

Exxon Valdez Oil Spill
Restoration Project Annual Report

**THE BREEDING AND FEEDING ECOLOGY
OF PIGEON GUILLEMOTS AT NAKED ISLAND,
PRINCE WILLIAM SOUND, ALASKA**

Restoration Project 98163F
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

Gregory H. Golet

U.S. Fish and Wildlife Service
1011 E. Tudor Rd.
Anchorage, AK 99503

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Study History: The field work for APEX subproject 98163F was conducted during the summer of 1998. Previous related field work was conducted during the summer of 1995-7 as part of APEX subprojects 95163 F and 96-97163. A study of similar scope took place in 1994 as Project 94173. Previous related projects have been funded by the Trustee Council. Oakley and Kuletz (1996) undertook a study in 1989-1990 to compare various population and reproductive parameters of pigeon guillemots before (Oakley and Kuletz 1979, Kuletz 1981, 1983, Oakley 1981) and after the spill. Also, Project 93034, an extensive survey of pigeon guillemot colonies throughout Prince William Sound, was conducted during the summer of 1993 (Sanger and Cody 1994).

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DRAFT

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SEABIRD POPULATION DECLINE LINKED TO CHANGES IN PREY TYPES

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Katherine J. Kuletz*
Gregory H. Golet*
David C. Duffy †

Address correspondence to:

*Katherine J. Kuletz
U.S. Fish and Wildlife Service
1011 East Tudor Road
Anchorage, Alaska 99503
phone: (907) 786-3453
FAX: (907) 786-3641
e-mail: kathy_kuletz@mail.fws.gov

*Gregory H. Golet
U.S. Fish and Wildlife Service
1011 East Tudor Road
Anchorage, Alaska 99503
phone: (907) 786-3423

†David C. Duffy
Pacific Cooperative Studies Unit
Department of Botany
University of Hawaii Manoa
Honolulu, Hawaii 96822-2279
dduffy@hawaii.edu

Seabird population decline linked to changes in prey types

K.J. Kuletz*, G.H. Golet*, & D. Duffy†

*U.S. Fish & Wildlife Service, 1011 E. Tudor Rd., Anchorage, AK 99503, USA

†PCSU/Dept. Botany, University of Hawaii Manoa, Honolulu, HI 96822-2279, USA

Population sizes and distributions of seabirds are believed ultimately to be limited by food, but the mechanisms responsible remain unclear¹⁻⁴. Food stress may be highest when birds concentrate at colonies and feed chicks in addition to themselves²⁻⁴. The polyphagous pigeon guillemot (*Cepphus columba*) should be less subject to prey fluctuations than other seabirds^{5,7}. From 1979-1997, however, guillemot populations in Prince William Sound (PWS) fluctuated, apparently in response to changes in the relative abundance of two prey types that occupy different habitats and have differing degrees of aggregation. Demersal fishes are more predictable and constant⁶ but spatially limited, and appear to support only a limited number of guillemot pairs. The surface-schooling fishes are patchy and variable in abundance over time^{7,8}, but their use by guillemots results in high chick growth rates⁹. The decline in guillemots in PWS tracked a decline in the proportion of surface-schooling fishes in chick diets. Despite advantages to raising chicks on high-lipid schooling fish^{9,10}, those guillemots using demersal fishes now comprise the majority that breed in this area.

During 1972 to 1997, the total PWS population of pigeon guillemots declined from 15,000 to <3,500 today^{11, 12, & unpubl.}. Although the guillemot population was affected by the 1989 *Exxon Valdez* Oil Spill, the decline began prior to the spill¹¹, and its magnitude suggests a pervasive

environmental factor. To examine the reasons for this decline and subsequent lack of recovery, we examined long-term data from Naked Island, where nearly one-fourth of PWS pigeon guillemots nest. We studied population trends, foraging, productivity, and chick diet at this island for nine years.

Guillemots usually lay two eggs, forage <4 km from their nest^{13, 14}, and bring their chicks single, whole fish, which can be visually identified. In most of their range, (California to the Bering Strait), guillemots feed themselves and their chicks primarily benthic fishes¹³⁻¹⁷ such as blennies (gunnels [Pholidae] and pricklebacks [Stichaeidae]), sculpin (Cottidae), and juvenile cod and pollock (Gadidae). Although typically less common in the diet, guillemots also eat surface-schooling fishes such as Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), and smelts (*Osmeridae*)¹³⁻¹⁷.

In the years 1979-81 sand lance was the largest component of chick diet (\bar{x} = 42.1%, SD = 17.3%) at Naked Is., with decreasing percentages of sand lance in following years (Fig. 1). In the six years during 1989-90 and 1994-97, sand lance was a much smaller fraction of chick diet (\bar{x} = 14.5%, SD = 5.0%), as the use of blennies, sculpin, and gadids increased. Herring were prominent in 1981 and 1989.

The principal surface-schooling fish at Naked was sand lance and the annual percentage of sand lance in the chick diet was positively related to both the total number of guillemots at the colonies ($r = 0.66$, $P = 0.014$; Fig. 2) and to the number of active nests ($r = 0.69$, $P = 0.010$). We did not, however, find a relationship between sand lance in the diet and the proportion of birds breeding at the colonies, suggesting population decline as opposed to higher instances of

nonbreeding.

We expected annual reproductive success to be higher in years with more sand lance in the chick diet. Although overall productivity did not differ significantly among years, there have been confounding factors such as nest predation and disturbances related to the oil spill¹¹. For years where both diet and substantial numbers of chicks were measured (1989-1997), there was a positive relation between the proportion of schooling fishes brought to the nest and chick growth rate and nestling survival⁹. These direct measures of productivity reflect the higher energy densities of most pelagic fishes compared to most demersal fishes^{10, 18}, and indicate advantages to foraging on surface-schooling fishes.

Marked individuals at Naked Is. displayed prey specialization in the food delivered to chicks^{9, 14, unpublished data}. Individual adults tended to bring their chicks either surface-schooling fishes (sand lance, herring, smelt) or demersal fishes (blennies, sculpin, flatfish, cod)¹⁴. Between 1979-1981, 12 of 23 marked individuals specialized in sand lance (>50% of deliveries), whereas in 1989-1996, only 3 of 22 individuals were sand lance specialists.

Colony size is hypothesized to be determined by the abundance of food within foraging distance from the colony^{2, 4, 19}. For pigeon guillemots, which have small dispersed colonies^{5, 13}, local demersal fish abundance is likely an important limiting factor. However, a sustained influx of pelagic prey such as sand lance through the colony forage area during chick rearing could greatly increase local carrying capacity^{4, 20}. Like most seabirds, guillemots are highly tenacious in choice of breeding site¹³. For polyphagous guillemots, a numerical response at breeding colonies resulting from changes in local prey might only be evident over many years. Prey

preferences of guillemots have been associated with habitat use ^{14,21} and demersal fishes tend to show greater predictability in abundance within their preferred habitats ⁶⁻⁸. A decline in sand lance could have changed the profitability of forage habitats, thus generating an ideal-free distribution among breeding birds ²².

The mechanism for reallocation of diet preferences among guillemots feeding chicks at Naked Is. is not clear. Both the pigeon guillemot and its congener, the black guillemot (*C. grylle*), demonstrate individual specialization in prey within a season ^{9, 13,14,15,21}. Evidence for diet preferences across years is less conclusive, but the link in utilization of the nearshore pelagic sand lance, herring and smelts suggests learned foraging behaviors ¹⁴. Individuals may have difficulty switching between prey guilds, and guillemots that are demersal feeders may dominate the population now because they are successful. The present guillemot population at Naked is half what it was in 1979-1980, which is consistent with the decline in sand lance specialists among marked individuals.

Regardless of the mechanism, the influx of high-quality pelagic fishes, and of sand lance in particular, is apparently important for maintaining large colonies of guillemots in Alaska. The high proportion of sand lance use by guillemots at Naked Is. is not typical of guillemot diet throughout its range, and may partly explain the higher chick growth rates at Naked, compared to populations where chicks are fed primarily demersal fishes ⁹. We propose that the biomass of demersal fishes alone is not sufficient to support the PWS guillemot population at the numbers observed in the 1970s.

Numerous sources indicate that there has been a change in the Gulf of Alaska that began in

the late 1970s, which has probably affected marine bird populations²³⁻²⁵. In PWS, seabird diets suggest a decrease in sand lance availability, with corresponding population changes in many piscivorous birds and mammals²⁶. We demonstrate population changes in response to those ecosystem changes and suggest potential mechanisms leading to the population changes. Our data also suggest that since 1996, sand lance use has begun to increase (Fig. 1), and we will be able to determine if the guillemot population increases in the coming years.

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FIGURE CAPTIONS

Figure 1. Prey types and their relative proportions in the diet of pigeon guillemot chicks on Naked Island, Prince William Sound, Alaska in 1979-81, 1989-90 and 1994-97. Blennies included primarily Pholidae and Stichidae. Sample sizes are above bars. We used binoculars and spotting scopes to monitor guillemot chick provisioning at five sub-colonies on Naked Island. From blinds, we identified prey items to the nearest possible taxon. Prey items were periodically verified by taking delivered items from chicks and adults, and via minnow traps and beach seining.

Figure 2. Pigeon guillemot population at Naked Island, Prince William Sound, Alaska as a function of proportion of sand lance in diet of chicks. Data from 1979-1980, 1989-1990, and 1994-1997 (in 1981 there was no population census). The total population was counted by circumnavigating Naked Island during morning high tides in early June, when colony attendance was highest.

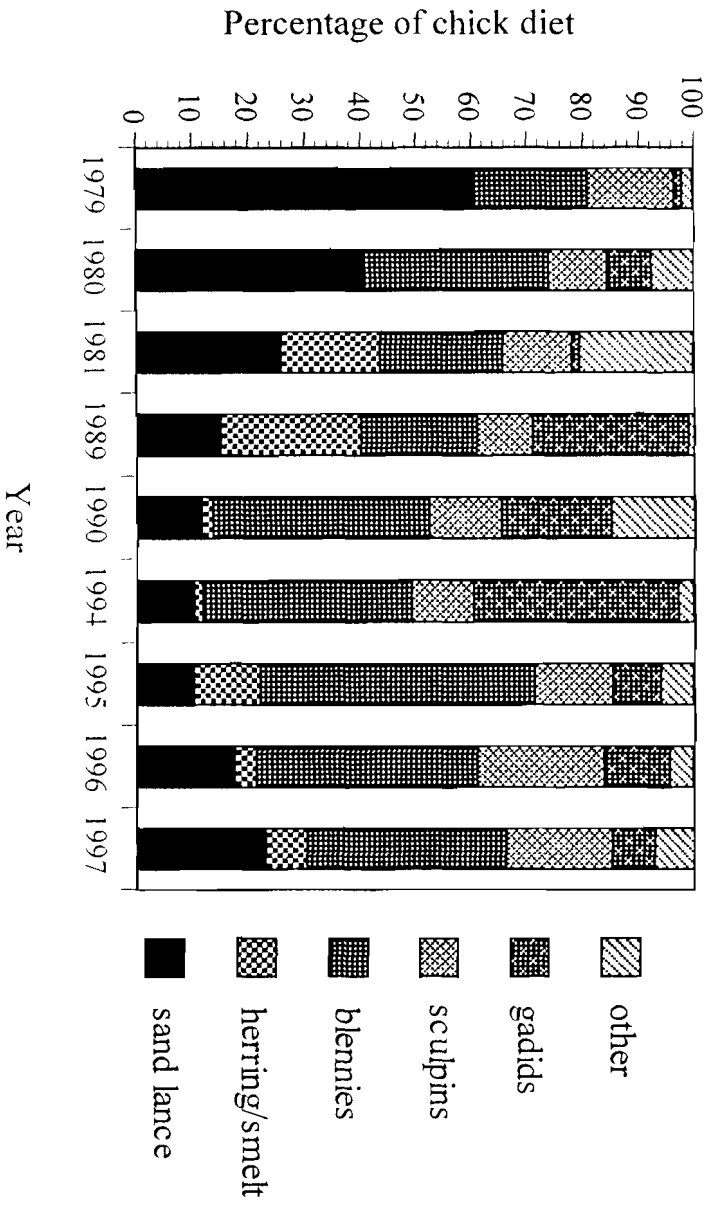
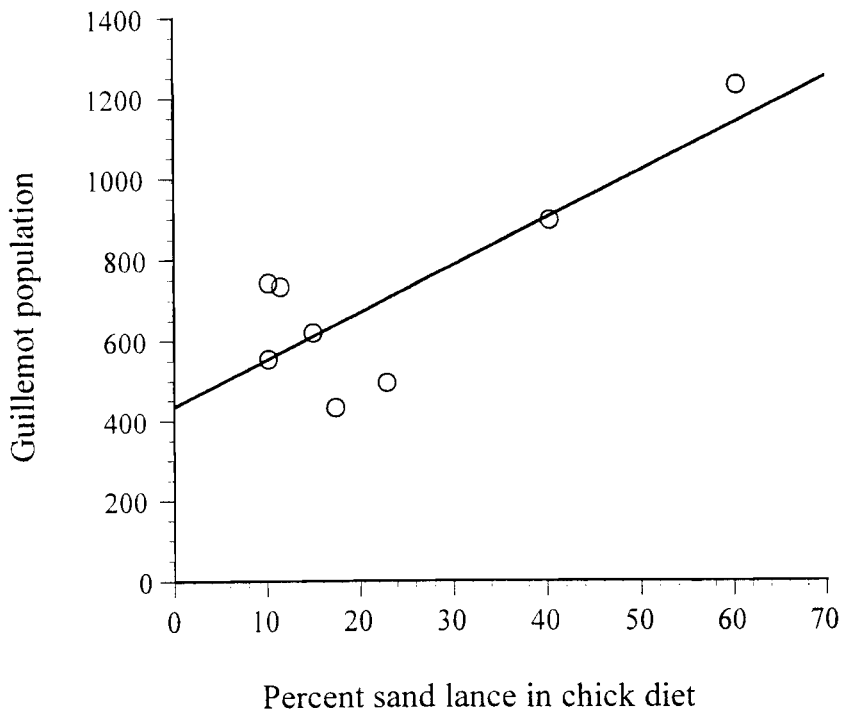


Fig. 2
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LRH: Golet et al.

RRH: *Prey Choice in Guillemots*

ADULT PREY CHOICE AFFECTS CHICK GROWTH
AND REPRODUCTIVE SUCCESS OF PIGEON GUILLEMOTS

GREGORY H. GOLET^{1,3}, KATHERINE J. KULETZ¹, DANIEL D. ROBY², AND DAVID B.
IRONS¹

¹*U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503, USA; and*

²*Oregon Cooperative Fish and Wildlife Research Unit, Biological Resources Division-U.S.G.S.
and Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331,
USA*

³E-mail: Greg_Golet@mail.fws.gov

ABSTRACT.--Pigeon Guillemots, *Cepphus columba*, are diving seabirds that forage near shore and feed their chicks both demersal and schooling fishes. During nine years between 1979 and 1997, we studied chick diet, chick growth rate, and reproductive success of Pigeon Guillemots at Naked Island, Prince William Sound, Alaska, to determine factors limiting guillemot breeding populations. We found evidence for prey specialization among guillemot breeding pairs, and detected differences in reproductive success between specialists and generalists. Pairs that specialized in particular prey types when foraging for their chicks fledged more chicks than those that generalized, apparently because they delivered larger individual prey items. Reproductive performance also varied among guillemot pairs as a function of the proportion of high-lipid schooling fishes fed to the chicks. Pairs that delivered primarily high-lipid fishes (Pacific sand lance, *Ammodytes hexapterus*, and Pacific herring, *Clupea pallasii*) attained higher overall reproductive success than pairs that delivered primarily low-lipid demersal fishes (e.g., sculpins, Cottidae spp., blennies, Stichaeidae and Pholididae spp.) and gadids (Gadidae spp.). The proportion of high-lipid fishes in the diet was positively related to chick growth, suggesting that piscivorous seabird chicks benefit from diets with high energy densities during early stages of development. Pigeon Guillemot chick diet showed high annual variation from 1979 to 1997, presumably because of fluctuations in abundance of Pacific sand lance, a high-lipid schooling fish. Regression analyses suggest that, at the population level, the percent occurrence of high-lipid fishes in the diet affected chick growth rate. We conclude that Pigeon Guillemots benefit by specializing when selecting prey for their chicks, and that high-lipid schooling fishes promote higher chick growth and reproductive success than low-lipid demersal fishes.

Within both marine and terrestrial populations of generalist predators, individuals have been identified that demonstrate high degrees of prey specialization (Tinbergen 1960, West 1988, Werner and Sherry 1987, Wendeln et al. 1994). Differences in patterns of prey choice between individuals within populations are of interest from an ecological standpoint because they represent alternate strategies to the general life history challenge of maximizing lifetime reproductive success. Despite this, relatively few studies have compared the reproductive performance of adults within a population that specialize on different prey types (but see Trillmich 1978, Trivelpiece et al. 1980, Pierotti and Annett 1991, Spear 1993). Much more common are studies that relate intra-annual or inter-colony differences in diet to reproductive performance (e.g. Harris and Hislop 1978, Monaghan et al. 1989, Hamer et al. 1991).

Cephus guillemots eat a wide range of prey types (Bradstreet and Brown 1985, Ewins 1993). Individuals are often highly specialized, however, with adult prey selection patterns differing markedly among conspecifics within the same breeding colony (*C. columba*: Drent 1965, Koelink 1972, Kuletz 1983, Emms and Verbeek 1991; *C. grylle*: Slater and Slater 1972, Cairns 1981, 1984). Guillemot colonies thus present valuable opportunities for studies relating foraging ecology to reproductive performance. Because adults with differing prey selection patterns are found within the same breeding colony, chick growth and reproductive success can be related to adult prey selection patterns without having to account for confounding variables present in inter-annual or inter-colony comparisons.

The guillemot foraging strategy differs from that of other piscivorous alcids. Guillemots often forage solitarily, or in small groups, and primarily select nearshore demersal fishes (e.g., sculpins Cottidae spp., blennies Stichaeidae and Pholididae spp.) for their chicks (Winn 1950,

Drent 1965, Cairns 1987a, Ewins 1993). These prey tend to be dispersed, but may be predictable in time and space (Rosenthal 1979, Cairns 1987a). In contrast, most other piscivorous alcid, (e.g., murre *Uria* spp., puffins *Fratercula* spp.) feed in foraging flocks on dense aggregations of pelagic schooling fishes (e.g., Pacific sand lance *Ammodytes hexapterus*, Capelin *Mallotus villosus*, Pacific herring *Clupea pallasii*, Gadidae spp.) (Barrett et al. 1987, Piatt 1990, Hatch and Sanger 1992). Given that many pelagic schooling fishes have higher lipid content (gadids are an exception), and consequently higher energy density, than demersal fishes (Montevecchi et al. 1984, Barrett et al. 1987, Hislop et al. 1991, Martensson et al. 1996, Van Pelt et al. 1997, Anthony and Roby 1997), it is perhaps surprising that guillemots do not prey on schooling fishes more extensively. At times high-lipid schooling fishes are available to guillemots, as instances of individual birds specializing in them demonstrate (Slater and Slater 1972, Cairns 1981, Kuletz 1983). Only rarely, however, has it been reported that guillemots exploit schooling fishes to a large degree (see Kuletz 1983).

To better understand the foraging ecology of guillemots we studied chick diet, chick growth, and reproductive success. We tested two main hypotheses, the first being that adults that are highly specialized when selecting prey items for their chicks have higher reproductive success than adults that are less specialized. This might be expected if specializing increases foraging efficiency by reducing prey handling time or enabling adults to select larger or more nutrient-rich prey (Slobodkin and Sanders 1969, Futuyma and Moreno 1988). The second hypothesis is that reproductive success varies as a function of the percent of high-lipid prey items in the chick diet. Adults that select high-lipid prey for their chicks may be expected to have higher reproductive success than those that select low-lipid prey for a number of reasons. Field

and laboratory studies of seabird nestling growth suggest that chicks fed high-lipid prey grow faster than chicks fed low-lipid prey because lipids are energy-rich (Harris and Hislop 1978, Massias and Becker 1990, Roby 1991). Because lipids tend to replace water and not protein, high-lipid prey fishes are not typically lacking in other nutrients (Harris and Hislop 1978). A further benefit of high-lipid prey for seabirds is that they generally yield higher assimilation efficiencies than low-lipid prey (Massias and Becker 1990, Brekke and Gabrielsen 1994). By investigating how prey selection habits relate to reproductive performance in Pigeon Guillemots, we gain a better understanding of the selective forces that have shaped the foraging patterns of this unique seabird.

METHODS

Study site.--We studied Pigeon Guillemots during nine years (from 1979 to 1981, 1989 to 1990, and 1994 to 1997) at Naked Island, Alaska (Fig. 1). Naked Island (ca. 3,862 ha) is located in central Prince William Sound (PWS), and is part of a three-island complex. The near shore habitat of this region is characterized by numerous bays and passages with shallow shelf habitat (<30 m) radiating about one kilometer from shore. Naked Island is forested to its 371 m summit, mostly with sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Guillemots nest semi-colonially along the island's rocky shorelines. They nest in cavities beneath tree roots overhanging crumbling cliffs, in rock crevices, or among boulders on talus slopes. From 1979 to 1997 the guillemot population at the Naked Island complex declined from 1,871 to 670 birds (Oakley and Kuletz 1996, Golet *unpublished data*). Other members of the Alcidae breeding on these islands include Marbled Murrelets (*Brachyramphus marmoratus*), Parakeet Auklets (*Cyclorhynchus psittacula*), Tufted Puffins (*Fratercula cirrhata*), and Horned

Puffins (*F. corniculata*). Populations of these species have also declined appreciably in PWS since the 1970's (Irons *unpubl. data*).

Chick diet and prey specialization.--We determined chick diet composition and delivery rates by observing prey items held crosswise in the bills of adults guillemots as they provisioned their chicks. Feeding observations were made with binoculars and spotting scopes from land-based blinds at five colonies. We watched from each blind for an average of four full days, alternating our observations among colonies to ensure that the diet of chicks aged 8 to 30 days was well documented. Because guillemots often pause on the water or on rocks in front of their nests before making deliveries to their chicks, we were usually able to identify the prey items they carried in their bills. Prey items were identified to the lowest possible taxon that we could visually distinguish, and then grouped into the six categories listed in Table 1. Lengths of prey items were estimated visually as multiples of guillemot bill lengths. Because chick diet composition was determined through observation alone, adult behavior and chick growth were not negatively affected.

Guillemot pairs were classified as generalists or one of five specialist types. We classified pairs rather than individual birds because we usually could not distinguish among mates. This classification was appropriate, however, because the reproductive parameters we studied were dependant upon both adult's prey deliveries. We included pairs in our analyses only if ≥ 10 deliveries were observed in which prey items were identified (as per Pierotti and Annett (1991)), although, on average, 29.3 (max = 148) deliveries were identified per pair. Pairs were classified as specialists (SPEC) when particular prey items or classes of prey items (as defined in Table 1) comprised $> 50\%$ of their deliveries, and as generalists (GEN) when they did

not meet this criterion. Based on these classifications we examined the distribution of specialist types among colonies and years.

To examine the effects of the proportion of high-lipid fishes in the diet on chick growth and reproductive success, we pooled specialist types according to the energy density of their prey. Sand lance specialists were grouped with herring/smelt specialists because these prey typically are energy-rich (energy densities range from 6 to 8 kJ/g fresh mass, Anthony and Roby 1997). The non-schooling fishes, the gadids (which school, but have low lipid content in the size classes that guillemots select), were combined to form the low-lipid category (energy densities typically < 5 kJ/g fresh mass, Anthony and Roby 1997). Generalists were also included in this category because they delivered only 25.3 % high-lipid fishes, on average.

Data from 1979-1981 were excluded in these analyses because there were few nests in which chick diet, nestling growth and productivity were simultaneously studied. We report diet data from these early years (see Table 1), however, because they relate to the population level effects that we describe between diet and growth rate (see Discussion).

Chick growth and reproductive success.--We determined chick growth and reproductive success at guillemot nests to examine the effects of prey choice on reproductive performance. At hatching we recorded brood size and hatching order. We marked the web of the foot of alpha (the first to hatch, or larger chick, of two-chick nests), and beta (the second to hatch, or smaller chick, of two-chick nests) chicks with a permanent pen to distinguish them from one another until they were old enough for banding. Chicks were weighed and measured at least once every five days from hatching until fledging. Growth rate was calculated as the slope of the regression of mass on age for chicks between 8 and 18 days, the linear phase of the growth cycle (Emms and

Verbeek 1991, Ewins 1993). Because this growth measure is not influenced by the particular asymptote that individual chicks attain (Hussel 1972, Gaston 1985), it has the advantage of being independent of peak and fledging mass, which we also report. We define peak mass as the highest mass measured, and fledging mass as the last mass measured prior to fledging. Peak and fledging mass have been shown to affect fledgling success and subsequent survival, and may well represent the condition of nestlings at their time of highest energetic demand (Perrins et al. 1973). Based on observations made during nest visits we determined hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid).

Statistics.--General linear models (GLMs) were used to test for effects of prey specialization and the proportion of high-lipid prey in the diet on reproductive performance. We determined the degree of specialization of guillemot pairs with the modified Hill's ratio, $F_{2,1}$ (Alatalo 1981):

$$F_{2,1} = \frac{\frac{1}{\sum_{i=1}^n p_i^2} - 1}{\exp\left(-\sum_{i=1}^n \ln p_i\right) - 1}$$

In this equation, p_i is defined as the number of prey type i delivered by the pair in a season divided by the total number of all prey types delivered by that pair in that season, and n equals the total number of prey types ($n = 6$, see Table 1). This diversity index has the advantage of not requiring an independent assessment of species richness, which is often a function of sample size (Alatalo 1981). We incorporated this diversity index as an independent variable into our GLMs

to test for effects of specialization on reproductive performance. To examine the effects of the proportion of high-lipid prey in the diet on reproductive performance we calculated a high-lipid prey index, which we also included in our GLMs. This was defined as the proportion of prey items observed delivered to each nest that were sand lance or herring/smelt. We also included "year" as a categorical random factor in all GLMs. For binomially distributed data we compared multiple logistic regression models, and tested for significance by assessing the deviance (expressed as a likelihood ratio statistic) of saturated models and models lacking particular effects (Agresti 1990, 1996). We used the Lilliefors test to assess normality with variables having continuous frequency distributions, and compared variables identified as non-parametric with the Kruskal Wallis test or the Mann Whitney *U*-test. The remainder were contrasted with ANOVAs or *t*-tests assuming equal or unequal variance as appropriate. For contingency table analyses, we used loglinear models (SYSTAT 1996), log-likelihood ratio tests (*G*-tests) (Fienberg 1970, Bishop et al. 1975), and Fisher's exact test. For *G*-tests involving only two classes, the Williams correction was applied to reduce the likelihood of type 1 errors (Sokal and Rohlf 1995). Means are presented \pm 1 SE. All tests are two-tailed.

RESULTS

Effects of specialization and high-lipid diet on reproductive performance.--Dietary diversity (degree of specialization) and proportion of high-lipid prey in the diet both affected reproductive performance of adult guillemots (Table 2). Dietary diversity was negatively related to overall productivity, suggesting that adults that specialize when selecting prey items for their chicks can raise more young than those that generalize. The difference in reproductive output

between specialists and generalists resulted largely from differences in nestling survival, suggesting that the benefits of specializing came during the later part of the nestling stage. Dietary diversity was not found to affect hatching success, chick growth rate, peak or fledge mass. Differences in nestling survival apparently resulted from differences in the size of prey items delivered to chicks, as dietary diversity was negatively related to prey size ($F_{1,79} = 4.57$, $P = 0.036$), but not prey delivery rate ($F_{1,70} = 0.09$, $P = 0.77$).

The percent of high-lipid prey items in the diet was positively related to both nestling survival and overall productivity (Fig. 2). Benefits of feeding chicks high-lipid prey fishes appeared early in the chick-rearing phase, when a significant effect was detected on chick growth rate. The growth rate difference appeared pronounced only among two-chick nests (Fig. 3). In nests with single chicks, growth did not differ according to diet. In two-chick nests, the difference was most apparent among beta chicks, although alpha chicks also had lower mean growth rates when fed mostly low-lipid fishes. Chicks fed more high-lipid fishes did not, however, attain higher peak or fledging masses than chicks fed low-lipid fishes. The higher reproductive performance found among adults that delivered more high-lipid prey apparently resulted from the differences in the nutritional status of the prey, as neither prey size ($F_{1,79} = 1.42$, $P = 0.24$), nor prey delivery rate ($F_{1,70} = 1.6$, $P = 0.22$) varied according to the percent of high-lipid prey delivered by adults.

Prey specialization patterns.--Adult guillemots demonstrated preferences when selecting prey items for their chicks. From 1989 to 1990 and 1994 to 1997, 59% of nests had a particular prey type that comprised >50% of the observed deliveries (Table 3). The actual proportion of individuals specializing was likely greater than this, however, because mates within a given nest

sometimes differed in their prey selection habits. Guillemots clearly differed in the diversity of prey items that they delivered to their chicks. In 1995 there was even a flatfish specialist ($n = 34$ identified deliveries, 62% flatfish Bothidae spp.), although this prey item comprised $< 5\%$ of the diet in the population that year. The proportion of pairs that delivered primarily high-lipid fishes did not differ significantly among the three main colony areas between 1989 and 1997 ($n = 95$ pairs, $G = 2.00$, $P = 0.59$). Thus the availability of high-lipid fishes did not appear to vary among the Naked Island guillemot colonies. We did, however, find significant variability in the relative abundances of particular specialist types from year to year ($n = 114$ identified specialists, $G = 37.9$, $P = 0.009$; Table 3). This variability appeared to be influenced by the overall abundance of particular prey items in the diet (compare Table 1 with Table 3). Because guillemots have strong nest site fidelity (Drent 1965), consistency in prey specialization may be examined by comparing prey selection patterns at individual nests over multiple years. Among nests classified as a particular specialist type in one year, 50% were classified as the same specialist type in the subsequent year. This level of consistency is substantially greater than what would be expected at random (20%). Interannual consistency appeared strongest among blenny specialists (73%) and generalists (55%).

Differences among Years.--On average $82 \pm 4\%$ of the prey items observed delivered to the chicks were identified each year. Significant variability was found among years in the items delivered ($n = 5,534$ prey deliveries, $G = 1908$, $P < 0.001$; Table 1), with schooling fishes fluctuating most in their percent occurrence. Pacific sand lance declined steadily from a high of 60% of the prey deliveries in 1979 to a low of 10% in 1994 & 1995. Variability was also high in the herring/smelt category (0 - 25%), and among the gadids (1 - 37%). In contrast, demersal

fishes, such as blennies and sculpins, remained relatively constant in the chick diet among years.

DISCUSSION

Benefits of prey specialization in guillemots.--Adults that specialized when selecting prey items for their chicks had higher reproductive success than those that generalized, apparently due to differences in foraging efficiency. This finding is important, as empirical support for a trade-off between foraging efficiency and dietary diversity has seldom been found (Leigh 1990, Cockburn 1991).

To forage efficiently, organisms must develop and maintain accurate environmental representations of prey distribution and abundance (Dall and Cuthill 1997). Such representations are always incomplete, however, because individuals are limited in terms of the time, energy, and cognitive resources that they can allocate to prey sampling (Real 1992). Moreover, for generalists, representations of particular prey are expected to be less accurate than for specialists, due to differences in prey sampling frequency (Dall and Cuthill 1997). Apparently this was the case for guillemots in our study, although the particular mechanism whereby specialization led to increased foraging efficiency deserves further explanation.

Specialists did better than generalists not because they selected more energy-rich prey (this effect was factored out in the GLM), nor because they delivered prey more frequently, but rather because they selected larger prey for their chicks. In guillemots, which deliver prey items one at a time to their chicks, it may be more advantageous to modify the size of the prey items delivered than their rate of delivery. Although both modifications may increase the rate at which energy is provisioned to the nestlings, delivering larger prey likely entails lesser increases in energy expenditure than delivering prey more frequently, since it does not require additional trips

to and from the foraging grounds. A further benefit of increasing the size of the prey delivered is that it does not necessarily increase the exposure of the nestlings to predators, as more frequent nest visitation might. The main benefit of specializing appeared to be increased nestling survival. Specialization did not affect chick growth rates, suggesting that during the early stages of nestling development prey quantity may be less important than prey quality (see below).

Patterns of prey choice in generalist predators. --Benefits of a high-lipid diet were evident early in the nestling period. Chick growth rates were positively related to the percent of high-lipid prey in the diet, and this effect was especially pronounced among beta chicks. This finding supports the prediction of Kuletz (1983), who suggested that adults that deliver primarily low-lipid fishes are less likely to fledge a second chick. High-lipid fishes may be a better food source for guillemot chicks because they tend to be more energy-rich, yield higher assimilation efficiencies (Massias and Becker 1990, Brekke and Gabrielsen 1994), and have less cartilaginous and bony parts than their low-lipid counterparts.

In other studies that demonstrated effects of diet choice on reproductive performance, the advantages of foraging on particular prey types varied. Delivery rates appeared important in several studies that attributed high reproductive success of particular groups of birds to close proximity of reliable prey. For example, South Polar (*Catharacta maccormicki*) and Brown (*C. lonnbergi*) skuas that specialized on nearby penguin eggs and chicks were more successful raising chicks than those that fed mainly at sea on fish (Trillmich 1978, Trivelpiece et al. 1980). Similarly, Western Gulls (*Larus occidentalis*) that exploited nearby Common Murres (*Uria aalge*) or Brandt's Cormorants (*Phalacrocorax penicillatus*) had higher breeding success than gulls from the same colony that foraged elsewhere (Spear 1993). Among Herring Gulls (*Larus*

argentatus), however, adults specializing in mussels had higher reproductive success than those specializing on petrels or human refuse not because of differences in energy densities or delivery rates of their prey, but instead because mussels contained a more complete complement of the nutrients required for laying viable eggs (Pierotti and Annett 1991). Thus the mechanisms by which particular prey items benefit individuals appear to vary, supporting the view of Futuyma and Moreno (1988) that there are many sources of natural selection that may favor one foraging strategy or another.

Population level effects.--At the population level the percent of high-lipid fishes in the diet also appears to have affected chick growth rates at Naked Island (Fig. 4). Chicks grew faster from 1979 to 1981, when high-lipid fishes comprised 40 to 60% of their diet, than in 1990 and 1994, when high-lipid fishes comprised only about 10% of their diet. Other studies of guillemots similarly suggest that chicks grow slowly when there are few high-lipid fishes in the diet (Fig. 4). At Mandarte Island, chick growth was 15.6 g/day (linear slope analysis of chick measurements in Drent (1965)) when *Ammodytes* (a high-lipid schooling fish) comprised 4.7% of the diet. At Mitlenatch Island, Emms and Verbeek (1991) measured a growth rate of 14.5 g/day when chicks received 4.6% *Ammodytes* and 1% *Clupea*, and at Skidegate Inlet, Vermeer et al. (1993) measured a growth rate of 15.5 g/day when *Ammodytes* comprised 10% of the chick diet (although their sample size for chick diet was small, $n = 20$). These growth measurements are comparable to the values we recorded at Naked Island when the percent of high-lipid fishes in the chick diet was lowest in nine years of study.

Studies of Black Guillemots in the North Atlantic Ocean further suggest that the proportion of high-lipid fishes in the diet affects chick growth. In Shetland, Black Guillemot

growth rates were among the highest recorded for this species (16.9 g/day) when *Ammodytes* was 52% of the chick diet (Ewins 1990, 1992). This contrasts the relatively low growth rate (14.2 g/day) measured for Black Guillemots in Hudson Bay when *Ammodytes* was < 1% of the chick diet (Cairns 1987a).

An effect of diet on reproductive performance was also found in guillemots at the Farallon Islands (Ainley et al. 1990). In cold water years, when rockfish (*Sebastes* spp.) comprised a large portion of the chick diet, fledging weights and reproductive success were higher than in warm water years when rockfish were less often fed to chicks. Although growth rates of chicks were not affected by the percent rockfish in the diet, chicks grew slowly in all years at the Farallons (16.5 g/day, $n = 6$ years), relative to what we observed at Naked Island (19.1 g/day, $n = 9$ years). Perhaps chicks grew more slowly at the Farallons because high-lipid fishes were lacking in their diet. Rockfish tend to have lower lipid content, and hence lower energy density (kJ/g wet mass) than *Ammodytes*, *Clupea*, or *Mallotus* (Van Pelt et al. 1997). Rockfish may also be less easily digested and assimilated than high-lipid fishes due to their numerous spines and thick scales (Eschmeyer and Herald 1983).

Cairns (1987b) hypothesized that among polyphagous seabirds, the availability of a principle prey item may vary considerably before changes occur in parameters such as chick growth rates. Our findings, however, suggest otherwise: In years when the proportion of high-lipid fishes was low in the chick diet, growth rates were also low (Fig. 4). Similar results were found in a 15-year study of the Great Skua (*Catharacta skua*), in Shetland (Hamer et al. 1991). Sandeels (*Ammodytes marinus*), a high-lipid fish, varied from 5 to 95% of the skua chick diet, and their use was positively correlated with chick growth rate. Apparently, for some generalist

foragers, there are no suitable replacements for high-lipid fishes in years when they are absent from the chick diet. These results suggest that chick growth may be sensitive to the percent occurrence of a principle prey item in the diet, particularly when there are pervasive differences in prey quality.

Foraging strategies of guillemots. --Our comparisons among years, and among studies, suggest that guillemot chick growth and productivity is maximized when high-lipid fishes comprise a major portion of the prey fed to chicks. Nonetheless, low-lipid fishes (e.g., blennies and sculpins) form the staple of the chick diet for most guillemot populations. These findings present an interesting question to the evolutionary ecologist: Given the apparent selective advantage of foraging on high-lipid schooling fishes, why haven't guillemots evolved (as other piscivorous alcids have) to become more highly specialized in feeding on these prey? The explanation may lie in the relative predictability of prey types. In Prince William Sound, high-lipid fishes, such as *Ammodytes*, have a distribution that is temporally and spatially variable (Blackburn 1979). Low-lipid fishes, by contrast, are predictable; they do not show marked movements during the breeding season (Rosenthal 1979). As a result, low-lipid fishes are probably easier for guillemots to specialize in than high-lipid fishes. Because there are benefits in specialization per se (e.g., increased prey size), foraging on predictable, low-lipid fishes may present a viable alternative to the more common alcid strategy of foraging on ephemeral high-lipid schooling prey.

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TABLE 1. Diet of Pigeon Guillemot chicks at Naked Island, PWS, Alaska. Values reported are percents of the identified deliveries, which averaged $81.5 \pm 3.5\%$ of the total deliveries. Prey specialization was studied from 1989-1997.

Year	<i>n</i>	Blennies ^a	Gadids ^b	Herring/smelt ^c	Sand lance ^d	Sculpins ^e	Other ^f
1979	525	20.6	1.5	0	60.4	15.4	2.1
1980	622	33.8	7.9	0	40.4	10.3	7.7
1981	431	22.3	1.4	17.6	25.8	12.3	20.7
1989	508	21.1	27.8	25.0	15.0	10.0	1.2
1990	646	38.7	19.7	2.2	11.5	13.0	15.4
1994	927	37.3	36.7	1.6	10.1	11.2	3.0
1995	689	49.3	8.7	11.8	10.2	13.9	6.1
1996	645	39.8	11.8	3.9	17.4	22.6	4.5
1997	541	35.9	7.6	7.0	22.9	19.0	7.6
mean	5,534	33.2	13.7	7.7	23.7	14.2	7.5

^acrescent gunnel *Pholis laeta*, slender eelblenny *Lumpenus fabricii*, snake prickleback *L.sagitta*, daubed shanny *L. maculatus*, black prickleback *Xiphister atropurpureus*, y-prickleback *Allolumpenus hypochromus*, high cockscomb *Anoplarchus purpureus*, penpoint gunnel *Apodichthys flavidus*, northern ronquil *Ronquilis jordani*, searcher *Bathymaster signatus*, arctic shanny *Stichaeus punctatus*, snailfish *Liparis* spp.

^bPacific cod *Gadus macrocephalus*, Pacific tomcod *Microgadus proximus*, walleye pollock *Theragra chalcogramma*.

^cPacific herring *Clupea pallasii*, smelt Osmeridae, including capelin *Mallotus villosus*.

^dPacific sand lance *Ammodytes hexapterus*.

^eribbed sculpin *Triglops pingelii*, slim sculpin *Radulimus asperllus*, tidepool sculpin *Oligocottus maculosus*, plain sculpin *Myoxocephalus jaok*, roughspine sculpin *Triglops macellus*, armorhead sculpin *Gymnocanthus galeatus*, grunt sculpin *Rhamphocottus richardsonii*, red irish lord *Hemilepidotus hemilepidotus*.

flatfish Bothidae, including rex sole *Glyptocephalus zachirus*, slender sole *Lyopsetta exilis*, dover sole *Microstomus pacificus*, rockfish *Sebastes* spp., Pacific sandfish *Trichodon trichodon*, greenling *Hexagrammos* spp., lingcod *Ophiodon elongatus*, salmon Salmonidae, invertebrates (shrimp *Pandalus* spp., squid *Rossia pacifica*, and crabs).

TABLE 2. Results of general linear model analyses testing for effects of dietary diversity and % high-lipid fishes in the chick diet on Pigeon Guillemot reproductive parameters at Naked Island, PWS, Alaska (1989-1990 and 1994-1997). Multiple logistic regression models^a of the following type were constructed: Parameter = diversity index (Hill's ratio $F_{2,1}$) + % high-lipid fish (SAN and H/S) in the diet + year. The G statistic is a measure of deviance between the fully saturated model and the model lacking a particular effect. Improved reproductive performance was associated with *reduced* dietary diversity (increased specialization) and *increased* selection of high-lipid prey. Significant P values are in bold face type.

Parameter	Effect ^b	Test statistic	n	P value
Chick growth rate (g/day)	diversity	$F = 0.00$	41	0.99
	% high-lipid	$F = 5.7$	41	0.023
Peak mass ^c (g)	diversity	$F = 1.1$	62	0.31
	% high-lipid	$F = 1.1$	62	0.24
Fledge mass ^c (g)	diversity	$F = 2.6$	63	0.12
	% high-lipid	$F = 1.6$	63	0.21
Hatching success (eggs hatched per egg laid)	diversity	$G = 0.77$	65	0.68
	% high-lipid	$G = 3.7$	65	0.16
Nestling survival (chicks fledged per egg hatched)	diversity	$G = 4.5$	58	0.034
	% high-lipid	$G = 4.2$	58	0.041
Productivity (chicks fledged per egg laid)	diversity	$G = 6.7$	58	0.01
	% high-lipid	$G = 8.8$	58	0.003

^aDiversity and proportion high-lipid prey were not autocorrelated (Pearson correlation coefficient = 0.096, Bonferroni probability $P = 0.32$).

^bThe interaction term, diversity x % high-lipid, was nonsignificant in all cases.

^cYear effect was also significant.

TABLE 3. Percent of guillemot pairs that specialized in particular prey items at Naked Island, PWS, Alaska (1989-1990 and 1994-1997). Values listed are percents of total pairs classified in that year.

Year	<i>n</i>	Sand lance	Herring /smelt	Blennies	Gadids	Sculpins	Total specialists	Generalists
1989	28	5.9	23.5	17.7	11.8	0	58.9	41.1
1990	25	5.6	0	22.2	5.6	5.6	39.0	61.0
1994	55	9.4	0	34.4	25.0	3.1	71.9	28.1
1995	29	11.8	11.8	41.2	0	5.9	76.5 ^a	23.5
1996	18	0	0	38.5	0	7.7	46.2	53.8
1997	29	11.1	0	38.9	0	11.1	61.1	38.9
All	184	8.8	5.8	32.2	7.1	5.6	58.9	41.1

^aIn addition to the specialists listed, one flatfish specialist was identified in 1995.

FIGURE LEGENDS

FIG. 1. The Naked Island group with the locations of the five Pigeon Guillemot study colonies indicated by numbered circles. Inset maps show the location of the Naked Island group within Prince William Sound (PWS), and the location of PWS within Alaska.

FIG. 2. Hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid), at nests with adults specializing in either high-lipid or low-lipid fishes at Naked Island, PWS, Alaska, 1989-1990, and 1994-1997.

FIG. 3. Growth rates (g/day) of Pigeon Guillemot chicks 8-18 days post-hatch fed by adults specializing in either high-lipid or low-lipid fishes at Naked Island, PWS, Alaska, 1989-1990, and 1994-1997.

FIG. 4. Regression of Pigeon Guillemot average chick growth rate on average percent high-lipid fishes in the diet ($Y = 1.17X + 15.1$, $n = 13$ colony-years, $r^2 = 0.70$, $P < 0.001$). The significant regression indicates that a high proportion of high-lipid fishes in the diet has a beneficial effect on chick growth. In all studies the primary high-lipid fish was Pacific Sand lance, *Ammodytes hexapterus*. This figure incorporates data from 5 studies [Naked Island, PWS, Alaska, this study; Mandarte Island, Haro Straight, BC, Drent (1965); Mitlenatch Island, Straight of Georgia, BC, Emms and Verbeek (1991); Skidegate Inlet, Queen Charlotte Islands, BC, Vermeer et al. (1993); and Farallon Islands, CA, Ainley et al. (1990)]. The regression is significant for Naked Island alone, as well ($n = 9$ years, $r^2 = 0.53$, $P = 0.026$). Growth rate values presented were calculated with the linear slope method (Emms and Verbeek 1991, Ewins 1993)

by the original authors, except for Mandarte Island, where values were derived from our analyses of Drent's (1965) chick mass measurements.

Pigeon Guillemot Colonies

- ① Igloo
- ② Nomad
- ③ Row
- ④ Hook
- ⑤ Tuft

