

Causes and consequences of timing of breeding in Common Guillemot, *Uria aalge*, in the Baltic Sea

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Abstract

Timing of breeding in Common guillemots at Stora Karlsö, central Baltic Sea, is determined by the size of the sprat stock and March sea surface temperature. These factors together explains 64 % of the inter-annual variation, based on data from the 1970ths and 2000ths. However, in the recent years, temperature seems less important, and I interpret this as guillemots are nowadays not physically constrained for breeding early because of the increased Baltic Sea sprat stock. Guillemots in the Baltic Sea feed almost exclusively on sprat, which has a spawning period with larger inter-annual variation in timing (several weeks) than guillemots (7-10 days). Using survival data for chicks ringed during the 2000ths, my results suggests that optimal timing of breeding for guillemots varies between years, and is probably linked to spawning timing in sprats.

Keywords: Common guillemot, *Uria aalge*, Sprat, *Sprattus sprattus*, timing, match, mismatch, sea surface temperature, Baltic Sea.

Introduction

Throughout the planet, there is a growing awareness of ecological consequences of the global warming (Walther et al 2002, Parmesan & Yohe 2003, Root et al 2003). Animals in the temperate zone usually reproduce during spring as an evolutionary adaption for maximizing food requirement and thus breeding output (Lack 1968) and a change in animal spring phenology is one widely documented ecological effect of global warming (Forchhammer et al 1998, Stenseth & Mysterud 2002). Originally intended as an explanation of inter-annual variation in cod *Gadus morhua* recruitment, Cushing (1969)

introduced the match-mismatch hypothesis. He hypothesized that there is an optimal timing for cod spawning, and variation in timing mediated through climate will sometimes mismatch food demand and food supply resulting in failed recruitment. Since introduction, the match-mismatch hypothesis has been used to describe variation in recruitment in various systems. In marine systems, fish-plankton (Cushing 1990, Platt et al 2003, Beugrand et al 2003), bivalve-plankton (Phillipart et al 2003), crab-bivalve (Strasser & Günter 2001), Daphnia-diatom (Windler & Schindler 2004) and seabird-fish (Durant et al 2005) interactions have been observed to have underlying match-mismatch dynamics. The perspective of match-mismatch has recently been broadened to an explanation model for various predator-prey interactions with a seasonal timing aspect (Thomas et al 2001, Durant et al 2007). In an extended context, it states that a predator, which depends more or less on any specific food-supply with an intra-annual variation in abundance, might be sensitive to variation in the prey abundance peak (Durant et al 2007). In a rapidly changing environment, e.g. as a result of the global warming, the ability of a predator to adjust to a change in timing of prey abundance is a key feature to maintain fitness (Durant et al 2007) and many studies have proposed or documented fitness drawbacks as a result of mismatch, including a broad spectrum of “predators” (soy sheep: Durant et al 2005, Atlantic puffin: Durant et al 2005, American Robin: Inouye et al 2000, pied flycatcher: Both & Visser 2001, Sanz et al 2003, Both et al 2006, blue tit: Visser et al 1998, Thomas et al 2001, winter moth: Visser & Holleman 2001). However, there are also studies, which have documented a remarkable ability to adjust breeding parameters to a variable environment in order to maintain a match breeding with food availability (e.g. Cresswell & McCleery 2003). Overall, bird species and amphibians currently show a consistent trend towards earlier phenology (Crick et al 1997, Forchhammer et al 1998, Stenseth & Mysterud 2002), but it is unclear whether this is a sufficient adjustment to a changing environment. Knowledge of which intrinsic and/or extrinsic factors that are behind the timing of breeding onset is a prerequisite in assessing how adaptable the predator is likely to be to a changing environment (Reed et al 2006).

The Baltic Sea is a brackish sea area which is relatively species poor and inhabits a mixture of marine and freshwater organisms (Elmgren & Hill 1997, Österblom et al 2007). The Baltic Sea ecosystem has

during the past 100 years undergone large human-induced ecosystem changes through hunting of seals, increased nutrient loading and intensive cod fisheries (Österblom et al 2007). The present state of the Baltic Sea is characterized by a dominance of sprat *Sprattus sprattus*, which has been favored by a small cod stock (Österblom et al 2007), and warmer winter climate (MacKenzie & Köster 2004). The Baltic Sea sprat stock in 2006 was estimated to almost 2000 thousand tons which is substantially lower than in the peak in the mid 1990ths (1995: around 3000 thousand tons) but is still about 10 times greater than the total Baltic Sea cod stock (2005: about 200 thousand tons) (ICES 2007a). Recent analyses using 30 years of data have shown trophic cascades induced by cod fisheries down to phytoplankton level (Casini et al 2008), proposing that top-down effects are very important constituting forces for fish stocks and zooplankton communities in the Baltic Sea. However, climate variations through river runoffs, the inflow of saline water, sea temperatures and ice coverage (Hänninen et al 2000) have also several documented effects on the Baltic ecosystem (Möllman et al 2003, Köster & McKenzie 2004) which emphasizes that a future climate change will likely have profound effects on the Baltic Ecosystem as well (MacKenzie et al 2007).

Common guillemots *Uria aalge* (hereafter: guillemots) are long-lived seabirds with delayed maturity and low annual breeding output. Seabirds are, although they breed on land, an integrated part of the marine ecosystem and can thus act as valuable indicators of the state of the seas (Cairns 1987, Furness & Camphuysen 1997, Piatt et al 2007). In the Baltic Sea, guillemot breeding ecology has been shown to be affected by a change in the sprat stock, through a decline in chick weights in parallel with a decline in sprat energy content (Österblom et al 2006). The declining energy content in sprat is in turn a result of an increased sprat stock due to less predation from the over-fished cod stock and climate-induced changes in the zooplankton community (Möllman et al 2005, Casini et al 2006, Österblom et al 2007). Guillemot in the Baltic Sea feeds almost exclusively on sprat (Hedgren 1976, Lyngs & Durinck 1998) which has a seasonal dependent distribution pattern (Aro 1989). Hence guillemots are likely to be sensitive to a change in sprat intra-annual spatiotemporal distribution, following the reasoning outlined by Durant et al (2007) of both spatial and temporal dimensions in match-mismatch dynamics.

In guillemots, breeding is highly synchronized (Hedgren & Linnman 1979, Wanless & Harris 1988, Hatchwell 1991) and many studies have documented seasonal declines in growth rate and breeding success, highlighting the importance of the timing parameter. Reasons proposed for this decline have been deterioration of food quality (Hedgren & Linnman 1979), age and/or experience differences among the breeding birds (Hedgren 1980, [Brünnich's Guillemots], de Forest & Gaston 1996, Hipfner et al 1999) and increased predation pressure with lower bird density at breeding sites (Birkhead 1977). In the life history of seabirds, pre-breeding survival is often considered as a less important parameter than e.g. adult survival but can nevertheless account for a large amount of the inter-annual variation in recruitment (Harris et al 2007). Post-fledging survival has been linked to timing of breeding in Isle of May, Scotland (Harris et al 2007), but studies performed in the Baltic Sea have so far not described any covariates that could describe the individual- or cohort level variation in survival (Hedgren 1981, Kadin 2007), although sea temperature the preceding winter has been proposed as one factor (Kadin 2007).

Perrins (1970) proposed that the timing of breeding in birds is determined by the time the female has gathered enough energy to form an egg and thus initiate breeding, i.e. a *constraints hypothesis*. Later studies have stated that energy might not be as important as any specific compound needed for the embryo in the egg, e.g. protein (Houston et al 1995). On the other hand, some experimental studies with supplementary feeding of the adults, has had little or no effect on either laying date (Bolton et al 1992, Arnold 1994) or breeding success (Nager et al 1997), which indicates that all species and/or populations of birds are not physically constrained at the moment of egg production but might instead use cues to breed at an optimal timing, which is when maximum food requirement are matched maximum with food supply (*anticipation hypothesis*, Lack 1954). Whether guillemots use cues to match energy requirements for optimal breeding timing or if they are limited by physical constraints is unknown (Frederiksen et al 2004) and in this thesis I will test both hypotheses.

In one of few studies performed regarding factors determining the inter-annual variation in timing of breeding in seabirds, Frederiksen (et al 2004) found a positive correlation between guillemot timing of breeding and North Atlantic Oscillation (NAO) index. The NAO index

describes the pressure anomalies between Gibraltar and Iceland, where positive values indicate high winter temperatures and frequent westerly winds whereas negative values describe cold and less windy conditions (Hurrell 1995). In the Black-legged Kittiwake *Rissa tridactyla* timing of breeding was also positively correlated with NAO index, whereas European shag *Phalacrocorax aristotelis* which is less dispersed during winters was more dependent on local sea surface temperature. They interpreted their results as those birds use large scale weather events and sea temperatures, respectively, as cues for breeding at ultimate timing (Frederiksen et al 2004).

Methods

Studies at breeding ledges

The colony of Stora Karlsö located in the central Baltic Sea, 57°17'N, 17°58'E (fig. 1). In 1998-1999 and 2005-2007 timing of breeding was studied on a daily basis during May-July (i.e. the whole breeding season) on a number of breeding ledges (*n* between 3 and 6). Dates for hatching- and fledging on a total of 293 (annual number 47-81) chicks were analyzed to assess whether there was inter-annual variation in chick fledging age. The brooding period was assumed not to vary between years.

Ringling of chicks and measuring timing of breeding

Guillemot chicks were ringed while fledging (i.e. jumping from their breeding ledges) in June-July 2000-2007. Ringing started within a few days after the first chicks fledged and ended when a year-specific quota was reached, varying between 500 and 2000, total *n* = 9982. In the beginning of the fledging seasons, few chicks in combination with high catching effort implied that the absolute majority of the chicks were ringed; hence fledging onset was measured with high accuracy. Between 1972 and 1977 all fledging chicks were ringed and in parallel counted (Hedgren 1979, S. Hedgren unpublished data) and there was an almost perfect correlation between these two timing measures (linear regression, “number chicks counted” = “number chicks ringed” *1.14 + 4.14, *P*<0.001,

$R^2=0.993$). Hence, ringing (hereafter: fledging) frequency worked as a good measure of frequency of fledging.

A consistent intra-annual pattern of fledging frequency was shown by Hedgren (1979). In his dataset, spanning over the years 1972-1977, a strong correlation was found between the date of fledging onset (first day with over 100 chicks fledging) and median fledging date (linear regression, “median fledging” = “100 fledging” * 0.91 + 5.57, $P<0.001$, $R^2=0.987$). The 100 fledging date (hereafter: fledging date) were used as timing measure in all analyses.

Estimating minimum survival

Re-sightings of ringed individuals were made at breeding ledges and adjacent areas in the colony (a total of 484 h in 2002-2007). All observed individuals from three different observation schemes were used in the analysis ($n = 1095$) which implies that observation effort and methodology were not constant between years. This should not lead to any bias in calculating differences within cohorts but any resulting differences between cohorts should be treated with caution. For a detailed method description, see Kadin (2007). Ring-recoveries of birds reported to be alive after March 31st the year following their birth was also included in the analysis ($n = 233$). Those data was received from the Bird Ringing Center, Swedish Museum of Natural History. Minimum survival rates were calculated as number of chicks survived / number of chicks ringed.

Potential biases in measuring timing of fledging

Some potential biases need to be mentioned about the method of obtaining a comparative measure of fledging date. In 1974 the guillemot population at Stora Karlsö was estimated to 6400 pairs based on a combination of counts of adult birds at breeding ledges, fledging chicks and eggs and chicks at breeding ledges (Hedgren 1975). In a recent count of individuals resting at the sea surface at the colony during pre-breeding season in 2005 the number of breeding pairs was estimated to 6000-6500 pairs (Hedgren & Kolehmainen 2006) which indicates a long-term stable population, although the methodologies are not fully comparable. Other authors have estimated the population to have

increased to between 8000 and 10000 pairs in the late 1990ths, yet without any described methodology (Olsson et al 2000). In conclusion, there is no evidence that any major change in the size of the breeding population has occurred, and at least there is no indication of a long-term decline. A hypothetical population increase of up to 30 % (as indicated by recent estimates) would have slightly advanced the first day of 100 fledging chicks compared to the population median fledging date, but the uncertainty and inconclusiveness of the estimations makes it impossible to take into account.

Another potential bias is coupled to a change in the appearance of the beach where the fledged chicks are caught. Since 1970ths landslide has lead to a larger amount of limestone boulders at the beach, making chicks slightly more difficult to catch in the 2000ths than in the 1970ths. This could potentially delay the date when 100 chicks first was caught compared to the median fledging date but a major catch-effort in the beginning of the season in recent years is likely compensating for that decline in chick “catchability” and is therefore assumed to not account for any major biases in finding a comparative measure on fledging date.

Complementary data

Data on sea surface temperatures was extracted from ICES Oceanographic Database. The sea area used in all analyses was 57°20' to 56°10' N and 16°45' to 18°45' E (fig. 1) which is the likely feeding area for the Stora Karlsö guillemots during pre-breeding season. Monthly mean sea surface temperatures (SST) were calculated for January – April and December for each year.

Data on sprat abundance and stock size was derived from the ICES Stock Assessment Summary database (ICES 2007a). Abundance estimates and stock size were derived from XSA analyses. Mean weight was extracted from the 2007 Baltic Fisheries Assessment Working Group (WGBFAS) report (table 7.7) (ICES 2007b).

Results

Timing of breeding of guillemots at Stora Karlsö

Age at fledging and timing of breeding are listed in table 1. Chick age at fledging in short term perspective was not different between the years with available data (1998-1999, 2005-2007, ANOVA, $F_{4,280}=1,78$, $P=0.132$). However, according to published data from studies during the 1970ths (table 1, from Hedgren & Linnman 1979), guillemot chicks are slightly older at fledging the 1998-2007 than in the 1970ths, probably as a compensation for decreased growth rate as a result of lower energy content in sprat (Österblom & Olsson 2002, Enekvist 2003). There was a strong tendency towards earlier timing in the 2000ths compared to 1970ths but the difference was not significant (Mann-Whitney test, $U=60.0$, P adjusted for ties = 0.058).

Long-term determinants of timing of breeding

Multiple regression analysis with timing as dependent and different sprat population parameters, sea surface temperature and NAO index as independent variables revealed that both fish- and temperature parameters are important for timing of breeding in guillemots. Using “best subsets regression” procedure in Minitab 15 (Minitab inc.) and model selection based on R^2_{adj} , sprat weight at age 4 was the strongest predictor of timing of breeding, interestingly with a positive sign which implies that guillemots breed late in years with sprats in good physical condition. Inter-annual variation in sprat energy content is negatively density dependent (Casini et al 2006) and sprat energy content is likely a confounding variable whereas the real determinant for timing of breeding is sprat abundance or biomass, which both also were significant predictors with a negative sign, i.e. early breeding in years with high abundance and biomass in sprat. After considering sprat weight at age 4 as a nonsense parameter, the model with the highest R^2_{adj} (0.64) was when sprat total biomass and March sea surface temperature were included (table 2, figure 2a). The parameter values imply that for every degree Celsius in increased water temperature, guillemots breed 2.7 days earlier and for every 1 million tons more sprat guillemots breed 8.7 days earlier.

The 1970ths versus the 2000ths

When analyzing the multiple regression model obtained by the procedure above, the residuals show a clear non-random pattern, in the 1970ths all were positive whereas in the 2000ths all but one were negative, which indicates auto-correlated residuals (Bowerman et al 2005) (fig. 2b). In this case, however, the residual plot rather indicated a difference between the two time periods in the study. Figure 3 a) and b) show the correlation of timing of breeding versus sea surface temperature and sprat stock size, respectively, where the two panels represents the two time periods in the study. The figure indicates that a change in the dependence has occurred; in the 1970ths both sprat stock size and sea surface temperature was important for timing of breeding whereas in the 2000ths sprat stock size seems to be the only determinate of inter-annual timing of breeding. There is no sign of any long-term increase in water temperature in this dataset that could have moved guillemot breeding timing to a threshold level; both mean and variance are almost equal the two time periods. However, the sprat stock has increased since the 1970ths, which could have uncoupled possible constraints in adult condition.

Consequences on post-fledging survival of timing of breeding

To test whether there was a timing dependence on post-fledging survival, linear regression analysis was used. This analytical method was used because other authors have documented a linear decrease in post-fledging survival, probably linked to differences in parental quality among early- and late breeding individuals (Harris et al 2007). When ringing dates with less than 20 individuals was excluded from the analysis, survival decreased with timing of fledging in all 7 years (fig. 4) when data from ring-recoveries and observation studies was included in the analysis. I conclude that the decrease is significant because all years shows a negative regression slope with time, although they are not independently significant ($P_{\text{negative slope}} = P_{\text{positive slope}} = 0.5$, $P_{7 \text{ negative slopes}} = 0.5^7 = 0.0078$).

In a complementary analysis, to get comparable results with Hedgren (1981), only ring recoveries were used. The consistent declining trend in survival in relation to timing of fledging then disappeared (fig. 5), some years even showed a increasing survival with timing of fledging. This finding was unexpected and indicates that there might be a difference in emigration rates or age-

dependent behavior (colony attendance, pair-bonding, prospecting behavior etc.) between early and late chicks, i.e. early chicks have been either more frequently attending to their natal colony or more visible than late ones. Although the sample size are being reduced in the latter analysis, ring recoveries constitute no spatial or behavioral bias as might be present in observation studies at the colony and the results on timing-dependent survival are thus likely more reliable.

Modeling optimal timing

Knowing that timing of spawning in sprat is normally distributed (Kraus & Köster 2001) one could also expect a normally distributed survival function in post-fledging guillemots, assuming a link between timing in sprat spawning and guillemot breeding. A large timing overlap will result in high survival and vice versa. The survival rates from the analysis only including ring-recoveries were used in a year-specific normal distribution function model:

$$f(x, \mu, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\left(\frac{(x-\mu)^2}{2\sigma^2}\right)}$$

Where μ and σ , the mean and standard deviation, respectively, was estimated using an un-weighted least squares analysis, using “Solver” function in Microsoft Excel 2007 (Microsoft Inc.). The outcome of the analysis is presented in fig. 5 where the optimal timing = mean value is the peak of the curve.

Discussion

Timing of breeding in Guillemots at Stora Karlsö

Although there is no high resolution data on timing of spawning of sprat in the Baltic Sea, the timing of breeding of guillemot at Stora Karlsö (egg laying in early May and chick fledging in late June/early July) seems to more or less coincide with the sprat spawning period in the Gotland deep (location indicated in fig. 1), which according to sampling of eggs, ichthyoplankton and adult in spawning condition during research trips performed 1996-1999 starts in April, peaks in June-July and end in August (STORE 2000). Factors proposed in determining timing of spawning in sprat is sea temperature (Karasiova 2002) and sprat stock size (Kraus & Köster 2001). The difference in temperature regime between Bornholm deep and Gotland deep is the likely reason to an observed

difference in sprat timing of spawning between the areas (STORE 2000). According to observations at “Hoburgen” 57°17'N 17°58'E (indicated in fig. 1) in April-June 2003, large amounts of alcids (both razorbills and guillemots) are observed daily during foraging trips, obviously heading in the direction of the sprat spawning grounds in the Gotland deep (Martinsson 2004).

Timing of breeding – a result of a constraint or an optimal decision?

There are many long-term studies which have correlated seabird timing and reproductive success with sea temperature (or climate indices linked to sea temperature) (Fredriksen et al 2004, Hedd et al 2002, Ramos et al 2002, Gjedrum et al 2003, Roth et al 2005, Barbraud & Weimerskirch 2006, Møller et al 2006) but the picture seems to be more complex than the large amount of studies linking global warming and phenology in terrestrial and temperate bird communities (e.g. Crick et al 1997, Forchhammer et al 1998, Cotton 2003). Actually, the majority of studies are documenting delays in breeding timing, often followed by reduced breeding success, as a result of increasing sea temperatures (North Pacific: Hedd et al 2002, Gjedrum et al 2003, Roth et al 2005, Indian Ocean: Ramos et al 2002, Antarctic Ocean: Barbraud & Weimerskirch 2006). The only exception I find is the North Sea and North Atlantic where a negative correlation between timing of breeding and sea temperature in seabirds have been reported (Fredriksen et al 2004, Greenwood 2007, Møller et al 2006). In this study, breeding timing was negatively correlated with sea temperature, in accordance with the North Sea- and North Atlantic studies. A probable reason behind the difference found between this study from the Baltic Sea and the majority of studies performed in the open sea areas in the references above, is that the Baltic Sea shows less variable oceanographic conditions. Likely, a temperature increase in the Baltic Sea directly affects e.g. onset and intensity of fish spawning (Karasiova 2002, Köster & McKenzie 2004), whereas a temperature increase in open marine systems may lead to unpredicted ecosystem changes e.g. as a result of a change in lower trophic level species-composition leading to less favorable seabird feeding conditions (e.g. Hedd et al 2002, Roth et al 2005).

Beside temperature, I can also show that abundance of the guillemots' principal prey, sprat, is a significant predictor of timing of breeding. This finding has a potential to answer the

questions whether timing of breeding in seabirds is a result of physical constraints or optimal decisions, i.e. the *constraint hypothesis* versus the *anticipation hypothesis*. On one hand, a high abundance of sprat during winter may lead to guillemots in better physical condition which in turn may allow them to breed early, if it is preferable (*constraint hypothesis*). Data on adult condition during winter could answer the question whether guillemots are depressed in condition during harsh condition (cold weather, small sprat stock). On the other hand, if sprat spawning onset is used as a cue for initiate breeding, guillemots are likely detecting an absolute number rather than a proportion of the total stock. During years with a large sprat stock, this absolute number is reached earlier which signals guillemot breeding onset (*anticipation hypothesis*). Analogue to the discussed reasons to the dependence on sprat abundance, temperature could theoretically fit in to both hypotheses. Low winter sea temperature will likely depress adult condition (Daunt et al 2006) but temperature could also be a reliable cue for timing in the marine ecosystem (Frederiksen et al 2004), both having a direct effect on seabirds and an indirect effect through triggering onset in lower trophic levels.

Comparing guillemot timing with another Stora Karlsö breeding alcid, razorbill *Alca torda*, could potentially shed some light on the underlying mechanisms behind timing of breeding. Diving depth of guillemots and razorbills in Newfoundland, Canada have been examined from drowned birds in fishing gear, and the study revealed that razorbills are able to dive down to 120 meters and guillemots to 180 meters (Piatt & Nettleship 1985). Guillemots (n=12243) occurred frequently down to 80 meters whereas the small sample size of razorbills (n=9) made it impossible to draw any general conclusions (Piatt & Nettleship 1985). A comparative study between the two species in north Norway in 1989 (Barrett & Furness 1990) concluded that razorbills dive less deep than guillemots (median 25.4 and 45.4 meters, respectively) and that razorbills have a preference for smaller prey compared to guillemots. Razorbills studied in southern Baltic Sea performed the most of their dives in the depth interval between 5 and 10 meters and very rarely dived deeper than 40 meters (Benvenuti et al 2001), but no comparative studies have been performed on guillemots. At Stora Karlsö, razorbills breed two to three weeks later (J. Sundberg & H. Österblom unpublished), and they also feed mainly on sprat in the Baltic Sea (Lyngs 2001). Sprat is hypothesized, especially in cold

winters, to be distributed at the bottom of the Baltic Sea deep basins and start spawn near the bottom in April (STORE 2000). In line of the argument that the Baltic Sea alcids are constrained to breed earlier because of insufficient adult condition, the shallow-diving razorbills must wait until May-June to breed with the background of the sprat spatiotemporal distribution. On the other hand, older sprats spawn earlier than young ones (Torstensen 1998) which is another potential explanation to the earlier breeding of guillemots compared to razorbills, rather supporting the *anticipation hypothesis*.

Long-term changes in the dynamics behind timing of breeding

The dynamics behind breeding onset seems to have changed, comparing the 1970ths and the 2000ths. Where the size of the sprat stock are roughly equally important now and then, temperature which alone accounted for 39 % percent of the variation in the 1970ths, did not describe any of the variation in the data in the 2000ths.

In an investigation of spawning timing of sprat between three time periods in the Gdansk deep, 1947-1955, 1968-1977 and 1996-1999 abundance of eggs and larva in May compared to July was higher in the late 1990ths than in 1968-1977 which indicates a shift towards earlier spawning (Karasiova 2002). Kraus & Köster (2001) analyzed surveys performed between 1996 and 1999 in all three spawning areas of sprat in the Baltic Sea and concluded that timing of spawning those years was not temperature dependent, but negatively correlated with sprat stock size, which implies that spawning was early in years with a large sprat stock. This could be an explanation to why guillemots breed early during years with a large sprat stock irrespective of any possible dependence on adult winter condition. The inter-annual variation in peak timing in sprat reported from Kraus & Köster (2001) is much larger than the measured timing variation in the breeding guillemots (span: several weeks during 4 study years compared to 10 days over of 35 year period in guillemots) which indicates that there is a low probability of a true match (or mismatch) between the peak sprat spawning and guillemot breeding. Rather there is more or less overlap of spatiotemporal distribution.

Schultz (1991) reviewed studies investigating factors behind timing of breeding in animals with focus on physical constraints. The conclusion was that physical constraints account for

much of the inter- and intra-annual variation in timing among wild populations, but there are sometimes possible to find a saturation level where physical constraints does not account for the breeding timing variation (Schultz 1991). In summary this is a combination of the *constraint* and *anticipation* hypotheses, which could fit in very well to the observed timing dynamics in guillemots at Stora Karlsö. In the 1970ths, the sprat stock was comparatively low which in years with low sea temperature, constrained guillemots physically to breed early. In the 2000ths, the larger sprat stock has favored guillemot winter condition, reaching a saturation point, which allows the birds to adjust breeding timing fully according to environmental cues, i.e. timing of sprat spawning. Using fish data with the highest possible temporal and spatial resolution, sprat abundance estimated from May acoustic survey in Baltic Sea subdivision 24-28 (southern Baltic Sea including west and east from Gotland, data from ICES 2007b), illustrates how strong this dependence appear to have been in recent years (fig 6, linear regression, $R^2 = 0.872$, $P = 0.006$).

A possible link between timing and post-fledging behavior

Kadin (2007) studied behavior of immature guillemots of known age and fledging weight and found that birds that weighted less at fledging matured earlier than chicks of normal fledging weight. Also, behavior of immature birds was clearly age-dependent (Kadin 2007). In this analysis, data indicates that early fledged chicks were observed at the colony with a higher probability than late chicks, irrespective of any difference in survival. This implies that the timing of fledging parameter might contain some information, e.g. a chick quality aspect, which later turns out in a difference in post-fledging behavior. Knowing that experienced parents are generally breeding early (e.g. Sydeman et al 1991, Hipfner 1997, Hipfner et al 1999, Arnold et al 2004) this is certainly not impossible. Deeper analyses of behavior of late versus early chicks, could answer the question whether timing in any way affects recruitment and behavior of immature guillemots, and whether this should be incorporated in e.g. survival estimation models. This is crucially important in guillemots whose behavior and thus detection probability is clearly age dependent. A difference in emigration rates between early and late chicks could be another explanation to the observed difference in detection; it might be possible to examine through a deeper analysis of ring recovery data.

An indication of match-mismatch dynamics in post-fledging survival

Guillemots have a so called intermediate fledging strategy, i.e. the male parent escorts the chick to the sea (Sealy 1973), and the birds breeding at Stora Karlsö are known to swim southwards after fledging (Olsson et al 1999). This strategy has been described as a trade-off between mortality and growth; while in the water the chances to gain energy increases but chick mortality increases too (Ydenberg 1989). Recent studies at Stora Karlsö have shown marked inter-annual variation in duration of foraging trips during chick rearing (Österblom & Olsson 2002, Enekvist 2003, Kylberg 2006) which is probably linked to inter-annual variation in food availability (unpublished data). After fledging, the chick and the parent are more spatially restricted and variation in local fish abundance would then have an even more direct effect on foraging efficiency and thus chick growth rate, and possibly also chick survival. The variation in fish abundance between years would intuitively (in combination with other possible factors) result in an effects in average survival between cohorts, and fish spatiotemporal distribution within years would result in timing-dependent variation within cohorts, which is analogue to a novel model for recruitment incorporating both abundance- and timing aspects (Durant et al 2005). To examine variation in survival between cohorts, detailed modeling must be performed which was out of the scope for this study. However, when analyzing the modeled year-specific optimal timing, indicated as the mean of the normal distribution curves in fig.5, temperature in March the preceding winter described a substantial part of the variation (fig. 7). In years with low winter temperature, late chicks had higher survival and high winter temperature favored early chicks. There is no time series of timing of sprat spawning, but winter sea temperature is likely one influencing factor (Karasiova 2002). I interpret this finding as an indication of breeding in some years is later and some years is earlier than optimal, which implies that this result is basically a measure of temporal mismatch between sprat spawning and guillemot timing in the Baltic Sea. A remark is that Kraus & Köster (2001) did not find any correlation between spawning timing and temperature when analyzing data from a few years in the late 1990ths but proposed that timing of spawning derives from the size of the sprat stock (a density dependent mechanism). However, these years were characterized of extremely large inter-annual variations in the stock size compared to recent years (ICES 2007a).

A glimpse into the future

There is presently a lot of concern of ecological consequences of the global change, where fisheries and global warming are likely the most influencing in marine systems (Cury et al 2008). The main driver of change in fish stocks in the Baltic Sea is certainly fisheries (Casini et al 2006, 2008) and variation in fish stocks have documented effects on breeding guillemots (Österblom et al 2006).

According to this study, variation in fish communities does also have effects on guillemots in terms of timing of breeding and post-fledging survival. In a future-scenario for the Baltic Sea, MacKenzie et al (2007) proposed that a species like sprat, for which the Baltic Sea constitutes the northern limit of its distribution area, will be favored by increasing temperatures. Furthermore, cod will suffer from even lower salinities which could possibly stabilize the present clupeid-dominated ecosystem of the Baltic Sea (MacKenzie et al 2007). In that broad sense, guillemots are not facing any direct risks with lost forage base, but the dynamics in all aspects of the breeding biology must be better understood to assess population sustainability. In a shorter time-frame, there are plans on local reduction of the sprat stock attempting to increase zooplankton abundance and possibly also cod abundance (Fiskeriverket 2008). Which effects on fish-seabird dynamics this will have is certainly important to monitor, at relevant spatial and temporal scales.

Match-mismatch in an extended ecosystem context in the Baltic Sea

To assess how sensitive guillemots are to changing timing dynamics in the Baltic Sea, sprat is the obvious component to focus on. It appears that the variation in timing is more pronounced in sprat than guillemots which is consistent with findings from other marine systems from where the match-mismatch hypothesis once where derived (Cushing 1969, 1990), although e.g. cod in the Baltic Sea during the late 1990ths shifted its spawning season with a magnitude of approximately 2 months, likely as a result of a change in the age-composition of the stock, lower size at age and low sea temperatures (Wieland et al 2000). A permanent shift towards earlier or later spawning in sprat leading to more frequently mismatched guillemot breeding seasons would probably result in increased mortality, but it is presently unknown whether mismatch leads to increased mortality or if sprat abundance or other factors (e.g. winter weather) are more important. However, the dynamics behind

timing of the sprat spawning season is unknown and it is therefore presently impossible to build reliable scenarios on possible changes of temperature and fish community changes. Analogue with the above discussed timing aspects of the breeding biology in birds, there are likely some kind of physical constraints associated with water temperature and ice coverage, especially because the Baltic Sea is around the northern limit of sprat distribution area (e.g. McKenzie & Köster 2004). But compared to birds in general, the inter-annual variation in sprat physical condition varies enormously (ICES 2007b) which is mainly a result of intra-specific competition (Casini et al 2006) which is likely interacting with sea temperature in constraining spawning, which is known to be an energy-costing process in fishes (e.g. Kjesbu 1994, Slotte 1999). For example, Kjesbu (1994) reported a delay in spawning timing in 8-10 days for Atlantic cod as an effect of 1°C decreased sea temperature. Furthermore, there could also be an effect of changes in timing related to age-composition of the stock, because older individuals are earlier and also likely able to spawn several batches compared to younger individuals (Alheit 1988). However, beyond age 4, sprat weight is fairly constant over age-classes (ICES 2007b).

Bottom-up dynamics through variation in plankton communities are also contributing to variation in sprat condition and stock size (Möllman et al 2003, Köster & McKenzie 2004), and possibly also timing of spawning. In fjords in Denmark, local eutrophication have advanced the spring bloom and consequently also zooplankton spawning, leading to advanced laying dates in arctic terns, irrespective of warming spring temperatures (Møller et al 2007). However, in the Baltic Sea, the general view is that the timing of the spring bloom is not coupled to nutrient concentrations, but to physical properties such as water stratification and sunlight.

Conclusions

The results presented in this study indicate that guillemots use sprat abundance as a cue for breeding at the right time. Sprats are likely gathering at spawning areas and initiate spawning, which signals breeding onset. In the 1970ths, in years with low sea temperature in combination with low sprat stock might have constrained guillemots to breed even earlier but this seems not to be case presently. Different years showed different patterns in survival in relation to timing, which was likely due to some amount of mismatch with sprat abundance; cold winters probably delayed sprat spawning which

avored late guillemot chicks whereas early chicks were favored breeding seasons following warm winters. Future studies should look at the importance of match-mismatch dynamics in sprat-seabird dynamics in the Baltic Sea and its importance for understanding consequences of fisheries and climate change on marine ecosystems.

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Tables and figures

year	fledging date ⁺	chick age at fledging ⁺⁺⁺
1972	June 29th	
1973	June 24th	
1974	June 25th	19,6
1975	June 30th	19,0
1976	July 1st	19,1
1977	July 4th	20,7
1998		21
1999		21,5
2000	June 26th	
2001	June 25th	
2002	June 25th	
2003	June 27th	
2004	June 21st	
2005	June 23rd	21
2006	June 24th	20,3
2007	June 25th	21

+ based on first day of 100 fledging chicks, see text.

+++ 1974-1977 from Hedgren & Linnman (1979)

table 1. Data on timing of fledging and chick age at fledging for guillemots at Stora Karlsö.

March Sea surface temperature (°C)			Biomass of sprats (million tons)			R ²	R ² _{adj}
<i>Koefficient</i>	<i>Standard error</i>	<i>type III P</i>	<i>Koefficient</i>	<i>Standard error</i>	<i>type III P</i>		
-2,568	1,11	0,048	-8,413	2,464	0,011	0,717	0,636

table 2. Multiple regression model for timing of breeding of guillemots at Stora Karlsö 1972-1977 and 2000-2007.

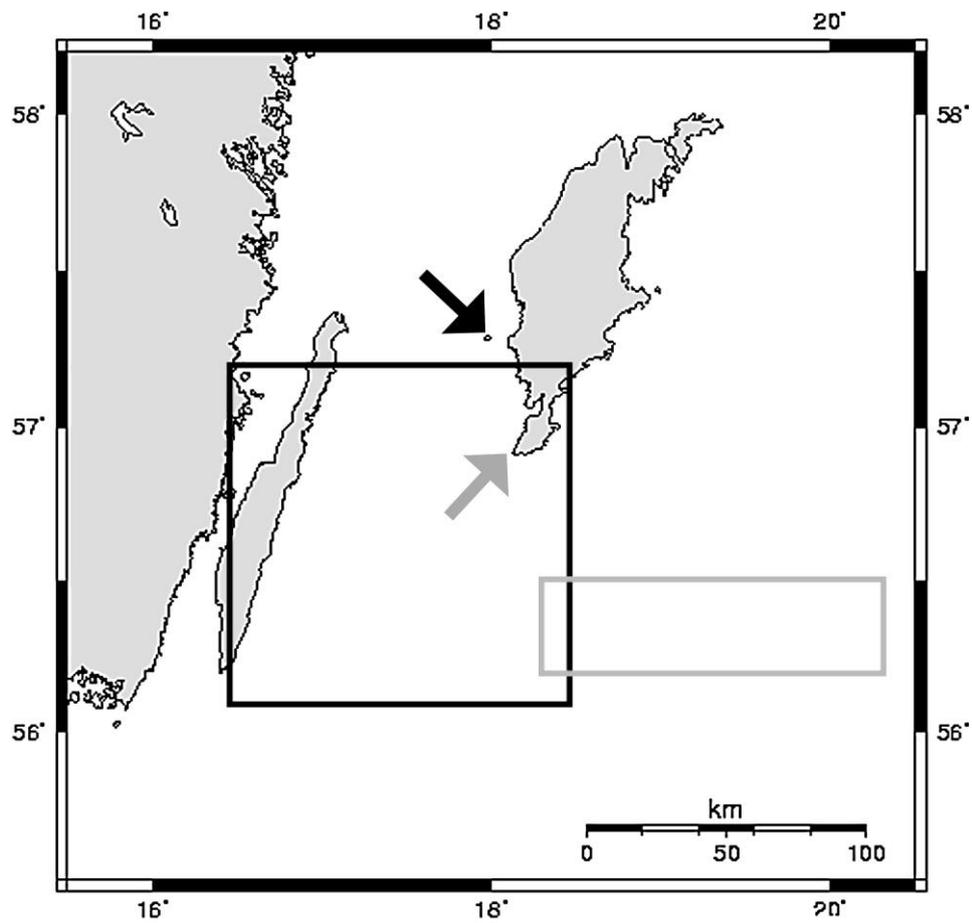
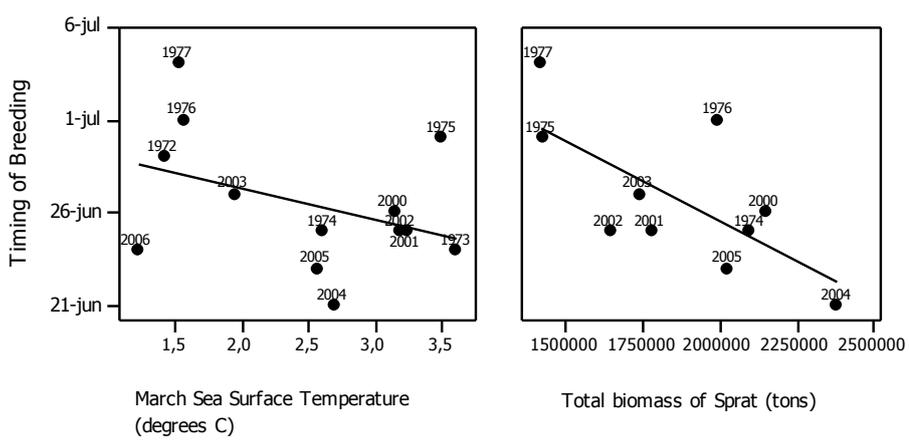


Fig 1. Black arrow indicates the study colony Stora Karlsö (57°17'N, 17°58'E) and grey arrow indicates Hoburg (56°55'N, 18°08'E, see text). Black box indicates the area where monthly sea surface temperatures were calculated and grey box indicates central Gotland deep, as defined by McKenzie & Köster (2004).

a.



b.

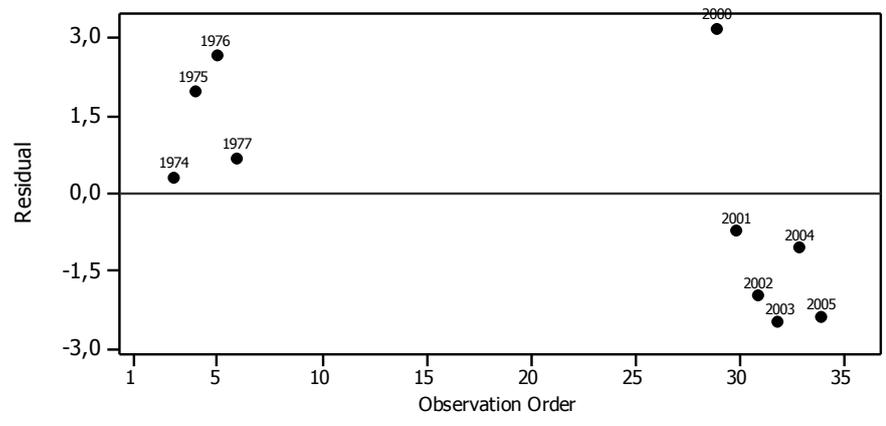


Figure 2. a) Correlations between timing of breeding and on Sea Surface Temperature in March and sprat abundance in the Baltic Sea. b) Residuals from estimated values for model described in table 2.

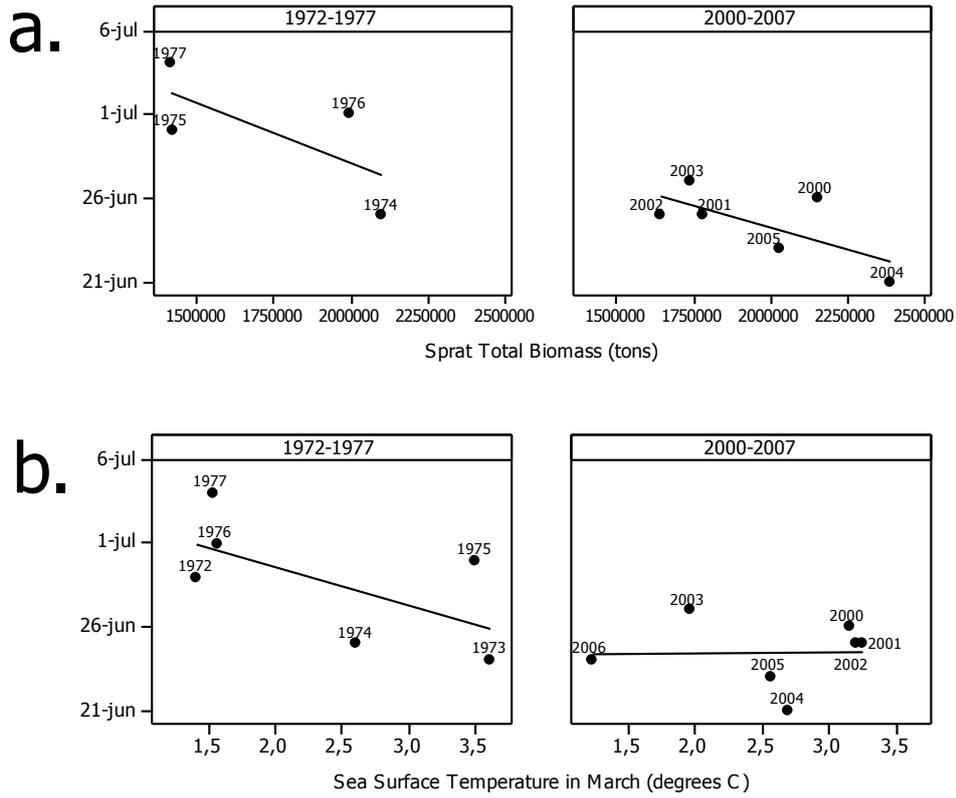


Fig 3. Correlation between timing of breeding and (a) sprat stock size (b) sea surface temperature, during the two study periods.

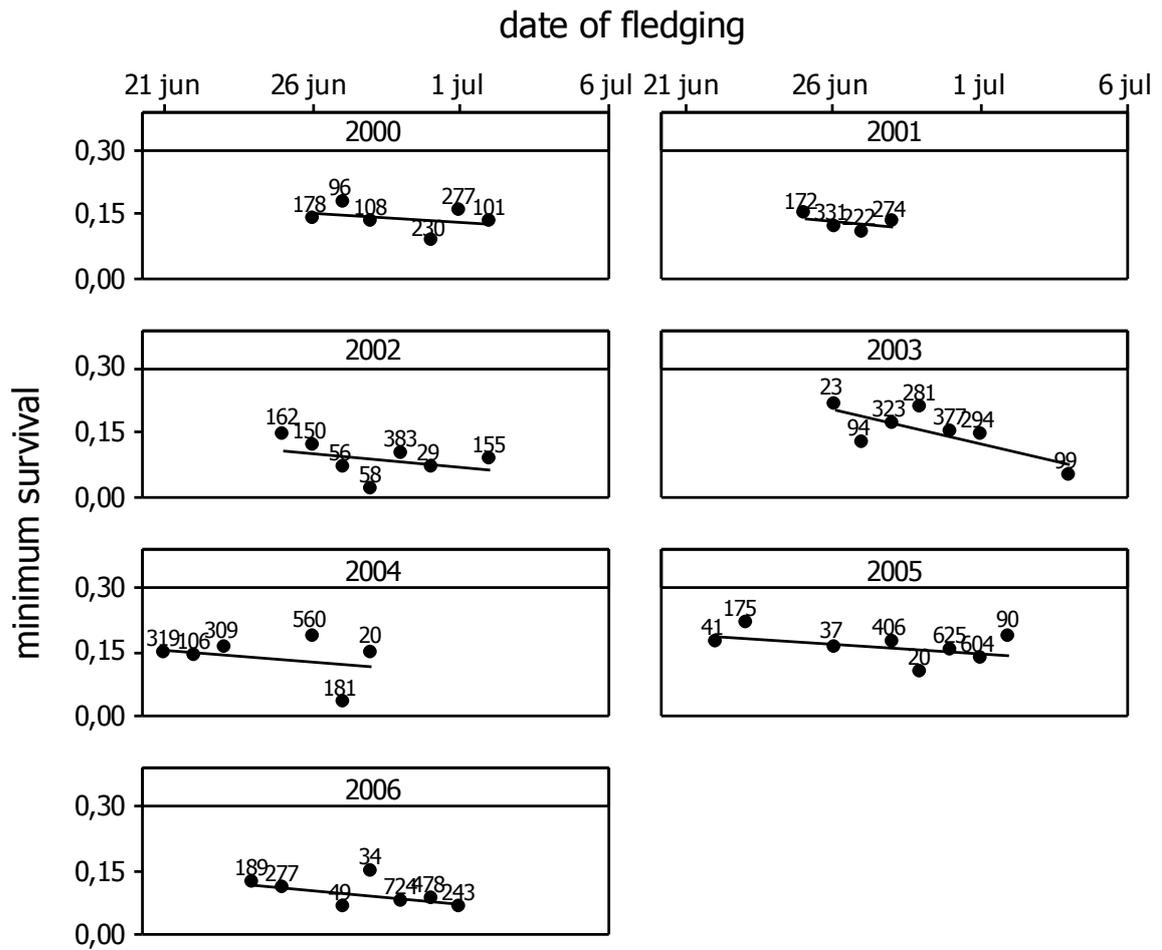


Figure 4. Minimum survival in relation to date of fledging 2000-2006. Data from both observation schemes at colony and ring-recoveries is used. Labels indicate n-numbers for ringed individuals. Days with less than 20 ringed individuals were excluded from the analysis.

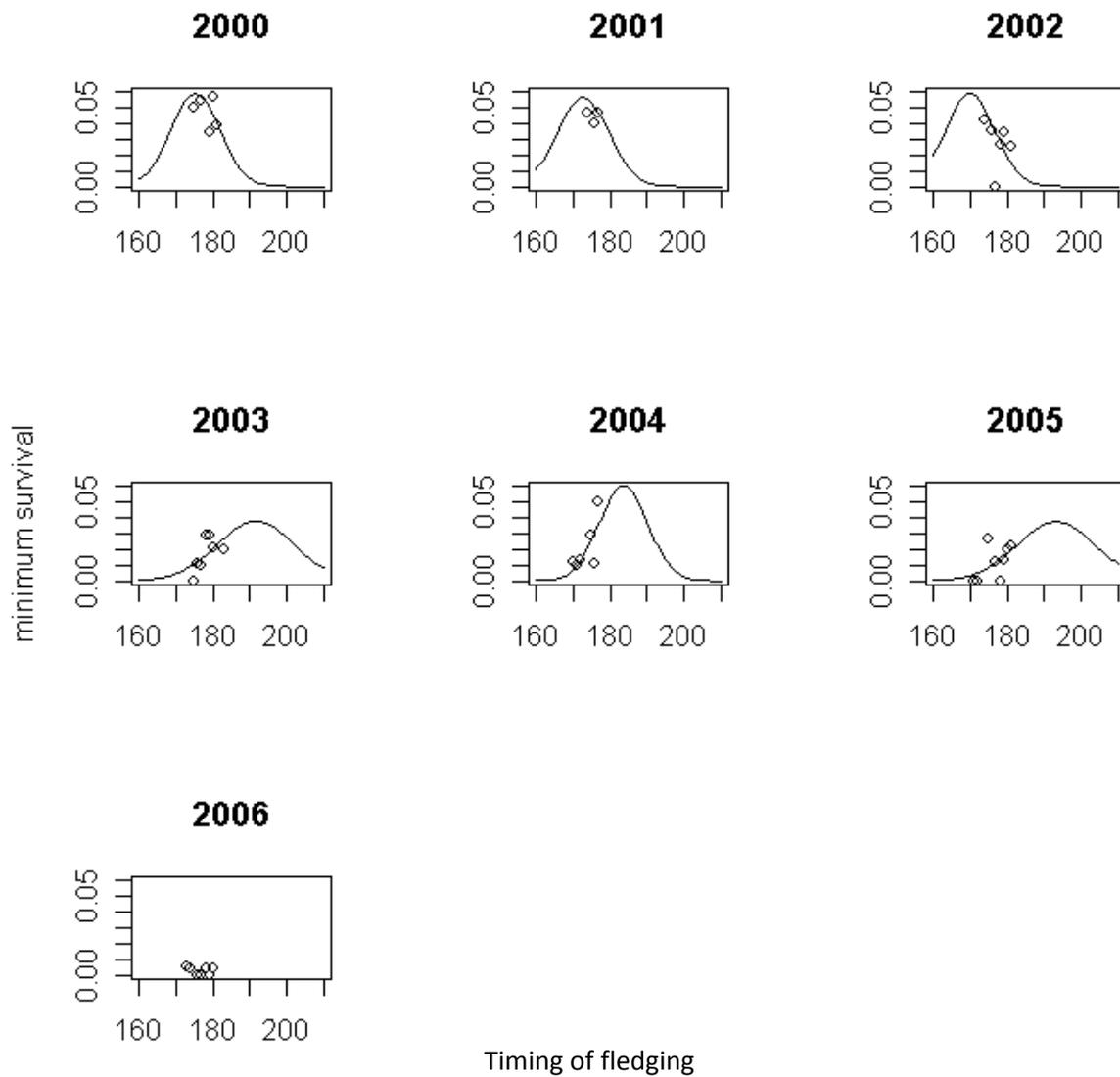


Figure 5. Minimum survival in relation to date of fledging 2000-2006. Only data from ring-recoveries were used. Days with less than 20 ringed individuals were excluded from the analysis. X-axis indicates timing of breeding in Julian days, where 160 = 11 June, 180 = 1 July and 200 = 21 July. The curve represents a normal distribution where the parameter values (mean and standard deviation) were estimated using an un-weighted least squares analysis, see Results.

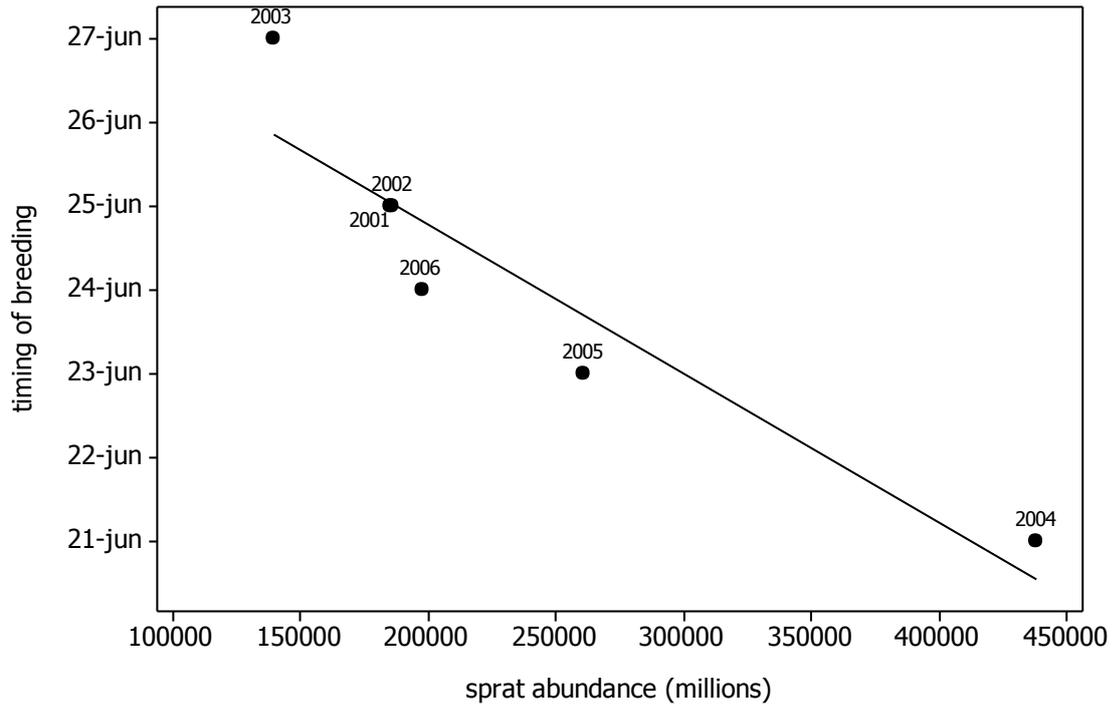


Fig 6. Correlation between timing of breeding and sprat abundance in Baltic Sea subdivisions 24-28 estimated from ICES May acoustic survey. Labels = study years.

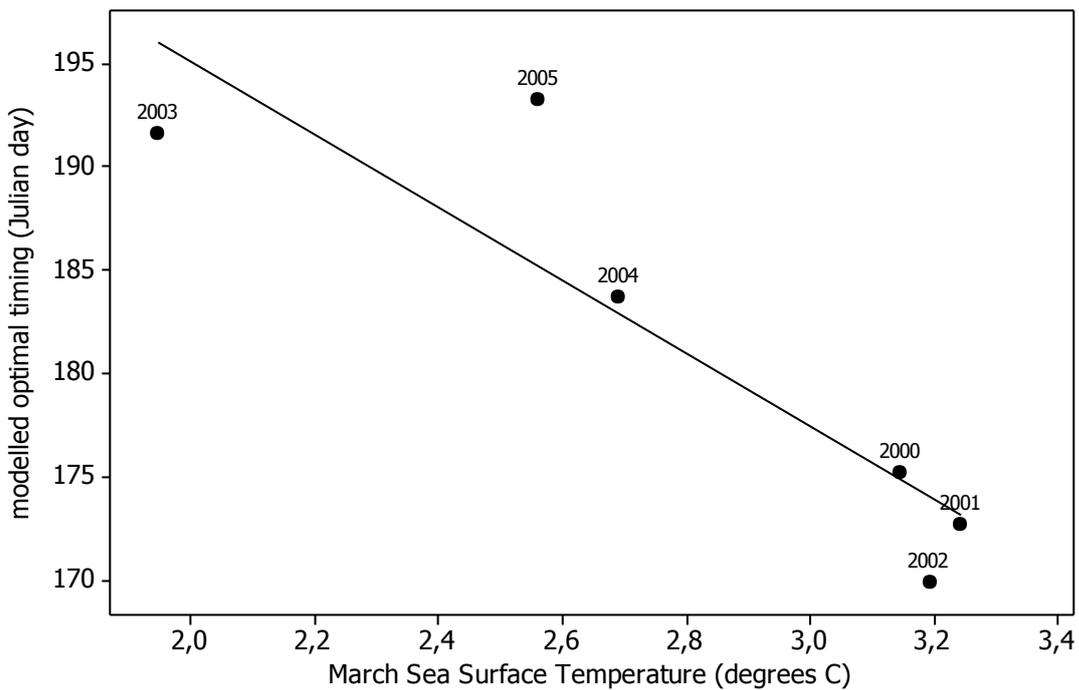


Fig 7. Correlation between modeled optimal timing (using method described under fig. 5) and March sea temperature in the Baltic Sea. Years with high temperature, sprat spawning is likely early which favors early guillemot chicks (years 2000-2002). Low temperature year spawning is likely delayed which favors late guillemot chicks, most obvious in 2003. Linear regression, $R^2 = 0.793$, $P = 0.017$.