

THE ECOLOGY AND ENERGETICS OF CHICK PROVISIONING BY BLACK GUILLEMOTS¹

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Abstract. I studied chick growth and parental provisioning behavior of Black Guillemots (*Cepphus grylle*) in Hudson Bay, Canada. Chicks received benthic blennies, principally *Stichaeus punctatus* and *Eumesogrammus praecisus*, which parents caught in water less than 40 m deep close to the colony. Chick feeds were more frequent in the morning but feeding rates did not vary with age of young. Size of prey items increased during the nestling period, and energy intake peaked at about 780 kJ/day/chick when chicks were 25 days of age. Black Guillemots can maintain higher reproductive rates than offshore-feeding Alcidae because their short foraging range and the temporal and spatial predictability of their benthic prey permit higher rates of chick provisioning.

Key words: *Black Guillemots; chick diet; chick growth; chick energy intake; feeding habitat selection; reproductive rates.*

INTRODUCTION

Seabirds have much lower reproductive rates than terrestrial birds (Lack 1968, Drent and Daan 1980). Lack (1968) proposed that seabirds' low reproductive rates are due to limitations in the ability of adults to supply food, and Ricklefs (1983) pointed out that seabird reproductive rates may be influenced by spatial heterogeneity in food sources, seasonal fluctuations in food availability, and the cost of transporting prey from the feeding area to the colony. Because seabirds typically obtain food for their chicks out of sight of their colonies, it has proven difficult to evaluate the relation between seabird reproductive rates and foraging methods and conditions. I gathered data on chick growth, energy intake, and adult foraging behavior of Black Guillemots (*Cepphus grylle*) to assess constraints on reproduction in this species. Black Guillemots forage near their colonies and carry single food items to their young in a manner which allows a clear view of the prey, and are therefore apt subjects for an integrated study of breeding and feeding ecology.

METHODS

This study was conducted in 1981 through 1983 at Pitsulak City (62°22'N, 78°08'W) and in 1983 at Piquiliit 5 (62°20'N, 78°09'W) in northeastern Hudson Bay, Canada. These low-lying and sparsely vegetated islands contained about 190 and 29 nesting pairs of Black Guillemots, respectively (Gaston et al. 1985). Hatching dates and growth rates were determined from visits at approximately 4-day intervals, which started midway through the incubation period. Because the constants derived from logistic and other curves described by Ricklefs (1967) are poorly suited to comparing growth data where asymptotes vary as a proportion of adult weight (Hussell 1972, Gaston 1985a), growth comparisons were based on maximum growth rate measured from a smoothed graph at the inflection point. Eggs were measured with vernier calipers and chicks were weighed with spring scales.

During chick rearing, observers recorded prey deliveries to nests, noting time, prey species, and estimated prey length. A 20-m tunnel (Cairns et al. 1987) allowed the observation blind to be reached without being seen by the birds, and the observation schedule uniformly represented the diel cycle and all phases of chick rearing except the first few days after hatching. Painted rulers were set near nest entrances to aid estimation of prey lengths. Identity of the adult was also recorded as most adults were color-marked. To

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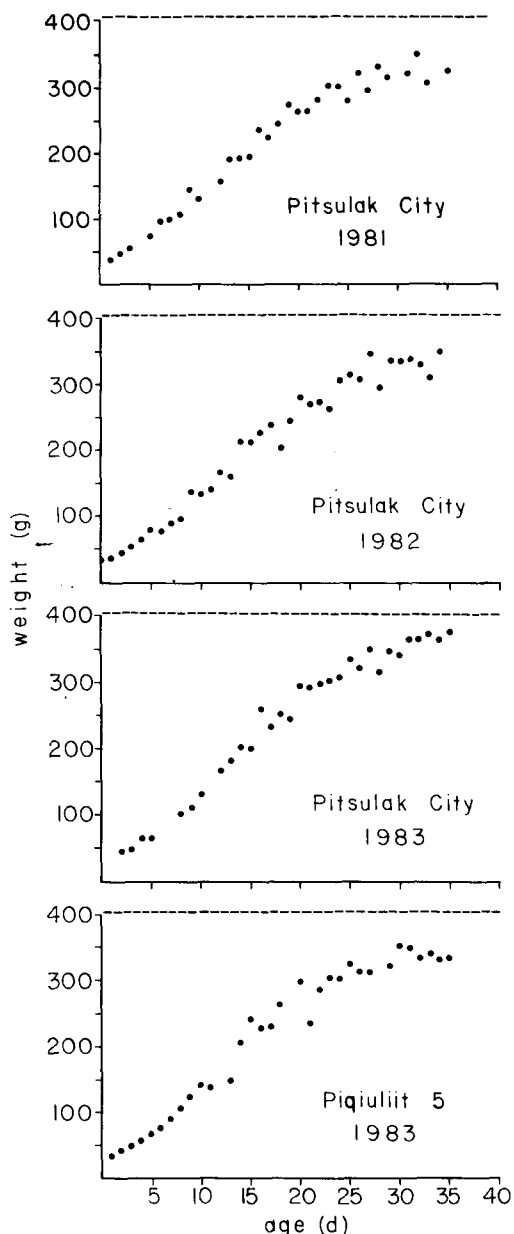


FIGURE 1. Weight growth of Black Guillemot chicks. Each dot is the mean weight of chicks measured at a specific age. The horizontal line is the mean weight of adults in the area (404.8 g, SD = 31.5, $n = 258$). 1981 data are from 85 measurements of 25 chicks, 1982 data from 239 measurements of 44 chicks, 1983 Pitsulak City data from 110 measurements of 19 chicks, and 1983 Piquiliit data from 78 measurements of 28 chicks.

determine locations where chick food was likely to be obtained I tracked guillemots leaving the colony after a food delivery during morning observation periods with binoculars or a 20 \times telescope. Sites where birds splashed down on the water were plotted on maps by estimating their positions relative to islands and a marker buoy, and by timing the trip from colony to splashdown and assuming a flight speed of 52 km/hr (Bradstreet 1982). Water depth at splashdown was taken from hydrographic charts supplemented by a dense network of depth profiles made with an echosounder.

Fish used in energy determinations were homogenized in a slurry for 5 to 10 min, frozen in an alcohol bath, freeze-dried for 48 hr, and weighed to the nearest mg to obtain dry weights. After reblending, specimens were pelletized and dried with CaSO_4 for 48 hr. Pellets were combusted in a Phillipson microbomb calorimeter and energetic values were determined from heat output measured by thermocouples.

RESULTS

EGG SIZE AND CHICK GROWTH

Egg lengths, diameters, and egg volume indices ($\text{length} \times \text{diameter}^2$) were similar among years and sites. Mean (\pm SD) dimensions of 229 eggs were $58.5 \pm 2.0 \times 39.6 \pm 1.2$ mm and mean volume index was $91,934 \pm 6,632$ mm³. Volume indices were not correlated with hatching date for Pitsulak City in 1982 ($r = 0.14$, $n = 40$, $P > 0.05$) but declined with hatching date at Piquiliit in 1983 ($r = -0.49$, $n = 30$, $P < 0.01$).

Median hatching dates for Pitsulak 1981, 1982, 1983, and Piquiliit 1983 were 30 July, 7 August, 31 July, and 30 July, respectively. Weight growth of guillemot chicks is plotted in Figure 1. After a brief period of slow growth, weight increased linearly until chicks were about 24 days old. Weight gain then slowed until fledging at about 34 days. Maximum growth rates were 13.6, 12.4, 14.7, and 16.2 g/day for Pitsulak City 1981, 1982, 1983, and Piquiliit 1983, respectively. Growth curves were similar across years and sites during the linear phase, but chicks in Pitsulak 1983 continued to grow until fledging, in contrast to chicks in other year-site categories whose weights stabilized at an asymptote. That weights were higher at Pitsulak 1983 than in other year-site categories was confirmed by comparison of weights of chicks

TABLE 1. Prey items delivered by Black Guillemots to nestlings at Pitsulak City and Piquiliit.^a

Taxon	Pitsulak						Piquiliit		Total	
	1981		1982		1983		1983		n	%
	n	% ^b	n	%	n	%	n	%		
Crustacea	1	0.7	1	0.1	0	0	0	0	2	0.1
Squid	0	0	1	0.1	0	0	0	0	1	0.1
<i>Boreogadus saida</i> (Arctic cod)	10	6.8	19	2.8	3	0.7	1	0.6	33	2.3
<i>Ammodytes</i> sp. (sand lance)	2	1.4	1	0.1	4	0.9	0	0	7	0.5
Blennioidea (blennies)										
<i>Eumesogrammus praecisus</i> (fourline snakeblenny)	(6)	(18.8) ^d	172	25.6	117	26.1	19	11.3	308	23.9 ^e
<i>Lumpenus maculatus</i> (daubed shanny)	(1)	(3.1)	0	0	0	0	0	0	0	0
<i>Stichaeus punctatus</i> (Arctic shanny)	(17)	(53.1)	309	45.9	197	43.9	126	75.0	632	49.0
<i>Gymnelus viridis</i> (fish doctor)	(2)	(6.3)	58	8.6	82	18.3	17	10.1	157	12.2
Unidentified Blennioidea	(0)	(0)	55	8.2	35	7.8	5	3.0	95	7.4
Total Blennioidea	127	85.8	594	88.3	431	96.0	167	99.4	1,319	91.7
Cottidae (sculpins)										
<i>Myoxocephalus</i> sp.	4	2.7	48	7.1	11	2.4	0	0	63	4.4
Unidentified Cottidae	4	2.7	0	0	0	0	0	0	4	0.3
Total Cottidae	8	5.4	48	7.1	11	2.4	0	0	67	4.7
<i>Liparis</i> sp. (seasnail)	0	0	9	1.3	0	0	0	0	9	0.6
Total identified	148		673		449		168		1,438	
Total items	280		819		518		171		1,788	
% Identified		52.9		82.2		86.7		98.2		80.4

^a Relative frequency of prey in each class varies with year-site category ($G = 60.2$, $P < 0.005$). For this test prey items were classed as "pelagics" (Crustacea, squid, *Boreogadus*, *Ammodytes*), Blennioidea, and "benthics" (Cottidae and *Liparis*). Frequency of blennioid species also varies among year-site classes ($G = 35.9$, $P < 0.005$). Pitsulak 1981 data used in this test were from fish recovered in hand. *Lumpenus maculatus* is excluded from the comparison.

^b Percentage of all prey items identified.

^c May include some *Gadus ogac*.

^d Blennies observed from the blind were not identified to species in 1981. Bracketed figures are from 32 prey items that were recovered and identified in hand.

^e Percentages for blenny species calculated from 1982 and 1983 data only.

measured at 30 or more days of age ($F = 7.0$, $P < 0.001$).

Weight of chicks at the end of the nestling period did not vary with fledging date; correlations between weights of 30+ day old chicks and their fledging dates were nonsignificant ($P > 0.05$) for all year and site categories.

CHICK DIET

All identified prey items were fish except two crustaceans (probably decapods) and one squid (Table 1). Diet was dominated by Blennioidea (blennies), which comprised 91.7% of identified deliveries. *Stichaeus punctatus* was the most frequently delivered blenny, followed by *Eumesogrammus praecisus* and *Gymnelus viridis*. Less common prey were benthic sculpins and sea-snails, and *Boreogadus saida* and *Ammodytes* sp., which swim pelagically but may also be found on the bottom.

Prey composition varied among years and sites (Table 1). Nonblenny species were a substantial fraction of identified deliveries at Pitsulak in 1981 and 1982 (14.2% and 11.7%) but dropped to 4% in 1983. At Piquiliit in 1983, 99.4% of identified deliveries were blennies. *S. punctatus* was invariably the most numerous prey species, comprising 44 to 75% of identified deliveries.

Chick diet varied significantly with time of day at Pitsulak in 1982 and 1983 ($G = 48.4$, $P < 0.005$, $n = 522$ for 1982; $G = 37.9$, $P < 0.05$, $n = 414$ for 1983; analysis by 3-hr periods), but not at Piquiliit in 1983 ($G = 16.5$, $P > 0.05$, $n = 163$). Occurrence of *E. praecisus* was highest early in the morning at all years and sites; otherwise diurnal variation in diet was not consistent among years and sites. Diet varied significantly with date at Pitsulak ($G = 83.1$, $P < 0.005$, $n = 522$ for 1982; $G = 29.3$, $P < 0.025$, $n = 414$ for 1983; analysis by 5-day periods), but not at Piquiliit

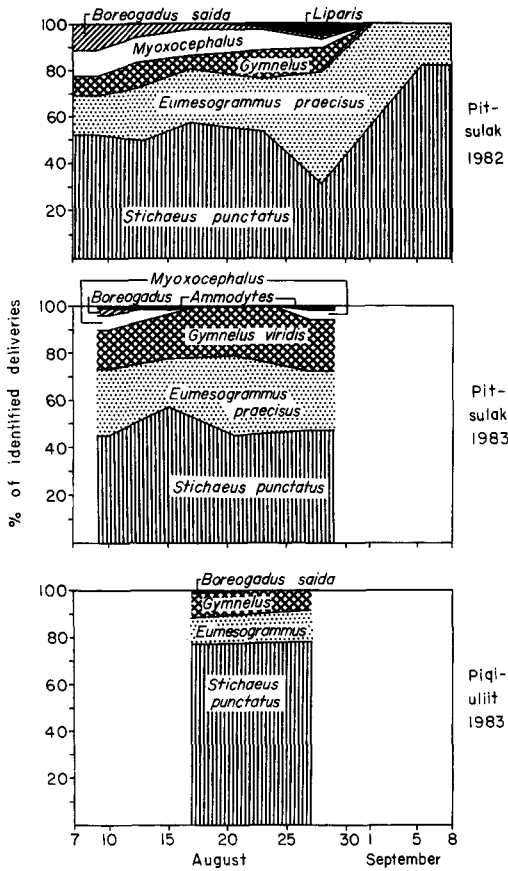


FIGURE 2. Diet of Black Guillemot chicks in relation to date. Based on 522 deliveries to Pitsulak in 1982, 414 deliveries to Pitsulak in 1983, and 163 deliveries to Piquiliit in 1983.

where the observation period was short ($G = 0.43, P > 0.05, n = 163$). However, there was no strong or consistent temporal variation in prey composition except for an increase in *E. praecisus* and *S. punctatus* late in the 1982 season at Pitsulak (Fig. 2).

PROVISIONING RATES

Feeding deliveries were more frequent in the morning than in the afternoon (Fig. 3). Rates peaked again in the evening at Pitsulak in 1981 and 1982 and Piquiliit in 1983, but not at Pitsulak in 1983. During chick rearing, guillemots attended the colony in large numbers in the morning, but few birds were visible in the afternoon other than chick-feeding birds during their brief visits.

The overall mean provisioning rate was 8.80 feeds/chick/day. Provisioning rates did not vary

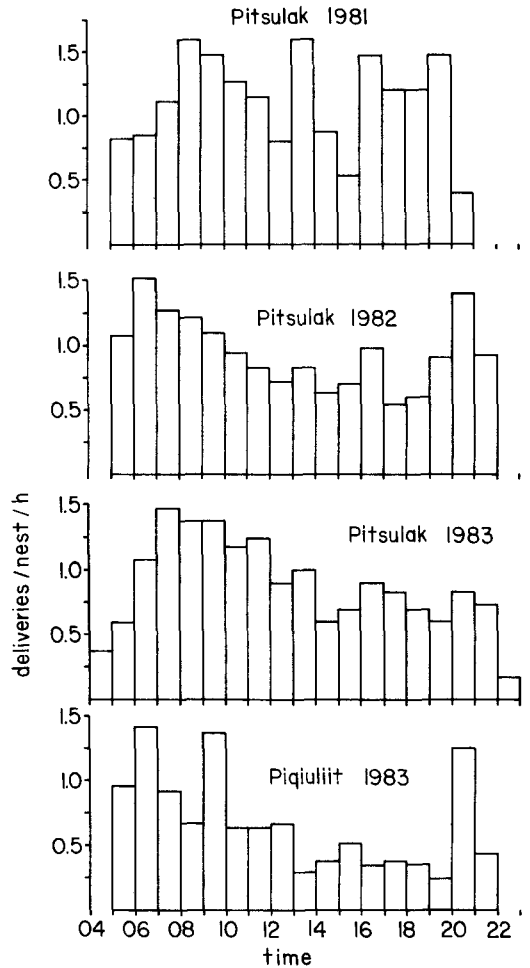


FIGURE 3. Prey deliveries to guillemot chicks in relation to time of day. No data available where abscissa is absent. Based on 492 deliveries in 1981, 633 deliveries in 1982, 518 deliveries to Pitsulak in 1983, and 171 deliveries to Piquiliit in 1983.

significantly among years and brood sizes ($F = 1.59, P > 0.05$; sample sizes given in Fig. 4) or with date (Fig. 4). Mean prey length, as estimated by observers in the blind, increased linearly during chick rearing (Fig. 5).

Of 1131 deliveries by known-sex guillemots to nestlings at Pitsulak City in 1982 and 1983, 581 were made by females and 550 were by males, suggesting that the sexes make similar contributions to chick provisioning.

ENERGY INTAKE OF CHICKS

Energy intake of chicks depends on size and energy density of prey, and feeding frequency. I measured energy densities of two *B. saida*, three

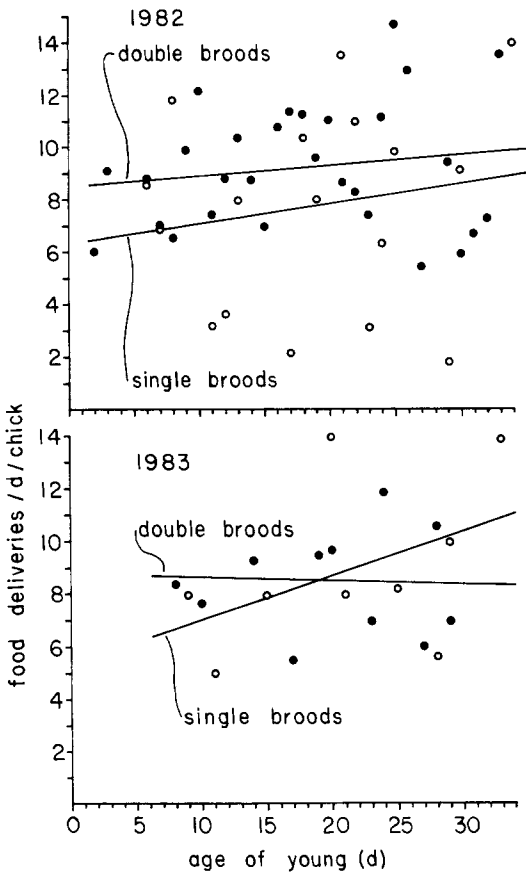


FIGURE 4. Prey delivered/chick/day at Pitsulak in 1982 and 1983. Each symbol represents observations of one nest on one day. Open circles represent single broods, solid circles represent double broods. For 1982 single broods, 1982 double broods, 1983 single broods, and 1983 double broods, $n = 70, 559, 65,$ and 453 deliveries, respectively. All regressions between food deliveries/chick/day vs. age of young are nonsignificant ($P > 0.05$).

E. praecisus, five *S. punctatus*, three *G. viridis* and four *Myoxocephalus*, using four samples per specimen. Energy densities did not differ significantly among species (nested ANOVA, $F = 2.61$, $P > 0.05$), and the overall mean density was 21.4 kJ/g dry weight. This value is similar to those reported by Koelink (1972) and Dunn (1975) for blennies and other benthic fish. Because specimens dried substantially before they reached the laboratory, I used Dunn's (1975) mean of 74% water content for several benthic fishes to calculate energy density of fresh prey. Mean energy density of the prey of guillemot chicks was thus 5.6 kJ/g wet weight.

Mean estimated lengths for each of the five

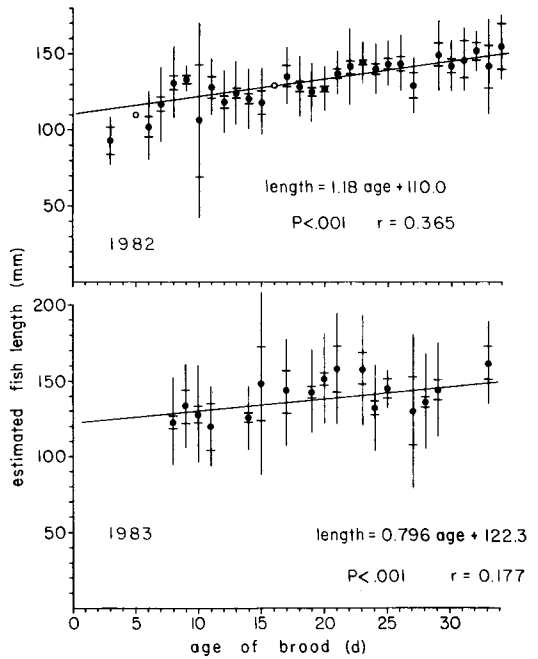


FIGURE 5. Estimated lengths of fish delivered to Black Guillemot nests at Pitsulak in 1982 and 1983 vs. age of young. Solid dots are means, vertical bars are standard deviations, and crossbars are standard errors. Open circles indicate a sample size of one. From 541 deliveries in 1982 and 441 deliveries in 1983.

major prey species are presented in Table 2. Since mean lengths within species did not vary between years or sites, I pooled data from Pitsulak 1982 and 1983 and Piquiliit 1983. Using length-weight regression equations derived from fish measured in hand, I calculated weights from the estimated lengths of each fish observed, and their energy values. Mean weights and energy contents for the various species varied widely; *E. praecisus*, the largest of the prey species, had nearly double the mean weight and energy content of *B. saida* (Table 2). *S. punctatus*, although similar in length to *E. praecisus*, was lighter and contained less energy.

Energy intake of chicks over the nestling period is plotted in Figure 6. Because composition of prey species did not vary strongly or consistently with date I assume in this analysis that prey composition was constant over chick rearing. The contribution of each species was based on weights calculated from estimated lengths, using pooled data from Pitsulak City 1982 and 1983. The weights of each species were scaled up according to the representation of each species

TABLE 2. Length-weight relations and estimated mean wet weight and energy content of fish prey from Pitsulak City 1982 and 1983 and Piquiliit 1983.

Species	Fish measured		Fish observed						
	n	Regression equation: weight (g) =	Estimated length (mm)		Calculated weight (g) ^a		Calculated kJ/fish		
			\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	
<i>Boreogadus saida</i>	6	$7.21 \times 10^{-7} \times \text{length}^{3.45}$	16	103.8	30.5	8.7	8.2	49.2	45.6
<i>Eumesogrammus praecisus</i>	12	$1.07 \times 10^{-6} \times \text{length}^{3.38}$	279	133.5	16.0	17.3	6.8	95.9	37.9
<i>Stichaeus punctatus</i>	32	$1.68 \times 10^{-6} \times \text{length}^{3.23}$	556	135.7	18.8	13.9	6.4	77.1	35.5
<i>Gymnelus viridis</i>	8	$4.53 \times 10^{-6} \times \text{length}^{2.9}$	142	158.9	40.2	13.2	11.0	73.2	61.3
<i>Myoxocephalus</i> sp.	7	$1.41 \times 10^{-5} \times \text{length}^{2.94}$	54	97.0	17.3	10.5	4.9	58.0	27.3

^a Weights are calculated from estimated lengths of observed fish according to the regression equation for each species. Since this method assumes that lengths were estimated in the field without error, standard deviations for weight and kJ/fish are less than those that would be produced if error of length estimates were included.

in total diet (Table 1), taken as a proportion of the overall mean of 8.80 feeds/chick/day (assumed to be constant over the season).

Estimated daily food deliveries rose from 80 to 85 g (460 kJ) for chicks a few days old to peak at 140 g (780 kJ) for 25-day-old chicks (Fig. 6). Weight of deliveries declined from this peak until fledging. Young chicks received much more food in proportion to their body weights than older chicks. Chicks under 5 days of age received more than their own weight in food daily, whereas 25-day-old chicks received about one half of their weight in food per day (Figs. 1 and 6).

The three species of blennies accounted for most of the food delivered to chicks; this reflects the blennies' numerical dominance and large body size. Most of the rise in estimated weight of fish delivered was due to increasing lengths of *S. punctatus*, whose daily contribution increased from 42 to 74 g over the nestling period. Sizes of *Eumesogrammus* and *Gymnelus* varied little, except in the week prior to fledging when a decline in the size of *Eumesogrammus* was re-

sponsible for the pre fledging reduction in overall energy intake.

CHOICE OF FEEDING HABITAT

Sites where birds splashed down on the water after delivering prey to Pitsulak City are indicated in Figure 7. All destinations of birds seen leaving Pitsulak were south or east of the island, but this distribution of splashdown sites may not reflect activities of the colony as a whole. Guillemots were frequently seen on the water north-east of the island; these birds presumably came from the central and eastern parts of the colony where no feeding observations were made.

Guillemots showed a marked preference for shallow water in their splashdown destinations, entirely avoiding the deep water west of Pitsulak

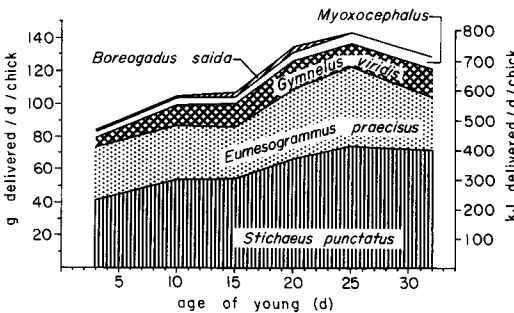


FIGURE 6. Estimated daily weight and energy contribution of fish species delivered to Black Guillemot chicks at Pitsulak in 1982 and 1983. See text for details of derivation.

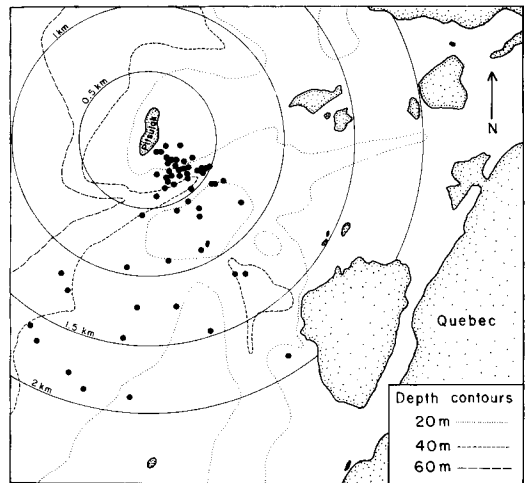


FIGURE 7. Sites where Black Guillemots splashed down on the water after delivering prey to Pitsulak City in August 1983. Distance circles are centered at the observation site on Pitsulak City.

City (Fig. 7). Figure 8 compares frequency of depth choice with availability of habitat of various depths within 2 km of the colony. Depths between 20 and 30 m were most strongly preferred, and most splashdowns occurred in water between 10 and 40 m deep.

Mean colony to splashdown distance was 677 m (SD = 528, $n = 56$) at Pitsulak, which is similar to splashdown distances of birds departing from Piquiliit ($\bar{x} = 686$, SD = 370, $n = 15$). The zone between 0.25 and 0.5 km from the colony was the most frequent destination of birds departing from Pitsulak (Fig. 9A). However, when splashdown rates are divided by the area of the preferred depth of 10 to 40 m within each distance zone, the most preferred destination is shown to be the zone adjacent to the colony (Fig. 9B). Preference decreases in the next two zones, and falls to low levels beyond 0.75 km.

TIMING AND COORDINATION OF ADULT FORAGING

If birds use a colony as a center where information on feeding sites is exchanged (Ward and Zahavi 1973), feeding departures should be synchronized as food-seeking birds follow successful foragers to good feeding sites. At Pitsulak City and Piquiliit, guillemots often left the colony in pairs or trios in the direction of the feeding grounds. However, in 56 cases where individual birds were visually followed from the colony to splashdown on the feeding grounds, any accompanying birds invariably separated from the birds that were tracked. In no case was more than one bird seen to splash down at the feeding ground in the same binocular or telescope field of view.

To measure synchrony of prey deliveries by guillemots, I calculated the coefficient of dispersion (s^2/\bar{x}) of feeding deliveries per 5-min period at Pitsulak City. Deliveries were weakly but significantly clumped in both 1982 and 1983 ($s^2/\bar{x} = 1.19$ for 1982, $s^2/\bar{x} = 1.22$ for 1983; both P 's < 0.05, Morisita's test, Southwood 1966).

DISCUSSION

CHICK GROWTH AND ENERGY INTAKE

Estimated food intake of guillemots peaked at ca. 25 days, and growth slowed after this age except at Pitsulak City in 1983, when chicks continued to grow until fledging (Fig. 1). This continuation of chick growth may have been due to favorable foraging conditions caused by decreased competition for food. Between 1982 and

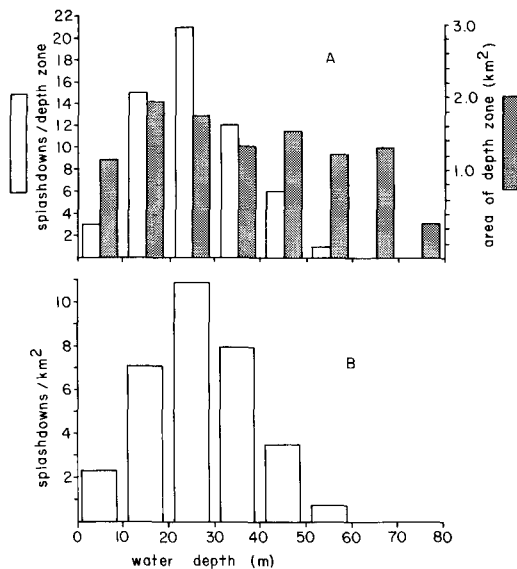


FIGURE 8. Depth preferences of Black Guillemots from 56 birds followed from Pitsulak City to splashdown in August 1983. (A) Frequency of use of depth zones compared to area of zones within 2 km of the colony. (B) Number of splashdowns in each depth zone divided by the area of that zone within 2 km of the colony. Frequency distribution of depth zones used differs from that expected if use were proportional to area ($G = 45.0$, $P < 0.005$).

1983 the number of guillemot pairs with chicks on Pitsulak City dropped from 134 to 49, apparently because of ermine (*Mustela erminea*) visitation (Cairns 1985). Chick growth at Piquiliit in 1983, which was not visited by ermine, showed the "normal" pattern of weight growth found at Pitsulak in other years (Fig. 1).

The maximum feeding rate of 140 g/chick/day estimated for Pitsulak guillemots is similar to that reported from Denmark (133 g, Asbirk 1979), but greater than the 100-g maximum reported for the closely related Pigeon Guillemot (*Cephus columba*, Koelink 1972), which is slightly larger than the Black Guillemot. However, comparisons of provisioning rates must be made with caution because of uncertainties in accurately estimating fish length (this study), in the use of discarded fish to indicate the size of fish consumed (Asbirk's study), and in identification of prey items from a film record (Koelink's study). Guillemots usually alter the amount of food brought to chicks by changing the size of prey items (Winn 1950, Koelink 1972, Asbirk 1979, this study) but intake adjustment may also be

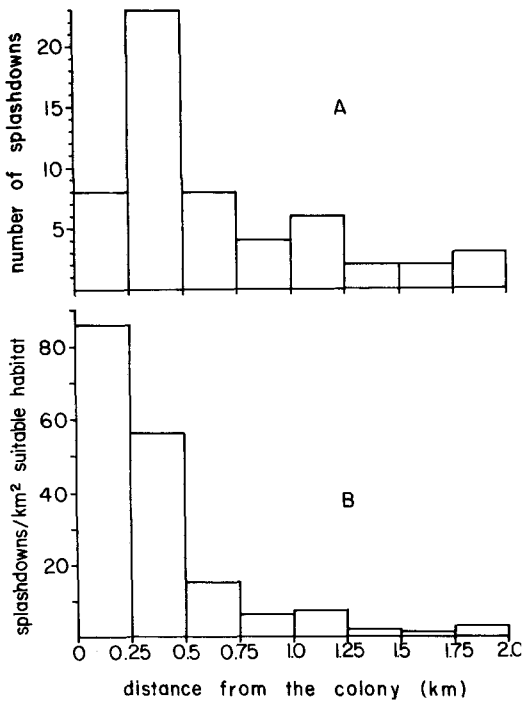


FIGURE 9. Distance from the colony at which Black Guillemots splashed down after delivering prey to Pitsulak City in August 1983, $n = 56$. (A) Number of splashdowns per distance zone. (B) Number of splashdowns per km² of suitable habitat (10 to 40 m depth) in each distance zone.

achieved by changing the feeding rate (Slater and Slater 1972).

FORAGING ECOLOGY

This study confirms that Black Guillemots obtain chick food in shallow water close to the colony, as suggested in other studies on the basis of food delivered to the colony (Winn 1950, Bergman 1971, Slater and Slater 1972, Cairns 1981, Petersen 1981). Adult guillemots also choose similar water depths when foraging for themselves, but adult foods are more diverse and are often obtained at greater distances from the colony (Cairns, in press). Although echo-sounder surveys showed that the deep water adjacent to Pitsulak City often contained abundant prey shoaling near the surface (unpubl. data), guillemots did not feed there. Guillemots occasionally took mid-water fishes such as arctic cod and sand lance in the shallow water zone, but these species also frequent the benthic zone and may have been caught there.

No evidence was found that Black Guillemots followed other birds to locate food for their chicks. Black Guillemot colonies are small in relation to those of most other seabirds, and the guillemot's solitary feeding habits are therefore consistent with the prediction that tendency to feed in groups should decline with decreasing colony size (Ward and Zahavi 1973, Erwin 1978, Waltz 1982). Solitary feeding is also appropriate because chick diet is mostly benthic blennies, which are dispersed and nonschooling (J. M. Green, pers. comm.).

THE RELATION BETWEEN FORAGING STRATEGY AND REPRODUCTIVE RATE

Black Guillemots produce more young and raise them at growth rates at least as rapid as the five other North Atlantic alcids (Gaston 1985a). This is consistent with the guillemot's role as an in-shore feeder whose delivery trips from the feeding grounds to the colony are shorter than those of offshore feeders (Lack 1968, Gaston 1985b). However, other features of guillemot foraging ecology may also be important in determining provisioning rates. Blennies fed to chicks at Pitsulak and Pigiuliit were large compared to fish typically delivered to chicks of other Atlantic Alcidae (Bradstreet and Brown 1985), thus allowing efficient energy transfer by the single-prey loading guillemots. Blennies are also relatively sedentary, so that prey distributions can be reliably known by foraging birds, which do not have to locate wide-ranging mobile prey. Blennies do not show marked movements during the guillemot breeding season, so prey is reliably available throughout. This constancy of prey supply is reflected in the absence of change with date in pre-fledging weights of chicks.

Studies with artificially enlarged broods have shown that guillemots are often capable of rearing three young (Koelink 1972, Asbirk 1979, Petersen 1981). These experiments have shown some depression of growth curves of triplets just before fledging, when the provisioning ability of adults is most likely to limit chick growth (Fagerstrom et al. 1983, Gaston 1985a), but this effect is probably not great enough to reduce subsequent survivorship (see Harris and Rothery 1985). Although guillemots frequently appear capable of rearing three chicks, their brood size may nevertheless be restricted to two because of their inability to incubate more than two eggs.

Growth rates of Black Guillemots are not only

higher than most others reported for Atlantic alcids, but they also tend to be less variable (Gaston 1985a). This constancy reflects the relative predictability of benthic prey exploited by guillemots in comparison with the mobile schooling prey used by offshore-feeding seabirds. Thus Black Guillemots can be considered "risk averse" foragers in contrast to "risk prone" offshore feeders (Caraco et al. 1980, Stephens 1981). The dichotomy of these strategies is most evident in the Pigeon Guillemot, in which individuals specializing in pelagic prey have greater variability in breeding productivity than those specializing in benthic prey (Kuletz 1983).

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