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Annual Variation in Seabird Attendance and Productivity on East Amatuli Island, Barren Islands, Alaska: Natural and Human-Induced Effects

Final Report 1992-1994

P. Dee Boersma Professor Julia K. Parrish Research Assistant Professor

Department of Zoology University of Washington Seattle, WA 98195

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P. Dee Boersma Professor

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Julia K. Parrish Research Assistant Professor

Department of Zoology University of Washington Seattle, WA 98195

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Minerals Management Service Environmnetal Studies Section 949 E. 36th Ave. Anchorage AK 99508

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PROJECT ORGANIZATION

Principle Investigator: Dr. P. Dee Boersma Professor, Zoology Department University of Washington Seattle, WA 98195

Project Manager: Dr. Julia K. Parrish Research Asst. Professor, Zoology Department University of Washington Seattle, WA 98195

Technician: Karen Jensen

Student Hourly Employees: Matt Wasson Jen Cesca Trista Patterson Johanna Salatas Nick Stathis Anna Stathis Jim Walseth

Time-Lapse Camera Consultants: Polar Alpine Inc.

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EXECUTIVE SUMMARY

The Barren Islands, (58° 55' N, 152° W), have the largest seabird breeding colonies in the North Gulf of Alaska (Bailey 1976). Because they are often abundant, conspicuous, and relatively high on the food chain, changes in seabird population dynamics can mirror changes in the bio-physical environment, including food supplies, oceanographic events such as El Niño-Southern Oscillation (ENSO), and marine pollution such as oil spills. Not all species will react similarly to a given environmental change; however, when several species within a single system are considered, patterns of environmental change may emerge. Aerial and ship-based surveys have shown that the waters surrounding the Barren Islands support a dense assemblage of foraging seabirds. However, the islands are particularly susceptible to marine perturbations, as evidenced by the Exxon Valdez oil spill of 1989. Some estimates of Barren Islands seabird losses resulting from this spill (e.g. murres) range as high as 50%. From 1990 through 1994, we monitored the population activity, diet, and reproductive success of two of the most abundant species of seabirds in the Barren Islands: Fork-tailed Storm-petrels (Oceanodroma furcata) and Common Murres (Uria aalge), in order to determine the degree to which each species responded to known changes in the environment, both natural and human-induced. For each species, methods were developed to monitor population activity, phenology, reproductive success, and, in the case of Fork-tailed Storm-petrels, chick growth. For the most part, methods and censusing sites were based on OSCEAP studies conducted by Boersma and Manuwal during the late 1970's and early 1980's. Seabird population monitoring usually commenced by the beginning of July and ended during the first week in September.

For Common Murres, patterns of population activity were estimated by counting murres present on four separate nesting areas (approximately 2-3% of total island attendance), after the murres had laid eggs but before chicks had fledged. Phenology was assessed from the timing of egg production on a 5x5m study plot on the top of Light Rock, established in 1977, as well as 35mm time-lapse movie cameras set up in 1991, 1993, and 1994. In addition, reproductive success was calculated for all pairs within the camera plots which could be visually followed. From 1975 through 1979, murre attendance estimates on East Amatuli Island ranged from a low of 19,000 to a high of 61,000. From 1990 to 1992, we counted between 31,000 and 35,000 murres in attendance on East Amatuli Island. Attendance in three of the four census areas increased steadily from 1990 to 1993; in total, attendance rose an estimated 18% annually. In all years, murres nesting on Light Rock produced eggs and chicks, although there were differences in both phenology and reproductive success. Egg laying on the 5

by 5 m plot in 1977 and 1978 was early relative to 1979; the former years are phenologically comparable to 1993 and 1994, while 1979 is closer to the timing of 1990. Reproductive success of murres in the time-lapse camera plots ranged from 0.65 to 0.93 fledglings per pair over the 243 pairs followed. Although there has been some concern that the *Exxon Valdez* oil spill caused a persistent decline in the reproductive output of the remaining East Amatuli population, we found no evidence to support or refute this contention. However, the pre-spill data available for accurate comparison was lacking, greatly weakening any firm conclusion about the effects of the spill.

For Fork-tailed Storm-petrels, patterns of population activity were estimated by assessing occupancy, reproductive success, and chick growth at approximately 650 marked burrows located in six study sites (A-E, Z). Throughout the 1990's, occupancy in marked nests has hovered between 40 and 50 percent. Hatching success and fledging success appeared to rise throughout the 1990's to a high of nearly 70% (hatching) and 90% (fledging) in 1994. Both tissue growth rate and weight gain fluctuated throughout the 1990's. In 1993 and 1994, it took approximately 57 days for the average chick to grow their wings from 10% (birth) to 90% of adult wingchord length. By contrast, the average length of time required in 1990 was 68 days, an approximately 20% difference. Weight gain followed a similar pattern. These dramatic differences in annual growth may reflect fledging success to some degree, but also reflect the fact that Fork-tailed Storm-petrel growth is regulated by food supply. Changes in weight gain probably reflect food quantity, while changes in wingchord growth rate reflect changes in food quality. Food availability may change on an intraseasonal basis and in an unpredictable fashion, while food quality may be changing over longer periods of time (e.g. decades).

Because seabirds can modify their behavior and foraging patterns, many species are able to ameliorate the effects of environmental change, regardless of source (i.e. natural or human-induced). For this reason, an understanding of natural biological variation and what causes variation to differ in direction or degree is also needed. Ainley, Sydeman and Norton (in press) argue that the intensity and geographical extent of the Aleutian Low Pressure System may alter wind patterns, upwelling patterns, and consequently affect the food supply, thereby affecting seabird reproductive and population biology in the Farallon Islands. It is interesting to note that in years when murre reproductive success is high in California, it is low on the Barren Islands. This "trade-off" effect may represent evidence of alternating strengths and weaknesses in the Alaska and California current systems, as both originate from the North Pacific Current. However, this alternating pattern is disrupted in years when the entire Pacific basin is affected, suggesting that major oceanographic perturbations can dwarf local

oceanographic trends. Thus, 1992 was a very poor reproductive year for murres in both the Farallon Islands and the Barren Islands, presumably because of El Niño.

In contrast to most natural perturbations, which can have either negative or positive impacts, most human perturbations have negative impacts on seabirds. Oil spills are among the most dramatic human perturbations in the marine environment. Without long-term monitoring of specific populations, it will be impossible to make blanket statements about the effects of oil spills on seabird populations, relative to other mortality agents, whether natural (e.g. ENSO, food availability, winterkill) or anthropogenic (e.g. gillnet bycatch, direct competition with fisheries, introduced predators). The Barren Islands data do not appear to shed light on this dilemma, in that although the Exxon Valdez oil spill killed many thousands of seabirds, it was impossible to detect long-term differences in response to the spill by Common Murres and Fork-tailed Storm-petrels. In part, our inability to detect change may be a result of the paucity of information on the non-breeding, or "at-sea" component of the Barren Islands population. Seabird populations may be buffered from adverse effects, both natural and human-induced, by their non-breeding pool. The level of resilience provided by non-breeders would thus be affected by the frequency and magnitude of disturbance. Additional human-induced disturbance in a system already susceptible to broad fluctuations in natural perturbation, may deplete the built-in reserve offered by non-breeders. Whether this is true, and how important the non-breeding pool of birds is, remains to be tested.

INTRODUCTION

Many authors argue for the use of seabirds as indicators of the marine environment (Boersma 1986, Furness 1987, Furness & Barrett 1991). Because they are often abundant, conspicuous, and relatively high on the food chain, changes in seabird population dynamics can mirror changes in: 1.) the food supply (Piatt 1990, Springer et al. 1986); 2.) oceanographic events such as El Niño-Southern Oscillation (ENSO) (Boersma 1978, Graybill & Hodder 1985, Wilson 1991, Massey et al. 1992); and 3.) levels of marine pollution, at the lethal (Piatt et al. 1990) as well as sublethal (Boersma 1986, Gilbertson et al. 1987) levels. It is generally accepted that not all species of seabirds will react similarly to a single environmental change (Furness & Barrett 1991). This is because each species has different foraging and nesting behavior, such that varying aspects of the physical/biological environment will impinge directly on each species' fitness. For instance, species with greater flight range may be less susceptible to changes in the food supply than species with limited range, because the former can adjust for nearshore food depletion by searching over greater distances from the colony.

Population-level measurements, such as attendance, diet, hatching success, chick growth rate, etc. may give us an integrated, albeit selective, window on the environment. However, when several species within a single system are considered, patterns of environmental change may emerge. The Barren Islands, with its abundant resident seabird colonies, provide such a system within which to quantify environmental change.

Located at the mouth of Cook Inlet, the Barren Islands, (58° 55' N, 152° W), have the largest seabird breeding colonies in the north Gulf of Alaska (Bailey 1976). East Amatuli Island, located on the east side of the island group (Figure 1), supports a particularly diverse assemblage of avian fauna that includes surface feeders and pursuit divers (Bailey 1976). These islands are ideally suited for seabirds due to three complimentary factors: First, the local topography and physical oceanography result in upwelling with a concomitant surge in productivity. Aerial and ship-based surveys have shown that the waters surrounding the Barren Islands support a dense assemblage of foraging seabirds (Piatt pers. comm.). Second, the system is not only uninhabited by man, but is protected as part of the Alaska Maritime National Wildlife Refuge (AMNWR). Lastly, although the island system supports a small number of raptors and river otters, predators are by-and-large absent. The latter two factors minimize disturbance to breeding habitats. All three factors contribute to the continuing reproductive success of the Barrens' seabirds and also highlight the importance of the islands as a population center for seabirds in the north Gulf of Alaska. However, the islands are particularly susceptible to marine perturbations because of their location at the mouth of Cook Inlet. As evidenced by the Exxon Valdez oil spill, pollutants that are introduced into Prince William Sound and the north Gulf of Alaska are likely to flow through the Barren Islands and may linger there for several weeks because of the large tidal exchange.

From 1990 through 1994, we monitored the population activity, diet, and reproductive success of two of the most abundant species of seabirds in the Barren Islands: Fork-tailed Storm-petrels (*Oceanodroma furcata*) and Common Murres (*Uria aalge*). Prior to 1990, extensive data was collected on Fork-tailed Storm-petrels (Boersma et al. 1980, Boersma unpub. data) and occasional data was collected on murres (Manuwal 1980). These datasets have allowed determinations of the degree to which each species responds to known changes in the environment, both natural and human-induced. For example, Fork-tailed Storm-petrel burrow occupancy (# occupied/# checked) and egg volumes were significantly lower in 1983 and 1984, years in which an El Niño-Southern Oscillation (ENSO) event was known to have affected physical oceanography conditions in the Pacific (see chapters in Diaz & Markgraf 1992). During

this period, sea-surface temperature (SST) anomalies in a four-degree sided square surrounding the Barren Islands were often in excess of 1.0°C (Figure 2). Anomalously high SST conditions have been associated with downturns in oceanic productivity (Sharp 1992), and thus potentially the food supply of lower food chain feeders such as Forktailed Storm-petrels (see references in Wooster & Fluharty 1985, Ainley & Boekelheide 1990). Thus, while not strictly causative, there is a definite, and biologically interpretable, correlation between a change in the larger physical environment and the reproductive biology of the seabird species.

Natural variation is not the only source of environmental change. Human-induced perturbations affect the environment on several scales. At a global level, changes such as rising CO^2 emissions can affect temperature, which in turn may affect both terrestrial and aquatic productivity (Halpert & Bell 1993). Regionally, human interaction with the oceanic environment may have produced changes in aquatic community structure due to fishing pressure (Springer et al. 1986). Such changes can often have far reaching effects on the food supply, and thus abundance, of regional seabird and marine mammal species (Springer et al. 1986).

Locally, point-source pollution can have a drastic effect on the marine environment. A case in point is the Exxon Valdez oil spill of 1989 (Piatt et al. 1990). Approximately 30,000 bird carcasses of 90 species were recovered following this spill (Piatt et al. 1990), and current estimates of total bird mortality have run as high as 500,000 (Parrish & Boersma, in press). Because over 70% of the recovered carcasses were murres, and the Barren Islands murre colonies (located on East Amatuli and Nord Island, respectively) comprise the largest murre colony in the path of the spill, both assessment of the damage to, and monitoring recovery of, the Barren Islands murre population is of serious scientific and management interest.

While it is possible to ascribe a potential cause, such as the Exxon Valdez oil spill, to a measured effect, such as a decline in the murre population, in general the pattern of population activity and reproductive effort of each species is going to be influenced by a complex combination of forces, both natural and anthropogenic (Hunt 1987). It thus becomes imperative to not only monitor seabird populations, but to also collect accurate measurements on the physical/biological environment (Hunt 1987, Parrish & Boersma 1995). These two pieces must then be superimposed such that measured environmental change is applicable on a biological scale appropriate to the species in question. In this context, scale is relevant to both time (as in the average life of a seabird) and space (as in the foraging range of the bird). For instance, nearshore changes in food supply may affect the alcids, (murres and puffins), more than Fork-tailed

Storm-petrels, because the former have a restricted foraging range around the nesting colony. Thus, localized shortages may affect the diet, and eventually the reproductive success, of these species. Fork-tailed Storm-petrels may be able to compensate for local shortages by increasing search distance and time. While this may increase egg neglect and slow chick growth, reproductive success, measured as fledglings per pair, may be unaffected. Furthermore, species with limited foraging ranges may be more susceptible to marine pollutants such as oil, should the oil cover a broad proportion of the species foraging range. During the breeding season, murres and Tufted Puffins should experience the brunt of any oiling in the Barren Islands' area, because their at-sea distribution is limited to close to the island. Thus, there is potential for naturally-induced downturns, such as those caused by changes in food supply, to be synergistically exacerbated by oiling events.

Because of the islands' high vulnerability to oil spill impacts due to its geographic location at the mouth of the Cook Inlet (an area of shipping traffic and potential oil and gas development), a three-year study to monitor the major marine avifauna was funded by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) from 1977 through 1979 (Manuwal 1980). That study concentrated primarily on three species: Fork-tailed Storm-petrels, Tufted Puffins and Common Murres. For each species, methods were developed to monitor population activity, phenology, reproductive success, and in some cases chick growth. From 1980 through 1984, these studies were continued under Boersma and concentrated on the Fork-tailed Storm-petrel. Monitoring of the Fork-tailed Storm-petrel population and, to a lesser extent, Tufted Puffins and Glaucouswinged Gulls (*Larus glaucescens*) was conducted intermittently from 1985-1989 by the U.S. Fish & Wildlife Service AMNWR staff (Nishimoto et al. 1986, Nishimoto et al. 1987, Nishimoto & Beringer 1988, Nishimoto & O'Reilly 1989). In 1990, Boersma resumed monitoring, and has continued surveying the seabird activity on East Amatuli Island through 1994.

METHODS

General

At the beginning of each field season (late June), a crew of field technicians and volunteers was transported from Homer to East Amatuli. As in previous years, camp was set up in a depression in the primary dune on the east side of Amatuli Cove. In 1993 and again in 1994, the camp was expanded to accommodate U. S. Fish & Wildlife Servicepersonnel. Seabird population monitoring usually commenced by the beginning of July and ended during the first week in September. In all years, camp was dismantled

by mid-September. During years in which time-lapse movie cameras were installed on Light Rock, a brief dismantling trip was made in October. In 1991 and again in 1993, data on Fork-tailed Storm-petrels was also collected during the October visit. In 1994, three separate visits were made to East Amatuli, en lieu of a permanent field camp. Visit timing and adverse weather conditions precluded collection of murre population information. However, these data were collected by US Fish & Wildlife Service personnel.

Common Murre

Attendance

From 1990 through 1992, island attendance was estimated by counting murres present on the island after the murres had laid eggs but before chicks had fledged (see Wanless et al. 1982, Hatch & Hatch 1989). Counts were made when the water around the island was relatively calm (seas less than 1 m) and visibility was good. All counts were restricted to between 1100 H and 1900 H. Before censuses began, observers practiced counting selected areas by making independent counts and then comparing data. The practice area was then censused more closely by both observers counting together. Independent counts were then made again. If these counts differed by more than ten percent, the entire process was repeated until the counters agreed which birds had been missed or invented. Attendance was defined as the number of murres directly counted on the cliffs. This figure does not take into account the percentage of the population that was not present, (i.e. foraging). Therefore, we did not attempt to use the attendance count to calculate the number of pairs nesting on the island. Instead, islandwide attendance censuses were used to provide a broad-brush picture of changes in East Amatuli colony size. In 1993, US Fish & Wildlife Service personnel assumed the responsibility of estimating island murre attendance.

In addition to the island census, four areas (Oval, Swatch, and Triangle Rock NW and S, respectively; Figure 1) were censused several times throughout the day on different dates throughout the breeding season to provide a more in-depth dataset for the determination of interannual trends (1990-1993). Counts were made as described above. In 1990-1992, counts were made from beyond the kelp bed (far), at unspecified locations affording a clear view of the area. In 1993, counts were made much closer from within the kelp (near). It is possible that closer counts could be higher because individual birds would be easier to spot. To test for methods effects, far and near counts were conducted in 1993 on the same day and compared. There were no statistical differences, indicating

near counts did not bias attendance upwards. In 1993 and 1994, U.S. Fish & Wildlife Service personnel also made duplicate counts of these multiple-count areas.

Reproductive Activity

During all boat surveys murre phenology was qualitatively assessed. Specifically, we observed: 1) whether the murres were occupying breeding ledges or continuing to raft, and 2) whether "flyoffs", defined as large numbers of murres (>100) flying from the cliffs in unison, occurred. Flyoffs were taken as an indirect indication that laying had not started in an area. We also noted whether recently laid murre eggs or freshly eaten eggs were seen on Light Rock during occasional visits. As our field season started in early July, it was impossible to determine when ledges were initially colonized. However, we operationally defined the beginning of reproductive activity as the time when the majority of the murre population was present on the breeding ledges and remained there throughout the day (i.e. no flyoffs).

Phenology was also assessed from the timing of egg production on a study plot on the top of Light Rock, established in the densest part of the colony in 1977 (Manuwal 1980). Originally 17.6 m², the plot was expanded to 25 m² in 1978 and located in the same general area as in the previous year (Boersma pers. obs.). The plot was reestablished in 1990, and surveyed through 1992. As in the 1970's the plot was visited after the initiation of egg laying (7 July and 1 August) and again after chicks started to hatch (1 September) in order to count eggs and chicks. Visits invariably flushed the resident adults, so an attendance count was never possible. The number of eggs and chicks appearing on the 5 x 5 m plot was used as an indication of relative reproductive success for the murre population. During the first two visits, all eggs within the plot were marked such that a loss rate between visits could be calculated. This loss rate is assumed to be the result of disturbance, primarily created by visiting the plot. Losses occurred because Glaucous-winged Gulls entered the plots after murres flushed, and preyed upon some percentage of the eggs. Because of this disturbance, our measures of egg and chick production from the 5 x 5 m plot are somewhat lower than what would actually have been produced.

During 1991, two 35mm time-lapse movie cameras were installed on Light Rock, one on the flat top and one on the North-sloping side. In 1993 and 1994, four such cameras were installed (1993 - two on flat top, two on North side; 1994 - three on flat top, one on North side). Cameras were set-up before the onset of the murre laying season (late June) and removed after murres had left for the season (late September - early October). Cameras took pictures every 6 (1991) or 10 minutes (1993; 1994), from dawn

to dusk. Subplots within the frame of each camera were used to assess daily and seasonal patterns of attendance and phenology. Reproductive success was calculated for all pairs within the plot which could be visually followed. Pairs whose position on the camera subplot occluded them from clear view were not followed, as it was difficult to impossible to clearly distinguish their reproductive output. Pair occlusion was a particular problem in the sloping plots, which led to the reduction in sloping camera plots from 1993 to 1994 as they were not useful with respect to accurate assessment of murre reproductive success. Although this method may be somewhat ambiguous, we had no *a priori* reason to believe there was a potential correlation between proximity to the camera and reproductive success.

For clearly visible pairs, all frames within each day were examined for sightings of eggs or chicks. As murres are protective of their eggs/chicks, and the cameras were taking "snapshots" in time (albeit tens of frames/day), there were days in which clear sightings for each pair's reproductive output were not possible. This was particularly true during stormy weather, when picture quality was reduced, as well as during hatching when parents remainded extremely close to new chicks. Therefore, we used a series of conservative operational definitions, based on range of days an egg or chick was sighted, to categorize the likelihood of hatching and fleding success. For each pair, successful fledgling production was operationally defined by one of the following: 1.) chick sightings over an 18+ day period, or 2.) chick sightings and sightings of adults with wings down (indirect evidence of chick presence) over a 20 day period, or 3.) chick sightings over a 30+ day period. Chicks were defined as having probably fledged if they were sighted directly or indirectly or less than 18 days and/or their eggs were sighted less than 30 days. Therefore, reproductive success was defined conservatively as:

fledglings/(eggs - relays)

and liberally as:

(fledglings + probable fledglings/(eggs - relays)

Fork-tailed Storm-petrel

Monitoring Areas

All permanently staked burrows in 6 study areas (A, B, C, D, E, and Z; Figure 1) were examined for evidence of nesting activity at the beginning, middle, and end of each field season. During each year, new burrows were identified and added to the

permanently staked list. Area checks were used to determine burrow usage and reproductive success of a known population as follows:

occupied burrow=presence of adult, egg, or chick burrow occupancy=occupied burrows/total burrows checked active burrow=presence of an egg or chick burrow activity=active burrows/total burrows checked hatching success=chicks produced/eggs chick mortality=dead chicks/chicks produced fledging success=chicks fledged/chicks produced

reproductive success=chicks fledged/active burrows

Because the field season ended before all chicks had actually fledged, the chick fledged category included actual fledgers plus all chicks in healthy condition at the end of the field season.

After the first complete area check, all active burrows were marked for the season with surveying flags. Active burrows were then monitored at three-day intervals throughout the nesting season as follows: Adults in the burrow were checked for band identification. Unbanded adults were banded. Once both birds of a pair were banded, adults were no longer removed from the burrow. If the burrow did not contain an egg or chick, and no adult was found for three consecutive visits, then the burrow was removed from the monitoring list. Burrow condition (dry, damp, wet, flooded) was also noted.

Eggs were removed from the burrow and measured to the nearest 0.1 mm with vernier calipers (length and width). Until hatching, relative egg temperature was consistently checked as a measure of incubation (warm, cool, or cold), and hatching state was recorded (presence and number of stars and pips). Pipped eggs usually hatched within 1-5 days. If an egg was cold for more than 6 sequential visits, it was considered dead and the nest was removed from the monitoring list.

Once the chick had hatched it was not removed from the burrow until the adult was no longer present, usually 2-5 days from hatching. Chicks were aged by classifying feather tracts on the back (small dots, large dots, lines), back skin color (red, pink, white/grey), and tarsus color (white, grey) Chick activity was noted on each visit as follows: responsiveness (active, lethargic, torporous), wing and feet temperature (warm, cool, cold), down condition (dry, damp, wet). Chick weight (to the nearest g) and wing measurements (to the nearest mm) were made on every visit. Wing chord was defined as the distance, on an unstretched wing, from the carpal joint to end of the bone, down, shaft, and/or feather as they appeared during chick growth. Chicks that were considered to be near fledging (identified by the presence of fully grown flight feathers and no

down) were banded. The yearly chick growth rate was calculated by taking mean weight and wing measurements from Day 1 through fledging and performing a best-fit growthcurve regression on the points (Boersma & Parrish, in prep.).

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RESULTS AND DISCUSSION

Common Murre

Attendance Patterns

From 1990 to 1992, we counted between 31,000 and 35,000 murres in attendance on East Amatuli Island (Boersma et al. 1995). In 1993, US Fish & Wildlife Service personnel estimated the East Amatuli population at 33,000 (Roseneau pers. comm.). Attendance figures were unavailable for the 1994 season. In all years the majority of the murre population nested on the southeast side of the main island, and secondarily on East Amatuli Light Rock. Because whole island censuses were only made once, these figures should not be taken as accurate representations of either island attendance or population size. Instead, these figures represent a broad estimate of annual attendance.

There has been a large amount of controversy surrounding the degree to which the *Exxon Valdez* oil spill impacted, and continues to impact, the Barren Islands murre population (Boersma et al. 1995, Nysewander et al. 1993, Parrish & Boersma 1995). Although the attendance figures reported here can be used as broad-brush baselines for future years, they are, unfortunately, not directly comparable to earlier census data as the latter were estimates rather than actual counts. In addition, specific information about counting methods, including number of observers, platform, optics, time of day and time of season are lacking. From 1975 through 1979, murre attendance estimates on East Amatuli Island ranged from a low of 19,000 to a high of 61,000 (Boersma et al. 1995).

Four areas: Oval, Swatch, Triangle Rock NW and S, respectively, were counted between 2 and 10 times per season, allowing a more accurate estimation of annual changes and variation in attendance. These four areas represent 2-3% of the total East Amatuli population, and are located in three separate locations along the periphery of the main island. Attendance in three of the four areas increased steadily from 1990 to 1993 (Figure 3). In total, attendance rose an estimated 118 murres per year, or approximately 18% annually (Figure 3). These high annual increases are the strongest indication that there was a large negative impact on the pre-1990 population (presumably the *Exxon Valdez* oil spill of 1989). Annual increases of +20% indicate that following the *Exxon Valdez* oil spill either breeding murres stayed away from the colony for several years (see Sydeman 1993), or adults were immigrating into the Barren Islands population, or some combination of the two. However, not all colony locations experienced such dramatic increases. On East Amatuli Light Rock, timelapse Camera 1 (located on the upper flat portion of the subcolony, to the immediate Northeast of the navigation light) attendance counts did not vary significantly (Table 1). That we did not see an island-wide pattern of dramatic increase suggests that all parts of the island are not necessarily affected in a similar manner by a single event such as an oil spill. Some locations on East Amatuli may be "optimal" nesting habitat, such that vacant spaces were quickly filled by migrating (local or regional) adults. There is some indication from long-term banded populations that movement between colonies of reproductively active adults does occur (Halley and Harris 1993). By 1991, the first year time-lapse camera data were collected, "optimal" locations may have already stabilized.

While the breeding population may appear to be in recovery, the total population (i.e. including the non-breeding component) may have sustained a serious loss. If what we are seeing is an equilibration of the breeding population at the expense of the "standing stock" of the non-breeding population, further perturbations could seriously affect murre population numbers and reproductive success. Thus, we still know little about the Exxon Valdez oil spill effect on murre population resiliency even though we can find no evidence of massive damage, either mortality or denigrated reproductive success, to the population.

Reproductive Success

In all years, murres nesting on Light Rock produced eggs and chicks, although there were differences in both phenology and reproductive success. During 1990-1992, eggs and chicks were observed directly by field personnel visiting Light Rock. In 1991, 1993, and 1994, time-lapse 35mm movie cameras recorded the reproductive activity of subplots of murres nesting on the flat top (1 to 3 cameras/year) and sloped sides (1 to 2 cameras/year) of the Rock. Because the latter method is remote and does not disturb the birds, a more accurate picture of reproductive success is possible.

For the time-lapse cameras, we defined reproductive success as a range of values bounding the probable true value (see Table 1). The pairs we followed do not represent 100% of the birds in each camera plot, but the number of pairs for which we were able to view eggs and/or chicks repeatedly. In the plots for which eggs, and especially chicks, could never be seen, the number of pairs followed is much lower than the probable number of reproductive pairs (i.e. Cameras 3 and 4). Reproductive success of followed pairs ranged from 0.65 to 0.93 fledglings per pair over the 243 pairs followed (Table 1). In 1993, pairs in the Camera 2 plot experienced lower reproductive success (0.58); however, this low value was not a result of natural processes but instead stemmed from a

Coast Guard helicopter landing on Light Rock on August 12, 1993 which caused many adults to temporarily desert and therefore led to the loss of eleven eggs. If these birds are not included in the reproductive success calculation, success increases to 0.79 fledglings per pair. In general, once eggs had hatched, the chance of chick mortality was quite small, even during large disturbances such as that caused by the helicopter landing in 1993.

In 1991, 1993, and 1994, phenology could be explicitly assessed on the timelapse camera plots. In other years (1977-1979; 1992) visits were made to the $5 \times 5 \text{ m}$ plot (location of Camera 2 in 1993 and 1994), and the number of eggs were counted. Thus, it is possible to assess whether egg presence is consistent with phenology patterns on the camera plots, or whether phenology was earlier in non-timelapse years. It is difficult to determine whether phenology was ever later, as lower egg values might be due to either later laying, lower overall production, or both. Because visits to the $5 \times 5 \text{ m}$ plot disturbed the murres, there was associated egg loss, primarily due to predation by Glaucous-winged Gulls. Although there was re-alying, egg predation undoubtedly decreased production, making absolute comparisons with time-lapse camera data inappropriate.

There are two evident phenological patterns. Within a year, laying was not necessarily synchronous across Light Rock, although it appeared to be synchronous within each camera plot. In 1993, murres nesting on the flat top of the rock laid 6 days earlier than murres nesting along side ledges. Between years phenology also changed (Figure 4). From 1991 on, lay date appears to get progressively earlier, although this pattern is somewhat confounded by 1992 (Figure 4). There have been claims that murre phenology following the Exxon Valdez oil spill has been significantly later than in previous years. It appears that egg laying on the 5 x 5 m plot in 1977 and 1978 was early relative to 1979, and that egg production in 1977 was very high. Visual inspection indicates that 1978 is phenologically comparable to 1993 and 1994, while 1979 is closer to 1990 (Figure 4). Acknowledging that these data are severely limited, we find no consistent pre-post spill pattern.

Although there has been some concern that the Exxon Valdez oil spill caused a persistent decline in the reproductive output of the remaining East Amatuli population, we found no evidence to support this contention. In reality, pre-spill reproductive data do not provide an accurate picture of reproductive success, as the only available data come from visits to the 5 x 5 m plot (Boersma et al. 1995). If the post-spill population was indeed severely hampered in egg and chick production, we would have expected that reproductive success in 1991 would have been low relative to other closely monitored

populations in Alaska. In fact, this is not the case. It is possible that the birds nesting on Light Rock occupy the most optimal habitat and, as such, experienced little of the postspill repercussions ascribed to other sectors of the Barren Islands murre population. In 1993 and 1994, the U.S. Fish & Wildlife Service personnel collected data on reproductive success of pairs nesting on the East Amatuli headland immediately east of Light Rock.

Fork-tailed Storm-petrel

Reproductive Success

Throughout the 1990's, occupancy in marked nests has hovered between 40 and 50 percent (Figure 5, Table 2). Although occupancy in 1991 appears to drop, it is actually higher than calculated because unfound nests (i.e. previously marked nests which remained un-located through the season presumably because the stake disappeared; NNF) and collapsed nests (nest collapse occurred over the winter; COLL.) were not recorded, erroneously inflating the number of available but unoccupied nests. Hatching success (chicks/eggs) and fledging success (fledgings + healthy end-of-season chicks/hatchlings) of both marked and new nests appeared to rise throughout the 1990's (Figures 6 & 7). This pattern may be an artifact of a change in methods from 1990-1993 to 1994. During 1994, nests were only checked intermittently (2-3 times per trip), as opposed to a regular three-day schedule in prior years. The number of nest checks prior to mean hatch date for the colony within year is negatively correlated with hatching success in a stepwise fashion (Figure 8). In other words, five or fewer nest checks result in lower abandonment, and thus higher hatching success. Therefore, the higher hatching and potential fledging success in 1994 could be partially the result of lowered disturbance levels. For nests checked on a regular basis (i.e. 1990-1994), experienced adults from marked burrows appeared more likely to desert (as measured by relative hatching success) than unbanded adults from nests which were newly found that year (i.e. birds inexperienced with humans). It is unclear what is determining this behavioral pattern in the adults. However, once chicks had hatched, nest status (marked or new), as well as number of times nests were checked prior to fledging, appeared to have little influence on fledging success.

The negative correlation between nest-check frequency and hatching success, combined with the counter-intuitive difference in hatching success between old (marked) and new nests, suggests that long-term monitoring projects need to seriously consider researcher effects. Chronic trampling of the vegetation results in soil compaction and gulley formation. Eventually, this erosional process may decrease the inherent worth of

nearby nests, forcing the residents to find new nest sites. Therefore, long-term monitoring programs need to first assess what level of reproductive information is necessary relative to the expected reproductive impairment of the population as a result of collecting those data. We suggest a hierarchical approach: 1.) long-term marked nests should be used for chick growth studies as the latter does not appear to be affected by human disturbance and 2.) new nests in similar habitat to the marked nests should be used to determine annual reproductive success. Ideally, the nests used for reproductive success should be checked intermittently, 2-3 times early in the season to assess occupancy and forecast mean hatch, 3-4 times around mean hatch, and 2-4 times late in the season just prior to fledging.

Chick Growth

Both tissue growth rate and weight gain fluctuated throughout the 1990's (Figures 9A-E). In 1993 and 1994, it took approximately 57 days for the average chick to grow their wings from 10% (birth) to 90% of adult wingchord length (full adult wingchord length was set at 162 mm). By contrast, the average length of time required in 1990 was 68 days, an approximately 20% difference. Weight gain followed a similar pattern: at 70 days the average chick weighed 96 grams in 1994 and only 75 grams in 1990. These dramatic differences in annual growth may reflect fledging success to some degree, as a higher percentage of chicks fledged in faster growth, heavier years (i.e. 1994).

Boersma and Parrish (in prep.) hypothesize that the demonstrable changes in mean annual growth rate reflect the fact that Fork-tailed Storm-petrel growth is primarily externally regulated by food supply. Changes in weight gain probably reflect food quantity, while changes in wingchord growth rate reflect changes in food quality. Thus it is possible to have high availability of low quality prey (i.e. high lipid, low protein producing fat chicks with slow wing growth), as may have been the case in the 1990's. Conversely, it is also possible to have high availability of high quality food (i.e. high protein leading to fast wing growth) as was seen in the 1980's. This challenges the idea that seabird growth, particularly in the storm-petrels, is regulated by bottlenecks in anatomical development (Ricklefs 1979). Changes in both wing growth patterns and weight gain are likely the synergistic result of changing food availability as well as changing food quality. Food availability may change on an intraseasonal basis and in an unpredictable fashion. Food quality may be changing over longer periods of time (e.g. decades) as a result of several potentially interacting events: decadal shifts in oceanic warming (Royer 1989), chaotic disturbance such as El Niño-Southern Oscillation, shifts

in trophic structure as a result of long-term fishing pressure (Springer et al. 1986), and short-term shifts in trophic structure caused by oil pollution.

General Discussion

Determining how perturbations affect seabird biology is particularly difficult because both natural and human induced changes are occurring continuously. Furthermore, the strength and direction of natural perturbations are both variable and chaotic. However, if we can use these "natural experiments" as indicators of how the changing environmental conditions will impact seabirds, we will perhaps be able to forecast how additional human-induced changes will alter seabird population biology.

Because seabirds can modify their behavior and foraging patterns, many species are able to ameliorate the effects of environmental change. For this reason, it is difficult to use seabirds as indicators of environmental change without extensive information on their biology. An understanding of natural biological variation and what causes variation to differ in direction or degree is also needed (Wiens 1995).

Physical oceanography is largely driven by climatic changes. Intensity of upwelling and sea-surface temperature are known to be linked to some seabird demographic parameters (Boersma 1978). There is increasing evidence that seabirds are sensitive to changes in these physical variables. Population changes of seabirds in the Farallons appear to track temporal variation in some large-scale oceanic conditions (Ainley and Lewis 1974). Ainley, Sydeman and Norton (in press) argue that the intensity and geographical extent of the Aleutian Low Pressure System may alter wind patterns, upwelling patterns, and consequently affect the food supply, thereby affecting seabird reproductive and population biology in the Farallon Islands. For example, breeding of Common Murres in the Farallon Islands has become earlier and is correlated with an increase in sea-surface temperature along the coast of California from the 1970's through the 1990's (Sydeman and Ainley 1994). Both the Common Murre and Cassin's Auklet (Ptychoramphus aleuticus) delayed reproduction in the Farallon Islands in 1982-1983 and 1992-1993, apparently in response to El Niño. Apparently, higher productivity is associated with earlier egg laying dates in murres (Sydeman and Ainley 1994). Interestingly, only two species of seabirds on the Farallon Islands, both storm-petrels, appeared to show little response to annual variability in marine productivity.

Our data from the Barren Islands characterizes a very different system, but a strikingly similar pattern. Royer (1989) reports that the Gulf of Alaska has been warming since the mid-1970's. In general, warmer waters are associated with lower productivity. The negative trend in the onset of egg laying (i.e. delayed) in the Barren Islands murre

population is correlated with a general increase in sea surface temperature in the north Gulf of Alaska.

One of the most striking aspects of this comparison is the apparent dovetail effect of north versus south. For instance, egg laying of murres on East Amatuli Island appeared to be earlier in 1977 and 1978 and later in 1979. The opposite pattern is shown by murres on the Farallon Islands which laid later in 1977 and 1978 than they did in 1979. Egg laying in 1979 and 1991 appeared to be earlier than normal in the Farallon Islands but later than normal in the Barren Islands. This opposition may represent evidence of alternating strengths and weaknesses in the Alaska and California current systems, as both originate from the North Pacific Current. However, this alternating pattern is disrupted in years when the entire Pacific basin is affected, such as an ENSO year, suggesting that major oceanographic perturbations can dwarf local oceanographic trends. Thus, 1992 was a very poor reproductive year for murres in both the Farallon Islands and the Barren Islands, presumably because of El Niño.

Fork-tailed Storm-petrel data from the Barren Islands are consistent with the interpretation that major oceanographic changes are occurring in the north Gulf of Alaska. Generally, growth rates of storm-petrel chicks have been slower in the 1990's than in the mid-1970's and early 1980's, suggesting that food availability and/or quality has changed. This is perhaps a surprising result given that of the 12 species of breeding birds on the Farallon Islands, only 2 species showed little response to annual variability: Fork-tailed and Leach's storm-petrels.

In contrast to most natural perturbations, which can have either negative or positive impacts, most human perturbations have negative impacts on seabirds. Oil spills are among the most dramatic human perturbations in the marine environment. However, the relative importance of massive versus chronic oil spills in structuring seabird breeding populations is unclear. Oil spills often result in a spike in adult seabird mortality; however, the long-term effects on seabird populations are not known. Some researchers have pointed out that although oil spills undoubtedly kill thousands of seabirds, average winterkill can reduce a population by 5-20% each year (Dunnet 1982, Clark 1984), leading one to the conclusion that oil spills are a minor component of seabird mortality. However, other authors have pointed out that winterkill disproportionately removes young-of-the-year and juvenile birds, while oil spills can principally affect breeders, particularly if the spill occurs close to breeding colonies during the breeding season (Piatt et al. 1991). In sum, without long-term monitoring of specific populations, it will be impossible to make blanket statements about the effects of oil spills on seabird populations, relative to other mortality. agents, whether natural (e.g. ENSO, food

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availability, winterkill) or anthropogenic (e.g. gillnet bycatch, direct competition with fisheries, introduced predators).

The Barren Islands data do not appear to shed light on this dilemma, in that although the *Exxon Valdez* oil spill killed many thousands of seabirds, it was impossible to detect long-term differences in response to the spill by Common Murres and Fork-tailed Storm-petrels. The impact on these two species was expected to differ, as large numbers of murres were killed by the oil and apparently few Fork-tailed Storm-petrels were killed by the oil (Piatt et al. 1990).

Since we first began working in the Barren Islands in 1976, use of the waters around the islands and of the islands themselves has increased dramatically due to increased boat traffic, fishing, scientific visits, and tourism (Boersma pers. obs.). Distinguishing the negative effects on area seabirds of these increasing human uses of the area from impacts associated with oil development and transport in the Cook Inlet area would be difficult. When coupled with natural perturbations and long-term oceanographic trends, teasing out cause-and-effect becomes impossible without a solid, long-term database designed to detect subtle changes in population parameters on a broad scale.

With the effects of several scales of perturbations occurring why haven't there been more obvious changes in seabird populations in the Barren Islands? The answer to this question lies in seabird breeding biology. Seabirds are long-lived and hence changes in reproductive success may not be apparent for a decade or more. Many species have the ability to switch food sources should conditions change, a further buffer against environmental variability. Changes in the level of adult mortality are expected to produce long-term effects in population structure and reproductive function. Why then did we see few changes, other than direct mortality, from the Exxon Valdez oil spill? The answer may be in the non-breeding component of seabird populations. We know almost nothing about this component of the population: how big it is, its age structure, and its geographic range. Seabird populations may be buffered from adverse effects, both natural and human-induced, by their non-breeding pool. The level of resilience provided by non-breeders would thus be affected by the frequency and magnitude of disturbance. Additional human-induced disturbance in a system already susceptible to broad fluctuations in natural perturbation may deplete the built-in reserve offered by nonbreeders. Whether this is true, and how important the non-breeding pool of birds is, remains to be tested.

The *Exxon Valdez* oil spill demonstrated that the Barren Islands are likely to be an important reference site. The location of the Barren Islands and extreme tidal

exchange that characterizes the area make them ideal for examining the effects of both natural and anthropogenic disturbance on seabird populations. Some baseline information is available and patterns of change can be detected. Reference areas will become increasingly important in determining both short and long-term environmental change. However, routine monitoring without scientific innovation will not be adequate for the challenge, because refinements in data collection must be made over time in order to test relevant, time-sensitive hypotheses. For instance, it is clear from our study and others (e.g. Hatch and Hatch 1989) that single, yearly censuses can only provide a broad estimate of population size, rather than a specific statistically robust number. However, the effort required to collect statistically adequate data at the level of entire colonies may be economically unfeasible in the long-term. Therefore, we recommend the adoption of methods, such as our timelapse camera system (allowing extremely accurate data collection on a small part of the colony), which speak to both long-term monitoring and statistical robustness; both are needed should future injury and damage assessment be necessary.

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Table 1	Reprod	uctive succ	ess for all pa	airs of Commo	n Murres that	could be fol	lowed
within	each time	-lapse came	era plot, East	Amatuli Ligh	t Rock, Barre	n Islands, Al	aska.

within each time-tapse camera plot, East Amatun Light Rock, Darren Islands, Alaska.								
Camera-Year	Attendance $(X \pm SD)$	Number of eggs	Number of relays	Number of chicks	Reproductive Success			
C1 - 1991	57 <u>+</u> 5.1	46	4	34	0.74-0.76			
C1 - 1993	57 <u>+</u> 9.6	41	1	34	0.76-0.89			
C2 - 1993	58 <u>+</u> 3.0	44	4	24	0.58-0.79			
C3 - 1993	35 ± 5.0	19	-	17	0.79-0.89			
C4 - 1993	62 ± 7.9	24	1	19	0.65-0.83			
C1 - 1994	52 ± 3.7	39	0	36	0.90-0.92			
C2 - 1994	59 ± 5.1	41	1	38	0.93			

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Table 2. Reproductive success for all marked burrows of Fork-tailed Storm-petrels within 6 study sites (A-E, Z). Status refers to whether the burrow was marked in a previous year (OLD) or newly marked that year (NEW). Within a year, old burrows (TOTAL), could be either not found (NNF), found but collapsed (COLL.), or occupied by at least one adult on one occasion (OCC.). Within the category occupied, the majority of the burrows had actively reproducing pairs (ACTIVE), indicated by the presence of an egg. Fledging was defined as chicks which fledged during our field season, or chicks in healthy condition at the end of the season.

					1990					
	STATUS	AREA	TOTAL	NNF	COLL.	OCC.	ACTIVE	CHICKS	FLEDGED	
	OLD	A	143	1	1	67	66	17 -	- 5 .	-
		В	53	0	1	30	30	3	2	
		C	29	0	0	13	• 13	2	0.	~
	•	D	174	1	0	91	89	14	5	
		E	122	2.	0	56	56	15	7	·
=		Z		0	0	<u> </u>	17	6	4 -	-
	NEW	A	14			14	14	6	1	
		В	7			7	7	0	0	
		C	0 -	•		0	. 0	0	0	
		D	37			36	36	9	3	
		E	62			60	60	26	7	
		Z	1			1	· 1	0	0	
					1001			-, ·	1.	
		*			1991	•		<u> </u>	•	
	STATUS	AREA	TOTAL	NNF	1991 COLL.	OCC.	ACTIVE	CHICKS	FLEDGED	-
-	STATUS OLD	AREA	TOTAL	NNF	1991 COLL.	OCC. 51	ACTIVE 31	CHICKS 8	FLEDGED 4	-
-	STATUS OLD	AREA A B	TOTAL 152 53	<u>NNF</u> -	1991 COLL.	OCC. 51 18	ACTIVE 31 15	CHICKS 8 1	FLEDGED 4	-
_	STATUS OLD	AREA A B C	TOTAL 152 53 29	NNF - - -	1991 COĽL. -	OCC. 51 18 11	ACTIVE 31 15 11	CHICKS 8 1 2	FLEDGED 4 1 1	-
_	STATUS OLD	AREA A B C D	TOTAL 152 53 29 184	NNF - - - -	1991 COLL. - - -	OCC. 51 18 11 42	ACTIVE 31 15 11 36	CHICKS 8 1 2 12	FLEDGED 4 1 1 - 11	-
_	STATUS OLD	AREA A B C D E	TOTAL 152 53 29 184 130	NNF - - - - -	1991 COLL. - - - -	OCC. 51 18 11 42 26	ACTIVE 31 15 11 36 21	CHICKS 8 1 2 12 3	FLEDGED 4 1 1 - 11 2	-
	STATUS OLD	AREA A B C D E Z	TOTAL 152 53 29 184 130 35	NNF - - - - -	1991 COLL. - - - - - -	OCC. 51 18 11 42 26 11	ACTIVE 31 15 11 36 21 9	CHICKS 8 1 2 12 3 2	FLEDGED 4 1 1 1 - 11 - 2 1	-
-	STATUS OLD NEW	AREA A B C D E Z A	TOTAL 152 53 29 184 130 35 12	NNF - - - - - -	1991 COLL. - - - - -	OCC. 51 18 11 42 26 11 12	ACTIVE 31 15 11 36 21 9 12	CHICKS 8 1 2 12 3 2 3	FLEDGED 4 - 1 1 - 11 - 2 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1	-
-	STATUS OLD NEW	AREA A B C D E Z A B	TOTAL 152 53 29 184 130 35 12 0	NNF - - - - - -	1991 COLL. - - - - -	OCC. 51 18 11 42 26 11 12 0	ACTIVE 31 15 11 36 21 9 12 0	CHICKS 8 1 2 12 3 2 3 0	FLEDGED 4 -1 1 -1 -1 -1 -1 -1 -1 -1 -1	-
-	STATUS OLD NEW	AREA A B C D E Z A B C	TOTAL 152 53 29 184 130 35 12 0 0	NNF - - - - -	1991 COLL. - - - - -	OCC. 51 18 11 42 26 11 12 0 0	ACTIVE 31 15 11 36 21 9 12 0 0 0	CHICKS 8 1 2 12 3 2 3 0 0 0	FLEDGED 4 - 1 1 - 11 2 1 - 1 0 0	-
	STATUS OLD NEW	AREA A B C D E Z A B C D	TOTAL 152 53 29 184 130 35 12 0 0 28	NNF - - - - -	1991 <u>COL'L.</u> - - - - -	OCC. 51 18 11 42 26 11 12 0 0 28	ACTIVE 31 15 11 36 21 9 12 0 0 28	CHICKS 8 1 2 12 3 2 3 0 0 5	FLEDGED 4 - 1 1 - 11 - 11 - 2 - 1 - 1 - 0 - 0 - 3	-
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	STATUS	AREA	TOTAL	NNF	COLL	OCC.	ACTIVE	CHICKS	FLEDGED	• •	
	OLD	A	180	6	6	72	68	28	18		
		B	54 29	2	4 7	33 12	33	14 5	9.		
		D	215	27	1	97	97	54	29		
		E Z	177 37	28 4	7	74 16	74	32	14		
	NEW	<u> </u>	10			8	7	3	2		
		B	1		· ·	1	1	0	0		
		D	0 10		~	0 7	0 7	0 5	0		
		E	8		•	4	4	3	1		
		Z	I			1	1	1	0		
•					1993						
	STATUS	AREA	TOTAL	NNF	COLL.	<u> </u>	ACTIVE	CHICKS	FLEDGED		
	ULD	B	54	0	5	28	23	8	5		
		C	29	0	0	10	9	3	2		
		E D	230 196	24 33	4 6	60	99 56	54 28	23 15		
		<u>Z</u>	37	3	0	17	16	5	4		
	NEW	A B	1			1	1	1	1		
		Č	0			0	0	$\overset{1}{0}$	0		
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	STATUS	AREA	TOTAL	NNF	COLL.	OCC.	ACTIVE	CHICKS	FLEDGED
-	OLD	A	176	8	8	68	63	48	45
		B	56	0	7	24	20	16	15
			29	07	2	10 86	8 79	0 58	5 57
		Ĕ	200	6	1	83	74	57	51
_		Z	34	0	2	10	8	6	6
	NEW	A	6			6	5	4	4
		, B	_ 3			3	3	. 2	, 2
			12			<u>;</u> 0 12	10	9	9
		Ē	28	2		28	25	17	17
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Figure 1. Topographic map of East Amatuli Island, Barren Islands, Alaska, showing the placement of six Fork-tailed Storm-petrel study areas with permanently marked burrows (A, B, C, D, E, Z), the Common Murre census areas (Oval, Swatch, Triangle Rock), and Light Rock - the site of Common Murre reproductive success assessment (5x5m plot; 35mm time-lapse camera plots). Inset is location of East Amatuli relative to the Barren Islands system.



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Figure 2. Sea surface temperature anomaly, by month, integrated over a 2° square centered on the Barren Islands (1975-1991). Temperatures greater or less than 1° are shown by open circles. All data from COADS.



Figure 3. The average annual attendance of Common Murres at four multiple-count areas (Oval, Swatch, Triangle Rock South and Northwest, respectively). Lines are least-squares fit. Slopes are indicated as the average gain in attendance per year. R² values indicate slope fit. Total attendance summed over all four areas, and the corresponding percentage increase is indicated below each year. Percent increase is calculated as (1-(larger value/smaller value)) to correct for polarization.



Figure 4. Phenology in Julian days, as assessed by the number or percentage of eggs laid, of Common Murres nesting on East Amatuli Light Rock from 1977 to 1994. 5x5 - the original plot set up by Manuwal and Boersma, which was visited 1-3 times each year (data are actual number of eggs on the plot); TLC - time-lapse camera #1 plot located above and west of 5x5 plot (data are percent of total eggs laid). A zero (0) indicates a visit was made but no eggs were present. TLC data are cut off when all eggs are laid (i.e. 100% is reached).

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Figure 5. Nest occupancy in permanently marked burrows of Fork-tailed Storm-petrels, 1990-1994.

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Figure 8. Hatching success of Fork-tailed Storm-petrels as a function of the average number of nest checks before mean hatch date, by year. Permanently marked nests are filled circles, new nests, by year, are open circles. Numbers above each filled circle are years.





