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NO EVIDENCE OF OPTIMAL FORAGING IN CHICK-RAISING BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*) IN THE SOUTHERN BARENTS SEA

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NO EVIDENCE OF OPTIMAL FORAGING IN CHICK-RAISING BLACK-LEGGED KITTIWAKES (*RISSA TRIDACTYLA*) IN THE SOUTHERN BARENTS SEA

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The black-legged kittiwake (*Rissa Tridactyla*) situation is getting more serious as the population numbers have declined over the last decades, and this well-known species is now considered endangered (EN) in the Norwegian redlist 2010. This study investigates the differences between adult and chick diet considering prey selection to be an important point. Earlier chick diet has been considered a proxy for adult diet, but the optimal-foraging theory suggests that this may not be accurate. Knowing the composition of both adult and chick diet is important for further preservation of the species. Studies of differences between self-feeding and chick provisioning have been carried out on several occasions, and the theory has been confirmed in several species such as the common guillemot (*Uria aalge*) and cape petrel (*Daption capense*), but never in kittiwakes. The water offloading method was used to sample stomach samples that were compared to regurgitated samples that indicate chick diet. Differences in diet were based on frequency of occurrence, and differences in total fish length of prey animals. Knowing the true diet of adult kittiwakes has important implications on how to manage the Norwegian populations. This study showed no signs of optimal foraging for kittiwakes during the 2012 breeding season. The main prey for both adults and chicks was capelin.

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INTRODUCTION

The study species

The species of this study, the black-legged kittiwake (*Rissa tridactyla, L. 1758*) is a medium-sized gull with a more specialized diet than many other gulls who are often scavengers or more generalist feeders. They belong to the family Laridae within the order Charadriiformes (Nelson 1980). The loud outbreak of calls sounding like “kittiwaak” has given them their English common-name, kittiwake.

They are easy to recognize from other similar gulls by their white and grey plumage, completely black wing-tips and black legs. Black-legged kittiwakes share a similar grey colouration on the wings as the herring gull (*Larus argentatus*) but the herring gull is considerably larger. A similar sized gull often confused with kittiwakes is the common gull (*Larus canus*) but they can easily be separated from each other by the colour of their legs. The common gull has yellow legs. Another species with similar characteristics is the red-legged kittiwake (*Rissa brevirostris*), but as the name indicates this species has red and not black legs. On the other hand there are individual differences in the colouration of the feet, and *R. brevirostris* with dark legs can be confused with an *R. tridactyla* if observed during flight. On closer inspection the two species can be separated on some other characteristics like the shorter beak, rounder eyes and slightly greyer plumage of *R. brevirostris.* The distribution of *R. brevirostris* is more limited than *R. tridactyla* and they are considered endemic to the Bering Sea (Kildaw 1999). About 20% of the world's population of *R. brevirostris* occurs in the Aleutians, primarily at the Bogoslof and Buldir islands. The remainder occurs in the Pribilof and Commander Islands (Vernon et al. 2005). Since this study is made outside the distribution range of *R. brevirostris*, using only kittiwake as species name in this text always refers to the black-legged kittiwake.

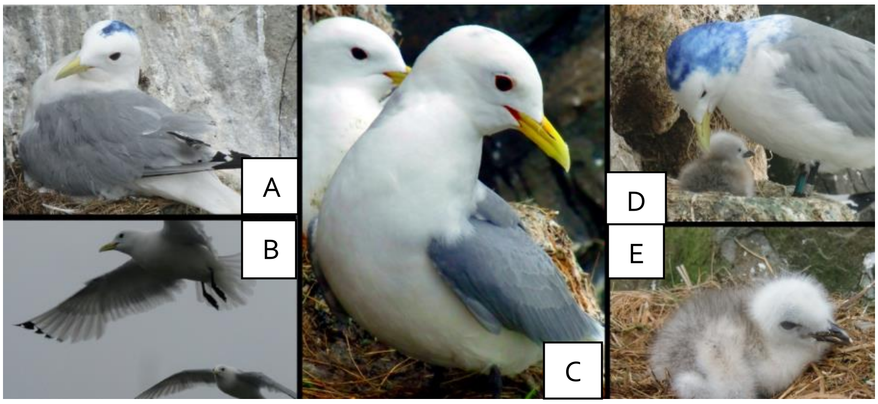


Figure 1. A.) Adult kittiwake that had returned to the nest to continue incubating only short time after being caught for sampling. All sampled kittiwakes were ringed and marked with a blue felt-tip pen to avoid recapture. B.) Kittiwakes are easily recognized in flight by their black legs and completely black wing tips. They are easily told apart from similar species in Norway by these traits. C.) Adult specimens in breeding plumage. D.) After disturbance most birds, like this one, returned to their nests after 1-3 minutes showing no abnormal behavior or signs of unnecessary stress from the capture and handling. E.) 2-day old chick. Photos: Renate Thorvaldsen.

Species distribution

The Kittiwake is common all over the North Atlantic (Fig 2.). Geolocation data loggers were deployed on kittiwakes from 19 different breeding colonies including colonies from both sides of the North Atlantic in 2008-2010. Hornøya was among these colonies and contributed with a number of 6 geolocation data loggers from 2008/2009 and 14 from 2009/2010 (Table 1, Frederiksen et al. 2012). The geolocation data loggers retrieved in this study showed that their main winter distribution is in the West Atlantic, between Newfoundland and the Mid-Atlantic ridge (Frederiksen et al. 2012). Frederiksen et al.'s study also showed a great overlap between the different colonies, and that 80 % of 4.5 million breeding pairs of Kittiwakes in the Atlantic spent the winter west of the Mid-Atlantic ridge.

The breeding distribution in the North Atlantic stretches from the high Arctic (80° N) to mid-temperate latitudes (40-45° N) on both sides of the ocean (Frederiksen et al. 2012). During the breeding season they colonize cliffs close to the sea and make nests of grass and seaweed on the steep cliff surfaces. They often breed in large colonies.

Kittiwakes are common seabirds in Norway and breed in colonies all along the Norwegian coastline with the majority in the north. They also breed on Svalbard and Jan Mayen. The population of black-legged kittiwakes in the whole Varanger-area was estimated to approximately 32 000 breeding pairs (Krasnov et al. 2007). The population growth of kittiwakes has been significantly negative since 1980 (Seapop report. 2011). On Hornøya there were estimated 11 500-12 000 breeding pairs in 2006 (Krasnov et al. 2007). During the 2012 breeding season, the population on Hornøya was estimated to be 7500 breeding pairs (Barrett, pers.com,).

Population dynamics

Kittiwake populations have declined strongly, and the North Atlantic population has declined by more than 50% since 1990 (Frederiksen et al. 2004; Barrett et al. 2006). The total population of kittiwakes in Norway was estimated to be 336 000 pairs and this is 13-15 % of the whole North Atlantic population which is approximately 2.3-2.6 million pairs (Barrett et al. 2006).

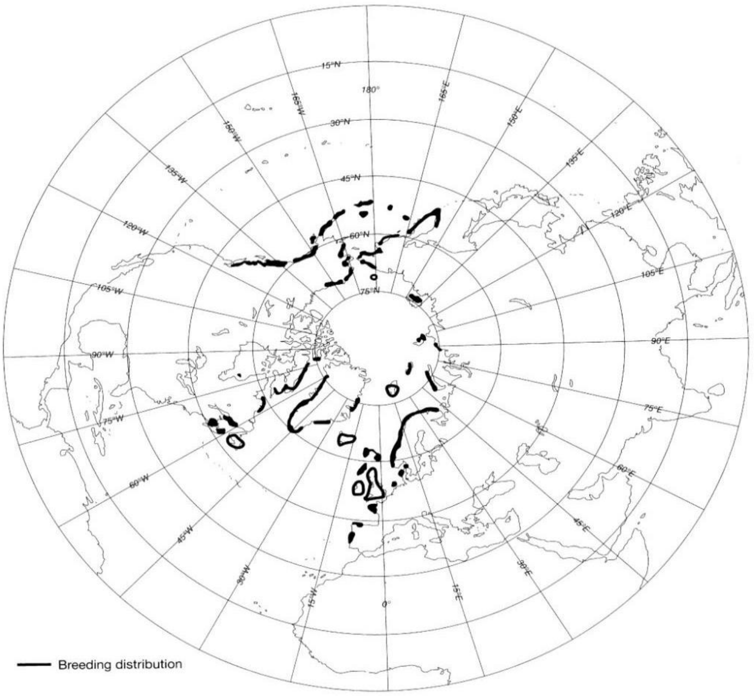


Figure 2. Distribution of kittiwakes during the breeding season (Map taken from "The Kittiwake", John C.Coulson, 2011 p.19).

Prior to the decline this Norwegian population was estimated to 500 000 pairs in 1980 (Barrett & Vader 1984). There is evidence of decline in all monitored Norwegian colonies, and there is evidence of acceleration of the decline to up to 10-15 p.a. since the mid-1990s (Barrett 2003; Lorentsen 2005). The average decrease has been 6 % p.a in the Barents Sea colonies and 8% p.a for the Norwegian colonies (Barrett et al. 2006). Monitoring plots on Hornøya have shown a 50 % decrease in apparently occupied nests since the mid-1980s. Even if the population numbers are still high they are now listed on the IUCN Red List of threatened Species. In the Norwegian 2010 red list Kittiwakes are listed as endangered (EN) (Kålås et al. 2010).

The reason for the dramatic decline is unknown, but rising water temperatures due to climate change might be an important factor (Varty &Tanner 2010). The sea surface temperature (SST) can have indirect effects of kittiwake breeding success in several ways. One argument is that there is a positive correlation between increased SST and recruitment of herring (*Clupea harengus*), which feeds on capelin, the preferred food of kittiwakes and several of the other seabirds in the southern Barents Sea. Herring preying on capelin is thought to lowers the total biomass available for seabirds to prey upon (Hjermann et al. 2004; Barrett 2007).

Kittiwakes, with a long lifespan typical for many seabirds, are likely to have many active breeding seasons during their lifespan. One breeding seabird only needs to bring one offspring to reproductive age for the population to remain stable. They can therefore afford to have a low annual reproduction and they have a general unwillingness to jeopardize their own survival for their chicks. This unwillingness to risk their lives for their young should be reflected in the population if they respond to climate fluctuations, since the adult birds can be expected to leave their offspring if feeding conditions get worse due to climate changes (Gaillard & Yoccoz 2003). Whether or not climate changes affect kittiwake survival is not documented, but a possible effect on adult mortality can have a dramatic effect on long-lived species with low annual reproduction rates such as kittiwakes (Sandvik et al. 2005). Overall there are indications that lower SSTs correlate with higher survival rates, and that the effect SST can have through the food chain can trigger adult mortality (Sandvik et al. 2005).

Diet and feeding strategies in kittiwakes

Kittiwakes differ from many other gull species by being more specialist feeders. Since kittiwakes are surface feeders that feed in the upper meter of the water column, they depend on eating whatever they can find in the surface layer. They are thought to be able to feed down to 1 meter under the surface, but since they don’t attempt to dive its more likely that they feed in the upper 0.5 meter (Lønne & Gabrielsen 1992). This means that even if there are a lot of fish in the area they may be unavailable for the kittiwakes unless they rise to the surface layers. They are also common scavengers at prawn or fishing boats (Galbraith 1983). The diet of kittiwakes can vary between the different areas since they depend on finding prey on the surface. Other seabirds which catch prey underwater can hunt in larger parts of the water column, and might be able to hunt closer to the colony compared to kittiwakes who may spend a larger amount of time searching for feeding grounds (Galbraith 1983; Kotzerka et al. 2010). Sandeels (*Ammodytes* *sp*.) are an important part of the diet for kittiwakes nesting in much of the Northern Sea (Pearson 1968; Furness & Cooper 1982). On Hornøya E. Finnmark, capelin is an important food prey for kittiwakes since capelin are very common in the Barents Sea and is the dominating pelagic species in the area (Bakketeig et al. 2005). Capelin come in to spawn along the coast of Finnmark in late winter/early spring, but some parts of the stock spawn during summer. (Barrett et al. 2006). This means that spawning capelin is often present close to Hornøya during parts of the breeding season. Monitoring studies have also shown that capelin is important in chick diet (Barrett 2007).

Also when the birds are breeding they will bring food back to the colony to feed their chicks. There are also several ways in which a bird can do this. They can swallow the food and keep it in their throat pouch, like the little Auk (*Alle alle),* or keep it in their proventriculus ready to regurgitate when they return to their offspring, like most gulls. They can also carry the food back to the colony freshly caught in their beaks, either as a mating display or food for their chick. Then they can be either a single-prey loader bringing only one fish in their beak like the common guillemot (*Uria aalge*) or they can bring back a number of smaller fish or fish larvae like the puffin (*Fratercula arctica*) or the razorbill (*Alca torda*).

Central place foraging theory – Self-feeding and Chick provisioning

There are few diet studies that distinguish between self-feeding and chick diet (Davoren et al. 1999) even if this has been recognized for some time (Kacelnik 1984; Swihart & Johnson 1986). Birds often collect a different prey of higher quality when hunting for their chicks to ensure that their offspring gets high quality food (Bradstreet & Brown 1985; Swihart & Johnson 1986). During the breeding season, the adult bird needs to optimize the energy yield per unit foraging effort to optimize their chick’s energy gain per unit time according to the central place foraging theory as described by Orians and Pearson (1979). This theory was supported in a study of chick diet and self-provisioning on common guillemots by Wilson et al. (2004) and further confirmed by similar study on common guillemots on Hornøya (Bugge et al. 2011).

The selection of prey fed to the chicks has long been considered a proxy for the adult-diet during breeding season (Wilson et al. 2004; Bugge et al. 2011), but central-place foraging theory predicts that there might be a difference. More recent studies have shown a difference in food quality between adult birds and chicks (Mehlum 2001; Shealer 1998; Wilson et al. 2004; Bugge et al. 2011; Fijn et al. 2012). More specific studies made on foraging strategies in kittiwakes using GPS tracking devices have shown that there might be a bimodal pattern in foraging trips with shorter trips that are likely to be for chick provisioning, and longer trips that are likely to be self-feeding trips (Kotzerka et al. 2010). This foraging strategy has also been suggested for chick-rearing procellariiformes in other earlier studies also (Congdon et al. 2005; Weimerskirch et al. 2001). These findings of differences in foraging trips might also mean that the prey items for chick-provisioning differ from the prey meant for self-feeding.

Comparative studies of the difference between chick-provisioning and self-feeding in other species of seabirds

Similar studies comparing self-feeding and chick-diet have been made on several occasions. Some studies good for comparison to this are the study made by Fijn et al. (2012) on the diet of Procellariids in Antarctica, the study made by Wilson et al. (2004) and Bugge et al. (2011) on common guillemots, and Shealers (1998) studies on terns in Puerto Rico. These were studies testing the difference between self-feeding and chick-provisioning, and all were made on different species. Some of the studies were made on seabirds with hunting strategies similar to those of kittiwakes like Shealer (1998) and Fijn et al (2012). The studies by Wilson et al. (2004) and Bugge et al. (2011) tested for differences in diet on common guillemots that have a very different hunting strategy from kittiwakes.

The study by Fijn et al. (2012) compared the diet of two procellariid species, snow petrel (*Pagodroma nivea*) and cape petrel (*Daption capense*) that are numerous in the Antarctic, and are important species since they stand for 20-40% of the overall consumption by seabirds in that area (Fijn et al. 2012). Food samples were obtained by using the same stomach flushing technique, both on chick-feeding birds and self-provisioning birds. Fijn et al. (2012) then used identifiable remains to reconstruct the original prey mass, and with this found that there was a significant difference on the diet of chick feeding and self-provisioning birds in cape petrels, whereas there were no such difference in snow petrels. In cape petrels they found a higher proportion of fish in chick-feeding birds than self-provisioning birds, as well as a smaller amount of crustaceans. Fijn et al. (2012) points out the importance of taking variation in food availability between areas into consideration when studying seabird diet on a certain location. There have been several studies on differences between self-feeding and chick provisioning diets in fulmarine petrels that did find a quality difference (Creet et al. 1994; Lorentsen et al.1998; Van Franeker et al. 2001). Fijn et al (2012) suggests that compositional differences may be caused by local abundance of prey items. They found that snow petrels had a higher percentage of krill and lower fraction of fish in both self-feeding and chick-provisioning birds than in other studies, and a reasonable explanation for this difference could simply be the local high abundance of Antarctic krill (Fijn et al. 2012)

Shealer (1998) has also showed a difference in diet in two species of terns, roseate terns (*Sterna duogallii*) and sandwich terns (*Sterna sandvicensis*) in Puerto Rico. Terns are more similar to kittiwakes in hunting strategies since they plunge dive to catch fish, but can only reach the surface layers (Nelson 1980). Both these species showed a difference in diet between adults and chicks, and in both of the species the chicks were fed a diet consisting of a higher proportion of clupeid fish than the adults ate themselves (Shealer 1998). In addition to investigating the diet choices made by terns for chick-provisioning and self-feeding, Shealer (1998) also investigated the fish available in the area for the terns to catch. This investigation showed that the terns fed their chicks fish in proportions different to those of fish caught in the lagoon during sampling. These terns bring whole fish back to their chicks instead of regurgitating, and according to central place foraging theory it is easy to improve chick's energy gain per unit time by bringing back more energy-rich fish for their chicks than what they eat themselves (Orians & Pearsons 1979).

Bugge et al.`s (2011) study is of a particular interest since it is performed at the same location as this study, but with another species, the common guillemot, that has a different hunting and feeding strategy than the kittiwake. Guillemots are like other auks specialized divers and are able to feed from a wider range of the water column than kittiwakes that are restricted to the surface layers. This makes this study an interesting comparative study since they are both from the same area with the same prey species available. The same sampling and analyzing techniques were used also in the two studies. Wilson et al. (2004) did the first detailed comparison on diet in adult and chick guillemots on the Isle of May in Scotland, and their findings strongly supported that breeding adults select higher quality prey for chick-provisioning. Their findings were that chicks were fed primarily energy rich sprats (*Sprattus sprattus*) and lesser sandeels (*Ammodytes marinus*) and that adults mainly fed on 0 and 1+ group lesser sandeels (Wilson et al. 2004). The study by Bugge et al. (2011) also showed that there is a quality difference between the fish caught for self-feeding and the fish caught for chick provisioning with adults eating mainly the youngest year-classes of gadids, whilst feeding mainly capelin and sandeels to their chicks. Guillemots are also single-prey loaders. Both diet studies on guillemots showed that there is a quality difference between the fish caught for self-feeding and the fish caught for chick provisioning.

Aim of the study and expected results

The decrease of the kittiwake population and the fact that it is now considered an endangered red-list species makes it more important than ever to document as many aspects of their feeding-ecology as possible. Since changes in food availability may have an effect on population numbers, knowing more about their feeding strategies during the breeding season is important. Also general food web knowledge is very important to maintain a good resource management which this study can contribute to. Good knowledge of the food web is particularly important in the area around Hornøya where the bird colony shares resources with fisheries. It is also important to understand the feeding ecology of adult birds and not just chick-provisioning birds. Most dietary studies focus on the diet of chick provisioning birds, but to fully understand the feeding ecology of a species, the difference between chick provisioning and self-feeding should be investigated, especially since chick provisioning accounts for only a small amount of annual food intake (e.g., 5% in fulmarine petrels) (Van Franeker et al. 2001). Estimated energy demands on kittiwakes on Hornøya showed that the total annual requirements for kittiwakes were $568*10^7$ kJ, and that chick energy demands counts for $73.5*10^7$ kJ of this number (Table 5; Furness & Barrett 1985) which is 12.9 % of the total annual energy demands. However this estimation was made when the population was much larger.

The aim of this study was to check for a quality difference in food between kittiwake adults and chicks. Hornøya is a locality where several surveillance studies have taken place since 1980, and it is now under surveillance of the SEAPOP programme. Kittiwakes on Hornøya have been the subject of a variety of studies in this time period, including diet studies (Barrett 2007). In 21 of the 22 seasons up to an including 2006 for which data are available for masses of prey landings, capelin and/or herring comprised 70% or more of the diet by mass in kittiwakes on Hornøya (Barrett 2007). The same was true for six of the seven subsequent years (Barrett pers.comm.).

Both Wilson et al. (2004) and Bugge et al. (2011) found quality differences in diet of adults and chicks, which is as expected since guillemots are divers and can pursuit prey under water, and can therefore pick prey that are present in a larger part of the water column, and not just at the surface. However studies between adult and chick diet in surface feeders have documented varying results. In Fijn et al. (2012) one of the two petrel species showed a difference in diet between self-feeding and chick-provisioning. Shealer’s (1998) study on terns also showed a quality difference between chick provisioning and self-feeding. So even if these birds are surface feeders there is a possibility to find differences in adult and chick diet, also with this hunting strategy. However it is expected that this is strongly linked to the availability of food in the surface layer, and this can differ geographically. Capelin is the main pelagic species in the area around Hornøya (Barrett et al. 2007). Since kittiwakes are pelagic feeders it is expected that these species are highly represented in the diet samples for both adults and chicks also in this study.

Optimizing energy load may be achieved by selecting fatty fish such as clupeids, sandeels, capelin, or mackerel (*Scomber scombrus*), but also by selecting larger or gravid fish, because these generally contain more energy per item (Montevecchi & Piatt 1984; Hislop et al. 1991; Lawson et al.1998 in Barrett et al. 2007). At Hornøya, the diet is predominantly capelin and/or I-group herring and the adults readily switch between the two species (Barrett 2007), but tendencies toward a lower breeding success when herring is present and a higher success when capelin is present, point to capelin as the preferred prey for kittiwakes (Barrett 2007).

Since capelin is a schooling species that is favourable for kittiwakes, because attacks from predatory fish bring them to the surface, they are likely to be easier to catch for kittiwakes than herring (Barrett 2007). As long as capelin is abundant in the area we expect kittiwakes to choose mainly capelin both for chick-provisioning and self-feeding.

METHODS

Location

The study took place on Hornøya during the late incubating period, hatching and most of the chick-raising period from June 14th and July 18th 2012. Hornøya (72°22`N, 31°10`E) is a small island (900 x 650 m) in the southern Barents Sea (Fig 3). It is a nature reserve serving as a reservoir for several different species of seabirds in addition to kittiwakes, such as common guillemots (*Uria aalge*), black guillemots (*Cepphus grille*), razorbills (*Alca torda*), Brünnich's guillemots (*Uria lomvia*), puffins (*Fratercula arctica*), shags (*Phalacrocorax aristotelis*), herring gull (*Larus argentatus*) and great-black back gull (*Larus marinus*). Ravens (*Corvus corax*) and Gyrfalcons (*Falco rusticolus*) are common predators in the colony. White-tailed eagles (*Haliaeetus albicilla*) are also present, and the during the 2012 season they were exceptionally numerous. Ravens mainly steal chicks and eggs from unguarded nests, but Gyrfalcons and White-tailed eagles can take adult birds.

Kittiwakes breed in steep cliffs and the kittiwake population of Hornøya is spread all around the island were the surface is suitable. The population is thus divided into many smaller colonies separated from each other all over the island. The sampling for this study was focused on one of these smaller colonies rather than sampling at random in the whole Hornøya population.

Figure 3. Map showing the geographical location of Hornøya. The highest point on the island is approximately 60 meters above sea level. The size of the island is c. 900x650 m.

Water off-loading method

The technique used in this study is commonly used in seabird diet studies (Catard et al. 2000; Cooper et al. 1992; Creet et al. 1994.) and is called "the water offloading technique" or stomach flushing and is described by Wilson (1984). The method has been used with success in other studies testing for differences between adult and chick diet in guillemots (Wilson et al. 2004; Bugge et al. 2011), and on petrels (Fijn et al. 2012). This method is simple, efficient and accepted as the most humane method for diet sampling of stomach content (Robertson et al. 1994). This was the diet-sampling method found most appropriate for this study.

The weakness of the method is that it is hard to do any quantitative analysis without risking a large bias. In this study, focus was on the frequency of occurrence of prey and therefore the water offloading technique seemed to be the better choice.

Treatment groups

The birds sampled from were separated into three different treatment groups:

1. Adult Kittiwakes incubating eggs
2. Adult Kittiwakes raising chicks
3. Adult Kittiwakes at empty nests

The reason for the separation of groups was to be able to detect differences in diet more easily. Since we could collect the samples from incubating birds in the beginning of the breeding season, and from birds at empty nests towards the end of the season, there was an opportunity to address any differences in diet in relation to time, while group 1 and 3 also represents adult diet for birds without chicks. By getting stomach samples from adult bird representing adult diet, from both bird without and without chicks, it was possible to check if there were any differences in adult diet during the change from incubating to raising chicks.

The birds raising chicks is the group where a difference between adult and chick diet could be addressed since the regurgitation from the birds sampled in this group were most likely meant for their chicks and not for self-feeding. Regurgitation from adults with chicks is therefore possibly a good indication of chick diet. In addition, assuming the stomach content from birds raising chicks is meant for self-feeding, in this group alone we can get an idea of both adult diet and the diet for chick-provisioning.

Capturing and diet sampling

The birds were caught using a noose pole while they were resting on their nest. Preferably, birds that came straight from the feeding grounds were picked for the study, since they are more likely to have stomach content, and possibly something in their proventriculus to regurgitate. Birds that have just been feeding often regurgitate the content in their proventriculus as a defense mechanism against predators or disturbance when they are caught. This regurgitated food was collected into separate zip-lock bags. Each bird was ringed, weighed in a bag with a spring balance (± 5 g). Measurements of head+beak, beak, and wings were measured with a wing rule and vernier calipers.

Finally the stomach content was sampled using the water off-loading method. With this method described by Wilson et al. (1984), a soft plastic tube of approximately 10 mm in diameter was inserted to the bird stomach through their esophagus. The tube was then connected to a 0.5 l water bottle filled with air tempered fresh water. Water was then flushed down into the birds stomach until water dripped from the beak. Then the bird was turned upside-down over a plastic box to collect the water running out while the plastic tube was gently drawn out from the stomach, making the stomach content flush out together with the water. This procedure was repeated a maximum of three times to make sure all the stomach content had been flushed out. If stomach flushing seemed empty the first time and if water came out clear the second time, we assumed that the bird was empty and avoided to flush the third time to reduce the amount of unnecessary 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 flew off, taking a few circles around the area. After a few minutes, most of them returned to their nest. There were no sign of harm, stress or behavioral change in the period after the sampling. This fits with the findings of Wilson et al. (2004) that the method does not harm the birds.

The samples were stored in zip-lock plastic bags, with the regurgitation in separate bags from the stomach content. All samples were frozen after each working shift for later analysis in the lab.

Lab analysis of diet samples

After thawing in the lab the sample was identified into lowest possible taxa before further digestion. Some of the samples were already almost entirely digested, and we could then start identifying directly. The rest of the samples were further digested using a saturated solution of biological detergent (Biotex). The samples were incubated overnight in an oven at 50°C. After incubation, the samples were shaken, flushed with warm tap water, and decanted carefully to get rid of the last pieces flesh without losing the fish bones and otoliths. The bones, otoliths and other leftovers after the digestion were investigated under a light microscope. Using the vertebrae of the fish we could identify them down to species using Härkonen (1986) and Watt et al. (1997).

Diet composition was expressed by frequency of occurrence of the different species. Due to large differences in the degree of digestion and the fact that otoliths were missing in many of the samples, further quantifications were impossible to make.

Fish size analysis

Otoliths made identification of some species very easy. Especially capelin (*Mallotus Villosus*) and sandeel (*Ammodytes sp*) are very characteristic. After identification, all otoliths were measured under a light microscope using a calibrated eyepiece graticule. The measurements were used to calculate total fish length (mm) using eq. 1 for capelin (Barrett & Furness 1990) and eq. 2 for sandeel (Jobling & Breiby's 1986).

$$\text{TFL (mm)} = 25.8 + 48.0 * \text{OL (mm)} \qquad \text{(Eq. 1)}$$

$$\text{TFL (mm)} = 14.93 + 40.8 * \text{OL (mm)} \qquad \text{(Eq. 2)}$$

Where OL is the otolith length in mm, and TFL is total fish length in mm. When possible the matching otoliths found in the stomach and regurgitate samples were paired to avoid counting one fish as two individuals.

Data analysis

Diet composition is expressed as frequency of occurrence based on counts of the different prey species found in each sample. For the statistical analysis for differences between the amounts of capelin brought in by the treatment group a Pearson's chi-square (χ^2) goodness of fit was performed. The software program was Excel 2013. A sign test was run on the treatment group of adults with chicks. In this group we had enough birds which both regurgitated and had identifiable content in their stomachs and therefore we could do a sign test to check for differences in the frequency of capelin between STO and REG samples at individual level. This test was run in R 2.15.2. A two-sample student's t-test with common variance was performed to check for differences in mean length of prey (Run in Excel).

RESULTS

Diet composition and prey frequency

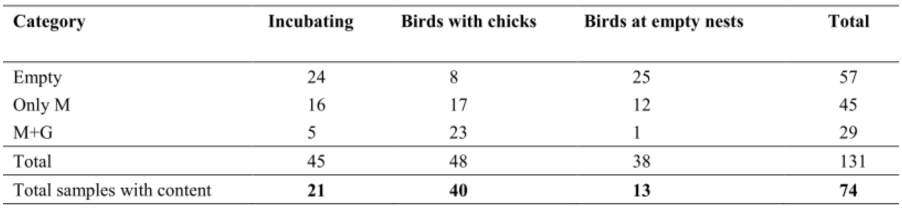
A total of 131 birds were sampled, and of these, 57 had no stomach content and were thus impossible to use further in the analysis. The total number of food samples, including all treatment groups and both regurgitations and samples from stomach pumping, was 160.

Eight of 48 samples from birds with chicks were empty, 24 of 45 of the samples from incubating birds were empty, and 25 of 38 samples from birds at empty nests. This account for 17 % of empty samples from birds with chicks, 53.6 % in incubating birds and 65.8 % in birds sitting on empty nests. Using a Pearson's chi-square test for three groups to test if there is a significant difference between the amount of empty samples from the different groups we found that $\chi^2 = 23.51_{,}$ df = 2, P = 0.00001. There was no difference between incubating birds and birds at empty nests ($\chi^2 = 1.32_{,}$ df = 1, P = 0.25).

As table 1 shows the total numbers of STO samples from the different treatment groups were 21 for incubating birds, 40 for birds with chicks and 13 for birds at empty nests. Of the three groups, birds with chicks was the group with the highest amount of REG samples with a number of 23 birds that regurgitated. Five of the 45 incubating birds sampled from regurgitated and only one of 38 birds on empty nests did the same.

Many of the birds handled did not regurgitate, but still had content in their stomachs. Seventeen of the 48 birds with chicks had only content in their stomachs but nothing to regurgitate. For incubating birds this number were 16 out of 45 samples, and for birds at empty nests 12 of 38 did not regurgitate but did have identifiable content in their stomachs.

Table 1. Number of samples collected during the breeding season in the different treatment groups. M is stomach sample and G is regurgitation sample. Empty means the samples collected that did not contain anything that could be identified. M+G are the number of birds caught that both regurgitated and were stomach flushed.



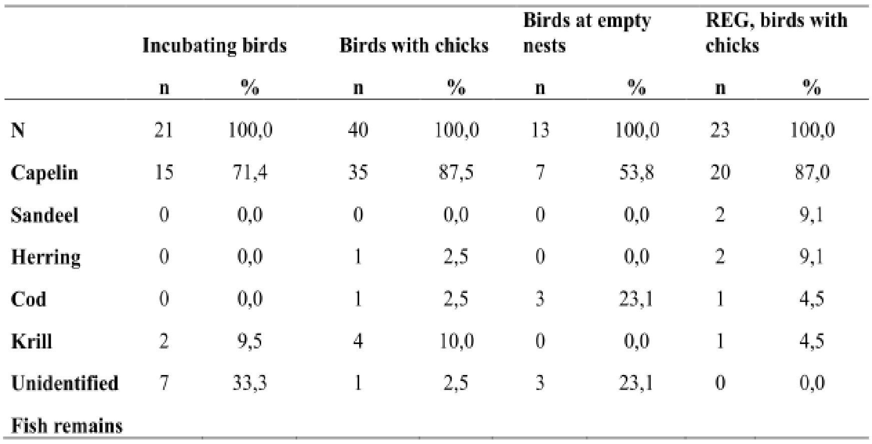
Category	Incubating	Birds with chicks	Birds at empty nests	Total
Empty	24	8	25	57
Only M	16	17	12	45
M+G	5	23	1	29
Total	45	48	38	131
Total samples with content	**21**	**40**	**13**	**74**

In all the different groups, Capelin was the most common prey animal found. Table 2 and Fig. 4 show the frequency of occurrence of all prey animals found in the different groups. In incubating birds, capelin was found in 74 % of the samples, in birds with chicks the percentages were 87.5 % in STO samples and 87 % in REG samples. The lowest occurrence of capelin was found in birds at empty nests with only 53.8 %.

Both in incubating birds, and REG from birds with chicks the second most common prey animal was krill, found in two (9.5 % of the samples) of the incubating birds and four (10 % of the samples) in the birds with chicks . In birds on empty nests the second most common prey were cod, found in three individuals accounting for 23.1 % of the samples.

Herring and sandeel were only found in REG of adults with chicks. Two individuals contained herring, and two different individuals contained sandeel, both counting as 9.1 % of the samples.

Table 2. Frequency of occurrence of the different prey items found in the stomach content of all the different treatment groups. The content of regurgitations from adult kittiwakes on nests with chicks is shown in the last column. N is number of samples, n is number of samples with occurrence of a given prey.



	Incubating birds		**Birds with chicks**		**Birds at empty nests**		**REG, birds with chicks**	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**
N	21	100,0	40	100,0	13	100,0	23	100,0
Capelin	15	71,4	35	87,5	7	53,8	20	87,0
Sandeel	0	0,0	0	0,0	0	0,0	2	9,1
Herring	0	0,0	1	2,5	0	0,0	2	9,1
Cod	0	0,0	1	2,5	3	23,1	1	4,5
Krill	2	9,5	4	10,0	0	0,0	1	4,5
Unidentified Fish remains	7	33,3	1	2,5	3	23,1	0	0,0

Unidentified remains are fish bones that were too well digested to use for any identification purposes. These bone leftovers could only confirm that the bird had been eating some kind of fish. In the REG samples from birds with chicks the amount of unidentified remains were naturally zero (0 % of the samples) since food in the proventriculus is only in the beginning of digestion and nothing were digested far enough to be unidentifiable. The amount of unidentifiable remains in STO of the different group were 2.5 % for birds with chicks, 33.3% for incubating birds, and 23.1 % for birds at empty nest. The difference between adults with chicks and incubating birds is significant (χ^2 = 10.29, df =1, P = 0.0013). So was the difference between adults with chicks and birds at empty nests (χ^2 = 6.31, df = 1, P = 0.012).

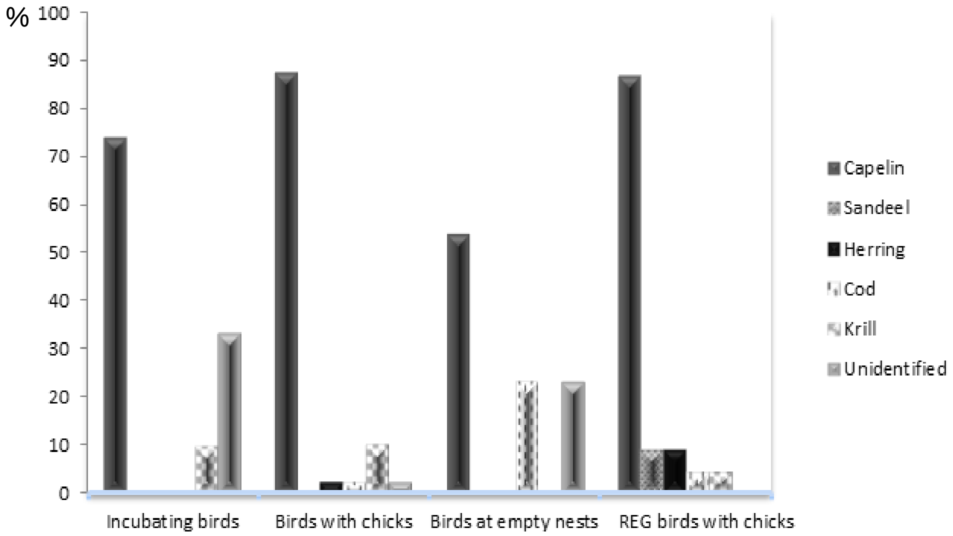


Figure 4: Percentage of occurrence of all the different prey animals found in the stomachs of incubating birds, birds with chicks, and birds at empty nest. Regurgitation samples (REG) from birds with chicks are shown in the last section.

Since only one of the birds at empty nests regurgitated, the sample number is too small to test for any differences between STO and REG both at group level and individual level. Although the number of regurgitates from incubating birds was a little bigger, it was also too small (n = 5) to test statistically. All of the samples from both groups (n = 6) contained 100% capelin remains, and no other prey species were found in these samples.

A Pearson's chi-square test was used to test if frequency of prey differed at the group level between the three treatment groups. Differences between expected and observed values are shown in Fig. 5. Testing for differences at group level of the frequencies of occurrence of capelin in stomach samples of incubating birds and birds at empty nests showed no significant difference in capelin found in the samples (χ^2 = 1.09, df = 1, P = 0.30). Except for capelin only two birds from incubating birds had krill in their stomachs and three birds at empty nests contained cod. The treatment-groups "Incubating birds" and "Birds at empty nests" can therefore be combined in one group, "birds without chicks". The number of samples containing capelin in all the three treatment groups are shown in Fig. 5 where they are compared to the total number of samples made and the values you would expect if everything was random (expected values from χ^2). As seen in Fig. 5, the observed values are close to the expected values in all treatment groups, but slightly higher than expected in birds with chicks and slightly lower than expected in birds at empty nests.

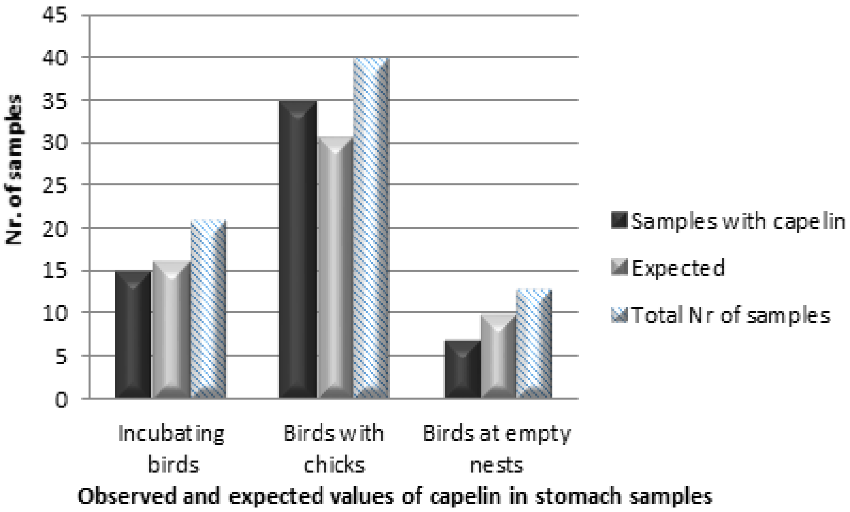


Figure 5: Observed and expected numbers of stomach samples containing capelin from all the different treatment groups.

When combining the data from the two treatment groups without chicks the total number of samples from “birds without chicks” were 34 STO samples and 6 REG samples. All REG samples contained 100 % capelin as mentioned earlier. The composition of the two groups of birds without chicks combined for capelin:sandeel:herring:cod:krill in STO samples is 22:0:0:3:2.

There was a significant difference in the frequency of capelin in STO samples of adults with and without chicks ($\chi^2 = 5.40$, df = 1, P = 0.02). The difference is due to the higher percentage of capelin in the samples from adults with chicks. So even if there was no significant difference between in the frequency of capelin found in the birds incubating and the birds on empty nests, there was a significant difference in the frequency of capelin found in birds with and without chicks.

The frequency of occurrence in STO and REG from adults with chicks is shown in Fig 6. With the results from the individuals who regurgitated in addition to having stomach contend (n = 23) we could check for differences at an individual level using a sign-test. One test for differences in capelin, and one for all the other prey species combined. The reason for putting all other prey species together in an “other species” group was that there were not enough samples containing species other than capelin to allow individual tests. With a p-value of 0.5 for differences in capelin between STO and REG, and p-value of 1 in the test for differences in other species, the sign-test showed that there was no significant difference between the content in the stomach and the content of the regurgitation of adult kittiwakes with chicks.

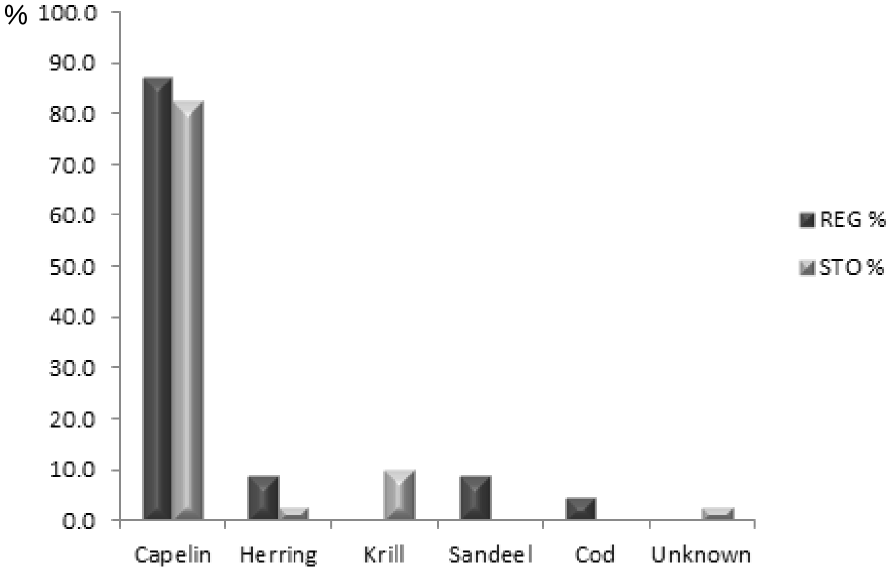


Figure 6: Frequency of occurrence of the different prey items found in REG and STO samples from kittiwakes with chicks (N = 40).

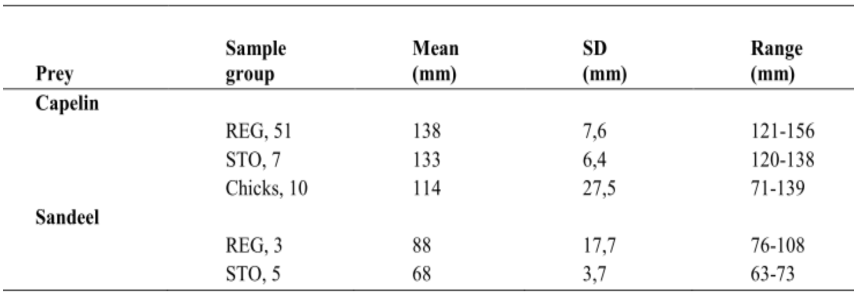
A comparison of REG with STO content at the individual level in the group of kittiwakes without chicks proved very difficult. Of the six birds that regurgitated, two of these had empty stomachs, leaving only four samples to compare between REG and STO. Of the six birds, the only prey item found in the samples was capelin. Despite the scarcity of samples, there was no indication of any difference between regurgitation and stomach content at the individual level for birds without chicks.

The number of REG samples collected from chicks was low due to chicks not being a main target of this study. The total of six regurgitation samples from chicks varied little with five chicks containing 100% capelin, and one containing capelin and cod.

Fish size

Otoliths were used to calculate total fish length (TFL) to investigate if there were any signs of difference between TFL of capelin found in REG and STO of birds with chicks. The distribution of TFL of capelin in STO and REG from adults with chicks is shown in Fig. 7. A comparison of TFL of capelin in REG from adults with chicks is shown in Fig 8.

Table 3. Total fish length of capelin and sandeel found in REG and STO samples of adults with chicks, and REG samples of chicks.



Prey	Sample group	Mean (mm)	SD (mm)	Range (mm)
Capelin				
	REG, 51	138	7,6	121-156
	STO, 7	133	6,4	120-138
	Chicks, 10	114	27,5	71-139
Sandeel				
	REG, 3	88	17,7	76-108
	STO, 5	68	3,7	63-73

Otoliths found were mainly from capelin, and the number of fish found based on otoliths were 51 in REG of adults with chicks, seven in STO of adults with chicks and 10 in REG from chicks (Table 3). TFL of capelin did not differ significantly between the REG and STO of adults ($t = 2.3$, $df = 8$, $P = 0.0847$) or between STO of adults and REG from chicks ($t = 2.2$, $df = 10$, $P = 0.06$). However, mean lengths of capelin were significantly longer in the REG samples of adults than in the chicks samples ($t = 2.26$, $df = 9$, $P = 0.02$).

Only two birds came back to their nest with otoliths from sandeel, both had chicks, and both had sandeel in the REG samples. Both of them also contained capelin. One bird had otoliths from five sandeels with total fish lengths of 63, 66, 68, 69 and 73 mm. The other bird had otoliths from three individual fish with lengths of 76, 79 and 108 mm. The mean fish lengths from the two birds were 67.8 mm (SD = 3.7) and 87.7 mm (SD = 17.7).

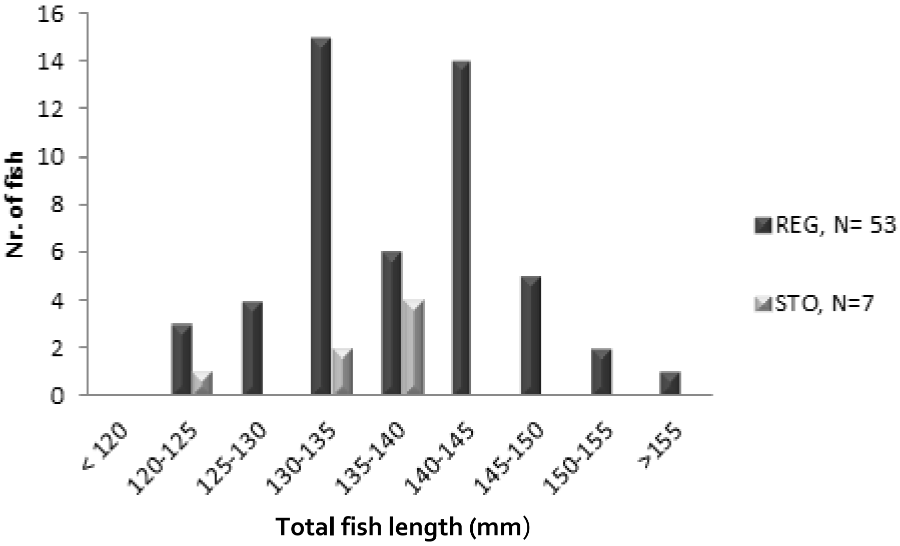


Figure 7: Frequency distributions of total fish lengths for REG and STO samples. Total fish length was calculated from the length of otoliths found in regurgitation (blue) and stomach samples (red) from adult birds with chicks. Considerably higher number of otoliths were found in regurgitation (53 fish) than in the stomach samples (7 fish).

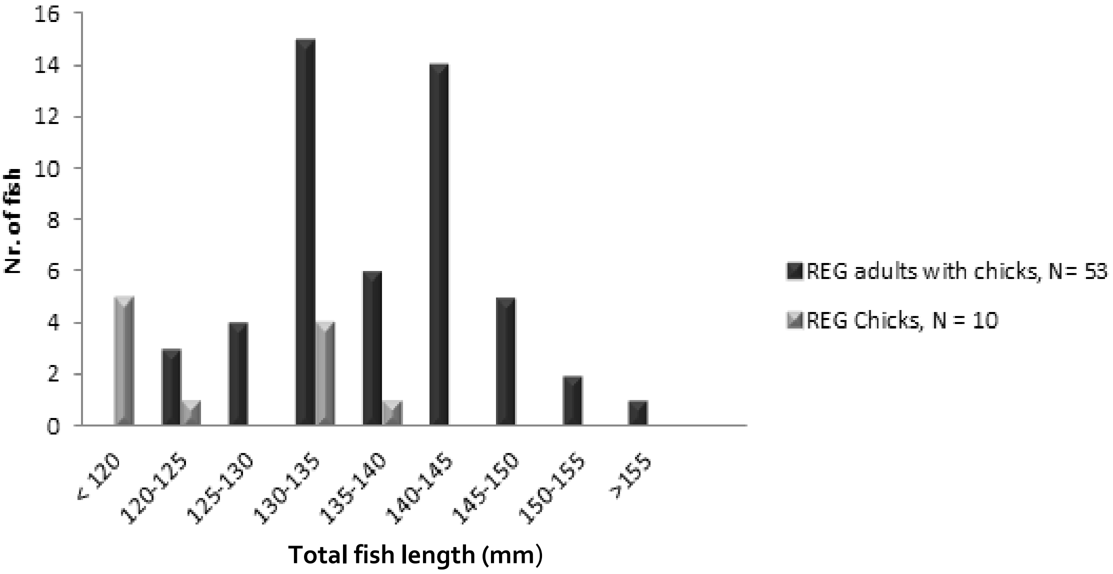


Figure 8: Total fish length of capelin found in regurgitation from chicks (6 individuals) and adults with chicks (16 individuals).

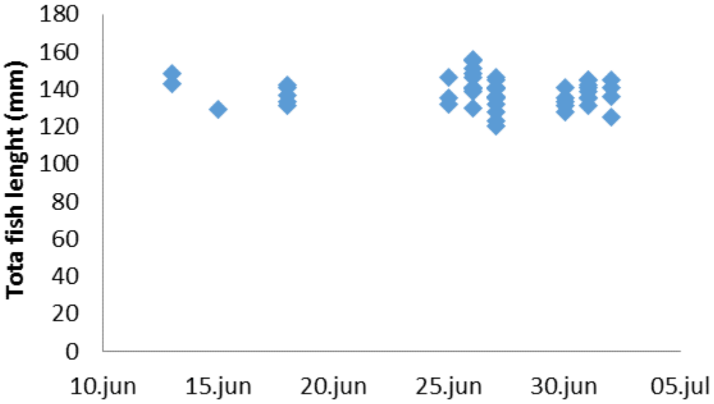


Figure 9: Total fish length of capelin found in REG of adults with chicks in relation to sampling date.

There seemed to be little variation in TFL of capelin throughout the season when we look at the size of capelin found in REG from adults with chicks (Fig. 9). TFL from the STO samples were too few and with too much variation to be able to draw any results for comparison between TFL in REG and STO in relation to time.

DISCUSSION

Evaluation of the method and its efficiency on kittiwakes

The water-off-loading method used by Wilson et al. (2004) and Bugge et al. (2011) on guillemots seemed to be a successful method to use also on kittiwakes. Since they regurgitate more or less voluntarily when threatened or harassed by other birds, or in this case catching and handling by humans, they were unproblematic to sample. This method was successfully used on non-regurgitating common guillemots Isle of May by Wilson et al. (2004), and on Hornøya in the study of Bugge et al. (2011). The overall success rate of samples collected with the water off-loading method was 56.5 %, which is slightly lower than the success rate of both Bugge et al. (2011) of 58% and Wilson et al. (2004) of 68%. This means that 43.5 % of the kittiwakes caught and sampled were completely empty. This does not necessarily mean that this method is inefficient on kittiwakes. It can however reflect that the retention time can differ between bird species. The numbers of empty samples from chick-rearing birds were much lower than in birds without chicks. This may be because kittiwakes with offspring return to the colony with food still in their stomachs and proventriculus in order to feed their young, while those without chicks can choose to digest their meals at sea and return to the colony with an emptier and therefore lighter stomach to reduce energy expenses when flying.

The limitation of this method is the same for kittiwakes as the limitations pointed out by Wilson et al. (2004) and Bugge et al. (2011) on their work on guillemots. The use of skeletal and otolith remains is limited due to different retention time of different prey types (Jobling & Breiby 1986; Johnstone et al. 1990; Hilton et al. 2000; Wilson et al. 2004). Quantification of diet data is therefore difficult with this method, and the focus is therefore on frequency of occurrence.

Even though handling and sampling is stressful for the birds, none of them showed abnormal behaviour after being released. Most of them took off and returned to their nest after 1-2 minutes.

Empty stomach samples and unidentifiable fish remains

Due to different retention times between species and samples collected without us knowing when the bird had its last meal, the stage of digestion differs between individuals, and this can make the otoliths and vertebrae hard to identify (Jobling & Breiby 1986; Johnstone et al. 1990; Wilson et al. 2004). This was not a problem for otoliths in this study, since none of them seemed to be excessively eroded and was easy to identify. Bugge et al. (2011) also concluded that very few of the otoliths found in guillemots had eroded so much that they could not be used, and the majority were found to be suitable for measurements, and this was the case also for otoliths found in kittiwakes in this study. Unfortunately, there was a considerable amount of samples containing only 1-2 vertebrae too extensively eroded to be identifiable. Many of these vertebrae looked like they could belong to capelin from their similar shape to the less eroded vertebrae found in other samples, but they were too far eroded for any certain identification of the species. All the samples containing only a few well-eroded vertebrae were classified as having unidentifiable fish remains, meaning that the only conclusion made from these samples was that the kittiwake had eaten fish. To avoid any possible bias, no attempt to further identify the eroded vertebrae were made.

There was a higher percentage of unidentified fish remains in the two groups without chicks compared to birds with chicks (Table 2). Birds with chicks had only 2.5 % unidentified fish remains in their stomach samples (1 of 40), while incubating birds had 33.3 % (7 of 21), and birds at empty nests had 23.1 % (3 of 13). As shown earlier these differences are significant both between adults with chicks and incubating bird, and adults with chicks and birds at empty nests. It is not surprising that the frequency of unidentified fish remains proved to be significantly higher in the birds without chick compared to birds with chicks, and this can be partly explained by their feeding behaviour when they have chicks compared to when they do not. Furthermore the speed of digestion, and the foraging trips and foraging behavior may be an important point to why the stomach samples from incubating birds and birds at empty nests seems to be further digested than the stomach samples from adults with chicks.

A seabird digestion system is simple, consisting of oesophagus, a simple acid-proteolytic stomach (with proventriculus and gizzard), a tubular small intestine and a short colon (Hilton et al. 2000). This is typical also for kittiwakes. A comparative study of digestion in North Atlantic seabirds by Hilton et al. (2000) found that the kittiwake retention time is 6.43 ± 0.38 (SD) hours for sandeel and 7.02 ± 1.12 (SD) hours for whiting. Capelin is probably closer to sandeel in retention time, since they are both fat and energy rich fish. Since the digestion is rather quick, the time from the moment the meal is consumed and until it is no longer possible to collect through stomach flushing may thus be a matter of hours. Species specializing on eating fish that are easy to digest (Jackson et al. 1987) and dense in energy (Hislop et al.1991, in Hilton et al. 2000) tend to have shorter retention time than birds with a more varied diet of lower quality (Hilton et al. 2000). It has been suggested that a short retention time is beneficial for birds with a pursuing hunting strategy because it decreases their mass and may increase hunting success for these hunters who are strongly mass-dependent (Sibly 1981). Sibly (1981) suggested that birds who pursuit their prey have a capture rate that is depending on performance, and a lowering of body mass can possibly increase capture rate. This is particularly likely in raptor species that catch avian prey during flight, but it may also be of significance to kittiwakes that need to take longer feeding trips. It should be an advantage for them to quickly reduce mass to save energy expenses flying back and forth to the colony.

Sibly (1981) showed that stomach mass correlated with stomach retention time was a very important influence on stomach retention time, and also food were retained in the stomach for a longer time in species with a heavy stomach. Kittiwakes are not considered pursuit foragers, but the mass of the stomach (measured as dry-mass) as a function of body mass in kittiwakes is very low (Fig 3a in Hilton et al. 2000). This can be an indication that even for kittiwakes with a non-pursuing hunting strategy it is important to decrease mass. Mass savings are likely to reduce cost during flight (Pennycuick 1989). Since a low mass may be important for kittiwakes to avoid using too much energy while flying back to the colony after feeding trips, birds without chicks may choose to digest at sea to avoid making the trip back to the colony with the extra weight of a meal

This strategy combined with the rapid digestion may help to explain why so many more of the birds without chicks came in with empty stomachs compared to birds with chicks.

A rapid digestion can also be a strategy to avoid “ingestion bottleneck”. Since they feed infrequently during the breeding season at foraging sites possibly far away from the breeding colony, they need to eat large meals on each feeding trip to meet their energy demands. On each feeding trip, the birds are constrained to eating only the amount of food they can consume until the gut is filled. Rapid digestion will minimize the impact of such a bottleneck (Hilton et al. 2000). In general, a specialization on high quality food is associated with rapid digestion, which is the case for kittiwakes feeding on energy rich capelin. The amount of empty stomach samples, and the lack of regurgitations from kittiwakes without chicks, can be a reflection of their high-quality diet. Furthermore, the higher fraction of empty stomachs in birds without chicks indicates that they rather digest at sea.

Behaviour in the colony

Spot-check studies of colour-dyed breeding kittiwakes have shown that the birds do not normally loaf around in the colony but fly straight off to sea after being relieved by their partner, which returned straight from being out at sea to the nest (Galbraith 1983). This conforms with observations during the breeding season on Hornøya in 2012. When one of the birds in a pair with chicks returned from the sea, they only stayed together on the nest for a short amount of time before the other bird flew away 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 more often observed loafing around in the colony before changing with their partner at the nest. This may also be one of the reasons for the higher amount of empty samples in birds on empty nests and with eggs. They may have been sitting in the colony elsewhere for a while before relieving their partner at the nest. Most of the birds in this study were caught right after they had been observed to relieve their partner at their nest to increase the chance of getting REG samples. This tactic appeared to be efficient in the birds with chicks, but the birds without chicks could be often completely empty with a negative stomach sample and no regurgitation upon capture even right after they had returned to their partner. This further supports our suspicions that birds without chicks to feed may choose to digest at sea. This difference in behavior of kittiwakes with chicks, and kittiwakes without chicks helps us explain why there were fewer regurgitates and stomach samples in the birds without offspring in the colony.

The composition of diet

There was a clear dominance of capelin in both STO and REG from adults with chicks and adults without chicks (Table 2 & Fig. 4). The second most common prey species was sandeel, but they were found only in a few individuals. Other prey animals found in the samples were herring, krill and cod; although none of these prey items were found in more than a few individuals each. The overall dominance of capelin in both STO and REG samples from all the groups was very clear and no other prey species were even close to being as abundant as capelin. However, there was a difference for the amount of capelin within the different groups. Incubating birds had capelin in 74 % of the samples and birds at empty nests had capelin in 53.8 % of the samples. In birds with chicks, the percentages of samples containing capelin were 87.5 % in STO and 87 % in REG samples. As confirmed with the χ^2 – test there was no significant difference in the frequency of capelin found in the samples from incubating birds and from birds at empty nests, meaning these groups can be treated as one, birds without chicks. The testing for differences in frequency of capelin in birds with chicks and birds without chicks after combination of the two groups without chicks proved to be significant. However, many of the sample containing unidentified fish remains, consisting mainly of 1-2 vertebrae, found in birds without chicks (Table 2) may have originally contained capelin, and that the percentage of capelin found in both birds with and without chicks would be much more similar if the samples from incubating birds and birds without chicks had been less digested. Even though there was an apparent significant difference in the amounts of capelin brought in by birds with chicks and birds without chicks, it does not necessarily mean that birds with chicks caught capelin more often than other prey compared to birds without chicks. This difference was probably due to the birds without chicks not having to bring back food to the colony for chick provisioning, but could choose to digest at sea.

In addition to capelin, three birds without chicks had krill in their stomachs and two birds had cod. All three birds with krill belonged to the group with incubating birds, and the two with cod were birds at empty nests. Although this is a very low number to draw any firm conclusions from, it may simply mean that krill was a little more available than cod in the beginning of the breeding season, and that cod was easier to catch later in the season. The possibility of chance cannot, however, be excluded.

In guillemots the differences in diet between adults and chicks were very clear. In the study by Bugge et al. (2011) the frequency of prey in adults were 89.8 % gadid, 25.4 % capelin and 11.9 % sandeel from the 59 adults sampled from. The 79 fish collected that was meant for chicks was mainly capelin (82.3 %). In this study they also used paired samples and found that the frequency of occurrence of capelin was significantly higher in chick food (77.2 %) than in adult stomachs (26.3 %). In Wilson et al. (2004) the adults mainly ate 0 and 1+ groups lesser sandeel, while 79 % of the chicks got energy rich sprats. Both these studies were made on the same bird species, but there was a difference in prey species due to the studies being made in different areas with different stocks of fish. Still, the difference between adult and chick diet were strongly significant.

Shealers (1998) study was made on two tern species who both are surface feeders and single-prey loaders. That means that they are more similar to kittiwakes in their hunting strategies, but that they only bring back one whole fish in their beaks for chick provisioning like the guillemots. Adult roseate terns fed primarily on dwarf herrings and anchovies, and fed mainly dwarf herring and sardines to their chicks. Sandwich terns ate mainly silversides and sardines for themselves, while providing their chicks with mainly dwarf herring and sardines to their chicks. The proportions of food in diet of adults differ from that of chicks in both roseate and sandwich terns. While there was a difference in composition, it was not as clear as shown in both studies of guillemots. The diet of roseate and sandwich terns also showed more variation in prey species. This is probably due to the fact that they are surface feeders like kittiwakes and no diving pursuit hunting birds like guillemots. Fijn et al. (2012) studied petrels who are probably the most similar to kittiwakes in these comparisons. Both the snow and cape petrels in Fijn et al.'s (2012) study were surface feeders and fed their chicks by regurgitating to them. Only cape petrels showed a significant difference in diet. Diet composition of chick provisioning cape petrels (fish:crustacean:squid:other) were 39:61:00:00 while for self-feeding birds the composition were 28:65:07:01. Even if the differences are significant, they are still not at clear as in guillemots. Snow petrels had no significant differences in adult and chick diet.

Differences between adult and chick diet

As in the samples from birds without chicks, only a few individuals from adults with chicks had STO or REG samples that contained prey other than capelin. Capelin was the clearly dominant prey in both STO and REG in chick-raising adults (Fig. 7).

In the group of adults with chicks we should be possible to get a clearer picture of the diet of adults in comparison to the diet of chicks. Instead of looking at differences at group level, a sign test was performed to spot differences at individual level. The theory suggests that if there is no significant difference at individual level, it is unlikely that we would find one at group level. The difference in frequency of capelin between adults and chicks was insignificant. Nor were there significant differences for the other species found in the samples. Since there were no significant differences between REG and STO when we look at species composition of each individual using sign tests, there were probably no differences in the prey selection in self-feeding or chick provisioning. Both adults and chicks seemed to rely on capelin as the main prey item. The importance of capelin as prey was expected, and has been documented as a very important pelagic prey species in the southern Barents Sea on several occasions (Erikstad 1990; Barrett 2007).

A quality difference in diet between adults and chicks has been found in several earlier studies both on divers (Wilson et al. 2004; Bugge et al. 2011) and on surface feeders (Fijn et al. 2012) as described earlier. Common guillemots in the studies of Wilson et al. (2004) and Bugge et al. (2011) clearly have an advantage with their diving and pursuing hunting strategy if they want to selectively choose the best prey for their chicks. Surface feeders like kittiwakes are limited to having to feed in the upper layers of the water column, and thereby eating what they can find there. The diet of surface feeders should, therefore, reflect what prey species is available in the surface layers. In Fijn et al.'s (2012) study of snow and cape petrels they found a difference in quality between adult and chick diet in one of the species, while in the other species it was insignificant. The reason for this can be that prey species in the surface varies geographically, and that the two species had different hunting grounds. Fijn et al. (2012) points out that the diet composition had been highly variable between site and year in cape petrels. Several studies have also shown differences between chick provisioning and self-feeding in fulmarine petrels (Creet et al.1994; Lorentsen et al.1998; Van Franeker et al. 2001). Also Shealer (1998) found a difference in diet of chicks and adults in roseate terns (*Sterna duogallii*) and sandwich terns (*Sterna sandvicensis).* Even if the birds of both Shealer (1998) and Fijn et al. (2012) studies were surface feeders, they found a difference between adult and chick diet in three of the four species in the two studies. These findings strongly indicate that an optimal foraging is a possibility also in surface feeders. Although, the diet showed more variation in terns than in guillemots (Shealer 1998), and that even if the difference in cape petrels were significant (Fijn et al. 2012) the differences were not at clear as with guillemots in both Wilson et al (2004) and Bugge et als (2011) studies.

Availabiliy of prey

It has long been though that the seabirds on Hornøya may exploit a late-spawning component of the capelin stock during the chick-rearing period (Barrett et al. 1990), and capelin have been considered the preferred food for kittiwakes breeding in East Finnmark Furness & Barrett (1985) and Krasnov & Barrett (1995). Because of this late-spawning stock, it is likely that capelin is both abundant and easy to catch when at the surface at least in parts of the breeding season. Personal observations during fieldwork showed that kittiwakes came in with spawning capelin (confirmed later in the laboratory by the amounts of capelin eggs found in the samples) mainly during the incubating and chick-rearing part of the season. As the season progressed, kittiwakes brought in fewer spawning capelin, while other deep diving species like guillemots continued to bring in spawning capelin and sandeel. This suggested that the capelin may have moved deeper in the water column, thereby becoming less available for kittiwakes, but still available for guillemots. Short-term fluctuations in prey availability have shown to be responsible for dramatic within-season changes in breeding conditions for kittiwakes (Suryan et al. 2002). In Labrador and Witless Bay (Newfoundland) in the 1990s, kittiwakes experienced breeding failures because of the lack of capelin while common guillemots were able to find alternate prey and bred successfully. This is likely due to the kittiwakes' inability to dive (Carscadden et al. 2002). Even if it seemed that capelin were less available for surface feeders in the late chick-raising period of the season, there were no apparent changes in prey composition, and it seemed that the kittiwakes continued to feed mainly on capelin. The adults seemed, however, to take longer foraging trips at the later part of the chick-rearing period as one could often observe chicks sitting alone at their nests while both adults were out foraging. This was an indication of lower availability of food, and the adults may have had to take longer foraging trips to find food in the surface layers.

Different strategies for chick provisioning

The different bird species in the articles by Shealer (1998), Wilson et al. (2004), Bugge et al. (2011) and Fijn et al. (2012) and kittiwake in this study displayed two different strategies in bringing food back to their chicks. The cape and snow petrels in Fijn et al.’s (2012) study regurgitate food to their chicks like kittiwakes do. Guillemots in the studies of Wilson et al. (2004) and Bugge et al. (2011) and roseate and sandwich terns in Shealer’s (1998) study all bring back one whole fish to their chicks. All of the bird who brought back whole fish for chick provisioning showed a significant difference between the diet of adults and chicks. In the birds who regurgitated food to their chicks, only one out of the three species showed a similar difference. It may be more common to see a quality difference in diet between adults and chicks in species who brings back one whole fish to their chicks since they more easily can maximize energy yield by choosing one larger and more energy rich fish, like capelin or sandeel, for their chicks. For species who regurgitate to their chicks, the content in their proventriculus are likely to contain more than just one fish. Therefore, they may not be able to be too 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 hunt on the surface.

Sizes of capelin and sandeel

None of the otoliths found in the samples showed excess signs of erosion, and only one was broken and considered unsuitable for measurements. Otoliths from all the different prey species were found (capelin, sandeel and cod) but not herring otoliths. Although herring otoliths are small in size and digested more rapidly than capelin otoliths (Johnstone et al. 1990), it should have been possible to find the bullae which are more resistant to digestion (Bugge et al. 2011). The only remains from herring found were a few vertebrae in the stomach samples, and a few pieces of herring bait from the fishing vessels in the regurgitations. Since the number and size of vertebrae in the stomach samples was about the same as found in the pieces of bait after digesting it in the lab, all the leftovers found from herring were assumed to be fish bait and not living fish. This suggests that herring were not readily available for kittiwake feeding in the surface layers. Instead, it seems that the few remains of herring found all originate from fishing baits.

The group of kittiwakes with chicks was the group where the largest amount of otoliths was found, and by using them to calculate total fish length, it was possible check for differences in size. Since the easiest way to increase energy gain per unit time is to increase the size of the fish (Wilson et al. 2004, Bugge et al. 2011), a quality difference between adult and chick diet can be shown in a difference in fish size and not only prey composition. There was, however, no significant difference in mean sizes of capelin in REG and STO samples from adults (Table 3.) It is unfortunate that the number of fish in STO (n = 7) is so much lower than in the REG (n = 57) samples, but this again indicates the rapid digestion of kittiwakes (Hilton et al. 2000). Otoliths from 10 capelin were retrieved from the six chick samples and their mean size was significantly lower than in REG of adults. However, both REG from adults and REG from chicks represented chick diet, since REG from adults with chicks was considered a proxy for chick diet. In addition, the TFL of capelin of the 10 capelins found in REG from chicks were from only six individuals. The smaller average size from these samples may be a slightly biased since they are from a low number of individuals. Besides, the neither the differences between REG and STO from adults (*t*-test, P = 0.08) or STO from adults and REG from chick (*t*-test, P = 0.06) were found significantly different, meaning that we did not find any difference in size of capelin between adult and chick diet.

Sandeels otoliths were found in only two REG samples, both from birds with chicks. Unfortunately, no sandeel otoliths were found in the STO samples so a comparison between sizes caught for self-feeding and for chick provisioning was not possible.

The size range of TFL of Capelin in all the samples was 71-156 mm and this is likely to represent fish from several year classes. Metamorphosis in capelin starts when they are around 75 mm (Vesin et al. 1981), and this normally takes place in their second year of life. The immature phase lasts from metamorphosis until maturation that is normally in their third and fourth year and most of the growth takes place at this phase (Gjøsæter 1998). Based on this the capelin found in the diet samples are likely to be mostly capelin of three and four years of age with the exception of the few number of immature capelin from the chick REG samples. From REG samples of adults, the range was from 121-156 mm. All the smallest fishes were found in two individuals of chicks. Overall, TFL of capelin found in chicks were 71-139 mm. The two individuals who had eaten smaller capelin may just be a result of a foraging trip where the adult encountered smaller fish than usual. Recordings from 1980-1994 showed that capelin <120 mm was caught only in two of these years (1981 and 1989) for chick provisioning by kittiwakes (Barrett & Krasnov 1996). The small average TFL of capelin (114 mm) found in chick regurgitation is considered not typical. The smaller fish size found in the REG from the two chicks was not found in the REG of adults with chicks. In adult REG we found the smallest capelin to be 121 mm. Due to the low number of chicks sampled from, and the two individual chicks with smaller than average fish, we assume that REG of adults with chicks gives a better picture of the size range of fish fed to chicks than the few samples from the chicks themselves. The TFL of capelin in REG from adults with chicks seemed to be stable throughout the breeding-season (Fig. 10.)

CONCLUSION

In this study, no significant differences in either prey composition or prey size were found between kittiwake adult and chick diet. The differences found for samples and amount of capelin found in birds with chicks compared to birds without chicks were considered more a result of the difference in behaviour of the two groups. If the birds without chicks had been sampled closer to the time they ingested their last meal, the differences in diet between chick-raising birds and birds without chicks would be expected to be insignificant. However, differences in diet of surface feeders can 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. Studies on cape petrels in Signy island have shown variability in composition between years. The composition of fish:crustacean:squid:other have been 15:64:0:21 (Beck 1969, recalculated in Croxall & Prince 1980), 65:35:0:0 (Coria et al. 1997), 2:97:0:1 (Soave et al. 1996), and 28:65:7:1 (Fijn et al. 2012). Further analysis are necessary to investigate if adult kittiwakes will show a similar degree of difference in diet between seasons and whether or not it effects the significance of difference in diet between adults and chicks.

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