

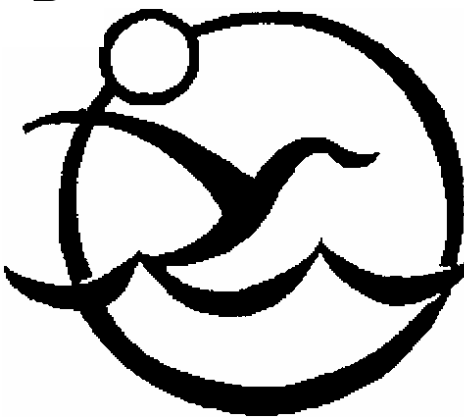
STOCKHOLMS UNIVERSITET

Systemekologiska Institutionen

**The effects of ecosystem changes on
the reproductive success and
feeding behaviour of the common
guillemot, *Uria aalge***

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The effects of ecosystem changes on the reproductive success and feeding behaviour of the common guillemot, *Uria aalge*

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During recent decades, fish stocks in the Baltic Sea have undergone considerable changes. Cod has decreased in abundance and sprat is more abundant than ever before. In response to this increased abundance, the size of sprat, *Sprattus sprattus*, has declined. The seabird, guillemot (*Uria aalge*), feeds almost entirely on sprat and the change in sprat stock could potentially change the reproductive success, feeding behaviour and adult time budget of the guillemot. The results from this study indicate a correlation between the reproductive success of the guillemot and the weight of Baltic sprat. Changes in mean fledging date also seem to have occurred, as well as the number of feeds chicks receive every day. Thus, changes in fish stocks appear to have cascaded through the food web and impacted the bird community.

Introduction

The fish stocks in the Baltic Sea have changed considerably during recent decades, due to several factors, e.g. fishing pressure, predation and conditions for reproduction (ICES 2005). Sprat, *Sprattus sprattus*, is zooplanktivorous (Casini et al 2005) and one of the most abundant fish species. The sprat stock has increased dramatically during the 1990's (Casini et al 2005). Declining salinity levels in the Baltic Sea during the 1990's have been correlated to changes in the zooplankton (Casini et al 2005). However, the changes in the zooplankton population may also be a result of increased predation pressure from sprat and herring, *Clupea harengus* (Casini et al 2005). Both sprat and herring prey on marine zooplankton such as copepods (Möllmann & Köster 2002).

A decrease in zooplankton density has impacted the food availability for sprat and their average weight decreased during the 1990's. The decline in salinity levels combined with a high fishing pressure has substantially reduced the cod stock (Kornilovs et al 2001). The sprat population increased as cod decreased (Nissling 2005, Harvey et al 2003). A reduced predation pressure on sprat by cod produces more and smaller sprat (Möllmann et al. 2004). More sprat leads to greater predation pressure on cod eggs and larvae, potentially making it harder for the cod stock to

recover (Möllman & Köster 1999). Possibly, the Baltic Sea has become a clupeid-dominated system rather than the cod-dominated one it used to be (Casini et al 2005).

During the early-mid 1990's, the condition of sprat (length to weight relationship) dropped by 24%. However, it increased slightly again by the end of the 1990's, only to decline again at the beginning of 2000 (Casini et al 2005). As the weight of sprat varies, this may have influenced animals that feed on them, such as the common guillemot *Uria aalge*.

The common guillemot is a single-prey loader that breeds mainly in the northern part of the boreal zone, with the most northern colonies situated on Bjørnøya, Spitsbergen and Novaya Zemlya (Nettleship & Birkhead 1985, Bergström & Lundevall 1996, Wanless et al 2005) In the Baltic region the guillemot is found primarily on Stora Karlsö (Bergström & Lundevall 1996). The colony on Stora Karlsö is the biggest in the Baltic Sea with its 10000 breeding pairs, and is likely to act as a source population for the whole of the Baltic Sea (Olsson et al. 2000). The guillemots spend most of their life at sea, only returning to land for a few months every spring/summer to breed. The breeding sites are on steep cliffs, often on a bare narrow ledge. The average age at the first breeding attempt is 5-6 years (Mitchell et al 2004). They lay a single egg directly on the bare ledge, which is brooded by both parents for about 32 days (Nettleship & Birkhead 1985). The egg is pyriform and can vary in colour, from bright green to white, often with black markings. Each egg has a special colour and marking, making it possible for parents to recognize their own egg (Nettleship & Birkhead 1985). Due to the fact that the birds lay a single egg, the guillemot cannot adjust their breeding effort by altering clutch size. Instead the parents can adjust the time the chick spends together with both parents on the ledge (Uttley et al 1994). Chicks spend approximately 20 days on the ledge (Hedgren 1980).

Food supplies can have a significant effect on seabirds. Guillemots breed earlier, have a greater fledging success and chicks fledge earlier when food supplies are more abundant (Hatchwell, 1991). Feeding trip duration, feeding behaviour and adult time budgets of seabirds can potentially indicate changes in food availability (Cairns 1987).

Trip duration of foraging in seabirds can be affected by several factors, e.g. by abundance, availability or type of prey. Therefore, the duration of foraging trips, may indicate the availability of guillemots' prey species (Davoren & Montevecchi 2003). The adult time budget is another parameter that can be affected by the amount of fish present. When feeding conditions are poor, parent birds spend more time foraging, than when food is abundant; thus spending less time together on the ledge (Wanless et al 2005). In 1990, a poor food year, guillemots on the Shetlands were found to forage for significantly longer time than in a good food year, thus spending less time at the breeding site (Uttley et al 1994). Another way of measuring food availability is by studying variations in feeding behaviour. Differences in feeding rates between years at the same colony may indicate a change in food availability (Hatchwell 1991). Since, the guillemot only brings one fish at a time to the chick and hence cannot compensate small/low calorie fish by bringing several fish in each foraging trip, the parents make more foraging trips when the quality of individual prey is poor (Zador & Piatt 1999). On the other hand, the chick is only able to digest a certain amount of fish per day, and can potentially fill up on small, low calorie fish during poor conditions. This is known as the junk-food hypothesis (Rosen & Trites 2000).

This paper aims at studying the potential effects on reproductive success, feeding behaviour and adult time budget of the common guillemot on the island of Stora Karlsö, from observed changes in sprat abundance and quality (i.e. condition, weight and presumably energy content: Casini et al 2005, ICES 2005). Common guillemot in the Baltic Sea feeds almost exclusively on sprat (Österblom & Olsson 2002). As the population of common guillemot appears to depend on this species, we anticipate that changes in the sprat stock will affect the breeding ecology of the species, i.e. the reproductive success and feeding behaviour.

I hypothesize that common guillemot breeding success is positively correlated to sprat spawning biomass, and that feeding behaviour, trip duration and adult time budgets should also be affected by changes in the fish stock, i.e. I suggest that feeding rates should be higher, trip duration shorter and adults to spend more time together on the breeding ledges when sprat spawning biomass is high. I also investigated a potential method for monitoring the size of fish, caught by guillemots.

Methods

Between the 2nd of May and 4th of July, 2005, the reproductive success, feeding behaviour, energy intake of the chicks and adult time budget of the common guillemot, *Uria aalge* was studied on the island of Stora Karlsö (57°17'N, 17°58'E). A method was also developed to assess the size of the fish caught by guillemots.

Several previous studies have been made on this colony. Between 1974-1977, Hedgren (1979, 1980) studied the breeding success, feeding behaviour, size of fish fed to chicks as well as chick growth and fledging weight. In 1998-99, Österblom & Olsson (2002) documented reproductive success, adult time budgets, feeding behaviour and species composition of fish caught by guillemots. In 2002, Enekvist (2003) analysed feeding behaviour and estimated the energy intake of the chicks.

This study was conducted on five breeding ledges (81 pairs of breeding birds) on the northwest side of the island. The ledges were studied every day for 10 weeks (during a total of 192 hours) from when the eggs were laid until the chicks fledged. The dates of egg laying, chick hatching and fledging were registered. The ledges were situated between 3 and 15 metres away from the observation point. Monitoring was done with binoculars, telescope, a digital SLR Nikon camera and a digital Sony video camera. Individuals/pairs were identified by plastic and metal tarsus rings (birds were ringed in 1997) or by other distinguishing features. As guillemots are relatively stationary on their ledges, it was easy to individually identify parents and chicks. As research had been carried out on these ledges prior to this study, the studies conducted during 2005 presented no new level of disturbance.

Results were compared to previous studies in 1974-1977 (Hedgren 1976, 1979, 1980), in 1998-1999 (Österblom & Olsson 2002) and in 2002 (Enekvist, 2003). The results from studies during the breeding season in 2005 and from previous seasons in the breeding colony were correlated with available information on the sprat stock from ICES assessments (ICES 2005).

Reproductive success

Reproductive success (fledged chicks/breeding pairs), hatching success (chicks hatched/breeding pairs), chick survival (successfully fledged chicks/eggs hatched), egg survival (number of eggs hatched/eggs laid) and replacement egg rate (number of replacement eggs laid/total number of eggs laid) were studied on all 81 breeding pairs during the 10 week period. Pairs laying replacement eggs were not included, as they generally suffer from higher mortality (Hedgren, 1980). The potential risk of fatality when chicks left the ledge were not accounted for in this study. Only a small proportion of chicks die at fledging, when landing on the beach (Hedgren 1980).

Chicks that disappeared after reaching the age of 15 days were classified as fledged. Chicks that had not reached the age of 15 days by the 4th July were not included in the study.

Feeding frequency, trip duration and adult time budget

The feeding behaviour, trip duration and adult time budget (time each pair spent together at the site between trips, during the breeding season) were observed for 24 out of 33 pairs that nested on a ledge about 35 metres above sea level and at an observation distance of approximately three metres. This study was conducted during three dawn-to-dusk sessions (03.00-23.00 hrs) on the 9th, 14th and 19th June, for a total of 1101 chick hours. The number of chicks present at the ledge differed between days due to differences in hatching- or fledging date. Observations were made continuously throughout the day, each observer spending a maximum of four hours at the observation point, in order to prevent observer fatigue. Photographs were taken of roughly two thirds of all fish brought to the ledge; video camera footage was also taken during one entire dawn-to-dusk session. All arrivals and departures of adult birds were recorded, giving us data on the amount of time parents spent together on the ledge. Only one fish at a time was brought to the chicks, with no exceptions.

The number of feeds and size of fish fed to the chicks, as well as the type of fish species delivered to chicks, was recorded. It was noted whether the trip was a success or not (i.e. a fish was caught). The time of feeding and whether the chick accepted the fish or not was documented (i.e. if the feeding succeeded or not). When comparing results to the previous study by Österblom & Olsson (2002) and Enekvist (2003), non-successful feeds and successful feeds were pooled, as these authors had not distinguished between the two. Hedgren and Linnman (1979) did, however, distinguish between successful and non-successful feeds.

Estimated fish size and energy content

The average size of sprat delivered to chicks was estimated from the relationship between the dorsal fin-to-caudal fin length and standard length of the fish and with the guillemot bill as a reference (average length 46 mm; Hatchwell 1991). The fish were sized either on the spot or by analysing photographs taken with the SLR camera. The length relationships in sprat were derived from photographs taken by the Swedish Board of Fisheries 2004.

Fish size was divided into four size classes, I-IV (Table 1). As eight year old or older sprat in the Baltic Sea (1974-2003, ICES) has a weight of 15g, the fish in size class IV (estimated weight 18.2 g) were assumed to be 1-2 year old Herring, *Clupea herengus* (ICES 2004). Sprat and Herring were jointly classed as Clupeids.

The standard length of the different size classes of fish, were used to estimate the calorific content and weight of the various fish sizes, utilizing Harris and Wanless (1985) calorie and weight equation from 1985.

1. Sprat (KJ) = $0,0096 * \text{length (cm)}^{3,845}$

2. Sprat (g) = $0,00971 * \text{length (cm)}^{2,855}$

By using equations 1 and 2, a mean intake of calories and biomass per chick could be estimated, as well as an average intake for all chicks. The same equations were used for size class IV fish, as no, to the author, known equations exist for estimating calorific content of herring. Two methods were used to calculate calorific content in fish; the above method by Harris and Wanless and the direct method which entails drying and then combusting the fish in a Gallenkamp Adiabatic Bomb Calorimeter. The latter method was used in 2002 by Enekvist (2003) to estimate the calorific content of fish caught by the guillemots. Enekvist too, used average bill length to estimate fish length

Results

Reproductive success

All results under the reproductive success subheading, including the level of significance with Yates correction, can be found in table 2.

The reproductive success in 2005 was 0.74 fledged chicks/breeding pair. Results from previous years indicate a significantly lower reproductive success in the period 1998-2005 than in the period 1974-77. There was no significant difference in the reproductive success within the periods 1974-1977 or 1998-2005.

The total number of eggs laid, including eggs that never hatched, replacement eggs, eggs that fell off the ledge or eggs that disappeared, totalled 84. Three eggs were laid as replacement eggs, resulting in a replacement egg rate of 3.7% (n=84). There was a significant difference in replacement egg rate between 1999 and 2005 (Tables 2 and 3), i.e. significantly fewer replacement eggs were laid in 2005 compared to 1999.

There was a significant difference in egg survival rates between 1974 and 2005 and also within the periods 1974-77 and 1999-2005. Hatching success has (chicks hatched/breeding pair) decreased since the 1970's. However, there was a tendency toward significant differences also within the periods 1974-77 and 1999-2005. Chick survival (chicks fledged/ eggs hatched), showed no sign of having changed during the study period.

The youngest chick to be fledged was 16 days old and the mean age at fledging was 20.8 days, slightly older than in previous studies; 19, 6 days in 1998 and 19.0 days in 1975 (Table 2).

A weak significant negative correlation was found between sprat spawning biomass and common guillemot breeding success (Linear regression analysis, $P < 0.05$, d.f=1) when using data for all years between 1974-1977, 1998, 1999 and 2005 (Figure 1). There was a significant positive correlation ($P < 0,05$, d.f=1) between common guillemot breeding success and sprat weight at age 4 (Figure 2).

Median fledging date

The median fledging date in 2005 was 24-25th June; in 1998 it was 27th June (Österblom & Olsson 2002) and during the period 1974-1977 it fluctuated between 30th June and 10th July (Hedgren & Linnman 1979). The common guillemot at Stora Karlsö have started breeding earlier during recent years (Figure 3), as chicks are not fledging at an earlier age and the incubation period is not likely to have changed. There was no correlation between mean deviation from long term average spring air temperatures and median fledging date. Presumably, chicks are not fledging at an earlier date due to warmer spring air temperatures (Figure 4).

Adult time budget

The average amount of time both parents spent together at the site in 1998 and 2005 was almost identical (Table 4). Also the numbers of trips/day/pair (successful and non-successful trips pooled) were very similar. In 2005 each pair made 5.5 trips/day and in 1998 each pair made 5.1 trips/day (Österblom & Olsson 2002). Numbers of trips/day/pair were not included in Enekvist's studies during 2002.

Trip duration

Out of 308 foraging trips in 2005, 13% were unsuccessful in the sense that no fish was brought back to the chick. In 3.5% of the cases ($n = 11$), the chick refused feeds. The longest successful foraging trip was 780 minutes (13 hours), and the shortest only 5 minutes. In 2002, the shortest trip was 25 minutes and the longest 750 minutes. The average time spent on a successful foraging trip was the longest in 2002 compared to 2005 and 1998 (Table 4). 33% of all foraging trips were shorter than one hour in 2005 (Figure 5). There was no significant difference in the number of trips less than one hour in 1998 and 2005 ($\chi^2=0.73$, $d.f= 1$, NS, Yates correction) (Table 4). However, when comparing results from 2005 and 1998, a significant difference in the proportion of foraging trips under 20 minutes was found ($\chi^2=17.18$, $d.f=1$, $P<0.001$, Yates correction) (Table 4). In other words birds are most likely foraging farther away from the breeding site in 2005 than in 1998.

Feeding behaviour

During three dawn-to-dusk periods, 258 successful foraging trips were recorded and 247 resulted in a successful feeding of the chick (95.7%) We recorded an additional 39 failed foraging trips (Table 5).

The total number of chicks observed during the three dawn-to-dusk periods was 56 and the average daily intake was 4.6 feeds/chick/day (Table 4). In 2003, chicks received 4.6 feeds/chick/day (Enekvist 2003) and in 1998 they were fed 4.3 times/day (Österblom & Olsson 2002). However, Österblom and Olsson and Enekvist did not make a distinction between successful- and non-successful feeds. When combining both successful and non-successful feeds in 2005, the feeding frequency was 4.8 feeds/day/chick. In other words the chicks were provided with 4.8 fish/day, although not all fish were eaten. The difference was not significant between the three years (T-test). Thus, feeding frequency appears to have been almost the same in 1998, 2002 and 2005. In 1975-76, however, Hedgren and Linnman (1979) observed 2.2 feeds/day.

There was no correlation between the age of the chick and the feeding frequency (Figure 6). However, it seems as if younger and older individuals were fed fewer fish/day than other chicks. In addition, there was no indication of a relationship between chick age and size of fish fed to chicks (Figure 7).

Chicks were fed throughout the day, but with peaks in early morning and late afternoon (Figure 8). Similar results were found by Österblom & Olsson (2002), Hedgren & Linnman (1979) and Enekvist (2003).

Estimated fish size and energy content

All fish fed to the chicks were identified as clupeids, besides one that appeared to be a sandeel (*Ammodytes* sp). During the years 1972-76 the average fish length was 132 mm ($n=32$) (Hedgren, 1976) and the average weight 13,3g ($n=25$) (Table 4). In 2005 the average length was estimated to 118 mm ($n=24$) and the average weight was estimated to 11,7g ($n=24$). Actual length data were not available for the 1972-76 samples, so to evaluate if fish in 2005 were significantly

smaller, a bootstrap technique was used. Based on random sampling with replacements from the 2005 fish data, 10 000 datasets were created and the average length was calculated from each set. Only 0.15% of these datasets had mean values of 132 mm or larger. The conclusion is thus that the fish were larger in 1972-76 than in 2005.

Most of the fish caught by guillemots and brought to the chicks were 10-12 cm (size class 2), which were assumed to be fish of 2-3 years of age (Figure 9).

Chicks in the 2005 study were estimated to have been fed 501 kJ or 46,7g fish per day (Table 4). These results were almost identical to Enekvist's estimations in 2002 (502 kJ/chick/day and 46.7 g/chick/day, using the same method of estimating calorific content and sprat weight as in this study). Mean weight of sprat in a trawled sample in 2002 was approximately 10.3 g (Enekvist, 2003). Estimated energy intakes using Hedgren's results from 1975 (Harris and Wanless, 1985) indicate a daily intake of 368 kJ/day and 32g of fish/day. Average energetic content of sprat in this study was estimated at 10.65 kJ/g. No such estimations were done by Hedgren during the 1970's on Stora Karlsö.

Discussion

There have been slight changes in the breeding success of the common guillemot on Stora Karlsö since the 1970's which could possibly be due to changes in the sprat stock. Chicks appear to be fed more frequently today than 30 years ago, although feeding behaviour has remained remarkably similar between 1998 and 2005.

Reproductive success

When comparing data from 1998 and 2005, there was no significant difference in reproductive success. However, there was a significant difference between the periods 1998-2005 and 1974-1977. Available data indicate a decline in reproductive success since the 1970's. However, due to similar reproductive success in 1974, 1998 and 2005, it can be questioned whether fewer chicks are fledged/breeding pair today than previously. The results may indicate a decline in reproductive success, but may also be an effect of natural fluctuations. It is uncertain why the reproductive rate is lower now than during the 1970's, however this could be due to different ledges being observed in the two periods (due to landslides on the cliff face which has created new ledges), or a real difference resulting from the decreased size of sprat.

The negative correlation between breeding success and fish biomass could be an indication that smaller sized fish, with a lower nutritional value, cause a decline in the reproductive success of the Baltic guillemot. Both Kornilovs et al. (2001) and Casini et al. (2005) suggest that a reduction in sprat condition has taken place. Also, there is a strong correlation between increasing sprat biomass and declining sprat weight (Figure 10). A weak positive correlation was found between sprat weight at age and breeding success, i.e. fish with a higher weight (and presumably nutritional value) may positively affect the bird's breeding success. However, the limited number

of years included in this study and the weak correlation between breeding success and mean weight of sprat indicate these results should be interpreted with some caution. The temporal trends of sprat condition (Casini personal communication), mean weight of sprat and common guillemot chicks fledging mass (Österblom et al 2001) illustrate similar trends, i.e. a decline at the end of the 1990's (Figures 11 & 12). Thus, this could indicate a link between these factors.

According to Hedgren (1980), guillemots with breeding experience are more likely to succeed in their attempt to produce a fledged chick than inexperienced parents. Results indicated that less replacement eggs were being laid in 2005. This could be due to fewer eggs accidentally falling off the ledge (and therefore less reason to lay a replacement egg).

I am unable to explain why hatching success was significantly higher in 2005 than in 1999. According to Österblom (Österblom & Olsson, 2002), the low hatching success in 1999 could have been due to predation by herring gulls. This factor was not thought to be a reason for the decline in fledged chicks observed in 2005 as only one egg was seen taken by a herring gull. Furthermore, the herring gull population has declined by approximately 40% since 1998 (Tuomo Kolehmainen, personal communication). Most likely, the majority of all eggs lost, fell off the ledge e.g. due to inexperienced breeders or disturbances.

Egg survival has varied between all years, and no trend could be established. However, egg survival was significantly higher today than in 1999. This could be a sign of an improvement in sprat condition since the 1990's; when their condition was at an all time low.

Chick survival did not appear to have changed during the study period. This may reflect the real situation, or be a result of too few years of data.

Adult time budget

When food abundance is high, guillemots tend to spend less time foraging and more time together with their partner and chick (Uttley et al 1994, Bryant et al 1999). Parents spent twice as long time foraging in years when food abundance was low than in years with high food availability (Uttley et al 1994). In this study adults spent 22% of the day together at the breeding site, which when compared to other studies, does not indicate a shortage of food. However, fish are now smaller than before. Hence, more feeds/day are needed for an equal energy intake. Foraging time has also been a good tool for estimating the distance travelled to feeding site. However, care needs to be taken when using time away from breeding site as an indicator of kilometres travelled, as guillemots spend time on the sea surface before and after diving (foraging) (Monaghan et al 1994).

The adult time budget appears to be identical between the years 1998 and 2005. Sprat abundance was similar between the years as well. However, adult birds spent more time together with the chick in 2002, although sprat abundance was lower this year.

Trip duration

The trip duration of guillemots, can be a good indicator of how hard the birds need to work in order to attain food (Uttley et al 1994). Shorter and fewer foraging trips, may suggest a greater supply of food. Foraging trips under 20 minutes were significantly fewer in 2005 than in 1998. This could be due to birds foraging further away from the colony. However, we have limited information about what the birds do during foraging trips. The observed results could also be due to a scarcity of sprat in the vicinity of Stora Karlsö, which forces the guillemots to seek food elsewhere.

Feeding behaviour

The guillemot catches only one fish at a time, and in the North Sea they have been observed to change diet in response to prey availability (Wanless et al 2005). This can thus be used as a short-term indicator of what fish are abundant (Barret 2002). By knowing a species preferences and daily intake of fish, a picture of the local fish community can be derived. This is well reflected in this study, in the difference in numbers of fish caught and fed to chicks in the 1970's and fish caught and fed to young in the late 1990's and 2005. Chicks are fed more fish/day today, than 30 years ago and subsequently also have a higher daily calorific intake. However, chicks are being fed twice as many fish/day today, but were estimated to only obtain 25% more calories now than during the 1970's. This could indicate a decline in fish energy content, most likely due to the diminishing size of sprat in the Baltic Sea.

The daily energy requirement of an adult guillemot is approximately 30% of its body mass (Hedgren 1976). If guillemots on Stora Karlsö are not acquiring the necessary energy input, this could have repercussions on their reproductive success. However, it should be taken into consideration that the fish had recently undergone spawning, which most likely decreases energy content further still. At other times of the year, the attained nutritional value may be different.

When correlating chick age and number of feeds/chick/day, it appears that chicks approximately 10 days of age receive the most feeds/day, chicks older or younger than this, obtain fewer feeds. This corresponds well to other reports (Birkhead & Nettleship 1986, Uttley et al 1994).

Estimated fish size and energy content

The condition of sprat was low during the mid to late 1990's, increased between 1998 and 2002, only to decrease again in 2002-2004 (Casini et al 2005). Unfortunately no estimates of fish size and energy content were made in 1998. However, comparing energy intake between years has proven to be a complex problem. Contradictory results were found when using Wanless & Harris (1985) method as apposed to the direct method used by Enekvist (2003). Trawled fish were used by Enekvist (2003) in the direct method, whereas fish caught by the birds were used in Wanless & Harris (1985) method. When comparing results, the latter method was used for the reason that

it had been used in previous studies on guillemot prey at Stora Karlsö. However, North Sea sprat tends to have a higher fat content than Baltic sprat (Hansson, 2001), which may make Wanless and Harris' method slightly misguide when applying it to Baltic fish. Nonetheless, the method can be used in a relative way to compare results throughout the years at Stora Karlsö, as seen in table 4.

According to ICES 48 % of the entire sprat stock in the Baltic Sea 2005 are 2 years of age (ICES, 2004). This corresponds well to results obtained in this study, where 43% of all fish caught for chicks were size class 2 (2-3 year old sprat).

Climate variations

The earlier median fledging date observed during recent years could indirectly be caused by climate change. Sea-surface temperature is most likely linked to air temperature. For every one degree decrease in sea-surface temperature, breeding of common guillemots has been observed to be delayed by 3 days (Nettleship & Birkhead 1985). Thus, when sea-surface temperature is elevated, birds breed earlier. Sea-surface temperature was not observed in this study. However, no relationship could be found between mean spring air temperature and median fledging date using the available results (Figure 4).

The amount of zooplankton, prey for sprat, also varies with temperature. Warmer surface water usually results in more plankton and sprat condition has been known to be positively correlated to the total zooplankton biomass (Casini et al 2005). Climate changes can also affect the female's condition. Colder weather requires spending more energy on self-maintenance than on egg formation (Nettleship & Birkhead, 1985). It appears most likely that there is no correlation between mean spring air temperature and chick fledging date. There are a few other possibilities as to why fledging has become earlier.

Older and thus more experienced birds tend to breed earlier in the season (Hedgren, 1980). Therefore, the change in fledging date may possibly be a sign of a change in the demography of the guillemots on Stora Karlsö or differences between nesting sites. If the breeding success has declined since the 1970's, there may be a greater amount of older guillemots today; which could possibly make egg laying earlier now than previously.

Another possible reason for this could be the birds trying to compensate a shortage of fish with high nutritional value, by initiating breeding at an earlier date. By doing this, they would be feeding their chicks fish from an earlier stage of the spawning period, which most likely would weigh more and be of a higher nutritional value.

Conclusion

This study indicates a significant negative correlation between sprat spawning biomass and breeding success, rather than the positive correlation that was hypothesized. Most likely this was due to the declining condition of sprat.

The results also indicate that mean spring temperature has no influence on the timing of reproduction, contrary to what was observed during the 1970's (Hedgren, 1979). Instead the results give the impression that other factors such as e.g. fish condition and bird demography could be possible causes.

The feeding behaviour and adult time budget did not differ much between years, although chicks are fed more feeds/day in the late 1990's and early 2000's, than during the 1970's. Possibly this was due to the deteriorating nutritional value of sprat.

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Appendix

Table 1. Size of sprat, divided into size classes; I-IV.

	Size class I	Size class II	Size class III	Size class IV
Fish length (mm)	< 100 mm (mean 98 mm)	100-120 mm (mean 112 mm)	120-130 mm (mean 121 mm)	130-150 mm (mean 140 mm)

Table 2. Reproductive and fledging data for the common guillemot on Stora Karlsö, 1974-77, 1998, 1999 and 2005. Reproductive success = fledged chicks/breeding pairs, egg survival = number of eggs hatched/eggs laid, hatching success = chicks hatched/pair, chick survival = chicks fledged successfully/of all eggs hatched. Statistical analyses, where e.g. the numbers of pairs that successfully produced a fledged chick, were contrasted to the number of pairs that failed in doing so. This was done for all years and the success frequencies were then compared with χ^2 tests.

	1972	1973	1974	1975	1976	1977	1998	1999	2005	Significant/non significant	χ^2	d.f.
Pairs			287	372	389	427	67	99	81			
Reproductive success			0.77	0.80	0.82	0.82	0.72	0.63	0.74	*** (1974-2005) NS (1974-77) NS (1998-2005)	24.5 3.4 3.1	6 3 2
Egg survival			0.72	0.82	0.82	0.79		0.61	0.77	*** (1974-2005) *** (1974-77) * (1999-2005)	33.5 13.2 6.18	5 3 1
Hatching success			0.79	0.85	0.87	0.85		0.69	0.80	*** (1974-2005) 0.07 (1974-77) 0.07 (1999-2005)	23.2 6.9 3.14	5 3 1
Chick survival			0.96	0.94	0.94	0.97		0.91	0.92	NS (1974-2005) NS (1974-77) NS (1999-2005)	8.1 4.8 0.16	5 3 1
Replacement egg rate			6.4%					13.1%	3.7%	* (1999&2005)	5.5	1
Median fledging date	5 July	30 June	30 June	5 July	7 July	10 July	27 June	26 June	24-25 June			
Mean age at fledging			19 days				19,6 days		20,8 days			

Table 3. Number of replacement eggs laid in 2005 and 1999.

	Replacement egg	No replacement egg
2005	3	81
1999	13	86

Table 4. Average adult time budgets and feeding behaviour of common guillemot on Stora Karlsö, 1975, 1998, 2002 and 2005.

	1975	1998	2002	2005
Time spent together at site		271 min/day	348 min/day	272 min/day
% of time spent together		22%	29%	22%
Trips < 1 h		36,5%	Ca 6%	33%
Trips < 20 min		9,6%		4,2%
Feeds/day/chick	2,2	4,3	4,6	4,8
Proportion clupeids	96,6%	96,5%	98,3%	99,6%
Estimated average fish length	132 mm		116 mm	118 mm
Estimated average fish weight	13,3 g		10,3	11,7
Mean trip duration		129 min	228 min	147 min
kJfish/day/chick	368		502	501
g fish/day/chick	32		46,7	46,7

Table 5. Results from foraging trips during three dawn-to-dusk periods, 2005.

	9 th June	14 th June	19 th June	Total
No. successful foraging trips	89	92	77	258
Failed feeding	3	3	5	11
Failed fishing trips	11	10	18	39
Observed chicks	19	20	17	56

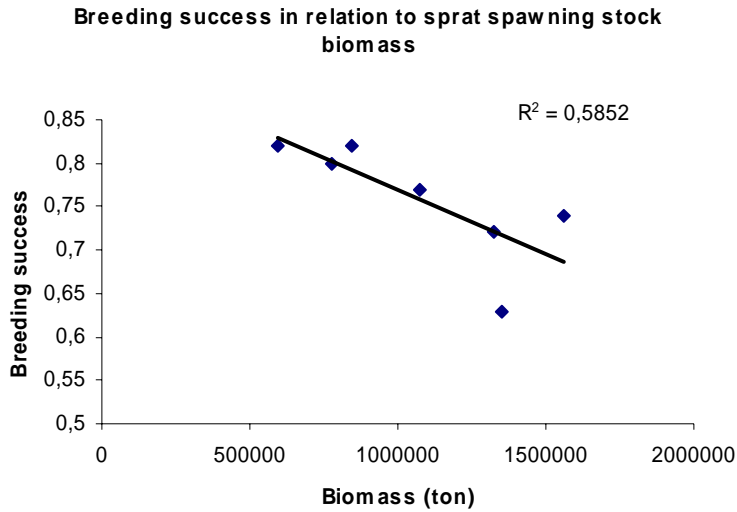


Figure 1. A significant, but weak, negative correlation between sprat spawning biomass and breeding success ($P < 0.05$, $d.f = 1$). An increase in fish biomass may be linked to a decline in reproductive success of the common guillemot.

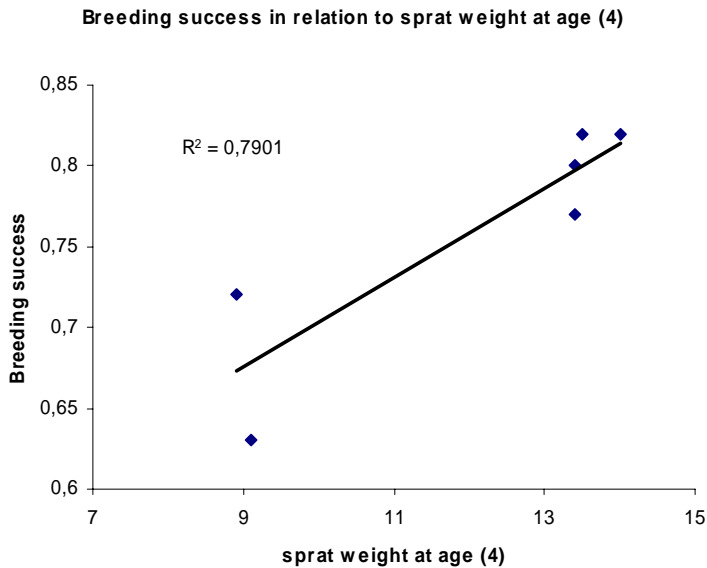


Figure 2. Graph indicates an increase in breeding success when linked to sprat weight at age (age4) ($P < 0.02$, $d.f = 1$). This suggests that an increase in sprat weight could be related to an elevated breeding success.

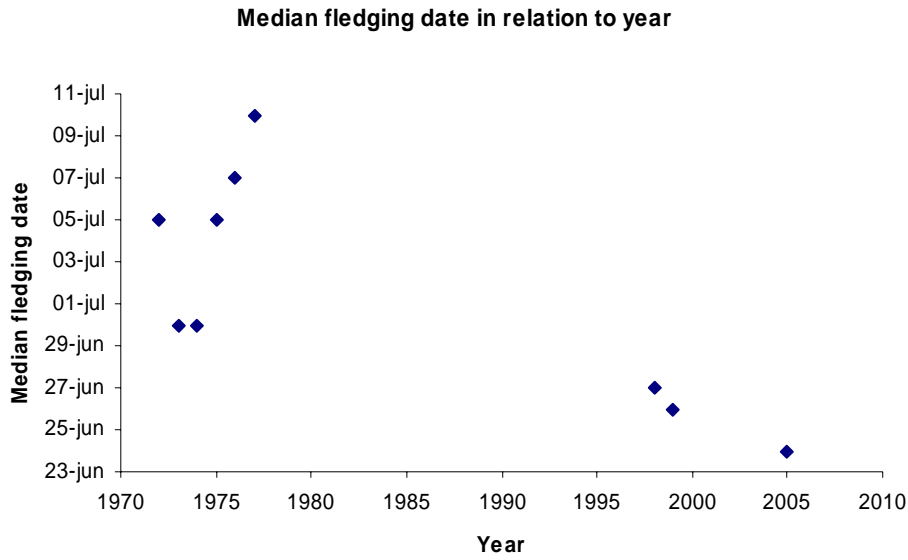


Figure 3. The guillemot fledging date has become earlier throughout the years at Stora Karlsö, 1974-2005.

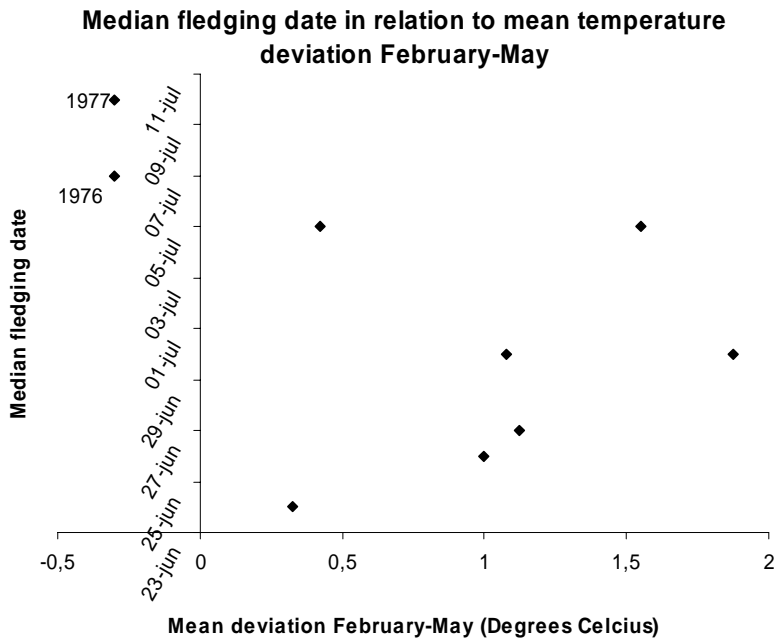


Figure 4. Median fledging date in relation to mean deviation from long term average air temperature ($^{\circ}\text{C}$) in February-May.

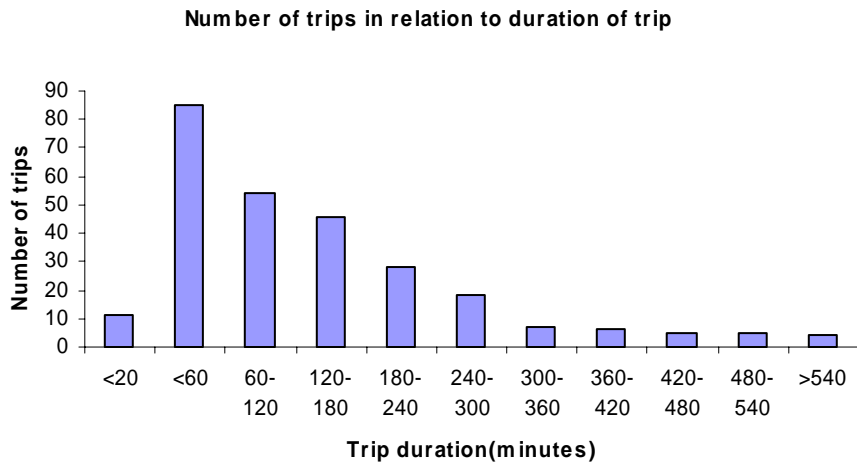


Figure 5. The number of successful foraging trips, during three dawn-to-dusk sessions, in comparison to the duration of the trip, counted in minutes.

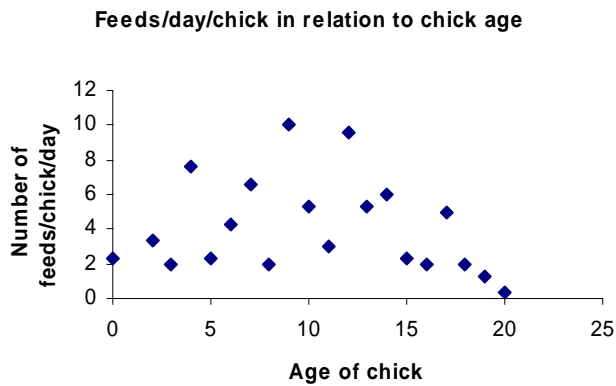


Figure 6. Average number of feeds/chick/day in relation to chick age. Graph indicates there is no correlation between age and number of feeds/day. However, the younger and older chicks received less feeds/day.

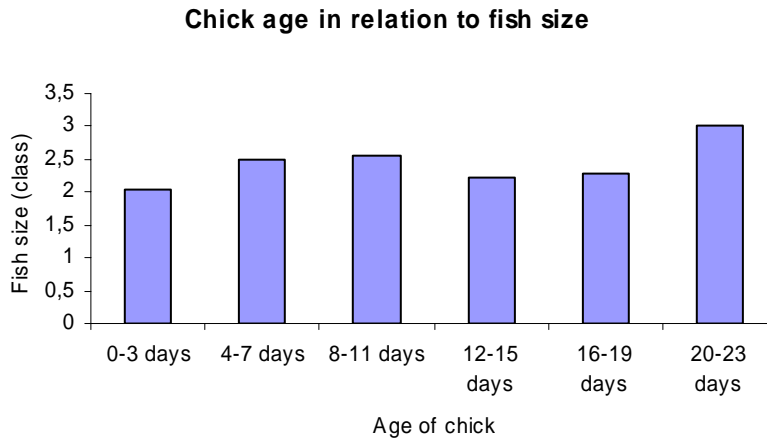


Figure 7. Size class of fish fed to chicks of different age. There is no indication of a relationship between age of chicks and size of fish fed to chicks.

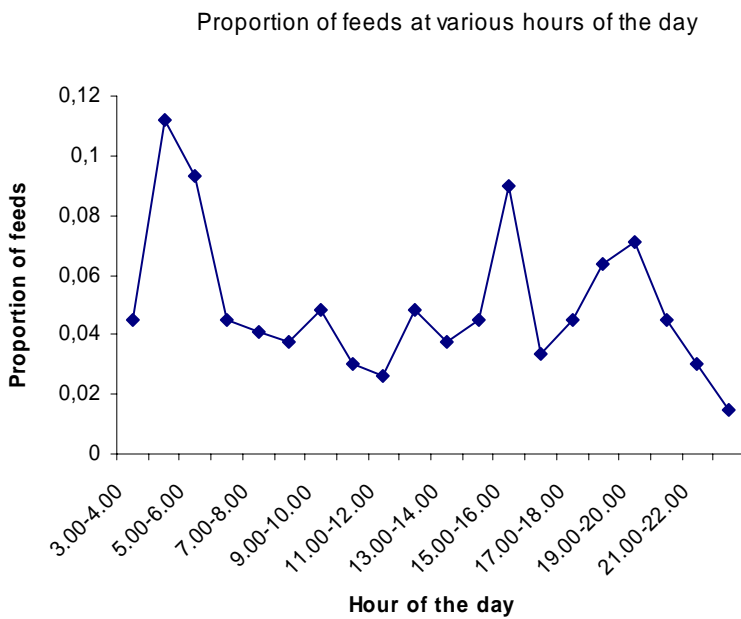


Figure 8. Proportion of feeds at different hours of the day. Data is taken from 3 dawn-to-dusk observations. Most feeds occur early morning and late afternoon. Corresponds with data from Österblom 2001, Hedgren 1975 and Enekvist 2003.

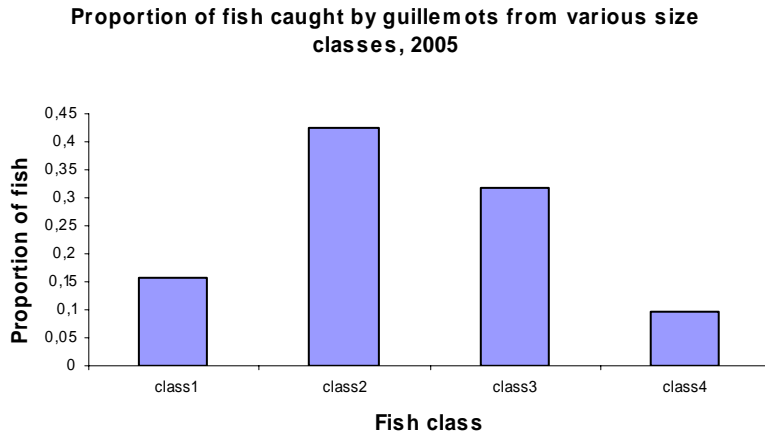


Figure 9. Proportion of fish caught by guillemots from various size classes on Stora Karlsö, 2005.

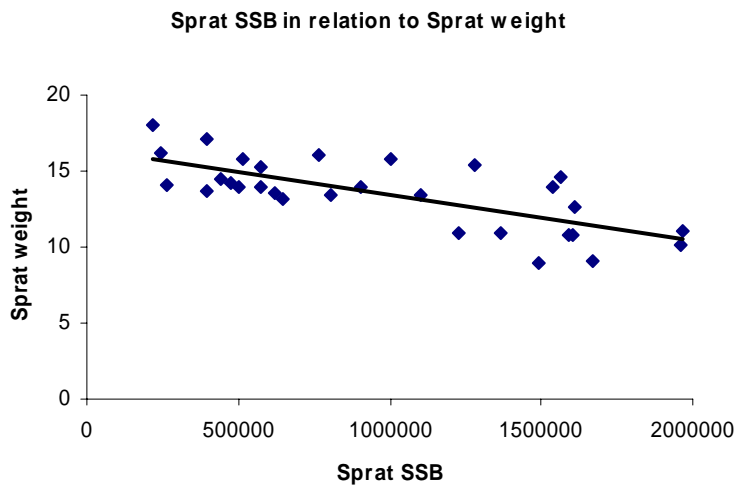


Figure 10. Sprat spawning stock biomass in relation to sprat weight 1974-2003. As sprat biomass increases, sprat weight decreases (ICES 2005).

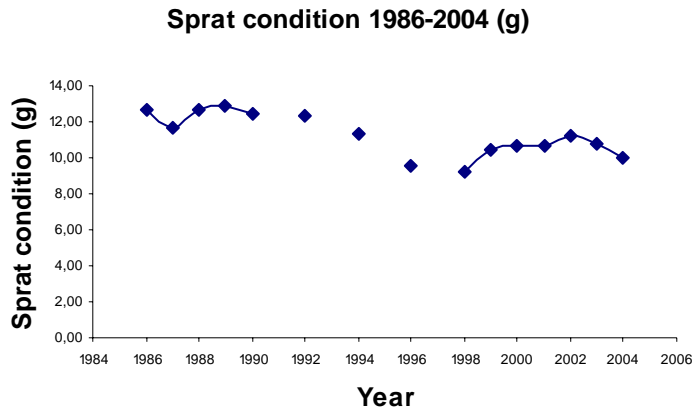


Figure 11. Figure indicates changes in condition of the Baltic sprat in the years 1986-2004 (ICES 2005).

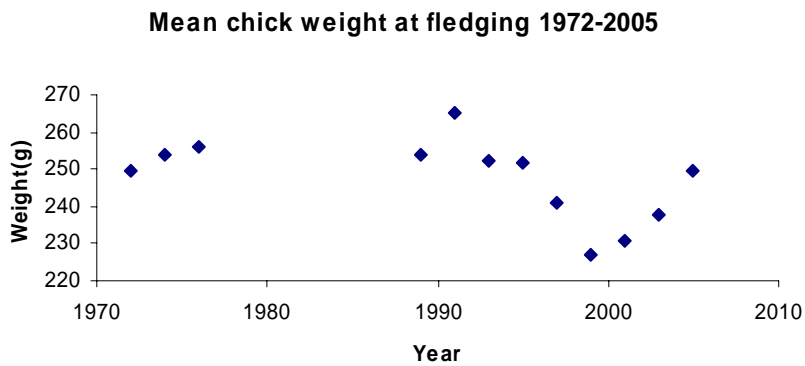


Figure 12. Mean weight of chicks at fledging age. Mean weight at fledging was at an all time low at the end of the 1990's.

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