Seasonal changes in clupeids maturation constrains the food quality of chicks of the common guillemot (*Uria aalge*)

- A case study of a potential mismatch, from the perspective of the common guillemot chicks on Stora Karlsö, the Baltic Sea.

Emelie Delphin
Abstract

Background Common guillemots are integral elements of the Baltic Sea marine ecosystem. They possess life-history characteristics such as relatively long lifespan, quite low fecundity resulting in only one egg per breeding season – characteristics that make them particularly vulnerable to even small changes in the environment. Higher weight of their single chick, gained during the breeding season, ensures higher survival rates for Guillemot fledglings. Hence, during the breeding season not only quantity but also quality of prey within the foraging area are central for their reproduction success.

Objectives This study applies the match-mismatch hypothesis on a predator-prey relationship by investigating common guillemot chicks’ fledgling weight on Stora Karlsö in relation to their key prey, sprat and herring. Maturity in sprat and herring were used as an indicator for fitness and spawning abundance of food quality for parental guillemot for raising chicks’.

Data The study used data of chicks’ weights when leaving their nests from common guillemots (40,936 chicks) collected between 2007 and 2017 from the Swedish Baltic Sea Bird Project. Data of sprat and herring gonadal maturity was obtained from the PLANFISH project and inspections of catches from the commercial and industrial fisheries.

Method Common guillemot chick fledgling weights between years were analysed by Analysis of Variance (ANOVA). Maturity in sprat and herring were used as a proxy to estimate spawning state and predict the peak day of highest abundance of potential spawners. A Generalized Additive Model (GAM) was used to predict the peak day of highest abundance of potential spawners. For estimating match-mismatch lags, a cross-correlation function analysis (CCF) was conducted to analyse chick fledgling weight in relation to sprat and herring’s maturity states (fitness).

Results The study showed that common guillemot chicks have decreased in weight annually between 2002 and 2017. The results further show that it is obviously more advantageous for chicks to leave their breeding ledge during the first part of the fledgling period (end of June) since chicks that leave their breeding ledge during the end (mid July) of the period showed a lower mean weight. The statistical analysis also showed that chicks had a significant weight loss of approximately 3 % between all pairwise compared consecutive years (2009-2017). The analysis of sprat and herring maturity (fitness) resulted in strong inter-annual variation, and
analysis showed that intra-annual fish maturity has an influence on chick weight. Cross correlation analysis revealed a significant positive correlation lag between herring mean maturity and chick mean weight during the fledgling period at day 0-2 days before leaving nest and a significant negative correlation at lag days 3-20 (approximate time period of hatching to young chick) but a negative correlation between sprat mean maturity and chick fledgling weight at lag 5-9 days after leaving nest and a significantly positive correlation between day 9-19 (approximate date of hatching). These results indicate that sprat might be the essential and necessary food during the chicks’ first period while herring comes to play a more vital role in the later.

**Conclusion** This study shows that breeding success in common guillemots not only strongly depends on quantity of essential fish prey species but also on the food quality (fitness) of the fish prey species. Moreover, chicks’ weight, and thus their potential later survival, is strongly dependent on the right timing of abundance of the developed maturity stages of the two relevant fish species, sprat and herring, during the 21 days of the breeding season. The study thus helps to clarify final causes and consequences of seasonal phenological changes in species’ life-history traits and the effects on other species.

**Keywords:** Common guillemot (*Uria aalge*), Sprat (*Sprattus sprattus*), Herring (*Clupea herengus*), Match-mismatch hypothesis, the Baltic Sea.

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<td>Chick weight that they have the day leaving their breeding sites.</td>
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1 Introduction

The ecological dynamics, with trophic interactions between species across the food web is a platform that builds up an ecosystem’s fundamental structure and function. The timing for related processes, such as reproduction, are regulated by adaptation within the population, other species and the environment. If those processes become disrupted by failures in species interaction, there is an increasing risk for the ecosystem to lose its capacity to maintain resilience against environmental changes, which in turn can lead to mismatches in species interactions and thereby cause ecosystem collapses and regime shifts (Durant et al. 2004).

Seabirds are long-lived top predators in the marine ecosystem and are known to respond quickly to changes in their environment. The breeding season is the most energy consuming phase for seabirds and are closely linked to the environmental condition and the quantity and quality of prey. Studies of the relationship between seabird-fish show that seabirds’ health are heavily influenced by the annual quantity and quality of their prey (Erikstad et al. 2013, Kadin et al. 2012, Kadin et al 2016). Chicks are the most vulnerable during the hatching and feeding period, as chicks depend on even more specific prey quantity and qualities. It is known that the food fed to chicks has a strong effect on their early growth pattern and survival (Barret et al. 2013, Becker and Specht 1991). Sustainable food supply delivered to chicks corresponds to increased growth, better development of vital organs and accumulating fat deposit (Sugishita et al. 2015). It is also known that higher body mass generally results in higher fledgling success and post-fledgling survival (Perrins 1973). However, many seabirds have a quite fixed breeding season, are single prey loaders and rely on one or few prey species which makes them particularly dependent on changes in their prey resource (Österblom et al. 2008, Shultz et al. 2009). Besides climate changes, a multitude of human activities such as extensive fishing release of toxic pollutions and other disturbances have a substantial effect on fish stocks which in turn has been shown to be pushing many seabird populations towards to the brink of extinction. Recent studies emphasise that an increasing number of seabird populations are suffering from both food scarcity and a lower energy content in their prey items. The capability for adaptation to new alternative prey substitutes is often difficult in many seabird populations. Moreover, there is often lack of alternatives and if alternatives are available, it is likely that the energy content and thus prey quality are changed to be lower.
Numerous studies have addressed that fish populations all over the world have also started to respond unpredictably and abruptly with alterations in their phenological attributes, e.g. shifting of timing of biological life-cycle events such as reproduction, age structured growth and development rate (Frederiksen et al. 2004, Both et al. 2009). This type of response is generally not isolated; they are connected through multiple interactions with other species at the same or at adjacent trophic levels (Both et al. 2009). For example, it has been shown that changes in seasonal timing of phytoplankton and zooplankton can be linked to changed timing of spawning within fish stocks, which also has shown crucial effects on e.g. seabird populations, where changes in breeding success, migration pattern, chick growth and survival have been observed (Durant et al. 2003, Genner et al. 2010). Sensitivity to environmental changes and adaptation capacity will likely differ among species, populations and trophic. This may result in an increased frequency of seasonal mismatches between trophic strongly interlinked predator-prey species interrelationships.

This thesis will be focusing on the common guillemot population on the island Stora Karlsö in the Baltic Sea. The population had a decrease during the 1960s and 1970s - possible due to high concentrations of human released toxins, PCB and DDT (Activity Report Baltic Seabird Project 2016). Today, the population is currently increasing again and has been stabilized during most part of the 21st century (Olsson & Hentati-Sundberg 2017). Even if the populations increasing, the common guillemots are quite sensitive to environmental changes.

There is a high human pressure on the Baltic Sea environment today, which has already undergone multiple transformative phases including a large-scale regime shift, where the system has changed from a cod dominated ecosystem to a sprat dominated ecosystem, mainly assigned to an interaction of high human fishing pressure and potentially unfavourable climate related changes which have had consequences for the whole ecosystem (Österblom et al. 2007). Common guillemots are, however strongly, constrained by their food preferences and foraging capacity as they are heavily relying on clupeids (sprat and herring) as prey. This strong dependency becomes especially important during the breeding season where not only quantity of the right prey but also quality delivered to the chick is relevant to cover the chick’s food requirements. Thus, high quality prey resources can potentially compensate low abundances, adult birds need to increase their energy demanding foraging trips leaving less available to the chicks. However, this might not always be possible, so the chick depends on the parental capacity to maximise foraging (Kadin et al.2016). Moreover, especially during chick-rearing phase common guillemot chicks also depend on certain prey size. Common guillemots are
single prey loaders which means that they can only catch one fish at a time. The only way to increase the amount of food brought to the chick is by increasing the number of foraging trips which is time consuming and not always possible. Further, common guillemots only hatch once per year and cannot produce more than one single egg per hatching. This implies that common guillemots depend on the survival of that one chick to successfully reproduce.

Many studies of seabirds have reported dramatic changes such as breeding failure and decreased chick weight due to alteration of their foraging species (Durant et al. 2005, Durant et al. 2003, Kadin et al. 2012). This thesis will investigate how seasonal changes in sprat and herring maturity, and thus their quality as prey, may influence common guillemot chick fledgling weight on Stora Karlsö, in the Baltic Sea.
2 Objectives

This thesis will investigate and expand the match mismatch hypothesis by focusing on common guillemot chicks fledgling weight on Stora Karlsö and the maturity (fitness) of their major prey sprat and herring in the Baltic Sea. The aim is to investigate if sprat and herring maturity stage, during guillemot chicks fledgling period, affect common guillemot chick mean weight. Understanding chick weight variability is a vital biological parameter, essential for survival and in turn successful reproduction.

Four research questions were formulated and are presented below with its related hypothesis (Figure 1).

Figure 1 Four hypotheses which guides this thesis.
2.1 Research Questions 1

Is there is an interannual difference in common guillemot chicks fledgling weight on Stora Karlsö between 2002-2017?

2.1.1 Hypothesis 1

Seabirds are highly sensitive to alterations in their environment especially chicks that tend to respond quickly towards changes. Changes in a seabird population are likely a result of alterations in their prey species population (Cairns 1987). Common guillemot chicks on Stora Karlsö have shown decreased body mass and fledgling weight in the past (Österblom et al. 2001, Kadin et al. 2016). This thesis hypothesises therefore that a decrease in chick fledgling weight between 2002-2017 has occurred.

2.2 Research Question 2

Is there an inter-annual difference between 2002-2017 in chick fledgling weight depending on when chicks leave their breeding site during the season?

2.2.1 Hypothesis 2

Spawning and maturation pattern in clupeids have been shown to fluctuate and be linked to the availability of zooplankton. The peak of available zooplankton for clupeids is driven by the annual phytoplankton bloom which in turn is influenced by temperatures where warmer temperatures correspond to earlier availability of phytoplankton and thereby earlier occurrence of zooplankton for clupeids. This may be linked to earlier maturation and spawning (Karasiova 2013, Ohlberger et al. 2014), that might constrain the food availability for common guillemots, where chicks that leave their breeding ledge at the end of the fledgling season have less available food and clupeids have lower maturity (lower fitness). This thesis hypothesises that common guillemot chicks that leave their breeding ledge during the end of the fledgling period (day 5-8) have a lower mean weight than chicks that leave their breeding ledge early (day 1-4) during the fledgling period.
2.3 Research Question 3

Is there a variability in sprat (between 2011-2015) and herring (2007-2014) inter- and intra-annual peak day of highest abundance of potential spawners in the Baltic Sea?

2.3.1 Hypothesis 3

This question is focusing on the whole Baltic Sea, an overview of the environment that common guillemots are facing when they not are breeding on Stora Karlsö. Moreover, as mentioned above, clupeids spawning patterns are linked to the availability of zooplankton which are linked to phytoplankton bloom that are highly influenced by temperature (Karasiova 2013). During the last decades fluctuations in the water temperature in the Baltic Sea have occurred, which influence the annual phytoplankton bloom. This may cause an earlier and more dynamical variation in the timing of spawning (Carscadden et al. 1997, Davoren & Montevecchi 2003, Kristiansen et al. 2011). This thesis hypothesizes that common guillemot chicks that leave their breeding ledge during the end of the fledgling period (day 5-8 mid-July) have a lower mean weight than chicks that leaves their breeding ledge early (day 1-4, the end of June) during the fledgling period.

2.4 Research Question 4

Is there a mismatch between common guillemot chick fledgling weight on Stora Karlsö and the fitness of sprat and herring in their foraging area between 2009-2015?

2.4.1 Hypothesis 4

Seasonal mismatches between seabirds and their prey have been shown in various ecosystems and have had devastating effects for those seabird populations where breeding failure and decreasing chick survival has been observed (Durant et al. 2005, Kadin et al. 2012). This thesis hypothesizes that common guillemot chick mean weight during the fledgling period are influenced by sprat and herring’s maturity.
3 Theoretical framework

This thesis will be guided by two key theories; the life-history theory and the match-mismatch theory. The life-history theory will address annually recurring life cycle events and the importance to collect knowledge about species phenological characteristics. The match-mismatch theory will be used in this thesis to explain why the timing of annual lifecycle events and their synchronization in marine ecosystems are important.

3.1 The life-history theory

Phenology refers to studies of annually recurring life-history events and has been used for centuries to determine timing of seasonal stages of development reached by an organism or a population (Edwards & Richardson 2004). Species have historically developed unique cues to match timing-related events in their environment by interacting with other organisms (through e.g. competition for food sources, migration and prey-predator interactions) and with their abiotic environment, e.g. temperature, photoperiod or food availability (Forrest and Miller-Rushing 2010). However, many marine areas are currently changing rapidly. During the last decades, moreover, the effects of climate change have started to become increasingly apparent and have been showed to directly affect the distribution, abundance and population dynamics of many marine organisms (IPCC, 2001). Numerous studies have documented that various organisms have started to respond in more dynamic and thus unpredictable ways of certain phenological shifts, e.g. timing-related reproductive events, changes in age structured growth, and general reproductive success (Iwasa & Levin 1995, Ohlberg et al. 2014). It has been observed that the phenological response to climate changes can differ within a population and between populations of the same species, depending on their local environment (Walther 2010).
Moreover, species can respond with phenological shifts either directly or indirectly. Directly by e.g. changed timing of seasonal events, due to abiotic changes which indirectly affect other species’ seasonal activities (e.g. timing of reproduction, migration etc). Indirect effects are suggested to have an overall stronger impact by affecting trophic interaction in general and can therefore result in more severe consequences, including massive biodiversity loss (Parmesan 2006, Rafferty et al. 2013). The different rates and ways of phenological response have been suggested to be explained by constraints on the phenological plasticity of species within ecosystems (Both et al. 2009).

There is a growing interest in research concerning how phenological shifts in one single species will influence interactive processes among species in the food web. Research of this type require knowledge of (1) the optimal window with favourable environmental conditions for reproduction (2) to what extent climate change or other external factors affect this window, (3) species’ adaptation abilities, and (4) effects on interactive processes between trophic levels. For many species the optimal window for reproduction and growth are mainly determined by food availability.

Young & Rudolf (2010) developed a mechanistic framework, *the phenology-ontogeny landscape*; an approach to examine ecosystem consequences of phenological shifts in species. Numerous studies usually have focused on a single species, while the framework of Yang & Rudolf (2010) emphasises the importance of investigating multiple factors that may cause phenological mismatches and interaction failure between species and their environment with consequences for the entire ecosystem. However, a key limitation with this approach, that the authors mention, is the absence of long-term data that include coordinated, repeated observations of various species across multiple trophic levels during the same spatial and temporal scales. Long-term time series are often needed to observe phenological changes. There is also a disconnection between studies that address phenological alterations which makes it difficult to detect general changes in the timing of e.g. reproduction. Robust indicators of early phenological changes are critical in order to understand the magnitude of ecosystem response and to maintain the resilience in marine ecosystems.
3.2 The match-mismatch theory

*It should not surprise us that fish stocks respond to climatic factors and to climatic change because they live their lives within the weight of the waters.*


The citation by Cushing (1982) refers to the match-mismatch theory (MMH) which is widely studied in the academic fields of biology and ecology. The original idea was invented by Hjort (1914) who suggested that the timing of phytoplankton blooms might have a significant effect on the survival of larval fishes. Cushing (1975) explained this idea in the field of fish biology and coined the match-mismatch hypothesis. He suggested that most fish species in temperate waters spawn at a fixed time annually, while zooplankton, which is the prey of larval fish, are controlled by the spring bloom and direct water temperatures. Annual variation in recruitment success of a fish population is therefore a function of a spatial and temporal match or mismatch of timing of spawning/hatching and the overlap of food availability during early larval stage. A mismatch between the requirement of food and food availability is linked to recruitment variability and year-class strength in fish populations (Hjort 1914, Cushing 1969, Cushing 1990, Durant et al. 2003).

During the last decades, the theory has been expanded and applied to various organisms and ecosystems (Nakazawa and Doi 2012). The theory has for instance been applied to different seabird populations and their prey (Regular et al. 2014, Buren et al. 2012). Seabirds hold a position as top predators of many marine ecosystems and have been used as a valuable indicator of changes in marine ecosystems since they usually return to the same spot for breeding and are thus relatively easy to monitor. They often rely on one or only a few prey species and change in their food resources would therefore likely affect their health directly, either through phenological and/or behavioural changes which can provide information of changes in its prey resources (Rindorf et al. 2000, Lewis et al. 2001, Durant et al. 2003, Durant et al. 2006).

Environmental changes can desynchronise interactive processes between species which can result in temporal mismatches (Figure 2) (Both et al 2006, Nakazawa & Doi 2012). Research states that changes in phytoplankton and zooplankton production may cause a variability in timing of spawning in many fish stocks, usually with a spawning peak earlier during warm periods (Carscadden et al. 1997, Davoren & Montevecchi 2003, Kristiansen et al. 2011). Studies of seabirds indicate that they have difficulties to adjust their biological breeding rhythm, to a
substantial degree, to temperature changes in the ocean. This may result in lack of synchrony with their prey and will likely affect the survival of many threatened populations and negatively affect populations that today are counted as "healthy" (Koegan et al. 2018). A study by Davoren & Montevecchi (2003) addresses common guillemot (*Uria aalge*) ability to indicate early biological signals in the capelin (*Mallotus villosus*) stock on the north-east coast of Newfoundland during the 1990’s. The study showed that common guillemots delayed breeding occurred when the percentage of mature capelin, which has the highest energy content, declined. The study proposes a potential mismatch between common guillemots and capelin since they were unable to match the temporal window when capelin was abundant and spawn. The mismatch between common guillemots and capelin is also suggested to be caused by the shift in the capelin stock from high size diversity to smaller size which results in less energy. Figure 2 gives an example that visualises the match-mismatch hypothesis in relation to this thesis.

Figure 2 Food interaction between a predator (common guillemot; black line) and their prey (sprat and herring; red and blue). A high match is represented by a temporal overlap of common guillemots and sprat and herring, (the red area). An increase in the time-lag between common guillemot’s food requirement and the availability of sprat and herring leads to a low match illustrated with the time lag between common guillemots and sprat and herring (the blue area). Adapted from Cushing (1990).
4 Methodology

4.1 Study locations

There are two study locations that have been investigated in this study; The Baltic Sea and Stora Karlsö.

Figure 3 Map of the Baltic Sea (subdivisions 23-32) and the location of Stora Karlsö in subdivision 27, where Skagerrak (subdivision 20) and Kattegatt (subdivision 21) are included.
4.1.1 The Baltic Sea

The Baltic Sea, (Figure 3) is geographically located in Northern Europe (between 54° and 66° N and 10° 30° - 31° E) and is a relatively small, shallow and semi-enclosed brackish water area (422,000 km² with an average depth of 55 m). The Baltic Sea is a young water basin which historically has undergone a wide variation in its environmental conditions. The current state with brackish water was established when the last glaciation retreated from Northern Europe; approximately 10,000 years ago (Ojaveer et al. 2010, Suikkanen et al. 2007). The only passage to the North Sea where exchanges of saline water occur is through the narrow sounds between Sweden and Denmark. Freshwater comes continuously through rivers and streams to the Baltic Sea. The Baltic Sea is characterised by a pronounced latitudinal gradient in salinity and temperature. The salinity gradient also changes horizontally, ranging from 15-25 ‰ in Kattegatt subdivision 21 to 7-8 ‰ in the central Baltic Sea to about 1-4 ‰ in the northern Gulf of Bothnia and the Gulf of Finland. Additionally, the Baltic Sea has low biodiversity with few species at each trophic level, connected through strong trophic interactions. Species in the Baltic Sea are constrained both by the environmental conditions and the accelerating human activities which impose a constant stress (Österblom et al. 2007, Tomczak et al. 2012, Niiranen et al. 2013).

4.1.2 Stora Karlsö

Stora Karlsö (Figure 3) is an island located in the Baltic Sea (57°17’N, 17°58’). The island provides the most important breeding habitat for common guillemots in the Baltic Sea area. Common guillemots have been monitored at Stora Karlsö for a long time and since 1997, the Baltic Seabird Project has the main responsibility for the monitoring program (Activity Report Baltic Seabird Project 2016). Ringing, weighing and extracting blood samples from the chicks takes place annually during the peak fledgling time when the chicks leave their breeding ledge. This normally occurs around the last week of June and the first week of July. On Stora Karlsö chicks can, relatively easy, be caught on the beach since they land there after leaving their nests on their way towards the sea. A major purpose of the Baltic Seabird Project is to gain an increased understanding of the common guillemot population on Stora Karlsö by studying e.g. population trends, breeding success and foraging behaviour. The common guillemots are also used as indicators e.g. changes in fish stocks.
4.2 Study species

4.2.1 Common guillemot

Common guillemot is a long-living, circumpolar, boreal and low Arctic auk (Barrett & Erikstad 2013, Barrett et al. 2015). The island Stora Karlsö (57°17’ N, 17°58’ E) holds the largest colony in the Baltic Sea where up to 90 % (~ 20,000 breeding pairs) of the Baltic Sea population hedges (Olsson & Hentati-Sundberg 2017). Common guillemots have low fecundity and lay one single egg per season in the beginning of May and both parents incubate the egg for approximately 32 days (Österblom et al. 2001, Österblom et al. 2006). The chick leaves its nesting site at the age of 15-21 days. The fledgling procedure occurs during the last week of June and the first week of July. Chicks are not able to fly but can jump from their breeding ledges and land on the beach or in the water where the male parent is waiting for the chick, to together swim out to sea (Österblom et al. 2001). The fledgling procedure is described in detail by Greenwood (1964) and is similar to the procedure on Stora Karlsö.

Moreover, the breeding season is the most energy demanding phase in common guillemot’s annual cycle and foraging is time-consuming and parents are limited in the number of trips they can make each day without compromising their own health. Sprat and herring are known as major food resources for common guillemots but literature describing detailed information regarding diet preferences for common guillemot is scarce. Some studies have however been conducted, both by Madsen (Madsen 1957) and Hedgren (Hedgren 1976) that investigated adult common guillemots in the Southern Baltic Sea and found that small herring (6 cm) were the major pray, while recent studies from Stora Karlsö found sprat being the major prey for adult common guillemot’s (sprat 91.5 %, herring 5.1 % and sand lance 3.2 %). Furthermore, the first study of food preference for common guillemots on Stora Karlsö was done by Berglund (Berglund 2016), the study investigated common guillemot chicks stomach content during 2005-2014. The results indicated that clupeids represented the main diet and the stomach analysis showed sprat as main prey (29 individuals, 71 %) and herring (12 individuals, 29 %).
However, previous studies have showed that both sprat and herring have decreased in condition from the 1990’s (Casini et al. 2006, Bignert et al. 2009). Österblom et al. (2001) and Österblom et al. (2006) observed that there was a decrease in common guillemot chick body mass between 1989-2000 that could be linked to weight-at-age in sprat. Additionally, in a study by Kadin et al. (2012), a correlation was found between common guillemot chick fledgling success on Stora Karlsö and weight-at-age in sprat and herring. This indicates that availability, size and energy content of food is important in the narrow window of chick-rearing period.

4.2.2 Sprat and herring

The mid-trophic pelagic fish sprat and herring carry a central position in the Baltic Sea food web where they manifest a link between both zooplankton and top predators (Figure 4), as well as to the fishery industry where they are economically valuable species. Moreover, sprat and herring build up energy reserves over the year as a preparation for the spawning season. Sprat and young herring feed on zooplankton and mainly pelagic copepods Temora longicornis, Bosmina maritima and Pseudocalanus elongatus, while larger herring feeds on nektobenthos Mysis mixta, amphipods and polychaetes (Casini et al. 2004). During the last three decades, Baltic sprat and herring have expressed fluctuations in their condition (weight-at-age and length-specific weight) (Möllmann et al. 2004a, Möllmann et al. 2004b). Changes in condition will likely have implications on phenological attributes, e.g. fecundity/maturity, migration, reproductive success and survival, which in turn will affect other species that depend on sprat and herring, e.g. larger predatory fish, mammals and seabirds (Casini et al. 2011). Further, changes in sprat and herring condition are suggested to be related to e.g. variations in the zooplankton community, size-selective fishery and/or the dramatic increase of sprat during 1990s when predation of cod decreased due to the cod collapse, which increased the intra- and inter specific competition between sprat and herring (Cardinale & Arrhenius 2000, Cardinale et al. 2002, Möllmann et al. 2004b, Ojaveer et al. 2010).
4.2.3 Maturation and spawning biology

Both sprat and herring spawning patterns are influenced by environmental conditions, i.e. availability of food and spring water temperature (Karasiova 2002). The environmental condition during the spawning period is important for reproductive success and an unfavourably environment can be linked to variability in the reproductive output, e.g. batch fecundity, spawning fraction and frequency and egg quality (Alheit 1993, Tripple et al. 1997). Herring and sprat have some differences in their maturation and spawning biology.

Sprat start to spawn at 2-3 years of age and are multiple batch-spawners which means they spawn several times during one season with up to 2,000-5,000 egg releases periodically over long intervals. Spawning takes place in coastal and offshore areas in the upper part of the halocline at a depth around 10-40 m. Thereafter the eggs are powered by sea currents and hatch 3-7 days later. The Gdansk deep, Bornholm and the Gotland basin are three major spawning areas in the Baltic Sea. The spawning season spanning from March to August with a main peak during May-June. Sprat are divided into two groups, spring- and autumn-spawners, where spring-spawners are most common in the Baltic Sea (ICES 2011).
Baltic herring reach sexual maturity about the age of 2-3 years and are a determinate spawner with spawning concentrated for 1-2 days per season at a depth between 0.5-100 m. Most herring are spring-spawners in the Baltic Sea, segregated into local spawning stocks. Autumn-spawners dominated until the 1950s but are rare today (ICES 2011). The spawning season usually starts in early April and continues uninterrupted for about 2-3 months (Rajasilta et al. 1993). Herring spawn in water temperatures between 8-12 °C, close to coastal areas with rich vegetation. This makes herring vulnerable to human activities, e.g. offshore oil and gas industries, gravel extraction and the increasing eutrophication causing less oxygen. Eggs sink to the bottom and form large aggregates.
5 Data

The data for detailed comparisons of seabird and fish distributions are lacking between 2002-2008 and 2016-2017, which is why this study uses different year intervals in the analysis.

5.1 Data collection of common guillemots

Data of common guillemots has been provided by the Swedish Baltic Sea Bird Project (BSP). BSP has collected data of common guillemots annually since 1997 on Stora Karlsö during their breeding season. Chicks have been ringed annually during their fledgling period (with an individual code ring), weighed and sampled for DNA (Figure 5). This study uses data from 2002 to 2017 (total 40,936 chicks) and includes fledgling weight and time-related variables (day, month, year).

![Figure 5 Procedure of collecting annual data of common guillemot chicks on Stora Karlsö.](image)

5.2 Data collection of sprat and herring

Data of sprat and herring has been provided by the Institute of Marine Research which is a part of the Swedish University of Agricultural Science (SLU). Samples of individuals were taken from acoustic surveys and the PLANFISH project (Appleberg et al. 2013) at SLU and from the commercial- and industrial fisheries to SLU’s fish database over the Baltic Sea. Variables selected for this analysis are time-related variables (year, month, day), ICES statistical rectangles called subdivisions (divided areas over the Baltic Sea aimed for specific regional
statistical analyses). Individual maturity stages data were used, where microscope observations determined the gonads’ size, consistency colour and shape. (DTU Aqua report 197-2008 Manual to determine gonadal maturity of herring (*Clupea harengus* L)). Some research questions required filtering of the data by maturity and year. The maturity classifications are described in Table 1, Table 2 and Table 3.

Table 1 The nine-grade scale of maturity stage for sprat and herring in the Baltic Sea, used by the Swedish University of Agricultural Science (SLU) to macroscopically assess which maturity stage individuals are in by investigating gonads’, size, consistency, colour and shape (DTU Aqua report 197-2008 Manual to determine gonadal maturity of herring (*Clupea harengus* L)).

<table>
<thead>
<tr>
<th>Stages</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Immature / juvenile</td>
<td>Testes are small and glassy transparent</td>
<td>Gonad are yellow-red translucent, small and threadlike.</td>
</tr>
<tr>
<td>2. Early maturation</td>
<td>Testes takes up 1/2 of the body length. Are bigger than 1-3 cm, have varying colour.</td>
<td>Ovaries are grey-read non-transparent, no visible oocytes.</td>
</tr>
<tr>
<td>3. Early maturation</td>
<td>Testes with swelling grey lobules, takes up 2/3 and the entire length of the body.</td>
<td>Ovaries are grey-red, visible oocytes.</td>
</tr>
<tr>
<td>4. Final maturation</td>
<td>Lobules fully grown but not purely white.</td>
<td>Ovaries fully grown and are transparent, oocytes are absent</td>
</tr>
<tr>
<td>5. Spawning prepared</td>
<td>Lobules fully grown and mostly white</td>
<td>Ovaries fully grown with few large transparent oocytes.</td>
</tr>
<tr>
<td>6. Spawning</td>
<td>Lobules are white and milky, semen flows after light pressure.</td>
<td>More than half if the oocytes are transparent and flows after light pressure.</td>
</tr>
<tr>
<td>7. Spent</td>
<td>Lobules are flabby some rest of milky, semen.</td>
<td>Ovaries are shrunk and often visible blood stains, some oocytes can be present.</td>
</tr>
<tr>
<td>8. Resting</td>
<td>Resting, Lobules are contracted and empty.</td>
<td>Ovaries are contracted and empty.</td>
</tr>
<tr>
<td>9. Abnormal</td>
<td>For example, diseases, birth defect, impaired maturation development, two-sexed individuals, poor sperm and egg quality. Abnormal individuals can also be caused by environmental condition</td>
<td></td>
</tr>
</tbody>
</table>
**Figure 6** Illustration of the maturity cycle for sprat and herring in the Baltic Sea according to the Swedish University of Agricultural Science (SLU) (DTU Aqua report 197-2008 Manual to determine gonadal maturity of herring (*Clupea harengus L*). Description of the different stages, Table 1. (1) Immature / juvenile, (2) Early maturation, (3) Early maturation, (4) Final maturation, (5) Spawning prepared, (6) Spawning, (7) Spent, (8) Resting.

**Table 2** Variables used to determine the predicted peak day of the highest abundance of potential spawners in the Baltic Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Data variables</th>
<th>Data range</th>
<th>Number of individuals</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprat</td>
<td>Maturity stage 1-8</td>
<td>2011-2015</td>
<td>45,370</td>
<td>The Baltic Sea</td>
</tr>
<tr>
<td>Herring</td>
<td>Maturity stage 1-8</td>
<td>2007-2014</td>
<td>227,596</td>
<td>The Baltic Sea</td>
</tr>
</tbody>
</table>

**Table 3** Variables used to determine the fitness of sprat and herring in common guillemots foraging area subdivision 27 in the Baltic Sea.

<table>
<thead>
<tr>
<th>Species</th>
<th>Data variables</th>
<th>Data range</th>
<th>Number of individuals</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sprat</td>
<td>Maturity stage 1-6</td>
<td>2009-2015</td>
<td>16450</td>
<td>Subdivision 27</td>
</tr>
<tr>
<td>Herring</td>
<td>Maturity stage 1-6</td>
<td>2009-2015</td>
<td>26101</td>
<td>Subdivision 27</td>
</tr>
</tbody>
</table>
5.3 Software

Data analysis and statistics were performed using R Ver. 3.4.4 (The R Core Team 2018) and Microsoft Excel version 15.39 (Excel 2017).
6 Analysis

The first part describes the data analysis for common guillemot chick fledgling weight on Stora Karlsö, while the second part describes the data analysis for sprat and herring predicted peak day of the highest abundance of potential spawners in the whole Baltic Sea. The third part describes the data analysis for the match-mismatch hypothesis - how sprat and herring maturity (fitness) in the guillemots foraging area during the breeding season (Stora Karlsö vicinity subdivision 27 of the Baltic Sea) influences common guillemot chick mean weight during the fledgling period.

6.1 Estimation of common guillemot chicks fledgling weight on Stora Karlsö.

For estimating mean annual fledgling weight for each year and day the weight of the steel ring (3 gram) was subtracted from all reported chicks’ weights. Individuals with fledgling weights > 600 grams were excluded from the analysis as unrealistic high and considered as misreporting in the protocol. In order to identify and explore whether there was a difference in fledgling weight depending on which day the chicks left their breeding ledge during the fledgling period, chicks that jumped during the first part of the season (day 1-4) were classified as early and chicks that jumped during (day 5-8) as late. The difference between early and late chick mean fledgling weight was then calculated for each year. Julian day start at date 2002-01-01 for the overall analysis for guillemots.

6.1.1 Statistical analysis of common guillemot chick mean fledgling weight

An ANOVA (Analysis of Variance) analysis for the general analysis followed by a post-hoc-tukey HSD test was performed in order to test for differences in mean values between all pairwise consecutive years between 2009-2017.
6.2 Estimation of predicted peak day of highest abundance of potential spawners

To assess sprat and herring peak day of the highest abundance of potential spawners in the Baltic Sea, the maturity scale was used in the following way; sprat and herring maturity stages were bundled into classes of either inactive spawning (0 %) or active spawning (100 %). The classification was based on when it is most likely that an individual is pre-spawning or spawning. Individuals in maturity stages 1-3 were defined as ‘inactive spawners’, either because they were immature or only in the start of their maturity process. Individuals in maturity stages 4-7 were defined as ‘active spawners’ since they are about to spawn, are spawning or have recently spawned. Individuals in maturity stage 8 where defined as ‘inactive spawners’ since they have finished their spawn and are resting. The start of julian date for sprat was set to 2010-01-01 and for herring to 2007-10-01. The start date for herring was set to October in order to capture potential autumn spawners. The mean maturity was then calculated for each year and julian day. There were some gaps in the data, due to absence of trawling, so it was not possible to use the same data range for sprat and herring. The analysis of sprat covers the years 2001-2015 and the years 2007-2014 for herring.

6.2.1 Statistical analysis of predicted peak day of highest abundance of potential spawners

A Generalized Additive Model (GAM) was applied to model the predicted annual peak day for the highest abundance of potential spawners as well as visualize the spawning cycle. For detailed information about GAM see Hastie and Tibshirani (1986,1990).

6.2.2 Estimation of fish maturity (fitness)

The analysis investigated sprat and herring maturity as an indicator for fitness in ICES subdivision 27 (the foraging area for common guillemots during the breeding season). To assess sprat and herring fitness, individual maturity stages 1-6 were used. Data for the years 2009-2015 were used, since this was the time period when data was available for both fish and chicks in the data sets. Julian day starts 2009-01-01 for both sprat and herring. The annual mean maturity was calculated for each julian day.
6.3 Statistical test of the match-mismatch hypothesis

To identify long-term pattern for sprat and herring maturity stages (fitness) and common guillemot daily mean fledgling weight, time series were used where the annual maturity occurrence of herring and sprat for each trawl day and fledgling weights for observation days were used, as well as time series of the mean and SD for the annual maturity and annual mean fledgling weight of chicks between 2009-2015. Moreover, approximate time from chicks hatching to fledgling is 21 days. In order to examine how sprat and herring maturity (fitness) in subdivision 27 affect chicks’ decrease in mean fledgling weight, each day over a 21-day period was analysed for each year. To investigate possible direct correlation of annual mean chick fledgling weight and sprat and herring’s maturity (fitness) an ANOVA (Analysis of Variance) analysis and a post-hoc-tukey HSD test were conducted. For estimating match-mismatches of chick weights and the appearance of mean maturity stages of sprat and herring, a time lag cross-correlation test was conducted to gain information regarding the variability of a given value over time. To estimate the mean maturity for sprat and herring, a weighted mean for maturity per day for each season was calculated which was then compared to annual mean weight per season, separated into early and late nest leavers. In this case maturity (fitness) over time (2009-2015) in relation to chick mean weight during the fledgling period (2009-2015).
7 Results

The results section is divided into three parts, the first presents results from the analysis of common guillemot chicks fledgling weight (7.1) and the second presents results from the analysis of sprat and herrings spawning cycle with the predicted peak day (7.2). The third section presents result from the match mismatch hypothesis (7.3).

7.1 Common guillemot chick fledgling weight

Throughout the period studied, 2002-2017, 40,936 fledglings were captured, weighted and ringed. The analysis of common guillemot chick mean weight on Stora Karlsö during their fledgling period shows an annual decrease between 2002-2017. The lowest mean weight was 224.92 grams (in year 2016) and the highest mean weight recorded in chicks was 247.45 grams (in year 2002) and 244.57 grams (2017), Table 4 and Figure 7.

![Figure 7 Annual mean weight loss for common guillemot chicks during the fledgling period between year 2002-2017.](image.png)
Table 4 Common guillemot chicks’ annual mean weight and the differences between chicks that leave their breeding ledges early respective late during the fledgling period on Stora Karlsö between year 2002-2017.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean Weight (g)</th>
<th>Early mean weight (g)</th>
<th>Late mean weight (g)</th>
<th>Abs. Weight diff late/early (g)</th>
<th>Relative Weight diff late/early (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>247.45</td>
<td>245.63</td>
<td>249.06</td>
<td>3.4</td>
<td>1.4%</td>
</tr>
<tr>
<td>2003</td>
<td>233.80</td>
<td>234.24</td>
<td>233.40</td>
<td>-0.8</td>
<td>-0.4%</td>
</tr>
<tr>
<td>2004</td>
<td>244.53</td>
<td>246.77</td>
<td>242.39</td>
<td>-4.4</td>
<td>-1.8%</td>
</tr>
<tr>
<td>2005</td>
<td>245.64</td>
<td>247.35</td>
<td>245.40</td>
<td>-2.0</td>
<td>-0.8%</td>
</tr>
<tr>
<td>2006</td>
<td>234.10</td>
<td>238.07</td>
<td>232.88</td>
<td>-5.2</td>
<td>-2.2%</td>
</tr>
<tr>
<td>2007</td>
<td>239.19</td>
<td>243.11</td>
<td>238.60</td>
<td>-4.5</td>
<td>-1.9%</td>
</tr>
<tr>
<td>2008</td>
<td>242.60</td>
<td>251.29</td>
<td>240.21</td>
<td>-11.1</td>
<td>-4.4%</td>
</tr>
<tr>
<td>2009</td>
<td>235.34</td>
<td>238.28</td>
<td>233.98</td>
<td>-4.3</td>
<td>-1.8%</td>
</tr>
<tr>
<td>2010</td>
<td>232.74</td>
<td>237.75</td>
<td>231.80</td>
<td>-6.0</td>
<td>-2.5%</td>
</tr>
<tr>
<td>2011</td>
<td>228.26</td>
<td>236.31</td>
<td>226.74</td>
<td>-9.6</td>
<td>-4.1%</td>
</tr>
<tr>
<td>2012</td>
<td>234.60</td>
<td>241.37</td>
<td>234.38</td>
<td>-7.0</td>
<td>-2.9%</td>
</tr>
<tr>
<td>2013</td>
<td>227.17</td>
<td>229.14</td>
<td>227.00</td>
<td>-2.1</td>
<td>-0.9%</td>
</tr>
<tr>
<td>2014</td>
<td>238.28</td>
<td>241.46</td>
<td>237.39</td>
<td>-4.1</td>
<td>-1.7%</td>
</tr>
<tr>
<td>2015</td>
<td>227.06</td>
<td>233.86</td>
<td>227.02</td>
<td>-6.8</td>
<td>-2.9%</td>
</tr>
<tr>
<td>2016</td>
<td>224.92</td>
<td>231.11</td>
<td>222.64</td>
<td>-8.5</td>
<td>-3.7%</td>
</tr>
<tr>
<td>2017</td>
<td>244.57</td>
<td>241.86</td>
<td>244.78</td>
<td>2.9</td>
<td>1.2%</td>
</tr>
</tbody>
</table>

The study also confirmed Hypothesis 2, the results show that there is a clear trend of a decreasing mean weight that depends on which day the chicks leave their breeding ledges. Early chicks that leaves their ledges during the first 4 days of the fledgling period showed a higher mean weight than late chicks that leaves their ledge between day 5-8. The biggest gap between early and late chicks was 2008 when early chicks had a mean weight of 251.29 grams and late chicks 240.21 grams, a percentage weight difference of 4.4%. 2002 and 2017 were the only years when late chicks had a higher mean weight than general (Figure 8 and Table 4).
Figure 8 Early and late chick mean fledgling weight. Time series with annual mean weight (g) between year 2002-2017 during the fledgling period at the end of June and the beginning of July. Early (day 1-4) chicks; blue line and late (day 5-8) chicks red line.

Moreover, Figure 9 visualizes the daily mean weight recordings for chicks during their fledgling period for year. All years except 2017 have a clear pattern of a decrease in weight in relation to days. Chicks that leave their breeding ledge during the end of the season have a lower fledgling weight.
Figure 9 Trend of annual mean fledgling weight (g)/Julian day of common guillemot chicks on Stora Karlsö between year 2002-2017.

The ANOVA and subsequent post-hoc analysis (Table 5 and Table 6) showed a significance in mean weight loss between all consecutive years 2009-2017. Hence there is a significant relationship between chick decrease in mean weight over time between all consecutive years 2009-2017.

Table 5 Output from the ANOVA for the inter-annual differences in common guillemot chicks mean weight between 2009-2017.

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Sum sq</th>
<th>F value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Factor Year</td>
<td>8</td>
<td>935621</td>
<td>183.3</td>
<td>&lt;2e-16</td>
</tr>
<tr>
<td>Residuals</td>
<td>29377</td>
<td>18738722</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

***: p = 0


Table 6 Output of the pairwise post-hoc test analysis, shows the multiple inter-annual comparison of significant chick mean weight comparisons of consecutive years 2009-2017 at p<0.05 significance level.

<table>
<thead>
<tr>
<th>Year</th>
<th>P adj</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009-2010</td>
<td>0.0021725</td>
</tr>
<tr>
<td>2011-2010</td>
<td>0.0000000</td>
</tr>
<tr>
<td>2012-2011</td>
<td>0.0000000</td>
</tr>
<tr>
<td>2013-2012</td>
<td>0.0000000</td>
</tr>
<tr>
<td>2014-2013</td>
<td>0.0000000</td>
</tr>
<tr>
<td>2015-2014</td>
<td>0.0000000</td>
</tr>
<tr>
<td>2016-2015</td>
<td>0.0014107</td>
</tr>
<tr>
<td>2017-2016</td>
<td>0.0000000</td>
</tr>
</tbody>
</table>

7.2 Sprat and herring

The result from the GAM analysis of sprat and herring predicted peak day of highest abundance of potential spawners.

7.2.1 Herring

Herring predicted spawning peak day shows a wide inter-annual variation among the peak day, spanning from day 176 (in year 2011) to day 236 (in year 2012). The predicted peak day of highest abundance of potential spawners for herring occurred between March-May, Table 7. The spawning cycle for herring was plotted using GAM predictions in Figure 10 shows a clear peak of predicted spawners. After the peak, spawning decreases markedly.
**Figure 10** Intra- and interannual time series of the predicted peak day during the year (julian day starting at date 2007-10-01) of the highest abundance of potential spawners for herring between 2007-2014 derived from GAMS fitting. The dashed line represents the peak day of the highest abundance of spawners.

**Table 7** Intra- and interannual predicted peak day (julian day with starting date 2011-01-01) for herring of the highest abundance of potential spawners year 2007-2014, derived from GAMS (levels 4-7) (see also dashed line in Figure 5).

<table>
<thead>
<tr>
<th>Year</th>
<th>Peak julian day of spawning</th>
<th>Month</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>229</td>
<td>May</td>
</tr>
<tr>
<td>2008</td>
<td>210</td>
<td>May</td>
</tr>
<tr>
<td>2009</td>
<td>193</td>
<td>April</td>
</tr>
<tr>
<td>2010</td>
<td>196</td>
<td>April</td>
</tr>
<tr>
<td>2011</td>
<td>176</td>
<td>March</td>
</tr>
<tr>
<td>2012</td>
<td>236</td>
<td>May</td>
</tr>
<tr>
<td>2013</td>
<td>200</td>
<td>April</td>
</tr>
<tr>
<td>2014</td>
<td>218</td>
<td>May</td>
</tr>
</tbody>
</table>
7.2.2  *Sprat*

Sprat spawning cycle and the predicted peak day shows less variation, interannual differences between the spawning time were overall small, spanning from day 130 (in year 2014) to day 151 (in year 2015). The predicted peak day of the highest abundance of potential spawners for sprat occurred in May, except in year 2015 when the predicted peak day occurred in June day 151 (Table 8). The visualization of the spawning cycle for sprat and the highest abundance of spawners, which was plotted using GAM, shows a similar result as for herring with a clear peak of predicted spawners (Figure 9). After the peak, spawning markedly decreases. In 2014, the cycle is flatter due to data limitations of trawl samples, however the peak is still visible (Figure 11).

![Figure 11](image)

*Figure 11* Intra- and interannual time series of the predicted peak day during the year (julian day starting date 2007-01-01) of the highest abundance of potential spawners for sprat between 2007-2014 derived from GAMS fitting. The dashed line represents the peak day of the highest abundance of spawners.
Table 8 Intra- and interannual predicted peak day (julian day with starting date 2011-01-01) for sprat of the highest abundance of potential spawners year 2007-2014, derived from GAMS (levels 4-7) (see also dashed line in Figure 5).

<table>
<thead>
<tr>
<th>Year</th>
<th>Peak Julian day spawning</th>
<th>Month</th>
</tr>
</thead>
<tbody>
<tr>
<td>2011</td>
<td>149</td>
<td>May</td>
</tr>
<tr>
<td>2012</td>
<td>135</td>
<td>May</td>
</tr>
<tr>
<td>2013</td>
<td>135</td>
<td>May</td>
</tr>
<tr>
<td>2014</td>
<td>130</td>
<td>May</td>
</tr>
<tr>
<td>2015</td>
<td>151</td>
<td>June</td>
</tr>
</tbody>
</table>

7.3 Match-mismatch

The results from the match-mismatch analysis of how sprat and herring’s maturity (fitness) influence common guillemot chicks mean weight during the fledgling period.

Figure 12 Variation in frequencies of individuals in the different maturity stages for sprat and herring between 2009-2015 in subdivision 27 in the Baltic Sea.

Figure 12 shows the frequencies of individuals in the different maturity stages (1-6) between 2009-2015 in common guillemot foraging area, subdivision 27. The majority of individuals during the years were in maturity stage 2 and 3.
Moreover, Figure 13, plot A shows the mean annual maturity occurrence of herring and sprat for each day and chick mean weights for observation days between 2009-2015 during the fledgling period. The plot indicates that chick fledgling periods are relatively fixed during the time period, hence, the peak period of fledgling has not changed over time. Moreover, during the fledgling period, sprat and herring in maturity stages 1-2 are the most available. Table 9 shows the annual mean maturity, especially sprat indicates a slightly decreasing mean maturity maximum stage of 2.87 in year 2010 and a minimum maturity stage of 2.25 in year 2014 while herring exhibit more variation. The pattern clearly shows that chick mean weight during the fledgling period are higher when sprat and herring maturity stage increases and vice versa - when sprat and herring maturity stage are below maturity stage 2, the chick mean weight are lowest (Figure 13).

**Table 9** Sprat and herring annual mean maturity.

<table>
<thead>
<tr>
<th>Year</th>
<th>Herring mean maturity</th>
<th>Sprat mean maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td>2.51</td>
<td>2.38</td>
</tr>
<tr>
<td>2010</td>
<td>2.82</td>
<td>2.87</td>
</tr>
<tr>
<td>2011</td>
<td>2.54</td>
<td>2.84</td>
</tr>
<tr>
<td>2012</td>
<td>2.59</td>
<td>2.64</td>
</tr>
<tr>
<td>2013</td>
<td>2.81</td>
<td>2.38</td>
</tr>
<tr>
<td>2014</td>
<td>2.83</td>
<td>2.25</td>
</tr>
<tr>
<td>2015</td>
<td>2.40</td>
<td>2.42</td>
</tr>
</tbody>
</table>
In subfigure A, time series of the mean annual maturity occurrence of herring and sprat for each trawl day and fledgling weights (green) for observation days between years 2009-2015 are illustrated. Grey bars lines represent timespan between hatching and leaving of the nest. Subfigure B shows the time series of the mean and standard deviation for the annual maturity and annual mean fledgling weight of chicks between years 2009-2015. Variability of sprat (blue) and herrings (black) mean maturity dynamics and common guillemot chicks mean fledgling weights as points (green) with julian day starting at date 2009-01-01.

The results of a cross-correlation analysis between annual mean chick weight and the mean maturity state of sprat and herring, respectively is shown in Figure 14. Figure 14A shows a positive lag correlation between herring mean maturity and chick mean weight at day 0-2 days before leaving nest during the fledgling period, however a significant negative one at lag days 3-20 (approximately time period of hatching to young chick). Obviously only the oldest chicks, just before leaving nest, benefit from high abundance of very mature herring. Moreover, Figure 14B shows a negative correlation at lag 5-9 days after leaving nest between sprat mean maturity...
and chick fledgling weight and a significantly positive correlation between 9-19 days (app. date of hatching). Early chicks seem to benefit from high abundance of mature sprat in the early period while it may have a negative effect if highly abundant sprat at the late period as potentially demand is higher than adults can provide when fishing small sprat (Figure 14B). Thus, presence of large mature herring in the later period is better as supported by the positive lag correlation just before chicks leaving their nests (Figure 14A). However, a presence of large mature herring in the early period after hatching has strong negative correlation on the chick weight as these fish might be too large to be eaten by the small chicks (Figure 14A).

**Figure 14** Mean chick weight vs (A) mean herring maturity and (B) mean sprat maturity. Autocorrelation lag of sprat and herring mean maturity and common guillemot chicks mean fledgling weight. The x-axis indicates the daily lag and leads up to 30 days and the y-axis shows the correlation coefficient. The arrow on the y-axis represent hatching day-day 21 and fledgling day-day 0.
8 Discussion

This section discusses the major findings from the analysis in relation to the research questions and the fundamental theory of the study. The first section discuss data limitations followed by three sections that cover common guillemot, sprat and herring, and match-mismatch hypothesis. These sections are followed by an outlook and conclusion.

8.1 Data limitations

This study has been working with extensive fish (272,966 observations) and seabird data (40,936 observations). Samples of common guillemots have annually been monitored which yielded a unique opportunity to analyze their fledgling weight over a 16-year period. However, samples from sprat and herring have been more difficult to analyze since trawl samples have been taken more irregularly and for some periods did not match with years where chick weights were obtained. Therefore, data for many years during the breeding season were lacking.

8.2 Common guillemot chicks weight

This thesis hypothesised that there is an inter-annual difference in common guillemot chick fledgling weight on Stora Karlsö between 2002-2017 in order i) to investigate what is the general values of chick weights and ii) to detect patterns and trends. I also investigated whether there is a difference of mean weight in common guillemot chicks that leave their breeding ledge during the end of the fledgling period (day 5-8) than chicks that leave their breeding ledge early (day 1-4) during the fledgling period.
Studies on chicks fledgling weights on Stora Karlsö have been conducted since 1970’s. There are several interesting observations from those studies, worth discussing together with results from this study (Hedgren 1979, Hedgren 1981, Österblom et al. 2006). Österblom et al (2006) found in their study between 1989-2004 that chick body mass (the same as fledgling weight) was higher during the early 1980’s, similar as chick body mass observed during 1970s (253.7 g, Hedgren 1979). Thus, chick mean body mass started to decrease significantly after the 1990s. They found a decrease in chick mean body mass over time of about 0.5 % per year from the 1990’s to beginning of 2000, which was about 6 % decrease in mean body mass during the entire study period. My thesis adds the most recent data of chick fledgling weight that corresponds to their result (Figure 7, Table 4). This study shows a higher decrease in chick mean fledgling weight between 2002-2017. The lowest recorded mean weight was in year 2016 of 224 grams and the highest recorded mean weight was observed in year 2002 of 247 grams (Table 4). The mean fledgling weight during my study period was lower than fledgling weights recorded during 1970s and 1980s. The statistical analysis, in this study showed that chicks had a significant weight loss of about 3 % between all consecutive years 2009-2017, which is an annually higher percental decrease in chick mean fledgling weight comparison to Österblom et al. (2001).

Further, this study identified that the actual day when chicks leave their breeding ledge during the breeding period influence their mean weight (figure 9 and 10, Table 4). Chicks that leave their breeding ledge during the first part of the fledgling period (day 1-4) showed a higher mean weight compared to chicks that leave during the end of the fledgling period (day 5-8). It is interesting because, this seasonal pattern of decreasing fledgling weights was observed already in 1972-1976 by Hedgren (1979 and 1981), Hedgren could not show any decrease in chick fledgling weight between 1972-1976 but found that chicks that hatched late during the fledgling season also exhibited a lower growth rate, than chicks that hatched early during the fledgling season which had a higher mean fledgling weight in comparison with chicks that fledge late during the season – after the median peak day, chicks mean fledgling weight decreased with about 2.6 grams d–1 between 1972-1976.
8.3 Sprat and herring

Within this part of the thesis, I investigate if there is an inter-annual variation in spawning for sprat and herring in the Baltic Sea and its patterns. The aim for this was to determine sprat and herring spawning dynamics that common guillemots generally experience most of the year in the Baltic Sea. Sprat and herring intra- and inter-annual spawning cycles were investigated as well as the potential peak day with the highest abundance of potential spawners where maturity stage was used as a proxy for spawning. This study illustrates a unique description of sprat and herring spawning pattern and maturity stages in the Baltic Sea and within common guillemots foraging area. The literature of those biological processes is rare for the Baltic Sea, so this study is expanding the current existing literature. Findings from the analysis of herring spawning patterns (Figure 10, Table 7) showed a large inter-annual difference among peak days, spanning from day 176 (in year 2011) until day 236 (in year 2012). The analysis of sprat (Figure 11, Table 8) showed a less varied inter-annual peak day spanning from day 130 (in year 2014) until day 151 (in year 2015). Both sprat and herring spawning cycle (Figure 10 herring, Figure 11 sprat) have a distinct peak day with a following clear decline in spawning activity. Hence, the results indicate that the peak day of the highest abundance of potential spawners temporally varied between years especially for herring.

The result from this study where clupeids shows a wide temporal variation in spawning activity may be linked to supporting evidence of seasonal alterations in the phytoplankton and zooplankton community in the Baltic Sea. Studies (Möllmann et al. 2004a, Möllmann et al 2004b, Lewandowska and Sommer 2010) have linked rising water temperatures to seasonal changes in phytoplankton and zooplankton communities, which have been showed to peak with a greater variation during the last decades and in more irregular patterns. Both sprat and herring spawning are suggested to be determined by zooplankton food availability and sea water temperature (Cushing 1975, Anner 1985), where warm winters might result in an earlier spring bloom inducing also earlier spawning and cold winters postpone the spring bloom and, hence, the spawning (Karasiova 2002, Peck et al. 2012). These factors could be a potential explanation in the temporal variation of spawning that this study emphasises, however, this needs to be further investigated. Furthermore, variation in the clupeid seasonal spawning patterns in the Baltic Sea also support the notion that ecosystem are facing greater unpredictability today.
8.4 Match-mismatch

This thesis investigated whether common guillemot chick mean weight is influenced by sprat and herring’s maturity during the 21 day feeding period after hatching and before leaving their nests.

My study found that sprat and herring maturity stages (fitness) appear to be an influential factor that influence common guillemot chick mean weight during their first weeks from hatching to fledgling (Figures 14 and 15). Between 2009-2015 both abundance (Figure 12) and mean maturity (fitness) (Figure 13) have decreased constantly during the observed years for sprat and herring. Additionally, the amount of sprat and herring individuals in maturity stages 4-6 has become smaller. These results confirm that both prey quantity and quality have strongly decreased in common guillemots foraging area at Stora Karlsö. These results are therefore explaining the significant mean weight loss of about 3 % of mean weight between consecutive years (Table 6) that chicks showed during the same period. Österblom et al (2006) found in the Stora Karlsö section an annual decrease of about 0.5 % per year in common chicks mean body mass during the period of 1989 – 2004. They also related this decrease to changes in decreasing sprat quality, but they did not include herring. Findings from my study confirm that there is a general decreasing quality in clupeids that is responsible for the decreasing mean weight in common guillemot chicks for the period 2002 -2017. My study thus, indicates that the abundance and level of maturity (fitness) in sprat and herring were more favorable for common guillemot mean weight during the fledgling period than to low maturity clupeids that were correlated to lower mean fledgling weight in chicks (Figure 13).

However, during the study period 2002-2017 common guillemots’ breeding and fledgling periods were found to be very fixed to a certain period (mid of May-July) and did not adjust to sprat and herring’s maturity that, on the contrary, showed more inter-annual varying patterns (Figure 13). Patterns indicate a potential risk of annual mismatch where sprat and herring have stronger distinction in both timing of spawning and maturity that did not fit to the breeding cycles of the common guillemots. Moreover, there was a decrease in both abundance (quantity) and high maturation stages (quality) during the breeding season makes it even more difficult for the guillemots foraging for some years (e.g. years 2013 and 2014 – see Figure 13). Studies for auks population in the North Sea have also been reported to be facing changes in their prey availability and quality where temporal mismatches occurrence with the consequences of breeding failures including decreased fledgling weight and post-fledgling survival (Wanless et
al. 2005, Anker-Nilssen & Aarvak, Durant et al. 2003). Wanless et al. 2005 investigated one of the largest common guillemot population in the North Sea during year 2004 when population exhibited breeding failure when they changed food resource from their key prey sandeels (*Ammodytes marinus*) to sprat. Chicks that survived during the period of the study were in poor condition compared to the years when sandeels were abundant around their foraging area. Even if the population found alternative preys during the period when sandeels were less available they were affected negatively – since the sprat had lower energy content than sandeels. A similar case, reported by Anker-Nilssen & Aarvak (2003) and Durant et al. (2003), observed that herring abundance strongly affects chick survival of Atlantic Puffins *Fratercula arctica* on the island Røst in Northern Norway, North Sea. And were considered to be the key factor determining Atlantic Puffins breeding success. Mismatches between puffins and herring have been seen, when a delay of herring that drift with the coastal current to Røst from their spawning banks southward occurred (Anker-Nilssen & Aarvak 2003, Durant et al. 2003). Thus, both these examples emphasise how vulnerable common guillemot populations are and that a population can change drastically.

Moreover, my study contributes with novel knowledge of an analysis where common guillemot chick prey preferences is investigated from hatching to fledgling (Figure 15). The results show that the occurrence of high quality of a certain prey type is obviously very essential for the chick mean weight. My findings that the fledgling period from hatching day to fledgling day (21 days), chicks seem to be particularly sensitive for changes in prey resources and depend the first period after hatching when the chicks are still small on high quality small-body size sprat (Figure 14B) and only in their last fledgling period on larger -body sized herrings (Figure 14A). The daily diet overlap appears to be important for common guillemot chicks that mainly preferred mature sprat during the first 9-19 days before fledgling while herring seems to be more important 0-2 days before fledgling and assumed even more important for chicks after fledgling. In most recent study of chicks feeding (Berglund 2016), sprat is the main prey (29 individuals, 71 %) and herring second (12 individuals, 29 %).
The study also indicated that clupeids around 16 cm is the maximum length that chicks eat on the breeding ledge (Berglund 2016). This may also make sense as guillemots chicks, even though highly available, swallow large herrings in their first days after hatching but when they become larger, small sprat (and keeping in mind that adult guillemots can only carry one fish to the nests) do not meet the demand of the growing chicks any more. Here occurrence of high quality and larger herring is of strong benefit for the chicks to gain weight. Thus, this confirms that even minute changes in prey type, even for a very short period like few days, can be crucial for the final fledgling weight. This shows how fine-tuned interaction of occurrence of abundant of certain high-quality prey species is essential for the survival of chicks and the breeding success of common guillemots in the Stora Karlsö region.
9 Conclusion

This study, which is based on a unique long-term, large dataset of common guillemot and clupeids data contributes to a growing body of literature within the field of complex ecosystem interactions with focus on seabird-fish relationship and mismatches. This study provides a unique description of a consistent, short- and long-term relationship between common guillemot chick mean weight during their fledgling period and the maturity (fitness) of sprat and herring in their foraging area. The quality-aspect, that this study highlights, where common guillemot chick response with annual decrease in fledgling weight due to temporal changes in their prey resource, sprat and herring adds a level of complexity when managing marine ecosystem. Since both common guillemots and clupeids have their life-history and phenology of seasonality which are linked to specific environmental conditions, this needs to be taken into account for adequate management decisions and avoid mismatches in the future. Sprat and herring in the Baltic Sea are probably still of “sufficient” quality and available during the breeding season and chick-rearing period since the population have increased. However, results from this study show that common guillemots’ prey’s environment are in a changing state that influence them now, which is why this study is so important.
10 Outlook

This study found that common guillemot chicks on Stora Karlsö had have an annual decrease in mean weight during the fledgling period due to temporal changes in their prey resource, sprat and herring in their foraging area. Future recommendations that would result in deeper insights within this research field are divided into spatial areas on a local, regional and global scale.

On the local scale it would be valuable with a better constructed and timed monitoring program over the foraging area during the breeding season, especially timed studies of sprat and herring which sometimes lacked in this study. On a local scale, I suggest a protection around the water of the breeding colony (subdivision 27) during the breeding season with trawl prohibition or more restricted trawling decisions.

On a regional scale would it be valuable with additional studies of sprat and herring spawning pattern as well as studied the fisheries influence on year-classes, maturity stages and spawning stocks. It would also on a regional scale be interesting to monitor other seabird’s response to changes in prey resources.

On a global scale would it be valuable to make a literature review and a global monitoring program that may include core populations of common guillemots and their prey species. Finally, a rewarding complement to this study would be to investigate multiple species interactions in order to investigate causes to the temporal variation in clupeids spawning and maturity (fitness) in the Baltic Sea.
11 References


