Changes in feeding behaviour and reproductive success in the Common Guillemot *Uria aalge* on the island of Stora Karlsö

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―――――――――― **Abstract** ――――――――――

We studied the feeding behaviour and reproductive success in Common Guillemots *Uria aalge* at the island of Stora Karlsö to reveal effects of an increased density of the prey fish Sprat *Sprattus sprattus*. Feeding rates were almost twice as high in 1998 (4.3 feeds/chick/day) as in 1975 (2.2 feeds/chick/day), and feeding trips were short. The adult birds spent a large proportion of the day together at the site during the chick–rearing period, indicating that the birds were not under significant food stress. Contrary to what we had expected, reproductive success was lower in 1998 and 1999 (0.671, SE = ±0.045, n = 2) than in 1974–1977 (0.803, SE =±0.010, n = 4) and chick survival and age at fledging was unchanged despite the increase of available prey. We speculate that the condition (nutritional value), rather than the abundance of Sprat, has been important in changing the Guillemots feeding behaviour. The study indicates that the reason for the observed lower reproductive success was lower egg survival, most likely an effect of an increased predation pressure from Herring Gulls *Larus argentatus*.

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The population of several seabird species has increased throughout the last century in the northeast Atlantic and the North Sea. This is thought to be a response to ecosystem changes from over-harvesting in the commercial fishery, where the removal of large predatory fish has led to an increased availability of seabird food items (Furness 1984). A number of Common Guillemot *Uria aalge* populations in the North Atlantic have increased during the period of 1950–1990 (Gaston et al. 1998). However, also some populations in Norway and the Barents Sea have decreased substantially because their prey has been the target of a large-scale fishery (Vader et al. 1990).

Several authors have studied the relationship between food abundance, feeding behaviour and reproductive success for Common Guillemots. Feeding rates and chick survival did not differ in response to food availability, because the Common Guillemots changed their diet and/or the time the adult birds spent together at the breeding sites, allocating more time to foraging when food was scarce (Burger & Piatt 1990, Zador & Piatt 1999).

Hence, adult Common Guillemots can compensate changes in food availability by switching prey item or by adjusting their time budget. Adult birds spend relatively more time together at the breeding site when food is abundant and less time when food is scarce. However, Uttley et al. (1994) found that feeding rates and chick survival was lower when food abundance was very low in a colony where the Common Guillemots prey almost exclusively on one species. Hence, the flexible adult time budget was not sufficient to compensate for a reduced abundance of prey when the only main prey species was available only in very low quantities.

The Common Guillemot in the Baltic Sea feed their chick almost exclusively on Sprat *Sprattus sprattus*. The majority of all Sprat fed to young in 1975 were two years or older, with a small proportion of first year fish (Hedgren 1976). The biomass of Sprat has increased dramatically since the mid seventies, mainly as a consequence of reduced abundance of Cod *Gadus morhua* (Anon. 2000a, Hjerne 2000). The majority of Sprat spawn for their first time at an age of two years and the spawning

biomass in 1998 was roughly twice that of 1975 (Anon. 2000b). Thus, the abundance of prey for Common Guillemots in 1998 was much higher than in 1975. Sprat is of increasing commercial importance as fishmeal in the Baltic Sea, and the current high intensity fishing for Sprat is unsustainable (Hansson 2000).

Stora Karlsö supports the largest colony of Common Guillemot in the Baltic Sea, containing two thirds of the Baltic population. The number of breeding pairs has increased during the last century (Hedgren 1975). In 1974 there were 6400 pairs (Hedgren 1980), in 1984/85 it had increased to 7500 pairs (Hedgren & Kolehmainen 2000), and today even more areas are occupied by breeding birds than in the eighties. Almost all Common guillemots breeding in the Baltic Sea stay in this area all year around (Olsson et al. 2000). The Stora Karlsö colony is probably a source for establishing new colonies in the Baltic Sea and it has been estimated that 12% of the recruitment at Græsholmen (55°19'N, 15°12'E) near Bornholm come from Stora Karlsö (Lyngs 1993). The breeding biology of Common Guillemots was studied at Stora Karlsö during the mid-seventies (Hedgren 1975, 1976, 1979, 1980, Hedgren & Linnman 1979).

The aim of this study was to investigate whether increased food abundance has had any effect on the feeding behaviour and reproductive success for the Common Guillemots breeding at Stora Karlsö. The data from this study were compared with published data from the mid-seventies regarding both feeding behaviour (Hedgren & Linnman 1979, Hedgren 1976) and reproductive success (Hedgren 1979, 1980).

Methods

The feeding behaviour of Common Guillemots breeding on the island of Stora Karlsö (57°17'N, 17°58'E) was observed on 6, 7, 9, 14, 21 and 27 June 1998, for a total of 90 hours (mean 15 h, range 10–20 h). The feeding rates, trip duration and adult time budgets were determined during three dusk-dawn observations (on 9, 14 and 21 June) between 0300 and 2300 hrs. In 1997, breeding birds on a focal ledge were marked with individual two-letter plastic tarsus rings. The ledge contained 36 breeding pairs and 25 of these were included in the feeding study (all chicks were not present during all watches, e.g. late hatched or early fledged chicks). Both individuals were marked in five pairs, one individual marked in 14 pairs and the remaining six pairs contained unmarked individuals that were easily identified (incomplete head moult or distinctively coloured feet). Only chicks hatched from first eggs were studied. For all arrivals we recorded the time, site, individual, whether a fish was carried or not and the type of prey. Due to the difficulty to distinguish Sprat from Herring *Clupea harengus* in the field, both species were recorded as clupeids. To the extent it was possible, we also recorded the time, site and individual for all departures. If this could not be determined to within five minutes (from attendance checks when available), it was not registered. All observations of feeding were made from four meters above the ledge by using binoculars. These results were compared to those obtained by Hedgren & Linnman (1979) and Hedgren (1976).

During 1998 and 1999 we measured reproductive success of 67 and 99 pairs, respectively. 24.6% of the birds in 1998 and 18.7% in 1999 were ringed as breeding birds in 1997. The previous breeding history of the remaining birds was unclear. Each individual pair was identified in sketches of the breeding ledges and we determined whether a breeding pair had an egg or a chick by making regular observations. In 1998, all pairs were observed daily in the beginning and end of the breeding season in order to determine the presence of an egg or chick. In 1999, all pairs were observed daily throughout the entire breeding season in order to make a more accurate measure of the number of eggs laid and eggs hatched. The breeding ledges were observed through binoculars or spotting scope. Chicks were assumed to have fledged successfully when they had reached an age of at least 15 days. The results from these two years were compared with the corresponding values for reproductive success between 1974–1977 (Hedgren 1980).

Results

Prey species

During 1770 chick hours of observations we registered 344 feeds, of which 332 (96.5%) were identified as clupeids. The remaining 3.5% were either Sandeel *Ammodytes* sp. or unidentified. Hedgren (1976) recorded 91.5% Sprat, 5.1% Herring and 2.3% Sandeel in a sample of 176 fish taken from breeding ledges during the chick-rearing period.

Feeding rates

Each chick received on average 0.22 feeds/hour (SE = ±0.02, n = 20) and there was a morning and an
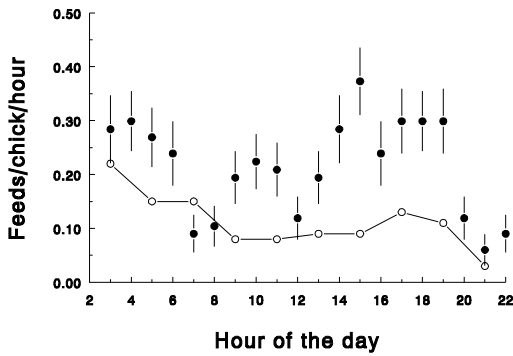
Figure 1. The mean number of feeds/chick/hour (± 1 se) during three dusk-dawn observations (June 9, 14 and 21) in relation to the time of day. The line with open circles refers to data for early chicks in 1975 (redrawn from Hedgren and Linnman 1979).
Medelantalet matningar/unge/timme (± 1 SE) under tre gry-ning-skymnings observationer (9, 14 och 21 juni) i förhållan-de till tid på dygnet. Linjen med öppna cirklar indikerar motsvarande värden från 1975 (återgiven från Hedgren & Linnman 1979).

afternoon peak (Figure 1), averaging 4.3 feeds/day (SE = ±0.2, n = 67 chick-days). In 1979 the chicks received on average 0.11 feeds/hour and 2.2 feeds/day (Figure 1; Hedgren & Linnman 1979). There was no relationship between feeding rate and chick age (r = 0.17, NS, n = 67 chick-days, Figure 2). However, the only chick that did not receive any food during the three dusk-dawn observations was a chick with an age of 21 days. If this chick-day is excluded from the sample, there is a positive correlation between feeding rate and chick-age (r = 0.29, P <

0.05, n = 66 chick-days). The mean age of the chicks in the feeding study was 9.0 days (SE = ±0.7, n = 67).

Trip duration

The shortest observed foraging trip when a bird returned with a fish was eight minutes, and 9.6% of all foraging trips were shorter than 20 min (n = 178). A large proportion (36.5%) of all foraging trips was shorter than one hour (Figure 3). During three dusk-dawn observations, we registered 291 successful foraging trips where the bird returned with a fish. The mean duration for a successful foraging trip was 129 minutes (SE = ±8.8, n = 178).

Adult time budgets

Each pair spent an average of 53 minutes together at the site between trips (SE = ±4.8, n = 249) during the chick-rearing season. Each pair made on average 5.1 trips/day (SE = ±0.2, n = 67, successful foraging trips and non-successful foraging trips pooled) and each pair thus spent an average of 271 minutes/day together at the site, or 22.6% of the day (data from dusk-dawn observations only).

Reproductive success

The average reproductive success (fledged chicks/ breeding pairs, possible mortality when the chicks leave the cliffs is not included) between 1998 and 1999 was 0.671 (SE = ±0.045, n = 2) (Table 1), and according to Hedgren (1980) the average reproductive
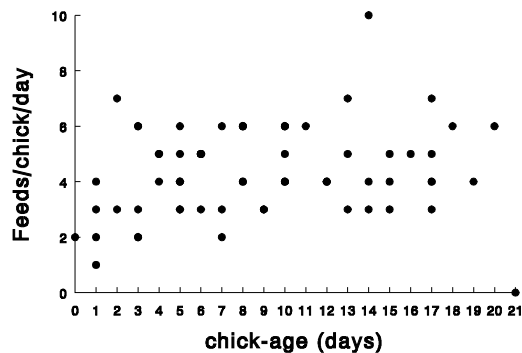

Figure 2. The mean number of feeds/chick/day (± 1 se) during three dusk-dawn observations (June 9, 14 and 21) in relation to chick-age.
Medelantalet matningar/unge/timme (± 1 SE) under tre gry-ning-skymnings observationer (9, 14 och 21 juni) i förhållan-de till ungens ålder.
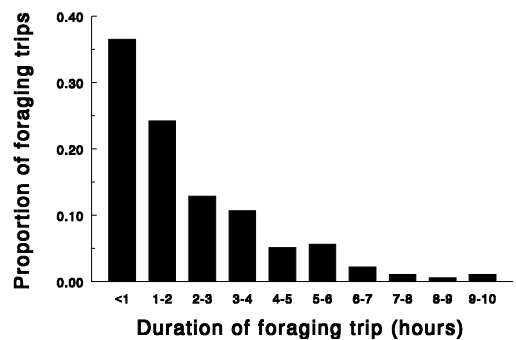

Figure 3. The proportion of all successful foraging trips during three dusk-dawn observations (June 9, 14 and 21) in relation to the duration of the foraging trip.
Proportionen av samtliga framgångsrika födosöksturer under tre gryning-skymnings observationer (9, 14 och 21 juni) i förhållande till längden av födosöksturen.

Table 1. Reproductive data for Common Guillemots on the island of Stora Karlsö between 1974–1977, from Hedgren (1980), and 1998–1999. Replacement eggs are included.
Häckningsdata för sillgrisslor på Stora Karlsö mellan 1974–1977, från Hedgren (1980) och 1998–1999. Siffrorna inkluderar omlagda ägg.

| Year | Pairs | Eggs | Hatched | Fledged | Eggs/ pair | Egg survival | Hatching success | Chick survival | Reproductive success |
År	*Par*	*Ägg*	*Kläckta*	*Flygga*	*Ägg/ par*	*Ägg-överlevnad*	*Kläcknings-framgång*	*Ung-överlevnad*	*Häcknings-framgång*
1974	287	316	228	220	1.10	0.72	0.79	0.96	0.77
1975	372	387	317	298	1.04	0.82	0.85	0.94	0.80
1976	389	411	337	318	1.06	0.82	0.87	0.94	0.82
1977	427	455	361	350	1.07	0.79	0.85	0.97	0.82
1974–77	1475	1569	1243	1186	1.064 ±0.006	0.793 ±0.010	0.843 ±0.009	0.953 ±0.006	0.803 ±0.010
1998	67			48					0.72
1999	99	112	68	62	1.131	0.607	0.687	0.912	0.63
1998–99									0.671 ±0.045

success between 1974–1977 was 0.803 (SE = ±0.010, n = 4). The difference in mean reproductive success between these two periods was statistically significant (Chi^2 = 17.13, d.f. = 1, P < 0.001, with Yates' correction). There was no significant difference between years in 1998 and 1999 (Chi^2 = 1.08, d.f. = 1, NS, with Yates' correction) or between ledges within years (1998: Chi^2 = 0.62, d.f. = 2, NS, 1999: Chi^2 = 2.51, d.f. = 2, NS). There was no difference between or within years between 1974–1977 (Hedgren 1980). Hence the overall reproductive success was lower in 1998 and 1999 compared to the period between 1974–1977.

The median fledging date was 27 June in 1998 and 26 June in 1999. The median fledging date between 1974–1977 varied between 30 June and 10 July (Hedgren 1979, 1980).

In 1974–1977, 6.4% (n = 1475) of the breeding pairs laid replacement eggs (Hedgren 1980); the corresponding figure for 1999 was 13.1% (n = 99). This difference was statistically significantly (Chi^2 = 5.66, d.f. = 1, P < 0.05, with Yates' correction). The number of eggs hatched per egg laid (egg survival), was lower in 1999 (0.607) than it was between 1974–1977 (0.793, SE = ±0.01, n = 4). The difference was statistically significantly (Chi^2 = 19.8, d.f. = 1, P < 0.001, with Yates' correction). Also, the number of chicks hatched per pair (hatching success) was lower in 1999 (0.687) than between 1974–1977 (0.843, SE = ±0.009, n = 4; Chi^2 = 15.09, d.f. = 1, P < 0.001, with Yates' correction).

The proportion of chicks that fledged successfully (chick survival) out of all eggs hatched in 1974–1977 was 0.953 (SE = ±0.006, n = 4) and in 1999, 0.912. There was no significant difference in chick survival between the period between 1974–1977 and 1999 (Chi^2 = 1.69, d.f. = 1, NS, with Yates' correction).

The mean age at fledging in 1998 was 19.6 days (SE = ±0.4, n = 48). The corresponding mean age at fledging in 1975 was 19.0 days (SE = ±0.6, n = 15) (Hedgren & Linnman 1979). Thus, we found no difference in mean age at fledging between 1975 and 1998.

Discussion

Sprat is currently extremely abundant in the Baltic Sea, and the spawning biomass in 1998 was roughly twice that of 1975 (Anon. 2000b). The total biomass of Herring has decreased by 70% during the same time period (Anon. 2000b). The main food fed to Common Guillemot chicks at Stora Karlsö in 1975 was Sprat (Hedgren 1976). Sprat has a higher calorific value than young herring and adult Common Guillemots appear to feed selectively on Sprat in the Baltic Sea (Lyngs & Durinck 1998). Thus, we assume that although we were not able to distinguish between Sprat and Herring in this study, it is likely that Sprat has continued to be the main prey fed to the chicks also in 1998 when our study was done.

Feeding rates

Common Guillemots almost always bring a single fish to their chick (Bradstreet & Brown 1985). The

feeding rate and size or quality of the prey determine the daily calorific intake of the chick, hence the only ways to increase the energy delivered to the chick is by increasing the feeding rate or by feeding the chick with larger or higher quality prey. The feeding rate in this study was almost twice as high as that obtained by Hedgren & Linnman (1979) in the same colony, but at similar level to rates observed elsewhere (Gaston et al. 1998).

The Common Guillemots breeding at the Shetland Islands fed their chicks almost exclusively on Lesser Sandeel *Ammodytes marinus*. The feeding rate increased in response to a greater abundance of prey (Uttley et al. 1994). However, in a bad year, the Common Guillemots tended to compensate the lower feeding rate by bringing larger prey to the chicks. At the Gannet Islands, Labrador, chicks were fed more frequently in a year when food was less abundant, but received poorer quality fish. The calorific intake was lower in the poor year despite the higher feeding rate (Birkhead & Nettleship 1987a).

Reproductive success and chick survival at Stora Karlsö was high between 1974–1977 (Hedgren 1980), indicating that the Common Guillemots feeding conditions were good during this period. However, in 1975, late hatched chicks had a lower growth rate than early hatched chicks despite a similar feeding rate (2.8 and 2.2 feeds/day for late and early chicks respectively). The reason for this was thought to be due to a seasonal deterioration in prey quality (Hedgren & Linnman 1979). The growth and fat content of Herring has decreased since the early 1980s in the Baltic proper (Ådjers et al. 2000). The condition (mean mass at age) of Sprat of all age classes of one year and older has decreased by 30% in the Baltic Sea from 1975 to 1998 (Anon. 2000b). The decrease was most evident during the 1990s (Anon. 2000b, Kaljuste 1999). Common Guillemot chick fledging body mass at Stora Karlsö has decreased significantly during the 1990s, indicating that feeding condition has deteriorated throughout this decade (Österblom et al. 2001). A reduction in the mass of Sprat and hence calorific content is the most likely explanation for the increased feeding rates observed for the Common Guillemots breeding in the Baltic Sea. Hence, we do not believe that the increased feeding rate is primarily a response to increased prey abundance, but rather a way to compensate for a low calorific intake in a single feed (see Österblom et al. 2001). Thus, when Common Guillemots are almost exclusively dependent on one prey type, large changes in the abundance or quality of this prey change their foraging behaviour.

Feeding rate in relation to chick-age varies with food availability. In the Shetland Islands, in a year when food was scarce, feeding rates increased to beyond 20 days chick age, but in a year when food was abundant, feeding rates peaked at 10 days (Uttley et al. 1994). There was no marked peak in feeding rate at any age in this study. Instead, the feeding rate in relation to chick-age showed a pattern more similar to that obtained during a poor food year by Uttley et al. (1994).

Trip duration and estimated foraging range

We observed several successful foraging trips where the birds returned to the colony after less than 20 min. A large proportion of all successful foraging trips were less than an hour, suggesting that food was easily accessible for the Common Guillemots. Uttley et al. (1994) found that successful foraging trips were shorter in a year when food abundance was high and several other studies have shown that Common Guillemots can make extremely short, yet successful foraging trips when food is abundant (Furness & Barrett 1985, Harris & Wanless 1985, Monaghan et al. 1994).

Studies by Cairns et al. (1987, 1990) and Monaghan et al. (1994) measured the activity budgets of Common Guillemots during foraging trips. A mean of 2.7–9.6% of the foraging trip was spent flying. There is some evidence that birds fly directly to the foraging area (Monaghan et al. 1994), enabling us to estimate the foraging range of the Common Guillemots breeding at Stora Karlsö. Using 2.7–9.6% of the mean trip duration (129 min) and a flight speed of 69 km/h (Pennycuick 1987), this represents a foraging range of 2.0–7.1 km during the chick-rearing period in still wind condition. These results are very similar to those obtained by Cairns et al. (1987, 1990) and Monaghan et al. (1994).

Adult time budgets

Adult Common Guillemots can compensate a low food supply by foraging more and thus spending less time together at the breeding site during the chick-rearing period. At two adjacent colonies in Alaska, where food varied 10-fold, breeding pairs of Common Guillemots spent 8% and 24% together at the site in the colony where food was scarce and abundant, respectively (Zador & Piatt 1999). Uttley et al. (1994) found that the adults spent 2.4% of the day together at the site in a poor year and 40% in a good year in the Shetland Islands. The mean duration of

periods when both members of a pair were together at the colony was about six times longer in a good year (50 minutes) than in a poor year (8 minutes, Uttley et al. 1994). In our study, both parents spent 22.6% of the day together at the site during the chick-rearing period and the mean duration of period that both members were together at the site was 53 minutes. This suggests that the birds not were under significant food stress. However, digestive constraints have been shown to affect the time budget of some birds (Diamond et al. 1986) and it has been suggested by Burger & Piatt (1990) that small Common Guillemot chicks eating large fish may influence their parents time budgets.

Data in support of the hypothesis that breeding pairs of Common and Brünnich's Guillemots *Uria lomvia* spend relatively much time together at a site when food abundance is high and relatively little time when food abundance is low has been provided by Burger & Piatt (1990), Furness & Barrett (1985), Harris & Wanless (1985, 1988) and Falk et al. (2000).

Monaghan (1996) has suggested that this type of data also can be a useful and inexpensive tool in order to provide indirect information on fish abundance. The data we have provided in this study may thus be useful for future management purposes.

Reproductive success

Cairns (1987) suggested that changes in food availability from poor to moderate would rapidly increase reproductive success, but that reproductive success would only increase gradually when food availability changes from moderate to good. In the Baltic Sea, food availability most likely changed from moderate to good, or from good to extremely good from 1974–1977 to 1998 and 1999. However, instead of an increase, we observed a decrease in reproductive success.

It is unclear why the measured reproductive success was lower in 1998 and 1999 than it was in the period between 1974–1977. The measured reproductive success in 1998 and 1999 was low compared to several Atlantic Common Guillemot colonies (Birkhead & Hudson 1977, Hatchwell & Birkhead 1991, Harris & Wanless 1988, Birkhead & Nettleship 1987b, Bryant et al. 1999). However, there are several potential reasons. One possible explanation may be a result of a difference in the breeding ledges observed. However no differences in reproductive success within years when comparing different ledges were found in this study or by Hedgren (1980). However,

the same ledges were not used in the two studies (see below).

Hedgren (1980) found that late-laying pairs had significantly lower reproductive success compared to early and mid season laying pairs. There was, however, no difference in reproductive success in early and mid season pairs. The reason for the seasonal decline in breeding was mainly due to the fact that young and inexperienced birds laid their eggs later. The median fledging dates in this study were early compared to those obtained by Hedgren (1979, 1980), thus the observed pairs in this study should be regarded as early breeders (i.e. experienced birds with a relatively high reproductive success). Early laying pairs are more likely to re-lay if they loose their first egg (Harris & Birkhead 1985, Birkhead & Hudson 1977), but replacement eggs are less likely to hatch (Hedgren 1980).

There is a significant relationship between the timing of breeding and mean deviation from long term average air temperature in February–May, where two degrees warmer result in one week earlier breeding season at Stora Karlsö (Hedgren 1979). The mean deviation from the long term average temperature was +1.13 and +1.00 degrees in 1998 and 1999 respectively (Swedish Meteorological and Hydrological Institute) and between -0.5 and +1.5 degrees between 1974–1977 (Hedgren 1979). Hence the timing of all breeding seasons are sufficiently similar for a comparison and we conclude that differences in timing is not a likely reason for differences in reproductive success between the seventies and the nineties.

One possible explanation to the observed lower hatching success and higher number of replacement eggs laid in 1999 may be predation by Herring Gulls *Larus argentatus*. The Herring Gull population on Stora Karlsö has increased dramatically from an estimated 300 pairs in 1974–1977 (Hedgren 1980), via 414 breeding pairs in 1984–1985 to 826 breeding pairs in 1998 (Hedgren & Kolehmainen 2000). In 1974–1977, Hedgren (1980) observed only one out of 325 lost eggs to be taken by a Herring Gull, although the causes of all failed eggs were not known. We have on some occasions observed Herring Gulls taking eggs from breeding birds on the ledges but we have not been able to quantify the extent. Ravens *Corvus corax* predating on Brünnich's Guillemot eggs and chicks took almost exclusively eggs (Gaston & Elliot 1996) and all predation observed by Birkhead (1977) by Great Black-backed Gulls *Larus marinus* on Common Guillemots were on eggs rather than chicks. Thus gull predation at

Stora Karlsö is likely to be higher on eggs than on chicks, something that could explain the observed low egg survival in this study. We believe that increased predation on eggs is the most likely explanation for the observed lower reproductive success in 1998 and 1999 compared to 1974–1977.

The reason why chick survival was not higher in 1999 than in 1974–1977 despite the increased food abundance is not clear. At Skomer Island, Wales, Common Guillemot chick survival was not affected by an increased feeding rate (Hatchwell 1991). In the Shetland Islands, Common Guillemot chick survival was lower in a year when food abundance was low (Uttley et al. 1994). Also, fledging age was lower in a year when food was more abundant (Uttley et al. 1994). In this study, fledging age was not affected by the increased food abundance. The high abundance of Sprat in the Baltic Sea is a measure of biomass and not the availability of suitable prey fish to Common Guillemots. As the condition of the main prey Sprat has deteriorated, chicks at Stora Karlsö may not have received a higher daily calorific intake despite the higher feeding rate. A similar result, where parents traded off feeding rate and prey quality, was found at the Gannet Islands, Labrador. Chicks were fed at a higher rate, but with lower quality fish when preferred food appeared to be less abundant, resulting in a lower calorific intake despite a higher feeding rate (Birkhead & Nettleship 1987a).

No known environmental contaminants can explain the observed lower egg survival. The concentrations of sDDT and PCBs in eggs of Common Guillemots on Stora Karlsö have decreased significantly since the seventies (Bignert et al. 1995). The eggshell thickness has increased in response to this factor and is currently at a level similar to pre-1946 eggs (A. Bignert pers. comm.). These factors taken together would suggest that egg survival should be higher presently than during the period 1974–1977. However, this study provides the opposite result.

In summary, food was extremely abundant in the Baltic Sea, and feeding rates were almost twice as high in 1998 than in 1975. Both adults spent a large proportion of the day together at the site, indicating that food was easily accessible. The condition of Sprat in the Baltic Sea has deteriorated during the last decade and we suggest that the higher feeding rates may be a response to this fact. Calorific intake may thus not be higher despite the higher feeding rates, something that could explain why chick survival and age at fledging was unaffected. Reproductive success was, contrary to what we had expected, lower in 1998 and 1999 than in 1974–1977. This was probably as a result of the lower egg survival observed in 1999. We speculate that predation by gulls is the most likely explanation for this observed lower reproductive success.

References

Anon. 2000a. *Report of the Working Group on Ecosystem Effects of fishing activities*. ICES CM 2000/ACME: 02.

Anon. 2000b. *Report of the Working Group on Baltic Fisheries Assessment*. ICES CM 2000/ACFM:14. Part 2, Pp. 362.

Bignert, A., Litzén, K., Odsjö, T., Olsson, M., Persson, W. & Reutergårdh, L. 1995. Time-related factors influence the concentrations of sDDT, PCBs and shell parameters in eggs of Baltic Guillemot (*Uria aalge*), 1861–1989. *Environ. Pollut.* 89: 27–36.

Birkhead, T.R. 1977. The effects of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *J. Anim. Ecol.* 46: 751–764.

Birkhead, T.R. & Hudson, P.J. 1977. Population parameters for the Common Guillemot *Uria aalge*. *Ornis Scand.* 8: 145–154.

Birkhead, T.R. & Nettleship, D.N. 1987a. Ecological relationship between Common Murres, *Uria aalge*, and Thick-Billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador III. Feeding ecology of the young. *Can. J. Zool.* 65: 1638–49.

Birkhead, T.R. & Nettleship, D.N. 1987b. Ecological relationship between Common Murres, *Uria aalge*, and Thick-Billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador II. Breeding success and site characteristics. *Can. J. Zool.* 65: 1630–37.

Bradstreet, M.S.W. & Brown, R.G.B. 1985. Feeding Ecology of the Atlantic Alcidae. Pp. 263–318 in *The Atlantic Alcidae, The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas*. (Nettleship, D.N. & Birkhead, T.R. eds). Academic Press, London.

Bryant, R., Jones, I.L. & Hipfner, M. 1999. Responses to changes in prey availability by Common Murres and Thick-billed Murres at the Gannet Islands, Labrador. *Can. J. Zool.* 77: 1278–1287.

Burger, A.E. & Piatt, J.F. 1990. Flexible time budgets in breeding Common Murres: Buffers against variable prey abundance. *Stud. Avian Biol.* 14: 71–83.

Cairns, D.K. 1987. Seabirds as Indicators of Marine Food Supplies. *Biol. Oceanogr.* 5: 261–271.

Cairns, D.K., Bredin, K.A. & Montevecchi, W.A. 1987. Activity budgets and foraging ranges of breeding Common Murres. *Auk* 104: 218–224.

Cairns, D.K., Montevecchi, W.A., Birt-Friesen, V.L. & Macko, S.A. 1990. Energy expenditures, ativity budgets, and prey harvest of breeding Common Murres. *Stud. Avian Biol.* 14: 84–92.

Diamond, J.M., Karasov, W.H., Phan, D. & Carpenter, F.L. 1986. Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature* 320: 62–63.

Falk, K., Benvenutti, S., Dall'antonia, L., Kampp, K. & Ribolin, A. 2000. Time allocation and foraging behaviour of chick-rearing Brünnich's Guillemots *Uria lomvia* in high-arctic Greenland. *Ibis* 142: 82–92.

Furness, R.W. 1984. Seabird- fisheries relationships in the northeast Atlantic and North Sea. Pp. 162–169 in: *Marine birds: their feeding ecology and commercial fisheries relationship* (Nettleship, D.N. Sanger, G.A. Springer, P.F. eds). Supply and Services, Ottawa.

Furness, R.W. & Barrett, R.T. 1985. The food requirements and ecological relationships of a seabird community in North Norway. *Ornis Scand.* 16: 305–313.

Gaston, A.J. & Elliot R.D. 1996. Predation by Ravens *Corvus corax* on Brünnich's Guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. *Ibis* 138: 742–748.

Gaston, A.J., Jones, I.L. & Lewington, I. 1998. *The Auks: Alcidae (Bird Families of the World, Vol. 5).* Oxford University Press, Oxford.

Hansson, S. 2000. Östersjöns fisk – i kläm mellan fiske och övergödning (Baltic fish – sandwiched between the fishery and eutrophication). *Fauna och Flora* 95: 169–176.

Harris, M.P. & Birkhead, T.R. 1985. Breeding Ecology of the Atlantic Alcidae. Pp. 156–204 in *The Atlantic Alcidae, The Evolution, Distribution and Biology of the Auks Inhabiting the Atlantic Ocean and Adjacent Water Areas* (Nettleship, D.N. & Birkhead, T.R. eds). Academic Press, London.

Harris, M.P. & Wanless, S. 1985. Fish fed to young Guillemots, *Uria aalge*, and used in display on the Isle of May, Scotland. *J. Zool., Lond.* 207: 441–458.

Harris, M.P. & Wanless, S. 1988. The breeding biology of Guillemots *Uria aalge* on the Isle of May over a six year period. *Ibis* 130: 172–92.

Hatchwell, B.J. 1991. The feeding ecology of young Guillemots *Uria aalge* on Skomer Island, Wales. *Ibis* 133: 153–161.

Hatchwell, B.J. & Birkhead, T.R. 1991. Population dynamics of Common guillemots *Uria aalge* on Skomer Island, Whales. *Ornis Scand.* 22: 55–59.

Hedgren, S. 1975. Det häckande beståndet av sillgrissla *Uria aalge* i Östersjön. (The breeding population of Guillemots *Uria aalge* in the Baltic Sea.) *Vår fågelvärld* 34: 43–52.

Hedgren, S. 1976. Om sillgrisslans *Uria aalge* föda på Stora Karlsö. (On the food of the Guillemot *Uria aalge* at the island of Stora Karlsö, the Baltic Sea). *Vår Fågelvärld* 35: 287–290.

Hedgren, S. 1979. Seasonal variation in fledging weight of Guillemots *Uria aalge. Ibis* 121: 357–361.

Hedgren, S. 1980. Reproductive success of Guillemots *Uria aalge* on the island of Stora Karlsö. *Ornis Fenn.* 57: 49–57.

Hedgren, S. & Kolehmainen, T. 2000. *Häckande fåglar på Stora Karlsö 1998.* Länsstyrelsen i Gotlands län, livsmiljöenheten. Rapport nr 2, 2000.

Hedgren, S. & Linnman, Å. 1979. Growth of Guillemot Uria aalge chicks in relation to time of hatching. *Ornis Scand.* 10: 29–36.

Hjerne, O. 2000. *Fish and fisheries management in an ecological context, with emphasis to the Baltic Sea.* Lic. Thesis. Stockholm University, Department of Systems Ecology.

Kaljuste, O. 1999. Changes in the growth and stock structure of Baltic Sprat (*Sprattus sprattus balticus*) in the Gulf of Finland in 1986–97. *Proc. Estonian Acad. Sci. Biol. Ecol.* 48: 296–309.

Lyngs, P. 1993. Colony interchange in Baltic Guillemots *Uria aalge. Dansk. Orn. Foren. Tidsskr.* 87: 247–250.

Lyngs, P. & Durinck, J. 1998. Diet of Guillemots *Uria aalge* in the central Baltic Sea. *Dansk. Orn. Foren. Tidsskr.* 92: 197–200.

Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos* 77: 227–237.

Monaghan, P., Walton, P., Wanless, S., Uttley, J.D. & Burns, M.D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge. Ibis* 136: 214–222.

Olsson, O., Nilsson, T. & Fransson, T. 2000. *Long-term study of mortality in the Common Guillemot in the Baltic Sea.* Swedish Environmental Protection Agency Report 5057.

Pennycuick, C.J. 1987. Flights of auks (Alcidae) and northern seabirds compared with southern procellariiforms. *J. Exp. Biol.* 128: 335–347.

Uttley, J.D., Walton, P., Monaghan, P. & Austin, G. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge. Ibis* 136: 205–213.

Vader, W., Barrett, R.T., Erikstad, K.E. & Strann, K.-B. 1990. Differential responses of Common and Thick-Billed Murres to a crash in the Capelin Stock in the Southern Barents Sea. *Stud. Avian Biol.* 14: 175–180.

Zador, S.G. & Piatt, J.F. 1999. Time-budgets of Common Murres at a declining and increasing colony in Alaska. *The Condor* 101: 149–152.

Ådjers, K., Sandström, O. & Bignert, A. 2000. Fisk och fiske – fisketrycket för hårt (Fishery in trouble). Pp. 35–36 in *Östersjö '99 Årsrapport från miljöövervakningen i egentliga Östersjön (Swedish Marine Monitoring in the Baltic Proper).* (Tidlund, A. & Brenner, U. eds). Stockholm Marine Research Center.

Österblom, H., Bignert, A., Fransson, T. & Olsson, O. 2001. A decrease in fledging body mass in Common Guillemot *Uria aalge* chicks in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 224: 305–309.

Sammanfattning

Förändringar i matningsbeteende och häcknings-framgång hos sillgrissla Uria aalge *på Stora Karlsö*

Ett flertal havsfågelpopulationer i norra Atlanten har ökat under det senaste århundradet, något som tros vara en effekt av det kommersiella fisket (Furness 1984). Ett hårt fisketryck på stora predatorer har ökat den tillgängliga mängden födofisk för fåglar. När

däremot de fiskarter som fåglarna föredrar fångas kommersiellt i stora mängder, har detta fått negativa konsekvenser för havsfåglar i exempelvis Norge och Barents hav (Vader et al. 1990).

Sillgrissla är en havsfågel som är relativt okänslig för förändringar i födotillgång, då de har en flexibel tidsbudget. Det innebär att de kan öka tiden som utnyttjas till att söka föda om mängden tillgänglig fisk är liten. Om andra fiskarter finns kan de utnyttjas som ett alternativ till den huvudsakliga födan (Burger & Piatt 1990, Zador & Piatt 1999). Då födotillgången däremot är mycket låg och inga alternativa arter finns att utnyttja, kan den flexibla tidsbudgeten i vissa fall inte kompensera för låga koncentrationer av föda (Monaghan et al. 1994, Uttley et al. 1994).

Sillgrisslor på Stora Karlsö matar sina ungar nästan uteslutande med skarpsill *Sprattus sprattus*, en art som har ökat dramatiskt sedan 70-talet (Hedgren 1976, Anon. 2000b). Kolonin på Stora Karlsö är den största i Sverige och har ökat under det senaste århundradet (Hedgren 1975, 1980, Hedgren & Kolehmainen 2000).

Syftet med den här studien var att undersöka om en ökade födotillgång har påverkat matningsbeteende och häckningsframgång hos sillgrisslor på Stora Karlsö. Data från vår studie jämförs med liknande data från 70-talet (Hedgren 1976, 1979, Hedgren & Linnman 1979, Hedgren 1980).

Metoder

Matningsbeteendet studerades den 6, 7, 9, 14, 21 och 27 juni 1998 under sammanlagt 90 timmar. Tre dygns kontinuerlig observation (9, 14 och 21 juni) användes för att beräkna matningsfrekvens, tiden för födosök och fåglarnas tidsbudget. 25 par ingick i matningsstudien. Då en medlem i en av dessa par anlände till hyllan registrerade vi tidpunkt, position på hyllan, om fågeln bar en fisk och vilken fiskart. Vi kunde inte skilja mellan skarpsill och strömming *Clupea harengus* i fält, utan båda arter registrerades som clupeider. Vi noterade även så långt det var möjligt, tid och plats för fåglar som lämnade hyllan.

Häckningsframgången studerades 1998 och 1999 för 67 och 99 par respektive år. Under 1998 gjordes dagliga observationer under början och slutet på häckningssäsongen för att bestämma om paret hade ett ägg eller en unge. Under 1999 gjordes dessa observationer under hela häckningssäsongen. Vi antog att en unge lämnat boet med framgång då den var borta vid en ålder av 15 dagar.

Resultat

Matningsbeteende

Av 344 registrerade fiskar var 96.5% clupeider. De återstående 3.5% var antingen tobisfiskar *Ammodytes* sp. eller ej identifierade. Varje unge matades med 4.3 fiskar/ dag 1998 och 2.2 fiskar/ dag 1975 (Hedgren & Linnman 1979, Figur 1). Födan verkade vara lättillgänglig, då 9.6% av alla framgångsrika födosöksturer var kortare än 20 minuter (n = 178, Figur 3). Paren var i medeltal tillsammans på häckningsplatsen 22.6% av dagen.

Häckningsframgång

Häckningsframgången under 1998 och 1999 (0.671 ungar/par, SE = ±0.045, n = 2, Tabell 1) var lägre än under perioden 1974–1977 (0.803 ungar/ par, SE = ±0.010, n = 4). Skillnaden var signifikant (Chi^2= 17.13, d.f. = 1, P < 0.001, med Yates korrektion). Under perioden 1974–1977 lade 6.4% av paren ett andra ägg då det första gått förlorat (Hedgren 1980). Motsvarande siffra 1999 var 13.1% (n = 99), vilket var signifikant fler (Chi^2= 5.66, d.f. = 1, P < 0.05, med Yates korrektion). Äggöverlevnaden var lägre 1999 (0.607) än mellan 1974–1977 (0.793, se = 0.01, n = 4, Chi^2= 19.8, d.f. = 1, P < 0.001, med Yates korrektion). Ungöverlevnaden mellan 1974–1977 var 0.953 flygga ungar/ kläckta ägg (SE = ±0.006, n = 4), vilket inte var skilt från 1999: 0.912, Chi^2 = 1.69, d.f. = 1, NS, med Yates korrektion). Ungarna lämnade boet vid en ålder av 19.6 dagar 1998 och 19.0 dagar 1975.

Diskussion

Vi antar att samtliga observerade clupeider var skarpsill, då: 1) skarpsillpopulationen har ökat dramatiskt och strömmingpopulationen minskat dramatiskt sedan 70-talet (Anon. 2000b) och 2) sillgrisslor föredrar skarpsill framför strömming (Hedgren 1976, Lyngs & Durinck 1998). Eftersom sillgrisslan nästan uteslutande matar ungen med en fisk åt gången (Bradstreet & Brown 1985) är det enda sättet att öka ungens dagliga kaloriintag att öka matningsfrekvensen eller storleken på fisken (då fiskar med ett högre näringsvärde inte finns som ett alternativ). Matningsfrekvensen 1998 var nästan dubbelt så hög som 1975. Häckningsframgången mellan 1974–1977 var hög, vilket tyder på att födotillgången var god. Ungar som kläcktes sent 1975 hade en långsammare tillväxt, trots att de matades med mer fisk (2.8 fiskar/

dag) än de ungar som kläcktes tidigt samma år (2.2 fiskar/ dag), något som antogs bero på en försämring i fiskens näringsinnehåll (Hedgren & Linnman 1979). Skarpsillens medelvikt i alla åldersklasser > 1 år har minskat mellan 1975 till 1998 och minskningen var mest dramatiskt under 90-talet (Anon 2000b). Under 90-talet minskade även vikten på ringmärkta sillgrissleungar (Österblom et al. 2001). En försämring i födans näringsinnehåll är den mest troliga förklaringen till den ökade matningsfrekvensen. De korta födosöksturerna pekar på att födotillgången var mycket god. Båda individerna i paret var tillsammans på häckningsplatsen en stor del av dagen, vilket visar att de inte var stressade för att söka föda (Burger & Piatt 1990, Bryant et al. 1999, Furness & Barrett 1985, Harris & Wanless 1985, 1988, Uttley et al. 1994, Zador & Piatt 1999).

Cairns et al. (1987) föreslog att en ökad födotillgång bör förbättra häckningsframgången. I Östersjön har tillgången på skarpsill troligtvis gått från god till mycket god mellan 1975 och 1998. Men trots detta har sillgrisslans häckningsframgången inte ökat, utan i stället minskat. Den mest troliga förklaringen till detta är en ökad predation från gråtrut. Populationen av gråtrut på Stora Karlsö har ökat från uppskatt-ningsvis 300 par 1974–1977 (Hedgren 1989), 414 par 1984/85 till 828 par 1998 (Hedgren & Kolehmaninen 2000). Under perioden 1974–1977 försvann 325 ägg, och endast ett kunde härledas till trutpredation, men orsaken till förlusten av samtliga ägg var inte känd (Hedgren 1980). Vi har vid ett flertal tillfällen observerat trutar med sillgrissleägg i munnen utan att kunna bestämma omfattningen av predationen. Havstrut *Larus marinus* tar i större utsträckning sillgrisslans ägg än dess ungar (Birkhead 1977) och korp *Corvus corax* tar en större andel ägg av spetsbergsgrisslor *Uria lomvia* (Gaston & Elliot 1996). Om gråtrut jagar på ett liknande sätt kan det vara en del av förklaringen till att en större andel par lade ett andra ägg lades 1999 och att den observerade äggöverlevnaden var låg.

Anledningen till att ungöverlevnaden inte var högre 1999 än mellan 1974–1977 trots en ökad födotillgång är inte klar. Då konditionen hos skarpsill har försämrats är det tänkbart att ungarna på Stora Karlsö inte hade ett högre dagligt kaloriintag 1998 trots den ökade matningsfrekvensen. En observerad förändring i ungarnas hoppvikter tyder på att energimängden i skarpsill har minskat (Österblom et al. 2001)