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DETERMINANTS OF POPULATION SIZE
OF PIGEON GUILLEMOTS *Cepphus columba*
AT NAKED ISLAND, PRINCE WILLIAM SOUND, ALASKA

A THESIS

Presented to the Faculty of the
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ABSTRACT

Nesting distribution, habitat use, food habits, and reproduction of Pigeon Guillemots Cepphus columba breeding at Naked Island, Prince William Sound, Alaska, were studied in 1978 to determine the factors that allow this species to occur abundantly there. The dominance of the shoreline by habitats containing natural nesting crevices accounted, in part, for guillemot abundance. Foraging occurred in bays; juvenile cods and sand lance were the most important prey. The population was relatively asynchronous in its reproductive activities due to the lack of predation and to the lengthy period of food availability. Nesting success rates were high. Nestlings gained weight faster and fledged at significantly higher weights than nestlings raised elsewhere. I concluded that Pigeon Guillemot population size and distribution are determined primarily by density independent factors.

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Brina Kessel provided guidance throughout my stay at this university. Stephen F. MacLean, Jr. suggested a change in this manuscript which decreased its size and enhanced its clarity. C. Peter McRoy taught me much about biological oceanography, thus

filling a large void in my understanding of seabird biology and behavior. I thank my committee for their efforts in my behalf.

INTRODUCTION

The Pigeon Guillemot *Cepphus columba* is one of 22 extant species of wing-propelled divers (Alcidae) occurring in the neritic waters of the northern oceans. This species and its two congeners, *C. grylle* and *C. carbo*, are distinguished ecologically from other alcids, and from most other seabirds, by two phenomena: (1) During breeding, they feed inshore, primarily on epibenthic fishes, and (2) they breed ubiquitously in low numbers throughout their ranges. In contrast, most seabirds feed offshore and breed in a few large colonies. This correlation between foraging zone and the size and dispersion of colonies is pervasive, both within and between families of seabirds (Lack 1968), although as yet there has been no functional explanation for it.

A seabird census in 1977 in the vicinity of Naked Island, Prince William Sound, Alaska (Sangster et al. 1978), revealed that large numbers of Pigeon Guillemots bred there. In 1978, I undertook studies to discover the ecological factors that allowed such abundance of Pigeon Guillemots at Naked Island. Guillemots are crevice nesters, and, at some locations, the number and dispersion of breeding guillemots is apparently determined by the availability of nest sites (Winn 1950, Drent 1965, Ainley and Lewis 1974). Alternatively, Asbirk (1979) suggested that guillemots nest in a dispersed fashion to avoid depletion of a dispersed and low density food supply. Thus, I examined both nesting habitat use and foods of the Naked Island guillemots.

Nesting chronology, success, and nestling growth were studied to provide indirect information on the availability and quality of food and nest sites.

The apparent stability of bird populations is generally attributed to density dependent mechanisms, notably competition for food, nesting sites, or both (Lack 1966, and others). I designed this study to reveal the relative importance of density independent and density dependent factors in determining guillemot population size and why guillemots nest ubiquitously in low numbers.

STUDY AREA

The study area was located in the center of Prince William Sound (PWS), a fjord-type estuarine system located off the northern Gulf of Alaska. The study area comprised Naked (36 km^2), Peak (5 km^2), Storey (8 km^2), Smith (3 km^2), and Little Smith (0.5 km^2) islands, and their adjoining waters (Fig. 1). The PWS region is part of the Pacific coastal belt of spruce *Picea sitchensis* and hemlock *Tsuga heterophylla* forest (Cooper 1942). The islands are low (less than 400 m) and wooded to their summits. Shores in the Naked Island area are rocky and consist of cliffs, broken cliffs, and escarpments interspersed with boulder beaches. They are composed of slightly metamorphosed, complexly folded marine Tertiary sandstones, primarily siltstone and argillite (Case et al. 1966). Shoreline habitats are described in Table 1, and their distribution is shown in Fig. 2. The Naked Island area was uplifted about 1 m during a major earthquake on 27 March 1964 (Plafker 1969). Tidal range is 3-4 m.

The climate of PWS is maritime, characterized by moderate temperature ranges and much precipitation. PWS weather is determined by the positions of the Aleutian Low and the Pacific High pressure systems (Royer 1975). During summer 1978, nearly 70% of the days were overcast, and rain, totalling 760 mm, fell on about half of the days. Winds recorded at the field camp, a protected location, were generally slight and were from the SE or SW; NW winds occurred infrequently.

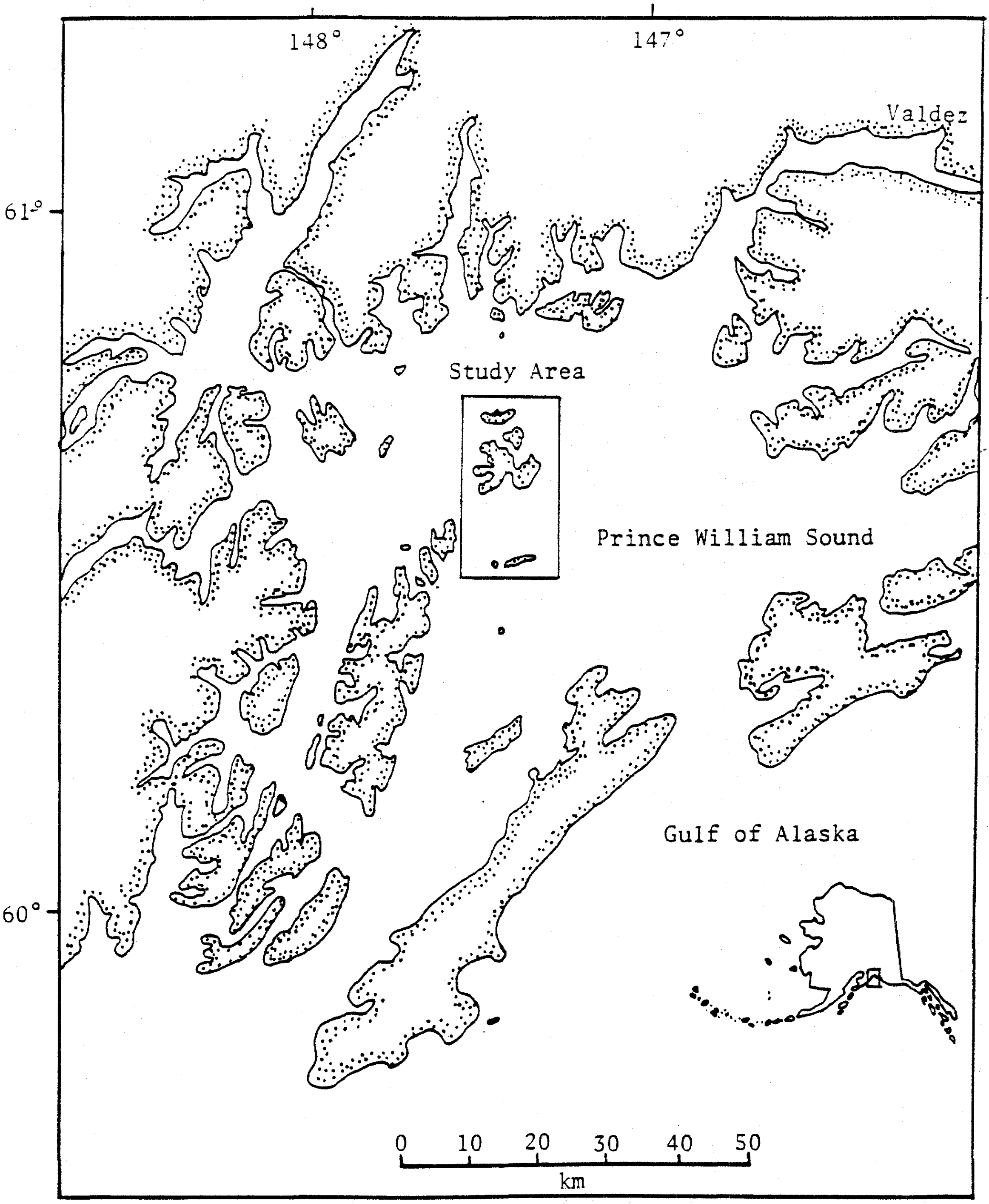

FIGURE 1. Map of Prince William Sound, Alaska, showing location of the study area.

TABLE 1. Definitions of shoreline habitats in the Naked Island area, Alaska.

Habitat	Definition
beach	gravel and boulder beaches that grade directly into island vegetation; could have rock outcrops or banks less than 5 m in height interspersed
cliff	vertical or nearly vertical section of rock with no significant vegetation; either grades directly into the *Fucus* zone or has talus boulders or a rounded boulder beach below; could have overhanging trees, generally alder *Alnus sinuata*, but also spruce *Picea sitchensis* and hemlock *Tsuga heterophylla*
broken cliff	less than vertical section of rock with vegetated ledges and cracks and with talus boulders on or below
escarpment	rock outcrops on steep vegetated slopes

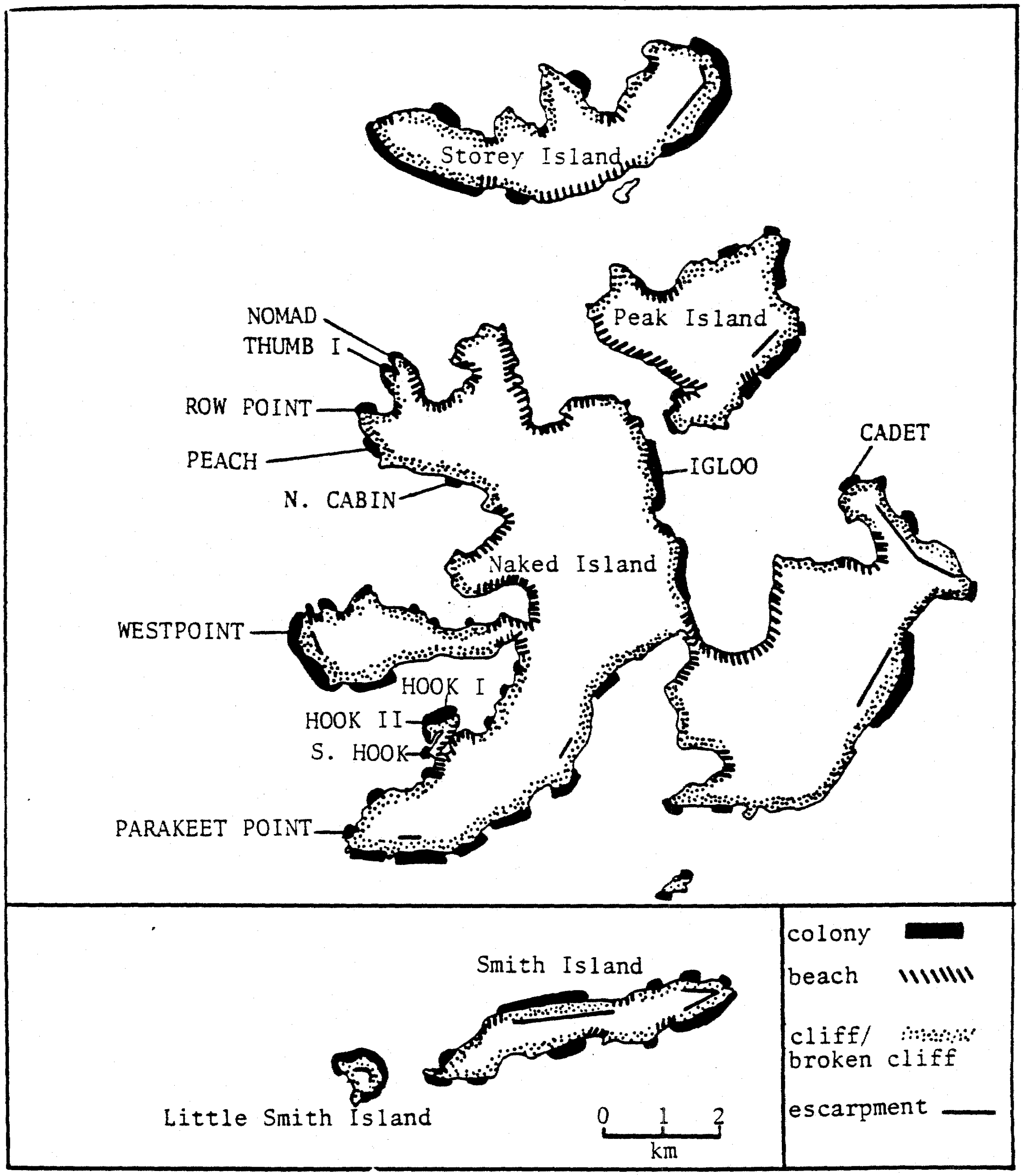

FIGURE 2. Location of Pigeon Guillemot colonies relative to the distribution of shoreline habitats in the Naked Island area, Alaska, and location of colonies referred to in the text.

The bathymetry and chemical and physical oceanographic properties of PWS have been described by Muench and Schmidt (1975). Surface water temperatures range from -2°C to 18°C. Surface salinities are strongly influenced by input of glacial and river fresh water and range from 20 o/oo in summer to 30 o/oo in winter. PWS is deep--over 70% is deeper than 100 m and over 40% is deeper than 200 m (C.P. McRoy, pers. comm.). The deepest part is an 800 m trench just west of Naked Island. The three main bays of Naked Island, and the passages between Naked, Peak, and Storey islands, form a large area of waters less than 100 m in depth; thus the study area can be considered an "island" of shallow water surrounded by much deeper water.

Marine plants, including Zostera marina, Nereocystis lutkeana, and Laminaria saccharinea, are a conspicuous component of the biological system. The inshore fishes of PWS, studied recently by Feder and Paul (1977) and Rosenthal (1979), are part of the Aleutian faunistic group (Peden and Wilson 1976).

Isleib and Kessel (1973) provided a general account of the avifauna of the PWS region. Six alcid and one larid species breed at Naked Island (Table 2). Other breeding birds that use marine habitats are the Bald Eagle Haliaeetus leucocephalus, Common Raven Corvus corax, and Northwestern Crow C. caurinus. Nonbreeding birds, including Pelagic Cormorants Phalacrocorax pelagicus,

TABLE 2. Seabird species breeding in the Naked Island area, Alaska, and their approximate population sizes in 1978 (after Oakley and Kuletz 1979).

Species	No. of Birds
Arctic Tern *Sterna paradisaea*	100
Pigeon Guillemot *Cepphus columba*	2500
Marbled Murrelet *Brachyramphus marmoratus*	3000
Parakeet Auklet *Cyclorrhynchus psittacula*	500
Rhinoceros Auklet *Cerorhinca monocerata*	5
Horned Puffin *Fratercula corniculata*	150
Tufted Puffin *Lunda cirrhata*	1000

Glaucous-winged Gulls Larus glaucescens, Black-legged Kittiwakes Rissa tridactyla, and Common Murres Uria aalge are an important part of the marine avifauna.

There is a small run of pink salmon Oncorhynchus gorbuscha on Naked Island, but it is rarely exploited. Storey, Peak, and the Smith islands were all stocked with fox Alopex lagopus around 1900 (Witten 1903), and they were present until the 1930's. With the exception of a private residence on Peak Island, the islands are uninhabited and undeveloped at this time.

METHODS

Each island was censused using a small boat at least three times during the summer, at about monthly intervals. The time of day varied, but most counts were between 04:00 and 09:30 Alaska Standard Time (AST). Weather during most censuses was clear or overcast with light winds. Each island was circumnavigated 50-100 m from shore, and the number, location, and activity of all guillemots was noted.

Censuses of a 100 m-wide strip were made from a small boat on five inshore and three offshore transects (Fig. 3). Counts were made by a single observer either to 100 m on one side of the boat or to 50 m on both sides, depending on light conditions. Speed averaged 20 km/h. Repeated observations were made on the inshore transects; offshore transects were conducted less frequently. All transects were made opportunistically and only when sea and light conditions were favorable; transects therefore occurred at various times of day. The number of each species on each transect was summed and the density (no. birds/km) calculated.

To estimate the proportion of the guillemot population that was nonbreeding, the number of nesting birds was compared with the number of birds counted during the early morning June censuses for 11 colonies.

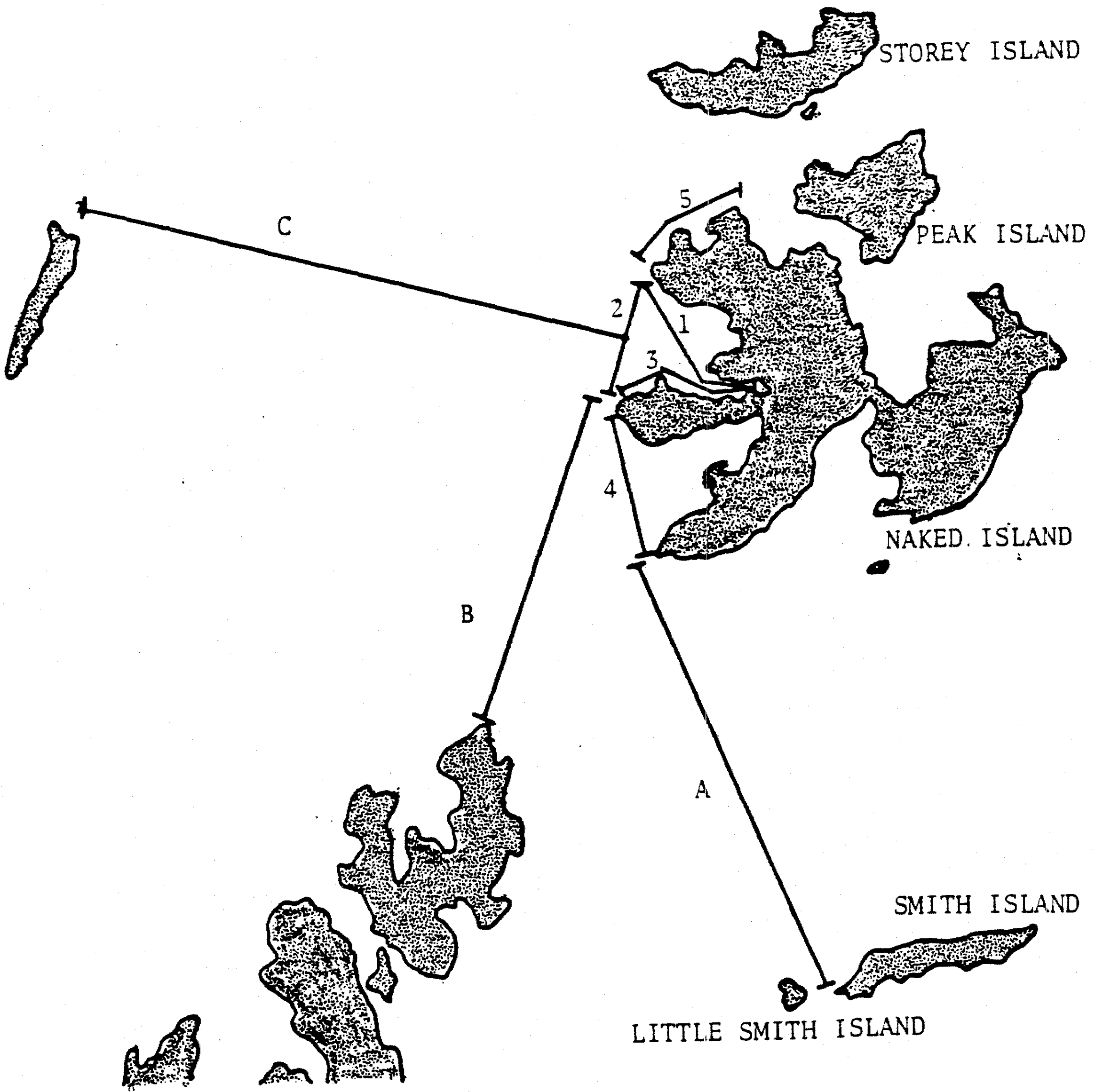

FIGURE 3. Location of the five inshore (1-5) and three offshore (A-C) transects on which seabird observations were made during summer 1978, at Naked Island, Alaska.

In total, 146 nest sites were observed for which nest type could be determined. Nest entrance dimensions, the distance from the entrance to the eggs, and the elevation above high tide line were measured on accessible nests.

Observations totalling 10.2 h were made of food items fed to chicks at Row Point and Westpoint colonies (see Fig. 2) between 12 July and 10 August. Observation periods occurred during midday (10:00-15:30 AST) and ranged from 0.25-2.0 h. Each fish observed was classified as a gadid, sand lance, cottid, or other, including unidentified fishes, and its length relative to the length of the bird's bill was estimated.

Food items lying in or near nests were recovered during regular visits. If chicks had been fed just prior to my arrival, I was often able to remove the fish from the chick's esophagus. All 29 items thus recovered were weighed to the nearest gram on a Pesola 100-g scale, and the total length of the item was measured to the nearest millimeter.

Excrement was collected from 14 nests, and all whole otoliths and large otolith pieces were examined. An estimate of the number of whole cod otoliths represented was obtained by weighing all cod otolith pieces from a nest to 0.001 g on a Sartorius digital balance and dividing that weight by 0.010 g, the average weight of five 5-mm Gadus/Theragra otoliths.

Fourteen Pigeon Guillemots were collected in June and late August to provide information on foods which were not necessarily fed to chicks. Birds were taken within 500 m of shore, mostly within 200 m. Immediately upon collection, each bird was weighed, and then formalin, diluted to 10% with seawater, was poured into the stomach. Later, stomachs were removed and preserved in additional formalin. When stomach contents were analyzed, food items were weighed to 0.1 g on a triple beam balance, and volume to 0.1 ml was determined by displacement.

Nomenclature of fish and invertebrate species follows Hart (1973) and Mueller (1976), respectively.

Transects and incidental observations provided information on foraging areas.

Information on the timing of reproductive activities was obtained from 10 nests found during the egg stage and 22 nests found during the chick stage. All nests were monitored until the chicks fledged; the date of fledging was known within 1 d for most chicks. A chronology for all breeding events was reconstructed from known dates of fledging, using the mean values for chick period (35 d) and incubation period (32 and 30 d, for first and second eggs, respectively) reported by Drent (1965).

Nesting success was studied at 32 nests for which clutch size was known. The estimate for hatching success was based on 10 nests found during the egg stage. Two nests with one chick were excluded from the analysis because they could not be searched to determine if another egg or chick had been present. Four nests with one chick were searched with no sign of a dead egg or chick.

In a related study of the Black Guillemot near Barrow, Alaska, and in this study, I found that unhatched eggs and dead chicks remain in nests, generally in a corner or partially buried in nest substrate. Hence, the four presumed one-egg clutches were included in the analysis of nesting success.

Various measures of growth were taken about every other day on 29 chicks, 12 of known age. Measurement of total culmen was made to 0.5 mm with vernier calipers and of wing chord to the nearest millimeter with a ruler. Weight was measured on a Pesola spring-balance scale appropriate to the weight at a given age (100 ± 1 g; 500 ± 10 g; 2.5 kg ± 25 g). Twenty-four chicks measured within 24 h of fledging were considered in the estimation of average fledging weight and size. Average weight gain (g/d) between 8 and 18 d of age was calculated for 12 chicks at Naked Island and 4 chicks at Fish Island, Alaska, and the Mann-Whitney test was used to test for differences between these chicks′ growth rates.

RESULTS

Population Characteristics

The number of Pigeon Guillemots counted at each island during censuses in 1978 is shown in Table 3. The number of guillemots seen in the June early morning counts was 1969. If the highest counts for each section of coast are summed, regardless of the date or time they occurred, a figure of 2228 is obtained. Hence, I estimate that 2000-2500 Pigeon Guillemots summered in the Naked Island area in 1978.

Nesting Pigeon Guillemots occurred in 34 of the 116 km of shoreline (Fig. 2). Guillemots were often present throughout sections of coast several kilometers long within which it was impossible to delineate discrete colonies. Some nests were solitary, and none of the 13 colonies--here defined as geographically distinct breeding sites--studied had more than 20 nests (Fig. 2). Pigeon Guillemots bred at all sites used by the other alcid species, as well as at many other sites.

The density of Pigeon Guillemots on inshore transects at Naked Island was high compared to their density on similar transects in Chiniak and Marmot bays, Kodiak Island, Alaska (Table 4). The relative abundances of seabird species also differed; Marbled Murrelets and Pigeon Guillemots dominated Naked Island waters, while Tufted Puffins dominated Kodiak Island waters.

TABLE 3. Counts of Pigeon Guillemots at colonies in the Naked Island area, Prince William Sound, Alaska, in 1978. Population size was estimated by (1) summing early morning counts in June (counts with *) and (2) summing high counts regardless of the date or time they occurred.

Location	May-June			July			August		
	day	time	no. birds	day	time	no. birds	day	time	no. birds
NAKED ISLAND									
Cabin Bay	26 MY	11:45-14:40	60				29 AU	05:35-10:05	11
	27 MY	09:00-18:30	58						
	3 JN	05:10-08:05	118*						
northwest side	27 MY	09:40-09:50	38	20 JL	09:25-09:45	39	29 AU	06:00-06:30	8
	3 JN	05:50-06:10	100*						
	4 JN	03:40-04:00	44						
McPherson Bay	27 MY	11:00-13:00	73	20 JL	09:25-09:45	188	29 AU	06:35-07:00	14
	4 JN	04:00-05:30	180*						
east side	27 MY	13:00-15:30	45	27 JL	09:30-11:30	118	1 AU	11:30-13:40	109
	4 JN	05:30-06:30	243*				29 AU	07:25-07:55	1
Bass Harbor (inner)	27 MY	16:00-17:00	36				29 AU	08:15-08:45	6
	4 JN	06:30-06:45	115*						
Bass Harbor (outer)	27 MY	15:30-17:45	20	27 JL	08:40-13:30	166	23 AU	13:00-13:30	1
	3 JN	07:00-07:20	66				29 AU	08:45-09:15	0
	4 JN	07:45-08:00	101*						
	8 JN	16:40-16:50	43						
	20 JN	08:50-09:35	78						
Outside Bay	26 MY	11:45-14:40	105				29 AU	09:15-09:50	12
	3 JN	06:15-07:00	290*						
	28 JN	04:50-06:30	196						
STOREY ISLAND	28 MY	10:45-14:25	84	27 JN	08:50-13:15	465	24 AU	06:15-07:25	50
	7 JN	04:20-05:35	364*						
PEAK ISLAND	28 MY	14:30-16:30	86	28 JL	07:10-09:35	164	24 AU	07:45-09:50	12
	7 JN	05:35-06:20	94*						
SMITH ISLAND	24 JN	04:00-05:45	292*	29 JL	06:00-09:30	271	23 AU	09:40-12:30	10
LITTLE SMITH ISLAND	24 JN	04:00-05:45	72*	29 JL	06:00-09:30	54	23 AU	09:40-12:30	1

TABLE 4. Average density (no. birds/km^2) and relative abundance (percent of total density) of seabird species during summer near Naked and Kodiak islands, Alaska, based on transect observations from small boats.

Species	Naked Island[1]		Kodiak Island[2]	
	av. density	rel. abund.	av. density	rel. abund.
Cormorant sp. *Phalacrocorax sp.*	0.3	0.2	2.6	2.4
Glaucous-winged Gull *Larus glaucescens*	4.8	2.5	10.4	9.4
Black-legged Kittiwake *Rissa tridactyla*	37.3	19.3	22.7	20.6
Arctic Tern *Sterna paradisaea*	2.9	1.5	1.1	1.0
Common Murre *Uria aalge*	4.6	2.4	2.1	1.9
Pigeon Guillemot *Cepphus columba*	43.8	22.7	4.6	4.2
Marbled Murrelet *Brachyramphus marmoratus*	91.8	47.6	4.0	3.6
Horned Puffin *Fratercula corniculata*	1.1	0.6	5.0	4.5
Tufted Puffin *Lunda cirrhata*	1.0	0.5	50.6	45.8
Other	5.2	2.7	7.3	6.6
All species	192.8	100	110.4	100

[1] inshore transects 1-5 [2] Dick et al. 1976

Nonbreeders, consisting of 1- and 2-year-old birds (identified by plumage) and adult-plumaged birds of unknown age, may represent 30-55% of the guillemots present at colonies (Winn 1950, Drent 1965, Preston 1968, Henderson MS). For 11 colonies on Naked Island, the number of birds attending the colony was correlated with the number nesting ($r=.86$, $df=9$, $p<0.01$), and the slope of the regression line was significantly less than one ($t=.72$, $df=9$, $p<0.001$; Fig. 4). The sample regression coefficient (b) should indicate the percent of those birds attending the colony that actually bred. Here, b equals 0.57, with the lower and upper limits of the 95% confidence interval equal to 0.44 and 0.70, respectively. Based on these data, an estimated 60% of the 1978 population at Naked Island, or 600-750 pairs, bred.

Nest Sites

At Naked Island, the distribution of nesting Pigeon Guillemots was correlated with the distribution of cliff, broken cliff, and escarpment habitats (Fig. 2); this correlation was explicable on the basis of the crevices available for and used for nesting.

1. talus crevice. A nest located under boulders that had fallen from a cliff and lay either at the base or on ledges of the cliff, or in boulders which had fallen between layers of the cliff which had separated. The crevice was often a round chamber with no strong linear component.

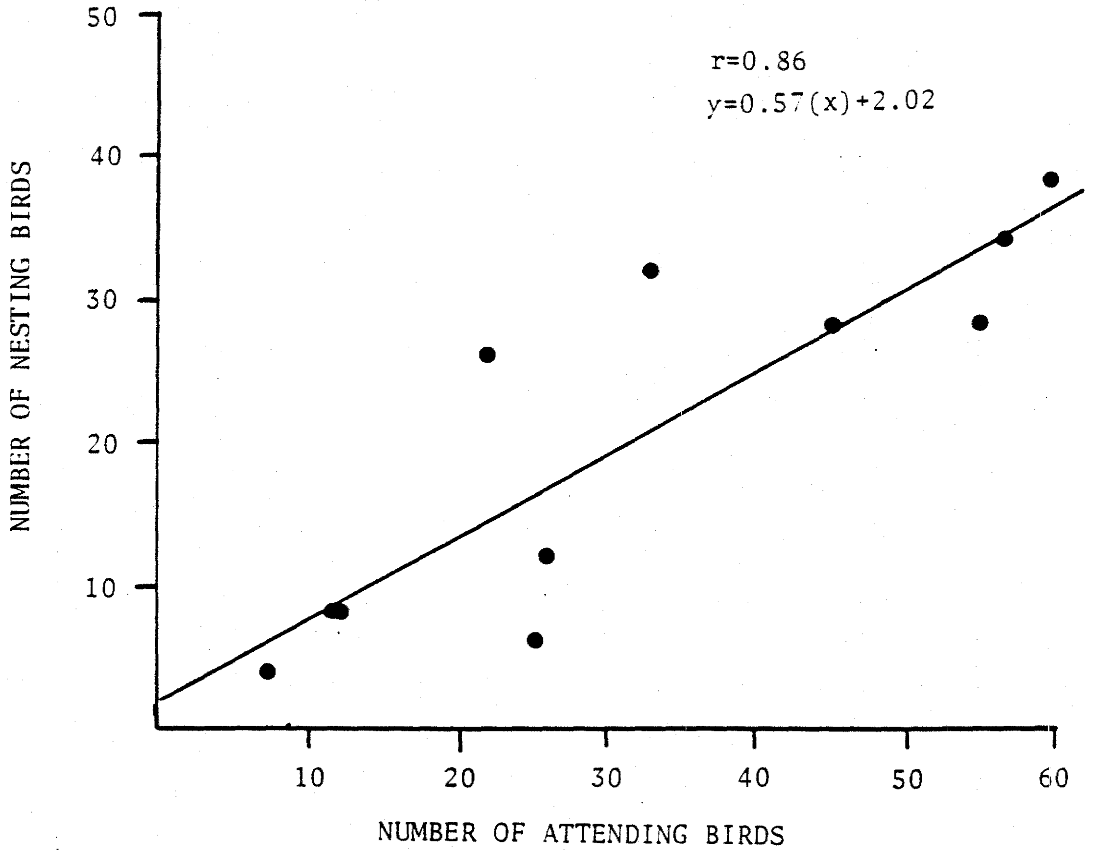

FIGURE 4. Comparison of the number of Pigeon Guillemots counted during June censuses to the number known to have bred at 11 colonies on Naked Island, Alaska, in 1978.

2. cliff crevice. A nest located in cracks of cliffs, often where stata had separated. Generally, these nests were narrow and up to several meters long. Cliff crevice nests often had little or no roof and were protected from rain only by the presence of an overhanging cliff face above the nest.

3. cliff-edge burrow. A nest at the cliff-edge where the forest floor hung over the edge. These nests were always associated with overhanging trees (mostly alder, some spruce and hemlock). The nest was either among or next to roots, or between rocks that had been pulled apart by the force of the overhanging tree. These nests had a strong linear component, generally extending about 1 m back from the cliff edge. These nests were not excavated by the guillemots and so were not true burrows.

Measurements of nest entrance dimensions, nest length, and elevation of nests at Naked Island are given in Table 5, with comparable data from Fish Island, Alaska, from Lehnhausen (1980). While there were significant differences in entrance width of cliff crevice nests and in entrance height of all nests between Naked and Fish islands, the entrance areas were similar, being smaller than 300 x 300 mm, regardless of nest type (Fig. 5). At both locations, the distributions of entrance dimension values were significantly skewed toward smaller values.

Nest length, the distance from the nest entrance to the eggs, averaged 0.9 m in Naked Island nests, and was not significantly different from the average length of Pigeon Guillemot nests at

TABLE 5. Comparison of entrance dimensions, length, and height of Pigeon Guillemot nests at Naked and Fish (Lehnhausen 1980) islands, Alaska.

	All Nest Types		Cliff Crevices		Talus Crevices		Cliff-edge Burrows	
	Naked	Fish	Naked	Fish	Naked	Fish	Naked	Fish
nest entrance width (mm)								
n	33	21	7	11	21	10	5	0
x̄	167.6	191.0	94.3	* 201.8	184.3	179.0	200.0	-
SD	123.3sk	99.2sk	51.3	127.2s	133.6s	59.9	127.5	-
height (mm)								
n	33	21	7	11	21	10	5	0
x̄	284.9	* 156.7	378.6	181.8	264.3	** 129.0	240.0	-
SD	218.0sk	88.9sk	318.7	112.5sk	202.4sk	43.3	54.8	-
area (m^2)								
n	33	21	7	11	21	10	5	0
x̄	0.05	0.03	0.05	0.03	0.06	0.02	0.05	-
SD	0.06sk	0.01s	0.04	0.01	0.08sk	0.01	0.03	-
nest length (m)								
n	45	11	11	4	26	7	8	0
x̄	0.93	0.79	1.04	0.90	0.85	0.73	1.08	-
SD	0.63sk	0.46	0.70	0.50	0.60sk	0.47	0.66	-
nest height (m)								
n	45	9	11	0	26	9	8	0
x̄	6.5 **	13.4	7.6	-	4.7 **	13.4	11.1	-
SD	4.2s	2.3	3.9	-	2.5	2.3	5.3	-

* $p < 0.05$ s distribution significantly skewed

** $p < 0.01$ k distribution significantly kurtotic

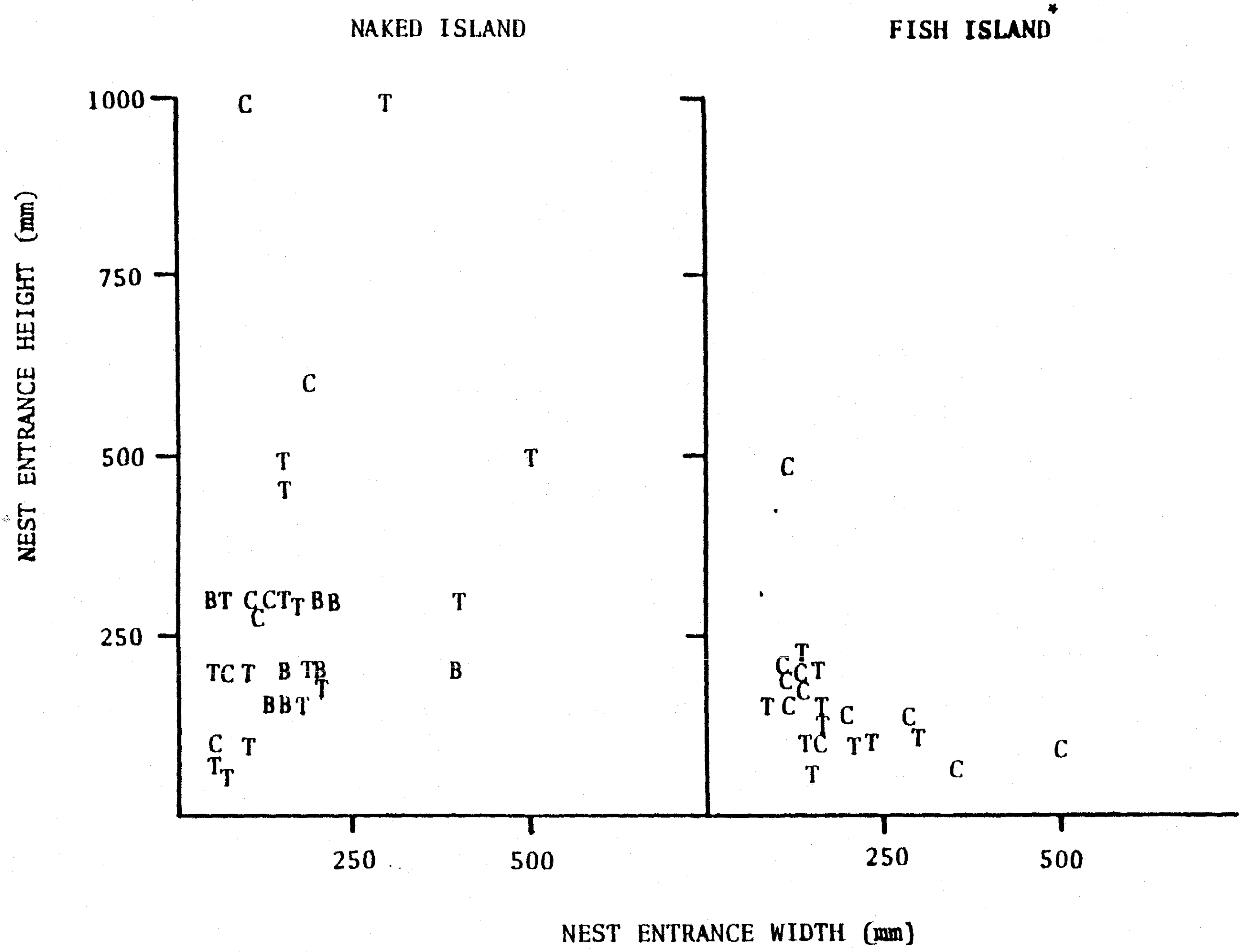

FIGURE 5. Comparison of entrance width to height of Pigeon Guillemot nests at Naked and Fish islands, Alaska. T=talus crevice, C=cliff crevice, B=cliff-edge burrow. *Lehnhausen 1980

Fish Island. Similar values for nest length have been reported for Black Guillemot nests (Asbirk 1979, Cairns 1980).

The average elevation above high tide line of nests at Naked Island was only 6.5 m. The average elevation of talus crevice nests at Fish Island was twice as high, 13.4 m, probably due to geomorphological differences between the islands. At Naked Island, significant differences between the three nest types were found only with respect to nest height ($p<0.001$). Because talus occurs at the bottom of cliffs, talus crevice nests were at lower elevations than cliff crevice nests and cliff-edge burrows.

Of 146 nests, 58 (40%) were cliff-edge burrows, 52 (36%) were in cliff crevices, and 36 (24%) were in talus crevices; thus, no nest type was used with significantly greater frequency on a populational basis ($\chi^2=5.31$, $p>0.05$). However, the frequency of each nest type varied among colonies (Table 6). In areas where cliffs graded directly into the sea, colonies could consist totally of cliff-edge burrows. In broken cliff areas, all nest types could be found.

One feature common to all colonies was the presence of a cliff. Cliffs were an integral part of the cliff-edge burrow and cliff crevice nests, and all talus nests were located at the base of cliffs or on ledges of broken cliffs. Most talus nests occurred within 1-3 m of the base of the cliff, a phenomenon also noted for the Black Guillemot (Belopolskii 1961, Lack 1967).

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TABLE 6. Predominant features of shoreline habitat, number of talus crevice, cliff crevice, and cliff-edge burrow nests, and nest density (no. nests/km) at 11 Pigeon Guillemot colonies on Naked Island, Alaska.

Colony	Shoreline Features				Nest Types			Density (no. nests/km)
	cliff	broken cliff	talus	overhanging vegetation	talus crevice	cliff crevice	cliff-edge burrow	
Nomad	X	X	X		2	3	2	70
Thumb I	X	X	X	X	8	1	2	55
Row	X	X	X	X	6	1	3	25
Peach	X		X	X	0	0	4	10
N. Cabin	X		X	X	0	3	0	30
Westpoint	X	X	X	X	0	5	8	33
Hook I and II	X	X	X	X	8	6	8	24
S. Hook	X	X			0	2	0	20
Parakeet Point	X	X	X	X	9	7	3	63
Igloo	X	X		X	0	1	16	34
Cadet	X				0	4	0	20

I did not measure distances between nests, but within colonies, nests were 10 m or more apart. Given that 600-750 guillemot pairs nested in the Naked Island area, and that nesting occurred within 34 km of shoreline, average nesting density was roughly 18-22 nests/km. Actual nesting density, based on the number of nests in a colony and the length of shoreline occuppied (Table 6), averaged slightly higher, 34.9 nests/km, and there was wide variation among colonies (SD=19.3, range 10-70).

Summer Foods

Prey species of Pigeon Guillemots in the Naked Island area in 1978 are listed in Table 7. The relative importance of each prey type was indicated by their frequency in stomach contents of collected birds (Fig. 6), in observations of items carried to chicks (Fig. 7), and in recoveries of otoliths from nests (Fig. 7 and Table 8).

Fish were the most important prey type, occurring in all collected birds and representing the bulk of material found in stomachs. With the exception of one squid found beside a nest, fish were the only food type I saw fed to chicks.

Gadidae. Cods represented 52% of the fish seen delivered to chicks and 58% of all otoliths recovered. Cod otoliths were found in 13 of 14 nests searched. Species identification was not possible during chick feeding observations, but based on otoliths, Pacific cod *Gadus macrocephalus*, walleye pollock *Theragra*

TABLE 7. Prey species of Pigeon Guillemots at Naked Island, Alaska, during summer 1978.

Prey species	Recovered from nest or chick	Sight record	Found in stomachs	Otolith recovery (nests)
Phylum Mollusca				
Class Cephalapoda				
Sepiolidae				
Rossia pacifica	X			
Phylum Arthropoda				
Class Crustacea				
Order Decapoda				
Hippolytidae				
Lebbeus sp.			X	
Crangonidae				
Crangon dalli			X	
C. septemspinosa			X	
Paguridae				
Pagurus sp.			X	
Galatheidae				
Munida quadrispina			X	
Majiidae				
Oregonia sp.			X	
Cancridae				
Cancer sp.			X	
C. magister			X	

TABLE 7. (continued)

Prey species	Recovered from nest or chick	Sight record	Found in stomachs	Otolith recovery (nests)
Phylum Chordata				
Class Osteichthyes				
Gadidae				
Eleginus gracilis			X	X
Gadus macrocephalus	X	X		X
Theragra chalcogramma	X	X		X
Zoarcidae				
Lycodes sp.				X
Bathymasteridae				
Ronquilus jordani				X
Stichaeidae				
Lumpenus maculatus	X			
L. sagitta	X	X		
Pholidae				
Apodichthys flavidus	X			
Pholis laeta	X	X		
Ammodytidae				
Ammodytes hexapterus		X		X
Cottidae				
Artedius sp.				X
Gymnocanthus tricuspis			X	X

TABLE 7. (continued)

Prey species	Recovered from nest or chick	Sight record	Found in stomachs	Otolith recovery (nests)
Cottidae (cont'd)				
Icelus spiniger				X
Myoxocephalus sp.				X
Agonidae				
Occella dodecaedron				X
Cyclopteridae				
Liparis sp.				X
Pleuronectidae				
Limanda proboscidea				X
Lyopsetta exilis	X			

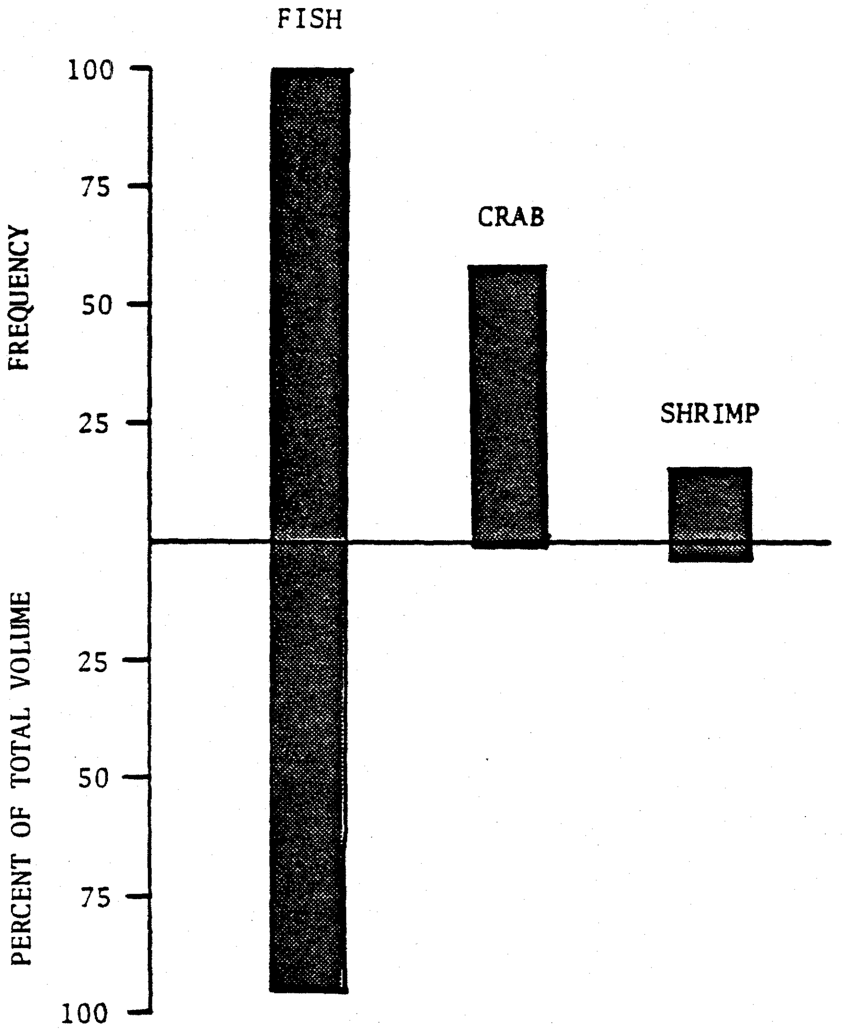

FIGURE 6. Frequency and percent of total volume of fish, crab, and shrimp in stomach contents of 14 Pigeon Guillemots collected in the vicinity of Naked Island, Alaska, during summer 1978.

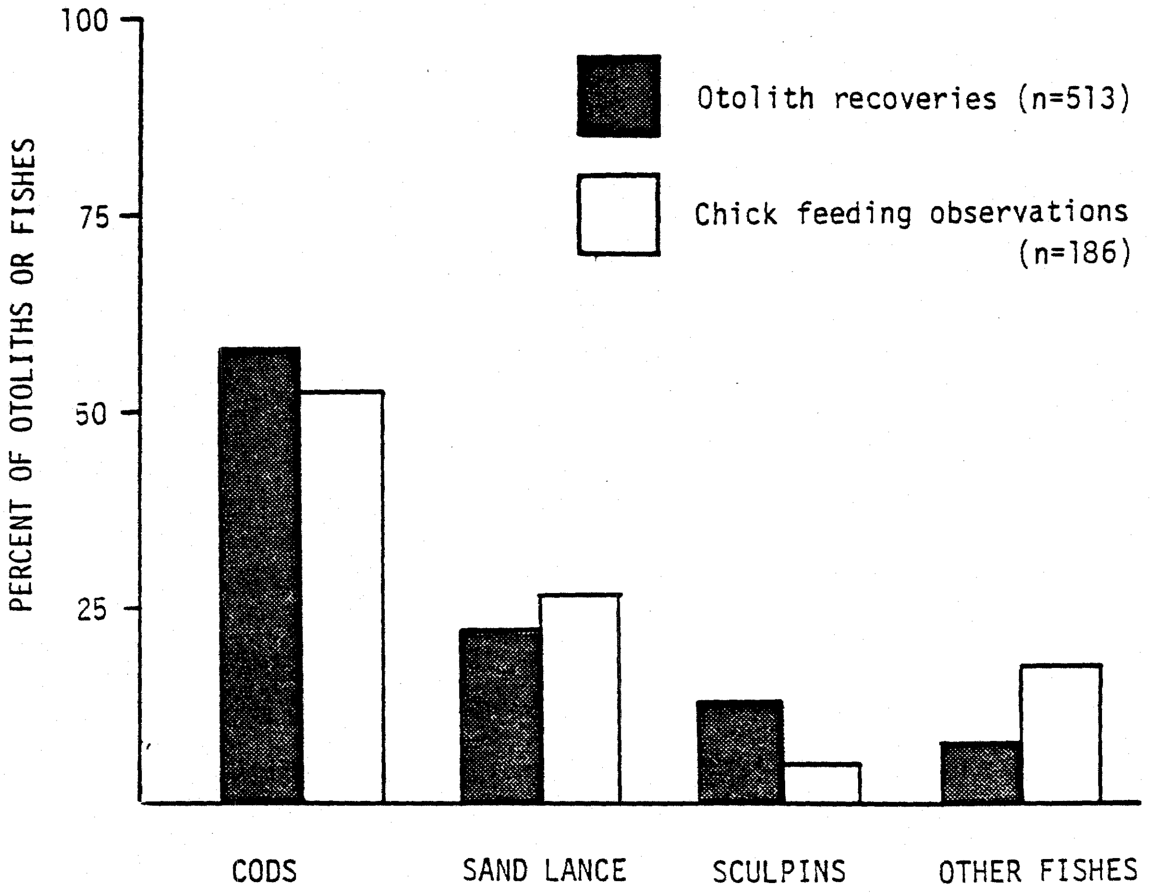

FIGURE 7. Percent of otoliths recovered from nests and of fishes brought to chicks that were cods (Gadidae), sand lance (*Ammodytes hexapterus*), sculpins (Cottidae), or other fishes (includes Bathymasteridae, Cyclopteridae, Zoarcidae, Agonidae, Pleuronectidae, and unidentified) at Pigeon Guillemot colonies on Naked Island, Alaska, in summer 1978.

Cottidae. Only eight sculpins were identified during chick feeding observations, though some of the unidentified fish could have been of this family. Otolith recoveries indicated that sculpins were taken more frequently than indicated by chick feeding observations. Sculpin otoliths of six types were found and represented 11% of those recovered. Nine of the 14 nests had cottid otoliths. One nest had 12 whole otoliths and 35 large otolith fragments from an unidentified sculpin, indicating that some birds took substantial numbers of sculpins.

Pleuronectidae. Two flatfish were seen during chick feeding observations; no otoliths were recovered. Single specimens of Limanda proboscidea and Lyopsetta exilis were found, indicating that right-eye flounders were taken. Left-eye flounders (Bothidae) could have been taken as well.

The number of otoliths from each fish species varied among nests and colonies (Table 8). Cod otoliths were present in all but one of the nests, but varied from 6 to 100% of the total recovered from those nests. Cod otoliths occurred more frequently and in larger numbers in nests at the northern colonies, Nomad, Thumb, and Row; sand lance otoliths occurred more frequently and in larger numbers in nests at the southern colonies, Hook and Parakeet Point.

A wide range of fish sizes was taken by the guillemots (Table 9), reflecting the diversity of species used as food. Weights of recovered fishes ranged from 3.5 g (Lumpenus maculatus) to 56 g

(Theragra chalcogramma); lengths ranged from 77 mm (L. maculatus) to 275 mm (L. sagitta). This latter fish had been swallowed by a 15-day old chick, and the tail protruded several centimeters from the bird's mouth. The length of this fish was not an obstacle to its use as food; excessive width can be (Drent 1965; Divoky et al. 1974).

The number of cod, sand lance, and all other fishes in size classes ranging from 1.0 to 5.0 bill lengths (BL) is shown in Fig. 8. These data show again the wide range of fish sizes used as prey, but indicate that most of the fishes were between 2.0 and 4.0 BL. The average culmen length of adult Pigeon Guillemots at Naked Island was 33.0 mm (unpubl. data), so these most frequent size classes correspond to fish lengths ranging from about 66 to 132 mm. The average length of four Pacific cod recovered from nests was 132.2 mm (Table 9) and thus considerably longer (by 1 BL) than the modal length for cod of 3 BL or 99 mm. Comparison of fish length to bill length provided only an index to the length of the fish and could have underestimated their lengths.

Both the cod and sand lance taken by Pigeon Guillemots at Naked Island in 1978 were juvenile fishes. The sand lance were in the age 1+ class, as revealed by aging of recovered otoliths. Their modal length of roughly 130 mm is within the range of lengths of age 1+ sand lance in nearshore waters of Kodiak Island (Harris and Hartt 1977) and in Kachemak Bay (Blackburn 1979a), Alaska.

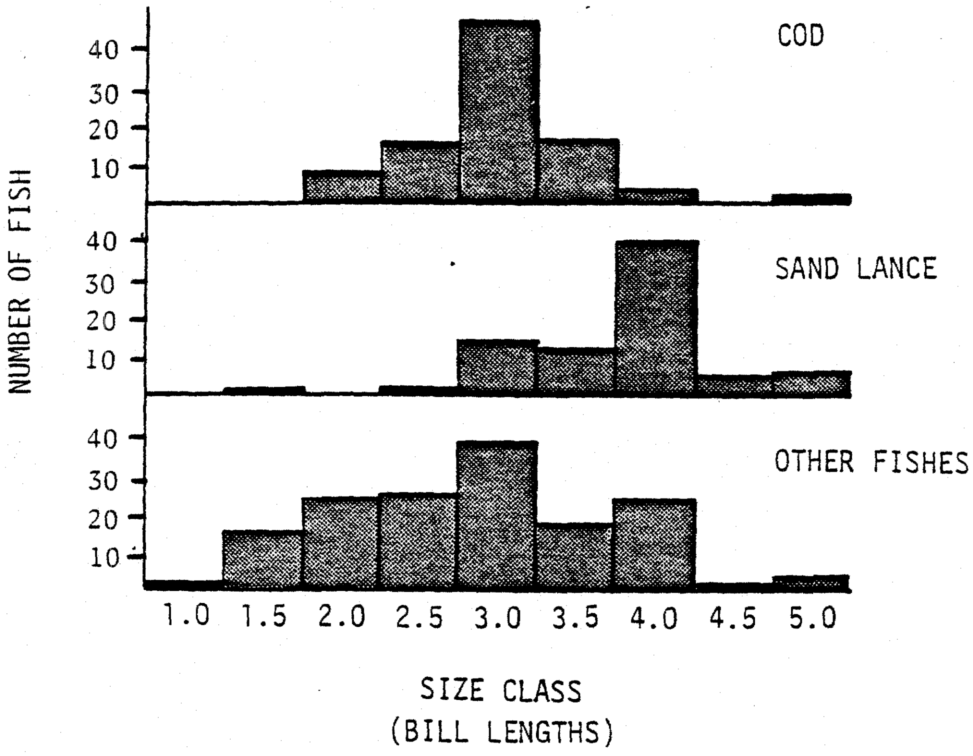

FIGURE 8. Number of cod, sand lance, and other fishes observed delivered to Pigeon Guillemot nests on Naked Island, Alaska, in 1978, in size classes created by estimating the length of the fish to the length of the bird's bill.

Most of the recovered cod otoliths were broken, so I used the approximated lengths of the fishes for assessing age. The lengths of most of the cods taken by the guillemots were between 75 and 150 mm; this range of lengths encompasses the age 0+ class for both Pacific cod and walleye pollock. Ketchen (1961) found that age 0 Pacific cod in British Columbia grew to an average length of 107 mm (range, 80 to 140 mm) by July of their first year. Whether the same early spawning time and growth rates apply to cod in more northerly Prince William Sound is unknown. Blackburn (1979a) observed an August mode in the size of Pacific cod in Lower Cook Inlet, Alaska, between 180 and 280 mm which he inferred were age 1+ fish. The Pacific cod taken by Pigeon Guillemots at Naked Island in 1978 were smaller than 200 mm, which suggests that they were age 0+ fish. Age-length relationships of walleye pollock in Alaskan waters are better known. Age 0+ pollock in the late summer of their first year ranged in length from 50 to 80 mm in the southeast Bering Sea (Smith 1979) and from 75 to 150 mm in Lower Cook Inlet (Blackburn 1979a). Pollock at age 1 (median birthday 1 April) have generally been about 150 mm (Yamaguchi and Takahashi 1972, Smith 1979). Most of the pollock taken by guillemots at Naked Island were smaller than that and must have been age 0 fish.

Crabs and/or shrimp occurred in 8 of 14 birds collected (Fig. 6). Crab remains were present in trace amounts, always in association with fish. Two stomachs contained whole shrimp along with substantial volumes of fish. Thus, invertebrate food was taken regularly by the guillemots, but was volumetrically unimportant.

Foraging Areas

The Pigeon Guillemot has been described as an "inshore feeder" (Bedard 1969); at Naked Island, all foraging occurred within the 100-m depth contour. Pigeon Guillemot density was highest in bays and passages, where they averaged 43.8 birds/km^2 (Table 4). Guillemots occurred on four of the six offshore transects conducted, but their density averaged only 0.87 birds/km^2.

Guillemot traffic past certain headlands demonstrated the use and importance of bays for feeding (Fig. 9). Between 12:45 and 13:20 (AST) on 27 July, 58 guillemots went past Nose headland; 27 were headed west, then south, into east McPherson Bay; 31 birds, all carrying fish, were headed southeastward toward colonies on the east side of Naked Island. Similar but unquantified observations were made at Tuft, Storey, and Tall headlands, and indicated that guillemots breeding on the more exposed sections of coast were flying into nearby bays to feed.

Within the bays, coves were used as foraging areas. Guillemots from Hook colony often flew to the cove a few hundred meters east of their colony. The Nose headland traffic was going to and from the cove in the most eastern part of McPherson Bay.

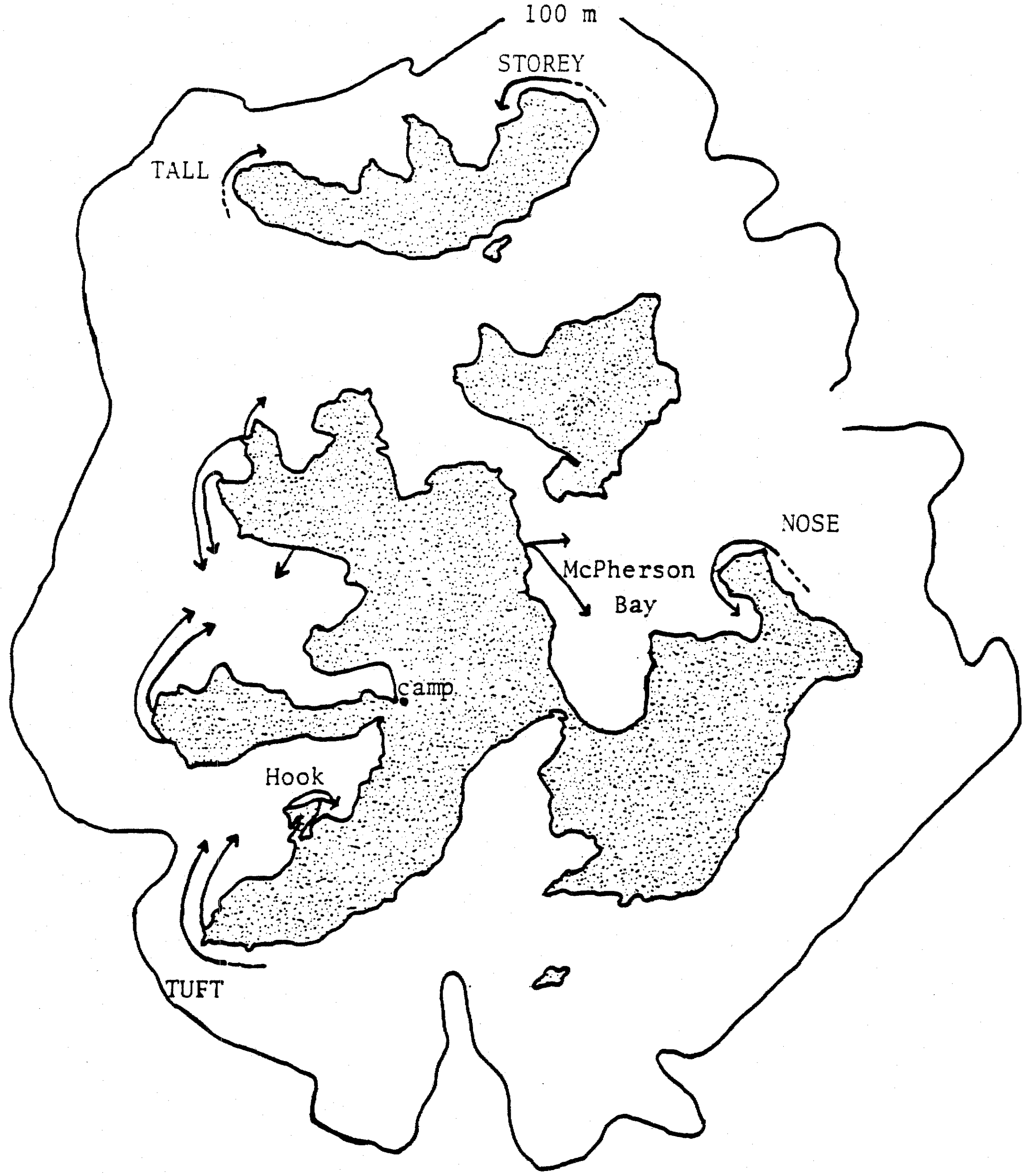

FIGURE 9. Flight directions of Pigeon Guillemots enroute to foraging grounds in the vicinity of Naked Island, Alaska, in summer 1978.

The cove on which the field camp was located was used regularly by foraging guillemots.

Based on these general observations of the location of foraging areas and on knowledge of the location of colony sites (Fig. 2), the distance that Naked Island guillemots traveled between their nesting and foraging sites ranged from a few hundred meters to 2 to 3 km. The direction of travel was along shore, rather than away from shore.

The presence of crabs, cods, and cottids in the guillemot's diet indicated that they fed on and near the bottom. Sand lance can feed in the water column diurnally (Inoue et al. 1967, Meyer et al. 1979), and their presence in the guillemots' diet suggests that guillemots can also feed in the water column.

Nesting Chronology

Pigeon Guillemots were conspicuously present in the Naked Island area when I arrived on 8 May 1978. Due to logistic problems, no observations of pre-laying behavior were made until 26 May, by which date guillemots were active both on rocks and on the water near their breeding sites.

During June, the birds were involved in egg laying and incubation. The first nest, containing two fresh eggs, was found on 8 June. Nests were difficult to find during incubation, and only nine more nests with eggs were found, seven in June and two in July. Two of three females collected in June had post-ovulatory follicles, and two adult males collected in June had enlarged testes. All of these birds had well-vascularized brood patches.

The first nestlings were found on 27 June, which was also the first day that adults were seen carrying fish. The last egg in a monitored nest hatched on 26 July, the same day that the first fledgling was seen on the water. In the monitored nests, the first chick fledged on 31 July; the last chick was still in its nest on 31 August and probably fledged soon thereafter. During the last census of Naked Island on 29 August (Table 3), relatively few adults were present at colonies and most of these were carrying fish. The chick-rearing period at Naked Island thus extended over 2 mo, July and August.

These observations on the timing of breeding activities corroborate an estimated chronology based on known fledging dates (Fig. 10). Nest initiation, and subsequently, hatching and fledging, each occurred over a month-long period.

The nests on which the Naked Island chronology (Fig. 10) was based were located in several colonies (see Fig. 2), and the average, standard error, and range of fledging dates for these colonies are shown in Fig. 11. Variation in average fledging date among these colonies was not significant (ANOVA, p=0.0597). However, the Nomad, Row, and Thumb colonies were adjacent, and the

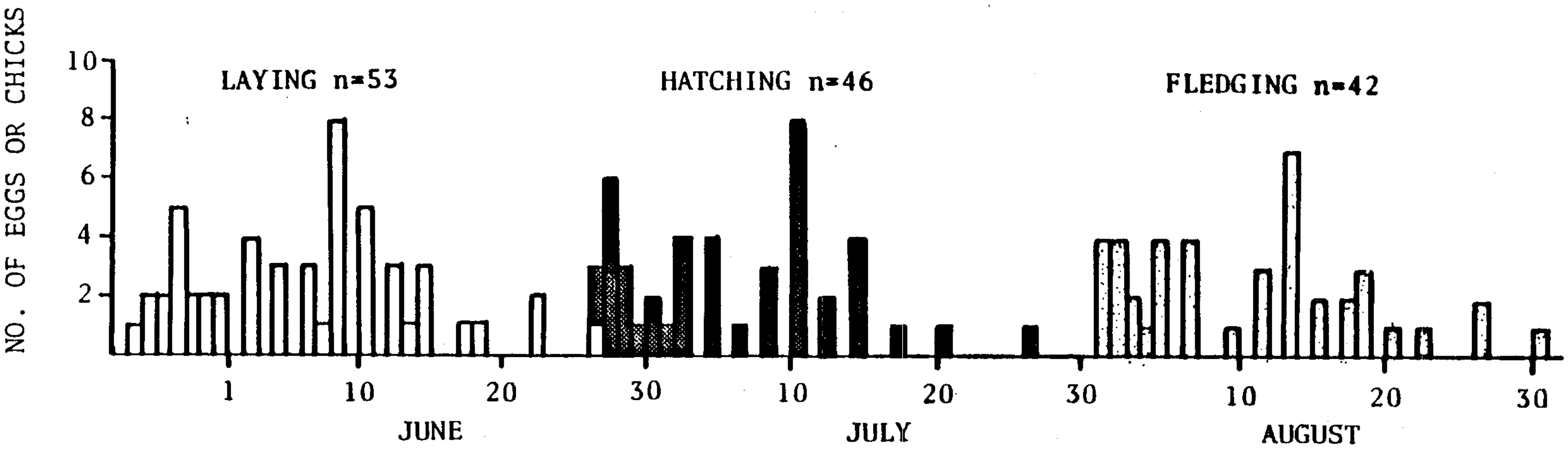

FIGURE 10. Breeding chronology of Pigeon Guillemots at Naked Island, Alaska, in 1978.

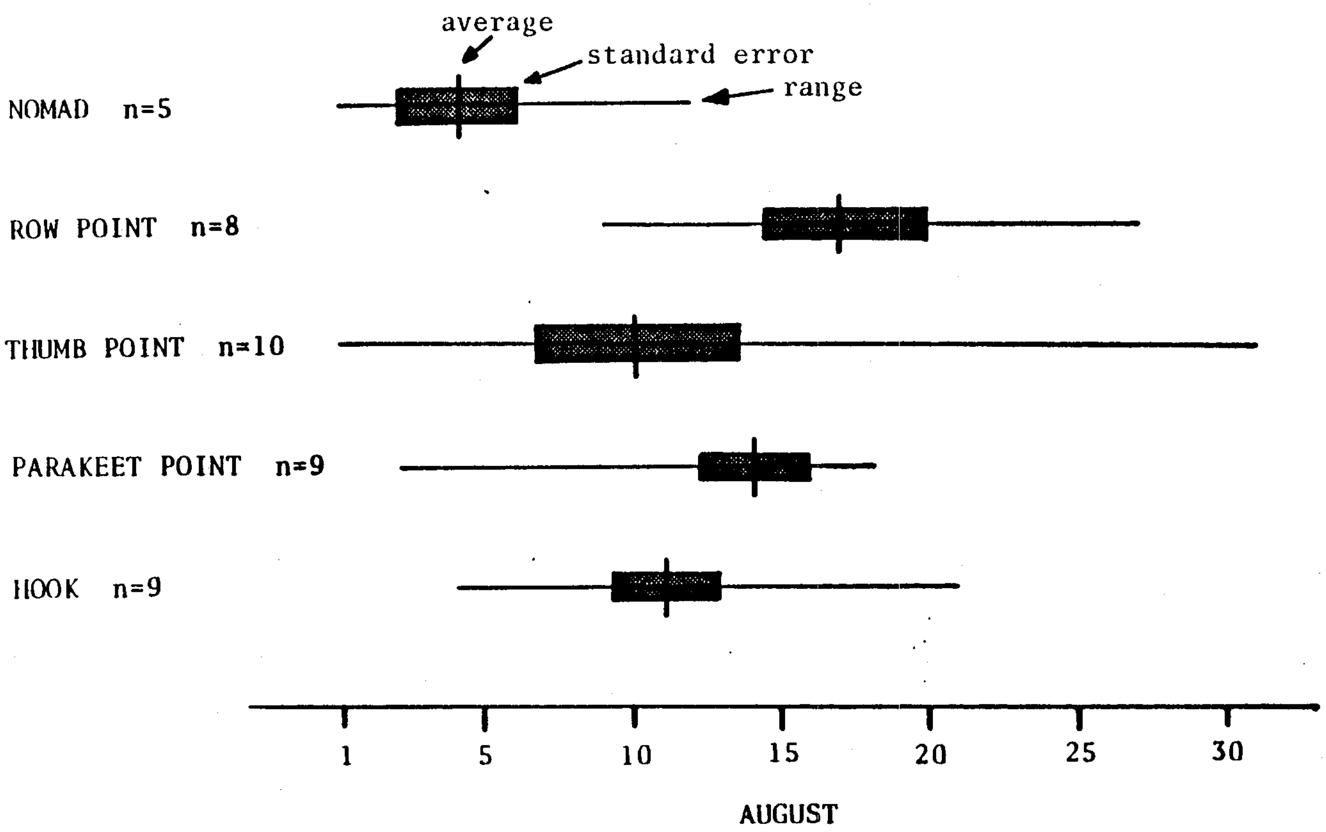

FIGURE 11. Average, standard error, and range of fledging dates of Pigeon Guillemot chicks at five colonies on Naked Island, Alaska, in 1978.

differences in average fledging date among them indicate that guillemots nesting in proximity were not synchronized in their breeding activities.

Nesting Success

Nesting success of guillemots at Naked Island in 1978 is shown in Table 10, with comparative information from other guillemot populations. The value for hatching success at Naked Island is an estimate based on the 10 nests found in the egg stage. Adults were banded at five of these nests, and three of these were subsequently abandoned; hatching success may therefore be underestimated. Causes of egg mortality were few. One nest was deserted for unknown reasons and in two nests, found during the chick stage, one egg of a two-egg clutch failed to hatch.

Once hatched, the probability of fledging was high (0.96). Among the 32 monitored nests, all nests which hatched young, also fledged young, with one exception. The two chicks in this nest disappeared within a week of hatching, and their fate is unknown. My only direct observation of chick mortality was of a nearly full-grown chick that fell about 6 m from a cliff-edge burrow. (This nest was inaccessible and thus had not been monitored.)

There were no significant differences in nesting success among the three types of nests used by Pigeon Guillemots at Naked

TABLE 10. Nesting success of Pigeon Guillemots at various localities.

Location	No. of nests	Average clutch size	Hatching success (%)	Fledging success (%)	Nesting success (%)	No. fledged per pair	Reference
Naked Island, Alaska	32	1.78	75.0	95.9	71.9	1.28	this study
Fish Island, Alaska	14	1.78	84.0	81.0	68.0	1.21	W. H. Lehnhausen (pers. comm.)
Shumagin Islands, Alaska	14	1.92	55.6	33.3	18.5	0.36	Moe and Day (1979)
Mandarte Island, British Columbia	58	1.86 n=220	61.8	83.8	51.8	0.96	Aitchison (1972)
Puget Sound, Washington	42	1.76	53.8	86.2	46.4	0.82	Thoreson and Booth (1958)
Protection Island, Washington	31	1.48	91.3	66.6	60.0	0.89	Leschner and Hirsch (1980)

Island, but the high success and small sample sizes for cliff crevice and cliff-edge burrow nests could have obscured any relationship.

Fledging Weight and Size and Nestling Growth Rates

The average weight of Pigeon Guillemot fledglings at Naked Island in 1978 was significantly greater than that of fledglings at Fish Island in 1976-77 (Table 11, Mann-Whitney, $T=218$, $p<0.05$); it is clear from the distribution of the data that the large difference in average weight between fledglings at Naked Island and Mandarte Island is real as well (Fig. 12).

Growth in weight of Pigeon Guillemot chicks at Mandarte Island, Puget Sound, and Fish Island was similar; chicks at Naked Island appeared to grow faster (Fig. 13). Tests for differences in growth rate were only possible between Naked Island and Fish Island; Naked Island chicks gained weight significantly faster ($t=6.41$, $df=14$, $p<0.05$).

In contrast, the growth rates of culmen and wing did not differ among populations (Fig. 14). The length of culmen at fledging was not different between Naked and Fish island (Table 11, $T=0.28$, $p>0.05$). Methods of wing measurement differed among sites, so no test was performed.

There was no correlation between weight and fledging date.

TABLE 11. Average weight and culmen and wing length of Pigeon Guillemot fledglings in various populations. Standard deviations, if known, are in parentheses.

Location	Year	Weight (g)	Culmen (mm)	Wing (mm)	Reference
Naked Island, Alaska n=24	1978	470.6 (51.7)	28.2 (1.2)	135.6[1] (5.9)	This study
Fish Island, Alaska n=12	1976& 1977	424.7 (65.9)	28.1 (1.0)	148.6[2] (7.2)	W. A. Lehnhausen (pers. comm.)
Mandarte Island, British Columbia n=20	1959& 1960	411	--	--	Drent (1965)
Puget Sound, Washington n=3	1957	438	28.8	138.7[1]	Thoreson and Booth (1958)
Farallon Islands, California n=31		452	--	--	Ainley et al. (1971)

[1] wing chord [2] flattened wing

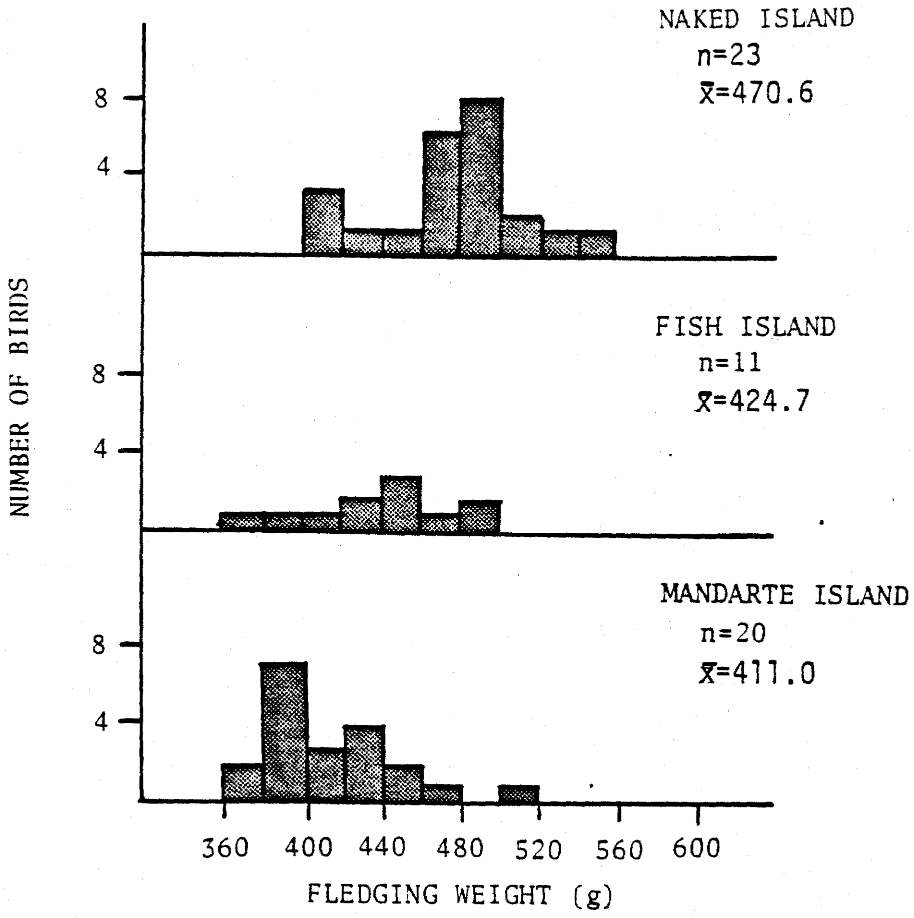

FIGURE 12. Fledging weights of Pigeon Guillemot chicks at Naked Island, Alaska, in 1978, Fish Island, Alaska, 1976-77 (W. A. Lehnhausen, pers. comm.), and Mandarte Island, British Columbia, 1959-60 (Drent 1965).

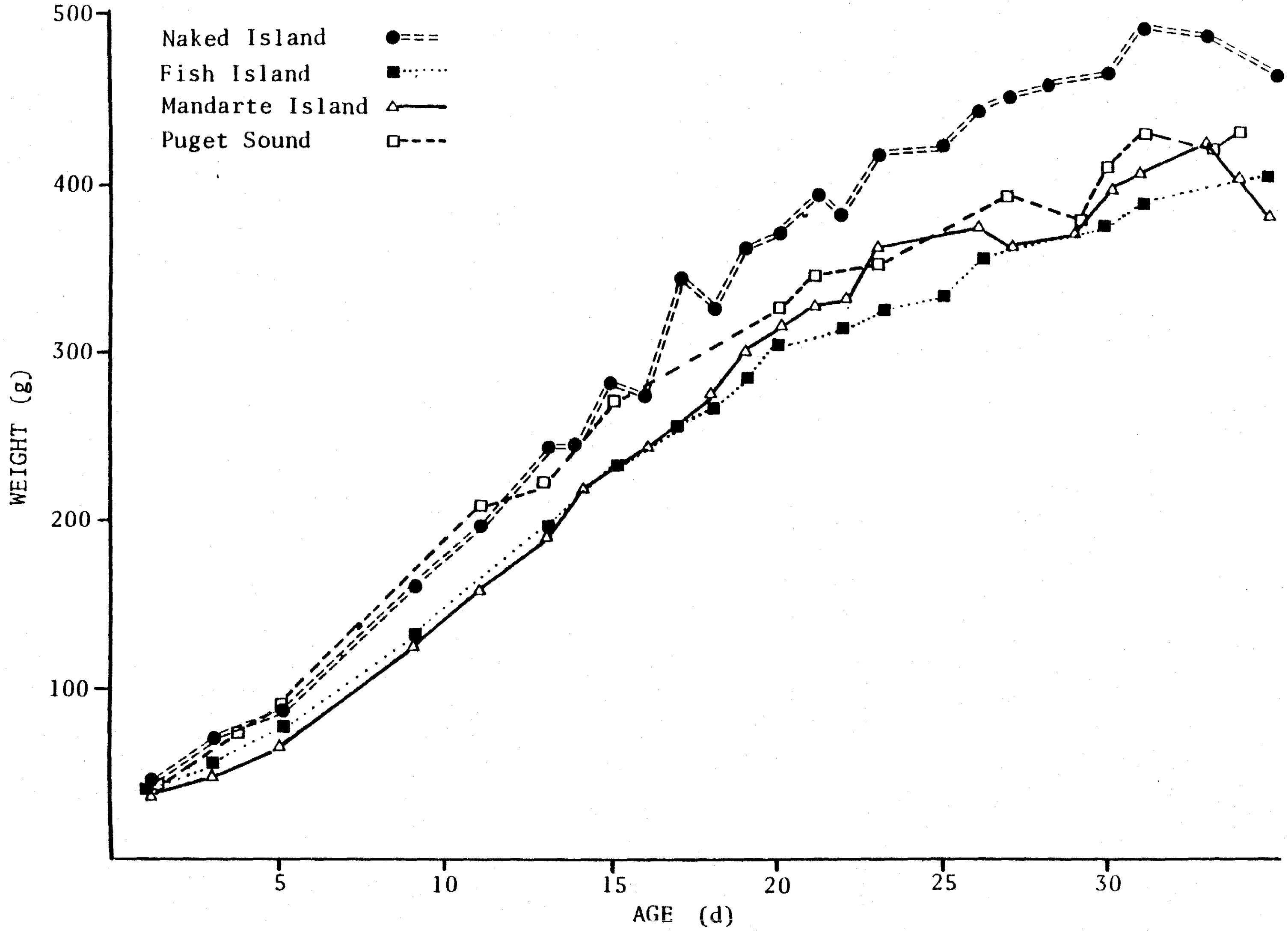

FIGURE 13. Average weights of known-age Pigeon Guillemot nestlings from Naked and Fish (W. A. Lehnhausen, pers. comm.) islands, Alaska, Mandarte Island, British Columbia (Drent 1965), and Puget Sound, Washington (Thoreson and Booth 1958).

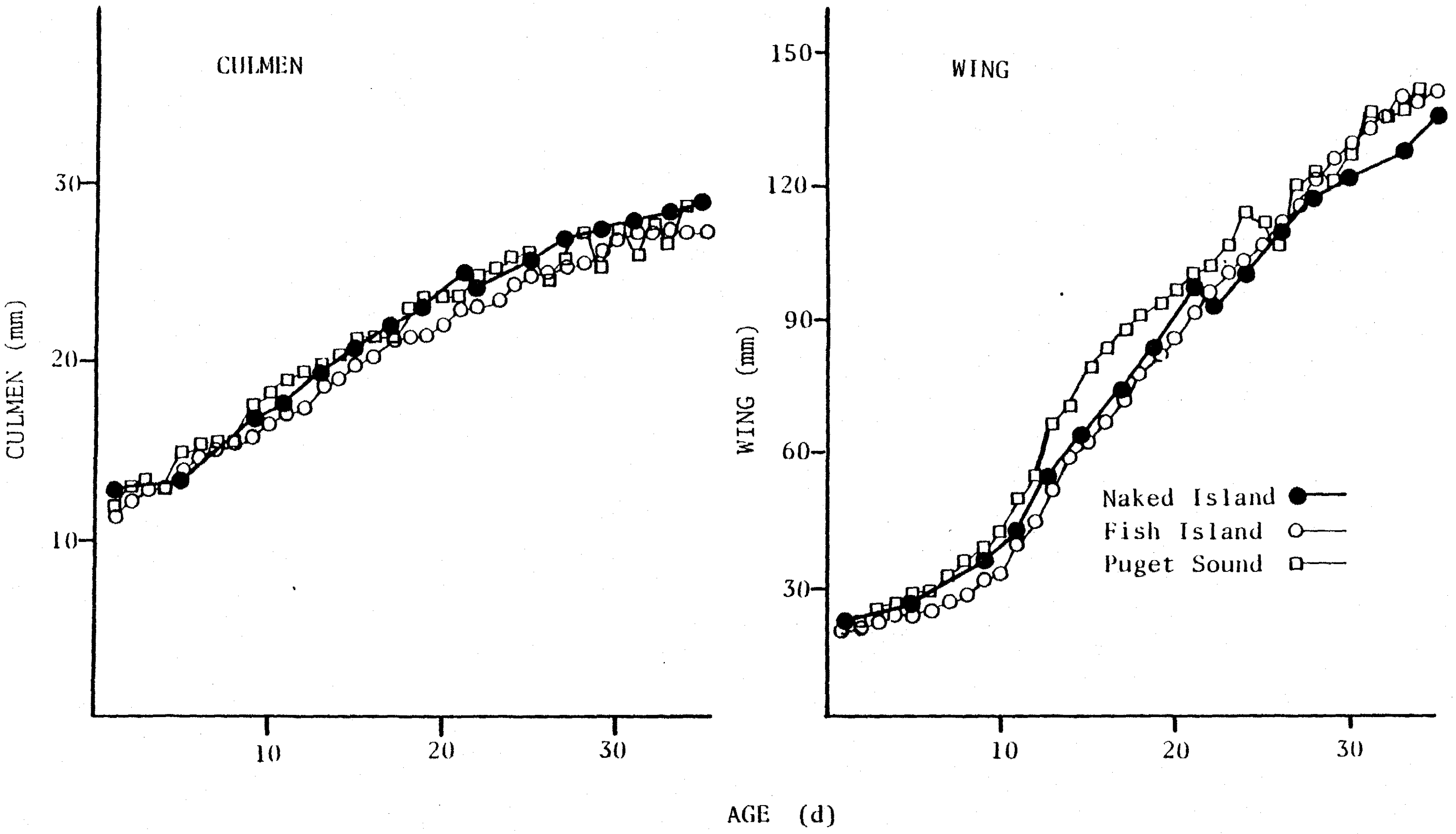

FIGURE 14. Average culmen and wing lengths of known-age Pigeon Guillemot nestlings from Naked and Fish (W. A. Lehnhausen, pers. comm.) islands, Alaska, and Puget Sound, Washington (Thoreson and Booth 1958).

DISCUSSION

The abundance of guillemots at Naked Island can, in part, be attributed to the dominance of the shoreline by habitats that contained three types of suitable nesting crevices. Nearly 80% of the shoreline was cliff or broken cliff, and guillemots were not restricted by habitat to only one or a few breeding sites. While guillemots nested throughout the study area, they occupied only 38% of the shoreline that was cliff or broken cliff, suggesting that the availability of nest sites had not limited the number of nesting birds. However, it is hard to reconcile the large number of nonbreeding guillemots at Naked Island with a picture of limitless nesting sites. That nests were not infinitely available was circumstantially indicated by the wide spacing of nests and the variation in frequency of nest types among colonies. Further, some guillemots did not nest in direct proximity to their foraging grounds, necessitating flights into or between bays while feeding young. Thus, the distribution of suitable nesting crevices influenced nesting dispersion. Further data are needed to determine if nest sites are limited in number and the extent to which the distribution of crevices determines the nesting dispersion of guillemots at Naked Island.

Gull and crow predation on eggs and chicks has accounted for a considerable proportion of nesting failure at some guillemot colonies (Heath 1915, Winn 1950, Preston 1968, Aitchison 1972, Divoky et al. 1974, Asbirk 1979); its incidence is correlated with the amount of cover provided by the nest (Divoky et al. 1974, Asbirk 1979). At Naked Island, most nests were at the cliff-edge or on cliff faces and were therefore inaccessible. Nest density was low, and neighboring nests were often of different types; hence, predators could not easily have formed a search image for guillemot nests. The physical factors which determined the nature and distribution of potential nesting crevices apparently precluded predation as a significant cause of mortality. Mortality which was unrelated to nest site quality, such as genetic death or failure of chicks to establish thermoregulation, was also uncommon at Naked Island, and there were no observed incidences of starvation. The comparatively high number of young fledged per nest (1.28 young/nest) in 1978, which was due to high success of both hatching and fledging, can be attributed to the combined effects of inaccessible nesting sites and adequate food.

The food of Pigeon Guillemot chicks at Naked Island in 1978 differed from that of guillemot chicks raised at other locations (Fig. 15). Cods and sand lance were the most important prey; other prey were blenniods, sculpins, a ronquil, and flatfish. At Mandarte Island, blenniods and sculpins formed the bulk of fishes delivered to chicks in all years studied (Drent 1965, Aitchison 1972, Koelink 1972). Cods were absent, and sand lance represented 5% or less of chick food deliveries. In Puget Sound, chicks were fed sand lance, smelt _Hypomesus_, blenniods, lampreys _Lampreta_, and flatfish, but Thoreson and Booth (1958) did not report a quantita-

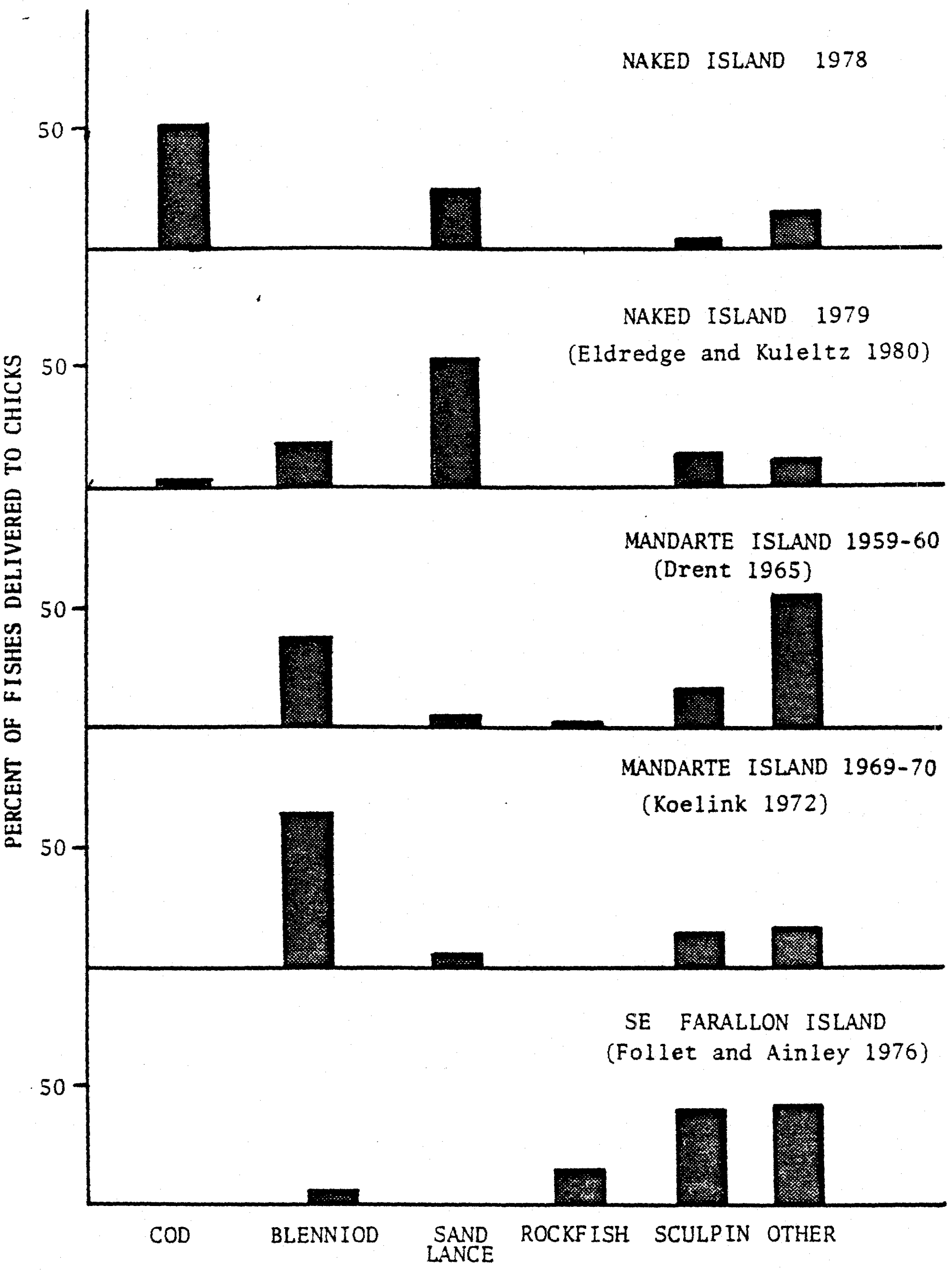

FIGURE 15. Percent of chick food deliveries that were cods, blenniods, sand lance, rockfish, sculpins, and other fishes at Pigeon Guillemot colonies on Naked Island, Alaska, Mandarte Island, British Columbia, SE Farallon Island, California.

tive assessment of each species' importance. The information on chick diet from the Farallon Islands (Follett and Ainley 1976) is based on fishes found at nests over a 4-yr period and so is not directly comparable, but sculpins and rockfish (Scorpaenidae) occurred most frequently; blenniod fishes were less common.

There were differences also in the location of the foraging areas among the localities considered here. At Naked Island, guillemots foraged from a few hundred meters to 2-3 km from their colonies. At Deception Island (Puget Sound) and at the Farallon Islands, guillemots foraged in the general vicinity of the island, often within 200 m. At Mandarte Island, the foraging grounds were 4-5 km distant.

In other inshore-feeding seabirds, notably cormorants (Lumsden and Haddow 1946, Hubbs et al. 1970), differences in diet and in the location of foraging grounds among localities are related to differences in the subtidal and nearshore habitats and their associated fish faunas. Young cods and sand lance make distinct inshore movements in summer, and the Naked Island area apparently provided excellent nursery grounds for them. Cods overwinter in deep water (Ketchen 1961), and the occurrence of a trench just a few kilometers west of the shallow waters of Naked Island could explain why cods were so abundant. At Mandarte Island the guillemots' diet consisted of fishes which are more permanent residents of inshore waters. At the Farallones, an isolated island group on the edge of the continental shelf, the guillemots primarily ate fishes inhabiting rocky substrates.

Individual specificity in the items fed to their chicks has been observed also by Drent (1965), Slater and Slater (1972), and Cairns (1978). Slater and Slater (1972) suggested that this specialization resulted from differences in the location where each bird feeds. That cods and sand lance were of differing importance between northern and southern colonies at Naked Island suggests that their respective foraging grounds differed in the relative abundances of fishes. Just as differences in diet among guillemot populations are due to differences in benthic habitats on a large scale, differences in diet within a guillemot population can be due to differences in benthic habitats on a small scale.

The comparatively high rate of weight gain and fledging weight of chicks at Naked Island can be attributed to the availability and quality of food in 1978. Cods and sand lance appeared to be readily available in the waters around Naked Island. Feeding flocks of Black-legged Kittiwakes, Marbled Murrelets, and Common Murres were common, and sand lance and walleye pollock were present in the stomachs of these three species (Oakley and Kuletz 1979). Minke Whales Balaenoptera acutorostrata, which feed primarily on inshore schooling fishes such as sand lance (Sergeant 1963), were also common.

Nutritional quality of the diet is also important and could supersede availability *per se* as the main factor affecting nestling growth (Leschner 1976, Harris and Hislop 1978, Wehle 1980). While there is no information on chick feeding rates to supplement the comparison of chick growth rates among localities, guillemots apparently were not under food stress at any of the sites. Thus, the differences in growth rate could have been due to the qualitative differences in their diets. Variations in fledging weight of Rhinoceros Auklet chicks among years (Leschner 1976) and among locations (Summers and Drent 1979) have been correlated with differences in composition of the diet. The protein and calorific content of fish species differ (Slobodkin and Richman 1961, Love 1970, Harris and Hislop 1978). Harris and Hislop (1978) showed that young puffins *Fratercula arctica* fed sand eels *Ammodytes* reached higher peak weights than those fed whiting *Merlangius merlangus*, a gadoid fish. The protein and fat content of sand lance is high (Love 1970, Harris and Hislop 1978), and their importance in the diet of guillemots at Naked Island could have positively influenced the growth of chicks.

In Alaska, Tufted Puffin chicks fed sand lance and capelin *Mallotus villosus* grew faster than chicks fed either sand lance or capelin (Wehle 1980), suggesting that the quality of the diet is determined not only by the nutritional composition of individual prey species, but by the suite of species that constitute the diet. Pigeon Guillemot chicks at Naked Island were fed a diversity of species. The number of otolith types recovered per nest averaged 5 and ranged from 1 to 14. Six of the 14 nests had both cod and sand lance otoliths. The general diversity of the chick's diet could have contributed to their high rate of weight gain and fledging weight in 1978.

At Naked Island, Pigeon Guillemot nests were initiated (or reinitiated) within a 4-6 wk period (late May and June); the date of breeding within that period apparently had little influence on reproductive success or chick growth. Chicks had the same high probability of fledging regardless of the date they hatched, and there was no correlation between fledging date and weight. For other seabirds, the date of breeding, particularly the date relative to the remainder of the colony, can have a significant influence on nesting success. The adaptiveness of synchrony is generally attributed to the decrease in predation rates as the amount of prey increases, a phenomenon certainly true for larids (Patterson 1965, Nisbet 1975, Hunt and Hunt 1976, Parsons 1976). Predation rates at guillemot colonies are linked to use of inadequate nest sites, primarily by young birds which also breed later in the season (Asbirk 1979). Hence, predation rates on guillemot nests are only secondarily influenced by the date of laying. Under this selective regime there would be an advantage to breeding early to obtain a good nest site, but no advantage to synchronization with neighbors. Predation was negligible at Naked

Island, hence it could not have exerted a significant selective force towards synchrony.

The wide spread in reproductive timing within the Naked Island Pigeon Guillemot population can be attributed ultimately to the length of the period of food availability, which extended into the early post-fledging period. Inshore fishes are abundant in Prince William Sound from April throughout October (Rosenthal 1979). Adult Pigeon Guillemots remained in the Naked Island area to complete their post-nuptial molt, while murres, which did not breed at Naked Island, came to Naked Island in large numbers during mid-August to molt. The concentration of post-breeding seabirds in the Naked Island area suggested that food remained available at least through early fall. Because food was available over such a long period, guillemot nesting success and chick growth was not disadvantaged by breeding early or late in the season. Post-fledging survival rates of guillemots relative to the date of fledging are unknown, but for two other inshore-feeding seabirds, the Shag *Phalacrocorax aristotelis* and Yellow-eyed Penguin *Megadyptes antipodes*, post-fledging survival was not influenced by fledging date (Richdale 1957, Potts 1969).

Determinants of Population Size and Distribution

In temperate regions, seabird reproduction coincides with a manyfold increase in oceanic productivity, and the idea that there is competition for food during breeding is unconvincing for at least some northern seabirds (Nelson 1966, 1967, 1970; Harris 1966). For most guillemot populations, it appears that food is generally abundant during breeding: Starvation of chicks is uncommon; guillemots can lay replacement clutches (Thoreson and Booth 1958, Drent et al. 1974, Asbirk 1979), which could only be possible if food were readily available; and, both Black and Pigeon guillemots can raise triplets (Koelink 1972, Aitchison 1972, Asbirk 1979).

Annual changes in food availability occur, but without respect to the numbers of guillemots. The disappearance of Zoarces viviparus from the foraging grounds of the Black Guillemots studied by Bergmann (1971, 1978) was correlated with decline in water temperature. Cod abundance and presence in inshore waters is dependent on the temperature regime during spawning and in summer (Ketchen 1961, Alderdice and Forrester 1971, Dickson et al. 1974), and the absence of cods from the diet of guillemots at Naked Island in 1979 (Eldredge and Kuletz 1980) could have been due to a change in water temperature. Sand lance are notoriously patchy in distribution (Blackburn 1979b), and their size and abundance are related to the degree of intraspecific competition for copepods, which are the mainstay of their diet (Hamada 1967). Sand lance are eaten by Shags Phalacrocorax aristotelis in Britian, and Potts (1969) found that shortages of sand lance were coincident with persistent winds. Food shortages did not become more frequent or more intense as the

Shag population increased, and he concluded that the availability of food was not influenced by the number of Shags. For guillemots, food shortages during breeding are rare and can be attributed to factors other than the density of guillemots. If summer food availability is not responsive to population size, it cannot function as a population regulator, nor is it likely to determine the population level.

Limitation of populations of crevice-nesting seabirds due to the availability of their specialized nests is always a possibility (von Haartman 1971), and there is good evidence that guillemot populations are so limited. A large proportion of the guillemots attending colonies are nonbreeding birds, and, while some of these birds are immatures, the ready use of nesting sites created by investigators (Winn 1950, Bianki 1967, Koelink 1972, Aitchison 1972, Divoky et al. 1974) indicates that some were prevented from breeding by the lack of a nest site.

Long term studies at Mandarte Island indicated that this guillemot population was stable, with all available nesting sites in use (Drent 1965, Aitchison 1972, Koelink 1972). The Farallon Island population was decimated by oil pollution in the early 1900's, but has since recovered and is now stable with all nest sites in use (Ainley and Lewis 1974:438). At Nordre Ronner, Denmark, some nest sites were unused during the years of Asbirk's (1979) study, but few nonbreeders were present. This population was recovering from decimation by oil pollution and had not increased to the limit set by available nesting sites. Cairns (1980) concluded that not all of the available nesting sites were used at the Black Guillemot colonies he studied, but again, few nonbreeders were present (Cairns 1978:48), suggesting that the population was in flux--a possibility not considered by Cairns (1980).

The ready use of man-made structures has been responsible for the range extension of the Black Guillemot to arctic North America (Divoky et al. 1974, Kuyt et al. 1976) and has allowed Pigeon Guillemots to breed in areas previously unoccupied (Campbell 1974, Byrd et al. 1974, pers. obs.). There are a number of reports of Pigeon Guillemots attempting to nest in bizarre sites, such as runways in grass or even on open ledges (Storer 1952, Thoreson and Booth 1958); these attempts can be interpreted as efforts by birds faced with the option of not breeding at all. The lability in nest site selection exhibited by the guillemots has obvious adaptive significance if nest sites are scarce.

Asbirk (1979) found the survivorship of adults attempting but failing to raise offspring was greater than the survivorship of adults successfully raising offspring. The survivorship of prevented breeders may not be appreciably greater than that of failed breeders, or the process of attempting to breed (i.e., gaining a mate and nest) could increase nesting skill and success in subsequent years and therefore offset any decrease in survivorship. The high incidence of nesting failure due to characteristics of the nest indicates that guillemots will nest in any crevice providing a modicum of cover and suggests that guillemots attempting to breed are at a selective advantage compared to those that do not attempt to breed. The limited availability of crevices makes attempts to breed in marginally suitable crevices adaptive. Thus, the availability of nest sites could not only set a limit to the number of guillemots which can breed, but the suitability of potential nesting sites could modify population productivity in a density dependent fashion.

For many bird species, the nest spacing pattern has important influences on nest success, but for Black Guillemots, nest success has not been influenced by density in any consistent manner: At Nordre Ronner, Denmark, nest success was higher in the high density portion of the colony (Asbirk 1979), while at Kent Island, New Brunswick, nest success was lower in the high density portion of the colony (Preston 1968). At two colonies in Quebec, Cairns (1980) found that nest density did not influence nest success. The high success rate in the high density area at Nordre Ronner was attributable to the fact that these were nests in rock crevices and were much less accessible to predators than were the driftwood nests that formed the majority of low density nests. Hence, at Nordre Ronner, nest success was influenced primarily by nest type; nest density was merely a reflection of the distribution of available nesting sites and did not, in itself, influence nest success.

At Kent Island, the reduced reproductive output from nests in the high density area was not due to an increased rate of nest failure _per se_ but to decreased clutch size. Preston (1968) speculated that the increased rate of agonistic encounters between birds in the high density area somehow influenced egg laying. These observations were suggestive of a population regulation mechanism (Preston 1968). If increased density does reduce reproductive rate, it would be adaptive for guillemots to seek nest sites far from their neighbors; this could explain, in part, the dispersed nesting distribution of guillemots. However, Cairns (1980), who also noted that the rate of agonistic encounters was greatest in high density areas, found no differences in reproductive output between high and low density areas. Preston's (1968) observations cannot be interpreted fully without more knowledge, particularly of the nest types involved and their distribution between high and low density areas (Cairns 1978).

Lack (1966) stated that where nest sites are limited, nonbreeders will accumulate until some other density dependent check is reached. While nonbreeding, in itself, can be considered a density dependent check on population growth (von Haartman 1971), other factors, most likely related to winter food availability, will determine the number of nonbreeders that can be supported in a temperate breeding seabird population (Harris 1966, Nelson 1966).

The inshore waters of Prince William Sound are almost devoid of forage fishes between November and March, in contrast to their abundance during the remainder of the year (Rosenthal 1979). The macrophyte forests which dominate subtidal habitats during summer deteriorate during winter, and the loss of cover must influence the distribution and abundance of epibenthic fishes and invertebrates living in those zones (Rosenthal 1979, Hodgson and Waaland 1979).

There is little information on the response of Pigeon Guillemots to this drastic seasonal change in their foraging environment. They appear to eat more invertebrate foods in winter (Preble and McAtee 1923, Munro and Clemens 1931, Krasnow et al. 1979, Sanger et al. 1980), probably because fishes are not as available. While Bent (1919) stated that Pigeon Guillemots winter offshore, recent data indicate that they remain inshore. Scott (1973) made inshore and offshore transect observations of marine birds in the vicinity of Yaquina Head, Oregon, in both summer and winter. Pigeon Guillemots were completely absent from the area in winter, and Scott suggested that open coast populations migrated to the protected waters of Puget Sound and British Columbia's inland passage, ostensibly because of improved foraging conditions there. Storer (1952) made this same suggestion and speculated that variations in wing length among Pigeon Guillemot populations were due to the migratory habits of the northern and southern populations and the more sedentary habits of the British Columbia and Washington populations.

Examination of the numbers of Pigeon Guillemots counted at coastal sites on the west coast of North America on Christmas Bird Counts between 1970 and 1979 (Fig. 16) provides some information on the winter dispersion of Pigeon Guillemots. They were largely absent from the open coasts of California, Oregon, and Washington, while they were abundant in Puget Sound and the Strait of Georgia, indicating that the southern open coast populations do indeed migrate. I found no Pigeon Guillemots breeding at Tacoma, Washington, during census work in May and June 1975 (unpubl. data), so the high numbers counted there in winter strongly suggests that southern Puget Sound is a wintering ground for birds breeding elsewhere. Similarly, Pigeon Guillemots breeding in the Bering Strait region withdraw in winter (Bent 1919) and probably account for the population which is present at the Pribilof Islands in winter (Preble and McAtee 1923). These data indicate that Pigeon Guillemots remain in inshore waters during winter and at least some open coast populations migrate to inshore wintering grounds.

Estimates of overwinter survival rates of Black Guillemots are on the order of 80-90% (Preston 1968, Asbirk 1979), and rates are probably similar for the Pigeon Guillemot. There has been no study of annual variations in overwinter survival of guillemots, so it is unknown if increases in productivity are balanced by

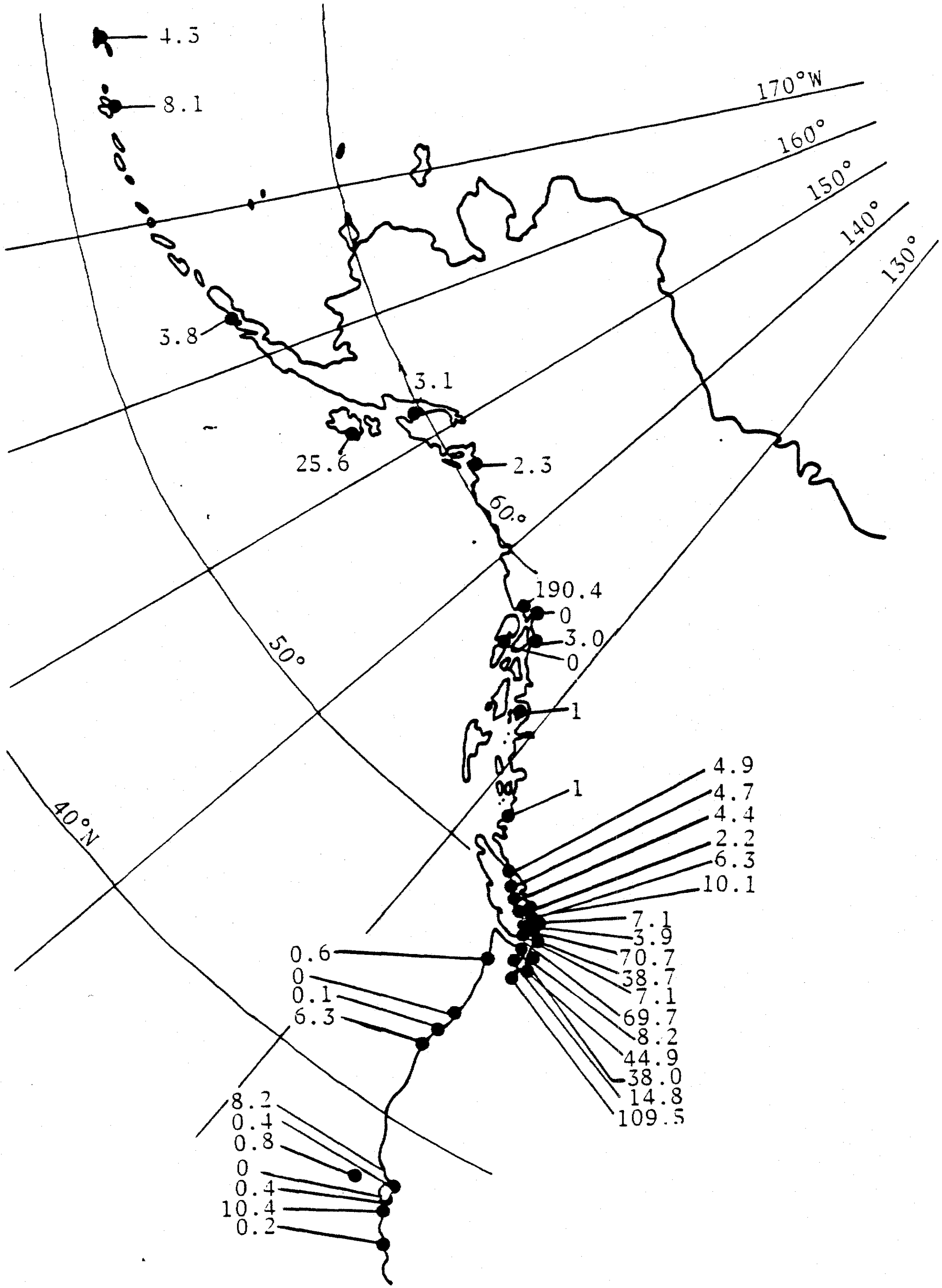

FIGURE 16. Average number of Pigeon Guillemots on Christmas Bird Counts between 1970 and 1979 at sites on the western coast of North America. Data abstracted from American Birds vols. 25-30, no. 2 and vols. 31-34, no. 4.

decreased overwinter survival. The concentration of Pigeon Guillemots at wintering grounds could provide a mechanism for density dependent mortality if the populations of winter prey are depleted, but evidence for this is lacking. That more guillemots survive the winter than can breed due to a lack of nest sites indicates that overwinter mortality is a less important determinant of population size than the number of nesting sites.

Many authors have noted that guillemot breeding distribution is governed or limited by the distribution of suitable nesting habitat (Soper 1940, Bianki 1967, MacLean and Verbeek 1968); the cause of their ubiquitous, low density breeding distribution appears to be the scarcity of nesting sites. As the number of birds able to breed but prevented from doing so by the lack of a nest site increases at a colony, it will become increasingly adaptive for these individuals to seek out new locations. Black Guillemot tracks going in and among the many discarded oil barrels on an arctic barrier island (pers. obs.) demonstrate that guillemots "prospect" for nesting sites. Their propensity to explore and their flexibility in choice of nesting site are traits which allow guillemots to breed in as much of the area that has adequate food as possible.

The breeding distribution of a seabird species must reflect the availability of both nest sites and food (Ashmole 1971). Preston (1968), reiterated by Sealy (1972) and Asbirk (1979), stated that the breeding distribution of guillemots was determined proximately by the distribution of nesting sites, but ultimately by their use of inshore waters for feeding. These authors state that guillemots use a food source that is distributed evenly throughout their foraging areas; the breeding distribution of *Cepphus* can thus be simply explained as a correlation between the distribution of a predator and its prey (Preston 1968:92, Sealy 1972:86). However, the statement that the guillemots' food source is dispersed or distributed evenly is merely an inference--no studies of the guillemots' prey species were cited--and the statement that their breeding distribution is determined ultimately by their use of a dispersed food source is misleading, because it implies that it is adaptive for guillemots to nest in a dispersed fashion, as required by the nature of their food source. Dispersion of nests could be adaptive in a food-related way if summer food supplies were depleted by the summering population, but there is no evidence of this phenomenon in guillemots. I contend that forage fishes are widely available in temperate inshore waters during summer and that they are more widely available than is suitable nesting habitat. The guillemots' dispersed breeding distribution is due to the strong pressure to find a nest, not to pressure to find food or to avoid competition for food.

That fishes are widely available in temperate inshore waters during summer can be inferred from the fact that guillemots can breed at so many locations. It cannot be inferred that the density of guillemots is low because the density of fishes is low.

Inshore fish faunas differ among sites because of oceanographic and substrate conditions, and the prey of guillemots differs accordingly among localities. Guillemots appear to be as labile in foraging habits as they are in nest site selection (Storer 1952). At some sites, guillemots may indeed feed on cryptic, armored, non-schooling species, such as sculpins and blenniods, which have a relatively dispersed distribution in the benthic environment. (However, at Mandarte Island, where Pigeon Guillemots fed on sculpins and blenniods, they fed at a single shoaling ground; hence, the distribution of even these fishes was clumped, not dispersed.) At other sites, such as Naked Island, St. Mary's Island (Cairns 1978), and Cooper Island (Divoky et al. 1974), guillemots fed on the young of schooling fishes, such as cod or sand lance, which had moved inshore for the summer and were concentrated there. Thus, the general statement that the guillemots' food source is dispersed is not justified, and the conclusion of the aforementioned authors that the guillemots' breeding distribution is ultimately determined by their use of a presumably dispersed food source is not warranted.

Guillemots can nest in large concentrations. Austin (fide Storer 1952) reported a Sooty Guillemot _C. carbo_ colony of 5000 pairs on Hokkaido, Japan. In Alaska, recent seabird censuses have discovered several Pigeon Guillemot colonies of 3000-4000 birds (Sowls et al. 1978). There are 2000 Pigeon Guillemots on the Farallon Islands, California (Ainley and Lewis 1974). In arctic

Canada, there are several nesting concentrations of Black Guillemots numbering in the thousands (Brown et al. 1975), including one of 10,000 pairs on Devon Island (Nettleship 1974). Certainly the food resources in the areas of these large concentrations of nesting guillemots must be propitious, but the existence of these colonies is predicated upon an abundance of nesting sites.

CONCLUSION

Nesting and foraging habitats were propitious for Pigeon Guillemots at Naked Island. Because shorelines were dominated by cliffs and broken cliffs, guillemots were not restricted to one or a few breeding sites; because most nests were inaccessible, predation was negligible. The high fledging weights of chicks in 1978 was due to an available and nutritional food supply. Based on the large number of nonbreeders, food was apparently more available than nest sites. As at other locations, breeding population size was determined by the number of nest sites. The comparative abundance of guillemots at Naked Island was due to the comparatively many nest sites found there.

SUMMARY

1. The Naked Island area was exceptional for the many Pigeon Guillemots which bred and summered there. In 1978, the population was estimated to be 2000-2500 birds. Guillemots were the second most abundant marine bird species. Their density on five inshore transects averaged 43.8 birds/ km^2 and was high compared to other areas. The abundance of Pigeon Guillemots at Naked Island can be attributed to bountiful foraging grounds and a shoreline dominated by habitats which provided nesting crevices.

2. Comparison of the number of Pigeon Guillemots attending colonies with the number known to breed indicated that approximately 40% of guillemots summering at Naked Island were nonbreeders.

3. Nesting occurred in talus and cliff crevices and cliff-edge burrows. Most nests had entrances smaller than 300 x 300 mm, and were about 1 m in length. Average elevation of nests was 6.5 m, reflecting the low height of Naked Island cliffs.

4. Nesting density averaged 34.9 nests/ km of shoreline in which nesting occurred, but showed wide variation among colonies. The frequency of each nest type also varied among colonies.

5. Juvenile cod and sand lance formed the bulk of the summer diet in 1978. A variety of other fishes and decapods were also eaten. This prey spectrum was unique compared to the prey sprectra of Pigeon Guillemots at other areas, where other fishes, notably blenniods and sculpins, were more important.

6. The principal foraging areas were bays and coves, and the distance between colonies and foraging sites ranged from a few hundred m to 2-3 km. Differences in the diet of guillemots from different colonies could have been due to differences in the relative abundance of fishes at their respective foraging grounds.

7. There was wide spread in timing of reproductive activities within the population due to the lack of predation and to the lengthy period of food availability.

8. The comparatively high number of young fledged per nest (1.28 young/nest) in 1978, can be attributed to the inaccessibility of nests which precluded predation and the abundance and quality of food.

9. The comparatively high rate of weight gain and fledging weight of chicks at Naked Island can be attributed to the availability and quality of food in 1978.

10. Both guillemot population size and distribution are overwhelmingly influenced by density independent factors.

The number and distribution of potential nesting crevices limits the number and distribution of breeders. The inshore fishes eaten by guillemots are generally abundant during summer, hence guillemots do not compete for food while breeding. Scarcity of food during summer can usually be attributed to physical or chemical oceanographic factors. Guillemot population productivity could be modified in a density dependent fashion if guillemots nest in suboptimal sites when population density is high. Overwinter survival rates could also be density dependent if the concentration of guillemots on winter foraging grounds depletes winter food supplies.

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