Optimal foraging in chick-raising Common Guillemots (*Uria aalge*)

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Abstract The Norwegian population of the Common Guillemot *Uria aalge* has declined by >95% since the 1960s, and is classified as critically endangered in the Norwegian Red List. Much of the recent decline has been attributed to reduced food availability, but without extensive documentation of adult diet. Instead, chick diet has been considered a proxy of adult diet during the breeding season in many Norwegian studies. However, central-place foraging theory, especially for single-prey loaders, predicts that this may not be so, and this study directly compares the diet of adult and chick Common Guillemots during the breeding season at a colony in NE Norway. Whereas chicks were fed mainly capelin (*Mallotus villosus*) and sandeels (*Ammodytes* sp.), most of the adult diet consisted of the two youngest year classes of Gadidae, probably cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). A successful ecosystem management of seabirds is dependent on a full understanding of how prey quality, abundance and availability influence seabird populations and their viability, such that knowing the true diet of adult Common Guillemots has important implications in the modelling and management of the Norwegian populations.

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Introduction

The Common Guillemot (*Uria aalge*) is a widespread, circumpolar, boreal and low Arctic species. Although numerous in the North Atlantic (ca. 3 million breeding pairs) and generally increasing in numbers after years of human persecution, the Norwegian population has declined by >95% since the 1960s to ca. 15,000 pairs in 2005 (Gaston and Jones 1998; Barrett et al. 2006). This decline was initially a result of direct and indirect human pressure, but subsequent breakdown of social structure and harassment from White-tailed Eagles (*Haliaeetus albicilla*) exacerbated the situation causing several colonies to be in danger of extinction (Barrett et al. 2006; Erikstad et al. 2007). The Common Guillemot is consequently classified as critically endangered in the Norwegian Red List (Kålås et al. 2006).

The vast majority of seabird feeding ecology studies has been restricted to breeding sites and seasons when birds are easy to access (Shealer 2002). Since seabirds spend most of the year at sea, such short-term sampling results in bias when evaluating the overall impact of food availability on population dynamics. This is exacerbated by the fact that most colony-based studies are of chick diet, and that the comparatively few studies that have directly compared the diets of breeding adults to those of chicks (or non-breeding adults) have revealed substantial differences (e.g. Ydenberg 1994; Brown and Ewins 1996; Davoren and Burger 1999; Dierschke and Hüppop 2003; Wilson et al. 2004).

This difference is partially due to constraints such as number of prey brought to the chick, size of prey and

distance to foraging grounds. These constraints lead to a differentiation between prey eaten by adults and prey that are most profitable regarding size and energetic content for chick rearing. During the breeding season, parent birds have to optimally allocate their resources between sustaining themselves and their chick(s). Central-place foraging theory (Orians and Pearson 1979) predicts that adults should maximise energy yield per unit foraging effort and thus their chick's energy gain per unit time. For single-prey loaders (such as guillemots *Uria* spp.), this might be obtained by bringing larger and more energy-rich prey to their chicks than they eat themselves (i.e. adults should be more selective regarding chick food than food for themselves). Thus, the allocation of food between the parents and the chicks could take the form of optimal sharing, with the threshold being determined by the relative needs of the parents and their chick(s) (Wilson et al. 2004; Sonntag and Hüppop 2005; McLeay et al. 2009).

In the 1986/1987 winter, food shortages caused a die-off of adult birds and a serious decline in the population of Common Guillemots in Norway (e.g. Vader et al. 1990; Barrett and Krasnov 1996). It was assumed then that the cause was a collapse in the capelin (*Mallotus villosus*) stocks in the Barents Sea. However, while detailed, long-term studies of chick diet are in progress in Norway, little is known about adult diet. Small, energy-rich fish such as capelin, I-group herring (*Clupea harengus*) and sandeels (*Ammodytes* sp.) are well documented as important chick food in N Norway and NW Russia (Barrett et al. 1997; Barrett and Golovkin 2000; Barrett 2002), but adults have also been shown to feed on euphausiids and gadids (Anker-Nilssen and Nygård 1987; Barrett et al. 1997; Mehlum 2001). Because the need to return regularly to the colony constrains adult foraging to a maximum during the breeding season, improved knowledge of adult diet during the breeding season is required for more precise predictive modelling and better management of this threatened population (Erikstad et al. 2007). For example, a better documentation of adult diet would help clarify the relationships between Common Guillemot population dynamics, prey availability and fisheries in Norwegian waters.

In 2003, Wilson et al. (2004) tested the foraging theory and prediction that adult Common Guillemots would bring better quality prey to their chicks than they ate themselves, and were the first to directly compare adult and chick diet in the same colony. They found that adults did indeed feed on smaller prey items, mainly 0-group lesser sandeels *A. marinus* whereas chicks were fed energy-rich sprats *Sprattus sprattus* and adult lesser sandeels. Their study was in a region where sandeels are the dominant prey among breeding seabirds whereas this study tested the same prediction in a region where capelin and small herring are also dominant prey (Barrett and Furness 1990; Barrett et al. 2002).

Methods

The study was carried out during the hatching and main chick-rearing period in a colony of ca. 8,000 pairs of Common Guillemots (RT Barrett, unpublished data) on Hornøya (72°22′N, 31°10′E), a small island in NE Norway between 16 June and 17 July 2008. One hundred and two adults were caught using a noose pole as they came in with fish for the chick. All birds were ringed, weighed (±5 g) and measured (wing, culmen and head + bill lengths ±0.5 mm using a stopped wing rule and vernier calipers), a small blood sample (max. 50 μl) was taken from the brachial vein for later sex determination, and a stomach content sample obtained using the water off-loading method as described by Wilson et al. (2004). Each adult was flushed a maximum three times to ensure a complete emptying of the stomach, and was finally marked with a felt-tipped pen to avoid unnecessary recapture. On release, some birds flew down to the sea before returning to the nest site after a short time whereas others scrambled down the slope and returned immediately to their chick. There was no evidence that the handling of the birds caused any harm, as also found by Wilson et al. (2004). The off-loaded food remains were stored in a plastic bag, marked, and deep-frozen for later analysis. When possible, the fish being carried by the adult was also collected and individually frozen.

After thawing, a preliminary identification to lowest possible taxon of undigested remains [mainly otoliths, fish scales and pro-otic bullae (characteristic for herring) and fish eggs (characteristic for capelin)] in the stomach samples was noted (using Härkonen 1986; Watt et al. 1997; and our own reference collection). The samples were then further digested in a saturated solution of biological washing powder (Biotex©) in an oven at 50°C for at least 24 h after which additional otoliths were identified. Because otoliths of cod (*Gadus morhua*), saithe (*Pollachius virens*) and haddock (*Melanogrammus aeglefinus*) (the three most likely gadids to be caught off Hornøya) are extremely difficult to distinguish when small, they were initially classified as gadid (family Gadidae). The lengths and widths of all otoliths were measured using a calibrated eye-piece graticule in a binocular microscope and used to determine total fish lengths (FL) using equations in Barrett and Furness (1990) for capelin and Jobling and Breiby (1986) for sandeel that are both based on fish caught in the southern Barents Sea. Because Jobling and Breiby's (1986) equation is based on standard fish length, the results were converted to total fish length using a factor of 1.01 (based on own measurements). For the gadids, three alternative equations were used to estimate their size, one for each of the three likely species (Table 1). These equations were based on our own measurements of otoliths and fish caught in the region and gave similar results for the youngest year

Table 1 Polynomial coefficients of relationships between otolith width (OW) and total fish length (FL) based on measurements of fish caught in the southern Barents Sea

	a	b	c	d
Cod *Gadus morhua*	1.079	4.293	1.521	−0.110
Saithe *Pollachius virens*	−3.805	12.269	−1.012	0.412
Haddock *Melanogrammus aeglefinus*	2.357	4.704	−0.372	0.104

$FL = a + b \times OW + c \times OW^2 + d \times OW^3$
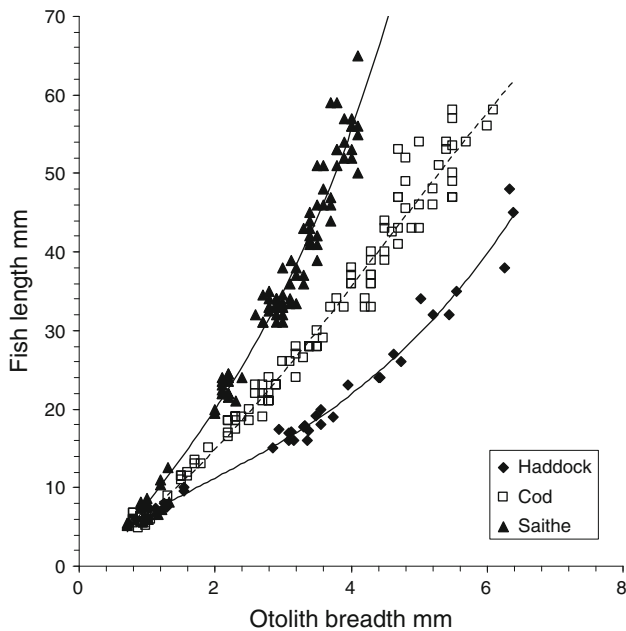

Fig. 1 Relationship between total fish length and otolith breadth for three species of gadid, haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) and cod (*Gadus morhua*) based on measurements of specimens from the southern Barents Sea (T Pedersen, unpublished data). (Equations for trend lines in Table 1)

Table 2 Frequency of occurrence of prey types in the diet of Common Guillemot (*Uria aalge*) adults and chicks at Hornøya, North Norway, 2008

Prey type	Adult (n = 59)		Chick (n = 79)	
	No. of samples containing prey type	% of samples	No. of samples containing prey type	% of samples
Gadid	53	89.8	2	2.5
Capelin	15	25.4	65	82.3
Sandeel	7	11.9	10	12.6
Herring	10[a]	16.9	2	2.5
Squid	1	1.7	0	0

[a] Including one with herring larvae

Results

Fifty-nine (58%) of the 102 stomach samples contained enough material to be included in the analyses and 79 fish carried by the adults were collected. The remaining fish were lost on capture among the birds on the breeding shelf.

Adult and chick diet composition

Of the 59 adult stomach samples, 56 contained 1–56 otoliths (mean = 7.1 ± 8.8), 4 contained only herring bullae and 6 both otoliths and bullae. No herring otoliths were found. Gadids were the most frequent prey, being found in 53 (89.8%) of the 59 samples. Capelin was found in 25.4% and sandeels in 11.9% of the samples (Table 2).

Of the 79 fish collected that were meant for chicks, 65 (82.3%) were capelin, 10 (12.6%) were sandeels, 2 (2.5%) were gadids and 2 (2.5%) were herring (Table 2).

There was a clear difference in diet of the adults and their chicks with adults eating mainly gadids while the chicks were fed mostly capelin and sandeel ($\chi^2 = 53.2$, $df = 4$, $P < 0.001$). Using paired samples ($n = 57$), the frequency of occurrence (FO) of capelin in chick food (77.2%) was significantly higher than that in adult stomachs (26.3%, sign-test, $P < 0.001$). In contrast, for gadoid prey, the FO in the diet of adults (91.2%) was higher than for chicks (3.5%) ($P < 0.001$). For herring, FO was also higher (19.3%) for adults than for chicks (1.8%) ($P = 0.006$), whereas for sandeel, the FO for adults (10.5%) did not differ significantly from that of chicks (17.5%) ($P = 0.45$).

Size distribution of prey

The mean lengths of the capelin and sandeels fed to chicks were 141.6 and 125.4 mm, respectively and were significantly larger than those eaten by the adults (by 30 and 12 mm, respectively, Student's *t* test, $P < 0.05$; Table 3).

class of fish (0-group) but were more critical for older fish (Fig. 1).

Diet composition is 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 the uncertainty as to how many meals each regurgitation represented. To avoid possible pseudoreplication through possible diet specialization by individual birds (Woo et al. 2008), only one diet sample (stomach and/or chick) was collected from an adult. Means are given ±1 standard deviation. Differences in diet between adults and chicks were tested using Chi-square (χ^2) goodness of fit of all the samples, supplemented by a sign-test for paired (adult and chick) sample comparisons (Zar 1999), when a stomach and chick food sample was collected from the same adult. Differences in mean lengths of prey were tested using Student's *t* test.

Table 3 Size of capelin and sandeels eaten by adults and those caught to feed to chicks of Common Guillemots (*Uria aalge*) at Hornøya, North Norway, 2008

	Capelin				Sandeel			
	Mean (mm)	SD	Range (mm)	n	Mean (mm)	SD	Range (mm)	n
Adult	111.5	14.2	89–131	12	113.3	22.9	64–156	29
Chick	141.6	14.2	99–168	65	125.4	9.5	113–136	10
	$t = -6.75$, $P < 0.001$				$t = -2.31$, $P = 0.027$			

The gadids eaten by the adults fell into two distinct size groups, irrespective of which species is considered (Fig. 2). The majority (76% of 340 otoliths) fell within a common 20–80 mm group ($\equiv$ 0-group cod, saithe and haddock) but in separate species groups for the larger fish; 140–200 mm for haddock, 220–290 mm for cod, and 300–410 mm for saithe. The two gadids fed to chicks were 52 and 65 mm, i.e. also 0-group fish.

Whereas there was no change in size of capelin and sandeels fed to chicks during the period of the study, the mean size of both species eaten by the adults decreased considerably (capelin: $r^2 = 0.43$, $P = 0.029$, $n = 11$; sandeel: $r^2 = 0.64$, $P < 0.001$, $n = 29$) (Fig. 3). Similarly and using haddock as the most likely prey (see
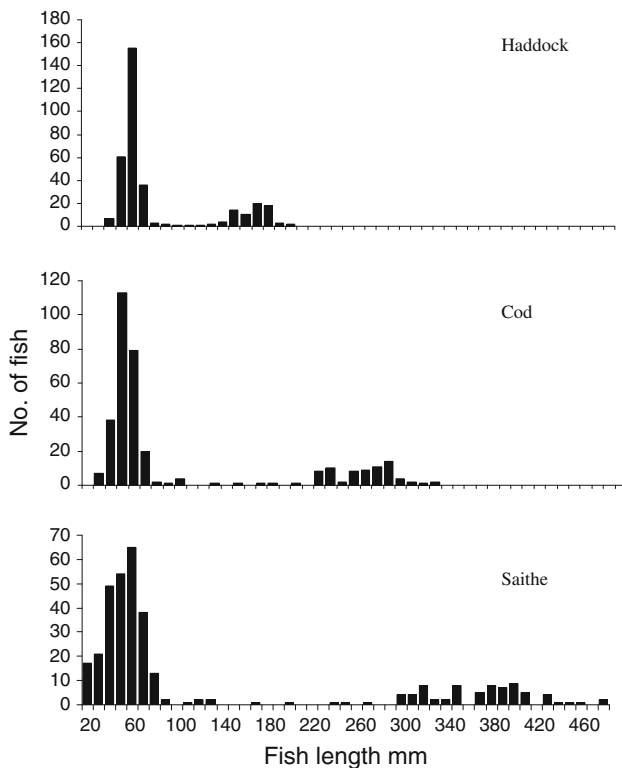

Fig. 2 Size distributions of gadids possibly eaten by adult Common Guillemots (*Uria aalge*) at Hornøya, N Norway, 2008 (using alternative equations for cod, saithe and haddock; Table 2)
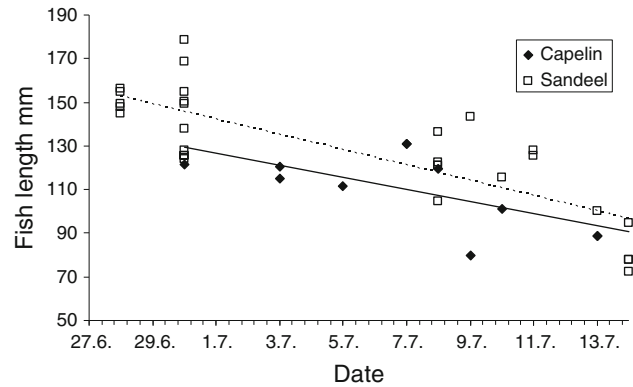

Fig. 3 Estimated lengths of capelin and sandeels eaten by adult Common Guillemots (*Uria aalge*) in relation to date at Hornøya, North Norway, 2008
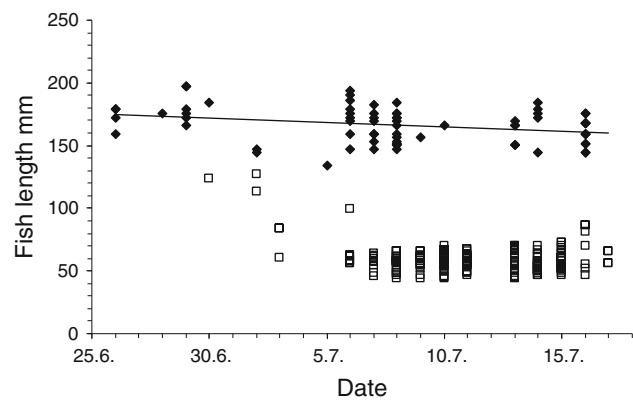

Fig. 4 Estimated lengths of gadids (using equation for haddock) eaten by adult Common Guillemots *Uria aalge* in relation to date at Hornøya, North Norway, 2008. *Squares* fish <130 mm, *diamonds* fish >130 mm. The *trend line* is fitted to fish >130 mm only

"Discussion"), the size of the largest (>130 mm) gadids dropped slightly as the season progressed ($r^2 = 0.08$, $P = 0.013$, $n = 72$) while that of the 0-group fish (<80 mm) that appeared about halfway through the study period did not change (Fig. 4).

Discussion

Wilson et al. (2004) were probably the first to use the water off-loading method on a species that does not normally regurgitate, and had a success rate of 68%, i.e. 62 samples from 91 adults caught. Although the success rate of this study (58%) was a little lower, the observed rapid return rates of the adults to the nest site after treatment shows that, at least for Common Guillemots, the method can be recommended. The use of skeletal remains and otoliths to identify and estimate size of prey does, however, have limitations due to differential retention times of different prey types and differential digestion rates of otoliths (e.g.

Jobling and Breiby 1986; Johnstone et al. 1990; Wilson et al. 2004; Barrett et al. 2007), but this bias in diet determination was partially overcome in this and Wilson et al.'s (2004) study by restricting the quantification of the data to frequency of occurrence. That said, few of the otoliths found in this study had signs of excess erosion and the majority were considered suitable for measurement and determination of fish size. The lack of herring otoliths in the samples, however, may be due to their small size and rapid digestion (Johnstone et al. 1990), but the species was represented by the bullae that are more resistant to digestion, and their presence in the samples precludes any underrepresentation of the species in the diet.

One unfortunate shortcoming in this study was the lack of a definitive identification of the gadids to species or even genus level. I-group cod and saithe can, however, be eliminated as having been too large for a Guillemot to handle in the quantities found (Fig. 1). Among the many published studies of adult Common Guillemot diet, very few document gadids >200 mm. Lorentsen and Anker-Nilssen (1999) found only 1 (213.7 mm) among 156 unidentified gadids (Lorentsen, personal communication) whereas Ouwehand et al. (2004) found 9 among 75. In the latter study, most of the maximum lengths of eight named gadid species (totalling 102 fish) were 150–195 mm. Furthermore, Swennen and Duiven (1977) found that the height of gadid fish and not their length was the decisive factor. Fish preferred by Common Guillemots had a height of 23 mm and the largest fish a height of 41 mm. With a length/height ratio of 4.78 for haddock (measured on 13 fish of relevant size; T Pedersen, unpublished data), these are equivalent to total fish lengths of ca. 110 and 196 mm, respectively. This corresponds to the size interval for haddock in Fig. 2 and supports the elimination of cod and saithe as being among the larger fish caught by the Common Guillemots in this study. Haddock in the size range 140–190 mm (Fig. 2) are I-group fish, i.e. they hatched the previous year. With respect to the 0-group fish, all three species are common off Hornøya in summer, but cod are normally most abundant (T Pedersen, unpublished data).

Irrespective of the final identification, 0-group gadids are all much smaller and hence of poorer individual quality than the energy-rich prey fed to the chicks (e.g. Pedersen and Hislop 2001). The dominance of capelin and sandeels in the chick diet was corroborated by a contemporary but independent survey on Hornøya in which 75% of 1,360 fish observed being brought into the colony were capelin, 16% sandeel, 6% herring and 2% "other" (R.T. Barrett, personal observation). The large differences between adult and chick diet supported the prediction that chicks would be fed larger and more energy-rich fish than the adults ate themselves. While both age groups ate capelin, sandeels, herring

and gadids, the chicks were fed >80% capelin and the adults ate >60% gadid. This is in full accordance with Wilson et al. (2004) who found that Scottish adults ate mainly 0-group sandeels while 79% of the fish fed to the chicks were energy-rich sprats and 20% I-group sandeels, and Sonntag and Hüppop (2005) who found that Helgoland adults fed their chicks a higher proportion of, and larger, sandeels and clupeids than they ate themselves. These findings all support the hypothesis that single prey-loading Common Guillemots maximise net energy gain per unit time for their chicks, as predicted by theories of optimal foraging (Orians and Pearson 1979; Thaxter et al. 2009).

It has long been thought that capelin is the main diet of Common Guillemots in North Norway, and that a 70–90% collapse in the breeding population due to an extraordinary adult mortality in winter 1986/1987 was explained by a similar collapse in the capelin stocks (Erikstad 1990; Vader et al. 1990; Krasnov and Barrett 1995). Although capelin has since been shown to be a major prey of Common Guillemot in the region in early spring (Erikstad and Vader 1989), this study shows that other prey items such as 0-group gadids may be equally important. Prior to the collapse in Guillemot numbers in 1987, the adult stocks of cod in the Barents Sea had also dropped, from >6 million t in mid-1942 to ca 1 million t in 1987, and the index of year class abundance for 0-group cod was at a minimum in 1987 (Mehl 1991; Hopkins and Nilssen 1991). Similarly, the abundance of 0-group saithe and haddock were also at a minimum in 1987 (ICES Advice 2009, http://www.ices.dk/advice/icesadvice.asp). During the time of the present study, the capelin stocks and 0-group abundance of the three gadids were high. Thus, the absence of small gadids, in addition to (or instead of) the collapse in the capelin stocks, may have played an important but previously unrecognized role in the extraordinary mortality of Common Guillemots in 1986/1987.

The dependence by adults on poorer quality prey than fed to chicks is corroborated by studies in the non-breeding season, i.e. away from the colonies and not connected to chick-provisioning. These studies suggest seabirds then take a larger variety of prey, including many species that are relatively low in energy density (e.g. Bradstreet and Brown 1985; Sonntag and Hüppop 2005; Hedd and Montevecchi 2006), and often at a lower trophic level (Bearhop et al. 2001). In Norwegian waters, Mehlum (2001) showed that Barents Sea Common Guillemots and Brünnich's Guillemots (Uria lomvia) that brought fish to their young had much smaller prey, e.g. euphausiids, as their own staple diet. Anker-Nilssen and Nygård (1987) also found that adult Common Guillemots accompanying chicks in mid-Norway soon after they had left the colony had fed mainly on gadids. In contrast, a study of food requirements by seabirds on Hornøya assumed that chick

and adult diets were similar and that capelin was an important constituent (50%) of adult diet (Furness and Barrett 1985). A later study of seabird consumption in Norwegian waters (Barrett et al. 2002) was based on the same assumption, even after evidence that adults may eat prey other than that fed to their chicks had been published (Anker-Nilssen and Nygård 1987; Mehlum 2001). Although not a large source of error considering the final figures, the fact that diet may vary considerably with time and that gadids are, at times, more important in the diet of Common Guillemots (and probably also other species) than previously considered means that such assumptions need to be reconsidered in future.

Although carried out in very different waters, this study corroborated that of Wilson et al. (2004) in its support of the prediction that adults ate poorer quality prey than that fed to their chicks, thereby providing further support for the central-place foraging theory. It also highlights the importance of including previously unrecognized prey types such as 0-group cod and I-group haddock (in addition to capelin, sandeels and young herring) in future models of consumption and population dynamics of the locally threatened Common Guillemots in North Norwegian waters, as well as raising the question as to whether other seabird species breeding in the region rely more on gadids than previously thought. In this region, where there are large changes in seabird populations and where forage fish populations fluctuate greatly (Barrett et al. 2006), a successful ecosystem management of seabirds is dependent on a full understanding of how prey quality, abundance and availability influence seabird populations and their viability (Österblom et al. 2008).

Zusammenfassung

Optimale Nahrungswahl bei Küken aufziehenden Trottellummen Uria aalge

Die norwegische Population der Trottellumme Uria aalge hat seit den 1960er Jahren um mehr als 95% abgenommen, und diese Art wird in der norwegischen roten Liste als vom Aussterben bedroht geführt. Der Großteil der jüngsten Abnahme ist verminderter Nahrungsverfügbarkeit zugeschrieben worden, ohne jedoch die Nahrung von Altvögeln ausführlich zu dokumentieren. Stattdessen wurde in vielen norwegischen Studien die Kükennahrung als ein Maß für die Nahrung von Altvögeln während der Brutsaison betrachtet. Die Theorie des „central place foraging" (wiederholte Rückkehr in dasselbe Nahrungsgebiet) sagt jedoch insbesondere für Arten, die nur ein einziges Beutestück transportieren, vorher, dass dies nicht unbedingt der Fall sein muss, und die vorliegende Studie vergleicht die Nahrung von Küken und adulten Trottellummen während der Brutsaison in einer Kolonie in Nordostnorwegen direkt miteinander. Während die Küken hauptsächlich mit Lodde (Mallotus villosus) und Sandaalen (Ammodytes sp.) gefüttert wurden, bestand der Großteil der Nahrung von Altvögeln aus den beiden jüngsten Altersklassen von Dorschen (Gadidae), wahrscheinlich Kabeljau (Gadus morhua) und Schellfisch (Melanogrammus aeglefinus). Ein erfolgreiches Ökosystemmanagement von Seevögeln hängt von einem vollständigen Verständnis davon ab, wie Qualität, Abundanz und Verfügbarkeit von Beute Seevogelpopulationen und ihre Lebensfähigkeit beeinflussen, so dass eine Kenntnis der genauen Nahrung adulter Trottellummen wichtige Folgen für das Modellieren und das Management der norwegischen Populationen hat.

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