

# The history and effects of seal–fishery conflicts in Denmark

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**ABSTRACT:** Growing marine mammal populations have led to renewed conflicts with fisheries and discussions of culling as a management measure. In order to evaluate the effects of such measures, lessons from previous culling efforts and historic data on marine mammal abundance and distribution in response to different hunting and management regimes are pertinent. Here, we combined multiple data sources, including bounty data from the Danish seal culling programme of 1889 to 1927, zooarchaeological records, historical written accounts, 20th century hunting statistics on seals and recent population survey data, in order to assess the prehistoric and historic occurrence of seals in Denmark, and to evaluate the effects of hunting and culling on seal populations, as well as its efficacy as a mitigation measure in seal–fisheries conflicts. We found that past conflicts were driven primarily by developments of passive fishing gear technology in the late 19th century, and that—contrary to several modern interpretations—the primary motivation for culling was damage to catch and gear, not resource competition. Furthermore, we demonstrate that it took decades of heavy-handed culling to minimize the historic seal–fisheries conflicts. Moreover, the culling programme should be regarded in a broader context, where preceding hunting had already decimated grey seal stocks, and subsequent hunting led to an all-time low of a few thousand harbour seals in the early 1970s. We recommend that 21st century seal–fisheries conflicts, debates and associated management decisions should be seen in a historical context, and that there should be an aim towards the development of sustainable fisheries and ecotourism, rather than culling.

**KEY WORDS:** Culling · Hunting · Pinnipeds · Management

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## INTRODUCTION

Competition between fisheries and marine mammals is an old story which has received renewed attention in recent years (Morissette et al. 2012, Bowen & Lidgard 2013). Following substantial population declines caused by centuries of hunting, culling and human disturbance, many marine mammal populations have increased (Roman et al. 2015). Similar to other seal populations, the abundance of Danish harbour seals *Phoca vitulina* has increased from a few thousand in the mid-1970s to close to 20 000 (Olsen et al. 2010, Galatius et al. 2017), and grey seals *Halichoerus*

*grypus* have recently resumed breeding at some of their former haul-out sites after a century of absence (Fietz et al. 2016, Galatius et al. 2017). Across the North Atlantic, such growing seal populations have been accompanied by conflicts with the fishing industry, including competition for fish stocks (Harwood & Walton 2002, Benoit et al. 2011), seal-induced damage to catches and gear (Kauppinen et al. 2005, Königson et al. 2007b, Varjopuro 2011) and increased loads of parasites (e.g. *Pseudoterranova decipiens* and *Contracaecum osculatum*) in commercial fish species (Buchmann & Kania 2012, Haarder et al. 2014), as well as opportunistic predation in fish farms (Quick et al.

2004, Thompson et al. 2007). Damage to gear and catch mostly affect the passive gear fisheries, whereas fisheries with active gear, comprising about 90% of total catches, have no or only minor direct conflicts with marine mammals (Prime & Hammond 1990, Hammond & Grellier 2005, Smout et al. 2014). However, although passive gear fisheries only account for a fraction of total catches, they are often regarded as culturally significant, play important roles in the local economy and are considered more environmentally benign than e.g. bottom trawling. Thus, in Denmark and elsewhere, growing seal populations have led to renewed debates about the seal–fisheries problem and discussions of possible management measures, including culling of seal stocks (Naturvårdsverket 2006, DFO 2011, DME 2013).

In order to evaluate the effects of such mitigation measures, lessons from previous conflicts are pertinent for the formulation of revised management programmes for both prey and predator (Bowen & Lidgard 2013). However, detailed baseline information is often unavailable or difficult to obtain (Pauly 1995). Thus, important aspects, such as the past distribution and abundance of seal populations, the background, purpose and effects of culling programmes, as well as preceding and subsequent human impacts, may be missing, providing an incomplete foundation for evaluating the appropriateness and effects of culling as a management measure. The Danish seal culling programme from 1889 to 1927 was among the first large-scale marine mammal control programmes, and provides an exceptional case for understanding the historic background and effects of seal culling. It has been described in a comprehensive review in Danish by Søndergaard et al. (1976) and in English in a shorter version by Joensen et al. (1976). More recent studies have presented subsets of the data and discussed some of the effects of this and similar culling programmes (Heide-Jørgensen & Härkönen 1988, Harding & Härkönen 1999, Härkönen et al. 2005, 2007). However, the most recent review confused local and regional target species and culling intensity (Bowen & Lidgard 2013), and few (if any) studies have considered the background and effects of preceding and subsequent hunting of seals. Thus, to date, an overall assessment of the background for seal–fisheries conflicts in Denmark, including the combined effects of seal culling and hunting through time, is not available, placing contemporary debates in an inaccurate context.

Here, we took a holistic approach, using multiple lines of evidence to assess the background of historic seal–fisheries conflicts and their effects on seal populations in Denmark. Specifically, we compiled zoo-

archaeological records, historical written accounts and hunting statistics (1) to provide an approximate description of the prehistoric and historic occurrence of seals in Denmark, and (2) to summarise all available information on the occurrence and magnitude of seal hunting in Denmark, including not just the culling programme of 1889 to 1927, but also preceding and subsequent hunting, in order to (3) discuss and evaluate the motivations for, and effects of, seal hunting and culling, and ultimately (4) discuss the efficiency of culling as a mitigation measure in light of 21st century fisheries conflicts.

## MATERIALS AND METHODS

### Data sources

The effects of seal hunting and culling were evaluated by compiling available information on seal occurrence and hunting in Denmark from 5 time periods: (1) prehistory; (2) the 16th to 19th century; (3) the Danish culling programme of 1889 to 1927; (4) the 1940s to the 1960s and 1970s, when seals were protected; and (5) the year 2015.

#### Prehistory to the 16th century

In order to establish baselines for comparison with current seal species composition and abundance, the prehistoric occurrence of seals was determined from the zooarchaeological record listed in the Natural History Museum of Denmark's database on quaternary zoology. This database contains information on all zooarchaeological findings in Denmark, including information presented by Møhl (1971) and Søndergaard et al. (1976), as well as later published accounts (Bennike et al. 2008, Aaris-Sørensen 2009) and unpublished inventories on zooarchaeological finds in the collections of the Natural History Museum of Denmark. Although the zooarchaeological record may be biased towards more easily hunted or otherwise preferred species, we assumed that it roughly reflects the occurrence of seals in prehistoric Denmark.

#### The 16th to the 19th century

Assessments of the 16th to 19th century occurrence of seals were based on observations and geographical localities extracted from historical records and contemporary accounts (Pontoppidan 1763–1781, Melchior

1834, Krøyer 1853, Skrydstrup 1875, Tauber 1880, 1882, 1892, Wulff 1881, Bøving-Petersen 1909, Søndergaard et al. 1976) located through searches for 'sæl' (seal) and 'sælhund' (alternative words for 'seal' in Danish) at the Royal Library of Denmark. Although the historical sources often did not provide the species of seal concerned, information on e.g. hunting locality, season and method could often be used to infer target species, and obtain crude assessments of seal occurrence and the magnitude of the hunt. For instance, pups hunted on land in summer were likely to be harbour seals, whereas pups hunted on land in winter were likely to be grey seals.

#### The Danish culling programme (1889 to 1927)

Statistics from the Danish culling programme from 1889 to 1927 were obtained from Søndergaard et al. (1976) and are based on the number of bounties paid to seal hunters. In 1889 and 1890, hunters were required to send the skull of the culled seal to the Natural History Museum of Denmark to collect their bounty. From 1890 to 1912, hunters only needed to provide the seal's tail as documentation for their claim; however, following suspicions of fraud, hunters were required to send both tail and lower jaw from 1913 until the end of the culling programme in 1927.

In addition to the number of bounties paid, the data provide information about seal species, age class, locality and hunting season for the period 1889 to 1890 and 1913 to 1927 (species and locality only). Information on culling effort was not available.

#### 1928 to present

Data on seal hunting in Denmark is lacking for the period between 1928 and 1940, but hunting statistics are available from 1941 until the mid-1970s, when protection of the harbour seal was initiated (grey seals were protected from 1967) (Søndergaard et al. 1976). The abundance and distribution of harbour seals just prior to their protection in 1976 were obtained from survey data presented in Søndergaard et al. (1976), while the current abundance and distribution of grey and harbour seals in Denmark were based on aerial survey data from 2015 (Galatius et al. 2017).

## RESULTS AND DISCUSSION

### Prehistoric occurrence of seals in Denmark

The zooarchaeological record suggests that seals occurred throughout prehistoric Denmark (Fig. 1B).

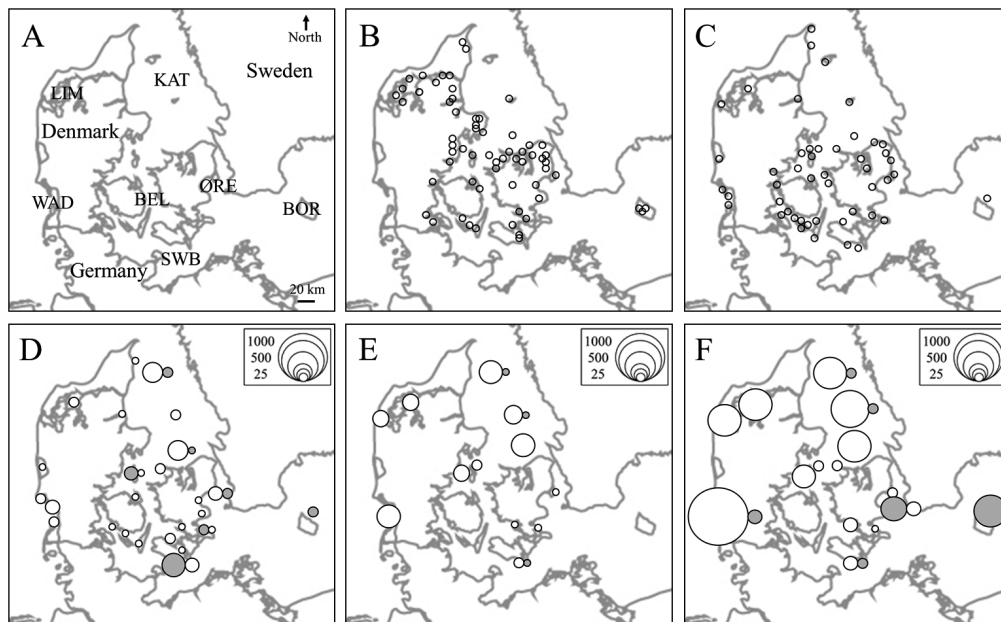


Fig. 1. Occurrence of seals in Denmark from prehistory to present. (A) Study area with region names (WAD: Wadden Sea; LIM: Limfjorden; KAT: Kattegat; BEL: The Belts; SWB: southwestern Baltic; ØRE: Øresund; BOR: Bornholm); (B) zooarchaeological finds of seals in Denmark, of which grey seals constitute the majority (see Fig. 3); (C) seal localities mentioned in 16th–19th century literature; (D) proportion of bounties paid during the first year (1889–1890) of the culling programme for harbour seal (white) and grey seal (grey) at different localities; (E) abundance and distribution of harbour and grey seals based on survey data from the early 1970s; (F) survey data from 2015. Inserts in (D–F) provide numbers of harbour and grey seals

Marine resources such as fish, mammals and molluscs were exploited by prehistoric human cultures across northern Europe, as evidenced by the presence of bones and shells at numerous historic and prehistoric coastal sites, although exploitation patterns varied greatly between regions, time periods and cultures (Møhl 1971, Storå & Lougas 2005, Eriksson & Liden 2013). Remains of grey seals and harp seals *Pagophilus groenlandicus* dominate in findings from cultural layers in the southern Baltic, the Kattegat and Limfjorden areas in the period 10 000 to 1500 yr BP (Lepiksaar 1986, Bennike et al. 2008). Scarcity of archaeological findings from harbour seals and ringed seals *Pusa hispida* suggests that these species did not regularly occur in the area in prehistoric times (Ukkonen et al. 2014). The harp seal disappeared from the zooarchaeological record about 1500 yr BP, likely due to hunting and environmental change (Storå & Lougas 2005, Bennike et al. 2008).

#### 16th to 19th century hunting

Our search in 16th to 19th century literature yielded more than 100 accounts on the occurrence of seals in different periods and geographical regions of Denmark (Fig. 1C). Although the historical literature does mention seal–fisheries conflicts as early as 1663, direct economic incentives (e.g. value of skin and blubber) seems to have been the main driver of seal hunting throughout the early part of the period. The economic importance of the hunt was confirmed by a declaration from 1523, in which the Danish king claimed property of half of the seals shot at the island of Hesselø, and another from 1579 in which the king banned public fishing and hunting at the island of Anholt to protect the royal seal hunt (Søndergaard et al. 1976). Such commercial hunting of seals has occurred throughout northern Europe for centuries. For instance, at least 15 000 ringed seals were killed annually in the northern Baltic Sea between 1550 and 1560 (Kvist 1991), and in the North Sea, large-scale hunting of harbour and grey seals has been practiced at least since the 1590s (Vooy et al. 2012). As in Denmark, the most important driver for the Baltic Sea was the high price of seal oil and skins (Kvist 1991), whereas fisheries conflicts appeared to have been the main motivation in the Netherlands (Vooy et al. 2012).

The earliest direct estimate of the magnitude of the commercial seal hunt in Denmark is from the late 18th century, where contemporary authors described how up to 1000 seals were clubbed, shot or caught in

nets on single days in the Kattegat and the southwestern Baltic (Pontoppidan 1763–1781). It is unclear whether these early numbers reflect the general magnitude of the hunt or particularly successful hunting events, but 100 yr later Tauber (1882) estimated the total hunt to be 300 to 400 seals yr<sup>-1</sup> in Denmark.

#### The Danish seal culling programme (1889 to 1927)

In the 18th and 19th century, there was a significant development of passive fishing gear technology in Denmark and the region as a whole, where pound nets, gill nets and new developments of fish traps were introduced. Pontoppidan (1763–1781) repeatedly mentioned the problems caused by seals in the southwestern Baltic, and Krøyer (1853) described how harbour seals damaged every fifth salmon caught in Randers Fjord on the western shore of the Kattegat, and that grey seals ate salmon off the hooks at Bornholm in the Baltic Sea. For instance, Krøyer (1853) noted that ‘it seems that these clever creatures know that it is difficult to catch the fast free-swimming salmon, but very easy when they are hooked on a line’. Seals also inflicted substantial damage to fish traps in the Belts and Øresund, and experienced fishermen complained that the catch had been reduced to 25 % of what it used to be (DFF 1892).

Danish fishermen had formed associations by the 1860s, and these soon began to apply political pressure for measures to counter the seal problem. Ultimately, this pressure resulted in the initiation of the Danish seal culling programme in 1889, and in 1890 the Danish Fisheries Organisation made official requests to fisheries organisations in Sweden, Finland and Russia to initiate a coordinated international campaign with the goal of minimizing seal–fisheries conflicts by exterminating seals (DFF 1892). Furthermore, the Danish government and Danish Fisheries Organisation supported the culling programme by supplying cheap or free rifles and ammunition to fishermen and hunters, paying bounties for killed seals and awarding prizes to the most effective hunters equivalent to several months’ wages (Søndergaard et al. 1976). Taken together, the historic references indicate that while seals were initially seen as a resource that was valued and to some extent ‘managed’ for sustainability, they were increasingly regarded as pests and competitors. Still, while the national and the fisheries’ interests then lay in culling seals to the indirect economic benefit of fisheries, the direct economic gain likely continued to

be a strong personal incentive for individual hunters, for whom the bounty and the additional value of blubber, skin and meat from an adult seal would equal a 2 wk salary.

The bounty system provided the first detailed accounts on hunting intensity in Denmark, with a total of 37 228 bounties paid during the nearly 4 decades of the culling programme (Figs. 1D & 2). The annual numbers of bounties ranged from a few hundred to almost 2000, with an average of 1300 to 1400 bounties paid  $\text{yr}^{-1}$  during the first 2 decades, and 300 to 400 bounties annually during the last decade of the programme. These numbers are not corrected for ‘struck and lost’, and should thus be taken as minimum estimates of hunting intensity. In the periods of 1889 to 1890 and 1918 to 1927, where species information is available from the records of the Natural History Museum of Denmark, harbour seals accounted for 71.7% of the culled seals, while grey seals accounted for 27.2% and ringed seals 1.1% (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m595p233\\_supp.pdf](http://www.int-res.com/articles/suppl/m595p233_supp.pdf)). If we assume that these proportions reflect the entire period, this corresponds to a total of 26 696 harbour seals, 10 130 grey seals and 402 ringed seals. The Danish culling programme has been described as including ‘decades of culls of ringed seals’ (Bowen & Lidgard 2013, p. 209), but, as we show here, it

mainly affected harbour and grey seals. During the first year of the culling programme, the vast majority of harbour seals that were killed were pups hunted during the summer and autumn (Fig. S2). The age distribution and seasonal timing for the rest of the period is unknown.

### Hunting from 1928 to the present

Seal hunting continued after the culling programme was abandoned. Data are unavailable from 1927 to 1940, but hunting statistics document that between 200 and 600 seals were killed annually in the period 1941 to 1973, which is comparable to the average annual cull during the latter part of the culling programme (Fig. 2). In the 1940s and early 1950s, the number of seals killed was likely underestimated due to unreturned hunting reports from hunters, and in general the numbers for that period can be regarded as minimum estimates as the hunting statistics do not account for struck and lost seals, illegal hunting and seals actively caught in nets by semi-professional seal hunters. Throughout the period, hunting continued to be a tool for minimizing seal–fisheries conflicts, encouraged by fisheries associations, but the hunt was also carried out for economic reasons by a handful of

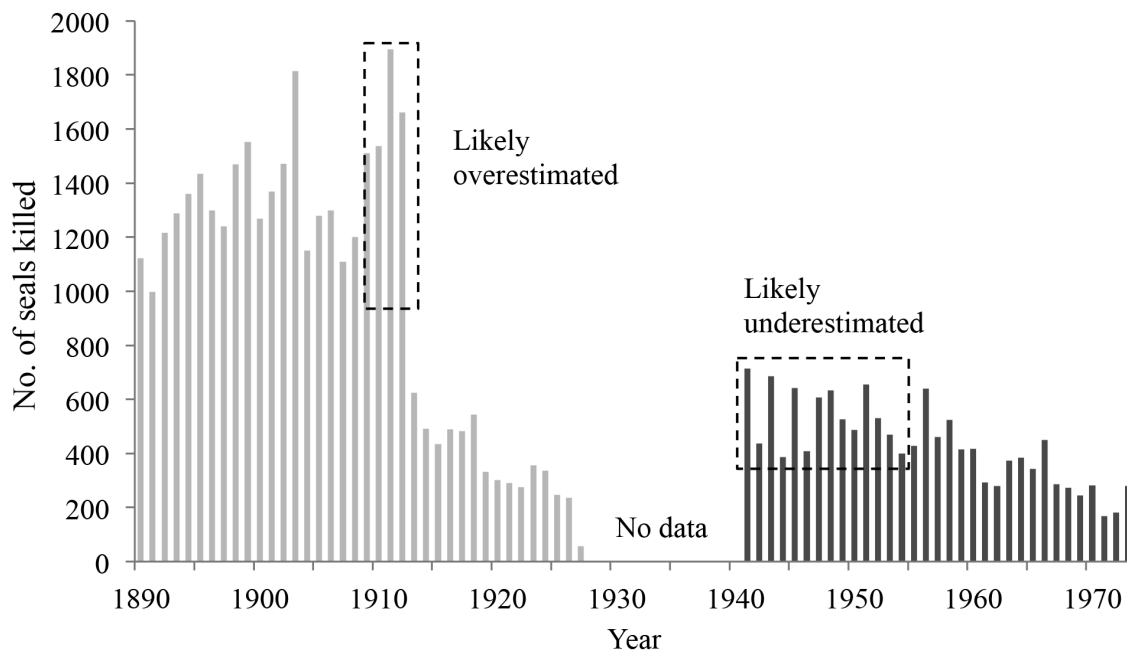


Fig. 2. The number of harbour, grey and ringed seals reported killed in Denmark during the culling programme (1889–1927; recorded as number of bounties paid) and the regular licensed hunt (1941–1973; reports by hunters of the number of seals killed). In the first period, harbour, grey and ringed seals constituted approximately 72, 27 and 1%, respectively, whereas almost all seals killed during the second period were harbour seals. The numbers for the 1910s are likely overestimated due to fraud with bounties, whereas the numbers from the 1940s and 1950s are likely underestimated due to underreporting by hunters. Data are missing from 1928 to 1940

professional seal hunters, each killing 25 to 50 seals yr<sup>-1</sup>. From the 1960s until the protection of grey seals in 1967 and harbour seals in 1976, the hunt was primarily for recreation (Joensen et al. 1976). Hunting of seals is currently illegal in Denmark, but fishermen can apply for license to regulate 'problem seals', defined as seals in the vicinity of passive fishing gear. Consequently, since 2005, on average 10 harbour seals yr<sup>-1</sup> have been regulated to reduce seal–fisheries conflicts.

### The effects of hunting and culling on seal distribution and abundance

The zooarchaeological record documents the long-term occurrence of seals throughout Danish waters, and many of the historical accounts describe seals as occurring 'everywhere', so the distribution of seals was probably more or less ubiquitous up until at least the 16th century (Fig. 1, Table 1). There are no direct estimates of the prehistoric or historic sizes of seal populations, but extrapolations from the bounty statistics suggest an 18th and 19th century abundance of 15 000 to 20 000 harbour and grey seals in Danish waters (Heide-Jørgensen & Härkönen 1988, Härkönen et al. 2007, Olsen et al. 2010). The first reliable population estimate is from the early 1970s, and suggests a total Danish abundance of 1500 to 3000 harbour seals; at this time the grey seal had vanished as a breeding species, and only occurred sporadically (Joensen et al. 1976) (Fig. 1E). In recent years, both species have increased in abundance compared to their levels in the 1970s, with the abundance of harbour seals reaching approximately 20 000, whereas grey seals visiting from the Baltic proper, the United Kingdom and the German and Dutch Wadden Sea occur in varying numbers of up to 850 animals, and

up to 10 grey seal pups are born each year (Fietz et al. 2016, Galatius et al. 2017) (Fig. 1F, Table 1). During this increase, both species exhibited a remarkable ability to return to previous haul-out sites. Still, some regions have not yet been recolonised. This particularly applies to the Belts around Funen—a region where seals were abundant in the 16th to 18th centuries but disappeared in the 19th century (Fryden-dahl 1939). Also, judging from historic hunting accounts, several fjord systems across the country, like Isefjorden and Roskilde Fjord, had large historic occurrences, but these have not yet been recolonised.

Taken together, these observations document substantial changes in seal occurrence and species composition (Fig. 3). Specifically, while the zooarchaeological record and historic literature indicate that the grey seal was the dominant species in Denmark until the 16th to 19th century, this species had already been decimated by the onset of the culling programme in 1889, at which time the harbour seal had become the most abundant species. The Danish culling programme (and similar programmes in the region) undoubtedly played a major role in these changes. However, given the magnitude of preceding and subsequent hunting for seal oil, skin and meat documented here, we suggest that these efforts outside the culling programme also played a substantial role in the reduction of the seal population, as has been seen elsewhere. For instance, grey seals were already hunted to extinction along the European mainland outside the Baltic in the 1500s (Härkönen et al. 2007), had vanished from Germany and Poland by the early 1910s (Gill 1978) and were later substantially decimated in the Swedish and Finnish Baltic Sea (Harding et al. 2007, Härkönen et al. 2007). In addition to hunting and culling, the change in abundance and species composition was likely affected by late Holocene environmental

Table 1. Temporal and spatial trends in grey and harbour seal hunting intensity and census population size in Denmark. Values are given as the proportion of the total number of seals within each of the periods 16th–19th century, 1889–1890, 1923–1927, 1960–1974, 1970 and 2015, respectively. The 16th–19th century hunting estimates are based on literature review, whereas estimates from the other periods are based on hunting statistics and survey counts. Values in **bold** include grey seals; all other values are harbour seals only

Region	Abbrev.	Hunt and culling				Survey	
		16th–19th Century	1889–1990	1923–1927	1960–1974	1970	2015
Wadden Sea	WAD	0.05	0.10	0.40	0.33	0.26	0.24
Limfjorden	LIM	0.07	0.00	0.01	0.12	0.09	0.13
Kattegat	KAT	<b>0.33</b>	<b>0.51</b>	0.19	0.43	0.61	0.49
The Belts	BEL	<b>0.19</b>	0.03	0.11	0.01	0.01	0.00
SW Baltic	SWB	<b>0.23</b>	<b>0.25</b>	<b>0.25</b>	0.09	0.01	<b>0.09</b>
Øresund	ØRE	<b>0.11</b>	0.09	0.03	0.02	0.02	0.00
Bornholm	BOR	<b>0.02</b>	<b>0.01</b>	<b>0.02</b>	<b>0.01</b>	<b>0.00</b>	<b>0.05</b>

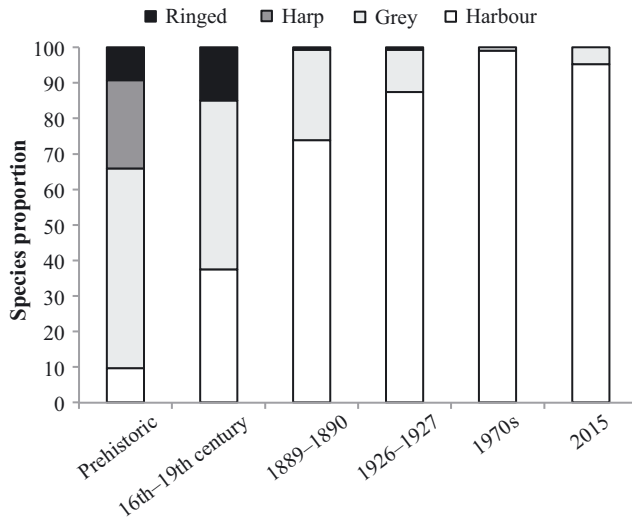


Fig. 3. Changes in the composition of the Danish seal fauna from prehistory to present expressed in terms of each species' proportion of the total occurrence. The prehistoric (6000–500 yr BP) data are based on zooarchaeological record, 16th–19th century data are from a review of historical written records, 1889–1890 and 1926–1927 are based on hunting statistics for subsets of the culling programme, and the 1970s and 2015 data were obtained from population surveys

changes reducing suitable habitats and range for e.g. the ice-associated ringed and harp seals (Bennike et al. 2008, Ukkonen et al. 2014), as well as interspecific competition (Svensson 2012) potentially giving an advantage to harbour seals in areas where grey seals disappeared. More recently, the populations have been affected by organochlorine pollution and associated health effects in Sweden and Finland (Bergman & Olsson 1986, Olsson et al. 1994) as well as disease outbreaks throughout northern Europe (Härkönen et al. 2006). Accordingly, the effects of the culling program cannot be evaluated in isolation, but must be considered in relation to previous and later anthropogenic and environmental impacts—an aspect which is often neglected in a fisheries and seal management context. This appears to specifically apply to the distribution and abundance of grey seals in Denmark, which had been substantially reduced by hunting even before the onset of the culling programme in 1889.

### Seal culling as conflict mitigation

It is often assumed that the motivation for the Danish seal culling programme (and similar programmes) was to protect fish stocks and reduce the competition between seals and fisheries for marine resources (Gulland 1987, Bowen & Lidgard 2013).

This assumption is incomplete and misleading. The current structure of the Danish fishery, with a dominance of active gear, contrasts to the situation that existed at the end of the 19th century, where most coastal fisheries were based on passive gear vulnerable to interactions with marine mammals. Indeed, several historical accounts concur that the main grievance of Danish fishermen was damage to static gear and catch (Melchior 1834, Krøyer 1853, Skrydstrup 1875, Tauber 1880, 1882, 1892, Wulff 1881, Bøving-Petersen 1909). Seal predation may have direct and substantial effects on fish abundance (Benoit et al. 2011, DFO 2011, Swain & Benoit 2015), and competition and displacement of coastal fish stocks by seals were mentioned in the historical Danish accounts, but it does not appear that these are the main motivations for culling seals. This also appears to have contributed to the motivation for pinniped culling programmes in other parts of the world. California sea lions *Zalophus californianus* were reported to steal fish and destroy gear at the time of the 1899 California sea lion cull (Kjønnøy 1899), and mitigation measures later discussed by the National Marine Fisheries Service of the United States specifically addressed removal of catch and damage to gear (NMFS 1997). Similar issues partly motivated the Norwegian grey seal culling programme of 1980 to 1990 (Kjønnøy 1990), and interactions with passive gear continue to be the main driver of seal–fisheries conflicts in Denmark and in the Baltic Sea region in general (Königson et al. 2003, 2006, 2007a,b, 2009, Kauppinen et al. 2005, Lundstrom et al. 2010, Varjopuro 2011).

Despite the widespread use of culling to minimize seal–fisheries conflicts, its effect as a mitigation measure has rarely been evaluated. The Danish culling programme was abandoned in 1927, but it is uncertain whether this happened because it was too expensive, and/or because the seal problem was considered resolved (Joensen et al. 1976, Søndergaard et al. 1976). As we have shown, culling was particularly intense during the first 2 decades of the programme, but the number of bounties declined steadily during the latter decades of the programme. Assuming that the intensity of the hunt correlated with the magnitude of the seal–fisheries conflict or the abundance of seals, the above numbers suggest that it took a long period of intense culling to effectively reduce seal numbers and associated impacts on the fisheries. Indeed, a decade into the programme, fishermen reported the costs associated with seal depredation to be greater than the income from the fishery (DFF 1899), and an interview survey conducted among

fishermen in 1908—nearly 2 decades into the programme—suggested that problems were still widespread (Bøving-Petersen 1909). Today, grey seals appear to cause more problems with fisheries than harbour seals in the Baltic Sea region (Königson et al. 2007a, 2009), so the historic conflict probably abated as grey seal populations were decimated in not only Denmark, but also neighboring Germany, Poland and Sweden. Furthermore, during the same period the fishery gradually developed into using more active gear, and correspondingly, landings from passive gear fisheries comprised a lesser and lesser part of the total revenue. Thus, the most likely reason for the cessation of the culling programme seems to be that the seal population had been decimated, that other types of fisheries had become more profitable, and hence that seal–fisheries conflicts were considered reduced to an acceptable level.

#### Lessons for 21st century seal–fisheries conflicts

In Denmark and elsewhere, the increased abundance of many marine mammal populations has raised concerns in coastal communities and maritime industries, and consequently in the political system. Typical complaints include (1) that populations are growing unnaturally and explosively, (2) that these are the main cause of declining fish stocks and landings and (3) that the ideal solution to the problem is culling (e.g. DME 2013, Meyer 2015, Åland fiskere 2015). However, as we and many others have shown (e.g. UNEP 1999), such statements are often short-sighted, ignoring longer term patterns and thus fail to capture the true nature of the marine mammal–fisheries conflict and population dynamics.

Firstly, most marine mammal populations were much larger in the past and are still depleted after previous pressures (Roman & Palumbi 2003, Kovacs et al. 2012, Roman et al. 2013). Also, exponential growth is a natural reaction of depleted populations when they are relieved of the pressures responsible for the depletion, and even top predators are obviously not immune to the effects of density dependence, so growth will not proceed uninhibited. Indeed, while e.g. harbour seal populations were growing at close to 12% yr<sup>-1</sup> in the Wadden Sea, the Skagerrak and the Kattegat until the phocine distemper virus (PDV) epidemic in 2002 (Härkönen et al. 2002), population growth rates are now levelling off at 6 to 8% yr<sup>-1</sup> (Galatius et al. 2017). These attitudes are reminiscent of the ‘shifting baseline syndrome’ coined by Pauly (1995) turned on its head: originally, this

syndrome described the gradual acceptance of depletion of species, as each new generation of scientists starts their careers with a new, still lower, baseline. In the case of seal–fishery conflicts, species with problematic interactions with humans recover and evoke heated debate as these interactions greatly exceed the accepted, modern baseline of low abundances. As highlighted above, grey seal abundance in Denmark is frequently described as growing ‘unnaturally’ and ‘explosively’, even though it is still at a small fraction of historic abundance, and breeding only occurs in very low numbers. Thus, there is a need to lift the baselines of what is perceived as ‘natural’ if the management objective is to allow depleted stocks to recover (Roman et al. 2015). Accordingly, the US Marine Mammal Protection Act is designed to return (or maintain) populations to their optimal sustainable population, which is defined as between 50 and 80% of virginial population levels (NOAA 2007, Roman et al. 2013). In contrast, the EU Marine Strategy Framework Directive does not include historical considerations at all, but strives to obtain ‘ecologically diverse and dynamic oceans and seas which are clean, healthy and productive within their intrinsic conditions, and the use of the marine environment is at a level that is sustainable’ (European Parliament and Council of the European Union 2008 (2008/56/EC)). Similarly, the EU Habitats Directive states that favourable reference levels for the range and size of populations should be ‘sufficiently large to allow the long term survival of the species’, but does not define these further, other than that reference levels should be ‘at least the size/range of the population, when the Directive came into force [in 1992]’ and that historic information ‘may be found useful’ (Council of the European Communities 1992 (92/43/EEC)).

Secondly, while marine mammals as top predators in the marine ecosystem undoubtedly have an impact on fish stocks, and may locally lead to declines and/or prevent recovery (Benoit et al. 2011, Swain & Benoit 2015), fish population dynamics are typically governed by multiple natural and anthropogenic processes, including exploitation and climate change, rather than marine mammal predation alone (Eero et al. 2011). Indeed, the removal of fish by fisheries in the Baltic Sea is at least three times higher than the combined removal by birds and seals (Hansson et al. 2017). Critics tend to disregard these facts, and—perhaps more perplexing—in particular seem to forget the impacts of a century of overexploitation (Christensen et al. 2003, Myers & Worm 2003, Thurstan et al. 2010), and that several sectors of the fishing industry—including



passive gear fisheries—are unprofitable and rely on substantial subsidies (Nielsen et al. 2013, UN 2017).

Thirdly, if culling is to be the standard response to growing marine mammal populations and associated fisheries conflicts, our data indicate that such culls need to be substantial to significantly reduce or eliminate the interactions. In Finland and Sweden, grey seals have been hunted to protect fisheries since 1998 and 2001, respectively. Several efforts have been made to direct this hunt towards ‘problem seals’, including special permits for hunting in the vicinity of fishing gear, higher quotas for areas with severe problems and hunting with seal traps. Despite this, seal-inflicted damage has increased significantly since its start, in concert with a generally increasing seal population (Königson et al. 2003, Lundstrom et al. 2010). This is consistent with our findings about culling as a mitigation approach; it was successfully employed in the late 19th to early 20th century, but required a protracted, heavy-handed effort that cost the extirpation of the grey seal as a breeding species in Denmark, and massive reductions of the Baltic Sea seal populations. The overall economic, publicity and ecosystem costs associated with a cull of such magnitude may well exceed the benefits.

If that is the case, what to do? In their discussion on lifting baselines, Roman et al. (2015) recommended that: (1) return of problematic species to their former areas of distribution should be communicated as the conservation success they represent; (2) their recovery should be presented in the light of their historical abundance, the ecosystem health and natural capital; (3) ecological changes should be monitored to anticipate arguments of failed resource management; and (4) the benefits of marine mammal populations, including costs and benefits of removal of ‘nuisance animals’, should be estimated (Roman et al. 2015). These recommendations are also valid here. However, in the case of seals—and in contrast to e.g. cetaceans—fisheries interactions are typically the primary aspect of their recovery to be evaluated and communicated. This is also the case in Denmark, where focus has been on the negative impacts of seals, and very little has been done to appreciate and estimate their potential value. Marine mammal watching has globally become a billion dollar industry with large unrealised economic potentials (Cisneros-Montemayor & Sumaila 2010), and on a global scale, the combined revenue of maritime and coastal tourism likely exceeds that from fisheries and aquaculture industries (Higham et al. 2014). In the EU, the maritime and coastal tourism sector employs more than 3 million people and is identified as a sector

with a high future potential for sustainable growth (European Commission 2017, ECORYS for DG Maritime Affairs & Fisheries 2013).

In light of this, the historic context of the current situation should be communicated, and the socio-economic benefits of a healthy and well-functioning marine environment, including all its inhabitants, should be explored; in particular with regards to the potentials of coastal and maritime ecotourism. This is not to say that passive gear fisheries should be abandoned. It is a trade of high social and cultural significance, provides jobs, income and atmosphere to local coastal communities, and is relatively sustainable with low environmental impact compared to e.g. trawling. However, we should recognize that in the case of marine mammal–fisheries conflicts, any solution (or no solution) will have negative effects on one or more stakeholders—be it fisheries, coastal communities, tourism, recreationists or environmentalists. The key is to minimize these effects while preserving a healthy marine environment.

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#### LITERATURE CITED

- Aaris-Sørensen K (2009) Diversity and dynamics of the mammalian fauna in Denmark throughout the last glacial-interglacial cycle, 115–0 kyr BP. *Fossils and Strata* 57:1–59
- Åland fiskere (Sveriges Fiskares Producentorganisation) (2015) Sæler får os til at miste fornuften. Politiken <http://politiken.dk/debat/debatindlaeg/ECE2955152/saeler-faar-os-til-at-miste-fornuften/>
- Anonymous (1899) Destructive sea lions. Thousands of salmon slaughtered in the Upper Bay. *San Fransisco Call*, Vol 85, 7 March 1899, p 6
- ✦ Bennike O, Rasmussen P, Aaris-Sørensen K (2008) The harp seal (*Phoca groenlandica* Erxleben) in Denmark, southern Scandinavia, during the Holocene. *Boreas* 37:263–272
- ✦ Benoit HP, Swain DP, Bowen WD, Breed GA, Hammill MO, Harvey V (2011) Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. *Mar Ecol Prog Ser* 442:149–167
- Bergman A, Olsson M (1986) Pathology of Baltic grey seal and ringed seal females with special reference to adrenocortical hyperplasia: Is environmental pollution the cause of a widely distributed disease syndrome? *Finnish Game Research* 44:47–62
- Bøving-Petersen JO (1909) Saltvandsfiskeriets skadedyr og kampen mod dem. Dansk Fiskeriforening, Fredericia

- Bowen WD, Lidgard D (2013) Marine mammal culling programs: review of effects on predator and prey populations. *Mammal Rev* 43:207–220
- Buchmann K, Kania P (2012) Emerging *Pseudoterranova decipiens* (Krabbe, 1878) problems in Baltic cod, *Gadus morhua* L., associated with grey seal colonization of spawning grounds. *J Fish Dis* 35:861–866
- Christensen V, Guénette S, Heymans JJ, Walters CJ, Watson R, Zeller D, Pauly D (2003) Hundred-year decline of North Atlantic predatory fishes. *Fish Fish* 4:1–24
- Cisneros-Montemayor AM, Sumaila UR (2010) A global estimate of benefits from ecosystem-based marine recreation: potential impacts and implications for management. *J Bioeconomics* 12:245–268
- Council of the European Communities (1992) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora, OJ L 206/9
- DFF (Dansk Fiskeriforening) (1892) Dansk fiskeriforenings medlemsblad. Copenhagen, p 512
- DFF (1899) Dansk fiskeriforenings medlemsblad. Copenhagen, p 548
- DFO (Department of Fisheries and Oceans Canada) (2011) Impacts of grey seals on fish populations in eastern Canada. Canadian Science Advisory Secretariat Science Advisory Report 2010/071. DFO, Ottawa
- DME (Danish Ministry of Environment) (2013) Danish Ministry of Environment. S 2100 endeligt svar, J.nr. NST-301-00299. [www.ft.dk/samling/20121/spoergsmaal/s2100/svar/1067379/1271979.pdf](http://www.ft.dk/samling/20121/spoergsmaal/s2100/svar/1067379/1271979.pdf)
- ECORYS for DG Maritime Affairs & Fisheries (2013) Study in support of policy measures for maritime and coastal tourism at EU level. Specific contract under FWC MARE/2012/06-SC D1/2013/01-S12.648530
- Eero M, MacKenzie BR, Köster FW, Gislason H (2011) Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. *Ecol Appl* 21:214–226
- Eriksson G, Liden K (2013) Dietary life histories in Stone Age Northern Europe. *J Anthropol Archaeol* 32:288–302
- European Commission (2017) Commission staff working document on nautical tourism. Brussels, 30.3.2017 SWD(2017) 126 final. [https://ec.europa.eu/maritimeaffairs/sites/maritimeaffairs/files/swd-2017-126\\_en](https://ec.europa.eu/maritimeaffairs/sites/maritimeaffairs/files/swd-2017-126_en)
- European Parliament and Council of the European Union (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive), OJ L 164/19
- Fietz K, Galatius A, Teilmann J, Dietz R and others (2016) Shift of grey seal subspecies boundaries in response to climate, culling and conservation. *Mol Ecol* 25:4097–4112
- Frydendahl HC (1939) Sælfangst i fynske farvande. *Fynsk Hjemstavn* 12:177–192
- Galatius A, Sveegaard S, Teilmann J (2017) Havpattedyr – sæler og marsvin. In: Hansen JW (ed) *Marine Områder 2015 – NOVANA*. Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, Aarhus, p 88–100
- Gill J (1978) Occurrence, legislation and protection of seals in Poland. *Finnish Game Research* 37:18–19
- Gulland JA (1987) Seals and fisheries: a case for predator control? *Trends Ecol Evol* 2:102–104
- Haarder S, Kania PW, Galatius A, Buchmann K (2014) Increased *Contracaecum osculatum* infection in Baltic cod (*Gadus morhua*) liver (1982–2012) associated with increasing grey seal (*Halichoerus grypus*) populations. *J Wildl Dis* 50:537–543
- Hammond PS, Grellier K (2005) Grey seal diet and fish consumption in the North Sea. Department for Environment, Food and Rural Affairs, London. [http://randd.defra.gov.uk/Document.aspx?Document=MF0319\\_3908\\_FRP.doc](http://randd.defra.gov.uk/Document.aspx?Document=MF0319_3908_FRP.doc)
- Hansson S, Bergström U, Bonsdorff E, Härkönen T and others (2017) Competition for the fish—fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. *ICES J Mar Sci* fsx207
- Harding KC, Härkönen TJ (1999) Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio* 28: 619–627
- Harding KC, Harkonen T, Helander B, Karlsson O (2007) Status of Baltic grey seals: population assessment and extinction risk. *NAMMCO Sci Publ* 6:33–56
- Härkönen T, Harding KC, Heide-Jørgensen MP (2002) Rates of increase in age-structured populations: a lesson from the European harbour seals. *Can J Zool* 80: 1498–1510
- Härkönen T, Harding KC, Goodman SJ, Johannesson K (2005) Colonization history of the Baltic harbour seals: integrating archaeological, behavioral, and genetic data. *Mar Mamm Sci* 21:695–716
- Härkönen T, Dietz R, Reijnders P, Teilmann J and others (2006) The 1988 and 2002 phocine distemper virus epidemics in European harbour seals. *Dis Aquat Org* 68: 115–130
- Härkönen T, Brasseur S, Teilmann J, Vincent C, Dietz R, Abt K, Reijnders P (2007) Status of grey seals along mainland Europe from southwestern Baltic to France. *NAMMCO Sci Publ* 6:57–68
- Harwood J, Walton M (2002) Interactions between seals and commercial fisheries in the north-east Atlantic. *Fisheries Series FISH* 110 EN. Working paper to the European Parliament's Committee on Fisheries European Parliament, Luxembourg. [www.europarl.europa.eu/RegData/etudes/etudes/join/2002/321146/DG-4-PECH\\_ET\(2002\)321146\\_EN.pdf](http://www.europarl.europa.eu/RegData/etudes/etudes/join/2002/321146/DG-4-PECH_ET(2002)321146_EN.pdf)
- Heide-Jørgensen MP, Härkönen TJ (1988) Rebuilding the seal stocks in the Kattegat-Skagerrak. *Mar Mamm Sci* 4: 231–246
- Higham J, Bejder L, Williams R (2014) *Whale-watching: sustainable tourism and ecological management*. Cambridge University Press, Cambridge
- Joensen AH, Sondergaard NO, Hansen EB (1976) Occurrence of seals and seal hunting in Denmark. *Dan Rev Game Biol* 10:1–20
- Kauppinen T, Siira A, Suuronen P (2005) Temporal and regional patterns in seal-induced catch and gear damage in the coastal trap-net fishery in the northern Baltic Sea: effect of netting material on damage. *Fish Res* 73:99–109
- Kjønnøy G (1990) Landsplan for forvaltning av kystsel. Fiskeridepartementet, Forvaltningstjenestene, Statens trykningskontor, Oslo
- Königson S, Lunneryd SG, Lundström K (2003) Damage to eel fisheries by seals along the Swedish west coast. A study of conflict and its possible solutions. *Finno Fiskeriverket Informerar* 9:1–24 (in Swedish with English Abstract)
- Königson SJ, Lundstrom KE, Hemmingsson MMB, Lunneryd SG, Westerberg H (2006) Feeding preferences of harbour seals (*Phoca vitulina*) specialised in raiding fishing gear. *Aquat Mamm* 32:152–156
- Königson S, Fjalling A, Lunneryd SG (2007a) Grey seal induced catch losses in the herring gillnet fisheries in the northern Baltic. *NAMMCO Sci Publ* 6:203–214
- Königson S, Hemmingsson M, Lunneryd SG, Lundstrom K

- (2007b) Seals and fyke nets: an investigation of the problem and its possible solution. *Mar Biol Res* 3:29–36
- ✦ Königson S, Lunneryd SG, Stridh H, Sundqvist F (2009) Grey seal predation in cod gillnet fisheries in the central Baltic Sea. *J Northwest Atl Fish Sci* 42:41–47
- ✦ Kovacs KM, Aguilar A, Aurioles D, Burkanov V and others (2012) Global threats to pinnipeds. *Mar Mamm Sci* 28: 414–436
- Krøyer HN (1853) Danmarks fiske, Vol. 3. Trier, Copenhagen
- ✦ Kvist R (1991) Sealing and sealing methods in the Bay of Bothnia 1551–70. *Polar Rec (Gr Brit)* 27:339–344
- Lepiksaar J (1986) The Holocene history of theriofauna in Fennoscandia and Baltic countries. *Nordic Late Quaternary Biology and Ecology (Striae)* 24:51–70
- ✦ Lundstrom K, Lunneryd SG, Königson S, Hemmingsson M (2010) Interactions between harbour seals (*Phoca vitulina*) and coastal fisheries along the Swedish west coast: an overview. *NAMMCO Sci Publ* 8:329–340
- Melchior HB (1834) Den danske Stats og Norges Pattedyr. Sophus Zahle
- Meyer I (2015) Voksende sælbestand truer fiskeriet. *Berlingske Tidende* [www.b.dk/nationalt/voksende-saelbestand-truer-fiskeriet](http://www.b.dk/nationalt/voksende-saelbestand-truer-fiskeriet)
- Møhl U (1971) Fangstdyrene ved de Danske strande. Den zoologiske baggrund for harpunerne (Game animals along the Danish beaches. The zoological background for the harpoons). *Årbog for Jysk Arkæologisk Selskab* 1971:297–329 (In Danish with English and German summaries)
- ✦ Morissette L, Christensen V, Pauly D (2012) Marine mammal impacts in exploited ecosystems: Would large scale culling benefit fisheries? *PLOS ONE* 7:e43966
- ✦ Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Naturvårdsverket (2006) Viltskadeanslaget, fisket och sälarna—utvärdering av viltskadeanslaget på sälskadeområdet. Naturvårdsverket, Stockholm
- Nielsen M, Larsen E, Egekvist J and others (2013) Dansk Kystfiskeri: Struktur og økonomi. Institut for Fødevarer og Ressourceøkonomi, Københavns Universitet, Copenhagen
- NMFS (National Marine Fisheries Service) (1997) Investigation of scientific information on the impacts of California sea lions and Pacific harbor seals on Pacific coast salmonids and on the coastal ecosystems of Washington, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-28. US Department of Commerce, Washington, DC
- NOAA (2007) The marine mammal protection act of 1972 as amended 2007. NOAA National Marine Fisheries Service, Silver Spring, MD
- ✦ Olsen MT, Andersen SM, Teilmann J, Dietz R, Edrén SMC, Linné A, Härkönen T (2010) Status of the harbour seal (*Phoca vitulina*) in southern Scandinavia. *NAMMCO Sci Publ* 8:77–94
- ✦ Olsson M, Karlsson B, Ahnland E (1994) Diseases and environmental contaminants in seals from the Baltic and the Swedish west coast. *Sci Total Environ* 154:217–227
- ✦ Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol Evol* 10:430
- Pontoppidan E (1763–1781) Den danske atlas eller Kongeriget Danemark. Godiche, Copenhagen
- ✦ Prime JH, Hammond PS (1990) The diet of gray seals from south-western North Sea assessed from analyses of hard parts found in feces. *J Appl Ecol* 27:435–447
- ✦ Quick NJ, Middlemas SJ, Armstrong JD (2004) A survey of antipredator controls at marine salmon farms in Scotland. *Aquaculture* 230:169–180
- ✦ Roman J, Palumbi SR (2003) Whales before whaling in the North Atlantic. *Science* 301:508–510
- Roman J, Altman I, Dunphy-Daly MM, Campbell C, Jasny M, Read AJ (2013) The Marine Mammal Protection Act at 40: status, recovery, and future of US marine mammals. *Ann N Y Acad Sci* 1286:29–49
- ✦ Roman J, Dunphy-Daly MM, Johnston DW, Read AJ (2015) Lifting baselines to address the consequences of conservation success. *Trends Ecol Evol* 30:299–302
- Skrydstrup V (1875) Laksefiskeriet ved Bornholm. *Nordisk Tidsskrift for Fiskeriet* 8:24–25
- ✦ Smout S, Rindorf A, Hammond PS, Harwood J, Matthiopoulos J (2014) Modelling prey consumption and switching by UK grey seals. *ICES J Mar Sci* 71:81–89
- Søndergaard NO, Joensen AH, Hansen EB (1976) Seals in Denmark. *Danske Vildtundersøgelser* 26 (in Danish with English summary)
- Storå J, Lougas L (2005) Human exploitation and history of seals in the Baltic during the Late Holocene. In: Monks GG (ed) *Exploitation and cultural importance of sea mammals*. Oxbow Books, Oxford, p 95–106
- ✦ Svensson CJ (2012) Seal dynamics on the Swedish west coast: scenarios of competition as Baltic grey seal intrude on harbour seal territory. *J Sea Res* 71:9–13
- ✦ Swain DP, Benoit HP (2015) Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. *Mar Ecol Prog Ser* 519:165–182
- Tauber JP (1880) Forekomsten af havpattedyr ved dansk Kyst. *Geogr Tidsskr* 4:91–103
- Tauber JP (1882) Sælhundene. *Fiskeritidende* 12:89–124
- Tauber JP (1892) *Zoologica Danica*. Hvirveldyr, Vol 1: Pattedyr. E Jespersen, Copenhagen
- ✦ Thompson PM, Mackey B, Barton TR, Duck C, Butler JRA (2007) Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals (*Phoca vitulina*) in north-east Scotland. *Anim Conserv* 10:48–56
- ✦ Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nat Commun* 1:15
- Ukkonen P, Aaris-Sørensen K, Arppe L, Daugnora L and others (2014) An Arctic seal in temperate waters: history of the ringed seal (*Pusa hispida*) in the Baltic Sea and its adaptation to the changing environment. *Holocene* 24: 1694–1706
- UN (2017) Report of the United Nations Conference to Support the Implementation of Sustainable Development Goal 14: conserve and sustainably use the oceans, seas and marine resources for sustainable development. A/CONF.230/14, United Nations, New York, NY. <https://undocs.org/A/CONF.230/14>
- UNEP (United Nations Environment Programme) (1999) Protocol for the scientific evaluation of proposals to cull marine mammals. Report of the Scientific Advisory Committee of the Marine Mammals Action Plan. UNEP, Rome
- ✦ Varjopuro R (2011) Co-existence of seals and fisheries? Adaptation of a coastal fishery for recovery of the Baltic grey seal. *Mar Policy* 35:450–456
- Vooy CGN, Brasseur S, Meer J, Reijnders P (2012) Analyses of four centuries of bounty hunting on seals in Zeeland, SW-Netherlands. *Lutra* 55:55–65
- Wulff J (1881) Danmarks pattedyr: en populær vejledning. PG Philipsens Forlag, Copenhagen