

Marine Record

Cite this article: Galatius A, Dietz R, Olsen MT, Teilmann J (2024). Recolonisation of former habitat by harbour seals in southern Denmark despite intense anthropogenic activity. *Journal of the Marine Biological Association of the United Kingdom* **104**, e85, 1–5. <https://doi.org/10.1017/S0025315424000717>

Received: 22 March 2024

Revised: 10 June 2024

Accepted: 23 July 2024

Keywords:

distribution; extinction; Funen; harbour seal; little belt; metapopulation; monitoring; pinnipeds; recolonisation

Corresponding author:

Anders Galatius;

Email: agj@ecos.au.dk

© The Author(s), 2024. Published by Cambridge University Press on behalf of Marine Biological Association of the United Kingdom. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.



Recolonisation of former habitat by harbour seals in southern Denmark despite intense anthropogenic activity

Anders Galatius¹ , Rune Dietz¹, Morten Tange Olsen^{1,2} and Jonas Teilmann¹

¹Section for Marine Mammal Research, Department of Ecoscience, Aarhus University, DK-4000 Roskilde, Denmark

and ²Section for Molecular Ecology and Evolution, Globe Institute, University of Copenhagen, DK-1353

Copenhagen K, Denmark

Abstract

Harbour seals were extensively hunted in Denmark, but have only been driven to local extinction in one larger area, the South Funen Archipelago and Little Belt, where the species has been absent throughout the 20th century. Despite high growth rates of the Danish harbour seal populations after protection from hunting in 1976, seals have only been observed sporadically in the South Funen Archipelago and Little Belt until recent years, where recolonisation now causes conflicts with fisheries. Here, we review historical sources documenting the local extinction of harbour seals in the area during the 19th century and report the results of aerial surveys of haul-out sites during moulting seasons of 2021–2023 and pupping seasons of 2022 and 2023. Historical sources reveal that seal hunting was a common practice in southern Denmark, but catches dwindled to rarities during the 19th century. During recent surveys, seals were detected at six of the identified potential haul-out sites. Around Aarø Island, an average of 141 (range: 92–186) harbour seals were recorded over four moulting season surveys, constituting the majority (90%) of the total counts of the surveyed area. During the pupping seasons, a total of five pups was encountered at two different haulouts. As none of the haulouts are protected during the pupping and breeding seasons, protective measures may support this recolonisation of the historic harbour seal breeding range.

Introduction

Harbour seals (*Phoca vitulina*) have a wide range in the northern hemisphere, occupying temperate and arctic coastal habitats (Teilmann *et al.*, 2023). Compared to other pinnipeds, individual home ranges for harbour seals are small, with most movement distances from the key haul-out site being below 50–100 km, resulting in genetic differentiation and creation of subpopulations over relatively small distances (Liu *et al.*, 2022). Today, the harbour seal is the most abundant seal species in Danish waters and was historically found in all parts of Denmark, where it was extensively hunted for its fur, blubber and to mitigate damages and competition with fisheries (Søndergaard *et al.*, 1976; Olsen *et al.*, 2018). The sympatric grey seal (*Halichoerus grypus*) was historically even more numerous than the harbour seal, but was driven to local extinction by a culling campaign from 1889 to 1927 and centuries of previous hunting (Søndergaard *et al.*, 1976; Olsen *et al.*, 2018). The Danish harbour seal populations were likewise targeted by the culling campaign and severely reduced in numbers, but survived at low abundances throughout the country from 1927 to the protection in 1976, with the exception of one larger area: the South Funen Archipelago and Little Belt, where harbour seals disappeared (Figure 1). Despite dedicated management efforts, including establishment of seal reserves from the 1950s to the 1980s, the protection of seals from hunting (grey seals in 1967 and harbour seals in 1976) and subsequent growth of the harbour seal populations in other parts of Denmark, seals have only been sporadically observed in South Funen Archipelago and Little Belt during the 20th century (Søndergaard *et al.*, 1976).

Historical sources document the long-term presence of seals in the area leading up to the local extinction. An early source is a local record book describing the case of a poacher caught on Drejø (Figure 1), who was pardoned on the condition that he supplied the landowner with three seals and their skin and blubber before Whit Sunday (7 June 1663), after which he was hired as a seal hunter (Rohmann, 1861). A source from the late 18th century indicates a substantial contemporary seal abundance based on a sermon from a priest at Avernakø (Figure 1), who lamented the ‘sacrilege’ of most of his male congregation favouring seal hunting to church service on a New Year’s Day (Søkilde, 1875). In the late 1930s, Frydendahl (1939) conducted an interview survey with people on Funen and in the South Funen Archipelago, who had personal memories of the historic seal hunting and/or had parents or grandparents who had been active hunters. These interviews document the gradual local extinction of seals during the 19th century: the interviewees relay that in their childhood, parents, grandparents and ‘old people’ told stories of hunts with daily catch numbers of 23, 16 and 10 seals. These numbers dwindle with time, and recollections from the interviewees’ own lifetimes concern rare encounters with single or few seals, mostly from their childhood. One person tells that admissions were sold to see a seal caught around 1870. Thus, seals seem to have disappeared from the South Funen

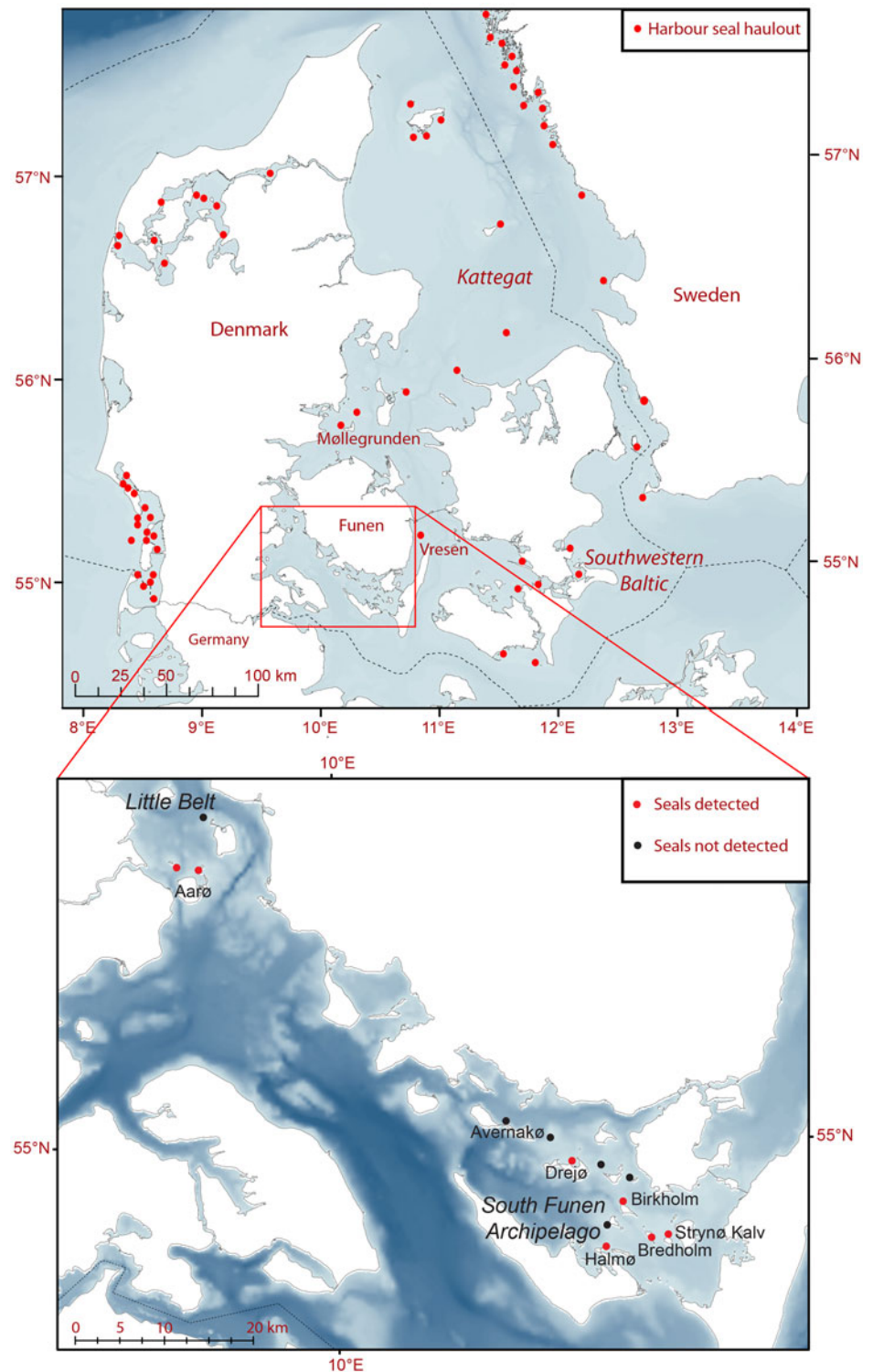


Figure 1. Map of Denmark with harbour seal haul-out sites in the four management units shown (top) and study area (bottom) with place names from the text. In the South Funen Archipelago and Little Belt, the 13 surveyed localities are shown. Localities with seals detected during surveys have red markers, while areas surveyed without seal observations are marked in black.

Archipelago at the initiation of the bounty campaign to cull seals in Denmark in 1889 (Olsen *et al.*, 2018). Information from Frydendahl (1939) indicates that a substantial part of the hunted seals were taken at breathing holes in the ice during cold winters, suggesting the historic occurrence of grey seals or even ringed seals (*Pusa hispida*) in the area, in addition to harbour seals.

In recent years, there have been increased reports of harbour seal occurrence in the South Funen Archipelago, not least from fishermen, who experience damaged or lost catches (Milling, 2021; Printzlau, 2021). This renewed occurrence of seals at least 130 years after their local extinction inspired our initiation of our aerial surveys in 2021 for potential seal haulouts during the harbour seal pupping and moulting season in June and August,

respectively. Here we report the results of the first three years of monitoring 2021–2023, documenting the return of harbour seals to the South Funen Archipelago and Little Belt in Denmark.

Materials and methods

To compile a list of potential haul-out sites in the South Funen Archipelago and Little Belt we enquired for sightings of hauled out seals in our network of people reporting stranded marine mammals in the area, as well as game wardens at the Danish Environmental Protection and Nature Agencies (Danish Ministry of Environment). These initiatives resulted in 13 localities where harbour seals had anecdotally been observed in recent

years (Figure 1). These localities were surveyed once during the moulting season in August 2021 to 2023 (twice in 2023, as many haulouts were flooded during the first survey) and once around the pupping season peak estimated in Denmark at 22nd June (Seganfredo *et al.*, 2023) in 2022 and 2023.

Surveys were conducted between 10:00 and 16:00 local time at wind speeds below 10 m s^{-1} and without precipitation at any locality in the preceding 6 hrs. As tidal amplitude in the survey area is negligible (10–15 cm), surveys were flown without consideration of tide. Two observers both took overlapping digital photographs from the right side of the plane of all groups of seals through an open window from a single-engine Cessna 172, flying 500–700 feet over the haul-out sites, using DSLR cameras with 70–200 mm lenses. The digital photographs were subsequently used to count the number of seals present by two independent observers. If the counts for a location differed by more than 5% between the two observers, a third (or more) count(s) was performed until there was agreement between the counts.

Results

In the August moulting season surveys, seals were detected at seven of the identified potential haul-out sites. At Aarø, an average of 141 harbour seals (min 93; max 186) was recorded over the three moulting seasons, constituting 90% of the total numbers in the South Funen Archipelago and Little Belt (Table 1). During the survey on August 9th 2023, the haulouts of Strynø Kalv, Bredholm, Birkholm and Drejø were flooded after a period of strong westerly winds, potentially causing a low count of seals. Thus, another survey was conducted on 22nd August 2023 during which 12 animals were recorded at Strynø Kalv. During the June pupping season surveys, a total of five pups were encountered at two different haul-out sites, Bredholm and Aarø (Table 1; Figure 1). One grey seal was recorded during the surveys, on 22nd August 2023 at Aarø.

Discussion

The harbour seal moulting and pupping season surveys conducted in 2021–2023 confirm the presence of substantial numbers of seals in the South Funen Archipelago and Little Belt after at least 130 years without regular presence in the area. The total of 667 seals (of which some may be resightings) recorded during the six surveys in 2021 to 2023 were all harbour seals, with the exception of a single grey seal. Harbour seals in Denmark have recovered from an estimated abundance of ca. 2000 individuals in the mid-1970s (Søndergaard *et al.*, 1976) to around 9000

counted at haul-out sites during the moult throughout Denmark in recent years (Sveegaard *et al.*, 2023). The successful recovery of the harbour seals in Denmark has been credited to protection of seals in 1976 and establishment of seal reserves at key sites with restricted access starting in 1951 (Heide-Jørgensen and Härkönen, 1988).

As other pinnipeds, harbour seals are vulnerable to disturbance at their haul-out sites, particularly during the breeding and moulting seasons (Andersen *et al.*, 2012). In other Danish regions, seal reserves and protected areas with restricted access to the public mitigate some of the human impacts caused by disturbance. However, there are currently no seal reserves or protected areas in the South Funen Archipelago and Little Belt; a populated area with many houses along the shores that is busy in terms of recreational traffic (e.g. motor boats, sailing boats, kayaks and paddle boards) and commercial activities (ferries and freight ships). Recolonisation is apparently occurring despite the high levels of disturbance, but on the other hand disturbance may have hindered an earlier or greater recovery of the seals. Previous studies of harbour seals have indicated that to some extent, they can habituate to anthropogenic disturbances in areas with high activity levels (Cates and Acevedo-Gutiérrez, 2017; Bankhead *et al.*, 2023).

During the pupping surveys, we only recorded three pups in 2022 at Aarø in southern Little Belt and two pups in 2023, at Bredholm in the South Funen Archipelago. Harbour seals have strong site fidelity, particularly adults during the breeding season (Härkönen and Harding, 2001; Dietz *et al.*, 2013). A likely consequence of this is that breeding activity lags behind other occurrence in a newly colonised area, a phenomenon that is also seen for grey seals currently recolonising previous ranges (Brasseur *et al.*, 2015; Galatius *et al.*, 2020; Wood *et al.*, 2020; Galatius *et al.*, 2024). Given the high level of human recreational activities in the area, disturbance may particularly limit future pupping activity without protective measures (Becker *et al.*, 2011). The South Funen Archipelago and Little Belt area neighbours two genetically separated harbour seal population areas from where animals may have immigrated: the Kattegat to the north and the southwestern Baltic to the east (Olsen *et al.*, 2014) (Figure 1). In the Little Belt, the distance by sea is shortest from the nearest Kattegat haulout at ca. 70 km from Møllegården to Aarø, while in the South Funen Archipelago, the distance is shortest from the southwestern Baltic haul-out site at Vresen at ca. 40 km to Strynø Kalv (Figure 1). In the Kattegat population, abundance has been relatively stable since 2010, indicating density dependence (Silva *et al.*, 2021), potentially spurring migration to new areas, similar to harbour seal and grey seal metapopulation

Table 1. Aerial survey counts of harbour seals from the seven haulouts where seals were detected during the seven surveys

Date	Strynø Kalv	Bredholm	Halmø	Birkholm	Drejø	Aarø NE	Aarø NW	Total
Harbour seal moulting season counts								
3rd August 2021	40	0	0	0	3	186	0	229
5th August 2022	3	0	0	0	0	135	0	138
9th August 2023	0	0	1	0	0	89	3	93
22nd August 2023	12	0	0	0	0	114 ^a	35	161
Moult average	13.75	0	0.25	0	0.75	131	9.5	155.25
Harbour seal pupping season counts								
21st June 2022	0(0)	0(0)	0(0)	0(0)	0(0)	39(3)	0(0)	39(3)
22nd June 2023	0(0)	16(2)	0(0)	0(0)	0(0)	0(0)	0(0)	16(2)

For the pupping season, the total count of harbour seals including pups is given with the number of pups in parentheses.

^aA single grey seal was detected on 22nd August 2023 at Aarø NE.

dynamics in other regions (Gaggiotti *et al.*, 2002; Russell *et al.*, 2019; Carroll *et al.*, 2020). In this way, the South Funen Archipelago and Little Belt could potentially act as a population sink for the Kattegat source population. Counts from the harbour seal population in the southwestern Baltic, on the other hand, are still growing exponentially (Galatius *et al.*, 2021), indicating that harbour seals here are not yet at their carrying capacity. Still, given increased competition with recovering grey seals (Galatius *et al.*, 2020) and associated changes in haul-out preferences, these southwestern Baltic harbour seals could also be a source population. Ultimately, genetic analyses will be necessary to ascertain the population origin(s) of the seals that have immigrated to the South Funen Archipelago and Little Belt area.

The century-long period of harbour seal absence from the area, persisting also after its nation-wide protection in 1976, highlights the potentially slow recovery and recolonisation of a species with relatively slow intrinsic growth rate (average <1 pup per year) and high site fidelity, when neighbouring populations are also depleted. Even at this early stage of recolonisation, harbour seals (perhaps in combination with visiting grey seals) are starting to cause controversy with fishery due to damage to the catch in static fishing gear and a simultaneous crash in commercial fishery (Milling, 2021; Printzlau, 2021). These seal-fishery conflicts are likely to increase if the recolonisation proceeds as expected.

Recommendations

Harbour seals are listed under Annex V in the EU Habitats Directive. To achieve favourable conservation status under the Habitats Directive, the range of a species should be aligned with its expected natural range. To ensure the achievement of this goal for harbour seals, we recommend the establishment of new seal reserves and/or protected areas in the South Funen Archipelago and Little Belt to minimise human impacts on the recolonisation of harbour seals here. In this regard, establishing seal reserves around the Aarø and Strynø Kalv – Bredholm haul-out sites may have the greatest impact, given the observed use of these areas for both moulting and breeding. Likewise, we recommend to conduct genetic sampling and analyses to ascertain the origin(s) of the harbour seals that have immigrated to the South Funen Archipelago and Little Belt area.

Acknowledgements. We thank Henrik Egede-Lassen, Vibe Schourup-Kristensen, Marc Allentoft-Larsen and Emily Griffiths for their dedicated work as assisting observers and photographers on the aerial surveys. Lotte Knudsen, Danish Environmental Protection Agency, Frederik Laursen and Frederik Lassen provided information on seal sightings in the survey area. The South Funen Archipelago and Little Belt harbour seal surveys were funded by the Danish Environmental Protection Agency under the Ministry of Environment.

Author Contributions. AG designed the study, AG and RD led the surveys, all authors interpreted the findings, AG wrote the draft article, all authors edited and approved of the final draft.

Financial Support. The Danish harbour seal monitoring programmes are funded by Danish Environmental Protection Agency

Conflicts of interest. The authors declare no conflict of interests.

Data Availability. The data that support this study are available in Table 1.

References

- Andersen SM, Teilmann J, Dietz R, Schmidt NM and Miller LA (2012) Behavioural responses of harbour seals to human-induced disturbances. *Aquatic Conservation-Marine and Freshwater Ecosystems* **22**, 113–121.
- Bankhead K, Freeman G, Goebel WH and Acevedo-Gutiérrez A (2023) Effects of anthropogenic noise on haul-out numbers of harbor seals (*Phoca vitulina*). *Canadian Journal of Zoology* **101**, 720–728.
- Becker BH, Press DT and Allen SG (2011) Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquatic Conservation-Marine and Freshwater Ecosystems* **21**, 247–260.
- Brasseur SMJM, Patel TDV, Gerrodette T, Meesters EHWG, Reijnders PJH and Aarts G (2015) Rapid recovery of Dutch gray seal colonies fueled by immigration. *Marine Mammal Science* **31**, 405–426.
- Carroll EL, Hall A, Olsen MT, Onoufriou AB, Gaggiotti OE and Russell DJF (2020) Perturbation drives changing metapopulation dynamics in a top marine predator. *Proceedings of the Royal Society B-Biological Sciences* **287**, 20200318.
- Cates K and Acevedo-Gutiérrez A (2017) Harbor seal (*Phoca vitulina*) tolerance to vessels under different levels of boat traffic. *Aquatic Mammals* **43**, 193–200.
- Dietz R, Teilmann J, Andersen SM, Riget F and Olsen MT (2013) Movements and site fidelity of harbour seals (*Phoca vitulina*) in Kattegat, Denmark, with implications for the epidemiology of the phocine distemper virus. *ICES Journal of Marine Science* **70**, 186–195.
- Frydendahl HC (1939) Sælfangst i fynske farvande. *Fynsk Hjemstavn* **12**, 177–192.
- Gaggiotti OE, Jones F, Lee WM, Amos W, Harwood J and Nichols RA (2002) Patterns of colonization in a metapopulation of grey seals. *Nature* **416**, 424–427.
- Galatius A, Teilmann J, Dahne M, Ahola M, Westphal L, Kyhn LA, Pawliczka I, Olsen MT and Dietz R (2020) Grey seal *Halichoerus grypus* recolonisation of the southern Baltic Sea, Danish Straits and Kattegat. *Wildlife Biology* **2020**, wlb.00711.
- Galatius A, Engbo SG, Teilmann J and van Beest FM (2021) Using environmental variation to optimize aerial surveys of harbour seals. *ICES Journal of Marine Science* **78**, 1500–1507.
- Galatius A, Olsen MT, Allentoft-Larsen M, Balle JD, Kyhn LA, Sveegaard S and Teilmann J (2024) Evidence of distribution overlap between Atlantic and Baltic grey seals. *Journal of the Marine Biological Association of the United Kingdom* **104**, e30.
- Härkönen T and Harding KC (2001) Spatial structure of harbour seal populations and the implications thereof. *Canadian Journal of Zoology* **79**, 2115–2127.
- Heide-Jørgensen MP and Härkönen TJ (1988) Rebuilding seal stocks in the Kattegat-Skagerrak. *Marine Mammal Science* **4**, 231–246.
- Liu XD, Schjøtt SR, Granquist SM, Rosing-Asvid A, Dietz R, Teilmann J, Galatius A, Cammen K, O'Corry-Crowe G, Harding K, Harkonen T, Hall A, Carroll EL, Kobayashi Y, Hammill M, Stenson G, Frie AK, Lydersen C, Kovacs KM, Andersen LW, Hoffman JI, Goodman SJ, Vieira FG, Heller R, Moltke I and Olsen MT (2022) Origin and expansion of the world's most widespread pinniped: range-wide population genomics of the harbour seal (*Phoca vitulina*). *Molecular Ecology* **31**, 1682–1699.
- Milling M (2021) *16 borgmestre i opråb: Dårligt havmiljø tager livet af mindre erhvervsfiskere*. vol. 2023. Odense, Denmark: TV2 Fyn. Available at <https://www.tv2fyn.dk/fyn/16-borgmestre-i-opraab-daarligt-havmiljoe-tager-livet-af-mindre-erhvervsfiskere>
- Olsen MT, Andersen LW, Dietz R, Teilmann J, Härkönen T and Siegismund HR (2014) Integrating genetic data and population viability analyses for the identification of harbour seal (*Phoca vitulina*) populations and management units. *Molecular Ecology* **23**, 815–831.
- Olsen MT, Galatius A and Härkönen T (2018) The history and effects of seal-fishery conflicts in Denmark. *Marine Ecology Progress Series* **595**, 233–243.
- Printzlau MG (2021) *Fiskeriet i Marstal er presset af parasit-inficerede sæler: Kampen er kun lige begyndt*. vol. 2021. Svendborg, Denmark: Fyns Amts Avis. Available at <https://faa.dk/aeroe/fiskeriet-i-marstal-er-presset-af-parasit-inficerede-saeler-kampen-er-kun-lige-begyndt>
- Rohmann JL (1861) *Bidrag Til Det Fyenske Archipelags Smaaøers Historie Efter Utrykte Kilder*. Odense, Denmark: Hempelske Bogtrykkeri.
- Russell DJF, Morris CD, Duck CD, Thompson D and Hiby L (2019) Monitoring long-term changes in UK grey seal pup production. *Aquatic Conservation-Marine and Freshwater Ecosystems* **29**, 24–39.
- Seganfredo S, Teilmann J, van Beest FM and Galatius A (2023) Phenology of harbor seal pupping and the influence of weather on pup counts, investigated by UAV. *Marine Mammal Science* **39**, 906–917.
- Silva WTAF, Bottagisio E, Härkönen T, Galatius A, Olsen MT and Harding KC (2021) Risk for overexploiting a seemingly stable seal population: influence of multiple stressors and hunting. *Ecosphere (Washington, D.C)* **12**, e03343.
- Søkilde NR (1875) *Holstenshus og Nakkebølle med Tilliggende Sogne og Øer Samt Udsigt Over Egnens Almindelige Historie fra Oldtiden til Vore Dage*. Odense, Denmark: Hempelske Boghandel.

- Søndergaard NO, Joensen AH and Hansen EB** (1976) Sælernes forekomst og sæljagten i Danmark. *Dansk Vildtundersøgelser* **26**, 1–80.
- Sveegaard S, Galatius A, Kyhn L and Teilmann J** (2023) Havpattedyr – sæler og marsvin. In Hansen JW and Høgslund S (eds), *Marine Områder 2021*. Aarhus: Aarhus Universitet – DCE – Nationalt Center for Miljø og Energi, pp. 122–133.
- Teilmann J, Olsen MT and Galatius A** (2023) Harbor seal *Phoca vitulina* Linnaeus, 1758. In Hackländer K and Zacos FE (eds), *Handbook of the Mammals of Europe*. Cham: Springer.
- Wood SA, Murray KT, Josephson E and Gilbert J** (2020) Rates of increase in gray seal (*Halichoerus grypus atlantica*) pupping at recolonized sites in the United States, 1988–2019. *Journal of Mammalogy* **101**, 121–128.