

Review

Harbour Seals: Population Structure, Status, and Threats in a Rapidly Changing Environment

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Abstract: The harbour seal (*Phoca vitulina*) is the world’s most widely distributed pinniped species ranging from temperate to Arctic regions (30–78.5° N in the Atlantic, 28–61.2° N in the Pacific), but no detailed overview of the species status exists. The aims of this review are to (i) provide current information on the genetic structure, population status, and threats; (ii) review potential consequences of a changing climate; and (iii) identify knowledge gaps to guide future research and monitoring. Although the species is globally abundant, wide differences exist across the species’ broad range. As climate warms, populations at the edges of the species’ distributional range are likely to be more affected. The primary climate-related drivers include: (i) changes in weather patterns, which can affect thermoregulation; (ii) decrease in availability of haul-out substrates; (iii) large-scale changes in prey availability and inter-specific competition; (iv) shifts in the range of pathogens; (v) increase in temperature favouring the biotransformation of contaminants; and (vi) increased exposure to pollutant from increased freshwater run-off. Multiple anthropogenic stressors may collectively impact some populations. Coordinated monitoring efforts across and within regions is needed. This would allow for a spatially explicit management approach including population-specific responses to known stressors.

Keywords: harbour seal; *Phoca vitulina*; pinniped; distribution; population status; climate change; edge effect; knowledge gaps



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1. Introduction

The harbour seal or common seal (*Phoca vitulina* Linnaeus 1758) is the most widely distributed pinniped in the northern hemisphere and ranges from temperate to Arctic regions. Due to its extensive range, nearshore coastal distribution, site fidelity, and high visibility, it is one of the most well-studied pinnipeds in the world [1,2]. Harbour seals use an array of habitats including bays, rivers, lakes, estuaries, intertidal habitats, sea ice, and icebergs in tidewater glacier fjords [3–8]. Harbour seals typically use solid substrates for birthing, nursing their young, resting and moulting, and can undertake extensive at-sea foraging trips lasting several days to weeks [9–11]. Harbour seals typically produce one pup each year in the late spring to early autumn depending upon the region [12], and mating occurs towards the end of the brief lactation period. Given that harbour seals occupy habitats that are in close proximity to human populations, the species has the potential to be exposed to a variety of anthropogenic activities including harvest,

population reduction programs, coastal development, agricultural runoff and pollution, and interactions with fisheries [13,14].

Similar to other marine mammal species, harbour seals are expected to undergo changes in all or part of their range due to climate related changes which include ocean warming [15], ocean acidification, changes in the precipitation, decreases in sea ice and sea level rise. Collectively, these factors are altering the physical and biological environment occupied by marine species [16,17], and in many cases challenging their capacity to adapt [18–20]. It has been suggested that climate-related changes may be a predominant threat to pinnipeds, through changes in ecological processes especially in polar regions [20–26].

The harbour seal has the widest distribution of any coastal pinniped, ranging continuously from 28° to 78.5° of latitude north [2]. Given this broad geographic distribution the species encounters an extensive gradient of environmental conditions from temperate to Arctic regions. Thus, it presents a unique case study to understand the influence of changing environmental conditions on a single species. Here, we (i) review current information on the harbour seal genetic structure, population status, and threats; (ii) assess potential consequences of a changing climate; and (iii) identify knowledge gaps to guide future research and monitoring.

2. Distribution and Genetic Structure

In this review, we use “population” as a unit where virtually no gene flow would be expected within one generation and “stock” as a management unit. Hence one population can be composed of one or several stocks [27].

Harbour seal were previously recognized as five subspecies based on differences in morphological characteristics and geographic distribution. However, recent genetic analysis suggests three primary subspecies [28,29]. There are currently three recognized subspecies of harbour seal: the Atlantic harbour seal (*P. v. vitulina*, Linnaeus 1758), the Pacific harbour seal (*P. v. richardii*, Gray 1864), and the Ungava harbour seal (*P. v. mellonae*, Doutt 1942), which is endemic to a freshwater system in Canada [30] (Figure 1). Pacific harbour seals occur along the North Pacific Rim ranging from southern Japan, the western Aleutians and Bering Sea; Alaska; the Pacific coast of North America including British Columbia, Washington, Oregon and California (USA) to Baja California (Mexico). Atlantic harbour seals occur along the East Atlantic Ocean from Brittany (France) to the Barents Sea (Norway) including the British Isles, Iceland, and Greenland. In the western Atlantic, they range from New York (USA) to the Canadian Arctic. They are occasionally seen as far south as South Carolina (USA). Currently, the Atlantic and Pacific harbour seals are isolated from one another by the high Arctic coasts of Russia and Canada.

Pacific and Atlantic populations are sister clades with genetic differences within each subspecies at the local scale [28,31]. These differences occur between neighbouring colonies despite the absence of major geographical barriers [29,31–34] and are likely due to the species’ relatively small scale movements at a maximum range of 300–500 km [35]. Genetic differentiation among groups of *P. vitulina* has been detected on a scale of only a few hundred kilometres in the northeast Pacific along their 16,000 km continuous distribution [29,31,36,37]. It appears that dispersal patterns of harbour seals are behaviourally restricted, and follow specific geographic features that likely limit gene flow between neighbouring regions [38]. This genetic variation is reflected in differences in phenology and morphology observed within the North Pacific Region following an axis along the Pacific coastlines and varying with geographic features including the continental shelf. Recent studies suggest that harbour seals in Japan originate from more than two lineages and secondary contacts between populations after long isolation [37,39]. In Alaska, harbour seals were previously managed as three stocks, but more recent evidence suggests structuring at a finer scale and twelve stocks are now recognized [40]. In the Atlantic Ocean, taxonomic schemes have recognized divisions between Greenland, North America and Europe [31]. Based on neutral genetic markers twelve genetically distinct populations across the north Atlantic Ocean are now identified [33]. The northernmost population

on Svalbard in the Barents Sea is currently recognized as an independent, highly distinct genetic unit along with the small population in southern Greenland [41]. Surprisingly, despite low numbers and an apparent separation between the two populations in Greenland, the population in southern Greenland exhibits a high level of genetic diversity. It is as high as in the much larger population in Europe. This is also the case in the UK where stronger connections exist between the populations in the southeast of England and those in Europe, than between England and the neighbouring harbour seals from eastern Scotland [42]. Recently these two British populations have been further divided into four geographically distinct clusters [43].

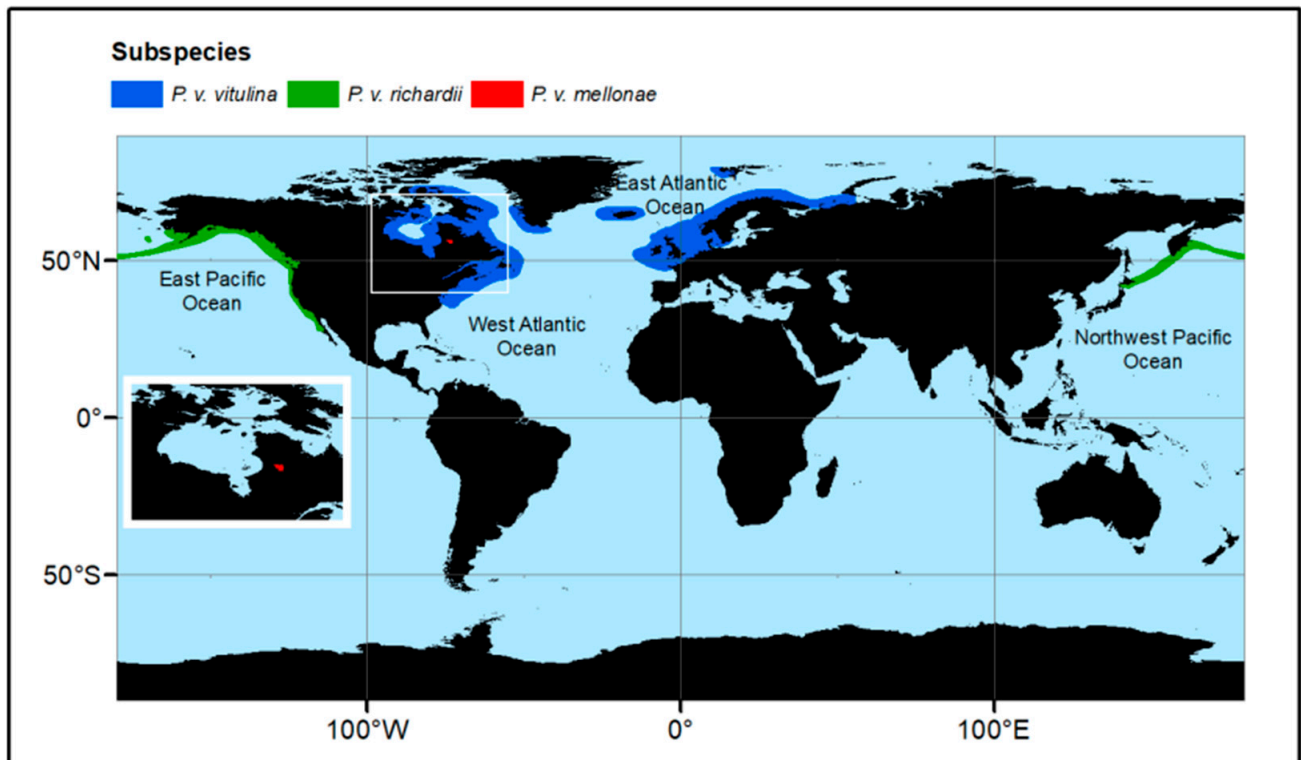


Figure 1. Distribution of harbour seals (*Phoca vitulina*). Colours correspond to each subspecies. The inset is a close-up on the region where *Phoca vitulina mellonae* is distributed. Modified from the International Union for the Conservation of Nature (IUCN) according to [2].

3. Status of the Main Populations and Current Threats

The worldwide population size of harbour seals is estimated between 610,000–640,000 individuals [44]. Although the global population trend is currently unknown, this species is listed as “Least concern” by the International Union for the Conservation of Nature (IUCN) red list [45]. However, given the broad geographic distribution, dramatic differences exist between subspecies, regions or populations in terms of minimum population estimates and population dynamics. Some populations are stable or increasing whereas others are experiencing declines leading to conservation concerns [21,44–47]. In addition, there are a wide variety of approaches that are used for monitoring, management, and conservation across the range of harbour seals.

3.1. Western Pacific Coast

Population dynamics of *P. v. richardii* in the western North Pacific region are not well documented due to an uneven distribution covering numerous remote islands [46,48]. In coastal regions of Russia, harbour seals occur on the Kuril Islands in the Okhotsk Sea and on the Commander Islands in the Bering Sea [49]. The Kuril Islands’ population is thought to be around 3000 and seemed stable in the early 2000s [49]. The most recent count from

the Commander Islands gives a total of 3344 individuals during the breeding season in July 2017 [50]. In the early 1990s a small population in the Kamchatka Peninsula was estimated at around 200 individuals [51], but no recent estimate exists. The harbour seal is listed in the Red Data Book of the Russian Federation and protected [50]. In Japan, harbour seals occur on the Pacific side of the island of Hokkaido and have decreased precipitously from the 1940s to only few hundred individuals in the 1970s [46]. Reasons for this decline are not clear but may include commercial hunting, bycatch in salmon nets, and interactions with coastal fisheries. In addition, the destruction of haul-out sites to improve substrates for commercial kelp production has likely contributed to this population's decline in the past [37]. However, recent trends show a yearly population growth rate of 4% and more than 1000 seals were recorded in the 2008 survey [37,46]. This is likely due to the cessation of the commercial seal harvest and the species' protection in Japan, although bycatch in salmon nets remains a concern in this region [37,46].

3.2. Eastern Pacific Coast

Harbour seals in the eastern north Pacific spans a diverse array of habitats across an extensive geographic range of over 8000 kilometres from the Aleutian Islands in western Alaska to Baja, California. Given this extensive range, the populations status varies between regions.

3.2.1. Alaska

Harbour seals range from Dixon Entrance in southeast Alaska to the Aleutian Islands and Bering Sea in southwestern Alaska. Although previously managed as three stocks, twelve stocks of harbour seals are currently recognized based primarily on genetics, movement data, and traditional ecological knowledge [40,52]. Harbour seals use a diverse range of habitats including beaches, sand bars, rocky islets, a freshwater lake, and icebergs that are calved from tidewater glaciers. Some of the largest aggregations of harbour seals in the world occur seasonally in tidewater glaciers fjords in Alaska, where they use ice that emanates from tidewater glaciers as habitat for pupping, moulting, and resting [53]. Although tidewater glaciers are naturally dynamic [54], the majority are retreating and thinning with unknown impacts on the seals that use iceberg habitat. A small, presumably isolated population of harbour seals (~400 seals) occurs in Iliamna Lake, a large freshwater lake that is connected to Bristol Bay by the Kvichak River [55]. Seals appear to be resident in the lake throughout the year and remain in the vicinity of cracks in the ice during winter [55,56]; however, the extent to which exchange occurs with seals in Bristol Bay is unknown [55].

Population status and their trajectories vary by region. Populations in the Bering Sea and Aleutian Islands were considered stable in the 1960s and 1970s [57–59]; however, surveys from the late 1990s documented precipitous declines [57,59,60]. Declines also occurred in the Gulf of Alaska [60–63]; however, more recent data suggests that some declines may have lessened [60,64]. In Glacier Bay, a tidewater glacier fjord and marine protected area in southeastern Alaska, precipitous declines in the number of harbour seals have occurred over the last 26 years [65–67]. Declines have also been documented in seabirds and other pinniped species and suggest that large scale changes in ocean climate and/or regime shifts [68,69] may have played a role [63,70–72]. Between 2014 and 2016, anomalously warm waters occurred in the eastern Gulf of Alaska due to a combination of a large warm water mass and a strong El Niño [73] which coincided with changes in lower and mid-trophic levels [74]. This also coincided with lower abundance estimates for harbour seals in Glacier Bay [68]. Collectively, given the extensive geographic range of harbour seals across Alaska, it is likely that a combination of larger-scale and local factors, such as variation in prey availability, predation, and/or habitat may have played a role in population trajectories over the last few decades [66,67,70,74,75].

3.2.2. British Columbia, Washington, Oregon, and California

Current population trends and abundance of harbour seals in British Columbia (B.C.) are assessed based on aerial surveys conducted from 1966 to 2014. Total abundance of harbour seals on the B.C. coast in 2008 was estimated to be 105,000 seals (95% CI: 90,900 to 118,900) [76]. Reconstruction of historical data indicates that the population was depleted during a period of commercial harvesting from 1879 to 1914, and subsequently maintained below natural levels by predator control programs until the early 1960s. The population was further depleted in the 1960s but now appears to have fully recovered [76]. Seal populations from coastal Oregon through Southern California seem to be generally increasing showing impressive recovery after discontinuation of historical state-financed bounties [77–79]. However, these populations seem to have reached now an asymptotic growth suggesting that they may be approaching carrying capacity [77,80]. Harbour seals in Washington state are divided into coastal and inland water stocks [77,81]. Their number approximates 30,000 individuals, although current data are not available. The primary population-level stressors likely include shifts in productivity and prey availability, organic pollutants, predation, and interaction with fisheries. In Oregon, harbour seals are estimated to be 10,000 individuals, based on aerial surveys in 2003 [77] and seem stable. Along the Oregon Coast, harbour seals occupy more than 90 haul-out locations including rocky shorelines, beaches, bays, estuaries, and outlying rocks [77,78]. They extensively utilize the continental shelf to forage, spending a great amount of time in highly productive areas with offshore seamounts and rocky substrates [38]. Current stock assessments treat the Oregon and Washington coastal stocks as one unit. However, seals in this region seem further subdivided based on geophysical barriers [38] such as Cape Blanco, where there is a narrowing of the continental shelf that separates the Central and Southern Oregon coasts. The California stock is estimated at 31,000 seals and appears stable in recent years [81]. The main limiting factors of population growth include changes in prey availability that are influenced by larger-scale inter-annual oceanographic processes such as El-Niño. In addition, a lack of undisturbed or available habitats, bycatch in commercial fisheries, and/or predation have been shown to negatively affect local harbour seal populations [82,83]. In Mexico, along the Pacific coast, harbour seals are found on several islands and the region represents the southern limit of the species' distribution [82,83]. The estimated number of seals is approximately 1000 individuals, but limited information regarding trends or threats exists [5].

3.3. Western North Atlantic Coast

Western Atlantic harbour seals range along the northern coast of Canada and the US from Baffin Island through North Carolina [84–86]. In Canada, three distinct units are recognized and include populations in Hudson Bay, Gulf of St Lawrence, and Sable Island [85,87]. A variety of survey methods have been used along the coast of Canada; and minimum population estimates range between 8000 and 12,000 seals, excluding Newfoundland [87]. In the US, coast-wide aerial surveys are primarily available for coastal Maine, with the last survey being conducted in 2012, providing a minimum population estimate of 75,834 seals (CV = 0.15) [88]. At Sable Island, the population has decreased dramatically since the early 1990s [89,90]. This decline appears to be due to a combination of shark-inflicted mortality and inter-specific competition with grey seals (*Halichoerus grypus*) [89,90]. The main threat to these populations is linked to interactions with fisheries through bycatch and reduced food availability [85,86]. A significant number of animals is caught each year in gillnets, bottom and mid-water trawls and small trap-nets, although it is unclear whether this translates to population-scale impacts [91,92].

P.v. mellonae is an endemic subspecies of harbour seals and the only that occurs throughout the year in freshwater. This population occurs along the Ungava peninsula in northern Quebec and has been isolated from harbour seals in the neighbouring Hudson Bay since the most recent glaciation, between 3000 and 8000 years ago. During winter, the seals are confined in ice-free areas and travel on snow between neighbouring lakes. They are

genetically distinct from harbour seals in Hudson Bay and they also have darker pelage and a flatter skull. They typically breed earlier than individuals from the saltwater subspecies in the same region. The population size is small, estimated between 50–600 animals [30] which represents a threat to its viability. Additional threats to this population include the development of hydroelectric dams that could decrease areas of open water during winter and mercury contamination from fish [30]. Due to the limited adaptive capabilities of this small and isolated population, climate-related disturbances are also of concern [30]. In 2018, this population was designated as Endangered in Canada due to cumulative anthropogenic disturbances [92].

3.4. Greenland

Historically, harbour seals were widely distributed throughout Greenland although not numerous. In recent years they became rare in most areas and in some cases extinct [3]. Currently, their status is “critically endangered” on the Greenlandic Red List and they are protected from hunting throughout the year. Two primary populations exist; one located on the west coast of Greenland and a second limited to the southeastern tip of the island. The population along the west coast is closely related to the West Atlantic populations whereas seals from the southern population are genetically closer to the Icelandic and Svalbard populations [41]. Current population estimates are not available; however, there is some historical information based on catch and skin statistics [47]. The number of seals has declined rapidly in West Greenland since the 1950s, most likely due to unsustainable hunting pressure. On the other hand catches in the southern part of Greenland remained stable between 1960–1980 and there were active breeding sites through the 1990s [3,93]. Harbour seals in Greenland were believed to number fewer than 1000 in the mid-2000s, representing one-third, of the estimated population size in the 1950s [47]. The primary threat to these populations is their small size and apparent separation, which makes them particularly vulnerable to stochastic events.

3.5. Svalbard

The Svalbard harbour seal constitutes the northernmost population of this species. It is genetically distinct from neighbouring populations and apparently isolated [4,94–96]. It is the only population to inhabit a true Arctic environment throughout the year [95,96]. Adults and juveniles are observed along the west coast of Spitsbergen throughout the year, with the northernmost record being as far north as 80.5° N [10,97]. They are very rarely observed past the southern tip of the island. Along the eastern coast of Svalbard, their distribution is limited by the occurrence and the thickness of sea ice [10,98–100]. Surveys were conducted in 2009 and 2010 and estimated a total of 2000 seals [4]. Individuals from this population tend to be shorter and more rotund compared to their southern counterparts suggesting adaptations to a colder environment [99]. The Svalbard population exhibits a high degree of sexual dimorphism compared to more southerly populations, with adult males being significantly heavier and longer than adult females [4]. The longevity of Svalbard harbour seals seems somewhat shorter than in other populations. The apparent lack of individuals older than 16 years is surprising given limited the human-seal interactions and the absence of acute source of mortality from epizootic outbreak. This skewed demographic distribution, with few older individuals might be linked to pressure from terrestrial predators such as polar bears (*Ursus maritimus*), or marine predators, such as killer whales (*Orcinus orca*) or Greenland sharks (*Somnius microcephalus*) [100]. Recent studies on contaminants show that this population is exposed to a wide variety of pollutants; however, measured levels suggest that these are not an immediate threat to their health [101]. The main threat to this population is linked to its small size and low genetic diversity which could reduce its resilience to stochastic events such as oil spill or disease outbreaks [41]. Presently, this population is red-listed in Norway and protected from exploitation.

3.6. Iceland and Faroe Islands

The harbour seal is the most abundant pinniped in Iceland [102–104] and has likely been exploited by humans since the settlement of the region, but nowadays, there is no commercial harvesting. In an effort to subsidise the seal industry and to control the incidence of roundworm (*Pseudoterranova* sp.) in commercial fish, a bounty program was introduced between 1982 and 1989 resulting in high levels of adult mortality [104]. Until 2018, harbour seal culling remained subsidised by the angling industry to protect salmonids from predation as this fishery is economically important in Iceland [105–107]. Regular aerial surveys since the early 1980s show that the population has decreased dramatically from approximately 33,000 individuals in 1980 to 12,000 in 2006 [107] and to about 7700 animals in 2016 [108]. The latest surveys in 2018 indicates that the population has now increased to about 9400 individuals [108]. However, this number remains 21% lower than the 2006 government issued management objective for a minimum population size of 12,000 animals [108]. Reasons for this decline are not well understood but may include over-harvesting, changes in prey availability, bycatch, environmental changes, and anthropogenic disturbances [108]. In the Faroe Islands, harbour seals were common in sheltered fjords, and likely more common than grey seals until the mid-19th century, when the species was extirpated through extensive harvesting [109]. Since then, harbour seals have been observed during bounty hunts, from 1889 to 1891 and again from 1963 to 1967 when one and four seals were caught respectively, in the southernmost part of the Southern Island [109]. Since then, only three observations of seals have been made in this region in 2001, 2005 and 2019 [110].

3.7. Continental Europe

Harbour seals in continental Europe are distributed over a wide latitudinal range from France (48° N) to northern Norway and the Murman peninsula (70° N) [111,112]. Through most of its historical distribution, the species has been harvested for fur or meat [32,113]. In addition, seals were also considered as competitors by fisheries, and long-term bounty programs depleted several populations until the mid-1970s [14,51,114]. Following the reduction in hunting pressure most populations in continental Europe started to recover, although in an unequal way. This recovery has, however, been hampered by two consecutive epidemics of Phocine distemper virus (PDV). These epidemics that swept through most of the European populations causing the death of 230,000 and 30,000 seals in 1988 and 2002, respectively, which represented over half of the total population [9,115].

3.7.1. Northern Europe

Harbour seals occur along the northernmost coast of Europe from northern Norway to the Eastern Murman coast in Russia where the easternmost breeding colony of *P. v. vitulina* subspecies is found [116,117]. The latest population estimate in the late 1990s ranged from 400–500 seals [116]. The main threat to this remote population is human disturbances at breeding sites, poaching, bycatch and shooting at salmon nets. Currently, the species is listed in the Red List of the Murman area and hence banned from harvesting. In mainland Norway, a system of quotas that was established after the culling period 1980–1987 regulates the hunt [115]. Quotas were increased substantially from 2003. In 2010, a management plan for harbour seals was implemented, with quotas aimed at maintaining the population at target level and surveys occurring every five years. The estimated number of seals in mainland Norway is approximately 7500 individuals during the 2011–2015 period. The number of seals appears stable compared to previous periods (2003–2006 and 1996–1999) [118]. Harbour seals along the Norwegian coast are threatened mainly by fisheries through bycatch and interactions with fish farms [114], although shooting at fish farms was prohibited in November 2019 (executive order FOR-2019-11-28-1593).

In southern Scandinavia and southern Baltic, harbour seals are divided into four populations, the Limfjord, the Kattegat, the Southern Baltic Sea and the Kalmarsund [119]. Heavy hunting pressure brought these populations of harbour seals to a historical low in the 1920s [120]. In the late 2000s the estimated number of seals in Southern Scandinavia and

Baltic was estimated between 26,350–33,450 individuals but has subsequently increased. Significant number of seals died in mass mortality events in 1998 and 2002, due to PDV, in 2007 due to an unknown cause, and in 2014 due to avian influenza [115,121–123]. Currently all populations in Southern Scandinavia are increasing and, except for the Kalmarsund one, seem to have reached or be approaching carrying capacity [121,123]. The Kalmarsund population a small, genetically isolated population has been increasing at 8% per year over the period from 2003 to 2016 reaching 1000 seals in 2014 [124]. The main pressures affecting seals in southern Scandinavia include bycatch, shooting, exposure to contaminants, human-related disturbances at breeding sites, and interspecific competition with grey seals [121,123,124]. However, given the recent increasing population trends it is difficult to assess whether these sources of mortality have population-level effects. In the Baltic region, infertility due to organohalogen pollution was identified as a problem for harbour, ringed and grey seals in the 1970s but since that time these effects seem to have decreased [123,125].

3.7.2. Southern Europe

In southern Europe, from the Netherlands through France, harbour seal populations appear to be increasing despite their proximity to human activities and heavy exploitation of the coastal areas that they inhabit. The population in the Wadden Sea is estimated to be between 25,000 and 31,800 individuals and has shown a quick recovery after two PDV epizootics [12,14,126]. The most recent total population estimate in 2019 was 40,800 in the Danish, Dutch and German Wadden Sea [126]. Increasing exploitation of coastal areas and shipping in the North Sea represent the primary threats to the Wadden/North Sea population. In particular, offshore wind farms may have the potential to interfere with foraging and migratory behaviour; although no impact studies have been conducted [127]. In France, where only three colonies exist, harbour seals have been completely protected since 1995. The three colonies show increasing trends with a minimum population estimate of 830 animals during the moult [128]. Observation of individuals from neighbouring colonies indicate some exchange with populations from the southern part of the United Kingdom (UK) and the Netherlands.

3.8. United Kingdom and Ireland

Approximately 40% of the European harbour seal population occurs in the UK with the majority around the coast of Scotland [129–135]. The most recent estimate in 2016 was 43,450 (95% CI: 35,550–57,900) seals [129]. Colonies on the northwest and southeast coasts appear to be stable or increasing [130,131]. Scottish colonies have experienced dramatic declines, especially on the east coast (Orkneys and Shetland) where populations have decreased by 85% between 2000 and 2010 [133,134]. Reasons for these widespread declines are yet unclear, but research efforts are currently focussed on competition with grey seals, predation from killer whales, and exposure to toxins from harmful algal blooms [133,134,136]. Recent studies reveal that harbour seals in declining colonies are significantly more exposed to harmful algal toxins, such as domoic acid and saxitoxins, which may be a contributing factor to the observed declines [136]. It is interesting to note that although the population in the Wash, England, is increasing, the rate of increase is still lower than in the neighbouring population in the Wadden Sea [130]. Harbour seals are relatively common in coastal waters of the Republic of Ireland at the edge of the species' range in Northwest Europe. Although haul-out sites cover the entire coast, scarce information is available regarding the population's trajectory [137–140]. A survey conducted in the early 2000s yielded a minimum population estimate of approximately 2,905 individuals [139], but no population trend is currently available due to the lack of historical and current data. Anecdotal data indicates increasing numbers of animals in southwest Ireland. Seal predation and damage to fishing gear is currently not monitored, but fishers and aquaculture operators are still licensed to shoot seals interacting with fishing equipment. An additional threat to this population includes bycatch, especially in the vicinity of major colonies [141,142].

4. Environmental Changes and Potential Consequences on Harbour Seals Populations

4.1. Increased Temperatures and Extreme Weather Events Affect Haul-Out Patterns

The average global land and ocean surface temperature for January–August 2019 was 0.94 °C (1.69 °F) above the 20th century average [143]. Ocean warming dominates the increase in energy stored in the climate system [18]. Changes in weather patterns have occurred over the last 50 years with an increased probability of extreme weather events such as heat waves, storms and large amount of precipitations [144]. These changes in the physical environment are expected to directly and indirectly influence marine mammals, especially amphibious species such as pinnipeds that use land, aquatic and ice environments. Harbour seal haul-out patterns are directly influenced by water and air temperature because thermoregulation is energetically costly [145–147]. Thus, in cold environments, harbour seals must continually thermoregulate to mitigate heat loss at sea, on land and ice [101,145–147]. For example, in Svalbard, at the northern limit of their distributional range, harbour seals typically spend more time at sea, during stormy weather conditions, even if the temperature is high because of the wind chill effect [101]. Given that the frequency of storms is predicted to increase in the Svalbard archipelago, it is expected that haul-out patterns could change and influence harbour seal energy budget. At the southern limit of their distributional range, harbour seals face the opposite problem. Hyperthermia is observed in juvenile seals at an ambient air temperature of 35 °C [147], a temperature that is easily reached in Southern California, Mexico, and France. This is especially critical for new-born pups that haul out for the majority of their time in the first weeks after birth [147]. Adult animals are also subject to overheating which can be a limiting factor in hauling out. Thus, a northward shift in distribution can be expected if southern populations cannot cope with high temperatures at least during the breeding and moulting periods. For northern populations, an increase of water and air temperatures may actually decrease thermic stress during the winter months and be an advantage [101].

4.2. Changes in Physical Habitat Affect Distribution Patterns

Sea ice cover in Arctic and sub-Arctic regions has dramatically decreased in recent decades, reaching historic minimums in 2007 and 2012 [18,148,149]. Throughout most of their range, harbour seals are not typically associated with sea ice. They even tend to avoid areas with thick ice where they cannot maintain breathing holes and are at risk of predation by polar bears [10,150]. As such, decreasing sea ice may increase the available habitat for harbour seals in seasonally ice-covered areas such as Svalbard, the western Hudson Bay, the St Lawrence Estuary or Greenland [150–152], which in turn could result in a northwards range expansion. However, other features, such as bathymetry, may still limit their expansion, as harbour seals are generally considered relatively shallow divers [100,153,154]. Harbour seals occasionally use ice floes and land-fast ice as a resting platform close to foraging sites during the winter like on Svalbard. Whether the reduced availability of such platforms would be detrimental for harbour seals is unknown [67,99,117]. In the Murman region, it has been suggested that hauling out on ice may reduce the risk of predation from land-based predators [117]. In south Greenland, low inflows of drift ice have resulted in abnormally high catches of harbour seals because drift ice used to shelter the seals' terrestrial haul-outs from the hunters [3,47].

In southeastern and southcentral Alaskan fjords, glacier ice and icebergs that emanate from tidewater glaciers are important habitat for harbour seals. However, the majority of tidewater glaciers are thinning and retreating [155,156]. It is not known whether the decrease of ice as a platform will affect harbour seals during critical life history events such as pupping and moulting [157,158]. The use of glacier ice habitat may confer several benefits including reducing the risk of predation, disease and pathogen transmission and providing a stable platform for nursing young that is not subject to tidal inundation [158,159]. Thus, reduction in the availability of glacier ice as habitat could potentially have population-level consequences [160]. Additionally, in Arctic and subarctic regions harbour seal distribution and niche often overlap with the ones of ringed seals and harp seals (*Pagophilus Groenlandi-*

cus). This could lead to interspecific resource competition and changes in predator-prey interactions, if harbour seal distributional range expands northwards and the species becomes more abundant [158,159,161,162].

4.3. Large-Scale Oceanic Events and Changes in Community Structure Affect Foraging

Patterns of the North Atlantic Oscillation (NAO) and the El Niño-Southern Oscillation (ENSO) have contributed to major variations in climate worldwide and directly or indirectly influence animal populations [163,164]. Strong ENSO events and cyclic patterns of the NAO have been linked to failed reproduction and decreased attendance at haul out sites in several pinniped species through changes in prey abundance and distribution [80,87,163]. Population trends in harbour seals in Alaska generally follow those of sympatric Steller sea lions (*Eumetopias jubatus*) and northern fur seals (*Callorhinus ursinus*), suggesting drivers linked to large-scale regime shifts [69,164]. On the west coast of North America, in particular Oregon and Washington, a recurrent pattern of seasonal areas of upwelling-driven hypoxia and anoxia on the continental shelf has caused die-offs of invertebrates and redistribution of many important preys including schooling fish and bottom fish. These deoxygenation events are thought to have secondary effects on the foraging efficiency of air breathing predators, such as harbour seals, as their prey experience physiological stress and habitat compression [165,166].

Changes in community structure can affect predators foraging patterns and diet composition. For example, large changes have been observed in the Barents Sea communities [167–171] due to dramatic increase in the influx and temperature of Atlantic water. This boreal water mass enters the Arctic Ocean and changes the characteristics of the Barents Sea/Fram Strait region from Arctic to Atlantic [167–171]. The range of Atlantic cod (*Gadus morhua*) has expanded northwards and they may even occupy areas of the Arctic continental shelf threatening local species such as polar cod (*Boreogadus saida*) [171]. Harbour seals on Svalbard have now shifted to feeding mainly on Atlantic species such as the Atlantic cod and haddock (*Melanogrammus aeglefinus*) [172,173]. The seals react to upwelling phenomenon that brings Atlantic water onto the West Spitsbergen shelf and they likely target associated Atlantic fish species under these events [98]. Predicted increase influx of Atlantic water in this region in combination with decreased sea ice are likely going to favour the growth and geographic expansion of the harbour seal population. However, diet changes might come at a fitness cost in other regions such as in Scotland [174]. Harbour seals were in poorer body condition during years of low herring (*Clupea harengus*) abundance when switching to alternative preys such as gadoids and showed signs of fish-induced anaemia [175]. In the past 40 years in the North Sea major climate-induced regime shifts have caused changes in community structures with effects rippling through the entire trophic chain up to top predators [176,177]. Such large-scale regime shifts are predicted to increase in the future and will disrupt local conditions and ecological relationships. Generalist top predators such as harbour seals have a flexible and broad diet which allow them to switch between several trophic niches if they can cope with the physical environment. Such species have the potential to establish in new areas, such as the high Arctic [178], and often have a competitive advantage over true Arctic species, such as ringed seals. Changes in community structure are not limited to prey but may also involve predators. For example, killer whale sightings have been more frequent in the Canadian Arctic, suggesting that the species is becoming more established in the region at least seasonally [179,180]. Harbour seals are regularly consumed by killer whales and the spatial overlap between these two species in the Arctic is likely to increase in the future. Polar bears are also known to prey upon harbour seals in the Hudson Bay and Svalbard. In these regions, the decrease in ringed seals abundance, the polar bear main prey, might increase the predation on harbour seals (Kovacs and Lydersen pers. comm.).

4.4. Shift in Pathogen Ranges May Affect Populations' Trajectories

Warmer air and water also affect the susceptibility of harbour seals to infections by pathogens [181,182]. The susceptibility of a population to pathogens depends on several factors. They include pathogens' geographic range, altered host-parasite dynamics, changes in life cycle, increased virulence, and unpredictable patterns of diseases [183–185]. A warming environment means that minimum temperature thresholds that acted as limiting factors for parasite and bacterial survival and growth are raised, leading to increased environmental prevalence of free-living pathogens [185]. In particular, overwinter survival of pathogens or parasites can dramatically increase their range expansion, density-dependent transmission, reaching new host populations or even species [186–191]. Pathogens are more likely to be transmitted to immunologically naïve host populations via a range of mechanisms, including: invasive species; species and population overlap; shifts in prey consumption; seasonal migrations; and shifting habitat availability [186,189,191]. In addition, climate-mediated physiological stresses and exposure to environmental pollutants have been shown to compromise host immune function and thus increase the clinical occurrence of opportunistic diseases [192]. Epizootic viral diseases causing mass mortality in harbour seals have been mainly reported from Europe and the USA [115,193,194]. In 1988, 60% of the North Sea harbour seals died during an outbreak of PDV followed by a subsequent outbreak in 2002 [115,193]. Above-average mean monthly air temperatures in Europe and an increase in density of hauled-out seals have been linked to mass mortality events [194]. During both outbreaks, the first cases were reported in the late spring when harbour seals start hauling out in larger groups for the breeding period, which is likely to enhance rates of transmission of density-dependent diseases [194]. In Arctic regions where harbour seals haul-out on ice, the disappearance of this platform might force the seals to haul-out on land in denser aggregations as observed in Pacific walrus. This will potentially increase the risk of transmission of infectious diseases and parasites. In the particular case of the PDV, grey seals have been suggested to be vectors infecting geographically distinct harbour seal populations [115,194]. Although harbour seal populations north of 65° N have not been affected by these recurrent epidemics, grey seals could also expand their distributional range northwards and therefore be in contact with immunologically naïve northern populations of harbour seals such as in Greenland [195]. Such epidemic outbreaks could potentially have a disastrous effect on small, genetically distinct populations with limited immunological robustness that might not be able to withstand a great loss of individuals, such as the Svalbard and Greenlandic populations [196]. Antibodies for PDV have been detected in harp seals from Canada, Greenland and the Barents Sea meaning this species might act as a reservoir for the virus. PDV antibodies have also been detected on the Pacific side in Kuril harbour seals where the prevalence is high (up to 100% in some sites) and the seals haul-out in dense groups [197]. Five species of seals (harbour, spotted (*Phoca largha*), ringed, ribbon (*Histiophoca fasciata*) and bearded (*Erignathus barbatus*)) overlap in this region, increasing risks of inter-specific transmission [197]. In addition, PDV has been detected in sea otters (*Enhydra lutris*) [198], which likely creates a potential threat to harbour seals and other pinnipeds that overlap with sea otters in the North Pacific [198]. Along the north-eastern coast of the US, harbour seal mass mortality events have been attributed to the Influenza A virus which occurred several times in the early 1980s. Thus far, this virus has only been isolated from harbour seals from the east coast of the US but is thought to be transmitted via pelagic birds which can cover large areas and could potentially infect other populations of marine mammals [190]. Additionally, pinnipeds that inhabit nearshore regions near human settlements and have a semi-aquatic lifestyle will likely be at increased risk of pathogen exposure [186,187,199,200]. A variety of pinniped-related parasites have begun to expand their range mainly northwards under the influence of environmental parameters [200,201]. In one example of this, the obligate intercellular parasite *Toxoplasma gondii* has appeared in the Arctic food chain and the transmission path and complete lifecycle of this organism in the Arctic environment is still not clear [200]. Warmer seas have resulted in influxes of temperate marine species that could serve as vector for this

parasite in the Svalbard Archipelago, even in the absence of the terrestrial definitive host. This might explain the high prevalence of the parasite in top predators in this region [200]. In the Kuril harbour seal, the increase of river runoff due to heavy precipitation has been linked to the appearance of oocysts of the protozoal endoparasites *T. gondii* and *Neospora caninum* in the marine ecosystem [199]. Warmer local sea temperatures have, in addition, enhanced survival of the parasite [197]. Although these parasites are not directly associated with mortality in harbour seals, an increased parasite burden can compromise the host's immunological function resulting in increased susceptibility to other pathogens or environmental stressors [201]. Mass mortality events in marine megafauna can lead to dramatic changes in abundance of lower trophic level species and community structure, playing an important role in shaping population dynamics and trajectories. Populations recovering from mass mortality events have a very different structure compared to the initial populations which renders difficult their management [14]. These abrupt changes in population structure may mask additive or synergistic drivers, such as anthropogenic disturbances or climate-related changes.

4.5. Increased Anthropogenic Disturbances May Affect Pristine Populations

As Arctic sea ice declines, new trans-Arctic shipping routes are being established, increasing vessel traffic. This will result in noise and chemical pollution [202,203]. For harbour seals, disturbances have the greatest effect near haul-out sites and during the reproductive season when they tend to spend more time ashore. In particular, the northern populations in Svalbard or Greenland could be disproportionately impacted while Southern populations might be more resilient to anthropogenic factors to which they are already exposed.

Pollution loads are very different among harbour seal populations. Southern populations in close proximity to human settlements, typically carry heavier pollutant loads compared to their northern counterparts. Heavy contaminant loads in marine mammals are associated with compromised immune systems, hormonal disruptions and increased parasite burden [204–206]. Although few major sources of pollution typically originate in the Arctic, this region is nevertheless exposed to pollutants through atmospheric and marine transport and freshwater runoff. Climate-related changes may affect these pathways and could therefore affect the exposure in Arctic regions. There is also compelling evidence that increasing temperature could be deleterious to pollutant-exposed wildlife through alterations in the biotransformation of contaminants [206]. Biological pollution is also an emerging issue with an increased presence of terrestrial pathogens in the marine system. This is due partly to an increase of anthropological use of coastal areas, but also to the increase of watershed runoff after bouts of increasingly dramatic precipitation events. For example, significant amounts of faecal coliform bacteria have been detected in harbour seals living near human settlements [206]. Biotoxins released from marine phytoplankton blooms have been recently found in harbour seals from Scotland [136] and linked to a possible decline in local populations. These harmful algal blooms have globally increased in distribution and intensity since the 1980s and new areas can be exposed such as the Norwegian coast [207].

5. Management and Knowledge Gaps under Rapidly Increasing Environmental Changes

5.1. Current Management Framework

Harbour seals are under a wide array of conservation status and management regimes across their broad geographic range. The species is listed as “Least Concern” on the global IUCN Red List, as it is very widely distributed and the total population size numbers in the 600,000 [45,208,209]. The Eastern Pacific subspecies is either stable or increasing in most of its range [210], while trends remain unknown for the Atlantic subspecies. Both of these subspecies are listed as “Least Concern” in regional Red Lists [208,209]. Some smaller, distinct populations are locally listed as “Endangered” (Canada endemic Ungava

seal), “Critically Endangered” (Greenlandic and Icelandic populations), or “Vulnerable” (Japan, Svalbard, Russian Federation, and Kalmarsund populations). Bounty systems were historically in place in Canada, the United States, Norway, and Iceland. They aimed at controlling local harbour seal populations in areas where fisheries and angling took place to reduce competition with fisheries and, in one case, to reduce the incidence of roundworm in commercial fish. Presently, there are no bounty systems remaining in place. However, harbour seals may be shot anytime for protection of fishing operations [130] in Scotland (under license), England and in Wales. The shooting of seals at fish farms was forbidden in 2019 in Norway and in 2020 in Canada. The harvest of harbour seals is allowed, but seasonally and/or is quota regulated, in England, Wales and Norway. In Iceland, harbour seals may be hunted under a special licence for traditional use.

Currently, harbour seals are protected from hunting:

- Under the Marine Mammal Protection Act in the USA (enacted in 1972) throughout its range, although subsistence hunting and traditional use are permitted for coastal Alaskan natives.
- By the Marine Mammal Regulations under the Fisheries Act in the non-Arctic part of Canada (since 1967 for the Pacific population and 1970 for the Atlantic population), while in the Arctic, subsistence hunting is permitted for both the marine and fresh water subspecies. The species is not managed in Nunavut.
- In Greenland (since 2010).
- In Iceland (since 2019).
- In Svalbard (since 1970s).
- Under the EU Habitats and Species Directive 1992 (Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora). The species is listed in Annex II (species requiring the designation of special areas of conservation, SAC, or marine protected areas, MPAs) and V (species whose taking from the wild can be restricted by European law). The monitoring of their population abundance and distribution is requested under the Marine Strategy Framework Directive (MSFD).
- In the Russian Federation (since 1975).
- In Japan under the Wildlife Protection, Management and the Hunting Law (since 2003) with some specific local population control plans.

The harbour seal is not listed in the appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). It is cited in Appendix III (Protected fauna species) of the Berne Convention. The Baltic and Wadden Sea populations are listed on Appendix II of the Convention of Migratory Species (species that need or would significantly benefit from international co-operation). The Baltic population is coordinated by the HELCOM seal Expert Group.

5.2. Knowledge Gaps

As environmental conditions change, up-to-date baseline data is important to inform conservation and management of harbour seals.

Genetic studies at local scale are still lacking in many regions. Further genetic sampling will facilitate stocks assessment and understanding of population dynamics at a regional scale. Some stocks, including several genetically distinct populations are still managed as single units even if some very contrasting population trends are apparent. More information on the degree of immigration and interbreeding between populations is also needed in some areas, especially if one of the populations is small, for example, between the Limfjord population and the Wadden Sea population. In this context, movement studies (biotelemetry) are useful for understanding the spatial distribution of individuals across the annual cycle and for understanding overlap with potential threats (see for example [11,38,98]).

Health and Disease Monitoring aiming at establishing baselines for health parameters and disease status, identifying causes of death as well as isolation and characterization of infectious agents are still lacking. However, some local initiatives exist [123,187]. Collecting

data on health parameters, distribution, epidemiology and effects of pathogens is essential to understand the impacts of pathogens range shift [184]. Since the relatively recent discovery of the PDV in 1988, this virus has become the most ecologically significant pathogen in harbour seals [193]. Some populations have not been tested for the prevalence of the virus, rendering difficult the monitoring of a range expansions of this pathogen in relation to movements between colonies of harbour seals and of other pinnipeds and demographic impacts. The epidemics of the virus are still unclear in the northeast Atlantic especially with respect to potential reservoir species such as harp and grey seals, which are sympatric with harbour seals.

Bycatch is recognised as a source of mortality in many areas, e.g., [108,141,210]; however, estimates and observer programs are limited in most regions.

Cumulative effect of stressors represents a key knowledge gap, especially as effects might not be simply additives but synergistic. Harbour seal populations are impacted at different rates by a variety of stressors and exhibit contrasting trends even at small regional scales. Comparing populations' parameters relative to the dynamics of their stressors would allow to better understand the range of potential responses. It would help informing the degree of harbour seals biological and behavioural plasticity and in turn populations' resilience and adaptive potential.

Survey efforts varies across the distributional range. In some areas, such as in Alaska, surveys occur regularly, whereas in other regions monitoring efforts have not been conducted recently. The remote nature of many of the population creates logistical challenges for population monitoring. However, with expected environmental changes and increased anthropogenic stressors, it is essential to have up-to-date population estimates and reliable trends in abundance. This is especially important for the smallest populations with low genetic diversity and populations at the edges of the species range. When possible, coordinated and consistent monitoring methods between regions would be useful. They would facilitate comparative studies and thus increase the value of data from local populations, particularly for populations of conservation concern.

5.3. Adaptive Management of Harbour Seals Following a Precautionary Approach

Climate and environmental changes impose growing pressure on global biodiversity, which requires that managers have access to up-to-date information on ecosystems to make timely and informed decisions. Hence, consistent monitoring is an essential aspect of informed management and conservation. In some regions, monitoring programs remain largely uncoordinated, limiting the ability to monitor, understand and respond effectively to trends. Marine mammals are prime sentinels of marine ecosystem changes because they integrate and reflect ecological variation across large spatial and temporal scales. Spatially explicit management recommendations are needed to support the resilience of (sub)populations at all scales. For example, in Japan, the population is generally increasing, but some previously depleted sites have not been recolonized [46]. This local specificity increases the probability of local extinctions through stochastic events. Small populations, particularly those at the edge of the distributional range, i.e., likely close to their adaptation capabilities, are particularly vulnerable. Hence, future objectives must give a particular attention to small entities and ensure that anthropogenic activities do not jeopardize their future persistence. It is also crucial that target population level objectives are based on biological criteria [118]. Adaptive management based on regular monitoring is needed more than ever under the current rate of environmental changes.

6. Conclusions

This review summarizes wide disparities in populations and conservation status of harbour seal populations across their broad geographic range. These disparities are not surprising given the extensive geographic range that harbour seals occupy. Large differences also exist with respect to the level of information available. Some populations in the UK, southern Europe, southern Scandinavia, Western Canada and Alaska are well-

monitored, while recent data are lacking for Eastern Canadian, Greenlandic, Icelandic, Russian and Japanese harbour seals. The European populations are still recovering after massive epizootic events that wiped out a large number of individuals rendering it difficult the estimation of true population trends and predict their fate once at carrying capacity. Climate-related change will likely play a significant role in observed and future trends in population dynamics and will also likely be synergistic with direct human disturbances such as bycatch, pollution and exploitation of coastal areas. Cumulative stressors might be further detrimental to already vulnerable populations, and populations at the edge of the range may have limited adaptation capabilities. Climate predictions indicate a unilateral warming of the atmosphere and oceans. This is already causing a northward shift of the distributional range of numerous species likely including the harbour seal. Harbour seals may expand northwards, and the southernmost populations may possibly be lost permanently. Ultimately, to facilitate and further complete our understanding of harbour seal populations trends, it will be necessary to have a more integrated approach to ecological monitoring that also includes monitoring associated with bottom-up (e.g., oceanography and mid-trophic levels) and top-down (e.g., predation) processes that are known to influence harbour seal populations across their broad geographic range.

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