BLACK-LEGGED KITTIWAKE *RISSA TRIDACTYLA* ADULTS AND CHICKS SHARE THE SAME DIET IN THE SOUTHERN BARENTS SEA

RENATE THORVALDSEN[1,2], ROBERT T. BARRETT[1] & TORSTEIN PEDERSEN[2]

[1]*Department of Natural Sciences, Tromsø University Museum, PO Box 6050, NO-9037 Tromsø, Norway (rob.barrett@uit.no)*
[2]*Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, Tromsø University, NO-9037 Tromsø, Norway*

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SUMMARY

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The Black-legged Kittiwake *Rissa tridactyla* population is declining throughout its North Atlantic range. In Norway, the species is classified as *Endangered* on the Norwegian Red List. Studies of diet are one important requirement for effective management of any species. Because it is easier to sample, chick diet has often been considered a proxy for adult diet in many seabird studies, but the optimal-foraging theory predicts that this may not be accurate. This study found, however, contrary to the theory, no significant differences in either prey composition or prey size in the diets of adult kittiwakes and their chicks in a north Norwegian colony during the 2012 breeding season. The main prey for both adults and chicks was capelin *Mallotus villosus*. Fewer samples were obtained from birds without chicks than from birds with chicks; this was considered to be a consequence of the former digesting their meals at sea before returning to the colony. Differences in diet of surface feeders can, however, be both seasonal and geographically dependent, and a similar study on kittiwakes in a different location or in a different breeding season may show a quality difference in diet between adults and chicks.

Key words: Barents Sea, Black-legged Kittiwake, *Rissa tridactyla*, optimal foraging, prey quality

INTRODUCTION

During the breeding season, parent birds need to sustain both themselves and their offspring. At this time, however, they are bound to the nest and need to optimize their energy yield, according to central-place foraging theory (Orians & Pearson 1979). Because parents can eat and digest their own food away from the nest, this theory predicts that they bring more energy-rich prey to their chicks than they eat themselves and that the allocation of food between the parents and the chicks takes the form of optimal sharing. This theory is especially applicable to birds with high transport costs between the nest and source of food or to birds that cannot deliver more than a few food items at a time (e.g. Shealer 1998, Wilson *et al.* 2004, Bugge *et al.* 2011). However, other studies of seabirds have suggested that the theory also holds true for multiple prey loaders among the auks (Alcidae) and for birds returning with food in their proventriculus. For example, adult Rhinoceros Auklets *Cerorhinca monocerata* collect larger fish for their chicks than for themselves (Davoren & Burger 1999), and dietary differences have also been found in fulmarine petrels (Procellariidae; Van Franeker *et al.* 2001, Fijn *et al.* 2012). Such differentiation is sometimes manifested in bimodal foraging strategies of adults, with shorter trips being made for chick provisioning, and longer trips for self-feeding (e.g. Weimerskirch *et al.* 2001, Congdon *et al.* 2005, Kotzerka *et al.* 2010).

In Norway, large declines in several important seabird populations have been documented since the 1960s (Brun 1979, Barrett *et al.* 2006). One such population is that of the Black-legged Kittiwake *Rissa tridactyla* (hereafter "kittiwake"), which, on the mainland, has declined at a rate of 6–8% per year since 1980, with evidence of an acceleration of up to 10–15% per year since the mid-1990s (Barrett *et al.* 2006). This decline is mirrored in a large part of the distribution of this bird in the northeast Atlantic (Frederiksen *et al.* 2012). The mainland population in Norway constitutes 13–15% of the North Atlantic population (Barrett *et al.* 2006) and is presently categorized as *Endangered* (EN) in the Norwegian 2010 Red List (Kålås *et al.* 2010).

Why the kittiwake population is declining is unknown, but the widespread nature of declines suggests a common causation linked to large-scale climate patterns (e.g. altered oceanography is indicated by rising water temperatures), facilitated perhaps by shared winter quarters (Frederiksen *et al.* 2004, 2011; Reiertsen *et al*. 2014). During the breeding season, ocean changes associated with rising sea surface temperatures (SST) may have negative effects on the availability of capelin *Mallotus villosus*, a preferred food for kittiwakes in the southern Barents Sea. Part of the story may involve the positive correlation between increased SST and recruitment of another predator, the Atlantic Herring *Clupea harengus*. Large stocks of herring feed on capelin larvae, ultimately reducing the total biomass of capelin available to kittiwakes (Hjermann *et al.* 2004, Barrett 2007). A recent study in the southern Barents Sea showed that short-term changes in diet and prey distribution can have dramatic effects on kittiwake breeding success (Ponchon *et al.* 2014), implying that studies of kittiwake diet are an important requirement for effective management of the species.

Perhaps because they are relatively easy, many dietary studies have focused on chick-provisioning birds and, in seabirds, prey fed to the chicks has often been used as a proxy for the adult diet during breeding season (e.g. Barrett *et al.* 2002, 2007; Robinette *et al.*

2007). This assumption has often, but not always, been shown to be incorrect, even among birds that regurgitate food to their chicks (e.g. Davoren & Burger 1999, Van Franeker *et al.* 2001, Fijn *et al.* 2012). Thus, to fully understand the feeding ecology of a species, both adult and chick diets need to be determined. This is especially true for seabirds, since chick provisioning accounts for only a small amount of annual food intake (e.g. 5% in fulmarine petrels, <10 % in kittiwakes; Furness & Barrett 1985, Van Franeker *et al.* 2001).

In this study, we investigated possible quality differences in food between kittiwake adults and chicks in a colony in the southern Barents Sea and tested the prediction that chicks are fed prey of a better quality than that eaten by their parents. When feeding chicks, kittiwakes regurgitate food carried back to the colony in their proventriculus. We assumed that, when foraging, adult kittiwakes first catch and partly (or wholly) digest prey for self-feeding before catching prey for their chicks. Prey remains that had passed to the most distal parts of the proventriculus would be a proxy of adult diet, and we expected the prey choice in these samples to be of poorer quality than that regurgitated by the adult when captured, which we assumed to be intended for the chick.

METHODS

This study was carried out between 14 June and 18 July 2012 on Hornøya (72°22′N, 31°10′E), a small island in the southern Barents Sea where an estimated 10 000 pairs of kittiwake bred the same year (Barrett, pers. obs.). The dates corresponded to the late incubating, hatching and most of the chick-raising periods. Prey samples were collected from three groups of adults: those incubating eggs, those raising chicks and, also during the chick-rearing period, those attending empty nests. The samples from incubating birds and from birds at empty nests towards the end of the season thus represented adult diets. Samples regurgitated by adults with chicks were considered to be food for chicks, whereas their stomach contents were considered to represent food for self-feeding.

Adult birds were caught on the nest using a noose pole as soon as they were seen to return to the nest from the feeding grounds. At that time, we considered stomach contents, and most food in their proventriculus, to be least digested. Kittiwakes that have just returned from foraging trips often regurgitate food as a reaction to capture, and these regurgitations were collected in zip-lock plastic

TABLE 1
Numbers of food samples collected during the breeding season from three groups of Black-legged Kittiwake breeding at Hornøya, northeast Norway

	Incubating		Birds with chicks		Birds at empty nests		Total	
Category[a]	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
Empty	24	53.3	8	11.2	25	64.1	57	35.6
Only STO	16	35.5	17	23.9	12	30.8	45	28.1
STO (with REG)	5	11.1	23	32.4	1	2.6	29	18.1
REG (with STO)	5	11.1	23	32.4	1	2.6	29	18.1
Total samples with identified content	26	57.7	63	88.7	14	35.9	103	64.4
Total	45	100	71	100	39	100	160	100

[a] STO is stomach-pumped sample and REG is regurgitation sample. Samples collected that did not contain anything that could be identified were designated as Empty. STO (with REG) and REG (with STO) are the birds whose stomach samples contained identifiable remains and who regurgitated.

TABLE 2
Frequency of occurrence of the various prey items found in the stomach content of three groups of Black-legged Kittiwake at Hornøya, northeast Norway[a]

	Incubating birds		Birds with chicks		Birds at empty nests		REG, birds with chicks	
Prey item	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
N	21	100	40	100	13	100	23	100
Capelin	15	71.4	35	87.5	7	53.8	20	87.0
Sandeel	0	0	0	0	0	0	2	9.1
Herring	0	0	1	2.5	0	0	2	9.1
Cod	0	0	1	2.5	3	23.1	1	4.5
Krill	2	9.5	4	10.0	0	0	1	4.5
Unidentified fish	7	33.3	1	2.5	3	23.1	0	0

[a] The content of regurgitations from adult kittiwakes with chicks is shown in the last column. N = total number of samples from each category, n = number of samples containing a given prey in each category.

bags. Each bird was ringed, weighed and measured (for other studies) before an attempt was made to sample its stomach content using the water offloading method (Wilson 1984) (under licence no. 2012/28101-id4116 of the Norwegian Animal Research Authority). The procedure was repeated once or, at most, twice. If stomach flushing seemed to be successful the first time and if water came out clear the second time, the stomach was assumed to be empty and the third flushing was avoided to reduce stress for the bird.

Before release, the bird was marked with a blue felt-tipped pen on the back of its head to avoid recapture. After release, most birds returned to their nest within a few minutes. There were no signs of harm, stress or behavioural change in the period after the sampling.

The samples were stored frozen. On return to the laboratory, each sample was thawed and weighed to the nearest 0.1 g. A preliminary identification to the lowest possible taxon of the remains was noted before the remains were further digested in a saturated solution of biological washing powder (Biotex) in an oven at 50 °C for at least 24 h. The remaining hard parts (mainly otoliths, vertebrae and pro-otic bullae [characteristic of herring]) were identified using Breiby (1985), Härkonen (1986), Watt *et al.* (1997) and a reference collection. Diet composition was expressed as frequency of occurrence based on counts of taxa in each sample. It was impossible to improve this quantification due to large differences in the degree of digestion of the samples and uncertainty concerning how many meals each regurgitation or stomach sample represented. To avoid possible pseudoreplication due to diet specialization by individual birds (Woo *et al.* 2008), only one diet sample (stomach and/or regurgitation) was collected from each adult.

After identification, all otoliths were measured under a light microscope using a calibrated eyepiece graticule. When possible, the matching otoliths were paired to avoid counting one fish as two individuals. The measurements were used to calculate total fish length (mm) using the equation TFL = 25.8 + 48.0 * OL (where TFL = total fish length in mm and OL = otolith length in mm) for capelin (Barrett & Furness 1990).

Differences between the amounts of capelin brought in by the treatment groups were tested using Pearson's *chi*-square goodness of fit in Excel 2013. To test for differences in the frequency of capelin at the individual level in regurgitations and stomach contents among adults with chicks, a sign test was run in R version 2.15.2. A two-sample *t*-test with common variance was used to check for differences in mean prey length.

TABLE 3
Mean total fish length (TFL) of capelin found in regurgitations (REG) and stomach-pumped (STO) samples of adult Black-legged Kittiwakes with chicks, and REG samples of chicks at Hornøya, northeast Norway

Sample group	n	TFL (mm)	SD (mm)	Range (mm)
REG	51	138	7.6	121–156
STO	7	133	6.4	120–138
REG (chick)	10	114	27.5	71–139

RESULTS

Diet composition

One hundred and sixty food samples were collected from 131 birds, including both regurgitations (REG) and samples from stomach pumping (STO) (Table 1). Fifty-seven birds had no apparent gut content. The difference between the proportions of empty samples from the different treatment groups was significant (Pearson's $\chi^2 = 23.51$, $df = 2$, $P < 0.001$), but there was no difference between incubating birds and birds at empty nests ($\chi^2 = 1.32$, $df = 1$, $P = 0.25$). Most REG samples were collected from birds with chicks, and many of the birds handled did not regurgitate, but had content in their stomachs (Table 1).

Capelin was the most common prey found in the samples (Table 2). Other prey types included krill (euphausiids) in STO from incubating birds and birds with chicks. In birds on empty nests, the second most common prey was Atlantic Cod *Gadus morhua*.

Unidentified remains consisted of fish bones that were too well digested to identify and could only confirm that the bird had eaten some kind of fish. No REG samples from birds with chicks contained unidentified remains, whereas the amount of unidentifiable remains in STO of the different groups varied between 2.5% and 33.3% (Table 2). The difference between adults with chicks and incubating birds was significant ($\chi^2 = 10.29$, $df = 1$, $P = 0.001$), as was the difference between adults with chicks and birds at empty nests ($\chi^2 = 6.31$, $df = 1$, $P = 0.012$).

Since only five incubating birds and one bird at empty nests regurgitated, the sample numbers were too small to test for any differences between STO and REG both at group level and individual level. All six samples contained capelin only.

The frequency of capelin in STO samples from adults with chicks was higher than in samples from adults without chicks ($\chi^2 = 5.40$, $df = 1$, $P = 0.02$); however, there was no significant difference in the frequencies of capelin found in the birds incubating and those on empty nests ($\chi^2 = 1.09$, $df = 1$, $P = 0.3$). Only two incubating birds had krill in their stomachs, and three birds at empty nests had cod. The treatment groups "incubating birds" and "birds at empty nests"

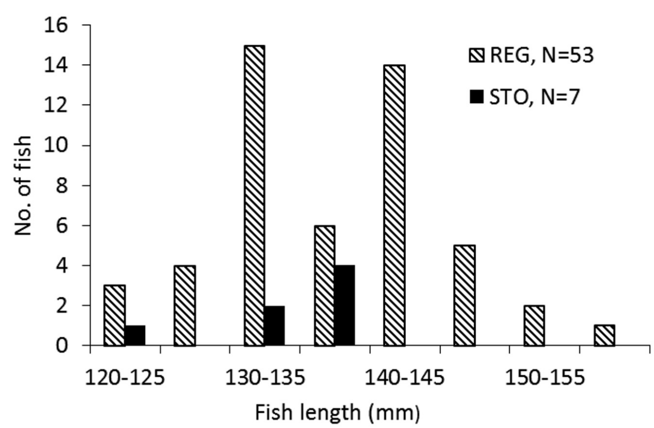

Fig. 1. Frequency distributions of total fish lengths of capelin from regurgitated (REG) and stomach-pumped (STO) food samples from adult Black-legged Kittiwakes at Hornøya, northeast Norway.

can therefore be combined in one group, "birds without chicks," resulting in 34 STO samples and 6 REG samples. All REG samples contained 100% capelin, as mentioned earlier.

Using data from the 23 individuals from which both REG and STO samples were obtained, and combining all prey species other than capelin (due to small sample sizes), the sign-test showed that there was no significant difference between the STO and REG contents of adult kittiwakes with chicks ($P = 0.5$ for differences in capelin between STO and REG, and $P = 1$ in the test for differences in other species).

A comparison of REG with STO content at the individual level in the group of kittiwakes without chicks was not statistically possible. Of the six birds that regurgitated, two had empty stomachs, leaving only four samples to compare between REG and STO. The only prey item found in the 10 samples was, however, capelin, suggesting no difference between REG and STO content at the individual level for birds without chicks.

Fish size

Only samples of capelin were large enough to analyze statistically. The total lengths of capelin in STO and REG samples from adults with chicks ranged between 120 and 156 mm (Table 3, Fig. 1) but did not differ significantly between the two groups ($t = 2.3$, $df = 8$, $P = 0.085$).

DISCUSSION

Evaluation of the water offloading method on kittiwakes

The overall success rate of samples collected from kittiwakes using the water offloading method in this study was 56.5%, which is similar to or slightly lower than the success rates of Bugge *et al.* (2011) (58%) and Wilson *et al.* (2004) (68%), who collected samples from Common Guillemots *Uria aalge*. There was, however, a large difference in sample returns between chick-rearing birds and birds without chicks, with the 83% of the former having food remains in their stomachs compared with 41% of the latter. This is probably because kittiwakes with offspring need to return to the colony quickly to feed chicks, whereas those without chicks can choose to digest their meals at sea and return to the colony with an empty and therefore lighter stomach, thus reducing energy expenses when flying. Thus, by choosing birds returning to nests with chicks, a higher rate of success using the technique can be expected from kittiwakes rather than from, for example, large auks.

Empty stomachs and unidentifiable fish remains

One drawback of the water offloading method is that identification is limited to otoliths and skeletal remains, thus restricting the quantification of diet data to frequency of occurrence. Furthermore, soft-bodied animals may be hard to find or even missing completely in the STO samples. Because prey species have different retention times and the interval between the bird's last meal and sampling time is unknown, the stages of digestion may differ between individuals, sometimes making otoliths and vertebrae hard to identify (Jobling & Breiby 1986, Johnstone *et al.* 1990, Wilson *et al.* 2004). This was not, however, a problem for otoliths in this study, since none were excessively eroded, and all were easy to identify and measure (as also found by Bugge *et al.* [2011] in Common Guillemots from the same colony). Some samples, however, contained only one or two vertebrae that were too extensively eroded to be identifiable. Many resembled those of capelin found in other samples, but were nevertheless too eroded for certain identification and were classified as unidentifiable fish remains.

More samples in the two groups of adults without chicks contained unidentified fish remains than samples in the birds with chicks (Table 2). We suggest that this is because birds without chicks digest most of their food at sea. Digesting food at sea has been suggested to be beneficial for birds that are pursuit hunters because it decreases their mass and thereby increases their hunting success (Sibly 1981). This may also apply to kittiwakes that need to take longer foraging flights, as it would be an advantage for them to quickly reduce mass to save energy cost during flight (Pennycuick 1989). Thus, birds without chicks may choose to digest their meals at sea to avoid making the trip back to the colony with the extra weight of a meal. Furthermore, capelin is a lipid-rich fish, making digestion quick and helping avoid an "ingestion bottleneck" (Hilton *et al.* 2000a, b). Since kittiwakes feed infrequently during the breeding season and their foraging sites are often far from the breeding colony (Ponchon *et al.* 2014, Redfern & Bevan 2014), they need to eat large meals on each feeding trip to meet their energy demands. On each feeding trip, however, the amount of food the birds can eat is constrained by the size of the gut, and rapid digestion minimizes the impact of such a bottleneck (Hilton *et al.* 2000a). Therefore, rapid digestion, empty stomach samples and the lack of regurgitations from kittiwakes without chicks could reflect a high-quality diet (e.g. capelin). Furthermore, the higher fraction of empty stomachs in birds without chicks indicates that they digested their meals at sea.

Behaviour in the colony

Spot-check studies of colour-dyed breeding kittiwakes have shown that birds attending eggs or chicks do not normally loaf in the colony but fly straight off to sea once relieved by their partner, which in turn had returned straight from the sea to the nest (Galbraith 1983, Coulson 2011). This was also noted incidentally during the breeding season on Hornøya in 2012 (pers. obs.). When one of the birds of a pair with chicks returned from the sea, the pair stayed together on the nest for only a short time before the relieved partner flew off to search for food. This differed from the behaviour of the birds on the empty nests, and to some extent to the birds with eggs. They were observed more often loafing in the colony before changing with their partner at the nest. This may be another reason for the higher frequency of empty samples among birds on empty nests and with eggs. Most of the birds in this study were caught as soon they were seen to relieve their partner at their nest to increase the chance of getting REG samples. This tactic appeared to be efficient for the birds with chicks, but birds without chicks often did not regurgitate or had empty stomachs, further supporting our suspicion that birds without chicks digest their food at sea.

Diet composition

There was a clear dominance of capelin in both STO and REG samples in all groups of adults, and no other prey species was even close to being as abundant. Although the differences in frequency of capelin in birds with or without chicks was significant, many of the latter samples contained unidentifiable remains (one or two vertebrae) of fish that were suspected to have been capelin. Hence, the proportion of capelin found in both birds with and without chicks was probably more similar than suggested by the statistics. The importance of capelin as prey was expected, consistent with other studies in the southern Barents Sea (Erikstad 1990, Krasnov & Barrett 1995, Barrett 2007). Although we found no differences between the type of prey in kittiwake adult and chick diets, a similar study at Hornøya documented clear differences in the diet of Common Guillemot adults and chicks, with the frequency of prey in the former being 89.8% gadid, 25.4% capelin and 11.9% Sandeel *Ammodytes* spp., and in the latter 82.3% capelin (Bugge *et al.* 2011). In their study, Bugge *et al.* also used paired samples and found that the frequency of occurrence of energy-rich capelin was significantly higher in chick food (77.2%) than in adult stomachs (26.3%). Similarly, in a second study of Common Guillemots in Scotland, the adults ate mainly 0 and 1+ groups of Lesser Sandeel *Ammodytes tobianus*, while 79% of the chicks were fed energy-rich Sprats *Sprattus sprattus* (Wilson *et al.* 2004). In studies of two other single-prey loaders, but surface-feeders, Shealer (1998) found that adult Roseate Terns *Sterna duogallii* fed primarily on Dwarf Herring *Jenkinsia lamprotaenia* and Anchovies *Anchoa* spp., but fed their chicks mainly Dwarf Herring and sardines *Harengula* and *Opisthomena* spp. Similarly, adult Sandwich Terns *Sterna sandvicensis* ate mainly Silversides *Hypoatherina harringtonensis* and sardines, while providing their chicks with mainly Dwarf Herring and sardines. In both cases, the proportions of food in diet of adults differed from those of the chicks, but the difference was not as clear as shown in both studies of guillemots. The diet compositions of Roseate and Sandwich terns were also more varied than those of guillemots, probably because they are surface feeders like kittiwakes and not pursuit divers like guillemots.

Although the prey composition of adult kittiwakes and chicks did not differ in our study, one way to increase energy gain per unit time would be to increase the size (and hence energy content) of the fish caught for the chicks. This was found in both studies of Common Guillemots (Wilson *et al.* 2004, Bugge *et al.* 2011), but not in this study (Table 3). This held true when supplementing the sample with few capelin from REG with 10 capelin retrieved from the six regurgitations from chicks (pers. obs., *t*-test, $P = 0.06$). It thus seems that a quality difference in diet between adults and chicks is more common in species that provision chicks with whole fish, since they can more easily maximize energy yield by choosing one larger and more energy-rich fish. Species that regurgitate chick food may not be able to be equally selective when hunting for their chicks, since filling their proventriculus with several energy-rich fish before returning to their chicks is likely to be far more energy- and time-consuming than picking just one, as the single-prey loaders do. This is probably particularly true for species that are restricted to hunting on the surface. That being said, optimal foraging has been suggested as a possibility among surface-feeding petrels (Lorentsen *et al.* 1998, van Franeker *et al.* 2001, Fijn *et al.* 2012), but we did not find optimal foraging in this study.

Conclusion

No significant differences in either prey composition or prey size were found between kittiwake adult and chick diet at Hornøya, northeast Norway, in 2012. As such, kittiwake chick diet was a good proxy of adult diet during the breeding season in question. Fewer samples were obtained from birds without chicks than from birds with chicks, probably as a result of the former digesting their meals before returning to the colony. Differences in diet of surface feeders can, however, be both seasonal and geographically dependent. A similar study of kittiwakes in a different location or in a different breeding season may show a quality difference in diet between adults and chicks.

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