

Exxon Valdez Oil Spill
Restoration Project Final Report

Recovery Monitoring of Pigeon Guillemot Populations
in Prince William Sound, Alaska

Restoration Project 94173
Final Report

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May 1995

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Study History: The field work for Restoration Project 94173 was conducted during the summer of 1994. Previous related projects have been funded by the Trustee Council. Bird Study Number 9 (Oakley and Kuletz 1994), begun in 1989 immediately after the oil spill, compared various population and reproductive parameters of pigeon guillemots before (Oakley and Kuletz 1979, Kuletz 1981, 1983, Oakley 1981) and after the spill. Also, Project 93034, an extensive survey of pigeon guillemot colonies throughout Prince William Sound, was conducted during the summer of 1993 (Sanger and Cody 1994).

Abstract: The population of pigeon guillemots in Prince William Sound decreased from about 15,000 (1970's) to about 5,000 (present). Some local populations were affected by the *T/V Exxon Valdez* oil spill in 1989, but there is evidence suggesting the Sound-wide population was already declining. In 1994, we monitored 22 guillemot nests on Naked Island (NI) and 24 on Jackpot Island (JI) from egg stage through fledging. Hatching success was 0.90 (n = 39, NI) and 0.80 (n = 46, JI); fledging success was 0.51 (n = 35, NI) and 0.76 (n = 37, JI). On NI, predation was the cause of numerous nesting failures. The most likely predators were mustelids. Predation on eggs by corvids was also suspected. Although predation was infrequent or nonexistent on JI, abandonment of eggs was high. Sand lance accounted for about 1% and 8% of prey items delivered to guillemot chicks at JI and NI in 1994; before the spill, sand lance were the single most important component of chick diet at NI. Gadids were more prevalent in the diet of guillemot chicks at NI in 1994 (ca. 30%) than in 1979-1981 (< 7%). Changes in the relative proportions of benthic and schooling fish in the diet of guillemot chicks might represent a key change in the ecosystem that is affecting other species of marine birds and mammals in the Sound.

Key Words: Alaska, *Cephus columba*, foraging ecology, Jackpot Island, Naked Island, oil spill, pigeon guillemot, population, Prince William Sound, predation, productivity, *T/V Exxon Valdez*

Citation: Hayes, D.L. 1995. Recovery monitoring of pigeon guillemot populations in Prince William Sound, Alaska, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94173), U.S. Fish and Wildlife Service, Anchorage, Alaska.

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ACKNOWLEDGMENTS

I thank Mary Cody, Kirk Lenington, John Maniscalco, Bev Short, and Ed Vorisek for help in the field, and Mark Esslinger and Burt Pratte for help with logistics. The crew of the Alaskan Gypsy and the marbled murrelet field team helped with the capture of adult pigeon guillemots. The U.S. Forest Service granted us permission to use Naked Island as our base of operations while in the field. I also thank Debbie Flint for making the maps and Mary Blake for typing the tables. Bryan Manly suggested the use of certain statistical analyses for some of the data and performed the randomization analysis of the growth data. Discussions with George Divoky, David Irons, Kathy Kuletz, and Dan Roby regarding various aspects of this project have been most helpful. The original manuscript of this report has been greatly improved through many helpful suggestions by Tony DeGange.

EXECUTIVE SUMMARY

The pigeon guillemot (*Cepphus columba*) is a cavity-nesting, pursuit-diving seabird that forages in nearshore waters. Guillemots are common, easily observed birds in parts of coastal Alaska. Between the early 1970's and the early 1990's, the population of pigeon guillemots in Prince William Sound (PWS) decreased from about 15,000 to less than 5,000. Over 600 carcasses of pigeon guillemots were recovered in the four months following the *T/V Exxon Valdez* oil spill in March of 1989, and these probably represent only a fraction (ca. 10-30%) of the actual number killed. Although some local populations of guillemots were affected by the spill, there is evidence suggesting that the Sound-wide population was already declining.

We studied the breeding and feeding ecology of pigeon guillemots nesting on two islands in the western part of PWS during the 1994 field season. Our objectives were to examine the effects of food availability and diet, predation, and adult survival and recruitment on productivity and numbers of guillemots in different parts of PWS.

We marked 51 pigeon guillemot nests on Naked Island (NI) and 37 nests on Jackpot Island (JI). Of these nests, we monitored 22 on Naked I. and 24 on Jackpot I. from the egg stage through fledging. Hatching success was 0.90 (n = 39, NI) and 0.80 (n = 46, JI); fledging success was 0.51 (n = 35, NI) and 0.76 (n = 37, JI). Chicks raised on Jackpot I. grew at a faster rate and fledged at significantly greater weights than chicks raised on Naked I.

On Naked I., predation during the chick stage was the cause of numerous nesting failures (8 of 35 nests, or 23%). Decapitated carcasses of chicks found near depredated nests suggest that the predators were mustelids. River otters (*Lutra canadensis*) were often seen around the guillemot colonies, and were the most likely predator, although mink might also have been responsible. Predation on eggs by corvids was also suspected. Although we saw the same species of potential avian and mammalian predators on or around Jackpot I., we found no evidence of predation. However, the abandonment of eggs on Jackpot I. was much higher than on Naked I. Depredation of guillemot nests on Naked I. was not common during previous studies, but is now a major factor affecting their reproductive success. Studies at other guillemot colonies have related lowered productivity or emigration to the presence of mammalian predators, especially otters and mink.

The adults breeding on Naked I. foraged mostly in the shallow waters surrounding the island. Guillemots breeding on Jackpot I. foraged farther from their colony, apparently because of the lack of shallow water around Jackpot I. Based on their flight directions, these birds presumably foraged near Jackpot Bay and Icy Bay. There was a marked difference in the proportion of schooling fish in the diet of chicks at the two islands. Sand lance accounted for about 1% and 8% of prey items delivered to guillemot chicks at Jackpot I. and Naked I. in 1994. Before the spill, this species was the single most important component of the chick

diet at Naked I. Gadids were much more prevalent in the diet of guillemot chicks at Naked I. in 1994 (ca. 30%) than in 1979-1981 (< 7%). There are no historical data for Jackpot I. The apparent decline in the abundance of sand lance and changes in the relative proportion of benthic and schooling fish in the diet of guillemot chicks might represent a shift in the ecosystem that is affecting other species of marine birds and mammals in PWS.

INTRODUCTION

The pigeon guillemot (*Cepphus columba*) is a pursuit-diving seabird that forages mostly in nearshore waters about 10-30 m deep (Storer 1952, Ewins 1993). Adults feed primarily on benthic fish and invertebrates, but also on schooling fish. Chicks are fed mostly fish. Guillemots nest in small scattered colonies or in solitary pairs in natural cavities along rocky shorelines. Unlike most other members of the family Alcidae, the pigeon guillemot typically lays a clutch of two eggs. The chicks are semiprecocial, usually spending about 35 to 45 days in the nest. During the daylight hours, they are fed by both parents, which return to the nest with one fish at a time in their bills.

The population of pigeon guillemots in Prince William Sound (PWS) has decreased from about 15,000 in the 1970's (Dwyer et al. ND) to less than about 5,000 in the 1990's (Agler et al. 1994, Sanger and Cody 1994). There is some evidence suggesting that this population was in decline before the *T/V Exxon Valdez* oil spill in March of 1989 (Oakley and Kuletz 1994). Over 600 guillemot carcasses were recovered after the spill, but this might represent only 10-30% of the actual number killed (Piatt et al. 1990). Based on censuses taken around the Naked Island complex (Naked, Peak, Storey, Smith, and Little Smith Islands), prespill counts (ca. 2,000 guillemots) were roughly twice as high as postspill counts (ca. 1,000 guillemots; Oakley and Kuletz 1994). Also, on Naked I., the relative decline in the numbers of guillemots was greater along oiled shorelines than along unoiled shorelines (Oakley and Kuletz 1994).

King and Sanger (1979) considered the pigeon guillemot to be one of the birds that is most vulnerable to oil spills because of its nearshore foraging habits. Several studies have reported sublethal toxic effects of oil on marine birds (Peakall et al. 1980, Peakall et al. 1982, 1983 as cited in Oakley and Kuletz 1994). Marked declines in populations of the pigeon guillemot or its congener, the black guillemot (*C. grylle*) have been attributed to oil pollution (Ainley and Lewis 1974, Asbirk 1978, Ewins and Tasker 1985).

At Naked I., adult guillemots delivered fewer schooling fish, particularly sand lance (*Ammodytes hexapterus*), to their chicks after the spill than before the spill (Oakley and Kuletz 1994). Numerous studies have shown that changes in the availability of prey species can result in widespread reproductive failure of seabirds (Vermeer et al. 1979, Anderson et al. 1982, Springer et al. 1986, Safina et al. 1988, Uttley et al. 1989, Furness and Barrett 1991; but see Burger and Piatt 1990).

Predation on eggs and chicks, not important previously on Naked I. (Oakley 1981, Kuletz 1983), was a major factor contributing to the lower reproductive success of guillemots after the spill (Oakley and Kuletz 1994). Studies at other guillemot colonies have related lowered productivity or emigration to the presence of mammalian predators (Asbirk 1978, Petersen 1979, Cairns 1985, Ewins 1985, 1989).

Thus, because 1) pigeon guillemots constitute an injured resource, 2) their population has been declining for some time, 3) there has been a marked change in their diet, 4) predation at the nest is more prevalent than in the past, and 5) there exist valuable prepill data for this species in PWS, they have been selected for intensive study. We studied the breeding and feeding ecology of pigeon guillemots nesting on two islands in the western part of PWS and found important differences between the two populations relative to the productivity of the colonies, the foraging habits of adults, diet of chicks, and the levels of predation occurring during the chick stage.

OBJECTIVES

1. Determine if availability of food is limiting reproductive success of guillemots by collecting the following kinds of data:
 - a. Measuring breeding parameters, including phenology, chick growth rates, fledging weights, and reproductive success at colonies on Naked and Jackpot Islands.
 - b. Measuring foraging parameters, including diet and provisioning rates of chicks, and location of foraging areas.
2. Determine if predation on eggs or chicks is limiting reproductive success by measuring relative rates of predation during the egg and chick stage in different habitats and at different colonies.
3. Determine if adult survival and recruitment are affecting the population of guillemots by banding adults and chicks.

METHODS

Study Area

Our field season extended from 19 May through 22 August 1994. Our two principal study sites were located on Naked I. and Jackpot I. in PWS (Fig. 1). Naked I. (ca. 3,862 ha) has a maximum elevation of 400 m and is part of a group of three main islands. The bays of Naked I., and the passages between it and the two neighboring islands, Peak and Storey, form an expanse of water that is less than 100 m deep. Jackpot I. (ca. 1.6 ha) has a maximum elevation of about 15 m and is located near the mouth of Jackpot Bay and the southern entrance to Dangerous Passage. Fool I. (ca. 12 ha, Fig. 1) was also a study site initially, but was discontinued later in the season. It lies in Wells Passage between Perry and Esther Islands, has a maximum elevation of about 20 m, and is surrounded by deep water on all sides. The shoreline of each of these islands is characterized by low cliffs and cobble or boulder beaches; high, steep, exposed cliffs occur along portions of the eastern shores of the Naked Island group. Each is forested to its summit; the principal species of tree are Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*). All of these islands are part of the Chugach National Forest.

Naked I., about 30 km southwest of the site where the *T/V Exxon Valdez* ran aground on Bligh Reef, was one of the first areas to be oiled (see Fig. 3, Kuletz 1994:35). Between 27 March and 2 April, 1989, portions of the eastern, northern, and northwestern shorelines were oiled. The prevailing winds moved most of the oil to the south, away from the island, but between 7 and 9 April, southerly winds brought the oil into contact with the southern and western shorelines of Naked I. again. Neither Jackpot nor Fool Island were oiled.

Selection of Study Sites

We chose Naked I. as one of our principal study sites and as a base of operations. This island has been used as a base camp for several previous guillemot studies (Oakley and Kuletz 1979, 1993, Eldridge and Kuletz 1980, Kuletz 1981, 1983, Oakley 1981). We made numerous trips to other areas of PWS looking for additional colonies that might also serve as study sites. The two main criteria for determining the potential of a new guillemot colony as a study site were the number of breeding guillemots in that colony and the accessibility of the nest sites. We examined guillemot colonies in some of the fjords of northwestern PWS: Passage Canal, Blackstone Bay, the Barry Arm off Harriman Fjord, and the Yale Arm off College Fjord (Fig. 1). We also examined several island colonies: the Pleiades, Fool I., Jackpot I., Bligh I., and Hinchinbrook I. (Fig. 1). We investigated several colonies on Storey and Peak Islands of the Naked Island group, as well as many scattered around Naked I. itself.

Censusing: Population and Colony Attendance

Pigeon guillemot populations of Naked, Peak, Storey, Smith, and Little Smith Islands (the Naked Island complex, Fig. 2) were censused by circumnavigating each island in a small boat at a distance of between 50 m and 100 m from the shore when the weather was good and the tides were near high. These censuses were conducted from 30 May to 1 June during the same time of day (0400-1000 Alaska Daylight Time) and at the same time of year that previous censuses of the this area were made. Guillemots at Jackpot I. were censused near the high tide on 11 June, but at 1330 instead of in the morning. Guillemots around Fool I. were counted on 15 June at 0530, which corresponded to peak tide. Also, throughout the breeding season, but mostly during the chick-rearing period, counts of the maximum number of guillemots present at a particular colony were made at 15-minute intervals whenever that colony was being monitored from a boat or a blind.

To examine colony attendance as a function of time of day, we made continuous 24-h watches at each of two guillemot colonies on Naked I. on 13-14 June and on 5-6 July. Observation shifts ranged from three to four hours.

Nest Sites and Monitoring

We marked 51 nests on Naked I., mostly at colonies along the western shoreline (Fig. 3), and 37 nests on Jackpot I. by painting a black number inside a white spot on nearby rocks. Some of the nests on Naked I. were known from previous studies, but most (65%) nests on Naked I. and all nests on Jackpot I. were found during the 1994 field season. We found some guillemot nests by searching potential nest sites in known colonies. Throughout the breeding season, but especially during the chick-rearing period, many new nests were opportunistically added to our sample as guillemots were discovered entering or leaving nest sites. Because of their inaccessibility or our inability to determine their contents, some of these nests were monitored only during feeding observations and were not used as part of our productivity sample. Nest sites were classified according to the type of habitat in which they occurred: tree root systems, rock crevices, or talus piles.

On Naked I., we checked nests at approximately four-day intervals initially, and then about every two days during the fledging period. Because of the distance from our base camp to Jackpot I., we checked nests there at eight- to eleven-day intervals initially, and then at four- to five-day intervals or more frequently later in the season.

Banding and Morphometrics

Adults were caught in mist nets over the water, in noose mats on communal rocks, or by hand or net at the nest. Adults were banded on the left foot with a USFWS metal band (bottom) and a color plastic cohort band (top), and on the right foot with a unique combination of two color plastic bands. Chicks were banded on the right foot with a USFWS metal band (bottom) and a color plastic cohort band (top) and on the left foot with a unique combination of two color plastic bands. The 1994 cohort plastic band was yellow. We banded 19 adults and 61 chicks. All birds received a USFWS band; all adults and most of the chicks also received the color bands.

We measured all adults that we handled and all accessible chicks. We measured tarsus, culmen, and gape to the nearest tenth of a millimeter with vernier or dial calipers and maximum wing chord with a rule to the nearest millimeter. We weighed birds with Pesola™ spring scales (0-100 g x 1 g, 0-500 g x 5 g, and 0-1 kg x 10 g) using the scale with the greatest precision possible. Newly hatched chicks were marked on the right foot and on the down of their head with paint markers to distinguish between alpha (first-hatched) and beta (second-hatched) chicks until they were large enough to be banded.

Nesting Chronology

Only nests that were discovered during the egg stage were used to construct the nesting chronology of guillemots at Naked and Jackpot Islands. For nests with two-egg clutches, eggs were assumed to have been laid on the same day and chicks to have hatched on the same day. If the laying date of the first egg of a two-egg clutch was known, the following day was used as the laying date for both eggs. Laying dates were sometimes back-calculated from hatching dates using 31 days as the incubation period for both eggs. Oakley and Kuletz (1994) used 32 days and 30 days for the incubation periods of the first and second chicks, respectively. For determining fledging dates of chicks still present in the nest when we left the study area, a chick was assumed to have fledged on the date of our last visit if the chick had been in the nest for 37 days or more. If the chick had not yet been in the nest for 37 days, then it was assumed to have fledged on that date in the future equivalent to a 37-day nestling period, which is the mean reported by Oakley and Kuletz (1994) for Naked I.

Productivity

We estimated productivity by two different methods. During the incubation stage, a nest was considered to be active and included in our sample if it contained at least one egg and if an adult was seen in that nest at least once. If we knew two eggs had been laid in a nest but saw only one chick and no sign of the other egg, we assumed that both eggs hatched and one chick died. It seems unlikely that a predator entering an active nest would take only one egg and leave the other intact. Also, based on other guillemot studies (G. Divoky, personal communication; D.L. Hayes, personal observation), the proportion of two-egg nests in which only one egg hatches is fairly low.

In the first method, we used only those nests that we followed from incubation through fledging. Productivity (chicks fledged/eggs laid) was defined as hatching success (eggs hatched/eggs laid) times fledging success (chicks fledged/eggs hatched). Thirty days is approximately the minimum time spent in the nest by guillemot chicks; the actual time is often much longer. For purposes of estimating fledging, however, any chick surviving in the nest for 30 days was assumed to have fledged.

Because there must have been some nests we never found that had lost eggs or chicks, and consequently our estimates of productivity were probably biased high, we also estimated productivity using the methods of Mayfield (1961, 1975). The Mayfield method eliminates some of this bias by recognizing that the number of nests lost will vary with the number of nests in the sample and with the length of time for which the sample is monitored. The probability that an egg present at the start of incubation will produce a fledgling was calculated as the product of A (the probability an egg will survive a 31-day incubation period); B (the hatching success rate of those eggs present in the nest throughout the incubation period);

and C (the probability a chick will survive a 30-day nestling period). Values for B were calculated as in the method described previously. Values for A and C were calculated from survival rates, which were based upon the "exposure" that each had in egg- or chick-days, respectively. When calculating exposure, if the number of eggs or chicks in a particular nest changed between visits, the change was assumed to have occurred at the midpoint of the interval, unless there was evidence to indicate otherwise, in which case the evidence was used to determine the date of the change. We used any nest for which we knew the contents on two or more dates, regardless of when the nest was found or how long we monitored it. This allowed us to increase our sample size and to make use of nests found later in the season.

Predation

Potential nest predators include the river otter (*Lutra canadensis*), mink (*Mustela vison*), northwestern crow (*Corvus caurinus*), common raven (*C. corax*), Steller's jay (*Cyanocitta stelleri*), and black-billed magpie (*Pica pica*). Bald eagles (*Haliaeetus leucocephalus*), peregrine falcons (*Falco peregrinus*), and other raptors might be predatory on adult and fledgling guillemots.

We set Havahart™ traps and checked them daily in an attempt to capture and identify potential predators. We disguised three traps as burrows by covering all but the entrance with moss, then baited them, first with eggs and later with fish. These were placed near guillemot nest sites in Cabin Bay that showed evidence of predation (an egg shell found in the open with a hole chewed in it but otherwise intact) and attempted predation (signs of scratching and digging directly above an active guillemot nest). They were monitored from 19 June through 1 July, which approximately coincided with the latter portion of the incubation period. We reset the traps at a new location in Cabin Bay and monitored them from 8 July through 27 July, which marked the early stages of the chick-rearing period. We did not disguise the traps at this new location and used various pieces of meat or fish as bait.

If eggs disappeared from nests between visits, we assumed that predation was the cause. If chicks too young to fledge (i.e., younger than 30 days) disappeared from nests between visits, we assumed predation was the cause only if we were reasonably certain that no chick was still in some hidden corner of the nest. In some instances, where the nest cavity was too long or labyrinthine, it was not possible to make this determination. If after repeated visits to this type of nest, we never saw the chick(s) again, we listed the cause of failure as unknown.

Chick Growth and Fledging Weights

We calculated the growth rates of chicks as the change in weight (g/d) during the linear phase of their growth, which is the period eight to 18 days after hatching (Koelink 1972). We measured few known-age chicks, so used wing length

as an index of developmental stage. Wing length can be measured easily and relatively consistently on chicks of all ages, especially after the feathers begin to develop. Also, the wing grows continually from hatching to fledging and is less sensitive than body mass to short-term deficiencies in nutrition (Ricklefs and White 1975).

A second-order polynomial was used to fit a curve to the data, where \ln body mass was plotted as a function of \ln wing length. The comparison between the growth rates of chicks on the two islands is confounded by the availability of different numbers of measurements on different chicks and different numbers of chicks in different nests. Thus, there is a complicated structure of interdependence among observations on each island. If this were not so, and observations from each chick were independent from those of other chicks on that island, then it would be possible to compare curves relating \ln body mass to \ln wing length by standard regression methods. Therefore, a randomization-based approach was used (Manly 1991). Preliminary analysis indicated that the relationship between body mass (B) and wing length (W) is well approximated on each island by an equation of the form

$$\ln(B) = B_0 + B_1 * \ln(W) + B_2 * \ln(W)^2. \quad (1)$$

Assuming this to be so, a measure of the extent to which the data are fitted better by separate equations for each island than by a single equation for both islands is the reduction in the coefficient of multiple determination (R^2), obtained when separate equations are fitted rather than a single equation. A test for whether this is a reduction is achieved by determining whether the observed reduction is significantly large in comparison to the distribution obtained for the same statistic by randomly reallocating nests (with all their associated measurements on one or two chicks) between the two islands, while keeping the number of nests on each island equal to the observed number.

Fledging weight was assumed to be the last recorded weight of a chick that was measured within one week of its departure from the nest. Chicks still in the nest when we left the study area were not included in the calculation of fledging weights.

Chick Provisioning and Diet

Either from blinds or from boats we observed adult guillemots bringing food items to their chicks throughout the chick-rearing period. Feeding watches ranged from 1.25 h to 24 h for a total of 388.75 h at Naked I. and 82.5 h at Jackpot I. Usually just one observer was in the blind at a time; shifts ranged up to six hours). Binoculars and spotting scopes were used to identify prey items in the bills of guillemots to the lowest possible taxon or "type" of prey. When time and visibility permitted, we also estimated the length of the prey item as a multiple of the guillemot's bill to the nearest half bill length. We recorded the time of each delivery and the number of the nest to which the prey was delivered, as well as how long the adult first remained on the water with the fish before delivering it.

We also recorded instances of attempts at kleptoparasitism or predation by gulls and raptors.

To test whether deliveries were distributed more or less evenly throughout the daylight hours, the day was divided into three approximately equal periods: early (0600-1100), mid-day (1100-1700), and late (1700-2200). Although a few deliveries occurred very early and very late, when it was too dark to make reliable observations, the period used for analysis was truncated at both ends in accordance with the times listed above. Using a Chi-square goodness-of-fit test, the actual number of deliveries observed during each of the three periods was compared to the expected number of deliveries in those periods if they had been distributed evenly throughout the day.

Identification and Sampling of Fish Types

We occasionally sampled waters (< ca. 15 m) around Naked I. with fish traps set on the bottom or occasionally above it to obtain specimens of fish to aid us in identifying those in the bills of guillemots. We measured wet weight and total length of all fish. Unless used as an identification sample, each fish was released after being weighed and measured. Occasionally, we retrieved fish of species not caught in the traps that we found in or near guillemot nests and used these as identification samples.

Data Analysis

Comparisons between Naked and Jackpot Islands or between years were made with two-tailed t-tests, 2 x 2 contingency tables analyzed with a G-test and corrected for continuity, Chi-square tests, ratio estimation with Z statistics, and randomization techniques. The level of significance was set at $\alpha = 0.05$. All means are reported as the mean plus or minus one standard deviation.

RESULTS

Censusing: Population and Colony Attendance

In 1994, 1,262 pigeon guillemots were counted around the shorelines of the Naked Island complex during the early-season census (30 May - 1 June, Table 1). On 11 June, 34 guillemots were counted around Jackpot I. The maximum number counted, however, was 74 at 0530 on 6 August. This latter count was conducted from an anchored boat during feeding watches and therefore only includes birds seen from that vantage point. The birds were in several large rafts, gradually moving closer to the island as daylight increased. Thus, it is possible that these rafts included most of the Jackpot I. population. On 15 June, 74 birds were counted around Fool I.

During the incubation period (Fig. 4) and early hatching period (Fig. 5), maximum counts of pigeon guillemots usually occurred in the early morning hours, shortly after first light. The birds were first detected in rafts a considerable distance from shore, then gradually moved closer to the colony. Time of day appeared to be more important than the tidal cycle in affecting colony attendance. Secondary peaks of guillemots later in the day often corresponded to high tide. Although no continuous 24-h observations were made in August, numerous counts made during extended feeding watches suggest that the tidal cycle had much less effect on colony attendance of guillemots while they were provisioning their young.

The maximum number of guillemots counted at the colonies we studied around Naked I. (Fig. 3) was as follows: Igloo I (37 on 26 July), Igloo II (14 on 2 August), Nomad (27 on 8 August), Row (20 on 10 July), Thumb (9 on 30 May), Hook I (17 on 23 July), and Hook II (11 on 24 July). The numbers of active guillemot nests at five study colonies on the western side of Naked I. are compared with similar data from previous years in Table 2. Since the last count in 1990, the number declined at three colonies and increased at two, although the number at every colony has declined since the 1978 count. The combined number of active nests at all five colonies in 1994 was only about half the number found in 1978 and 1979.

Of the 51 marked nest sites on Naked I., 15 (29%) were among tree roots, 28 (55%) were in rock crevices, and eight (16%) were in the talus. All but one of the 37 marked nest sites on Jackpot I. were among tree roots and the remaining one was in a rock crevice. There were few suitable rock crevices on Jackpot I. and no talus piles.

Nesting Chronology

Nesting chronology was similar at both islands (Naked I., Fig. 6.; Jackpot I., Fig. 7). The median laying date was 4 June at Naked I. (range = 19 May - 17 June) and 3 June at Jackpot I. (range = 24 May - 13 June). The median hatching date was 3 July at both Naked I. (range = 19 June - 18 July) and Jackpot I. (range = 24 June - 14 July). The median fledging date was 14 August at Naked I. (range = 2 August - 24 August) and 9 August at Jackpot I. (range = 30 July - 21 August). However, out of this sample, two chicks from each island were still present in the nest on our last day of observation (Naked I., 22 August; Jackpot I., 18 August).

The mean number of days that chicks spent in the nest was not significantly different between the two islands ($t = 1.922$, $df = 43$, $P > 0.05$). Chicks were in the nest an average of 39.3 ± 5.5 d on Naked I. ($n = 18$, range = 30-48 d) and 36.6 ± 3.8 d on Jackpot I. ($n = 27$, range = 30-47 d).

Productivity

The mean clutch size was 1.70 ± 0.47 ($n = 23$) on Naked I. and 1.92 ± 0.28 ($n = 24$) on Jackpot I. The difference between clutch sizes on the two islands was not significant ($G = 2.480$, $df = 1$, $P > 0.10$). Of a total of 39 eggs (23 clutches; 16 with 2 eggs, 7 with 1 egg) on Naked I., 35 hatched, two were abandoned, and two were probably taken by predators. Of a total of 46 eggs (24 clutches; 22 with 2 eggs, 2 with 1 egg) on Jackpot I., 37 hatched and nine were abandoned. Of a total of 53 chicks (32 broods; 21 with 2 chicks, 11 with 1 chick) on Naked I. that were monitored at some stage of the breeding cycle, 30 chicks fledged, eight were found dead in the nest, 11 were probably taken by predators, and the fate of four others is unknown. Of a total of 45 chicks (23 broods; 22 with 2 chicks, 1 with 1 chick) similarly monitored on Jackpot I., 35 chicks fledged, three were found dead in the nest, and the fate of seven others is unknown. The difference between brood sizes was not tested for significance because we were not sure of the original number of chicks in some of the "one-chick" nests found after the egg stage.

Hatching and fledging success and productivity, as determined by the "traditional" method, were based on 23 clutches from 22 nests (one pair relaid after their nest was depredated during the egg stage) at Naked I. and 24 nests on Jackpot I. Hatching success was 0.90 ($n = 39$) at Naked I. and 0.80 ($n = 46$) at Jackpot I.; it was not significantly different between islands ($Z = 0.90$, $P = 0.1841$). Fledging success was 0.51 ($n = 35$) at Naked I. and 0.76 ($n = 37$) at Jackpot I.; it was significantly different between islands ($Z = 2.13$, $P = 0.0166$). Overall productivity (i.e., chicks fledged/eggs laid) was 0.46 at Naked I. and 0.61 at Jackpot I. The Mayfield method yielded similar productivity values of 0.42 ($n = 36$) at Naked I. and 0.61 ($n = 29$) at Jackpot I.

Fourteen of 23 nests (61%) at Naked I. produced at least one fledgling compared to 18 of 24 nests (75%) at Jackpot I. This difference between the proportion of successful nests was not significant ($G = 0.528$, $df = 1$, $P > 0.25$) between the two islands.

Predation

Of the 35 nests on Naked I. that we monitored for productivity, two nests were depredated during the egg stage and eight nests were depredated during the chick stage. Although potential predators were seen on both islands, none were actually seen taking eggs or chicks. There was no evidence of predation on Jackpot I., but we found evidence suggesting mammalian predation on Naked I. in the form of guillemot carcasses with the heads chewed off, signs of scratching and digging at nest entrances, and mammalian hair found near a depredated nest. Guillemots often reacted to the presence of bald eagles around the colonies by flushing from the rocks or nearshore waters and settling farther offshore. Gulls and raptors were occasionally seen chasing guillemots with food, but in almost all instances, this behavior appeared to be kleptoparasitic rather than predatory.

Black-billed magpies were often seen near guillemot nest sites and were sometimes seen entering the nests. The shells of several apparently depredated guillemot eggs were also found, but it was not possible to identify the predator from this evidence.

Chick Growth and Fledging Weights

The mean growth rate of chicks during the linear phase of their growth was 15.7 ± 6.6 g/d ($n = 10$, range = 5.0-29.0 g/d) at Naked I. and 20.3 ± 3.5 g/d ($n = 6$, range = 15.0-23.5 g/d) at Jackpot I. The difference was not significant ($t = 1.570$, $df = 14$, $P > 0.10$).

The relationship between \ln body mass and \ln wing length of chicks on Naked and Jackpot Islands is compared in Figure 8. Fitting a common curve of the form of equation (1) to the results for both islands gives $R^2 = 0.9284$. Fitting separate curves gives $R^2 = 0.9352$. The increase in R^2 obtained by fitting separate curves is therefore 0.0068. To test whether this increase is significantly large, the randomization distribution of the increase in R^2 was approximated by the observed value plus 999 values obtained by randomly reallocating the available data set of 41 nests to a set of 24 nests on Naked Island and 17 nests on Jackpot Island. Only 12 of the 1000 values were equal to or greater than 0.0068. Therefore, the increase of 0.0068 is significantly large ($P = 0.012$), clearly indicating a difference in the body mass - wing length relationships for the two islands (Manly 1991).

The mean fledging weight of chicks was 453 ± 55 g ($n = 17$, range = 357-525 g) at Naked I. and 508 ± 39 g ($n = 17$, range = 440-585 g) at Jackpot I. This difference was significant ($t = 3.410$, $df = 32$, $P < 0.002$).

Chick Provisioning and Diet

Collectively, guillemots delivered fish to their chicks throughout the daylight hours at Naked I. (Fig. 9) and at Jackpot I. (Fig. 10). Neither distribution was significantly different from a theoretical even distribution of deliveries made throughout the day (Naked I., $\chi^2 = 3.709$, $df = 2$, $P > 0.10$; Jackpot I., $\chi^2 = 0.936$, $df = 2$, $P > 0.50$). Feeding rates varied considerably among nests. At any particular nest, there were periods of several hours in which no deliveries were made; also adults sometimes stopped delivering shortly after mid-day (Naked I., Figs. 11 and 12; Jackpot I., Fig. 13).

Pigeon guillemots at Naked I. sometimes foraged directly in front of their colony in water less than 15 m deep, but usually foraged in nearby bays or on the broad, shallow-water (< 25 m deep) shelves surrounding Naked I. (Fig. 14). Guillemots were never seen foraging in the immediate vicinity of Jackpot I., but instead flew toward shallower waters near the mouths of Jackpot Bay or Icy Bay (each ca. 2-4 km distant, Fig. 15), presumably foraging there. Guillemots carrying fish were observed returning to the colony at Jackpot I. from the general direction of either of these two bays.

The diet of pigeon guillemot chicks at the two islands was different with respect to types of fish. At Jackpot I., herring or smelt accounted for at least 32.3% of the prey items fed to chicks, whereas at Naked I., these types of fish accounted for only 1.2% of the chick diet (Fig. 16). Gadids were prevalent in the diet of chicks at both islands (Naked I., 29.5%; Jackpot I., 18.5%). Sand lance accounted for at least 7.9% of prey items delivered at Naked I., but were virtually absent (0.8%) from the chicks' diet at Jackpot I. Because of the relatively large proportion of fish that could not be identified (Naked I., 25.4%; Jackpot I., 24.2%), the values reported above represent minimum percentage contributions of those types of fish to the total delivered.

Fish Types Caught in Traps

Shrimp (mostly *Pandalus danae* and *Eualus gaimardii*) were the most frequently taken animal in the fish traps, but were not counted because they were never seen being delivered to guillemot nests in 1994. Of 106 fish caught in the traps, the relative proportions of each type were as follows: 40 arctic shannies (*Stichaeus punctatus*), 25 gadids (presumably mostly Pacific tomcod *Microgadus proximus*, possibly also Pacific cod *Gadus macrocephalus*, and walleye pollock *Theragra chalcogramma*), 19 *Lumpenus* spp. (probably mostly snake pricklebacks *L. sagitta*), nine sculpins (mostly tidepool sculpins *Oligocottus maculosus*, also one *Nautichthys* sp.), eight crescent gunnels (*Pholis laeta*), three masked greenlings (*Hexagrammos octogrammus*), one juvenile lingcod (*Ophiodon elongatus*), and one warbonnet (*Chirolophis* sp.).

DISCUSSION

Censusing: Population and Colony Attendance

Early season counts of pigeon guillemots in the Naked Island complex suggest that their population has decreased considerably from 1978 and 1979 (Table 1). These censuses, which were conducted at the breeding colonies during roughly the same phase of the breeding cycle, at approximately the same time of day, and under similar weather and tidal conditions, probably are better indicators of trends in guillemot numbers than are counts made during other types of surveys in PWS. Observed colony attendance patterns of guillemots at Naked I. (Figs. 4 and 5) and Jackpot I. indicate that the time of day is extremely important when planning guillemot censuses. A morning peak in colony attendance seems to hold true for pigeon and black guillemots throughout most of their range (Drent 1965, Cairns 1979, Vermeer et al. 1989). Vermeer et al. (1989) reported that the optimal time to determine the population of nesting guillemots was at high tide in the morning. They found colony attendance to be correlated most strongly with tide height, but also with time of day and tide direction, at three colonies in Skidegate Inlet, Queen Charlotte Islands. However, at Mandarte

Island, British Columbia, time of day was the only factor influencing colony attendance. They suggested that the maximum tidal range was responsible for the observed differences in colony attendance. The range at Skidegate Inlet is 7.8 m, but only 3.8 m at Mandarte Island; it is 5.8 m in the Naked Island area. Another indication of a marked decline is the total number of active nests at five previously monitored colonies on Naked I., which in 1994 was only about half of what it was in 1978 and 1979 (Table 2).

Other surveys such as those of Dwyer et al. (ND; ca.15,700 in 1972-1973), those of Klosiewski and Laing (1994; ca. 3,000-6,600 in 1989-1991), and most recently by Agler et al. (1994; ca. 4,000 in 1993) also suggest a general decline in the numbers of pigeon guillemots in PWS. Sanger and Cody (1994) surveyed 98% of the PWS shoreline between May and June of 1993 and counted 3,028 guillemots. Because the primary objective of their survey was to locate pigeon guillemot colonies, their methods were different from the previous censuses conducted around the Naked Island complex, and the lower count for 1993 in this area most likely reflects these differences in methods. A comparison of the counts by Sanger and Cody (1994) with other recent counts (see Table 1) made before and after suggests that their estimates might be about 35% low.

Productivity

The ideal and most straightforward method of calculating productivity is from a sample of known nests that are followed from before egg-laying through fledging. Use of this "traditional" or cohort method was not an option during the 1994 field season. First, in most instances, we did not know about a nest site until we discovered eggs or chicks, because guillemots build no nest and use only a rudimentary nest scrape in which to lay their eggs. Second, we found most nests either well into the incubation period or during the chick-rearing period, when parents were observed delivering food to their chicks. If all nests that were found later in the breeding season are included in the sample, one runs the risk of biasing the results toward successful nesting attempts. This is because those nests that failed without ever having been found are not accounted for in calculations of productivity. As a compromise, we included in our sample those nests whose contents were monitored from incubation through fledging. The problem with this method is that we are restricted to small sample sizes (Naked I., 23 clutches from 22 nests; Jackpot I., 24 nests).

The cryptic nature of guillemot nests makes it likely that in most studies (especially during the first year), a large proportion of the nests monitored will be those that are discovered later in the breeding season. The Mayfield method allowed us to use those nests found later in the breeding season and thus increase our sample sizes (Naked I., 36 clutches from 35 nests; Jackpot I., 29 nests). The Mayfield method provides a useful means of comparing data between studies when appropriately sized cohorts cannot be followed throughout the breeding season.

Oakley and Kuletz (1994) included several tables in their report, each of which relates to some measure of pigeon guillemot productivity. These tables have been reproduced (see Appendix, Tables A1-A5) with only minor modifications in this report, and updated with the appropriate values for 1994. Although the original tables contained information from Naked I. only, data from Jackpot I. have been included for comparative purposes.

Predation

From our productivity sample, nests of each type were depredated in 1994: tree roots (4 of 10, or 40%), rock crevices (4 of 19, or 21%), and talus (2 of 6, or 33%). In 1978, of 146 known nest sites on Naked I., 40% of the nests were among tree roots, 36% in rock crevices, and 24% in talus (Oakley 1981). The high proportion of nests in rock crevices (55%, usually on cliff faces) on Naked I. in 1994 suggests that guillemots might be selecting this type of nest site to be less accessible to predators. The difference in the proportion of nests of each type between 1978 and 1994 was not significant ($\chi^2 = 5.455$, $df = 2$, $P > 0.05$). However, the number of rock crevice nests in 1994 was higher than the expected and this component made the largest contribution to the calculated Chi-square value. Not all of these nests were accessible, so we could not determine the fate of eggs or chicks in some. Jackpot I. has little shoreline (ca. 1 km) and low cliffs (typically < 3-4 m high) with few suitable crevices and no talus piles. Therefore, almost all guillemots breeding on the island use tree roots as nest sites. Although all or most of the tree root nests on Jackpot I. were seemingly accessible to mammalian predators, we found no evidence of predation there. In Shetland and Orkney, the use of available breeding habitat by black guillemots was influenced by the distribution of mammalian ground predators (Ewins and Tasker 1985). Nest sites accessible to ground predators were used on islands that were free of brown rats (*Rattus norvegicus*) and ermine (*Mustela erminea*), but on islands where these mammals were present, guillemots bred only in higher cliffs.

Oakley and Kuletz (1994) noted that the primary difference in productivity of pigeon guillemots on Naked I. that they observed following the oil spill was lowered nesting success, which was the result of nest predation during the chick stage. On Naked I. in 1994, we found carcasses of guillemot chicks with the heads chewed off, suggesting that some kind of mustelid is likely responsible for the predation. The most likely predator is the river otter. These animals were seen frequently around Naked I. in the vicinity of guillemot colonies. Ewins (1985) reported that on the island of Mousa in Shetland, otters (*Lutra lutra*) killed both chicks and incubating adults, and that decapitated carcasses were a sure sign of these predators. Ewins also noted that there were few nests inaccessible to them. Likewise, many of the nest sites on Naked I. are probably accessible to otters, including some of those in rock crevices.

Few, if any, nest sites would be inaccessible to the more agile mink. We never saw mink in 1994. Although mink were common on Naked I. during the

summer after the oil spill, no mink were seen in 1991 and only scant evidence of their presence was found in 1992 despite some trapping effort (J. Faro, personal communication). River otters and mink typically forage in the intertidal zone. A study that compared the diet of river otters in two areas of PWS before and after the spill showed that there were significant declines in species richness and diversity (mostly bony fish and molluscs) in otter diets on the oiled area compared to the unoiled area (Bowyer et al. 1994). Another study, also conducted in PWS, clearly indicated that oil contamination was affecting the health of river otters up to two years after the spill (Duffy et al. 1993, 1994). Contamination of the normal intertidal food supply of river otters and mink might have ultimately caused some of these predators to switch to other types of prey, including guillemot chicks.

Whatever mammalian predator is responsible for killing chicks on Naked I., the increased predation pressure there might have caused breeding guillemots to move elsewhere. It is possible that guillemots in PWS are emigrating from some colonies on the mainland and large islands like Naked I. to smaller ones like Jackpot I., where ground predators have not become established. Emigration of black guillemots from colonies in Sweden and Iceland have been attributed to predation by mink (Asbirk 1978, Petersen 1979). These kinds of movement would not necessarily show up in Sound-wide surveys such as those of Agler et al. (1994), but rather in censuses designed to count guillemots at their colonies during the breeding or prebreeding season. All black guillemot colonies in Scotland were surveyed in the mid-1980's using standardized methods (i.e., early morning counts in the prebreeding period; M.L. Tasker, personal communication). In several of the areas, more recent counts have provided useful indices of change. The principal factor controlling local distributions in Scotland appears to be introduced mammals.

Avian predation also probably accounts for some of the nesting failures on Naked I. Of the corvids, magpies are the likeliest predator. They were seen on several occasions either entering guillemot nests or repeatedly following adult guillemots to the nest entrance. During a previous field season, a magpie was seen dragging a guillemot chick from its nest (K. Kuletz, personal communication). Crows are apparently aware of the locations of marked guillemot nests and were seen in 1994 and in previous years "systematically" moving from one marked nest to another. Other studies indicate that crows are a major source of egg predation and sometimes take young chicks as well (Emms and Verbeek 1989, Ewins 1989).

Adults, and especially fledglings, are probably sometimes taken by large raptors. Bald eagles are known predators of adult guillemots in British Columbia (Vermeer et al. 1989 as cited in Ewins et al. 1993). Beaks of guillemots were found beneath an eagle's nest on Naked I. during a previous study (K. Kuletz, personal communication). We often witnessed a change in the guillemots' behavior when an eagle flew into the area. The guillemots' reactions to the presence of bald eagles (e.g., flushing, moving farther offshore, alarm calling, and diving) suggest that they perceive this potential predator as a real threat. However, any interactions between an eagle and a single guillemot were assumed

to be kleptoparasitic because we only observed these when a guillemot had a fish in its bill.

Other Causes of Nesting Failure

Only two eggs from a single nest were abandoned on Naked I., but nine eggs from five nests were abandoned on Jackpot I. The abandoned nest on Naked I. was in a crevice that had little cover. Abandoned nests on Jackpot I. were typically deep cavities in expansive tree root systems. An adult was flushed twice from the nest on Naked I. and twice from one of the nests on Jackpot I. It is possible that our repeated visits to these nests was the cause of this abandonment. Several investigators at other guillemot colonies have observed reduced productivity apparently associated with human disturbance (Bergman 1971, Cairns 1980, Vermeer et al. 1993). The fact that the rate of abandonment on Jackpot I. was higher, although nests were visited more frequently on Naked I., might be explained by the lack of previous research on Jackpot I. On Naked I., some of the same colonies have been studied for years and the guillemots there might have habituated to some extent to the presence of biologists walking through their breeding habitat.

One chick on Naked I., and two chicks on Jackpot I., died within their first week of life. The cause of death in each instance was unknown. Other studies have also reported deaths among young chicks (Preston 1968 and Kaftanovski 1951 as cited therein; Divoky et al. 1974, Kuletz 1983, D.L. Hayes, personal observation). Preston (1968) suggested the cause might be related to prolonged chilling or failure to become homoiothermic. On Naked I. in 1994, two chicks apparently died from exposure after heavy rains and one chick died after its wing had been pinned down by a fallen rock.

Chick Growth and Fledging Weights

Our estimates of growth rates during the linear phase of growth (Naked I., 15.7 g/d; Jackpot I., 20.3 g/d) were similar to those of Oakley and Kuletz (1994) at Naked I. (range = 16.6-23.8 g/d for all years combined, Table 3), as were our estimates of fledging weights (Table 4). Growth rates were also similar to those reported by Koelink (1972) at Mandarte Island (15.9 g/d) and Ainley and Boekelheide (1990) on the Farallon Islands (16.5 g/d). In the absence of known-age chicks, we used our plots of ln body mass vs. ln wing length as a condition index to the developmental stage of the chicks. Manipulation of food intake of alcid chicks by several researchers has shown that the rate of growth of wing feathers is unaffected by nutrition (Gaston 1985 and references therein). Randomization techniques showed that the two data sets graphically compared in Figure 8 were significantly different. On average, chicks on Jackpot I. also fledged at greater weights and spent less time in the nest than those on Naked I.

Peakall et al. (1982, 1983 as cited in Oakley and Kuletz 1994) have shown that ingestion of a small amount of oil by waterbirds can produce a variety of sublethal, physiological effects that might affect their fitness. Black guillemot chicks dosed with crude oil and raised by their parents in the nest grew significantly more slowly than controls, and also showed signs of impaired osmoregulatory function (Peakall et al. 1980). Although it is unlikely that direct ingestion of oil or external oiling is affecting the birds five years after the spill, indirect effects of the oil might be important. Hemosiderosis has been observed in demersal fish collected from oiled eel grass beds in Herring Bay, Knight Island, PWS (S. Jewett, personal communication). Hemosiderin is the result of excessive destruction of erythrocytes and collects in the liver and spleen. Polycyclic aromatic hydrocarbons (PAHs) found in crude oil are known to cause the lysis of red blood cells. Of a sample of 10 pricklebacks (*Anoplarchus* spp.) and 10 crescent gunnels (*Pholis laeta*) collected from each of two areas of the bay (oiled and unoiled), all specimens from the oiled beds showed signs of hemosiderosis and none in the control beds showed any signs of this disorder. Many of the fish from the oiled beds were in poor condition, as judged by lipid and glycogen stores. Long-term exposure of marine fish to crude oil results in lowering of lipid reserves (Thomas et al. 1980 and Dey et al. 1983, both cited in Duffy et al. 1993). If guillemots are regularly feeding their offspring fish from oiled areas, the chicks could be accumulating PAHs in concentrations that might cause sublethal toxic effects. Either reduced energy content of food fish or accumulation of PAHs could adversely affect chick metabolism and growth.

Differences in diet might also explain the differences in growth rates between the two populations. The energy density of lipid is about twice that of protein or carbohydrate. The lipid content of herring, capelin, and sand lance is typically high relative to that of gadids, which tend to be poor in lipids (D. Roby, personal communication). Also, research on adult kittiwakes and murrelets by Brekke and Gabrielsen (1994) suggests that assimilation efficiency is directly proportional to the fat content of the prey. This same relationship might hold for some seabird chicks as well. The relative proportions of these types of fish delivered to guillemot chicks (especially the large component of herring or smelt at Jackpot I.) suggest that chicks raised on Jackpot I. are, on average, receiving meals of higher energy content than those chicks raised on Naked I.

The mean fledging weight of guillemot chicks raised on Naked I. (453 g) was 95% of the mean adult weight of 477 ± 38 g (range = 420-569 g, n = 19, SE = 8.8), while the mean fledging weight of chicks raised on Jackpot I. (508 g) was 106% of this value. Supra-adult weights of chicks are not common among the alcids (Sealy 1973). Other studies have shown that pigeon guillemots typically weigh less than adults when they fledge and that their peak weight is reached at fledging. On Mandarte Island, the mean fledging weight was 411 g, or 91% of the mean adult weight (Drent 1965); in Puget Sound, the mean fledging weight was 438 g, or 92% of the mean adult weight (Thoresen and Booth 1958). The fact that the mean fledging weight of Jackpot I. chicks was greater than the mean adult weight might

be explained by the fact that all the adults measured were from Naked I. and the mean adult weight of the Jackpot I. population could be greater, or that sample sizes were too small and thus had too much variance. However, Eldridge and Kuletz (1980) reported a mean adult weight of 504 ± 25 g ($n = 42$, $SE = 3.8$) for Naked I. pigeon guillemots that they measured in 1979; mean fledging weights were 506 ± 38 g ($n = 18$ chicks measured within four days of fledging) and 503 ± 43 g ($n = 8$ chicks measured within 24 hours of fledging). When making these comparisons, it is also important to remember that the mass of chicks can vary considerably (up to 30-40 g/d) during the final portion of the nestling period (Emms and Verbeek 1991).

It seems reasonable to assume that in species such as the pigeon guillemot, where the chicks are independent upon fledging, fledging weight would be important to survival (i.e., heavier chicks with larger fat stores would have an added buffer while learning to forage efficiently, especially if food is scarce or bad weather prevents them from foraging). There are no conclusive data indicating that fledging weight in auks influences their postfledging survival (Harris and Rotherby 1985). Other studies of species whose chicks are independent at fledging (e.g., Manx shearwater, Perrins et al. 1973; cape gannet, Jarvis 1974 as cited in Harris and Rotherby 1985) have shown that there is a significant positive correlation between weight at fledging and postfledging survival (but see Schreiber 1994).

Chick Provisioning

Members of the genus *Cephus* typically lay two eggs. Most other alcids lay only a single egg, but the near-shore foraging habits of guillemots probably account for their ability to raise two chicks. Mehlum et al. (1993) maintain that long-distance foraging by black guillemots, which typically raise two-chick broods and have a high wing loading relative to most other seabirds, is too energetically demanding and might exceed their maximum sustainable working level. Koelink (1972) argues this same point for chick-rearing pigeon guillemots. In his study, although artificial broods of three were successfully raised to fledging, there was a proportional decrease in the amount of food delivered per chick throughout the nestling period. In black guillemots also, artificial triplets have been successfully raised but with differing results regarding fledging weights. In Denmark, the mean fledging weight of triplets was higher than that of chicks from normal broods (Asbirk 1979 as cited in Harris and Birkhead 1985). In Iceland, triplets fledged at lower mean weights than chicks from normal broods (Petersen 1981 as cited in Harris and Birkhead 1985).

Our measured rates of food deliveries to individual nests (range = 0.67-1.39/nest/h; Naked I., Figs. 11 and 12; Jackpot I., Fig. 13) are comparable to those of other studies of *Cephus* guillemots (Thoresen and Booth 1958, Bergman 1971, Asbirk 1979 as cited in Harris and Birkhead 1985, Cairns 1981, 1987, Kuletz 1983). Unfortunately, we did not always know the number of chicks inside each

nest. Without this information, and without a knowledge of the weight of each prey item delivered, a comparison of provisioning rates (i.e., g/h/chick) is impossible. Furthermore, fish vary considerably in their composition of lipids, proteins, and carbohydrates. Fish higher in lipids have a higher energy content, which can be particularly relevant to the reproductive success of the seabirds feeding upon them. Also, the lipid content even within a single species of fish can vary widely with season, sex, reproductive status, and age class (D. Roby, personal communication). It is almost impossible to accurately estimate the weight of prey items delivered to chicks noninvasively. Measuring the actual energy content of the prey cannot be done by noninvasive means; prey must be intercepted and analyzed in the laboratory. Obviously, this cannot be done repeatedly at the same nest without affecting the food intake of the chicks involved.

Foraging

The maximum diving depth of black guillemots is about 50 m (Piatt and Nettleship 1985). Assuming that the pigeon guillemot has similar diving capabilities, it is restricted to waters no deeper than this when feeding on benthic prey items. The pigeon guillemots breeding on Naked I. generally forage around the island, usually within about 600 m of the shore and in water shallower than 25 m (Kuletz 1983). There is a broad, shallow-water shelf surrounding Naked I. and the neighboring islands (Fig. 14), which allows guillemots to forage nearby. On Jackpot I., there is very little shallow water immediately around the island (Fig. 15), and thus guillemots breeding there fly greater distances to obtain food for their chicks. These birds apparently find it necessary to fly several kilometers to Jackpot Bay or Icy Bay to find food for their chicks instead of trying to forage around Jackpot I. However, the extra amount of energy expended by adults feeding chicks on Jackpot I. seems to be offset by the increased growth rates, fledging weights, and productivity measured at this colony relative to colonies on Naked I.

Chick Diet

The most obvious difference in the diet of chicks between Naked and Jackpot Islands in 1994 was in the proportion of herring or smelt (Fig. 16), accounting for approximately one third of all prey items delivered to Jackpot I. chicks, but only slightly more than one percent of those delivered to Naked I. chicks. Interestingly, herring or smelt were not noted in the diet of chicks on Naked I. in 1979 or 1980, then accounted for about 16% and 23% of the diet in 1981 and 1989, respectively, and only about two percent in 1990 (Oakley and Kuletz 1994). In 1994, sand lance accounted for less than one percent of all prey items delivered to chicks on Jackpot I., and about eight percent on Naked I. Data from before the oil spill show that sand lance had been the single most important prey item in the diet of chicks at Naked I. (55% in 1979, 35% in 1980, and 23% in

1981; Kuletz 1983). After the spill, in the two years when data are available, sand lance accounted for about 14% and eight percent of the chick diet (Oakley and Kuletz 1994). In 1994, gadids, which were relatively unimportant in the chick diet at Naked I. until after the spill, were the most frequently delivered type of prey at Naked I., and second only to herring or smelt at Jackpot I. The proportion of herring or smelt in the diet of chicks might be related to the ephemeral nature of schools of this type of fish and their presence within the foraging range of guillemots. Their capture might occur only coincidentally when behavioral factors (e.g., spawning) or oceanographic factors (e.g., currents, upwelling) bring these prey into shallower nearshore waters. However, the relative increase in the proportion of gadids, presumably caught by the guillemots on or near the bottom, could indicate a pronounced shift in the ecosystem. The fact that gadids did not show up in fish traps in appreciable numbers (Kuletz 1983, Oakley and Kuletz 1994) until 1994 lends support to this hypothesis.

CONCLUSIONS

We found important differences between the pigeon guillemot populations of Naked and Jackpot Islands. On Naked I., we noticed increased predation pressure and a marked change in the diet of chicks compared to the late 1970's. Also, the numbers of guillemots in the Naked Island complex are about half of what they were in the late 1970's.

Productivity was lower on Naked I., primarily as a result of predation during the chick stage. The most likely predators are mustelids, especially river otters. Although we saw the same potential predator species on both islands and almost all of the nests on Jackpot I. appeared to be accessible to ground predators, we found no evidence of predation on that island. Egg abandonment was the main reason for nesting failures on Jackpot I. Our investigations might have caused the incubating adults to desert. The diet of chicks was substantially different between the two islands with respect to the proportion of schooling fish. Herring or smelt accounted for about one third of the chick diet on Jackpot I., but only about one percent on Naked I. The guillemots breeding at Jackpot I. foraged farther from their colonies than those breeding at Naked I. The extra energy expended by the Jackpot I. adults when foraging at greater distances seems to be offset by increased growth rates of chicks and greater fledging weights.

It is conceivable that residual oil contamination has caused river otters or other mustelids on Naked I. to switch to another food source. It is also possible that oil contamination has had sublethal toxic effects on both demersal fish and, at the next trophic level, on the guillemots that feed on them. In addition to accumulating polycyclic aromatic hydrocarbons in their tissues, stressed fish are likely to have lowered glycogen and lipid stores, and thus energy content. These trophic relationships certainly merit further study.

Sand lance were the single most important species in the diet of pigeon guillemot chicks on Naked I. in the late 1970's, but they accounted for only about

eight percent of the chick diet in 1994. Likewise, gadids were previously unimportant in the chick diet on Naked I., but in 1994 accounted for about 30% of the prey items delivered to chicks. The apparent decline in the availability of sand lance and changes in the relative proportions of benthic and schooling fish in the diet of guillemot chicks might represent a key change in the ecosystem that is affecting other marine birds and mammals in PWS.

Future work on pigeon guillemots in PWS should focus on 1) determining what animals are responsible for the increased levels of predation at the nest site on Naked I., 2) marking chicks and breeding adults for estimating recruitment and adult survival, 3) censusing designated colonies on a regular basis using standardized methods, and 4) diet composition and energy content of prey items as they relate to growth and productivity.

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Table 1. Counts of pigeon guillemots during June censuses at Naked, Peak, Storey, Smith, and Little Smith Islands, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill. Censuses conducted between 3 and 6 June unless otherwise noted. Dashes indicate no surveys were conducted.

Year	Naked Island	Storey Island	Peak Island	Smith Island	Little Smith Island	Total
Before spill						
1978	1115	392	94	175	72	1965
1979	1226	495	150	301	58	2230
1980	891	--	--	--	--	--
After spill						
1989 ^a	615	193	73	--	--	--
1990	729	293	102	124	31	1279
1991	755	293	102	76	35	1261
1992	586	230	87	100	23	1025
1993 ^b	385	242	94	75	32	828
1994 ^c	739	298	81	121	23	1262

^aCensus conducted on 13-14 June.

^bFrom Sanger and Cody 1994 (censuses in May or June 1993)

^cIn 1994 Naked Island census was done on 30 May, Storey and Peak Islands on 31 May, and Smith and Little Smith Islands on June 1.

Note: Data from all years except 1993 and 1994 from Table 1 (Oakley and Kuletz 1994).

Table 2. Number of active pigeon guillemot nests at five colonies on the western side of Naked Island, Prince William Sound, Alaska, before and after the *T/V Exxon Valdez* oil spill. Dashes indicate no surveys were conducted.

Year	Nomad	Thumb	Row	Hook	Tuft	Total
Before spill						
1978	7	11	9	12	19	58
1979	8	6	15	14	10	53
1980	5	4	10	8	6	33
1981	4	5	7	--	--	--
After spill						
1989	3	4	7	2	5	21
1990	4	3	13	2	12	34
1994	5	2	3	^a 11	10	29

^aThis value includes nests from both Hook I and Hook II colonies.

Note: Data from all years except 1994 from Table 2 (Oakley and Kuletz 1994).

Table 3. Growth rates of pigeon guillemot chicks raised at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of Chicks	Mean Growth Rate (g/d) ^a	Standard Error	Minimum Growth Rate (g/d)	Maximum Growth Rate (g/d)
Before spill					
1978	15	19.6	1.4	7.4	31.7
1979	16	23.8	1.2	17.1	32.0
1980	^b 1	19.0	--	--	--
1981	11	19.2	1.8	11.4	34.3
After spill					
1989	5	18.1	2.5	11.5	23.4
1990	12	16.6	1.2	10.1	23.6
1994	10	15.7	2.1	5.0	29.0
1994 (JI) ^c	6	20.3	1.4	15.0	23.5

^aMean number of grams gained per day during the linear growth phase, which is the period between 8 and 18 days after hatching (Koelink 1972).

^bFew chicks were measured in 1980 because of loss of nests from netting and tagging of adults for foraging studies (Kuletz 1983).

^c(JI) indicates data is from Jackpot Island.

Note: Data from all years except 1994 from Table 14 (Oakley and Kuletz 1994).

Table 4. Fledging weights^a of pigeon guillemot chicks raised at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of Chicks	Mean Fledging Weight (g)	Standard Error	Minimum Weight (g)	Maximum Weight (g)
Before spill					
1978	29	467	9	291	542
1979	17	506	12	427	590
1980	^b 2	517	52	466	569
1981	13	428	29	202	546
After spill					
1989	10	507	16	420	570
1990	13	438	16	310	510
1994	17	453	13	357	525
1994 (JI) ^c	17	508	9	440	585

^aThe last weight obtained from a chick that was measured within one week of fledging.

^bFew chicks were measured in 1980 because of loss of nests from netting and tagging of adults for foraging studies (Kuletz 1983).

^c(JI) indicates data is from Jackpot Island.

Note: Data from all years except 1994 from Table 13 (Oakley and Kuletz 1994).

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Figure 1. Locations (dots) investigated during the 1994 field season as potential study sites for pigeon guillemots breeding in Prince William Sound, Alaska.

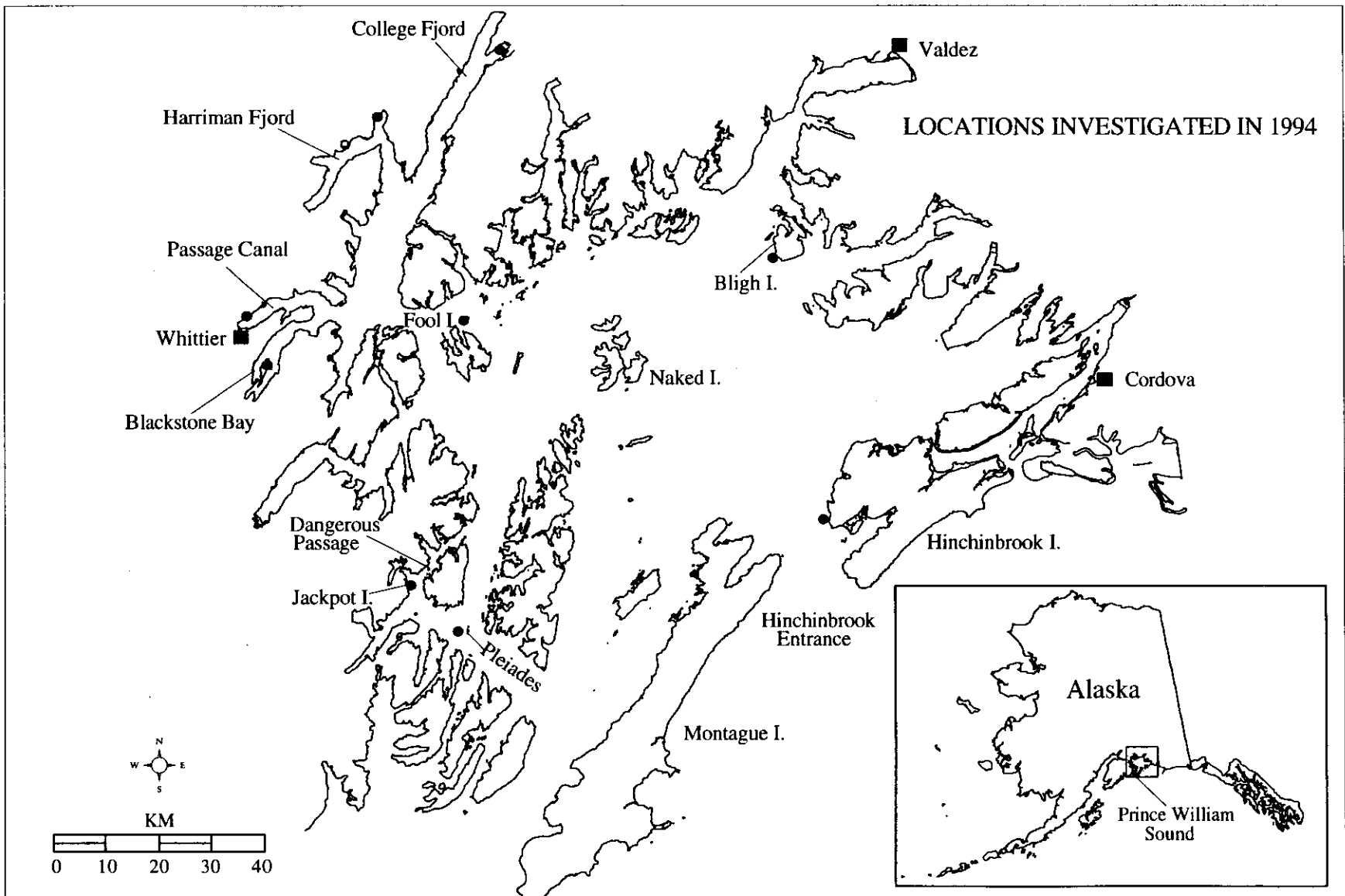


Figure 2. The Naked Island complex, comprising Naked, Peak, Storey, Smith, and Little Smith Islands, most of which were censused for pigeon guillemots by standardized methods in 1978-1980 and in 1989-1994.

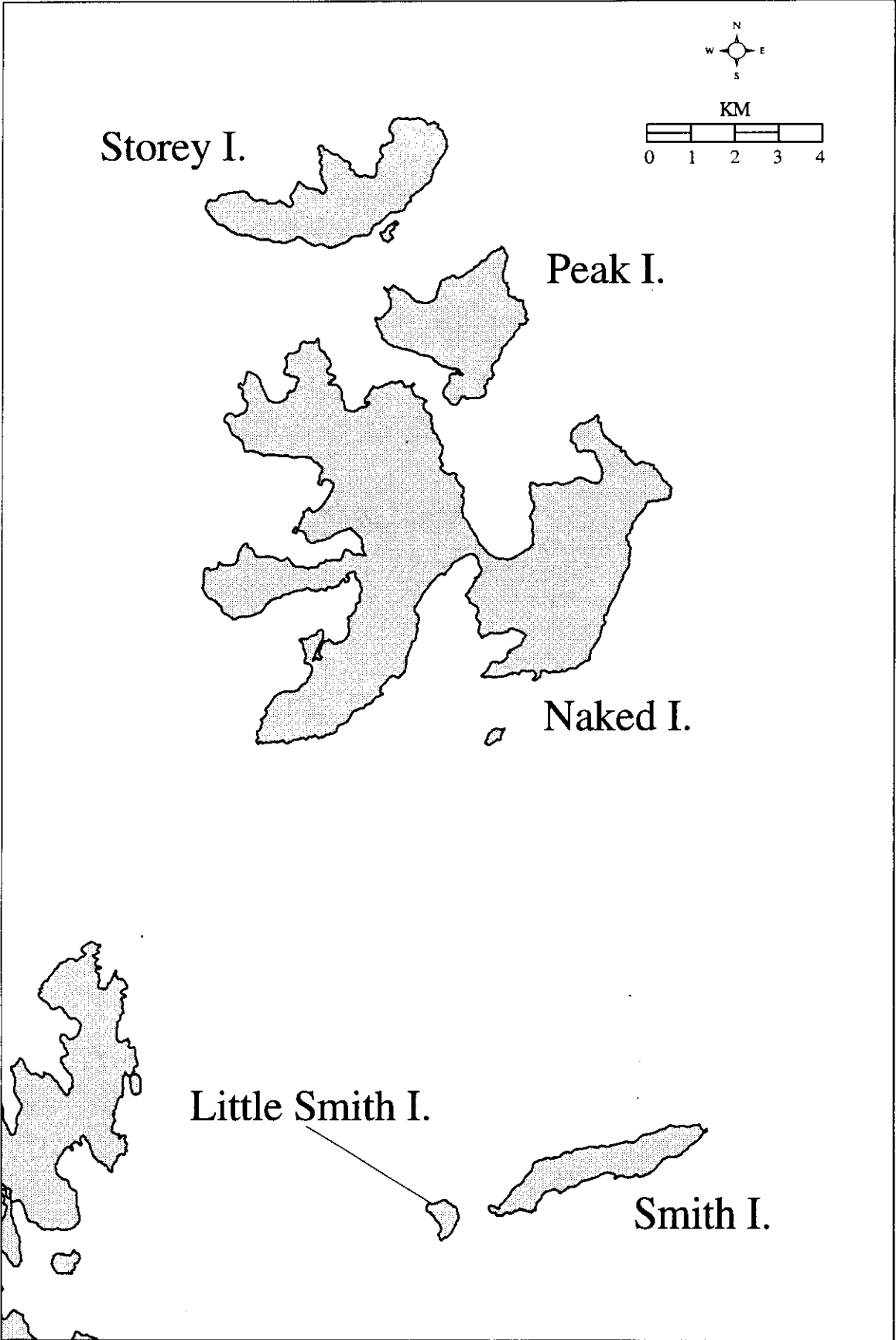


Figure 3. Locations of pigeon guillemot colonies (crosses) on Naked Island that were monitored during the 1994 field season.

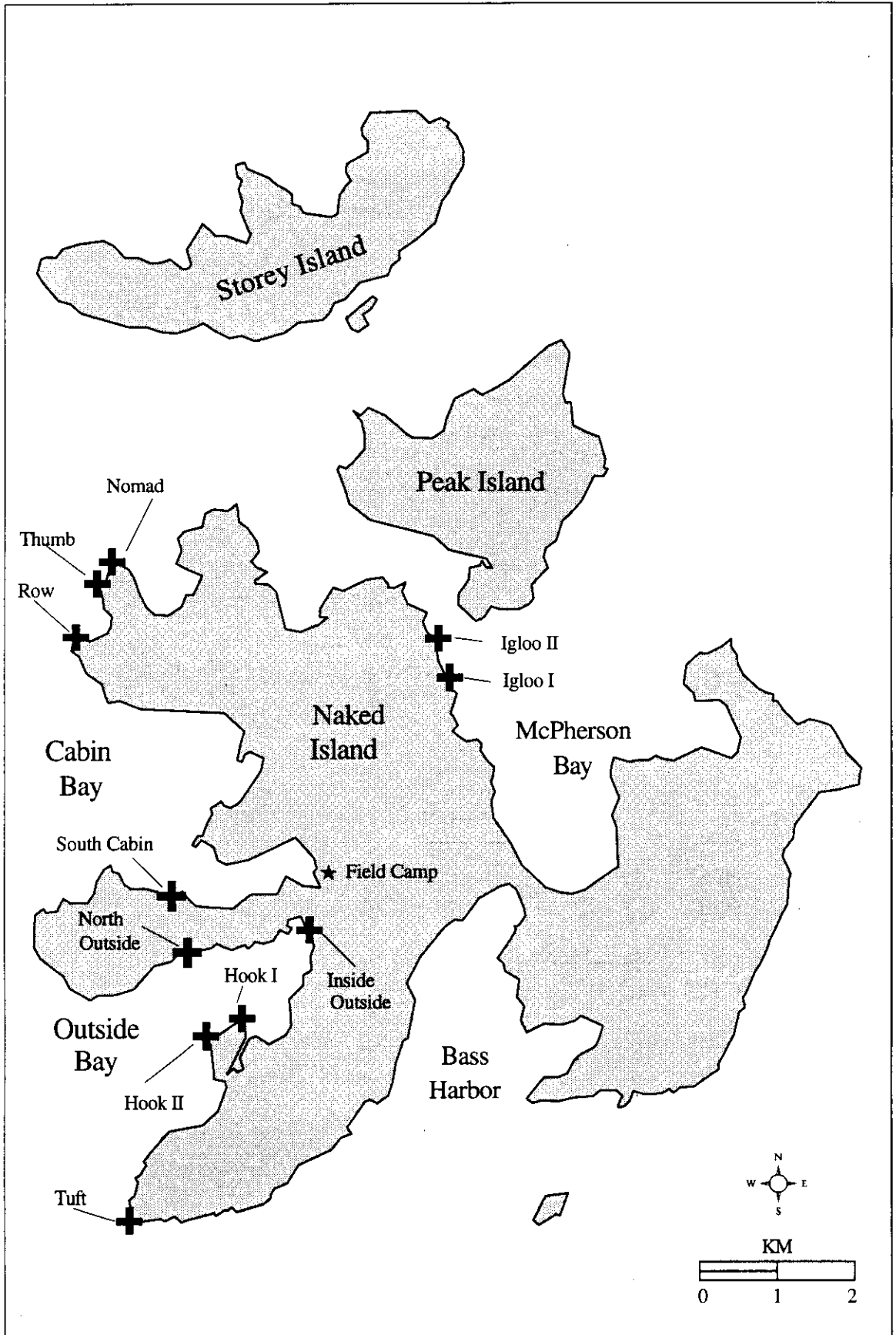


Figure 4. Attendance patterns of pigeon guillemots at two colonies on Naked Island (13-14 June 1994) during the incubation period. Times of high (H) and low (L) tides are indicated by letters at top of graph.

COLONY ATTENDANCE

NAKED I., 13-14 JUNE 1994

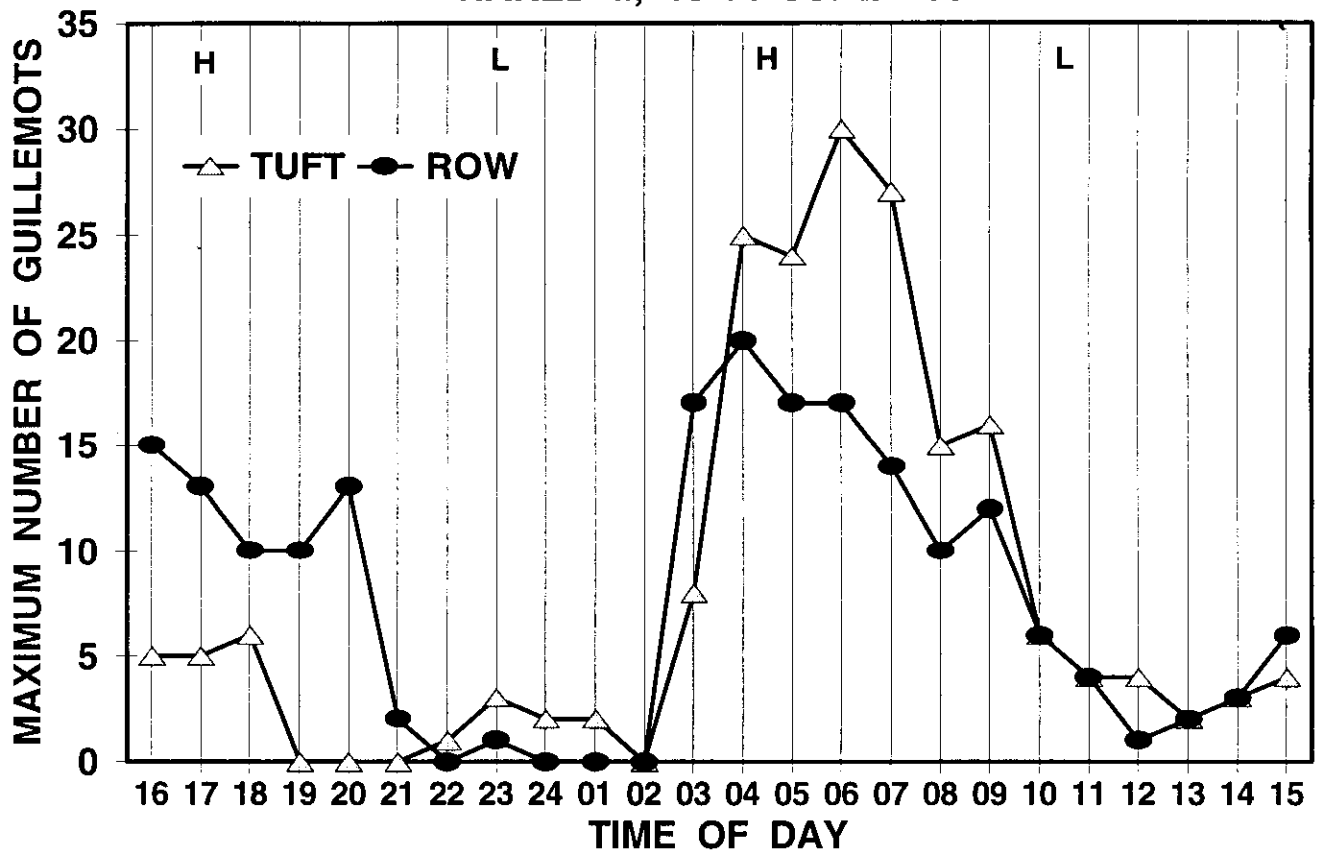


Figure 5. Attendance patterns of pigeon guillemots at two colonies on Naked Island (5-6 July 1994) during the early hatching period. Times of high (H) and low (L) tides are indicated by letters at top of graph.

COLONY ATTENDANCE NAKED I., 5-6 JULY 1994

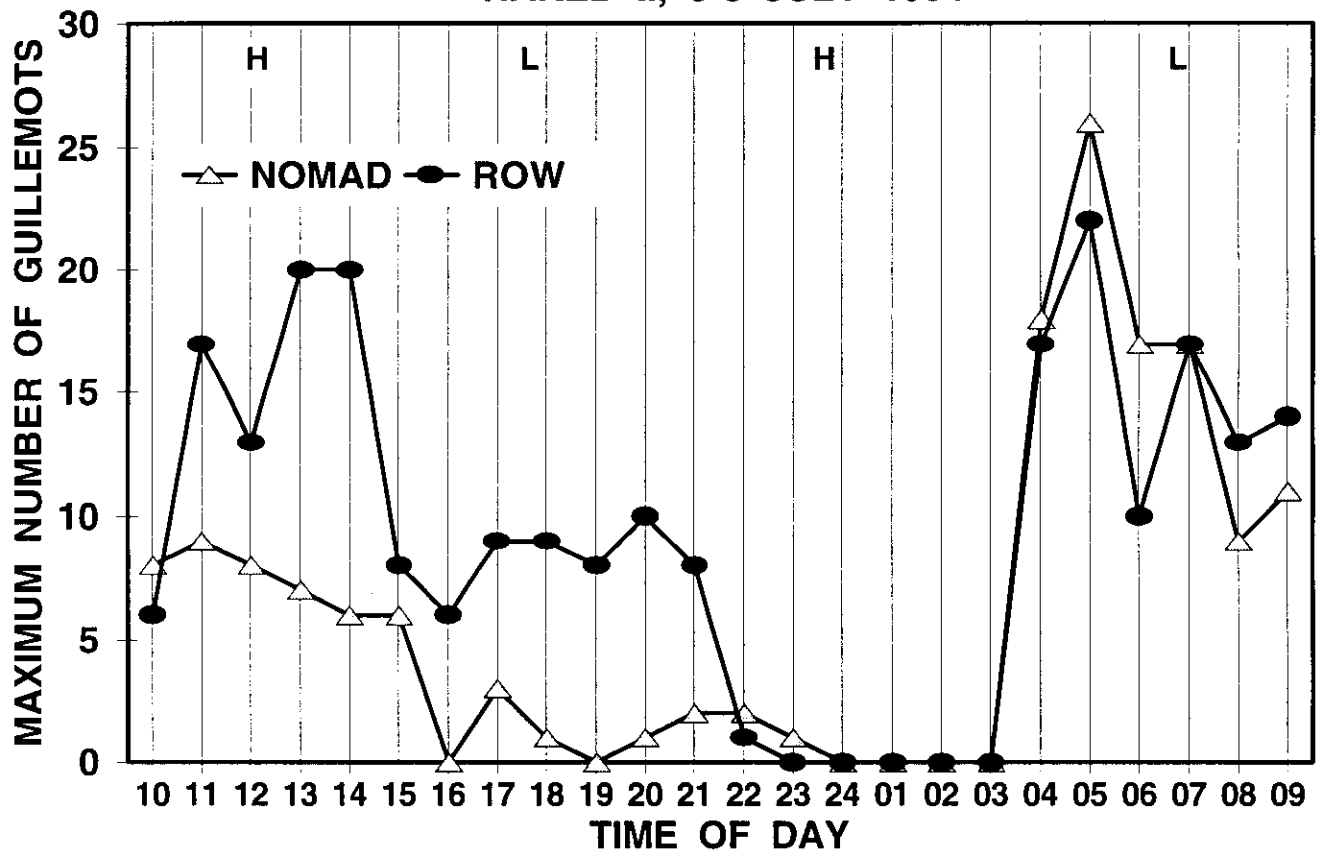


Figure 6. Nesting chronology of pigeon guillemots on Naked Island during the 1994 breeding season. Each bar represents one week beginning on the date below it. Only those nests followed from incubation through fledging were used to construct the chronology.

NAKED I. NESTING CHRONOLOGY -- 1994

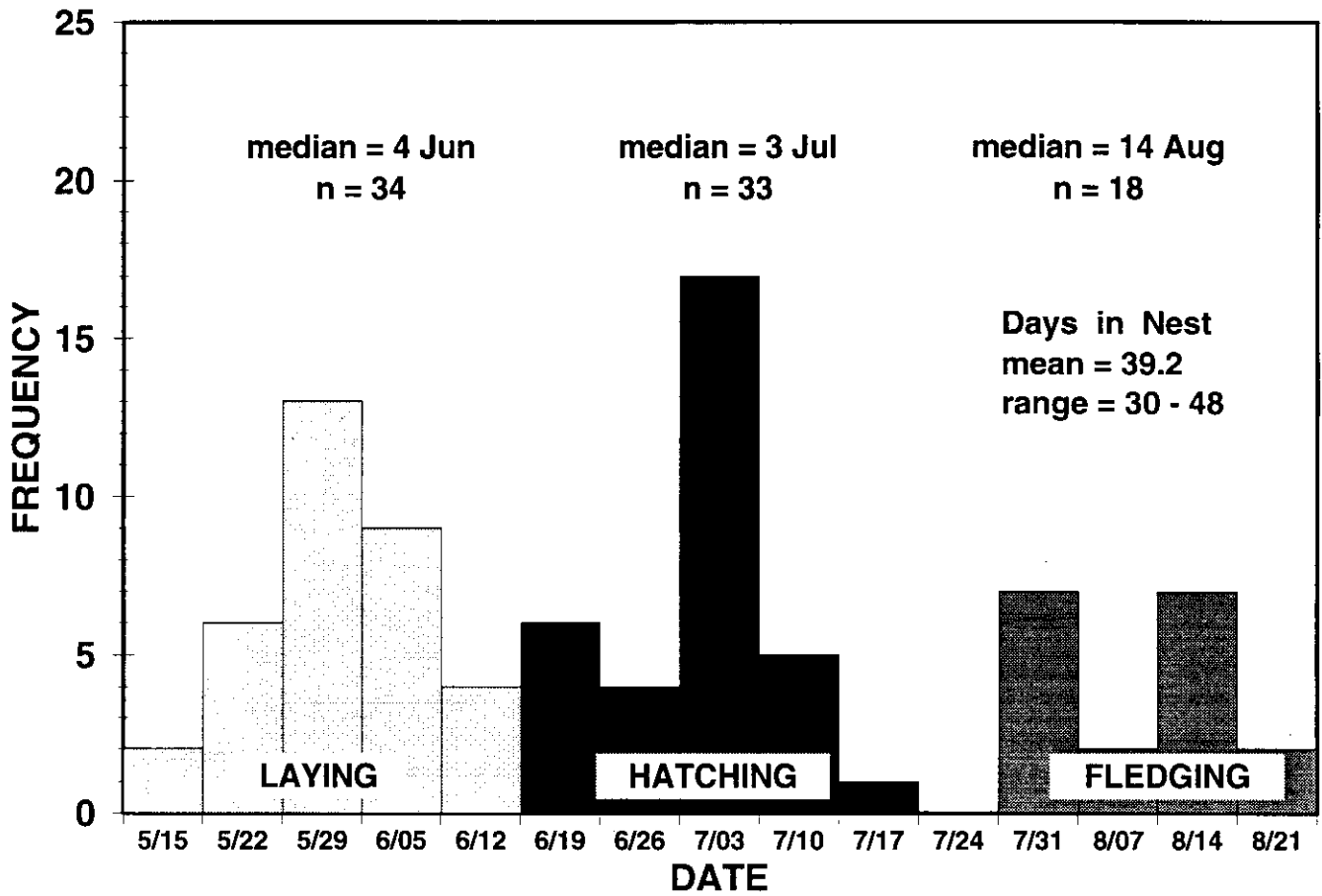


Figure 7. Nesting chronology of pigeon guillemots on Jackpot Island during the 1994 breeding season. Each bar represents one week beginning on the date below it. Only those nests followed from incubation through fledging were used to construct the chronology.

JACKPOT I. NESTING CHRONOLOGY -- 1994

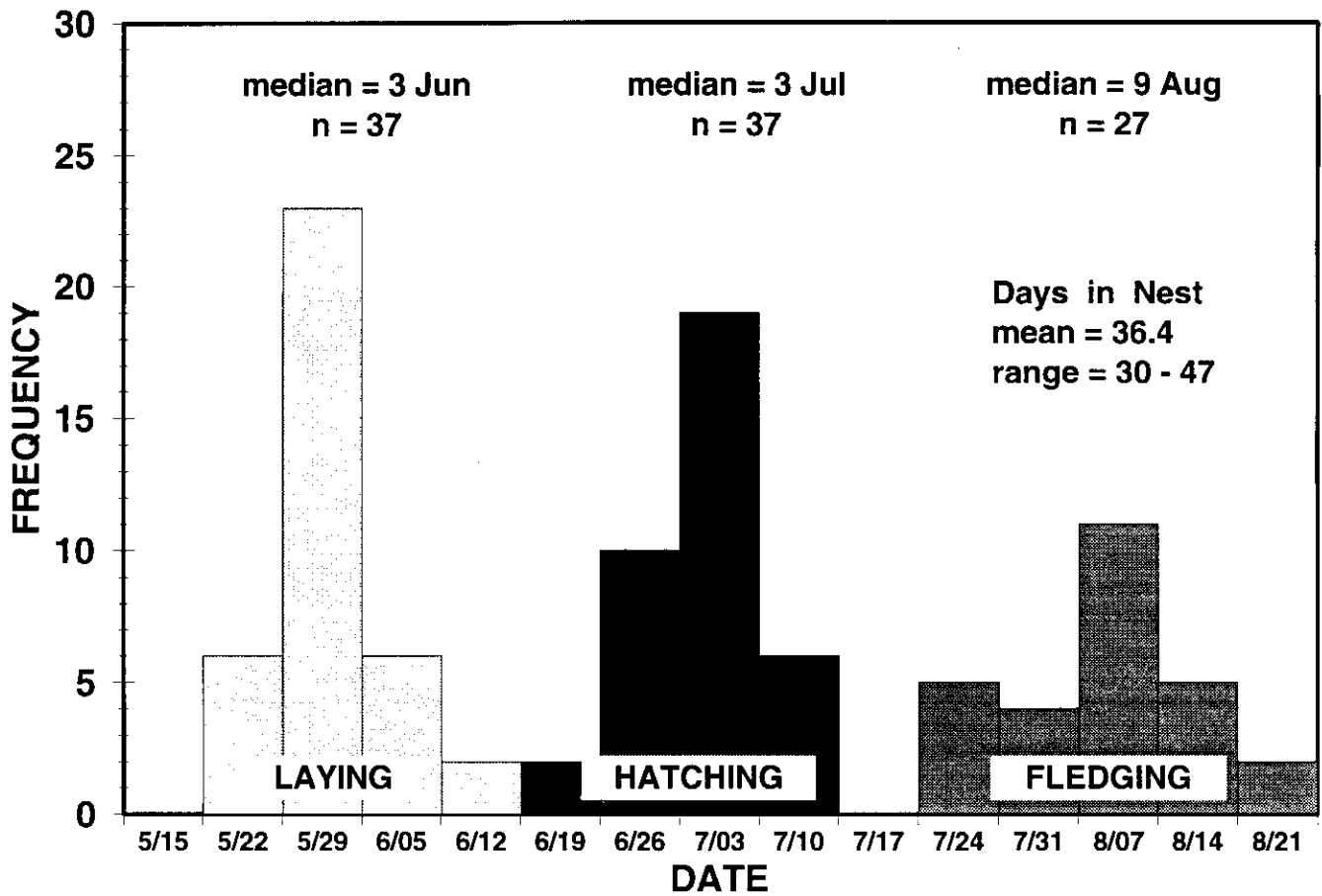


Figure 8. Comparison of \ln body mass vs. \ln wing length for chicks raised on Naked and Jackpot Islands. Second order polynomial equations for best-fit curves are shown.

PIGEON GUILLEMOT GROWTH

Comparison between Islands -- 1994

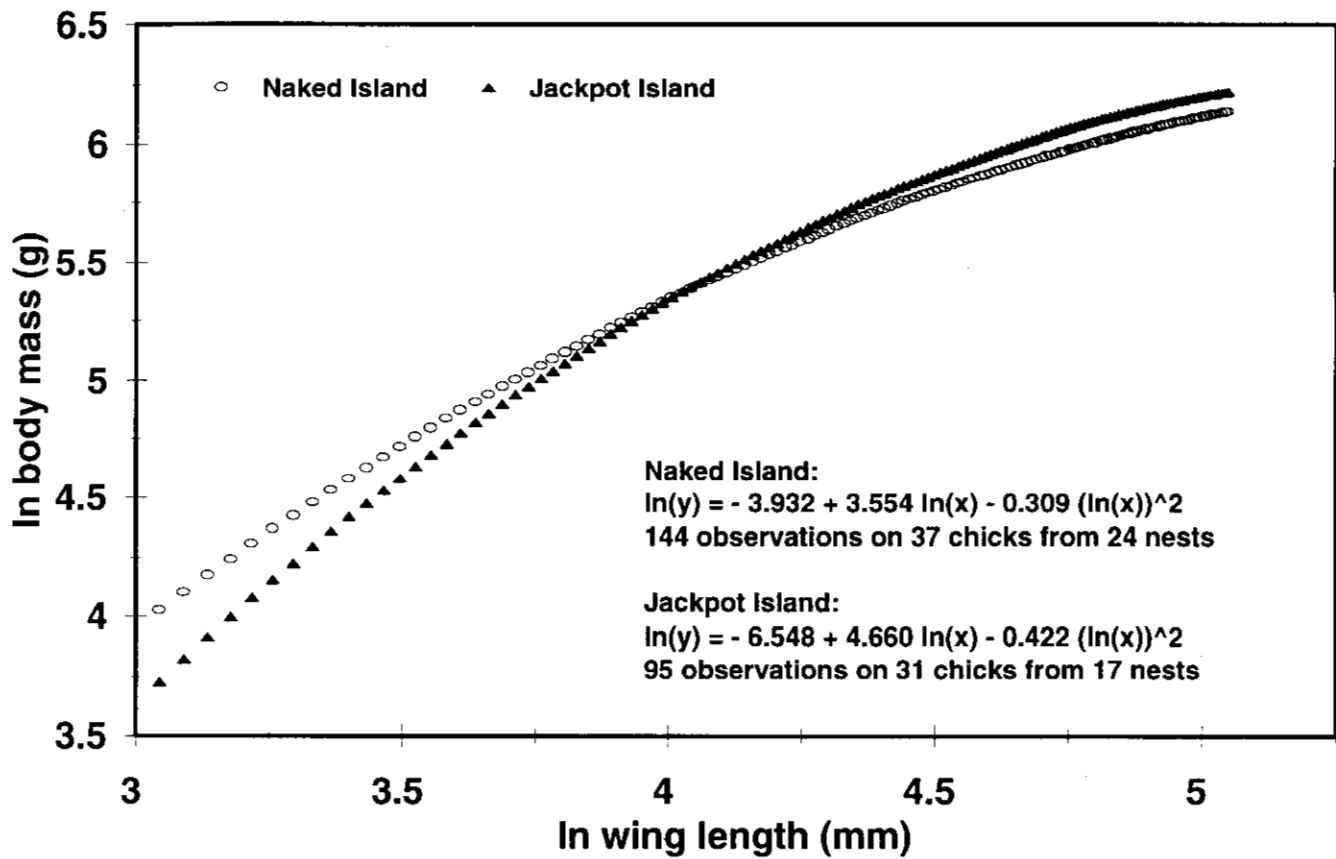


Figure 9. Temporal distribution of food deliveries by adult pigeon guillemots at several colonies on Naked Island during the 1994 breeding season.

TEMPORAL DISTRIBUTION OF DELIVERIES NAKED ISLAND -- 1994

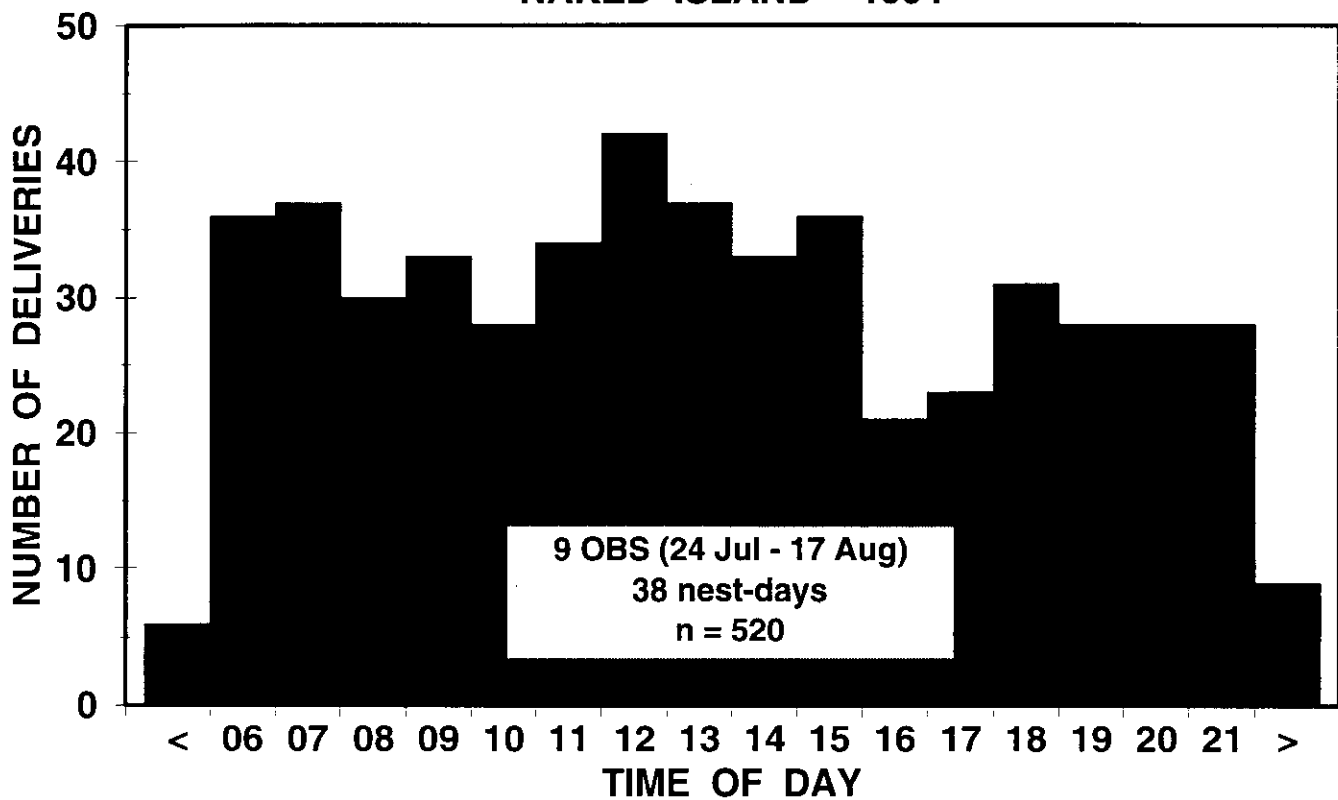


Figure 10. Temporal distribution of food deliveries by adult pigeon guillemots at Jackpot Island during the 1994 breeding season.

TEMPORAL DISTRIBUTION OF DELIVERIES JACKPOT ISLAND -- 1994

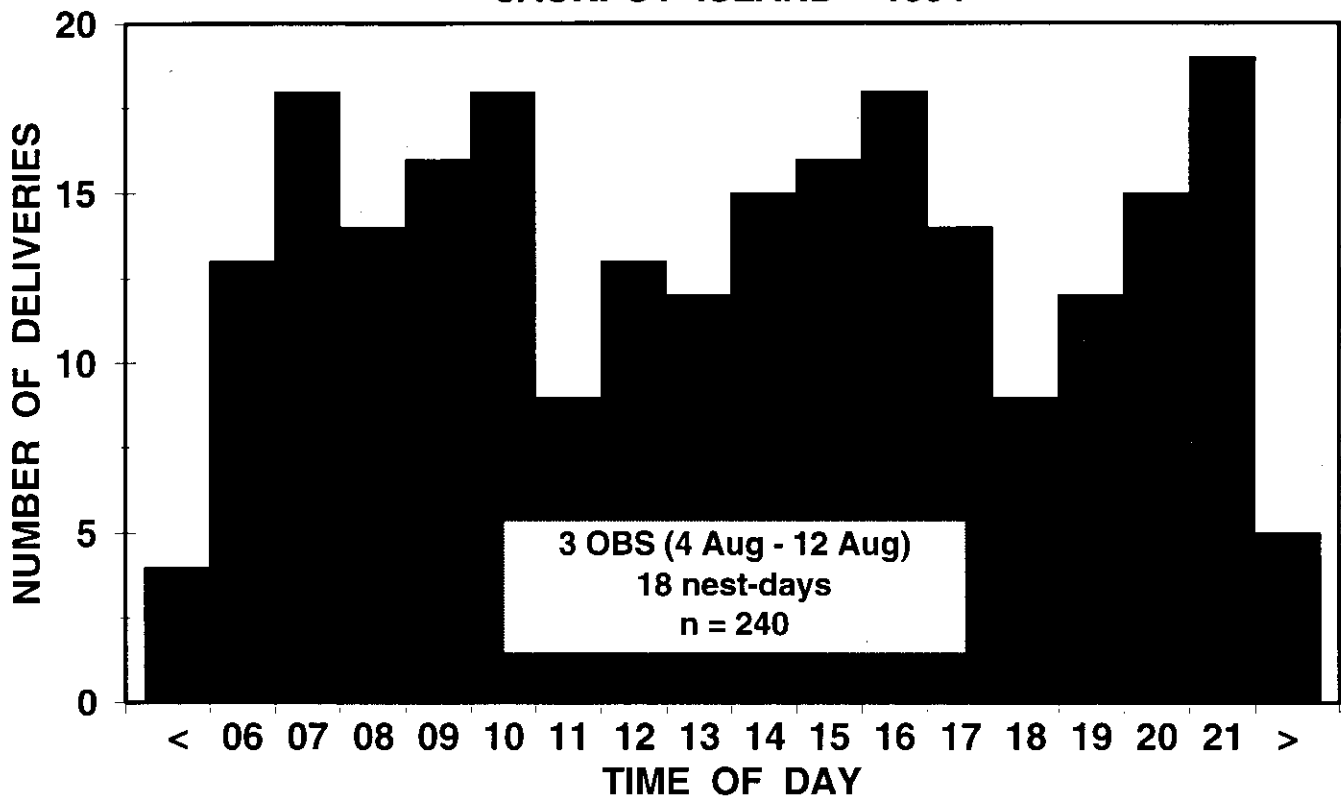


Figure 11. Temporal distribution of food deliveries (inverted triangles) to each of four guillemot nests at Tuft colony on Naked Island (3 August 1994). Notations above lines indicate total number of fish (f) delivered, delivery rate (f/h), and number of chicks (c) in the nest on that day. A "?" indicates the number of chicks in the nest on that day was not known and, if followed by a "(2)", that two chicks hatched in that nest. Two deliveries occurring within a three-minute period are indicated by a "+" above a triangle.

FOOD DELIVERIES

Tuft, Naked I. -- 3 Aug 1994

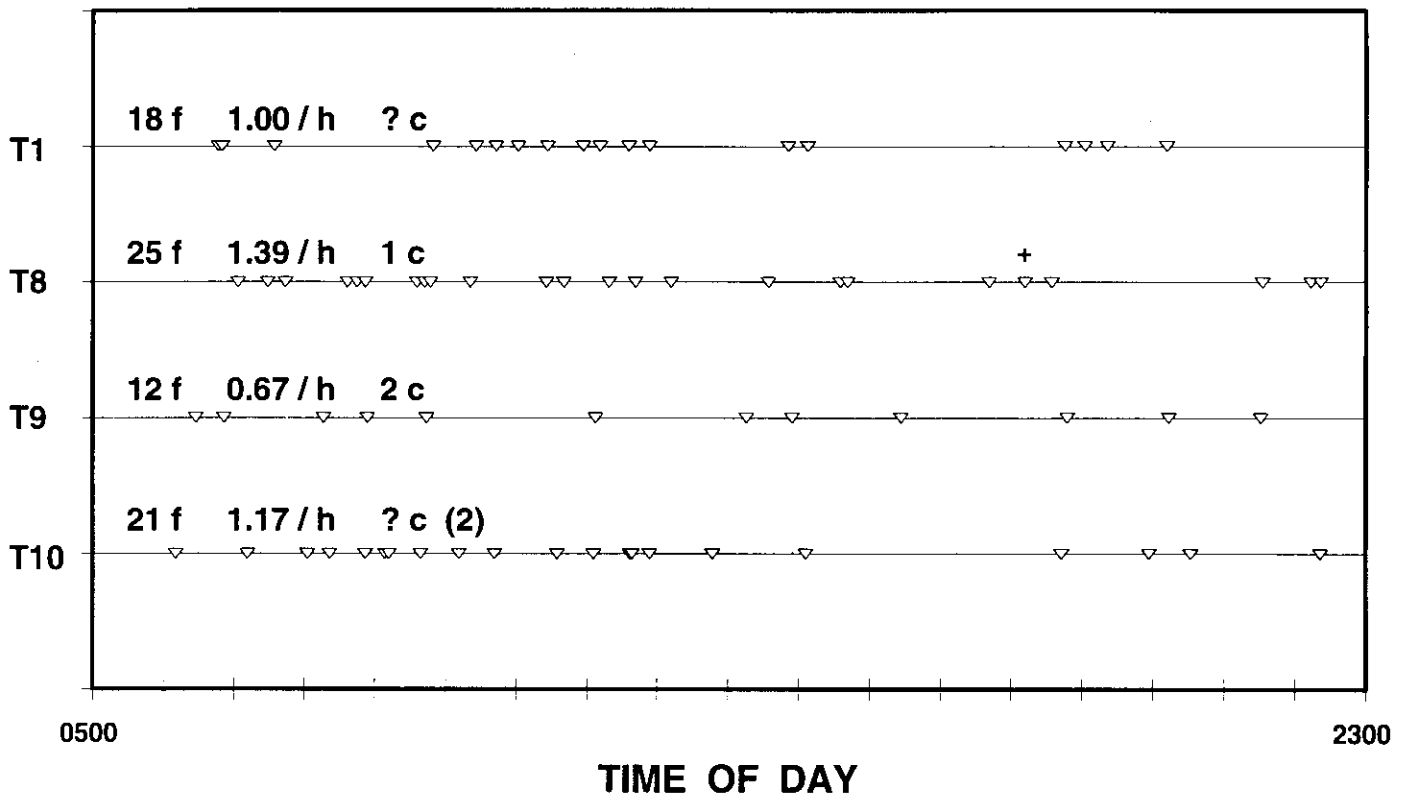


Figure 12. Temporal distribution of food deliveries (inverted triangles) to each of three guillemot nests at Nomad colony on Naked Island (7 August 1994). Notations above lines indicate total number of fish (f) delivered, delivery rate (f/h), and number of chicks (c) in the nest on that day. A "?" indicates the number of chicks in the nest on that day was not known and, if followed by a "(2)", that two chicks hatched in that nest. Two deliveries occurring within a three-minute period are indicated by a "+" above a triangle.

FOOD DELIVERIES

Nomad, Naked I. -- 7 Aug 1994

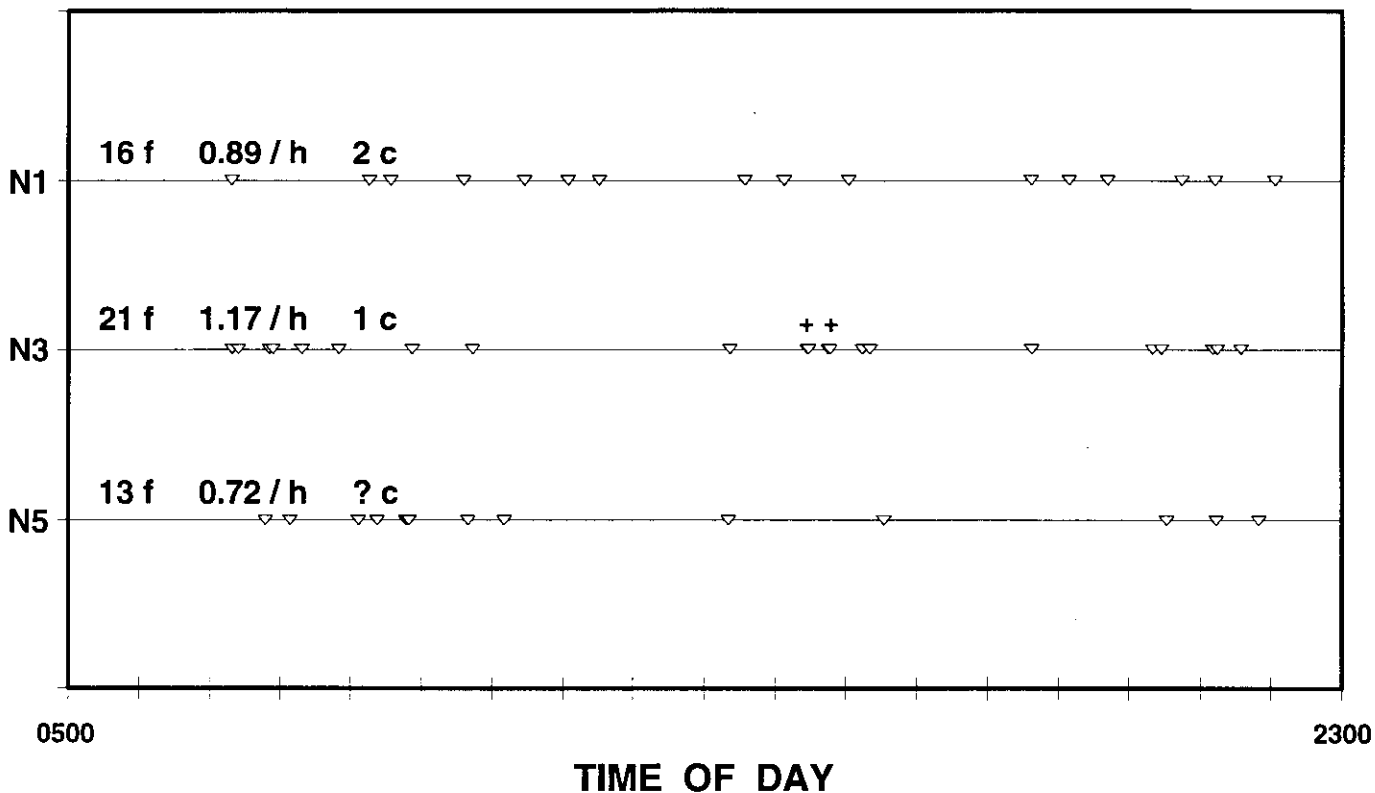


Figure 13. Temporal distribution of food deliveries (inverted triangles) to each of four guillemot nests on Jackpot Island (6 August 1994). Notations above lines indicate total number of fish (f) delivered, delivery rate (f/h), and number of chicks (c) in the nest on that day. A "?" indicates the number of chicks in the nest on that day was not known and, if followed by a "(2)", that two chicks hatched in that nest. Two deliveries occurring within a three-minute period are indicated by a "+" above a triangle.

FOOD DELIVERIES

Jackpot I. -- 6 Aug 1994

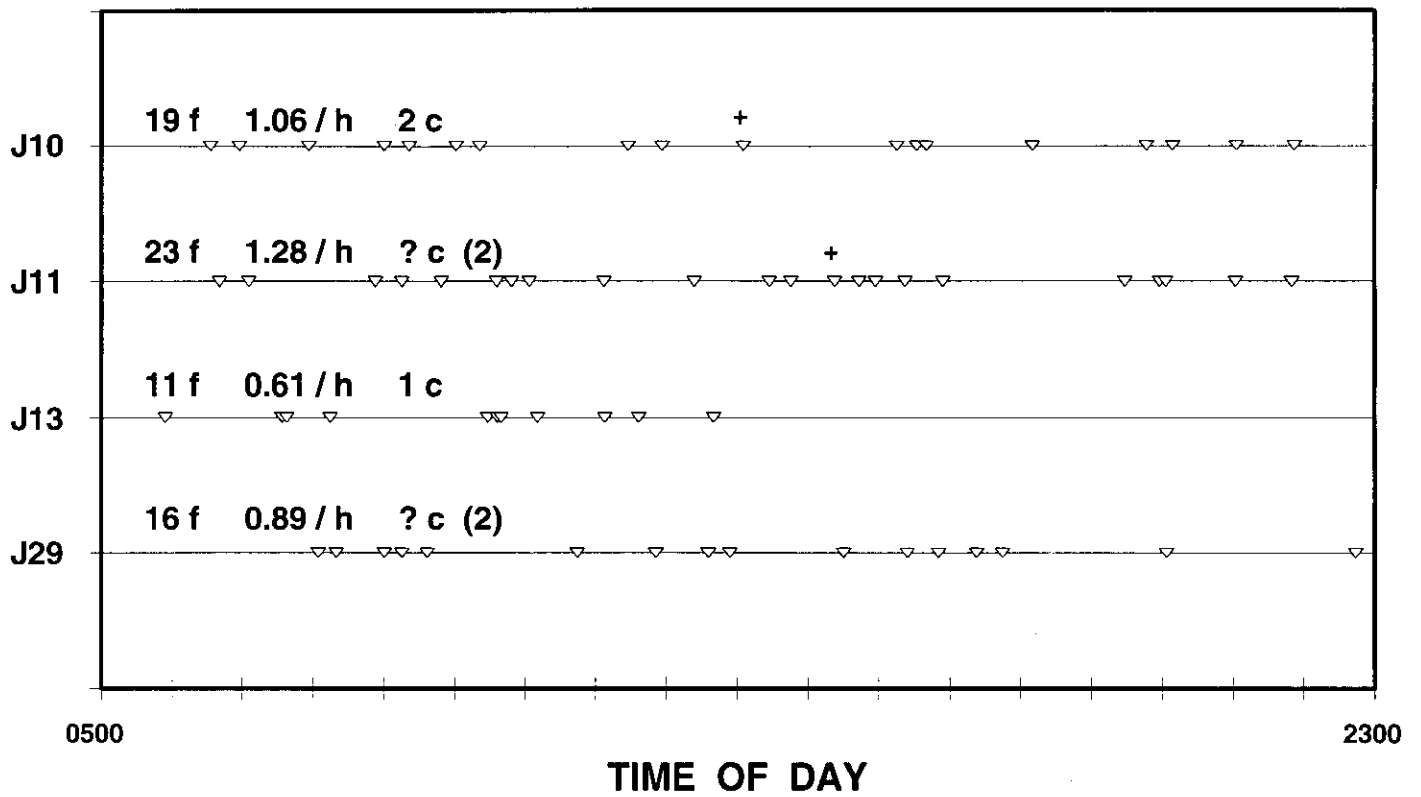


Figure 14. Bathymetry of the Naked Island area. Note the broad expanse of shallow water extending around most parts of Naked, Peak, and Storey Islands.

Bathymetric Depth Classification

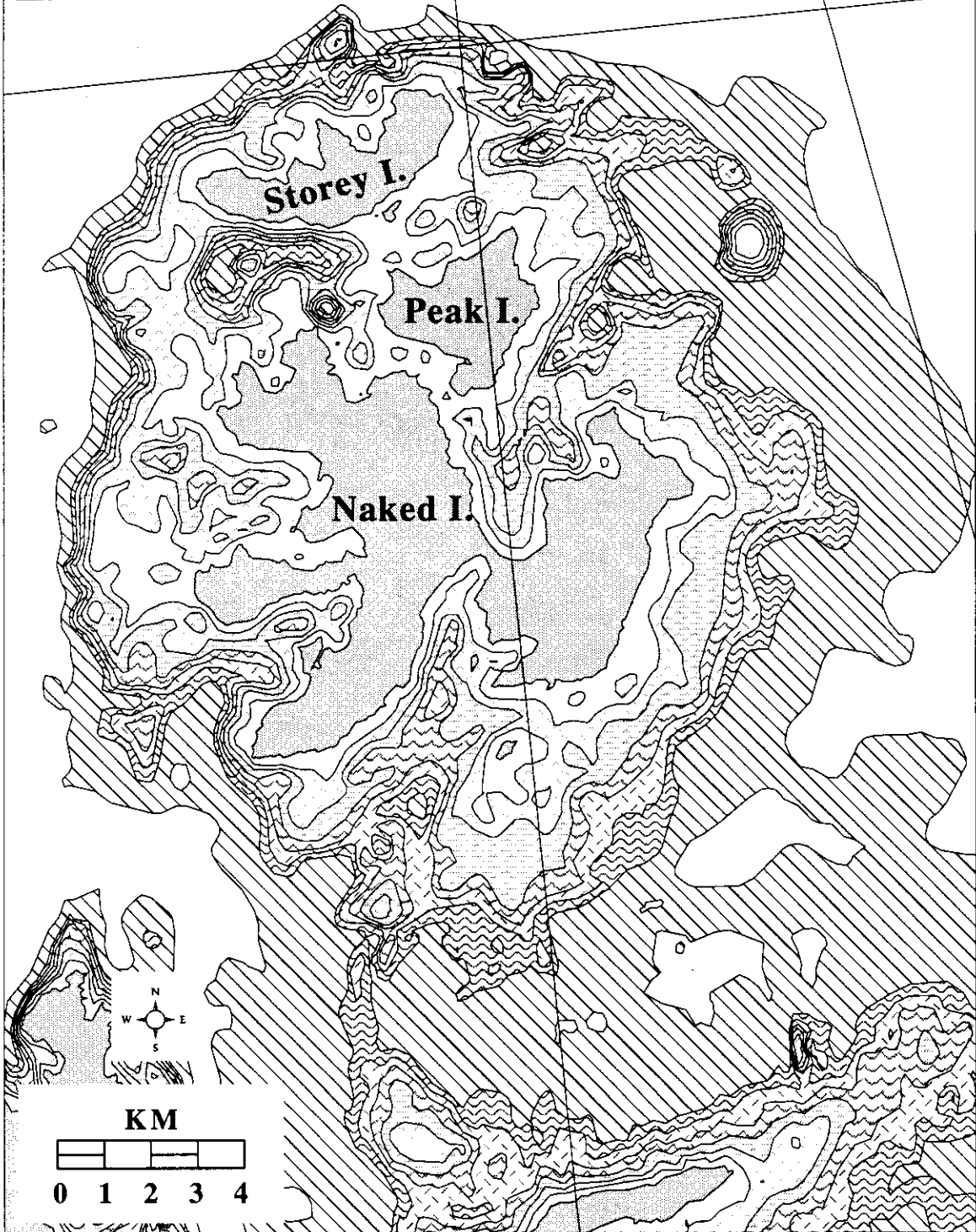
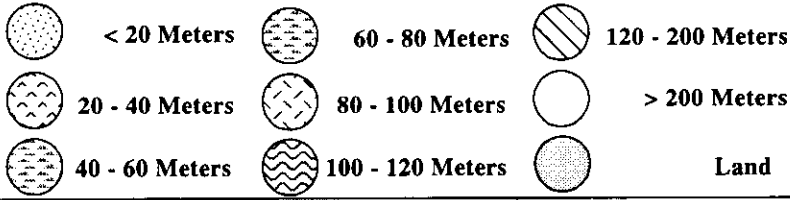


Figure 15. Bathymetry of the Jackpot Island area. Note the deep water surrounding Jackpot Island and shallower water near the mouths of Jackpot Bay and Icy Bay.

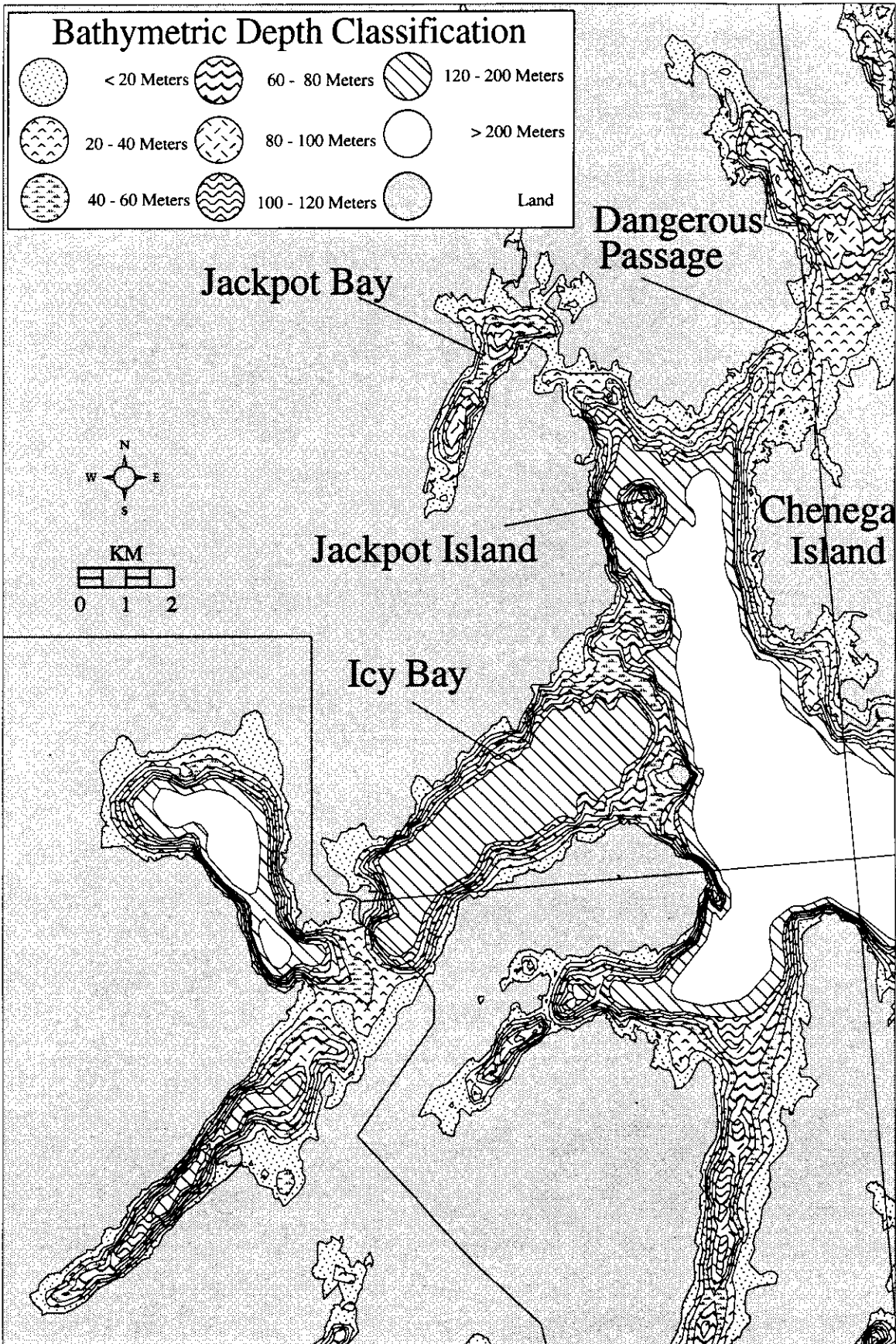
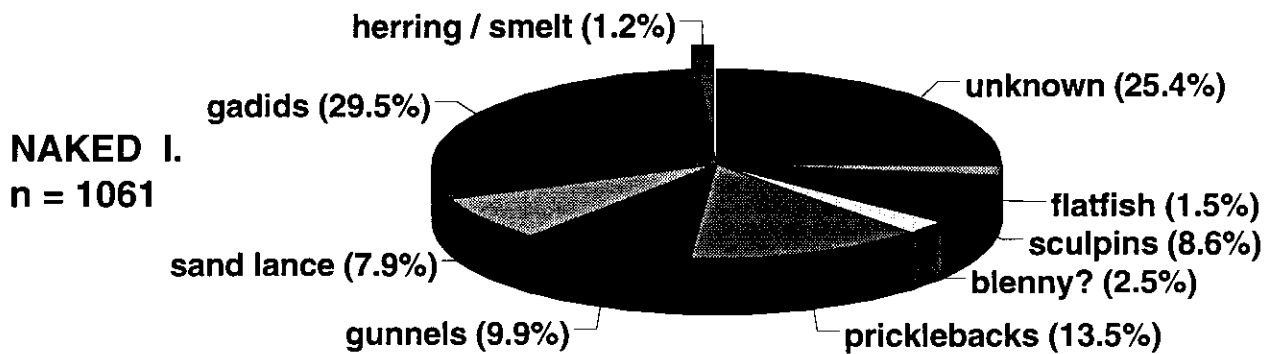
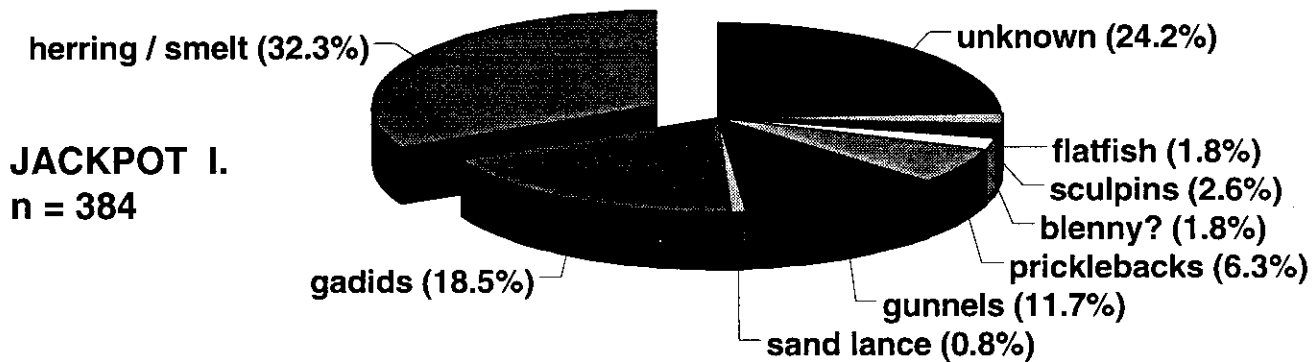


Figure 16. Comparison of prey types and relative proportions of each delivered by adult pigeon guillemots at several colonies on Naked Island (16 observations) and at Jackpot Island (3 observations). All observations were made between 17 July and 12 August 1994.

PREY TYPES & PROPORTIONS DELIVERED BY PIGEON GUILLEMOTS



All observations made between 17 July and 12 August 1994. NI = 16 obs, JI = 3 obs



APPENDIX

Oakley and Kuletz (1994) included several tables in their report, each of which relates to some measure of pigeon guillemot productivity. These tables have been reproduced here with only minor modifications, and updated with the appropriate values for 1994. Although the original tables contained information from Naked I. only, data from Jackpot I. have been included for comparative purposes.

Table A1.	Mean clutch size (mean number of eggs per nest found during the egg stage) of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the <i>T/V Exxon Valdez</i> oil spill	67
Table A2.	Mean number of chicks hatched per nest found in the egg stage of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the <i>T/V Exxon Valdez</i> oil spill	68
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Table A5.	Causes of nesting failure of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the <i>T/V Exxon Valdez</i> oil spill	71

Table A1. Mean clutch size (mean number of eggs per nest found during the egg stage)^a of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of nests	Mean clutch size	Standard error
Before spill			
1978	13	1.54	0.14
1979	33	1.85	0.06
1980	27	1.78	0.08
1981	22	1.59	0.11
1984	7	1.86	0.14
After spill			
1989	7	1.57	0.20
1990	27	1.78	0.10
1994	^b 23	1.70	0.10
1994 (JI) ^c	24	1.92	0.09

^aThe mean number of eggs per nest found during the egg stage is what Oakley and Kuletz (1994) refer to as mean clutch size; it is equivalent to mean clutch size as used in this report.

^bThis value includes 23 clutches from 22 nests.

^c(JI) indicates data from Jackpot Island.

Note: Data from all years except 1994 from Table 8 (Oakley and Kuletz 1994).

Table A2. Mean number of chicks hatched per nest found in the egg stage^a of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of nests	Mean number of chicks hatched	Standard error
Before spill			
1978	9	1.22	0.28
1979	32	1.34	0.15
1980	20	^b 1.05	0.20
1981	21	1.14	0.17
1984	7	1.43	0.37
After spill			
1989	7	1.43	0.30
1990	25	1.28	0.16
1994	^c 23	1.52	0.15
1994 (JI) ^d	24	1.54	0.17

^aThe mean number of chicks hatched per nest found in the egg stage is what Oakley and Kuletz (1994) refer to as hatching success rate; it is NOT equivalent to hatching success as used in this report.

^bNests of birds subjected to netting and tagging for foraging studies were not included, but reproduction of neighboring pairs at colonies where netting and tagging occurred might have been affected (Kuletz 1983).

^cThis value includes 23 clutches from 22 nests.

^d(JI) indicates data is from Jackpot Island.

Note: Data from all years except 1994 from Table 9 (Oakley and Kuletz 1994).

Table A3. Mean number of chicks fledged per nest found in the egg or chick stage^a of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of nests	Mean number of chicks fledged	Standard error
Before spill			
1978	30	1.60	0.10
1979	23	1.48	0.15
1980	12	^b 1.00	0.25
1981	17	1.06	0.18
1984	6	1.17	0.31
After spill			
1989	14	0.93	0.22
1990	29	0.79	0.14
1994	^c 35	0.86	0.13
1994 (JI)	28	1.25	0.15

^aThe mean number of chicks fledged per nest found in the egg or chick stage is what Oakley and Kuletz (1994) refer to as fledging success rate; it is NOT equivalent to fledging success as used in this report.

^bNests of birds subjected to netting and tagging for foraging studies were not included, but reproduction of neighboring pairs at colonies where netting and tagging occurred might have been affected (Kuletz 1983).

^cThis value includes 35 clutches from 34 nests.

^d(JI) indicates data is from Jackpot Island.

Note: Data from all years except 1994 from Table 10 (Oakley and Kuletz 1994).

Table A4. Mean number of chicks fledged per nest found in the egg stage^a of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill.

Year	Number of nests	Mean number of chicks fledged	Standard error
Before spill			
1978	8	1.25	0.20
1979	30	1.13	0.13
1980	18	^b 0.61	0.20
1981	19	0.74	0.17
1984	7	1.00	0.28
After spill			
1989	6	0.50	0.34
1990	24	0.68	0.16
1994	^c 23	0.78	0.17
1994 (JI) ^d	24	1.17	0.17

^aThe mean number of chicks fledged per nest found in the egg stage is what Oakley and Kuletz (1994) refer to as nesting success rate; it is NOT equivalent to nesting success as used in this report.

^bNests of birds subjected to netting and tagging for foraging studies were not included, but reproduction of neighboring pairs at colonies where netting and tagging occurred might have been affected (Kuletz 1983).

^cThis value includes 23 clutches from 22 nests.

^d(JI) indicates data is from Jackpot Island.

Note: Data for all years except 1994 from Table 11 (Oakley and Kuletz 1994).

Table A5. Causes of nesting failure of pigeon guillemots at Naked Island, Prince William Sound, Alaska, before and after the *T/V Exxon Valdez* oil spill.

Number of Nests in which at least one egg failed to hatch or at least one chick failed to fledge.							
Year	Number of Nests	Unhatched Egg ^a	Young Chick Death ^b	Predation of Egg ^c	Predation of Chick ^c	Starvation or Exposure	Unknown Reason
Before spill							
1978	32	4	0	0	0	0	2
1979	30	6	1	2	1	1	4
1980	19	5	0	2	0	4	2
1981	22	6	1	2	0	6	0
After spill							
1989	15	3	1	1	4	0	0
1990	38	2	1	3	4	1	5
1994	23 ^d	1	1	2	7	1	4
1994 (JI) ^e	24	5	2	0	0	0	6

^aIncludes eggs which failed to hatch due to infertility, embryo death, or nest desertion.

^bRefers to chicks, less than one week old, dying in the nest for no apparent reason.

^cIn previous years, predation was rarely witnessed; most instances of nesting failure attributed to predation were presumed based on disappearance of eggs or chicks. In 1994, predation was never witnessed, but conclusive evidence of predation was found.

^dThis value includes 23 clutches from 22 nests.

^e(JI) indicates data is from Jackpot Island.

Note: Data from all years except 1994 from Table 12 (Oakley and Kuletz 1994).