FISH AND SEABIRD SPATIAL DISTRIBUTION AND ABUNDANCE AROUND THE LARGEST SEABIRD COLONY IN THE BALTIC SEA

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ABSTRACT

HENTATI-SUNDBERG, J., EVANS, T., ÖSTERBLOM, H., HJELM, J., LARSON, N., BAKKEN, V., SVENSON, A. & OLSSON, O. 2018. Fish and seabird spatial distribution and abundance at the largest seabird colony in the Baltic Sea. *Marine Ornithology* 46: 61–68.

We studied the at-sea distribution of two auks (Common Murre *Uria aalge*, Razorbill *Alca torda*), two gulls (Lesser Black-backed Gull *Larus fuscus,* Herring Gull *Larus argentatus*), and Great Cormorant *Phalacrocorax carbo* during the peak breeding season of 2014 around Stora Karlsö, the main Baltic Sea seabird colony. Simultaneously, we quantified forage fish abundance and distribution using hydro-acoustics and pelagic trawling. The auks and gulls had a roughly similar distribution, foraging mainly about 40 km west-northwest from the colony. Great Cormorants were found only in inshore areas, close to the colony. Sprat *Sprattus sprattus* and herring *Clupea harengus* biomass was, respectively, 1.38 and 2.68 mt/km^2 averaged over the whole study area. These estimates represent a total biomass for small pelagic fish of 17 900 t in the 4 408 km^2 study area. The estimated prey consumption over the breeding season was 2 310 t for Common Murre and Razorbill combined. Thus, auks may have a non-negligible impact on their prey sources in the region. Common Murres foraged closer to the colony (median 36.3 km) than Razorbills (median 41.1 km), but we found no significant correlation between auk at-sea numbers and fish densities. We discuss how new technology can contribute to detailed monitoring of the interactions between seabirds and fish at different spatial and temporal scales, with the ultimate aim of providing a scientific basis for ecosystem-based management.

Key words: *Alca torda*, ecosystem-based management, ecosystem surveys, forage fish, *Larus argentatus*, *Larus fuscus*, *Phalacrocorax carbo*, *Uria aalge*

INTRODUCTION

Interactions between marine top predators (e.g., seabirds) and fisheries involve a trade-off between conservation and resource harvesting in marine systems (Lescroël *et al.* 2016). Seabird-fish-fisheries interactions include direct mortality due to bycatch (Lewison *et al.* 2014), seabirds foraging on fishing discards (Bartumeus *et al.* 2010, Votier *et al.* 2004), and resource competition (Cury *et al.* 2011, Furness & Camphuysen 1997). Identifying, analyzing, and negotiating such trade-offs between ecosystem uses is a key aspect in the ongoing move from sectorial management to ecosystem-based management (Jennings & Quesne 2012, Link & Browman 2014).

In the Baltic Sea, the problem of gillnet bycatch of seabirds and marine mammals has been extensively studied, eliciting far-reaching action to mitigate the problem (such as a ban on driftnet fishing in 2008) (Hentati-Sundberg *et al.* 2015, Žydelis *et al.* 2009, Österblom *et al.* 2002). Less is known about the ecological interaction among small pelagic fish, fishing, and seabirds. Earlier studies have indicated that Common Murre *Uria aalge* productivity and chick mass at fledging are correlated with the condition of its main forage species: sprat *Sprattus sprattus* (Kadin *et al.* 2012, Österblom *et al.* 2006). However, in the Baltic Sea, birds and fish have so far been compared only on coarse temporal (annual) and spatial scales, making it difficult both to disentangle the detailed ecological relationship and to devise concrete management actions. Further, these earlier studies considered only one species (Common Murre), for which there were long-term monitoring data, making it difficult to draw general conclusions on the links between seabirds and fish stocks in the area.

In this study, we investigated finer-scale spatio-temporal dimensions of seabirds and fish stock interactions around Stora Karlsö, the largest seabird colony in the Baltic Sea (57°17′1N, 17°58′2E; Fig. 1).
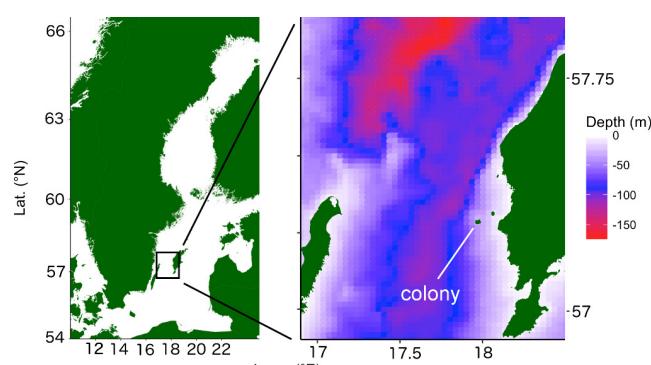

Fig. 1. Map of the study area with bathymetry indicated by colors.

Seabirds are central-place foragers during the breeding season, commuting to foraging areas, with the distance depending on phase in the breeding cycle and species-specific traits such as wing loading (Phillips *et al.* 2006, Quillfeldt *et al.* 2014, Croxall & Prince 1979, Pennycuick 1987). The ecological status of small pelagic fish, such as sprat and herring *Clupea harengus*, the key prey for pelagic seabirds in the Baltic Sea, is relatively well known at the scale of the whole Baltic Sea (ICES 2016). However, these species are known to conduct substantial intra-annual movements (Aro 1989), and the main scientific survey to determine density and distribution is performed in October—i.e., out of the seabird breeding season of May–July (ICES 2014). Thus, data for detailed comparisons of seabird and fish distributions have so far been lacking.

Analyzing fine-scale spatio-temporal dimensions of seabirds and fish has emerged in the last two to three decades, owing to improved hydro-acoustics technology as well as increasing availability of seabird-at-sea data (e.g., Piatt 1990, Fauchald *et al.* 2000, Grémillet *et al.* 2008, Fauchald *et al.* 2011). On large spatial scales, fish distributions can explain an important fraction of the variability in seabird numbers (Fauchald *et al.*, 2011). However, at scales of individual prey patches, spatial correlations are often only weakly positive, absent, or even negative, probably due to factors such as seabirds' (and researchers') imperfect information on prey densities and avoidance behavior in prey fish (Fauchald *et al.* 2011, Logerwell & Hargreaves 1996, Schneider & Piatt 1986, Schneider 1993, Weimerskirch 2007). Different seabird species often have differing at-sea distributions, despite relying on the same prey species (Certain *et al.* 2007, Croxall *et al.* 1997, Fauchald *et al.* 2011, Pettex *et al.* 2016). Describing and explaining such differences is a first step in identifying functional responses of seabirds to changing prey distributions, with the ultimate goal of identifying critical areas and periods for seabirds to inform dynamic ecosystem-based management (Dunn *et al.* 2016).

The goal of this paper is to present initial results relating at-sea distribution of seabirds from the Stora Karlsö colony to estimates of fish distribution in the area. Auk species at Stora Karlsö are at historically high levels, whereas gulls have shown a long-term decrease (Hentati-Sundberg & Olsson 2016, Olsson & Hentati-Sundberg 2017). A key question, therefore, is how much prey fish is necessary to sustain these colonies? We hypothesized that the distribution of the two auks and two gulls would be correlated with fish density, and specifically that: (1) Common Murres have the strongest spatial correlation with fish density, as they can dive to the bottom anywhere in the foraging area and thus are not limited by depth; (2) Razorbills *Alca torda* are also correlated with fish densities but are primarily found at shallower depths due to their limited diving ability; (3) gulls (Lesser Black-backed *Larus fuscus*, Herring *Larus argentatus*) forage further from the colony than the auks, because of their diving ability is limited, but they have the capacity to commute longer distances at a lower energy consumption; and (4) Great Cormorants *Phalacrocorax carbo* feed in inshore areas due to a different (benthic) forage base compared with the auks and gulls.

METHODS

Fish density and the spatial distribution of five fish-eating seabirds (Common Murre, Razorbill, Lesser Black-backed Gull, Herring Gull and Great Cormorant) were simultaneously monitored in the waters around the island of Stora Karlsö during the peak of seabird breeding, 15–19 June 2014. For this combined fish–bird survey, we used a 24 m commercial fishing vessel equipped with a scientific echo-sounder and a pelagic trawl, as detailed in the following paragraphs.

Birds were counted during daylight hours (03h30–23h00 UTC+2). The visibility was good during the whole survey, and wave height never exceeded 0.5 m. The following data were recorded for each observation: species, number, position, time, activity (on surface or flying), and flight direction. Only birds observed in the transect, 300 m in front and 300 m to either side (the side with the best visibility) of the vessel, were recorded, and there were two observers present at all times, according to the vector method of Spear *et al.* (2004). Observation height was 4 m, and the speed of the vessel was normally 5 knots. In the statistical analysis of the bird observations, we analyzed surface observations of auks and cormorants, and flight observations of gulls. This was motivated by the fact that auks and cormorant commute to foraging areas, where they actively forage by diving from the surface, whereas gulls move around searching for prey near the sea surface.

Fish densities were derived through integration of echoes recorded with a SIMRAD EK60 split-beam echo-sounder, equipped with a general-purpose transceiver (GPT) and a SIMRAD ES120-7C (120 kHz) transducer. The beam angle was 7°, implying a beam width of 21.3 m at 100 m depth. The raw data from the echo-sounder were integrated for each 0.05 nautical mile (92.6 m), which yielded spatially explicit S_a (nautical area backscatter coefficient) values in meters squared per nautical mile squared. To relate echo strengths to fish species and size class, three tows were made using a pelagic trawl with a 12 mm mesh size at the cod end (for sampling details, see ICES 2014). The tows were used to investigate species and size composition and to estimate total fish abundance and biomass in the survey area. This was done through distributing the total returned acoustic signal (S_a) based on the number of fish of different species and sizes recorded in the tows. Target strength (*TS*) of individual fish is given by the equation:

$$TS = a_i + b_i * \log (L)$$

Where a_i and b_i are species-specific constants, and *L* is the total length of individual fish measured in centimeters. We used *a* = -65 for cod (Rose & Porter 1996) and -74.2 for the other species (Saunders *et al.* 2012, ICES 2014). The value of *b* was set to 20 for all species, following ICES (2014). This analysis yielded a total figure of abundance per length class in the study area. As a next step, weight of individual fish from the trawls were used to calculate biomass per species and length class for the whole study area. Because only three tows were made, we did not make the translations of returned acoustic signal to biomass for the spatial-explicit analysis of fish. Thus, reported spatially explicit fish data are in the form of raw S_a values (densities), rather than quantities (number or biomass).

Three statistical tests were performed to investigate the bird foraging distribution in relation to fish density. First, the general foraging area of the species was compared by aggregating all observations with the observation effort (measured as km² surveyed) into an evenly spaced grid with a resolution of 9 km² (squares with 3 km sides). The distributions were compared using a Syrjala test, a non-parametric statistical test for two spatial distributions, that is sensitive to distributional differences but insensitive to abundance

differences (Syrjala 1996). The tests were run pairwise between all the studied species, with the null hypotheses that the distributions were the same.

Second, we ran statistical models to investigate whether bird density was affected by fish density, depth, and distance from the colony. We used the 9 km^2 grid, described above, but also grids with resolutions of 0.25, 1, 4, 25, and 50 km^2. We used such a broad spectrum of resolutions to attempt to find fine-scale spatial overlaps as well as more coarse-scale associations between seabirds and fish. Here, we used a multi-model inference approach, in which we fitted general additive models (GAMs) with all combinations of parameters, and calculated average parameter values based on Akaike's information criterion (AIC)-weighting of the different models (see Burnham *et al.* 2011). This was done separately for each spatial scale and separately for the two auk species. The models took the general form:

Bird density ~ α + Fish density + Depth + Colony distance + s(Lat, Long) + ε

Where α is the intercept, s denotes a smoothing spline to control for spatial autocorrelation, and ε is the error term.

In this analysis, we removed all observations farther than 60 km from the colony, as this was considered to be outside the foraging range for breeding auks. Bird density and fish density were log transformed (log X + 0.1) to achieve linearity. Using the same setup, we also looked at possible nonlinear associations of seabirds with prey abundance, colony distance, and depth, using smoothing splines also for these parameters. In this analysis, smoothing was limited to four degrees of freedom to avoid over-fitting of nonsensible biological relationships.

Last, we estimated total prey consumption for auks in the study area using an approach adopted from Roth *et al.* (2008). Here, we used literature values on field metabolic rate (FMR) and assimilation efficiency (Hilton *et al.* 2000) of Common Murre, together with previously reported data on colony size (Olsson & Hentati-Sundberg 2017) and prey energy content (Eneqvist 2003). The detailed figures for Common Murre were translated into a value for Razorbill, adjusted for differences in colony size and body mass. Consumption by gulls and Great Cormorant was not analyzed due to lack of data on diet and field metabolic rate for those species.

RESULTS

The spatial distributions of the five seabirds had some commonalities but were generally quite different from each other (Fig. 2). Common Murre was the most widely distributed species and was seen both in shallower areas close to the island of Öland, west of Stora Karlsö, and also in the relatively deep areas lying between the two islands (Fig.
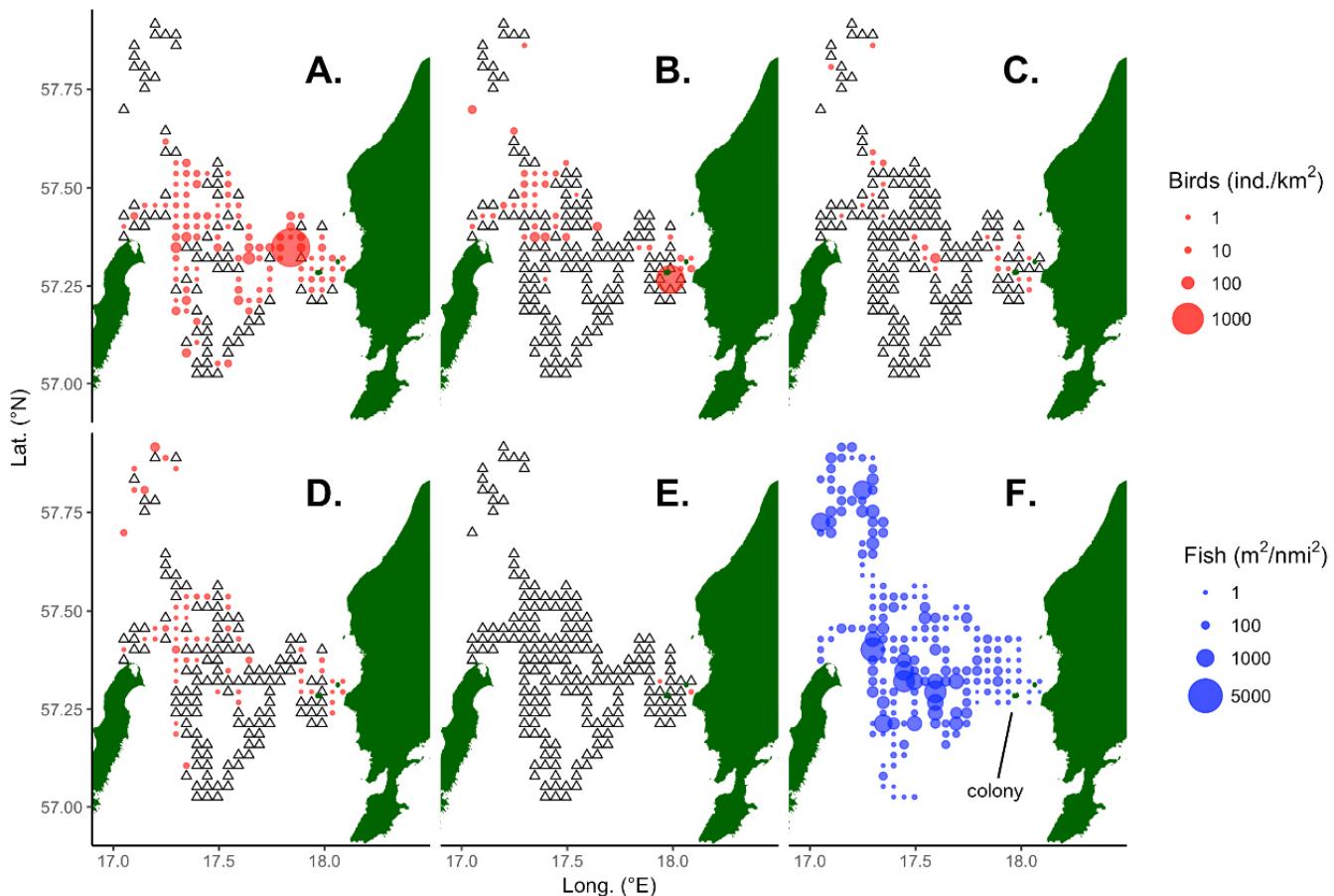
Fig. 2. At-sea distribution of five seabird species: (A) Common Murre, (B) Razorbill, (C) Lesser Black-Backed Gull, (D) Herring Gull, (E) Great Cormorant, and distribution of fish (F) around the Stora Karlsö colony, June 2014. All observations are summarized in an evenly spaced grid with a resolution of 9 km^2. Black triangles indicate that no birds were observed.

2A). Razorbills were more concentrated in the shallower areas about 40 km northwest of the colony (Fig. 2B). Lesser Black-backed Gulls were quite evenly distributed west and northwest of the colony (Fig. 2C), whereas Herring Gulls were more common further away from the colony (Fig. 2D). Last, Great Cormorants were seen only very close to the shore (Fig. 2E), which suggests a different forage base, also shown in earlier studies in the Baltic Sea (Lehikoinen *et al.* 2011, Östman *et al.* 2013). For the two gulls, by using flying observations we could not distinguish between birds that were commuting and those that were actively feeding. Further, their breeding numbers on Stora Karlsö are much lower (*Larus fuscus* 364 pairs, *Larus argentatus* 248 pairs) than the numbers of auks (*Uria aalge* 15 700 pairs, *Alca torda* ≈10 000 pairs) (Olsson & Hentati-Sundberg, 2017), which makes observation rates of the auks at sea higher. With this in mind, the distribution estimates and statistics should be interpreted with caution. However, a general foraging area for gulls and auks was detected, ca. 40 km west-northwest of the colony. All of the at-sea distribution differences between species were significant (Syrjala test, $P < 0.05$) at the 9 km^2 spatial resolution shown in Fig. 2.

Five fish species were recorded during the survey, with the following relative abundance (measured in numbers): sprat (58%), Atlantic herring (31%), three-spined stickleback *Gasterosteus aculeatus* (9.9%), Atlantic cod *Gadus morhua* (0.09%), and sandeel *Ammodytes tobianus* (0.006%). The length distribution and corresponding estimated biomass of the five fish species recorded during the survey is given in Fig. 3. As sprat and herring are known to be the dominant prey of Common Murre and Razorbill at Stora Karlsö (Kadin *et al.* 2015, pers. obs.), our detailed analysis focused on those species. Sprat and herring abundance was 11 300 and 8 400 individuals/km^2, corresponding to 1.38 and 2.68 t/km^2, respectively, averaged over the whole study area. These estimates represent a total biomass for small pelagic fish of 17 900 t in the 4 408 km^2 study area. The prey consumption of Common Murre and Razorbill over the breeding season was estimated to be 1 480 t and 840 t, respectively (Table 1). Thus, seabirds may have a non-negligible impact on fish resources around the colony.
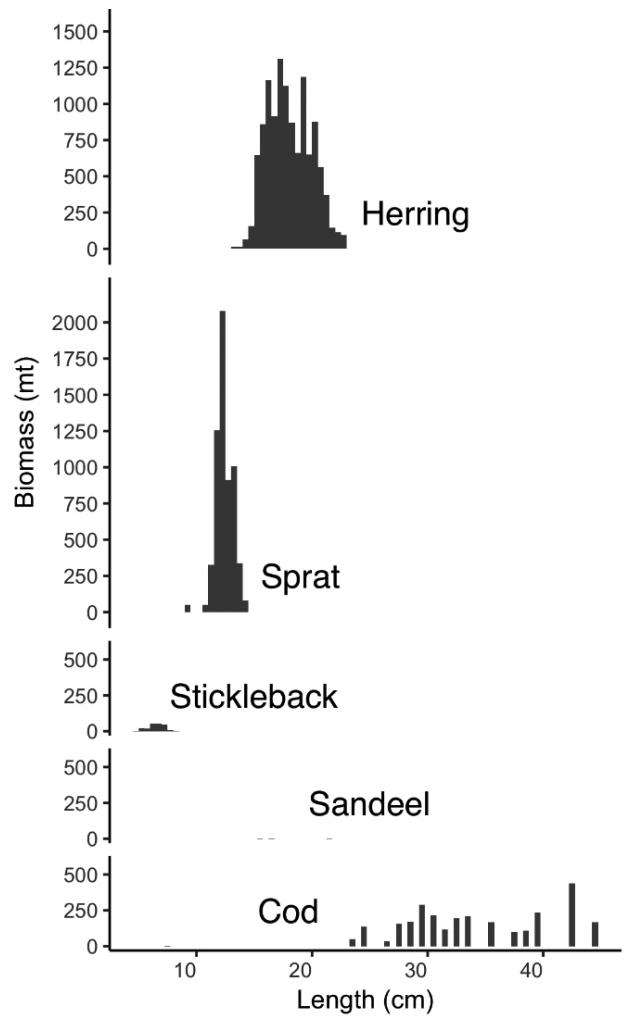
Fig 3. Total fish biomass by species and length class recorded in the study area around island of Stora Karlsö, June 2014.

TABLE 1
### Estimated prey consumption of Common Murres and Razorbills during breeding at Stora Karlsö

Parameter	Description and source	Value
Common Murres		
FMR breeders	Field metabolic rate (Roth *et al.* 2008)	1 530 kJ/d
FMR non-breeders	Field metabolic rate (Roth *et al.* 2008)	1 392 kJ/d
Assimilation efficiency	True metabolizable energy coefficient, (Hilton *et al.*, 2000)	0.78
Energy requirement breeders		1 784.62 kJ/d
Energy requirement non-breeders		1 961.54 kJ/d
Karlsö breeding individuals	(Olsson & Hentati-Sundberg 2017)	31 400
Karlsö non-breeders	Immature birds, estimated from unpublished data from ringing and resightings	15 700
Breeding season length		90 d
Total energy	Over the whole breeding season	8 064 969 231 kJ
Sprat energy content	(Enekvist, 2003)	5.46 kJ/g
Consumption		1 477.1 t
Razorbills		
Consumption	Based on consumption calculated for Common Murre adjusted for the difference in population numbers (Olsson & Hentati-Sundberg 2017) and in body mass	842.48 t

Razorbill was found to be foraging further from the colony than Common Murre (average 41.2 and 36.3 km, respectively; $P < 0.001$ for difference, non-parametric bootstrapping; Fig. 4A). Both species foraged farther from the colony than would have been observed if they had a uniform distribution in the study area (Fig. 4A). There also appeared to be a difference in depth at which the birds were foraging, but this difference was not statistically significant (Razorbill median 60.5 m, Common Murre median 70.1 m, $P > 0.05$; Fig. 4B). However, both species were found at depths shallower than would have been observed if they were uniformly distributed in the area (Fig. 4B). The main feeding area observed for both seabird species roughly corresponded to the area with the highest fish densities (Fig. 2F).

Our attempt to model the general distribution of the two auks revealed that none of our candidate predictors (fish distribution, distance from colony, and depth) could explain bird densities at any studied spatial scale (Fig. 5). In the models run, there was a clear spatial co-variance structure, but, after accounting for that, the three candidate predictors were insignificant. We also investigated possible nonlinear relationships between bird distribution and fish density, depth, and distance, and similarly found that they were insignificant in predicting bird distribution (results not shown).
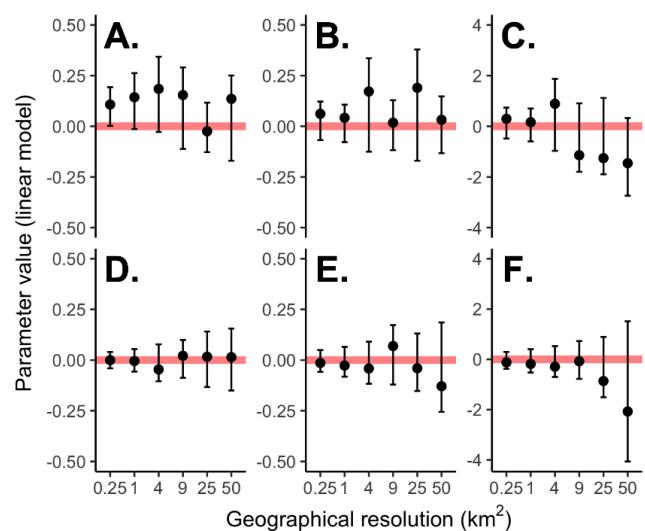
DISCUSSION

We simultaneously surveyed seabirds-at-sea in conjunction with hydro-acoustics and trawl sampling to determine whether seabirds tracked the prey distribution. Distinct differences in seabird distribution were found. Great cormorants were observed only very close to the colony. The two auks and two gulls had a roughly similar distribution (although significantly different) and were most likely feeding on the same prey, i.e., the most abundant species in the study area, sprat and small herring. For the two seabird species for which the most detailed foraging data are available, Common Murre and Razorbill, we found that Razorbill foraged further away from the colony and at shallower depths, whereas Common Murres foraged in deeper areas close to the colony. We see two likely explanations. Despite their similarities, Common Murre and Razorbill have slightly different physiological adaptations. Murres, having higher wing loading but comparatively better diving abilities, would benefit from shorter trips and from feeding in deeper waters
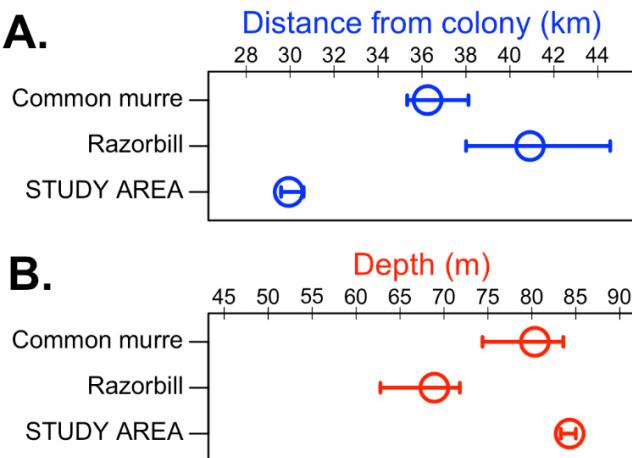
(Thaxter *et al.* 2010). A similar difference in behavior has also been reported between Common Murre and the closely related Thick-billed Murre *U. lomvia*, in which the former performed deeper dives and used their wings more frequently under water, indicating a higher capacity for catching fast-moving prey at deeper depths (Kokubun *et al.* 2015). The other possible explanation is related to a difference in breeding timing. On Stora Karlsö, murres breed about three weeks earlier than Razorbills, which means that murres were in the chick-rearing phase when this study was performed, whereas Razorbills were at the end of incubation. Seasonal differences in foraging behavior have been shown previously for both Common Murre (Cairns *et al.* 1987) and Thick-billed Murre (Falk *et al.* 2000) and for Lesser Black-backed Gulls breeding in Stora Karlsö (Isaksson *et al.* 2016). In the case of the murres, the need to feed chicks may have implied a need for shorter trips to maintain feeding rates, thus explaining the observed difference. At this stage, these two hypotheses are not mutually exclusive. There may be additional hypotheses, such as competitive exclusion between the species in foraging area use. Future studies studying detailed feeding behavior over a whole breeding season will be needed to distinguish among those hypotheses.

We did not find any statistically significant correlation between fish and seabird distributions at any studied scale (0.25–50 km^2). Although a visual inspection of the data indicated a coarse spatial overlap (Fig. 2), in the statistical models for Common Murre and Razorbill, smoothed spatial coordinates were the only significant predictors, and parameter values for fish density, distance from colony, and depth included 0 in the 95% confidence interval. This is similar to studies in other systems that have found similarly weak predator–prey correlations at small spatial scales (Fauchald *et al.* 2011, Logerwell & Hargreaves 1996, Schneider & Piatt 1986; but see Piatt 1990). Both imperfect information on detailed fish distribution among the birds and the fact that fish schools avoid areas with high bird densities, or even avoid the survey vessel, probably leading to the difficulty in finding fine-scale correlations.

Fig. 4. Characteristics of foraging habitat of Common Murre and Razorbill in terms of (A) distance from breeding colony and (B) depth.

Fig. 5. Parameter values for general linear models of at-sea distribution of auks at different geographical scales. Densities of Common Murres predicted by (A) fish abundance, (B) depth, and (C) distance from colony; and of Razorbills as predicted by (D) fish abundance, (E) depth, and (F) distance from colony.

The beam for collecting the acoustic data is very narrow (~90 m^2 at 50 m depth), whereas the area for the bird observations is around 90 000 m^2. Therefore, researchers have imperfect information on fish schools, too! Our dataset was also limited in time.

An improved methodology, in which the fish–bird interaction can be studied in even greater detail, e.g., with permanent acoustic buoys or autonomous vessels, could be an interesting way to better integrate fine-scale predator–prey patterns (e.g., Axelsen *et al.* 2001, Cimino *et al.* 2016, Solberg *et al.* 2015). In parallel, complementary seabird data could be obtained using emerging data-logger technologies (which could give detailed information on foraging of breeding birds) or possibly using radar, which would cover the whole breeding and non-breeding population (Assali *et al.* 2017, Lilliendahl *et al.* 2003).

Our data re-emphasize the result from earlier studies (Evans *et al.* 2013, Olsson *et al.* 1999) that have identified the area between islands of Öland and Gotland as a "hot spot" for seabirds in the Baltic Sea (Fig. 2). This area is also important for trawl fisheries for sprat and herring (Hentati-Sundberg *et al.* 2015). Fish biomass was surprisingly low, and in the same order of magnitude as the total consumption of the auks, over the entire breeding season. Compared with the regular scientific survey in October 2014, the abundance (numbers) of sprat and herring was about 1/6 and 1/3 of the area-corrected abundance in the same area (ICES statistical rectangle 43G7), indicating a strong intra-annual variation in fish abundance (ICES 2016).

The populations of both auk species have increased substantially at Stora Karlsö since the mid-1980s—by 130% and 600% for *Uria aalge* and *Alca torda,* respectively (Olsson & Hentati-Sundberg 2017)—and they may approach a point where population growth will be limited by prey availability. Gull numbers, on the other hand, have decreased over time, with rates of 5.0% and 6.2% per year for *L. fuscus* and *L. argentatus*, respectively, over the last 10 years (Olsson & Hentati-Sundberg 2017). One hypothesis to explain this diverging pattern could be that the surface-feeding gulls have a higher prey need for successful breeding, or, in other words, that the auks' buffering capacity is higher (e.g., Zador & Piatt 1999), giving them a more nonlinear functional response to prey abundance (Cury *et al.* 2011). Gulls may also have previously foraged on cod fisheries discards, but there is currently very little cod fishing in the area due to a spatial contraction of the Baltic Sea cod stock (Casini *et al.* 2012). An alternative hypothesis is that the increasing population of auks is reducing the abundance of small pelagic fish around the colony, negatively affecting gulls. Such competitive exclusion has been discussed earlier, e.g., between salmon (*Onchorhynchus* spp.) and seabirds in the California Current System (Ainley *et al.* 2009), and between sympatric petrels and albatrosses in South Georgia (Phillips *et al.* 2005). In any case, our preliminary results provide an argument for spatial protection around the breeding colony during summer, similar to management actions taken elsewhere (e.g., the North Sea sandeel box; Frederiksen *et al.* 2008).

The ICES Baltic Sea Integrated Assessment (Möllmann *et al.* 2013) and the global Ocean Health Index (Halpern *et al.* 2008) are examples of integrated assessment and indicator schemes that combine existing data from diverse sampling schemes and institutions from the conservation and fisheries sectors. In this study, we instead conducted simultaneous monitoring on multiple components of the ecosystem, in a study conceived, designed, and carried out in partnership between seabird ecologists and fisheries scientists. Despite the preliminary nature of our empirical findings, it is clear that the simultaneous monitoring scheme piloted through our study can be further developed to advance our spatial and temporal understanding of species' interactions and thereby to contribute to dynamic approaches to ocean management, for addressing specific, place-based ecosystem trade-offs (Dunn *et al.* 2016). In more practical terms, our study provides an example in a European context of how ecosystem surveys, used successfully elsewhere (e.g., Ainley *et al.* 2009, Santora *et al.* 2011), could be developed to provide the type of ecosystem data required to fulfil the obligations stipulated in the European Common Fisheries Policy (EC 2013) and Marine Strategy Framework Directive (EC 2008).

ACKNOWLEDGMENTS

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