

CONTRASTING DIET QUALITY OF NORTHERN GANNETS *MORUS BASSANUS* AT TWO COLONIES

SUE LEWIS¹*, THOMAS N. SHERRATT², KEITH C. HAMER³,
MIKE P. HARRIS¹ & SARAH WANLESS¹



Lewis S., T.N. Sherratt, K.C. Hamer, M.P. Harris & S. Wanless 2003. Contrasting diet quality of Northern Gannets *Morus bassanus* at two colonies. *Ardea* 91(2): 167-176.

The diet of Northern Gannets *Morus bassanus* during chick rearing was determined at two colonies in the UK and Ireland that differed markedly in size (the Bass Rock with c. 40 000 breeding pairs, and Great Saltee with 2000 breeding pairs). Gannets from the Bass Rock took a significantly higher proportion of Mackerel *Scomber scombrus* than birds from Great Saltee. There was no significant difference between colonies in the proportion of sandeels (Ammodytidae), clupeids (Clupeidae) or gadoids (Gadidae), but birds from Great Saltee took a significantly higher proportion of other species than birds from the Bass Rock. These differences in diet between the colonies resulted in the average energy density of food loads being significantly higher at the Bass Rock than at Great Saltee. This pattern may reflect differences in the distribution and abundance of prey around the two colonies, but intrinsic factors may also be important, and these warrant further investigation.

Key words: *Morus bassanus* - seabird diet - energy density - chick-provisioning

¹* NERC Centre for Hydrology and Ecology, Banchory Research Station, Hill of Brathens, Banchory, Aberdeenshire AB31 4BW, UK; E-mail: suele@ceh.ac.uk; ²Department of Biology, 1125 Colonel By Drive, Carleton University, Ottawa, Ontario, Canada, K1S 5B6; ³Ecology and Evolution Group, School of Biology, University of Leeds, Leeds, LS2 9JT, UK.

INTRODUCTION

The food and foraging ecology of seabirds has been widely studied (Barrett *et al.* 1997; Croxall *et al.* 1999; Velando & Freire 1999; Cherel *et al.* 2002; Ainley *et al.* 2003). While extrinsic factors such as local prey availability might influence what different populations within a species will feed on (Watanuki *et al.* 1993; Tremblay & Cherel 2003), anthropogenic fishing pressure for forage fish and/or predatory fish may also influence the relationship between seabirds and their prey (Gislason & Kirkegaard 1996; Furness & Tasker 2000; Furness 2002). However, variation in diet between seabird populations may also be caused

by intrinsic differences, such as density dependent competition for food (Ashmole 1963; Lewis *et al.* 2001). Therefore, quantifying diet composition for a given species at more than one location is important in understanding the interaction of extrinsic and intrinsic effects on seabird foraging ecology.

The Northern Gannet *Morus bassanus* is an important top predator within its breeding range in the North Atlantic, as it is the largest pelagic seabird breeding in the area with high mass-specific energy requirements (Birt-Friesen *et al.* 1989). The gannet is a generalist predator known to take a wide range of prey species and sizes (Nelson 1978). Gannetries are widely distributed

around the north Atlantic and prey availability is therefore likely to differ between colonies. In addition, previous work has demonstrated intrinsic effects on foraging ecology: provisioning rates to chicks are lower at larger colonies (Lewis *et al.* 2001). However, no previous attempt has been made to quantify diet composition or energetic value at gannetries of different sizes. In this paper, we describe the diet of Northern Gannets at two colonies in the UK and Ireland which differ markedly in size. Second, we quantify the energy value of food loads. Together with provisioning rates (Lewis *et al.* 2001; Lewis *et al.* 2002), this has enabled us to compare the energy delivered per day at a large and a small colony.

METHODS

The study was carried out on Great Saltee, off the coast of Wexford, SE Ireland (52°8'30"N; 6°41'W) which has a breeding population of 2000 pairs (O. Merne pers. comm.) and the Bass Rock which is situated in the Firth of Forth, SE Scotland (56°6'N; 2°36'W), and currently has over 40 000 breeding pairs (Nelson 2002). At both colonies diet samples were collected in the middle of chick-rearing when most young were between three and six weeks old. On Great Saltee, 40 food samples were obtained from chicks that regurgitated during routine handling for ringing on 19 Jun and 17 Jul 2000. On the Bass Rock, 48 food samples were collected between 19 Jun and 15 Aug 2001 from adult breeders that regurgitated voluntarily when approached.

Diet analysis

A qualitative assessment was made of the species composition of samples immediately after collection. For most samples (73% for Great Saltee and 77% for the Bass Rock), it was possible to identify prey items in the field. Among these samples, individual prey items (typically belonging to large species such as Mackerel *Scomber scombrus* or Garfish *Belone belone*) were also isolated and the maximum length was measured with a ruler. The remainder of items

were too small to be counted or measured in the field. At both colonies, between 20 and 30% of all samples were too digested for any field observations or measurements to be taken. All samples, both intact and fragmented, were digested, and prey composition and size was derived indirectly from sagittal otoliths or vertebrae length (Härkönen 1986; Watt *et al.* 1997). Each regurgitate was placed in a saturated solution of biological washing powder (Biotex) and kept in an oven at 40-50°C for at least 5 h until flesh and soft material had been digested. All the remaining otoliths and fish bones were identified using a binocular microscope (25x magnification) and keys in Härkönen (1986) and Watt *et al.* (1997). In all cases, species identification by visual assessment was confirmed by vertebrae and/or otoliths. Sandeels (Ammodytidae) were separated into two age groups: 0 group (young of the year) and 1+ group (1 year or older). All the otoliths present in each sample were counted and measured, except for those containing >100 otoliths. Where a subset of 50 otoliths was measured. The total number of fish in each sample was determined in two ways a) visually for large fish which could be identified; b) for all other cases, the number of otolith pairs or unique otoliths (fish have two identical sagittal otoliths (Härkönen 1986). The exception for case b) was samples containing 0 group sandeels where only a subsample of otoliths was measured and therefore could not be classed as unique or one of a pair, the number of fish present being the total number of otoliths divided by two.

Energy densities

The lengths of individual fish in each sample were determined using species-specific otolith length/width-fish length equations or species-specific vertebrae length-fish length equations (Härkönen 1986; Watt *et al.* 1997). Equations were available in the literature for all prey species except Garfish, for which we used the lengths measured in the field (all Garfish present after digestion had been identified and measured visually). The total energy content of each fish was calculated by multiplying the mass (g), obtained

from species-specific length-mass equations in the literature, by the energy density (kJ g^{-1}) of the fish, also obtained from species-specific (and size-specific for some species) values in the literature (see Appendix 1). Where more than one reference was available, the most recent one was used. For a few species we were unable to find appropriate equations in the literature, and in these cases, we used the equation for the most closely related species. The mean energy density (kJ g^{-1}) for each sample was calculated by dividing the total energy content (kJ) by the total mass (g).

Statistical analysis

The presence or absence of the four main prey types (sandeels, Mackerel, clupeids and gadoids) and a final category containing all “other” prey species was recorded for each diet sample. For each colony, the number of samples of each possible combination of presence/absence of the five prey types ($n = 32$) was counted. A table of diet distribution was formulated containing 64 rows (32×2 colonies) and seven columns (five prey types, colony, number of records). A type III generalised linear model (GLM) with a Poisson error distribution and a logarithm link function was fitted using Genstat 5, release 4.2, and the inter-colony diet differences assessed from the interactions between colony and prey type. The model was instructed to remove the two rows with forced zeros prior to analysis, where all prey types were absent, which could not occur because all our samples contained at least one of the five types. The deviance values show the effect of removing each term from the model and are distributed by χ^2 . The analysis was repeated using only the subset of the Bass Rock samples that spanned the same period of the season as the samples from Great Saltee. This sub-sample at the Bass Rock were collected from 19 Jun to 28 Jul ($n = 36$). In addition, seasonal changes in diet on the Bass Rock were tested for by carrying out a similar analysis design of the above. A table of diet composition on the Bass Rock was constructed with 96 rows (32 rows $\times 3$ months: Jun, Jul and Aug). A *t*-test was used to compare the energy values of food samples between the two colonies.

RESULTS

Prey species recorded at Great Saltee were sandeels (Lesser Sandeel *Ammodytes marinus* and Greater Sandeel *Hyperoplus lanceolatus*), gadoids (Whiting *Merlangius merlangus*, Norway Pout *Trisopterus esmarkii* and unidentified gadoids), Mackerel, Garfish, clupeids (Herring *Clupea harengus* and Sprat *Sprattus sprattus*), Plaice *Pleuronectes platessa*, Hake *Merluccius merluccius*, Red Gurnard *Aspitrigla cuculus*, Dragonet *Callionymus lyra*, Bull-rout *Myoxocephalus scorpius*, Salmon *Salmo salar* and Scad *Trachurus trachurus* (see Table 1a). 0 and 1 + group sandeels were present in samples in similar frequencies. The length of individual prey items varied widely from 55 mm (0-group sandeels) to 650 mm (Garfish) (see Table 2a). On the Bass Rock, prey recorded were Lesser Sandeel, Mackerel, clupeids (herring and sprat), gadoids (Cod *Gadus morhua*, Haddock *Melanogrammus aeglefinus*, Whiting, Norway Pout), flatfish (Habit *Hippoglossus hippoglossus* and Long Rough Dab *Hippoglossoides platessoides*), Hake, Red Gurnard and Dragonet (see Table 1b). 0 group sandeels were much more abundant than 1+: only two food samples contained 1+ sandeels, compared to 23 with 0 group. The length of individual prey items varied widely from 60 mm (0-group sandeels) to 407 mm (Mackerel) (see Table 2b).

There were no significant differences in the relative frequency of occurrence of sandeels, clupeids, or gadoids in each sample, between colonies (Fig. 1, GLM, sandeel * location: deviance = 1.73, $P = 0.19$; clupeid * location: deviance = 0.26, $P = 0.61$; gadoid * location: deviance = 0.91, $P = 0.33$). However, there were significant interactions between Mackerel and colony and “other” prey items and colony (Fig. 1, GLM, Mackerel * location: deviance = 9.53, $P = 0.002$; other * location: deviance = 15.21, $P < 0.001$). Thus, more food samples contained Mackerel on the Bass Rock than Great Saltee, while more samples from Great Saltee contained “other” prey types. Comparing just the sandeel component of the diet, samples from the Bass Rock were composed mainly of 0 group, while those from Great

Table 1. Diet of Northern Gannets *Morus bassanus* at (A) Great Saltee in 2000 ($n = 40$; from chicks) and from regurgitates from (b) the Bass Rock in 2001 ($n = 48$; from adults).

A) Species	Frequency of occurrence (%)		
	Jun ($n = 15$)	Jul ($n = 25$)	All ($n = 40$)
Ammodytidae	33	36	35
0 group	13	12	13
1+ group	20	28	25
Gadidae	33	16	23
Scombridae	13	24	20
Belonidae	7	20	15
Clupeidae	27	4	13
Pleuronectidae	7	16	13
Merlucciidae	7	8	8
Triglidae	13	4	8
Callionymidae	13	4	8
Cottidae	0	4	3
Salmonidae	7	0	3
Carandidae	7	0	3

B) Species	Frequency of occurrence (%)			
	Jun ($n = 8$)	Jul ($n = 29$)	Aug ($n = 11$)	All ($n = 48$)
Ammodytidae	50	55	36	48
0 group	50	55	36	48
1+ group	0	7	0	4
Scombridae	50	41	55	46
Clupeidae	0	10	36	15
Gadidae	25	14	0	13
Pleuronectidae	0	3	9	4
Merlucciidae	0	3	0	2
Triglidae	13	0	0	2
Callionymidae	0	3	0	2

Saltee were slightly biased towards older age classes (Table 1). Repeating the analysis using only those diet samples from the Bass Rock that were collected at the same time of season as on Great Saltee, very similar results were obtained (GLM, sandeel * location: deviance = 2.45, $P = 0.12$; clupeid * location: deviance = 0.17, $P = 0.68$; gadoid * location: deviance = 0.17, $P = 0.68$; Mackerel * location: deviance = 7.32, $P = 0.007$; other * location: deviance = 13.39, $P < 0.001$).

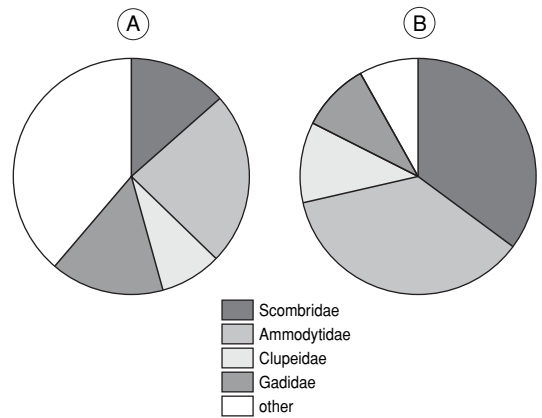


Fig. 1. Percentage of regurgitates from Northern Gannets containing Ammodytidae, Scombridae, Clupeidae, Gadidae and Other prey items at (a) Great Saltee in 2000 ($n = 40$) and (b) the Bass Rock in 2001 ($n = 48$).

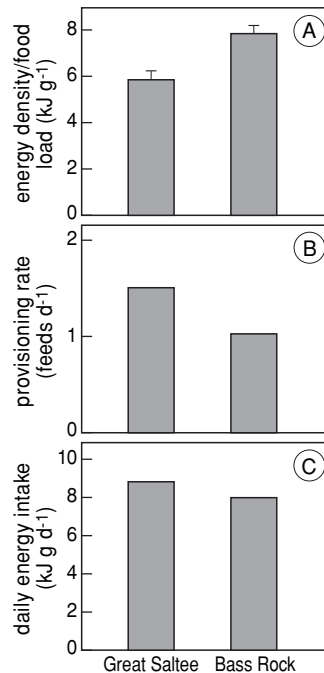


Fig. 2 (a) Mean \pm SE energy density (kJ g^{-1}) of a food sample, (b) mean daily provisioning rate (taken from Lewis *et al.* 2001) and (c) mean daily energy intake (kJ) by Northern Gannets on Great Saltee and the Bass Rock in 2000 and 2001 respectively.

Table 2a. Mean lengths (mm) and total number of fish present in 40 food samples from Northern Gannets *Morus bassanus* at Great Saltee in 2000.

Family	Species	<i>n</i> fish	length (mm)	SD	min	max
Ammodytidae	Lesser Sandeel					
	0 group	5	82.5	26.3	55	115
	1+ group	4	180.1	36.9	149	232
	Greater Sandeel					
	0 group	6	161.8	19.2	127	184
	1+ group	6	276.4	32.8	257	314
Scombridae	Mackerel	8	315.1	85.2	119	400
Clupeidae	Herring	9	158.3	103.7	78	410
Belonidae	Garfish	6	358.3	142.9	300	650
Pleuronectidae	Plaice	4	210.8	26.3	187	248
Gadidae	Whiting	6	293.1	6.2	187	375
	Norway Pout	1	217.0		217	
Merlucciidae	Hake	4	283.0	33.1	236	312
Triglidae	Red Gurnard	3	340.3	40.1	297	376
Callionymidae	Dragonet	3	256.3	21.9	239	281
Cottidae	Bull-rout	1	119.0		119	
Salmonidae	Salmon	1	241.0		241	
Carangidae	Scad	1	279.0		279	

There was no evidence for a change in diet composition through the season on the Bass Rock (GLM, sandeel * month: deviance = 0.94, $P = 0.39$; clupeid * month: deviance = 2.01, $P = 0.13$;

gadoid * month: deviance = 1.80, $P = 0.17$, Mackerel * month: deviance = 0.15, $P = 0.86$; other * month: deviance = 0.05, $P = 0.95$). Average energy densities of food samples collect-

Table 2b: Mean lengths (mm) and total number of fish present in 48 food samples from gannets *Morus bassanus* at the Bass Rock in 2001.

Family	Species	<i>n</i> fish	length (mm)	SD	min	max
Ammodytidae	Lesser Sandeel					
	0 group	1161	84.8 *	9.2	60	110
	1+ group	5	109.1	17.9	91	135
Scombridae	Mackerel	17	312.4	35.1	260	407
Clupeidae	Sprat	44	81.6	13.4	64	117
Gadidae	Cod	1	230.0		230	
	Haddock	7	240.6	68.9	155	343
	Whiting	3	246.7	55.0	192	302
	Norway Pout	1	99.0		99	
Pleuronectidae	Halibut	1	339.0		339	
	Long Rough Dab	2	95.5	14.9	85	106
Merlucciidae	Hake	1	220.0		220	
Callionymidae	Dragonet	1	219.0		219	
Triglidae	Red Gurnard	1	150.0		150	

* mean is based on a subsample of otoliths

ed from Great Saltee and the Bass Rock are shown in Fig. 2a. The mean energetic value of a food load was significantly greater for the Bass Rock than for Great Saltee (Fig. 2b, t -test $t_{73} = 3.421$, $P = 0.001$).

DISCUSSION

Our results accord well with those from previous studies. The Northern Gannet has a broad diet, taking very small prey such as 0 group sandeels and large species such as Mackerel (Nelson 1978; Montevocchi *et al.* 1984; Wanless 1984; Montevocchi & Barrett 1987; Martin 1989; Hamer *et al.* 2000). To our knowledge, our study is the first to describe diet data of Great Saltee gannets. However, we must acknowledge that our data come from only two sampling days. While we need to be cautious about generalising from these data, the sampling dates were well separated and reasonable sample sizes were collected each day. Clearly it would be useful to collect more data from this colony in the future. Bearing in mind these caveats, our results nevertheless indicate that diet at the two colonies differed to a large extent, with prey types differing in energy density by a factor of three (Murray & Burt 1969; Pedersen & Hislop 2001). Gannets on the Bass Rock took considerably more Mackerel than birds from Great Saltee, which took more items in the "other" prey category. Sandeels tended to be a more important part of the diet of birds from the Bass Rock although this difference was not statistically significant. There was no difference in the occurrence of clupeids and gadoids at the two colonies (see Fig. 1). The difference in energy density was largely explained by the greater importance of energy-rich Mackerel in the diet of birds at this colony. Our patterns were not caused by seasonal differences in sampling dates between the two colonies, because when we sub-sampled only those dates from the Bass Rock that coincided with the dates from Great Saltee the inter-colony patterns were the same. Moreover, we could not detect any seasonal pattern in diet composition at the Bass Rock.

A second potential reason for the difference in

diet between the two colonies could be that Great Saltee samples came from chicks while those from the Bass Rock were from adults. While this bias would be serious in species that carry food for the chick in the bill, such as some auks and terns (Davoren & Burger 1999), this is less serious for species such as gannets that feed their chicks by regurgitation. We therefore consider it unlikely that the food present in the stomach of parent birds at the colony is divided into food for its chick versus food retained for itself. Thus while we cannot rule this out explicitly it seems to us unlikely that this factor alone could explain the large variation in diet observed between the Bass Rock and Great Saltee.

A third potential explanation is a year effect since data were collected in two different seasons. However again we think this is an unlikely cause for the differences in diet observed between the two colonies. Although our study is the first to describe diet data at Great Saltee, diet data have been collected at the Bass Rock in several other years both before and since this study (1998; Hamer *et al.* 2000; 2002 and 2003; *pers. obs.*). Diet composition has been consistent during this time with Mackerel and 0 group sandeel dominating in all years. This consistency has been maintained despite variations in abundance and recruitment of Mackerel and 0 group sandeels among years (ICES 2002). The variation between colonies is much greater than variation within a colony between years. We think it unlikely therefore that, had we collected diet data on the Bass Rock in 2000, that the diet would have been dominated by similar species as Great Saltee.

We consider that a more likely explanation for the inter-colony differences in diet observed is that prey distribution and abundance differed between the North Sea and the Celtic Sea. Indeed differences in prey distribution was suggested by Hamer *et al.* (2001), as a possible reason for explaining why gannets on the Bass Rock showed a significantly higher degree of foraging site fidelity than those from Great Saltee. The 'other' species category was more widely represented at Great Saltee, including a number of species, particularly benthic fish (e.g., Plaice) that must have

come from fishery discards because Northern Gannets are not believed to be substrate feeders (Nelson 1978), although they have been observed down to 34m (Brierley & Fernandes 2001). Indeed the presence of Northern Gannets scavenging behind trawlers has already been highlighted (Furness *et al.* 1992; Camphuysen *et al.* 1995). Thus, it is possible that differences in the availability of this human source of food may contribute to the differences in diet observed between the colonies. Alternatively diet differences between the two colonies could also have arisen due to intrinsic effects. Recent evidence has shown that gannets from larger colonies travel further to collect food for their offspring (Lewis *et al.* 2001). Such trips last longer and chicks at larger colonies are therefore provisioned at a lower rate than those at smaller colonies. Results indicated that feeding rates were 32% lower at the Bass Rock in 2001 (Lewis *et al.* 2002) than Great Saltee in 2000 (Lewis *et al.* 2001). However, results from this study show that energy density of food was 34% higher at the Bass Rock. The net result is that in energetic terms the difference between the colonies was only 9% (Figure 2c). Since lower provisioning rates are predicted to affect population processes through breeding success and survival of adults and offspring (Ashmole 1963), the extent of intra-specific competition may affect the choice of prey. Thus, birds from larger colonies should select higher quality prey items in their diet to compensate for the lower provisioning rate. If this is the case, it would appear that the Bass Rock gannets are partially able to compensate, which may explain why breeding success in gannets does not differ in terms of colony size (Upton *et al.* 2000). Data from other UK gannetries at Hermaness and Ailsa Craig, have shown that diet can change over time (Wanless 1984; Martin 1989), but these shifts were associated with very marked changes in prey abundance during the study period. Ainley *et al.* (2003) found that diet variation did not explain differences in population growth and emigration rates among colonies of Adelie Penguins *Pygoscelis adeliae*. However, in their study all four colonies were situated within one cluster,

and therefore not geographically separate. To disentangle whether intra-specific variation in diet is due to geographic differences in prey, or active selection to compensate for density dependent effects clearly requires a much wider study on numerous, isolated colonies of different size. The Northern Gannet, with its generalised diet and established relationship between provisioning rate and colony size would potentially be a good model species for such an investigation.

ACKNOWLEDGEMENTS

We thank Francis Daunt, Oscar Merne, Luisa Money, Kelly Redman and Alyn Walsh for help in the field; Dave Carss and Mick Marquiss for assistance with prey identification; the Neale family for access to Great Saltee and Martin and Lynda Smyth for logistical support in Ireland; Sir Hew Hamilton-Dalrymple for access to the Bass Rock, and Bryan Nelson, the Marr Family and the McNicol Family for logistical support. Francis Daunt and two anonymous referees provided constructive comments on the manuscript and David Elston gave statistical advice. We thank John Croxall for support and assistance in developing the project on the Bass Rock. This work was funded by a Natural Environment Research Council Case Studentship GT04/99/55 to S.L. This work complies with the current laws within the UK.

REFERENCES

- Ainley D.G., G. Ballard, K.J. Barton, B.J. Karl, G.H. Rau, C.A. Ribic & P.R. Wilson 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. *Condor* 105: 95-106.
- Ashmole N.P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458-473.
- Barrett R.T., V. Bakken & J.V. Krasnov 1997. The diets of Common and Brunnich's Guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. *Polar Res.* 16: 73-84.
- Birt-Friesen V.L., W.A. Montevecchi, D.K. Cairns & S.A. Macko 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. *Ecology* 70: 357-367.
- Brierley A.S. & P.G. Fernandes 2001. Diving depths of Northern Gannets: acoustic observations of *Sula bassana* from an autonomous underwater vehicle. *Auk* 118: 529-534.
- Camphuysen C.J., Calvo B., Durinck J., Ensor K., Follestad A., Furness R.W., Garthe S., Leaper G., Skov H., Tasker M.L. & Winter C.J.N. 1995. Consumption of discards by seabirds in the North Sea. Final report to the European Comm., study contr. BIOECO/93/10, NIOZ-Report 1995-5, Netherlands Institute for Sea Research, Texel.
- Carss D.N. 1993. Shags *Phalacrocorax aristotelis* at cage farms in Argyll, western Scotland. *Bird Study* 40: 203-211.

- Cherel Y., P. Bocher, C. Trouve & H. Weimerskirch 2002. Diet and feeding ecology of Blue Petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar. Ecol. Prog. Ser.* 228: 283-299.
- Coull K.A., A.S. Jermyn, A.W. Newton, G.I. Henderson & W.B. Hall 1989. Length/weight relationships for 88 species of fish encountered in the north east Atlantic. Rep. Nr. 43. Scottish Fisheries Research. Department of Agriculture and Fisheries for Scotland.
- Croxall J.P., K. Reid & P.A. Prince 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar. Ecol. Prog. Ser.* 177: 115-131.
- Davoren G.K. & A.E. Burger 1999. Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Anim. Behav.* 58: 853-863.
- Elliot J.M. 1976. Body composition of Brown Trout (*Salmo trutta*) in relation to temperature and ration size. *J. Anim. Ecol.* 45: 273-289.
- Furness R.W. 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. *Ices J. Mar. Sci.* 59: 261-269.
- Furness R.W., K. Ensor & A.V. Hudson 1992. The use of fishery waste by gull populations around the British Isles. *Ardea* 80: 105-113.
- Furness R.W. & M.L. Tasker 2000. Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar. Ecol. Prog. Ser.* 202: 253-264.
- Gislason H. & E. Kirkegaard 1996. The industrial fishery and the North Sea sandeel stock Seminar on the Precautionary Approach to North Sea Fisheries Management, Oslo.
- Hamer K.C., R.A. Phillips, J.K. Hill, S. Wanless & A.G. Wood 2001. Contrasting foraging strategies of Gannets *Morus bassanus* at two North Atlantic colonies. *Mar. Ecol. Prog. Ser.* 224: 283-290.
- Hamer K.C., R.A. Phillips, S. Wanless, M.P. Harris & A.G. Wood 2000. Foraging ranges, diets and feeding locations of Gannets in the North Sea: evidence from satellite telemetry. *Mar. Ecol. Prog. Ser.* 200: 257-264.
- Härkönen T. 1986. Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu ApS, Hellerup, Denmark.
- Harris M.P. & J.R.G. Hislop 1978. The food of young Puffins *Fratercula arctica*. *J. Zool. Lond.* 185: 213-236.
- Hislop J.R.G., M.P. Harris & J.G.M. Smith 1991. Variation in the calorific value and total energy content of the Lesser Sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J. Zool.* 224: 501-517.
- ICES 2002. Report of the ICES Advisory Committee on the Fisheries Management, Copenhagen.
- Lewis S., S. Benvenuti, L. Dall'Antonia, R. Griffiths, L. Money, T.N. Sherratt, S. Wanless & K.C. Hamer 2002. Sex specific foraging behaviour in a monomorphic seabird. *Proc. Roy. Soc. Lond. B* 269: 1687-1693.
- Lewis S., T.N. Sherratt, K.C. Hamer & S. Wanless 2001. Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412: 816-819.
- Martin A.R. 1989. The diet of Atlantic puffin *Fratercula arctica* and Northern Gannet *Sula bassana* chicks at a Shetland colony during a period of changing prey availability. *Bird Study* 36: 170-180.
- Montevocchi W.A. & R.T. Barrett 1987. Prey selection by Gannets at breeding colonies in Norway. *Orn. Scand.* 18: 319-322.
- Montevocchi W.A., R.E. Ricklefs, I.R. Kirkham & D. Gabaldon 1984. Growth energetics of nestling Northern Gannets (*Sula bassanus*). *Auk* 101: 334-341.
- Murray J. & J.R. Burt 1969. The Composition of Fish. Report No. 38, Tory Research Station. Ministry of Agriculture Fisheries and Food.
- Nelson J.B. 1978. The Gannet. T. and A.D. Poyser, London.
- Nelson J.B. 2002. The Atlantic Gannet. Fenix Books Ltd., Norfolk.
- Pedersen J. & J.R.G. Hislop 2001. Seasonal variations in the energy density of fishes in the North Sea. *J. Fish Biol.* 59: 380-389.
- Sidwell V.D. 1981. Chemical and nutritional composition of finfishes, whales, crustaceans, mollusks and their products. NOAA technical memorandum NMFS FISEC-II.
- Thorpe J.E. 1979. A trout population survey of the major tributaries in August 1979. Unpublished report, Loch Leven Research Group 1978-1979.
- Tremblay Y. & Y. Cherel 2003. Geographic variation in the foraging behaviour, diet and chick growth of Rockhopper Penguins. *Mar. Ecol. Prog. Ser.* 251: 279-297.
- Upton A.J., G. Pickerell & M. Heubeck 2000. Seabird numbers and breeding success in Britain and Ireland, 1999. JNCC, Peterborough.
- Velando A. & J. Freire 1999. Intercolony and seasonal differences in the breeding diet of European shags on the Galician coast (NW Spain). *Mar. Ecol. Prog. Ser.* 188: 225-236.
- Wanless S. 1984. The growth and food of young Gannets *Sula bassana* on Ailsa Craig. *Seabird* 7: 62-70.
- Watanuki Y., A. Kato, Y. Mori & Y. Naito 1993. Diving performance of Adélie Penguins in relation to food availability in fast sea-ice areas: comparison between years. *J. Anim. Ecol.* 62: 634-646.
- Watt J., G.J. Pierce & P.R. Boyle 1997. Guide to the identification of North Sea fish using premaxillae and vertebrae. ICES Cooperative Research Report No. 220.

SAMENVATTING

Het menu van Jan van Genten *Morus bassanus* tijdens de kuikenzorg werd bestudeerd in een Schotse kolonie (Bass Rock, 40 000 paren) en in een Ierse kolonie (Great Saltee, 2000 paren). De Jan van Genten van Bass Rock consumeerden veel meer Makreel *Scomber scombrus* dan de vogels in Ierland. Er was geen significant verschil in de proporties zandspiering Ammodytidae, haringachtigen Clupeidae en kabeljauwachtigen Gadidae, maar het totaal aan andere vissoorten (dus geen Makreel) was op Great Saltee proportioneel groter dan op de Bass Rock. Het verschil in prooi-soorten resulteerde in gemiddeld veel energierijker voedsel voor de vogels in Schotland dan voor hun Ierse soortgenoten. Dit werd vermoedelijk veroorzaakt door een

verschil in voedselaanbod rondom de beide kolonies, maar intrinsieke factoren kunnen aan het gevonden verschil hebben bijgedragen. Hieraan zal in de toekomst aandacht worden besteed. Zo is recent aangetoond dat broedvogels van grotere kolonies veel langere voedselvluchten ondernemen, waardoor er veel langere tussenpozen tussen voedingssessies voorkomen. Een voorkeur voor energierijkere prooien ligt dan voor de hand ter compensatie van de schaarsere leveranties aan het jong. Op Bass Rock was de frequentie van voedselaanvoer voor de jongen 32% lager dan op Great Saltee, terwijl de energiedichtheid van de voedselbolussen op de

Bass Rock 34% hoger was. Het nettoverschil tussen beide kolonies bedroeg als gevolg daarvan slechts 9%. De resultaten suggereren dat de vogels van Bass Rock in staat waren om door het vinden van vette, energierijke vis te compenseren voor hun noodzaak tot het maken van lange voedselvluchten. Dit vermogen verklaart waarom grote kolonies niet per se tot een kleiner broedsucces aanleiding behoeven te geven. (CJC)

Corresponding editor C.J. Camphuysen

Received 1 October 2003; accepted 3 November 2003

Appendix 1. Species specific equations used to convert bone length to fish length (column two) and fish length to fresh mass (column three) and fresh mass/fish length to energy (column four). FL = fish length (mm for column two and cm for columns three and four), OL = otolith length (mm), OW = otolith width (mm) VL = vertebrae length (mm), M = mass (g), E = energy (kJ) and ED = energy density values (kJ g⁻¹). ln = natural log. * ED show size specific (mm) energy density ranges for Jul (kJ g⁻¹). References: (a) (Härkönen 1986); (b) (Watt *et al.* 1997); (c) (Harris & Hislop 1978); (d) (Coull *et al.* 1989); (e) (Carss 1993); (f) (Thorpe 1979); (g) (Hislop *et al.* 1991); (h) (Pedersen & Hislop 2001); (i) (Murray & Burt 1969); (j) (Sidwell 1981); (k) (Elliot 1976); (l) (Montevecchi *et al.* 1984).

Fish species	bone (mm) to fish length (mm)	ref	fish length (cm) to fish mass (g)	ref	fresh mass (g)/length (cm) to energy (kJ)	ref
Ammodytidae						
Lesser Sandeel <i>Ammodytes marinus</i>	FL=8.776+51.906 OL	a	M=0.00209 FL ^{3.148}	c	E=0.0081 FL ^{3.427}	g
Greater Sandeel <i>Hyperoplus lanceolatus</i>	FL=-4.024+56.84 OL	a	use Lesser Sandeel	c	ED=3.81	j
Belonidae						
Garfish <i>Belone belone</i>	measure intact fish		M=0.002 FL ^{3.442}	d	ED=3.52	j
Callyonymidae						
Dragonet <i>Callionymus lyra</i>	FL=VL/0.028	b	M=0.22 FL ^{2.5907}	d	use Red Gurnard	i
Carangidae						
Scad <i>Trachurus trachurus</i>	FL=VL/0.024	b	use Mackerel	d	ED=4.94	j
Clupeidae						
Herring <i>Clupea harengus</i>	FL=-87.49+184.39 OW	a	M=0.00254 FL ^{3.289}	c	* ED=4.1-11.9 (40-299)	h
Sprat <i>Sprattus sprattus</i>	FL=-25.28+137.24 OW	a	M=0.009708 FL ^{2.855}	c	E=0.0096 FL ^{3.845}	g
Cottidae						
Bull-rout <i>Myoxocephalus scorpius</i>	FL=VL/0.014	b	M=0.0096 FL ^{3.20}	e	use Red Gurnard	i
Gadidae						
Cod <i>Gadus morhua</i>	FL=-202.13+48.37 OL	a	M=0.00626 FL ^{3.109}	c	ED=3.06	j
Haddock <i>Melanogrammus aeglefinus</i>	FL=8.785 OL ^{1.38}	a	M=0.01 FL ^{2.914}	c	* ED=3.9-5.6 (100-549)	h
Whiting <i>Merlangius merlangus</i>	FL=-11.936+19.7 OL	a	M=0.00854 FL ^{2.978}	c	* ED=3.8-5.4 (50-299)	h
Norway Pout <i>Trisopterus esmarkii</i>	FL=-42.6+29.522 OL	a	M=0.0101 FL ^{2.730}	c	* ED=3.9-5.7 (40-199)	h
Merlucciidae						
Hake <i>Merluccius merluccius</i>	FL=-0.63+23.884 OL	a	M=0.0047 FL ^{3.099}	d	ED=3.43	j
Pleuronectidae						
Plaice <i>Pleuronectes platessa</i>	FL=-3.81+47.63 OL	a	use Long Rough Dab	d	ED=3.89	j
Halibut <i>Hippoglossus hippoglossus</i>	FL=-413.93+105.79 OL	a	use Long Rough Dab	d	ED=5.40	j
Long Rough Dab <i>H. platessoides</i>	FL=-24.52+48.35 OL	a	M=0.0044 FL ^{3.2039}	d	ED=2.40-3.60	j
Salmonidae						
Salmon <i>Salmo salar</i>	FL=4.7643+0.8239 ln VL	b	M=0.0195 FL ^{2.822}	f	ED=5.23	j
Scombridae						
Mackerel <i>Scomber scombrus</i>	FL=VL/0.024	b	M=0.00381 FL ^{3.21}	d	ED=10.3	k
Triglidae						
Red Gurnard <i>Aspitrigla cuculus</i>	FL=16.7+71.92 OL	a	M=0.0045 FL ^{3.2228}	d	ED=3.78-4.34	i