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Diet and prey size preference in Razorbills *Alca torda* breeding at Stora Karlsö, Sweden

Vilken typ och storlek av bytesdjur föredrar häckande tordmular Alca torda *vid Stora Karlsö?*

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THE RAZORBILL *Alca torda* is one of three auk species breeding in Sweden, often occurring in colonies with Common Guillemot *Uria aalge*. The largest colony in the Baltic Sea is situated on the island Stora Karlsö west of Gotland. During the chick-rearing phase, Razorbills forage at sea and return to feed the young with single or multiple prey carried sideways in the bill, unlike Common Guillemots that carry a single fish in the middle of the bill. Clupeids, especially sprat *Sprattus sprattus*, are the main prey of Baltic Sea Razorbills, but studies are scarce. Here, we investigate the diet preference of Razorbills at Stora Karlsö with regard to prey taxonomy and size, analysing photographs and applying morphometric equations. We show that most feeding attempts involved a single clupeid (88% of known fish taxonomy), in most cases likely sprat. The average prey size (115 mm) and prey species was similar to that of Common Guillemots in the same colony. The variation in size was much smaller in the Razorbill diet than the size distribution of clupeids at sea, indicating a strong prey size selectivity. The Razorbills' high specialisation underlines the importance of maintaining strong populations of clupeids in their foraging area, as these fish are also targeted by industrial fisheries.

Keywords: auk | Alcidae | Clupeidae | sprat| *Sprattus sprattus* | Baltic Sea

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Introduction

Seabirds are important indicator species for changes in fish stock composition, and thus the status of the marine food web and ecosystem as a whole (Furness & Camphuysen 1997, HELCOM 2018). As seabirds compete with forage fisheries for prey, estimating their prey requirements is essential for achieving good conservation status (Sydeman *et al.* 2017, Saraux *et al.* 2020, Hentati-Sundberg *et al.* 2021). Diet and prey choice are key parameters for estimating prey consumption and prey requirements, and good estimations of these parameters are necessary for evaluating potential overlap between fisheries and marine top predators (Hansson *et al.* 2018). Studying diets is also important for comparing the ecological niche of sympatrically breeding seabirds to evaluate their competitiveness in the light of changing environmental conditions and climate change.

The Baltic Sea food web has experienced dramatic changes over the previous decades, with fisheries, eutrophication, and climate change being important driving forces (Österblom *et al.* 2007, Casini *et al.* 2008, HELCOM 2018). Notably, the recent strong decline of cod *Gadus morhua* has led to higher abundances of its main prey, clupeids (sprat *Sprattus sprattus* and herring *Clupea harengus*), but also decreasing clupeid body mass and energy content, probably due to increased intraspecific competition (ICES 2020). Seabirds in the Baltic Sea have responded to these food web changes, being sensitive to both quantity (Hjernquist & Hjernquist 2010) and quality (Österblom *et al.* 2006, Kadin *et al.* 2012) of the available prey. The size and quality (measured as lipid and fatty acid content) of sprat are highly correlated (Røjbek *et al.* 2014), which suggests that seabirds would target the largest possible prey, especially when feeding their offspring at the colony and making energetically costly commuting trips to foraging grounds.

The auk family (Alcidae) are widely distributed across high latitudes in the Northern Hemisphere. Globally, several auk species are declining due to fisheries and habitat reduction (Descamps *et al.* 2013, Vilchis *et al.* 2015) but there are also examples of species that show increasing trends, at least for populations in parts of their distribution range (Meade *et al.* 2013, Berglund & Hentati-Sundberg 2015, Olsson & Hentati-Sundberg 2017). In the Baltic Sea there are three auk species: Common Guillemot *Uria aalge* (also called Common Murre), Razorbill *Alca torda*, and Black Guillemot *Cepphus grylle*, of which Razorbill and Common Guillemot has increased strongly in recent decades (Ottvall *et al.* 2009, Olsson & Hentati-Sundberg 2017, HELCOM 2018). Until 2018 the global trend was declining for Razorbill, with the species listed as Near Threatened on the global IUCN Red List (BirdLife International 2018). However, the 2021 assessment has this reversed (BirdLife International 2021).

Comparing the diet of sympatrically breeding species can reveal how slight variations in morphologies affect prey preferences. While the Razorbill is an expert at diving, it is not quite as proficient as the Common Guillemot (Thaxter *et al.* 2010). Foraging Razorbills can carry fish sideways in the bill, thereby enabling them to bring several fish back to the colony from a feeding trip (Thaxter *et al.* 2013). On the other hand, in sympatrically breeding populations, Razorbills have been shown to bring smaller prey items than Common Guillemots (Chivers *et al.* 2012, Thaxter *et al.* 2013).

In this study, we investigate the prey preference of Razorbills at Stora Karlsö, Baltic Sea, by studying the species and size composition of prey, and comparing the results with scientifically collected fish abundance data. We also compare the results with previously published results on diets of sympatrically breeding Common Guillemots. Since the Razorbills have shallower dive profiles than the Common Guillemots (Thaxter *et al.* 2010) they may not reach the same size and/or high-quality prey as Common Guillemots. On the other hand, lower quality fish may be compensated by a higher number of prey items per trip for Razorbills. We thus hypothesise that (1) Razorbills will bring a higher number of fish (more than one); (2) Razorbills will target smaller prey items than sympatrically breeding Common Guillemots; (3) the size distribution of Razorbill prey is narrower (has lower variance) than the size distribution in the sea; and (4) sprat is preferred over herring due to its more suitable size and higher energy content.

Methods

STUDY LOCATION AND FIELD METHODS

Stora Karlsö is an island west of Gotland (57°17'1"N, 17°58'2"E) in the Swedish part of the Baltic Sea (Figure 1), with 25–45 m high cliffs suitable for breeding auks. The island hosts large Razorbill and Common Guillemot colonies, c. 12,000 and 15,700 pairs, respectively, which equals 30% and 70% of the total Baltic Sea populations (Olsson & Hentati-Sundberg 2017). Photographs of breeding Razorbills with prey in the bill were taken in connection to observational studies of chick feeding. The photographs were taken with a digital SLR camera with a 75–300 mm zoom lens from a distance of 25–40 m on the southwest part of the island. An opportunistic sampling strategy was applied: any adult Razorbill delivering fish to the general breeding area was included in the study. The photographs were taken in three different years: 4–13 July 2009 (377 photographs), 4 July 2010 (86 photographs), and 8–19 July 2012 (226 photographs). Photographs were taken during daylight hours, i.e. between 04:00 and 21:30. By analysing each photograph, the number of prey per feeding attempt and their taxonomic group were estimated. Furthermore, for photographs of sufficient quality and containing clupeid prey, prey size was estimated.

MORPHOMETRIC MEASUREMENTS OF CLUPEIDS

A typical photograph included a Razorbill with a single fish, most often a clupeid (see below), carried sideways in the bill, but often taken from an angle that did not show the full length of the fish. To estimate clupeid size from the photographs, we developed a method to predict total fish length from other more visible body features. This was done using morphometric equations based on measurements of dead sprat and herring collected by professional trawl fishing north of the island Öland in May 2019. Sprat and herring were initially frozen but thawed and measured with a measuring board and callipers to the nearest mm in the laboratory in 2020.

Four size measurements were taken: mouth to gill, body height (at the highest point), standard length, and total length (Figure 2). Even though standard length was sometimes easier to see in photographs (especially when the caudal fin was unclear), total length was used in the analyses. The reason is twofold: first, it is widely used in the literature (e.g., Kadin *et al.* 2012, Røjbek *et al.* 2014), and second, it

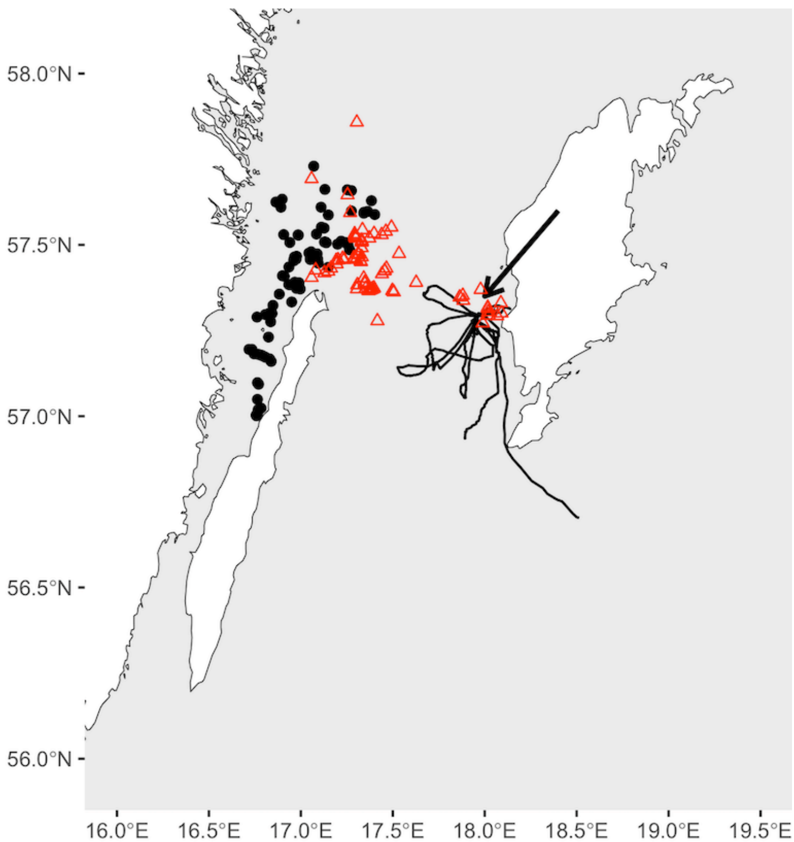

FIGURE 1. Location of Stora Karlsö (arrow) and location of PLAN FISH scientific fish samples (black dots), Razorbill *Alca torda* feeding locations in 2014 (red triangles), reported in Hentati-Sundberg *et al.* (2018), and Razorbill feeding trips in 2010–2015 (black lines), reported in Isaksson *et al.* (2019).
— Stora Karlsö (pil) och platserna för PLAN FISH vetenskapliga fiskprover (svarta cirklar), tordmularnas Alca torda *födosöksplatser 2014 (röda trianglar), enligt Hentati-Sundberg m. fl. (2018), samt tordmularnas födosöksturer 2010–2015 (svarta linjer), enligt Isaksson m. fl. (2019).*

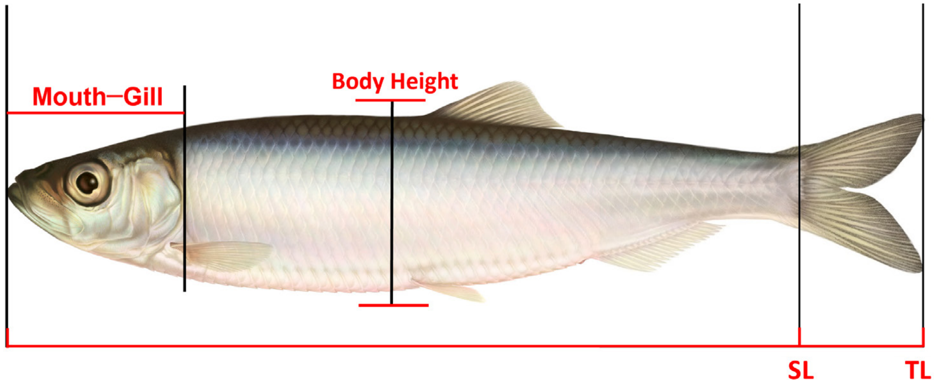

FIGURE 2. Measurements obtained from sprat *Sprattus sprattus* and herring *Clupea harengus* for morphology correlations. SL=standard length, TL=total length. Photo modified from © Linda Nyman/Artdatabanken.
— *Mått av skarpsill* Sprattus sprattus *och strömming* Clupea harengus *som tagits för morfologiska korrelationer. SL = standardlängd, TL = total kroppslängd, Mouth–Gill = mun till gäl, Body Height = kroppshöjd. Foto modifierat från © Linda Nyman/Artdatabanken.*

was the measurement used in the scientific data on fish abundance and size distribution, hence used as comparison to the Razorbill prey size (PLAN FISH, see below). As sprat is the most common food source recorded in earlier studies of Razorbills in the Baltic Sea (Lyngs 2001), and a preliminary analysis revealed that the prey sizes of Razorbills corresponded better to the size distribution of sprat, only sprat data was used to generate a method for prey size estimation. Linear regressions with the measurements of sprat with total length as the response variable and body height and head length as explanatory variables were made using R (version 2.6.0, R Core Team 2019) to find correlations with total length. From this data two equations were produced (Equation 1 and 2), see Results.

CLUPEID SIZE ESTIMATION

A total of 348 and 221 photographs from 2009 and 2012, respectively, showed Razorbills with forage fish in the bill. The photographs from 2010 were analysed like those from the other years but only contained a total of six feeding attempts and were therefore excluded from the size measurement aspect of the study. The final sample for size measurements included 125 clupeids at 117 feeding attempts documented in 189 photos.

Size estimation of clupeids in the Razorbill diet was done in the software ImageJ v. 1.52s (Schneider *et al.* 2012) with measurements from twelve Razorbills obtained from the Department of Zoology at the Swedish Museum of Natural History, used as scale. The measurements of the Razorbills included bill length (28.36 ± 2.2 mm), bill width, measured at the widest part of the bill, (10.04 ± 0.6 mm), head width, measured just behind the eyes, (40.55 ± 1.0 mm) and head height, measured at the position of the eyes, (51.30 ± 3.6 mm). Out of these, bill length (i.e. the hard part of the bill, measured from the bill tip to a point perpendicular to where the white eye line begins; see Figure 3) was used in most cases since the majority of the photographs clearly showed this feature. Field photographs were sometimes of low quality, and even when the bill was possible to measure the whole body of the fish could often not be seen, or the fish was captured in an angle that was not amenable to measuring. Therefore, body height or head length (mouth–gill) of the fish (whichever could be observed) was measured and Equations 1 or 2 was used to find an estimate of total length. If more than one photograph of the same feeding attempt was available, all photographs were measured and an average of the lengths of the fish were used. The same applied if more than one measurement could be recorded from one photograph, for example both total length and body height, in which case both measurements were recorded and the average total length used.

Every time a new measurement was taken, the reference scale of the Razorbill was added in the photograph and the fish length was measured at least three times to generate an average length. The process was

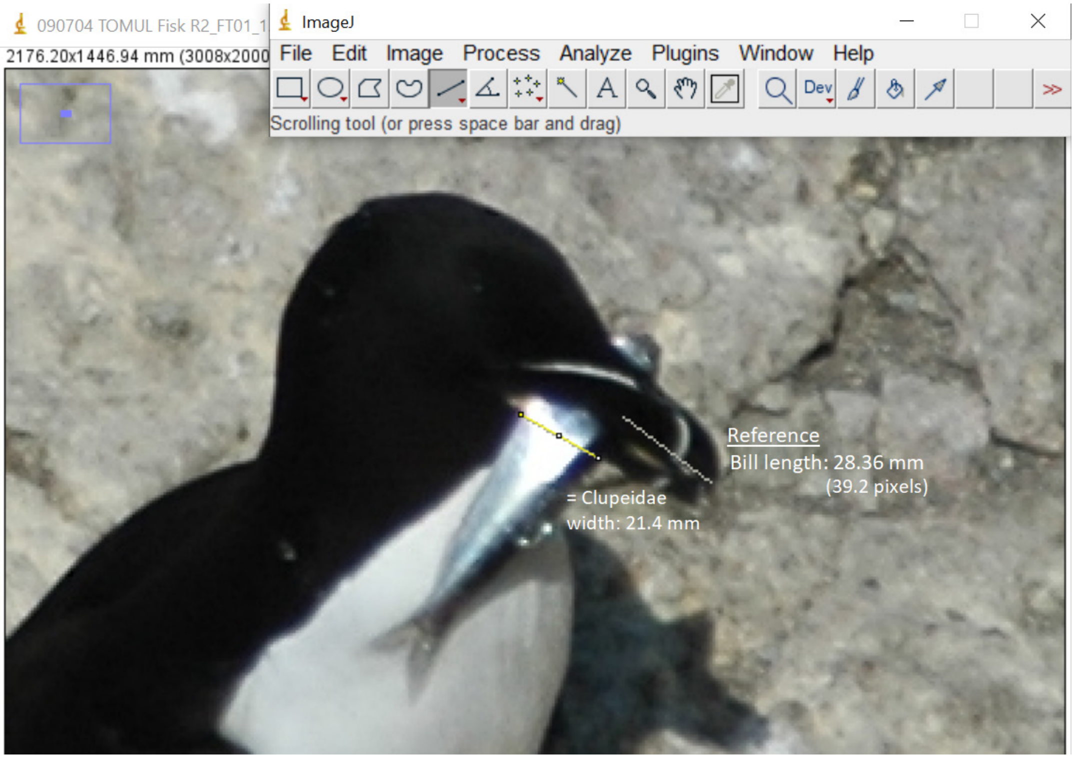

FIGURE 3. Example photograph from the software ImageJ v. 1.52s (Schneider ***et al.*** 2012) with the recorded bill length (reference scale 28.36 mm, equal to 39.2 pixels in this photograph) and the body height of the fish (21.4 mm), based on the reference bill length. In this example, bill length presented the clearest reference view, since bill width, head width, or head height cannot be assessed in this angle.
— Ett exempelfotografi i programmet ImageJ v. 1.52s (Schneider m. fl. 2012) med den uppmätta näblängden (referensskala 28,36 mm, motsvarande 39,2 pixlar i detta foto) och fiskens kroppshöjd (21,4 mm), baserat på näblängdens referensskala. I det här exemplet utgjorde näblängd den tydligaste referensen, då näbbredd, huvudbredd samt huvudhöjd är svårbedömda utifrån fotots vinkel.

then repeated for the same measurement, starting with the scale of the Razorbill, to get a more reliable result of that measurement of the fish. Every measurement had the scale redrawn at least twice. An average was taken and recorded together with other measurements of the same fish in the same or different photographs, if there were any. An example of how the reference scale and a fish measurement looked in ImageJ can be seen in Figure 3.

CLUPEID ABUNDANCE AND SIZE DISTRIBUTION

Data for relative abundance and size distribution of clupeid populations in the Baltic Sea were obtained from fish collected with a pelagic trawl with a 10 mm cod end, collected as a part of the PLAN FISH project at the Institute of Marine Research at the Department of Aquatic Resources, Swedish University of Agricultural Sciences (Figure 1). The dataset included the length of 5,460 sprat and 7,777 herring caught in May–August in 2009–2012 north of Öland, an area often used by the auks at Stora Karlsö to forage for prey (Evans *et al.* 2013, Hentati-Sundberg *et al.* 2018, Isaksson *et al.* 2019). To compare length distribution of prey in the Razorbill diet with length distribution of clupeids in the sea, we used the Welch t-test, which accommodates for the substantial difference in variance between the two datasets.

SENSITIVITY ANALYSIS

Due to the uncertainty of species composition in the Razorbill diets, there is a corresponding uncertainty in the size estimations obtained by the morphometric equations that were fitted for sprats. To evaluate this uncertainty, morphometric equations were developed also for herring, and the total lengths of clupeids in the

TABLE 1. Number of recorded prey from photographed Razorbills *Alca torda* at Stora Karlsö in the three study years. All fish were included if feeding attempts involved more than one fish.
— *Antal bytesfiskar som identifierats från fotograferade tordmular* Alca torda *vid Stora Karlsö under de tre studieåren. Alla fiskar inkluderades om matningen involverade mer än en fisk.*

Year *År*	Clupeidae	*Ammodytes* sp.	Unknown *Okänd*
2009	125	1	5
2010	6	–	–
2012	100	8	23
Total (%) *Totalt (%)*	232 (86.2%)	9 (3.4%)	28 (10.4%)

Razorbill diet was estimated separately assuming the prey was sprat or herring. Assuming a diet composition varying between 0% and 100% herring (at 10% increments) the mean and standard deviation of prey size were estimated. This analysis was repeated 100 times per diet composition category. The obtained prey size distributions were compared to the two years (2009 and 2012) of clupeid size distribution from the PLAN FISH dataset.

Results

TAXONOMIC COMPOSITION

A total of 239 feeding attempts comprising 268 fish were documented from the photographs, with 88% of feeding attempts involving a single fish and 12% involving two fish; no feeding attempt with more than two fish was recorded. In cases with two fish, 79% (23 feeding attempts) involved two clupeids. Species identity was generally difficult to determine from the photographs, especially between herring and sprat, which therefore were analysed together as clupeids. We could therefore not test hypothesis 4, that sprat would be preferred over herring. The vast majority (86.2%) of all prey were clupeids, 3.4% were sandeels *Ammodytes* sp., whereas 10.4% could not be determined (Table 1).

MORPHOMETRIC MEASUREMENTS OF CLUPEIDS

118 sprats with a total length varying between 83 mm and 133 mm and a mean of 107.8 ± 6.7 mm were measured. All measurements were not possible to obtain from each sprat, depending on their state. Given the angles of most Razorbill photographs, morphometric equations were used to estimate total length. These

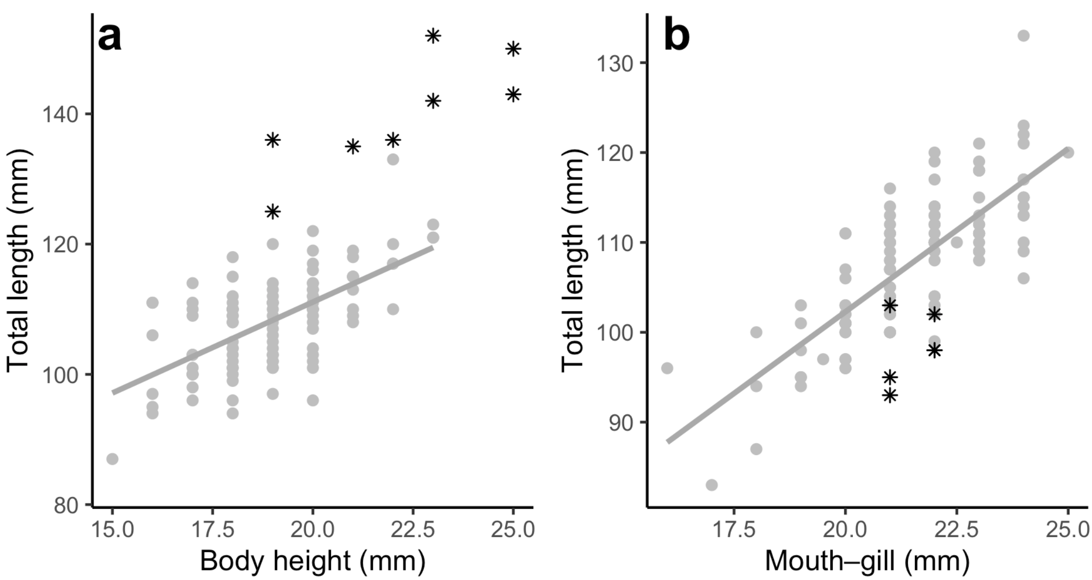

FIGURE 4. Regressions of the total length on (**a**) body height and (**b**) head length of sprat *Sprattus sprattus* (grey dots and line). Data for herring *Clupea harengus* (black stars) are added for reference.
— *Regression för skarpsillens* Sprattus sprattus *totala kroppslängd (grå punkter och linje) gentemot (**a**) kroppshöjd och (**b**) huvudlängd. Data för strömming* Clupea harengus *(svarta stjärnor) anges som referens.*

were derived from the regressions of body height and total length ($R2=0.39$; $F_{1,100}=64.07$; $P<0.001$; Figure 4a) and head length (mouth–gill distance) and total length ($R2=0.61$; $F_{1,113}=179$; $P<0.001$; Figure 4b). The equations are defined:

(1) Total length (mm) = 2.79 × body height + 55.24

(2) Total length (mm) = 3.63 × head length + 29.65

CLUPEID SIZE ESTIMATION

Of the 125 clupeids for which there were good enough photographs to estimate total fish length, body height (Equation 1) and head length (Equation 2) were used in 115 and 8 of the cases, respectively. The estimated total lengths were similar using the two methods (116.0 and 118.5 mm, respectively, Welch t-test: $t_{7.65}=0.77$, $P=0.46$) and the two samples were therefore pooled for the remaining analyses. The estimated total length of clupeids in the Razorbill diet varied between 84 mm and 140 mm. The average total length was similar between the two years with sufficient data (Welch t-test: $t_{88.17}=0.22$, $P>0.50$; Table 2) with a mean of 115.1 ± 8.5 mm (ranging from 84.4 to 139.7 mm) and 115.5 ± 9.7 mm (ranging from 93.8 to 137.5 mm), respectively. In recorded feeding attempts involving two fish, and where both could be measured, there was no considerable length difference (mean 5.1 mm difference of two clupeids in the same bill), although there were too few feeding attempts ($n=5$) to test this statistically. In 53 feeding attempts, there were more than one photograph (max = 4) of the same fish. The mean absolute error of fish length estimations from individual fish seen on several photographs was 5.3 mm, with an average coefficient of variation (CV) being 3.4%.

BALTIC SEA COMPARISON

For both years with comparable data (2009 and 2012), the prey length of Razorbills constituted a narrower span than the length distribution at sea (Figure 5), giving support to hypothesis 3. The length of the clupeids in photographs differed significantly from the length distribution at sea for all months and years (Welch t-test: $t_{148.73}=19.55$, $P<0.001$) as well as when comparing the two years separately (2009: Welch t-test: $t_{224.47}=6.33$, $P<0.001$; 2012: Welch t-test: $t_{61.37}=9.40$, $P<0.001$). All photographs were taken in July, and when

TABLE 2. Average fish length (total length; mm) and standard deviation of the clupeids measured from photographs as well as from the PLAN FISH data (sprat *Sprattus sprattus* and herring *Clupea harengus*). *— Genomsnittlig fisklängd (total kroppslängd; mm) och standardavvikelse för sillfiskar mätta från foton samt data från PLAN FISH (skarpsill* Sprattus sprattus *och strömming* Clupea harengus*).*

Data source *Datakälla*	Mean length (mm) *Snittlängd (mm)*
Photos 2009 *Foton 2009*	115.1 ± 8.5
Photos 2012 *Foton 2012*	115.5 ± 9.7
Photos both years *Foton båda åren*	115.2 ± 8.9
PLAN FISH 2009, *S. sprattus*	106.7 ± 12.7
PLAN FISH 2009, *C. harengus*	137.1 ± 24.5
PLAN FISH July *juli* 2012, *S. sprattus*	109.1 ± 14.5
PLAN FISH July *juli* 2012, *C. harengus*	135.4 ± 27.5

restricting the at-sea data to July only, all years pooled, the difference was also significant (PLAN FISH year 2010–2012, 2009 did not include July: Welch t-test: $t_{216.34}=14.95$, $P<0.001$). When separating herring and sprat in the PLAN FISH length distribution there was still a significant difference between this distribution and the length distribution from the photographs (sprat: Welch t-test: $t_{177.97}=3.93$, $P<0.001$; herring: Welch t-test: $t_{285.56}=27.40$, $P<0.001$). The Razorbill prey was larger than the average sprat and smaller than the average herring. Restricting the comparison to a period with directly comparable data (July 2012), the difference between the photographs and PLAN FISH July 2012 was also significant for the combined species (Welch t-test: $t_{73.46}=5.38$, $P<0.001$) as well as sprat (Welch t-test: $t_{64.71}=4.12$, $P<0.001$) and herring (Welch t-test: $t_{103.69}=11.48$, $P<0.001$) separately (Table 2, Figure 5).

The sensitivity analysis revealed that prey size is generally underestimated when assuming 100% sprat in the diet (as done above), and in the extreme case of 100% herring in the diet, the average prey size for the two years combined would have been 138.4 mm. The standard deviation of estimated sizes in the diet at different species compositions varied between 7.5 and 15.2 mm, with the largest span at mixed species composition (50% sprat and 50% herring). The standard deviation of clupeids in the sea was 33.3 and 29.1 mm for 2009 and 2012, respectively, i.e. markedly higher than the variation in the Razorbill diet, regardless of the assumption of prey composition. We could therefore conclude that the observed prey size preference (narrower span of fish sizes than in the sea) was not sensitive to our prey composition assumptions.

Discussion

By analysing photographs of Razorbills returning with prey it was clear that clupeids were the most common prey taxa at Stora Karlsö (Table 1). Distinguishing sprat from herring is difficult from photographs, but it is probable that the main proportion consisted of sprat, as the size distribution measured from the photographs was closer to that of sprat than that of herring in the PLAN FISH sea data (Table 2). The mean size of prey was similar across the two years with sufficient data (Table 2), and in most cases the birds carried a single fish home to the chicks.

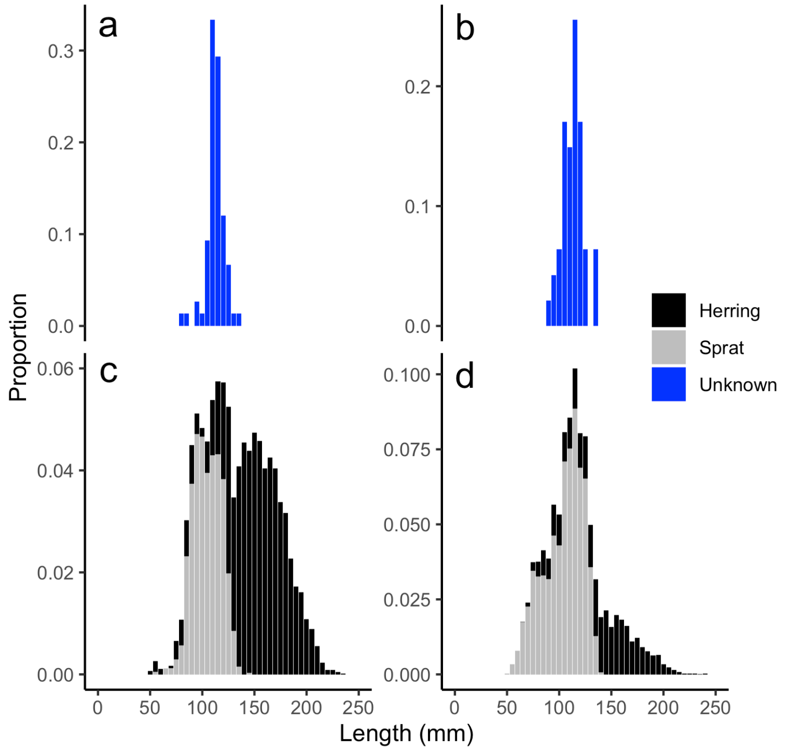

FIGURE 5. Length distribution of clupeid fish in Razorbill *Alca torda* diets in (**a**) 2009 and (**b**) 2012, and the corresponding length distribution among clupeids in the sea (**c**) 2009 and (**d**) 2012.
— Längdfördelning bland sillfiskar (svart = strömming, grå = skarpsill, blå = obestämd) i tordmulens Alca torda *diet (**a**) 2009 och (**b**) 2012, samt motsvarande längdfördelning i havet (**c**) 2009 och (**d**) 2012.*

The size of clupeids correlates with their quality as food (Røjbek *et al.* 2014): hence the larger the fish the better for the bird. However, catching large fish is likely associated with higher foraging costs, especially during the day, when larger sprats are distributed closer to the bottom (Cardinale *et al.* 2003, Andersen *et al.* 2017) and the birds have to dive deeper to catch them. The fact that clupeids caught by Razorbills were of a smaller average size than those sampled by PLAN FISH might indicate that larger clupeids occur deeper in the sea than the maximum Razorbill diving depth, or are too large for a Razorbill to catch (cf. Sanford & Harris (1967) for Common Guillemots). The sample size of recorded foraging bouts with more than one fish was limited (representing 12% of photographs), but the available data did not indicate an obvious size difference between the two prey items. This suggests that Razorbills at Stora Karlsö have the opportunity to double the prey per foraging flight but in most cases choose not to, which rejects hypothesis 1 that Razorbills would often target more than one prey per trip. Targeting several fish per trip likely involves a scaling of foraging costs, either because catching success decreases when already carrying prey, or because the cost of diving is higher relative to the cost of commuting. Some support for this comes from northern Norway, where 76% of recorded foraging bouts, across several seasons, contained a single fish (Barrett 2003). Similarly, a majority of the feeding attempts in Razorbill colonies on the island Røst comprise a single fish (Tycho Anker-Nilssen, *in litt.*).

The vast majority (79%) of feeding attempts that included more than one fish contained two clupeids. In fact, only six cases involved a prey species other than a clupeid, such as sandeel or an unknown species, and only one case involved two sandeels. This could reflect local prey conditions and schooling behaviour of fish. For instance, at Isle of May, Scotland, less than 3% of Razorbill feeding attempts comprised multiple species (Thaxter *et al.* 2013), normally of the same prey species as at Stora Karlsö. A higher percentage of multiple prey loadings in Razorbills have been recorded in northern Norway (Barrett 2003, Tycho Anker-Nilssen, *in litt.*), where the most common prey species, however, is also more slender (e.g. sandeels) than at Stora Karlsö. At Isle of May around 73.5% of the feeding attempts comprised two or more prey items (Thaxter *et al.* 2013), although earlier studies have found 63% being larger single fish (Harris & Wanless 1986). This illustrates how dynamic the marine environment is, and how seabirds can be indicators of such dynamics; depending on when and how long studies are carried out, results will differ, and comparisons may shed light on how fish stocks, seas, or birds are doing.

Given the clupeid dominance in the diet of Razorbills at Stora Karlsö, one may ask whether this reflects available prey items in the sea or a high prey specificity, either based on species or size. In Norway, the most common prey species at Røst were saithe *Pollachius virens* and sandeel together with some haddock *Melanogrammus aeglefinus* and herring (Tycho Anker-Nilssen *in litt.*), while at Hornøya in the Barent's Sea, the most common prey were sandeels and capelin *Mallotus villosus*, even if other fish species were also present around the colony (Barrett 2003). At Græsholmen in the Danish part of the Baltic Sea, Razorbills had a diet more similar that at Stora Karlsö, with the majority of prey being sprat, along with some sandeels as well as some three-spined sticklebacks *Gasterosteus aculeatus* (Lyngs 2001). Some sandeels occurred also at Stora Karlsö, as well as some prey items that due to poor photographs (blurry or taken from problematic angles) could not be identified to species. In summary, we conclude that the large dominance of clupeids in the Razorbill diet in this and earlier studies in the Baltic Sea (Lyngs 2001) reflects the abundance; herring and sprat are without doubt the dominant fish species in the pelagic ecosystem in the Baltic Sea (ICES 2020).

The average estimated prey length for Razorbills in 2009 and 2012 was 115.1 mm and 115.5 mm, respectively. However, there is some methodological uncertainty around these estimates, given that lengths are estimated from morphometric equations for sprat, and the samples could contain also small herring. Given the low number of herring available when developing the morphometric equations we were not able to establish morphometric relationships for herring, but the data available indicate that the length–body height relationship is different than for sprat, with the risk that fish lengths are underestimated. The estimated prey lengths for Razorbills do correspond to earlier reported prey of the sympatrically occurring and more numerous Common Guillemots at Stora Karlsö (112.7 mm, 2005–2009; Kadin *et al.* 2012). Despite the uncertainty in Razorbill diet estimates due to uncertain species determination, we can conclude that Razorbill prey items are not smaller than those of Common Guillemots, thus giving no support for our hypothesis 2 that Razorbills would target smaller prey than Common Guillemots. One difference between the species is that Razorbills generally fly further away from the colony to forage than Common Guillemots (Wanless *et al.* 1990, Thaxter *et al.* 2010, Hentati-Sundberg *et al.* 2018). This could make up for the better-quality sprat the Common Guillemots can catch closer to the colony since the Razorbills will have more access to food and can better deal with local depletions (Hentati-Sundberg *et al.* 2020). Studies using diving loggers have revealed that Common Guillemot dives are usually U-shaped (Evans *et al.* 2013) while Razorbills often perform sharper, V-shaped dives (Benvenuti *et al.* 2001, Shoji *et al.* 2015). However, at Stora Karlsö, Razorbills primarily use U-shaped dives with an average depth of 15.3 m and a maximum of 37 m (Isaksson *et al.* 2019), compared to Common Guillemots that also make U-shaped dives but often deeper than 60 m (Evans *et al.* 2013). The similarity in dive profiles for Common Guillemots and Razorbills at Stora Karlsö might suggest a more similar diet than in other sympatric colonies, but the diving depth difference is still puzzling. The similarity in diet but difference in diving preferences between the two species could potentially explain the three-week difference in onset of breeding in the two auk species at Stora Karlsö, i.e. that Common Guillemots but not Razorbills can access deeply distributed clupeids before their spawning onset in April–May.

The Razorbill has been increasing in Sweden for the last three to four decades (Ottvall *et al.* 2009, Olsson & Hentati-Sundberg 2017, HELCOM 2018). Ottvall *et al.* (2009) argued that this can be related to eutrophication and climate change, which can increase the amount of food and increase winter survival of the seabirds like the Razorbill (Heubeck *et al.* 2011, Eero *et al.* 2016). After the trophic cascade involving cod and sprat in the 1990s, the cod was thought to be recovering in the beginning of the 2000s (Eero *et al.* 2012, ICES 2020). However, this is not the case, and the cod were at the time of the study at record low levels whereas the sprat and herring stocks were considered to be within safe biological limits (ICES 2020). Continued high clupeid abundance within the breeding season foraging area is paramount for the future survival of this important Razorbill population, and a continuing increasing and least concern trend (BirdLife International 2021).

Razorbills are long-lived birds that lay only one egg per season, making them particularly vulnerable to changes in mortality. Complementing knowledge on prey choice for chick feeding with adult diets and foraging locations, and making detailed comparisons between prey abundance and prey capture, will reveal the amount of prey needed to sustain Razorbills in the Baltic Sea and within their global distribution.

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Svensk sammanfattning

Sjöfåglar är viktiga indikatorarter för förändringar i fiskbestånd och därför även för statusen av marina näringskedjor och ekosystem. Östersjöns näringskedja har över de senaste decennierna gått igenom stora förändringar med det kommersiella fisket, övergödning och klimatförändringar. Tordmule *Alca torda* är en av tre alkfåglar som häckar i Sverige, ofta i kolonier tillsammans med sillgrisslor *Uria aalge*. Globalt hade tordmularnas antal en nedåtgående trend fram till 2018, under 2021 ändrades dock detta till en uppåtgående trend. I Sverige har de dock ökat stabilt de senaste decennierna. Den största kolonin i Östersjön ligger på ön Stora Karlsö väster om Gotland. Under häckningssäsongen födosöker tordmularna till havs och återkommer bärande födan på tvären i näbben. På detta sätt kan tordmularna bära flera fiskar i näbben samtidigt, till skillnad från sillgrisslorna som endast bär en fisk i taget längs med mitten av näbben. Tidigare forskning har visat att sillfiskar Clupeidae (skarpsill *Sprattus sprattus* och strömming *Clupea harengus*) är den främsta födan för tordmular i Östersjön, särskilt skarpsill, men detta baseras på ett fåtal studier.

I denna studie undersöktes födopreferensen av tordmular på Stora Karlsö gällande bytesstorlek och taxonomi. Storleken jämfördes sedan med fiskstorlekar från Östersjön. Studien bestod av fotografier på tordmular med byte i näbben tagna på Stora Karlsö under 2009, 2010 och 2012. På dessa foton bestämdes fiskart, antal samt, där det var möjligt, storlek för sillfiskar. Fotona var ofta tagna från en vinkel som inte visade fiskens totala längd och därför uppskattades storleken på sillfiskarna med hjälp av morfometriska ekvationer framtagna från sillfiskar från samma plats, med tordmularnas näbblängd som storleksskala. Dessa storlekar jämfördes med storlekar på strömming och skarpsill från Östersjön 2009–2012.

Resultatet visar att majoriteten av födoförsöken involverade en enda fisk (88 %) och aldrig mer än två fiskar samtidigt. Majoriteten var sillfiskar (82,6 %), utöver det syntes tobisfiskar *Ammodytes* sp. samt fiskar som inte kunde artbestämmas. Den uppskattade totala längden på de mätta sillfiskarna varierade mellan 84 och 140 mm med medel på 115,1 mm (2009) och 115,5 mm (2012). Storleksspannet i havet var större än fördelningen av fiskar tagna av tordmular, vilket indikerar en selektivitet av tordmularna. Tordmularna valde signifikant större skarpsillar än medellängden i Östersjön, men signifikant mindre strömmingar än medellängden i havet. Det var däremot ingen direkt skillnad mellan storlekar på de fångade sillfiskarna jämfört med sillfiskar fångade av sillgrisslor i tidigare studier (~112,7 mm). Även bytesartskompositionen var liknande.

Tordmularnas specialiserade sillfiskdiet understryker vikten av att behålla starka populationer av skarpsill och strömming, vilka också påverkas av kommersiellt fiske inom tordmularnas födosöksområde.

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