GROWTH ENERGETICS OF NESTLING NORTHERN GANNETS (*SULA BASSANUS*)

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ABSTRACT.—We describe the energetics of postnatal growth and development of wild and captive Northern Gannet chicks. For 14 chicks 0–9 weeks old, a 24-week immature, and a breeding female, we determined water, lipid, and nonlipid content. During the 13-week nestling period, mass increased over 40-fold. Accumulation of lipid caused the energy density of chicks to increase steadily through 9 weeks. Lipid eventually accounted for about 60% of energy in tissues. Two captive chicks grew at rates comparable to wild young and consumed, on average, about 24 kg of fish containing 190,000 kJ during the nestling period. The energy density of chick guano was 13.3 ± 0.8 kJ/g. Estimated metabolizable energy (ME) rose rapidly from 952 kJ during week 1 to 19,318 kJ during week 6, after which ME fluctuated between about 9,000 and 16,400 kJ/week. During week 1, the growth increment (GI) was 801 kJ; GI increased sharply to 9,667 kJ during week 4 and peaked at 12,711 kJ in week 7. Net growth efficiency was 49% to 8 weeks of age and 33% to fledging at 13 weeks. The food requirement of the gannet population of Newfoundland is estimated. *Received 2 August 1982, resubmitted 28 January 1983, accepted 1 September 1983.*

CONSIDERATIONS of how parents and chicks are coupled by time, energy, and nutrition are crucial to an understanding of the evolution and ecological diversification of developmental and parental-care patterns among seabirds. Much more needs to be known about how growth energetics are related to parental investment and feeding ecology, particularly among large species that raise altricial young (see Dunn 1975a, b, 1980; Cooper 1978). In this paper developmental changes in the energy composition and requirements of Northern Gannet (*Sula bassanus*) chicks are analyzed as a step toward a better understanding of life-history patterns in marine birds.

Northern Gannets are large, long-lived, fish-eating seabirds that feed primarily inshore. They begin breeding at 5–7 yr and pair monogamously (Nelson 1978a, b). Each year the female lays one small egg (3.6% adult mass), which has little yolk (15.5% egg mass, Ricklefs and Montevecchi 1979). Hatching and fledging success are high, often greater than 80 and 90%, respectively (Nelson 1978a, b). Altricial young are cared for intensively by both parents at the nest for 13 weeks, after which chicks go to sea and parental care ends (Montevecchi and Porter 1980). Post-fledging mortality in the first year may be at least 60% (Nelson 1978a).

In this study we examined the water, lipid, and nonlipid contents and energy densities of different-aged nestlings. The food consumption of captive chicks was monitored over the nestling period, and the organic composition and energy contents of different foods were determined. Data were integrated to construct a nestling energy budget. We also estimated the gannets' harvest of their major foods (mackerel, herring, capelin, squid) in Newfoundland waters.

METHODS

In 1978–1979, four Northern Gannet chicks were removed from nests within 10 days of hatching on Baccalieu Island (48°07'N, 52°47'W), Newfoundland and were raised in captivity. For 4 weeks they were fed primarily capelin (*Mallotus villosus*), thereafter mackerel (*Scomber scombrus*); these fish are the most common items fed to chicks of these ages on Baccalieu Island (Montevecchi and Porter 1980). As in nature, neonates were fed frequent (up to 6 times per day), small meals, and older chicks were fed large

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pieces of mackerel once or twice daily. Our food consumption data are based on two chicks who were taken in 1979 and whose food intakes were precisely monitored.

Protein levels in food samples were measured by the Kjeldahl method. Lipids were extracted with diethyl ether, and their levels were determined by subtracting lipid-free mass from pre-extracted mass. Amino-acid compositions of foods were analyzed with a Beckman Amino Acid Analyzer (Model No. 121M) with AA-10 resin and manobore flow systems following a 24-h HCl hydrolysate at 110°C.

Body composition of 14 chicks (10 killed at the nest and 4 that died after brief periods in captivity but whose masses were within the ranges of noncaptive chicks of the same ages), a hand-reared 24-week immature, and a breeding female collected on Baccalieu Island in 1977 and frozen for later analyses was determined. Thawed birds were dissected into several components, which were air-dried at 68–70°C to constant mass. Lipids were extracted for 24 h in each of three fresh baths of a 5:1 mixture of petroleum ether: chloroform. From primary measurements (wet, dry, and lipid-free dry masses) we calculated water = wet − dry mass, lipid = dry − lipid-free dry mass, and lipid-free wet mass = wet mass − lipid. The energy equivalent of tissue was calculated by applying the conversion factors: 38 kJ/g lipid and 20 kJ/g lipid-free dry matter (Ricklefs 1974).

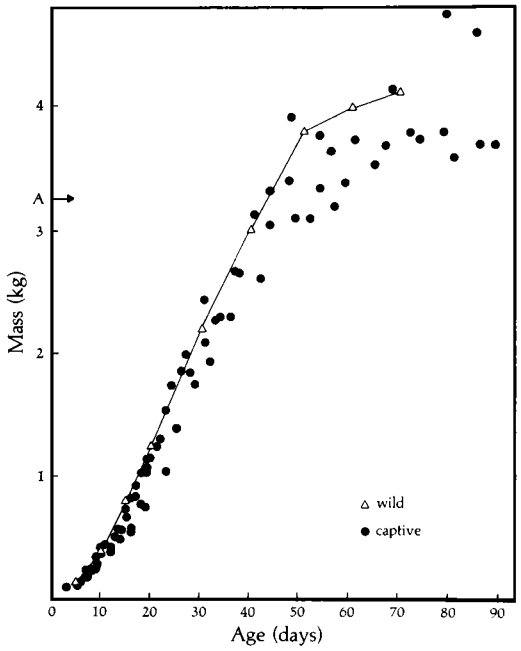

Fig. 1. Masses of wild (from Nelson 1964) and four hand-raised Northern Gannet chicks as a function of age. Average adult mass (A) is indicated on ordinate.

Results

Chicks averaged (± SD) 79.3 ± 11.2 g (n = 12) at hatching, about 70% of the fresh egg mass (114.1 ± 9.4 g; Ricklefs and Montevecchi 1979) and about 2.5% of adult mass (3,236.4 ± 41.9 g, n = 40). Young chicks increased their masses very rapidly, more than 10-fold in 3 weeks (Fig. 1). By 7 weeks, chicks were as heavy as adults, and by 10 weeks, they weighed about 4 kg, about 25% more than an adult (Fig. 1). Up to 60 days, our captive chicks did not differ significantly in mass from Nelson's (1964) sample of wild chicks at Bass Rock, Scotland. Weekly mass increments were relatively constant to about 50 days, after which further gain slowed and became quite variable. Using the Gompertz equation (Ricklefs 1968a), we found that the Northern Gannets' growth constant (K), calculated for Nelson's (1964) data, was 0.063 day^{-1}, similar to those of altricial landbirds of similar size (Ricklefs 1973). The K-value calculated for captive chicks in this study was 0.073 day^{-1}, but a lower asymptote was achieved. After masses peaked around 10 weeks, captive and wild chicks exhibited slight mass recessions before fledging age, when most weigh more than 3,500 g (Montevecchi unpubl. data, cf. Kirkham and Montevecchi 1982: adult mean = about 3,250 g). Captives near fledging age had similar masses to fledglings that had recently departed from the colony (Montevecchi unpubl. data).

Increases in water, lipid, and lipid-free dry matter during the first 60 days of postnatal development are illustrated in Fig. 2, and the total energy equivalent of these components is illustrated in Fig. 3. Four chicks aged 50–63 days contained an average of 965 g of lipid-free dry matter, equivalent to 19,300 kJ, and 729 g of lipid, equivalent to 27,702 kJ. Lipid therefore accounted for about 60% of the energy in the nestling's tissues around the time of peak mass. The energy densities of chicks increased with age, due largely to progressive accumulation of lipid, at least to 9 weeks (Fig. 4). The linear relationship, determined by a least squares fit of the data, may be expressed as energy density (kJ/g) = 3.35 + 0.16 age (days). The energy densities of two fully grown birds were similar to those of chicks at peak mass, about 13 kJ/g.

The organic composition and energy equiv-

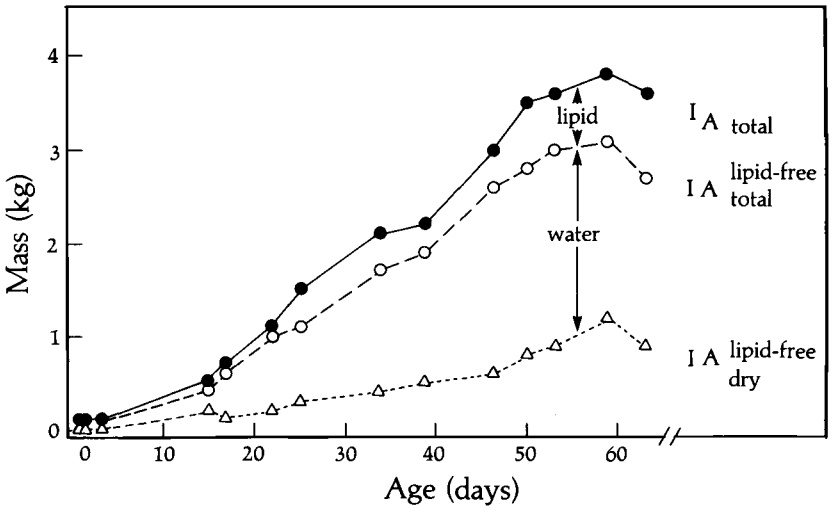

Fig. 2. Changes in lipid, lipid-free dry material, and water content of body tissues of Northern Gannet chicks as functions of age. Contents of a 24-week immature (I) and breeding female (A) are indicated.

alents of items most frequently fed chicks are presented in Table 1. Owing to high lipid content, mackerel is the most energy rich of the foods. Other foods have substantially lower lipid levels and higher protein indices (100 × g protein/kJ).

The amino acid composition of capelin, mackerel, squid (*Ilex illecebrosus*), and herring (*Clupea harengus*) were analyzed. The levels (nanomoles/mg of dry weight, including lipid) of all amino acids and ninhydrin positive substances, except hydroxyproline and hydroxylysine, were found to be higher in capelin, an important food for neonates, than in mackerel, the food most commonly fed older chicks. Capelin also contained substantially higher levels of most amino acids than did either squid or herring, foods also fed primarily to older chicks by parents (see Montevecchi and Porter 1980). Squid had relatively high amounts of cysteic acid/phosphoserine and taurine. The differences among these species generally reflect the varying ratios of protein to fat. Essential amino

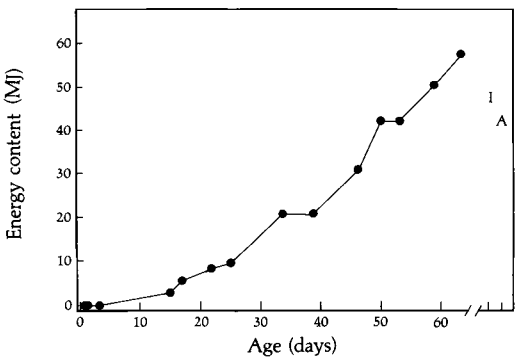

Fig. 3. Changes in energy content of Northern Gannet chicks as a function of age. Contents of a 24-week immature (I) and breeding female (A) are indicated.

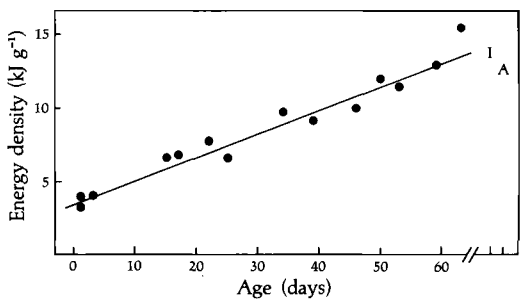

Fig. 4. Energy density (kJ/g) of Northern Gannet chicks as a function of age. Those of a 24-week immature (I) and breeding female (A) are indicated.

TABLE 1. Energy values and organic composition of foods most frequently fed to Northern Gannet chicks in Newfoundland.

Food	Energy[a] (kJ/g)	Percentage wet mass				Protein index[b]	Lipid index[c]
		H_2O	Protein	Lipid	Ash		
Mackerel (*Scomber scombrus*)	10.3	62.3	16.2	18.6	2.0	1.6	1.8
Capelin (*Mallotus villosus*)	4.2	78.4	14.9	3.3	2.0	3.6	0.8
Squid (*Ilex illecebrosus*)	4.3	78.2	15.9	3.0	1.8	3.7	0.7
Sand Lance (*Ammodytes hexapterus*)	7.3	63.5	19.5	8.9	7.3	2.7	1.2
Atlantic Saury (*Scomberesox saurus*)	6.8	70.1	19.6	7.6	1.5	2.8	1.1
Herring[d] (*Clupea harengus*)	9.2	62.9	20.0	13.6	—	2.2	1.5

[a] Wet mass, protein = 20 kJ/g, fat = 38 kJ/g.
[b] Percentage protein/energy.
[c] Percentage lipid/energy.
[d] Based on cleaned fish (Adams 1975); probable overestimates.

acids (Lloyd et al. 1978) varied by no more than a factor of two among prey types. Avian protein needs during growth are not well understood, and it is difficult at present to assess the nutritional significance of the different protein levels.

Over the 13-week nestling period, captive chicks consumed, on average, 24,174 g of food containing about 190,550 kJ. The guano samples, collected from captives of about 6 weeks of age and combusted in a bomb calorimeter, averaged (± SD) 13.3 ± 0.8 kJ/g, which did not differ significantly (*t*-test) from the average energy density (12.8 ± 1.2 kJ/g; $n = 10$; range = 12.1–15.2 kJ/g; calculated from Cooper 1978) of the guano of two hand-reared Cape Gannet (*Sula capensis*) chicks. Systematic records of chicks' excretion were not kept, and Cooper's (1978) assimilation efficiency of 76.1% was used to estimate metabolizable energy (ME). The assumption that the efficiencies of these two congeneric species are similar is supported on many counts: (1) taxonomic affinity of *bassanus* and *capensis* (Nelson 1978a, b), (2) diet similarity of the two species (Nelson 1978a, b), (3) similar energy densities of chick's guano, and (4) the narrow range of assimilation efficiencies of fish-eating seabirds in general (e.g. Dunn 1975a, 1980).

Assuming 76.1% assimilation efficiency, we estimated that about 45,550 kJ were excreted, leaving 145,000 kJ of ME for growth, maintenance, temperature regulation, and activity. The chick's average weekly energy intake (and estimated ME) increased rapidly up to 6 weeks of age, after which intake appeared to decrease slightly and then level off (Fig. 5).

The energy accumulated in a developing animal's tissues per unit of energy either consumed or assimilated is an index of growth efficiency (Kleiber 1961). Dividing the net increase in carcass energy content between the date of hatching and 13 weeks (47,835 kJ) by total energy intake (190,550 kJ) and total ME (145,000 kJ) yields estimates of gross and net growth efficiencies of 25.1 and 33.0%, respectively, over the nestling period. During the first 8 weeks, the period of most rapid growth, gross and net growth efficiencies were 37.0 and 48.6%. These efficiencies are on the same order as those reported for most passerines (22–29%, Drent and Daan 1980) and for many other fish-eating seabirds (e.g. Koelink 1972, Brisbin cited in Westerterp 1973, Ricklefs 1983).

DISCUSSION

Gannet chicks grow rapidly, achieving a 40-fold increase in mass in the first 2 months of life (see also Montevecchi and Porter 1980, Kirkham and Montevecchi 1982). Similar growth rates have been reported for Northern Gannets in Scotland (Nelson 1964) and for Cape Gannets (Cooper 1978). Other species of sulids, the tropical, pelagic boobies in particular, grow much more slowly (Nelson 1978a, b). In comparison with other nonsulid Pelecaniformes, Northern Gannets gain weight at a rate similar to that of Brown Pelicans (*Pelecanus occidentalis*, K = 0.071, Ricklefs 1973) but slower than that of the smaller Double-crested Cormorants (*Phalacrocorax auritus*, K = 0.208, Dunn 1975b).

Lipid increase accounted for 60% of the energy accumulated by Northern Gannets during growth. Rising lipid and decreasing water levels resulted in a linear increase in energy density

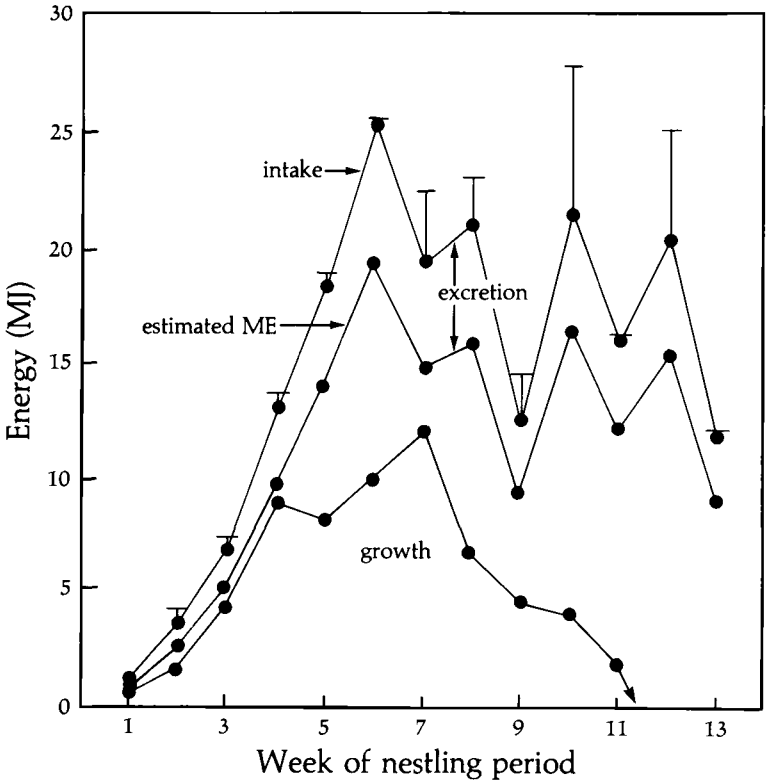

Fig. 5. Average (± SD) total energy intake of two captive Northern Gannet chicks and estimated metabolizable energy (ME) based on an assimilation efficiency of 76.1% (from Cooper 1978; see text for explanation).

with age, at least to 9 weeks (Fig. 4). Dunn (1975b) found a similar trend in Double-crested Cormorants and, after reviewing other studies, suggested that the energy densities of altricial chicks generally increase from about 3 kJ/g at hatching to 8 kJ/g at fledging. The energy densities of gannet neonates (3.4 kJ/g) are similar to that proposed by Dunn for other altricial neonates, but large lipid deposits in older chicks yielded densities (up to 14 kJ/g) that greatly exceeded those of other altricial fledglings.

Estimates of energy accumulated in tissues were obtained by converting lipid and non-lipid dry material to kJ (Fig. 3). Maintenance energy (activity and temperature regulation) was estimated as the difference between ME (Fig. 5) and growth energy and is compared to an estimate of BMR of gannet chicks, based on the Lasiewski and Dawson's (1967) equation for adult birds, in Table 2.

Growth requirements increased rapidly to a plateau between 6,000 and 12,000 kJ/week during weeks 4 through 8. Maintenance requirements showed wide weekly fluctuations, which we could not incorporate into our calculations of growth energy, that were probably due to changes in the chick's lipid content. Approximately 44% of the nestling's ME is allocated for growth (including the cost of biosynthesis); perhaps 33% is accumulated in tissues before fledging.

From 3 weeks, nestlings store increasing amounts of lipid, which accounts for most of the growth energy requirement. Parents tended to feed older chicks richer food (mackerel) than they fed to younger chicks which are more commonly fed capelin, a food with a higher protein to lipid ratio (see Montevecchi and Porter 1980). Subcutaneous fat reserves may be adaptive in the event of poor parental foraging

TABLE 2. Energy budget of a nestling Northern Gannet (see text).

Age (weeks)	Mass[a] (g)	Energy density[b] (kJ/g)	Accumulated energy (kJ)	Growth increment[c] (kJ/week)	Maintenance[d] (ME − GI) (kJ/week)	Maintenance[e] (equation) (kJ/week)
Hatch	79	3.35	265	—	—	—
1	194	4.47	867	801	151	701
2	409	5.59	2,286	1,888	737	1,202
3	834	6.71	5,596	4,402	793	2,013
4	1,643	7.83	12,865	9,667	113	3,286
5	2,122	8.95	18,992	8,149	5,674	3,954
6	2,632	10.07	26,504	9,991	9,327	4,620
7	3,189	11.19	35,685	12,211	2,532	5,307
8	3,282	12.31	40.401	6,273	9,733	5,419
9	3,425	13.0	44,525	4,124	5,302	5,588
10	3,732	13.0	48,516	3,991	12,411	5,947
11	3,877	13.0	50,401	1,885	10,245	6,113
12	3,702	13.0	48,126	−2,275	17,870	5,912
13	3,700	13.0	48,100	−26	9,021	5,910

[a] $\bar{x}$ weekly mass of two hand-raised chicks.
[b] From Fig. 4, energy density (kJ/g) = 3.35 + 0.16 age (days) up to 8 weeks, 13.0 thereafter.
[c] Assumes 75% production efficiency: 1.33 × weekly increment of accumulated energy.
[d] Metabolizable energy (ME) − growth increment (GI).
[e] BMR from Lasiewski and Dawson (1967) equation h: (kcal/day) = 78.3 M $(kg)^{0.723}$ multiplied by 7 to convert daily to weekly estimates and by 4.187 to convert kcals to Joules.

conditions (O'Connor 1978). Older gannet chicks show no overt deleterious effects from starvation lasting up to 2 weeks (Nelson 1978a, b; see also Schreiber 1976). With a maintenance requirement of no more than 6,000 kJ/week and a maximum lipid accumulation of 26,000 kJ (700 g), nestlings could easily survive extended periods without food. Lipid reserves must also sustain independent fledglings during their flightless period at sea.

Chicks lose weight during the third (and last) month of the nestling period, though they fledge with substantial fat reserves at masses in excess of those of adults (see Nelson 1978a, b). Accumulation of mass by nestlings in excess of adult levels, followed by prefledging recession, is common among marine birds with no postfledging care and among aerial foraging birds, such as hirundines (Harris 1966; Lack 1968; Ricklefs 1968a, b; Schreiber 1976; Ricklefs et al. 1980; cf. Sealy 1973, Dunn 1975b). Such mass recession is associated with decreased parental feeding rates, lowered feeding motivation among older chicks, and increased activity, mostly wing flapping (Montevecchi and Porter 1980; see also Ricklefs 1968b; Cooper 1978, 1979; Nelson 1978a).

Estimates of metabolizable energy requirements during the nestling period total 145,000 kJ (Table 2). On the basis of Lasiewski and Dawson's (1967) equation, adult resting metabolism equals 767 kJ/day or 5,369 kJ/week. The peak energy requirement of a chick, about 15,000 kJ/week, equals about 300% adult BMR, or about 150% per parent. Because females provide about 60% of the chick's food energy (Montevecchi and Porter 1980), the sexes make differential parental feeding investments: about 180% BMR/female and about 120% BMR/male. Males forage about 9 h/day and females about 6 h/day throughout the nesting season, based on periods of absence from the nest (Montevecchi and Porter 1980). Assuming a flight cost of 500% BMR (Cooper 1978, Hails 1979, Kirkham 1980), another 188% BMR would be added to the male's daily expenditure, 125% BMR to the female's, bringing the parental foraging and feeding energy totals of both sexes to virtual identity at 308% and 305% BMR, respectively. These hypothetical estimates are similar to those recently derived for Leach's Storm-Petrel (*Oceanodroma leucorhoa*, Ricklefs et al. 1980) and Lesser Sheathbills (*Chionis minor*, A. E. Burger pers. comm). Drent and Daan (1980) have estimated that the energy expenditure of breeding adults is about 400% BMR during sustained foraging.

The gannets' main foods (mackerel, capelin,

TABLE 3. Estimates of (A) the energy intake of the Northern Gannet population in Newfoundland and (B) their takes of different food items during the breeding season.

A

Age class	Number of birds	Energy intake (kJ/day)	Number of days	Total energy (kJ)
Breeding adults	18,688[a]	2,500[d]	210	9.81×10^9
Fledglings	6,728[b]	(190,500)		1.28×10^9
Nonbreeders	1,682[c]	2,000[e]	150[f]	0.51×10^9
Totals	27,098			11.60×10^9

B

Food item[g]	Percentage utilization[h]	Total energy take (kJ)	Tonnes[i]
Mackerel	46	5.34×10^9	518.5
Capelin	23	2.67×10^9	635.7
Squid	19	2.20×10^9	511.6
Herring	12	1.39×10^9	151.1

[a] Based on Montevecchi et al. (1980) and unpublished data.
[b] Assumes 80% hatching and 90% fledging success.
[c] Estimated at 9% of breeding population.
[d] 320% of estimated BMR.
[e] 250% of estimated BMR.
[f] Estimate of 5-month colony occupation for nonbreeders (Montevecchi unpubl. data).
[g] Gannets in Newfoundland also take other fish (see text).
[h] Derived from Kirkham et al. (MS).
[i] Total energy take/energy densities from Table 1.

squid, herring) in Newfoundland are commercially valuable, and it is useful to estimate the food needs of the population during the breeding season. In Newfoundland waters, gannets also take Atlantic saury (*Scomberesox saurus*), sand lance (*Ammodytes hexapterus*), cod (*Gadus morhua*), and salmon (*Salmo calar*), although, with the exception of saury, always in very small numbers (Kirkham et al. ms). The breeding population (about 9,344 pairs) in Newfoundland occupies three colonies for about 7 months (210 days, April–October), during which time they produce about 6,700 chicks (see Table 3). A substantial population of nonbreeders also occupies colony areas for about 5 months. These data are combined in Table 3 with energy intake estimates to yield an overall intake of 11.60×10^9 kJ of food. In Table 3, estimates of the population harvests of mackerel (518.5 t), capelin (635.7 t), squid (511.6 t), and herring (151.3 t) are derived. Whether these speculated levels of exploitation are in competition with local fisheries efforts (see Sanger 1972, Wiens and Scott 1975, Furness 1978) remains to be determined.

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