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Foraging efficiency in diving predators based on prey availability

Determining how prey schooling patterns and behaviour affect foraging strategies in two alcid divers

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Front cover: Common guillemots by Astrid A. Carlsen, SLU

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Abstract

Seabirds worldwide are under great pressure from overfishing, habitat loss, predation, disturbance and climate change, evident in the rapid decrease of their population sizes. To conserve these numerous species, the need to share resources have become central, where especially human competition over commercially sought prey species has been pointed out as a key issue. Although the foraging behaviour of seabirds have been extensively researched over the last half century, few studies have had the opportunity to simultaneously study the prey availability as well as predictability of availability. In this essay, I will provide the theoretical framework and knowledge gaps that gives the foundation for my Ph.D. thesis. Thus, the essay will go into detail on topics concerning seabird movement (as monitored using global location/position sensors and dive movement recorders) and the available prey stock dynamics (by echo sounder equipped autonomous sail drone and research vessel), to describe the effect of schooling behaviour on two alcid species foraging efficiency. Firstly, I will describe how schooling behaviour is known to be affected by biotic and abiotic factors concerning the fish itself (e.g. species, biomass, time of day/season, predators present). Secondly, I will explore which factors in schooling behaviour that influence foraging efficiency in diving seabirds the most and how, determining the keys to availability of prey dependent on distance for central place foragers. Third, I will discuss the micro-migration and foraging conditions outside breeding season and during the critical onset of breeding. Finally, I will outline possible effects of increased fishery, competition and climate change by changing variables in the fish school behaviour equations. I review relevant literature on the study species; two closely related seabirds, razorbills *Alca torda* and common guillemots *Uria aalge*, and their main prey species, sprat *Sprattus sprattus*, herring *Clupea harengus* and three-spined stickleback *Gasterosteus aculeatus*. The alcid species forage on the same prey species in partly overlapping areas, but with different physiological adaptations affecting preferred flight distance and dive depth. This gives a great opportunity to explore species variations in response to changes in a common foraging environment.

The foraging environment of pursuit diving predators

Top-predators, are a vulnerable group of animals due to their large metabolic demands, expansive habitats and niches that are often highly specialized to certain prey types (Ripple *et al.*, 2014). Worldwide, top-predators have been largely reduced in numbers over the last two centuries due to anthropogenic interventions including hunting, prey depletion and the restriction, degradation and defragmentation of their habitats (Dias *et al.*, 2019; Heithaus *et al.*, 2008; Ripple *et al.*, 2014). However, top predators have many important ecosystem functions, such as regulating food webs, contributing to nutrition cycling, shaping habitats and impeding ecological invasions amongst others (Hammerschlag *et al.*, 2019; Sergio *et al.*, 2008). The rapid removal of top predators from many ecosystems have thus created many unforeseen shifts in ecosystem services and food webs, affecting all species involved (Hammerschlag *et al.,*2019). Though many measures has been taken to restore and protect the larger predators, including international and national regulations for protecting species and habitats (IUCN, 2018) and raising awareness (e.g. media and documentaries, wildlife foundations and ecotourism), there is still a large issue connected to competition over resources with the human population (e.g. Grémillet *et al.*, 2018a). In marine systems, bycatch of larger predators such as mammals and seabirds in fishing gear and the competition for the prey resources are the most acute (Sydeman *et al.*, 2017). The conflict can be divided into two aspects; fisheries limiting the total food resources, and fisheries changing the foraging environment in some form that have consequences for the associated functional or numerical responses in prey-encounters (Sydeman *et al.,* 2017; Hammerschlag *et al.,* 2019).

Although measures are being taken to regulate and improve fishing gear and methods to avoid by-catch, the competition over food resources is only increasing (Grémillet *et al.,* 2018). As an example, 38% of the world's 346 seabird species are considered globally threatened or near-by threatened by the International Union for Conservation of Nature (IUCN, 2018) at present, with half of the seabird species populations declining. Whilst the global seabird population has seen a drastic reduction in size leading to lowered consumption of prey (a total of -19% from the years 1970's to 2000's; Grémillet *et al.*, 2018), the commercial fishery on the same prey types as those targeted by seabirds have increased during the same period (a total of +10% from the years 1970's to 2000's; Grémillet *et al.*, 2018).

Marine ecosystems are inherently stochastic foraging environments on both a short- and a long-term scale, due to large year-to-year variations in prey abundance within and among foraging locations (Weimerskirch, 2007). The ongoing climate change further adds complications to the animals by making prey movement patterns less predictable (Mahone *et al.,*2017), even for marine predators that have adapted to read the spatiotemporal patterns of their sought prey.

1 Theoretical framework

1.1 Central place foraging for divers

Dependent on bio-energetic demands and physical adaptations, seabirds that prey on fish will seek foraging locations with certain properties, such as upwelling areas or shallow waters where the preferred prey type may be reachable and abundant (Hunt *et al.*, 1999). To reach preferred foraging grounds many animals, and top predators in particular, must often commute large distances, especially during the breeding period when the position of the offspring (e.g. roost or nest) is a central place that all foraging revolves around (Orians & Pearson 1979). During the breeding season, parent animals have to choose between foraging patches and how much time to spend in them, by trading off known properties such as prey availability and commute distances. Such decision-making is commonly described by The Marginal Value Theorem (MVT, Charnov, 1976), an optimal foraging theory that predicts how much time or effort animals should invest in each fitness-enhancing opportunity (e.g. foraging) to optimize time usage and net energy gain (Fig. 1). A provisioning parent animal is expected to maximize food delivery per time unit by bringing home larger food loads from more distant patches involving longer travel times compared to closer patches (Orians & Pearson 1979). As a particular case of foraging theory/optimality, diving animals forage in 3 dimensional patches where the surface in itself becomes a central place that the round trip (i.e. travel time/ distance to and from preferred foraging depth) revolves around (Carlsen *et al.,* 2021). The deeper the dive, the longer the expected foraging time, once the preferred depth is reached (Carbone & Houston, 1996; Carlsen *et al.,* 2021; Walton *et al.,* 1998). In such systems, the foraging patches are indeed a matter of both vertical and horizontal localities, where the two may interact in determining foraging effort/demand and time allocation. The aspect of the diving depth as a travel distance is especially interesting for divers that spend the non-breeding season mainly at the sea surface, and thus spend very little time in commuting flight.

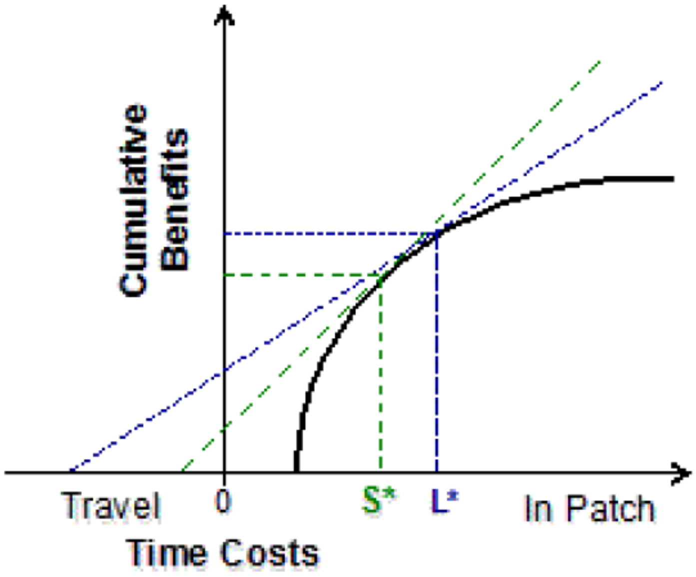

Fig. 1: Graphical representation of the marginal value theorem (MVT). Arrival in the patch (at time=0) is followed by a short delay before active foraging starts with an initial rapid increase in cumulative foraging benefits (thick black curve). Benefits per time in patch then decrease with diminishing returns due to processes such as prey depletion. The optimum times in the patch for short (S* in green) versus long (L* in blue) travel times is given by maximizing the slope of the tangent to the gain curve representing the benefits per total time (travel + in patch) costs. As travel time costs increase (to the left of y-axis), there is an increase in the optimum time spent in patch and the cumulative benefits gained per visit (modified from: Krebs and Kacelnik, 1991).

In any foraging situation food availability will follow a diminishing returns curve (Fig.1), either due to individual exhaustion from the hunt, the limited amount of food available, limitations in means of storage room during a trip (i.e. in the bill, mouth or stomach), or other physiological and ecological features (Charnov, 1976; Grémillet, 1996). During the breeding season, large numbers of diving animals tend to breed in dense colonies and concentrate foraging in the closest area. This can create progressions of prey depletion closest to the colony over the course of a breeding season, known as Storer-Ashmole's Halo (Ashmole, 1963; Gaston *et al.,* 2007; Elliott *et al.*, 2009), which consequently increases the distances of foraging trips over time. Studies on passerine birds show that parent birds consistently adjust the load size delivered as a function of round-trip time (i.e. the distance from the nest to the foraging patch, Fig.1), as well as making adjustments concerning prey quality versus quantity and the variances in prey rewards at different locations (see Wright *et al.,* 1998; Mathot *et al.,* 2017; Westneat *et al.,* 2017). Importantly, provisioning birds often perform self-feeding before searching for chick provisioning food (Ydenberg 1994; Ydenberg & Davies 2010), where some choose different types or sizes of prey and often in different patches for themselves before seeking prey for the offspring (Ydenberg 1994; Ydenberg & Davies 2010; Wilson *et al.*, 2004). This means that the cost gain curve for time spent catching provisioning prey should indeed be different from the time spent self-feeding.

1.2 Predictability of patch quality for divers

Due to the large distances animals often have to move to/between foraging sites, the predictability of detecting desirable prey becomes crucial (Weimerskirch, 2007). Though the marine environment is inherently stochastic (Giske *et al.,* 1998), the movement patterns of larger prey biomasses is in most cases driven by biotic and abiotic environmental ques that gives a certain level of predictability in space and time (e.g. Giske *et al.*, 1998; Magurran, 1990; Weimerskirch, 2007). Common ques in the marine environment are e.g. light conditions and daytime (Giske *et al.*, 1998; Regular *et al.*, 2011), seasonal dependent production (Weimerskirch, 2007), temperature, salinity and oxygen (Ojaveer & Kalejs, 2010), but can also be based on conspecific and/or interspecific communication (Jones *et al.*, 2018; Lachlan *et al.*, 1998; Lukoschek & McCormick, 2000). Additional to the predictability of sufficient prey detection, the prey must be available for the diver to catch at high enough rate such that the energetic gain is sufficiently much higher than the cost of foraging (Monaghan *et al.,* 1994; Reed *et al.,* 2015; Weimerskirch, 2007; Whelan *et al.,* 2021). The catch rate is dependent on prey density as a function of total biomass/number of prey items and/or schooling behaviour (Enstipp *et al.*, 2007). For diving animals hunting elusive fish prey, 'availability' may include depth of schools, among-school distance (Birt *et al.*, 1987; Weimerskirch, 2007), within-school density (i.e. distance between individual prey items) and schooling versus non-schooling behaviour (Miramontes *et al.*, 2012). Availability is however species specific, dependent on the foragers adaptations and niche use (e.g. Thaxter *et al.*, 2010), and prey distribution is perhaps especially important for central place foragers due to their restraint in available areas and time efficiency demands (Charnov, 1976; Walton *et al.,* 1998, Gaston *et al.,*2007). We know that for animals that dive to forage, the oxygen storage capacity and pressure tolerance (Ponganis, 2019; Walton *et al.*, 1998) intertwined with their adaptations that ensure efficient under-water movement (e.g. streamlined body shape, pelage/plumage that insulate whilst decrease friction etc.) is key to their successful foraging (e.g. Grémillet *et al.*, 2012; Lovvorn *et al.*, 1999; Lovvorn *et al.*, 2001; Thaxter *et al.*, 2010; Watanuki *et al.*, 2003). Additionally, most divers are considered primarily visual predators, meaning that they are dependent on some level of light to detect prey (Regular *et al.,* 2011). Thus, foraging in large depths with reduced light levels should result in lower success rates and more time/ energy invested in foraging (Regular *et al.,* 2011).

If a visited patch is of insufficient quality, the cost of continued prey search increases exponentially due to e.g. more or deeper dives needed (Carlsen *et al.*, 2021) or the need to explore more patches leading to increased commuting time and time spent away from the partner and/or offspring (e.g. Kadin *et al.*, 2016; Monaghan *et al.*, 1994). Ultimately the consequence could be that a parent must return to the offspring with insufficient prey (e.g. in size/shape, nutritional content), leading to a shorter rest before the next provisioning trip, which again is likely to be less than optimal if no new knowledge about a patch of sufficient quality was gained during the last trip. However, the complexity of optimal foraging and keeping up with time and/or energy efficiency in extreme foraging situations such as diving is still by large underexplored due to the lack of prey availability data at the spatial and temporal resolution needed. The spatiotemporal variation in prey availability should be reflected in the foraging efficiency of individual divers (number of dives and/or total time spent foraging per day; Monhagan *et al.,* 1994), and could potentially be used to describe the most important aspects of prey behaviour for central place foragers in general and in divers in particular.

1.3 Schooling behaviour and predator-prey dynamics

Many species of fish protect themselves against predators by aggregating into large, dense schools (Magurran, 1990; Krause *et al.*, 2002), which provides both opportunities and obstacles for diving predators. An advantage is, among others, that a school might be more easily detected (Miramontes *et al.,* 2012), but the main disadvantage is the confusion effect large schools has on a predator that both intimidates and makes its decisions on prey choice harder (Krause *et al.*, 2002), leading to predators in general being less successful during hunts (Neill & Cullen, 1974; Krause *et al.*, 2002). The schooling behaviour of fish is thought to be affected by several environmental cues and may vary greatly even within a population (see Fig. 2). There are indications that such variation in school aggregation patterns is somewhat predictable with time of day and within/among season (Nilsson *et al.*, 2003). When schools form, the distribution of individuals does not necessarily become homogenous, but instead it is likely that the distance between each individual increases with distance from the central point (Lawson *et al.*, 2001). In general, fish tend to form dense aggregations during daytime and disperse during the night. Aggregation patterns seem in some species to be tied to Diel Vertical Migration (DVM, Cardinale *et al.*, 2003; Nilsson *et al.*, 2003). Interestingly, the entire population may not form schools at the same time, but instead split into two or more different strategies simultaneously, where the proportion of schooling individuals can correlate with the density of conspecifics (Giske *et al.*, 1998; Holubová *et al.*, 2019).

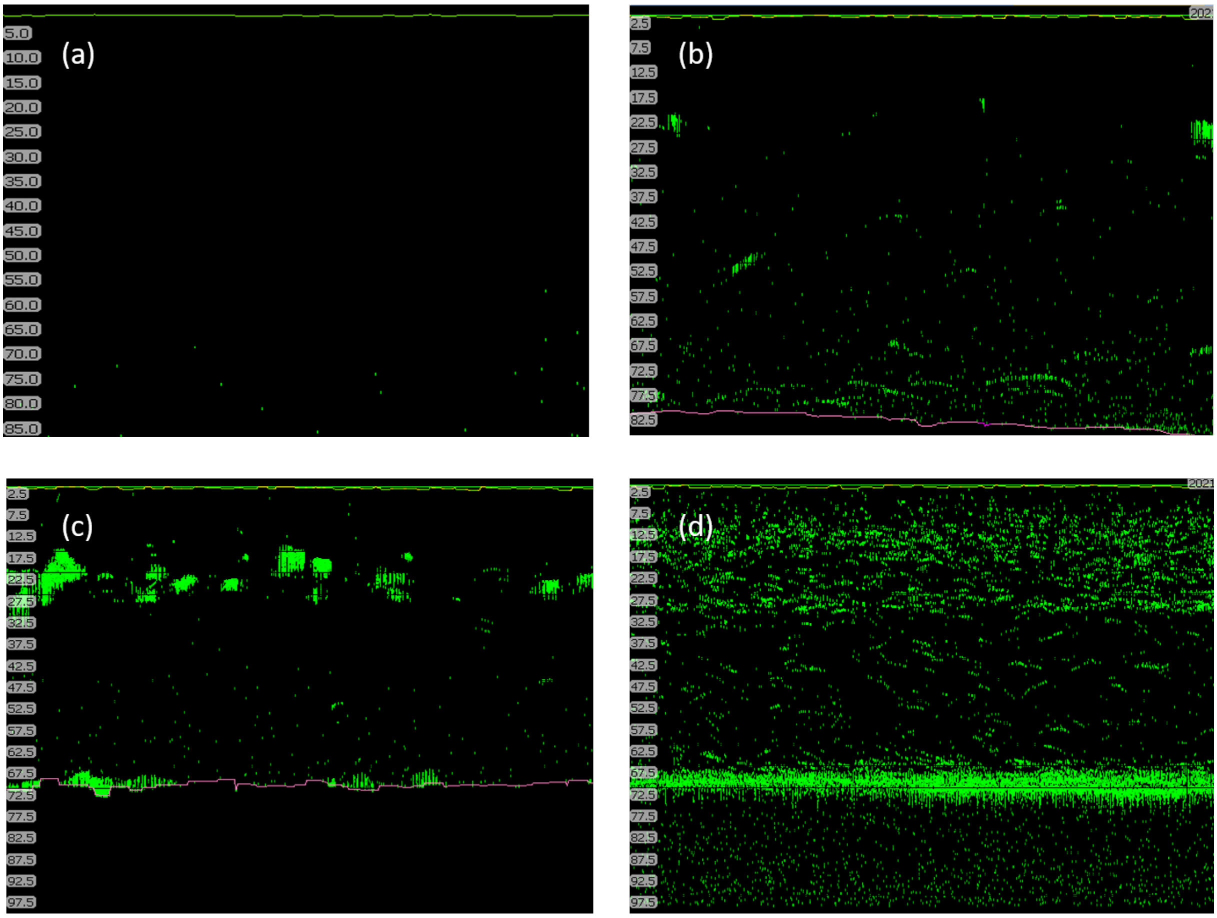

Fig. 2: Varying foraging environments within the range of Stora Karlsö seabird populations during breeding season 2020, collected by the autonomous saildrone Sailbuoy (Offshore Sensing AS). Shown is a 3-week snapshot (24.04.2021-13.05.2021), from very low to very high density of potential prey. Y-axes indicates depth (m). Foraging conditions are here (a) Close to absence of prey; (b) randomly scattered single targets; (c) dense clusters in shallow depth; (d) Two dense layers of fish. Pink lines at bottom in figs (b) and (c) are bottom exclusion lines, in figs (a) and (d) the bottom is below 100 m and thus not shown .

It is well established that fish schooling behaviour evolved as a defence mechanism against predators, and that the interchange between aggregation and dispersion may be a trade-off between enhancing foraging conditions and avoiding predation (Magurran, 1990). However, new evidence suggests a much more complex picture. It has for example been shown that a decrease in dissolved oxygen in the water affects schooling behaviour negatively (Bertrand *et al.*, 2006), which is coherent with dispersal in deep waters. There is also evidence for hydro-mechanical advantages when schooling with conspecifics of same size and shape that leads to reduced cost of movement (Weihs, 1973). One study suggest that as stock sizes in some fish and krill populations change the number of local schools changed too, though sizes of schools were maintained (Brierley & Cox, 2015), suggesting that there is an optimal school size. However, others have found that fish density is a triggering factor for an increase in school size (Holubová *et al.*, 2019), suggesting that density dependent schooling patterns may be species /foraging niche specific (Gulka *et al.*, 2019). Another study suggested that environmental conditions rather than stock size drove school sizes, based on a combination of field studies and laboratorial experiments (Hensor *et al.*, 2005). Whether the varying results is due to differences in species, niches and systems, or even spatiotemporal variations that can occur within these is unknown. However, determining behavioural patterns in the local prey species of divers can be a significant contribution to conservation of such higher predators and their functional role in the ecosystems.

Determining the prey fish’s schooling behaviour and how it changes with prey stock size and environmental factors is likely to explain changes in foraging activity, localities and patterns in diving animals (see Fig. 3). Many studies have looked at factors that directly or indirectly drive schooling behaviour in fish, but as shown here it is very unclear how aspects of the school itself interacts with the local environment to drive certain behavioural patterns. Once the connection between prey schooling patterns and foraging patterns of diving animals are described, it should be possible to predict how a change in schooling will affect the diving predators. Previous studies have focused on the foraging efficiency in diving animals, but never with data on real-time spatiotemporal abundance and schooling behaviour of prey. Importantly, predator species with different adaptations may react differently to changes in the same factors.

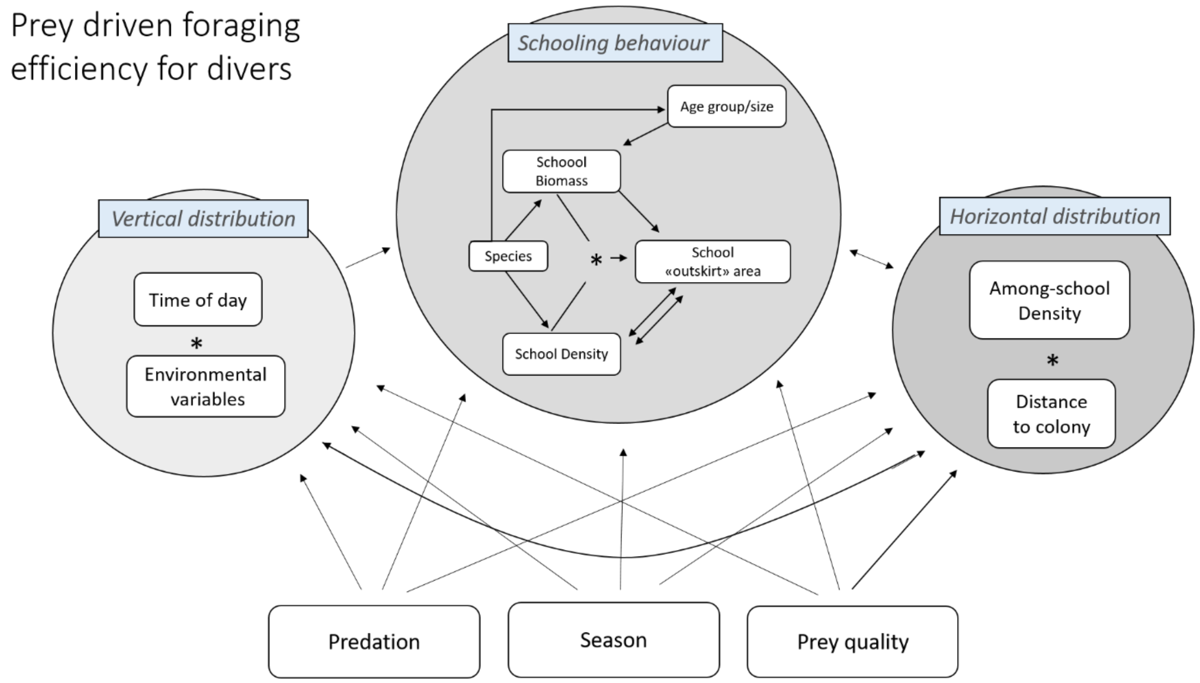

Fig. 3: Conceptual framework describing the most interesting aspects of foraging efficiency driven by the prey’s aggregation patterns and movements. Influencing aspects are divided into 3 main groups: Vertical prey distribution, schooling behaviour (i.e. aggregation patterns) and horizontal movement including prey quality (i.e. assuming that different patches or areas may contain prey of different quality). They are all assumed to vary with seasonal and environmental changes. Indirect effects on foraging efficiency via other parameters indicated with

arrows (small arrows for single parameters, large arrows for all parameters within group) and interactions among parameters indicated with asterix.

2 Ecological features of the study system

2.1 The Baltic Sea

The *alcidae* family in the order *Charadriiformes* consists seabird species that move with ease both in the air and under water. Two seabird species belonging to the *alcidae* family, in the Baltic Sea, the common guillemot (*Uria aalge*) and the razorbill (*Alca torda*). Both species have increased dramatically over the last 3-4 decades (Olsson & Hentati-Sundberg, 2017). The reason for this exponential population growth is thought to be the collapse of the population of one of their main food competitor, the cod (*Gadus morhua*). This leaves high abundances of the alcids preferred prey for chick provision and the crucial first winter survival (Sarzo *et al.*, 2021; Bradstreet & Brown 1985; ICES 2005a) in combination with lowered mortality in bycatches and oil spills (Hentati-Sundberg & Olsson, 2016). Since the 1970's, the populations of guillemots and razorbills breeding at their main breeding sites in the Baltic Sea, Stora Karlsö, has increased from 6.000 and 1.200 pairs to now an estimated 26.000 (JHS pers. Com.) and 12.500 pairs, respectively (Olssen and Hentati-Sundberg, 2017).

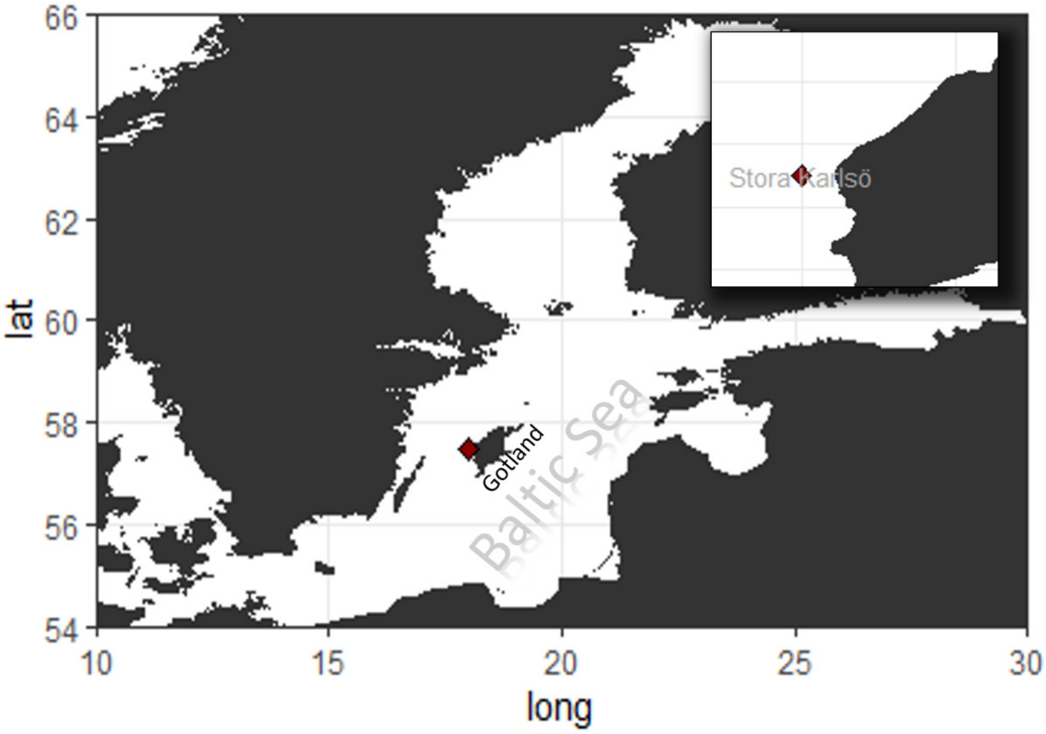

Fig. 4: Stora Karlsö, main site for breeding colonies of alcids in the Baltic Sea.

The diet of adult guillemots and razorbills in the area is little known, but analyses from chick studies suggest that three main species of prey dominate their diet, where >90% of provision and presumably adult feed is the Clupeids sprat S*pattus sprattus* and herring *Clupea harengus*, and the third is three-spined stickleback (hereafter: sticklebacks) *Gasterosteus sp*. (Kadin *et al.*, 2016; and JHS & PA Berglund pers. comm). All three fish species are considered abundant in the Baltic Sea, though whilst stickleback are on the rise, sprat and herring have been stabilizing and in some areas even slightly declined the last few years (ICES, 2021b). As the Baltic alcid species mainly forage on commercially sought clupeids (with the likely inclusion of sticklebacks in commercial fishery in close future, Olsson *et al.*, 2019), there is a conflict between the fishery and the conservation of biodiversity (Fransson *et al.,* 2002; Grémillet *et al.,* 2018; Hentati-Sundberg *et al.,*2021a). Inter-annual stock assessments of sprat and herring by the International Council for the Exploration of the Sea (ICES) provide estimates of the total abundance and biomass of fish stocks in the Baltic Sea, based on commercial catches and acoustic data (e.g. ICES, 2019; 2020). However, such coarse grained analyses gives little insight to crucial fine-scale distributions, such as fish abundance in close proximity to breeding colonies of species of conservatory interest. Due to the previous lack of long-term fine-scale data on fish populations and local fishery pressure, estimating the true level of local fishery-seabird competition and fish depletion during intense predation periods (e.g. breeding seasons) has been difficult (Hentati-Sundberg *et al.,* 2017). However, with new hydro-acoustic technology, such as sailing drones with echosounders, the within-season changes in prey abundance can provide insight into possible competition, through the possibility to track fine scale seasonal changes in clupeid and stickleback abundance.

2.2 Alcid birds

2.2.1 General foraging behaviour and environment

Alcids have found a way to exploit the marine environment by having a highly specialized morphology for underwater movement (Thaxter *et al.,* 2010). This gives flexibility in foraging area, depth and duration that leaves room for a buffer in energy and foraging efficiency for more demanding times (Burger & Piatt, 1990; Weimerskirch, 2007). Energetic demands are especially high during the breeding seasons (Gaston *et al.*, 2007; Hemerik *et al.*, 2014; Kadin *et al.*, 2016) as well as moulting and late winter (Burke & Montevecchi, 2018). The trade-off in flight abilities for efficient diving has however been large. As compared to great flyers such as albatrosses and petrels that only forage on the sea surface but cannot dive far below it, the alcids are adapted to spend time on and under the water surface, but less built for long distance movement (Thaxter *et al.,* 2010). Seabirds in general are long-lived animals, on the slower end of the pace-of-life spectrum (Stearns, 1992), and alcids spend on average several years learning how to forage efficiently enough before trying to breed (Birkhead & Hudson, 1977). When a breeding season has been successful, individuals will invest highly in keeping their valuable assets by returning to the exact same nest site, with the same partner and the same neighbours year after year (Hedgren, 1980). They often appear at the breeding site in good time to run their own prey stock assessment in the area before choosing the onset of breeding when all parameters are in favour of success (Whelan *et al.,* 2021). The alcids' assessments of prey populations may occur by visiting the same foraging locations that were successful the year before, using information they learned from other individuals in the colony during their pre-breeding years (Limmer & Becker, 2010). If foraging conditions are inadequate, guillemots have been seen to adjust or compromise brood investment in terms of provisioning effort or simply skip breeding seasons in extreme cases of low prey abundancy/quality (Reed *et al.*, 2015).

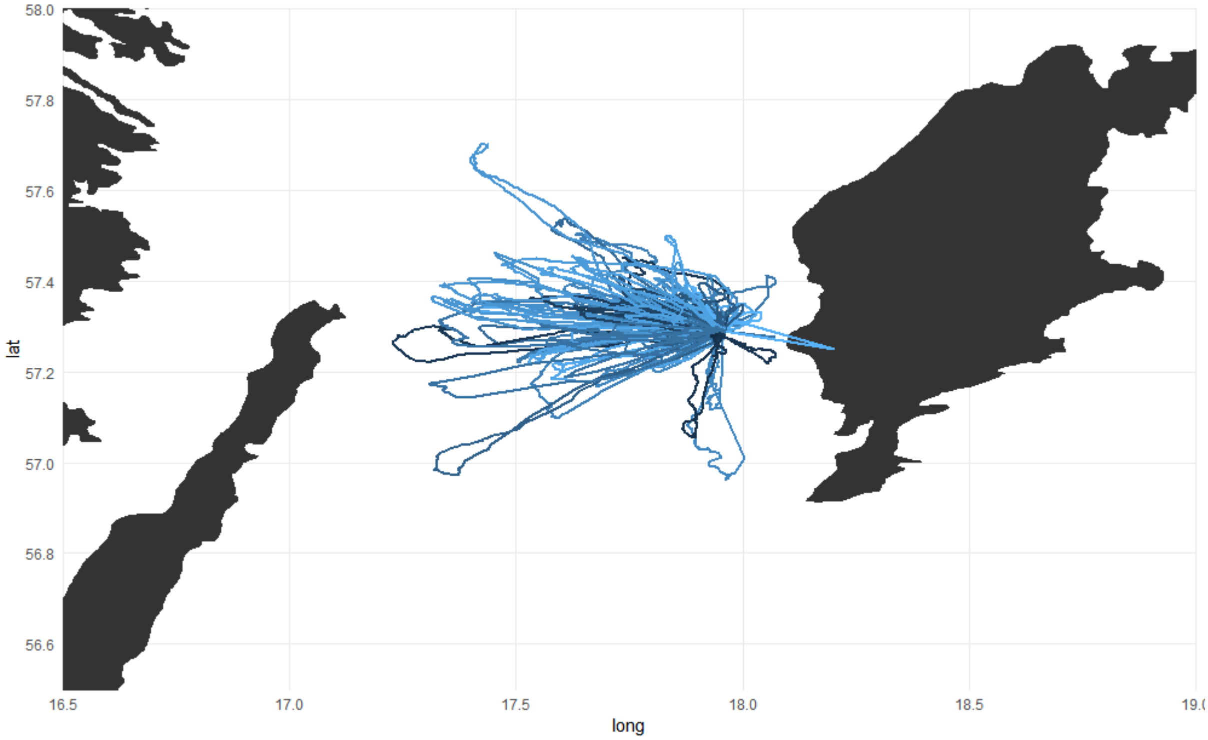

Fig. 5: Flight patterns of foraging trips in 25 guillemots and 3 razorbills breeding on Stora Karlsö from 2018-2020.

Even minor changes may be noted by these seabirds which with time will alter their foraging behaviour to meet the requirements as far as possible (Gulka *et al.*, 2019; Reed *et al.*, 2015). The effort spent foraging during a year, measured as time spent commuting to foraging locations, including both flight and diving depth/ duration per day (and perhaps number of dives/ trips), should infer their ability to meet demands under varying conditions (Monaghan *et al.,* 1994). Interestingly, species with different niche use and extent of behavioural plasticity may not respond equally to minor changes in the same environmental variables, even for closely related birds foraging on the same fish species (Thaxter *et al.*, 2010). Such environmental changes may include changes in foraging locations and distance from breeding colony, winter habitat, depth of dives and overall foraging efficiency, along with density and behavioural patterns (e.g. diurnal migratory patterns) of prey.

2.2.2 Species specific niches and morphological trade-offs

In the Baltic Sea, both guillemots and razorbills are increasing in numbers, and there is little sign of them outcompeting each other despite foraging on the same prey and in largely the same areas (Hentati-sundberg *et al.*, 2021a). The seeming lack of competition for food could be due to their differences in preferred foraging locations along with the general high abundance of prey, but this is not yet clear. Adaptations to be an efficient flyer versus an efficient wing propelled swimmer demands the exact opposite of a bird's morphology (Thaxter *et al.*, 2010); the comparably larger wings of a razorbill reduce the cost of long-distance flight (though probably still very energetically demanding compared to most species), but make dives energetically costly (see fig. 6). The opposite is true for the guillemot with smaller wings (Thaxter *et al.*, 2010), being very efficient deep divers but short-distance flyers. Additionally, razorbills are somewhat smaller than common guillemots (750g versus 915g; Baltic Seabird Project, hereby BSP, unpublished data.), and razorbills can, in contrast to guillemots, carry multiple prey in their bill (Thaxter *et al.*, 2010).

Fig. 6: Wing-to-body size ratio demonstrated during wing stretch in razorbill (left) versus the much larger common guillemot (photos by A.A. Carlsen 2018).

Additional to the among-species variation in niches (Gulka *et al.*, 2019), quite distinct within-year variation in time spent foraging has been recorded in other populations of guillemots (Burke & Montevecchi, 2018). Guillemots in Canada was flying on average <2% of the time in winter, whilst 9.6% diving, and the rest of the time was spent on the water surface (Burke & Montevecchi, 2018). Interestingly, their daily energetic expenditures doubled towards January and February compared to November and early December, probably because of an increase in metabolic costs related to thermoregulation due to low sea surface temperature (Burke & Montevecchi, 2018). Razorbills, during the breeding season, on the other hand, spent 15% of the time diving and 10% of the time to fly (i.e. commute to and from breeding site), implying a significant amount of time spent foraging (Fig. 7) (Isaksson *et al.*, 2019). The energetic needs of the late winter months in alcids is perhaps somewhat comparable to demands during the breeding season, but this still remains to be explored.

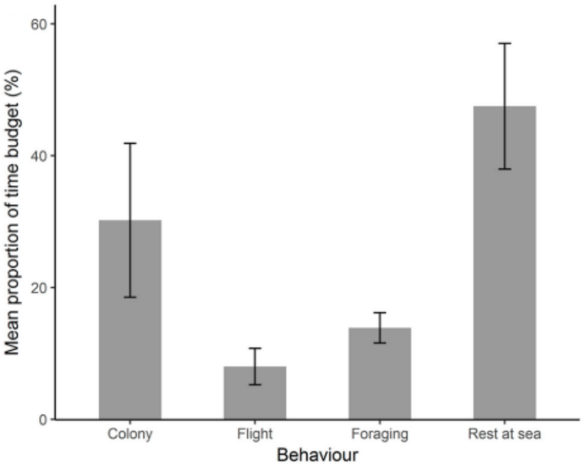

Fig. 7: Time budget for 22 adult razorbills during breeding between 7–18 July in 2010, 2011 and 2015 at Stora Karlsö (Isaksson *et al.*, 2019).

Further analyses showed that the Canadian guillemots' dives become much deeper in winter, where more than half of all dives are deeper than 50m, and the deepest winter dive recorded in another colony was approaching 250m (Chimienti *et al.,* 2017). The cost of foraging dives is likely to increase as depth increases, as decent is the most costly part of dives (Carlsen *et al.*, 2021; Enstipp *et al.*, 2005).

Different aspects of a foraging environment may have different effects on the foraging efficiency of birds depending on their adaptations, which is mirrored in differences in time allocation of closely related birds with similar niches (Thaxter *et al.*, 2010). This is likely to be dependent on the availability and/or predictability of prey, e.g. the density of schools may affect the foraging efficiency of seabirds differently depending on their capabilities as divers (Thaxter *et al.,* 2010). Where a more skilled diver could have enough time and speed to efficiently pursue and hunt highly dispersed prey, a less skilled diver may be more reliant on large, obvious schools in predictable places where less information sampling dives are needed (Carlsen *et al.,* 2021). Similarly, if the predictability of availability of prey in distant patches becomes low (i.e. increase in zero-catch patches visited), a long-distance flyer would perhaps have an advantage in multiple patch visits. This illustrates the benefits of including more than one species when investigating the impact of change to a foraging environment such as the Baltic Sea.

2.3 Forage fish

2.3.1 Fish stock features

The three fish species of interest in this study are sprat, herring and stickleback. The Baltic Sea spawning stock biomass (SSB) in 2020 was estimated to be 977 000 tonnes of sprat (ICES, 2021c) and 364 981 tonnes of herring (ICES, 2021b). Although there is no stock assessment for sticklebacks in the Baltic Sea, the relative abundance is monitored and has increased drastically in recent years (Bergström *et al.*, 2015; Olsson *et al.*, 2019). Average total lengths of adult sprat, herring and stickleback is 12, 18 and 6 cm, respectively (Casini *et al.*, 2011; Bergström *et al.*, 2015). Clupeids have high levels of lipids (Kondratjeva, 1993) and are sought prey for alcids provisioning offspring (Kadin *et al.*, 2016; Österblom *et al.*, 2006).

Fig. 8: Sailbuoy (Offshore Sensing AS, see www.sailbuoy.no) and its monitoring track around Stora Karlsö in 2020.

To protect themselves from predation, clupeids utilize DVM, staying by the surface at night, only to descend towards the bottom at dawn and return to the surface again at dusk (Nilsson *et al.*, 2003). Contrary, the smaller and leaner stickleback (Chellappa *et al.*, 1989) is famous for its defence against predators through its heavily built armour making it more difficult to handle (Wasserman *et al.*, 2021). With this armour they can afford staying closer to the surface (ca 6 m depth) to feed in the most productive zone under maximum light levels at daytime and so utilize a weaker form of DVM to 10-20 m depth (Jurvelius *et al.*, 1996). Though sticklebacks may be seen as lower quality prey compared to clupeids due to their smaller size, their large abundance close to the surface especially during daylight makes them highly available. This availability may make them more likely to be targeted by alcids, especially for self-feeding adult individuals, but are perhaps insufficient as long-term chick provision (Kadin *et al.*, 2016). All three fish species are facultative schooling fish that regulate their level of aggregation and schooling patterns dependent on numerous biotic and abiotic stimuli (Jurvelius *et al.*, 1996; Nilsson *et al.*, 2003).

2.3.2 Fish migration and seasonal movement

Historically there has been much overlap in preferred locations for clupeids and stickleback in the Baltic Sea, as they have largely the same food preference (Aro, 1989; Jakubavičiute *et al.,* 2017; Bergström *et al.,* 2015). Clupeids in the Baltic Sea migrate to minimize fluctuations in biotic and abiotic environmental parameters and for spawning, such as food availability and temperature (Aro, 1989). Data on stickleback migration is insufficient at this time (but see fig. 9). One known migration pattern is the movement to preferred spawning areas, which for herring and sprat in the Baltic Sea happens mainly in spring (though there still is some autumn spawning herrings), typically starting in March-April (Aro, 1989; ICES, 2021b). Herring and sprat have different spawning niches; while herring migrates closer to shore to spawn in shallow waters preferably in vegetative areas, sprat are pelagic spawners in deeper waters with large overlap with winter foraging areas (Aneer, 1989; Aro, 1989). The migration of herring can thus be summarized as going from mid-Baltic basins to shore in spring, and back from shore to deeper waters in summer. Sprat on the other hand tends to move slightly further north in the winter feeding period, and back south for spawning in the middle of the Baltic Sea (Fig. 10). This means that an accumulation of prey close to the Karlsö islands in spring and summer is likely (Aro, 1989), which may help sustain the seabird population during their breeding season from May to July. If so, the birds should not start breeding until the sprat spawning migration is fully started and the density of preferred prey in preferred locations is high enough to maximize foraging efficiency in the birds (Whelan *et al.,* 2021). The fish migration during spring and summer seems relatively constant, as herring spawn by age groups whilst sprat is flexible both in time and number of spawning's per individual (Aro, 1989). Thus, there should be a continuous refilling of food sources close to the breeding grounds of the seabirds. However, this also means that there should be signs of diminishing returns towards the end of the season when less and less fish come to spawn (perhaps from early July and onwards), and thus the food source becomes scarcer which then should lead birds to seek prey further away from the breeding colony. Unfortunately, there is a lack of up-to-date information about forage fish abundance and movement over the year. The last report of forage fish seasonal migration patterns are now three decades old while changes in sprat and herring stock sizes have been large (Aro, 1989; Casini *et al.*, 2011).

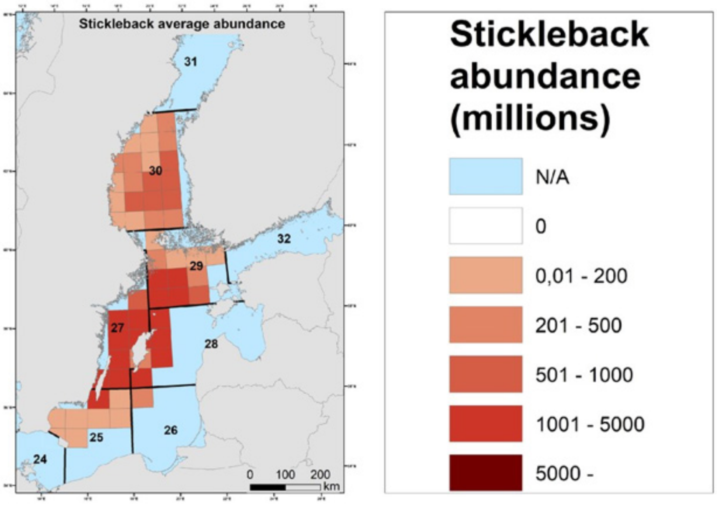

Fig. 9: Abundance of stickleback from western/northern Baltic Sea. Average abundance (millions per nautical mile^2) per ICES rectangle during 2001–2014. Colours represents differences in abundance (blue areas are not covered by survey, N/A). From Olsson *et al.*, 2019.

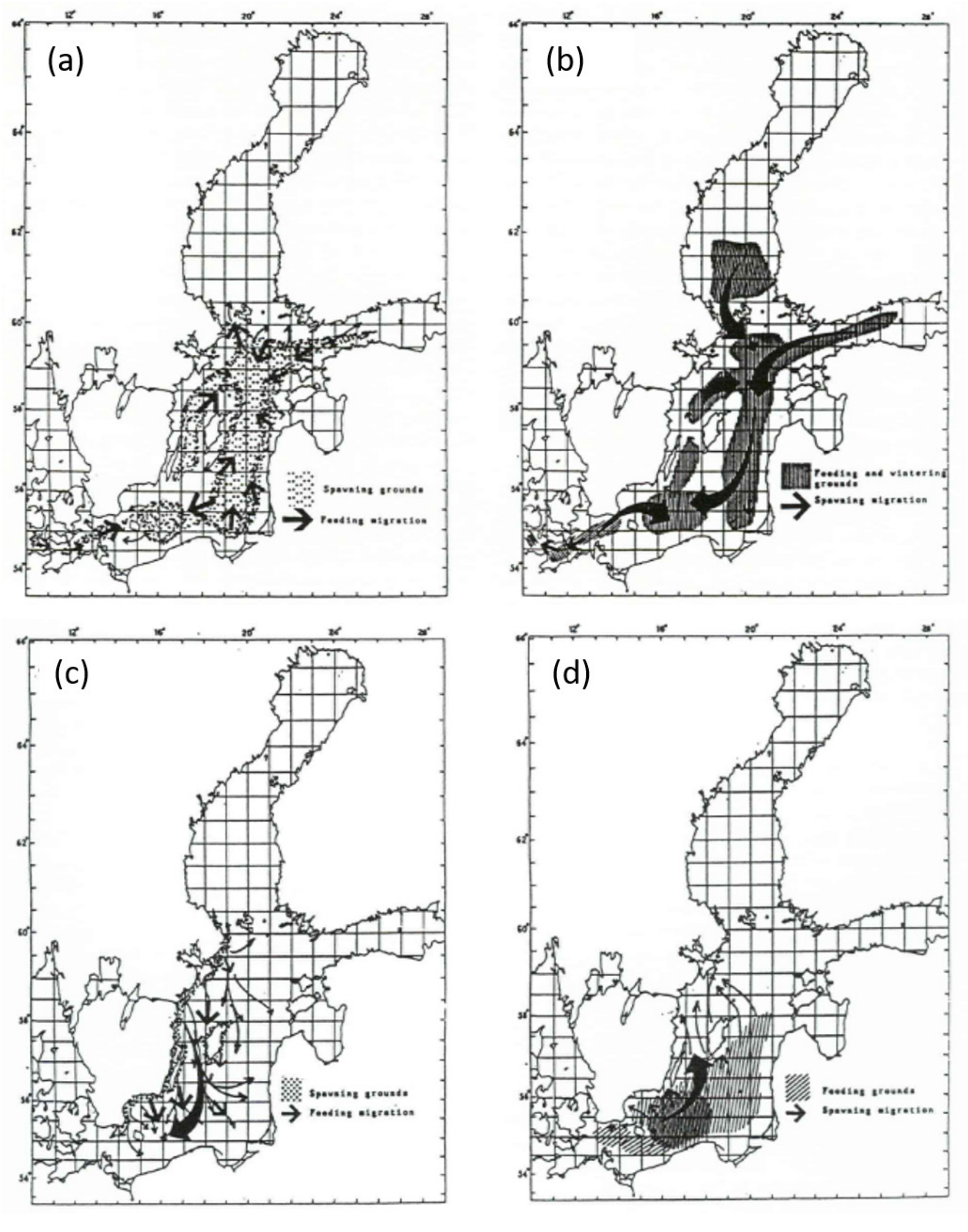

Fig. 10: Map over middle-southern Baltic Sea clupeid populations migratory movement (1989) for (a) Sprat spawning ground (residence from March-July), (b) Sprat feeding ground (residence from August-February), and spring-spawning open-sea herring in the Southwestern and Central Baltic (Subdivisions 25-27) (c) Spawning ground and (d) Feeding ground. Although much of the summer versus wintering ground is overlapping, there is a slight tendency to migrate further north in winter, and a larger accumulation between Öland and Gotland in summer (reprinted from: Aro, 1989).

2.4 Seabird and forage fish stock interactions

Although a sufficient abundance of preferred prey species is important for any seabird, the quality (i.e. nutritional content such as lipids, and overall size) is in some cases also an essential factor for survival and reproductive success (Österblom *et al.,*2008). In sprat and herring in the Baltic Sea, body condition have decreased over the last few decades as the population size, especially of sprat, has increased (Casini *et al.*, 2006; 2011). The large populations of sprat in the Baltic Sea, with little competition from other species, seem to regulate their own populations body condition by depressing the biomass of their food source (Casini *et al.*, 2006). Additionally, a few other biotic and abiotic factors, such as low salinity, has a negative effect on clupeid growth and body condition, further amplifying the density dependent effects (Casini *et al.*, 2006). When the clupeid-to-prey ratio is low, the clupeids have proven to grow larger and hold a higher body fat content, but as population size and density increases, the ratio increase leaving less food per individual (Casini *et al.*, 2011).

The intraspecific competition among sprat have implications for seabirds that provide single fish items to their chicks during breeding as each prey demands an entire foraging trip, where compensations for low quality prey with increased amount is costly. Hunting a low quality prey is likely to take the same amount of effort as a high quality prey, but gives a lower gain so that the overall foraging effort has to increase. It is likely that even if the abundance of prey was lower and thus more time in a patch was needed to catch prey, this would still have been more beneficial if the prey delivered to the chick was of high quality. That is because in particular guillemots only deliver one prey item to their chick per trip, and so a small change in prey size or nutritional content may lead to an entire foraging trip extra per day to successfully raise a chick, drastically affecting the overall foraging efficiency of provisioning adults. Foraging trips may last for hours at the time, and any time away from the nest may have further implications on the partner and other aspects of parental care (i.e. protection from predators or attacks from conspecifics, thermoregulation, etc.) (Monaghan *et al.,* 1994). For this reason, the chick rearing parents may choose to let the chick go hungry for longer instead of taking the extra trip, possibly leading to lower chick fledge weights/earlier fledging, perhaps especially likely as the fledge weight of chicks has shown to not affect post-fledge survival (Harris *et al.*, 2007; Hedgren, 1981). As population sizes in sprat has increased and body condition has gone down after the mid 1990s, fledging weight in guillemot chicks has have decreased and is today considerably lower than previously in the Stora Karlsö colony. The average fledge weight has been <235g in the latest few years hitting an all-time-low of 220g in 2021 (Fig. 11) as compared to >250g in the 70's (Hedgren, 1981; Österblom *et al.*, 2006).

Although not directly tested, there is reason to believe that the change in lipid content in clupeids is a significant factor affecting fledge weight in the local alcids. In a short-term perspective, an increased mortality in the clupeid stock may not be all bad, as a decrease in clupeid population sizes may have a positive influence on their body condition, and thus on the nutritional value for the seabirds (Casini *et al.*, 2006). However, further studies concerning the behavioural responses and physiological effects of clupeid body condition on adult birds is needed.

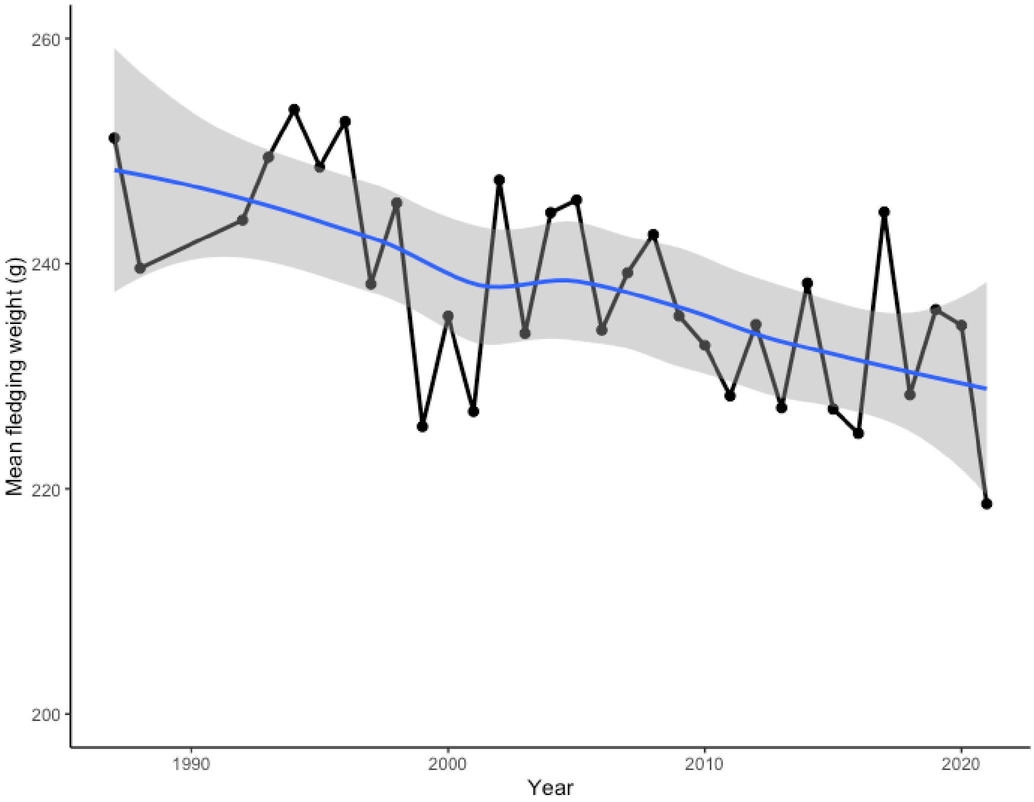

Fig. 11: Trend in mean fledging weight of common guillemot chicks at Stora Karlsö 1987 – 2021.

3 The effects of human interventions and climate in the Baltic Sea

3.1 Clupeid mortalities by fisheries and predation

The sprat and herring stocks of the Baltic Sea is utilized by both EU and Russia, with no agreement plan among the two (ICES, 2021c, 2021b). EU follows a Multiannual Plan (MAP) for the fishery on the Baltic clupeids. The plan is based on advice from ICES on the current estimates of biomass (B) and fishing mortality (F) in relation to the long-term management targets for biomass and fishing mortality (B_{MSY} and F_{MSY}). The Total Allowable Catch (TAC) is then the agreed total quota for EU that year, including a prognosis about the level of the Russian fishery. The agreed TAC for EU + Russia in 2021 was 126.051 tons of herring in the Central Baltic Sea and 268.458 tons of sprat in the entire Baltic Sea (ICES, 2021c, 2021b). There is currently no fishery and thus no stock assessment or catch advice for sticklebacks. Following the F_{MSY} is thought to be precautionary by leaving healthy population sizes and sufficient recruitment for the fish species of interest in future years (ICES, 2021c, 2021b).

As noted above, the stock size of sprat in particular has, since the mid. 1990s, been so large that the population have shown density-dependent deprivations in individual growth and condition (Casini *et al.*, 2006, 2010), and top-down regulating sources such as cod, marine mammal and seabird predation are unlikely to impose an impact strong enough to regulate forage fish numbers (Hansson *et al.*, 2018). However, such assessments of Baltic sprat and herring are coarse and do not take into account fine scale differences in natural mortality such as in close proximity to breeding colonies of seabirds. An earlier estimate from the Stora Karlsö colony estimated the alcids' prey consumption to more than 2.300 tons (13%) of clupeids out of the total 17.900 tons estimated to be available in the 4.408 km^2 feeding area during the breeding season (Hentati-Sundberg *et al.,* 2017). This means that the alcid population is very likely to have a large impact on prey abundance in the area during breeding, unless there is continuous refilling by migrating spawning fish in this period. Not only are the alcid population estimated to have increased on Stora Karlsö since the study in 2017, but so has the local population of grey seals *(Halichoerus grypus*) that forage on clupeids (Hansson *et al.*, 2018) and great cormorants (*Phalacrocorax carbo*) that by large targets sticklebacks (BSP unpublished data, 2008). Undeniably, the Stora Karlsö area is critical during breeding for several Baltic seabird populations (Hentati-Sundberg *et al.,* 2017), but simultaneously an important ground for fishery (Hentati-Sundberg *et al.*, 2015) which creates the foundation for conflict between fishery and conservation of top predators. Though it is likely that clupeid abundance decrease from breeding season (mid. June) to autumn (October) (Hentati-Sundberg *et al.*, 2015) in this area, we do not know whether this is only due to clupeid mortality (i.e. from fishery or predation), or partly because of seasonal migration (see Aro, 1989). Thus, taking the fish consumption of locally bound (i.e. breeding) seabird populations into consideration may be of great importance when managing seabird conservation and the effect of local fishery pressure. With the locally increasing alcid and grey seal population, relatively high abundance of great cormorants and the effort made to re-establish the cod population (ICES, 2021a) we should expect a locally increased natural mortality in clupeids and perhaps sticklebacks in the near-by future. Additionally, the possible impact of fisheries in interaction with the predicted climate change effects leaves large uncertainties in the future of food availability to all top-predators in the area.

3.2 Climate change

Climate change is thought to reinforce the environmental changes already seen in the Baltic Sea (e.g. decreased salinity, increased eutrophication and increased variations in temperatures and extreme weather events) (Meier *et al.*, 2021). The ongoing change in biotic and abiotic factors, linked to anthropogenic disturbance and climate change, has strongly affected the species composition, proportion of species and consequently food web interactions in the Baltic Sea (e.g. Möllmann *et al.,* 2009; Bergström *et al.,* 2015; Meier *et al.*, 2021), which combined with overfishing ultimately led to the collapse of one of the main predators of clupeids, the cod (ICES, 2021a). Also zooplankton species cope with abiotic factors differently, where a change in salinity and oxygenation of the water has driven a change in proportion of important copepod species where some (e.g. *Pseudocalanus elongates, Temora longicornis* and Cladocerans) have decreased in abundance, whilst others (e.g. *Acartia spp*.) has increased (Möllmann *et al.,* 2009). This has altered the prey composition for zooplanktivorus species, where generalists (i.e. with flexible traits in e.g. prey choice or spatial use) such as clupeids perhaps do better than specialists (i.e. highly specialized to one niche e.g. exploiting one specific food source or being stationary) (Davey *et al.,* 2012). The body condition of clupeid individuals vary among seasons and inter-annually (Casini *et al.,* 2006), and there has been signs of the growth of clupeid fish species being both affected by bottom-up (e.g. water salinity) and top-down (e.g. predation affecting the density of the clupeid populations) processes (Casini *et al.*, 2006; Casini *et al.*, 2010; Majaneva *et al.*, 2020). Thus, climate change can affect the seabirds foraging indirectly by decreasing their prey's reproductive success and food source (Casini *et al.*, 2010; Österblom *et al.*, 2006). Rapid negative changes in prey availability may directly lead to seabird couples choosing not to breed for years in a row, resulting in a steep decrease in recruitment and population fitness (Reed *et al.*, 2015). Should inadequate foraging conditions or lack of 'intuitive' prey movement patterns become long lasting, the implications on seabird populations may be serious (Reed *et al.*, 2015).

3.3 Eutrophication

Excessive input of nutrients (i.e. nitrogen and phosphorous) into the water has driven an increased eutrophication and led to hypoxic or even anoxic waters beneath the halocline (HELCOM, 2018; Rönnberg & Bonsdorff, 2004; Saraiva *et al.*, 2019). The effects of eutrophication on the dive efficiency in breath-holding marine birds and mammals is an interesting, and very little investigated area of research, but there are reasons to believe the effects could be both positive and negative on the divers foraging efficiency (Grémillet *et al.*, 2012; Strod *et al.*, 2008). Eutrophication can lead to increased algal blooms, in turn resulting in turbid waters where little light reaches through and distance of vision is reduced drastically (Grémillet *et al.*, 2012; Strod *et al.*, 2008). This may then result in reduced foraging efficiency as visual predators will have their sight reduced, thus altering dive strategies including preferred depth, duration and number of dives needed to reach a sufficient prey load. However, increased eutrophication has also overall lead to higher production, meaning more available food for forage fish species (Aro, 1989; Eero *et al.*, 2016) and perhaps leading to prey being closer to the surface to feed or avoid anoxic deep waters, which would then perhaps balance out the disadvantages for the birds.

4 Knowledge gaps and outstanding research questions

Though some of the aspects outlined in this essay has been somewhat considered in isolation, very few studies have had anything close to spatiotemporally matching data on prey abundance and patterns of distribution, let alone tested the effects of prey aggregation patterns on divers. The uniqueness with this project is the potential to tie together the alcids movement data and foraging efficiency analyses with correspondent actual fish distribution and behaviour. My thesis should be able to aid fishery management in its development to consider optimal harvest levels not only from the fisheries point of view, but also from an extended ecosystems point of view.

In my PhD project, I aim to explain the most important aspects around the foraging conditions for common guillemots and razorbills in the Baltic Sea, by drawing lines from the ecology of their prey species to the variations in seabird-species specific foraging efficiency. Firstly, I will focus on the prey species behaviour with respect to depth per time of day, density of individuals and available prey biomasses at different distances to the seabird colony. Secondly, the time budget of the birds will be explored with focus on their species-specific adaptations to the Baltic Sea environment. Here I aim to explain how the spatiotemporal variation in patch quality (i.e.

based on aggregation patterns in the previous analyses) is key for a seabird seeking maximum foraging efficiency. Thirdly, the migratory and dive behaviour of the seabirds will be investigated whilst inferring (and perhaps periodically ‘ground-truthing’ with acoustic surveys) prey abundance and/or aggregation patterns based on dive behaviour. Lastly, the long-term effects and future prospects of predicted fishery and climate change will be explored with focus on availability and predictability of prey. Below, I outline some possible routs towards solving these questions in more detail.

4.3 Research questions

1) What are the spatiotemporal school behaviour in the prey species of Baltic alcids?

The foraging efficiency of seabirds should rely highly on prey availability, movement, behaviour and predictability of detection. Data on school aggregation and movement of important prey species will be collected using an echo-sounder operated from a sailing drone. Through analyses in Echoview and R I hope to reveal the foraging conditions of Baltic alcids on different spatiotemporal scales (i.e. within a day, a season, a year, and among years). Prey species schooling pattern /aggregation may be dependent on many different parameters of the school itself such as species, school biomass/ number of individuals in the area or density among schools, density within school (i.e. average distance between individuals), depth of school (by time of day/season), condition of individuals, the age groups, but possibly also on abiotic factors such as oxygen level in the water, salinity and turbidity (i.e. visual conditions). These relationships could be analysed using Hidden Markov Models. School pattern may also be dependent on predation pressure, and the direction of predation (i.e. above from seabirds, below from larger typically benthic predators such as cod, or more pelagic such as seals). Large predators are possible to distinguish in acoustic data, allowing for correlating predator presence and schooling patterns. Most importantly, I could test if any of the patterns simply can be explained by the time of day within species, because if this is the case it should be directly relatable to the birds foraging behaviour. Using information theoretical approaches for model selection, the most important parameters will be detected and their effect sizes estimated.

2) How does foraging efficiency in guillemots versus razorbills vary with prey stock dynamics and aggregation patterns?

The parameters explored in the first research question will here be applied to the foraging efficiency of seabirds in different areas and time of day within the breeding season. This specific time is chosen due to the intensive collection of prey data in the same areas and time that the seabirds use to forage, and in a life stage where the birds have a very high energetic demand and efficiency therefore crucial for success. Data on the time allocation, chosen foraging areas and depths of dives will be collected using light-level Global Location Sensors (GLS) and Time/Temperature Depth Recorders (TDR's) fitted to the leg rings of the birds.

There are two interesting aspects to consider here. First, it is important to determine what aspects of prey availability, seen as fish schooling patterns, that is most important for the foraging time allocation and dive efficiency in the birds. This includes depth per time of day/within season, biomass, density of individuals within schools/ schools in an area, and perhaps species/ body condition of prey. The variation in clupeids and sticklebacks aggregation patterns should have a predictable effect on alcids foraging efficiency. Secondly, we need to take the bird's optimal time budget into consideration, and how this varies with alcid species adapted to different niches. According to the marginal value theorem, the birds should aim to correlate the time spent actively foraging (i.e. diving) with time spent travelling for maximum efficiency, but this relationship should vary with the cost of commute (i.e. both commute from nest to foraging site and descent/ascent between surface and foraging depth). The relationship between surface duration and dive duration may be an alternative measure for dive efficiency. Here, the predictability of prey detection is crucial, as the arrival to a distant empty foraging patch may increase the time spent searching exponentially with no predictable gain. The most interesting factor here is prey availability in relation to distance to patch, both under flight distance and dive distance, what leads to patch dissertation and/or trip termination (including determining possible cost of "empty patch" visits).

The difference in preferred time allocation among the two alcid species should lead to difference in sensitivity to changes in the foraging system, and so they may not respond identically to the same environmental changes. Guillemots may be the most sensitive to (i.e. efficiency is most impacted by) changes in distance from breeding colony to high quality foraging patches, but the razorbill on the other hand may be severely affected by any sub-surface changes in prey abundance such as depth, density and distance between prey items, abundance and thus also proportion of prey species. A skilled diver with information about the overall patch parameters may have good chances at reaching the energetic goal by simply investing more time foraging (Thaxter *et al.*, 2010). A poor diver, however, may struggle to find good patches as diving is needed for information sampling of the environment, especially in the case of less predictable foraging grounds. Additionally, one should expect less skilled divers to dive shallower during daytime as compared to more skilled divers, perhaps having to rely more on prey species that do not utilize DVM to save time and energy, and thus intensify diving during dusk and dawn when high quality prey is thought to be more available.

3) Where does the birds overwinter, and how are foraging conditions in the area and at the time affecting the foraging efficiency?

In this part, the foraging efficiency will be determined with respect to high versus low energy expenditure periods, where high energy expenditure is expected during chick rearing, possibly "post-fledging chick dive training", moulting, late winter and perhaps migration to breeding site (dependent on overwintering area), and low energy expenditure in any other time periods. GLS loggers detect movement continuously, whilst dive data is collected continuously from the beginning of June till the end of August, and then for one week every month until May. Firstly, I will investigate detectable differences in time spent foraging among these time periods and with season. During non-breeding seasons the alcids are unlikely to move large distances on a daily basis, as there is no nest to return to after foraging. Thus, changes in foraging effort from the first arrival in a new patch/area to the final abandonment after some time should indicate prey depletion unless the birds nomadically "herd" (i.e. follow) the fish prey's natural movement and migration patterns. Non-mutually exclusive is the prediction that increasing intraspecific competition affects prey abundance, where the birds continue moving as they themselves exhaust the local fish stocks. Increased competition could either lead to earlier abandonment of a patch or increased variation in spatiotemporal movement pattern, but should still be reflected in increased foraging effort as compared to a new or better patch (e.g. due to less competition). Changes in the foraging environment needs also to be taken into account, as factors such as eutrophication, temperature, prey-food sources and light levels change.

Secondly, I will specifically address the alcids spring time movement, when birds start to return to the breeding site and begin to run assessments of prey availability and prey condition before the onset of breeding. If there is an accumulation of prey (data collected during the Sprat Acoustic Survey, SPRAS, survey in May from R/V Svea) as compared to late summer and autumn (data collected during the Baltic International Acoustic Survey, BIAS, survey in October from RV Svea), I might be able to detect signs of a threshold in stability of efficiency (e.g. maximum foraging efficiency over a certain number of days) for foraging alcids that can indicate/ predict onset of breeding. Ideally, some prey data (e.g. biomass and depth per time of day) would be available from each season across the year, which would complement the data from larger acoustic surveys (i.e. from Sailbuoy and R/V Svea) so that general supporting information on prey availability can be presented for both assessments of foraging efficiency in non-breeding seasons and at the onset-of-breeding period.

4) What are the expected effects of fishery and climate change on the Baltic Sea alcids foraging environment?

Based on the newly gained knowledge of school aggregation patterns effect on alcids foraging efficiency, I wish to describe possible scenarios of how interactions between fishery and predation intensity and climate may affect the schooling behaviour of the fish and thus the foraging efficiency of the birds. This part can be based on transferring probable effects from fishery and climate change on fish school behaviour (e.g. depth, density, abundance, body conditions). This should mainly mean adjusting the most important aspects of fish schooling behaviour to predict impacts of e.g. increasing temperature, decreasing O_2 levels, decreasing biomass and perhaps both increasing and decreasing individual body conditions on seabird foraging efficiency. The core in this matter is whether the buffer seabirds have in terms of foraging time and energy is likely to be enough for them to cope with years of unpredictable or less-optimal foraging conditions compared to the present conditions.

Litterature:

Aneer, G. (1989). Herring (Clupea harengus L.) spawning and spawning ground characteristics in the Baltic Sea. Fisheries Research, 8, 169–195. https://doi.org/10.1016/0165-7836(89)90030-1

Aro, E. (1989). A review of fish migration patterns in the Baltic. Rapports et Procès-Verbaux Des Réunions / Conseil Permanent International Pour l'Exploration de La Mer, 190, 72–96. http://en.scientificcommons.org/26047672

Bergström, U., Olsson, J., Casini, M., Eriksson, B. K., Fredriksson, R., Wennhage, H., & Appelberg, M. (2015). Stickleback increase in the Baltic Sea - A thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science, 163, 134–142. https://doi.org/10.1016/j.ecss.2015.06.017

Bertrand, A., Barbieri, M. A., Gerlotto, F., Leiva, F., & Córdova, J. (2006). Determinism and plasticity of fish schooling behaviour as exemplified by the South Pacific jack mackerel Trachurus murphyi. Marine Ecology Progress Series, 311, 145–156. https://doi.org/10.3354/meps311145

Birkhead, A. T. R., & Hudson, P. J. (1977). Population Parameters for the Common Guillemot Uria aalge. Ornis Scandinavica, 8, 145–154.

Birt, V. L., Birt, T. P., Goulet, D., Cairnse, D. K., & Montevecchi, W. A. (1987). Ashmole ' s halo : direct evidence for prey depletion by a seabird. Marine Ecology, 40, 205–208.

Brierley, A. S., & Cox, M. J. (2015). Fewer but not smaller schools in declining fish and krill populations. Current Biology, 25, 75–79. https://doi.org/10.1016/j.cub.2014.10.062

Burger, A. E., & Piatt, J. F. (1990). Flexible time budgets in breeding common murres: buffers against variable prey abundance. Studies in Avian Biology, 14, 71–83.

Burke, C. M., & Montevecchi, W. A. (2018). Taking the bite out of winter: Common murres (Uria aalge) push their dive limits to surmount energy constraints. Frontiers in Marine Science, 5, 1–13. https://doi.org/10.3389/fmars.2018.00063

Carbone, C., & Houston, A. I. (1996). The optimal allocation of time over the dive cycle: An approach based on aerobic and anaerobic respiration. Animal Behaviour, 51, 1247–1255. https://doi.org/10.1006/anbe.1996.0129

Cardinale, M., Casini, M., Arrhenius, F., & Håkansson, N. (2003). Diel spatial distribution and feeding activity of herring (Clupea harengus) and sprat (Sprattus sprattus) in the Baltic Sea. Aquatic Living Resources, 16, 283–292. https://doi.org/10.1016/S0990-7440(03)00007-X

Carlsen, A. A., Lorentsen, S. H., & Wright, J. (2021). Recovery, body mass and buoyancy: a detailed analysis of foraging dive cycles in the European shag. Animal Behaviour, 178, 247–265. https://doi.org/10.1016/j.anbehav.2021.05.010

Casini, M., Bartolino, V., Molinero, J. C., & Kornilovs, G. (2010). Linking fisheries , trophic interactions and climate : threshold dynamics drive herring Clupea harengus growth in the central Baltic Sea. Marine Ecology Progress Series, 413, 241–252. https://doi.org/10.3354/meps08592

Casini, M., Cardinale, M., & Hjelm, J. (2006). Inter-annual variation in herring , Clupea harengus , and sprat , Sprattus sprattus , condition in the central Baltic Sea : what gives the tune ? Oikos, 112, 638–650.

Casini, M., Kornilovs, G., Cardinale, M., Mo, C., Grygiel, W., Jonsson, P., Raid, T., Flinkman, J., & Feldman, V. (2011). Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids : compelling evidence using an extensive international acoustic survey. Population Ecology, 53, 511–523. https://doi.org/10.1007/s10144-011-0269-2

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. Theoretical Population Biology, 9, 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chellappa, S., Huntingford, F. A., Strang, R. H. C., & Thomson, R. Y. (1989). Annual variation in energy reserves in male three-spined stickleback, Gasterosteus aculeatm L. (Pisces, Gasterosteidae). Journal of Fish Biology, 35, 275–286. https://doi.org/10.1111/j.1095-8649.1989.tb02976.x

Davey, C. M., Chamberlain, D. E., Newson, S. E., Noble, D. G., & Johnston, A. (2012). Rise of the generalists: Evidence for climate driven homogenization in avian communities. Global Ecology and Biogeography, 21, 568–578. https://doi.org/10.1111/j.1466-8238.2011.00693.x

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. Biological Conservation, 237, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033

Eero, M., Andersson, H. C., Almroth-Rosell, E., & MacKenzie, B. R. (2016). Has eutrophication promoted forage fish production in the Baltic Sea? In Ambio, 45, 649–660. https://doi.org/10.1007/s13280-016-0788-3

Elliott, K. H., Woo, K. J., Gaston, A. J., Benvenuti., S., Dall'Antonia, L., & Davoren, G. K. (2009). Central-place foraging in an arctic seabird provides evidence for Storer-Ashmole's halo. Auk, 126, 613–625. https://doi.org/10.1525/auk.2009.08245

Enstipp, M. R., Grémillet, D., & Jones, D. R. (2007). Investigating the functional link between prey abundance and seabird predatory performance. Marine Ecology Progress Series, 331, 267–279. https://doi.org/10.3354/meps331267

Enstipp, M. R., Grémillet, D., & Lorentsen, S. (2005). Energetic costs of diving and thermal status in European shags (Phalacrocorax aristotelis). Experimental Biology, 208, 3451–3461. https://doi.org/10.1242/jeb.01791

Gaston, A. J., Ydenberg, R. C., & Smith, G. E. J. (2007). Ashmole's halo and population regulation in seabirds. Marine Ornithology, 35, 119–126.

Giske, J., Huse, G., & Fiksen, Ø. (1998). Modelling spatial dynamics of fish. Reviews in Fish Biology and Fisheries, 8, 57–91. https://doi.org/10.1023/A:1008864517488

Grémillet, D., Nazirides, T., Nikolaou, H., & Crivelli, A. J. (2012). Fish are not safe from great cormorants in turbid water. Aquatic Biology, 15, 187–194. https://doi.org/10.3354/ab00430

Grémillet, D., Ponchon, A., Paleczny, M., Palomares, M. L. D., Karpouzi, V., & Pauly, D. (2018). Persisting Worldwide Seabird-Fishery Competition Despite Seabird Community Decline. Current Biology, 28, 4009–4013. https://doi.org/10.1016/j.cub.2018.10.051

Gulka, J., Ronconi, R. A., & Davoren, G. K. (2019). Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability. In Marine Biology, 166, 1–17. https://doi.org/10.1007/s00227-019-3553-x

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., Gallagher, A. J., Irschick, D. J., Skubel, R., & Cooke, S. J. (2019). Ecosystem Function and Services of Aquatic Predators in the Anthropocene. In Trends in Ecology and Evolution, 34, 369–383. https://doi.org/10.1016/j.tree.2019.01.005

Hansson, S., Bergström, U., Bonsdorff, E., Härkönen, T., Jepsen, N., Kautsky, L., Lundström, K., Lunneryd, S. G., Ovegård, M., Salmi, J., Sendek, D., & Vetemaa, M. (2018). Competition for the fish - Fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. ICES Journal of Marine Science, 75, 999–1008. https://doi.org/10.1093/icesjms/fsx207

Harris, M. P., Frederiksen, M., & Wanless, S. (2007). Within- and between-year variation in the juvenile survival of Common Guillemots Uria aalge. Ibis, 149, 472–481. https://doi.org/10.1111/j.1474-919X.2007.00667.x

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution, 23, 202–210. https://doi.org/10.1016/j.tree.2008.01.003

HELCOM. (2018). Eutrophication: Supplementary report. Baltic Sea Environment Proceedings, 156, 183. http://stateofthebalticsea.helcom.fi/wp-content/uploads/2019/09/BSEP156-Eutrophication.pdf

Hemerik, L., Van Opheusden, M. V., & Ydenberg, R. (2014). Ashmole's halo as the outcome of a predator-prey game. Marine Ornithology, 42, 125–136.

Hensor, E., Couzin, I. D., James, R., & Krause, J. (2005). Modelling density-dependent fish shoal distributions in the laboratory and field. In Oikos, 110, 344–352. https://doi.org/10.1111/j.0030-1299.2005.13513.x

Hentati-Sundberg, J., Hjelm, J., Boonstra, W. J., & Österblom, H. (2015). Management Forcing Increased Specialization in a Fishery System. Ecosystems, 18, 45–61. https://doi.org/10.1007/s10021-014-9811-3

Hentati-Sundberg, J., & Olsson, O. (2016). Amateur photographs reveal population history of a colonial seabird. Current Biology, 26, 226–228. https://doi.org/10.1016/j.cub.2016.02.007

Hentati-Sundberg, J., Olin, A. B., Evans, T. J., Isaksson, N., Berglund, P. A., & Olsson, O. (2021). A mechanistic framework to inform the spatial management of conflicting fisheries and top predators. Journal of Applied Ecology, 58, 125–134. https://doi.org/10.1111/1365-2664.13759

Holubová, M., Čech, M., Vašek, M., & Peterka, J. (2019). Density dependent attributes of fish aggregative behaviour. PeerJ, 2019, 1–16. https://doi.org/10.7717/peerj.6378

ICES. (2021a). Cod (Gadus morhua) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). In ICES Advisory Committee.

ICES. (2021b). Herring (Clupea harengus) in subdivisions 25–29 and 32, excluding the Gulf of Riga (central Baltic Sea). In ICES Advisory Committee. https://doi.org/10.17895/ices.advice.4748

ICES. (2021c). Sprat (Sprattus sprattus) in subdivisions 22–32 (Baltic Sea). In ICES Advisory Committee. https://doi.org/10.17895/ices.advice.4754

Isaksson, N., Evans, T. J., Olsson, O., & Åkesson, S. (2019). Foraging behaviour of Razorbills Alca torda during chick-rearing at the largest colony in the Baltic Sea. Bird Study, 66, 11–21. https://doi.org/10.1080/00063657.2018.1563044

Jakubavičiute, E., Casini, M., Ložys, L., & Olsson, J. (2017). Seasonal dynamics in the diet of pelagic fish species in the southwest Baltic Proper. ICES Journal of Marine Science, 74, 750–758. https://doi.org/10.1093/icesjms/fsw224

Jones, T. B., Patrick, S. C., Arnould, J. P. Y., Rodriguez-Malagon, M. A., Wells, M. R., & Green, J. A. (2018). Evidence of sociality in the timing and location of foraging in a colonial seabird. Biology Letters, 14, 1–4. https://doi.org/10.1098/rsbl.2018.0214

Jurvelius, J., Leinikki, J., Mamylov, V., & Pushkin, S. (1996). Stock assessment of pelagic three-spined stickleback (Gasterosteus aculeatus): A simultaneous up- and down-looking echo-sounding study. Fisheries Research, 27, 227–241. https://doi.org/10.1016/0165-7836(95)00464-5

Kadin, M., Olsson, O., Hentati-Sundberg, J., Ehrning, E. W., & Blenckner, T. (2016). Common Guillemot Uria aalge parents adjust provisioning rates to compensate for low food quality. Ibis, 158, 167–178. https://doi.org/10.1111/ibi.12335

Kondratjeva, N. (1993). Biochemical and morphophysiological parameters of Baltic sprat in relation to age and annual cycle periods. Ices C.M., 25, 1–5.

Krebs, J.R., Kacelnik, A., (1991). Decision making. In: Krebs, J.R.,Davies, N.B., (Eds.), *Behavioural Ecology: An EvolutionaryApproach*. Blackwell Science, Oxford, 110 pp

Lachlan, R. F., Crooks, L., & Laland, K. N. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Animal Behaviour, 56, 181–190. https://doi.org/10.1006/anbe.1998.0760

Lawson, G. L., Barange, M., & Fréon, P. (2001). Species identification of pelagic fish schools on the South African continental shelf using acoustic descriptors and ancillary information. ICES Journal of Marine Science, 58, 275–287. https://doi.org/10.1006/jmsc.2000.1009

Limmer, B., & Becker, P. H. (2010). Improvement of reproductive performance with age and breeding experience depends on recruitment age in a long-lived seabird. Oikos, 119, 500–507. https://doi.org/10.1111/j.1600-0706.2009.16673.x

Lovvorn, J R, Croll, D. A., & Liggins, G. A. (1999). Mechanical Versus Physiological Determinants Of Swimming Speeds In Diving Brünnich's Guillemots. Experimental Biology, 202, 1741–1752.

Lovvorn, James R, Liggins, G. A., Borstad, M. H., Calisal, S. M., & Mikkelsen, J. O. N. (2001). Hydrodynamic Drag Of Diving Birds : Effects Of Body Size, Body Shape And Feathers At Steady Speeds. Experimental Biology, 204, 1547–1557.

Lukoschek, V., & McCormick, M. I. (2000). A review of multi-species foraging associations in fishes and their ecological significance. Proceedings of the Ninth International Coral Reef Symposium, I, 467–474.

Magurran, A. E. (1990). The adaptive significance of schooling as an anti-predator defence in fish. Annales Zoologici Fennici, 27, 51–66.

Majaneva, S., Fridolfsson, E., Casini, M., Legrand, C., Lindehoff, E., Margonski, P., Majaneva, M., Nilsson, J., Rubene, G., Wasmund, N., & Hylander, S. (2020). Deficiency syndromes in top predators associated with large-scale changes in the Baltic Sea ecosystem. PLoS ONE, 15, 1–21. https://doi.org/10.1371/journal.pone.0227714

Meier, H. E. M., Kniebusch, M., Dieterich, C., Gröger, M., Zorita, E., Elmgren, R., Myrberg, K., Ahola, M., Bartosova, A., Bonsdorff, E., Börgel, F., Capell, R., Carlén, I., Carlund, T., Carstensen, J., Christensen, O., Dierschke, V., Frauen, C., Frederiksen, M., Zhang, W. (2021). Climate Change in the Baltic Sea Region: A Summary. Earth System Dynamics Discussions, 1–205. https://doi.org/10.5194/esd-2021-67

Miramontes, O., Boyer, D., & Bartumeus, F. (2012). The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds. PLoS ONE, 7, 1–9. https://doi.org/10.1371/journal.pone.0034317

Monaghan, P., Walton, P., Wanless, S., Uttley, J. D., & Burns, M. D. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots Uria aalge. Ibis, 136, 214–222. https://doi.org/10.1111/j.1474-919X.1994.tb01087.x

Nilsson, L. A. F., Høgsbro, U., Lundgren, B., Friis, B., Nielsen, J. R., & Beyer, J. E. (2003). Vertical migration and dispersion of sprat (Sprattus sprattus) and herring (Clupea harengus) schools at dusk in the Baltic Sea. Aquatic Living Resources, 16, 317–324. https://doi.org/10.1016/S0990-7440(03)00039-1

Ojaveer, E., & Kalejs, M. (2010). Ecology and long-term forecasting of sprat (Sprattus sprattus balticus) stock in the Baltic Sea: A review. Reviews in Fish Biology and Fisheries, 20, 203–217. https://doi.org/10.1007/s11160-009-9130-5

Olsson, J., Jakubavičiūte, E., Kaljuste, O., Larsson, N., Bergström, U., Casini, M., Cardinale, M., Hjelm, J., Byström, P., & Anderson, E. (2019). The first large-scale assessment of three-spined stickleback (Gasterosteus aculeatus) biomass and spatial distribution in the Baltic Sea. ICES Journal of Marine Science, 76, 1653–1665. https://doi.org/10.1093/icesjms/fsz078

Olsson, O., and J. Hentati-Sundberg. (2017). Population Trends and Status of Four Seabird Species (Uria Aalge, Alca Torda, Larus Fuscus, Larus Argentatus) at Stora Karlsö in the Baltic Sea. Ornis Svecica 27: 64–93.

Österblom, H., O. Olsson, T. Blenckner, and R. W. Furness. 2008. “Junk-Food in Marine Ecosystems.” Oikos 117, 967–77.

Österblom, H., Casini, M., Olsson, O., & Bignert, A. (2006). Fish, seabirds and trophic cascades in the Baltic Sea. Marine Ecology Progress Series, 323, 233–238.

Österblom, H., Fransson, T., & Olsson, O. (2002). Bycatches of common guillemot (Uria aalge) in the Baltic Sea gillnet fishery. Biological Conservation, 105, 309–319. https://doi.org/10.1016/S0006-3207(01)00211-7

Ponganis, P. J. (2019). State of the art review: From the seaside to the bedside: Insights from comparative diving physiology into respiratory, sleep and critical care. Thorax, 74, 512–518. https://doi.org/10.1136/thoraxjnl-2018-212136

Reed, T. E., Harris, M. P., & Wanless, S. (2015). Skipped breeding in common guillemots in a changing climate: Restraint or constraint? Frontiers in Ecology and Evolution, 3, 1–13. https://doi.org/10.3389/fevo.2015.00001

Regular, P. M., Hedd, A., & Montevecchi, W. A. (2011). Fishing in the dark: A pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. PLoS ONE, 6, 1–6. https://doi.org/10.1371/journal.pone.0026763

Rinjdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., Pinnegar, J. K. (2009). Resolving the effect of climate change on fish populations. ICES Journal of Marine Science, 66, 1570–1583.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., Schmitz, O. J., Smith, D. W., Wallach, A. D., & Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. Science, 343, 151–164. https://doi.org/10.1126/science.1241484

Rönnberg, C., & Bonsdorff, E. (2004). Baltic Sea eutrophication: Area-specific ecological consequences. Hydrobiologia, 514, 227–241. https://doi.org/10.1023/B:HYDR.0000019238.84989.7f

Saraiva, S., Markus Meier, H. E., Andersson, H., Höglund, A., Dieterich, C., Gröger, M., Hordoir, R., & Eilola, K. (2019). Uncertainties in projections of the baltic sea ecosystem driven by an ensemble of global climate models. Frontiers in Earth Science, 6, 1–18. https://doi.org/10.3389/feart.2018.00244

Sarzo, B., King, R., Conesa, D., & Hentati-Sundberg, J. (2021). Correcting Bias in Survival Probabilities for Partially Monitored Populations via Integrated Models. Journal of Agricultural, Biological, and Environmental Statistics, 26, 200–219. https://doi.org/10.1007/s13253-020-00423-1

Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., & Hiraldo, F. (2008). Top predators as conservation tools: Ecological rationale, assumptions, and efficacy. Annual Review of Ecology, Evolution, and Systematics, 39, 1–19. https://doi.org/10.1146/annurev.ecolsys.39.110707.173545

Strod, T., Izhaki, I., Arad, Z., & Katzir, G. (2008). Prey detection by great cormorant (Phalacrocorax carbo sinensis) in clear and in turbid water. Journal of Experimental Biology, 211, 866–872. https://doi.org/10.1242/jeb.014324

Sydeman, W. J., Thompson, S. A., Anker-Nilssen, T., Arimitsu, M., Bennison, A., Bertrand, S., Boersch-Supan, P., Boyd, C., Bransome, N. C., Crawford, R. J. M., Daunt, F., Furness, R. W., Gianuca, D., Gladics, A., Koehn, L., Lang, J. W., Logerwell, E., Morris, T. L., Phillips, E. M., … Zador, S. (2017). Best practices for assessing forage fish fisheries-seabird resource competition. Fisheries Research, 194, 209–221. https://doi.org/10.1016/j.fishres.2017.05.018

Thaxter, C. B., Wanless, S., Daunt, F., Harris, M. P., Benvenuti, S., Watanuki, Y., Grémillet, D., & Hamer, K. C. (2010). Influence of wing loading on the trade-off between pursuit-diving and flight in common guillemots and razorbills. Journal of Experimental Biology, 213, 1018–1025. https://doi.org/10.1242/jeb.037390

Walton, P., Ruxton, G. D., & Monaghan, P. A. T. (1998). Avian diving , respiratory physiology and the marginal value theorem. Animal Behaviour, 56, 165–174.

Wasserman, B. A., Reid, K., Arredondo, O. M., Osterback, A. M. K., Kern, C. H., Kiernan, J.

D., & Palkovacs, E. P. (2021). Predator life history and prey ontogeny limit natural selection on the major armour gene, Eda, in threespine stickleback. Ecology of Freshwater Fish, 00, 1–9. https://doi.org/10.1111/eff.12630

Watanuki, Y., Niizuma, Y., Gabrielsen, G. W., Sato, K., & Naito, Y. (2003). Stroke and glide of wing-propelled divers: Deep diving seabirds adjust surge frequency to buoyancy change with depth. In Proceedings of the Royal Society B: Biological Sciences, 270, 483–488. https://doi.org/10.1098/rspb.2002.2252

Weihs, D. (1973). Hydromechanics of fish schooling. Nature, 241, 290–291.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? Deep-Sea Research Part II, 54, 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Whelan, S., Hatch, S. A., Benowitz-Fredericks, Z. M., Parenteau, C., Chastel, O., & Elliott, K. H. (2021). The effects of food supply on reproductive hormones and timing of reproduction in an income-breeding seabird. Hormones and Behavior, 127, 1–21. https://doi.org/10.1016/j.yhbeh.2020.104874

Wilson, L. J. (2004). Self-feeding and chick provisioning diet differ in the Common Guillemot Uria aalge. Ardea, 92, 197-208.