious artifact of statistical analyses. For example, the difference of 2 versus 3 walls in a nest is probably not important. These results do indicate that the same proportion of burrow, crevice and open nests are found within the major habitats and locations on the island. This is a worthwhile result as future work on Razorbills on MSI can be representative if only a fraction of the island is used for treatments.

Were there any differences in microclimate among breeding sites? Ambient temperature increased throughout the 2001 season on MSI but was unrelated to relative temperature amplitude (AMP). I detected an effect of roof height on AMP but the differences were quite small. AMP was greater in nest sites without overhead cover because they did not have any protective barrier from either heating or cooling. The effect of nest sites with any amount of roof was to flatten the amplitude response of nest site temperature. Nest sites with overhead cover has the lowest AMP, but higher breeding success. There might have been a connection here but I had not way of testing it. A future study could look at the temperature of eggs in various nesting sites, remove the effect of the incubating parent, and test for differences in AMP again.

Was there any pattern of how adults of varying quality (as indicated by egg laying date) distributed themselves among breeding sites? This study did not detect a type of breeding site that is preferred by adults. This observation suggests that adults of varying quality are randomly distributed among the whole suite of nest site characteristics. There

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was no pattern linking laying date with any particular characteristic. I believe that virtually no predation and the availability of breeding habitat are the reasons that the distribution of adults of varying quality (as indicated by laying date) is not patterned to any description of breeding site. If these two factors were to change, competition for nest sites might erupt on MSI and a pattern of laying date variation among site types may emerge.

Did breeding success vary among breeding sites?

This study failed to detect a difference in breeding success in relation to ambient nest site temperature but an effect on breeding success was detected for cover and substrate. During 2000 and 2001, there was higher breeding success in covered nest sites. The reason for this is not clear. There is virtually no predation, there is available breeding habitat, and there is no preference for one type of nest site over another. A possible conclusion of these observations could be that Razorbills could breed anywhere on MSI and be successful. The population is expanding on MSI, even between 2000 and 2001 (assumed from the increase in distribution of breeding Razorbills to area not used in 2000, and from anecdotal light-keeper evidence of where Razorbills have traditionally bred on MSI, VDG), so another possible conclusion might be that the Razorbill population at MSI is still a young colony, and complex social-colonial structure has not developed. The associations between breeding success and nest site characteristics that may be assumed to be important may still be developing. A third possible explanation may be that this study did not measure the correct parameters that are influencing Razorbill breeding success.

On MSI in 2000 and 2001, the majority of egg losses were not attributed to breakage, chipping or cracking, but failing to hatch. If egg loss, or non-hatching of eggs is the greatest loss to Razorbill breeding success it is plausible why vegetation in a nest site would increase breeding success. Any amount of vegetation could dampen the movement of the egg and decrease the potential for chips and cracks.

If certain nest sites offer advantages and do not require parents to work harder, or expend more energy, then those nest types would be expected to be preferred and thus have higher success. The amount of burrow nesting on MSI may indicate prolonged avian predation in the past, but does not explain fully the difference in breeding success observed during 2000 and 2001.

Did laying date affect egg size, growth and breeding success?

Egg size, growth and breeding success declined with increasing laying date. Part of the probable explanation for these results rests in the relation of breeding biology to Razorbill adult condition and history. The age of breeding Razorbills on MSI was not known so the results of this study can not directly support the age/experience hypothesis concerning decreases in egg size, chick growth and breeding success. However, this hypothesis seems the most likely to explain the seasonal effects observed, based on the parameters that were studied. Older Razorbills do lay larger eggs, and breed earlier in the season and this is the most reasonable explanation for the response of size, mass gain and breeding success. The response of wing gain to laying date is unexpected and remains unexplained.

5 TABLES

Table 1   Mean number of Razorbills counted on selected dates or periods from the light house tower on Machias Seal Island from 12 May through 18 Aug 2000.

Date or Period	0700-0730	Number of Counts	1900-1930	Number of Counts
Max Count (Season)	977	2	1282	2
Min Count (Season)	0	2	0	2
Peak Lay Date (21 May)	719	2	705	2
Mid Season (20 June)	674	2	176	2
Mean (Whole Season)	503	65	196	65
Mean (12 May – 12 July)	570	45	270	42

Table 2   Number of occupied Razorbill breeding sites found on complete survey

(10-14 June 2000, Machias Seal Island).

Area or Gridline (see Fig 2-2)	Location on Island	Burrow	Crevice	Open	Total
South of Tramway	South	5	1	0	6
NE MSI	West				20
Northwest, MSI	West				25
C7-C8	West	34	3	3	40
C8-C9	West	29	2	3	34
E14-E13	South	9	1	0	10
E13-D13	South	122	14	4	140
D11-C11	Southwest	1	1	0	2
F13-F14	South	13	1	0	14
D5-C5	West	16	1	1	18
D13-D12	South	5	0	0	5
D12-C12	South	7	2	0	9
D11-C11	Southwest	14	3	1	18
C12-C11	Southwest	47	7	6	60
C11-C10	Southwest	46	12	11	69
Total		343	47	29	470

Table 3   Sensitivity of Razorbill breeding population estimates to one or two more

radio-marked Razorbills occupying a site that could (+) or could not (-) be detected by

the visual survey.

No. of sites detected only by radio-transmitter	No. of sites detected by radio-transmitter and survey	No. of Razorbill sites counted in survey	Correction	Other sites	[1]Corrected No. of Sites	Percent Difference
5 (++)	19	419	1.208	51	557	- 5.9 %
6 (+)	18	419	1.250	51	575	- 2.7 %
7	17	419	1.292	51	592	
8 (-)	16	419	1.333	51	608	+ 2.7 %
9 (--)	15	419	1.375	51	627	+ 5.9 %

[1]Corrected No.of Sites=[1+(No. of sites detected by radio-transmitter/24)]*419+51

Table 4 The number (percentage) of breeding sites, by cover, within location, habitat, substrate, roof height and the number of walls for 520 Razorbill nest sites on MSI, NB, Canada in 2000 and 2001 combined.

Breeding Site Characteristics	Burrow N = 307	Crevice N = 134	Open N = 79	Total 520
Location				
South	109 (21)	53 (10)	27 (5)	189
Southwest	95 (18)	41 (8)	31 (6)	167
West	103 (20)	40 (8)	21 (4)	164
Habitat				
Boulder	267 (51)	121 (23)	71 (14)	459
Granite	34 (7)	12 (2)	6 (1)	52
Vegetation	6 (1)	1 (<1)	2 (<1)	9
Substrate				
Granite	80 (15)	33 (6)	22 (4)	135
Granite and Rocks	26 (5)	16 (3)	9 (2)	51
Granite and Veg	21 (4)	6 (1)	8 (2)	35
Rock	83 (16)	40 (8)	23 (4)	146
Rock and Veg	44 (8)	25 (5)	7 (1)	76
Veg	53 (10)	14 (3)	10 (2)	77
Roof Height				
High	181 (35)	94 (18)	0 (0)	275
Low	126 (24)	40 (8)	0 (0)	166
None	0 (0)	0 (0)	79 (15)	79
Number of Walls				
<2	98 (19)	13 (3)	7 (1)	118
2	163 (31)	85 (16)	46 (9)	294
>2	46 (9)	36 (7)	26 (5)	108

Table 5   Results of Chi-Square analysis testing for differences in the number of

nests, by cover, for location, habitat, substrate, roof height, and number of walls for 519

nesting sites on MSI, NB, Canada in 2000 and 2001.

Breeding Site Characteristic	N	df	Critical Value	Pearson Chi-Square	P
Location	519	4	9.488	3.15	0.533
Habitat	519	4	9.488	2.23	0.693
Substrate	519	10	18.307	10.78	0.375
Roof Height	435	1	3.842	11.54	0.001
Number of Walls	519	4	9.488	42.91	< 0.0001

Table 6   General summary of Razorbill breeding site temperature monitoring from

26 May to 18 July 2001 at MSI, NB, Canada.

Period	Recording Days	Sites	*Mean Period Amplitude (^{o}C)
26 May - 29 May	4	10	9.287
29 May - 01 Jun	4	9	8.923
01 Jun - 06 Jun	6	9	6.031
06 Jun - 10 Jun	5	9	5.02
10 Jun - 13 Jun	4	9	6.38
13 Jun - 18 Jun	6	9	6.356
18 Jun - 22 Jun	5	8	7.291
22 Jun - 25 Jun	4	6	6.143
25 Jun - 29 Jun	5	9	7.015
29 Jun - 03 Jul	5	8	5.372
03 Jul - 06 Jul	4	9	4.116
06 Jul - 13 Jul	8	9	5.122
13 Jul - 18 Jul	6	8	7.746

*Mean Period amplitude is the mean temperature amplitude of all sites recorded

in one period.

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Table 7 (A) General linear model (ANOVA) for AMP at Razorbill nest sites (N = 112) on MSI, NB, Canada, in 2001. (see Appendix 1 for calculation of AMP) (B) Post-hoc comparisons that are the result of multiple pair-wise Bonferroni tests significant at α = 0.017 following significant ANOVAs on AMP. Values that are not significantly different are underlined together.

(A)				
Parameter	df_1	df_2	F	P
Cover	2	96	0.55	0.58
Location	2	96	0.11	0.89
Substrate	5	96	1.61	0.16
Walls	2	96	0.63	0.54
Roof	2	96	3.99	0.02
(B)	Post-hoc Comparisons			
Cover	ns			
Location	ns			
Substrate	ns			
Walls	ns			
*Roof	> 25 cm	< 25 cm	No	

*Roof - High – greater than 25 cm, Low – less than 25 cm, None – sites with no roof.

Table 8   The effect of roof height on the mean (SE), SD, maximum and minimum

values of relative temperature amplitude (AMP) in 112 Razorbill nest sites on MSI, NB,

Canada in 2001. See Appendix 1 for AMP calculation methods.

Roof Height	N	High	Low	None
	112	40	33	39
Mean (SE)		-1.14 (0.30)	-1.23 (0.34)	2.22 (0.53)
SD		1.92	1.94	3.31
Maximum Amplitude		4.46	3.31	9.99
Minimum Amplitude		-4.20	-6.03	-4.37

Table 9   Logistic regression analysis of breeding success (number of eggs that hatch and survive in the nest for 14 days) for Razorbill breeding site characteristics on MSI, NB, Canada in 2000 and 2001.

Source	N	Df	Wald	P
Cover	519	2	13.23	0.0013
Habitat	519	2	3.3792	0.19
Location	519	2	4.06	0.13
Year	519	1	0.0135	0.91
Roof Height	519	1	0.42	0.81
Number of Walls	519	2	1.99	0.37
Substrate	519	5	13.34	0.02
Amplitude Temperature	112	1	0.0014	0.97

Table 10   The effect of cover and substrate on hatching, nestling, and breeding

success for 194 Razorbill nest sites used for analyses in 2000 from MSI, NB Canada.

(Hatching success = Eggs Laid/Hatched Eggs, Hatchling success = number of Chicks

Present at 14 Days/Hatched Eggs, Breeding success = the number of chicks surviving in

nest for 14 days/Eggs Laid).

	Eggs Laid	Hatched Eggs	Hatching Success %	Chicks Present at 14 Days	Nestling Success %	Breeding Success %
2000 Total	194	123	63	107	87	55
Cover						
Burrow	107	81	76	68	84	64
Crevice	58	28	48	27	96	47
Open	29	14	48	12	86	41
Substrate						
Granite	56	30	54	24	80	43
Granite and Rocks	20	11	55	9	82	45
Granite and Vegetation	11	8	73	8	100	73
Rock	56	37	66	34	92	61
Rock and Vegetation	24	15	63	14	93	58
Vegetation	27	22	81	18	82	67

Table 11   The effect of cover and substrate on hatching, nestling and breeding

success for 326 Razorbill nest sites used for analyses in 2001 on MSI, NB Canada.

(Hatching success = Eggs Laid/Hatched Eggs, Hatchling success = number of Chicks

Present at 14 Days/Hatched Eggs, Breeding success = the number of chicks surviving in

nest for 14 days/Eggs Laid)

	Eggs Laid	Hatched Eggs	Hatching Success %	Chicks Present at 14 days	Nestling Success %	Breeding Success %
2001 Total	326	230	71	191	83	58
Cover						
Burrow	200	154	77	134	87	67
Crevice	76	49	64	34	69	45
Open	50	28	56	23	82	46
Substrate						
Granite	79	54	68	45	83	57
Granite and Rocks	31	18	58	15	83	48
Granite and Vegetation	24	21	88	18	85	75
Rocks	90	60	67	44	73	49
Rock and Vegetation	52	38	75	33	84	63
Vegetation	50	39	78	36	92	72

Table 12   Summary of recent Razorbill modal laying and hatching dates on MSI,

NB, Canada from 1995 - 2001. Data from 1995 - 1999 are from Charette *et al.* 2004.

Year	Peak Egg Laying	First Chick Hatched	Peak Hatch	Incubation Period
1995	21 May	16 June	27 June	37[*]
1996	23 May	15 June	5 July	40[*]
1997	26 May	16 June	2 July	37[*]
1998	20 May	20 June	24 June	35[*]
1999	20 May	15 June	23 June	34[*]
2000	17 May	13 June 165	23 June 173	35[**]
2001	22 May	16 June 169	24 June 175	36[**]

[*] estimated incubation period
[**] based on known lay and hatch dates.

Table 13 Razorbill egg measurements from other North American colonies (Mean ± SD, with range in brackets) expanded from Hipfner and Chapdelaine 2002 (Table 3). Data from MSI (VDG).

Colony	Year	N	Length (mm)	Breadth (mm)	Length* breadth^2 (cm^3)
Machias Seal Is.	2000	131	76.2 ± 3.1 (67.2-89.4)	48.1 ± 1.6 (43.6-52.8)	176.0 ± 16.0 (132.5-231.7)
	2001	291	76.5 ± 2.7 (69.6-84.2)	48.2 ± 1.9 (41.6-52.6)	176.2 ± 14.7 (123.9-225.5)
Is. Ste.-Marie	1963	100	74.5 (69.4-84.4)	48.5 (44.8-52.0)	
	1988	125	75.5 ± 3.0 (69.4-84.4)	48.3 ± 1.6 (44.8-52.0)	176.9 ± 14.9 (137.4-204.2)
	1992	59	75.7 ± 3.1 (68.4-82.9)	48.3 ± 1.7 (43.1-51.6)	177.4 ± 18.0 (129.4-220.7)
St. Lawrence Est.	1988	71	74.3 ± 2.6 (68.2-80.5)	47.9 ± 3.4 (42.0-52.6)	170.7 ± 16.4 (132.1-215.8)
Corossol I.	1988	31	75.8 ± 3.3 (68.9-81.7)	46.9 ± 2.1 (42.1-51.4)	167.9 ± 19.7 (132.8-206.6)
Boat I.	1988	39	75.0 ± 3.0 (70.7-85.2)	48.2 ± 1.5 (42.8-51.7)	174.3 ± 16.4 (142.1-227.7)
Wolf Bay	1988	13	76.8 ± 3.1 (72.4-81.4)	48.0 ± 1.7 (45.0-50.7)	178.0 ± 15.8 (153.9-207.7)
Gannet Is.	1981	339			180.1 ± 13.8
	1982	293			176.3 ± 14.5
	1983	361			176.0 ± 14.5
	1996	117	74.5 ± 2.7 (67.8-81.2)	48.4 ± 1.5 (44.3-52.5)	174.9 ± 14.8 (133.1-214.2)
	1997	102	75.0 ± 2.7 (69.8-82.1)	48.6 ± 1.6 (44.6-51.5)	177.4 ± 15.6 (139.6-217.7)

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Table 14 A) Multivariate Analysis of Variance (MANOVA) test results for egg size, mass gain, and wing gain of 196 Razorbill chicks in 2000 and 2001 on Machias Seal Island, NB, Canada, and B) ANOVA (Univariate F-tests with 3,135 df.) for effect of laying date on egg size, mass gain, and wing gain.

A)

	Pillai's Trace	F	df	Error df	Sig
Intercept	0.990	4147.58	3	131	<0.0001
Year	0.012	0.52	3	131	0.669
Laying date	0.351	9.38	6	264	<0.0001
Cover	0.056	1.26	6	264	0.276

B)

	MS	F	Sig
Egg Size	1293.88 178.72	7.24	<0.0001
Mass Gain	4226.90 511.76	8.26	<0.0001
Wing Gain	107.09 49.69	2.16	0.096

Table 15   Logistic regressions for breeding success of 240 Razorbill nest sites on

MSI, NB, Canada in 2000 and 2001 combined. Data are from those sites where laying

date was known.

Parameter	df	Wald χ^2	P
Year	1	1.75	0.186
Laying Date	1	10.02	0.0024
Egg Size (cm^3)	1	4.11	0.043

Table 16 ANOVAs comparing the mean laying date and mean egg size for Razorbill hatching success (eggs that hatched or not - HS), and reproductive success (chicks that departed or not - RS), from MSI, NB, Canada in 2000 and 2001 combined. The degrees of freedom for laying date are 1 and 281 and for egg size 1 and 238. Mean laying date is the mean number of days from peak, and mean egg size is the mean cm^3 of first eggs.

Component of Breeding Success	Variable	Success	N	Mean ± SE	F, P value
HS	Laying Date	Yes	198	2.0 ± 0.4	20.98, <0.0001
		No	85	5.8 ± 0.8	
	Egg Size	Yes	165	179.3 ± 1.1	14.62, <0.0001
		No	75	171.6 ± 1.7	
RS	Laying Date	Yes	162	1.4 ± 0.4	31.07, <0.0001
		No	121	5.6 ± 0.7	
	Egg Size	Yes	135	179.7 ± 1.3	11.78, 0.001
		No	105	173.2 ± 1.4	

Table 17 The number and probable fate of unhatched eggs on Machias Seal Island during 2000 and 2001 as percent of unhatched eggs and as percent of all eggs laid during both years of the study.

Egg Fate	Died While Hatching[1]	Drowned[2]	Hole/Cracked[3]	Mini[4]	Predated/Missing[5]	Roll From Site[6]	Abandoned[7]	Present[8]	Total Unhatched
Number	7	2	25	1	13	9	22	72	151
% of unhatched	4.6	1.3	16.6	0.7	8.6	5.9	14.6	47.7	
% of all eggs	1.3	0.4	4.8	0.2	2.5	1.7	4.22	13.8	28.9

([1] – chick did not emerge after egg starred or pipped. [2] – egg apparently drowned in burrow after rain storm. [3] – eggs that developed holes or cracks between visits to site. [4] – undersized egg. [5] – eggs that went missing from nest site before scheduled hatch date, no sign of egg hatch or predation. [6] – egg rolls sufficiently under or out of a nest site that adult can not incubate it. [7] – eggs that were not incubated at all or stopped incubation (cold egg). [8] – eggs that continued to be incubated well past the scheduled hatch date, includes full or intermittent incubation.)

6 FIGURES
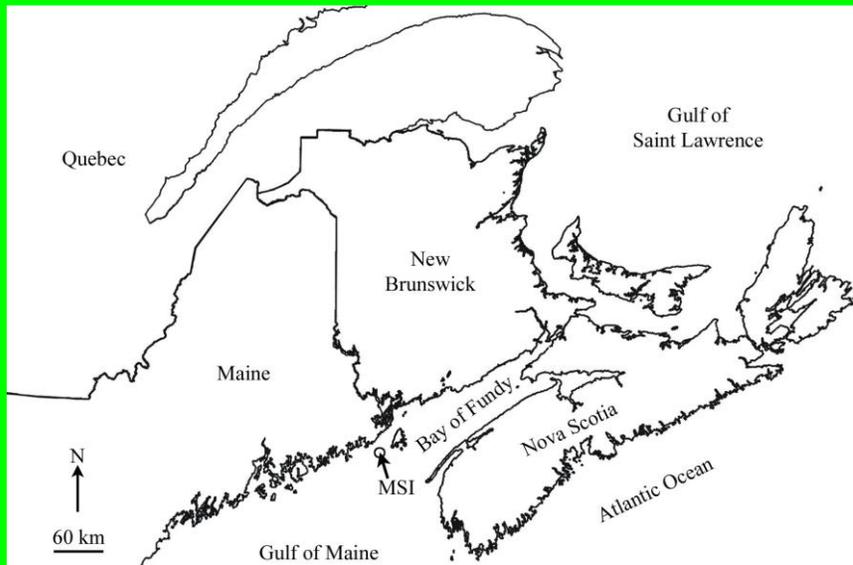
Figure 1 Location of Machias Seal Island (MSI) in the Bay of Fundy, New

Brunswick, Canada.
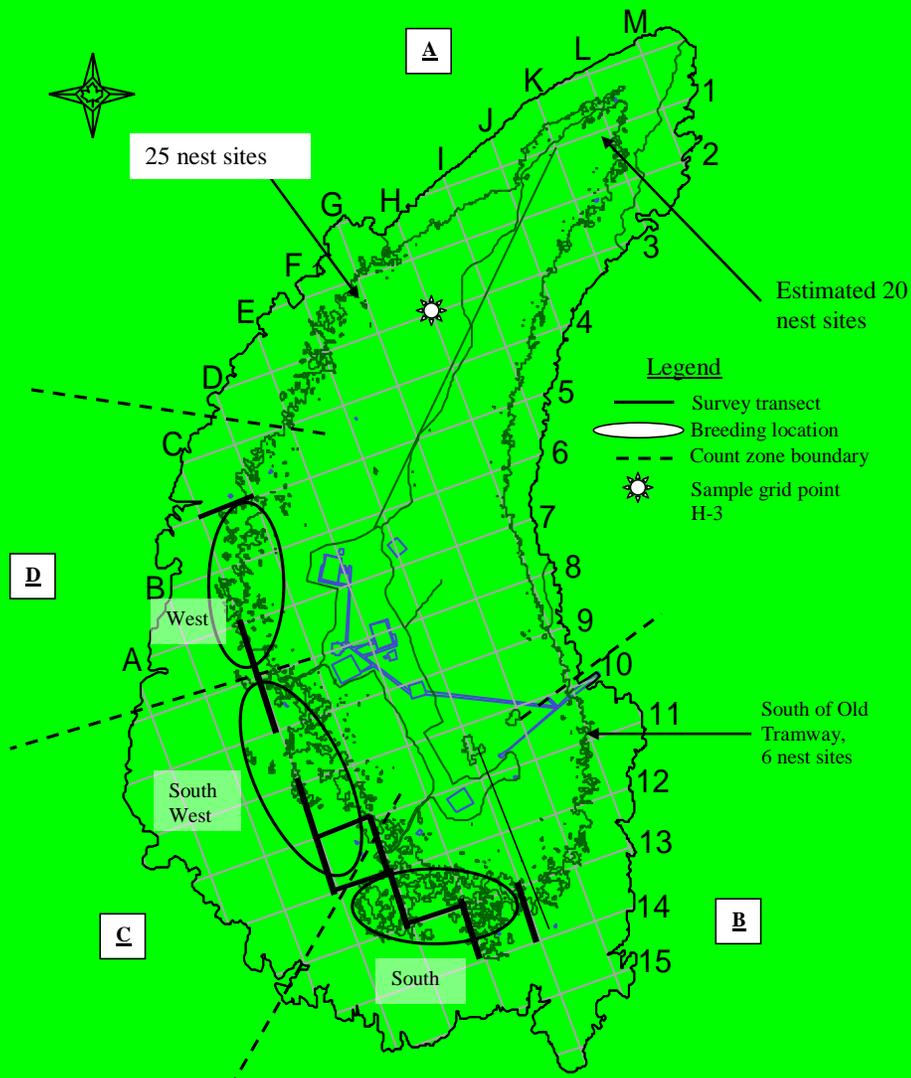
Figure 2   General Map of MSI showing tower counting zones (A,B,C,D), main
breeding areas (South, Southwest, West), survey transects and locations where additional
nests were added to the population estimate (not in survey).
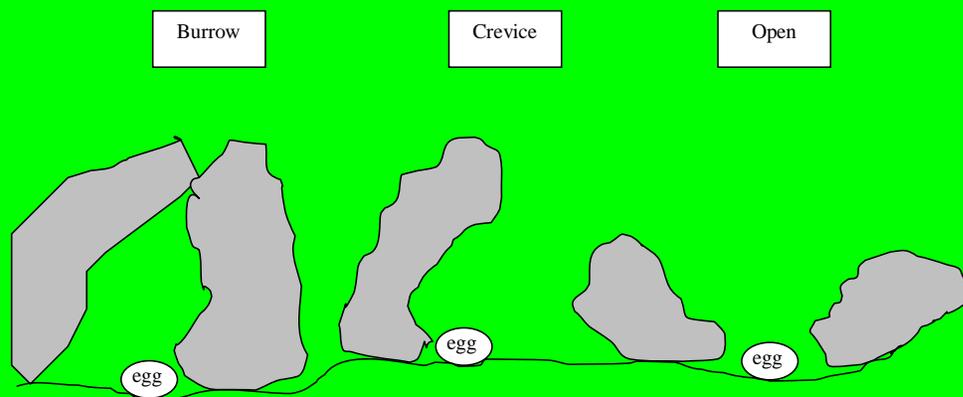
Figure 3 Schematic drawing of three Razorbill nest site types based on the amount of overhead cover on MSI, NB, Canada.

Coiled Internal Antenna

Epoxy Coating

Radio Transmitter

Battery

13 mm

10 mm
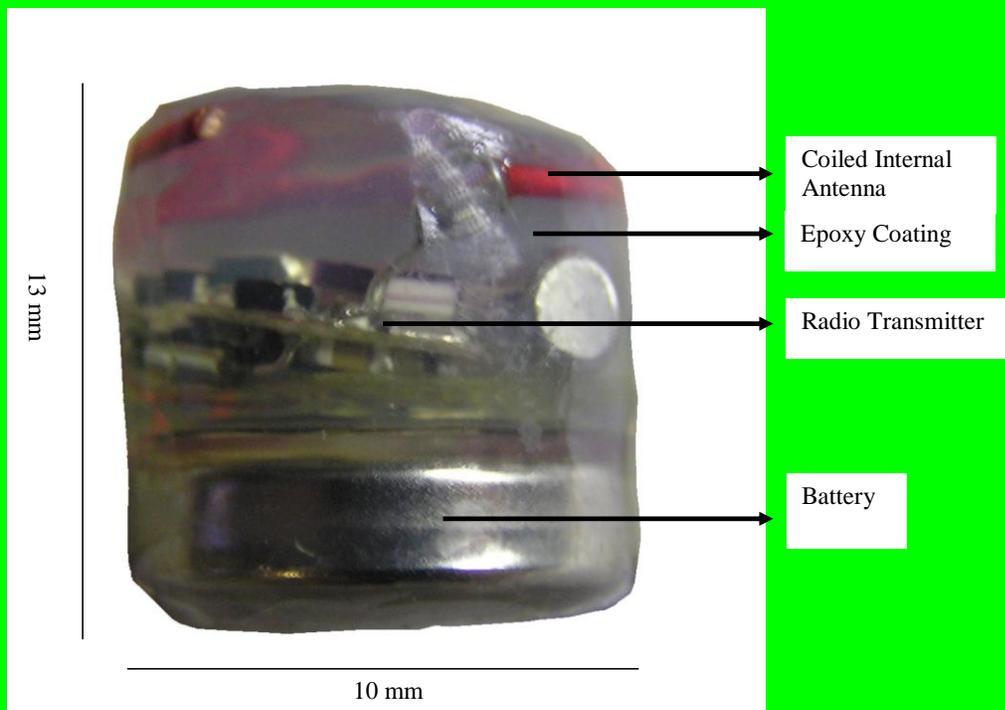
Figure 4   Radio transmitter designed for Razorbills nesting on MSI. (Specifics – Battery 1.5v,
pulse rate 60 ppm, pulse width 21 ms, current 0.04 ma and mass 3.7 g, straight distance range
is 400+ m).
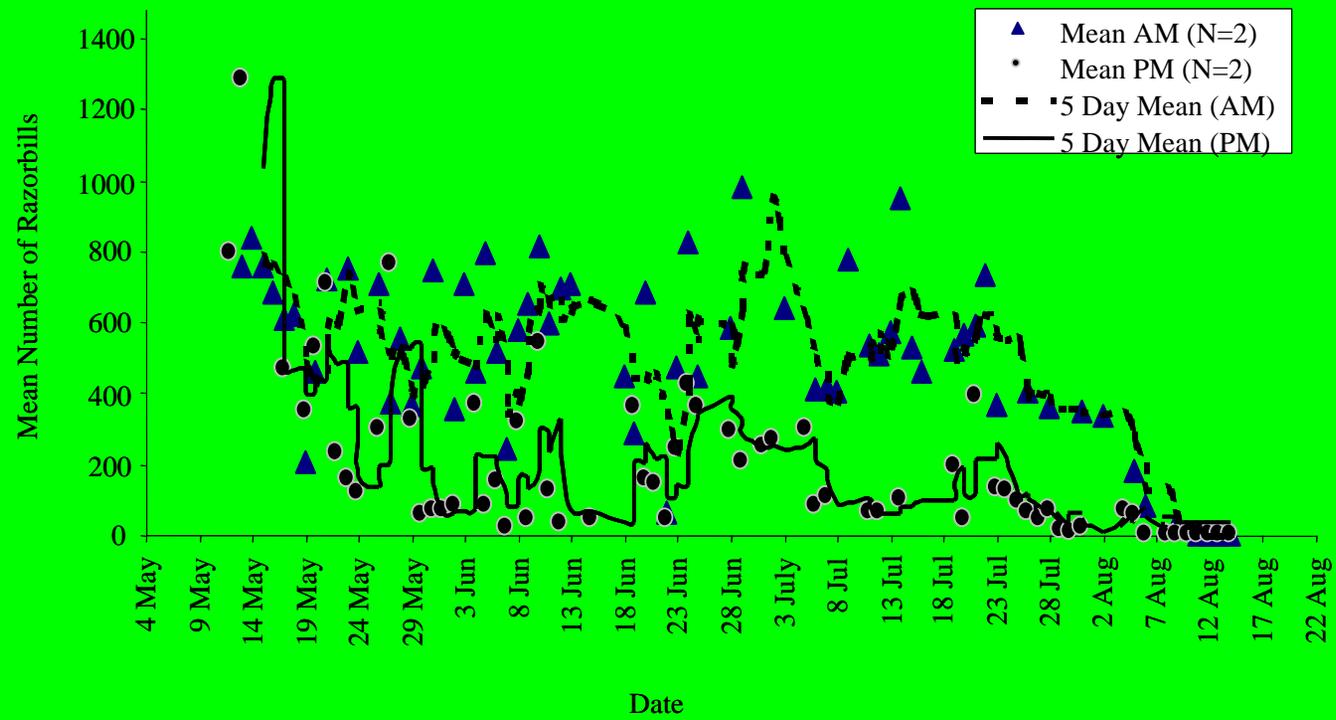
Figure 5   Mean counts of Razorbills from an 18 m light tower on Machias Seal Island during 2000. Each point is a mean of two counts and each line is a five day mean for that counting period (AM or PM).
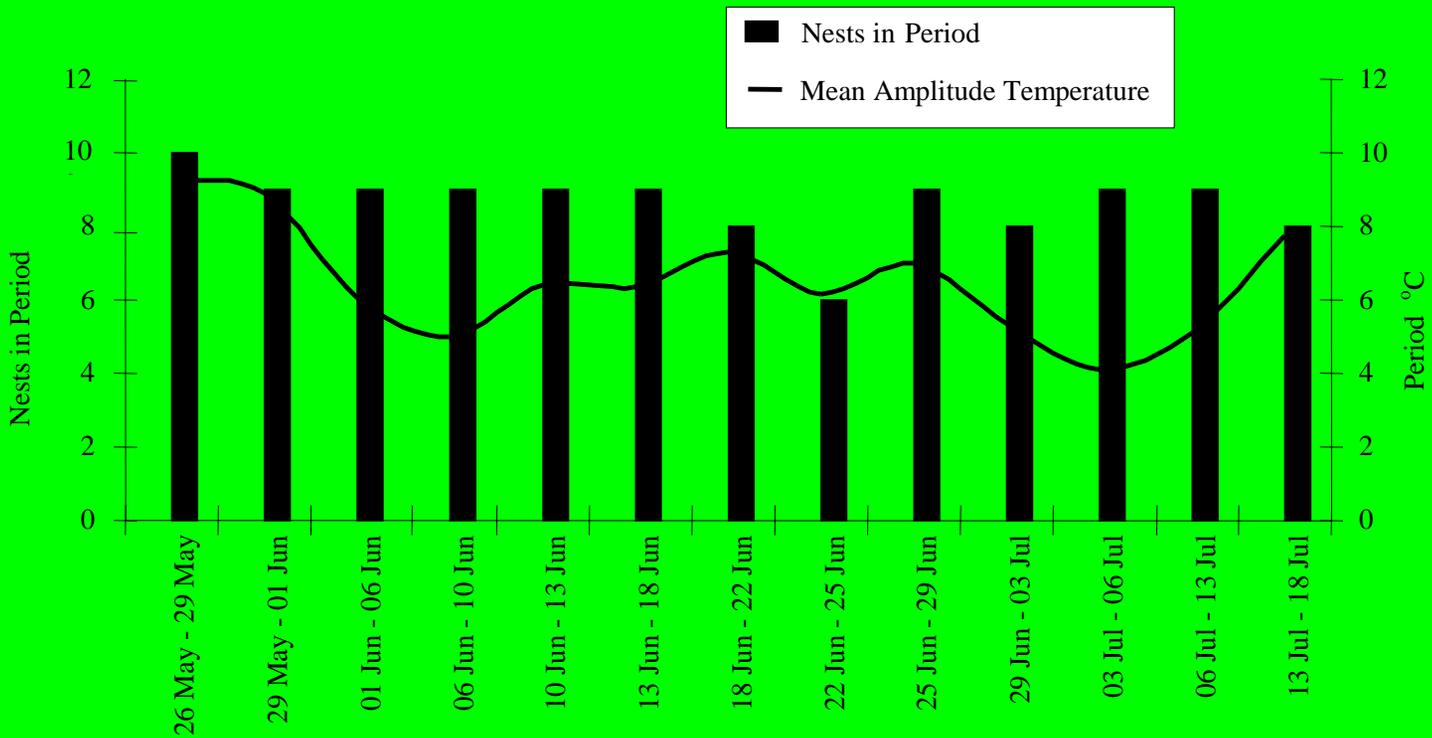
Figure 6   The mean period amplitude calculated for 13 time periods from 26 May to18 July 2001 on MSI, NB, Canada. The number of nest sites where temperature was recorded varies due to battery failure in some data loggers, and the removal of temperature probes by Razorbills. Data were recorded from 112 different Razorbill nest sites that were randomly selected by cover and location.
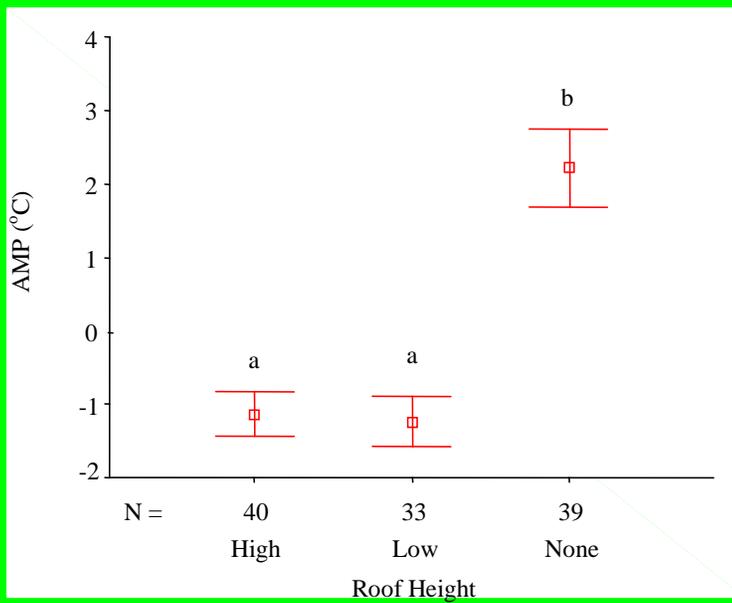
Figure 7   The effect of roof height, high (> 25 cm), low (< 25 cm), and no roof on mean (± SE) of AMP for Razorbill nest sites on MSI, NB, Canada in 2001. Similar letters are significant pairwise comparisons and Bonferroni post-hoc tests significant at P = 0.017.
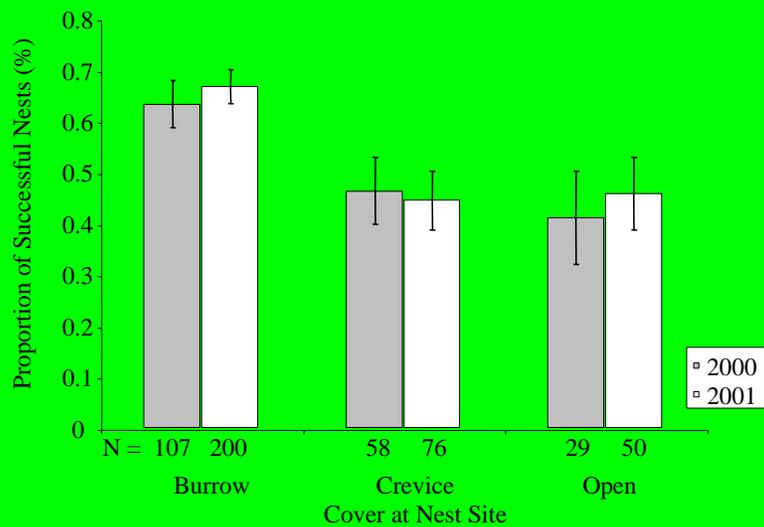
Figure 8 The effect of cover on breeding success (proportion of successful Razorbill

nest sites) on MSI, NB, Canada in 2000 and 2001. Breeding success (eggs laid that

hatched and chicks survived in the nest for 14 days) is shown as a proportion ($\pm$ 1

SE) of the total number of nest sites in each category.
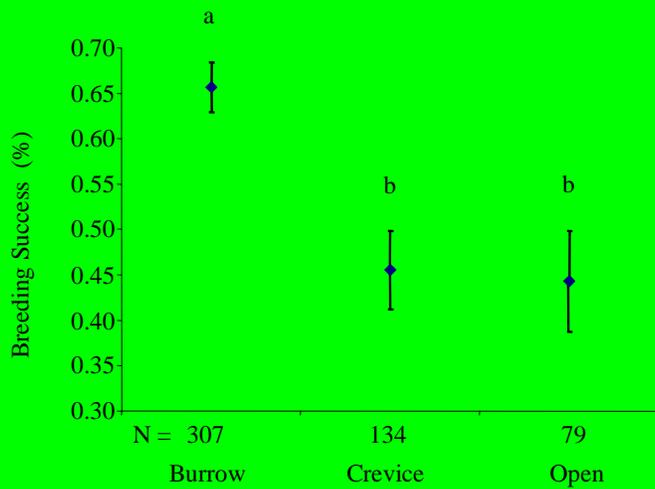
Figure 9   The effect of cover on the number of nest sites where breeding was successful on MSI, NB, Canada in 2000 and 2001. Breeding success (eggs laid that hatched and chicks survived to 14 days) is shown as a proportion (± 1 SE) of the total number of Razorbill nest sites in each category. Similar letters denote proportions where standard errors overlap.
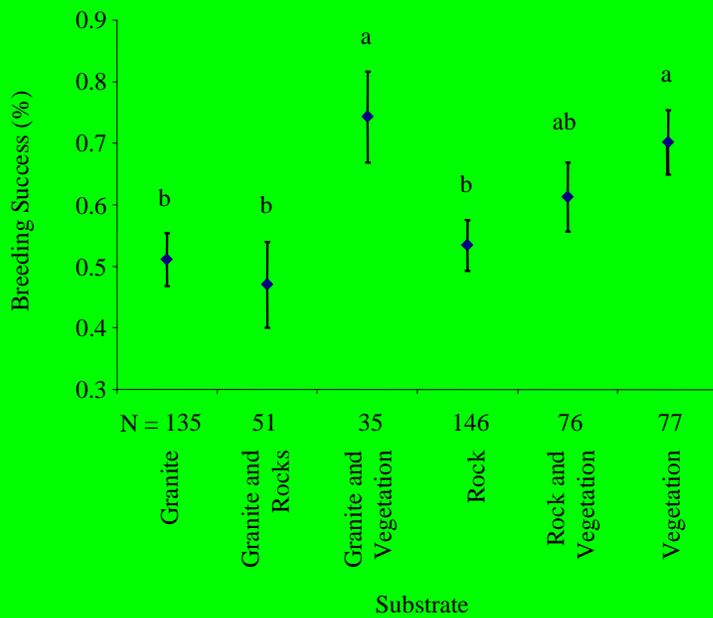
Figure 10   The effect of substrate on the number of Razorbill nest sites where breeding was successful on MSI, NB, Canada in 2000 and 2001. Breeding success (eggs laid that hatched and chicks survived to 14 days of age) is shown as a proportion (± 1 SE) of total number of eggs in each category. Similar letters denote proportions where standard errors overlap.

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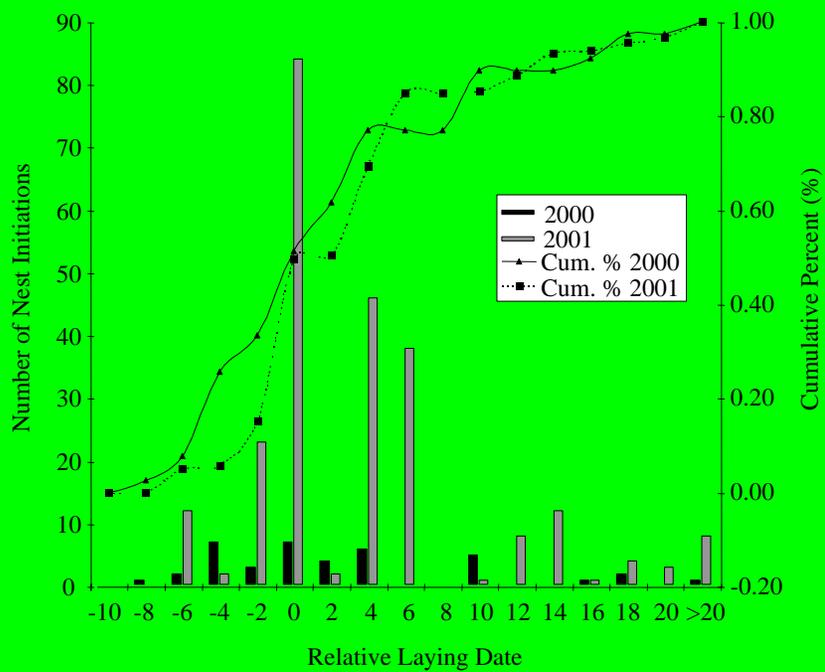
Figure 11 Number of Razorbill eggs laid at two-day intervals throughout season on MSI, NB, Canada in 2000 and 2001. Relative laying date is the difference between the observed laying date and the peak laying date.
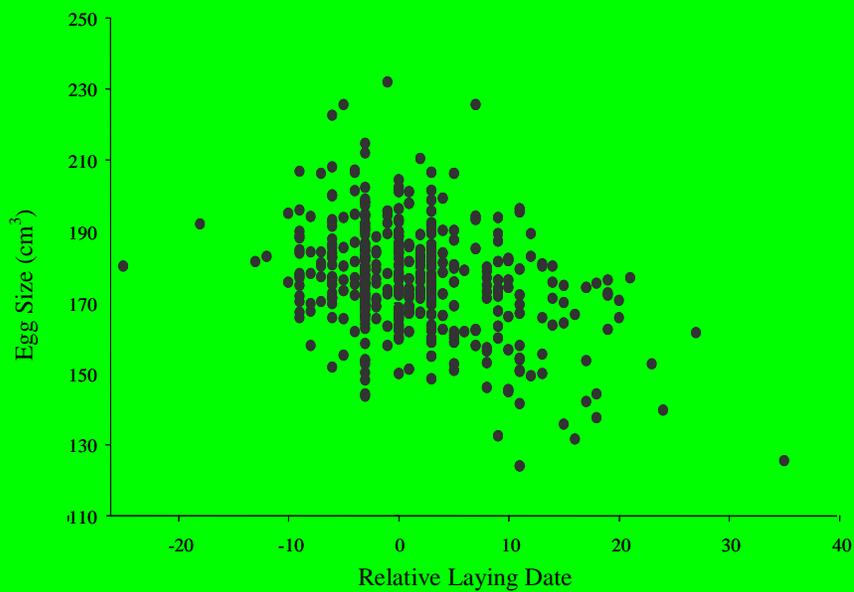
Figure 12 The effect of laying date on Razorbill egg size at MSI, NB, Canada in 2000 and 2001. The relative laying date is calculated from the laying date for each egg in each year minus the modal laying date for that year. Laying Date = -0.151(Egg Size) + 29.9, adj r^2 = 0.124, N = 283, P < 0.05.

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8 APPENDICIES

Appendix 1   Summary of Relative AMP calculation from sample raw data, for period of 25 June – 29 June 2001. Each day, each

site has a maximum and minimum temperature calculated, representing the highest and lowest temperature on that day. Mean AMP is

the mean amplitude for that site in this period. Mean Period AMP is the mean of all mean AMP calculated in this period. Relative

AMP is the difference between the Mean AMP for a site, and the Mean Period AMP. Relative AMP is used in all analyses with

temperature.

Logger	Midpoint of Period	Days in Period	Location	Temp	Site	Type	25-Jun	26-Jun	27-Jun	28-Jun	29-Jun	Mean AMP	Mean Period AMP	Relative AMP
	27 June	5	Sowest	Max	sTRA	O	16.38	22.48	23.24	28.31	22.09			
				Min			12.55	10.99	11.77	12.55	11.77			
				Max-Min			3.83	11.49	11.47	15.76	10.32	10.574	7.015	3.559
B-540	27 June	5	Sowest	Max	sTRB	C	16	20.19	16.38	18.66	15.62			
				Min			11.77	10.99	11.77	12.55	12.93			
				Max-Min			4.23	9.2	4.61	6.11	2.69	5.368	7.015	-1.647
	27 June	5	Sowest	Max	w5	C	15.62	18.28	14.85	39.22	23.63			
				Min			10.21	9.82	10.21	10.99	12.55			
				Max-Min			5.41	8.46	4.64	28.23	11.08	11.564	7.015	4.549
	27 June	5	Sowest	Max	n nw5	C	12.93	15.62	12.55	14.09	12.93			
				Min			9.42	8.23	10.99	12.55	9.42			
				Max-Min			3.51	7.39	1.56	1.54	3.51	3.502	7.015	-3.513
C-541	27 June	5	Sowest	Max	nw5	B	18.66	15.23	14.09	16.38	13.32			
				Min			9.82	9.42	10.21	11.38	11.77			
				Max-Min			8.84	5.81	3.88	5	1.55	5.016	7.015	-1.999
	27 June	5	Sowest	Max	lnw5	O	20.57	15.62	20.57	25.17	15.62			
				Min			11.38	9.82	10.99	12.93	11.77			
				Max-Min			9.19	5.8	9.58	12.24	3.85	8.132	7.015	1.117

Appendix 1 (cont)   Summary of Relative AMP calculation from sample raw data, for period of 25 June – 29 June 2001. Each day, each site has a maximum and minimum temperature calculated, representing the highest and lowest temperature on that day. Mean AMP is the mean amplitude for that site in this period. Mean Period AMP is the mean of all mean AMP calculated in this period. Relative AMP is the difference between the Mean AMP for a site, and the Mean Period AMP. Relative AMP is used in all analyses with temperature.

Logger	Midpoint of Period	Days in Period	Location	Temp	Site	Type	25-Jun	26-Jun	27-Jun	28-Jun	29-Jun	Mean AMP	Mean Period AMP	Relative AMP
	27 June	5	South	Max	60	B	18.69	16.83	15.92	15.92	14.58			
				Min			12.83	11.97	13.27	13.27	11.97			
				Max-Min			5.86	4.86	2.65	2.65	2.61	3.726	7.015	-3.289
	27 June	5	South	Max	20	B	19.81	17.52	16.76	16.76	14.47			
				Min			12.55	11.38	12.55	12.93	10.99			
A-542				Max-Min			7.26	6.14	4.21	3.83	3.48	4.984	7.015	-2.031
	27 June	5	South	Max	e20	O	27.52	20.19	25.95	29.1	25.17			
				Min			12.93	11.38	12.55	11.38	9.42			
				Max-Min			14.59	8.81	13.4	17.72	15.75	14.054	7.015	7.039
	27 June	5	South	Max	59	C	26.34	17.52	15.62	17.9	21.33			
				Min			13.32	12.55	13.32	12.16	11.38			
				Max-Min			13.02	4.97	2.3	5.74	9.95	7.196	7.015	0.181

Appendix 2   Results of various logistic regression models for physical and biological characteristics that had an effect on breeding success. The models predictive capability for a successful or unsuccessful nest is given as a percentage.

Logistic Model	N	df	Classification Success (%)		
			Success %Yes	Unsuccessful %No	Overall
Cover	283	2	66	55	61
Substrate	283	5	93	14	59
Laying Date	283	1	80	40	63
Egg Size	240	1	81	31	60
Cover + Substrate	283	7	77	46	64
Cover + Laying Date	283	4	85	42	66
Cover + Egg Size	283	3	74	45	61
Substrate + Laying Date	283	7	82	40	64
Substrate + Egg Size	240	6	76	53	66
Laying Date + Egg Size	240	3	84	37	63
Cover + Substrate + Laying Date	283	9	80	49	67
Cover + Substrate + Egg Size	240	8	76	54	66
Substrate + Laying Date + Egg Size	240	8	76	50	65
Cover + Substrate + Laying Date + Egg Size	240	10	78	54	68

Comment [TD22]: Does this mean that the model correctly predicts 81% of successful sites but only 30% of unsuccessful? If so, none of the models are very good, are they?

Appendix 3 Summary of Razorbill breeding biology data at MSI, NB, Canada for 2000

and 2001.

		2000		2001
		Mean ± SE		Mean ± SE
Eggs	194		325	
Laying Date	39	17 May	244	22 May
Fresh Egg Mass	27	92.9 ± 1.8	260	95.0 ± 0.5
Length (mm)	131	76.2 ± 0.3	291	76.2 ± 0.2
Breadth (mm)	131	48.0 ± 0.1	291	48.1 ± 0.01
Volume Index (cm^3)	131	175.9 ± 1.4	291	176.2 ± 0.9
Incubation Period	29	35.7 ± 0.5	173	36.1 ± 0.3
Hatching Success (%)	123	63%	230	71%
Chicks	60		136	
Hatching Date	29	23 June	173	24 June
Hatchling Mass (g)	6	68.9 ± 3.9	10	66.3 ± 2.4
Hatchling Wing (mm)	6	26.9 ± 0.8	10	25.4 ± 0.4
Mean Mass Gain (g)*	60	26.4 ± 0.9	135	26.2 ± 0.6
Mean Wing Gain (mm)	59	33.6 ± 1.3	135	35.2 ± 0.6
Breeding Success (%)	107	55%	190	58%

* Corrected for egg size

Curriculum Vitae

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Publications

Boyne, A.W., D. Grecian, and J. Hudson. 2001. Census of terns and other colonial
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