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 97163F
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.

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Study History: The field work for APEX subproject 97163F was conducted during the summer of 1997. Previous related field work was conducted during the summer of 1995-6 as part of APEX subprojects 95163 F and 96163. 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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ADULT PREY CHOICE AFFECTS CHICK GROWTH AND REPRODUCTIVE SUCCESS OF PIGEON GUILLEMOTS

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Running Title: *Prey Specialization in Guillemots*

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Abstract. Pigeon Guillemots, *Cepphus columba*, are diving seabirds that forage near shore and feed on both demersal and schooling fishes. During nine years between 1979-1997, we made intensive studies of chick diet, chick growth rate, and reproductive success at Naked Island, Prince William Sound, Alaska, in an attempt to understand factors limiting Pigeon Guillemot breeding populations.

We found evidence for prey specialization among adult Pigeon Guillemots, but detected no differences in reproductive performance between specialists and generalists. We did, however, find significant differences in chick growth and reproductive success between pairs that fed their chicks primarily high energy density fishes and those that delivered primarily low energy density fishes.

Chicks that were fed high energy density fishes (e.g., sand lance, herring) had significantly higher growth rates (21.4 ± 0.8 vs. 17.4 ± 1.0 g/d), and tended to attain higher peak masses (486 ± 16 vs. 445 ± 9 g) than those that were fed primarily low energy density fishes (e.g., blennies, sculpins, gadids). The improved growth of guillemot chicks fed more high energy density fishes may in part be a function of the relatively high lipid content and of these prey; however, pairs delivering primarily high energy density fishes had higher rates of prey delivery than pairs delivering primarily low energy density fishes (1.11 ± 0.1 vs. 0.8 ± 0.04 deliveries$\cdot$pair$^{-1}\cdot$h^{-1}).

Pairs that delivered primarily high energy density fishes had significantly higher productivity than pairs that delivered primarily low energy density fishes (0.90 ± 0.07 vs. 0.69 ± 0.04 fledglings/egg), this difference being primarily attributable to a trend of increased nestling survival among pairs delivering high energy density fishes (0.95 ± 0.04 vs. 0.77 ± 0.04 fledglings/hatchling). At fledging, pairs that delivered primarily high energy density fishes also had a significantly larger mean brood size than pairs that delivered primarily low energy density fishes (1.64 ± 0.15 vs. 1.29 ± 0.06 chicks/pair).

Pigeon Guillemot chick diet varied widely from 1979 to 1997. Most of the variability was attributable to fluctuations in schooling fishes, particularly Pacific Sand lance, *Ammodytes hexapterus*, a high energy density fish. Regression analyses suggest that, at the population level, the percent occurrence of high energy density fishes in the diet affected chick growth rate. We conclude that chicks grow fastest, and reproductive success is highest, when high energy density fishes comprise a major portion of the diet.

KEY WORDS: *Alaska;* Cepphus columba; *chick growth; diet choice; dietary generalist; prey preference; prey specialization; reproductive success; seabird.*

KEY PHRASES:

-- *Pigeon Guillemots are generalist predators that demonstrate a high degree of individual specialization when selecting prey items for their chicks.*

-- *Specializing in particular prey items for provisioning chicks does not appear to promote higher reproductive success than generalizing.*

-- *Reproductive success, chick growth rates, and prey delivery rates are greater in Pigeon Guillemots that deliver primarily high energy prey fishes than in guillemots that deliver primarily low energy density fishes.*

-- *Populations of both Pigeon and Black Guillemots that feed their chicks more high*

energy density fishes have higher mean chick growth rates than populations that feed their chicks less high energy density fishes.

-- Pigeon Guillemots are polyphagous marine predators that appear to demonstrate a linear relationship between the availability of a preferred prey item and chick growth rate.

INTRODUCTION

Within both marine and terrestrial populations of generalist predators, individuals have been identified that demonstrate high degrees of prey specialization (Tinbergen 1960, Harris 1965, McCleery and Sibley 1986, 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, few studies have compared the reproductive performance of different specialist types within populations (but see Trillmich 1978, Trivelpiece et al. 1980, Pierotti and Annett 1987, 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, Barrett et al. 1987, Monaghan et al. 1989, Van Heezik and Davis 1990, Hamer et al. 1991, Hatchwell 1991, Uttley et al. 1994, Phillips et al. 1996).

Cepphus guillemots, of the seabird family Alcidae, may be considered dietary generalists. Compared with other alcids, the range of prey items that they exploit is wide (Bradstreet and Brown 1985, Cramp 1985, Ewins 1990, 1993). On the individual level, however, guillemots often display a high degree of prey specialization. Studies of both Pigeon, *C. columba,* (Drent 1965, Koelink 1972, Kuletz 1983, Emms and Verbeek 1991) and Black, *C. grylle,* (Slater and Slater 1972, Cairns 1981, 1984) Guillemots have noted that prey selection patterns of individual adults often differ markedly from those of conspecifics within the same breeding colony. As a generalist forager that shows the propensity to specialize, *Cepphus* guillemots are well suited for studies that relate patterns of prey choice to chick growth and reproductive performance. Comparisons can be made of guillemot pairs that feed their chicks different prey items, without having to account for confounding variables that are present in inter-annual or inter-colony comparisons. Furthermore, because guillemots are conspicuous in their prey delivery habits (they carry single, intact prey items held crosswise in the bill to their chicks), chick diet composition can be determined through observation alone, thus minimizing effects of human disturbance on chick growth.

We studied chick diet, chick growth rates, and reproductive success of Pigeon Guillemots to test two main hypotheses. First, we asked if specialists have higher reproductive performance than generalists. This might be expected if specialization reduces prey handling time (Slobokin and Sanders 1969) thereby increasing chick provisioning rates. Second, we asked if adults that deliver primarily high energy density fishes have chicks that grow faster and achieve higher overall reproductive success than those that deliver primarily low energy density prey fishes. In the first hypothesis we ask if specialization *per se* is important, while in the second we ask if the particular prey selected matters.

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 for their chicks (e.g., sculpins Cottidae spp., blennies Stichaeidae and Pholididae spp.) (Winn 1950, Drent 1965, Slater and Slater 1972, Cairns 1981, Cairns 1987a, Emms and Verbeek 1991, Ewins 1990, 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 alcids, (e.g., murres *Uria* spp., murrelets *Brachyramphus* 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, Nelson 1997). Given that pelagic schooling fishes tend to have higher energy densities than demersal fishes (with the exception of the gadids) (Montevecchi et al. 1984, Barret 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 schooling fishes are available to guillemots, as instances of individual birds specializing in them demonstrate (Slater and Slater 1972, Cairns 1981, Kuletz 1983), however, only rarely do guillemot populations exploit schooling fishes to a large degree (see Kuletz 1983). During our study, most guillemots specialized in nearshore demersal fishes or were generalist, however some guillemots specialized in schooling fishes. In testing our energy-density hypothesis, we compared the reproductive performance of guillemots that specialized in high-energy schooling fishes with other guillemots in the population. In so doing, we ask not only if energy density matters, but also if the more common alcid strategy of preying on pelagic schooling fishes may at times be favorable for guillemots.

METHODS

Study Site

We studied Pigeon Guillemots (hereafter referred to as guillemots) from 1979-1981, 1989-1991, and 1994-1997 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 a series of bays and passages with shelf habitat <30 meters deep radiating approximately one kilometer from shore. Naked Island is forested to its 371 meter summit, and the principle tree species are sitka spruce, *Picea sitchensis,* and western hemlock, *Tsuga heterophylla,*. Guillemots nest semi-colonially along the island's rocky shorelines. They nest beneath tree roots overhanging crumbling cliffs, in rock crevices, on sea stacks, 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*). During 1993, the entire Prince William Sound was surveyed for guillemots, and 3,028 birds were counted (Sanger and Cody 1994). Other members of the Alcidae breeding on these islands include Marbled Murrelets, *Brachyramphus marmoratus*, Parakeet Auklets *Cyclorrhynchus psittacula*, Tufted Puffins, *Fratercula cirrhata*, and Horned Puffins, *F. corniculata.*

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 provisioning their chicks. We observed from land-based blinds with binoculars and spotting scopes. We watched from each blind an average of four full days per breeding season, spacing our days of observation in a systematic manner to ensure representative coverage of the entire chick-rearing period. Because guillemots often pause on the water or on rocks in front of their nests before making deliveries to their chicks, the prey items they carry in their bills can usually be identified. We identified prey items to the lowest possible taxon that we could visually distinguish, and then grouped them into the six categories listed in Table 4.

Guillemot pairs were classified as generalists or one of five specialist types based on our observations of adults delivering prey items to their chicks (Table 1). We classified pairs rather than individual birds because most often we could not distinguish between mates. This classification was appropriate, however, because the 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 deliveries were identified per pair (max = 148). Pairs were classified as specialists (SPEC) when particular prey items or classes of prey items comprised > 50% of the deliveries, and as generalists (GEN) when they did not meet this criterion. We compared specialists and generalists to test our first hypothesis. To test our second hypothesis we compared pairs that delivered primarily high energy density (HED) fishes with pairs that delivered primarily low energy density (LED) fishes. We grouped the non-schooling fishes, the gadids (which school, but are of low energy density in the size classes that guillemots select), and the generalists into the low energy density category. Generalist were included in this category because they delivered only 25.3 % high energy density fishes, on average.

We calculated the dietary diversity of each pair with the modified Hill's ratio, $F_{2,1}$ (Alatalo 1981, Grundel 1990):

(equation is at end with figures)

In this equation, p_i is defined as the number of prey type I delivered by the pair in a year divided by the total number of all prey types delivered by that pair in that year, and n equals the total number of prey types ($n = 6$, see Table 4). 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 compared the dietary diversity of pairs classified as specialists and generalists to determine if pairs we defined as specialists had lower dietary diversity than pairs we defined as generalist.

We examined the effects of diet choice on growth and reproductive success for all but the early years of the study (1979-1981). These years were excluded because there were too few nests for which both specialization and growth or productivity measures were taken. We report diet data from these early years (see Table 4), 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 compared chick growth and reproductive success between generalists and specialists and between pairs that delivered primarily high energy density fishes and pairs that delivered primarily low energy density fishes. Growth patterns were quantified for alpha (the first to hatch, or larger chick, of two-chick nests), beta (the second to hatch, or smaller chick, of two-chick nests), and single (the lone chick of one-chick nests) chicks by weighing and measuring chicks at least once every five days. The growth rate we report is 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 Veerbeek 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 (provided the chick was weighed ≤ seven days before 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). By assessing chick growth in this manner we were able to compare our results to those of prior studies.

We compared the following reproductive success parameters between specialists and generalists, and between pairs that delivered primarily high energy density fishes and pairs that delivered primarily low energy density fishes: clutch size, hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), brood size at fledging, and productivity (chicks fledged per egg laid). Productivity is the most comprehensive measure of reproductive success that we report.

Statistics

Before testing the effects of diet on delivery rate, growth rate, or reproductive success, we tested for differences among years in each of these parameters. First, we used the Lilliefors test to assess normality with variables having continuous frequency distributions. Then, we compared variables identified as non-parametric with the Kruskal Wallis test or the Mann Whitney *U*- test, and contrasted the remainder with *ANOVA*s or *t*-tests assuming equal or unequal variance as appropriate. When significant year effects were found, we used general linear models to test for parameter effects. For contingency table analyses, we used loglinear models (LOGIN command, 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). Mean values are presented ± standard error, while proportions are reported ± standard deviation. All tests are two-tailed, and significance is assigned at the 0.05 level.

RESULTS

Effect of Prey Specialization on Growth and Reproductive Success

Pigeon Guillemots that specialized in particular prey types when foraging for their chicks did not have higher meal delivery rates, chick growth rates, or reproductive success than guillemots that delivered a wider variety of prey (Table 2). Thus, during the years of our study, it appeared that there was no selective advantage in simply being a specialist as opposed to a generalist. However, guillemots that delivered primarily high energy density prey had significantly greater reproductive performance than those that delivered primarily low energy density prey, suggesting that preferentially selecting certain prey items may help maximize lifetime reproductive success.

Chicks fed high energy density fishes had significantly higher linear growth rates of mass than those fed low energy density fishes (HED: 21.4 ± 0.8 g/d, n = 11 chicks; LED: 17.4 ± 1 g/d, n = 32 chicks; F = 5.13, P = 0.030; Fig. 2). The difference between the two groups was apparent only among the two chick nests; in nests with single chicks linear growth did not differ according to diet. In two chick nests, the difference was most pronounced among beta chicks, although alpha chicks also had lower mean growth rates when fed low energy density fishes. Chicks fed high energy density fishes also tended to attain higher peak masses than chicks fed low energy density fishes (HED: 486 ± 16 g, n = 13; LED: 445 ± 9 g, n = 49 chicks; U = 210.5, P = 0.062; Fig. 3a), and although not statistically significant, the difference in fledging masses was in the expected direction (HED: 471 ± 18 g, n = 13; LED: 432 ± 10 g, n = 49 chicks; U = 247, P = 0.22; Fig. 3b). As with growth rates, the differences in peak and fledging masses between the two groups were most apparent in the beta chick category.

Guillemot pairs that provisioned their chicks with high energy density fishes made significantly more deliveries per hour than adults that delivered low energy density fishes (HED: 1.11 ± 0.1 deliveries$\cdot$nest$^{-1}\cdot$h^{-1}, n = 11 nests; LED: 0.8 ± 0.04 deliveries$\cdot$nest$^{-1}\cdot$h^{-1}, n = 59 nests; F = 6.38, P = 0.014).

Guillemot pairs that delivered high energy density fishes to their chicks had significantly higher productivity than pairs that delivered low energy density fishes (HED: 0.90 ± 0.07 fledglings/egg, n = 10 eggs; LED: 0.69±0.04 fledglings/egg, n = 50 eggs; U = 153.0, P = 0.029; Fig. 4). Pairs that delivered high energy density fishes also had a larger brood size at fledging than pairs that delivered low energy density fishes (HED: 1.64 ± 0.15 chicks/nest, n = 11 nests; LED: 1.29 ± 0.06 chicks/nest, n = 52 nests; Fisher's exact test P = 0.039). These differences in reproductive success were primarily attributable to a trend of higher nestling survival among adults that delivered high energy density fishes compared with those that delivered low energy density fishes (HED: 0.95 ± 0.04 fledglings/hatchling, n = 10 chicks; LED: 0.77 ± 0.04 fledglings/hatchling, n = 54 chicks; U = 181.0, P = 0.052). There were no differences in hatching success (HED: 0.95 ± 0.04 hatchlings/egg, n = 11 eggs; LED: 0.93 ± 0.03 hatchlings/egg, n = 54 eggs; U = 285.0, P = 0.71), or clutch size (HED: 1.91 ± 0.09 eggs/nest, n = 11 nests; LED: 1.84 ± 0.05 eggs/nest, n = 55 nests; U = 280.5, P = 0.54) between the two groups.

Prey Specialization Patterns

Adult guillemots demonstrated distinct preferences in the prey items they selected for their young. In the six years during which we quantified specialization patterns, 58.9% of the 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 this year. Nests we classified as specialists had significantly lower dietary diversity ($F_{2,1}$) than nests we classified as generalists (SPEC: 0.69 ± 0.01, $n = 40$; GEN: 0.84 ± 0.01, $n = 74$; $t = 7.02$, $P < 0.0001$), further demonstrating that guillemots differed in their prey selection habits. The proportion of pairs that delivered primarily high energy density fishes did not differ significantly between the three main colony areas between 1989 and 1997 ($n = 95$ pairs, $G = 2.00$, $P = 0.59$). Thus the availability of high energy density fishes did not appear to vary among the Naked Island guillemot colonies. However, we did 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 tended to reflect the overall abundance of particular prey items in the diet. Among nests classified as a particular specialist type in one year, 50.2% 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 and generalists.

Differences among Years

Chick diet varied significantly during the years in which we studied adult prey specialization (1989-1990 & 1994-1997, $n = 3{,}956$ identified prey items, $G = 787.5$, $P < 0.001$; Table 4). However, even greater variability in chick diet was observed from 1979-1981. Overall, the schooling fishes fluctuated most in the diet. Pacific sand lance, *Ammodytes hexapterus,* declined steadily from a high of 60% of the identified prey items in the diet 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, blennies and sculpins remained fairly constant in the chick diet. On average 81.5 ± 3.5% of prey items were positively identified.

Although delivery rates differed significantly ($n = 80$ nests, $F = 5.75$, $P < 0.001$), we found no significant differences in chick growth rates ($n = 102$ chicks, $F = 1.75$, $P = 0.13$) from 1989 to 1997 (Table 5). Both peak ($n = 137$ chicks, $H = 15.69$, $P = 0.008$) and fledging ($n = 135$ chicks, $H = 13.08$, $P = 0.023$) masses were, however, significantly different among years.

We found no differences in reproductive success from 1989-1997. Productivity was not significantly different among years ($n = 181$ nests, $G = 2.70$, $P = 0.75$), nor was hatching success ($n = 320$ eggs; $G = 5.09$, $P = 0.41$) or nestling survival ($n = 245$ chicks, $G = 1.54$, $P = 0.91$).

DISCUSSION

Effect of Prey Choice on Growth and Reproductive Success

Pigeon Guillemots that specialized on particular prey types when foraging for their chicks did not appear to have any reproductive advantage over guillemots that generalized. However, adults that delivered primarily high energy density prey fishes had chicks that grew faster, and had higher overall reproductive success than those that delivered primarily low energy density prey fishes. Thus although specializing *per se* appeared to confer no fitness advantage, there may have been a benefit to preferentially selecting prey items of high energy density. A similar conclusion was reached by Fox and Morrow (1981), who found that insect herbivores that specialized on particular plants appeared to have no selective advantage over those that had greater host breadth. Differences in insect growth, they found, depended more upon the nutritional quality of the plants consumed.

Differences in reproductive performance between guillemot pairs that delivered high energy density fishes and those that delivered low energy density fishes were apparent during the early stages of chick development. Young chicks fed primarily high energy density fishes had growth rates that were significantly higher than those of chicks fed primarily low energy density fishes. The difference in growth rates was pronounced, however, only in nests with two chicks, and was greatest between groups of beta chicks, suggesting that adults that deliver primarily low energy density fishes are less likely to successfully fledge a second chick (as predicted by Kuletz 1983). Differences in reproductive performance between the two groups persisted throughout the chick-rearing period, and at fledging, pairs that delivered primarily high energy density fishes had significantly larger brood sizes than pairs that delivered primarily low energy density fishes.

On the population level the percent of high energy density fishes in the diet also appears to have affected chick growth rates at Naked Island (Fig. 5). Chicks grew fastest from 1979 - 1981, when high energy density fishes comprised from 40 - 60% of their diet. By contrast, in 1990 and 1994, when high energy density fishes comprised only ~ 10% of their diet, chicks grew more slowly.

Ainley et al. (1990) also found an effect of diet on reproductive success in their studies of guillemots at the Farallon Islands. They found that reproductive success was highest in cold water years, when rockfish, *Sebastes* spp., comprised a large portion of the chick diet. They further determined that mean fledging weight was greater in high rockfish years, although they found no correlation between diet and growth rate. The mean growth rate that Ainley et al. (1990) reported for guillemot chicks was low (16.5 g/d), relative to the nine-year mean that we measured at Naked Island (19.1 g/d). In part, this may be attributable to an absence of high energy density fishes in the diet of guillemot chicks at the Farallons. Rockfish generally have lower energy density (kJ/g wet mass) than *Ammodytes*, *Clupea*, or *Mallotus* (Van Pelt et al. 1997), and may be less easily digested and assimilated by young chicks due to their numerous spines and thick scales (Eschmeyer and Herald 1983).

At times when high energy density fishes are locally abundant they may be the preferred prey of guillemots (Ewins 1990). On a long-term basis, however, low energy density fishes (e.g., blennies and sculpins) appear to form the staple of the chick diet for most guillemot populations. Abundances of *Ammodytes, Clupea,* and *Mallotus* may be too variable for these prey to form the primary component of the chick diet in most years. In Prince William Sound, high energy density fishes, such as *Ammodytes*, are notoriously patchy (Blackburn 1979). We found that blennies and sculpins showed the lowest variability in their percent occurrence in the chick diet from year to year, which may be explained by the sedentary nature of these nearshore demersal fishes, which do not show marked movements during the guillemot breeding season (Rosenthal 1979, Cairns 1987a).

In general, studies of Pigeon Guillemots reveal relatively low growth rates when the percent occurrence of high energy density fishes in the chick diet is low (Fig. 5). At Mandarte Island, chick growth was 15.6 g/d (linear slope analysis of Drent's 1965 published data) when *Ammodytes* comprised 4.7% of the diet. At Mitlenatch Island, Emms and Verbeek (1991) measured a growth rate of 14.5 g/d 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/d 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 lowest values we recorded at Naked Island (in 1990 and 1994), when the percent of high energy density fishes in the diet was at its lowest in our nine years of study.

Studies of the Pigeon Guillemot's congener in the North Atlantic Ocean further suggest that the proportion of high energy density fish in the diet may affect chick growth rates. Black Guillemot growth rates in Shetland were among the highest recorded for this species (16.9 g/d, Ewins 1992) when *Ammodytes* was 52% of the chick diet (Ewins 1990). This contrasts the relatively low growth rate (14.2 g/d) measured for Black Guillemots in Hudson Bay when *Ammodytes* was < 1% of the chick diet (Cairns 1987a). Apparently for both Pigeon and Black Guillemots, chick growth is maximized when high energy density fishes comprise a substantial portion of the chick diet.

Relationship between Diet and Growth in a Polyphagous Predator

Cairns (1987b, p. 267) suggested 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 studies of guillemots, however, suggest that this may not be the case. In years when the proportion of high energy density fishes were reduced in the chick diet, growth rates were lower ($n = 9$ years, $r^2 = 0.53$, $P = 0.026$, Fig. 6). Apparently, there was no suitable replacement for high energy density fishes in the years when they were less common in the diet. Hamer et al. (1991) also found a significant linear relationship between chick diet and growth. In their 15-year study of the Great Skua, *Catharacta skua*, a generalist scavenger, they found that sandeels, *Ammodytes marinus*, a high energy density fish, varied from 5 - 95% of the chick diet, and their use was positively correlated with chick growth rate ($n = 15$ years, $r^2 = 0.52$, $P = 0.002$, p.182). Thus, it appears that species that feed their chicks a wide array of prey items may not show the same threshold responses that characterize the relationship between prey availability and growth in species with fewer alternate prey (e.g. Phillips et al. 1996). In polyphagous generalist predators, chick growth rates may be linearly related to the percent occurrence of a preferred prey type in the diet, as we found for guillemots, and Hamer et al. (1991) found for skuas.

Prey Specialization (Diet Choice) of Generalist Predators

Although individual prey specialization has been documented in birds, the effects of specialization on reproductive performance have rarely been quantified. Studies of gulls, *Larus* spp., (Pierotti and Annett 1991, Spear 1993) and skuas, *Catharacta* spp., (Trillmich 1978, Trivelpiece et al. 1980) provide notable exceptions. In our study, as well as in those mentioned above, groups of birds that selected one prey type reproduced more successfully than others. We found that pairs that delivered primarily high energy density fishes had higher reproductive success than pairs that delivered primarily low energy density fishes because they had a higher probability of fledging chicks once the eggs hatched. Apparently delivering more high energy density fishes maximized the chick's rate of caloric intake, as evinced by the significantly higher growth rates we measured at these nests. Higher chick growth and productivity of pairs delivering primarily high energy density fishes may have been a function of the higher lipid content of their prey compared with low energy density fishes. It is also possible, however, that the difference in reproductive performance between these two groups was simply a function of differences in the amount of food delivered to the nestlings. We found that pairs that delivered primarily high energy density fishes had a significantly higher rate of prey delivery than pairs that delivered more low energy density fishes. If average prey mass was comparable between the two groups, then an increased rate of prey delivery could, in itself, explain the difference in productivity.

In other studies, delivery rates may have been important, as high levels of reproductive success of particular groups of birds were attributed to close proximity to a reliable prey source. Trillmich (1978) and Trivelpiece et al. (1980) found that South Polar, *C. maccormicki,* and Brown, *C. lonnberg,* Skuas that specialized on nearby penguin eggs and chicks were more successful raising chicks than those that fed mainly at sea on fish. Similarly, Spear (1993) found that Western Gull, *L. occidentalis,* specialists exploiting nearby Common Murres, *Uria aalge,* or Brandt's Cormorants, *Phalacrocorax penicillatus,* had higher breeding success than gulls from the same colony that foraged elsewhere.

In contrast to these studies, differences in reproductive success of Herring Gull, *L. argentatus,* specialists were largely a function of differences in hatching success (Pierotti and Annett 1991). Presumably one specialist's diet yielded a more complete complement of nutrients essential for producing viable eggs. Among Herring Gulls the reproductively most successful specialists were the most common, and the most consistent in their prey specialization patterns from year to year (Pierotti and Annett 1991). By contrast, we found that pairs that delivered primarily high energy density fishes, which were the most successful raising chicks, were less common in the population between 1989-1997, and less consistent from year to year than other specialist types. At Naked Island, it is likely that pairs that delivered primarily high energy density fishes were relatively uncommon in our study population because their principal prey, *Ammodytes,* tends to be both ephemeral and patchy in Prince William Sound (Blackburn 1979). Such a distribution may make *Ammodytes* difficult for guillemots to routinely exploit, except when it is superabundant. Nonetheless, other studies have documented similar instances of guillemots specializing on *Ammodytes,* even when its percent occurrence in the diet was relatively low in the population at large: Slater and Slater (1972) found that *Ammodytes* comprised 64% of the diet at one Black Guillemot nest (n = 89 deliveries), although this prey accounted for only 17% of the chick diet at the colony; and Cairns (1981) found that an individual Black Guillemot brought 100% *Ammodytes* to its chicks (n = 17 deliveries) at a colony where *Ammodytes* averaged only 8% of the deliveries.

In summary, we found that even in years when high energy density fishes were not abundant (as appeared to be the case from 1990 - 1997), individual guillemots that delivered them had chicks that grew faster and had higher reproductive success than guillemots that delivered primarily low energy density fishes. In years when schooling fishes are more abundant, we expect that the differences in growth and reproductive performance between pairs that deliver primarily high energy density fishes and those that deliver primarily low energy density fishes would be even more pronounced. As the comparisons within populations, among years, and among studies indicate, guillemots chick growth and productivity appears to be maximized when high energy density fishes comprise a major portion of the chick diet. Such a finding presents an interesting question to the evolutionary ecologist: Given the apparent selective advantage of foraging on high energy density fishes, why haven't guillemots evolved (as other alcids have) to become more highly specialized on these prey? In the highly variable pelagic environment of the pigeon guillemot, there must be a long-term advantage to foraging on the widely dispersed, but predictable demersal fishes, even if they are of lower energy density.

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Table 1. Groups used to classify Pigeon Guillemot pairs at Naked Island, PWS, Alaska (1989-1990 & 1994-1997). Pairs were classified based on the prey types they delivered to their chicks, and were identified as specialists when a particular prey type comprised >50% of the deliveries.

group	definition
SAN	sand lance[a] specialist
H/S	herring/smelt[a] specialist
BL	blenny[a] specialist
GAD	gadid[a] specialist
SCU	sculpin[a] specialist
SPEC[b]	specialist (includes SCH, BL, GAD, and SCU)
GEN[b]	generalist (no particular prey type comprised >50% of the deliveries)
HED[c]	high energy density (includes SAN and H/S)
LED[c]	low energy density (includes BL, GAD, SCU, and GEN[d])

[a] The taxonomic composition of these groups is defined in Table 4.

[b] The specialist and generalist groupings were made to test the hypothesis that specialists have higher productivity than generalists (SPEC vs. GEN).

[c] The low energy density and high energy density groupings were made to test the hypothesis that adults that feed their chicks primarily high energy density prey have higher productivity than those that feed their chicks primarily low energy density prey (SCH vs. LED).

[d] Because generalists delivered only 25.3% high energy density fishes, they were included in the LED grouping to test the energy-density hypothesis.

Table 2. Comparisons of growth and reproductive performance between adult Pigeon Guillemots classified as specialists[a] and generalists at Naked Island, PWS, Alaska (1989-1990 & 1994-1997). Means are reported ± standard error.

parameter	specialists	generalists	test statistic	*P* value
meal delivery rate	0.88 ± 0.05	0.80 ± 0.05	$F = 1.03$	0.31
n	42	28		
chick growth rate	18.1 ± 0.9	16.4 ± 1.8	$F = 2.82$	0.10
n	27	10		
chick peak weight	458 ± 11	451 ± 11	$U = 405$	0.60
n	40	22		
chick fledging weight	441 ± 12	444 ± 11	$U = 471$	0.88
n	40	23		
clutch size	1.8 ± 0.06	1.9 ± 0.07	$U = 527$	0.47
n	41	24		
hatching success	0.93 ± 0.04	0.94 ± 0.03	$U = 417$	0.93
n	35	24		
nestling survival	0.82 ± 0.04	0.79 ± 0.06	$U = 385$	0.84
n	33	24		
brood size at fledging	1.4 ± 0.08	1.3 ± 0.10	$G = 0.019$	0.89
n	40	24		
productivity	0.77 ± 0.04	0.71 ± 0.06	$U = 354$	0.44
n	33	24		

[a] Nests were classified as specialists if a particular prey item or class of prey items comprised >50% of the deliveries made to the chicks, otherwise, nests were classified as generalists.

Table 3. Percent of total nests at which Pigeon Guillemots were specialists and generalists at Naked Island, PWS, Alaska (1989-1980 & 1994-1997).

year	n	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
mean	%	8.8	5.8	32.2	7.1	5.6	58.9	41.1

[a] In addition to the specialists listed, one flatfish specialist was identified in 1995.

Table 4. Diet of Pigeon Guillemot chicks at Naked Island, PWS, Alaska. Values reported are percents of the identified deliveries, which averaged 81.5 ± 3.5% of the total deliveries. Prey specialization was studied from 1989-1997.

year		blennies[a]	gadids[b]	herring/smelt[c]	sand lance[d]	sculpins[e]	other[f]
1979	%	20.6	1.5	0	60.4	15.4	2.1
	n	108	8	0	317	81	11
1980	%	33.8	7.9	0	40.4	10.3	7.7
	n	210	49	0	251	64	48
1981	%	22.3	1.4	17.6	25.8	12.3	20.7
	n	96	6	76	111	53	89
1989	%	21.1	27.8	25.0	15.0	10.0	1.2
	n	107	141	127	76	51	6
1990	%	38.7	19.7	2.2	11.5	13.0	15.4
	n	250	127	14	74	84	97
1994	%	37.3	36.7	1.6	10.1	11.2	3.0
	n	346	340	15	94	104	28
1995	%	49.3	8.7	11.8	10.2	13.9	6.1
	n	340	60	81	70	96	42
1996	%	39.8	11.8	3.9	17.4	22.6	4.5
	n	257	76	25	112	146	29
1997	%	35.9	7.6	7.0	22.9	19.0	7.6
	n	194	41	38	124	103	41
Mean	%	33.2	13.7	7.7	23.7	14.2	7.5

[a]blennies	crescent 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 purpurescens*, penpoint gunnel *Apodichthys flavidus*, northern ronquil *Ronquilis jordani*, searcher *Bathymaster signatus*, arctic shanny *Stichaeus punctatus,* snailfish *Liparis* spp.
[b]gadids	Pacific cod *Gadus macrocephalus*, Pacific tomcod *Microgadus proximus*, walleye pollock *Theragra chalcogramma.*
[c]herring/smelt	Pacific herring *Clupea pallasii*, smelt Osmeridae, including capelin *Mallotus villosus.*
[d]sand lance	Pacific sandlance *Ammodytes hexapterus.*
[e]sculpins	ribbed sculpin *Triglops pingelii*, slim sculpin *Radulinus 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.*
[f]other	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 5. Delivery rates and growth parameters at Pigeon Guillemot nests on Naked Island, PWS, Alaska (1989-1990 & 1994-1997)[a]. Means are reported ± standard error.

year	delivery rate (deliveries·nest^{-1}·hr^{-1})	growth rate (g/d)	peak mass (g)	fledge mass (g)
1989	1.0±0.07	18.1±2.5	511±16	507±20
n	16	5	10	10
1990	0.95±0.08	16.7±1.2	542±17	438±18
n	12	12	13	13
1994	0.83±0.11	15.7±2.1	469±12	458±15
n	7	10	18	18
1995	0.62±0.10	19.5±1.4	480±14	455±14
n	18	13	22	22
1996	0.61±0.07	20.8±1.1	482±18	455±15
n	18	22	15	15
1997	0.75±0.07	18.9±0.8	442±7.4	431±8.4
n	18	42	59	57
mean	0.79±0.07	18.3±0.8	488±14	457±11

[a] See Oakley and Kuletz (1996) for 1979-1981 values.

FIGURE LEGENDS

Figure 1. Map of the Naked Island group with the locations of the 5 Pigeon Guillemot study colonies indicated by numbered circles. Inset maps show the location of the Naked Island group within Prince William Sound, and the location of Prince William Sound (PWS) within Alaska.

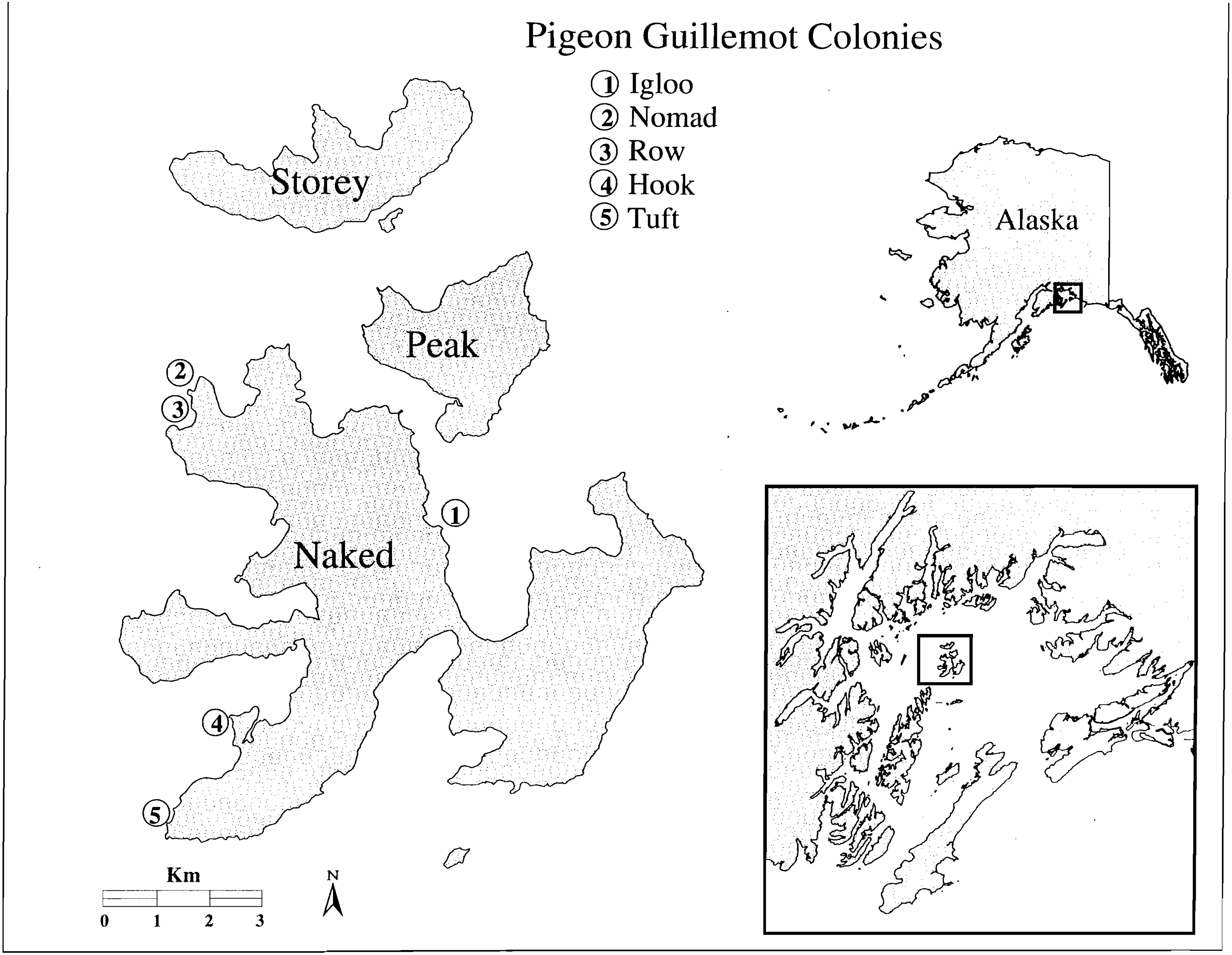
Figure 2. Growth rates (g/d) of Pigeon Guillemot chicks 8-18 days post-hatch fed by adults specializing in either high energy density (HED) or demersal (DEM) fishes at Naked Island, PWS, Alaska (1989-1990 & 1994-1997).

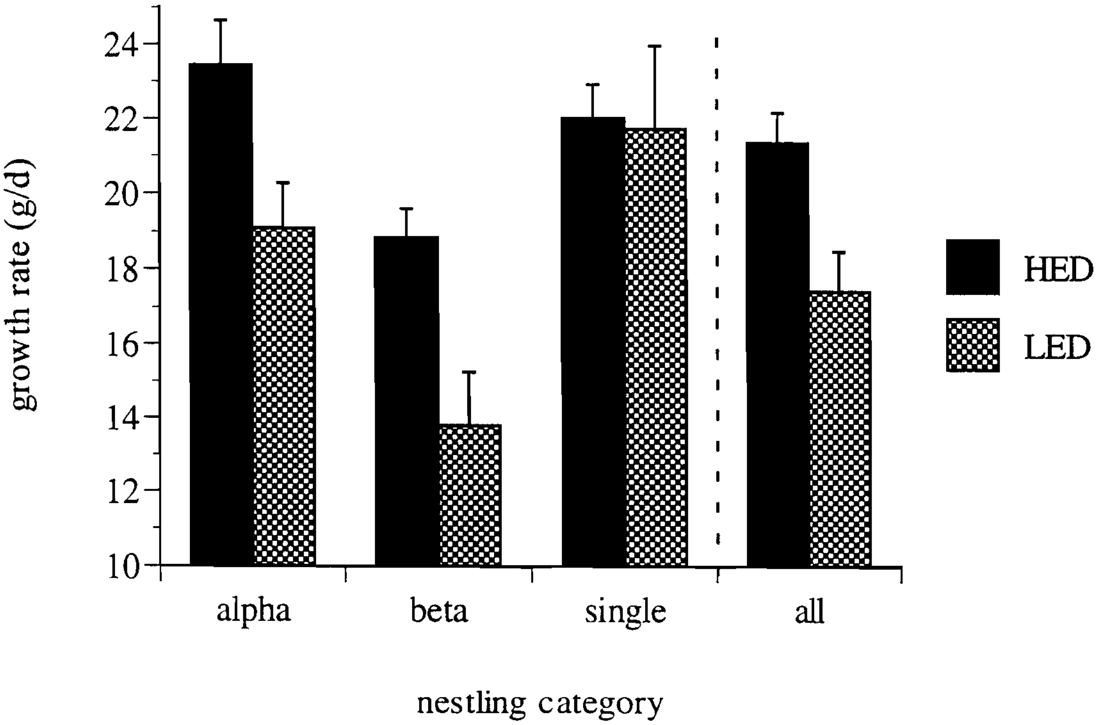
Figure 3. Peak (a) and fledging mass (b) of Pigeon Guillemot chicks fed by adults specializing in either high energy density (HED) or demersal (DEM) fishes at Naked Island, PWS, Alaska (1989-1990 & 1994-1997).

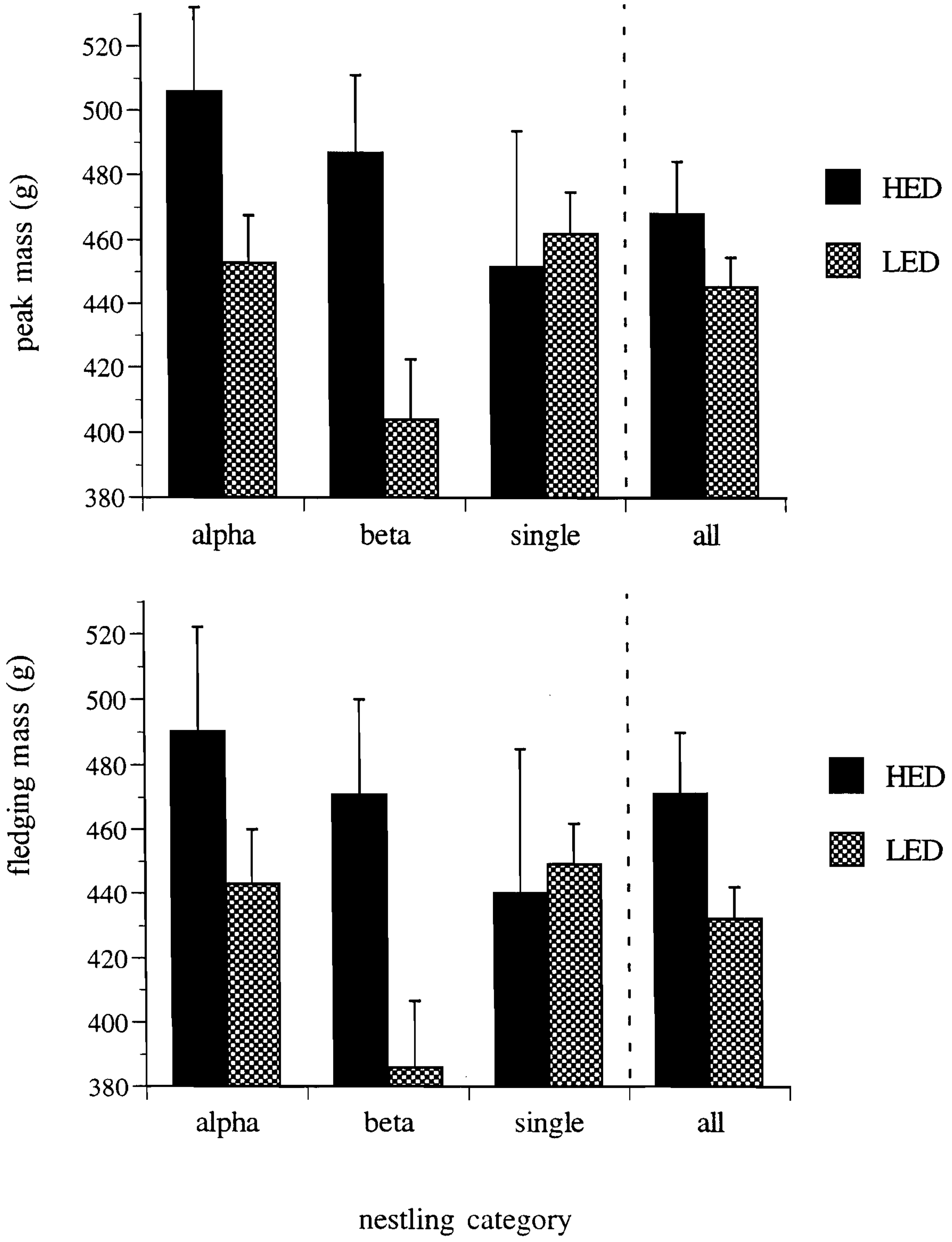
Figure 4. Hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid), at nests with adults specializing in either high energy density (HED) or demersal (DEM) fishes at Naked Island, PWS, Alaska (1989-1990 & 1994-1997).

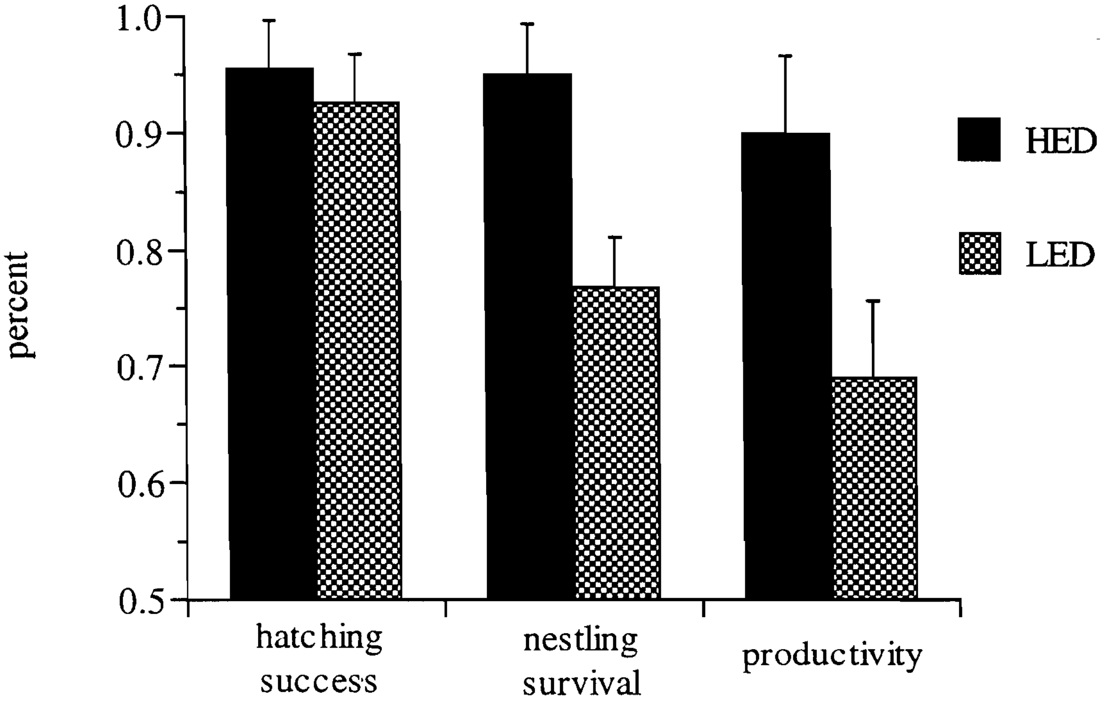
Figure 5. Regression of Pigeon Guillemot chick growth rate on percent high energy density fishes in the diet ($Y = 1.17X + 15.1$, n=13 colony-years, r^2=0.70, $P < 0.001$). The significant regression indicates that a high proportion of high energy density fishes in the diet has a beneficial effect on chick growth. In all studies the primary high energy density 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 relation holds for Naked Island alone, as well (n=9 years, r^2=0.53, P=0.026).

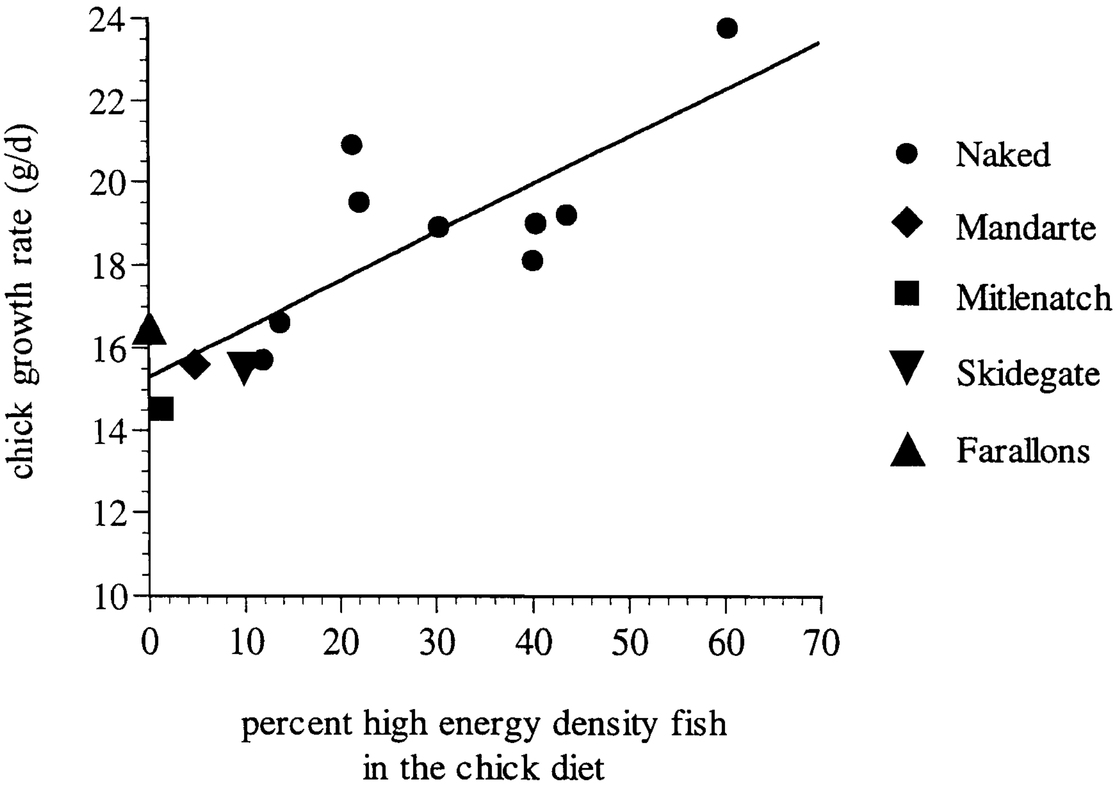
$$F_{2,1} = \frac{\dfrac{1}{\sum\limits_{i=1}^{n} p_i^2} - 1}{\exp\left(-\sum\limits_{i=1}^{n} p_{\mathrm{i}} \ln p_{\mathrm{i}}\right) - 1}$$


Pigeon Guillemot Colonies
① Igloo
② Nomad
③ Row
④ Hook
⑤ Tuft
Storey
Peak
Naked
Alaska
Km
0
1
2
3
N


growth rate (g/d)
24
22
20
18
16
14
12
10
alpha
beta
single
all
nestling category
HED
LED


peak mass (g)
520
500
480
460
440
420
400
380
alpha
beta
single
all
■ HED
▨ LED
fledging mass (g)
520
500
480
460
440
420
400
380
alpha
beta
single
all
■ HED
▨ LED
nestling category

percent
1.0
0.9
0.8
0.7
0.6
0.5
hatching success
nestling survival
productivity
HED
LED


chick growth rate (g/d)
24
22
20
18
16
14
12
10
0
10
20
30
40
50
60
70
percent high energy density fish in the chick diet
● Naked
◆ Mandarte
■ Mitlenatch
▼ Skidegate
▲ Farallons