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The thesis of Katherine J. Kuletz is approved:

Gayle J. Hurdley

John J. Hurdley

F. Lynn Carpenter

George L. Hurdley

Committee Chair

University of California, Irvine

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## ABSTRACT OF THE THESIS

### Mechanisms and Consequences of Foraging Behavior in a Population of Breeding Pigeon Guillemots

by

Katherine J. Kuletz

Master of Science in Biological Sciences

University of California, Irvine, 1983

Professor George L. Hunt, Jr., Chair

The diet, habitat use and reproductive success of Pigeon Guillemots (Cepphus columba) at three small adjoining colonies were followed from 1979 to 1981 at Naked Island, Prince William Sound, Alaska. Individual birds displayed foraging site and prey preferences which were generally maintained within a season and between years. There were significant correlations between the use of certain habitats and prey species, but differential prey selection between birds using the same or similar habitats did occur. Although most birds sampled a variety of prey during the course of a season, they tended to either specialize on surface schooling fish, primarily sandlance (Ammodytes hexapterus), or use a wide range of bottom fish.

The use of sandlance in 1979 correlated with higher reproductive success for the population and higher fledging success for

pairs. However, inclement weather in 1981 had a detrimental affect on foraging efficiency, particularly for sandlance, and correlated with higher daily percentages of bottom fish.

Differences in diet between individuals appeared to be correlated with laying date, habitat use and possibly an acquired search image. Polymorphism in foraging behavior for this population is likely to be influenced by the frequency of environmental fluctuations which affect the efficiencies of different foraging behaviors.



## INTRODUCTION

Foraging behavior depends on the abundance, distribution and predictability of prey. A resource base with a few primary prey species that are abundant should favor specialists, while an environment with many species, each with low abundance and wide dispersal, should favor generalists (MacArthur 1968, Cody 1974). However, the diet breadth of a species or population may be greater than that of individuals that are responding to local habitat conditions. The variability within a population may depend on the complexity of the habitat and the prey diversity associated with different habitats (Morse 1980, Fox and Morrow 1981, Werner et al. 1981). Implicit in these predictions is the importance of encounter rate and experience in the search for, pursuit and capture of prey (MacArthur and Pianka 1966, Levins 1968, Murton 1971, Schoener 1971, Roughgarden 1974, Strickler 1979). As a result, changes in resource abundance force an organism into a compromise between familiarity with habitats or prey and flexibility to changes in prey (Heinrich 1979).

Because of the complexity of interacting factors, the adaptive significance of foraging patterns in higher vertebrates has not been adequately studied in the field, particularly in relation to individual reproductive fitness. This study focused

on intraspecific variation in diet in a breeding population of Pigeon Guillemots (Cepphus columba), members of the alcid genus in which individuals exhibit prey preferences. At Naked Island, Alaska, I examined the following questions: 1) How persistent are individuals in their choice of prey and does this correspond to habitat preference? 2) Are there differences in foraging routine and efficiency between individuals which can be related to their prey? 3) Does the type of prey fed to chicks affect reproductive success?

For seabirds the pressures of resource fluctuation are strongest when they must feed offspring in addition to themselves. Ninety-eight percent of seabird species nest colonially (Lack 1968), typically in large aggregations near access to a few prey species which tend to be temporarily abundant. In contrast, guillemots are widely dispersed at low densities, nesting in multi-species colonies, small conspecific colonies, or singly. The foraging behavior of the genus is that of "generalist", with records of over fifty prey species of sub-littoral epibenthic fish, mid-water and surface schooling fish, plus various crustacea and squid (Follett and Ainley 1976). However, breeding birds often display prey specificity, with great variety between individuals (Drent 1965, Koelink 1972, Slater and Slater 1972, Eldridge and Kuletz 1980).

Because of their dietary differences, individual foraging behaviors (ie, temporal and spatial patterns and diet breadth)

should be diverse and correspond to the properties of "preferred" prey. Guillemots have been observed to maintain unique diet preferences despite the use of obvious and abundant different prey by neighbors (Drent 1965, Slater and Slater 1972, this study). These behavioral patterns challenge certain "optimal foraging" predictions as well as the concept of seabird colonies serving as "information centers" (Ward and Zahavi 1973) and require further studies to determine their adaptive advantages. Two mechanisms suggested by Drent (1965) and Slater and Slater (1972) were 1) the operation of a "search image" and 2) forage site attachment. Both authors favored the idea that the forage site determined diet, but no quantitative studies were done.

Storer (1952) suggested that guillemot's generalist feeding habits minimized the impact of resource fluctuation on their breeding success and distribution, but this theory assumes that all individuals use the full range of available prey. If habitat or prey choice persist over time, whether seasonally or year-to-year, individuals should experience different environmental pressures and consequently differential breeding success. The capacity of guillemots to lay two eggs (most alcids lay one) would accentuate differences in fledging success between pairs.

Guillemots are uniquely suited to the study of different foraging strategies under similar climatic and habitat conditions. Their small colonies and nearshore feeding habits permit one to follow individuals from specific nests. Monogamous pairing and

nest site tenacity allows successive years of observations on the foraging of individuals and the fledging success of the pair. In this study, differences in guillemot foraging patterns are analyzed in conjunction with the food returned to chicks and the reproductive outcome of three seasons. The results suggest some probable mechanisms and potential costs and benefits of specializing or generalizing on different types of prey. The discussion will address why behavioral variation is maintained in a population, and how this relates to the distribution and abundance of C. columba.

## THE STUDY AREA

Naked Island ( $35 \text{ km}^2$ ) is located in Prince William Sound, southcentral Alaska on a shallow water plateau less than 100 meters deep (Fig. 1). Peak ( $5 \text{ km}^2$ ) and Storey ( $8 \text{ km}^2$ ) Islands are one and three km north and the two Smith Islands 10 km to the south. The sound is a fjord-type system with prevailing SE/SW winds (Royer 1975). Surface water temperatures range from  $-2^\circ\text{C}$  to  $18^\circ\text{C}$  and the tide range is 3-4 m (Muench and Schmidt 1975). The leeward west side of Naked Island has protected bays and coves with eelgrass (Zostera ssp.) and beaches of mud and cobble. The outer shoreline is primarily boulder beaches with talus slides and low cliffs 5-20 meters high. Intertidal and subtidal algae, primarily Ulva, Laminaria and Fucus ssp., are abundant.

The island is uninhabited except for occasional fishermen and fall deer hunters. Potential nest predators include river otter (Lutra canadensis), northwestern crow (Corvus caurinus) and common raven (C. corax). There are small colonies of three other alcids and one larid species, four species of nonbreeding seabirds and a variety of marine mammals (Sangster et al. 1978, Oakley and Kuletz 1979). There are an estimated 700 breeding pairs of pigeon guillemots, and a total population of 2500 guillemots, about a third of all the seabirds in the study area. Breeding was followed at the colonies named "Parakeet", "Hook", "Row", "Thumb",

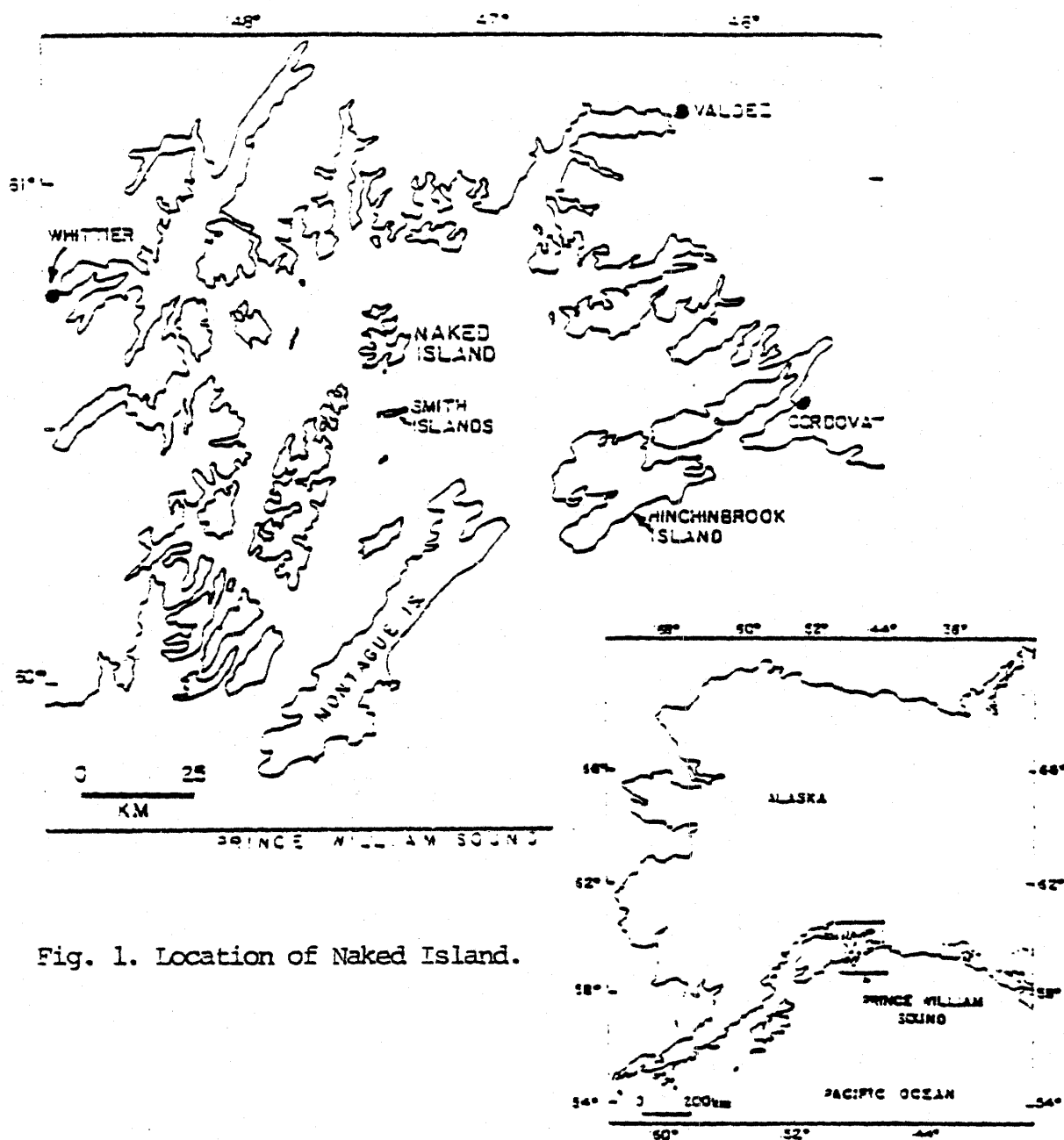


Fig. 1. Location of Naked Island.

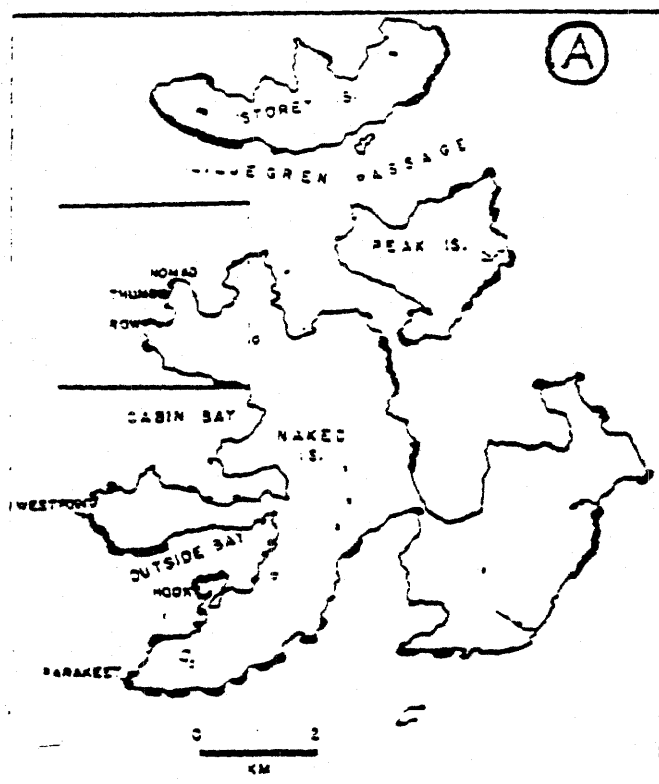
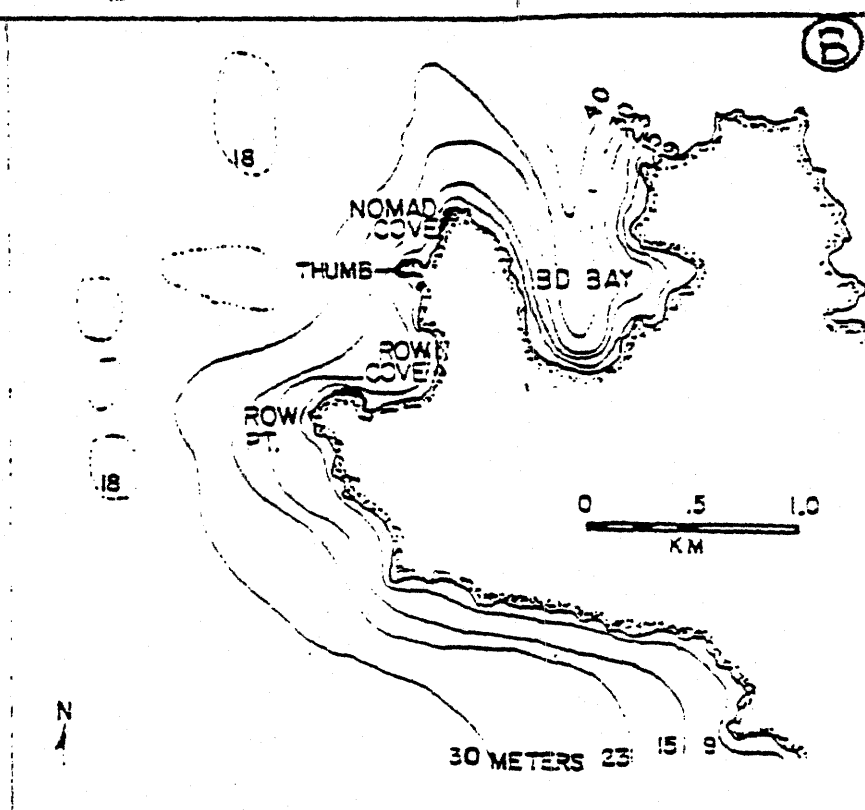


Figure 2.

Colonies observed and water depths of main study area. Darkened shoreline in A indicates pigeon guillemot nesting areas. Dotted water depth contours in B were taken from USGS maps, solid lines from depth sounder transects done for this study by the author.



and "Nomad" (Fig. 2A). Occasional feeding watches were done at Hook and Parakeet, but the majority were done at Row and Nomad in 1980 and 1981, with Thumb included in 1981 (Fig. 2B).

#### PHENOLOGY OF NAKED ISLAND GUILLEMOTS

Pigeon guillemots were present upon our arrival in May. The birds nested in cliff-top burrows (40%), cliff crevices (36%) and talus (24%) (Oakley and Kuletz 1979). Courtship and mating extended through May, with most eggs laid by early June. The one or two eggs are incubated by both parents an average of 32 days. Chick rearing, averaging 37 days, spans July and August. Nest mates, which continued pair bonding activities regardless of egg or chick survivorship, gathered at the colonies in the early morning and at the following high tide. Non-breeding birds also attended the social gatherings and comprised between 40% to 60% of a colony. Non-breeders left the area earlier in the season than birds raising chicks and by late August only a small proportion of adults still feeding young remained. Fledglings were present up to our departure 30 August. Guillemots are not present in the study area in winter (Islieb & Kessel 1973). Audubon Christmas counts indicate they may over-winter in waters off British Columbia or Puget Sound (Oakley 1981).



## METHODS

The methods were designed to: 1) Gather data on the full range of available prey and general foraging patterns of the local population by monitoring individuals from different colonies. 2) Compare the temporal foraging patterns and efficiency of birds preying on different types of fish. 3) Determine the reproductive success of the population and of specific pairs with respect to diet.

### I. Foraging Habitat and Diet

Feeding watches were rotated among colonies with each colony observed at least every 2-4 days, usually for six daylight hours. The flight directions of birds provisioning chicks or their diving sites were recorded using a compass, prominent landmarks and buoys set to aid distance judgements for some areas. In 1980 and 1981 diving sites not visible from the colony blind were reported via radio by an observer stationed near the foraging area. Diving sites were plotted on a map divided into 200 m quadrats, since individuals often covered 50-200 m during a foraging sequence. Individual birds could be identified if one or both nest mates were marked with colored leg bands or painted wing patches. Because birds typically paused on the water or rocks before delivery, prey could be identified with binoculars or spotting telescope.

Two "suites" of prey were recognized, based on their distribution patterns and habitat utilization. The "schooling fish" are the Sandlance (Ammodytidae), herring (Clupeidae) and smelt (Osmeridae), which usually occupy surface waters. Although sandlance burrow in sand, guillemots appeared to be preying on them only when these fish were schooling near the surface. The "bottom fish" suite includes the remaining fish and invertebrates. The eleven prey categories were based on taxonomic groups and the ability to distinguish prey through the spotting scope. The "Unidentified" returns were due to rapid deliveries which were the major cause of lack of identification; unidentified returns comprised only 9 to 13% of a year's total and, therefore, should not significantly bias the results. Identification to species was possible for certain prey and deliveries were occasionally retrieved from chicks for verification. We obtained samples of bottom fish with baited minnow traps set at various sites at depths of 3-26 meters, with each set consisting of three traps anchored together on the seafloor for 8-24 hours.

Prey returns of different birds using similar habitats were compared by a two-way heterogeneity G-test (Sokal and Rolf 1969). Habitats were scaled into quadrats, zones and domains. Quadrates 400-600 m offshore were combined into units of 4-6 quadrats to compensate for observer bias in estimating distances, with an attempt to follow the shoreline and water depth contours. At greater distances 12 quadrats were combined. The zones were

geographically defined areas such as bays, coves, or stretches of shoreline. The domains were defined by water depth and distance offshore: Nearshore (<200 m offshore, <15 m deep), Shelf (middle regions of bays, and waters 200-600 m offshore, 16-23 m deep) and Offshore (>600 m offshore, >23 m deep).

## II. Temporal Foraging Patterns and Feeding Rate

A bird's arrival with food and the actual delivery to the nest were recorded to the nearest minute; trip time was from delivery to the next arrival. Since individuals could not always be distinguished a second measure of trip time was the time between two consecutive deliveries to a nest.

In 1980 28 birds were wing-tagged to facilitate foraging observations. Since no tagged birds hatched chicks they were not included in the reproductive analysis. Their foraging appeared to be affected in late summer, when some birds suffered obvious impairment or death. Forage areas were checked periodically for tagged birds, their locations noted and diving patterns monitored for 10-60 min. Untagged birds were observed if they could be individually followed. Time spent under water and on the surface between dives was recorded to the nearest second.

Daily weather records were kept using a rain gauge, min-max thermometer and anemometer or radio reports of wind speed. Sea conditions were rated on a scale of one to five (Appendix A). In 1981 weather and sea conditions were noted hourly during the

feeding watches.

### III. Estimating Reproductive Success

Colony attendance counts were taken hourly during the watches and nesting activities noted. Different individuals were observed each year, due to unsuccessful nesting attempts (apparently) caused by human disturbance and weather, or failure to attempt nesting by some experienced pairs. Since guillemots display nest site fidelity (Storer 1952, Drent 1965, Preston 1968, Asbirk 1979, this study), all reused nests were assumed to be occupied by the same pair even when members weren't tagged. This assumption was probably valid; in three nests a tagged bird deserted and did not return the following year, although the nests were active, whereas, comparison, 12 banded birds with more than one year of breeding records returned to the same nest for a total of 37 bird-years.

Laying and hatching dates were determined by daily nest checks or calculated by backdating from the date of hatching or estimated from the date of fledging. The chronologies of inaccessible nests were estimated by feeding activities. At accessible nests chick growth was measured every three days, weather permitting. Wing chord, tarsi and culmen length were measured to the nearest mm and chick weight to the nearest gram using hand held pesola scales.

## RESULTS

### FORAGING HABITAT AND DIET

To determine the association between habitat use and diet, I examine: 1) the distribution of foraging birds and individual habitat use; 2) the prey delivered to specific nests and the total for the population; 3) estimated distribution of prey species based on deliveries for which the bird's forage site was known; and 4) tests for heterogeneity of prey selection between birds using the same or similar habitats.

#### 1. Distribution of Foraging Birds

Birds from the same colony tended to concentrate their foraging in the same general area (Fig. 3), so there was some overlap in forage sites among colony members. Guillemots are often reported to travel 3-4 km foraging for chicks (Storer 1952, Drent 1965, Slater and Slater 1972, Cairns 1980) and the colonies I studied were 1 km or less from each other. This indicates that birds were not restricting their foraging due to a lack of other potential sites in the vicinity. Some year-to-year variation in foraging areas may reflect the presence of new individuals rather than changes by the same individuals.

The colony foraging areas were basically consistent all three years except for a reduced use of offshore areas in 1981, a year

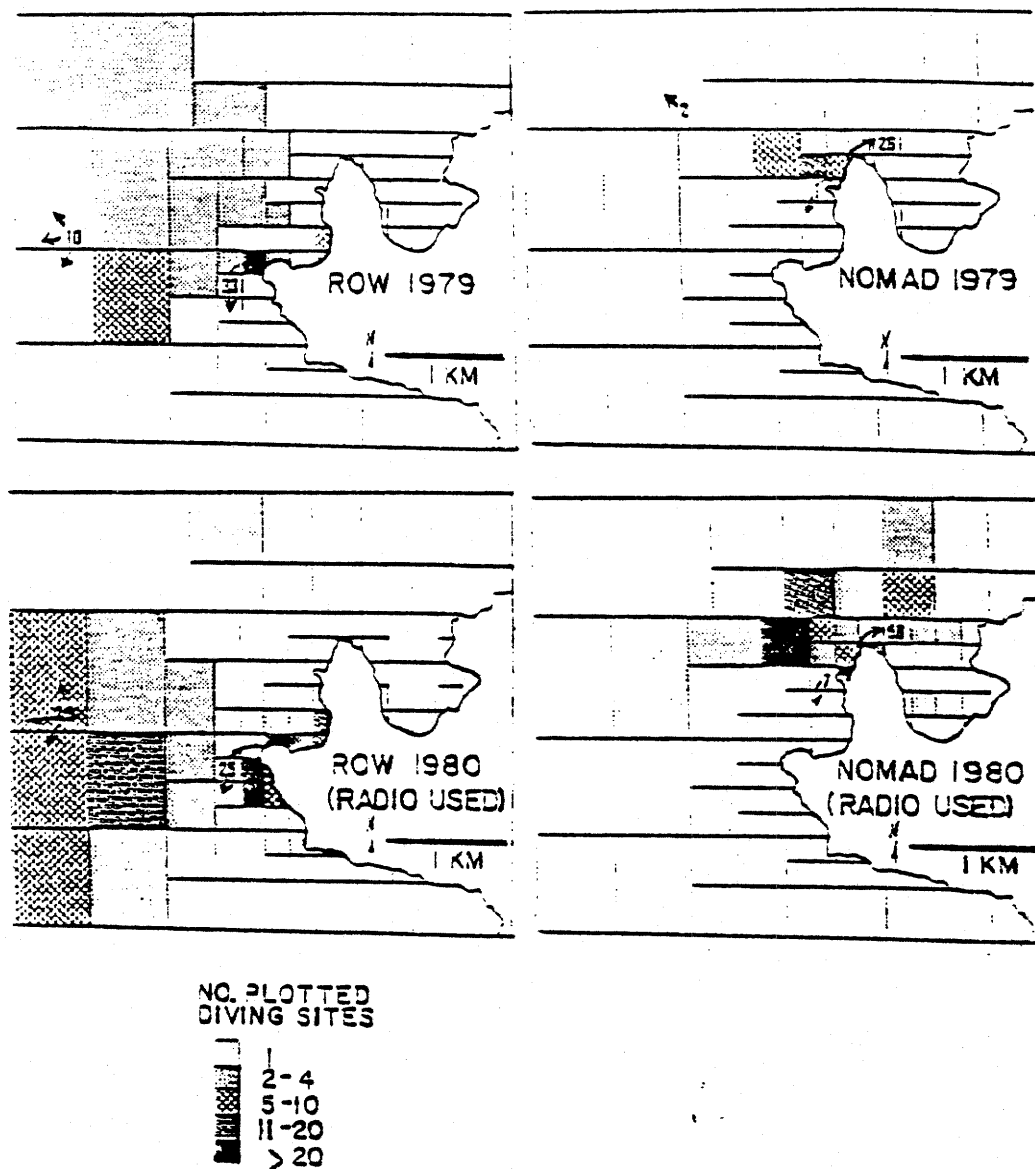


Figure 3. Recorded diving sites by birds of known nest association, plotted near land map seen in Fig. 2B. Numbers indicate flight directions beyond site of colony observer. The most accurate records for foraging sites were obtained in 1980.

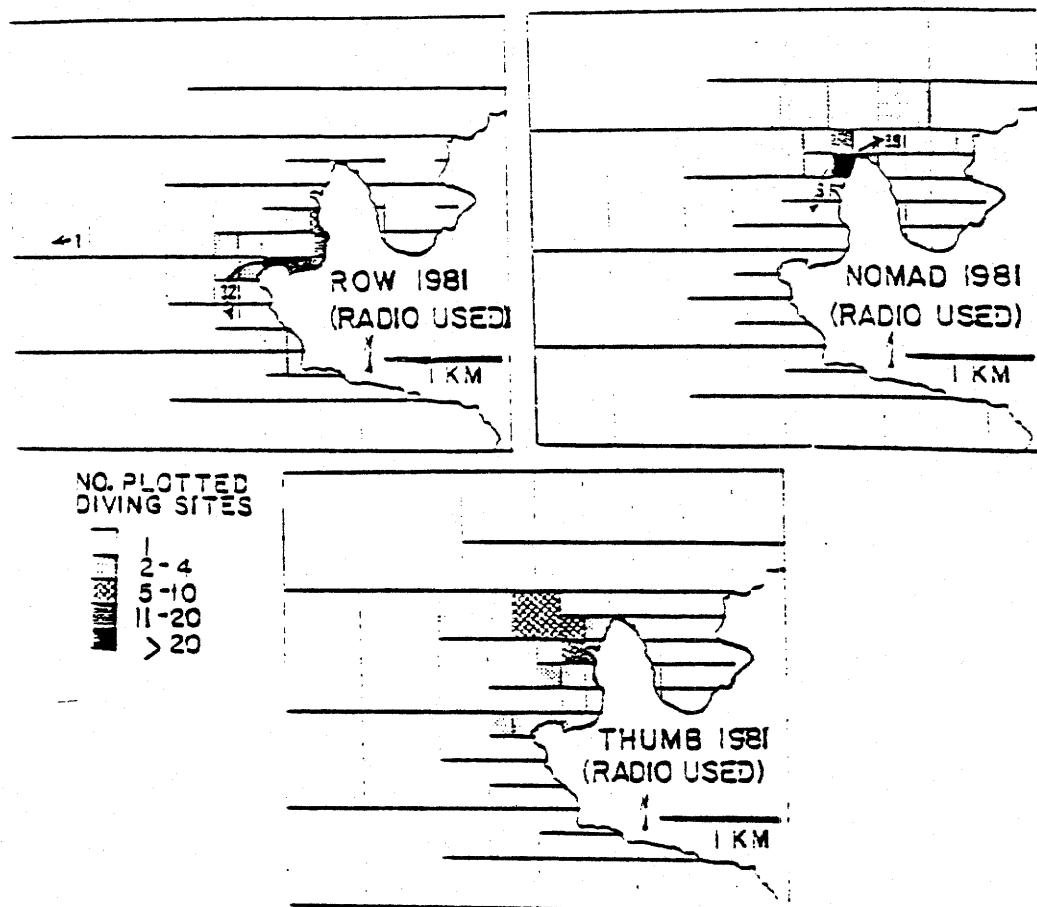


Figure 3. (cont.)

with frequent storms. This reduced use was real because we used an off-colony radio observer in 1980 and 1981. In addition, birds foraged near their colonies more each year. In 1979 only 9% of all foraging flights (N=180) ended within 200 m of the foraging bird's colony, compared to 21% of all observations in 1980 (N=440) and 35% in 1981 (N=226). This gradual increase seems to relate to the increase in strong winds and total rainfall each year (Appendix B). The low number of distant foraging sites was not due to rainy weather interfering with our ability to follow the birds, since the proportion of flight observations lost by observers was actually higher in 1979 and 1980 and they were usually caused by sun glare.

Over the course of a season certain quadrats were visited by more birds than other quadrats (Fig. 4), especially areas of underwater rises or shelf breaks in 1980 (see Fig. 2B) and areas near colonies in 1981. However, quadrats most often used by any one bird did not usually overlap those used frequently by another. The zone visited more than 50% of the days on which a bird was sighted was considered its "primary" zone and the zone used 25-50% termed "secondary". Zones visited less than 25% were termed "minor" sites, the majority of which were single visits. Single visits to quadrats were 14% of all plotted diving sites (N=555) for nesting pairs. Since records for a pair represent the foraging movements of two birds, these trips may be exploratory and are a relatively small proportion of guillemot foraging activi-



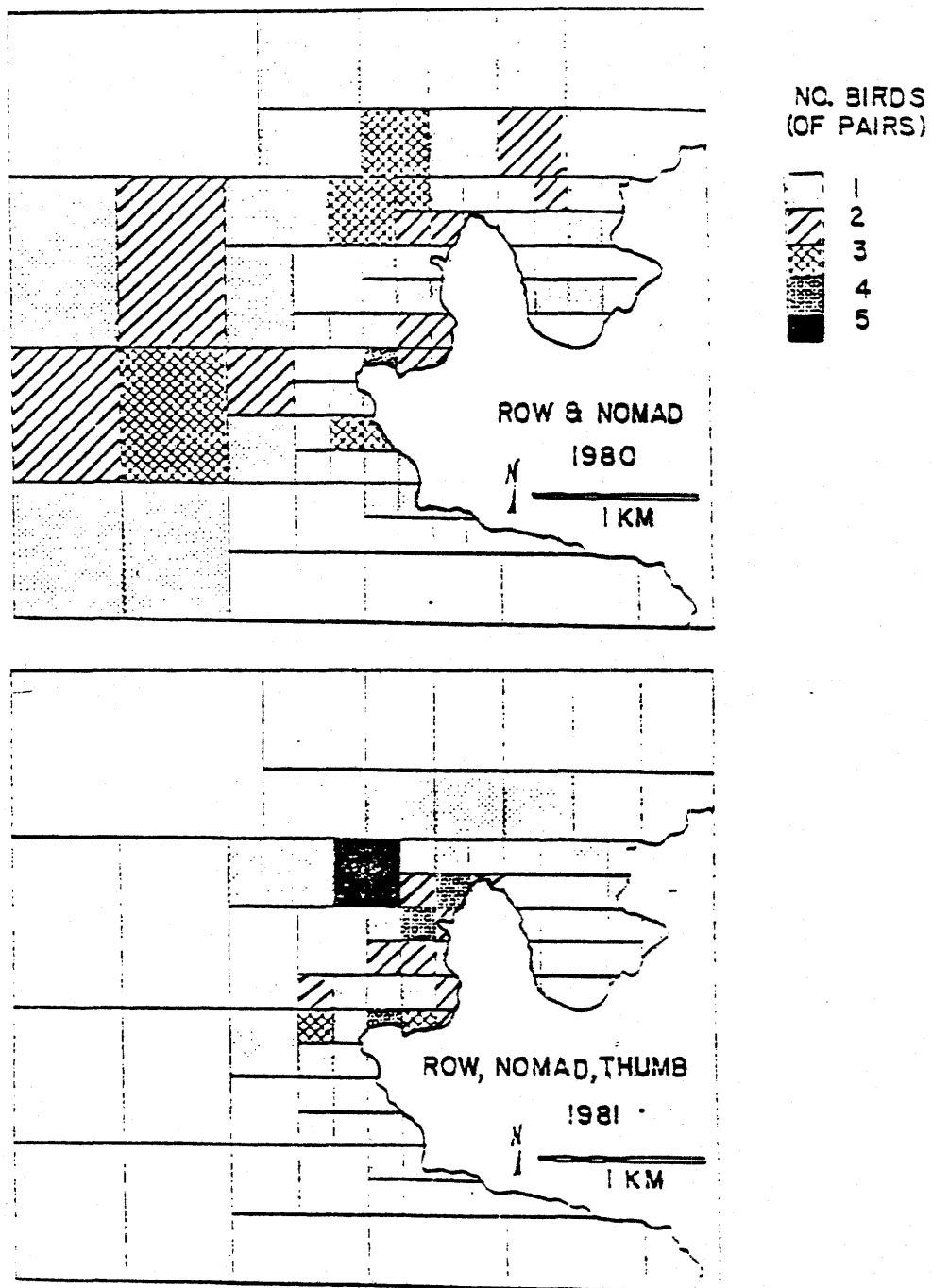


Figure 4. The total number of nest provisioners which visited each forage site within the seasons of 1980 (Row and Nomad birds only) and 1981 (Row, Nomad and Thumb).

ties.

The foraging data for pairs were substantiated by observations of marked individuals, which used the same primary forage zone, usually a specific area of that zone, throughout the year. This was true for banded birds provisioning chicks as well as for non-breeding wing-tagged birds (Table 1). Individual movement during the season was estimated from the number of quadrats visited, which averaged 3.5 quadrats/bird ( $SD=1.55$ ). Results varied between birds, but averages were similar for those provisioning chicks and tagged birds without young. There was no significant difference between years, nor between birds concentrating on schooling fish ( $\bar{x}=3.25$ ,  $SD=.05$ ) or on bottom fish ( $\bar{x}=3.9$ ,  $SD=1.19$ ). The slightly greater area covered by birds preying on bottom fish may have been due to observer inaccuracy in pinpointing the distant sites those birds typically used.

Pairs and individuals observed for more than one year rarely altered their primary forage zone between years. For eight pairs with two or more years of data ( $N=18$  nest-years), there were only two major changes. For five marked individuals ( $N=11$  bird-years) there was one change, to the bird's minor site of the previous year. Forage site fidelity may continue regardless of chick-feeding responsibilities; two birds tagged in 1980 which failed to hatch eggs that year but raised broods in 1979 and 1981, had the same primary forage zones all three years.

## 2. Prey Delivered to Chicks

**Table 1.** Summary of forage site use for banded birds feeding chicks and wing-tagged birds foraging for themselves.

Forage Zone Use	<u>Bird-days of observation</u>		<u>Prey returns from known forage sites</u>	
	Tagged birds without chicks (N=11)	Banded birds with chicks (N=21)	Banded birds with chicks (N=21)	
Bird-days at Primary Zone (%)	49 (94%)	98 (78%)	212	(85%)
Bird-days at Secondary Zone (%)	0 (0%)	13 (11%)	20	(8%)
Bird-days at Minor Sites (%)	3 (6%)	13 (11%)	17	(7%)
<u>Observation Intensity</u>				
$\bar{x}$ No. of quadrats/bird	3.2 $\pm 1.4$	3.6 $\pm 2.3$		
$\bar{x}$ days of observation/bird	4.9 $\pm 1.7$	5.4 $\pm 2.6$		
Total Bird-days of observation	52	124	249	

In total prey returns for three years (Table 2) sandlance were always important, but their use decreased each year. The most pronounced change occurred in 1981 when herring, smelt and lingcod became important food items and together composed 28% of the total. Seasonal fluctuations in prey species were suggested by the birds' returns (Fig. 5) and indicate that sandlance were available throughout the season in 1979 and to a lesser degree in 1980, but in 1981 they were absent by August. In 1981, with the appearance of lingcod, the proportion of blennoids relative to other bottom fish decreased in the latter half of the season.

Most nesting pairs and individuals showed preferential use of certain prey (Table 3). Sample sizes, though small, represent the entire chick-rearing period of a pair and daily results were usually consistent with respect to schooling fish or bottom fish usage (Appendix C). In 1980 and 1981, 88% of the pairs were consistent throughout the season. In 1979 half of the pairs were not homogeneous between days, but these nests had less than 6 days of observation and the nest mates appeared to have different preferences. Of 19 individuals with at least 6 days of observations (from 1980 and 1981), 17 maintained their preference for schooling or bottom fish within a given year.

For eight pairs observed two or more seasons, five had the same prey bias as in previous years. The three which changed, all between 1979 and 1980 at Row colony, included one case of a change of mate and two nests with unbanded birds. Only one of these

Table 2. Summary of food items fed to Pigeon Guillemot chicks.

FOOD GROUP	PERCENT OF TOTAL FOR EACH SEASON		
	1979	1980	1981
<b>Surface School fish</b>			
1 Sandlance	54.6	35.3	22.6
2 Herring	*	*	7.7
3 Smelt	*	*	7.8
<b>Bottom fish &amp; Inverts</b>			
4 Blenny/Ronquil	18.6	29.5	19.4
5 Lingcod	*	*	12.6
6 Sculpin	14.0	9.0	10.7
7 Cod	1.4	6.9	1.2
8 Flatfish	1.7	5.5	1.2
9 Rockfish	*	*	3.6
10 Invertebrates	0.3	1.3	0.7
Unidentified	9.3	12.5	12.8
* Fish rarely observed and never recovered at nests. Included with Unidentified.			

**Identified Species**

- |   |                         |
|---|-------------------------|
| 1. Ammodytes hexapterus                     | 7. Pacific tomcod       |
| 2. Clupea pallasii                          | (Microgadus proximus)   |
| 3. Osmeridae ssp                            | Pacific cod             |
| 4. Crescent Gunnel (Pholis laeta)           | (Gadus macrocephalus)   |
| Snake prickleback (Lumpenus sagitta)        | Walleva pollock         |
| Y-Prickleback (Allolumpenus hypochromus)    | (Theragra chalcogramma) |
| Daubed shanny (Lumpenus maculatus)          | 8. Bothidae ssp         |
| Penpoint gunnel (Apodichthys flavidus)      | Pleuronectidae ssp      |
| Northern Ronquil (Ronquilus jordani)        | Slender Sole (Lyposetta |
| Searcher (Bathymaster signatus)             | exilis)                 |
| Liparis ssp (Cyclopteridae)                 | 9. Sebastes ssp         |
| 5. Ophiodon elongatus                       | 10. Shrimp              |
| 6. Tidepool sculpin (Oligocollus maculosus) | Squid                   |
| Cottidae ssp                                |                         |
| Agonidae ssp                                |                         |

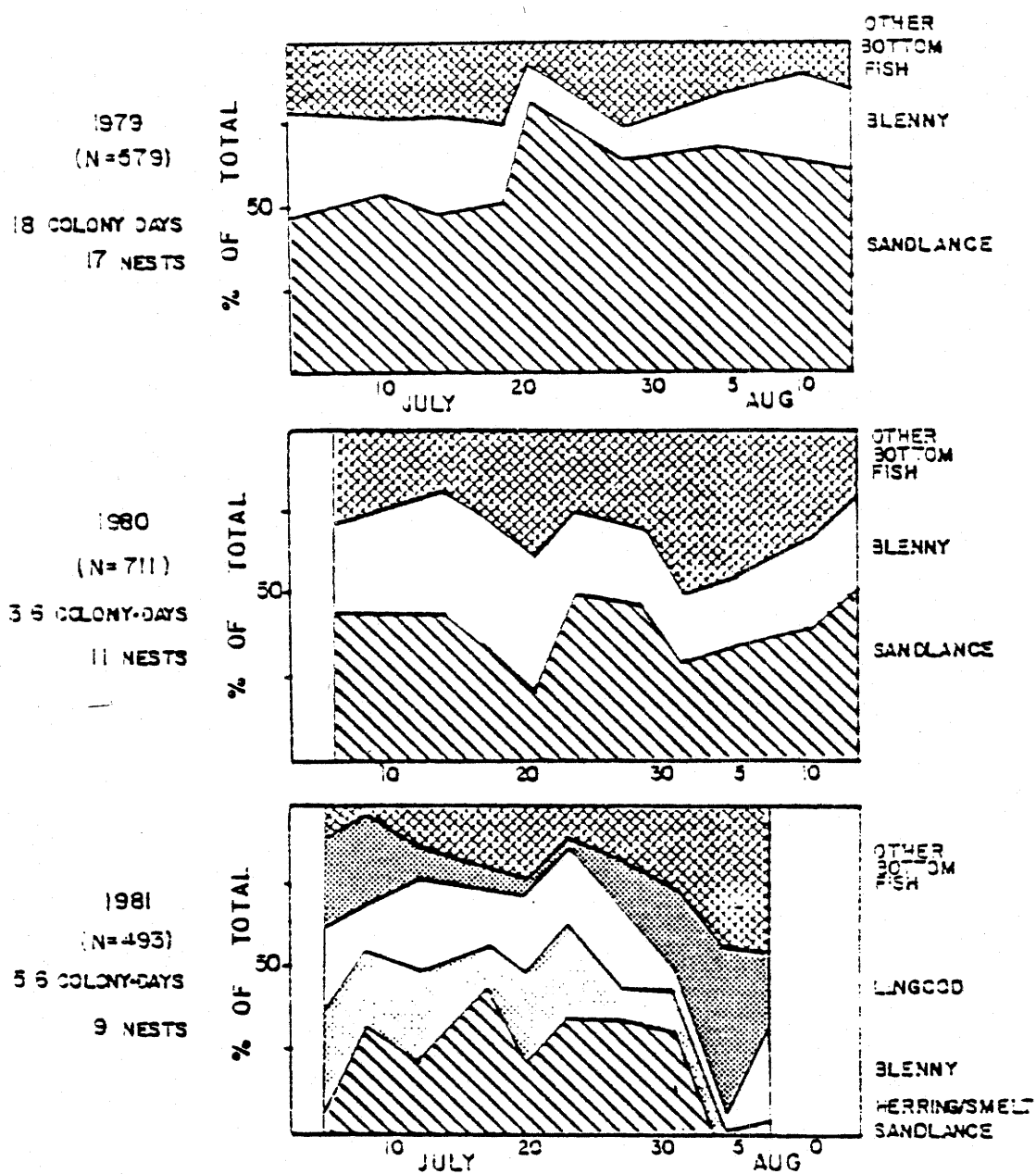


Figure 5. Seasonal prey fluctuations for 1979-1981, based on pigeon guillemot prey returns.

**Table 3.** Prey returns of major fish groups given as percentages of the total returns for each nest. Values less than expected (-) and more than expected (+) were based on the number of fish observed for the nest, compared to expected values derived from the total prey returns of all birds for the given year, with a Chi-square test for significance.

Year	Nest	No. Fish	Percent of nest total				Other bottom fish	Lingcod
			Schooling fish	Blenny	Sculpin			
1979	1	48	(-) 6***	(*) 50***	(+) 37***		7	
	2	36	35	28	14	(+) 23***		
	3	47	72	15	13	0		
	4	57	(+) 74*	20	6	(-) 0*		
	5	40	50	13	20	(+) 17*		
	6	38	71	16	13	0		
	7	42	(+) 69*	26	5	0		
	8	24	87	9	4	0		
	9	27	48	30	15	7		
	10	38	(+) 82*	(-) 3**	15	0		
	11	22	(+) 95**	(-) 0*	5	0		
	12	36	64	(+) 30*	3	3		
	13	34	64	36	0	0		
	14	42	(-) 31**	(-) 2**	(+) 48**	(+) 19***		
1980	1	49	(+) 88***	(-) 5***	5	(-) 2**		
	2	49	(+) 68**	25	2	5		
	3	58	27	(+) 63***	4	6		
	4	60	(+) 57*	41	(-) 0**	(-) 2**		
	5	132	(+) 59**	27	8	(-) 6**		
	6	47	(-) 10**	26	(+) 51***	13		
	7	100	(-) 24*	(-) 13***	(+) 21**	(+) 42***		
	8	59	(-) 17***	24	15	(+) 44***		
	9	163	31	(+) 47***	6	16		
	10	61	(-) 16**	56	14	14		
1981	1	66	30	(+) 40**	5	5	20	
	2	92	(+) 94***	(-) 4***	(-) 0**	(-) 0*	(-) 2**	
	3	67	(-) 8***	(+) 55***	16	5	16	
	4	64	(-) 14***	25	17	(+) 19**	25	
	5	76	53	18	(-) 3*	10	16	
	6	30	(+) 83**	7	0	0	10	
	7	51	(-) 13**	19	(+) 28**	14	26	
	8	45	41	21	12	17	9	
	9	57	40	20	(+) 36***	2	2	

\*p<.05, \*\*p<.025, \*\*\*p<.001

three pairs bred in 1981, but it failed to hatch chicks. For five individuals with more than one year of observation (N=11 bird-years), there were two changes, one of which accompanied a change in forage site. In both cases the schooling fish preference displayed in 1979 and 1980 became a bottom fish preference in 1981. In summary, both prey preference and forage site fidelity were usually consistent within a year and between years. The prey returns of some birds within a year suggest that changes in prey may be more common than changes in forage site.

When sandlance were an important part of the season's returns for any one pair or marked individual, diet breadth was low, with a Shannon-Wiener diversity index of less than .447 in 1979 and 1980 (Fig. 6). In contrast, the diet breadth of individuals and pairs using bottom fish was relatively high, ranging from .504 to .813. However, in 1981 birds using sandlance had diet breadths similar to birds using bottom fish, in part due to the inclusion of herring and smelt. The average diet diversity of individuals was significantly higher in 1981 than 1979 (t-test;  $t=2.53$ ,  $p<.05$ ). As a result, in 1981 there was actually less variability between individuals in terms of diet breadth, since no birds were displaying the degree of specialization that had distinguished the sandlance specialists in 1979 and 1980.

The higher prey diversity of birds using bottom fish occurred despite forage site fidelity. In comparison, birds preying on sandlance rarely returned with other species from their primary



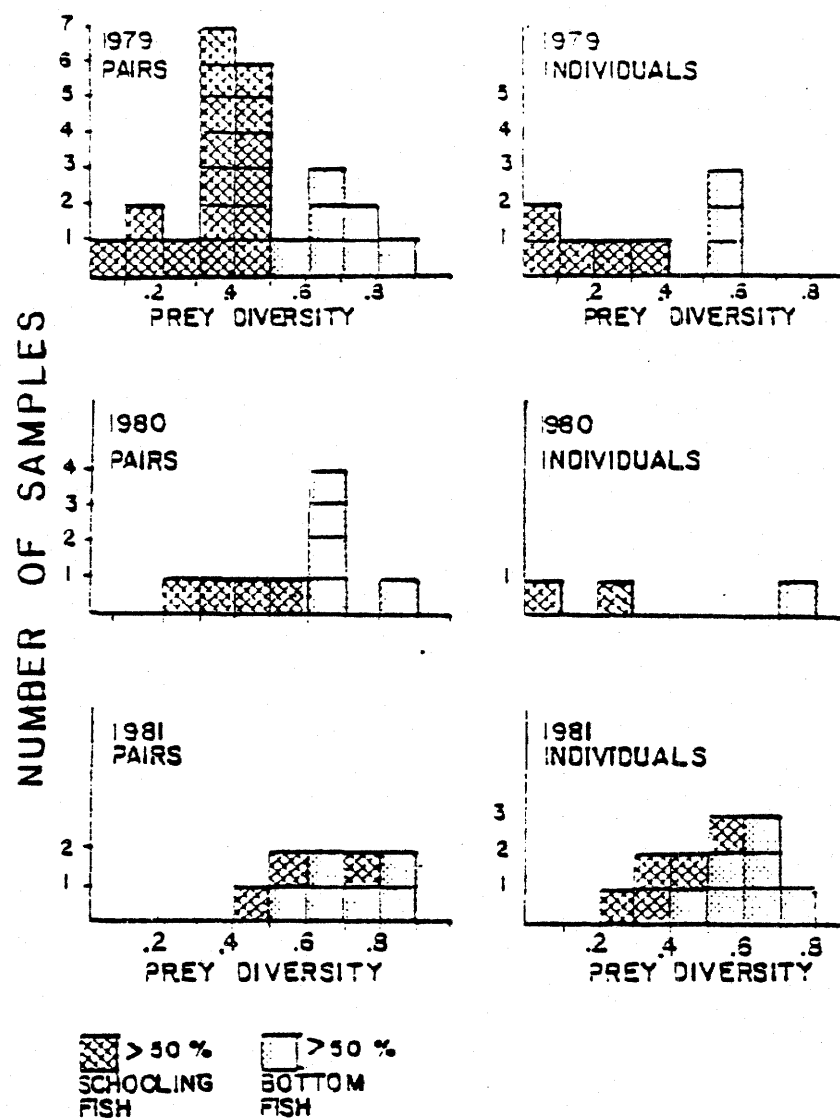


Figure 6. Prey diversity of pairs and individual birds provisioning chicks, using Shannon-Wiener diversity index. In the left-hand series, each square represents the total returns of a pair. In the right-hand series, each square represents the total returns of a marked individual which could be identified throughout the season.

site, except in 1981 when they also returned herring and smelt. That year, individuals with higher than expected frequencies of sandlance (based on total prey returns of the population) also had higher frequencies of herring and smelt, whereas birds with lower than expected frequencies of sandlance had low frequencies of herring and smelt (Table 4; Sign test;  $r=.64$ ,  $p<.01$ ). Thus despite their higher prey diversity, bottom feeders did not use herring and smelt in 1981 to the same extent that birds feeding on sandlance did.

For birds concentrating on bottom fish, the degree of specialization may depend on the species most commonly used, since some bottom fish had higher frequencies of sequential returns by the same bird than others (Fig. 7A). In addition, a bottom feeder's total returns on any one day emphasized a particular species and showed a positive correlation between degree of specialization and number of fish returned (Fig. 7B). On a short term basis, this supports the hypothesis of a search image mechanism, or might result from the discovery of single-species patches of prey.

### 3. Estimation of Prey Distributions

Preferential use of different habitats between birds of Row and Nomad colonies corresponded to their trends in prey use, even though they are only 1 km apart (Table 5). In 1980 birds from Row foraged more often in nearshore shallow waters ( $p<.001$ ) and had

**Table 4.** Sign test on the sandlance and herring/smelt returns for individual birds in 1981. Deviations below expected frequencies (-) and above expected (+) are compared for each bird. Expected frequencies were based on the total guillemot prey returns of 1981.

Bird	No. of		No. of		Direction from expected	
	<u>sandlance</u>	<u>expected</u>	<u>herring/smelt</u>	<u>expected</u>	<u>sandlance</u>	<u>herring/smelt</u>
1.	0	9.5	1	5.1	-	-
2.	2	7.0	3	3.9	-	-
3.	1	6.7	2	3.6	-	-
4.	15	10.9	10	5.9	+	+
5.	15	8.0	6	4.3	+	+
6.	24	12.6	11	6.8	+	+
7.	44	17.5	3	9.5	+	-
8.	0	5.6	2	3.0	-	-
9.	0	7.7	1	4.2	-	-
10.	0	7.7	2	4.2	-	-
11.	0	9.1	14	4.9	-	+

$$r_n = 0.64, p < .01$$

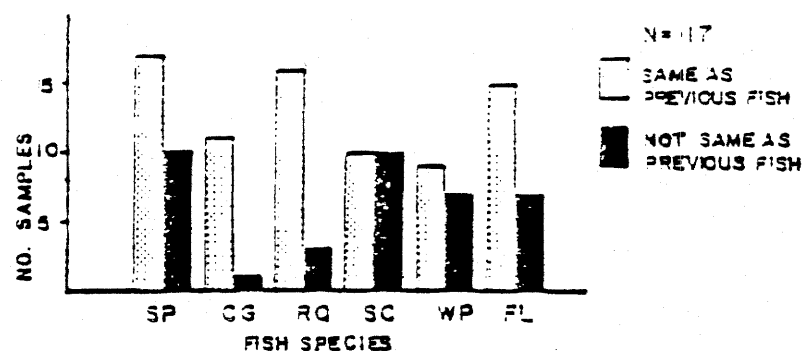


Figure 7A. Consecutive deliveries by the same bird for snake prickleback (SP), crescent gunnel (CG), Ronquil (RQ), sculpin (SC), walleye pollock (WP) and flatfish (FL).

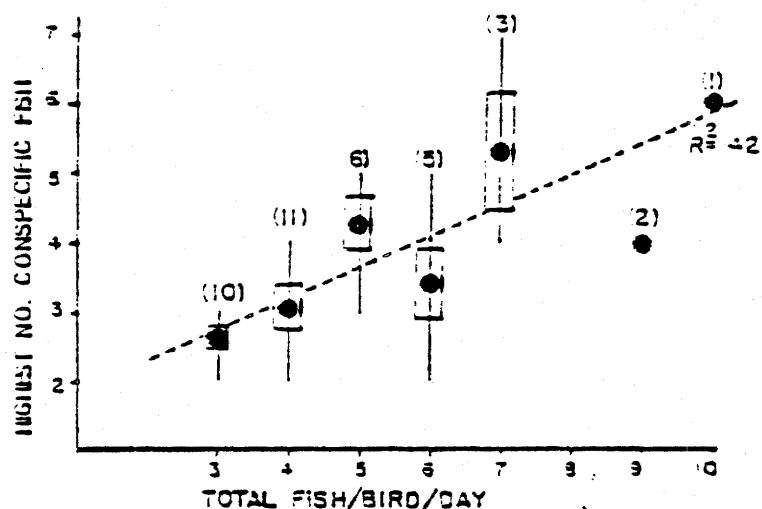


Figure 7B. Highest number of similar fish for all deliveries by a single bird on a given day. Data taken from birds preying on bottom fish.

higher sandlance returns than Nomad birds ( $p < .001$ ). More specifically, prey zonation by water depth is evident in the prey returns from known forage sites pooled in 1980 and 1981 (Fig. 8). Although sandlance did not dominate the returns from nearshore waters in 1981 as much as they did in 1980, the low number of offshore returns in 1981 made it necessary to pool the years for an accurate assessment of relative fish returns for those water depths. Sandlance and crescent gunnel (Pholis laeta) were usually returned from nearshore waters of  $< 15$  m; flatfish and lingcod from areas of intermediate depth; sculpin from intermediate and deeper areas; ronquil, cod and snake prickleback (Lumpenus sagitta) from water  $> 23$  m deep. Consequently, there was a greater diversity of prey returned from shelf and offshore areas compared to nearshore.

The birds' prey returns do not necessarily reflect the actual distribution of the fish. For example, the increase in bottom fish returns from nearshore waters in 1981 suggests that they were likely present in those waters in previous years but were not being taken by many birds when sandlance were abundant. In addition, snake pricklebacks and ronquils were primarily returned from offshore sites by the birds, but trap captures verified their presence in the intertidal and shallow water zones. Fish trapping efforts were not systematic enough for inferences on abundance and may have attracted only certain species, but results roughly correspond to guillemot prey use (Table 6). Blennies (primarily crescent gunnel and snake prickleback) were frequent trap cap-

Table 5. Forage site and prey returns for 10 nests in 1980.

A. Identified fish returns from known foraging locations

	<u>Water Depth</u>		
	<15 m	>15 m	
Sandlance	132	4	$N = 308$ $\chi^2 = 149.54$ $df = 1$ $p < .001$
Bottom Fish	48	124	

B. Colony use at known foraging locations

	<u>Water Depth</u>		
	<15 m	>15 m	
Nomad Birds	69	141	$N = 369$ $\chi^2 = 50.8$ $df = 1$ $p < .001$
Row Birds	121	38	

C. Total fish returns

	<u>Bottom</u>		
	Fish	Sandlance	
Nomad Birds	258	93	$N = 659$ $\chi^2 = 21.79$ $df = 1$ $p < .001$
Row Birds	135	173	

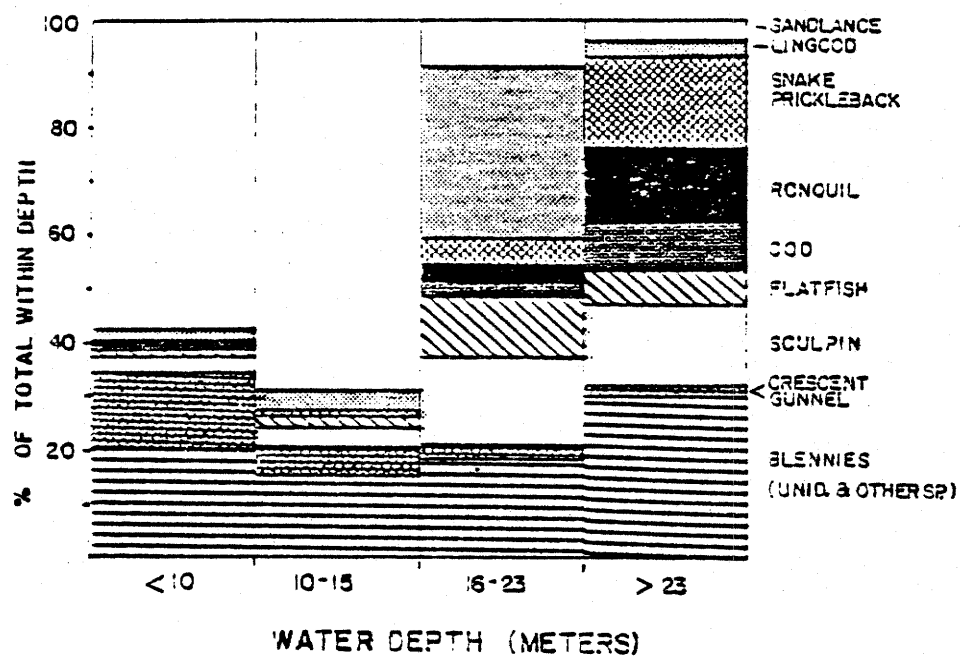


Figure 8. Distribution of prey returns (1980 and 1981 combined) relative to water depth of the birds' forage sites.

tures, followed by sculpin, ronquils and pacific tomcod (Microgadus proximus). By far the most abundant catch were shrimp (Appendix D), which were rarely returned to chicks by a few birds which normally returned bottom fish. However, shrimp were found in adults collected at Naked Island and may be important in the adult diet (Eldridge and Kuletz 1980).

#### 4. Prey Selection Within Habitats

The results of the two-way heterogeneity-G test (Table 7) for prey returns of birds using the same domain (ie., Nearshore, Shelf or Offshore) indicate there was differential prey selection between individual birds. However, the pooled prey returns often showed a significant trend toward one type of prey within a given domain. In all three years, prey returns from the Nearshore domain were proportionately higher in schooling fish than in bottom fish ( $p < .001$ ). The Shelf domain also yielded significantly more schooling fish in 1979 than other types of fish ( $p < .001$ ) but there was a reverse, non-significant trend in 1980 and 1981. In 1980, returns from the Offshore domain were significantly greater for blenny and other bottom fish ( $p < .001$ ), and the same trend, but non-significant, occurred in 1979.

Total heterogeneity for two of three forage zones (bays and coves) analyzed also indicated significant differences between birds, although like the domains, pooled returns showed a trend toward one prey type. On a finer scale, testing the prey choice of different birds at the same quadrat was restricted by the low



Table 6. Numbers and relative values of fish trap captures compared to yearly guillemot prey returns for those groups caught in traps.

	<u>Blenny</u>		<u>Sculpin</u>		<u>Ronquil</u>		<u>Tomcod</u>
<u>Traps</u> (1979-1981)	70	>	15	>	5	=	5
<u>Guillemots</u>							
1979	120	>	87	>	9	≥	7
1980	175	>	70	>	35	>	8
1981	114	>	76	>	8	≥	7

**Table 7.** Results of Two-way Heterogeneity-G test for identified birds and their prey returns from known foraging locations. Prey categories were Schooling Fish (SF), Blenny (BL) and other Bottom Fish (BF). The G-Pooled tests for heterogeneity of prey returns for all birds combined,  $G_H$  compares the prey returns of different birds using similar habitats.

YEAR	FORAGE LOCATION	NO. BIRDS	TOTAL RETURNS	NO.			G-POOLED	G <sub>H</sub>
				SF	BL	BF		

---

Domains

1979	Nearshore	10	46	36	5	5	39.04***	32.5**
	Shelf	9	45	27	11	7	14.25***	49.98***
	Offshore	10	33	14	14	9	1.23	36.08*
1980	Nearshore	8	154	119	29	6	141.20***	33.80**
	Shelf	8	35	6	16	13	4.94	18.84
	Offshore	7	94	3	45	46	53.82***	43.92***
1981	Nearshore	10	110	61	13	36	47.31***	129.42***
	Shelf	8	50	9	14	28	4.47	37.19**
	Offshore	Insufficient returns						

-

Forage Zones

1979	BD Bay	4	22	5	9	8	1.25	12.16
1980	Row Cove	5	60	40	17	3	38.54***	22.23**
1981	Row Cove	7	88	46	19	23	32.84***	96.75***
1980	Nomad Cove	4	70	46	20	4	42.17***	13.76*
1981	Nomad Cove	8	49	28	3	18	36.75***	56.23***

\* .025 < p < .05

\*\* .005 < p < .01

\*\*\* p < .001

number of identified prey returns outside a bird's primary forage site. For quadrats with more than 10 identified prey returns from three or more birds ( $N=6$ ), I compared returns of birds using their primary site with the combined returns of other birds which visited the site. Results varied, with three birds at their primary site coinciding with the prey returns of "visitors" and three showing significant deviation from the visitors.

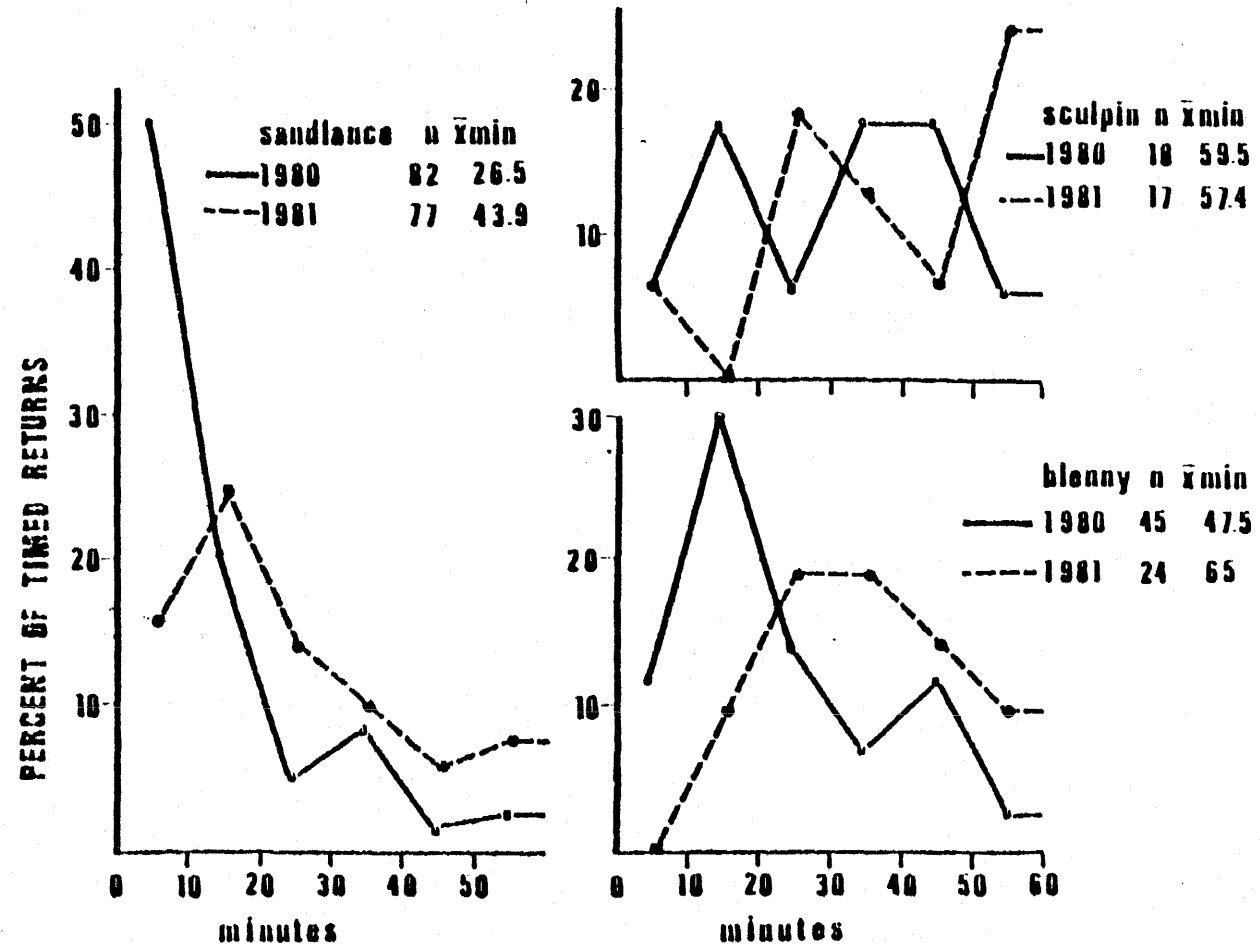
## II. Temporal Foraging Patterns and Feeding Rate

Intuitively, different prey must vary in their energetic cost and benefit to the predator. A direct measure of the energetics involved was not within the scope of this study, but estimates of predator foraging routine and efficiency were determined by: 1) the time required to obtain prey; 2) forage site distance and water depth; 3) guillemot diving patterns; 4) possible tidal influence on foraging; 5) chick feeding rate; and 6) the effect of weather on feeding rate and prey choice.

### **1. Trip Times**

The fish groups had different patterns of return frequencies (Fig. 9). In 1980 the median trip time for birds returning sandlance was the lowest ( $<10$  min), followed by blennies (11-20 min) and flatfish and ronquil (21-30 min). Sculpin showed no consistent pattern, which may reflect the variety of species and habitats they came from. All fish groups except sculpin had longer mean return times in 1981 than in 1980. For sandlance the percen-

Figure 9  
TRIP TIME DISTRIBUTIONS FOR THREE MAJOR PREY

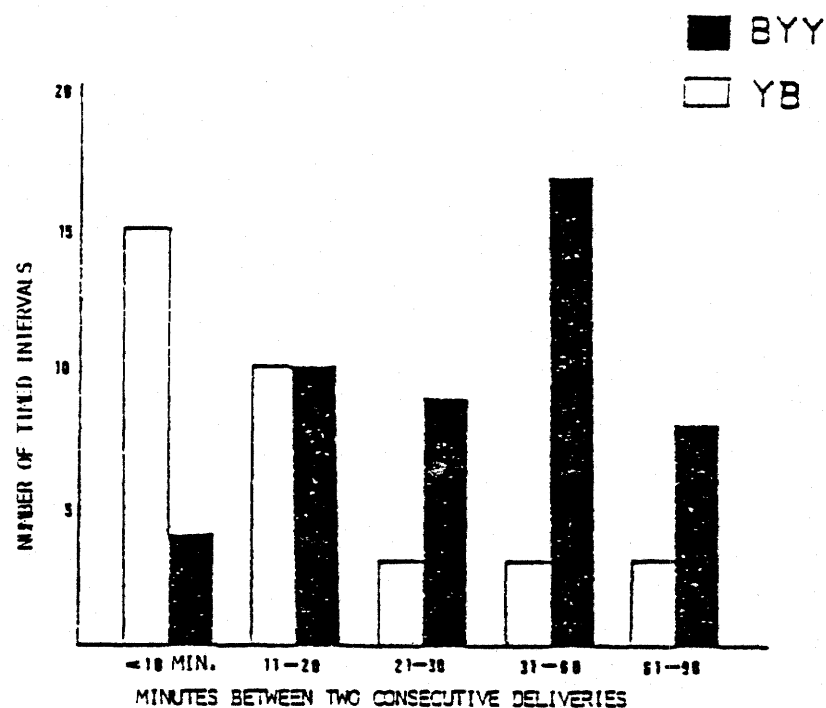


tage of returns taking less than 10 min went from 50% in 1980 to 25% in 1981. This implies a considerable decrease in abundance or accessibility. The mean time between two consecutive deliveries at the same nest was also higher in 1981 than in 1980 (t-test;  $t=2.77$ ,  $p<.02$ ).

The effect of prey choice on feeding schedules can be demonstrated by comparing two birds with distinctly different foraging behaviors (Fig. 10). Most returns by the sandlance specialist were less than 20 min apart. The bottom fish generalist usually required 20-60 min. The greater foraging distance, deeper water and diversity of prey used by the latter are all likely to have affected feeding frequency.

## 2. Forage Site Distance and Water Depth

Most of the birds foraged at distances c $\approx$  100-600 m from their colony, although a few traveled up to 2 km. The average distances to both primary and secondary forage sites were further for birds using bottom fish than for those using schooling fish. This difference was significant only for the secondary sites (t-test;  $t=2.92$ ,  $p<.02$ ). For birds preying on bottom fish, the secondary site was also significantly further from the colony than their primary site (t-test;  $t=2.48$ ,  $p<.02$ ). As expected from the habitat distributions of prey, birds concentrating on bottom fish used sites >15 m deep more often than birds concentrating on schooling fish ( $\chi^2=6.56$ ,  $p<.025$ ). Even when birds which preyed on



BIRD	% PREY						N
	SANDL	BLenny	SCULP	FLATF	COD	SQUID	
BYY	2	16	25	30	25	2	63
YB	96	4	0	0	0	0	50

Figure 10. Trip times for two banded birds (BYY and YB) in 1980, with their total 1980 prey returns.

schooling fish traveled relatively long distances, they were using nearshore sites.

### 3. Diving Observations

Diving birds were observed at two foraging areas of similar water depth but with total returns of different fish groups. Birds diving at BD Bay (Fig. 11), where the predominant prey was bottom fish, had mean underwater times of 86 sec (SE=4.4) and surface times between dives of 40 sec (SE=3.2). At Row Pt., where sandlance were commonly taken, underwater times averaged 47 sec (SE=6.9), and surface time 18 sec (SE=2.2). Birds pursuing sandlance also used a rapid series of dives less than 5 sec each just below the surface. The results indicate that first, bottom feeders require more time underwater to search out and/or capture prey. Second, longer dives are associated with longer intervals between dives, perhaps an indication of greater physiological stress. I was unable to determine the success rate per unit time.

Data were not sufficient to analyze differences in handling times, but my observations were that sandlance took less than one minute. Blennies required several minutes to subdue (up to 10 min in some cases), often with several regurgitations, prey escapes and recapture dives. Birds were occasionally observed feeding themselves between deliveries to chicks. Considering the longer pursuit and handling time of bottom fish, such self-feeding would contribute to their longer trip times.

In general, birds preying on bottom fish were expending more

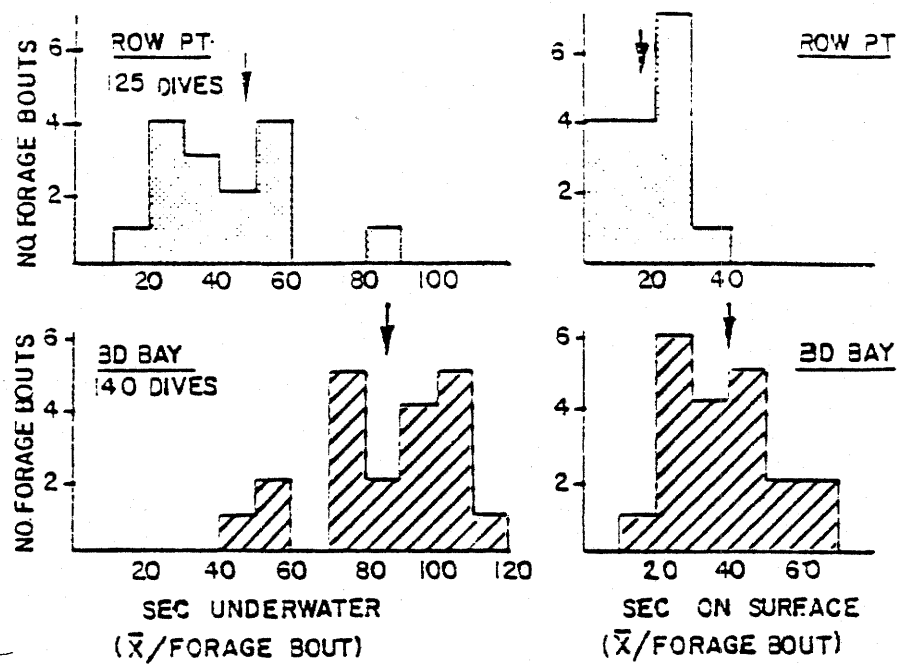


Figure 11. Guillemot diving times at two forage zones.  
Arrows indicate means.



effort per catch than birds preying on schooling fish. The compensation may be in the caloric gain per catch. There is considerable range in weight between fish species (2-40 g) and within the same species (Appendix E). Using the average species' weight from the trap captures ( $\bar{x}=15.5$ ,  $SD=15.0$ ), bottom fish were estimated to weight 1.5 times more than the average schooling fish. This difference may partly account for the profitability of using distant sites.

#### 4. Tidal Influence

To determine if birds were responding to tidal influences on prey availability, the birds' arrival times were noted relative to the hours before and after high tide. When all returns were combined there was no significant tidal correlation, although there were slightly more returns during low flood tides. However, return frequencies relative to tide were unique between fish groups and some fish showed distinct peaks at certain tidal stages (Fig. 12). Differences between fish groups may explain why Drent (1965) found no correlation between guillemot chick feeding and tides using the combined results of 11 nests.

#### 5. Feeding Rate

Feeding rates varied considerably between nesting pairs and for the same pair from day to day. Combined results for all nests from the feeding watches did not show a strongly preferred period for chick feeding, although there was a slightly higher feeding

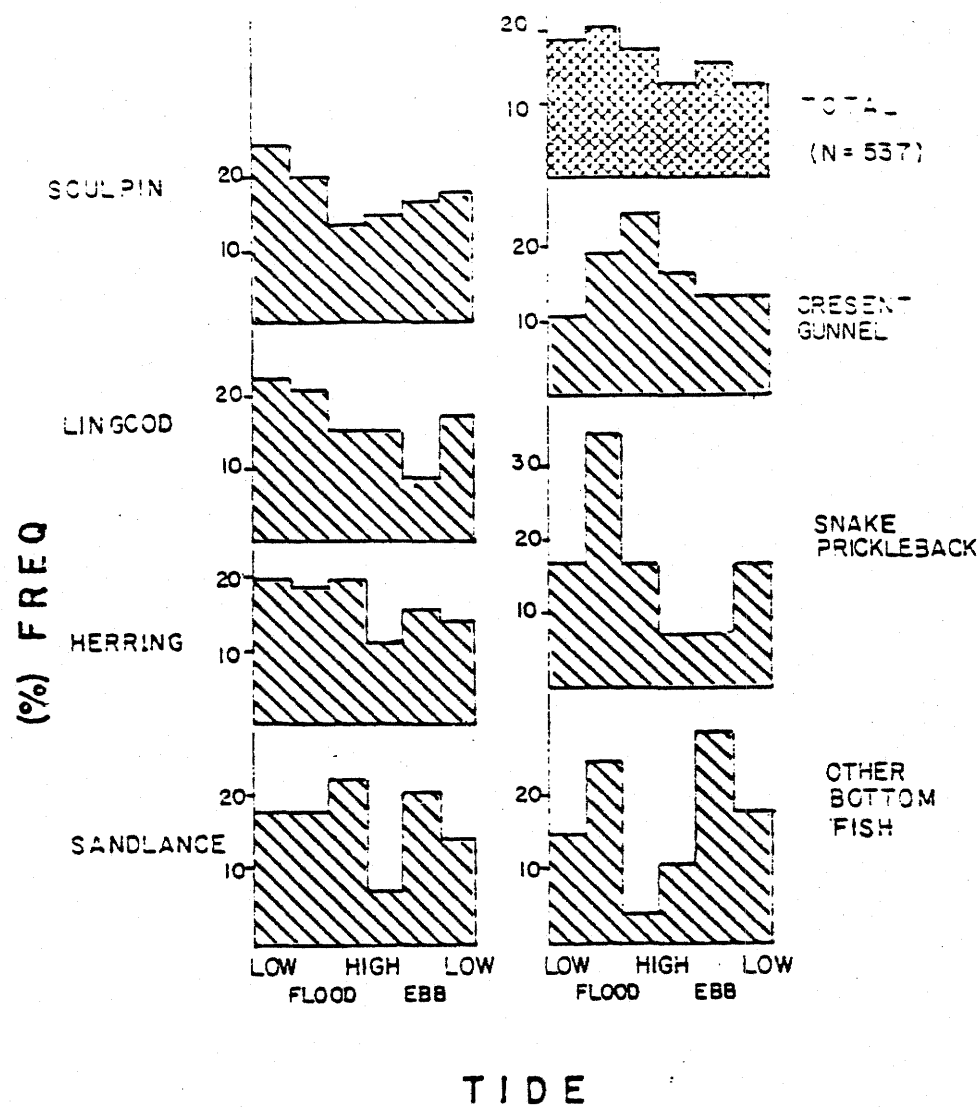


Figure 12. Deliveries of fish relative to tide.

rate during morning hours. These results are similar to those of Drent (1965), Koelink (1972) and Slater and Slater (1972). For one two-chick nest recorded with a time lapse camera, feeding gradually increased from first light to 1100 hours and continued sporadically through the afternoon until a second peak at 2000 hours (Eldridge and Kuletz 1980). These combined results from 13 days, however, mask daily variation.

Due to the brief sandlance trip times, I expected that the feeding rate (number of fish delivered per unit time) would be positively correlated with the percentage of sandlance in the returns of individuals or in daily totals. However, there was no consistent correlation on the colony, nest or individual level. The combined daily feeding rate of nests receiving more sandlance was higher than nests receiving bottom fish only in 1979. Furthermore, there was a significant decrease in feeding rate each year (ANOVA;  $F=11.94$ ,  $p<.001$ ), with no significant interaction with the diet preference of a pair ( $F=1.9$ ,  $p<.16$ ). Average daily feeding rate went from 1.06 fish/hour/nest in 1979 to 0.86 in 1980 and 0.65 in 1981.

The decline in feeding rate parallels the decrease in sandlance use, but might also have been weather related. Because of the wide variation in fish weights even within a species, I could not calculate feeding rate on a weight basis, which would have been a more important indicator of provisioning success. Even a direct measure of biomass could be misleading, since sandlance are

high in fat and protein per gram of body weight (Love 1980, Harris and Hislop 1978), whereas many bottom fish contain a large proportion of bone, fins, spines, and in some species, toxins (Gibson 1982).

## 6. Weather Effects

The increased foraging time of birds in 1981 coincided with more rain and wind that year (Appendix B). There was also an increase in the occurrence of northeast winds. Since these colonies were exposed to NE winds funnelling through Liljegren Passage, this may have contributed to the lower feeding rate. In 1981 there was a weak negative correlation between feeding rate per watch and rough seas. Simultaneously, there was a significant increase in the percentage of bottom fish returned to nests (Fig. 13;  $r=.44$ ,  $p<.02$ ). There was indirect evidence that birds preying on schooling fish were particularly affected as conditions deteriorated; two nests with previously high feeding rates of sand-lance lost chicks near fledging age during a three day storm. Other weather related mortality occurred when chicks were less than two weeks old.

## III. REPRODUCTIVE SUCCESS

The overwinter survivorship of guillemots by the breeding age of 3-4 years is high, estimated at 80-90% (Preston 1968, Asbirk 1979). Differences in foraging behavior which are not reflected in adult mortality would be of little consequence unless their

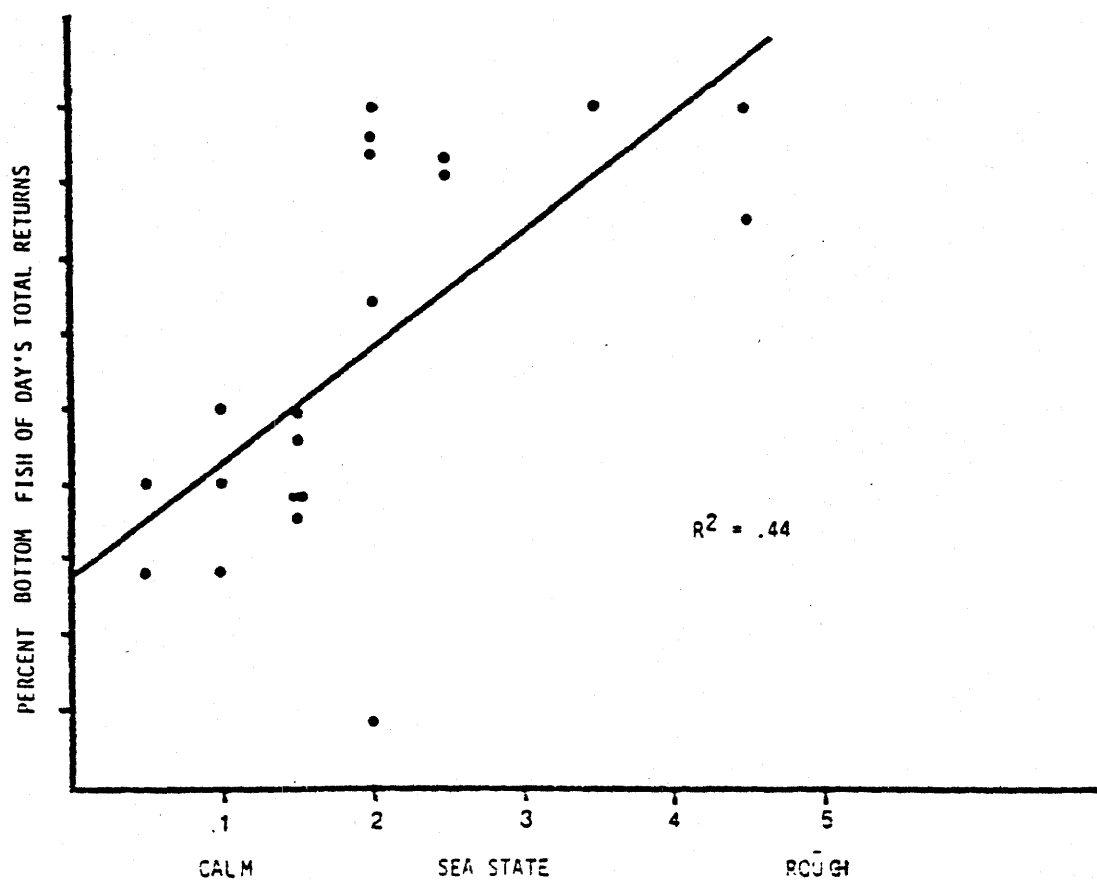


Figure 13. Daily percentage of bottom fish returns relative to sea conditions (mean of hourly rating for each day).

reproductive potential was affected. I assessed the effect of diet on reproduction by: 1) the number of nesting attempts each year; 2) the reproductive success of the population; and 3) the fledging success of pairs with respect to laying date and prey use.

### 1. Nesting Attempts

The percentage of nesting attempts relative to the maximum colony attendance varied between years (Table 8). Each colony showed more variation between years than it did with the other colonies in the same year (ANOVA;  $F=10.69$ ,  $p<.025$ ). The highest percentage of nesting birds was in 1979, when 53% of the birds made obvious nesting attempts. This dropped to 42% in 1980 and 37% in 1981. The Row colony, with the highest rate of sandlance use, had the greatest variation between years. A more conservative estimate of the stable colony population might be the average number congregated at high tide. Using these numbers, approximately 70% of the birds made nesting attempts in 1979, 55% in 1980 and 56% in 1981. It is possible that some nesting attempts went undetected, or that the 1980 tagging at Row and Nomad eliminated some potential 1981 breeders. Nonetheless, results suggest that birds at all three colonies were responding similarly to yearly fluctuations in environmental conditions.

### 2. Total Reproductive Success

Paralleling the percentage of nesting attempts, total repro-

**Table 8.** Percent of breeding birds for each colony.

Colony	1979			1980			1981			1979-1981	
	No. of Birds		Percent Nesting	No. of Birds		Percent Nesting	No. of Birds		Percent Nesting	Average % Nesting	
	Total	Nesting		Total	Nesting		Total	Nesting			
MAX Colony Count	Row	52	28	(54%)	55	22	(40%)	44	14	(32%)	42.0
	Thumb	23	12	(52%)	23	10	(43%)	22	10	(45%)	46.7
	Nomad	23	12	(52%)	23	10	(43%)	21	8	(38%)	44.3
	Year's Mean	98	52	(53%)	101	42	(42%)	87	32	(37%)	ANOVA: F=10.69 .025 <p<.01
X Daily High Tide Colony Count	Row	46	28	(61%)	50	22	(44%)	30	14	(47%)	50.1
	Thumb	16	12	(75%)	16	10	(63%)	15	10	(67%)	68.3
	Nomad	17	12	(71%)	17	10	(59%)	15	8	(53%)	61.0
	Year's Mean	70	52	(69%)	83	42	(55%)	60	32	(56%)	

ductive success (Table 9) was highest in 1979 and roughly equivalent in 1980 and 1981. There is a strong possibility that netting and tagging at the colonies in 1980 affected the reproductive results that year. The differences between years approached significance for the fledging success of nests which hatched chicks (ANOVA;  $F=3.023$ ,  $p<.06$ ). Chick growth rate and fledging weight was also higher in 1979 than in 1981 (Table 10; t-test;  $t=1.87$ ,  $p<.05$ ). Weather related mortality increased dramatically after 1979 and was highest in 1981 (27%). Chick mortality usually occurred during two or three day storms. Starvation or exposure and drowning could have been the cause, since some nest cavities showed evidence of flooding.

### 3. Fledging Success of Pairs

For 20 nests monitored more than one season the laying date of each pair was the same between years, relative to each year's mean. Drent (1965) had the same results for 13 banded female guillemots. There was no correlation between laying date and fledging success ( $x^2=.98$ ,  $p<.32$ ), but laying date did correlate with diet. Pairs with total returns of more schooling fish usually initiated nests earlier than the year's mean, whereas pairs with higher bottom fish returns tended to nest later ( $x^2=8.57$ ,  $p<.005$ ). The latter pairs also laid eggs over a wider range of dates than those using schooling fish; 19 and 15 days respectively in 1979; 32 and 26 days in 1981. In 1980 both groups had a



Table 9. Reproductive success of Naked Island pigeon guillemots.

	Mean $\pm$ SD per nest		
	1979	1980 <sup>a</sup>	1981
Clutch size	1.82 $\pm$ .39	1.73 $\pm$ .44	1.58 $\pm$ .50
No. Hatched per nest	1.36 $\pm$ .82	1.05 $\pm$ .84	1.15 $\pm$ .78
No. fledged per nest (all nests)	1.16 $\pm$ .90	0.68 $\pm$ .84	0.73 $\pm$ .78
No. fledged <sup>b</sup> per nest (with chicks)	1.48 $\pm$ .71	1.00 $\pm$ .85	1.00 $\pm$ .75
No. of nests	33	22	26
	Percent of total		
	1979	1980 <sup>a</sup>	1981
Chicks lost to non-elements <sup>c</sup>	.16	.14	.10
Chicks lost to starvation or exposure	.02	.21	.27
Hatched eggs that fledged	.82	.65	.63
Total eggs fledged	.62	.40	.46

a. Tagged birds from known nests were not included, but netting and tagging operations may have interfered with other nests.

b. ANOVA:  $F=3.0225$ ,  $p<.06$ .

c. Includes egg and chick predation and tick infestation (2 cases).

Table 10. Chick growth and fledging weights for 1979 and 1981. Due to tagging of adults in 1980, there were insufficient number of accessible chicks to include with this analysis.

		N	1979	N	1981
Growth rate (g/day)	All accessible chicks	17	18.76 $\pm$ 1.58	11	12.70 $\pm$ 2.68 <sup>a</sup>
	Chicks fed more schooling fish	6	no data	3	10.08 $\pm$ 1.96 <sup>b</sup>
	Chicks fed more bottom fish	5	no data	5	14.30 $\pm$ 1.56 <sup>b</sup>
Fledging weights (g)	All accessible chicks	17	504 $\pm$ 44 <sup>b</sup>	11	417 $\pm$ 102 <sup>c</sup>
	Chicks fed more schooling fish	6	499 $\pm$ 49	3	332 $\pm$ 68 <sup>d</sup>
	Chicks fed more bottom fish	5	495 $\pm$ 45	5	427 $\pm$ 100 <sup>d</sup>

- a. Difference between years for all nests; T-test;  $t=7.55$ ,  $p<.001$ .  
b. Difference between chicks receiving more schooling or bottom fish in 1981; T-test;  $t=3.37$ ,  $p<.01$ .  
c. Difference between years for all nests; T-test;  $t=1.87$ ,  $p<.05$ .  
d. Difference between chicks receiving more schooling or bottom fish in 1981; T-test;  $t=3.37$ ,  $p<.01$ .

nesting range of 18 days.

The low numbers of accessible nests with feeding observations made it necessary to combine three years of reproductive data to compare diet and fledging success. Disregarding brood size, success (ie, fledging at least one chick) was not significantly correlated with diet ( $\chi^2=0.98$ ,  $p<.322$ ). However, when brood size and diet were known ( $n=18$ ), pairs with high schooling fish returns fledged two chicks and those using more bottom fish fledged one chick ( $\chi^2=5.10$ ,  $p<.05$ ). In 1979, fledging weights were not correlated with diet, but in 1981 growth rates and fledging weights for three chicks fed schooling fish (Table 10) were lower than five chicks fed bottom fish (t-test;  $t=3.37$ ,  $p<.01$ ). The small sample size precludes generalizations, but does suggest that those pairs continuing to use sandlance may have been at a disadvantage during a year with apparent poor conditions for sandlance capture.

## DISCUSSION

The results of this study address three primary questions:

- 1) What mechanisms serve to maintain variation in diet within a population?
- 2) What is the relationship between diet and reproduction?
- 3) What selective pressures have influenced the evolution of foraging behavioral polymorphism in Cepphus?

### I. MECHANISMS MAINTAINING DIET VARIABILITY

Resource partitioning is commonly associated with habitat partitioning (Schoener 1974, Werner et al. 1977). The spatial distribution of individual guillemots was the most apparent mechanism responsible for the variation in diet within this population. An important aspect of guillemot foraging habitat is its three dimensionality. The vertical segregation of fish species within the water column has the potential for further dividing the resource. Ainley et al. (1981) related the diets of three co-existing cormorant species to their use of different zones of the water column. The diet of guillemots encompasses most of the prey species used by all three cormorants combined.

Guillemots fit the profile of solitary predators described by Custer and Osborn (1978) by following each other less and not shifting feeding sites as often as communal foragers. The tenacity of this behavior was evident in individual foraging movements and by the limited use of waters near the colonies,

despite the presence of fish. One outcome of solitary foraging is that individuals may not readily cue in on neighbors to take advantage of a clumped, temporarily abundant prey such as sandlance.

Site fidelity would seem to be a disadvantage for birds specializing on the more ephemeral sandlance, yet sandlance specialists did not differ from bottom feeders in this regard. However, seining surveys show specific and consistent nearshore locations of sandlance in years when they are abundant, perhaps due to local hydrology (Blackburn 1980). Thus sandlance are not entirely unpredictable spatially. When sandlance are present, schools may number in the thousands (Meyer et al. 1979). The low diversity diets of birds using primarily schooling fish is consistent with the optimal foraging theory that large or abundant patches should be used in a more specialized way than smaller patches (MacArthur and Pianka 1966, Emlen 1966).

An obvious advantage to site fidelity is familiarity with microhabitats and patterns of prey movement. Sealy (1972) suggested the circadian rhythms of alcid species in general were determined by cycles of their preferred food, and the diurnal movements of nearshore fish are largely controlled by the tide. There was some evidence for tidal influence in the return frequencies of certain fish in my study (Fig. 12). Since tidal effect varies between fish species and localities, depending on substrate, topography and exposure (Hoffman et al. 1981, Gibson

1982), birds may be responding to tidal influence on the availability of prey at preferred forage sites.

Consistent use of a forage site and encounter frequency or experience with certain prey are invariably connected, and thus their relative importance to diet is difficult to ascertain in the field. While habitat was strongly correlated with diet, it is also likely that a forage site was chosen because of its prey (Johnson 1980). The hypothesis of a search image cannot be rejected; there was differential prey selection between birds using the same or similar habitats.

One possible example of prey selectivity was the association between the use of sandlance, herring and smelt. A basic type of search image might be responsible, but could have been reinforced by surface foraging habits. In addition, juvenile sandlance and herring occasionally occur in mixed schools (Richards 1976). A second example was the tendency for bottom feeders to concentrate on certain types of bottom fish, particularly on any one day. Forage site tenacity could also promote this pattern, since benthic fish species do show zonation by water depth and small groups of conspecifics may aggregate under a rock ledge or within a patch of preferred algae (Blackburn 1980, Gibson 1982, Horn pers. comm.).

The patterns of both habitat use and prey use suggest that learning is an important mechanism determining guillemot diet. Since most birds sampled a range of prey in the course of a

season, behavioral flexibility obviously exists. The ability to alter foraging behavior between years was seen directly in a few individuals and indirectly by the increased proportions of birds utilizing bottom fish in 1981. Major diet changes within a season were even more rare. Time lags in predator response to prey fluctuations may be due to advantages of prior handling experience and habitat fixation, despite radical changes in prey abundance (Smith and Dawkins 1971, Murdoch et al. 1975, Hinrich 1979, Werner et al. 1981, Strickler 1979). The different pursuit techniques required for surface schooling fish and bottom fish may constrain behavioral flexibility. Among individual Great Tits (Parus major), Royama (1970) found a breakdown of prey into "suites" based on foraging technique. For guillemots, exposure to and thus experience with certain prey would be reinforced by selective use of available habitats.

Age and experience are recognized as important aspects of seabird foraging efficiency and breeding success (review in Buckley and Buckley 1980) and one possibility is that this is incurred through acquisition of superior forage areas (Wynne-Edwards 1962, Coulson and Dixon 1979). I only observed one aggressive encounter at a forage site; in 1981 a bird which had been breeding at least four years chased an "intruding" guillemot from its area. But agonistic and extensive social interactions are a large part of colony activity (Storer 1952, Thorensen and Booth 1958, Drent 1965, Pearson 1968, Divoky et al. 1974, Cairns 1980,

Kuletz, pers. obs.). It has been suggested that conflicts result from nest site limitation (Storer 1952, MacLean and Verbeek 1968, Divoky et al. 1974, Ainley and Lewis 1974). However, some populations show no evidence of nesting habitat restricting colony size (Asbirk 1979, Cairns 1980). At Naked Island "new" nests were initiated every year, unattended "old" nests were not appropriated and nesting boxes introduced by Oakley in 1978 were not used then or in following years. Available nest sites (by human estimates) were evident at the colonies and in the stretches of unpopulated shoreline. For this population, food availability is likely to be the current limiting factor.

Even without territoriality, some species show predilections to spacing which may function to limit over-crowding at a feeding site (Zwartz 1976, Salt and Willard 1971). At Naked Island, the distribution of foraging individuals suggests such a spacing mechanism. Earlier return to the breeding area by more experienced guillemots (Drent 1965, Preston 1968) could establish proprietorship of preferred sites without overt aggression. A study begun when the guillemots first arrive in April might elucidate the patterns already in operation during chick rearing. Considering the apparent importance of social dominance at the colony and the arrival of birds to the area at least a month before mating begins, it could prove advantageous to examine the connection between breeding status and habitat use.



## II. DIET AND REPRODUCTION

The correlation between diet and nest initiation is in accord with the seasonal patterns of the fish as described in the literature. In Prince William Sound, sandlance move inshore in early spring and successive waves of three different year-classes usually cease by mid summer, when they go offshore until a brief inshore fall migration (Rosenthal 1979). Schooling fish may remain inshore into late summer, depending on weather conditions (Rogers 1980). In contrast, bottom fish move inshore in spring and remain stable in total biomass until late fall, although the species composition changes as the season progresses (Oviatt and Nixon 1973, Rosenthal 1979). The greater range and typically later dates of nest initiation for bottom feeders, plus their higher prey diversity, may reflect the turnover of fish species. Evans (1982) concluded that the primary "evolutionary hurdle" separating 'specialist' and 'generalist' stinkbug species was the timing of reproduction. In a similar fashion, guillemot nesting asynchrony and individual consistency year-to-year constitute another mechanism fostering intrapopulation variability in diet.

Considering the range in fish weights, seasonal changes in the availability of different prey may affect the energetic gain per effort for certain habitats. The energetic constraints of provisioning chicks has important implications to colony location and diet (Lack 1968, Krebs 1974, Sealy 1972, Erwin 1978). Cairns (pers. comm.) noted black guillemots (Cepphus grylle) feeding

themselves on Arctic cod (Boreogadus saida) averaging 10 g, and transporting blennies (primarily Stichaeus punctatus) averaging 16 g the 3-4 km to the chicks. At Naked Island, sandlance averaging 8 g may have been profitable due to their nearshore availability. Most prey returned from distant sites were heavier bottom fish species, even though trap captures indicated their presence in shallow waters. Normally, foraging at outlying areas may function to partition the habitat, and the use of distant sites would require higher rewards per delivery. Although sandlance apparently were not as available nearshore in 1981 as in previous years, inclement weather could have resulted in more foraging near the colonies due to difficult foraging conditions or the effort of transporting food in heavy wind or rain. Slater and Slater (1972) gave evidence that birds had difficulty delivering food during high winds.

The relative effort required for prey acquisition is an indirect measure of the benefits of different prey. Sandlance appear to "cost" less than the other fish, as evidenced by the shorter trip times needed to obtain them. Slater and Slater (1972) also noted that guillemots using sandlance fished closer to the colony and had quicker return times. Besides occupying nearshore shallow waters, the large schools may promote predator efficiency by increased encounter rates and decreased handling time (Oaten and Murdoch 1975, Pyke et al. 1977).

A direct measure of the relative values of different diets is

reproductive success. At Naked Island, differences in sandlance availability over three years corresponded to more nesting attempts, higher fledging success and heavier fledging weights for the population. Compared to guillemot populations using predominately blenny and sculpin, when sandlance were available Naked Island chicks had significantly higher growth rates and fledgings weights in 1978 and 1979 (Oakley and Kuletz 1979, Kuletz 1980). Enhanced reproductive success with sandlance availability has been noted for other seabird species (Pearson 1968, Harris and Hislop 1978, Hunt et al. 1980, Vermeer 1979, 1980).

From these results, it would seem advantageous for all birds to utilize sandlance when they are available. Since guillemots must double their catch rate when raising chicks (Koelink 1972), taking the most immediately profitable prey could be one key to reproductive success. Large sandlance schools were clearly evident near all colonies in 1979 and 1980, yet many birds persisted in making long foraging excursions for bottom fish. Presumably there are selective advantages to maintaining such behavioral patterns.

### III. SELECTION FOR INTRAPOPULATION VARIABILITY

Habitat, experience and weather appear to influence diet, but what originally determines preferences? Heritable traits (ie., body size, wing length, bill size) may orient an individual toward the prey most often available to its population. Since guillemots, like many seabirds, show philopatry (Storer 1952, Preston

1968, Ashmole 1971, Kuletz, unpubl. data), local adaptations in this "generalist" genus may account for its many races and subspecies compared to other alcid genera (Storer 1952). However, in an environment with frequent fluctuations relative to the lifetime of the individual, genetic pre-conditioning could be less advantageous than some degree of behavioral flexibility.

The extent of genetic fixation or early exposure in determining foraging behavior in Cepphus was not within the scope of this study. However, the relatively low number of birds which changed their primary prey preference between years suggests that there are limitations to individual adaptability. Certainly the variability exhibited by the population was much greater than that displayed by any one individual.

Behavioral polymorphism in foraging has evolutionary advantages for the species and population. First, it maximizes resource partitioning in an environment of relatively low productivity and with a highly diverse resource base undergoing seasonal fluctuations. The small widely dispersed nature of guillemot colonies typical throughout most of its range is consistent with the distribution of the epibenthic prey commonly utilized. Second, with individuals depending on different resources the risk of drastic breeding failure for the population are reduced. There are guillemot colonies which do not exhibit extensive foraging variation and the consequences are similar to what occurs with other seabirds. A black guillemot colony in

Finland which depended almost entirely on Zoarces viviparus had nearly total breeding failure during a year when that prey was unavailable (Bergman 1971).

One explanation for the limited use of sandlance by roughly half of the population may be the unpredictability of these fish. Sandlance have shown yearly fluctuations of several orders of magnitude, perhaps due to marine conditions affecting the supply of copepods (Meyer et al. 1979, Blackburn 1980, Rosenthal 1979). Many seabird studies also attest to their year-to-year variability (Nettleship 1972, Erwin 1978, Hedgren 1979, Hunt et al. 1980, Vermeer 1980). Even if abundance is high, schooling fish may not move inshore during inclement weather (Dunn 1973, Rogers 1979). Vermeer (1980) and Potts (1969) noted low sandlance availability during seasons characterized by rough seas, extreme rains and low water temperature, all of which prevailed at Naked Island in 1981.

Weather can directly affect the foraging abilities of birds. The results of this study agree with others showing reduced feeding rates for alcids during high winds and rough seas (Baily and Davenport 1972, Slater and Slater 1972, Birkhead 1976). A possible advantage to diving deeper for bottom fish is the stratification of nearshore turbid waters. In a survey of subtidal benthic fish (Peden and Wilson 1976), divers noted a distinct halocline during inclement weather. Depending on location and severity of disturbance, the cline varied between depths of 7 and

12 m, with opaque surface waters and clear waters below. The divers noted an improved ability to locate fish below this visual barrier and guillemots might be similarly influenced in their ability to locate and pursue prey. There was indirect evidence of such an effect in the increased percentage of bottom fish returns on days with rough seas (see Fig. 13).

High resource variance can offset the advantages of high abundance (Real et al. 1982), which would be particularly important when stable chick provisioning is required (Krebs 1974). In this sense, birds concentrating on schooling fish could be considered "risk sensitive" and those maintaining a bottom fish diet "risk averse" (see Caraco et al. 1980).

The present data from Naked-Island are insufficient to test long-term reproductive success of individuals, but it is possible to calculate the combined breeding success (ie, fledging at least one chick) from 1978 to 1981. Nests with several years breeding data but only one with feeding observations were assumed to have been basically consistent in prey use. Every known nest was considered a potential success, whether or not the pair made an attempt that year (excluding tagged birds and new nests). The results (Table 11) show that pairs which used more bottom fish were fairly consistent, with 42-58% of the potential nests fledging young each year. The yearly success of pairs with higher schooling fish returns fluctuated from 29-80%. When all four years are combined, the latter group has marginally higher success

**Table 11.** Percentage of successful pairs from potential nesting pairs for nests with chick feeding data at Naked Island, Alaska.

Year	No. of Nests	<u>Majority of prey returns for pair</u>	
		Surface Schooling Fish	Bottom Fish
1978	potential	9	4
	successful	7	2
	percent successful	(77)	(50)
1979	potential	15	12
	successful	12	7
	percent successful	(80)	(58)
1980	potential	8	12
	successful	3	6
	percent successful	(38)	(50)
1981	potential	7	12
	successful	2	5
	percent successful	(29)	(42)
1978- 1981	potential	39	40
	successful	24	20
	percent successful	(62)	(50)

(50% and 62% respectively).

Although this test over-simplifies the real situation, it supports the concept that individuals are exhibiting different "strategies" toward maximizing reproductive fitness. Equally important, the two groups are roughly equivalent over a four year span. Further support comes from the reproductive success of nests for those years when their feeding was monitored. Averaging three years showed no difference between nests using more bottom fish and those using more schooling fish, but this analysis masked between-year differences. While the nests receiving more schooling fish may have had higher success in 1979 than nests receiving bottom fish, the reverse occurred in 1981. Averaging three years equalized the success of both types of nests, as would be expected with a balanced polymorphism.

In a computer simulated model Reddingius and den Boer (1970) showed that the stability of a population increased with the number of different patch sites over which it was distributed. This is not necessarily beneficial for the individual. A pair with one or both mates using a temporarily rich resource, ie., sandlance, increases its chances of fledging two chicks instead of one. However, the advantage could be lost in years of low sandlance abundance or inclement weather if the efficient use of alternate prey depends on special skills or habitat familiarity. Over a breeding span of about ten years (Preston 1968), birds with lower but more consistent fledging success are potentially equal



in fitness. The life time reproductive success between birds with different foraging behaviors, or with access to certain types of habitat, will depend on the relative frequencies of different environmental conditions. With a tendency for individuals to be consistent and frequent changes in the relative advantages of different foraging behaviors, the variability within the population will be maintained.

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Appendix A. Sea conditions rating scale.

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- 1.....Glassy to rippled on surface
- 2.....Rippled with small wavelets ( $< .3$  m)
- 3.....Small wavelets and swell (.3-.6 m)
- 4.....Chop with some whitecaps (.6-1.0 m)
- 5.....Chop with whitecaps and swell ( $> 1$  m)

Appendix B, Weather for Naked Island in July and August, 1979-1981

	July			August			July/August Combined		
	1979	1980	1981	1979	1980	1981	1979	1980	1981
Weather (% of days)									
Clear (50% clouds)	28	32	16	24	17	12	27	27	15
Overcast (no rain)	14	32	6	17	24	0	17	29	4
Rain	55	36	77	59	59	88	56	44	81
Wind Speed (% of days)									
<5 knots	60	45	35	29	20	18	49	37	29
6-20 knots	33	42	48	41	60	47	36	48	48
>20 knots	7	13	16	29	20	35	15	15	23
Wind Direction (% of days)									
SE	50	45	16	82	33	71	62	41	35
SW	23	21	16	6	7	0	17	16	10
NW	10	28	16	6	7	6	9	20	13
NE	0	3	45	0	33	18	0	14	35
Variable	17	3	6	6	20	6	13	9	6
Rain (cm)	9.7	30.2	32.8	11.4	22.0	61.9	21.1	52.3	94.6
Temperature (C)									
Ave daily Min.	10.1	10.1	10.2	9.8	10.1	10.2	10.0	10.1	10.2
Ave daily Max.	17.6	16.9	15.0	16.0	15.9	14.2	16.8	16.4	14.5

Appendix C. Wilcoxon's signed-rank test on the daily returns of each nest or individual bird. For each day of observation, negative values (-) were given when bottom fish (B) predominated. Positive values (+) were given when schooling fish (S) predominated. Ties (=) were not included. Days were then ranked according to their magnitude of differences and negative and positive values for the season summed and tested for significance. (\* = .025 < p < .05, \*\* = .005 < p < .01, \*\*\* = p < .001).

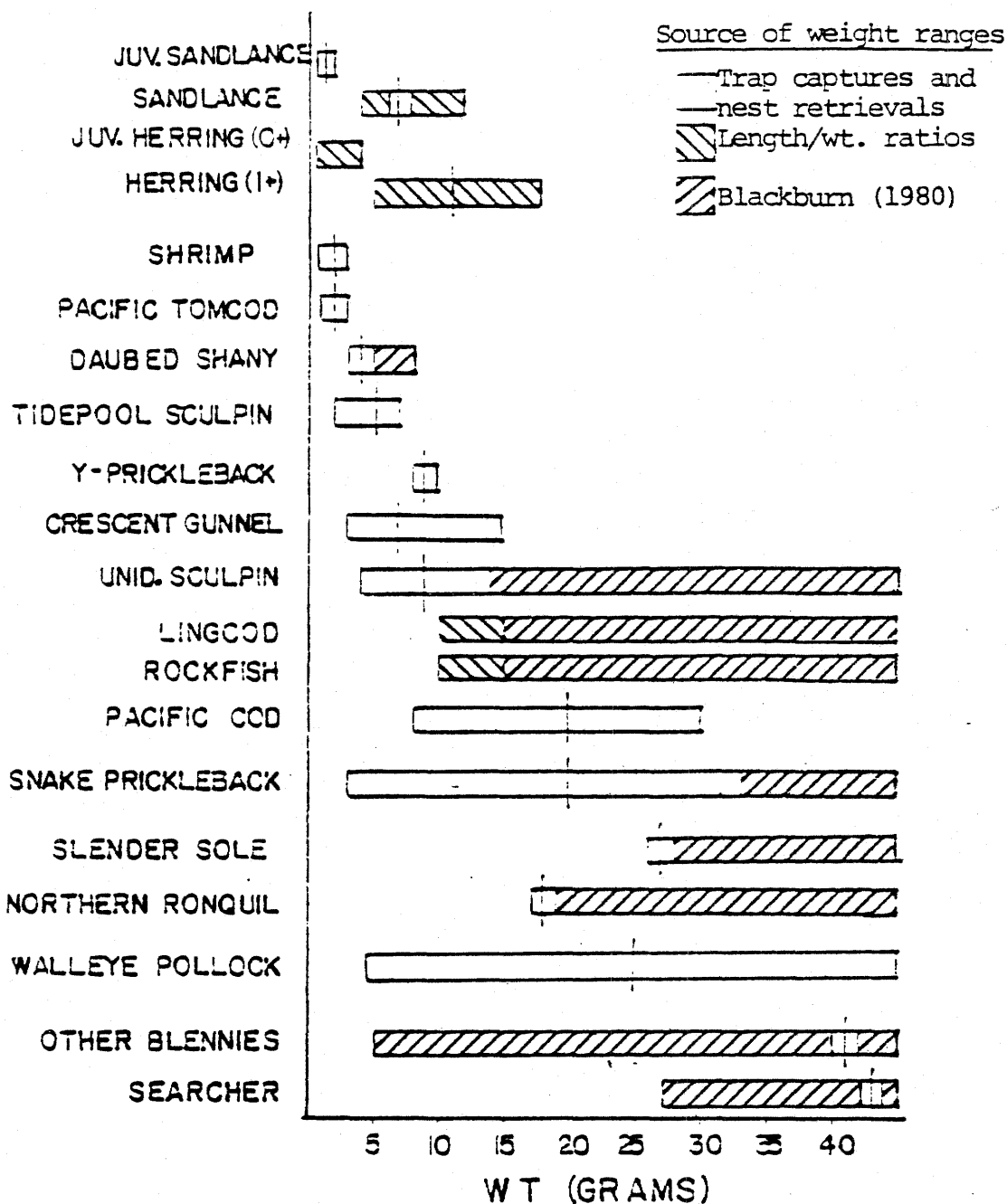
YEAR	PAIR OR BIRD	NO. OF DAYS				SUM OF		PRIMARY PREY	
		TOTAL	(-)	(+)	(=)	NEG	POS		
1979 Pairs	1	8	8	0	0	36	0	B	**
	2	6	4	1	1	13	2	B	ns
	3	6	2	3	1	11	4	B	ns
	4	8	1	7	0	2	34	S	**
	5	6	2	4	0	4	17	S	ns
	6	9	0	9	0	0	45	S	**
	7	8	5	3	0	21	16	B	ns
	8	9	0	8	1	0	36	S	**
	9	8	1	7	0	1	35	S	**
	10	7	4	1	2	13	2	B	ns
	11	8	2	5	2	2	19	S	*
	12	7	2	5	0	10	19	S	ns
	13	8	2	5	1	-	22	S	ns
1980 Pairs	1	14	12	1	1	85	6	B	**
	2	16	15	1	0	135	2	B	***
	3	14	12	2	0	94	11	B	**
	4	19	15	4	0	150	40	B	*
	5	15	12	3	0	107	13	B	**
	6	11	0	8	3	0	38	S	**
	7	12	3	7	2	14	43	S	ns
	8	11	9	0	2	47	0	B	**
	9	11	4	6	1	23	32	S	ns
1981 Pairs	1	17	11	3	3	84	22	B	*
	2	14	0	14	0	0	105	S	***
	3	20	20	0	0	210	0	B	***
	4	15	13	1	1	104	1	B	***
	5	16	6	7	3	39	48	S	ns
	6	13	2	10	1	5	73	S	**
	7	15	15	0	0	120	0	B	***
	8	14	7	4	3	37	29	B	ns
	9	10	8	1	1	41	4	B	**

## Appendix C. (continued)

YEAR	PAIR OR BIRD	NO. OF DAYS				SUM OF		PRIMARY PREY	
		TOTAL	(-)	(+)	(=)	NEG	POS		
1981 Bird	1	14	6	7	1	49	42	B	ns
	2	13	12	1	0	85	7	B	**
	3	15	15	0	0	120	0	B	***
	4	13	12	0	1	0	78	S	***
	5	14	12	0	2	0	78	S	***
	6	5	5	0	0	15	0	B	*
	7	8	6	1	1	26	2	B	*
	8	9	0	9	0	4	41	S	**
	9	10	0	9	1	0	45	S	***
	10	8	3	2	3	8	8	S	ns
	11	9	7	1	1	95	1	B	**
	12	13	11	0	2	66	0	B	***
	13	13	9	3	1	63	15	B	*
	14	10	8	0	2	36	0	B	**

Appendix D. Minnow trap captures from 1979-1981

SPECIES	No. Caught	$\bar{x}$ wt (grams)	sd	$\bar{x}$ length (mm)	sd
Pacific Tomcod ( <i>Microgadus proximus</i> )	5	2.0	-	69.0	-
Tidepool Sculpin ( <i>Oligocollus maculosus</i> )	10	5.4	3.2	84.4	13.1
Other Sculpin ( <i>Cottid</i> ssp.)	5	9.0	5.7	-	-
Northern Ronquil ( <i>Ronquilus jordani</i> )	4	17.6	-	110.0	-
Searcher ( <i>Bathymaster signatus</i> )	1	43.5	-	171.0	
Crescent Gunnel ( <i>Pholis laeta</i> )	36	6.9	2.3	134.4	14.3
Snake Prickleback ( <i>Lumpenus sagitta</i> )	30	19.8	8.9	216.2	45.5
Y-prickleback ( <i>Allolumpenus hypochromus</i> )	2	9.0	-	127.0	-
Daubed Shanny ( <i>Lumpenus maculatus</i> )	1	4.0	-	77.0	-
Penpoint Gunnel ( <i>Apodichthys flavidus</i> )	1	41.0	-	232.0	-
Shrimp:	279	2/ea			
<i>Eualus slickleyi</i>					
<i>Crangon alaskensi</i>					
<i>Pandalus hypsinotus</i>					
<i>P. danae</i>					
<i>P. platyceros</i>					



Appendix E. Weight ranges and means for fish used by Naked Island pigeon guillemots.