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Grey seal *Halichoerus grypus* recolonisation of the southern Baltic Sea, Danish Straits and Kattegat

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The grey seal became locally extinct in the southern Baltic Sea, Danish Straits and Kattegat in the early 1900s after prolonged culling campaigns. Here, we combine national monitoring and anecdotal data from Denmark, Sweden, Germany and Poland to report on the grey seal's recolonisation of those areas and the initial reestablishment of breeding colonies. Grey seal occurrence has steadily increased since year 2003 as evidenced by the coordinated Baltic Sea moult censuses. At the first census in 2003, there were 146 grey seals along the southern Baltic coasts of Sweden and Denmark, ca 1% of the total Baltic Sea population count. Since 2015, this has increased to 2000–2600 grey seals, or ca 7% of the total population count. Since the local extinction, there have been sporadic breeding events in the 1940s on sea ice around Bornholm and in the 1980s and 1990s on haul-outs in Kattegat. In 2003, the first two pups in the southern Baltic Sea were recorded at Rødsand, Denmark. This is to date the only site in the southern Baltic Sea with regular annual pupping since the recolonisation. Since 2000, there have also been sporadic breeding events in Danish Kattegat, southern Sweden, Poland and Germany. At Rødsand, there have been at least 3–10 pups recorded every year since initiation of monitoring in 2011, with an increasing tendency until 2017 with 10 pups counted, which subsequently decreased to 5–6 pups annually in 2018–2020. Compared to recolonising events in the Atlantic, the numbers of pups are low. This may be caused by differences in population dynamics, recolonisation distances, habitat and mortality and effects of rehabilitation programmes. It is likely that the breeding distribution will spread throughout the southern Baltic, Danish Straits and Kattegat if appropriate protection measures of seals and haul-outs are installed.

Keywords: abundance, distribution, management, Pinnipedia, population recovery, survey data

The grey seal *Halichoerus grypus* has historically occurred along the coasts of mainland Europe from Brittany to Murmansk (Härkönen et al. 2007, Nilssen and Haug 2007, Zirianov and Mishin 2007). Two subspecies with distinct breeding periods occur in Europe; the Baltic subspecies *H. g. grypus* and the Atlantic subspecies *H. g. atlantica* (Fietz et al. 2016, Olsen et al. 2016). Throughout their range in continental Europe, grey seals have been hunted extensively, resulting in local extinctions in the Wadden Sea in the late Middle Ages (Reijnders et al. 1995), and in the southwestern Baltic in early 20th century as the result of culling campaigns (Søndergaard et al. 1976, Gill 1978, Harding and Härkönen 1999).

In the entire Baltic Sea, the grey seal population was in the range of 88 000–100 000 at the onset of the 20th century (Harding and Härkönen 1999). Extensive culling rapidly reduced the numbers to about 20 000 animals in the 1940s (Harding et al. 2007). A further decline to about 3000–3600 animals by the mid-1970s was caused by environmental pollution by organochlorines, primarily PCBs and DDT, polychlorinated biphenyls and dichlorodiphenyltrichloroethanes, respectively (Jensen et al. 1969, Helle 1980, Harding and Härkönen 1999, Harding et al. 2007). Pregnancy rates as low as 20–30% were observed during the period 1973–1979 due to infertility in the females caused by occlusions and stenosis in their uterine horns (Bergman 1999, Harding and Härkönen 1999, Helle 1980). After the use of these contaminants has been abandoned and their effects have attenuated, and the introduction of a general culling and hunting ban, the population has been growing exponentially since the 1980s (Harding and Härkönen 1999,

Härkönen et al. 2007, HELCOM 2018). In the years 2014–2017, numbers have been stagnating around 30 000 individuals counted in the Baltic Sea at the haul-outs in the moulting season in late May and early June (ICES 2019). After this period of stagnation, ca 38 000 seals were counted in 2019 (ICES 2020).

In the southern Baltic Sea, the Danish Straits and Kattegat (Fig. 1), the number of grey seals was probably already much reduced at the onset of the culling campaigns in the late 19th century (Olsen et al. 2018). Ancient DNA analyses have shown that grey seals in the southern Baltic Sea genetically were part of the larger Baltic Sea population and subspecies (Fietz et al. 2016), and zooarchaeological findings indicate that grey seals were the most common species of seal in Kattegat and the southern Baltic Sea prehistorically (Møhl 1971, Lepiksaar 1986, Olsen et al. 2018). This is corroborated by historical sources which hint that until the early 19th century, the grey seal was the most common species of seal in Kattegat (Bynch 1801). In contemporary historic literature prior to the local extinction, there are descriptions of several grey seal breeding colonies in Kattegat and the southern Baltic Sea. In Kattegat and Skagerrak, between the Baltic Sea and the North Sea (Fig. 1), the peak pupping activity seems to have occurred in January historically, which is between the current pupping periods of grey seal populations in the Baltic Sea (February–March) and in the northeast Atlantic (October–December), respectively (Søndergaard et al. 1976). Danish breeding colonies mentioned are: Sønder Rønner near Læsø (Faber 1828), Anholt (Bynch 1801) and Rødsand (Fig. 2) (Tauber 1880, 1882). Historical seal hunting using clubs and hatchets, which is unlikely to target other seals than grey seal pups, is reported from Sjællands Rev and Hesselø (Søndergaard et al. 1976). Even after the local extinction in the late 19th century, several grey seal pups were seen on sea ice around Bornholm during the severe winters in the early 1940s (Søndergaard et al. 1976). Along the Swedish west coast, there were breeding grey seals in the early 19th century at Koster Islands, Väderöarna, Onsala, Varberg and probably Hallands Väderö (Malm 1877, Dahlbeck 1974). On the other hand, German references do not mention regular breeding sites in German waters (Mohr 1956), but there are several historical reports of newborn pups in Germany, sporadically documented along the coastline (Hornschuch and Schilling 1850, Friedel 1882). Already around 1850 the number of grey seals were severely reduced (Boll 1847).

In the southern Baltic Sea, Danish Straits and Kattegat, grey seals only occurred sporadically from the time of their local extinction in the late-19th and early-20th century until more frequent reports in Danish, German, Polish and southern Swedish waters in the early 21st century (Härkönen et al. 2007, Olsen et al. 2018, Von Nordheim et al. 2019). In this article, we document the recolonisation of haul-outs and reestablishment of breeding colonies, and report the combined

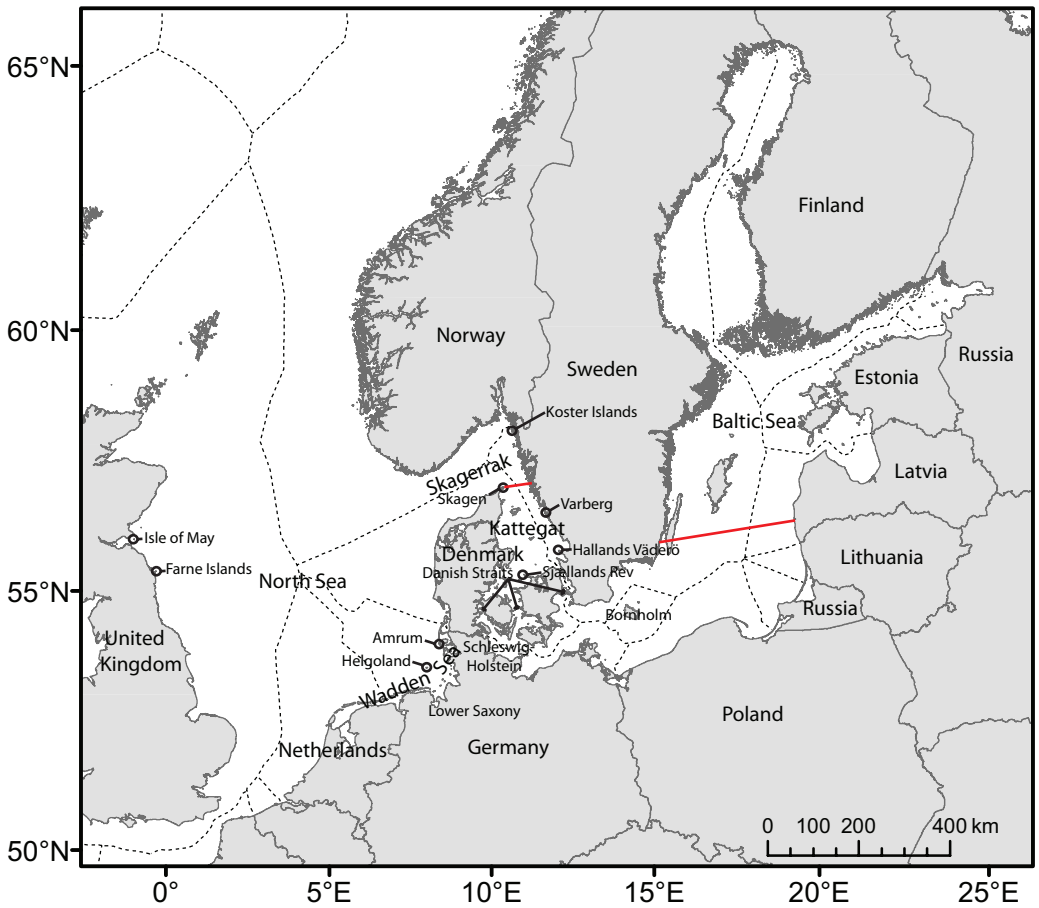

Figure 1. Map of the North and Baltic Seas with place names mentioned in the manuscript. Dashed lines indicate international borders. The limits of the study area are marked by red lines.

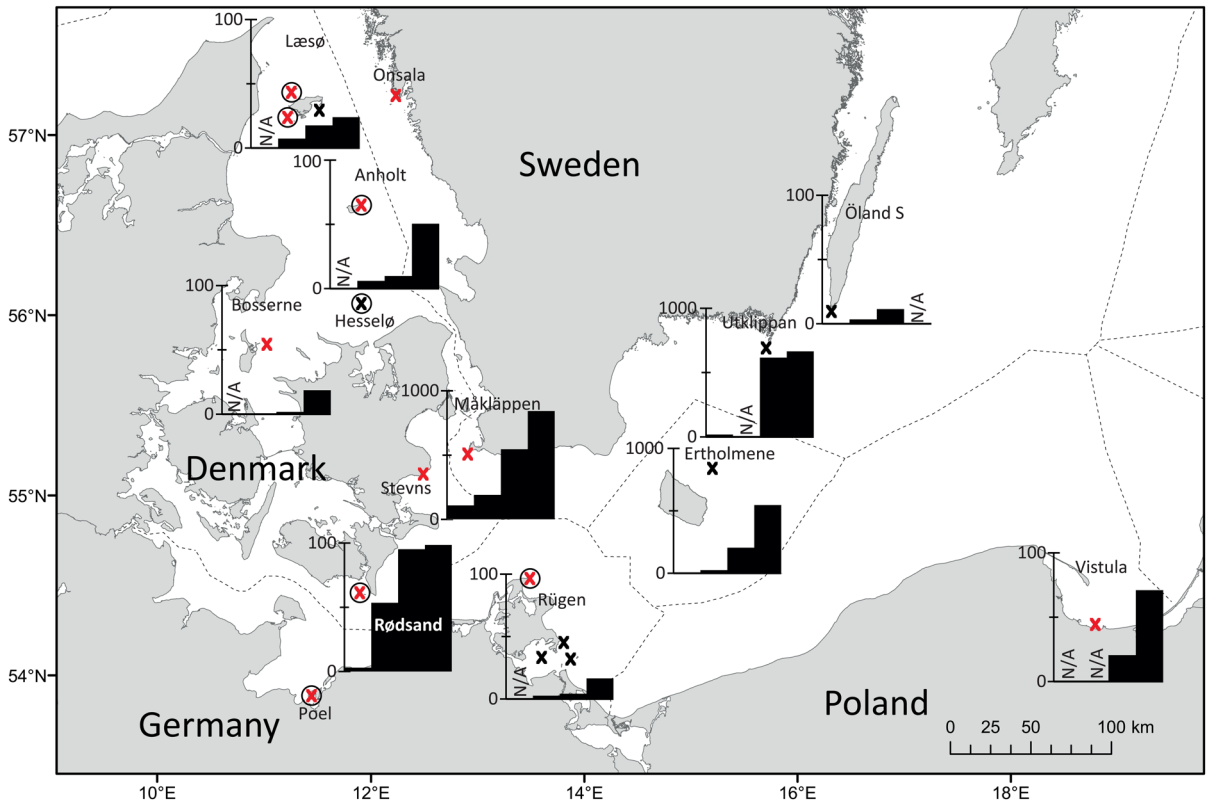

Figure 2. Map of important grey seal haul-out localities (crosses) in Kattegat and southern Baltic Sea. Column charts show moult abundance of grey seals for haul-out with more than 10 grey seals recorded, or total counts of several haul-outs around the main island in the cases of Rügen and Læsø. First bar represents the average count for the years 2001–2005, second bar 2006–2010, third bar 2011–2015 and fourth bar 2016–2019. Note, that Y-axis values range from 0 to 100 or 0 to 1000, depending on the size of the haul-out. N/A means that data are not available from the period in concern. Red crosses denote haul-outs with breeding activity after 1990, circled crosses denote haul-outs with historic breeding activity.

results of regional grey seal monitoring programmes, as well as anecdotal evidence of grey seal occurrence and breeding on localities in the southern Baltic Sea, Danish straits and Kattegat. Our findings have implications for understanding the factors affecting species recolonisation events, and feed directly into grey seal management and conflict mitigation both nationally and internationally, e.g. within the frameworks of the Helsinki Commission (HELCOM, the Baltic Marine Environment Commission) and EU's Habitats and Marine Strategy Framework Directives.

Material and methods

Grey seal population abundance and distribution during moult

We drew population abundance data from the HELCOM Seal Database, containing data from the coordinated censuses of moulting grey seals throughout the Baltic Sea (HELCOM 2019). We obtained additional data from the Danish Nature Agency's monitoring programme, the Swedish Agency for Marine and Water Management's marine environmental monitoring data (Swedish Oceanographic Archive 2019), Polish online camera surveillance at the haul-out at the mouth of the Vistula River and land and boat-based counts in Germany (Federal Agency for Nature Conservation and Southeast Rügen Biosphere Reserve). For all data presented here, we define the southern Baltic Sea, Danish Straits and Kattegat as south of the northern tip of Denmark (Skagen), through the Danish Straits and including the Baltic Sea south of 56.5°N (Fig. 1).

Since 2011, there have been three annual surveys of potential and known Danish grey seal localities in Kattegat, the Danish Straits and the southwestern Baltic, including the Swedish locality Måkläppen. The surveys use digital aerial photography from single-engine, high-winged aircrafts (Cessna 172 or 182). The first two annual surveys are conducted during the breeding season on approximately (± 2 days) 1 March and 15 March, respectively. The third annual survey takes place during the coordinated pan-Baltic grey seal moult survey, in late May–early June. During this period at least two surveys are completed at the Swedish localities The surveys were carried out with methodology according to Galatius et al. (2014). As the breeding season may extend beyond the survey period, pup counts are minimum estimates. If pupping in Kattegat occurs in January as has been the case historically, pups born at this time would not have been detected. In Poland, there has been continuous video monitoring of the single active grey seal haul-out at the mouth of the Vistula River since 2010. In Germany, grey seal localities have been frequently monitored from boats since 2006. This includes several observations during the pupping and moulting seasons.

Anecdotal data on breeding events

We aimed to document and compile all available records of Baltic grey seal breeding in the southern Baltic region during the Baltic subspecies' breeding season since 1980. Thus, in addition to data from the HELCOM and national monitoring programmes, we collected anecdotal records of breeding grey seals from Denmark, Germany, Poland, southern Sweden and the Swedish west coast from the literature, or from researchers and managers. In Kattegat, there are some records of breeding during the North Sea grey seal breeding period from October to December (Härkönen et al. 2007). These records were not included in this study.

Theoretical size of the Rødsand breeding population in 2020

We tested whether autochthonous recruitment could account for the growth of the only permanent breeding colony in the southern Baltic Sea, Rødsand. To this end, we used a matrix model to calculate a high range estimate of the current number of breeding females under the scenario of autochthonous recruitment. We set liberal values regarding age-specific survival relative to values for grey seals reviewed by Harding et al. (2007): first year survival was set at 60%, subsequent annual survival rates of 85% at ages 1–4 and 95% from 4 years of age. We assumed equal sex ratio in pups and 100% natal philopatry for pups born at Rødsand. Furthermore, we assumed that breeding at Rødsand began with two immigrating 5 year-old females in 2000, each bearing a pup in that year. We assumed age at first reproduction to be 5 years (Harding et al. 2007), and we set annual birth rate of the adult females at 100%.

Results

Grey seal abundance and distribution during moulting

Grey seals have frequently occurred in Kattegat, particularly at Anholt and Læsø in small groups of less than 10 seals since 1979. At the expansion of the Danish monitoring programme for harbour seals to the southwestern Baltic Sea in 1990, there were records of grey seals at Måkläppen in numbers up to 100 animals and at Rødsand in numbers up to 20. The first regular annual moult censuses of grey seals throughout the Baltic Sea were commenced in 2003. In that year, approximately 16 000 grey seals were counted throughout the Baltic Sea (maxima of two or three counts in each region), of which 146 seals were in the southern Baltic Sea corresponding to just below 1% of the total count (Fig. 3). Since then, the number of seals counted during the moulting season in the Baltic Sea has increased steadily, amounting to a maximum of 38 000 in 2019, of which ca 2537 were observed in the southern Baltic Sea, corresponding to almost 7% of the pan-Baltic Sea population. It must be noted that some Danish, German and Polish sites were not included in the counts before 2011, however, the contributions to the numbers from haul-outs in these countries would have been modest, probably in the range of tens. Importantly, at a local scale, while new sites have been continuously recolonised it

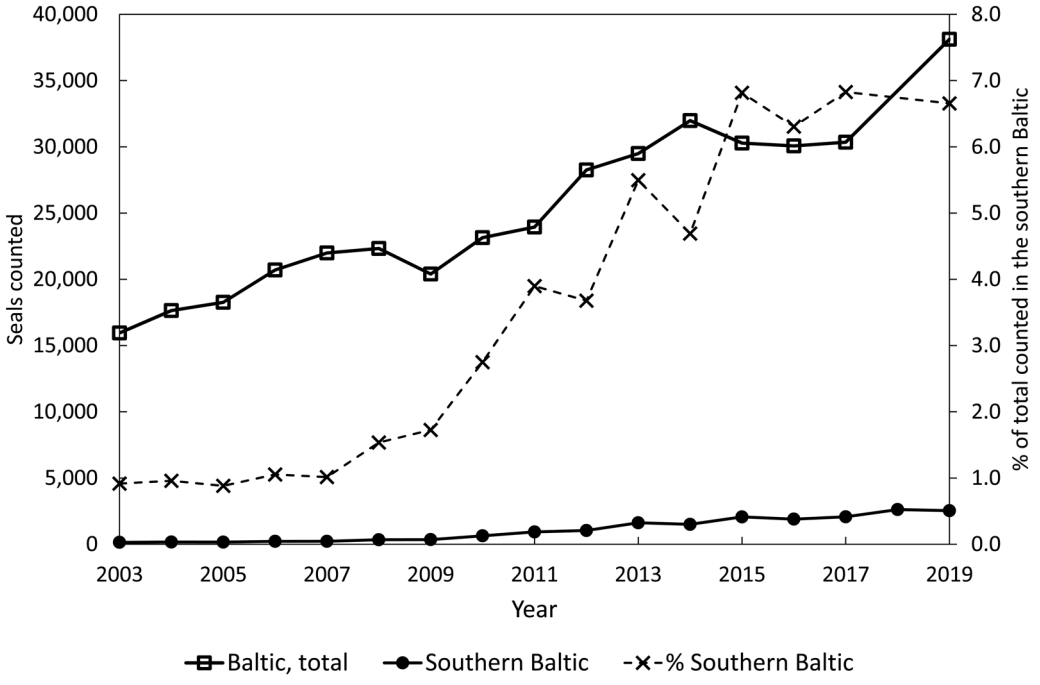

Figure 3. Counted seals during the moult aerial censuses of grey seals in the Baltic Sea area. Solid line, square markers (left axis): total number of grey seals counted on haul-outs throughout the Baltic Sea. Solid line, round markers (left axis): total number of grey seals counted on haul-outs in the southern Baltic, Danish Straits and Kattegat (southern Sweden, Denmark, Germany and Poland). Dashed line, crosses (right axis): percentage of total number of seals that were counted on haul-outs in the southern Baltic. In 2018, the coordinated count was not conducted in important areas in Finland, so a total number is not available.

Table 1. Maximum number of pups counted at each of the localities under the Danish monitoring programme since 2011. Ertholmene was added to the programme in 2012, Bosserne was added in 2017. Localities are given in Fig. 2. An 'X' denotes that the locality was not covered in the concerned year. Modelled pupping estimates for Rødsand are given in parentheses.

	Kattegat Læsø-Sønder Rønner	Kattegat Læsø-Borfeld	Kattegat Læsø-Knobgrundene	Kattegat Anholt	Kattegat Hesselø	Kattegat Bosserne	SW Baltic Rødsand	SW Baltic Måkläppen	Baltic Proper Ertholmene	Sum
2011	0	0	0	0	0	X	3 (3.1)	0	X	3
2012	0	0	0	0	0	X	3 (3.4)	0	0	3
2013	0	2	0	0	0	X	4 (3.6)	0	0	6
2014	0	0	0	0	0	X	3 (3.9)	0	0	3
2015	0	1	0	1	0	X	4 (4.2)	0	0	6
2016	0	0	0	0	0	X	8 (4.6)	0	0	8
2017	0	2	0	1	0	1	10 (4.9)	0	0	14
2018	0	0	0	0	0	0	6 (5.3)	0	0	6
2019	0	1	0	1	0	0	5 (5.7)	0	0	7
2020	0	0	0	0	0	0	6 (6.3)	1	0	7
Sum	0	6	0	3	0	1	52 (45)	1	0	63

seems that the overall increase of the southern Baltic grey seal population to date has been driven by a few major sites with hundreds of seals hauling out (Fig. 2). Also, while the absolute abundance has been increasing, the proportion of southern Baltic to total Baltic population has been stable at around 7% since 2015.

Grey seal pups and breeding sites – monitoring programmes

The Danish monitoring programme data show that a minimum of 63 grey seal pups were born in the Danish parts of the southern Baltic Sea, Danish straits and Kattegat in the period 2011–2020, of which 52 (83%) were observed at Rødsand, 6 at Borfeld and 3 at Anholt, respectively (Table 1, Fig. 2). The number of pups recorded at Rødsand ranged from 3 to 10 per year. In 2020, a minimum of 6 pups were born at Rødsand, which is slightly lower than the 6.3 breeding females estimated by the matrix model (Table 1). In Germany, the first evidence of pupping came in 2018, with one grey seal pup found dead near Cape Arkona on the northern tip of Rügen in early March (Von Nordheim et al. 2019), and a second pup was born in mid-March 2019 on the island Poel. For both of these pups, it was confirmed that they were born on site and not stillborn. Since there were no other obvious pathologies and meconium was still present in the intestine, death shortly after birth was most likely. In Poland, one mother–pup pair was observed at the end of February 2016 and then for a couple of weeks at the haul-out at the mouth of the Vistula river. Overall, the proportion of pups counted in the southern Baltic Sea in 2019 to the number of seals counted during the moult was approximately one to 370, corresponding to 0.2%.

Anecdotal reports of grey seal pups

The anecdotal reports and opportunistic surveys provide additional insights on grey seal breeding events not covered by the temporal or geographical range of the monitoring programme. The first pup in Kattegat was recorded as early as March 1982 on Anholt (Dietz and Heide-Jørgensen 1982), one was observed near Onsala in spring 1991 (Härkönen et al. 2007), and another on Anholt in March 1996 (Heide-Jørgensen et al. 1997). Also, during an opportunistic aerial survey of seal haul-outs in Kattegat on 10 March 2008, one grey seal pup was recorded at Sønder Rønner south of Læsø. In the southern Baltic Sea, Rødsand accounts for the first grey seal pups recorded with two pups observed in late February 2003, and another two in late February 2004 (Edren et al. 2010). In 2008, another survey of Rødsand was conducted during the Baltic Sea grey seal breeding period on March 10, with three live pups and one dead being recorded. Finally, an opportunistic survey was conducted in the southern Baltic on 26 February and 3 March 2010 – the year prior to the initiation of the monitoring programme – with no pups recorded on Rødsand, but a single pup at Måkläppen in southern Sweden. On 26 February 2020 a newborn, dead pup was found at Stevns in Denmark.

Discussion

Grey seal recolonisation of the southern Baltic Sea

Grey seals have been regarded as extinct as a breeding species in the Danish waters of the southern Baltic, Danish Straits and Kattegat since the early 20th century (Søndergaard et al. 1976). There have been frequent observations of small groups of grey seals (>10) in Kattegat at least since the 1970s and grey seals have used the haul-out at Måkläppen in southern Sweden in considerable numbers (~100) since the 1990s. However, until 2003, less than 1% of the moulting grey seals of the Baltic population count occurred south of 56.5°N. Since then, numbers have steadily increased, and in recent years, there have been counts of up to 2600 grey seals in the southern Baltic, constituting just below 7% of the total population for the entire Baltic Sea.

Despite up to 100 years of absence, the grey seals recolonising the southern Baltic and Kattegat appear to return to the same haul-out sites as those described in historical sources and prehistorical zooarchaeological finds. In Denmark and Sweden, this includes all the contemporary major haul-outs such as Læsø, Anholt, Bosserne, Rødsand, Måkläppen and Ertholmene (Bynch 1801, Faber 1828, Tauber 1880, Tauber 1882, Møhl 1971, Søndergaard et al. 1976, Lepiksaar 1986, Olsen et al. 2018). Still, several past haul-out sites have not yet been recolonised in Kattegat and the archipelago sea south of Funen, Denmark. Grith (1891) mentions several haul-outs in the inner waters of the Gulf of Gdańsk (Poland), but most of these have yet to be repopulated (Pawliczka 2011). Likewise, in Schleswig-Holstein and Mecklenburg-Vorpommern in Germany, there are also several known historical haul-outs and a rich prehistoric zooarchaeological record (Sommer and Benecke 2003, Glykou 2014), but some of these places have been lost through sand and stone mining along the coast (von Nordheim et al. 2011). Furthermore, the German and Polish coastline sees heavy use by tourists, and, in consequence, many historical sites are unlikely to be repopulated unless they are protected.

Establishment of breeding sites

After the extinction of grey seals in the southern Baltic Sea, the earliest observations of breeding are from the severe winters of the early 1940s, when a few grey seals were found breeding on sea ice near Bornholm (Søndergaard et al. 1976). As we review here, in the 1980s and 1990s there were sporadic observations of new-born grey seal pups being born on Danish and Swedish localities in Kattegat. In the southwestern Baltic, the first record of pups at Rødsand was in 2003, and since the initiation of the Danish monitoring programme in 2011, there have been births here every year. Moreover, a number of other localities in Sweden and Denmark, and in the last couple of years, Poland and Germany, have seen sporadic breeding activity. Still, Rødsand remains the only consistently used grey seal breeding locality in the southern Baltic Sea, Danish straits and Kattegat. It is peculiar that no or very little breeding occurs at Måkläppen, Utklippan and Ertholmene, where by far the largest aggregations of grey seals in the southern Baltic occur. However, we found no historical sources reporting breeding at Ertholmene, and the skerries around these islands are prone to flooding by large waves in windy conditions, making it an unfavourable breeding site where pups in lanugo fur risk getting flushed off the skerries. At Måkläppen, the haul-out is accessible from land, allowing foxes *Vulpes vulpes* and other terrestrial predators access, possibly detracting from its value as a safe breeding locality. Moreover, human disturbance occurs at most of the southern Baltic haul-out sites during parts of the year, whereas the breeding sites in the core area further north in the Baltic Sea are more inaccessible. These may be important prohibiting factors for reestablishment of breeding, as grey seals may show more precaution in their choice of breeding locality with respect to disturbance than harbour seals, whose pups have adult pelage and can swim immediately after birth (Teilmann and Galatius 2018) whereas grey seal pups are born with a lanugo fur (Hall and Russell 2018) and have limited capacity for swimming during the nursing period.

It is probable that the breeding activity at Rødsand began even before the first recorded pups in 2003, as there was no monitoring of the site during the breeding season. This is also possible with regard to the Swedish localities, where only opportunistic observations are available. Thus, an unknown (but low) proportion of the pupping events in southern Sweden are likely to be undetected. In Germany, local game wardens, tourist operators, and/or online cameras have regularly monitored relevant haul-outs since 2005. This means that the pups registered at Poel and Rügen islands in Germany in 2018 and 2019 are likely the first and only recent examples of breeding activity in this country. These births were live pups that died shortly after birth, indicating that the localities are inappropriate for giving birth and sustaining the lactation period, or that the females were inexperienced and left the pup. The theoretically most attractive breeding locality in the German part of the Baltic Sea is the already established haul-out site Greifswalder Oie off Rügen, which is sheltered from flooding and relatively undisturbed. However, despite weekly monitoring, pups have not been detected here. Historically, breeding in the northwestern part of our study area in Kattegat occurred in January, in between the breeding periods of North Sea and Baltic Sea. We do not know if this timing was peculiar to a now extinct hybrid population inhabiting this area or if pupping has also recently occurred in January in this area. If the latter is the case, such events will have gone undetected by the monitoring programme.

After at least 17 years of annual breeding activity in the southern Baltic Sea, Danish Straits and Kattegat, only 8 births were recorded in 2020, after a record of 14 in 2017. With values for age-specific survival and breeding philopatry set deliberately high, a theoretical breeding population at Rødsand in 2020 of ca 6 females given pure autochthonous recruitment was calculated. This matches the 6 pups observed in this year, but is lower than the 10 adult females breeding at Rødsand in 2017. In combination with the liberal values set for survival and birth rate, this indicates that even with the low rate of growth, recruitment cannot be exclusively autochthonous and that immigration of females born at other Baltic breeding sites occurs.

Hypotheses for the slow establishment of breeding sites

In the southern Baltic Sea, as in the Wadden Sea (Brasseur et al. 2015), there are much more abundant occurrences of grey seals than the local breeding population would support. The reestablishment of Rødsand and other southern Baltic haul-outs as breeding colonies has been slow compared to other examples of grey seal (re)colonisation, e.g. in the Wadden Sea. Here, grey seals have emigrated from colonies in the United Kingdom and began breeding in the Netherlands in 1980 (Reijnders et al. 1995, Czeck and Paul 2008, Brasseur et al. 2015). Breeding colonies in the Netherlands, Lower Saxony and Helgoland have all grown at much faster rates than what we have observed in the southern Baltic (Czeck and Paul 2008, Abt and Engler 2009, Brasseur et al. 2015). An exception is the colony of Jungnamensand off Amrum in the Schleswig-Holstein Wadden Sea, which initially, in the 1980s and early 1990s, grew at a rate similar to that of Rødsand, with a subsequent decline in the 1990s, probably caused by erosion, making the site susceptible to flooding (Abt et al. 2002). The site has not recovered, and currently, few if any pups are born annually in Schleswig-Holstein (Cremer et al. 2019). In the Northwest Atlantic, the population dynamics of grey seals have gone through similar dynamics as in Europe: hunting for oil, bounty hunting and lack of protection have reduced numbers dramatically, before recovery latter half of the 20th century (Wood et al. 2020). This led to local extinction in the United States. Early development in recolonised grey seal pupping sites in the United States during the 1990s and early 2000s are hard to compare to sites in the southern Baltic Sea as monitoring was not comprehensive in the early stages of colonisation in the United States. However, the Muskeget Island colony (Massachussetts) grew from a handful of pups to more than 300 annually within a decade, in a large part fuelled by immigration, while Monomoy Island (Massachussetts) data suggest pup production mostly in single digits for 18 years, before a rapid growth to many hundred pups annually (Wood et al. 2020).

Why has establishment of breeding colonies in the southern Baltic Sea progressed so slowly compared to what has been observed in other areas? We propose five hypotheses, with varying supporting evidence: 1) differences in population dynamics, 2) differences in recolonisation distances, 3) differences in habitat and 4) differences in mortality and finally 5) differences in rehabilitation programmes. 1) In the North Sea region, there have been large breeding colonies in the UK with declining increases of pup production during the colonisation of the Wadden Sea (Harrison et al. 2006, Abt and Engler 2009). This indicates a saturation of source colonies and therefore increases the incentive for individual seals to emigrate. The dynamics of pup production in Baltic colonies are largely unknown, as there is no monitoring of pup production in Sweden, and only partial coverage of Finnish and Estonian waters (Galatius et al. 2014). Furthermore, a large proportion of the Baltic grey seal stock breeds on sea ice, rather than in colonies on land, making the dynamics of breeding distribution hard to assess. In recent years, ice has been irregularly available in the Baltic grey seal core breeding area, but the islands and skerries suitable for breeding are still abundant in parts of the area, and contrary to the North Sea, saturation does not seem to be an issue in the Baltic core breeding area. Female grey seals are generally very philopatric to breeding sites (Pomeroy et al. 2000), and may rarely attempt breeding at sites outside their natal range. Thus, the low number of pups in the southern Baltic may partly be due to a lack of immigrating sexually mature females. 2) There is a large geographical hiatus between the breeding range of the grey seal in the central and northern Baltic Sea and the recorded pupping localities in the southern Baltic Sea. This is, however, also the case between the UK and the Wadden Sea, where the closest likely source colonies in the UK, Isle of May and Farne Islands (Abt and Engler 2009), are approximately 500–700 km from the Wadden Sea colonies, similar to the distances from breeding areas in the central Baltic to southern Baltic haul-outs. Even at smaller scales, distance to source colonies has been shown to be an important factor in the establishment and growth of grey seal breeding colonies (Gaggiotti et al. 2002). 3) In the Baltic Sea, there are differences between the available breeding sites and substrates in the south relative to the northern and central parts, where grey seals breed preferentially on sea ice, secondarily on rock skerries and sand/shingle islets, whereas most localities in the southern Baltic Sea are islets of sand or shingle. Baltic grey seal pups born on sea ice show higher pup survival rates and weaning weights than those born on land (Jüssi et al. 2008). Lower levels of infectious agents on ice and potentially fewer interactions with avian predators such as white-tailed eagles *Haliaetus albicilla* are thought to account for these observed differences (Jüssi et al. 2008). This may impede colonisation of the southern Baltic Sea by relatively lower pup survival in the southern Baltic Sea compared to the Baltic Proper (and the Wadden Sea) because most Baltic grey seals may be less adapted to land breeding than their Atlantic brethren. This could also entail a higher threshold for immigration for females primarily adapted for ice breeding. Indeed, at a time when sea ice was available for breeding in the southern Baltic Sea, a few breeding events were recorded as early as the 1940s on that substrate (Søndergaard et al. 1976). There have also been severe winters in the 1980s, without detection of grey seal pups on sea ice in the southern Baltic. 4) In the Wadden Sea, there have been efforts to rehabilitate hundreds of sick or abandoned pups, which may have led to increased pup and juvenile survival rates (Brasseur 2018), although Reijnders et al. (1995) estimated that this effect was low compared to the effects of immigration on the growth of the Dutch recovering breeding population. In comparison, there has been no rehabilitation of grey seals in Denmark, and only low numbers of rehabilitated pups or pups bred in captivity in southern Sweden and Poland (In Poland, there has been a recent increase from 40 pups 2018 to 72 pups in 2020 in Poland. In southern Sweden, single pups have sporadically been rehabilitated over the past 20 years). It is, however, still possible that these few animals have been instrumental in re-establishing breeding in the southern Baltic. Finally 5), some of the reproductively active female grey seals and their pups may have been accidentally bycaught or deliberately killed in fishing gear or illegally shot by fishermen in an attempt to reduce the negative impact of the growing grey seal population on the coastal fishery. Documentation of hefty illegal killing of grey seals

off Bornholm appeared in an interview study with anonymous fishermen from 2018 (Bisgaard 2018). In Germany, there has been potential deliberate drowning of 23 grey seals in fish traps in the fall of 2017 (Westphal, unpubl.). Given that adult females generally seem to stay in relatively small areas (Karlsson et al. 2005), it is likely that many females pupping at Rødsand stay in the southern Baltic Sea, using feeding grounds off Bornholm outside the pupping period. Thus, some of the few reproductively active females may be among the animals killed.

There are obviously many other differences between the North Sea and the Baltic Sea in terms of habitat and ecology which could potentially affect the rate of recolonisation and reestablishment of breeding sites in the southern Baltic. Except for the continuous breeding at Rødsand, there are no known consistent breeding haul-outs, but rather a pattern of sporadic breeding attempts at several localities. Links of direct causality are difficult to infer, but we hypothesize that the main factors accounting for the slow reestablishment of breeding in the southern Baltic are those listed above. Ten of the pups born at Rødsand between 2014 and 2019 were equipped with Argos satellite transmitters and/or plastic roto tags. Of these pups, at least four have died during their first year of life: one was reported as by-catch by a fisherman, two have been found dead on the coastline, and one Argos-equipped pup never left Rødsand, giving a minimum first year mortality of 40% among these 10 tagged pups.

Management implications

The return of the grey seal to the southern Baltic Sea, Danish straits and Kattegat is a conservation success, resulting from protection of the species from culling, banning of organochlorine pollutants and protection of haul-out sites, with prohibition of access on key haul-outs and the surrounding water area in sensitive periods. These management initiatives have allowed the Baltic grey seal population to recover and subsequently to expand its distribution into the southern Baltic Sea, the Danish Straits and Kattegat, where it has been the most abundant seal species within historic times. However, there are no protective measures during the grey seal breeding season at some known and potential breeding locations in Sweden. In Germany workshops were conducted in January 2020 by the German Oceanographic Museum in collaboration with national parks administration to educate the local authorities and municipalities about returning grey seals and easily implementable protective measures like short term exclusion zones to prevent harassment and injuries to seals, humans and dogs. In Poland the only active haul-out site is located in the area of a bird reserve in the Vistula river mouth and is therefore protected by the reserve regulation. During the breeding season, the area is free from disturbances and could potentially serve as a suitable breeding site. However since the video monitoring of the haul-out was established in 2010, only one mother–-pup pair was observed in 2016. The female which gave birth was rehabilitated as a pup and successfully released into nature (Pawliczka unpubl.).

The reappearance of grey seals in the southern Baltic Sea has caused conflicts with coastal fisheries (Olsen et al. 2018). This has led to legal regulation in Denmark (a quota of 40 grey seals will presumably be shot around Bornholm in 2019–2020) and illegal killing of potentially hundreds of grey seals in Denmark in the form of shooting and large mesh set nets targeting seals (Bisgaard 2018). In 2017, 23 healthy male grey seals were found dead at southeastern Rügen, Germany, and were diagnosed with signs of dying in large coastal fish traps, indicating that German fishermen also illegally target grey seals (Westphal et al. unpubl.). Those 23 seals likely represented 25–47% of the locally occurring animals at the time (Westphal et al. 2018). Although the great majority of the grey seals occurring in the southern Baltic Sea do not breed in the area, breeding seals may be among the victims of such actions, impeding recolonisation.

The recolonisation of the southern Baltic Sea as defined by a colony with annual breeding activity began around 100 years after the local extinction and more than 20 years after the recovery of the Baltic stock began in the 1970s. Even now, 17 years after the first recorded pups at Rødsand, with thousands of grey seals counted in southern Baltic during the moulting season, documented annual pup production is still in single digits in most years. All other localities than Rødsand only show sporadic breeding activity. This slow recovery of the breeding colonies in the southern Baltic is an example of a slow recovery of a long-lived, slow reproducing species after a severe population collapse, which is relevant in the future management of such species.

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