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Diet of Northern Gannet *Morus bassanus* chicks in North Norway

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Abstract. Northern Gannets *Morus bassanus* established colonies in North Norway in the 1960s, since when the breeding population has increased and spread north- and eastwards. Diet data collected at several colonies in North Norway confirm the Gannet's opportunistic foraging behaviour with Atlantic herring *Clupea harengus*, Atlantic mackerel *Scomber scombrus*, sandeels Ammodytidae and saithe *Pollachius virens* being the main prey brought to chicks. As such, climate change is unlikely to have a negative effect on the Gannet population in the region.

Key words: chick diet; climate; Norwegian Sea; Barents Sea

INTRODUCTION

Since the early 1900s, the population of the Northern Gannet (*Morus bassanus*, hereafter Gannet) has been increasing throughout its breeding range on both sides of the North Atlantic at a rate of about 3% y^{-1} (Nelson 2002, Murray et al. 2015a, Newton et al. 2015). The Gannet first colonised Norway in the southwest of the country (at Runde) in the mid-1940s and spread to three colonies in North Norway in the early 1960s (Brun 1967, 1970). Since then, North Norwegian numbers have risen steadily, albeit with some regional differences in progression, to 3300 pairs in 2015–2016 that bred on seven colonies spread along the coast between the tip of the Lofoten Islands and East Finnmark (Barrett unpubl. data).

The first birds to colonise North Norway were probably immigrants from the then (and still) rapidly increasing population in Britain. The first indications of this were pre-1971 controls outside breeding colonies in Norway of 31 birds ringed on colonies between the English Channel and Shetland followed by one bird ringed on Ailsa Craig, Scotland found breeding on Skarvklakken (Fig. 1) in 1970 and 1971 (Brun 1972).

The spread of Gannets to Norway was possibly associated with the highly productive waters and especially the large stocks of Norwegian spring-spawning Atlantic herring *Clupea harengus* that occur along the Norwegian coast (Brun 1970, 1972), although no empirical diet data were collected at the time. The periodical rich abundances of young saithe *Pollachius virens* in Vesterålen and spawning capelin *Mallotus villosus* in Finnmark (and sometimes as far west as Vesterålen in the Gannet pre-breeding period) were also suggested to have attracted the Gannets northwards (Brun 1972). That food for Gannets is plentiful in the region was partly corroborated by a later study that showed that prey availability was not a limiting factor during a period of population decrease and colony extinctions in the Lofoten/Vesterålen area between 1990 and 2006 (Pettex et al. 2015). Whereas adult survival rate is the most decisive demographic trait affecting population changes of long-lived seabirds, the survival and growth of chicks also play an important role (Sandvik et al. 2012). The latter is, in turn, much dependent on the quantity and quality of food brought by the parents. Changes in Gannet populations are often attributed to local food availability (e.g. Crawford et al. 2007) and this note summarizes all diet data collected at North Norwegian Gannet colonies between 1985 and 2016 as a contribution to understand better drivers of the increase in North Norway.

MATERIAL AND METHODS

Food samples were collected at four colonies: Storstappen (71° 09'N, 25° 19'E), Skarvklakken (69° 09'N, 15° 39'E), Store Ulvøyholmen (68° 31'N, 14° 31'E) and Hovsflesa (68° 22'N, 14° 00'E) (Figure 1). Due to very limited possibilities of access to the colonies, food data were generally collected during irregular and single 1–2 h visits to the colony early in the chick-rearing period when the main task was to ring chicks. Only Skarvklakken and Ulvøyholmen were visited on two or more days in a single season (Table 1). The study was based on regurgitates produced by adults and sometimes nestlings before our arrival or when disturbed by us. In early studies, any fish that could be identified were noted in the field. In some cases, approximate lengths of individual fish that had not been digested too much were also measured. After

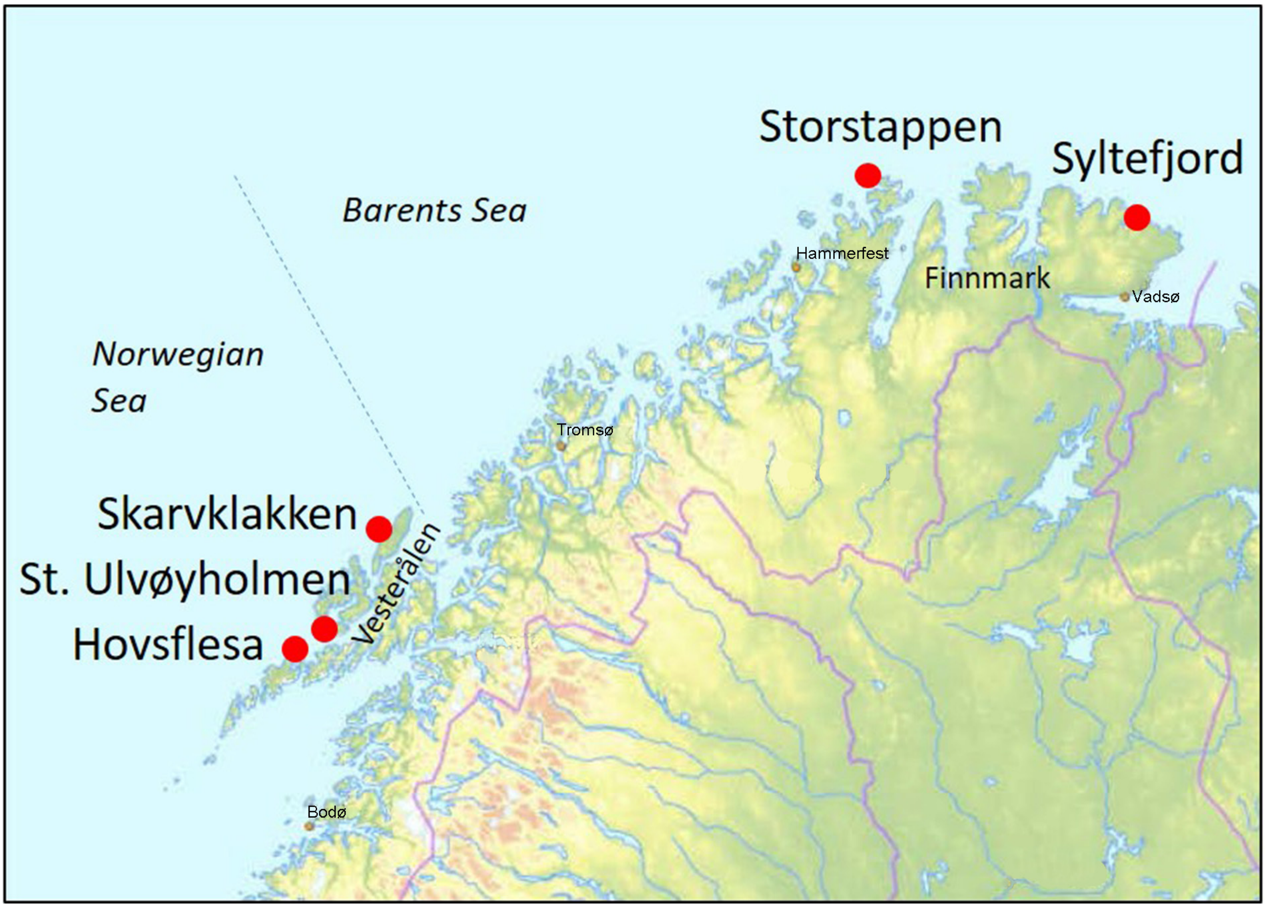

Figure 1. North Norwegian Northern Gannet colonies mentioned in the text. The dotted line indicates the approximate boundary between the Norwegian Sea and Barents Sea.

2008, regurgitations were collected and individually frozen in plastic bags for subsequent analysis in the laboratory. After thawing, preliminary identification and 24 h digestion at 50 °C in a strong solution of biological washing powder, the taxonomic composition of each sample was determined from the remaining otoliths, vertebrae and other hard body parts (see Pettex et al. 2015 for details). The overall compositions were expressed both as % by mass using Swanson et al.'s (1974) aggregated percentage of prey biomass method and as % by frequency of occurrence. Approximate prey size was determined from relationships between otolith and/or vertebrate lengths in Jobling and Breiby (1986) or Watt et al. (1997). To determine approximate lengths of Atlantic mackerel *Scomber scombrus*, a relationship between tail length (often little digested in regurgitations and easily measured) and total length determined from measurements of pictures of fish found in the internet (fish length/tail length, mean = 7.05, SE = 0.11, n = 31). Approximate fish masses were calculated using the relationship $M=aL^b$ (where M = mass in g, L = total length in cm and a and b are constants taken from Coull et al. 1989; Table 1)

Table 1. Constants a and b for mass-length relationships for fish regurgitated by Northern Gannets in Norway where Mass = a × Total length^b, from Coull et al. (1989)

	a	b
Atlantic Herring	3.01	0.01
Atlantic Mackerel	3.21	0.03
Sandeel	3.32	0.01
Saithe[A]	2.74	0.02

[A] gutted weight (GW). Total mass = GW×1.19

RESULTS

Four colonies (Figure 1) were sampled between 1985 and 2016. Hovsflesa was sampled twice, Skarvklakken and Storstappen four times and Store Ulvøyholmen six times (Table 2). Very brief field notes made on Skarvklakken in 1978 and 1981 and at Hovsflesa in 1979 were also included in the analysis. In 564 (93%) of the 605 samples collected or registered, regurgitations consisted of a single prey species such that the results are very similar when expressed as aggregate % of prey mass or % frequency of occurrence. Of the 41 multi-prey samples, 40 contained two species and one contained three species. At least four fish species

Table 2. Diet composition of Northern Gannets at four colonies in North Norway expressed as % by mass using Swanson' et al.'s (1974) aggregated percentage of prey biomass method and as % by frequency of occurrence.

	Hovsflesa		Store Ulvøyholmen						Skarvklakken				Storstappen			
Year:	1985	1986	2007[A]	2008[A]	2009	2014	2015	2016	1985	1997	1999	2001	2007[A]	2008[A]	2009	2010
Date (x July):	24	11	25[B]	9	4–8	15	13	5	10 & 23	10	29[B]	26-27[B]	17	26	25	21
Sample size:	26	40	2	4	35	24	17	17	202	73	23	26	24	3	39	50
Aggregated % by prey mass																
Atlantic herring *Clupea harengus*	69	75			37	4	24	44	37	12	61	79	88	67	93	31
Atlantic mackerel *Scomber scombrus*			100	75	14	58	38	6		62						54
Sandeels Ammodytidae	10	4		25	4	8	7	29	3	7	35					13
Saithe *Pollachius virens*	14	21			45	29	32	21	59	1	4	21			7	2
Atlantic cod *Gadus morhua*	6															
Garfish *Belone belone*													13			0
Atlantic salmon *Salmo salar*														33		
Redfish *Sebastes* sp.		1														
Flatfish Pleuronectidae	2															
Unidentified fish									2	18						
% by frequency of occurrence																
Atlantic herring *Clupea harengus*	73	80			37	4	29	53	38	12	61	81	88	67	95	36
Atlantic mackerel *Scomber scombrus*			100	75	14	58	41	6		62						56
Sandeels Ammodytidae	12	5		25	6	8	12	35	4	7	35					18
Saithe *Pollachius virens*	15	25			46	29	35	47	63	1	4	23			10	2
Atlantic cod *Gadus morhua*	8															
Garfish *Belone belone*													13			2
Atlantic salmon *Salmo salar*														33		
Flatfish Pleuronectidae	4															
Redfish *Sebastes* sp.		3														
Unidentified fish									3	18						

[A] From Pettex et al. 2015; [B] June

Table 3. Estimated total lengths (mean and SE in mm) of fish regurgitated by Northern Gannets at North Norwegian colonies. When N ≤ 3, individual lengths are given. M = method used to determine length where F = measured in the field, OL, VL and TF = estimated from otolith, vertebrate and tail fin lengths respectively (see Methods).

	Atlantic herring				Saithe				Sandeels				Atlantic mackerel			
	Mean	SE	N	M	Mean	SE	N	M	Mean	SE	N	M	Mean	SE	N	M
Skarvklakken 1985[A]	263	16	?	F	228	20	?	F								
Skarvklakken 1997	283	17	9	F	200		1	F	110, 220, 220		3	F	277	11	41	F
Skarvklakken 1999	232	13	19	F	150, 250		2	F	131	50	19	F				
Skarvklakken 2001	242	27	6	F												
Hovsflesa 1985	340	42	5	F	200, 200, 220		3	F	180		1	F				
Hovsflesa 1986	270	14	21	F	238	18	9	F	150, 150		2	F				
Storstappen 2009	302	4	34	VL	223, 328, 381		3	VL					350		1	F
	187, 251		2	OL	162		1	OL								
Storstappen 2010	139	10	23	OL	225		1	OL	139	3	25	OL	400		1	OL
Ulvøyholmen 2009	291	11	4	OL	185	5	14	OL	182, 182		2	OL				
Ulvøyholmen 2014	336	11	11	VL	88	4	25	OL	213	11	6	OL	332, 364, 407		3	OL
													356	12	9	TF
Ulvøyholmen 2015	195		1	OL	123	24	5	OL	192		1	OL	344	18	4	OL
	230, 280, 380		3	VL	250	11	7	VL					370	13	7	TF
Ulvøyholmen 2016	177, 198, 209		3	OL	72	4	26	OL	212	7	12	OL				
	254	9	4	VL												

[A] From Montevecchi & Barrett (1987)

Table 4. Rough estimates of mean mass (in g) of fish regurgitated by Northern Gannets in Norway as calculated from fish lengths given in Table 3.

	Atlantic herring	Saithe	Sandeels	Atlantic mackerel
Skarvklakken 1985	188	125		
Skarvklakken 1997	234	87	3, 29, 29	128
Skarvklakken 1999	129	40, 161	5	
Skarvklakken 2001	146			
Hovsflesa 1985	407	87, 87, 113	15	
Hovsflesa 1986	203	141	8	
Storstappen 2009	285 67, 183	118, 339, 511 49		271
Storstappen 2010	28	121	6	417
Ulvøyholmen 2009	255	71	15, 15	
Ulvøyholmen 2014	393	9	26	229, 308, 440 287
Ulvøyholmen 2015	76 126, 227, 569	23 161	18	257 324
Ulvøyholmen 2016	57, 80, 94 169	5	25	

constituted the main prey – herring, mackerel, sandeels Ammodytidae and saithe, albeit in proportions varying both in time and space (Table 2). Herring was common at Store Ulvøyholmen (in 3 of 4 years when sample sizes ≥ 17) and Skarvklakken and dominated (>60% of the samples) at Hovsflesa and Storstappen in all years (except at the latter in 2010 = 31%) and at Skarvklakken in two of four years. Mackerel made up 62% of the samples at Skarvklakken in 1997 and 40–60% of the samples at Storstappen in 2010 and Store Ulvøyholmen in 2014 and 2015. Mackerel possibly also dominated the Ulvøyholmen samples in 2007 and 2008, but the sample sizes were very small. Other prey included Atlantic cod *Gadus morhua*, garfish *Belone belone*, Atlantic salmon *Salmo salar*, redfish *Sebastes* sp. and flatfish Pleuronectidae.

The mean estimated lengths of fish varied between 72 mm saithe (Ulvøyholmen 2016) and 370 mm mackerel (Ulvøyholmen 2015) (Table 3). Of the four main species, mackerel were the largest, mostly between 350 and 400 mm (or 250–400 g, Table 4). Herring also tended to be large with fish >300 mm (≡ >280 g) being caught at Hovsflesa (1985), Storstappen (2009) and Ulvøyholmen (2014) and between 240 and 300 mm (150–280 g) at Skarvklakken (1985, 1997 and 2001), Hovsflesa (1986), Ulvøyholmen (2009 and 2016). Smaller herring (mean = 139 mm) were found at Storstappen in 2010. Saithe were overall smaller than herring and mackerel with a maximum mean of 250 mm (≡ 160 g) and ranging generally between 70 mm (5 g) and 220 mm (120 g). Smallest were the sandeels (131–213 mm, or 5–26 g).

DISCUSSION

Despite the ad hoc character of sampling in this study, there can be little doubt that North Norwegian Gannets target four main prey during the chick-rearing period; herring, mackerel, sandeels and saithe. The Gannet is a generalist predator and in his definitive account of the Gannet, Nelson (2002) lists 40 prey species recorded in the diet on both sides of the North Atlantic, but with herring, mackerel and sandeel as principal prey. These three prey types were also found later on Icelandic colonies (Vigfúsdottir et al. 2009). In addition, capelin is an important food item in eastern Canada (Montevecchi & Porter 1980, Bennett et al. 2013). Although no empirical diet data were collected, capelin was inferred as an important prey at Norway's easternmost colony at Syltefjord, East Finnmark (Fig. 1) and at the recently (mid-1990s) established colony at Kharlov on the Kola Peninsula (Brun 1967, Krasnov & Barrett 1997). As such, North Norwegian Gannets conform to their peers throughout the North Atlantic, with saithe as a fifth important local supplement. All five prey types are energy-rich, shoaling fish and, with the exception of sandeels that periodically hide in the sand on the sea floor, all occur in the upper water layers within the Gannets' normal diving range (0–15 m, Nelson (2002)). Furthermore, all are at times common in inshore waters in summer in North Norway (Pethon 2005, Olsen et al. 2010) and thus within the 20–100 km foraging range of chick-feeding adults (Pettex et al. 2012).

Mackerel of the size range registered in this study would have been mature fish of 3 years or older (Olafsdottir et al. 2016) as would have been the herring larger than ca. 250 mm (Prokopchuk 2009) that were found at most localities. The smaller herring found at Gjesvær in 2010 were most probably I-group (1-year-old) fish. Similarly, saithe between 200 and 300 mm were probably II-group whereas those <100 mm found at Ulvøyholmen in 2014 and 2016 were 0-group fish, i.e. fish that had hatched that year. Small 0- and I-group fish have often been recorded as important food for other seabirds in the region (Fauchald et al. 2012), whereas Great Cormorants *Phalacrocorax carbo* have also been recorded as preying on larger, II-group and older gadoids (Lorentsen et al. in press). Gannets, however, are the only species known to prey on even larger pelagic fish such as mature herring and mackerel and on large gadoids (up to ca. 300 mm) both in Norway and elsewhere in the breeding range (e.g. Lewis et al. 2003, Hamer et al. 2007, Garthe et al. 2014).

Being very lipid-rich, herring and mackerel have the highest energy density (herring 9–11 kJ g^{-1} wet weight, mackerel 7–10 kJ g^{-1} wet weight) of the four main prey, although values do vary in time and space. After an intense feeding period during the spring and summer, lipid levels reach a maximum during the third quarter (Pedersen & Hislop 2001, Olafsdottir et al. 2016) such they would be optimal prey for Gannets seeking high-energy food for rapidly-growing chicks (Montevecchi et al. 1984). Sandeels and saithe (<30 mm) have lower energy densities (5–7 kJ g^{-1} wet weight and 4–5 kJ g^{-1} wet weight respectively) (Montevecchi et al. 1984, Pedersen & Hislop 2001, Spitz et al. 2010). As such, the capture of herring or mackerel would give approximately the same energy returns per fish (2000–3000 kJ) and much higher than those of individual saithe or sandeels (<800 kJ). That being said, leaner saithe and sandeels might be more important as food for young, developing chicks due to their more manageable size and higher relative protein levels (Montevecchi & Barrett 1987).

An overwhelming dominance of single-species food loads despite a wide range of prey species found in any set of samples both in this study and e.g. in Canada (96% of 8239 samples, Montevecchi 2007) or Scotland (76% of 266 samples, Hamer et al. 2000) suggest that once a fish shoal has been detected, Gannets feed on that shoal until satiation or until the shoal dissolves or dives out of reach. This corroborates the finding that locating schools of suitable prey is a key component for Gannets when foraging (Garthe et al. 2014) such that, once detected, a school is utilized to the maximum. Furthermore, tracking studies of Gannets at Storstappen and Store Ulvøyholmen showed relatively short foraging trips (Pettex et al. 2015). This would have reduced the need to top up stomach loads (with possibly a different species) that otherwise would have been digested on long trips in order to have sufficient food for the chick (Lewis et al. 2004).

Herring, saithe and sandeels occur along the Norwegian coast throughout the year whereas mackerel, a warmer water species, are visitors to the more northern waters during their summer feeding migration (Loeng & Drinkwater 2007). Although mackerel was not earlier common in North Norway (Pethon 2005), a warming of the North Atlantic after the turn of the millennium led to an extension of its distribution and migration patterns as far north and west as Svalbard and Iceland (Astthorsson et al. 2012, Berge et al. 2015). This would have thus increased its availability also to Gannets foraging along the North Norwegian coast and this was especially evident in 2010 when mackerel constituted >50% of food samples collected as far north as Storstappen (Table 1). That being said, mackerel dominated the samples at Skarvklakken in 1997 when there was a large negative heat content anomaly over four years (1995–1998) in the Norwegian Sea (Mork 2016). Mackerel was also among the prey items (that also included herring, sandeels, saithe and cod) noted anecdotally at Skarvklakken and Hovsflesa during the short visits in July 1978 and 1979 respectively, indicating that some individuals were in the region even during an earlier period (1976–1989) of cold water in the Norwegian Sea (Mork 2016). A similar, but reverse situation occurred in eastern Canada when cold-water events off Newfoundland in the early 1990s inhibited the movement of mackerel and other warm-water species northwards with a consequent shift to cold-water pelagic prey by Gannets breeding in the region (Montevecchi 2007). That Gannets are opportunistic in their feeding habits and can readily respond to ocean climate changes by seeking out new prey partly explains their expansion into North Norwegian waters and beyond and will be beneficial for the species in times of climate change.

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