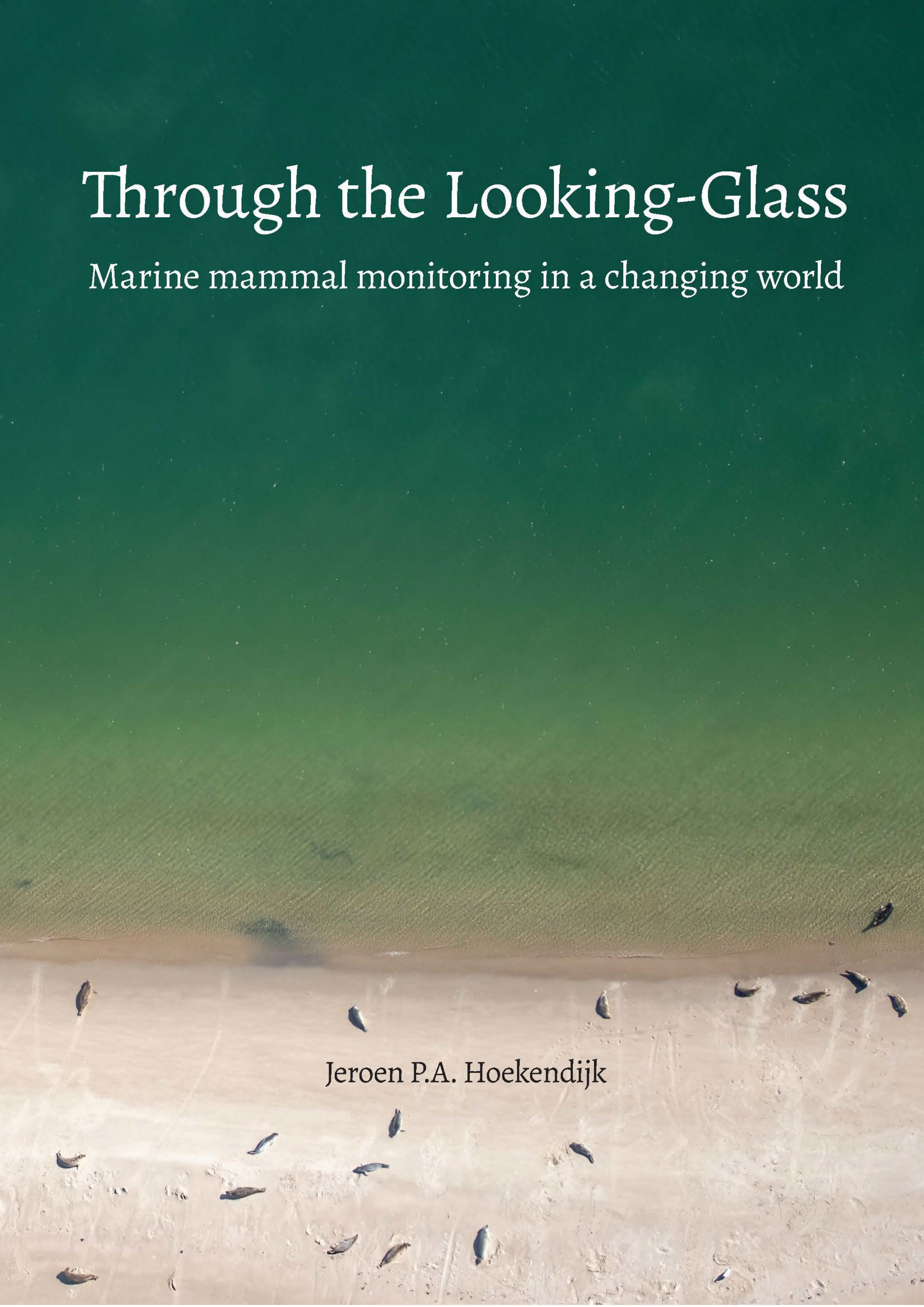

Through the Looking-Glass

Marine mammal monitoring in a changing world

Jeroen P.A. Hoekendijk

Propositions

1. Thanks to their amphibious phenology, pinnipeds are unmatched sentinels to monitor the marine realm.
   (this thesis)
2. Seen from space, individual seals, cows and pandas look remarkably similar.
   (this thesis)
3. More people know of the melting of Olaf – the talking snowman from 'Frozen' – than of the ongoing disintegration of the Arctic ecosystem.
4. The song 'Science' by System of a Down should be included in the curriculum of scientific integrity courses.
5. Wandering walruses pose no more threat to humanity than golden retrievers.
6. Censoring propositions beforehand clips the wings of the PhD candidate.

Propositions belonging to the thesis, entitled

Through the looking-glass: marine mammal monitoring in a changing world

JPA Hoekendijk Wageningen, 26/01/2024

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Chapter 1

General introduction

1.1 Background

1.1.1 Marine mammals in a rapidly changing Arctic

The Arctic climate is changing extremely fast. Climate models have systematically underestimated the temperature increase in this region and the latest findings now suggest that over the past 43 years, the Arctic has been warming up nearly four times faster than the globe on average (Rantanen *et al*., 2022). This temperature increase has led to a decrease in sea ice volume by 75% since the 1980s (Overland and Wang, 2013), putting many of the endemic Arctic marine mammal species that depend on the sea ice at risk (Kovacs *et al*., 2011). Negative impacts and anthropogenic activities are expected to increase (Kovacs *et al*, 2011) as the Arctic Ocean is predicted to be nearly ice-free as soon as summer 2035 (Guarino *et al*, 2020).

This is particularly problematic for Arctic pinnipeds (true seals, eared seals and walruses) that are all dependent on the sea-ice to different extents. The ribbon seal *Histriophoca fasciata*, harp seal *Pagophilis groenlandicus* and hooded seal *Cystophora cristata* for instance, all breed on pack ice in spring, but are also reported to spend long periods offshore in ice-free areas (Kovacs *et al*., 2011). Though all pinnipeds may haul out on the ice occasionally throughout the year, the ringed seal *Phoca hispida* and bearded seal *Erignathus barbatus* are particularly associated with sea ice year-round using it for breeding, resting and moulting (Kovacs *et al*., 2011). Finally, the walrus *Odobenus rosmarus* (Figure 1.1) – the only extant member of the Odobenidae family and not a true seal – also uses sea ice for breeding and resting. Walruses use sea ice seasonally as temporal haul-out sites to extend their feeding range, thereby minimizing the travel distance to bivalve beds that are otherwise too far from shore to commute from (Fay, 1982). Because of the retreating sea ice, walruses are in some locations forced to move to suboptimal haul-out sites on land in summer, which may lead to overcrowding and lower accessibility to foraging grounds (Jay *et al*., 2012; Cooper *et al*., 2006). In the Chuckchi Sea for instance, Pacific walruses *O. rosmarus divergens* now haul out on land more often, and concentrate there in larger numbers (Fishbach and Douglas, 2021).

Figure 1.1 One of the most recognizable animals on the planet, the walrus, is threatened by the disappearing sea ice.

But these consequences are not limited to pinnipeds. The disappearing sea ice is also expected to have negative impacts on endemic Arctic cetaceans. The narwhal *Monodon monoceros*, beluga *Delphinapterus leucas* and bowhead whale *Balaena mysticetus* are all associated with sea ice throughout most of the year (i.e., are pagophilic). Bowhead whales are baleen whales (Mysticeti) that filter feed on zooplankton, whereas narwhals and belugas are toothed whales (Odontoceti) that feed primarily on fish (and occasionally on invertebrates such as shrimp and squid). Although their diet differs greatly, their prey species are all associated with sea ice, which makes these cetaceans vulnerable to sea ice loss (Kovacs et al, 2011). Additionally, the sea ice also offers protection from predators, mainly killer whales (*Orcinus orca*). A reduction of sea ice cover makes it harder to hide from these predators, while at the same time allows for killer whales to become more abundant in the Arctic (Higdon and Ferguson, 2009; Ferguson et al., 2010).

Marine mammals are great indicators to study the state of the ecosystem in which they occur. To examine the effects of climate change and the resulting decreasing sea ice on Arctic marine mammals, detailed information on their abundance and distribution is essential. However, due to the remoteness and vastness of the polar area, the harsh environmental conditions and the polar night, it is extremely challenging to locate these animals and study them. Additionally, traditional ship and/or aerial surveys are often based on prior knowledge of marine mammal distribution. This is for instance the case for the most abundant Arctic marine mammal, the harp seal, which is estimated to number close to nine million individuals globally (Lavigne, 2009). Compared to cetaceans (that are in the water permanently), pinnipeds can be more easily observed, as they regularly return to the sea ice (or land for species at lower latitudes) to rest, moult and pup. During these periods, pinnipeds regularly form dense aggregations at haul-out sites; data on abundance and distribution is therefore generally collected in these periods. In the case of the harp seals, the surveying effort has been directed at specific ice fields where these seals are known to aggregate. The largest population of harp seals occurs in the Northwest Atlantic and was estimated to be 7.4 million individuals (Hammill et al., 2015). However, the 95% confidence interval ranged from 6.0 to 9.1 million individuals, which is indicative of the challenges that researchers face when estimating Arctic marine mammal abundance.

In response to the disappearing sea ice, it is expected that Arctic marine mammals change their current distribution. Consequently, these less predictable conditions will make monitoring of marine mammals increasingly difficult, and could (i) lead to even higher uncertainties in population size estimates, (ii) result in knowledge gaps regarding both population development and distribution, and (iii) make protection and management of the species increasingly challenging.

1.1.2 Monitoring marine mammal movement and distribution

Marine mammal distribution and abundance is monitored in various ways. A commonly used approach is to track individually recognisable animals through space and time, by leveraging permanent markings unique to each individual (such as pigmentation or scarring). This is particularly beneficial for animals that cover great distances and are hard to track otherwise, such as marine mammals (Figure 1.2). For cetaceans (e.g., whales, dolphins and porpoises), this approach has been used since the 1950s (Caldwell, 1955; Schevill and Backus, 1960) to follow movements of individual animals, and to study for instance connectivity between breeding and feeding grounds or site fidelity over consecutive years.

Figure 1.2 Individual markings such as scarring and pigmentation – particularly on the fluke – are used to distinguish between individual humpback whales *Megaptera novaeangliae*.

When these individually recognizable animals are photographed, photo-identification catalogues can be created, which can be leveraged to detect range shifts of animals moving to new regions. Photo-identification methods are now commonly employed in cetacean research, often in combination with capture-recapture models to make abundance estimates (e.g., Urian *et al.*, 2014) and an increasing body of work is now focusing on automated identification of individuals (e.g., Vidal *et al.*, 2021; Maglietta *et al.*, 2022). Photo-identification has also been applied in pinniped studies, for instance in grey seals *Halichoerus grypus* (Hiby and Lovell, 1990; Vincent *et al.*, 2001), harbour seals *Phoca vitulina* (Yochem *et al.*, 1999), monk seals *Monachus monachus* (Forcada and Aguilar, 2000), leopards seals *Hydrurga leptonyx* (Forcada and Robinson, 2006) and New Zealand sea lions *Phocarctos hookeri* (McConkey, 1999). However, not all marine mammal species have easily distinguishable individual markings. Furthermore, some marine mammal populations are very large and cover vast areas (e.g., harp seals, see above), which reduces the chance of resighting a specific individual. Finally, photo-identification methods require to be in close proximity to the animals repeatedly, which is particularly challenging in remote and inaccessible regions. Still, this approach might provide opportunities in scenarios where a limited number of individuals pioneer into new areas and data can be collected opportunistically. This was for instance the case when a walrus was sighted at various locations around Europe (Brasseur *et al.*, in press).

Figure 1.3 Pinnipeds, such as this harbour seal photographed in the Dutch Wadden Sea, can be equipped with satellite tags to track them, and log variables such as speed, diving depth and water temperature.

An alternative approach to study marine mammal movement and distribution is to track them using satellite telemetry (Figure 1.3), which allows to follow the animals continuously (e.g., Aarts *et al.*, 2019). This approach can also be combined with photo-identification, as was shown in a capture-recapture study to estimate leopard seal abundance (Forcada and Robinson, 2006). Although telemetry data provides accurate information on movement of individual animals, it is very challenging to achieve a representative sample of the distribution of the entire population, especially when populations are large.

To obtain more precise estimates of population abundance and distribution in specific areas, dedicated aerial surveys can be conducted. These surveys can capitalize on marine mammal phenology (e.g., seasonality) and coincide with predictable seasonal aggregations. Historically, surveys were conducted by plane and animals were counted manually during the survey (e.g., Steller sea lions *Eumetopias jubatus*; Kenyon and Rice, 1961), but since the introduction of digital photography, marine mammal aggregations can more easily be photographed and individuals can be counted afterwards. When the survey area is relatively small (e.g., a single haul-out site on land), unmanned aerial vehicles (UAVs) can be deployed to collect imagery (e.g., Infantes *et al*., 2022). Occasionally, thermal sensors are used to detect marine mammals, particularly pinnipeds; both on land (harbour seals; Christman *et al*., 2022) and on ice (walruses; Burn *et al*., 2010). Some studies have combined aerial surveys with telemetry, to estimate the proportion of animals at sea during the survey (walruses; Lydersen *et al*., 2007; grey seals; Lonergan *et al*., 2011). However, the manual processing of these remote sensing data is labour intensive (and therefore costly), particularly when the abundance and density of the surveyed marine mammals is high. Furthermore, as opposed to using satellite telemetry, unfavourable weather conditions (e.g., high wind speeds) can limit survey time.

Recently, more and more studies have explored the usage of submeter very high resolution (VHR) satellite imagery to count marine mammals (e.g., Khan *et al*., 2023). This approach can be particularly advantageous in remote and inaccessible regions and in principle allows to sample entire populations non-invasively. Unfortunately, the resolution of these images is too low to differentiate between most marine mammal species, particularly smaller ones. Furthermore, as for aerial surveys, the manual processing of satellite images is labour-intensive and costly. Alternatively, the detection of animals in remote sensing images can be automated (e.g., Weinstein, 2017; Tuia *et al*., 2022), thereby replacing (or reducing) the time-consuming manual detection of animals in newly acquired images. However, before this approach can be applied on a large scale, there are still many challenges to overcome, which are detailed below.

1.1.3 Automated detection of animals in remote sensing imagery

With recent developments in the field of machine learning and Computer Vision (CV), automated detection algorithms can now significantly reduce the time required for the labour-intensive manual processing of remote sensing imagery. Deep learning models – a family of machine learning models based on artificial neural networks – in particular have been successful to learn representations of complex data, such as images (LeCun *et al*., 2015). Although artificial neural networks date back to the 1940s (McCulloch and Pitts, 1943) and 1950s (Metropolis *et al*., 1953), deep learning models have only recently become increasingly performant, following the increase of computational power and (digitally) available data. A detailed review of the history and development of these models is beyond the scope of this introduction and can be found in Schmidhuber (2015). During the last decade, machine learning and CV have also found their way into the field of ecology (Tuia *et al*., 2022). In a review of different applications to automatically detect, count and study animals, Weinstein (2018) shows a strong increase in the number of ecology-oriented publications using CV methodologies. Convolutional Neural Networks (CNNs) in particular have shown a remarkable increase in ecological applications (Christin *et al*., 2019). The majority of literature about CNNs applied in animal ecology focuses on terrestrial animals (e.g. Kellenberger *et al*., 2018; Eikelboom *et al*., 2019).

Before a CNN can automatically detect and count animals in unseen images, it first has to be trained to recognise the target, which is done by exposing the model to many examples of annotated (i.e., labelled) images and adjusting the model's internal (learnable) parameters to closely match its predictions with the labels. Therefore, these training images require manual processing to generate a set of labels. Through the principles of transfer learning (Ng, 2016), standard CNN architectures can be pre-trained on large benchmark image datasets such as ImageNet (Deng *et al*., 2009) and then fine-tuned with smaller amounts of data pertaining to the specific application, thereby reducing the amount of required training data by orders of magnitude. Despite this, the paucity of annotated training data still remains the main bottleneck when employing CNNs for ecological objectives and datasets.

One way to reduce the time and costs of annotating the images is to use crowdsourcing. In this approach, non-expert observers can be involved to annotate the images used for training (Arteta *et al*., 2016; Attari *et al*., 2016; Ofli *et al*., 2016). However, when the problem is complex, such as the identification of animals difficult to discern on satellite imagery, the lack of experience may lead to inaccurate annotations. For instance, in a Weddell seals study using VHR satellite images, crowdsourcing resulted in a high rate (67%) of false positives (LaRue *et al*., 2020). An alternative approach to reduce time and costs of annotating data is to artificially create vast amounts of training data (e.g., Bondi *et al*., 2018). In rare occasions, annotations collected for other purposes, without the aim of deep learning applications (e.g., image level counts) might be available, circumventing the need to label imagery. In principle, creating a set of labelled images is required only once, after which a network can be trained. However, whenever the CNN is applied in a new scenario (on a new animal, a new background, or after changing equipment, etc.), the annotation and training process often needs to be repeated for that specific case.

After the model is trained, it can be used to make predictions in new images to automatically detect and count animals in newly acquired images, thereby replacing the labour-intensive (and therefore costly) manual processing. By significantly reducing the processing costs of newly collected images, it becomes possible to survey large areas with reduced expenses. Eikelboom *et al*. (2019), for instance, compared the performance of the object detection model RetinaNet (Lin *et al*., 2018) – trained to detect elephants, giraffes and zebras in aerial images – against manual detection. Their model found 95% of elephants, 91% of giraffes and 90% of zebras that were found manually by the combined efforts of four human observers. Interestingly, the model also detected additional animals that were missed by the human observers. There was however a high rate of false positives, i.e., detections where there was no animal. Therefore, they proposed a method where the detections of the model are verified by humans. By using this semi-automated approach, the processing time could be reduced, and the survey effort could be increased, without increasing the overall costs.

In many remote sensing scenarios, the targeted animals might be relatively rare and/or scarcely distributed over vast areas. As a consequence, the vast majority of the images will not contain the target animals (Xue *et al.*, 2017; Kellenberger *et al.*, 2018; Gonçalves *et al.*, 2020). This means that even relatively low rates of false positives of the trained model could lead to a high absolute number of false positives (Hollings *et al.*, 2018; Gonçalves *et al.*, 2020). For instance, Borowicz *et al.* (2019) and Guirado *et al.* (2019) detect whales from space. For both studies, the images were collected in areas known for some of the highest densities of whales in the world, and the detection network misidentified respectively 6.7% (Borowicz *et al.*, 2019) and 3.25% (Guirado *et al.*, 2019) of their non-whale tiles as whales. Consequently, if these approaches would be extrapolated to other areas, including those with few or no whales at all, the number of false positives relative to the actual number of whales is expected to increase dramatically. Furthermore, Borowicz *et al.* (2019) reported zero false negatives (i.e., whales identified as water) on the testing set. This might be attributed to the fact that their model is trained and tested on images with good weather, without waves, and that the model was not tested on other objects, such as ships or rocks. Therefore, it might effectively be a smooth water detector rather than an actual whale detector, which further limits the usability of the method in real world scenarios.

Where Borowicz *et al.* (2019) and Guirado *et al.* (2019) cut up their images in small tiles, and then treat the detection of whales as a classification problem, other detection algorithms are also applied (e.g., Eikelboom *et al.*, 2019). For instance, Corcoran *et al.* (2019) used a combination of two object detection models, Faster-RCNN (Ren *et al.*, 2015) and YOLO (Redmon and Farhadi, 2016), to detect koalas. In these cases, the networks were pretrained, and the architecture of the network was not changed. This 'off-the-shelf' approach has some strong benefits as it is ready to use, and the accuracy of the networks is generally good.

One of the downsides of using an object detection approach is that every single object needs to be annotated separately, either by bounding boxes or centroids. When many of the target objects (or animals) occur in a single image, annotating each individual object may become a tedious process (Wang *et al.*, 2018, Kellenberger *et al.*, 2019). This is for instance the case for pinnipeds on haul-out sites, where many individual animals are clustered closely together, or even overlap. In some scenarios, annotations of every individual object might even be impossible (e.g., Moen *et al.*, 2018).

In these scenarios, where there is a high density of objects, the image can be labelled with a single number describing the number of objects in the picture, instead of labelling each individual object (Figure 1.4). The problem can then be treated as a regression task and the CNN can be trained to output a single number of objects for each input image. In other words, the CNN is trained to regress the number of animals in the image. However, information on the exact location of the object in the picture will not be available and potentially relevant ecological information will be lost.

Figure 1.4 Different approaches to animal detection and counting: Image segmentation (left) predicts labels for every pixel (e.g., seal vs background), whereas object detection (middle) generally predicts bounding boxes around every object of interest (i.e., seals). Regression based approaches (right) predict an image-level count, and information on the exact location of seals not provided. Photograph Sophie Brasseur.

Very few automated approaches on pinniped detection have been published. Infantes *et al*. (2022) use a CNN to both count and measure body size of harbour seal adults and pups, using aerial images collected by UAVs. The counts are compared with ground-based counts using telescopes and a 95–97% accuracy is reported. Gonçalves *et al*. (2020) automatically detect four sympatric species of pack-ice seals (Weddell seals *Leptonychotes weddellii*; crabeater seals *Lobodon carcinophaga*; leopard seals *Hydrurga leptonyx*; Ross seals *Omnatophoca rossii*) from VHR satellite imagery. They modified the semantic segmentation (i.e., pixel-wise classification) model U-Net (Ronneberger *et al*., 2015) in such a way that it produces not only a heatmap, but also a presence/absence of seals and a seal count. Their training dataset contained 1,168 seals. Compared to the combined efforts of two human observers, the CNN detected only 35% of the seals that were manually annotated, while also finding 1,321 false positives. As the number of training images was relatively low, it is expected that the performance could increase by training the network with more images and seals. Later versions of their approach (Gonçalves *et al*. 2022) include a sea ice segmentation model to first find potential suitable seal habitats. However, when using VHR satellite imagery, it becomes extremely challenging to detect pups, which are smaller and generally better camouflaged (e.g., Fudala and Bialik, 2022) and to differentiate between sympatric pinniped species (e.g., Gonçalves *et al*., 2020).

1.1.4 The southern North Sea as laboratory to study methodologies for marine mammal monitoring

When studying Arctic marine mammals, the inaccessibility and remoteness of the Arctic region limits the possibilities to develop and test these new methodologies directly. To circumvent this challenge, the experimental work presented in this thesis was developed in a more easily accessible region, which allowed to leverage knowledge and existing data on marine mammal populations that occur at lower latitudes, the southern North Sea (including the Wadden Sea). I focus on the development and study of monitoring technologies in this area, by leveraging observational datasets on both pinnipeds and bottlenose dolphins.

First are pinnipeds. Two pinniped species occur in the southern North Sea, the harbour seal (Figure 1.3) and the grey seal (Figure 1.5). The harbour seal is the smaller of the two, with females growing up to 150 cm and males up to 160 cm. Grey seals are larger, and display a higher level of sexual dimorphism, with males reaching 210 cm on average, while females grow to 185 cm on average. Male grey seals are also significantly heavier than females at 300 kg and 200 kg, respectively.

Most Arctic pinnipeds haul out on sea ice to rest, moult and pup, whereas grey seals and harbour seals along the Dutch coasts haul out on land on intertidal flats, sand banks and beaches. While the sea ice moves due to currents and wind regimes, haul-out sites on land are more predictable and allow for more straightforward monitoring. Similar to most Arctic pinnipeds, grey seals and harbour seals haul out seasonally. Both species may form large aggregations and often return to the same haul-out sites in consecutive years. Grey seals and harbour seals have an overlapping habitat and distribution (i.e., are sympatric species), and are even found in mixed groups at haul-out sites (Figure 1.6; Jones *et al*., 2015, McConnell *et al*., 1999; Damseaux *et al*., 2021). However, grey seals generally have a preference to haul out on the highest sandbanks, which are less exposed to tidal and weather conditions, while harbour seals can also use sandbanks that are only available during low tide, which are more readily available.

In the Wadden Sea, bordering the southern North Sea, seals have been hunted for centuries, which led to the local extinction of grey seals in in the Middle Ages (Reijnders *et al*., 1995) and near-extinction of the harbour seal in the 20th century (Reijnders *et al*., 1992). Following the cessation of the hunt in 1960, populations of both species have shown steady recovery: grey seals recolonised the area (Brasseur *et al.,* 2015) and in the international Wadden Sea number over 8,000 individuals counted in 2023 (Schop *et al.,* 2023) and the number of harbour seals counted reached over 25,000 individuals, resulting in a population estimate of 40,000 individuals in 2014 (Brasseur *et al.,* 2018). Since then, the growth has stagnated and in 2022 slightly less than 25,000 animals were counted (Galatius *et al*., 2022).

Figure 1.5 A male grey seal during the mating season on Griend (Dutch Wadden Sea).

Figure 1.6 A haul-out site with both harbour and grey seals, in the Dutch Wadden Sea.

Compared to Arctic pinniped populations, the harbour and grey seals in the Wadden Sea can be considered data-rich species. Both have been studied extensively in this region. The numbers and pup production are recorded annually and hundreds of individual animals have been tracked throughout the years (Reijnders, 1976; Reijnders, 1986; Reijnders *et al.*, 1995; Ries *et al.*, 1998; Härkönen *et al.*, 2006; Reijnders *et al.*, 2010; Brasseur *et al.*, 2015; Brasseur *et al.*, 2018; Aarts *et al.*, 2019). Regular aerial monitoring started in the 1970s and is now done annually, with multiple surveys carried out during the respective breeding and moulting season. Since the 1990s, aerial images (Figure 1.7) are collected, resulting in a large database of thousands of aerial images. Additionally, a significant amount of tracking data is available, providing a detailed view on fine scale distribution and habitat use of both species from the 1990s onwards. Finally, the national inspection of land-use (i.e., land registry 'Kadaster') provide aerial images that occasionally include haul-out sites. These datasets provide a unique opportunity to develop and test new approaches to monitor pinniped haul-out sites, such as automated detection and the usage of lower resolution aerial or satellite imagery. These new approaches might not only offer new insights into the ecology of grey and harbour seals and reduce costs associated with data processing, but they can also provide valuable new tools – such as automated detection – to study pinnipeds in other more inaccessible regions.

Second are bottlenose dolphins. As opposed to grey and harbour seals, bottlenose dolphins are rarely observed in the Netherlands. These robust dolphins can grow up to 390 cm, and were once common in the North Sea. However, during the last century numbers have declined (Evans, 1980). Historically, these animals also regularly occurred in Dutch waters, particularly in a tidal inlet connecting the North Sea and Wadden Sea (i.e., the Marsdiep), but currently these dolphins are considered rare visitors (van Bree, 1977; Kompanje, 2001, 2005; Camphuysen and Peet, 2006).

As for the Dutch harbour seal and grey seal populations, bottlenose dolphins in the North Sea – such as the Eastern Scottish population (e.g., Cheney *et al.*, 2013) and even solitary individuals (e.g., Müller and Bossley, 2002) – are relatively well studied and can be considered data-rich when compared to Arctic marine mammal populations. For instance, a long-term photo-identification catalogue for the East Coast Scotland population is curated by the University of Aberdeen and the University of St. Andrews (Cheney et al., 2014). These type of extensive datasets from neighbouring populations, that cover a large part of the population, allow for comparison with opportunistically collected data from bottlenose dolphins in the Netherlands. The results can provide new insights into the distribution and potential range shifts of these dolphins, but can also be used to evaluate the benefits and drawbacks of applying this methodology on Arctic marine mammals.


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Figure 1.7 Aerial image of a harbour seal haul out site in the Dutch Wadden Sea, photographed from an airplane.

1.2 Knowledge gaps

In response to global warming, the distribution of many species is changing, often moving towards higher latitudes, either driven by their own temperature tolerance limitations, or by shifting distributions of their preferred prey (Huntington *et al*., 2020; Jensen *et al*., 2023). However, animals inhabiting polar regions – at the climatological limits of our globe – are geographically restricted and cannot shift their distribution towards cooler regions as the planet warms. Therefore, these animals might respond differently to cope with increasing temperatures. For instance, some Arctic migratory vertebrates could respond by shifting the timing of their annual migration between feeding and breeding areas, or alternatively change their distribution (i.e., range shifts). **A better overview of the responses of Arctic vertebrates to a warming Arctic is needed (KG 1).**

Species distributions may shift either due to demographic processes (i.e., latitudinal variation in mortality and birth rates) or shifts in distribution of individual animals. As a method of choice, photo-identification methods and catalogues (covering long time series) can be used to estimate and study such changes in distributions and range shifts of individual animals in more detail and is therefore a commonly used tool to study life-history traits. Additionally, range shifts can also have implications for conservation and management of marine mammals. Protective measures are often limited to confined geographical areas that are considered important for the species, such as known breeding or feeding grounds. When their local environment changes, e.g., due to climate change or other anthropogenic sources of disturbance, these mobile animals move away from their anticipated home range into areas without protective measurements, this potentially puts them at risk. **Better insights into (i) the movement of individual marine mammals using opportunistically collected images suitable for photo-identification and (ii) the potential consequences for adequate conservation are needed (KG 2).**

The variety of different marine mammal survey techniques (e.g., land-based observations, aerial surveys and satellite-based remote sensing) and the digitization of survey methods lead to a vast increase in photos that require processing. Manually counting marine mammals from the imagery collected during these surveys is labour-intensive and therefore costly. To this end, CV and deep learning allow to dramatically reduce the time required to process image data. However, these algorithms are data-hungry, and generally rely on manually annotated images to learn to recognise patterns within those images. Most commonly, deep learning algorithms developed in ecological studies are designed for object detection, which requires individual-level annotations with bounding boxes for each image. Manually annotating every object is labour-intensive, especially when individuals occur in high numbers and densities. Proceeding this way, the time required to manually annotate the images might undermine the speed gains of using an automated approach in the first place. **More research is needed to explore the potential of automated counting tasks in ecological applications (KG 3).**

The distribution of many species is changing due to global warming (e.g., KG 1). Central-place foragers (i.e., animals that return to a fixed point, such as pinnipeds and colony forming seabirds) might be particularly susceptible to climate change-induced shifts. For instance, Arctic pinnipeds have evolved to move and behave in relation to seasonal ice conditions (e.g., de la Vega *et al*., 2021; Hamilton *et al*., 2022). These animals time their breeding or moulting season to coincide with the availability of predictable safe ice and migrate to specific regions to make optimal use of expected seasonal changes to feed. In general, predictable distributions such as these often dictate the timing and location on which marine mammal surveys are based. However, given the uncertainties surrounding the response of Arctic marine mammals to the disappearing sea ice, these patterns are expected to become less predictable. Therefore, it will become increasingly challenging to study the distribution and abundance of these animals in this remote and inaccessible region. A potential solution to circumvent these uncertainties is to use VHR satellite imagery, which allows for (i) the detection of marine mammals from space (e.g., Khan *et al*., 2023), and to (ii) survey larger areas than with traditional aerial or ship-based surveys. However, even in satellite imagery with the highest available resolution, most marine mammal species are only a few pixels large.

Morphological characteristics alone are therefore often insufficient to differentiate between species in satellite imagery, especially when species are sympatric. Consequently, other information is needed to identify them. **More research is needed to determine whether characteristics other than morphological traits of the animals can be used to differentiate between marine mammal species in remote sensing applications (KG 4).**

1.3 Research questions and outline of the thesis

The knowledge gaps outlined above require specific solutions before these techniques can be applied on a large scale. This thesis aims to develop and apply new methodologies for marine mammal detection of data-rich marine mammal populations in the southern North Sea. This is addressed through the following research questions:

RQ 1. Which changes in migration timing or distribution do Arctic migratory vertebrates exhibit in response to global warming?

RQ 2. How can opportunistically collected data contribute to a better understanding of range shifts in marine mammals? A bottlenose dolphin case study.

RQ 3. How can image-level annotations be leveraged to train a deep learning model to count pinnipeds from aerial imagery, and what is the accuracy of this approach? A grey and harbour seal case study.

RQ 4. How can fine-scale spatial haul-out patterns in pinniped haul-out sites be used as a tool to differentiate between sympatric species, when using low-resolution remote sensing imagery?

This thesis consists of four chapters that were written as independent research papers. RQ 1 is addressed in Chapter 2 – where an extensive literature review is carried out to assess whether Arctic migratory vertebrates show shifts in migration timing or distribution in response to the current global warming (KG 1). In Chapter 3, I tackle RQ 2 by showing case studies where opportunistically collected image data is used to trace the movement of a marine mammal, the bottlenose dolphin (KG 2). In Chapter 4, a regression-based Deep Learning approach is employed to automate counting of seals, using image-level annotations, addressing KG 3 and answering RQ 3. Chapter 5 focusses on RQ 4 by examining fine-scale spatial patterns in pinniped haul-out sites formed by two sympatric seal species (KG 4). Finally, Chapter 6 brings together the developed methodology and results of all chapters and provides a synthesis of our key insights and suggestions for further research.

Chapter 2

Migratory vertebrates shift migration timing and distributions in a warming Arctic

Abstract. Climate warming in the Arctic has led to warmer and earlier springs, and as a result, many food resources for migratory animals become available earlier in the season, as well as become distributed further northwards. To optimally profit from these resources, migratory animals are expected to arrive earlier in the Arctic, as well as shift their own spatial distributions northwards. Here, we review literature to assess whether Arctic migratory birds and mammals already show shifts in migration timing or distribution in response to the warming climate. Distribution shifts were most prominent in marine mammals, as expected from observed northward shifts of their resources. At least for many bird species, the ability to shift distributions is likely constrained by available habitat further north. Shifts in timing have been shown in many species of terrestrial birds and ungulates, as well as for polar bears. Within species, we found strong variation in shifts in timing and distributions between populations. Our review thus shows that many migratory animals display shifts in migration timing and spatial distribution in reaction to a warming Arctic. Importantly, we identify large knowledge gaps especially concerning distribution shifts and timing of autumn migration, especially for marine mammals. Our understanding of how migratory animals respond to climate change appears to be mostly limited by the lack of long-term monitoring studies.

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2.1 Introduction

The Arctic region is characterised by strong seasonality. During winter, the Arctic forms an inhospitable environment for most animals, with low temperatures, extensive snow and ice cover and long phases of darkness. The summer season is relatively short with long light phases and temperatures above freezing, associated with strong changes in environmental conditions, including melt of snow and break-up of sea ice. In both terrestrial and marine ecosystems, the Arctic summer is also a period of peak productivity, creating a short period of high resource abundance for many species. These strong seasonal changes in environmental conditions explain why many vertebrates occurring in the Arctic have a migratory lifestyle (Fox TAD, 2021; Figure 2.1). This allows them to profit from high resource abundance in the Arctic summer, while escaping harsh climatic conditions during winter.

Figure 2.1 Examples of warm-blooded vertebrates migrating to the Arctic, showing (**A**) reindeer (*Rangifer tarandus*) crossing a frozen river on the way to their calving grounds, (**B**) red knots (*Calidris canutus*) on a spring staging site in northern Norway, (**C**) walrus (*Odobenus rosmarus*) resting on sea ice with their young, and (**D**) a minke whale (*Balaenoptera acutorostrata*) in a fjord in Svalbard. Photographs by Paul Asman and Jill Lenoble (A), GRID Arendal (B), Alaska Region US Fish and Wildlife (C), and Guillaeme Baviere (D).

The Arctic climate is changing disproportionally fast (Serreze *et al*., 2009), with temperature increases three times as fast as the rest of the globe (AMAP, 2021), especially accelerating in recent decades (Post *et al*., 2018). Increases in temperature throughout the year coincide with loss of Arctic sea ice, shorter seasonal duration of snow cover (Box *et al*., 2019), and overall increased 'greening' of tundra regions (but with strong variation between sites, Myers-Smith *et al*., 2020). Such changes are predicted to further accelerate in the near future (IPCC, 2019). The warming climate has strong impacts on the availability of resources for Arctic migratory animals. Earlier disappearance of ice and snow in the season can result in shifts in timing and distribution of the main food resources for migrants, including vegetation (Doiron *et al*., 2014; Lameris *et al*., 2017) and arthropods on land (Høye *et al*., 2021; Reneerkens *et al*., 2016; Tulp and Schekkerman, 2008), and phytoplankton abundances at sea (Asch *et al*., 2019; Henson *et al*., 2018). If migratory animals do not change the timing of their migration and reproduction or their summer distribution in response, phenological mismatches with their food resources may occur, potentially resulting in reduced fitness (Post and Forchhammer, 2008, Lameris *et al*., 2018) which might affect population dynamics.

To adjust to changes in the timing of resource availability in the Arctic, migratory animals could advance their timing of arrival on the breeding grounds. Given the limited leeway to increase the speed of migration once underway (Schmaljohann and Both, 2017; Alerstam and Bäckman, 2018) for birds which have relatively high travel speeds, this likely also necessitates advancements in migratory fuel deposition and departure from the wintering grounds (Lindström *et al*., 2019). Besides changes in spring migration in response to earlier resource availability, longer Arctic summer seasons associated with later freeze-up and snowfall (Box *et al*., 2019) could also drive delays in the timing of autumn migration (Xu and Si, 2019).

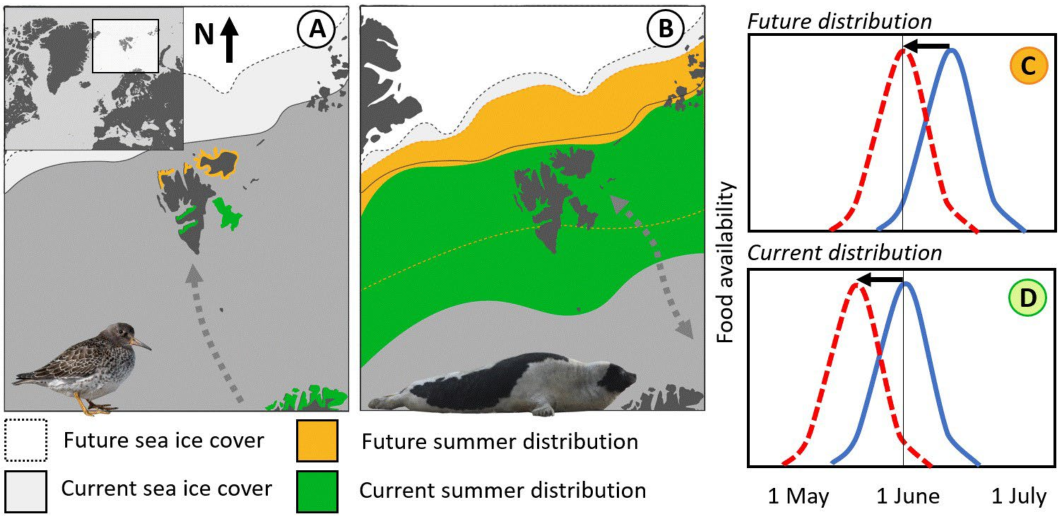

Figure 2.2 (**A-B**) Maps showing examples of current (green) and hypothetical future summer distributions (orange) of purple sandpipers *Calidris maritima* (**A**) and harp seals *Pagophilus groenlandicus* (**B**) around Svalbard. While harp seals can shift their distribution northward with retreating sea ice, purple sandpipers are constrained by available land mass of Svalbard to shift their distributions far north. Median sea ice cover (during summer months 1981 - 2010) is shown as light grey area in the north, outlined by a solid black line, and hypothetical change in future ice cover is depicted by the white area outlined by dashed black line. Grey dashed arrows show migration directions of the sandpipers and seals. Distributions and migration directions are based on (Svetochev *et al*., 2016; Jay *et al*., 2017; Birdlife International, 2021). (**C-D**) With a warming climate, timing of food availability (blue lines) is expected to advance (red dashed lines), both in current distributions (**D**) as well as hypothetical future distribution ranges (**C**). To maintain a synchrony with these peaks in food availability, animals are expected to advance their own timing of migration, but may also be able to maintain a synchrony by shifting their distribution northward (towards distribution **C**) where the food becomes available later in the season.

In addition to shifts in the timing of migration, animals may respond to a warming Arctic by shifting their summer distribution northward to locations with later phenology. Animals making this northward shift may then experience the same timing of resource availability in spring without advancing migration timing (Figure 2.2), although it could also result in later arrival given longer migration distances. However, distributional shifts might be limited by topography or by increased travel costs for some Arctic animals. First, many terrestrial animals in the Arctic already find themselves at the most northern edge of the continent, resulting in shrinking habitat range or "polar squeeze" (Figure 2.2). Second, suitable habitats may not be present further north. For example, marine mammals are largely reliant on sea ice for feeding (and reproducing in case of pinnipeds), and may find themselves without any available habitat with the predicted disappearance of sea ice in summer (Wang and Overland, 2009). Changes in timing of migration and reproduction (Rakhimberdiev *et al.*, 2018; Gurarie *et al.*, 2019), and to a limited extent shifts in breeding distribution (Brommer *et al.*, 2012; Severson *et al.*, 2021), have already been observed in Arctic migratory animals. Those species which have been unable to shift timing of reproduction sufficiently, often suffer from reductions in reproductive success and survival (Post and Forchhammer, 2008; Lameris *et al.*, 2018). As Arctic migratory animals are an essential part of local Arctic ecosystems (Bauer and Hoye, 2014; Choi *et al.*, 2019), as well as provide important resources for local Indigenous Peoples (Wenzel, 2009; , Martinez-Levasseur *et al.*, 2021), any changes in the migration timing and distribution of migratory animals will have far-reaching consequences.

Here we review literature on Arctic migratory animals for evidence of shifts in timing of migration and shifts in distribution. We focus on groups of endothermic migratory vertebrates that perform seasonal migrations to, or within, the Arctic, including terrestrial and marine birds, ungulates, cetaceans, pinnipeds and polar bears (Figure 2.1). These animals differ strongly in their habitats (marine, coastal and terrestrial habitats) as well as in their diet (plankton, benthic invertebrates, fish, pinnipeds, plants, arthropods, rodents). We expect to find variation in both shifts in timing and distribution across taxonomic groups of Arctic migratory animals. Concerning migration timing, we predict that long-distance migrants (most birds and cetaceans, with one-way journeys on average exceeding 2000 kilometres) will show smaller shifts in migration timing in comparison to short-distance migrants (including some cetaceans, all ungulates, pinnipeds and polar bear), as long-distance migrants cannot predict conditions in the Arctic from their distant wintering grounds (Kölzsch *et al.*, 2015; Lameris *et al.*, 2017). Concerning shifts in distribution, we expect terrestrial animals (including land-breeding marine birds), to be more constrained in making large shifts (Lenoir *et al.*, 2020) compared to marine animals. For terrestrial animals, suitable alternative habitat further northward may not be available due to lagging changes in suitable vegetation communities, or as it is limited by topographical barriers in the landscape such as the northern edge of the continent (Figure 2.2). In comparison, animals in marine environments that can freely navigate the oceans and enter the Arctic basin, may show stronger shifts in their distribution (Lenoir *et al.*, 2020), for example by following the edge of pack ice, or the distribution shifts of their main prey (Oziel L *et al.*, 2020; Sunday *et al.*, 2012).

In this review, we first introduce the focal taxonomic groups of endothermic vertebrates and their migrations. Thereafter we introduce the resources on which animals depend and discuss how the phenology and abundance of these resources are expected to change in a warming climate. Finally, following a systematic literature search, we review scientific literature on evidence for shifts in timing of migration and shifts in distribution of focal taxonomic groups, and quantify whether shifts in timing differ between taxonomic groups.

2.2 Migrations of Arctic, warm-blooded vertebrates

2.2.1 Bird migration

The most abundant birds with Arctic distributions are seabirds, shorebirds, and waterfowl, with other less represented species groups including passerines, grouse and birds of prey (Fox TAD, 2021). Most of these species are migratory (CAFF, 2013) and spend the winter in more southern regions. The extent of these migrations varies enormously, with some seabird species wintering in Arctic waters (Fort *et al.*, 2013; Linnebjerg *et al.*, 2018), most waterfowl, passerines, and birds of prey wintering in temperate regions (Curk *et al.*, 2020; Fox and Leafloor, 2018; Macdonald *et al.*, 2016), and many shorebird and seabird species wintering in areas that range from temperate and tropical regions (Bemmelen *et al.*, 2017; Meltofte, 1996; Reneerkens *et al.*, 2019) down to Antarctic waters (Egevang *et al.*, 2010; Fijn *et al.*, 2013). Differences in wintering areas, and therefore migration distance, likely relate strongly to availability of suitable wintering habitat with available resources. Fish-eating seabirds may be able to winter in Arctic waters as long as fish are available and accessible (Fort *et al.*, 2009; Hunt, 1990), while shorebirds, depending on benthic invertebrates, travel to temperate and tropical intertidal flats that do not freeze in winter (Reneerkens *et al.*, 2019). Given long migration distances, many bird species require stopover sites to gain energy stores between leaps of migration (Alerstam, 2011). During spring migration, at least some species of waterfowl appear to track peaks in food quality and availability (van der Graaf *et al.*, 2006; Shariatinajafabadi *et al.*, 2014; Wang *et al.*, 2019) and the onset of ice break-up and snowmelt at staging sites (Nuijten *et al.*, 2014; Li *et al.*, 2020). This, however, does not appear to be the case for all species of waterfowl (Wang *et al.*, 2019) nor for shorebirds (Tucker *et al.*, 2019). Birds of prey also track snowmelt during northward migration, possibly as areas with melting snow contain high availability of rodent prey (Curk *et al.*, 2020). All Arctic migratory birds reproduce during the Arctic summer, and many species (including waterfowl, shorebirds and marine birds) appear to attempt to synchronize their reproduction with prey availability for their offspring.

2.2.2 Ungulate migration

The Arctic is inhabited by a limited set of ungulate species, including reindeer (*Rangifer tarandus*), moose (*Alces alces*), muskox (*Ovibos moschatus*), Dall's sheep (*Ovis dalli*) and snow sheep (*Ovis nivicola*). Movements of the three latter species are limited to short-distances (up to 100 km), which can be seasonal but often follow nomadic patterns (Schmidt *et al.*, 2016) in search of suitable foraging grounds. On the other hand, moose (Ball *et al.*, 2001; Allen *et al.*, 2016) and reindeer are considered partial migrants, and especially some populations of reindeer make large migratory movements up to 1300 km (Joly *et al.*, 2016) from taiga wintering areas to calving grounds at coastal Arctic tundra zones. Other populations of reindeer migrate shorter distances (Mahoney and Schaefer, 2002) or are resident (Tyler and Øritsland, 1989). By migrating, ungulates can winter in areas with more suitable conditions for both adults and their offspring (Ball *et al.*, 2001), travel northwards in spring along a wave of vegetation green-up (Merkle *et al.*, 2016), and match calving with local peaks in food quality (Post and Forchhammer, 2008; Laforge *et al.*, 2021). Studies on the migrations of moose are largely limited to their southern ranges, and in this review we therefore focus on reindeer.

2.2.3 Cetacean migration

Cetaceans occurring in the Arctic are mostly represented by baleen whales (Mysticeti), including rorquals (Balaenopteridae) and grey whales (*Eschrichtius robustus*), and fewer toothed whales (Odontoceti), including belugas (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), sperm whales (*Physeter macrocephalus*) and northern bottlenose whales (*Hyperoodon ampullatus*). With the exception of the pagophilic (i.e. sea-ice loving) beluga, narwhal and bowhead whale (*Balaena mysticetus*), which make seasonal migrations within the Arctic, cetaceans are seasonal visitors to the Arctic. In contrast to birds and ungulates that migrate to the Arctic for reproduction, migratory whales use the high latitude summer grounds exclusively for feeding, while reproduction occurs in low latitude winter grounds, where food availability is generally scarce or non-existent (Fokkema *et al.*, 2020). The mechanism driving this migratory pattern remains largely unknown. It has been suggested that whales migrate to reduce predation pressure on calves (Connor and Corkeron, 2001; Corkeron and Connor, 1999), or that the higher temperatures of low latitude waters bring thermoregulation benefits for calves (and/or adults) (Lockyer and Brown, 1981; Pitman *et al.*, 2020). However, recent new evidence suggests that deferred skin moult could be the main driver of long-distance cetacean migration (Pitman *et al.*, 2020). In colder waters, cetaceans reduce blood flow to their skin to conserve body heat. It appears that cetaceans migrate to warmer waters at lower latitudes to reduce heat loss during moult, a period during which they enlarge blood flow through the skin. Similarly, the pagophilic species that remain in the Arctic year-round, make seasonal migrations towards warmer waters in estuaries and shallows to moult (Smith *et al.*, 1992; Chernova *et al.*, 2016; Fortune *et al.*, 2017).

2.2.4 Pinniped migration

Several pinniped species are year-round residents in the Arctic regions, like harp seal (*Pagophilus groenlandicus*), ringed seal (*Pusa hispida*), hooded seal (*Cystophora cristata*), bearded seal (*Erignathus barbatus*), spotted seal (*Phoca largha*), ribbon seal (*Histriophoca fasciata*) and walrus (*Odobenus rosmarus*). In addition, the distributions of other species like harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*), Steller sea lion (*Eumetopias jubatus*) and northern fur seal (*Callorhinus ursinus*) extend into the polar regions. While pinnipeds feed at sea, they require land or ice to reproduce, moult and periodically rest, which severely constrains their at-sea distribution. To avoid land predators, most Arctic pinnipeds spend the breeding and moulting season on land-fast ice or free-floating pack ice in late winter and spring (Kovacs and Lydersen, 2008), after which they disperse. While some individuals move long distances away from the ice (e.g. harp seals and walrus), most pinniped species remain associated with outer edges of the pack ice, where they feed on fish and invertebrates (Crawford *et al.*, 2015), while using the pack ice as resting platforms. Resident Arctic pinnipeds feed on prey that is present and accessible in the Arctic regions year-round, which provides no strong incentive to leave the Arctic region altogether, as opposed to most birds and cetaceans. However, pinnipeds do show seasonal long-distance movements (Svetochev *et al.*, 2016), but this seasonal migratory pattern mostly involves movement between foraging areas, breeding and moulting locations, largely driven by the extent of the pack ice (Kovacs *et al.*, 2016).

2.2.5 Polar bear migration

Polar bears (*Ursus maritimus*) depend on sea ice platforms to hunt fatty, energy-dense pinniped prey (Pilfold *et al.*, 2017), primarily ringed seals and bearded seals (Parks *et al.*, 2006). The bears consume around two-thirds of their annual food intake from February up to mid-April, when seals give birth on the sea ice (Pilfold *et al.*, 2017; Stirling and Oritsland, 1995). When sea ice melts and becomes fractured in spring, the polar bears' mobility and seal hunting technique become inefficient (Cherry *et al.*, 2013), and bears either move with the receding pack ice, or migrate towards terrestrial habitats (Pilfold *et al.*, 2017). The summer is typically a period of fasting for polar bears during which they rely on endogenous energy reserves (Molnár *et al.*, 2020). Most polar bears move back onto the pack ice after autumn, when pack ice extent increases, while pregnant female bears will enter terrestrial maternity dens along the coast where they give birth to their young (Ramsay, 1990).

2.3 Changing resources under climate warming

Temperatures in the Arctic are increasing year-round, with temperatures above freezing occurring earlier in spring (Assmann *et al.*, 2019), associated with earlier timing of snow melt, active layer melt and ice break-up (Box *et al.*, 2019). These climatic changes can result in earlier availability of resources for migrants (although the relative importance of climatic factors may differ at regional scales, e.g. (John *et al.*, 2020)). In addition, higher summer temperatures may lengthen the period of resource availability, and climatic changes may also cause a northward shift in the spatial distribution of resources, as well as of suitable habitats for migrants. We discuss these aspects in detail in the following sections.

2.3.1 Earlier resource availability

Lower trophic levels, including the food resources for many migratory animals (Figure 2.3), are known to rapidly adjust their phenology to a warming climate (Thackeray *et al.*, 2010). In terrestrial habitats, earlier snowmelt and increasing temperatures have led to an advancement in the growing season of many plants (Kelsey *et al.*, 2021), and thereby an advancement in the moment of peak quality and availability of forage plants for herbivorous birds and ungulates (Doiron *et al.*, 2014; Lameris *et al.*, 2017; Post *et al.*, 2008). Arthropods, which form the main prey for Arctic-breeding shorebirds and passerines (Wirta *et al.*, 2015), respond to earlier dates of snow and active layer melt and increasing temperatures by earlier emergence (Høye *et al.*, 2021; Rakhimberdiev *et al.*, 2018; Koltz *et al.*, 2018) and changes in their abundance (Høye *et al.*, 2021). The annual cycles of Arctic rodents, the main prey of Arctic raptors and skuas (Wiklund *et al.*, 1999), seem to be little impacted by a warming climate (Ehrich *et al.*, 2019) (but see reports on irregularity of these cycles (Nolet *et al.*, 2013)). At the same time, the accessibility of rodents as prey for birds is potentially dependent on snow cover, with high concentrations of accessible rodents around the time of snow melt (Curk *et al.*, 2020). Despite increasing temperatures, increasing precipitation in winter (another aspect of climate change in the Arctic, Vincent *et al.*, 2015) may also result in abundant

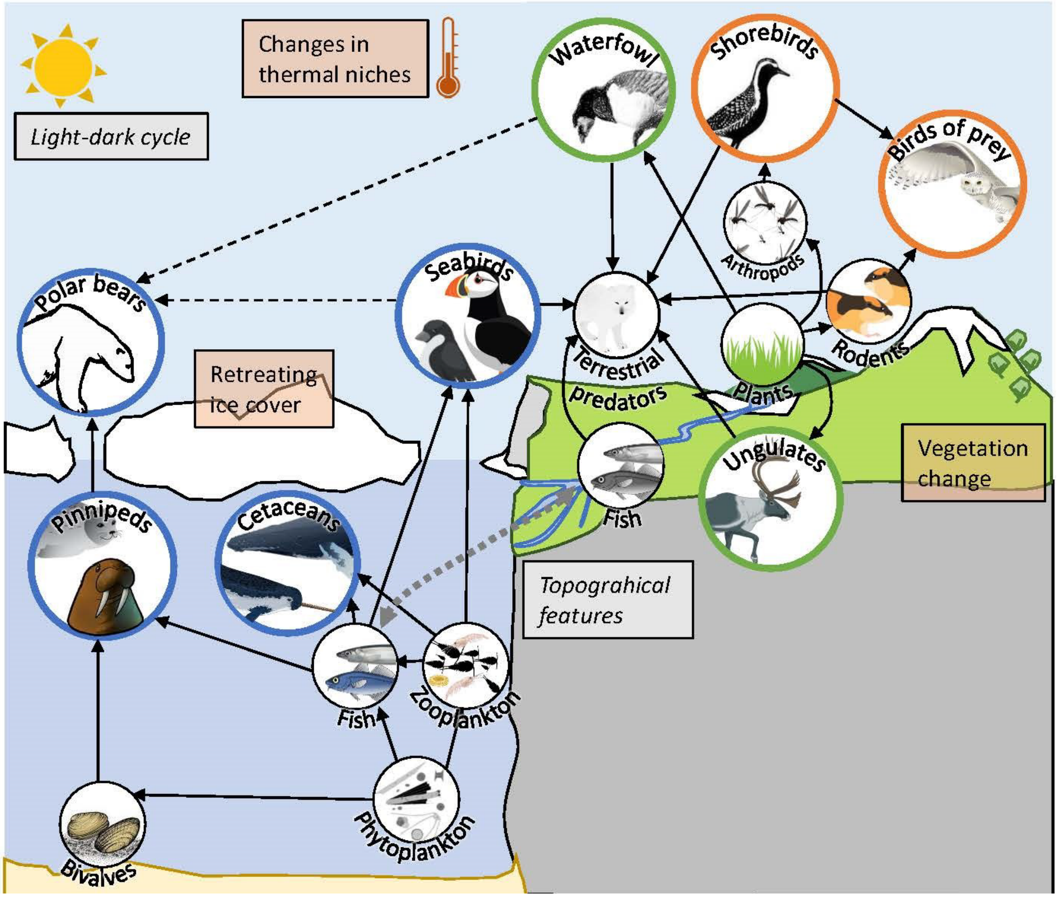

Figure 2.3 Simplified food webs in marine Arctic habitats (left) and terrestrial habitats (right), with the focal groups of marine migrants (blue), terrestrial herbivore migrants (green) and terrestrial carnivores (orange) displayed in circles. Resources, as well as predators which do not display typical migratory behaviour, are displayed in black, smaller circles. Several marine fish species make semelparous migrations to streams and rivers to spawn (as indicated by the grey dashed arrow), and are thus available as resource to both marine and terrestrial animals. In marine habitats, migratory seabirds, cetaceans and pinnipeds are expected to adjust timing of migration and / or distribution with availability of zooplankton, benthic organisms such as bivalves, and fish, which in turn rely on phytoplankton (including ice algae). Polar bears rely on the presence of pack ice to prey on pinnipeds during winter months, but with a warming climate spend more time in terrestrial habitats where they have started to prey on bird's eggs. In terrestrial habitats, herbivores feed on forage plants and time arrival with peaks in nutritional quality of plants. Shorebirds time migration in synchrony with availability of arthropods, and birds of prey rely on availability of rodents for successful reproduction. In turn, terrestrial predators such as Arctic foxes prey on bird's nests, especially in years when cyclic rodent populations are depressed. Besides shifts in phenology of resources, climate warming may also impact habitat suitability via changes in thermal niches, retreating pack ice and vegetation community change (shown in orange boxes). Other aspects such as light-dark cycles and topographical features (such as cliffs which seabirds require for nesting, shown in grey boxes) will not change, potentially constraining distribution shifts of animals.

snow and late melt thereof, which has the potential to largely disrupt reproduction of all terrestrial animals (Schmidt *et al.*, 2019).

In marine environments, ice algae and phytoplankton form the most important primary producers and are the basis of the Arctic marine food web (Post, 2017). Ice algae grow under thinning ice edges, and their phenology is regulated by light (Tedesco *et al.*, 2019). While a warming climate would result in a more permeable ice layer and earlier ice algal blooms may be expected, short day-length at high latitudes limit phenological advancements of ice algae (Tedesco *et al.*, 2019; ,95). The other main primary producer, phytoplankton, blooms occur later in the season at ice edges, regulated by light and nutrient upwelling (Ji *et al.*, 2013). Earlier ice disappearance has caused an advancement in timing of phytoplankton blooms (Kahru *et al.*, 2011) and a decreasing time-lag between ice algae and phytoplankton blooms (Ji *et al.*, 2013), which together form the main food resource for many species of bivalves and zooplankton (Søreide *et al.*, 2010). Zooplankton may suffer from reductions in survival (measured as lower available zooplankton biomass) when they are not able to adjust their phenology in response to advanced phytoplankton blooms (Søreide *et al.*, 2010; Leu *et al.*, 2011; Janout *et al.*, 2016), as well as possibly due to the segregation of ice algae and phytoplankton blooms. Nevertheless, other studies found stable zooplankton biomass following earlier phytoplankton blooms (Dalpadado *et al.*, 2020). Zooplankton is the main food resource for fish species, and both zooplankton and fish are eaten by most baleen whales, pinnipeds and seabirds (Dehn *et al.*, 2007; Wold *et al.*, 2011). Both timing and abundance of zooplankton may affect the abundance and availability of fish species as prey for higher trophic levels. For seabirds and whales, important prey fish species may occur earlier in the season, or decrease in abundance due to phenological mismatches with algal and plankton blooms.

2.3.2 Longer period of resource availability

While a warming climate will advance the timing when resources become available, it can also impact the abundance of resources (Høyen *et al.*, 2021), as well as result in a longer period of availability of resources. Although their nutritional value declines over the season, forage plants are available for herbivorous birds until covered by first snowfall in autumn, which is occurring later in the season in recent years (Box *et al.*, 2019). This is also beneficial for many ungulates, which, despite their ability to find forage plants under shallow layers of snow, cannot deal with deeper layers of snow (Heggberget *et al.*, 2002) or ice crust formation (Tyler, 2010). Terrestrial arthropods may remain active as long as temperatures are above freezing, but their availability to predators could be limited due to a restricted number of generations emerging in one season (Koltz and Culler, 2021) but see (Høye *et al.*, 2020), and Arctic shorebirds are thus unlikely to profit from a longer breeding season through re-nesting (Saalfeld *et al.*, 2021). With increasing temperatures, warming Arctic waters may facilitate longer resource availability, by driving the emergence of a second phytoplankton bloom (Dalpadado *et al.*, 2020; Ardyna *et al.*, 2014) and a second generation of copepods (Weydmann *et al.*, 2018) during autumn.

2.3.3 Northward shifts in suitable habitats and resources

A change in climate is expected to change the habitat suitability for migratory animals as well as for their resources, and both may show northward shifts of their distribution in response (Figure 2.2). First of all, many organisms thrive within a specific ‘thermal niche’ or ‘thermal preference’, and experience fitness reductions outside this niche (Buckley and Kingsolver, 2012; Lesica and McCune, 2004). With a warming climate, the location of this thermal niche and therefore the suitability of habitats is predicted to shift northwards (Sunday *et al.*, 2012; Pearson *et al.*, 2013). This may lead to distribution shifts for endothermic vertebrates, as well as for their food resources, often ectothermic animals or vegetation. Although at high latitudes most endothermic animals live at temperatures well below their thermal maximum and thus have leeway under increasing temperatures (Khaliq *et al.*, 2014; Sunday *et al.*, 2011), habitat suitability of ectothermic organisms is more sensitive to changing temperatures (Buckley and Kingsolver, 2012), and these potentially make larger distribution shifts (Sheldon *et al.*, 2011). At the same time, vegetation communities and thereby distribution of specific plant species appear to change at relatively slow rates (Myers-

Smith *et al.*, 2020; Bjorkman *et al.*, 2020). Such shifts in the distribution of resources will also change habitat suitability for migrants. For example, in marine environments, many fish species are showing northward distribution shifts, changing local community composition of potential prey species for marine predators (Fossheim *et al.*, 2015). At the same time, some fish species from lower latitudes may be unable to find refuge away from predators during the continuous light of polar summer, which may constrain their abundance under certain climate change scenarios (Ljungström *et al.*, 2021).

Some factors of habitat suitability are closely linked to climatic conditions, including the thermal niche and resource distribution as explained above, as well as specific environmental aspects of habitats, such as cover of sea ice as resting platforms for pinnipeds and hunting platforms for polar bears. While climate warming will directly change these aspects of habitat suitability, other aspects are geographically fixed, for example topographical features (e.g. cliffs making up suitable nesting habitat for seabirds) and the duration of the light-dark cycle (which is fixed by latitude and date). Advances in the timing of resource availability and rapid-changing aspects of habitat suitability as a result of climate warming may drive northward distribution shifts of animals, but slow-changing or fixed aspects of habitat suitability may at the same time form constraints for distribution shifts (Ljungström *et al.*, 2021; Huffeldt, 2020). Moreover, such differences in the rate of northward shifts could cause reductions in suitable habitat altogether.

2.4. Shifts in migration timing and distributions

2.4.1 Methods to quantify differences in responses between taxonomic groups

To review whether vertebrates display shifts in migration timing and distributions in response to a warming climate, we searched for relevant papers using the Web of Science database. We used the search term Arctic AND (range shift OR migration timing) AND (bird OR avian OR ungulate OR herbivore OR cetacean OR whale OR beluga OR narwal OR pinniped OR seal OR walrus OR polar bear). This query resulted in 486 papers, from which we only included papers that (1) dealt with Arctic migratory species, (2) reporting on changes in either timing of spring or autumn migration, timing of reproduction or changes in distribution, (3) either as trends over time (as measured over a period of at least 5 years) or (4) in relation to climatic and environmental conditions in the Arctic (as measured over a period of at least 3 years). To determine which species are considered 'Arctic species', we used species lists as provided by the Arctic Biodiversity Assessment (CAFF, 2013), with the exception that we only included bird species for which the majority or complete population breeds in the Arctic. We excluded papers that did not report species-specific results. Eventually this selection resulted in 32 papers. In addition to these papers, we added 35 relevant papers (matching the criteria mentioned above) that we found within reference lists of the 32 selected papers, as well as relevant papers found within the reference lists of two review studies on marine mammals (Kovacs *et al.*, 2011; van Weelden *et al.*, 2021).

For every paper, we recorded (1) the study species and taxonomic group (bird, ungulate, cetacean, pinniped, polar bear), (2) the region where the study was conducted, and (3) whether evidence was reported for shifts in timing of spring migration, reproduction and autumn migration and shifts in summering distribution. For shifts in timing, we considered evidence to be significant shifts in timing over years (considering study periods of at least 5 years) or with changing climatic variables. For shifts in distribution, we considered evidence to include both increases in the number of sightings (but only when evident that this was unrelated to population increase) as well as latitudinal change in observations (Bengtsson *et al.*, 2005). We noted the rate of change in timing of spring and autumn migration (in days per year) when this was reported in studies.

In order to quantify how taxonomic groups differed in responses to changing climatic conditions, we compared the relative number of species per taxonomic group for which shifts in migration and distribution were recorded. We quantified whether shifts in migration timing differed between taxonomic groups by comparing effect sizes of reported shifts in spring and autumn migration. In addition, comparing the number of species and study regions for which we found relevant studies allowed us to quantify how knowledge gaps differed between groups and regions.

2.4.2 Shifts in migration timing

2.4.2.1 Terrestrial and sea birds

Most of the time series available on migration timing of terrestrial birds show no clear advancements in the timing of migration departure from wintering areas (Lameris *et al.*, 2018; Rakhimberdiev *et al.*, 2018; Tombre *et al.*, 2008; Eichhorn *et al.*, 2009; Clausen and Clausen, 2013). However, in the last decades, some species of waterfowl and one shorebird have shown profound shifts in timing of departure (Eichhorn *et al.*, 209; Fox *et al.*, 2014; Nuijten *et al.*, 2020; Conklin *et al.*, 2021; Bauer *et al.*, 2008), but these shifts appear mostly linked to changes in suitable stopover sites along their migratory route. At the same time, many terrestrial bird species have advanced timing of arrival in the Arctic, with studies showing species to adjust migration timing to annual variation in climatic conditions in the Arctic (Lameris *et al.*, 2018; Rakhimberdiev *et al.*, 2018; , Ely *et al.*, 2018; Boelman *et al.*, 2017; Oliver *et al.*, 2018) and some studies also showing clear trends of advanced arrival over time (Rakhimberdiev *et al.*, 2018; , Boyd and Petersen, 2006; Ward *et al.*, 2016; Gunnarsson and Tómasson, 2011). While one study shows stronger shifts in advancement of arrival in short-distance migrants compared to long-distance migrants (Ward *et al.*, 2016), other studies find no clear differences between short- and long-distance migrants (Ely *et al.*, 2018). Along with advancements in migration timing, some terrestrial bird species show advancements in the timing of reproduction (Rakhimberdiev *et al.*, 2018; , Lameris *et al.*, 2019; Liebezeit *et al.*, 2014; Saalfeld and Lanctot, 2017; Smith *et al.*, 2010; Grabowski *et al.*, 2013), but this is not found for all species (Reneerkens *et al.*, 2016; Kwon *et al.*, 2018; Ross *et al.*, 2017), and advancements in reproduction timing can lag behind advancements in arrival (Lameris *et al.*, 2018). Trends in autumn migration are mixed, with some species showing delayed arrival in wintering grounds, associated with higher temperatures at northern summering and staging sites (Nuijten *et al.*, 2020; Lehikoinen and Jaatinen, 2012). Several other species show earlier arrivals of adult birds (Lehikoinen and Jaatinen, 2012; Barshep *et al.*, 2012), possibly explained by disrupted breeding seasons.

In contrast to many terrestrial bird species, less is known about changes in timing of migration in Arctic seabirds. For species for which data are available, advancements in migration timing are relatively small, with the exception of Arctic-breeding guillemots (*Uria* spp.) which have advanced arrival in breeding colonies all over the Arctic (Merkel *et al.*, 2019). A large meta-analysis, that included many Arctic breeding seabirds, showed that seabirds in general have not adjusted their timing of reproduction in response to higher sea-surface temperature (Keogan *et al.*, 2018). In the Arctic, advancements in reproduction phenology over time have been found for surface-feeding species (gulls and tubenoses) in the Pacific ocean but not in the Atlantic ocean, while pursuit-diving species (alcids) showed no trends in either ocean (Descamps *et al.*, 2019). While this may be the general pattern, some pursuit-diving and benthic-feeding species do show advancements in reproduction timing in response to local earlier ice break-up (Love *et al.*, 2010; Gaston *et al.*, 2005; Gaston *et al.*, 2009) and increases in air temperature (Moe *et al.*, 2009). We did not find studies reporting trends in timing of autumn migration in sea birds.

2.4.2.2. Ungulates

A variety of trends on reindeer migration timing emerge from the literature. A delay in spring migration over time was found for reindeer populations on Newfoundland up to the year 2000 (Mahoney and Schaefer, 2002), earlier spring departures but not earlier arrivals were shown for populations in Northern Quebec between 2000 and 2011 (Le Corre *et al.*, 2017) and no trends in departure dates but earlier arrival were found for populations in north-western Canada and Alaska between 2000 and 2017 (Gurarie *et al.*, 2019). It is suggested that reindeer adjust departure dates and travel speed to local as well as large-scale climatic conditions (Gurarie *et al.*, 2019), allowing them to pass through areas just prior to snowmelt (Laforge *et al.*, 2021), which facilitates easier passage over partly frozen soil and ice (Leblond *et al.*, 2015). In addition, by pacing migration speed with local timing of snowmelt, reindeer may be able to optimally time their arrival on the calving grounds to match local dates of snow melt and vegetation green-up (Gurarie *et al.*, 2019; Laforge *et al.*, 2021). As a result, calving date has advanced in several populations of reindeer in response to a warming climate (Davidson *et al.*, 2020). However, large variation exists in the extent to which reindeer appear to be able to keep up their timing of reproduction with the local climate. Domestic reindeer in Northern Finland have been able to advance timing of calving with earlier springs (Paoli *et al.*, 2018), which has benefitted reproductive success (Paoli *et al.*, 2020). On the other hand, reindeer populations in Svalbard and Western Greenland do not seem to advance calving dates with earlier springs (Post and Forchhammer, 2008; Danielsen, 2016), and a mismatch with phenology of local forage plants has resulted in a reduction in reproductive success in Western Greenland (Post and Forchhammer, 2008; Post *et al.*, 2008; Eikelenboom *et al.*, 2021; Kerby and Post, 2013). While longer summer seasons could extend the summer period during which forage plants are available, reindeer have been found to advance autumn migration timing (Mahoney and Schaefer,2002; Le Corre *et al.*, 2017). It is possible that such changes are a response to resource depletion, but it is yet unclear whether this is mainly driven by climate change or population dynamics.

2.4.2.3. Cetaceans

An increasing asynchrony between the arrival of migratory cetacean species and local abundance of prey (due to spatial and temporal shifts) has been predicted (Kovacs and Lydersen, 2008), but long-term data on the timing of migration of Arctic cetacean species is rare, and the few available studies paint a mixed picture (van Weelden *et al.*, 2021). Spring migration phenology shows either no change (beluga whales) or has been delayed (bowhead and grey whale), which could suggest that these species might not keep up with advancing phenology of their prey in the Arctic. In autumn, delays in departure from northern waters have been found for beluga whales, which appears to be a response to later ice formation (Hauser *et al.*, 2017). However, further south along the migration route, migrating baleen whales are observed on autumn migration earlier in recent years (Ramp *et al.*, 2015).

2.4.2.4. Pinnipeds

The seasonal distribution of pinnipeds in the Arctic is heavily influenced by the spatial extent of the sea pack ice, which shows large seasonal and inter-annual variation. Most pinnipeds associate with the ice well before the breeding season, which means that ice regions need to be accessible at the onset of the breeding season and remain stable throughout the breeding period in order to be suitable (Kovacs *et al.*, 2011). Some species (e.g. ringed seals) breed on (more stable) fast-ice, as they have a relatively long nursing period (~ 6 weeks) (Smith and Lydersen, 1991; Smith and Hammill, 1981). In contrast, pinnipeds that rely on floating pack ice such as hooded seals generally have a shorter nursing period. Hooded seals breed several weeks later than harp seals, during the start of the seasonal ice break-up. To combat the effect of drift, their lactation period is extremely short (~ 4 days). Due to the strong association with sea pack ice, Arctic pinnipeds will be highly influenced by climatic changes in temperature. However, currently, little information is available about changes in phenology of pinnipeds in response to increasing temperatures and changes in ice cover (Laidre *et al.*, 2015). We found only one study reporting on shifts in timing in pinnipeds, showing a long-term advancement in the arrival of walrus in their summering range, as observed by local Inuit hunters in the Canadian Arctic (Martinez-Levasseur *et al.*, 2021).

2.4.2.5. Polar bears

Although pinnipeds, the main prey of polar bears, have not been reported to display major shifts in phenology, climate warming is strongly reducing the seasonal availability of pack ice (Castro de la Guardia *et al.*, 2013; Guardia *et al.*, 2017), used by pinnipeds and polar bears as haul-out sites and foraging habitat, respectively. Polar bears time their migration towards terrestrial habitats with the break-up of pack ice in spring (Cherry *et al.*, 2016). As a result, bears have advanced their arrival in terrestrial habitats with earlier ice break-up (Cherry *et al.*, 2013; Guardia *et al.*, 2017), as well as delayed the time when they travel back to the pack ice in winter, which also impacts their condition when entering maternity dens (Derocher *et al.*, 2011). By shifting their migration timing, bears have increased the fasting period in terrestrial habitats during which they have no access to their pinniped prey (Cherry *et al.*, 2013). In addition, due to reduced availability of pack ice, bears often have to travel longer distances on terrestrial habitats and swim larger distances in order to migrate back to the pack ice (Pilfold *et al.*, 2017). Longer fasting periods and higher travelling costs have been shown to cause reductions in population vital rates (Pilfold *et al.*, 2017; Molnár *et al.*, 2020; Pagano *et al.*, 2018).

2.4.3. Changes in winter and summer distributions

2.4.3.1. Terrestrial and marine birds

Northward shifts in wintering distribution of Arctic migratory birds, also named 'short-stopping', have in the past decades been shown for multiple species of Arctic-breeding waterfowl and shorebirds (Nuijten *et al.*, 2020; Maclean *et al.*, 2008; Elmberg *et al.*, 2014; Clausen *et al.*, 2018). For birds wintering in Europe, this mostly translates to shifts in a north-easterly direction up to 13 km/year (as reported for Bewick's swans, Nuijten *et al.*, 2020). Changing energetic requirements and prey availability under different scenarios of future climate are also expected to affect the winter distributions of the five most numerous species of seabirds in the North Atlantic, many of which breed in the Arctic (Clairbaux *et al.*, 2021), but shifts in winter distributions have not yet been shown for these species.

The investigation of shifts in breeding distributions of Arctic species is in its infancy, but theoretical exercises predicting shifts in winter and summer ranges are contributing a basis for forecasting potential changes. Shifts in breeding distribution have been predicted for Arctic-breeding shorebirds (Wauchope *et al.*, 2017) as well as for Arctic seabirds (Clairbaux *et al.*, 2019) given the northward shifts of their prey (Frederiksen *et al.*, 2013). In this way, climate change may result in shifts in migration destinations and even flyways, for example the predicted establishment of wintering populations of little auks (*Alle alle*) in the Pacific, which would facilitate trans-Arctic migrations (Clairbaux *et al.*, 2019). Likewise, Arctic seabirds may also cease migration completely and become year-round residents of the Arctic. Nevertheless, so far there is little evidence that shifts in breeding distribution are already taking place. In part, this is because range shifts are typically picked up in long-term monitoring studies with high spatial coverage (Devictor *et al.*, 2012), which are rare in the Arctic. In Finland, an average northward shifts of 0.8 km/year have been observed in a suite of Arctic bird species (Brommer *et al.*, 2012). A long-term local study in Arctic Russia has revealed a strong decline in densities of typical high-Arctic breeding shorebird species, while species typical for southern tundra habitats have increased (Soloviev *et al.*, 2021).

2.4.3.2. Ungulates

Reindeer have often been considered to display strong site fidelity, especially during the calving season in summer (Ferguson and Elkie, 2004; Schaefer *et al.*, 2005). This idea of site fidelity is under discussion, as reindeer can shift their wintering ranges following overgrazing of pastures (Ferguson and Messier, 2000), and recently, two reindeer herds have started to adjust their calving grounds to annual variation in forage quality, moving further westwards into Alaska in earlier springs (Severson *et al.*, 2021; Gunn *et al.*, 2008). Similarly, moose in Alaska have shifted their summering ranges northwards following shrub encroachment in tundra habitats (Tape *et al.*, 2016).

2.4.3.3. Cetaceans

For cetacean species, it is predicted that the ranges of 88% of all cetaceans may be affected due to global warming (MacLeod, 2009). In accordance, northward shifts in distribution have been revealed for several migratory baleen whales, including typical southern Arctic species (Brower *et al.*, 2018; Storrie *et al.*, 2018). Also short-distance migrants, bowhead whales and beluga whales, are shifting their distributions within the Arctic, likely in response to changes in sea ice cover (Druckenmiller *et al.*, 2018; Heide-Jørgensen *et al.*, 2010). Killer whales (*Orcinus orca*) typically avoid heavy ice concentrations, and are increasingly occurring in the Arctic following reductions in sea ice cover which has opened up movement corridors (Higdon and Ferguson, 2009; Ferguson *et al.*, 2010). The increase of this top predator might in turn influence the distribution of cetaceans and pinnipeds restricted to the Arctic. Sea ice reduction might also provide opportunities for cetacean species to move between the North Pacific and North Atlantic, as is supported by recent reports of grey whales in the Mediterranean Sea (Drake, 2011).

2.4.3.4. Pinnipeds

Most species of pinnipeds restricted to the Arctic are heavily reliant on sea ice for reproduction, moult and resting. During the winter months the sea ice connects to all landmasses surrounding the Arctic Ocean (i.e. Russia, Alaska, Canada, Greenland). However, as a result of climate change, the Arctic sea ice extent, as well as its thickness and age, have decreased (Meier *et al.*, 2014), with the largest changes during the summer months. Currently, the summer sea ice only connects to the shallow waters of Greenland and Northern Canada (Perovich *et al.*, 2020), and, somewhere between 2030 and 2050, it is expected that the Arctic will be completely ice-free during summer (Xu and Si, 2019; IPCC, 2013). Since most arctic pinnipeds are reliant on sea ice and generally feed in shallower (and coastal) waters, the distribution of sea ice relative to the coastal waters will likely have a main impact on the distribution of Arctic pinnipeds. Probably in a result to changing sea ice conditions, range shifts in pupping grounds have been shown for harp seals (Rosing-Asvid, 2008; Stenson *et al.*, 2020), as well as in summering distributions of harp seal, bearded seal and ringed seal around Svalbard, which show a northward latitudinal trend (Bengtsson *et al.*, 2021). In addition, some species (e.g. walrus) are forced to haul-out on land more often in the absence of sea ice, and this may impose additional safety and energy expenditure costs (Jay *et al.*, 2017), also considering density-dependent effects as fewer haul-out sites are available (MacCracken, 2012). The disappearance of sea ice may also provide opportunities for the more temperate seal species that rely on land to rest, moult and reproduce, and these species, like harbour seals, which show an increase in numbers in the Arctic (Bengtsson *et al.*, 2021; Blanchet *et al.*, 2014).

2.4.3.5. Polar bears

Following reductions in pack ice and earlier ice break-up, polar bears have been observed to have shifted their winter ranges northward (Laidre *et al.*, 2018; Laidre *et al.*, 2020; Wilson *et al.*, 2016). Also, polar bears have shifted their maternity dens more often to terrestrial coastal areas rather than on pack ice, in response to absence of stable old ice (Fischbach *et al.*, 2007). In summer, available habitat on pack ice has contracted for several populations of polar bears (Laidre *et al.*, 2018; Wilson *et al.*, 2016), and the number of polar bears spending the summer in terrestrial habitats is increasing

(Prop *et al.*, 2015). In some regions polar bears are able to cope with sea ice loss by making use of coastal seasonal ice (Laidre *et al.*, 2020). However, the increasing distance between wintering habitats on pack ice and terrestrial summering habitats makes polar bears vulnerable to climate change (Pilfold *et al.*, 2017; Fischbach *et al.*, 2007).

2.4.4. Comparisons between species groups

2.4.4.1. Available data

Most of the studies that we found were on shifts in the timing of migration, while much fewer studies were available on changes in distribution (Figure 2.4A). Shifts in timing were more often studied for spring migrations and less often for autumn migrations. While terrestrial and marine birds, with data available for 46 out of 126 species, as well as ungulates and polar bear appeared to be well studied, much less studies were available for cetaceans and pinnipeds. Most studies originated from the American and Canadian Arctic, as well as from the Atlantic Arctic (Greenland and Svalbard) (Figure 2.4B). Much fewer studies were available for the European and West-Russian Arctic, and we found no studies reporting shifts in migration timing and distribution from the East-Russian Arctic.

2.4.4.2. Shifts in timing

Advancements in spring migration timing were reported for many terrestrial and marine birds, as well as for polar bear and some populations of reindeer, but less often for cetaceans and pinnipeds (Figure 2.4A). Although fewer studies were available, polar bears showed stronger advancements in spring migration timing compared to birds (Figure 2.4C). Unexpectedly, some cetacean species and populations of reindeer showed a delay in spring migration timing. Shifts in autumn migration timing also showed mixed results, with both delayed and advanced timing in birds and cetaceans, advancements in ungulates and a delay for one sub-population of polar bears (reported in one study, Figure 2.4C).

2.4.4.3. Shifts in distribution

Despite the low number of studies, it appears that a northward shift in distribution was found for relatively more species of both marine (cetaceans, pinnipeds and polar bear) and terrestrial mammals (ungulates) compared to bird species (Figure 2.4A).

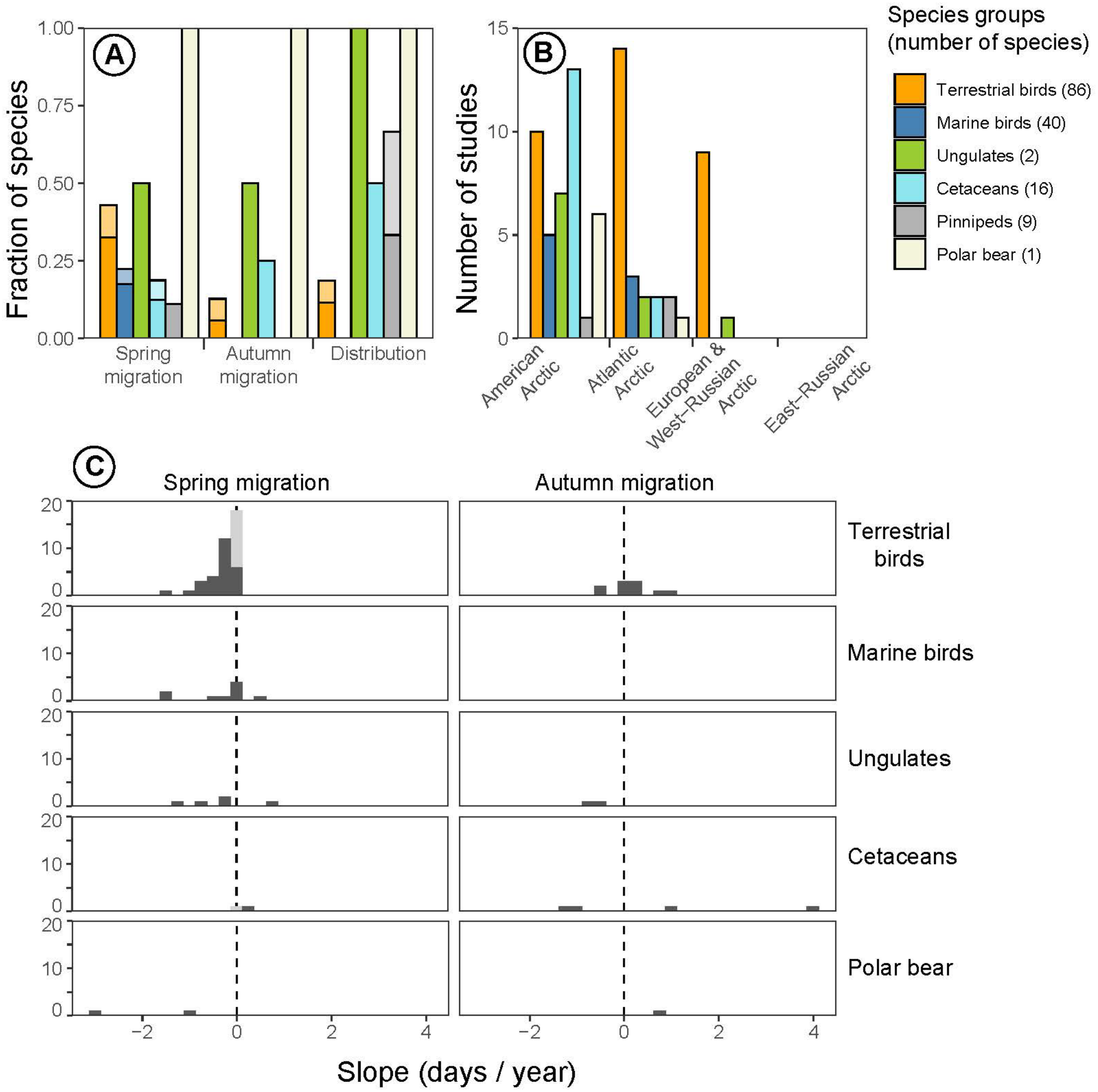

Figure 2.4 (**A**) The fraction of species per taxonomic group for which shifts in spring migration timing, autumn migration timing and distribution have been studied (light-coloured bars) and have been observed (dark-coloured bars). The total number of species for each group is noted in brackets in the legend. (**B**) The number of studies conducted within the four different geographic regions of the Arctic, shown per species group. (**C**) Histograms of reported trends in migration timing (as the slope in days of change over years), shown in bins of 0.25 as black bars. Grey bars show the number of studies reporting no change in migration timing over years without quantifying the slope. Histograms are shown for spring (left) and autumn migrations and for terrestrial birds, sea birds, ungulates, cetaceans and polar bear. For pinnipeds no trends were reported.

2.5 Discussion

2.5.1. Shifts in timing

While many studies highlight the potential for trophic mismatches for Arctic migrants due to their inadequate advancement of timing of arrival on their summering grounds in a warming climate (Post and Forchhammer, 2008; Lameris *et al.*, 2018; Saalfeld *et al.*, 2019), our review shows that there are many examples of advancement of migration timing of especially terrestrial Arctic-breeding birds, as well as for polar bears and some populations of ungulates. Advancements are observed both over long time spans (several decades) and in association with changing environmental conditions, such as increasing temperatures and earlier snowmelt and ice break-up. This suggests that animals adjust their migration timing to locally changing conditions, either as they aim to match reproduction timing with local food abundance, or simply because warmer conditions allow (Nuijten *et al*., 2014; Li *et al.*, 2020), or even force, earlier migrations (Cherry *et al.*, 2013). In comparison to most bird species, polar bears show especially rapid trends in migration timing, matching arrival and departure from pack ice with timing of ice freeze-up and break-up (Cherry *et al.*, 2013). However, not all species show such flexible changes in timing, as shown by observations of multiple species at a single study site, showing advancements in reproduction timing in some species but not for others (Grabowski *et al.*, 2013). Differential responses in migration timing may also occur within species, which is notable in the differential migration timing for different reindeer populations. Whereas we had expected to find stronger shifts in migration timing for short-distance migrants (ungulates, pinnipeds, polar bear and some cetaceans) compared to long-distance migrants (birds and most cetaceans), we find large variation in both short- and long-distance migrants. Whether or not species and populations advance migration timing therefore likely depends on other factors as well, for example (1) variation in the environmental change that species experience, (2) strategies which animals use for reproduction, as well as (3) potential physiological constraints for making changes in the timing of migration. All these factors may differ between species. First, Arctic regions differ in the rate of climate warming and local response in for example advancement of resource abundance (Kwon *et al.*, 2015), date of snowmelt (Lameris *et al.*, 2019) or sea ice dynamics (Hauser *et al.*, 2017), which can drive differentiation in responses in migration timing. Second, flexibility in migration timing may depend on reproduction strategies, depending on whether animals reproduce in the Arctic or southern wintering grounds (Hauser *et al.*, 2017; Ramp *et al.*, 2015), or whether animals rely more on internal energy reserves or on local resources for successful reproduction (Kerby and Post, 2013; Hupp *et al.*, 2018; Ejsmond *et al.*, 2021). Third, Arctic migrants may also be constrained to make advancements in timing by, for example, the time needed for fuel deposition (Lindström *et al.*, 2019; Lameris *et al.*, 2021), little potential to increase travel speed (Schmaljohann and Both, 2017), a lack of relevant cues to time their migration (Kölzsch *et al.*, 2015), or physical barriers during migration, such as earlier ice break-up in rivers (Leblond *et al.*, 2015; Kauffman *et al.*, 2021) or available light (Huffeldt, 2020).

Our review suggests that few species of cetaceans and pinnipeds display shifts in migration timing. Admittedly, very few data appear to be available to test for shifts in timing (Kovacs *et al.*, 2011; Laidre *et al.*, 2015), and it is therefore a possibility that the low number of observed shifts is caused by the difficulty in observing migration timing in these animals. Moreover, a publication bias might exists where studies finding no shifts are less often published. In theory, shifts in timing for marine mammals could be constrained by their relatively low travel speed (Alerstam and Bäckman, 2018), but given the short migration distances of Arctic pinnipeds, this should not form a major constraint for many species. While climate warming changes the trophic interactions between marine mammals and their prey resources, changes in abundance and distribution of resources may have a larger effect on populations than changes in timing. Therefore, as a primary response to a warming climate, marine mammals may be more likely to display shifts in distribution. The same may hold for marine Arctic-breeding birds, for which we find less evidence for shifts in migration timing as compared to terrestrial birds.

2.5.2 Shifts in distribution

Shifts in distribution over the past decades appear to occur more often in marine mammals, which is in confirmation of our hypothesis. For cetaceans, pinnipeds and polar bears, relatively many species display northward distribution shifts, and it is likely that such shifts are a response to changes in sea ice cover (Kovacs *et al.*, 2011) and associated shifts in suitable areas for feeding and reproduction. Most Arctic cetaceans and pinnipeds depend on high food abundance close to the edge of the pack ice, and as a result are expected to shift their ranges with retreating ice cover (Druckenmiller *et al.*, 2018). Moreover, pinnipeds also rely on sea ice as haul-out platforms for reproduction and moult, and their life-histories are strongly tied to sea ice (Stenson *et al.*, 2020). The close association with pack ice is also evident for polar bears, for which a large extent of available data shows a combination of northward shifts in winter, matching changes in pack ice, and shifts to terrestrial habitats during summer. With longer stays in terrestrial habitats, an increasing number of bears is preying on eggs of waterfowl and seabirds (Prop *et al.*, 2015; Hamilton *et al.*, 2017), even though this prey is unlikely to compensate for the increasing periods of fasting under declining sea ice (Dey *et al.*, 2017).

Our review suggests distribution shifts to be less evident for marine and terrestrial bird species. Although this could be explained by the rarity of long-term monitoring programmes with extensive cover, there are also ecological explanations. Marine birds, given observed distribution shifts of their prey (Fossheim *et al.*, 2015), would be expected to show shifts in distribution, similar to marine mammals. Instead, observed shifts in diet show that some species of marine birds may cope with shifts in prey species distribution by preying on different resources (Provencher *et al.*, 2012; Vihtakari *et al.*, 2017; J.Divoky *et al.*, 2015). While such diet shifts may be a possibility for generalist species, like certain cetacean and pinniped species (Yurkowski *et al.*, 2018), species with a more specialized diet (e.g. planktivorous marine birds) may not be able to switch prey, and face potentially severe fitness impacts following shifts in prey species distribution, should they not be able to respond adequately by shifting their own distribution (Dorresteijn *et al.*, 2012; Kitaysky and Golubova, 2000; Kitaysky *et al.*, 2006). In addition, distribution shifts in marine birds are also potentially constrained by available habitat for their breeding colonies at higher latitudes.

For terrestrial bird species, our review suggests relatively few distribution shifts, which is possibly explained by adequate responses in migration timing, as well as no clear evidence for shifts in distribution ranges of prey resources. In addition, several terrestrial bird species have been shown to be rather flexible in choice of habitat within their current range (Kondratyev *et al.*, 2013) and their choice for prey species (Fufachev *et al.*, 2019), which could also reduce the need for distribution shifts. For ungulates, several studies show shifts in calving grounds, presumably to locations with higher food abundance and more suitable habitats. Possibly, terrestrial ungulates possess such adaptive responses to changing conditions, as they continuously need to shift ranges in response to overgrazing events (Kauffman *et al.*, 2021).

Remarkably, in the cases where shifts in distributions are observed, these often show sub-Arctic species extending their range into the Arctic, such as common seals, southern cetacean species, and shorebird species of southern tundra regions (Kovacs *et al.*, 2011; Soloviev *et al.*, 2021; Blanchet *et al.*, 2014). At the same time, shifts in distribution for species within the Arctic are less often observed.

2.5.3 Implications of inadequate shifts in timing and distribution

Many populations of Arctic migratory endothermic vertebrates appear able to shift their timing of migration and their distributions, yet not all species are making such shifts, nor do we know whether such shifts are in fact adequate responses to changes in distribution and abundance of food. As a result from inadequate responses in either the timing of migration and reproduction, or inadequate shifts in distribution, phenological mismatches between the period of offspring growth and timing of peak food abundance may arise. Such mismatches have been shown for several species of Arctic terrestrial birds (Lameris *et al.*, 2018; Saalfeld *et al.*, 2019), marine birds (Gaston *et al.*, 2009) and terrestrial ungulates (Post and Forchhammer, 2008), resulting in reductions in reproductive success. In temperate-breeding migratory songbirds, slow adjustments in migration timing have even been linked to population declines (Saino *et al.*, 2011) but see (Reed *et al.*, 2013). At the same time, not all species which show little change in timing of breeding and reproduction, experience mismatches with reductions in reproductive success (e.g. Reneerkens *et al.*, 2016). While generally, timing of food availability may advance in a warming Arctic, and more rapidly when compared with temperate regions (Post *et al.*, 2018; Zhemchuzhnikov *et al.*, 2021), the rate of warming and the responses of prey species can strongly differ between regions (Kwon *et al.*, 2019). Such regional differences could be an important explanation for the absence of shifts in timing and distribution of migratory species, rather than it reflecting suboptimal behaviour. Fitness consequences for Arctic migratory species may also arise from increased competition with sub-Arctic species, extending their ranges into the Arctic. However, northward shifts in distribution by some species originating from outside the Arctic circle may be constrained by the unique light environment at high latitudes (Ljungström *et al.*, 2021; Huffeldt, 2020), complicating forecasts of future ranges of birds and mammals in the Arctic. As such, it is difficult to predict whether or not migratory populations will suffer from reproductive consequences in a warming climate, based on whether populations are showing shifts in their migratory behaviour and distributions.

2.5.4 Future outlook

This review suggests the potential for many Arctic migratory animals to make shifts in the timing of migration and in their distribution in the Arctic, potentially allowing them to adequately respond to changed resource distribution in a warming Arctic. Yet, our review also highlights potential constraints for animals to make such shifts, which could eventually result in inadequate or no shifts, with possible negative effects on fitness. The potential for animal populations to make shifts in distribution and timing likely relies on the potential for making shifts in migration schedules and strategies, either by individual flexibility (Conklin *et al.*, 2021), or by changes in subsequent generations (Gill *et al.*, 2014). In the latter case, the ability of populations to shift in response to a warming climate is linked to its reproductive success under current conditions.

Our review also suggests a severe lack of data, limiting our ability to identify shifts in timing and distribution. Data are especially lacking for migration timing in cetaceans and pinnipeds, but also in other taxonomic groups potential shifts in timing and distribution have not been studied. It is striking that shifts in spring migration timing have received much more attention than shifts in autumn migration timing (Gallinat *et al.*, 2015), and also there are relatively few studies on shifts in distribution. Our review also suggests strong regional differences in available data, with most data available for Arctic vertebrates in Alaska, Northern Canada, Greenland, Svalbard and Scandinavia, and fewer data for the European and Russian Arctic. The need for long-term data collection over the entire Arctic region is well recognised (Gauthier *et al.*, 2013), as advised in recent reports on population monitoring for marine as well as terrestrial monitoring (CAFF, 2017; Aronsson *et al.*, 2021). Given the rate of climatic changes in the Arctic, it is likely that shifts in timing of migration and distribution of migratory animals will become more prominent. Better monitoring of migratory animals will allow an increased understanding of the responses of these animals to global warming, which may help to identify the possible limitations that restrict adaptations of animals to the globally changing conditions, and the potential impacts on their populations. Such data will be essential for the conservation of migratory species in a warming climate, as well as for the persistence of Indigenous and local human communities in the Arctic, which are often culturally and nutritionally dependent on the presence of migratory vertebrates (Meakin *et al.*, 2014).

Chapter 3

Bottlenose dolphins in The Netherlands come from two sides: across the North Sea and through the English Channel

Abstract. On July 19th 2019 an estimated 20 bottlenose dolphins (*Tursiops truncatus*) were observed in the Marsdiep, a tidal inlet connecting the North Sea and the Dutch Wadden Sea, between Den Helder and the island of Texel. Photographs and video recordings were made and nine individuals were matched with known dolphins from the Moray Firth, NE Scotland. These are the first matches of this east coast of Scotland population outside the UK and Ireland. Subsequent observations of individuals from this group show that at least some of the animals have returned to Scottish waters, while others were photographed in Danish waters. Furthermore, we report on a photo identification match of a solitary bottlenose dolphin between France and The Netherlands. These matches suggest that bottlenose dolphins, in the Netherlands, originate from two different genetically distinct populations: 'Coastal South' and 'Coastal North'. This evidence of previously unknown long-range movements may have important implications for the conservation and management of this species in European waters.

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3.1 Introduction

Bottlenose dolphins *Tursiops truncatus* (Montagu, 1821) were once common in the North Sea, but during the last century numbers have declined (Evans, 1980) and they are now rarely observed here (Reid *et al*., 2006). The exception is a small population of ca. 195 animals on the east coast of Scotland (Wilson *et al*., 1997; Cheney *et al*., 2013). Many historical reports of free ranging animals, stranded individuals and catches show that bottlenose dolphins also used to inhabit Dutch waters (van Bree, 1977; Kompanje, 2001, 2005; Camphuysen and Peet, 2006). In the first half of the 20th century, groups of bottlenose dolphins were observed yearly in spring in the Marsdiep, a tidal inlet connecting the North Sea and the Dutch Wadden Sea, between Den Helder and the island of Texel. Here they foraged on herring migrating to the Zuiderzee to spawn. After the completion of the dam 'Afsluitdijk' in 1932, the Zuiderzee was closed off from the Wadden Sea and the local herring stock collapsed, with the dolphins disappearing soon after. Since 1965 the sightings of dolphins have also decreased in other parts of The Netherlands and bottlenose dolphins are now considered rare visitors (ter Pelkwijk, 1937; Verwey, 1975; Verwey and Wolff, 1981; van Bree, 1977; Kompanje, 2001, 2005; Camphuysen and Peet, 2006). Most reports since then have been of solitary individuals (Addink and Smeenk, 1990; Addink, 1991; van der Ham *et al*., 1992; Camphuysen and Peet, 2006). Most notably is a male identified as 'Dony' (also occasionally named 'Randy'), that stayed in The Netherlands for multiple weeks in November/December 2002. This individual yielded the first photo-identification match of a "foreign" bottlenose dolphin in The Netherlands (Camphuysen and Peet, 2006). He was first observed in Ireland (April 2001), and later in England and Belgium, before entering Dutch waters. Currently (April 2021) he is residing off Brittany, France (Nunny and Simmonds, 2019; Facebook page Dony, 2021). It is suggested that these solitary individuals came as a direct consequence of the decimation of bottlenose dolphins in European waters (Müller and Bossley, 2002), as a dispersing dolphin might not be able to find neighbouring populations and might socialize with people instead (Nunny and Simmonds, 2019).

In contrast, a group of 50-100 bottlenose dolphins was observed in the morning of August 12th 2004, swimming off Huisduinen (Figure 1), along the northwestern coastline of the Dutch mainland, until they entered the Marsdiep (Supplementary Figures S1), all the way to the Afsluitdijk (Leopold, 2004; Zeezoogdieren.org, 2004; Camphuysen and Peet, 2006). The animals returned to the North Sea in several smaller groups in the afternoon and evening and disappeared from view. One month later, on September 9th, a group of approximately 60 animals was seen in the same area (Supplementary Figures S1). Again, the dolphins were first observed in the morning, at 9:30 AM further south, off the Dutch mainland coast (Camperduin), by an experienced seawatcher (*pers. comm.* Nick van der Ham). The animals moved north and were picked up by other seawatchers at Callantsoog and Huisduinen before they entered the Marsdiep at approximately 12:30 PM. Here they swam eastwards up to the Den Helder-Texel ferry track line, where they turned north and returned to the North Sea, following the coastline of Texel (Camphuysen and Peet, 2006; van Bemmelen, 2009). Unfortunately, none of the photographs taken during these two occasions were suitable for photo-identification.

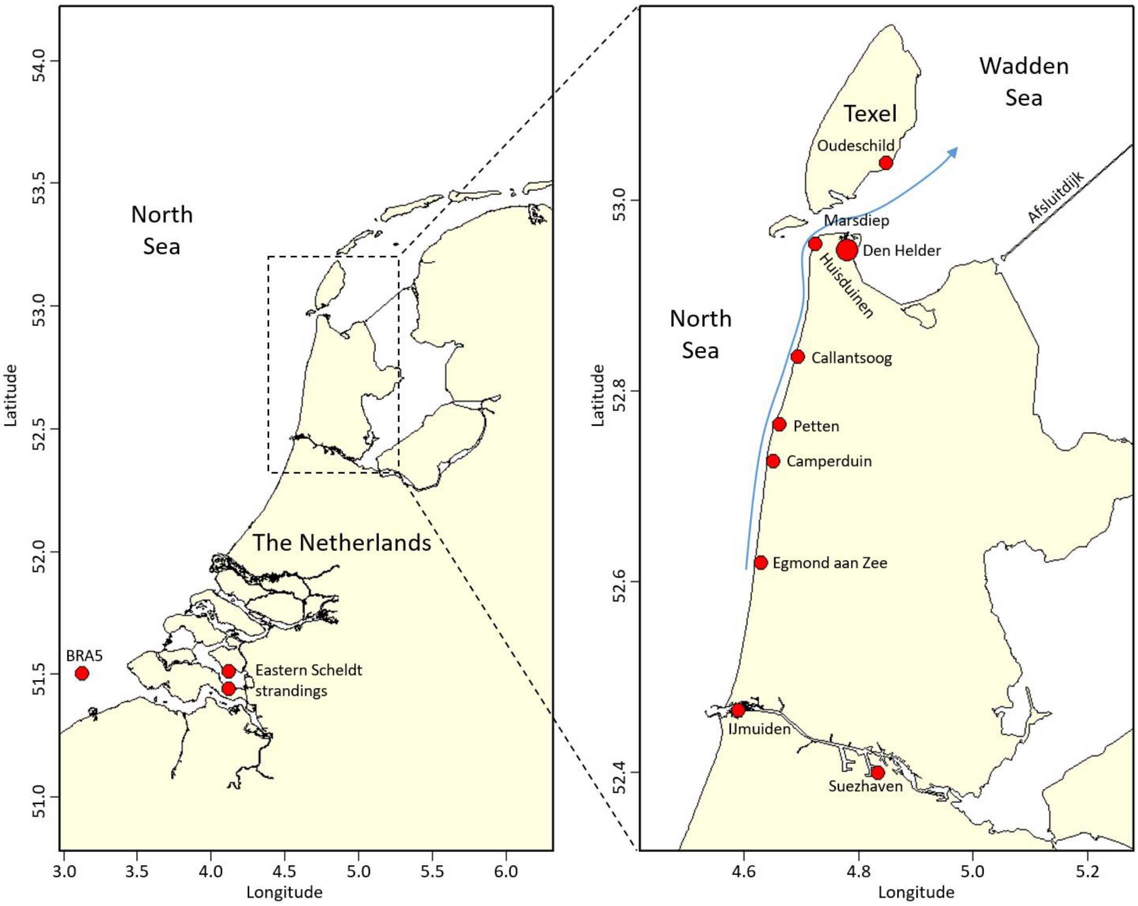

Figure 3.1 Maps of The Netherlands showing the locations mentioned in the main text. *Left panel:* The locations of the two stranded bottlenose dolphins (2007 top and 2013 bottom) in the Eastern Scheldt and the sightings from fishing vessel BRA5 (2014). *Right panel:* Map of the province North-Holland. The arrow depicts the estimated route of the bottlenose dolphins, sighted on July 19th, 2019.

A similarly large group was seen offshore, on October 3rd 2014 near the Dutch/Belgium border (51°30’00”N, 03°07’48”E, Figure 3.1), from the fishing vessel BRA5 (Natuurpunt, 2014). Animals accompanying the ship were videoed, but the image quality did not allow matching.

In this study we report on new sightings and photo-identification matches of bottlenose dolphins in Dutch waters (i.e. the Marsdiep and Amsterdam). Additionally, we present images of two bottlenose dolphins that were stranded in the Netherlands that could not be matched with previously known individuals.

3.2 Materials and Methods

Photographs and videos of bottlenose dolphins in Dutch waters were opportunistically collected, both of stranded (dead) and free ranging individuals. We compared these images manually (i.e. by eye) with photo-identification catalogues and pictures taken by the public, available on the internet, to examine the origins of these Dutch sightings.

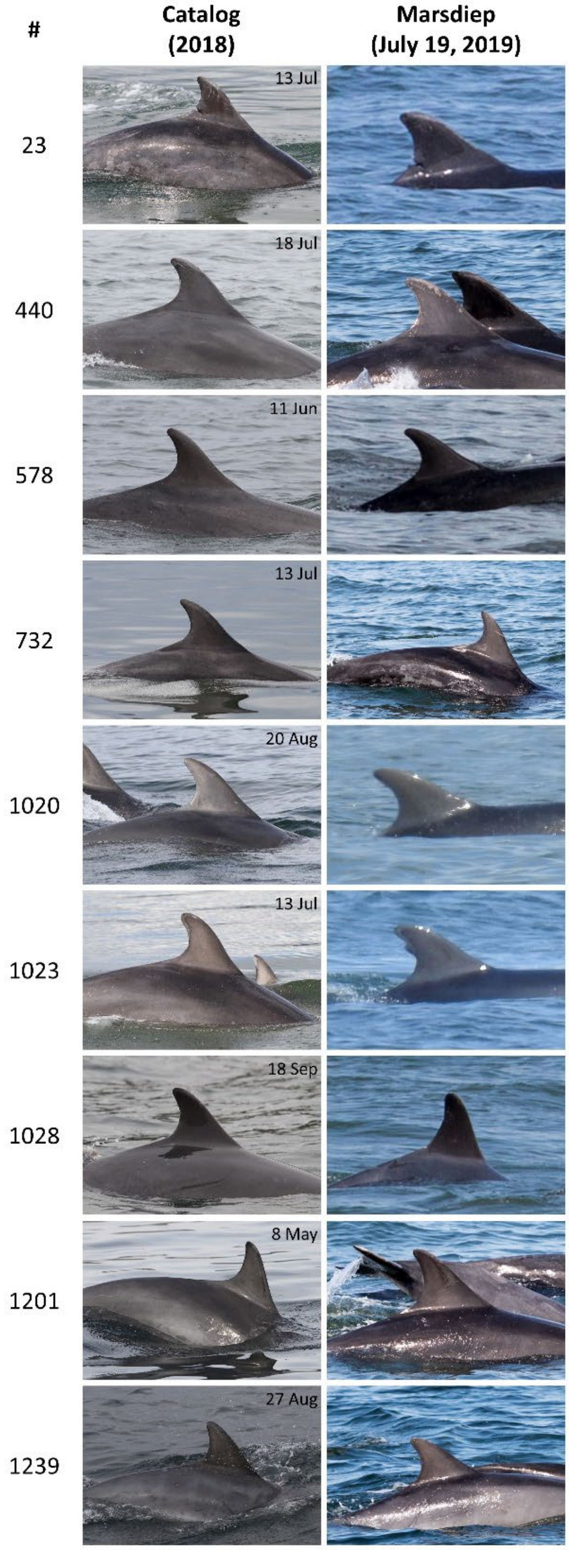

Figure 3.2 Photo identification of the Dutch bottlenose dolphins, sighted on July 19th, 2019. Pictures on the left are from the East Coast Scotland Bottlenose Dolphin Photo-ID Catalogue, pictures on the right are taken in the Marsdiep (by Tobias Brügging, JH and ML). High resolution versions and additional photos and video that were used to identify individuals can be found in Supplementary Figures S2 and Supplementary Video S3.

3.3 Results

3.3.1 Bottlenose dolphins in the Marsdiep

On Friday July 19th 2019, at 5:30 AM, a group of bottlenose dolphins was spotted off Egmond aan Zee (Dutch mainland coast) (Figure 3.1) (*pers. comm.* Jasper Rautenberg). The group travelled north and was observed off Camperduin (*pers. comm.* Bert de Haan and Nick van der Ham) and then photographed off Petten (*pers.comm.* Nils van Duivendijk) later that morning. At 10:32 AM the group swam past Huisduinen (*pers. obs.* JH), 30 km north of the first sighting location. At this point two groups were observed. Within each group, the animals were swimming closely together and both adults and juveniles were present. The first group swam northwards parallel to shore at 500-1000 m and consisted of approximately 10 individuals. The second group was swimming in the same direction, but closer to shore (50-100 m) and consisted of nine individuals. Whenever a boat passed close by, the animals dived longer and appeared to increase their swimming speed. Occasionally the dolphins were lobtailing. The first group continued to move northwards towards Texel, crossing the Marsdiep, and soon disappeared from sight, while the second group followed the coastline eastwards, deeper into the Marsdiep towards the Wadden Sea, where the animals were continuously seen until noon by multiple observers (*pers. obs.* ML). The last sighting was made from the vessel TX 10 at 15:27 PM in the Wadden Sea east off Texel, close to Oudeschild (Figure 3.1).

The first group was too far from shore to collect any images that could be used for photo-identification. The second group however, swam closer to shore and photos (Figure 3.2, Supplementary Figures S2) and video recordings (Supplementary Video S3) were made, both from shore and from seal watching boat 'Het Sop'. These images were compared to the East Coast Scotland Bottlenose Dolphin Photo-Identification Catalogue (Cheney *et al.*, 2014), curated by the University of Aberdeen and the University of St. Andrews. Eight individuals were positively identified, while one other individual was highly likely a match to the same population (Figure 3.2; Table 3.1; Supplementary Figures S2). Matches were made using multiple photographs from the Netherlands (see supplementary information) to individuals observed almost annually by the University of Aberdeen since at least 2006. The adult dolphins were matched using nicks (three dolphins) and/or tooth rakes and skin lesions (six dolphins), and the two juveniles were matched on observed association with their mothers and dorsal fin shape (Table 3.1). The group consisted of an adult and a juvenile male, 6 adult females and 1 juvenile of unknown sex (Table 3.1). None of these dolphins were observed by the University of Aberdeen in the Moray Firth Special Area of Conservation during their approximately weekly photo-identification surveys between May and September 2019, although all the adults had previously been photographed in this area every year since at least 2009.

In June 2020, two of these individuals (#1028 and #440) were observed and photographed in the Moray Firth, providing proof of the animals' return to their normal range after their excursion across the North Sea. However, three other individuals (#23, #578 and #732) were photographed in autumn 2020 on the west coast of Denmark (pers. comm. Carl Kinze). Whether this means that these three individuals stayed in the eastern part of North Sea, or returned to Scotland before traveling to Denmark remains unclear. However, in January 2020 one of these dolphins (#23) was sighted in the Moray Firth by a regular seawatcher familiar with this individual (*pers. comm.* Alan Airey). Unfortunately, this animal was not photographed, and the identification could not be confirmed.

Table 3.1 Overview of bottlenose dolphins photographed in the Marsdiep (The Netherlands) that are matched with the East Coast Scotland Bottlenose Dolphin Photo-ID Catalogue.

#	Name	Sex	Ageclass	Confidence	First seen	Matched using
23	Mischief	Male	Adult	Certain	1989	Multiple nicks
440	Sickle	Female	Adult	Certain	1994	Tooth rake and skin lesions
578	Chewbacca	Female	Adult	Certain	1996	Multiple nicks and skin lesions on body
732	Tall Fin	Female	Adult	Certain	1998	Fin shape and tooth rakes
1023	Sparkle	Female	Adult	Certain	2007	Skin lesions
1028	Lilith	Female	Adult	Certain	2006	Large nick
1020	Idris	Female	Adult	Probable	2007	Fin shape and association with known individuals
1201	Skywalker	Male	Juvenile	Certain	2015	Fin shape and association with mother (#578)
1239	Ruby	Unknown	Juvenile	Certain	2017	Fin shape and association with mother (#1028)

3.3.2 Solitary bottlenose dolphin in Amsterdam

A solitary bottlenose dolphin was observed on Saturday May 2nd 2020, swimming with the sailing vessel ‘Tres Hombres’. The crew first observed the dolphin off France 3 days earlier. The animal followed the ship to The Netherlands, into the Noordzeekanaal (North Sea Canal), passing the sluices in IJmuiden (Figure 3.1), up to the Suezhaven in Amsterdam where the ship docked. The dolphin appeared to be healthy, and was observed defecating. The dolphin stayed with the ship, and detailed photographs could be made. Comparison of the dorsal fin and facial features (Genov *et al*., 2018) with images of known individuals from the French coast showed that this individual is known as ‘Zafar’ (Figure 3.3, Supplementary Figures S2), a male solitary-sociable dolphin that shows a-typical behaviour seeking out human company (Nunny and Simmonds, 2019). This individual might have been observed as early as 2002, but the first confirmed sighting dates back to 2017, when he was seen off Lomener, Brittany, France (Zafar le dauphin blogspot, 2018). Since then, he was repeatedly observed off Brittany, mostly off Brest, until mid-February 2020. On May 3rd the dolphin was escorted back through the sluices, after which he resided in the Seaport of IJmuiden for two days. Here he interacted with various small boats, buoys and people, but was also observed foraging. The last confirmed sighting was from a fishing vessel off Callantsoog on May 5th, which he followed for multiple hours (Observation.org, 2020). Unfortunately, the dolphin was found dead with its tail amputated on May 12th, probably after a ship strike (IJsseldijk *et al*., 2020).

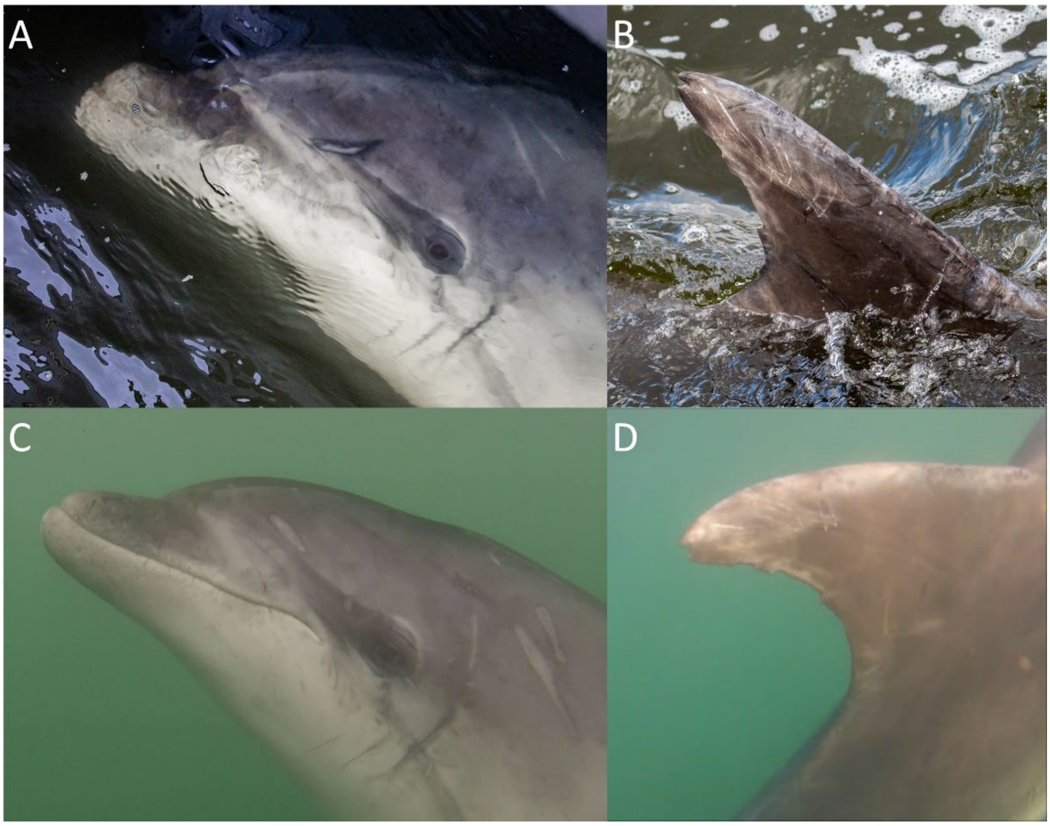

Figure 3.3 Photo identification of the Amsterdam bottlenose dolphin. The top images (A and B) were taken in Amsterdam (May 2nd 2020, by JH), the bottom images (C and D) were taken in France (Facebook page Zafar, 2019).

3.3.3 Recent strandings

Bottlenose dolphin strandings in The Netherlands over the last two decades were examined to look for other potential matches with the east coast of Scotland. An extensive overview of strandings and catches of bottlenose dolphins in the North Sea between 1534 and 2000 can be found in Kompanje (2001, 2005), but these do not show photographs of recent cases that might be matched with dolphins from other regions. Since 2000, 10 new strandings have been reported (Table 3.2). These records mostly concerned single bones, but there were two individuals found dead and photographed in the Eastern Scheldt, both of which were first observed alive in the same area.

Table 3.2 Summary of stranded bottlenose dolphins in The Netherlands since 2000 (Walvisstrandingen, 2020).

Date	Location	Description
September 12, 2007	Eastern Scheldt	Complete animal, see text
November 26, 2008	Wadden Sea, near Ameland	(Sub)fossil skull
April 14, 2012	Vliehors, Vlieland	Left lower jawbone
April 20, 2013	Hors, Texel	Vertebra
June 27, 2013	Krabbendijke (Eastern Scheldt)	Complete animal, see text
August, 2014	Terschelling	Right lower jawbone, 42.5 cm
January 4, 2015	Terschelling	Right lower jawbone
May 13, 2015	Noordwijk	Left lower jawbone, ~40 cm
December 18, 2015	Schiermonnikoog	(Sub)fossil vertebra

The first of these two dolphins was a female (262 cm, 221 kg), found on September 12th 2007 (Figure 3.4), floating in the Eastern Scheldt, between buoys LG10 and LG12 (Figure 3.1). This animal had been observed alive days before stranding in this semi-enclosed tidal bay. A necropsy, performed by Dr Thierry Jauniaux, indicated the cause of death was an infectious disease, specifically lung edema associated with pyemia/septicemia. Stomach content analysis found remains of (amongst others) 12 Atlantic cods *Gadus morhua*, six saithes *Pollachius virens* and two black gobies *Gobius niger*, a locally abundant goby species, indicating that the animal had been feeding locally, until shortly before her death.

A second female (266 cm, 196.5 kg) was found dead in the Eastern Scheldt near Krabbendijke (Figure 3.1) on June 27th 2013 (Figure 3.5), after she had been observed alive in the area since June 18th 2013. The stranded animal had died very recently (the body was still warm) and was necropsied the same day at Utrecht University. The stomach was empty, except for some tiny fish eye lenses and jaws of marine worms, both probably from small secondary prey, suggesting this dolphin had not eaten recently. Parasitic nematodes *Anisakis simplex* found in the fore stomach were still alive. All these findings suggest the animal live stranded following starvation and subsequently died (van Beurden *et al.*, 2015).

Neither of these dolphins from the Eastern Scheldt could be matched to the NE Scotland population, nor with solitary individuals documented online.

Figure 3.4 Bottlenose dolphin, retrieved from the Eastern Scheldt, SW Netherlands, Sept 12th 2007. Photo by Alfons Wijdeveld, provided by EHBZ Zuidwest (Walvisstrandingen, 2020).

3.4. Discussion

The photo-identification matches presented here show that bottlenose dolphins in The Netherlands originate from different locations. The Marsdiep group of 2019 comprised the first photo-identification match of bottlenose dolphins in The Netherlands with the NE Scotland population. Furthermore, this sighting provided the first matches of bottlenose dolphins from the east coast of Scotland population outside the UK and Ireland. The sightings of two individuals (#1028 and #440) from this group in 2020 back in the Moray Firth show that these dolphins made a round trip. Individual #23 may have returned to the Moray Firth before he was re-sighted in Danish waters, although without photographs or video footage this could not be confirmed. It is unknown whether individuals #578 and #732 also returned to the Moray Firth or stayed in eastern parts of the North Sea, before they were re-sighted with #23 in Danish waters. The fate of the other identified individuals is not presently known. Unfortunately, there is no high-resolution imagery available of the bottlenose dolphins sighted in 2004 in the Marsdiep, so their origin remains unknown.

In contrast to the group of dolphins photographed in the Marsdiep in 2019, two solitary bottlenose dolphins may have entered the North Sea from the south. The Amsterdam dolphin of 2020 ('Zafar') was matched with previous sightings off Brittany, which is close to a nearby population residing off Normandy, France, consisting of approximately 420 individuals (Louis *et al*., 2015). The behaviour of 'Zafar' allowed for confirmation that this dolphin entered the North Sea from the South via the English Channel, as he was seen by the crew of the 'Tres Hombres' for three consecutive days as they sailed through the Channel. The dolphin that resided in the SW of The Netherlands in 2002 ('Dony') was first observed in Ireland (Camphuysen and Peet, 2006), close to a genetically distinct population residing in the Shannon Estuary (Mirimin *et al*., 2011). It is likely that 'Dony' entered the North Sea via the English Channel as well. The two other solitary dolphins, observed and later found dead in the SW of The Netherlands in 2007 and 2013, did not match with any individuals from the east coast of Scotland population. Comparisons were also made with pictures of solitary individuals and groups sighted along the Belgium coast (Haelters and Kerckhof, 2010; Haelters *et al*., 2018), but no match could be established.

Figure 3.5 Bottlenose dolphin stranded near Krabbendijke, Eastern Scheldt, SW Netherlands, June 27th 2013. Photos by Liliane Solé (Walvisstrandingen, 2020).

Based on the genetic population structure, the North-East Atlantic coastal bottlenose dolphin ecotype can be divided in two populations, a 'Coastal South' (comprising the English Channel, Arcachon estuary and South Galicia resident groups) and a 'Coastal North' population (comprising the UK and Ireland resident or mobile coastal groups) (Louis *et al*., 2014). It is currently unclear to which populations 'Zafar', 'Dony' and the two stranded individuals belong, but this can potentially be resolved by future genetic analysis.

The results presented here could only be collected due to the (opportunistic) collaboration between land based 'seawatchers', observers at sea and marine scientists, augmented by public outreach in (social) media. This is indicative of the importance of long-term research and photo-identification catalogues such as the East Coast Scotland Bottlenose Dolphin Photo-Identification Catalogue, and also of publicly available platforms such as Observation.org (2020).

Small coastal populations that are relatively isolated are vulnerable to extinction (Louis *et al*., 2014). Already a population of North Sea bottlenose dolphins became extinct, namely the genetically distinct population in the Humber Estuary, East England (Nichols *et al.,* 2007). The bottlenose dolphins that visited the Marsdiep/Zuiderzee seasonally have disappeared from that area as well. As it remains unclear whether these animals were genetically differentiated from neighbouring populations, it is unknown whether they changed their distribution or that this population became extinct as well.

In Europe the there are two key conservation measures for bottlenose dolphins. Firstly, the designation of Special Areas of Conservation (SAC) under Annex II of the EU Habitats Directive (92/43/EEC), although the use of these static protection measures for mobile species has been debated (Hooker *et al*., 2011; Wilson, 2016). Secondly, bottlenose dolphins are European Protected

Species under Annex IV which is dynamic and protects bottlenose dolphins “across their entire natural range” within the EU, although unlike Annex II, this does not provide habitat protection. In Scotland, following EU exit, the Conservation (Natural Habitats, etc.) Regulations 1994 (as amended) continues to deliver these two conservation measures for territorial waters and provides that the population of bottlenose dolphins that use the Moray Firth SAC are protected across their known Scottish range. However, whether this same level of protection extends internationally is debatable, especially in areas this population was not known to frequent. The dolphins in Normandy live in an “Area of Special Interest.” that is being upgraded into a marine protected area, under the IUCN (category V: “protected seascape”) (Louis *et al*., 2015) and is being listed under Annex II of the Habitats Directive.

While movements of individual or groups of bottlenose dolphins outside their known range may facilitate gene flow between isolated populations, there is also the risk that individuals, from these already small, vulnerable populations (Louis *et al*., 2014) move into areas with different levels of protection. Evidence of long-range movements and/or confirmed presence in an area is required to ensure the correct implementation of existing EU conservation and management initiatives by member states to protect both individuals and their habitats. This previously unobserved connectivity of bottlenose dolphins between territorial waters exposes these individuals to widespread and persistent threats such as bycatch and anthropogenic noise (Nelms *et al*., 2021), highlighting the need for adaptive and integrated conservation and management of these mobile cetaceans.

Chapter 4

Counting using deep learning regression gives value to ecological surveys

Abstract. Many ecological studies rely on count data and involve manual counting of objects of interest, which is time-consuming and especially disadvantageous when time in the field or lab is limited. However, an increasing number of works uses digital imagery, which opens opportunities to automatise counting tasks. In this study, we use machine learning to automate counting objects of interest without the need to label individual objects. By leveraging already existing image-level annotations, this approach can also give value to historical data that were collected and annotated over longer time series (typical for many ecological studies), without the aim of deep learning applications. We demonstrate deep learning regression on two fundamentally different counting tasks: (i) daily growth rings from microscopic images of fish otolith (i.e., hearing stone) and (ii) hauled out seals from highly variable aerial imagery. In the otolith images, our deep learning-based regressor yields an *RMSE* of 3.40 dayrings and an R^2 of 0.92. Initial performance in the seal images is lower (*RMSE* of 23.46 seals and R^2 of 0.72), which can be attributed to a lack of images with a high number of seals in the initial training set, compared to the test set. We then show how to improve performance substantially (*RMSE* of 19.03 seals and R^2 of 0.77) by carefully selecting and relabelling just 100 additional training images based on initial model prediction discrepancy. The regression-based approach used here returns accurate counts (R^2 of 0.92 and 0.77 for the rings and seals, respectively), directly usable in ecological research.

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4.1 Introduction

Ecological studies aim to unravel the interactions between organisms and their environment at various spatial scales. In order to quantify these intricate relationships, many ecological studies rely on count data: for instance, during animal surveys, individuals are counted to estimate and monitor population size (Buckland *et al.*, 2001; Brasseur *et al.*, 2018) or to predict the spatial distribution of animals (Matthiopoulos *et al.*, 2020). On smaller scales, counting physical traits is widely used in, for example, plant phenotyping, where the number of leaves of a plant is a key trait to describe development and growth (Walter and Schurr, 1999; Dobrescu *et al.*, 2017). The usage of count data in ecology is also common on microscopic scales, for example to estimate the age of fish by counting daily growth rings that are visible in otoliths (i.e., hearing stones) (Poiesz *et al.*, 2019; Poiesz *et al.*, 2020).

Irrespective of the scale, counting objects of interest can be tedious and time-consuming, especially when objects occur in large numbers and/or densities (e.g., wildlife that clusters in colonies; Cremer *et al.*, 2017), when they overlap (e.g., leaves of plants; Walter and Schurr, 1999; Dobrescu *et al.*, 2017), or when they are less well-defined and cryptic (e.g., otolith rings; Poiesz *et al.*, 2019). Historically, many of these traits were counted directly by eye. Later, objects of interest were photographed, which allowed for optimisation of the time in the field (or lab) and repeatability of the counts. Nowadays, many studies increasingly take advantage of digital photography, allowing for more efficient ways of archiving the data. Crucially, these archived images can now potentially be used for digital processing and automated counting.

To this end, recent ecological studies have shown promising potential of using computer vision to count objects of interest from digital imagery (Weinstein, 2018; Christin *et al.*, 2019): they employ Machine Learning (ML) models, which are trained on a set of manually annotated (labelled) images to learn to recognise patterns (e.g., colours and shapes), and eventually objects, in those training images. Once trained, these ML models can be used to automatically recognize similar patterns in new images and perform tasks like species classification, animal detection, and more (Thessen, 2016). Most successful ML models belong to the family of Deep Learning (DL) (Schmidhuber, 2015), in particular Convolutional Neural Networks (CNNs) (LeCun *et al.*, 2015).

Most ecological studies that use computer vision for counting apply CNNs designed for object detection (Eikelboom *et al.*, 2019; Kellenberger *et al.*, 2018; Corcoran *et al.*, 2019). These object detectors are trained on images in which every object of interest is annotated individually, most commonly by a bounding box drawn around the object, or a location point at its centre. Alternatively, objects of interest can be counted using detectors based on image segmentation (Zabawa *et al.*, 2020), which require even more extensive annotations, as every pixel in the image must be labelled. Annotating training images for object detection and image segmentation can therefore be labour-intensive, especially for images where object counts are high. Hence, this could potentially undermine the time (and cost) reduction advantage promised by ML models in the first place.

An alternative is to instead annotate training images with a single value that represents the number of objects in an image. These image-level annotations pose significantly reduced annotation time and can directly be used to train regression-based CNNs. Perhaps more importantly, image-level counts are an often-used annotation format in ecological studies, for example in cases where objects are manually counted from digital imagery over longer time series. Furthermore, image-level annotations provide a viable solution for scenarios that are complicated to annotate otherwise, such as for overlapping objects (Dobrescu *et al.*, 2017), complex and atypically shaped objects like concentric rings (Moen *et al.*, 2018), or continuous variables like an individual's size or age (Vabø *et al.*, 2021).

In this study we highlight the value of regression-based CNNs for ecological studies. We present a relatively lightweight DL model for counting objects in digital imagery and evaluate it on two fundamentally different real-world datasets, that were originally collected without the aim of training DL models. The first dataset consists of microscopic images of plaice (*Pleuronectes platessa*) otoliths (i.e., hearing stones) in which concentric rings are visible. These rings represent daily growth layers and are used to estimate the age of the fish to reconstruct egg and larval drift and calculate the contribution of various spawning grounds to different settling areas (Poiesz *et al.*, 2019; Poiesz *et al.*, 2020). Plaice eggs and larvae are transported from their North Sea spawning grounds towards the coast of the North Sea and into the Wadden Sea (pelagic phase), where they settle (benthic phase). The transition of the pelagic phase to the benthic phase is visible in the otoliths. For this application, only the post-settlement benthic phase growth rings (visible directly after the pelagic phase centre) are counted. The already existing image-level annotations in this dataset are of high quality and are directly usable for DL applications.

The second dataset consists of aerial images of grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) hauled out on land, which are collected from an aircraft using a hand-held camera during annual surveys monitoring population size and distribution (Cremer *et al.*, 2017). These images are highly variable in light conditions, distance towards the seals, focal length and angle of view. For this second dataset, some of the existing image-level annotations were not directly usable for DL applications (see "Methods" section). Instead of recounting the seals and correcting the annotations for all images in this dataset, we propose a multi-step model building approach to handle scenarios where the quality of existing image-level annotations is insufficient to train a CNN. This approach can also be used to adapt the CNN to dataset variations that appear over time or with new acquisitions conditions.

These two real-world applications show that regression-based CNNs have the potential to greatly facilitate counting tasks in ecology. They allow researchers to reassign valuable resources and scale up their surveying effort, while potentially leveraging existing image-level annotations from archived datasets directly for the automation of counting.

4.2 Results

For the results reported in this section, we used a pre-trained ResNet-18 CNN (He *et al.*, 2016) and modified it for the task of regression. After various experiments with other architectures and hyperparameters (Supplementary Material S2), we found that this relatively lightweight (i.e., shallow) ResNet-18, trained with a Huber loss function (Girshick, 2015) and with the largest possible batch size (limited by hardware, n = 84 and n = 100 images for the otolith and seal application, respectively) gave the best performance on the validation set, for both the seal and otolith ring counting application. Details on the CNN architecture selection and training are provided in the "Methods" section.

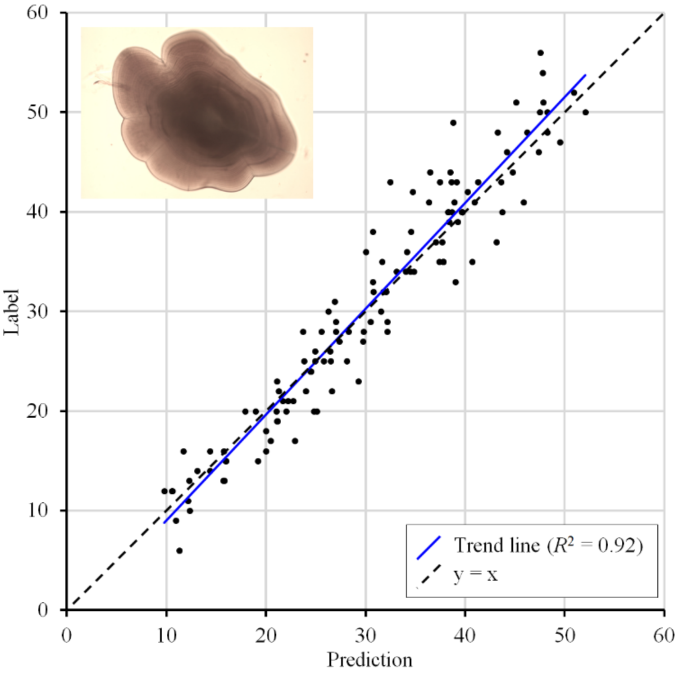

Figure 4.1 Numerical results on the otolith test set (*n* = 120), where the labels (i.e., manual counts of post-settlement growth rings) are plotted against the predicted counts. The dotted line corresponds to the optimum *y* = *x*.

4.2.1 Otolith daily growth rings from microscopic images

For the otolith growth ring counting application, the regression CNN was trained on 3465 microscopic images of otoliths. The results are provided in Figure 4.1. Here, the predicted counts on the randomly selected test set (n = 120) are plotted against the labels (i.e., the manual counts of the post-settlement growth rings). The CNN achieved an R^2 of 0.92, an *RMSE* of 3.40 day-rings and an *MAE* of 2.60 day-rings (Table 4.1), which corresponds to an average error of 9.9%.

4.2.2 Hauled out seals from aerial images

For the seal counting application, the existing image-level annotations were of insufficient quality (see "Methods" section) and manual recounting was required before training the CNN. Instead of recounting all the seals and correcting the annotations for all 11,087 aerial images in the main dataset, we applied a multi-step model building approach. First, two smaller subsets from the main dataset were selected, recounted and used for (i) a stratified random test set (n = 100) and for (ii) training/validation (named 'seal subset 1', n = 787) (see "Methods" section). Unlike the stratified random test set (which reflects the full distribution of available annotations from the main dataset), the images in 'seal subset 1' were selected (visually) for their high quality, which led to an under-representation of images with a high number of seals (which were generally of poorer quality). This first step greatly reduced the number of images that needed to be recounted and relabelled.

Table 4.1 Numerical performance of the proposed method on the randomly selected test sets for both applications. The performance of the seal counting application increased after fine-tuning the Step 1 model using 'seal subset 2' (Step 2 model).

	Otolith Rings	**Seals**	
		Step 1 model	*Step 2 model*
R^2	0.92	0.72	0.77
RMSE	3.40	23.46	19.03
MAE	2.60	10.47	8.14

Figure 4.2 (open dots, panels A and B) illustrates the predicted counts versus the real counts of the resulting model. This Step 1 model achieved an R^2 of 0.72, an *RMSE* of 23.46 seals and an *MAE* of 10.47 seals on the seal test set (Table 4.1). The next step allowed us to focus on images where the CNN was most incorrect. Here, the Step 1 model was used to predict counts on the 10,200 remaining images from the main dataset (that still included noisy labels). To train the model further, the images from the main dataset in which the number of seals was most overestimated (n = 50) and most underestimated (n = 50) with respect to the original (noisy) labels were selected ('seal subset 2'), manually recounted and relabelled and used to supplement 'seal subset 1'. By further tuning the model using this extended training/validation set, the performance on the test set improved (Figure 4.2, solid dots, panel A and C), with the model achieving an R^2 of 0.77, an *RMSE* of 19.03 seals and an *MAE* of 8.14 seals (Table 4.1). This can be attributed mostly to improved predictions for images with a higher number of seals. Experiments with a random sampling on the whole distribution of labels (i.e., 787 images randomly selected from 'seal subset 1' and 'seal subset 2' combined, including images with a high number of seals) did not lead to better performance of the Step 1 model (see Supplementary S4). Thus, the two-step strategy allowed us to significantly improve the model performance on the seals with only 100 images to be reannotated, reducing labelling efforts to a minimum.

In the test set, a total of 3,300 seals were annotated. With our multi-step approach, the predicted total number of seals on the test set increased from 2,372 (71.9% of the total) to 2,986 (90.5%) for the Step 1 and Step 2 model, respectively.

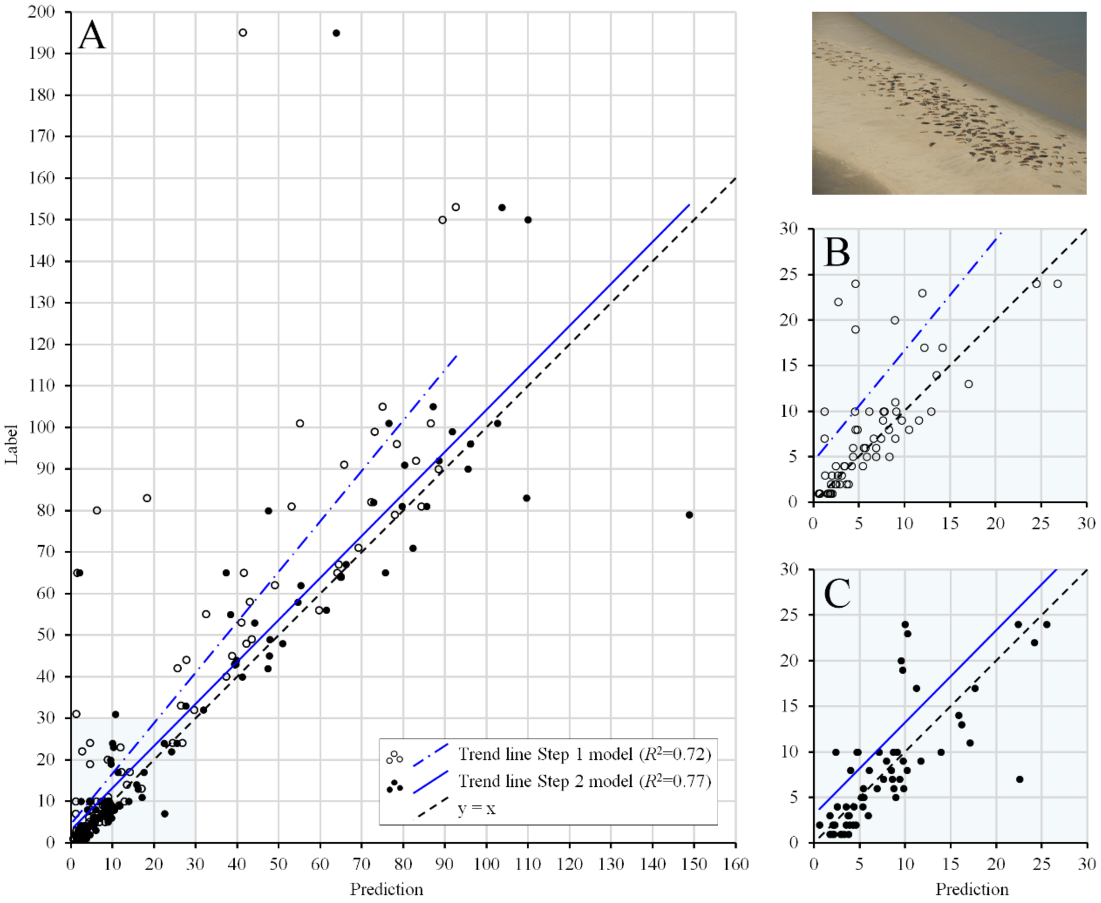

Figure 4.2 Numerical results on the seal test set (n = 100), where the labels (i.e., the manual counts of hauled-out seals) are plotted against the predicted counts. The black dotted lines resemble $y = x$. **(A)** The accuracy of the model trained on 'seal subset 1' (white dots) strongly improved after fine-tuning using training subset 2 (black dots). **(B,C)** Zoomed in (range 0-30) on predicted counts made by the Step 1 model **(B)** and the Step 2 model **(C)**.

4.2.3 Visualising counts

Class activation maps (CAM) (Zhou *et al.*, 2016; Howard and Gugger, 2020) of images from the test sets were used to further examine model performance. These heatmaps represent the regions of the original image that contributed the most to the final prediction of the CNN. The heatmaps of the otolith images (Figure 4.3) were less informative than those of the the seal images. However, they illustrate that areas with more contrasting post-settlement rings were highlighted, while the accessory growth centre (containing pre-settlement growth rings that are not targeted by this application) did not seem to contribute to the prediction (i.e., it remained darker). This underlines that the model is indeed focusing on the task of counting post-settlement growth rings.

For most seal images, the heatmaps show that the regions containing seals contributed the most to the final prediction. Unlike the cryptic concentric otolith rings, seals are clearly picked up by the model, according to the heatmaps (Figure 4.4).

4.3 Discussion

The regression-based CNN presented here performed well when trained on the two fundamentally different datasets. This was achieved without making any modifications to the architecture of the CNN between the two cases, except for training hyperparameters like the learning rate and number of epochs (see "Methods" section). By automating the counting tasks, the processing time of newly acquired images is dramatically reduced: processing 100 images using our trained CNN takes less than a minute, while manual processing the same amount of images is estimated to require at least one hour for the seals and three hours for the otoliths.

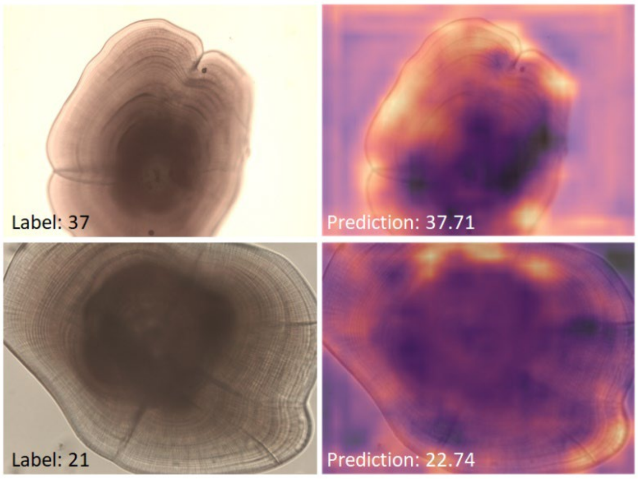

Figure 4.3 Examples of images (left) and CAMs (right), with good performance from the ring test set.

The accuracies reported here are directly usable in ecological research. For harbour seals, a correction factor of 0.68 is routinely used to extrapolate the survey counts to a population size estimate (Ries *et al.*, 1998). The 95% confidence interval of this correction factor is [0.47, 0.85]. In other words, the uncertainty in the population size estimate is minus 21% or plus 17%, which is substantially larger than the 9.5% underestimate in the total predicted counts of our Step 2 model. For the ring counting application, a coefficient of variation between multiple human experts was not available for daily growth rings of plaice. However, these are reported for yearly growth rings of Greenland halibut as 12% (Albert *et al.*, 2008) and 16.3% (Albert, 2016), which is higher than the reported 9.9% average error obtained by our deep counting regression approach.

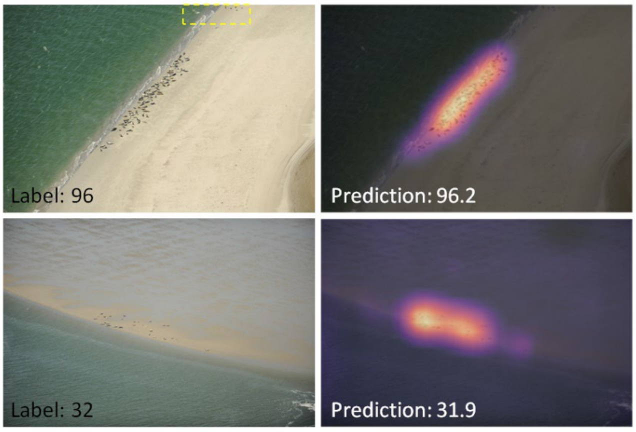

Figure 4.4 Examples of images (left) and CAMs (right), with good performance from the seal test set. Notice that in the top example some birds are visible (yellow dotted line), which are not counted by the model, which has specialised on seals.

The two datasets feature different challenges regarding both the quality of the existing annotations and the task complexity. In the case of the otoliths, the existing annotations were of good quality and could be used directly to train the model. These image-level annotations provide a solution to label the complex concentric growth rings, which would be extremely difficult to annotate using other approaches, such as bounding boxes. A DL regression-based approach was applied in previous research to count otolith growth rings (Moen *et al.*, 2018), which achieved a higher accuracy on their test-set (*MSE* of 2.99). However, the tasks considered in that study were radically different from ours: in their paper, Moen and colleagues (Moen *et al.*, 2018) considered year-rings, which are less cryptic than the post settlement day rings considered in this paper. Furthermore, our model was trained with fewer images (n = 3,585 instead of n = 8,875), to make predictions on a wider range of counts (1 to 63 day-rings instead of 1 to 26 year-rings). Finally, we evaluated the performance using a stratified random test set, which covers the ensemble of the distribution of possible values, while Moen and colleagues used a non-stratified test set, therefore reducing the number of occurrences of rare out-of-distribution cases in the test set.

In the case of the seals, the counting task was complex due to the high variability of the images (e.g., lighting conditions, distance from the seals and angle of view). Additionally, some of the existing count labels were not directly usable for training a CNN (see "Methods" section). However, this provided an opportunity to demonstrate the use of an iterative approach, in which the required re-annotation efforts could be minimized and focused on images where the model performed poorly. The CNN was first trained using only a subset containing recounted high-quality images ('seal subset 1'). As is common among DL applications, the resulting Step 1 model performed relatively poorly when it needed to make predictions that fell outside the range of the training images. This was the case for images in which a high number of seals were visible and/or when the seals appeared smaller (i.e., were photographed from a larger distance or a smaller focal length was used). The poor performance on these types of images could be attributed to 'seal subset 1' containing only images with clearly visible seals, ranging from zero to 99 individuals (see "Methods" section). By using the Step 1 model predictions to guide the selection of images that need to be reviewed, a relatively small number of images ('seal subset 2') was selected from the remaining images in the main database, to supplement 'seal subset 1'. This multi-step approach allows to focus on images with a large potential for improvement for the Step 2 model: many of the images in 'seal subset 2' contained a high number of seals and/or seals that appeared smaller. This approach can therefore also be used to cope with dataset variations that appear over time or with new acquisitions conditions. The high variability in the seal dataset (i.e., distance towards seals, angle of view and zoom level) suggests that a regression-based approach based on this data can also provide solutions for scenarios where the objects of interest move through a three-dimensional space (e.g., flocks of birds, schools of fish), provided that the model is trained with a wide variety of input data covering the expected variations.

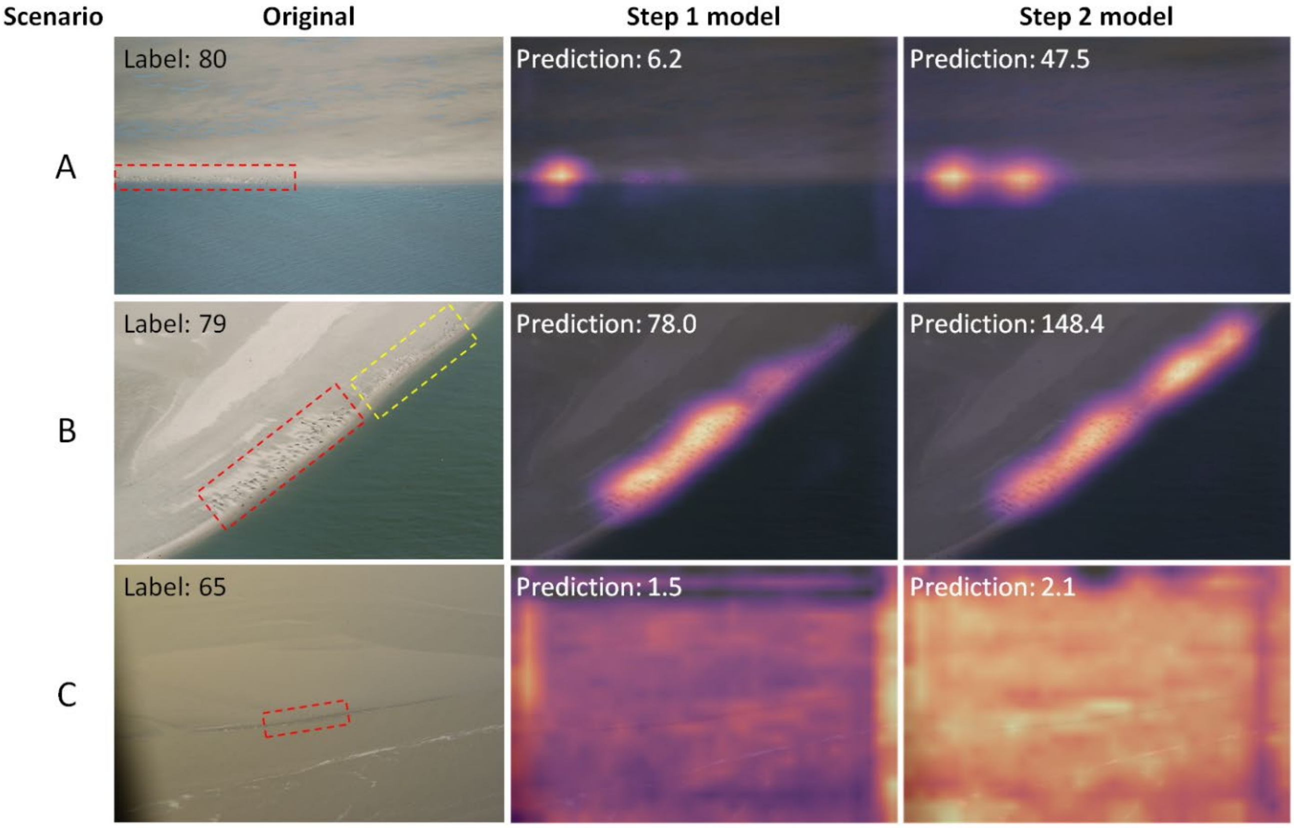

Figure 4.5 Examples of CAMs for cases with unsatisfactory performance. The first column shows the unedited aerial images, where the red dotted line marks the area where the seals are visible. The second and third columns show the heatmaps when predictions are made using the Step 1 and Step 2 model, respectively. For case (A) (small seals) the performance increased, but is still unsatisfactory, as seals remain only partially detected. For case (B) the performance decreased as birds (yellow dotted line) start to contribute to the predictions, while for case (C) (blurry and extremely small seals) the performance was poor for both models.

In contrast with an object detection approach, it is not possible to evaluate the predicted location of single objects in our regression-based approach, as the predictions are given as image-level counts. However, by using CAMs as presented here, model decisions can be visualised and used to evaluate the model performance in more detail. In case of the seals, these heatmaps were used to further compare the performance of the Step 1 and Step 2 model on the test set. The Step 2 model generally performed better, especially for images where seals appeared smaller (e.g., Figure 4.5, case A). For some images however, the model predictions deteriorated. This was for instance the case for an image with birds presents adjacent to the seals, which contributed to the predicted counts for the Step 2 model (Figure 4.5, case B). For some images that were particularly difficult (e.g., due to blur or extremely small seals), the Step 2 model remained unable to count seals adequately (Figure 4.5, case C).

For future applications, automated counts based on the regression approach presented here could potentially be further improved by changing the survey design to have lower variability in the images. In the case of the seals for instance, this could be obtained by photographing the seals from a more constant distance with a single focal length, although in practice this might be challenging. For existing data sets, the model could also deliberately be exposed to more appearance variability. This could for instance be done by resorting to un- or semi-supervised domain adaptation routines

(Wang and Deng, 2018). This requires no or only a few extra annotated images but result in more robustness of the model to the appearance variations inherent in the data. Alternatively, in cases such as the seals, where many images remain unused due to noisy labels, the iterative approach presented in this study could be repeated, which is expected to further improve the performance of the model.

In many computer vision disciplines, regression-based CNNs similar to the one employed here are commonly used for counting tasks, especially when the objects of interest occur in high densities and high numbers, such as human crowds (Ryan *et al.*, 2015; Sindagi and Patel, 2018) or buildings (Lobry and Tuia, 2019). They have also been used in some ecological applications, particularly when the objects of interest are hard to annotate using bounding boxes, for instance in the case of overlapping plant leaves (Dobrescu *et al.*, 2017; Jiang and Li, 2020; Li *et al.*, 2020). Wildlife counting is a domain that is typically addressed with spatially explicit object detection approaches (Eikelboom *et al.*, 2019; Kellenberger *et al.*, 2018). Few other works have addressed this task using regression-based CNNs (Kellenberger *et al.*, 2019; Marsden *et al.*, 2018), but they either had no explicit focus on wildlife detection (Marsden *et al.*, 2018) or used it to approximate spatial locations (Kellenberger *et al.*, 2019). Nonetheless, proceeding with a regression approach permits to process surveys where only global counts are provided, rather than precise annotations of individuals that would be required by object detection approaches. But even in the presence of individual annotations, the regression approach remains competitive in terms of final counts: when compared to a traditional deep object detection approach (Faster R-CNN; Ren *et al.*, 2015) on a manually annotated subset of the seals dataset, our regression approach remained more accurate (details in Supplementary Materials S3). Furthermore, it took approximately one hour to obtain the image-level annotations required to train the regression-based CNN, while it took over 8 hours to create the individual bounding boxes required to train the Faster R-CNN model.

Our study illustrates how a relatively lightweight regression CNN can be used to automatically count objects of interest from digital imagery in fundamentally different kinds of ecological applications. We have shown that it is well-suited to count wildlife (especially when individuals occur in high densities) and to count cryptic objects that are extremely difficult to annotate individually. Previous ecological studies have shown that by automating detection tasks, time and resources can be reassigned, allowing for an increase in sampling effort (Eikelboom *et al.*, 2019). By using annotations at the image-level, labelling efforts and costs can be reduced. Finally, a unique advantage of using a regression-based approach is that it has the potential to leverage already existing labels, collected without the aim of DL applications, thereby reducing labelling efforts and costs to zero.

4.4 Methods

4.4.1 Datasets

In this study, datasets from two fundamentally different real-world ecological use cases were employed. The objects of interest in these images were manually counted in previous studies (Brasseur *et al.*, 2018; Cremer *et al.*, 2017; Brasseur *et al.*, 2015; Van der Veer, in prep) without the aim of DL applications.

4.4.1.1 Microscopic images of otolith rings.

The first dataset consists of 3,585 microscopic images of otoliths (i.e., hearing stones) of plaice (*Pleuronectes platessa*). Newly settled juvenile plaice of various length classes were collected at stations along the North Sea and Wadden Sea coast during 23 sampling campaigns conducted over 6 years. Each individual fish was measured, the sagittal otoliths were removed and microscopic images of two zoom levels (10 × 20 and 10 × 10, depending on fish length) were made. Post-settlement daily growth rings outside the accessory growth centre were then counted by eye (Poiesz *et al.*, 2019; Poiesz *et al.*, 2020). In this dataset, images of otoliths with less than 16 and more than 45 rings were scarce (Figure 4.6). Therefore, a stratified random design was used to select 120 images to evaluate the model performance over the full range of ring counts: all 3,585 images were grouped in eight bins according to their label (Figure 4.6) and from each bin 15 images were randomly selected for the test set. Out of the remaining 3,465 images, 80% of the images were randomly selected for training and 20% were used as a validation set, which is used to estimate the model performance and optimise hyperparameters during training.

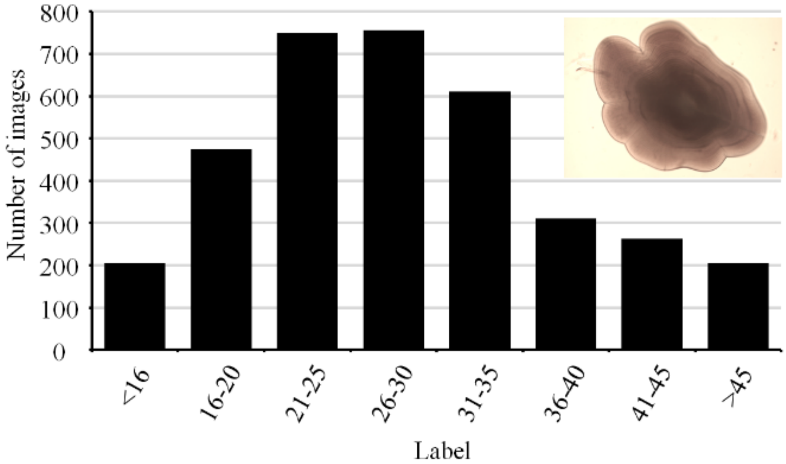

Figure 4.6 Distribution of the labels (i.e., number of post-settlement rings) of all images in the otolith dataset (n = 3585).

4.4.1.2 Aerial images of seals.

The second dataset consists of 11,087 aerial images (named ‘main dataset’ from now onwards) of hauled out grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*), collected between 2005 and 2019 in the Dutch part of the Wadden Sea (Brasseur *et al.*, 2018; Brasseur *et al.*, 2015). Surveys for both species were performed multiple times each year: approximately three times during pupping season and twice during the moult (Cremer *et al.*, 2017). During these periods, seals haul out on land in larger numbers. Images were taken manually through the airplane window whenever seals were sighted, while flying at a fixed height of approximately 150 m, using different focal lengths (80-400 mm). Due to variations in survey conditions (e.g., weather, lighting) and image composition (e.g., angle of view, distance towards seals), this main dataset is highly variable. Noisy labels further complicated the use of this dataset: seals present in multiple (partially) overlapping images were counted only once, and were therefore not included in the count label of each image. Recounting the seals on all images in this dataset to deal with these noisy labels would be a tedious task, compromising one of the main aims of this study of reducing annotation efforts. Instead, only a selection of the main dataset was recounted and used for training and testing. First, 100 images were randomly selected (and recounted) for the test set. In the main dataset, images with a high number of seals were scarce while images with a low number of seals were abundant (Figure 4.7, panel A).

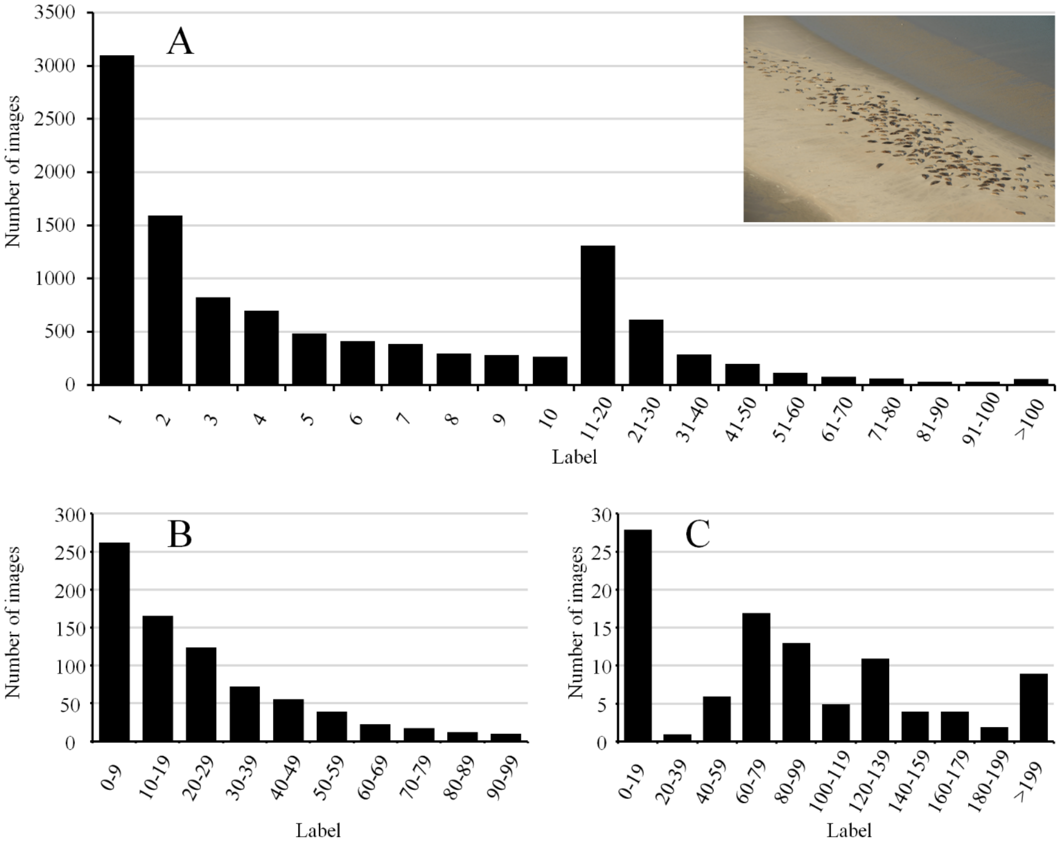

Figure 4.7 Distribution of the labels (i.e., number of seals) in (**A**) the seal main dataset (n = 11,087), (**B**) ‘seal subset 1’ (*n* = 787) and (**C**) ‘seal subset 2’ (*n* = 100).

Therefore, as with the otoliths, all 11,087 images were grouped into 20 bins according to their label (Figure 4.7, panel A), after which five images were randomly selected from each bin for the test set. Second, images of sufficient quality and containing easily identifiable were selected from the main dataset (and recounted) for training and validation, until 787 images were retained (named 'seal subset 1'). In order to create images with zero seals (i.e., just containing the background) and to remove seals that are only partly photographed along the image borders, some of these images were cropped. The dimensions of those cropped images were preserved and, if required, the image-level annotation was modified accordingly. The resulting 'seal subset 1' only contains images with zero to 99 seals (Figure 4.7, panel B). These 787 images were then randomly split in a training (80%) and validation set (20%). In order to still take advantage of the remaining 10,200 images from the main dataset, a two-step label refinement was performed (see the section "Dealing with noisy labels: two-step label refinement" below).

4.4.2 Convolutional neural networks

CNNs are a particular type of artificial neural network. Similar to a biological neural network, where many neurons are connected by synapses, these models consist of a series of connected artificial neurons (i.e., nodes), grouped into layers that are applied one by one. In a CNN, each layer receives an input and produces an output by performing a convolution between the neurons (now organised into a rectangular filter) and each spatial input location and its surroundings. This convolution operator computes a dot product at each location in the input (image or previous layer's output), encoding the correlation between the local input values and the learnable filter weights (i.e., neurons). After this convolution, an activation function is applied so that the final output of the network can represent more than just a linear combination of the inputs. Each layer performs calculations on the inputs it receives from the previous layer, before sending it to the next layer. Regular layers that ingest all previous outputs rather than a local neighbourhood are sometimes also employed at the end; these are called "fully-connected" layers. The number of layers determines the depth of the network. More layers introduce a larger number of free (learnable) parameters, as does a higher number of convolutional filters per layer or larger filter sizes. A final layer usually projects the intermediate, high-dimensional outputs into a vector of size C (the number of categories) in the case of classification, into a single number in the case of regression (ours), or into a custom number of outputs representing arbitrarily complex parameters, such as the class label and coordinates of a bounding box in the case of object detection. During training, the model is fed with many labelled examples to learn the task at hand: the parameters of the neurons are updated to minimise a loss (provided by an error function measuring the discrepancy between predictions and labels; in our case this is the Huber loss as described below). To do so, the gradient and its derivative with respect to each neuron in the last layer is computed; modifying neurons by following their gradients downwards allows reducing the loss (and thereby improving model prediction) for the current image accordingly. Since the series of layers in a CNN can be seen as a set of nested, differentiable functions, the chain rule can be applied to also compute gradients for the intermediate, hidden layers and modify neurons therein backwards until the first layer. This process is known as backpropagation (LeCun *et al.*, 1989). With the recent increase of computational power and labelled dataset sizes, these models are now of increasing complexity (i.e., they have higher numbers of learnable parameters in the convolutional filters and layers).

CNNs come in many layer configurations, or architectures. One of the most widely used CNN architecture is the ResNet (He *et al.*, 2016), which introduced the concept of residual blocks: in ResNets, the input to a residual block (i.e., a group of convolutional layers with nonlinear activations) is added to its output in an element-wise manner. This allows the block to focus on learning residual patterns on top of its inputs. Also, it enables learning signals to by-pass entire blocks, which stabilises training by avoiding the problem of vanishing gradients (Hochreiter *et al.*, 2001). As a consequence, ResNets were the first models that could be trained even with many layers in series and provided a significant increase in accuracy.

4.4.3 Model selection and training

For the otolith dataset, we employed ResNet (He *et al.*, 2016) architectures of various depths (i.e., ResNet18, ResNet34, ResNet50, ResNet101 and ResNet152, where the number corresponds to the number of hidden layers in the model, see Supplementary Materials S2). These ResNet models were pretrained on ImageNet (Deng *et al.*, 2009), which is a large benchmark dataset containing millions of natural images annotated with thousands of categories. Pre-training on ImageNet is a commonly employed methodology to train a CNN efficiently, as it will already have learned how to recognise common recurring features, such as edges and basic geometrical patterns, which would have to be learned from zero otherwise. Therefore, pre-training reduces the required amount of training data significantly.

We modified the ResNet architecture to perform a regression task. To do so, we replaced the classification output layer with two fully-connected layers that map to 512 neurons after the first layer and to a single continuous variable after the second layer (Howard and Gugger, 2020) (Figure 4.8). Since the final task to be performed is regression, the loss function is a loss function that is tailored for regression. In our experiments we tested both a Mean Squared Error and a Smooth L1 (i.e., Huber) loss (Girshick, 2015) (see Supplementary Materials S2). The Huber loss is more robust against outliers and is defined as follows:

$$\mathcal{L}(y, \hat{y}) = \frac{1}{n}\sum_{i}^{n} z_i$$

Where z_i is given by

$$z_i = \begin{cases} 0.5(y_i - \hat{y}_i)^2, & \text{if} |y_i - \hat{y}_i| < 1 \\ |y_i - \hat{y}_i| - 0.5, & \text{otherwise} \end{cases}$$

where $\hat{y}$ is the value predicted by the model, y is the true (ground truth) value (i.e., the label) and n is the batch size. Intuitively, the Huber loss assigns a strong (squared) penalty for predictions that are close to the target value, but not perfect (i.e., loss value < 1) and a smaller (linear) penalty for predictions far off, which increases tolerance towards potential outliers both in prediction and target.

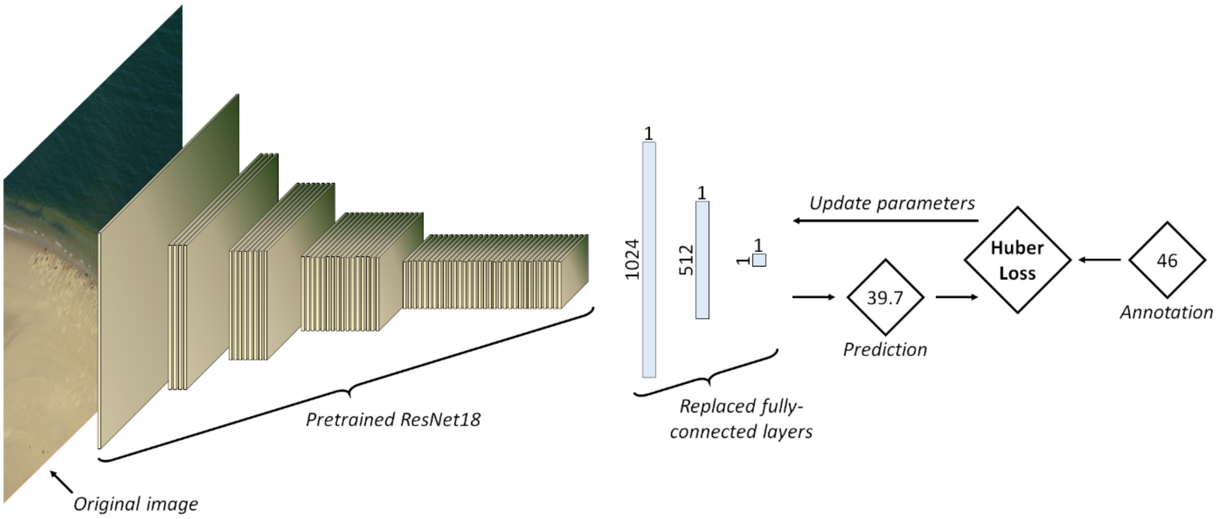

Figure 4.8 Schematic representation of the CNN used in this study. The classification output layer of the pretrained ResNet18 is replaced by two fully-connected layers. The model is trained with a Huber loss.

Computations were performed on a Linux server with four Nvidia GeForce GTX 1080 Ti graphics cards. The CNNs were trained using the FastAI library (Howard and Gugger, 2020) (version 2.0.13) in PyTorch (Paszke *et al.*, 2017) (version 1.6.0). FastAI's default settings were used for image normalisation, dropout (Srivastava *et al.*, 2014), weight decay and momentum (Howard and Gugger, 2020), and a batch size of 84 images was used for the otolith dataset. Whenever an image was used in a model iteration during training, a series of transformations was applied randomly to it for data augmentation (including resizing to 1,040 × 770 pixels, random horizontal flips, lighting, warping, zooming and zero-padding). When using image-level annotations, only limited degrees of zooming can be used, otherwise objects of interest might be cut out of the image, making the image-level annotations incorrect. For the same reason, images were squeezed instead of cropped whenever necessary to account for different image dimensions. Various Learning Rates (LR) and Batch Sizes (BS) were evaluated (see Supplementary Materials S2). A LR finder (Smith, 2018) was used to determine the initial LR values, and FastAIs default settings for discriminative LR were applied (Howard and Gugger, 2020). In discriminative LR, a lower LR is used to train the early layers of the model, while the later layers are trained using a higher LR. For this purpose, our model was divided into three sections (the pretrained part of the network is split into two sections, while the third section comprised the added fully-connected layers), that each had a different LR (specified below) during training. Additionally, we applied '1cycle training' (Howard and Gugger, 2020; Smith and Topin, 2019). Here, training is divided into two phases, one where the LR grows towards a maximum, followed by a phase where the LR is reduced to the original value again. Firstly, only the two fully-connected layers added for regression (i.e., the third section) were trained for 25 epochs (of which the best performing 24th epoch was saved) with an LR of $5e-2$, while the rest of the network remained frozen. After this, the entire network was unfrozen and all layers were further tuned using a discriminative LR ranging from $9e-7$ to $9e-5$, for another 50 epochs, of which the best performing epoch was saved (50th epoch). The same model architecture, training approach and hyperparameters were used for the seal images, with the following exceptions. The batch size was 100 and images were resized to 1,064 × 708 pixels. First, only the added layers were trained (analogue to the rings), with an LR of $3e-2$, for 50 epochs (of which the best performing 45th epoch was saved). After this, the entire network was unfrozen and further tuned for 50 epochs (of which the best performing epoch, the 49th, was saved), using a discriminative LR ranging from $3e-4$ to $3e-2$.

For both the otolith and seal cases, the trained models were evaluated on their respective test sets (described above). These test sets represent unseen data that is not used during the training and validation of the model. R^2, $RMSE$ and MAE were used as performance metrics, and predicted counts were plotted against the labels. Additionally, Class Activation Maps (CAM) were made to aid with interpreting the predictions of the model (Zhou *et al.*, 2016; Howard and Gugger, 2020).

4.4.4 Dealing with noisy labels: two-step label refinement

In order to take advantage of the additionally available noisy data during training, a two-step approach was employed that avoids the need to recount tens of thousands of seals. By using the Step 1 model (trained using 'seal subset 1') predictions, an additional 100 images were selected (and recounted) from the remaining main dataset (see "Results" section). For 35 images, the seals were not clearly identifiable by eye (i.e., they appeared too small) and the image was discarded and replaced by the next most poorly predicted image. These resulting 100 images (named 'seal subset 2', Figure 4.7, panel C) were expected to include cases with noisy labels, but also cases that were challenging for the model to predict (e.g., images with a high number of seals). After this, the entire model (i.e., all layers) was retrained using 'seal subset 1' supplemented with 'seal subset 2', randomly split in a training (80%) and validation set (20%), for an additional 50 epochs using the same hyperparameters as before, except for the LR. Various LR were evaluated and a discriminative LR ranging from $1e-5$ to $1e-3$ gave the best performance on the validation set, in the 48th epoch.

Chapter 5

Stay close, but not too close: aerial image analysis reveals patterns of social distancing in seal colonies

Abstract. Many species aggregate in dense colonies. Species-specific spatial patterns provide clues about how colonies are shaped by various (a-)biotic factors, including predation, temperature regulation, or disease transmission. Using aerial imagery, we examined these patterns in colonies on land of two sympatric seal species: the harbour seal and grey seal. Results show that the density of grey seals on land is twice as high as that of harbour seals. Furthermore, the nearest neighbour distance (NND) of harbour seals (median = 1.06 m) is significantly larger than that of grey seals (median = 0.53 m). Avoidance at small distances (i.e., social distancing) was supported by spatial simulation: when the observed seal locations were shuffled slightly, the frequency of the smallest NNDs (0-25 cm) increased, while the most frequently observed NNDs decreased. As harbour seals are more prone to infectious diseases, we hypothesize that the larger NNDs might be a behavioural response to reduce pathogen transmission. The approach presented here can potentially be used as a practical tool to differentiate between harbour and grey seals in remote sensing applications, particularly in low to medium resolution imagery (e.g., satellite imagery), where morphological characteristics alone are insufficient to differentiate between species.

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5.1 Introduction

Colony formation is an ecological trait that occurs in many animal taxa. The process of colony formation is driven by various biotic and abiotic costs and benefits (Brown, 2016). Potential benefits include protection from predators (i.e., predator swamping), thermoregulation, mating success, increased foraging efficiency and information transfer (Axelrod and Hamilton, 1981; Ward and Zahavi, 1972). Benefits associated with colony forming are case-specific and by no means universal among different species (Alexander, 1974; Hoogland, 1979). Colony formation also has costs. Two of these – namely increased competition for resources and an increased risk of pathogen transmission – are considered inevitable (Alexander, 1974; Hoogland, 1979; Townsend, 2020). The interplay between these various costs and benefits influences the size of colonies (i.e., the tendency to stay with many conspecifics, but not too many), and may lead to distinct fine scale spatial patterns (i.e., "stay close, but not too close"). These patterns are a potentially valuable tool for remote sensing applications: the distinct spatial distribution patterns may be used to identify species, which opens new possibilities to utilize lower resolution imagery (e.g., satellite imagery with 31 cm per pixel resolution) that is otherwise insufficient to differentiate species based on morphological characteristics of single individuals.

Pinnipeds (i.e., seals, sea lions, fur seals and walruses) occupy the boundary between the marine and terrestrial realm. They forage in a marine environment, but depend on land or ice to rest, moult and pup (Lydersen and Kovacs, 1999). Many pinniped species tend to cluster together when hauling out on land, regularly forming large aggregations. Previous research has shown that these colonies can increase pup survival in southern sea lions *Otaria byronia* (Campagna *et al*., 1992), while for elephant seals *Mirounga leonina*, pup mortality increases with higher densities in colonies (Baldi *et al*., 1996). For harbour seals *Phoca vitulina*, alertness increases with group size (Andersen *et al*., 2012; Da Silva and Terhune, 1988), which suggests that scanning for approaching danger could be another important benefit and driver for colony forming in pinnipeds. On the other hand, a commonly observed cost that limits pinniped group size and density is competition for haul-out space, which might result in agonistic behaviour (Conder, 1949; Wilson, 1978; Sullivan, 1982; Davis and Renouf, 1987; Neumann, 1999; Bradshaw *et al*., 2000; Grandi *et al*., 2008). This competition for space is potentially fiercer on land than on ice, as the sea-ice is generally more widely available than suitable haul-out sites on land. The various costs and benefits of colony forming have resulted in a wide range of – potentially species specific – fine scale haul-out patterns (Figure 5.1).

Figure 5.1 Fine scale haul-out patterns of pinnipeds. Haul-out patters of pinnipeds show high variation. Some species haul out solitarily, such as ringed seals (A), while others – such as harbour seals (B) and grey seals (C) – haul out in colonies while preserving some distance from conspecifics. Finally, some species – such as walruses (D) – may cluster together without any distance between individuals. Photos A and D by Eelke Folmer (Aeria).

In the southern North Sea and Dutch Wadden Sea, grey seals *Halichoerus grypus* and harbour seals *Phoca vitulina* are considered sympatric species (i.e., having an overlapping habitat and distribution) (Jones *et al*., 2015; McConnell *et al*., 1999, Damseaux *et al*., 2021). Both species haul out on intertidal flats, sand banks and beaches (Aarts *et al*., 2016). Grey seals generally haul out on the highest sandbanks, which are less exposed to tidal and weather conditions, while harbour seals most often use sandbanks that are only available during low tide. Especially during the pupping season, grey seals avoid tidal haul-out sites, as their pups need to remain on land for several weeks to moult and shed their birth coat (i.e., the lanugo) before going to sea (Reijnders *et al*., 1995, Brasseur *et al*., 2015). On the contrary, harbour seal pups moult their lanugo in utero and can swim within hours after birth, which allows them to utilize lower sandbanks and intertidal flats even during the breeding season. Consequently, harbour seals have more suitable haul-out sites available during the pupping season than grey seals. The preference of grey seals for higher grounds seems general and is also observed outside the breeding season, most notably during the moult when they aggregate in groups reaching over thousand individuals. Grey seals tend to undertake longer foraging trips and have longer resting times compared to harbour seals (Aarts *et al*., 2016), which might explain their preference for higher haul-out sites safe from tidal conditions. Despite these differences, there is occasional overlap, where grey and harbour seals are observed mixed together on a haul-out site.

The species-specific differences in haul-out behaviour most likely play an important role in explaining their population dynamics. While both species have historically been hunted extensively in the Wadden Sea, the breeding system of the grey seal may render this species more vulnerable. For grey seals, this led to their extinction in this area in the Middle Ages (Reijnders *et al.*, 1995). Protective measures and legislation in the UK in the early 20th century allowed neighbouring grey seal populations to recover and subsequently recolonize the Wadden Sea in the 1980s. Fuelled by this immigration (Brasseur *et al.*, 2015), the grey seal population in the Wadden Sea has grown to over 9000 individuals (counted during moult). Harbour seal pups on the other hand, are more mobile (even with pups) and difficult to approach and are more likely to escape into the water when facing threats. Compared to grey seals, they were therefore less vulnerable to historic hunting, which is reflected in an abundance estimate of 40,000 individuals in the Wadden Sea in 1900 (Reijnders, 1992; Brasseur *et al.*, 2018), despite centuries of hunting (de Vooys *et al.*, 2012). However, due to a more extensive use of firearms and industrial pollution, the harbour seal population decreased dramatically to around 4,500 individuals in 1960 (Reijnders *et al.*, 1992). After that, recovery was limited due to pollution (Reijnders, 1986) and two outbreaks of the Phocine Distemper Virus (PDV) in 1988 and 2002. During both outbreaks, the population was reduced to approximately 50% (Akineden *et al.*, 2007; Härkönen *et al.*, 2006; Svensson, 2012). Despite these massive reductions in the recent past, the harbour seal is currently the most abundant seal species in the Wadden Sea.

The influence of (a-)biotic factors – such as pathogen transmission, availability of preferred haul-out sites and requirements related to phenology or social cohesion – may result in species-specific fine scale haul-out patterns within grey and harbour seal colonies. To examine the fine scale spatial haul-out patterns of grey and harbour seals, we analyse measurements of densities and spatial distances between individual seals at various haul-out sites in the Netherlands, using high resolution aerial imagery. We then show that the observed densities and distances are species-specific and differ significantly between the two species, with harbour seals keeping larger distances from conspecifics than grey seals. By shuffling the observed distributions through spatial simulations, we then show that both species avoid getting too close to conspecifics and that distribution of inter-individual distances vary greatly between the species. This finding has implications to understand pinnipeds behaviour, but also could be used as a proxy for large scale species identification. Indeed, when detecting, counting and analysing sympatric behaviour of seals in lower resolution (satellite) imagery, one could use the inter-individual distances to characterise the species of the group. This could become a valuable tool to aid in species identification based on satellite images of inaccessible regions, such as the Arctic.

5.2 Methods

5.2.1 Data collection on fine scale distribution

The Dutch government has commissioned the collection of aerial images as part of the national inspection of land use change (i.e., land registry ‘Kadaster’), but some of these images also contain seal haul-out sites. Surveys were conducted once per year, during February–June, between 2016 and 2019. The images were georeferenced (projection: Amersfoort Rijksdriehoek; EPSG:28992) and have a resolution of either 7.5 cm (2019) or 10 cm (2016–2019). The distribution of individual grey (N=~80) and harbour seals (N=~250) tracked with GPS loggers was used to determine the exact location of seal colonies on land (i.e., haul-out sites). Aerial images that overlapped with these tracked animals were selected for visual inspection in QGIS (Version 3.10) and the colonies were categorised as grey seal (i), harbour seal (ii) or mixed (iii) colonies. All images that contained seals were then selected for analysis and each individual seal was manually labelled, by drawing a polygon following the outline of each seal, using the Picterra software suite (www.picterra.ch). The annotations were then exported as georeferenced spatial polygon shapefiles. Mixed colonies were excluded from further analysis.

5.2.2 Nearest neighbour distance and density estimation

To determine inter-animal distances and examine fine-scale spatial patterns, the polygons (each one corresponding to an individual seal) were analysed in the statistical software R (version 1.4.1106) (R Core Team, 2023) (for the complete R-code, see online Supplementary Materials). For each photographed haul-out site a distance matrix was created using the *gDistance* function from the *rgeos* R-package (Bivand *et al*., 2017), which contained the distances (in metres) between the edges of all polygons within the haul-out site. Assuming that the spatial position of every individual seal represents an independent decision, the smallest distance for each polygon – representing the nearest neighbour distance (NND) – was extracted from the distance matrix. The mean and median NND were calculated for both species. Since the mean NND is highly influenced by outliers, we tested if there was a significant difference in the median between the NNDs of grey seals and harbour seals by fitting a 0.5 quantile regression model (package *quantreg*, function *rq*, Koenker 2005, Koenker *et al*. 2017) to the data, where ‘species’ was included as factor variable.

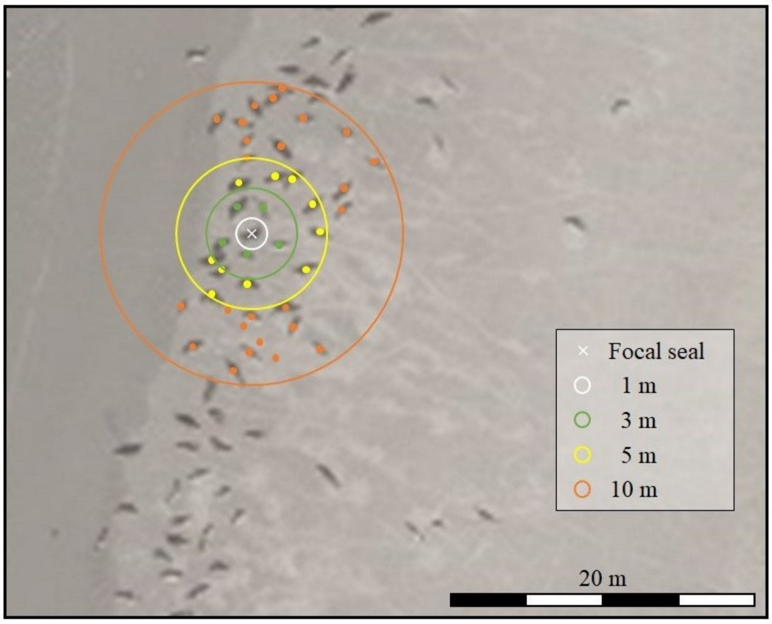

Figure 5.2 Visualisation of the density analysis. For a focal seal (white cross) all neighbouring seals were counted within a 1 (white), 3 (green), 5 (yellow) and 10 m (orange) radius. This was repeated for every seal.

Additionally, as a measure for density, we plotted circles with increasing radii (1, 3, 5 and 10 m) around the center point of a focal seal, and counted how many neighbouring seal center points were present within each circle (Figure 5.2). This was repeated for every seal. To test if there were significant differences between the densities of grey seals and harbour seals, a generalized linear model (GLM) was fitted to these count data, assuming a negative binomial error distribution to allow for possible over- or under-dispersion (package MASS, function glm.nb, Venables and Ripley, 2002), and including 'species' as factor variable. This analysis was repeated for all radii (1, 3, 5 and 10 m) separately.

5.2.3 Social distancing analysis

Hauled-out seals group together, but within these aggregations, seals may choose to maintain a small distance between individuals. To examine this social distancing, we simulated spatial arrangements of the colony via spatial perturbation of the seals positions: the annotated seals (i.e., the polygons) were semi-randomly moved to a new location within the colony while maintaining the heterogenous spatial density on the haul-out site, and the resulting simulated NNDs were compared with the original NNDs. To do this, the spatial distribution of seals on each individual haul-out site was defined by estimating a spatial kernel density (Package *spatstat*, function *densityfun*, Baddeley *et al*., 2014) based on the original observed distribution of all polygons (Figure 5.3). The bandwidth used for the kernel density was the average cross-validated bandwidth determined per haul-out site (Package *spatstat*, function *bw.diggle*, Baddeley *et al*., 2014). For each polygon, a new location was sampled based on the kernel around the centre of each polygon. The orientation of the seal was preserved. This way, the observed densities and colony forming behaviour of the seals was mimicked and the sampling space was limited to represent the original space in which the seals were distributed. The shuffled polygons often overlapped (35% for grey seals, 14% for harbour seals). As it is uncommon for either seal species to lay on top of each other, overlapping polygons were rotated (1-degree increments). If the overlap was not resolved after rotation, the polygon was moved slightly in a random direction with 10 cm increments until the overlap was resolved. Additionally, two alternative approaches for dealing with overlapping polygons were also analysed and can be found in Supplementary Materials S5.

We investigated whether seals keep a (small) distance from one another (i.e., social distancing), by comparing the NNDs of the non-shuffled polygons (i.e., the original observations) with the shuffled NNDs. This was tested for both species separately, by comparing the proportion of the polygons lying within 25 cm of each other in the observed and shuffled data set. This threshold distance of 25 cm was chosen to prevent any bias introduced by potential imprecise annotation caused by the image resolution (7.5 or 10cm per pixel). The statistical testing was done by fitting a GLM with binomial error distribution to the data (with the number of NNDs < 25 cm and > 25 cm as 'successes' and 'failures', respectively) and observed/shuffled as factor variable.

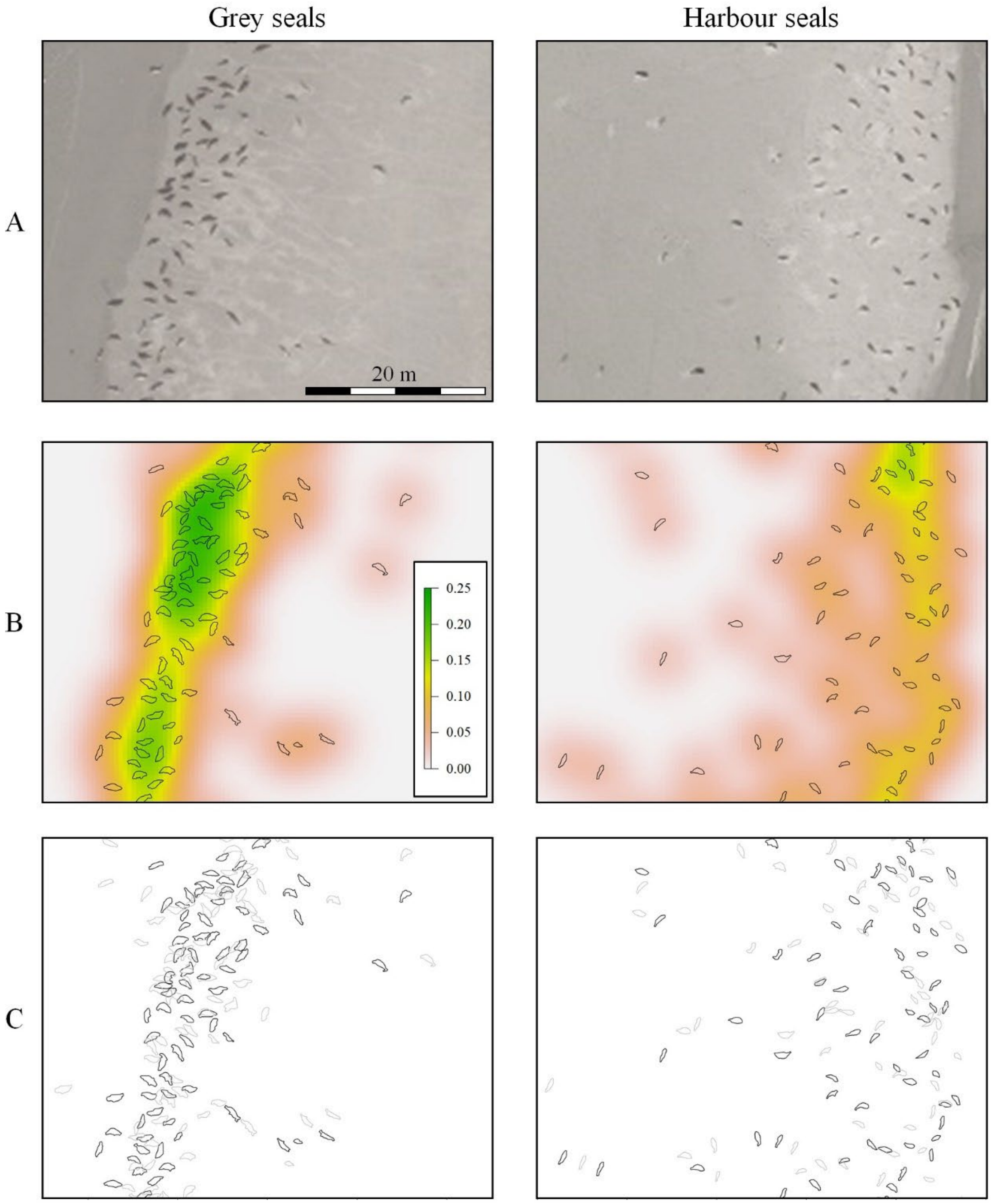

Figure 5.3 Density kernel and randomisation. **A**: Example of original aerial image of grey seals (left) and harbour seals (right). **B**: Visualisation of density kernels, with annotated seals, of the same region as A. **C**: Original distribution (black) and shuffled distribution (light grey), of the same region as A and B.

5.3 Results

As the National land registry focused on human terrestrial use, therefore neglecting tidal sites, relatively few seal haul-out sites were recorded in Dutch waters. After visual inspection of the aerial images that overlapped with the GPS tracking data, a total of 11 haul-out sites were found (Supplementary Materials S7). Based on the GPS tracking data, two of these sites were identified as grey seal colonies and six as harbour seal colonies. Three sites containing mixed groups of harbour and grey seals were excluded from further analysis, to allow for a comparison between species. The images of the grey seal sites were collected in March, during the moult. Most of the harbour seal images were collected in February–May, during the feeding season. However, one harbour seal haul-out site was photographed in June, during the pupping season of harbour seals, and multiple mother/pup pairs were visible. As mother/pup pairs tend to stay close together, and would bias the nearest-neighbour distance results, this site was excluded from the analysis. A detailed comparison of this site with non-pupping harbour seal haul-out sites can be found in Supplementary Materials S6.

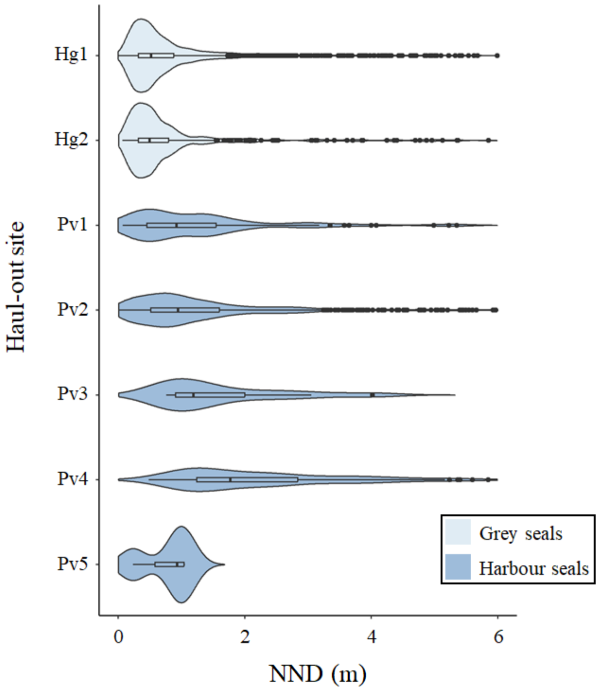

Figure 5.4 Distribution NNDs per site. Violin plots of NNDs for each grey seal (light blue) and harbour seal (dark blue) haul-out site

In the selected images, a total of 1574 harbour seals (February – May) and 3299 grey seals (March) were found and annotated. The mean NND for harbour seals was 1.62 m and 1.15 m for grey seals. The median NND for harbour seals was (1.06 m) was twice as large as that of grey seals (0.53 m). This difference was significant (Table 5.1). In line with Graves *et al.* (2022) we also calculated 25% quantiles, which were 0.32 m and 0.49 m for grey and harbour seals, respectively. These quartiles also significantly differed between species (t-value 8.32539, p< 0.001). The patterns observed for grey and harbour seals are consistent across the different haul-out sites (Figure 5.4). For all harbour seal haul-out sites, the median and interquartile range are larger than those of the grey seal sites.

Table 5.1 Summary statistics (t-test median based on quantile regression) comparing the NND of grey and harbour seals.

Species	N	Sites	Mean (m)	Median (m)	t-test median
Grey seal	3,299	2	1.15	0.53	t = 18.3 p-value <0.001
Harbour seal	1,574	5	1.62	1.06	

Table 5.2 Haul-out densities of grey seals (Hg) and harbour seals (Pv), for different radii around a focal polygon. The results of the GLM for all radii are provided, as well as the mean and median number of individuals and the 95% confidence interval (CI) for both species.

Radius (m)	**Mean**		**95% CI**		**Median**		**GLM**
	Hg	*Pv*	*Hg*	*Pv*	*Hg*	*Pv*	***(Hg versus Pv)***
1	1.86	0.63	1.81-1.91	0.59-0.68	2	0	z-value = -29.86 p-value < 0.0001
3	7.23	3.30	7.07-7.38	3.15-3.46	7	3	z-value = -34.06 p-value < 0.0001
5	14.01	6.97	13.73-14.29	6.68-7.27	15	5	z-value = -32.97 p-value < 0.0001
10	32.34	18.34	31.74-32.95	17.62-19.10	33	15	z-value = -28.48 p-value < 0.0001

The number of neighbouring polygons present within different radii (1, 3, 5, and 10 m) around a focal polygon differed significantly between grey and harbour seals for all radii, with grey seals having roughly two times higher density than harbour seals (Table 5.2).

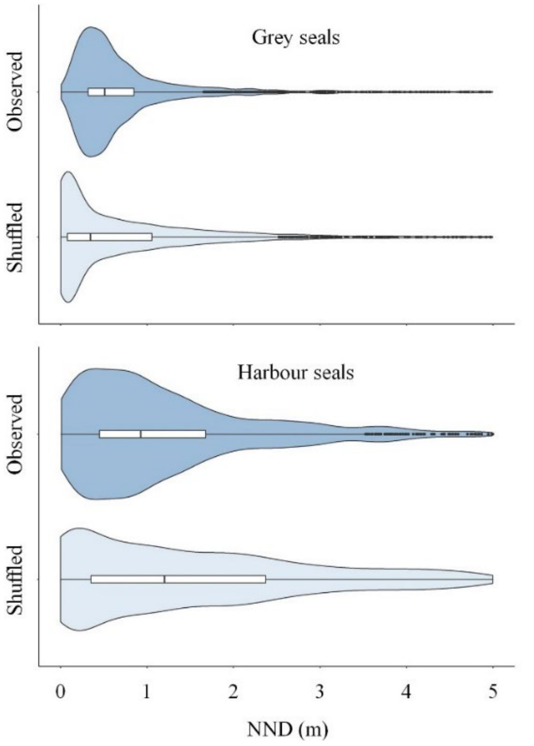

Figure 5.5 Violin plots of NNDs for both the observed (dark blue) and the shuffled distribution (light blue), for grey seals (top) and harbour seals (bottom).

After the random displacements of polygons (see Methods section; Figure 5.3), we found that for both grey and harbour seals the shuffled distribution of NNDs comprised a higher frequency of both smaller and larger NNDs, while fewer NNDs at intermediate distances were observed with respect to the NNDs of the original observations (Figure 5.5).

Compared to the observed distribution, the occurrences of the smallest NNDs (0–25 cm) increased for both species after the shuffling. For grey seals, 16% (537 out of 3299) of the observed seals are within 25 cm of their nearest neighbour, while this proportion increases to 44% after shuffling (1453 out of the 3299). This difference is statistically significant (GLM, z-value = 23.8, p-value < 0.001). For harbour seals, only 9% (148 out of 1574) observed individuals are within 25cm of their neighbour, while after shuffling this is increased to 22% (348 out of the 1574), which is also statistically significant different (GLM. z-value = 9.5, p-value <0.001). (Figure 5.6). This indicates that both seal species avoid the immediate proximity (<25 cm) of their neighbour.

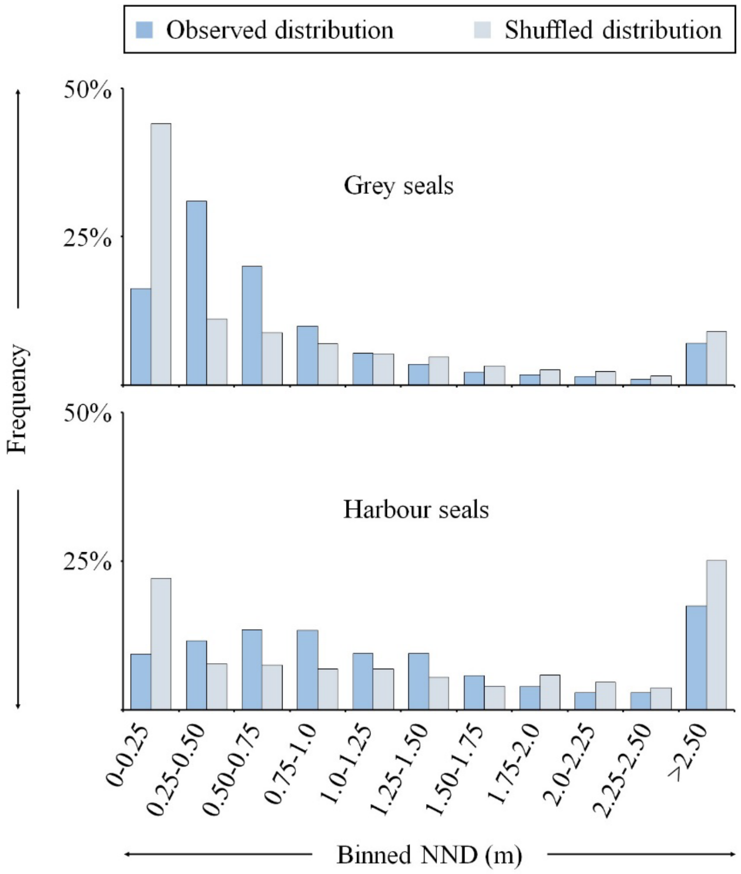

Figure 5.6 Distribution of the observed and shuffled NNDs in 0.25 m bins, for grey seals (top) and harbour seals (bottom). In the shuffled distribution (dark grey), the smallest NNDs are more common than in the observed distributions (light grey).

5.4 Discussion

Pinniped behaviour is strongly governed by their phenology and shows great seasonal variation. During approximately nine months of the year, seals spend most of their time at sea, while regularly coming back to shore to rest. However, during breeding and moulting they spend more time on land and seal numbers at haul-out sites are generally higher. Furthermore, seasonal variation in behaviour within colonies has also been recorded: during the breeding season of harbour seals for instance, the level of alertness is lower (Andersen *et al.*, 2012; Renouf *et al.*, 1981; Kovacs and Innes, 1990). This seasonal variation can potentially also affect the fine scale distribution (and the NNDs reported in this study). However, the aerial images available for this study did not allow to examine all periods (i.e., feeding, breeding and moult) for both seal species. The only images available for grey seals were collected in March during the moult, while for harbour seals, images from both the feeding season (February–May) and pupping season (June) were available. This allowed for the comparison between the two species in spring. Additionally, we provide an example of seasonal differences in haul-out patterns for harbour seals in- and outside the breeding season (Supplementary Materials S6). Here we found that pupping harbour seals display both significantly lower densities and median NNDs than non-pupping harbour seals. This can be explained by mother/pup pairs keeping more distance from conspecifics during nursing, while the pup stays in very close proximity to its mother. Additional survey data is required to further study seasonal variations and interspecific variation between colonies.

The manual processing of the aerial imagery as presented in our study is labour-intensive and time consuming. However, thanks to the recent rapid developments in the field of Computer Vision, it could be possible to utilize automated detection algorithms to reduce the time required to label individual animals in newly collected imagery (e.g., Oliveira *et al*., 2021; Infantes *et al*., 2022). The images and annotations collected in our study can be used to train such an algorithm for hauled out grey and harbour seals in the Wadden Sea.

Like most other pinnipeds, harbour and grey seals haul out in groups. In our study, harbour seals keep more distance – i.e., display greater NNDs – from conspecifics than grey seals do. Furthermore, harbour seals occur in significantly lower densities at haul-out sites compared to grey seals, despite being considerably smaller than (male) grey seals and therefore requiring less space. Both grey and harbour seal avoid close (less than 25cm) contact.

No other studies on harbour seal NNDs were found. Studies on fine scale haul-out patterns for grey seals are scarce and limited to the breeding season, whereas our grey seal images were collected during the moult. During the breeding season, grey seals form harems. Female grey seals have been estimated to haul out within 8 m of another female (Tinker *et al*., 1995), which is similar to an estimated NND of 5-10 m between multiple grey seal mother-pup pairs (Lydersen and Kovacs, 1999). Both studies examined grey seals hauled out on ice, where suitable habitat is generally less scarce than on land. On land, an NND of 6.07m was reported for breeding females (Twiss *et al*., 2012). The lower NNDs reported in our study could potentially be explained by the lack of aggression among males and among nursing females guarding their pups, a behaviour which commonly observed during the breeding season (Robinson and Pomeroy, 2022).

The underlying mechanisms driving the observed differences in the fine scale haul-out patterns of grey and harbour seals remain unclear. Although still speculative at this point, the two universal costs of colony formation – increased competition for resources and an increased risk of pathogen transmission – provide potential insights. Due to the preference of grey seals in the Wadden Sea area for relatively higher haul-out sites (Reijnders *et al*., 1995, Brasseur *et al*., 2015), suitable haul-out space for grey seals is more limited than for harbour seals. Consequently, competition for space is higher, which could potentially explain the smaller NNDs and higher haul-out densities of grey seal. However, on one of the two grey seal haul-out sites in this study, haul-out space does not seem to be a limiting factor, yet grey seals often tend to cluster in tight groups (Figure 5.7). Both grey seal haul-out sites are relatively high and also available during high tide, allowing seals to move up during incoming tide.

Figure 5.7 Aerial image of hauled-out grey seals. Even when suitable haul-out space is not limiting, grey seals often tend to cluster together in our study.

With a larger group size, the prevalence of pathogens (including parasites) increases (Andersen and May, 1979; Townsend *et al*., 2020; Rifkin *et al*., 2012). When facing emerging pathogens, both affected individuals and healthy individuals can mitigate infection risks by altering their behaviour and reducing their level of interaction (i.e., their sociality) as a precautionary measure (Townsend *et al*., 2020; Stockmaier *et al*., 2021). Therefore, pathogen occurrence not only limits group size, but also the level of sociality within a group (Prado *et al*., 2009). The effectiveness of this response was also illustrated in humans during the outbreak of the SARS-CoV-2 virus, as many countries implemented social distancing measures, which significantly reduced the transmission rate (McGrail *et al*., 2020; Stockmaier *et al*., 2021). Because seals haul out in close proximity of many other individuals and have high contact rates, they are particularly vulnerable to infectious diseases (Altizer *et al*., 2003). The two PDV outbreaks in 1988 and 2002 serve as an example of this: harbour seal populations were reduced by up to 50%, whereas grey seals remained relatively unharmed by the same virus. It is possible that the observed differences in fine scale haul-out patterns between the two species reflect an evolutionary response to pathogen occurrence. Interestingly, this behaviour – where individuals alter their level of sociality in response to an emerging pathogen (i.e., on an ecological timescale) – has been observed in other social animals (Stockmaier *et al*., 2021), such as mule deer *Odocoileus hemionus hemionus* (Mejía Salazar *et al*., 2016), wild house mice *Mus musculus domesticus* (Lopes *et al*., 2016) and social insects (Stroeymeyt *et al*., 2018). For Caribbean spiny lobsters, it has been shown that attraction to conspecifics has decreased in a region with a higher pathogen occurrence (Childress *et al*., 2015; Townsend *et al*., 2020), which is suggested to be an evolutionary response. Although our findings confirm the existence of social distancing in harbour and grey seals, it cannot be concluded whether or not it is an evolutionary response to limit pathogen transmission, because no data was available from before or during these outbreaks.

The observed fine scale haul-out patterns of grey and harbour seals are species-specific, which is particularly interesting for remote sensing applications. In the Netherlands, grey and harbour seals are sympatric, young and sub adult grey seals are of similar size as adult harbour seals, and both species haul out throughout the year. Consequently, it is challenging to differentiate the two species in remote sensing imagery with an insufficient resolution to identify the species based on morphological characteristics. Whereas the resolution of imagery used in our study is 7.5 and 10 cm per pixel, the resolution of the highest resolution of commercially available satellite imagery is currently 31 cm per pixel. Although this allows for the detection of individual seals (e.g., Gonçalves *et al*., 2020), it is impossible to differentiate between harbour and grey seals based on morphological characteristics alone. For this type of low-resolution imagery, additional variables such as seal phenology (e.g., seasonality) and habitat characteristics (e.g., height of haul-out sites) can aid in the identification of grey and harbour seal colonies to the species level. Our findings suggest that spatial patterns within a colony could provide another tool to differentiate between these species. This approach has potential for the characterization of colonies in remote and inaccessible regions such as the polar regions, where satellite images are routinely available.

Chapter 6

Synthesis

6.1. Main findings in relation to the research questions

The imminent disappearance of the sea ice, like the sword of Damocles, hangs over millions of Arctic marine mammals. Not only will this have severe consequences for the fragile Arctic ecosystem and marine mammal directly, but it will inevitably also lead to an increase of anthropogenic activities, which is expected to further disrupt the life cycle of Arctic animals. How Arctic marine mammals are responding to these changing conditions remains largely unclear (Chapter 2).

The focus of this thesis is to develop and apply methodologies for marine mammal detection and identification that can aid studying distribution and range shifts: examples of more traditional marine mammal photo-identification are given (considering bottlenose dolphins as study species, Chapter 3), and new approaches to automatically count individuals (with pinnipeds as a case study, Chapter 4) and to differentiate between species in low-resolution imagery (studying grey and harbour seals, Chapter 5) are developed and tested, by using data-rich marine mammal populations in the southern North Sea as ‘model organisms’.

These chapters are written as self-contained scientific papers (included without modifications as published in the respective journals), that jointly address the four research questions of this thesis, which were formulated in Chapter 1:

RQ 1. Which changes in migration timing or distribution do Arctic migratory vertebrates exhibit in response to global warming?

RQ 2. How can opportunistically collected data contribute to a better understanding of range shifts in marine mammals? A bottlenose dolphin case study.

RQ 3. How can image-level annotations be leveraged to train a deep learning model to count pinnipeds from aerial imagery, and what is the accuracy of this approach? A grey and harbour seal case study.

RQ 4. How can fine-scale spatial haul-out patterns in pinniped haul-out sites be used as a tool to differentiate between sympatric species, when using low-resolution remote sensing imagery?

In this final chapter, I synthesize the main findings and discuss the used methodology in relation to both the overall aim and individual research questions. Furthermore, I provide an outlook on future research to better detect and monitor marine mammals in Polar regions – mostly centred on the potential of remote sensing using satellite imagery – and discuss challenges that lay ahead.

6.1.1. Changes in migration timing and distribution of Arctic vertebrates in response to global warming

Climate change has led to a dramatic decrease in sea ice volume: the Arctic Ocean may be ice-free as soon as summer 2035 (Guarino *et al*, 2020). It is expected that this will have severe consequences for Arctic marine mammals, many of which are dependent on sea ice (Kovacs *et al*, 2011). Among marine mammals, Arctic pinnipeds are particularly vulnerable, as they need sea ice for resting, breeding and moulting.

In Chapter 2, an extensive literature review discusses observed shifts in both migration timing and distribution of Arctic animals in response to climate change. Due to increased temperatures, the distribution of some food resources shifted northwards, while others have become available earlier in the season. This chapter first discusses many examples of Arctic animals – particularly birds, polar bears and ungulates – that display shifts in migration timing reflecting adjustments to changing local conditions. Differently from those mostly non-marine species, very few species of marine mammals were found to shift the timing of their migration. Beluga whales now delay their departure from northern waters in autumn, which appears to be a response to later sea ice formation (Hauser, 2017). For pinnipeds, only one report on shifts in migration timing was found, which described how walruses advanced their arrival in their summering range (Martinez-Levasseur *et al*., 2021).

Notably, instead of changing their migration timing, most marine mammal species appear to shift their range in response to the changing environment. For cetaceans, both northwards shifts (migratory baleen whales, Brower *et al*., 2018; Storrie *et al*., 2018) and distribution shifts within the Arctic (bowhead whales, Druckenmiller *et al*., 2018; belugas, Heide-Jørgensen *et al*., 2010) were reported. The reduced sea ice has also allowed orcas *Orcinus orca* to enter Arctic areas that were previously inaccessible to this top predator (Higdon and Ferguson, 2009; Ferguson *et al*., 2010). The presence of orcas is expected to further influence the distribution of Arctic cetaceans and pinnipeds. For pinnipeds, range shifts have been observed in both pupping grounds (harp seals, Rosing-Asvid, 2008; Stenson *et al*., 2020) and in summer distribution (harp seal, bearded seal and ringed seal, Bengtsson *et al*., 2021). Other species (e.g., walruses) are now increasingly observed to haul out on land instead of sea ice, which may have effects on survival (e.g., safety from predators, energy expenditure costs (Jay *et al*., 2017) and density-dependent effects (MacCracken, 2012). Finally, more temperate pinniped species are now occurring in higher numbers in the Arctic (e.g., harbour seals, Bengtsson *et al*., 2021; Blanchet *et al*., 2014).

Most importantly, this chapter shows that large knowledge gaps remain, particularly for marine mammals. This finding underpins the urgent need to develop and test new approaches (e.g., Chapter 4 and 5) to aid in marine mammal monitoring (and especially identifying new distributions and range shifts) in a rapidly changing Arctic, since traditional approaches, such as capture-recapture methodologies are inadequate in this remote and inhospitable region. Pinnipeds in particular could benefit from automated image processing (Chapter 4), as they occur in very large numbers and form large seasonal aggregations (Chapter 1). Monitoring Arctic marine mammals is often depended on prior knowledge on the species' distribution, which provides additional challenges as the Arctic is rapidly changing. Consequently, when such priors (i) do not hold anymore, (ii) are unknown or (iii) difficult to quantify, alternative approaches to scale up surveys are needed (e.g., Chapter 4 and 5).

6.1.2. Bottlenose dolphins in the Netherlands come from two sides: across the North Sea and through the English Channel

Chapter 3 describes an approach based on photo-identification, with the aim of studying movement and range shifts of individual animals. Studying spatial distributions of marine mammals at sea is challenging, as they are only briefly (and partly) visible at the surface. Most pinnipeds form dense aggregations while hauled out on land/sea ice, which can be used to collect data on abundance and distribution, for instance by aerial surveys (see Chapter 4 and 5). Cetaceans however, permanently occupy the marine realm and seldom form predictable dense seasonal aggregations as most pinnipeds do (although they can occur in clusters during breeding or feeding). Therefore, photo-identification – often in combination with capture-recapture methodology – has been a commonly used tool to study individual cetacean distribution, especially when populations are relatively small and the chance of a recapture is relatively large. Chapter 3 provides multiple case studies centred around bottlenose dolphins and applies photo-identification methodologies to determine the origin of these species in the Netherlands.

Once common, bottlenose dolphins are now rarely observed in the Netherlands (van Bree, 1977; Kompanje, 2001, 2005; Camphuysen and Peet, 2006). Occasionally, these dolphins are observed in Dutch waters, both stranded (dead) and free ranging. In these cases, opportunistically collected imagery allows for comparison with well-studied and data-rich (and relatively small) neighbouring populations, highlighting the value of long-term monitoring schemes and photo-identification catalogues. In Chapter 3, multiple photo-identification matches of animals observed in the Netherlands could be made. Surprisingly, the identified dolphins originated from very different locations. The first case comprised a group of dolphins photographed entering the Dutch Wadden Sea, that was matched with the NE Scotland population. Not only was this the first match of bottlenose dolphins in the Netherlands with this Scottish population, but it was also the first sighting of individuals from that population outside the UK and Ireland. After their visit to Dutch waters, some individuals returned to their 'home' location, while others stayed on the eastern side of the North Sea and were sighted repeatedly off Denmark. The second case comprised a solitary dolphin photographed in Amsterdam, that was matched with previous sightings off Brittany (France). Unfortunately, this individual was later found stranded, with an amputated tail, presumably due to a ship strike.

Although the mechanisms underlying these previously unknown long-range movements remain unclear, these findings have important implications for the conservation and management of European bottlenose dolphins. As these dolphins move into areas that lack protective measurements, they are exposed to many anthropogenic threats, such as ship-strikes and by-catch. These findings are an example of the potential risks of range shifts of marine mammals. As the distribution of Artic marine mammals is expected to change in response to the disappearing sea ice (Chapter 2), this might make them more vulnerable to anthropogenic activities, which are expected to increase as the region is becoming more accessible.

The recent developments in the field of computer vision have allowed researchers to develop and apply automated approaches to match newly collected images with existing photo-identification catalogues. This field of research is denoted as individual re-identification and consists in identifying and matching defining patterns and shapes of individuals, across images. Hence, these methods only work for species with unique appearances that are easily visible, such as zebras (Crall *et al.*, 2013) and tigers (Shukla *et al.*, 2019). Crucially, they have also been successfully applied to cetaceans (Blount *et al.*, 2022; Maglietta *et al.*, 2022) and pinnipeds (Nepovinnykh *et al.*, 2023). Most recent and performant approaches apply deep learning (e.g., Vidal *et al.*, 2021; Patton *et al.*, 2023), and interpretable AI models allow to highlight the visual cues that led to the identification, which can then be used to recognize remarkable features of specific individuals such as scars or the shape of the fluke (Marcos *et al.*, 2022).

6.1.3. Leveraging existing image-level labels to automatically count pinnipeds from aerial imagery

While bottlenose dolphins are considered rare visitors in the Netherlands, both harbour and grey seals permanently reside in Dutch waters. However, while for cetaceans photo-identification is often the only suitable method to estimate their distribution and range shifts, for seal species that come to land to rest and reproduce, a larger suite of methods is available. The seasonal haul-out sites on land can be leveraged to estimate abundance and distribution and study range shifts, which is most conventionally done through aerial surveys. Regular aerial monitoring in this region started in the 1970s and multiple surveys are now carried out annually. Since the 1990s, aerial images are collected using hand-held cameras, which has resulted in a large database of thousands of aerial images of seals in Dutch waters.

Unfortunately, manual processing of this imagery can be extremely labour-intensive and time-consuming. Thanks to the recent developments in the field of computer vision, the processing of these images can now be automated (Chapter 1). Most ecological studies that apply computer vision approaches for counting or detecting animals utilise data where animals are annotated (or labelled) individually. This degree of label information, however, is often expensive as all individuals need to be annotated in every image, or, in the case of seals that form dense aggregations on land, nearly impossible to achieve. Chapter 4 provides an alternative approach that circumvents the need to label individual seals, but instead uses image-level counts and casts the problem as a regression task.

The results show that this approach provides accurate image-level counts, despite the sometimes relatively poor quality of the images and the oblique angle at which they were taken. Additionally, it serves as an example in which deep learning regression is particularly beneficial, especially given the lower effort needed to provide labels as image-level counts: as the seals in these images occur in very high densities (up to hundreds of animals in a single image), labelling every individual seal would be particularly time-consuming. Furthermore, determining the exact location of individual seals within an image is beyond what is needed in this monitoring scheme: obtaining image-level counts is sufficient. Finally, this method provides opportunities to leverage already existing image-level labels, which were collected without the aim of deep learning applications. This unique aspect has the potential to give additional value to years of field work and ecological studies.

The seal dataset employed in this study contained a high variability (i.e., distance to animals, angle of view, various weather conditions) and exposed a number of limitations of the methodology. Similar to human observers, the model performed worse when images depicted large groups that were taken at great distances, where pinnipeds appeared very small due to the camera resolution (e.g., Figure 4.5 A and C). The predictions on this type of images were often underestimated, which contributed greatly to the lower overall predicted total number of seals (e.g., Figure 4.2 A). In rare occasions, the model overestimated individual counts, due to large birds that were resting on land, as was indicated by the spatial heatmaps (e.g., Figure 4.5 B). Both these cases could also reflect the lack of these types of images in the training set, and performance could potentially be increased with more images with birds and/or small appearing seals being added to the training set. This could most conveniently be done through another iteration of the multi-step approach presented in

Chapter 4, where a specific subset of new images is added within which the model performs poorly, followed by model fine-tuning with this augmented dataset.

Another limitation of the presented approach is the inability to differentiate between grey and harbour seals; instead, the trained model predicts a general seal count. This is particularly troublesome for scenarios where grey and harbour seals form mixed groups (e.g., Figure 1.6), or in scenarios where no prior knowledge on seal distribution is available. Potential solutions for this limitation for future research could be to retrain the model on each species independently, or to modify the model to produce multiclass outputs (one for each species).

Unfortunately, our results also remain relative to the precision of the counts ground truth we used. A coefficient of variation between multiple human observers was not available for these seal data, and a detailed comparison between the error of multiple human observers was not made. To still provide some context of the reported underestimated predicted total number of seals, the total predicted counts were compared with the confidence interval used to extrapolate survey counts to a population size estimate. This illustrates that the reported inaccuracies of our model are within the range of what is accepted in this field of research and are directly usable in ecological research.

6.1.4. Fine-scale spatial haul-out patterns can be used to differentiate seal species in remote sensing applications

Differentiating sympatric grey and harbour seals in aerial imagery can be challenging, particularly when the resolution of the aerial imagery is relatively low (7.5 cm and 10 cm per pixel in the study in Chapter 5). Grey seals are sexually dimorphic, and females are significantly smaller than males (185 cm and 210 cm on average, respectively). Although European harbour seals are generally smaller (with females growing up to 150 cm and males up to 160 cm), from the air they can easily be confused with female or sub-adult grey seals. Fortunately, both species have been extensively studied in the Dutch Wadden sea. Multiple telemetry studies, for instance, have resulted in a detailed understanding of the fine-scale distribution and habitat use of both species. Therefore, the GPS tracking data provided an unbiased means to differentiate between grey seals, harbour seals and mixed groups at haul-out sites.

In Chapter 5, the fine-scale haul-out patterns within these grey seal haul-out sites are compared with those in harbour seal haul-out sites. The results show that fine-scale haul-out patterns in harbour seal and grey seal sites are species-specific and that both species avoid being too close to their conspecifics (i.e., they practice social distancing). This finding provides clues as to how these aggregations are shaped: compared to grey seals, harbour seals occur in lower densities and keep more distance to their nearest neighbour. As harbour seals are more prone to infectious respiratory diseases than grey seals (Gigliotti *et al*., 2022), the larger distances between harbour seals could potentially reflect a behavioural response to reduce pathogen transmission.

Besides its ecological value, this approach might also prove useful in a remote sensing context, as it allows to differentiate between the two species in imagery in which the resolution is too low to observe morphological characteristics (e.g., the shape of the head). This opens new possibilities to leverage lower-resolution imagery – such as public satellite imagery – to study and monitor these sympatric species. Furthermore, this approach can potentially also be applied to identify other species (such as other pinniped species or colony-forming birds) in satellite imagery. This could be particularly valuable in remote and inaccessible regions, where collecting higher resolution imagery using traditional aerial and ship-based surveys is extremely challenging.

The aerial images available for this study did not allow for a comparison between different seasons (i.e., feeding, breeding and moult), except for haul-out patterns of harbour seals in- and outside the breeding season (Supplementary Materials S6). Compared to non-pupping harbour seals, pupping harbour seals displayed both significantly lower densities and median NNDs. Unfortunately, for grey seals no imagery was available to compare haul-out patterns in different seasons. Furthermore, in the available data the haul-out sites were photographed only once, which prevented a detailed comparison of fine-scale haul-out patterns at different moments in time. Therefore, temporal (and tidal) effects could not be examined. However, the observed patterns were consisted across the different haul-out sites, which were photographed at different moments. Additional survey data is required to further study temporal variations and interspecific variation between haul-out sites.

Finally, some images of haul-out sites were available that potentially contained mixed groups of both grey and harbour seals. These mixed groups were categorized based on the distribution of approximately 80 individual grey seals and 250 harbour seals that were tracked with GPS loggers. However, grey and harbour seals could not be differentiated in the aerial imagery itself, due to the relatively low resolution. Therefore, the proportions of both species within the mixed groups could not be determined, and these mixed groups were excluded from the analysis. If higher resolution georeferenced data becomes available, a detailed analysis of these mixed groups could provide further insights into how these aggregations are shaped.

6.2 Relating the main findings to Arctic marine mammal monitoring

Despite the rapidly disappearing sea ice, it remains largely unclear how Arctic marine mammals are responding to these changing conditions (Chapter 2). This lack of knowledge can be partly explained by the vastness and conditions hostile for humans in the Arctic, which make it extremely challenging to locate marine mammals in this region, let alone record changes in ranges or species distributions. The remoteness and inaccessibility of the region further complicates collecting these data. In this section we sketch how the experimental work presented in Chapters 3–5, which was developed in a more easily accessible region (the southern North Sea) and leveraged data-rich marine mammal populations, can aid toward the monitoring of marine mammals in the Arctic.

Photo-identification methodologies can be effective tools to track marine mammals and study range shifts, as is shown in Chapter 3 for bottlenose dolphins in the Netherlands. However, as this approach requires to be in proximity with the animals, applying these methodologies in the remote and inhospitable Arctic is challenging. Furthermore, currently only few photo-identification catalogues exist for Arctic marine mammals, making it harder to compare opportunistically collected data with existing datasets, as was done in Chapter 3. Additionally, due to (i) the large population sizes of many Arctic marine mammals (particularly pinnipeds), (ii) vast distribution ranges and (iii) the inaccessibility of the region, it is unlikely that a representative sample can be collected to study range shifts on a population scale using photo-identification methodologies. Despite these challenges, photo-identification can be effective in specific scenarios – for instance when studying smaller isolated subpopulations – and some studies have applied this methodology on narwhals (Auger-Méthé *et al.*, 2010), belugas (Auger-Méthé *et al.*, 2010; McGuire *et al.*, 2020) and bowhead whales (e.g., Zeh *et al.*, 2002). Furthermore, individual Arctic marine mammals are occasionally found in new regions, as is for instance illustrated by (i) bowhead whale sightings off Ireland (de Boer *et al.*, 2017), (ii) the first ever record of a hooded seal birth in the Netherlands (unpublished data; Figure 6.1), and by multiple walruses that wandered through European waters (e.g., Figure 6.2; Brasseur *et al.*, in preparation). In these cases, photo-identification is a valuable tool to track such pioneering individuals, which in turn can be the first indicators of range shifts.

As photo-identification is of limited applicability and use in the Arctic, data on marine mammal distribution and abundance in this region is commonly collected by aerial and ship-based surveys (see Chapter 1). These survey efforts are generally directed at regions where marine mammals are historically known to aggregate. Despite their strong site fidelity, the distribution of Arctic marine mammals is expected to become less predictable as the sea ice continues to disappear (Kovacs *et al.*, 2011). Therefore – even though a decrease of sea ice will facilitate easier access to the region – traditional aerial and ship-based surveys might soon prove insufficient to monitor Arctic marine mammals: larger areas may need to be surveyed before marine mammals are located, which in turn will require more resources to be (re-) allocated to the data collection part of the research, and will therefore lead to larger amounts of data that require processing. To address these new challenges,

Figure 6.1 A hooded seal that was born on a sandy beach instead of the ice, on the island of Vlieland (the Netherlands).

Figure 6.2 A walrus hauled out a concrete pier in Harlingen (the Netherlands). She was observed at many locations throughout Europe, wounds and scars on her fore-flippers allowed for photo-identification. Although she appeared to be in healthy condition, she was later shot with a rifle in Norway, due to "concerns about her welfare and the public's safety".

both Chapter 4 and 5 set out to develop and test new tools to aid in marine mammal detection and monitoring that could be applied in the Arctic.

The methodology described in Chapter 4 allows to automatically process image data to provide accurate seal count estimates. This approach reduces the time required to manually process and interpret new data, and therefore potentially allows to reallocate resources to other parts of the research, such as data collection, which is particularly expensive in the remote and inaccessible Arctic. Furthermore, as the location of haul-out sites becomes less predictable, it might be necessary to survey larger areas, which will result in an increased amount of data that requires processing. An automated approach (such as the one presented in Chapter 4) allows to effectively process the expected increasing amounts of data. As some Arctic pinnipeds (such as walruses) occur in high numbers and densities at haul-out sites, a regression-based approach (that requires image-level counts) is particularly convenient, and it reduces the time required to generate a labelled dataset significantly. In some specific scenarios, cetacean surveys could also benefit from this approach, for instance in the case of belugas that occur in very high densities in fresh water estuaries during their moult. However, this approach also has limitations when applied in the Arctic. Some pinniped species in the Arctic are sympatric (e.g., harp and hooded seals). The approach presented in Chapter 4 is currently unable to make predictions for multiple classes simultaneously and is therefore unable to differentiate between species. The model could be configured to provide predictions for each species independently (as discussed in the previous section), but performance evaluation is subject to future research. Furthermore, the current model remains specific to given acquisition conditions (e.g., type of camera, angle of view and altitude). The influence of all these factors remains to be studied in details to see how robust the method would be when applied in the Arctic. Finally, some Arctic pinniped species (e.g., harp and hooded seals) occur in groups with a lower density that that of grey and harbour seals, and some species (e.g., ringed seals) are solitary, which reduces the benefits of a regression-based approach.

Using lower-resolution imagery could be an interesting lead to cover larger areas at a much lower cost. However, most individual marine mammals remain of small size and become undetectable in low-resolution imagery (generally at 10 m and above). Even in VHR satellite imagery, it is nearly impossible to differentiate most (smaller) marine mammal species. Nonetheless, by using prior knowledge on Arctic species distribution and haul-out locations, smaller marine mammals can in some cases be identified to the species level in this type of imagery. However, as marine mammal behaviour and distribution are expected to change as the sea ice disappears (Chapter 1), it might be increasingly difficult to predict the locations of marine mammal aggregations using such prior knowledge. Chapter 5 provides an alternative approach to differentiate between sympatric species, based on fine-scale haul-out patterns of pinnipeds, opening new opportunities to utilize this type of imagery in a rapidly changing Arctic. Moreover, using lower-resolution remote sensing imagery can have multiple additional benefits. For instance, when a specific region is photographed at a lower instead of a higher resolution, the total amount of data that requires processing (i.e., the total amount of pixels) is reduced. Furthermore, when lower-resolution images are sufficient, surveys can effectively cover larger areas with the same effort (e.g., cameras can use a lower focal length, or surveys can be flown at higher altitude). This is particularly beneficial in remote and inaccessible regions such as the Arctic, where survey costs are high. In the near future, using haul-out patterns (such as the density approach described in Chapter 5) might even allow to differentiate between pinniped species in satellite imagery: we discuss ideas in this direction in the next and final section of this manuscript.

6.3 Moving forward: detecting marine mammals from space

Remote sensing using satellite imagery has high potential: the data collection is repeatable, highly standardized and can be employed on spatial and temporal scales that are impossible to achieve using traditional aerial or ship-based methods (Pettorelli *et al.*, 2014). Furthermore, inaccessible areas that are challenging to survey using traditional aerial and ship-based methods can be monitored regularly when using satellite imagery, while also circumventing other (logistical) downsides, such as safety, carbon emissions and potential disturbance of wildlife. In this final section, potential avenues to move forward in this direction are reviewed.

Despite the potential of using satellite imagery in remote sensing applications, there are relatively few ecological studies that have used it to detect animals. In a literature review, Wang *et al.* (2019), reported only 15 studies to use satellite images to detect animals. Five of these studies focused on detecting terrestrial mammals (Yang *et al.*, 2014; Xue *et al.*, 2017; Platonov *et al.*, 2013; Stapleton *et al.*, 2014; LaRue *et al.*, 2017) and two on marine birds (Fretwell *et al.*, 2012; Fretwell *et al.*, 2017). But using satellite data to detect terrestrial animals is a blooming field (e.g., Duporge *et al.*, 2020; Wu *et al.*, 2023), and a sharp increase is also observed in literature considering marine animals: Khan *et al.* (2023) provided a summary of 29 studies that utilized satellite imagery to detect marine mammals. Of these studies, 17 focused on various species of cetaceans (Table 6.1), which are easier to detect than pinnipeds due to their larger size. One of the most notable examples is the work of Hodul *et al*, (2022), where a photo-identification match of an individual northern right whale was provided based on scarring patterns that were apparent even at such distance (Hodul *et al.*, 2022).

However, contrarily to cetaceans, pinnipeds occupy both the marine and the terrestrial realm, and often form seasonal aggregations on land or ice, which allows for easier detection. They are however significantly smaller than cetaceans. The highest resolution of satellite imagery that is currently available commercially is provided by the WorldView-3 satellite, which has a resolution of 31 cm panchromatic and 1.24 m multispectral. Despite this high resolution, detecting individual seals in the Arctic remains challenging (see e.g. Figure 6.3), as 31 cm resolution translates to a body length of only around 4 pixels for the smallest Arctic seals (the ringed seal, with some adults measuring just 1.0 m) to around 12 pixels for the largest Arctic pinniped (male walruses, which can grow up to 3.6 m).

Table 6.1 Overview of key papers on whale detection using satellite imagery, providing the species, sensor and image resolution.

Species	Sensor	Resolution	Source
orca humpback whales	IKONOS 2	0.8 m panchromatic 3.3 m multispectral	Abileah, 2002
bowhead whales	GeoEye-1	0.5 m panchromatic	Platonov *et al.*, 2013
southern right whales	WorldView II	0.5 m panchromatic 2.0 m multispectral	Fretwell *et al.*, 2014
sei whales	WorldView II	0.5 m panchromatic 2.0 m multispectral	Fretwell *et al.*, 2019
fin whales humpback whales southern right whales grey whales	WorldView III	0.31 m panchromatic 1.24 m multispectral	Cubaynes *et al.*, 2019
humpback whales southern right whales	WorldView III	0.31 m panchromatic 1.24 m multispectral	Borowicz *et al.*, 2019
unspecified whales	WorldView III, GeoEye-01, QuickBird-2, SPOT-6, US GeologicalSurvey orthoimagery, WorldView II	0.31 m panchromatic 1.24 m multispectral (0.15 m aerial)	Guirado *et al.*, 2019
unspecified whales	WorldView III	0.31 m panchromatic 1.24 m multispectral	Bamford *et al.*, 2020
beluga narwhal	WorldView III	0.31 m panchromatic 1.24 m multispectral	Charry *et al.*, 2021
northern right whale	WorldView III	0.31 m panchromatic 1.24 m multispectral	Hodul *et al.*, 2022
southern right whales humpback whales fin whales grey whale	WorldView II, WorldView III, GeoEye-1, Quickbird-2	various	Cubaynes and Fretwell, 2022

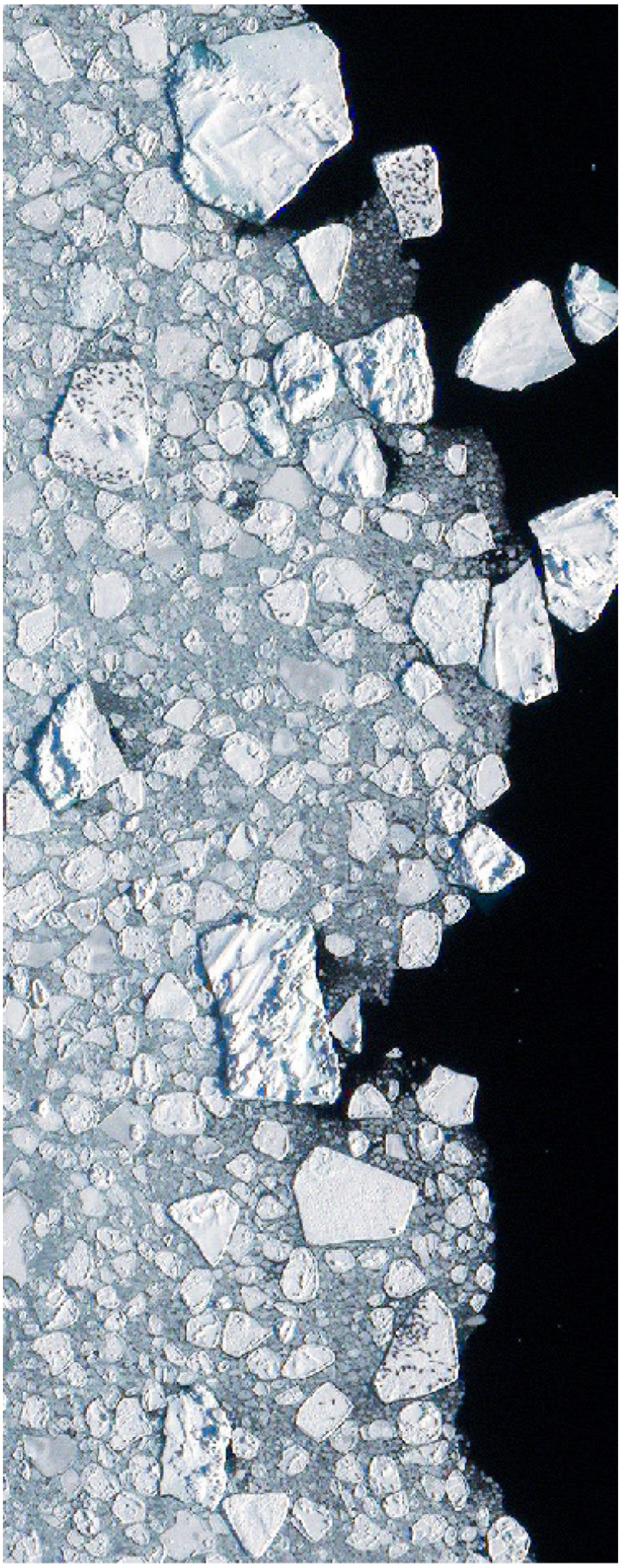

Figure 6.3 Arctic seals hauled out on the pack-ice, east of Greenland. Based on concurrent aerial surveys, it is most likely they are harp seals. Hooded seals are also present in these regions during the breeding season. © Maxar.

In the review provided by Khan *et al*. (2023), 10 out of 29 studies that utilized satellite imagery to detect marine mammals focus on pinnipeds, despite their smaller size. Walruses are relatively large and are known to periodically form very dense aggregations. Often, many individuals are laying against each other, forming a 'continuous mass', which allows for easier detection in satellite imagery (Figure 6.4; Figure 5.1; Lydersen, 2018). A regression-based approach (Chapter 4) could potentially be used to predict counts for these dense aggregations.

Multiple studies compared satellite-derived pinniped counts with aerial or ground counts, in order to verify pinniped detections on satellite imagery (LaRue *et al*., 2011; McMahon *et al*., 2014; Ainley *et al*., 2015; Fudala and Bialik, 2022). These studies show a strong positive correlation between the two counting sources, underpinning the potential of using commercial VHR satellite images to count pinnipeds. For the largest pinniped species – southern elephant seals *Mirounga leonine* – even males and females could be distinguished based on their sexual dimorphism, yet pup recognition was challenging (Fudala and Bialik, 2022). This resulted in many missed pups when using satellite imagery (i.e., false negatives), despite the large size of this species. As pup counts are the cornerstone of many pinniped monitoring schemes, this highlights an important limitation of using satellite imagery. Notably, if the disappearing sea ice causes Arctic seals to haul out on land – as is reported for walruses (e.g., Fischbach and Douglas, 2021) – it might make it easier to detect pups of some species (e.g., harp seals) as their light-coloured fur provides a high contrast against a dark background.

The manual processing of satellite imagery is a very labour-intensive – and therefore expensive – process. Some studies have therefore applied a citizen science approach to detect pinnipeds on satellite imagery (LaRue *et al.*, 2020). This can dramatically reduce the time and cost necessary to process the images, but the use of non-expert observers caused a high rate of false positives (LaRue *et al.*, 2020). Alternatively, Gonçalves *et al.* (2020) applied an automated approach to detect pinnipeds from satellite imagery, which was later improved by including a sea ice segmentation model (Gonçalves *et al.*, 2022). Both studies were unable to differentiate between four sympatric species, but still serve as first examples of the rapid recent developments in automated wildlife detection, thereby lowering the costs and time to process the images dramatically.

Figure 6.4 Walruses are known to periodically form very dense aggregations, with many individuals laying against each other, forming a 'continuous mass' of blubber and tusks.

Using satellite imagery to monitor pinniped distribution and range shifts shows great potential, as is supported by the examples above. However, some major challenges remain. Firstly, as satellite imagery allows for surveying larger areas, the amount of data that requires processing will also increase. Secondly, sympatric species are challenging to differentiate. This challenge will become harder for ice-breeding species, as the locations of haul-out sites become less predictable due to the disappearing sea ice. Thirdly, VHR satellite images are expensive; the price for 0.5 m resolution satellite imagery for example ranges from USD 14 to 29 per km^2 (Hollings *et al.*, 2017). Considering these challenges, I sketch the following approach for future surveys of Arctic pinnipeds as a combination of multiple data sources and methodologies.

Currently, aerial and ship-based surveys are directed at areas where marine mammals are known to aggregate, based on prior knowledge. However, due to the disappearing sea ice, these distribution patterns are expected to change, and large marine mammal aggregations might be missed. Freely available but low-resolution (10+ m), satellite imagery allows to scan large areas, potentially on a continental scale. The resolution of this type of imagery is too low to detect individual pinnipeds, but it can be used to detect potential, suitable habitats (i.e., specific sea ice conditions, proximity to the ice edge, etc.). This process could potentially also be automated (cf. Gonçalves *et al.*, 2022). After suitable sites are located, higher-resolution satellite images of these locations can be collected, within which seal aggregations can be detected. Automated detection algorithms can be applied to estimate seal counts in these images. By using regression-based approaches, similar to those presented in Chapter 4, labelling time can be reduced. Fine-scale haul-out patterns (i.e., densities within haul-out sites) can be leveraged to differentiate between species (Chapter 5). By leveraging the detections of pinniped aggregations from satellite imagery, the aerial/ship-based survey efforts can be directed towards areas of high interest, effectively replacing the current requirement of prior knowledge on the animals' distribution. Images collected during such surveys can subsequently again be processed automatically to provide more accurate counts (e.g., Chapter 4) and to detect well-camouflaged pups.

This proposed integrated approach remains a research idea for the future and will have to be thoroughly developed and validated. However, at this stage it seems particularly valuable in the face of climate change – as rapidly changing sea ice conditions will lead to less predictable haul-out locations – and holds the potential to survey large (possibly up to the continental-scale) regions, while reducing the chance that newly formed aggregations are missed.

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Supplementary materials

S1 – Supplementary materials for Chapter 3

Figure S1 Bottlenose dolphins in the Marsdiep, August 12th 2004. Photos by Rogier Kruger.

Figure S2 Bottlenose dolphins in the Marsdiep, September 9th 2004. Photo by Sophie Brasseur.

Additional supplementary materials for Chapter 3 (videos and images) can be found online.

S2 – Supplementary materials for Chapter 4

Table S1 Numerical results on the validation set of the otolith ring counting application, using various ResNet architectures, loss functions (Huber vs. MSE) and batchsizes (BS).

ResNet	Loss	BS	RMSE
18	Huber	84	2.47
18	Huber	16	3.69
34	Huber	64	2.55
34	MSE	64	2.58
34	Huber	32	2.43
34	MSE	32	2.54
34	Huber	16	3.66
50	Huber	16	3.34
101	Huber	16	3.33
152	Huber	12	4.03

Table S2 Numerical results on the validation set of the seal counting application, using various ResNet architectures, loss functions (Huber vs. MSE) and batchsizes (BS).

ResNet	Loss	BS	RMSE
18	Huber	100	4.48
18	Huber	64	4.38
18	Huber	16	5.21
34	Huber	64	5.50
34	MSE	64	5.45
34	Huber	32	5.28
34	MSE	32	7.62
34	Huber	16	10.01
50	Huber	16	7.06
101	Huber	16	8.84
152	Huber	12	9.90

S3 – Supplementary materials for Chapter 4

Wildlife counting is a domain that is typically dominated by object detection approaches. In this Supplementary materials S3, we compare the predicted counts on our 'seal test set' of an object detector (Faster R-CNN) with a regressor (as described in the main text for the 'Step 1 model'), both trained on a small subset of the available data.

Training an object detector requires individual seals to be annotated. Instead of annotating the entire seal dataset (987 images, containing 31,419 seals), we created a sub-set of 100 training images, randomly selected from 'seal subset 1' and 'seal subset 2' combined. This new sub-set contained 3,021 individual seals, that were then annotated individually using bounding boxes. Using these 100 images, we first trained a Faster R-CNN (Ren *et al*., 2015) on the bounding boxes directly. In detail, we split the images into non-overlapping patches of size 224x224 and trained on 16 patches at a time. We employed a ResNet-50 FPN as backbone and trained the model for 300,000 iterations with stochastic gradient descent and an initial learning rate of 0.01, divided by 10 after 100,000 and 200,000 iterations, respectively. During testing, we also predicted on patches of the same size and recorded the number of seals detected across all patches per image. Additionally, we trained a regressor (as described in main text for the 'Step 1 model') on the same 100 images and compared the predicted counts on the 'Seal test set'. The Faster R-CNN achieved an R^2 of 0.38 and an *RMSE* of 46.5 (Table S3). The poorest predictions were on images with a high number of (small) seals and images that contained many birds. The regressor performed significantly better Figure S3), with an *RMSE* of 32.2, although the R^2 was equivalent (0.36; Table S3). The results of this small-scale experiment are indicative that – for the seal application – a regression-based approach as the one presented here is a valid alternative for a detection/classification network. Furthermore, the annotation process by drawing bounding boxes took slightly over 8 hours, while obtaining image-level counts by manual counting took slightly over one hour.

Table S3 Numerical results on the test set of the seal counting application, using an object detector (faster R-CNN) and a regressor (as described in the main text for the 'Step 1 model')

	Faster R-CNN	**Regressor**
R^2	0.38	0.36
RMSE	46.5	32.2

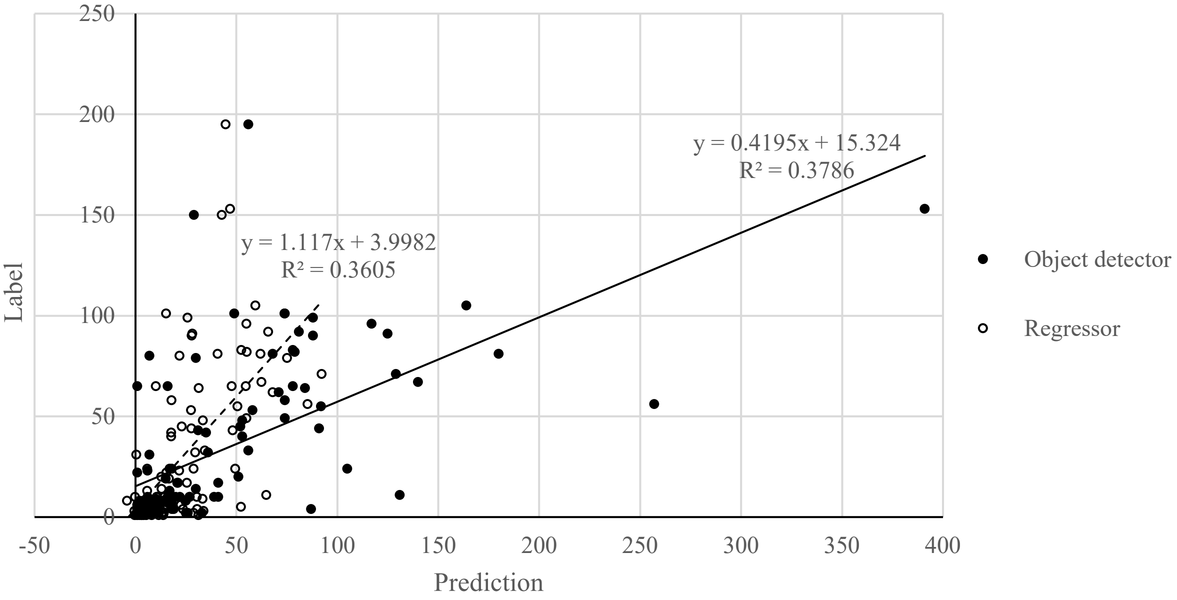

Figure S3 Numerical results on the test set of the seal counting application, where the labels (i.e., the manual counts of hauled out seals) are plotted against the predicted counts, using an object detector (Faster R-CNN, black dots) and a regressor (as described in the main text for the 'Step 1 model', white dots). Both are trained using a small subset (*n* = 100) of randomly selected images from 'seal subset 1' and 'seal subset 2' combined.

S4 – Supplementary materials for Chapter 4

In this Supplementary materials S4, we compare how our seal 'Step 1 model' compares to a model trained using a random training set, with the same number of images as 'seal subset 1', but sampled across the full distribution (including images with a high number of seals, similar as 'seal subset 2').

For this new model, we randomly selected 787 images from 'seal subset 1' and 'seal subset 2' combined. The 787 images in this new subset, named 'seal subset 3', now also include 32 images with 100+ seals. This 'seal subset 3' was then used to train a regressor, analogue to the 'Step 1 model' training described in the manuscript (but covering the whole range of animal counts). The resulting 'Step 3 model' slightly improved when compared to the 'Step 1 model' (*RMSE* = 22.3 instead of *RMSE* = 23.5; Table S4) but is still performing worse than the Step 2 model (*RMSE* = 19.0). Therefore, we argue that the increased performance can mostly be attributed to the iterative approach to model training (and an increased amount of training images) and not just to including the same types of images that appear in the test set. However, these effects are not mutually exclusive, and probably all contribute to the performance increase in the 'Step 2 model'.

Table S4 Numerical results on the test set of the seal counting application of the various models.

	Step 1	**Step 3**	**Step 2**
Number of training images	787	787	878
RMSE	23.5	22.3	19.0
R^2	0.7	0.7	0.8

S5 – Supplementary materials for Chapter 5

Overlapping polygons

In addition to the shuffling scenario described in the main text, we examined alternative shuffling methods. In the main text (see Methods section Chapter 5) overlapping polygons were rotated (1-degree increments) in an attempt to resolve the overlap. If the overlap was not resolved after this rotation, the polygon was moved slightly in a random direction with 10 cm increments until the overlap was solved. In this supplementary material, we name this scenario 'Random A', and test two additional scenarios to deal with polygons that overlap after rotation. In the second scenario ('Random B'), an overlapping polygon was removed and placed again, using the same placing strategy of Random A, until it found an unoccupied location. To some extent, this scenario mimics active social distancing: when polygons overlap (i.e., the polygon's 'chosen spot' is occupied), it samples a completely new location, thereby lowering the chance that it will end up very close to another polygon, whereas in Random A overlapping polygons result in laying very close to its original chosen (i.e., occupied) location. Finally, a scenario was included where polygons that overlapped after rotation were allowed ('Random C'). This scenario ignores the fact that seals in the Netherlands rarely lay on top of each other (Figure S4).

For the new shuffling methods (Random B and C), the NNDs were calculated and compared with the observed NNDs, analogously to the analysis in the main text for the Random A strategy: the proportion of the polygons laying within 25cm of each other in the observed and shuffled data set were compared by fitting a GLM to the data (also see Methods section Chapter 5). The resulting values for both the observed distribution and the randomized scenarios are presented in Table S5.

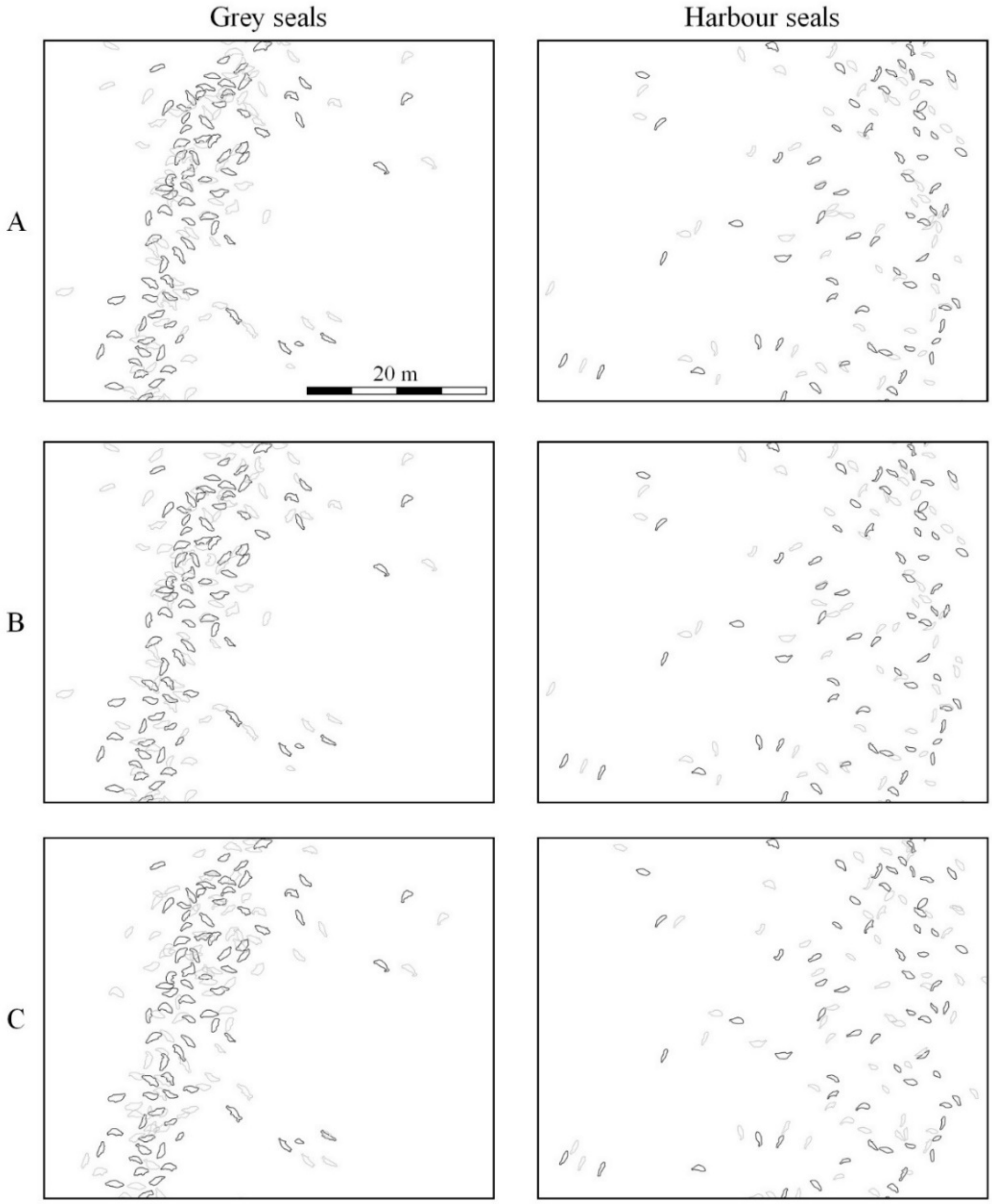

Figure S4 Example of original distribution (black) and shuffled distribution (light grey) of annotated grey seals (left) and harbour seals (right), for scenario Random A (top), Random B (middle) and Random C (bottom). Note that in Random C, polygons occasionally overlap.

Table S5 The results of the GLMs are provided for the observed NNDs and all shuffling scenarios (A, B and C), for both grey and harbour seals. Provided are the proportion (%) of polygons within 25cm of each other, as well as the z-values and p-values.

Scenario	**Grey seals (n = 3299)**			**Harbour seals (n = 1574)**		
	% (n)	*z*	*p*	*% (n)*	*z*	*P*
Observed	16 (537)	NA	NA	9 (148)	NA	NA
Random A	44 (1453)	23.8	< 0.001	22 (348)	9.5	< 0.001
Random B	22 (739)	6.275	< 0.001	10 (161)	0.779	0.436
Random C	48 (1579)	26.468	< 0.001	23 (359)	9.946	< 0.001

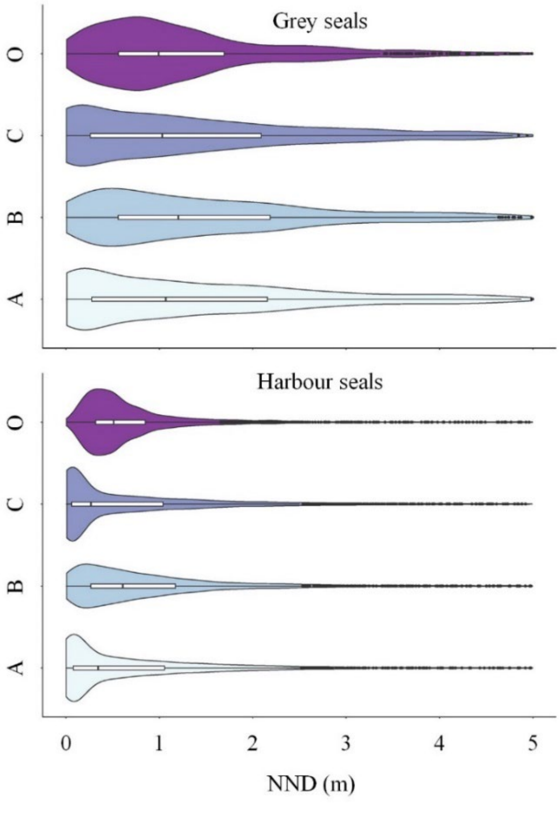

Figure S5 Distribution of NNDs for both the observed distributions (O) and all three shuffled distributions (Random A, B and C), for grey seals (top) and harbour seals (bottom).

For scenario Random B (where occupied locations are avoided, and therefore mimic social distancing), the proportion of polygons laying within 25 cm (Figure S5) is statistically different from the observed values only for grey seals (Table S5). For harbour seals however, no significant difference was found (Figure S5, Table S5).

For scenario Random C (where overlapping polygons are allowed), the proportion of polygons laying within 25 cm (Figure S5) is statistically different from the observed values, for both seal species (Table S5). Similar to Random A, this indicates that both species avoid the immediate proximity (<25 cm) of their neighbour.

S6 – Supplementary materials for Chapter 5

Harbour seals in- and outside the breeding season

While all images of grey seals were collected during their moult (in March), the images of harbour seals were collected both during their feeding season (February–May) and during their pupping season (June, not used for the results presented in the main body of the paper). This allowed for a comparison of pupping and non-pupping harbour seal NNDs.

Analogue to the approach described in the Methods section, we calculated the NNDs for the seals photographed during the pupping season, and tested if there was a significant difference in the median between the NNDs of pupping and non-pupping harbour seals by fitting a quantile regression model to the data, where 'pupping' was included as factor variable.

Furthermore, we calculated the number of neighbouring polygons present within different radii (1, 3, 5 and 10 m) for each polygon (as presented in the Methods section), and tested if there were significant differences between the densities of pupping and non-pupping harbour seals by fitting a GLM data, including pupping as factor variable

Table S6 Summary statistics (t-test median based on quantile regression) comparing the NND of pupping and non-pupping harbour seals.

Species	N	Sites	Mean (m)	Median (m)	t-test median
Pupping	349	1	4.29	0.59	t = -5.39 p-value <0.001
Non-pupping	1,574	5	1.62	1.06	

The pupping harbour seals displayed significantly lower NNDs than non-pupping harbour seals (Table S6). This is as we expected, as nursing harbour seals females have a single pup, which stays in very close proximity to its mother. However, the mother/pup pairs apparently are quite interspaced, hence the larger mean distance between individuals.

Table S7 Haul-out densities. The results of the GLM for all radii are provided, as well as the mean and median number of individuals and the 95% confidence interval (CI) for both species.

Radius (m)	**GLM (pupping × non-pupping)**	**Mean**		**95% CI**		**Median**	
		Non-pupping	*Pupping*	*Non-pupping*	*Pupping*	*Non-pupping*	*Pupping*
1	z-value = 0.69 p-value = 0.492	0.63	0.67	0.59-0.68	0.59-0.77	0	1
3	z-value = -14.1 p-value < 0.0001	3.30	1.31	3.15-3.46	1.18-1.45	3	1
5	z-value = -19.81 p-value < 0.0001	6.97	2.15	6.68-7.27	1.94-2.39	5	1
10	z-value = -26.54 p-value < 0.0001	18.34	4.46	17.62-19.10	4.03-4.93	15	3

For the density analysis, the number of neighbouring polygons present within a 1m radius around a focal polygon did not differ significantly between pupping and non-pupping harbour seals (Table S7). As for the differences in NND, this can also be explained by the close proximity between nursing mothers and their pups. These mother/pup pairs then generally avoid other seals, which is supported by the GLM results of the other radii. The number of neighbouring polygons present for 3, 5, and 10 m radii around a focal polygon were significantly lower for pupping harbour seals when compared to non-pupping harbour seals (Table S7).

These results show that fine scale haul-out patterns of harbour seals differ between seasons. The observed patterns could potentially be used to determine if a harbour seal colony is breeding, in imagery where the resolution is insufficient to differentiate between pups and adults.

S7 – Supplementary materials for Chapter 5

Map of the study area

The different haul-out sites used for this study (see Methods section) are found along the Dutch coast (Figure S6). Based on the GPS tracking data, the haul-out sites were identified as grey seal, harbour seal, or mixed (see Methods section Chapter 5).

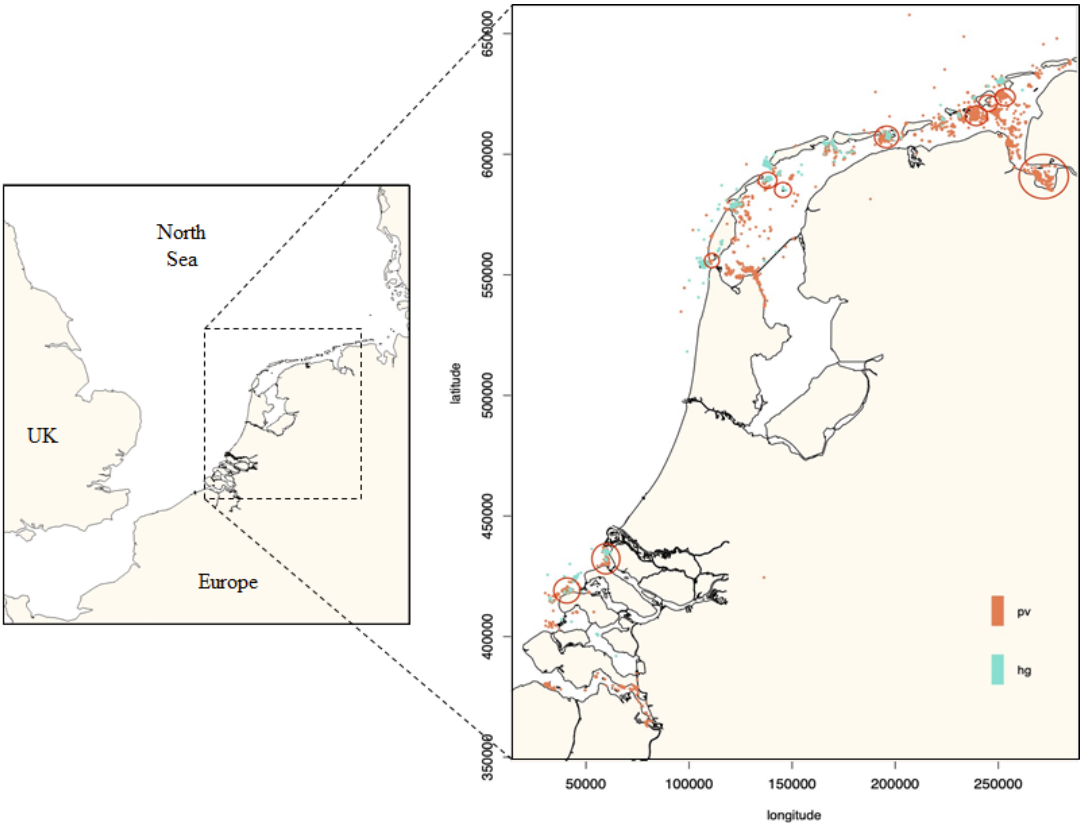

Figure S6 Study area. Map of the Netherlands, with GPS locations of harbour (orange) and grey seals (light blue). The red circles indicate the haul-out locations used in this study

Summary

The Arctic climate is changing extremely fast: as soon as 2035, the Arctic Ocean is predicted to be nearly ice-free. This is particularly problematic for Arctic pinnipeds (true seals, eared seals and walruses) that are dependent on the sea-ice for instance to rest and breed. How these animals will respond to these rapidly changing conditions, remains unclear and is highly unpredictable. Therefore, aerial and ship-based surveys might soon prove insufficient to monitor pinnipeds in the remote and vast Arctic.

This thesis aims to develop and apply methodologies for marine mammal monitoring, that can aid with studying distribution and range shifts. Data-rich marine mammal populations in the southern North Sea are used as 'model organisms' to test these new methods. The thesis addresses the following research questions:

RQ 1. Which changes in migration timing or distribution do Arctic migratory vertebrates exhibit in response to global warming?

RQ 2. How can opportunistically collected data contribute to a better understanding of range shifts in marine mammals? A bottlenose dolphin case study.

RQ 3. How can image-level annotations be leveraged to train a deep learning model to count pinnipeds from aerial imagery, and what is the accuracy of this approach? A grey and harbour seal case study.

RQ 4. How can fine-scale spatial haul-out patterns in pinniped haul-out sites be used as a tool to differentiate between sympatric species, when using low-resolution remote sensing imagery?

After a general introduction – where existing challenges and knowledge gaps are identified – the thesis contains four technical chapters:

Chapter 2. Migratory vertebrates shift migration timing and distributions in a warming Arctic

In Chapter 2, an extensive literature review discusses observed shifts in both migration timing and distribution of Arctic migratory vertebrates in response to climate warming. Very few species of marine mammals were found to shift the timing of their migration. Instead, most marine mammal species appear to shift their range in response to the changing environment. This chapter identifies

that large knowledge gaps remain, particularly for marine mammals, in terms of data-richness of observations and availability of open technology to monitor individuals in a semi-automated way. This finding underpins the urgent need to develop and test such new approaches to monitor these animals. The specific technologies are then explored in the following chapters.

Chapter 3. Bottlenose dolphins in The Netherlands come from two sides: across the North Sea and through the English Channel

Chapter 3 describes multiple case studies that apply photo-identification to examine distribution and range shifts in marine mammals, focussed on bottlenose dolphins. Photographs were opportunistically collected in the Netherlands and compared with images of dolphins from well-studied and data-rich neighbouring populations. The results provide proof that bottlenose dolphins observed in the Netherlands originate from two different populations (NE Scotland and Brittany, France). This evidence of previously unknown long-range movements may have important implications for the conservation and management of this species in European waters and highlights the importance to continuously monitor marine mammal distributions to identify potential range shifts.

Chapter 4. Counting using deep learning regression gives value to ecological surveys

In this chapter, computer vision and deep learning is used to automatically count grey and harbour seals from aerial images collected in the Dutch Wadden Sea. Most ecological studies that apply deep learning to detect and count animals, use data in which every individual animal is labelled to train a model. In this chapter, an alternative approach – based on deep learning regression – is presented, which uses image-level counts to train a model. As seals in these images occur in very high densities, this approach significantly reduces the time and costs required to label images for training. A unique aspect of this approach is that it can potentially leverage existing image-level counts (collected without the aim of deep learning applications) to train a model, thereby reducing the labelling time to zero.

Chapter 5. Stay close, but not too close: aerial image analysis reveals patterns of social distancing in seal colonies

Chapter 5 examines fine-scale haul-out patterns within grey seal and harbour seal colonies. Using aerial imagery, the nearest-neighbour distances and densities within the colonies were calculated and a detailed comparison between the two species was made. The results show that these haul-out patterns are species-specific: while both species avoid being too close to their conspecifics (i.e., practice social distancing), grey seals keep less distance from conspecifics than harbour seals do. Furthermore, the density of grey seals on land is twice as high as that of harbour seals. This finding sheds light on the mechanisms underlying colony forming, as larger distances between harbour seals could potentially reflect a behavioural response to reduce pathogen transmission. The species-specific haul-out patterns reported in this study can potentially also be used as a tool to differentiate between harbour and grey seals in remote sensing applications.

Photo-identification methodologies can be effective tools to track individual marine mammals, but applying this approach in the Arctic is challenging. It remains however a valuable tool to track pioneering individuals entering new areas, which in turn can be the first indicators of range shifts. Automated approaches to count Arctic pinnipeds reduce the time required to manually process new data – which are expected to increase due to uncertainties surrounding expected range shifts – while the increase in processing costs (i.e., computing time to make predictions) remain negligible. It could also aid in processing new sources of big data, such as satellite imagery, which would be particularly beneficial in this remote and inaccessible region. Leveraging species-specific fine-scale haul-out patterns might even allow to differentiate between pinniped species in this satellite imagery. Therefore, the methods presented in this thesis can contribute to a better understanding of Arctic pinniped distribution and expected range shifts.

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List of publications

Ben Chehida Y, Stelwagen T, **Hoekendijk JPA**, Ferreira M, Eira C, Torres-Pereira A, Nicolau L, Thumloup J, Fontaine MC. 2023 Harbor porpoise losing its edge: Genetic time series suggests a rapid population decline in Iberian waters over the last 30 years. *Ecology and Evolution* **13(12)**, e10819.

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review/project proposal (4.5 ECTS)

- Automated pinniped counts: a machine learning approach to count seals from aerial and satellite imagery

Post-graduate courses (6.3 ECTS)

- Consumer resource interactions; PE&RC (2018)
- Machine learning for spatial data; PE&RC (2019)
- Practical deep learning for coders; Fastai (2019)
- Cutting edge deep learning for coders; Fastai (2019/2020)
- HPC basic; WUR (2023)

Laboratory training and working visits (2 ECTS)

- Machine learning; Wageningen Food & Biobased Research (2019/2020)
- Seals from space; British Antarctic Survey, Cambridge (2019/2020)

Invited review of journal manuscripts (1 ECTS)

- Journal of Marine Science: regional scale patterns in marine mammals (2017)

Competence, skills and career-oriented activities (2 ECTS)

- Training course on marine remote sensing in Svalbard; SIOS (2019)
- Workshop computer vision for marine bird detection; WMR (2022)

Scientific integrity/ethics in science activities (0.3 ECTS)

- Integrity workshop; NIOZ (2022)

PE&RC Annual meetings, seminars and the PE&RC retreat (1.2 ECTS)

- PE&RC Last year retreat (2023)
- Netherlands annual ecology meeting (2020)

Discussion groups/local seminars or scientific meetings (7.5 ECTS)

- Zeezoogdierdagen Texel (2019)
- Netherlands annual ecology meeting (2019-2023)
- Machine learning discussion group NIOZ (2019-2023)

International symposia, workshops and conferences (3.2 ECTS)

- World marine mammal conference; Barcelona (2019)
- The Dutch conference on computer vision; Wageningen (2019)
- Imaka; Groningen (2023)
- Pool tot pool symposium; Leiden (2023)
- Seal rescue; Texel (2023)
- NWO Polar symposium; Den Haag (2023)

Societally relevant exposure (7.2 ECTS)

- Newspaper: Trouw, Volkskrant, NH Dagblad, Financieel dagblad FD talenten (2018, 2022, 2023)
- Radio: Vroege Vogels, 3fm, Op1 (2019, 2023)
- Blog: Whale scientists (2020)
- Blog: IFLS (US) (2022)
- CNN (Brasil) (2023)
- Al Jazeera (US) (2023)
- VICE News (US) (2023)
- Newspaper: Guardian (UK) (2023)
- International press release: Reuters (2023)
- TV: EenVandaag, NOS, NOS Jeugdjournaal, Hart van Nederland (2023)
- NH Nieuws (2023)
- Online: Nu.nl (2023)
- Radio: WOMR (US) (2023)

Lecturing/supervision of practicals/tutorials (0.3 ECTS)

- Seminar Utrecht Bioinformatics Center

BSc/MSc thesis supervision (4 ECTS)

- Wadden Sea seals from space
- Social distancing seals

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