Moving towards an Agent-based movement model for harbour seals in the Netherlands

Definition of knowledge gaps and initial development of AgentSeal NL

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Wageningen University & Research report: C054/23

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Wageningen Marine Research

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Photo cover: Tagged seal hauling out with another seal (S.Hielkema)

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Contents

Summary

Marine top predators play a crucial role in the North Sea ecosystem. Top predators may exert pressure on the lower trophic levels, so called top-down pressure as they feed. On the other hand, changes in the lower trophic levels may eventually propagate through the system and influence these top predators, causing for example changes in population or distribution. Top predators are therefore frequently used as ecosystem sentinels. Historically, humans have heavily depleted the higher trophic levels in the marine environment. Direct hunting has been the main cause of decrease of top predators in the past centuries. While several marine mammal populations have been recovered from these pressures, human activities at sea including fishing, oil and gas exploration, and the construction of offshore wind farms might again affect the populations, potentially influencing their pivotal role in marine ecosystems. In this report we investigate how Agent-Based Models (ABMs) could potentially be used to predict population-level responses to changes in the environment, like these types of human activities.

An ABM mimics species in their behaviour and (population) development as accurately as possible (i.e., digital twins), however, to build such a model extensive data are needed. The harbour seal population in the Netherlands has been monitored for decades and compared to other areas, many seals have been tracked, giving us a unique insight in the seals' population development and habitat use. Moreover, data on their diet and prey abundance, and other environmental factors such as bathymetry and sediment composition are available at a reasonable detail. In many cases additional data can be obtained from literature though essential data on for example life history, energetics and actual prey distribution are still missing. Throughout this project we have attempted to fill several important data and knowledge gaps.

In Chapter 2 we report on seal diet studies based on existing data (2.1) and using novel molecular e-DNA techniques (appendix 1). Collating existing data on fish distribution and abundance based in demersal fish surveys (2.2) and using this to estimate the top-down effect the harbour seals potentially have on the lower trophic levels they feed on (2.3). Here we find that if all estimates are correct the seals may locally deplete their prey to up to 50% (appendix 2). Finally, we report on a new research project initiated to determine the prey biomass in more detail by using a sampling method (triple D dredge) more appropriate to accurately sample small demersal fish, like sandeel, that form the most important prey of seals in the North Sea.

In Chapter 3, we describe the deployment of accelerometers and the development of techniques to extract biologically meaningful data from such tracking devices. But first, we compile all historical "traditional" telemetry data on distribution and diving behaviour that can be used to inform an ABM (3.1). Despite this, there are gaps in our understanding of where and how seals move, such as when fleeing or hunting. To facilitate the collection of such information, new transmitters are required. We deployed 5 accelerometer-equipped tags in this study (3.2). These accelerometery transmitters were used to aid in the development of the algorithms required to transform high-volume accelerometery data into biologically relevant summary data that could be transmitted via GSM network (3.3). Special care was taken to distinguish between the static (body orientation) and dynamic (body motion) components (Appendix 3). Based on existing data from recovered accelerometers, the method devised in Appendix 3 was then applied to classify harbour seals' behavioural states (Appendix 4).

In chapter 4 we report on how behavioural changes in seals caused by piledriving of wind turbines can be studied and how the effects could be quantified (Appendix 5). Here we use the data of seals that were intentionally tracked to study the effect of offshore wind farm construction (Gemini, Luchterduinen en Borssele wind park) and fortuitous data when animals were moving in areas where piledriving was ongoing. When mitigations were in place (i.e., most offshore windparks, except for those constructed in the early days, like Gemini and Luchterduinen), very few behavioural responses were apparent. However, this was mostly because very few seals venture in the direct vicinity of the constructed wind farm, which suggests avoidance of the park even before pile-driving commenced,

which could be because seals avoid the area based on previous exposure events or because they hear the preparation activities prior to pre-piling.

In the final chapter 5, we describe the Agent Based Model. First, in collaboration with international partners, we helped to develop an Agent Based Model for harbour seals (AgentSeal), which was first tested on seals foraging along the east coast of Scotland (Appendix 6). Next, the model was adapted for harbour seals hauling-out in the Dutch Wadden Sea and foraging in the adjacent North Sea. This included information on the distribution of haul-out sites, the location of obstacles (like island and intertidal mudflats) and a map of habitat suitability used as a proxy for the prey landscape. The ABM was used to simulate the movement, foraging and resting behaviour and physiological state (mass and energy reserve) of seals. One of the most critical elements of such an ABM is how much food seals can extract per unit of time, which depends on many variables, including the prey density, prey quality and the detection and capture probability. In this study, we varied the food richness. There appears to be a tipping point, where reduction in foraging efficiency (either due to lower food availability or lower catching efficiency) can rapidly lead to energy loss and mortality.

Individual-Based or Agent Based Models are the most promising tools for reconstructing the behaviour and physiology of animals, as well as examining the effect of human activities on population viability. However, even though such an ABM may be the best available tool, it remains difficult to estimate the absolute effect of human activities on marine mammals, primarily due to incomplete information, the existence of complex feedbacks (e.g., between predators and preys), and the complexity of ecosystem processes. For instance, human disturbance can result in lost foraging opportunities and increased competition elsewhere, but it can also reduce predation pressure in the impacted area, thereby positively or negatively influencing future foraging opportunities. Instead of attempting to estimate the absolute impact of non-lethal human activities, which is nearly impossible anyway, ABMs (such as AgentSeal) could be used for scenario studies and hypothesis testing. Such models could be used, for instance, to determine during which season marine mammals are most susceptible to disturbances and which regions or habitats have the greatest impact on population size. Currently, most impact assessments are based on local seal density, but the integration over time is entirely ignored. Even if the population density is low, some low-density areas may provide a lot of food for seals and be a key factor in the size of the population. For example, regions along the outer edges of their foraging distribution might receive low usage but could be critical for seals in periods when food is scarce (or energy demand is).

1 Introduction

1.1 Background

Gemini offshore wind farm is located in the Dutch part of the North Sea, 85 km north of the coast of Groningen, 60 km north of the island Schiermonnikoog (Figure 1.1). The Gemini wind farm consists of 150 wind turbines, totalling 600 MW and two offshore high voltage stations. Start of construction was mid-2015. Gemini was fully operational since 2017. The Environmental Impact Assessment for Gemini indicated that effects on harbour seals due to noise emission during offshore pile driving could not be ruled out beforehand (Burggraaf-van den Berg *et al.,* 2012). The impact zone for harbour seals was studied in detail in an Appropriate Assessment of Gemini. In this assessment, it was concluded that the animals can for the most part avoid the noise disturbance, both in terms of time and area, and therefore that effects on the conservation objective of the harbour seal were estimated to be non-significant (Arcadis 2012).

Figure 1.1. *General map of Gemini site in relation to the Wadden Sea*

To address some remaining knowledge gaps, Gemini Wind Park designed an environmental monitoring program. One component of that program was to study the possible effects of the construction on seals in and around the wind farm due to underwater noise using GPS data loggers. The study provided data for 30 harbour seals and over 800 days of tracking data (Brasseur *et al.,* 2018a). The report concluded that Individual Based Models (IBMs) or Agent Based Models (ABMs) designed using data on seal behaviour, distribution and abundance can be used to estimate and predict the effect of human activities on marine biota. However, before such predictive ABM can be developed for harbour seals in the Netherlands, some knowledge gaps needed to be addressed first. The objective of this study is to develop a framework and address some of the key knowledge gaps.

1.2 Addressing population level effects of human activities on marine top-predators

As top-level marine predators, marine mammals and seabirds are frequently referred to as "charismatic megafauna" (Reynolds *et al.*, 2009), and they play a crucial role in marine ecosystems. Changes in the marine system, such as changes in primary productivity at lower trophic levels, may eventually propagate through the system and influence these top predators. Consequently, marine mammals and birds have frequently served as ecosystem sentinels (Moore, 2008). These species groups can identify productivity hotspots, reflect changes in food webs, and accumulate contamination that can be used as a surrogate for environmental pollution. As top predators, they may also exert pressure on marine ecosystems feeding on lower trophic levels.

Both marine mammals and seabirds have been heavily hunted over the past two centuries, resulting in dwindling populations. Consequently, during and immediately after the era of intensive hunting, their top-down effect on marine systems was relatively small, especially when compared to total fishing pressure (Engelhard *et al.,* 2014). Increases in populations of marine mammals and seabirds as a result of the reduced hunting pressure, however, might eventually allow the top predators to re-establish their dominance of the marine food web (Baum and Worm, 2009; Aarts et al., 2019).

Other human pressures, such as fishing, oil and gas exploration, and the construction of wind farms, may however jeopardize the anticipated recuperation of the populations or even threaten them. Here, we investigate how Agent Based Models could potentially be used to predict population-level responses to changes in the environment such as these types of human activities.

1.3 Agent Based Models

Many processes in nature are stochastic. As a result, individuals may experience different prey encounters at the same site, which is likely to influence their future decision to return to that site or choose another patch. The movement of individuals, is also, at least partly, random. As a result, the accumulation of knowledge and experience is a stochastic process also. Finally, the behaviour of one individual, will influence the behaviour of others. These interactions can be direct or indirect, and positive and negative. For example, prey depletion at a patch by one individual, will influence prey density for others. Any model other than an Agent Based Model or ABM would be incapable to capture such random processes.

ABMs focus on individuals or agents and how they interact with their surroundings, which can also be allowed to be highly dynamic). ABMs are bottom-up models that are typically centred on the mechanisms that drive behaviour and physiology, while population distribution and abundance are emerging properties. Most ABMs are intended to imitate species as accurately as possible (i.e., digital twins), and in theory, all relevant characteristics of an individual and how it interacts with its environment can be included.

1.4 Knowledge gaps

Individual based models are typically data hungry. A perfect model would require detailed data on the needs of the individual to feed, rest or grow but also on the environmental variables including (in the case of seals) water depth, haul out locations but also distribution and abundance of prey and changes herein. Ideally it would also include mortality, reproduction, and other seasonal patterns, enabling to mimic changes in population development observed.

The harbour seal population in the Netherlands has been monitored for decades and compared to other areas, many seals have been tracked (see chapter 3.1 for an overview), giving us a unique insight in the seals' population development and habitat use (Brasseur *et al.*, 2018a; b). Moreover, data on (commercial) fish, and other environmental factors such as bathymetry and sediment composition are available at a reasonable detail. In many cases additional data can be obtained from literature, though some essential data is still missing. In this project we report on the different aspects we have attempted to study, ultimately enabling the construction of a realistic ABM model for the harbour seal in this region.

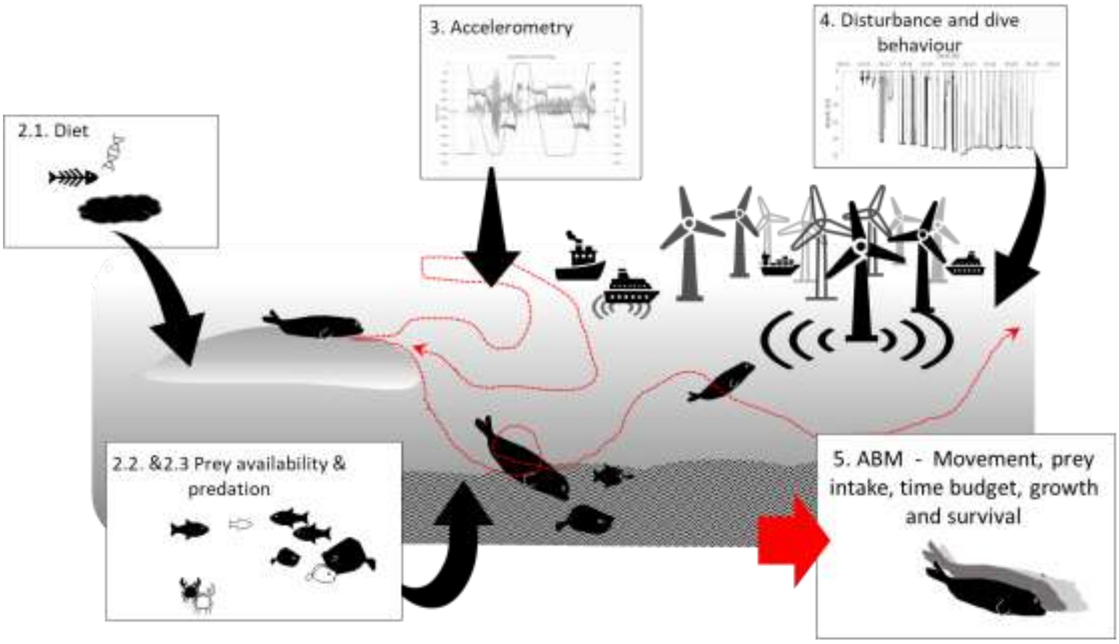


***Figure 1.2**. Overview of the studies treated in this report*

Various knowledge gaps are addressed in this report (Figure 1.2). The primary reason seals leave the Wadden Sea and venture into the North Sea is to find and catch prey. Therefore, information regarding the diet of seals (Chapter 2.1), the amount of available prey (Chapter 2.2) and whether prey availability could potentially be a limiting factor (i.e., whether there is evidence for density dependent effects) is required (Chapter 2.3). These studies revealed that estimates on the absolute availability of small prey species (such as sandeel) are still lacking, and as a result, a research proposal was developed. Also unknown is how harbour seals locate and capture prey, which has led to the development of accelerometery trackers (Chapter 3.1) and new methods for analysing such high-resolution data (Chapter 3.2). In addition to prey, anthropogenic disturbance also affects the distribution and behaviour of seals at sea. Using pile-driving data from German parks, we studied harbour seals' behavioural responses to the construction of wind farms (Chapter 4). However, since noise mitigation was in place at most other parks studied and few harbour seals venture into the parks' immediate vicinity, insufficient data were available to quantify population-level responses. Finally, in collaboration with an international team, an Agent Based Model for harbour seal (AgentSeal) was developed, and this model was subsequently adapted for seals in the Netherlands (Chapter 5). The estimation of the effect of absolute prey availability on fitness was given special consideration.

Here we report in the following chapters:

Chapter 2
- 2.1 Amelioration of diet studies, using new molecular techniques, e-DNA,
- 2.2 Measurement of available prey biomass
- 2.3 Estimating effects seals have on the biomass of their prey,

Chapter 3
- 3.1 Development of the use of accelerometery in current tags
- 3.2 Defining a smoother to analyse accelerometery data

Chapter 4
- Studying the effect of a human activity (pile driving) on the seals' behaviour

Chapter 5
- Development of an ABM for the harbour seals

2 Seal diet and prey distribution

Seals travel out to sea in search of prey. In this chapter we use data from fisheries surveys to estimate the abundance and distribution of their prey. Ideally, these prey-field data should be included in the ABM. However, the spatial resolution of the fish survey data is currently inadequate. The 'sandeel and seal' project was designed to address this knowledge gap. Estimating the energy landscape with more precise data on sandeel and other small demersal fish species is one of the anticipated outcomes. In the future, such a landscape of prey-energy can directly feed into the ABM.

2.1 Seal diet

To understand an animals' requirements and its role in the ecosystem, knowing what an animal feeds on is imperative (Pierce and Boyle, 1991; Trites, 1997; O'Boyle and Sinclair, 2012; Foo *et al.,* 2016; Trites and Spitz, 2018). However, as marine animals like seals feed at sea, it is complicated if not impossible to obtain direct information on the animals' dietary choices. Therefore, knowledge on diet is usually obtained via several indirect methods. These include methods to approximate diet, for example using stable isotopes $N^{14/15}$ ratio to determine the trophic level at which the animals feed on and with the $C^{12/13}$ ratio the proximity to coastal areas (Young and Ferguson, 2014; de la Vega *et al.*, 2016; Duffill Telsnig *et al.*, 2019). Depending on the tissues analysed, samples may represent recent feeding (i.e., from blood) or provide information on former feeding, even years back (i.e., teeth and baleens). Also, methods based on fatty acids that can or cannot be synthesised by the animals themselves have been developed, giving more detail on likely prey items, though the time scale is usually up to several months corresponding to the feeding seasons of the animals (Madgett *et al.*, 2019; Dannenberger *et al.*, 2020; Ross *et al.*, 2022; Stewart *et al.*, 2022). Finally, the most straightforward diet studies are based on analysis of stomach contents or scats, where the composition of the last meal is inferred from prey remains found. Especially the shell (of crustacean and molluscs) and bone (of fish or birds and mammals) remains have proven useful for identification and even estimation of prey size (Härkönen and Heide- Jørgensen, 1991; Kavanagh *et al.*, 2010; Scharff-Olsen *et al.*, 2018; Wilson and Hammond, 2019).

However, all the diet study methods do have some issues. For example, in theory the fatty acid composition of all potential prey and how these may vary with growth or season, should ideally be known to identify them when studying the fat tissues of the predator. Also a prey library to compare bones and shells is needed when studying the contents of stomachs and scats. Moreover, the recognition of prey remains requires highly skilled analysts, and even then, the complete analysis of one sample may require a days' work or more. In many cases the different methods are combined creating a more complete image of the diet (Madgett *et al.,* 2019; Ross *et al.,* 2022)

Biases involved also need to be considered as for example though often used, the stomach contents of stranded animals might show what a dying animal would eat rather than a healthy one. More importantly only robust remains can be found in scats and stomachs, so potentially when prey lack these or when the predator only consumed the soft parts of a prey, traces remain undetected.
To circumvent the latter issue, and potentially to facilitate and speed up the recognition of prey, new genetic techniques DNA metabarcoding could be developed. These would be targeting fragmented DNA of consumed prey (e-DNA), and could be used alongside scat/ stomach contents analysis to identify prey that lack digestion-resistant hard parts, prey that are more problematic to quantify (Tollit *et al.*, 2009) or to identify the species or sex of the predator (Wilson and Hammond, 2016). Studies are still needed to identify the best fragment of DNA to use, develop protocols and better understand if and how the amount of DNA could translate into prey quantity (Sørlie *et al.*, 2020; Thomas *et al.*, 2022).

In this study (Heidstra *et al., in prep*; Appendix 1) we investigated methods to infer the diet composition of the harbour seal *Phoca vitulina* and grey seal *Halichoerus grypus*, based on their faecal remains. Here we used both the traditional hard part analysis and DNA techniques for this. While hard part analysis is unique to determine prey size, it is, as said above, both labour intensive and inefficient in detecting species when hard parts are worn by digestion or only soft parts are ingested. We used frozen faecal samples collected in the wild (2011 - 2018) along the Dutch coast. Different methods were used to dissolve faecal samples and extract the genetic material: Ethanol followed by freeze-drying and phosphate-buffered saline (PBS). PBS was a better solvent, as Ethanol seemed to react with the faecal material, creating a paste which strongly adhered to hard parts complicating morphological identification. The Qiagen Fast DNA Stool Kit was used to extract DNA. To identify prey DNA, a ~75 base pair fragment of the 16S mt DNA was used. This fragment targets many chordate species, including seals. therefor a blocking primer was added to block the seal DNA. Next Generation Sequencing was used to sequence all amplified faeces DNA. Faecal samples were also washed and remaining hard parts were examined and brought to species level. By comparing the analysis of hard parts with that of DNA, we were able to obtain a (more) complete insight into the diet of harbour and grey seals identifying more species in the scats than could be identified by recognising the hard remains of the prey (Figure 2.1). Also, the DNA technique we developed allowed for multiple samples (over 90) to be analysed at once, reducing analysing time. The inspection of the hard parts has not become redundant however, as the size of the bones (especially the otoliths or ear bones of fish) remains the only way to estimate prey size.

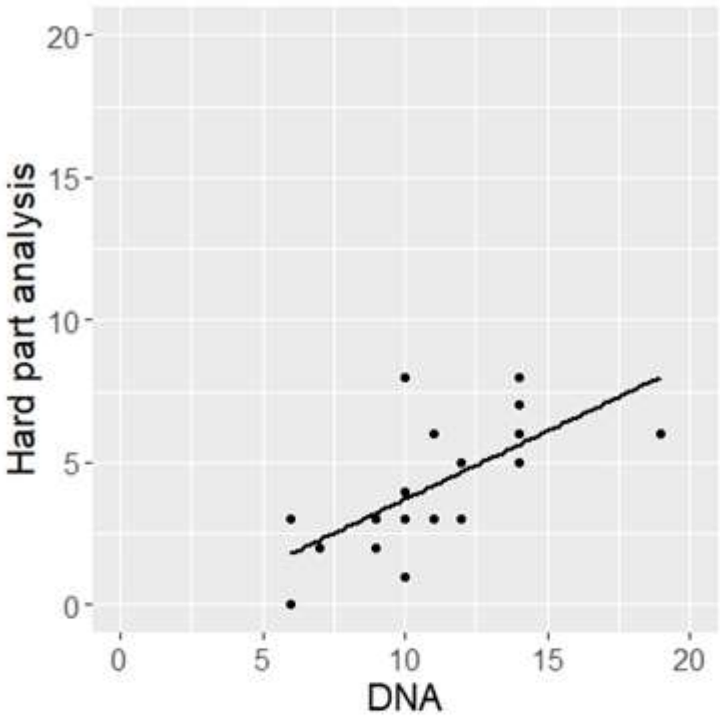


Figure 2.1 *Scatterplot showing species richness (S): Hard-part analysis (HPA) versus molecular analysis (DNA). Seal (host) species included. S was significantly higher when analysing faecal samples using DNA (paired-test: t = -12.516, df = 18, p = 2.556e-10).*

Based on earlier analysis (1999-2009) prey species identified in harbour seal scats collected throughout the Dutch coasts were summarized (Figure 2.2). The relative importance of the different prey for the seals can be expressed in the number of fish eaten, based on number of otoliths, or biomass, estimated length and weight (Aarts *et al.,* 2019). The latter can be derived using bones (most often otoliths) to estimate the length calculating weight base on existing standards of the prey. In the results, we see that though many sandeel otoliths were found, flatfish, specifically flounder, is of more importance for the seals in terms of biomass during the indicated study period. Interesting as well is the size distribution of the consumed prey, though on some occasions the seals do eat larger fish, most of the prey is smaller than 20 cm (Figure 2.3).

In general, harbour seals seem to feed mainly on non-commercial demersal fish species or size classes, i.e., these are prey that are generally not consumed by humans, either they are below the minimum landing size or non-commercial species.

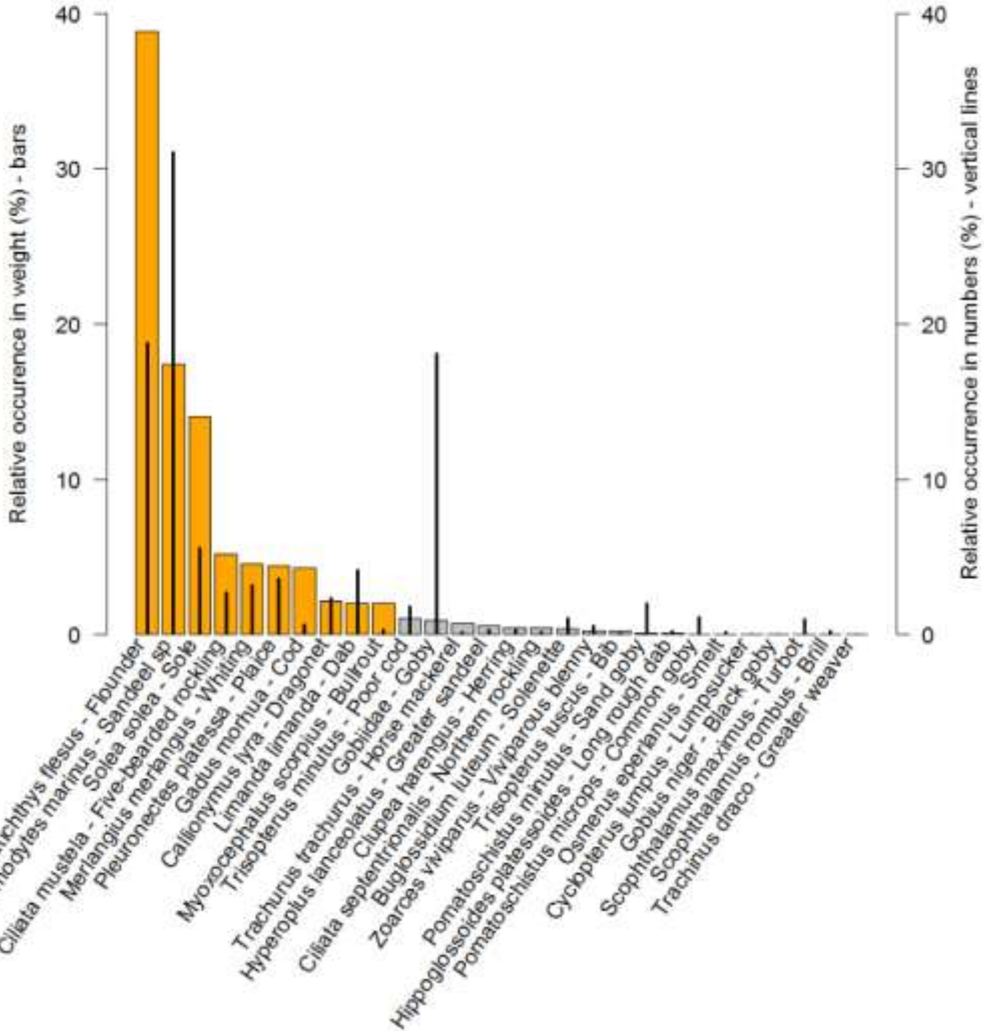


Figure 2.2. *The occurrence of fish species found in harbour seal scat samples collected in the Dutch Wadden Sea (1999-2009). These are defined as percentage of estimated fresh weight (bars, left axis) and relative number of otoliths (vertical lines, right axis) The 10 most important prey species (95% of biomass in the diet) are indicated using orange vertical bars (Aarts et al., 2019).*

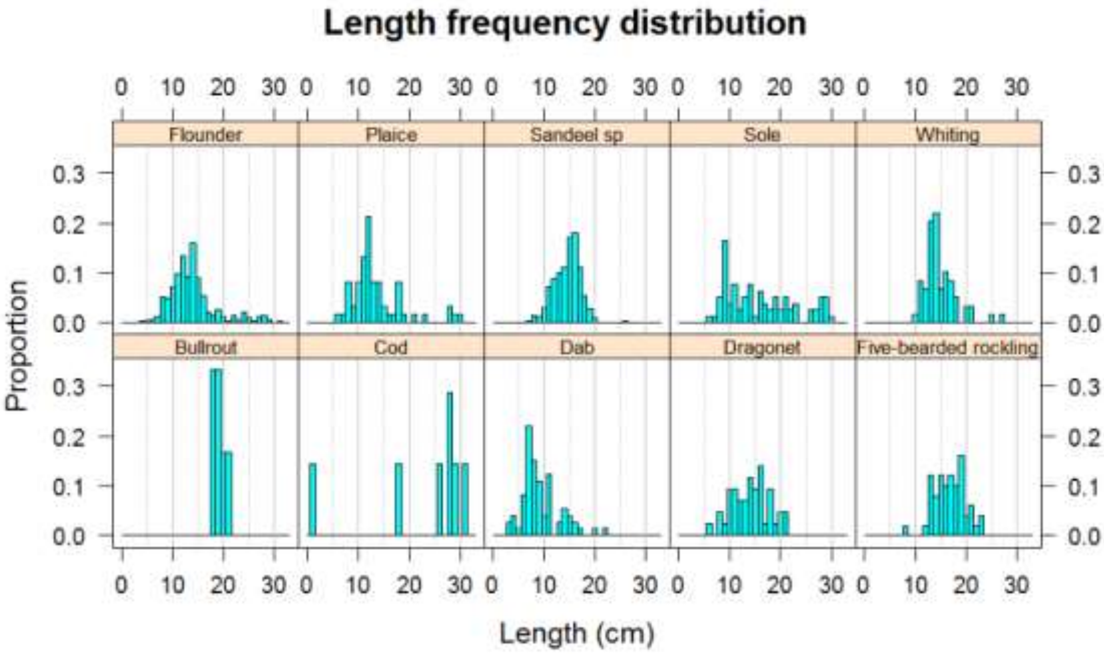


Figure 2.3. *Length distribution of the 10 most common fish species found in scat samples of harbour seals, collected 1999-2009 (Figure 2.2) (Aarts et al., 2019).*

2.2 Prey distribution and biomass

One of the reasons for estimating the prey distribution and biomass was to use these as input into the individual based model. Therefore, in this project we did collate all fish survey data collected within the Wadden Sea and adjacent North Sea (see Appendix 3 for more details). Data from two fish surveys were used; the demersal fish survey (DFS) and the Dutch beam trawl survey (BTS) (see Figure 2.4. for distribution of sample locations). The DFS has been conducted annually in September-October since 1970. The DFS covers the Wadden Sea and coastal waters (up to 25 m depth) from the southern border of the Netherlands to Esbjerg in Denmark (van Beek *et al.,* 1989). In the Wadden Sea, fishing was restricted to the tidal channels and gullies deeper than 2 m. The gear used is suitable for smaller demersal species (<20cm), but suboptimal for pelagic species such as herring and sprat. The Dutch BTS covers the central North Sea and is designed to sample the older flatfish species (i.e., ≥1 year old). Compared to the DFS, the BTS is carried out with a larger beam trawl (8 m), a higher speed (4 knots) and a larger mesh size of 120 mm, with 40 mm stretched mesh cod end (Rogers *et al.,* 1998). The data collected in quarter 3 (July- September) were used since this reflects the abundance of fish prior to the feeding season in the winter.

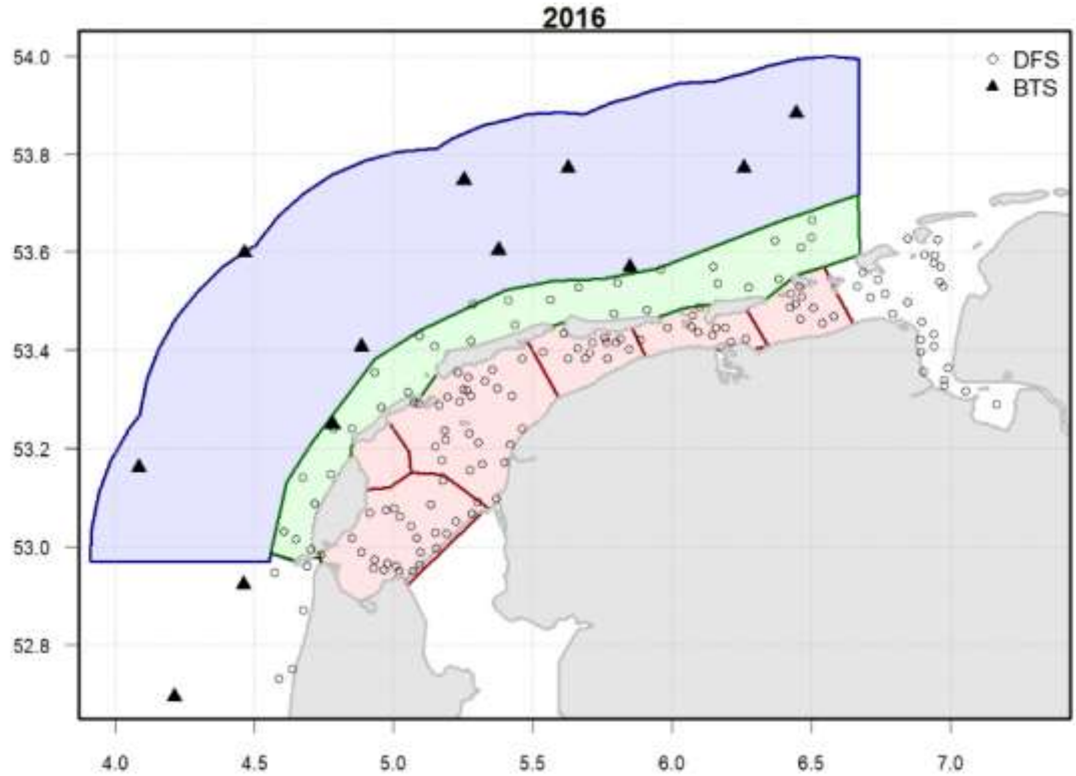
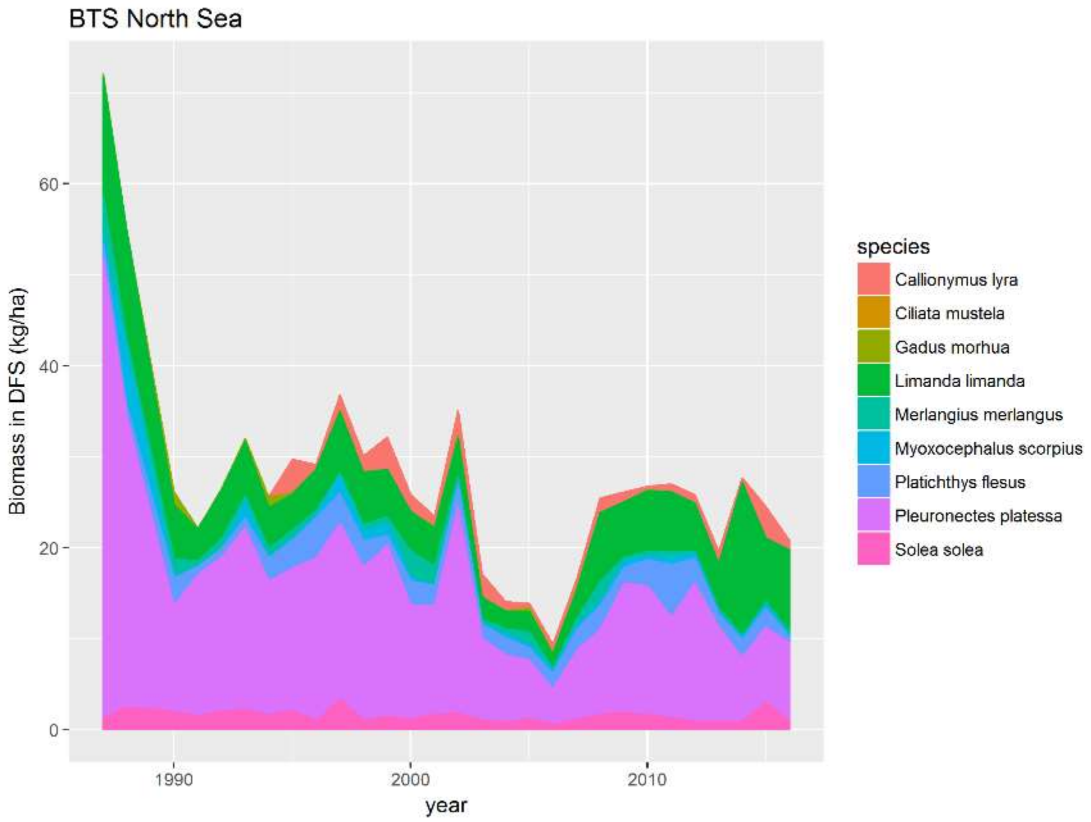


***Figure 2.4**. The distribution of fish survey locations of the DFS (circles) and BTS (triangles). The red, green, and blue region represent the Wadden Sea, Wadden coast and North Sea region. See Appendix 4 (Aarts et al., 2021), for more details.*

Both the DFS and BTS catch a large variety of species. Based on the seal diet data, we selected the 10 most abundant prey species (Figure 2.2), which are the European flounder (bot, *Platichthys flesus*), Sandeel (zandspiering, *Ammodytes sp.*), Dover sole (tong, *Solea solea*), Five-bearded rockling (vijf-dradige meun, *Ciliata mustela*), Whiting (wijting, *Merlangius merlangus*), European Plaice (schol, *Pleuronectes platessa*), Atlantic cod (kabeljauw, *Gadus morhua*), Common dragonet (pitvis, *Callionymus lyra*), Common dab (Schar, *Limanda limanda*), and Bull-rout (gewone zeedonderpad, *Myoxocephalus scorpius*). The relative abundances of these species are shown in Figure 2.5. By far plaice is the most abundant fish species caught during the fish surveys in the Wadden Sea and adjacent North Sea . Some species might be underrepresented in these surveys, such as gobies and sandeel due to net selectivity.



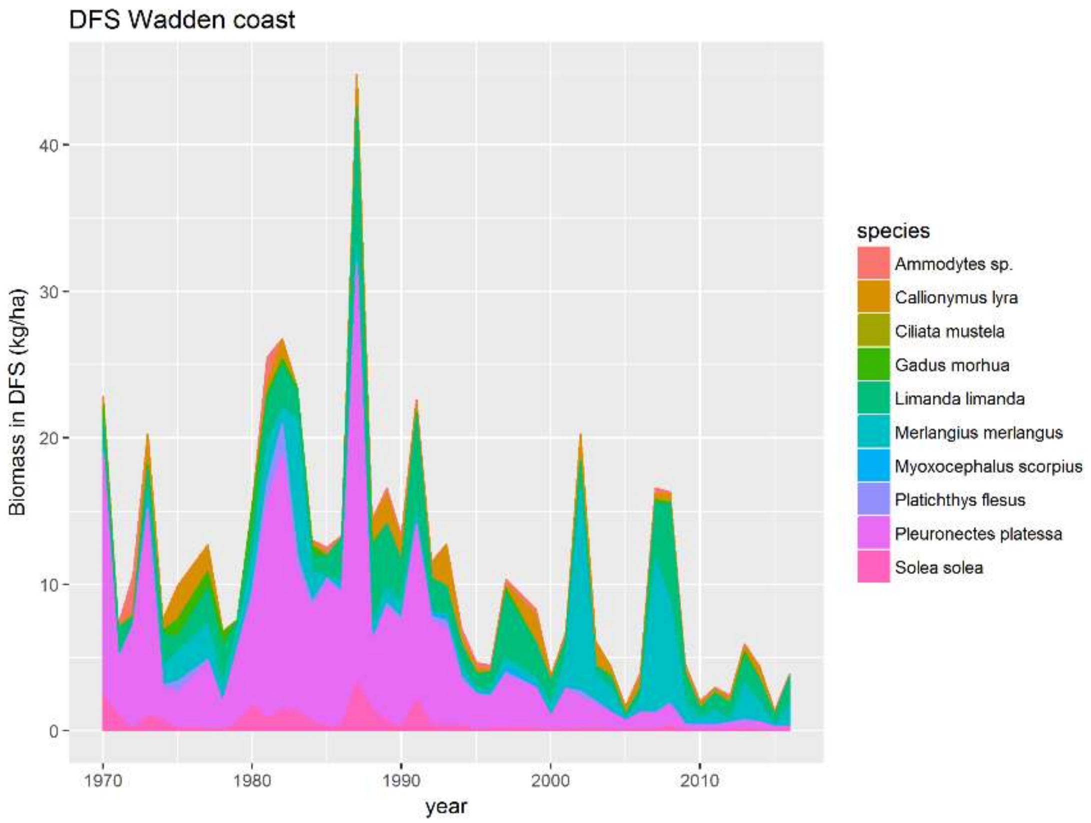


Figure 2.5. *Species composition. Biomass (kg/ha) in BTS (top figure) and DFS Wadden coast and Wadden Sea (bottom figure).*

2.3 Estimated effect of seals on fish biomass

Information on the distribution of fish is not only important for knowing where prey can be found, but also to estimate the impact of seals on fish abundance. If the fish abundance is relatively low compared to the total consumption by seals, high quality foraging areas close to the haul-out are only short-lived, forcing seals to move to areas further offshore to feed. This process is also known as density dependent competition and should ideally be captured by the ABM, showing a growing tendency to make longer foraging trips. To estimate if such density dependent effects are likely, we carried out an extensive study to estimate the total seal consumption relative to fish biomass (See Aarts *et al.*, 2019, Appendix 4). Our main conclusion was that based on the current estimates of fish density, harbour seals could significantly impact fish abundance, particularly in the vicinity of the haul-out site, where reduction of biomass during the winter months, could be as high as 50%. There were however large sources of uncertainty, including the migration of fish between the North Sea and Wadden Sea, and catchability estimates of the fish survey sampling gear, particularly for one of the most important prey species sandeel.

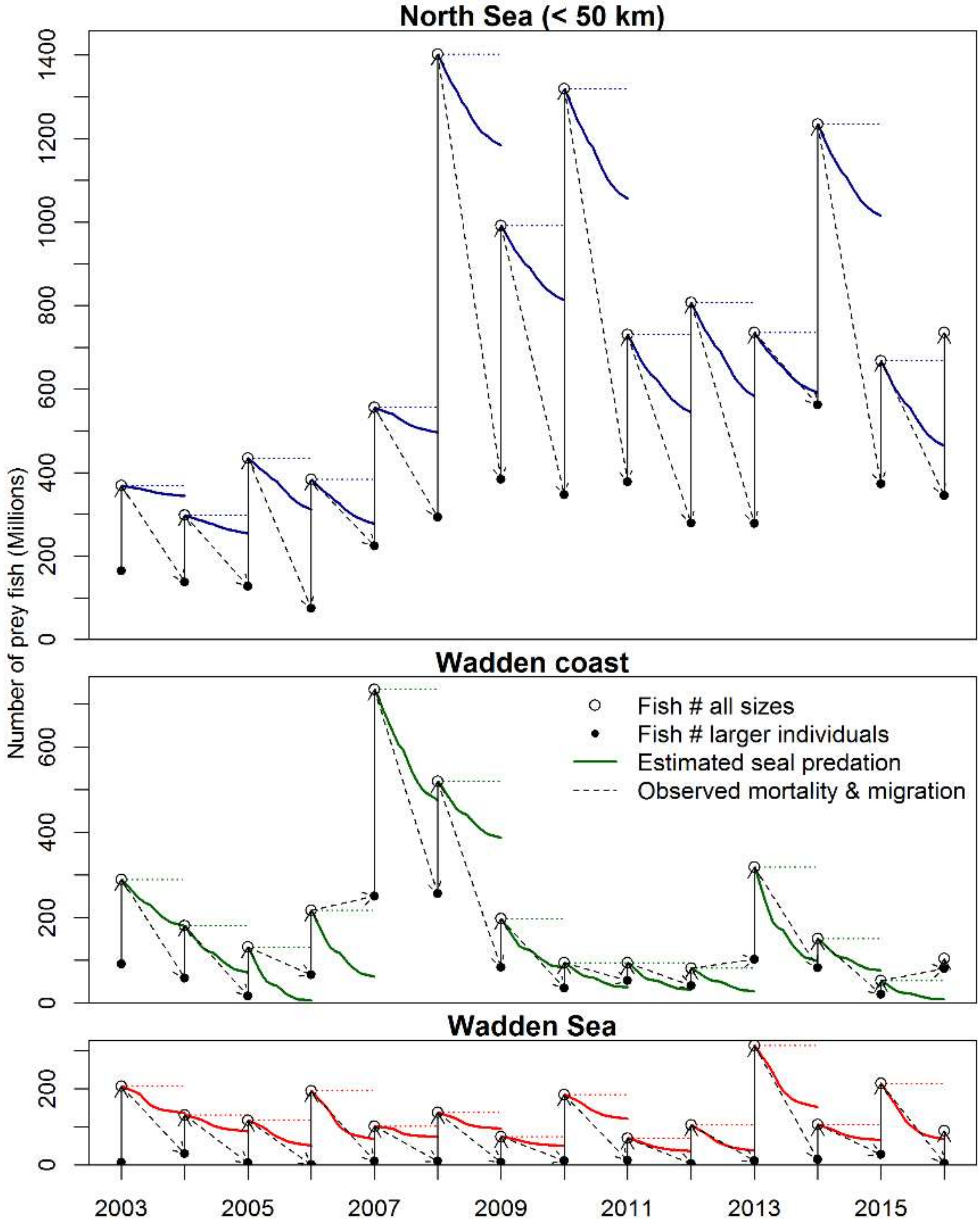


Figure 2.6. *The estimated effect of seal predation on the number of prey fish in the Wadden Sea (red lines; lower panel), Wadden coast (green lines; central panel) and remaining areas up to 50km from the haul-outs (blue line; upper panel). Regions are defined in Figure 2.4. The fish survey in September is the starting point (open circle, representing all size-classes), after which we estimate their decline during the winter months caused by seal predation (coloured lines). During the subsequent survey in September the following year, the number of remaining individuals from previous year can be estimated by only counting the larger individuals (>13.5cm, presumed 1+ year olds). These 1+ year olds are represented by the black dots. In the Wadden Sea, nearly all larger individuals (black dots) seem to disappear annually (either they died or moved elsewhere). However, throughout the summer new recruits replenish the area (upward arrow).*

2.4 Future directions

Sandeels (most often *Ammodytes marinus, Ammodytes tobianus* and *Hyperoplus lanceolatus)* are known to be the most dominant fish species in the North Sea (Engelhard *et al.,* 2014) and were found to be one of the most important prey species for both harbour seals (Figure 2.2) and grey seals (Wilson & Hammond 2016) in the southern North Sea. However, sandeels are not properly sampled in any of the existing fishery surveys, and information on their distribution and biomass lacks. Therefore, this prey species could not be included in the assessment concerning the top-down effect of seals described in previous sections. This also holds for other small, non-commercial demersal fish identified in the top predators' diets. Sandeel are a relatively predictable food source to exploit and key food web energy conveyers (Christensen *et al.,* 2013). The oil-rich, highly energetic fish forms an important trophic link between zooplankton and many predators including fish (such as Cod, Haddock, Whiting, Saithe and Mackerel), seabirds (Fulmar, Gannet, Kittiwake, Puffin, Sandwich tern, Razorbill and Guillemot), and marine mammals (harbour porpoises, grey seals and harbour seals (Reay 1970; Daan *et al.,* 1990; Thompson et al. 1996; Rindorf *et al.* 2000; McConnell et al. 1999; Santos & Pierce 2003; Wanless *et al*,. 2004; Temming *et al*., 2004; Wanless *et al.,* 2005; Pinnegar *et al.,* 2006; Aarts *et al.,* 2008; Engelhard *et al.,* 2013, 2014; Gilles *et al.*, 2016; Wilson & Hammond 2016). Because sandeel is such an abundant food source, changes in their abundance will also indirectly influence the population dynamics of other prey species (Smout *et al*., 2013). However, despite the importance of sandeels in the North Sea food web and being a relatively easy study species (because of their concentration in specific well-characterized habitats), a basic understanding of abundance, life history, population dynamics and fine scaled distribution is lacking for the Dutch part of the North Sea. With their elongated slender shape sandeel is not readily caught in standard demersal sampling gear. Specific gear and strategies are needed to study the sandeels and the other small demersal fish.

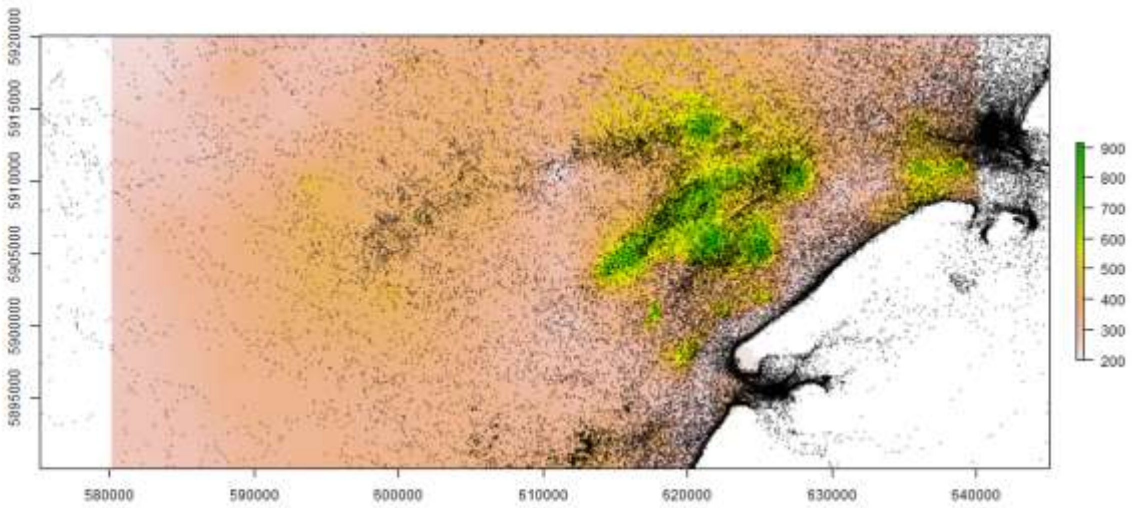


Figure 2.7 *Locations of seals determined by tracking (black points) and underlying habitat model for the area north of Texel*

To improve our understanding of sandeel ecology and create better maps of their distribution, a research proposal within this ABM project was developed. This research has been funded (Top Sector Water & Maritime: the Blue route) and a PhD, a Postdoc and a lab-assistant are currently working on this project. As part of this study, several research cruises have been organised. The first cruise took place in September 2019 on board of the Pelagia, where we sampled an area intensively used by grey and harbour seals and characterized by coarse sediment (Figure 2.7). These results indeed show high abundance of sandeel (>50% of total biomass in that area, see Figure 2.8). The total biomass of demersal fish locally up to 1000g/10 m2 (Figure 2.8) exceeds by far the estimates based on the DFS and BTS (which is in average 10-20 kg/10m2). In many areas sandeels are clearly the dominant fish, especially the more coastal areas with coarse sediment (stations 5-32, Figure 2.9). The data have not yet been incorporated into the Agent Based Model. However, estimates of absolute prey biomass found in this seal hotspot has been used to rescale maximum habitat suitability to maximum prey biomass per unit of area.

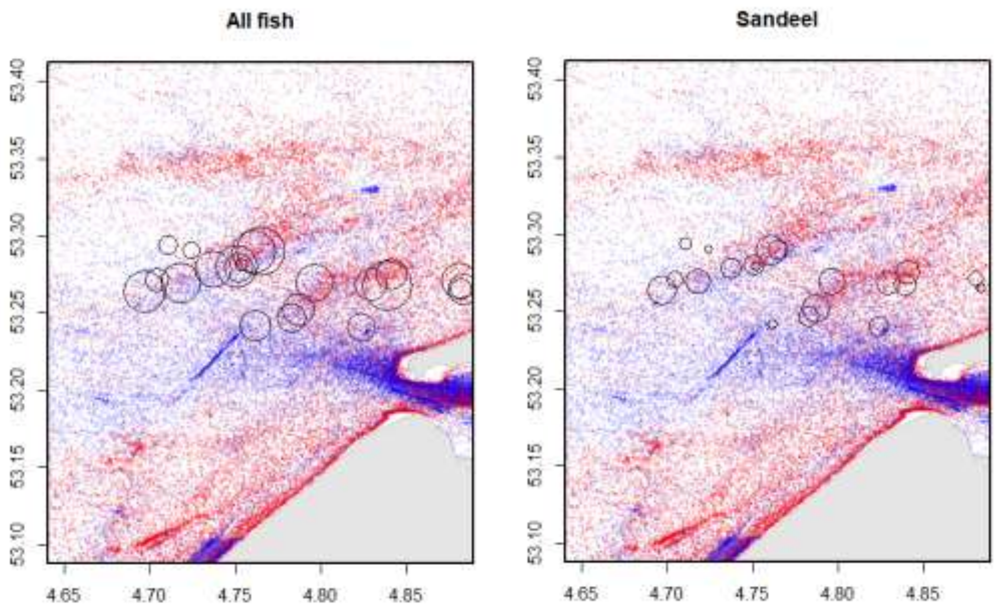


Figure 2.8. *Fish density per sample (black circles) left all species, right sandeels only. The blue dots are locations of tracked harbour seals, the red dot grey seals.*

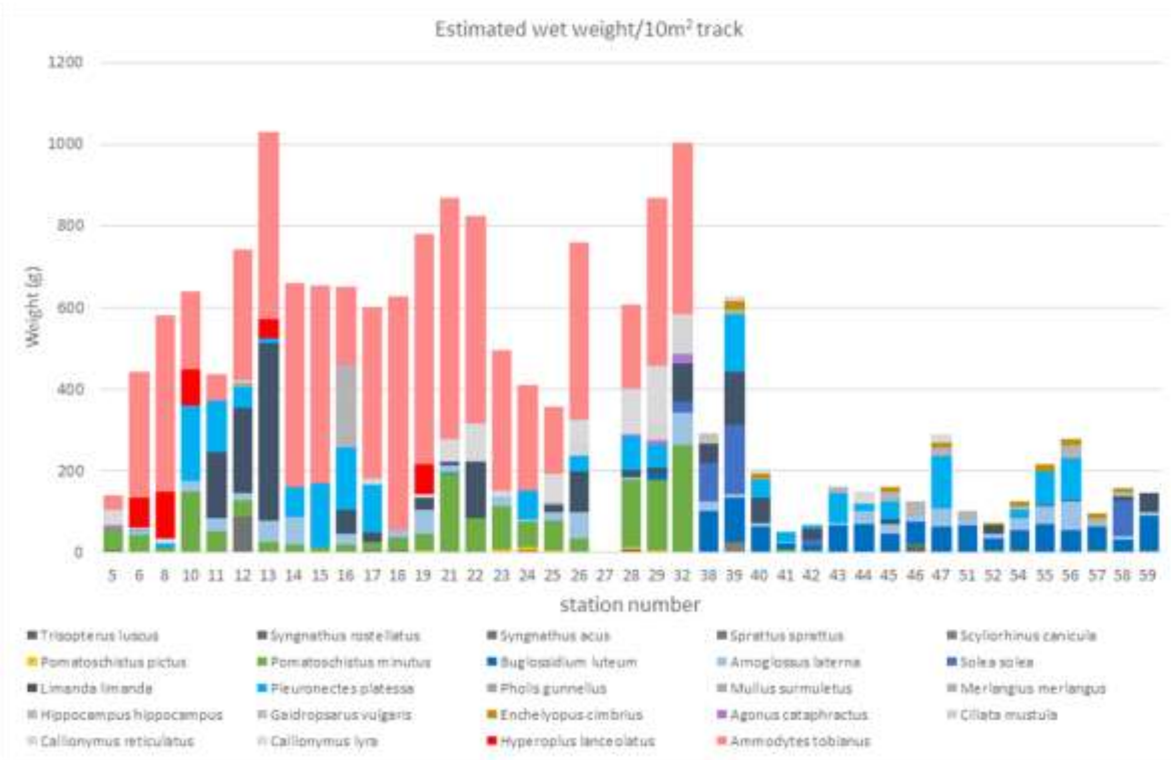


Figure 2.9. *Wet weight of fish sampled at the different stations. 1-32 represent coastal stations (like Figure 2.8) 38-59 are more offshore locations (beyond Friese front), a different habitat, with radically different species composition and lower overall fish biomass . Station 27 was not sampled.*

3 Developing accelerometery to quantify seal behaviour (TKI)

To bridge the gap between food density and actual prey intake rate, information on prey detection and capture probability is required. What is the seal's search area, and what is the likelihood that it will capture a prey once it is encountered? In this chapter we have develop accelerometery methods to measure such prey capture attempts. We argue that prey capture probability is one of the most neglected aspects of an ABM. By combining the fish energy landscape, accelerometery studies, and an ABM, it should be possible in the future to estimate how anthropogenic activities influence the prey capture probability and how this translates into effects on seal population size.

3.1 Background: Growing use of North Sea and seal populations

Historically humans along the North Sea coasts have affected the seal populations by hunting, leading to the extinction of the grey seals and critically endangering the harbour seal populations (Reijnders, 1985; Reijnders *et al.,* 1995; Brasseur *et al.,* 2015; Brasseur *et al.,* 2018c). Though direct mortality caused by humans still occurs in the form of by-catch in fisheries, nowadays, disturbance and pollution are probably the principal anthropogenic factor that may affect the recovering populations. In the 20th century, the marine environment has been increasingly industrialised and used in the light of energy, aquaculture, and transport. Most striking, in terms of growth speed and area used is the development of offshore windfarms (Figure 3.1).

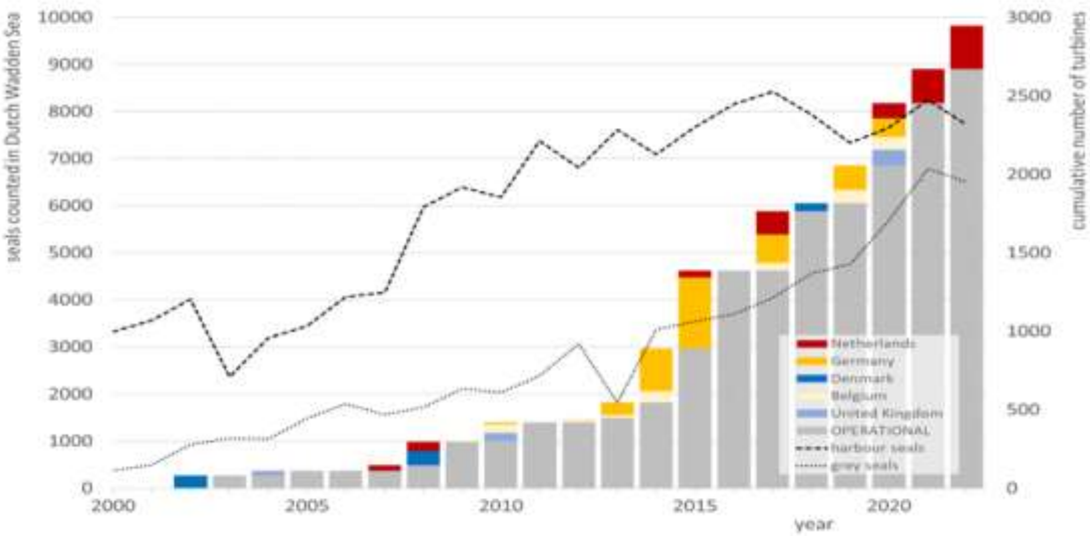


Figure 3.1. *Number of turbines constructed and operational in the southern North Sea and German Bight (Bars) and number of seals counted in the Dutch Wadden sea area (lines).*

As a result of disturbance or habitat degradation, behavioural changes such as less efficient foraging, flight reactions or shifts in habitat use could occur, leading indirectly to effects on populations. Anthropogenic activities such as construction are likely to affect habitat use, trophic relations and competition or reproduction and disease, having effect on birth and survival rates (Reijnders, 1986; Hall *et al.,* 2003; Van de Vijver *et al.,* 2005; Härkönen *et al.,* 2006). In order to limit the effects of the increasing economic activities at sea on seal populations, it is necessary not only to identify the immediate life-threatening dangers (i.e., accidental bycatch in fishery, or damage from pile driving) but also to understand how the human activities and pollution can disturb behaviour and thus affect a potentially much larger group of animals in the long term.

3.2 Tracking

In the past 30 years, seals have been tagged along the Dutch coasts in the context of understanding the animal's movement and behaviour. This is done especially in the framework of impact assessments for offshore wind turbines , tourism, or the construction of for example a seaport. The current trackers record GPS location and depth at various points in the dive. This provides a wealth of information about the movement and diving behaviour of animals at sea, which can be used to directly design recommendations regarding those human activities at sea that could potentially impact the seal population. However, the interpretation of detailed seal behaviour is complicated because the animals move three-dimensionally (x and y coordinate, and depth) while the available data only provide information on the tracks (x and y coordinates) and dives (depths) independently, and no information can be obtained with the current transmitters about the orientation or hunting behaviour of the animal underwater.

Research of animals in the wild has taken off enormously in recent years using transmitters to follow movement and behaviour of free-living species. Since 1997, several projects were carried out tracking both harbour and grey seals in the Netherlands (Table 3.1). Projects were mostly contracted in the context of the increasing economic activities in the coastal zones where seals reside. This provides for a fortuitous patchwork of information on the distribution and diving behaviour of seals in Dutch waters and changes herein. However, the data lacks consistency with variable effort to sample in different areas and seasons for both species (Brasseur and Reijnders, 2000; 2001; Brasseur *et al.,* 2009; Brasseur *et al.,* 2010; Brasseur *et al.,* 2018a; Brasseur *et al.,* 2018b).

Earlier trackers transmitted through the ARGOS system, limiting both the number of locations to 0-8/day and the amount of data that could be sent (typically 8 bits of data). After 2006, transmitters used in the Netherlands were changed to GSM/GPS tags enabling accurate (GPS) locations and collection of detailed dive information including several points at depth during a dive (see block). Yet, with only the vertical detail of a dive, it is complicated to explain the behaviour of the animals (for example discriminating between the foraging or transiting or fleeing behaviour) (Aarts *et al.,* 2011; Aarts *et al.,* 2013a; Aarts *et al.,* 2013b; Russell *et al.,* 2014; Aarts *et al.,* 2019).

Brief overview of telemetry

Tracking seals in the wild was potentially one of the most important technical advancements in the 20th century to better understand how the animals use their environment. Initially, radio transmitters were used. When applied on marine animals, additional data were obtained as visual tracking was discontinued as soon as the animals dived. This gave an indication of dive duration. Moreover, using signal modulation methods were developed to also collect physiological information such as body temperature or respiration or heart rates (Adams, 1965).

Since then, technical developments have allowed researchers to follow seals to great depths (with elephant seals displaying dives of over 1000m) and throughout their range. For this, three major components needed to be developed: data reception, recording location, type of data collected. Below are examples of these

Data reception:

The simplest trackers are so-called **recovery tags**. These can be attached to the animals and collect information that can be read upon recovery of the tag, for example when the tag become detached. In seals trackers are typically glued in the fur and are released when animals moult. Other mechanisms exist such as recapture or weak links that deteriorate or detach electronically.

VHF – trackers (radio transmitters) have been used for seals, allowing scientist to manually track them with a limited reception of several km's were developed to track animals on land; example: (Siniff and Tester, 1965). When animals remain in relatively small areas, reception can be automated, or arrays of receivers are used. Typically, the radio waves do not transport well in saltwater allowing for contact only when the tracker is at the surface.

Satellite transmission: many studies use the ARGOS system with a large number of satellites that circle the poles. Small amounts of data can be sent at fixed intervals (~45 sec) which is received by the satellite and conveyed to the ARGOS centre. This is ideal for animals that move over larger and uninhabited area. However, costs are often high.

GSM: as mobile telephone reception covers large areas of the northern hemisphere; track data can also be sent by telephone to an FTP site. This relatively new method gives the scientist the possibility to send much larger amounts of data and works well for animals, such as seals, that regularly come to shore allowing for the data to be downloaded.

Location:

Geo location: in some trackers (mostly with limited capacity) time of sunup and sundown is recorded. Based on this, an approximate location can be determined. Here the racker collects the information which is sent like other data collected by the tag.

Triangulation: For the VHF telemetry the approximate location of the animals is determined using the bearing of a so-called fix or, with other bearings, to triangulate the location. This can be automated and used in an array of receivers, though this is not commonly used with seals.

Doppler effect: the Argos system uses the doppler effect based on attenuation of the frequency to localise a tracker. For a reasonable location it needs to receive multiple signals which is often complicated when the seal is diving at sea

GPS: like in a car, trackers can be fitted with a GPS. The difference is however that the almanack is not downloaded, allowing for a location to be made in a fraction of a second. Like the Geo location the tracker collects the location information which is sent like other data collected by the tag.

Environmental/ physiological data

Next to location the tracker may collect aal kinds of data which is often summarised before being sent. This includes for example **depth**, in the current seal trackers a set number of depth readings, either at fixed moments in a dive or using the broken stick method: the moments where changes are the most prominent are sent, providing for an idea of the shape of the dive. Other environmental data like **temperature** and **connectivity** or data from other measurements including heart rate or **accelerometery** can be recorded. If and how the data is transmitted depends on many factors including the data reception system used, and the power required to do so.

Up until now seal studies mostly included location data and (often summarised or incomplete) dive data. In the Netherlands, with an almost full GSM coverage, the GSM/GPS trackers facilitated the collection of very regular seal locations at 10-15 min interval and a complete record of the dives during the tracking period of the seals (up to 270 days). Next to dive information and GPS location the trackers provide for so called haul out data defining the periods seals remain at the surface for >10 min.

Table 3.1. Overview of the number of transmitters deployed on harbour (PV) and grey seals (HG) tracked in the Netherlands using Argos or GSM devices.

aim	Population			Harbour	Offshore Wind								Other			
project	**Tourism**	**Habitat Use Rescue**		**Eems harbour**	**OWEZ**		**Gemini**		**Luchter-duinen**		**Borssele**		**Accelerometry**	**Total**		
species	**PV**	**PV**	**HG**	**PV**	**PV**	**HG**	**PV**	**HG**	**PV**	**HG**	**PV**	**HG**	**PV**	**PV**	**HG**	
								Argos								
1997	4													4		4
1998	17													17		17
1999	3	3												6		6
2000	9													9		9
2002		4												4		4
2003		7												7		7
2004		8												8		8
2005			6		12	6								12	12	24
2006						2									2	2
2007					12									12		12
Total Argos	**33**	**22**	**6**		**24**	**8**								**79**	**14**	**93**
								GSM/GPS								
2006						4									**4**	**6**
2007					***10***	***5***								**10**	**5**	**27**
2008						6									**6**	**6**
2009				45										**45**		**45**
2010				48										**48**		**48**
2011				48										**48**		**48**

2013							10	10	12	15				**22**	**25**	**47**
2014							10	1	20	20				**30**	**21**	**51**
2015							10	16	12	12				**22**	**28**	**50**
2016									12					**12**		**12**
2017									6					**6**		**6**
2019											10	10		**10**	**10**	**20**
2020		1												**1**		**1**
2022													5	**5**		**5**
Total GSM				**141**	**10**	**15**	**30**	**27**	**62**	**47**	**10**	**10**	**6**	**259**	**99**	**358**
Total	**33**	**22**	**6**	**141**	**34**	**23**	**30**	**27**	**62**	**47**	**10**	**10**	**6**	**338**	**113**	**451**

Although current GPS trackers may occasionally include accelerometers, their data resolution is far too high to be transmitted over a standard GSM network. In this project the aim is to develop algorithms to summarize the data in such a way that it can also be sent using the current GSM transmission. This involved both developing a smoothing algorithm to identify the body orientation and behaviour (theoretical study) and apply this in a GSM/GPS tracker so that the data can be transferred using the current GSM transmission.

3.3 Analysis of accelerometery data

Accelerometers measure on one hand the tri-axial total gravitational force (x,y,z; Figure 3.2). The division between the three orthogonal dimensions changes with the animal's body orientation relative to the Earth's gravitational field. This reflects the so-called *static component* defining for example how much an object is upright or tilted. Additionally, acceleration or deceleration in either dimension is measured reflecting the so-called *dynamic component* in the same orthogonal dimensions (i.e., surge, stroke and rolling). This would indicate for example movement forwards or swaying and heaving.

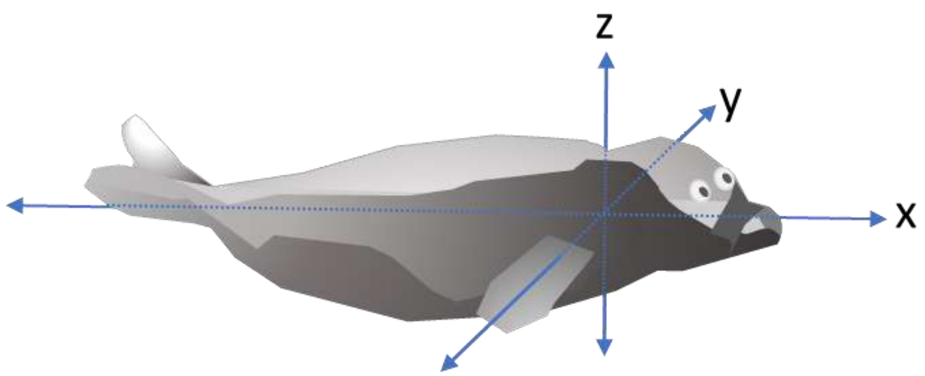


Figure 3.2. *Seal model showing the three axis directions measured with the accelerometers.*

Next to the GPS location and the dive depth, both information on the animals' orientation (and change herein) and the acceleration or deceleration would potentially help define the behaviour of the animals, especially at sea. For example, the acceleration in the ascent or descent (supported by the indication of orientation) could show if a seal is diving directly to the bottom to feed (seals most often feed at the bottom), or more diagonally to travel or to flee. Sudden changes in acceleration could indicate prey capture events. However, the data collected by the accelerometer is so detailed (approximately 120 measurements per second) and therefore of such an amount, that it cannot be sent in raw format by the current transmitters using the GSM links, though it can be archived on the tag. To access the data from accelerometers used currently on marine mammals (archival tags) they need to be retrieved (e.g., Vance *et al.,* 2021; Iorio-Merlo *et al.,* 2022). However, retrieving the tag is not always successful, leading to data loss and unnecessary disturbance of the animals.

Ideally, to enable receiving accelerometery data, the detailed data should be processed on board the tracker and only a summary could be sent. For example, in feeding events, where the animal does a burst in speed, potentially also changes orientation. This could be recognised by the tag and only the amplitude and maybe an angle of such a burst needs recording and sent. Similarly, to record fleeing behaviour, angle and speed of the descent and ascent of dives might suffice. However, too little is known on the detailed behaviour of the seals at sea to simply program the tracker to summarise the data. In this project we aimed to define algorithms to summarise the data ultimately to use in our current trackers.

3.3.1 Use of existing accelerometery data from captive and wild seals

Data from the accelerometer is the sum of the position of the seal (gravity recorded as an acceleration force towards the earth) and movement of the animal in the three directions. Changes in acceleration is caused by behaviour (for example the capture of a prey) but also movement (every swim stroke is recorded). To interpret what the animal is doing, these need to be separated (filtered). To do so basic data needs to be collected.
In first instance, we aimed at studying the detailed movements of seals that had been tagged with accelerometers in captivity using the data obtained to define different behavioural categories in relation to the accelerometery data. In summary, the intention was to observe the different orientations, behaviour, and movements in a controlled environment (for example: nose down, swimming, feeding). We obtained data from such an experiment from France. However, the tank size forced the seals to turn continuously avoiding the walls and it was impossible to obtain clean data. Luckily, other data became available from trackers that had accelerometers on a harbour seal in Scotland in the wild, and were retrieved. Though here observational data was not available, dive data and locations were, indicating when an animal was diving, resting, or swimming (Iorio-Merlo *et al.,* 2022). This provided us with the opportunity to define a correct smoother or filter for specifically harbour seals in the North Sea (see also Aarts et al in prep; Appendix 2).

3.3.2 Deployment of accelerometers on seals in the Netherlands

Using the smoother described above, data collected by a custom designed tag could now be summarised. To define the final settings seals were deployed with custom-designed tags that would relay both the data comparable to the existing GSM/GPS tags (location, haul out and dive data) and additionally collecting accelerometery. However, not all accelerometery data can be sent so, the tag was designed to send the complete data of a few dives per day.
Despite covid and the lack of available electronic parts we eventually managed to deploy 5 trackers on young, rehabilitated pups released in the wild (table 3.2).

Table 3.2 *Overview of seals tagged with accelerometery- GSM/GPS trackers.* ***Figure 3.5****. shows examples of the animals and their tracks.*

Tag no.	Seal name	Date of release	End	duration	sex
pv79-120-22	Jet	06/05/2022	22/06/2022	47	f
pv79-122-22	Malaika	01/09/2022	14/12/2022	104	f
pv79-121-22	Eddie	01/12/2022	22/04/2023	142	m
pv79-123-22	Jack	01/12/2022	13/5/2023	163	m
pv79-124-22	Emma	01/12/2022	17/04/2023	137	f

The first seal, pv79-120-22, was released in May 2022 assuming it would still collect data before the moult, usually in August. However, the animal spent most of the time on land preparing for moult (Figure 3.3). Possibly because it was well fed in captivity and did not need to feed in that period. Still 39 dives were recorded with accelerometery (Figure 3.4). As the seals in this experiment were rescued seals they could also be followed by the public (https://www.ecomare.nl/verdiep/volg-de-zeehonden/).

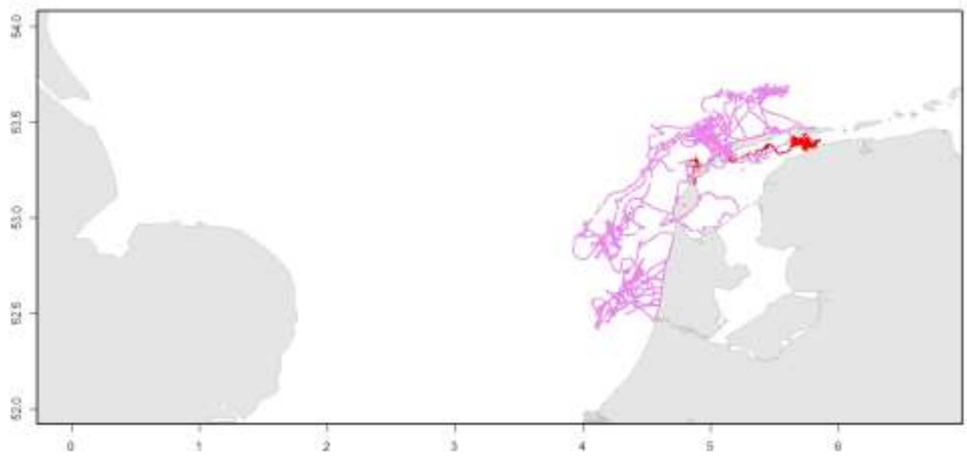


Figure 3.3. *Tracking results of pv79-120-22 (red) and pv79-122-22 (pink).*

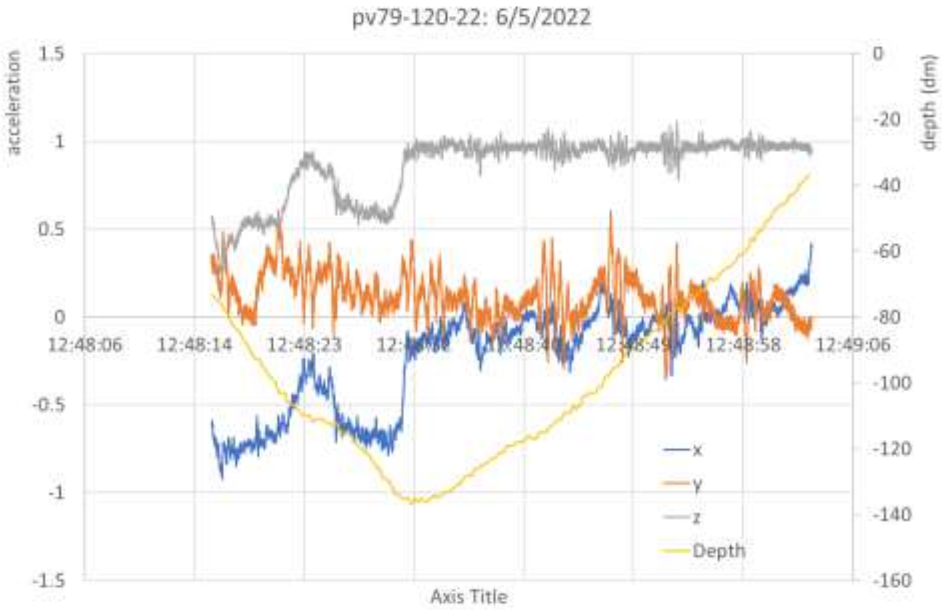


Figure 3.4. *First dive recorded using the accelerometery-GPS/GSM tag.*

The next seal deployment occurred in September 2022 avoiding the moulting period in the hope the seal would be more active. In this period, harbour seals recuperate from the moult and young animals learn to feed on their own exploring the surroundings.

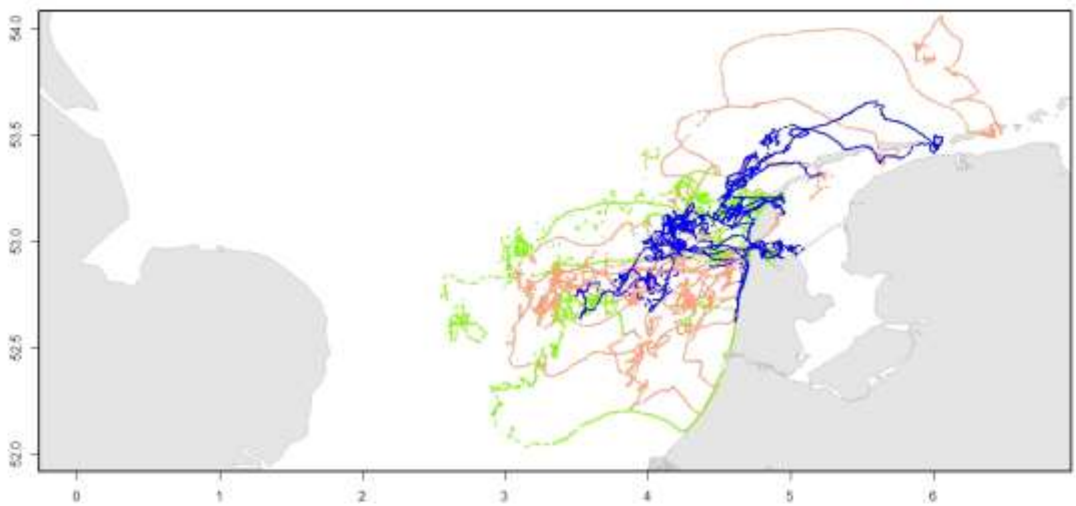
Table 3.3 *Overview of data obtained so far from experimental accelerometery- GSM/GPS trackers.*

			Number of dives		Dive duration (H:M:S)		Depth (m)	
Seal no.	month	year	Tot no.	accelerometery	Avg.	Max	Avg.	Max
pv79-120-22	May	2022	6160	20	00:01:45	00:05:01	5	46
	Jun	2022	5227	19	00:01:59	00:05:05	5	23
pv79-121-22	Dec	2022	3758	1	00:01:34	00:06:35	15	31
	Jan	2023	6161	1	00:01:50	00:03:59	17	42
	Feb	2023	10589	1	00:01:20	00:03:34	19	45
	Mar	2023	12971		00:01:19	00:03:35	18	44
	Apr	2023	13290		00:01:02	00:04:30	17	45
pv79-122-22	Sep	2022	5416	28	00:01:34	00:03:40	14	39
	Oct	2022	11675	39	00:01:49	00:04:10	18	37
	Nov	2022	12877		00:01:52	00:03:59	22	36

	Dec	2022	5612		00:01:25	00:02:55	19	29
pv79-123-22	Dec	2022	1189	6	00:01:21	00:04:25	8	29
	Jan	2023	6113	21	00:01:44	00:05:49	21	47
	Feb	2023	5350	30	00:01:51	00:04:48	20	47
	Mar	2023	11472	38	00:01:57	00:05:20	27	51
	Apr	2023	7130	28	00:01:37	00:04:45	21	38
	May	2023	6404		00:01:07	00:04:21	16	29
pv79-124-22	Dec	2022	1754	3	00:01:58	00:04:03	22	37
	Jan	2023	11539	36	00:01:46	00:04:13	20	46
	Feb	2023	5494	6	00:01:51	00:06:17	20	39
	Mar	2023	6863	19	00:02:07	00:08:00	23	36
	Apr	2023	6447		00:02:04	00:03:59	23	33

Finally, three seals were released in December (Figure 3.5), still in the period when they tend to explore and feed extensively. See also table 3.3. for a summary of the data. For an un know reason, the tag 79-121-22 did not function well and only sent a few accelerometery readings.

Figure 3.5. *Tagged seals and tracking results of pv79-121-22 (salmon), and pv79-123-22 (green) and pv79-124-22 (blue). Photo J. Hoekendijk.*



A good example of the accelerometery results is shown in Figure 3.6 where two consecutive dives by seal no 123 potentially have different results. The first dive the seal goes beyond 50m depth, and a clear regular acceleration is observed in the y-axis (from left to right; see also Figure 3.2) indicating a swim stroke pattern as the seal is moving horizontally along the bottom (the x is ~0). In the second dive, at about the same depth, the seal produces a "jerk" measured as substantial changes in acceleration in all three axes, potentially (attempting to) catching a fish, although this could also be the result of other types of behaviour.

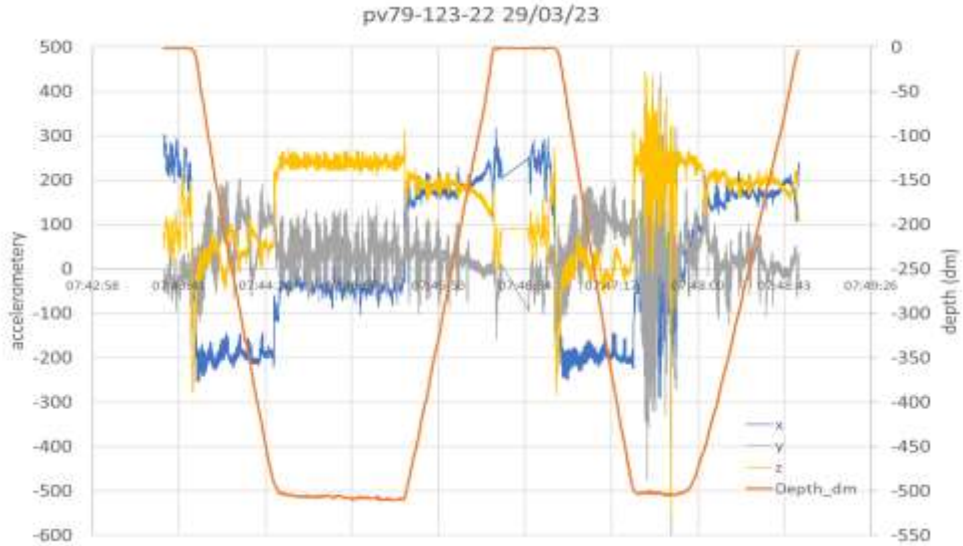


Figure 3.6. *Two consecutive dives recorded using the accelerometery-GPS/GSM tag*.

In the future, the tag will be programmed to summarise these differences in dive types identifying swimming and hunting behaviour. In addition, speed, and inclination during descent and ascent can for example be used to identify fleeing, diving, or transiting behaviour.

3.3.3 Behavioural classification

One of the aims of this research project was to use accelerometery data to classify and validate the behavioural states of seals. However, due to Covid 19 and global chip shortage, accelerometery data from Dutch seals could only be collected in the final stages of the project, and therefore was unavailable. Instead, for our analysis, we relied on data from retrieved accelerometery trackers from harbour seals tracked in Scotland, which became available for this research (see Figure 3.7).

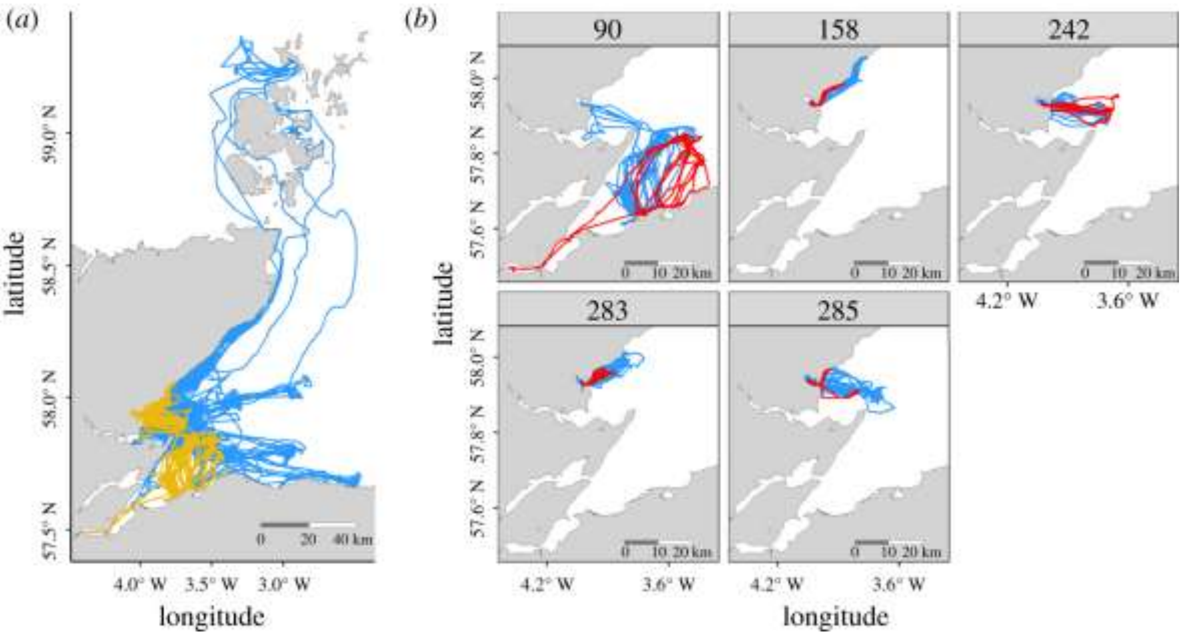


Figure 3.7. *(a) Maps displaying the movements of the 31 tagged harbour seals in the Moray Firth (Scotland), showing data from the five retrieved tags in yellow. (b) Tracks of the five focal seals where tags were recovered. The trips with accelerometer data that were included in the analysis are highlighted in red (Model 3), while the time period before and after is shown in blue. (from Iorio-Merlo et al., 2022)*

This led to a collaborative publication as shown in Appendix 4 (see https://royalsocietypublishing.org/doi/10.1098/rspb.2021.2261). Here we provide an extract of that publication that relates to the accelerometery data. For this analysis, the smoothing and filter techniques as described in Appendix 3, were applied to these accelerometery data. Also, that same method was used to apply a post-hoc calibration of the accelerometery measurements. See Appendix A in Iorio-Merlo *et al.,* (2022).

Next the accelerometery data were used to classify foraging and prey encounters: "We used two different methodologies to detect prey encounters. First, we identified sudden peaks in dynamic acceleration resulting from rapid head and body movements. This method has been validated with captive harbour seals and was able to identify prey capture attempts. We calculated the standard deviation in dynamic acceleration over a moving window of 1.5 s for each axis and used a k-means cluster analysis to group the standard deviation values into two activity states, 'high' and 'low'. We assumed an animal made a prey capture attempt and thus encountered a prey item when its activity was determined to be 'high' on all three axes. Second, we identified changes in body pitch angle, which have been used as indicators of the more subtle movements that harbour seals may use to catch benthic prey in shallow coastal waters. The pitch angle was calculated based on the estimated gravitational component of the measured g-forces. We calculated the differences between peaks and troughs in the time series of body pitch angle during each dive. Prey capture attempts were identified when a change in pitch angle greater than 20° occurred within a window of 5 s." (Iorio-Merlo *et al.,* 2022)

"Prey encounters were detected in all 51 foraging trips for which we had accelerometer data. Within each of these trips, 69.45% of dives had at least one prey encounter identified by one of the two methods. In total, 51 586 encounters were identified from peaks in acceleration and 78 441 encounters were identified from changes in body pitch angle towards the seabed. Of these, only 981 events overlapped in time, possibly suggesting that the methods had identified the same event. There was inter-individual variability in the detection of prey encounters by the two methods." (Iorio-Merlo *et al.,* 2022)

An example of prey encounters is shown in Figure 3.8. Most prey capture attempts took place on the outer margins of the foraging trips.

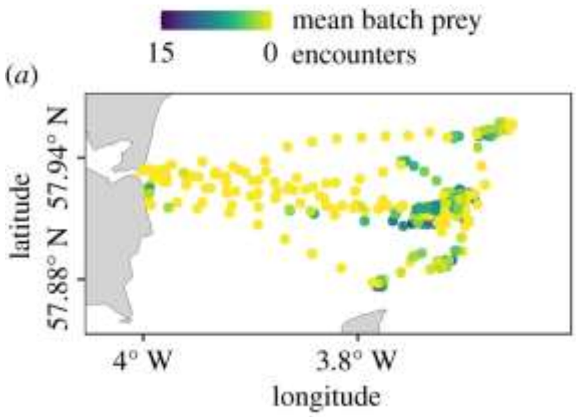


Figure 3.8. *Locations of dive batches, colour-coded by the mean number of prey encounters per dive batch.*

3.4 Conclusion and future directions

Telemetry has made it possible to “follow” even cryptic seals into their natural habitat. Initially, data relay via satellites made it possible to locate the seals at sea, albeit with limited information on their environment or diving behaviour. Through the use of GSM technology, scientists were able to transmit more data, resulting in more detailed behavioural information on diving and hauling-out. However, information on prey detection and capture probability is required to bridge the gap between food density and actual prey intake rate. In some regions, it is possible to deploy and retrieve archival trackers that can collect data for several days at sufficient resolution. To answer questions regarding the seal's search area and the likelihood of prey capture, however, new trackers must be developed. This device should collect accelerometery data and summarise these data on board so that it only transmits essential information so that the GSM-GPS tracker can work for months on end. For summarizing data, the data collected in this project will be required, as it indicated how accelerometery data changes as the seal moves through its environment. Eventually, trackers collecting and summarizing these kinds of measurements will provide the information needed to estimate the effect of environmental changes, such as those caused by (natural) variations in prey availability and capture probability, and human activities, and to include these into an Agent-Based model.

4 Effect of pile-driving on harbour and grey seals

In this chapter we look at the effect of pile-driving. If we know more precisely how seals respond to pile-driving, and at what distance from the piling-locations, these behavioural changes can be incorporated into an ABM.

4.1 Aim

Previous studies have investigated the effect of pile driving of the Luchterduinen and Gemini offshore wind park. As part of this project, a manuscript was prepared to describe the effect of the construction of both wind farms on grey seals. This manuscript can be found in Appendix 3. For this study however, the tracked harbour seals did not approach the pile driving locations of the Luchterduinen wind park and Gemini wind park often and as a consequence there was insufficient *harbour seal* tracking data to estimate the effect of pile driving on this species. Therefore, an analysis was proposed where all available construction data from the neighbouring countries Germany and Belgium would be included. A timeline of all known construction activities is shown in Figure 4.1.

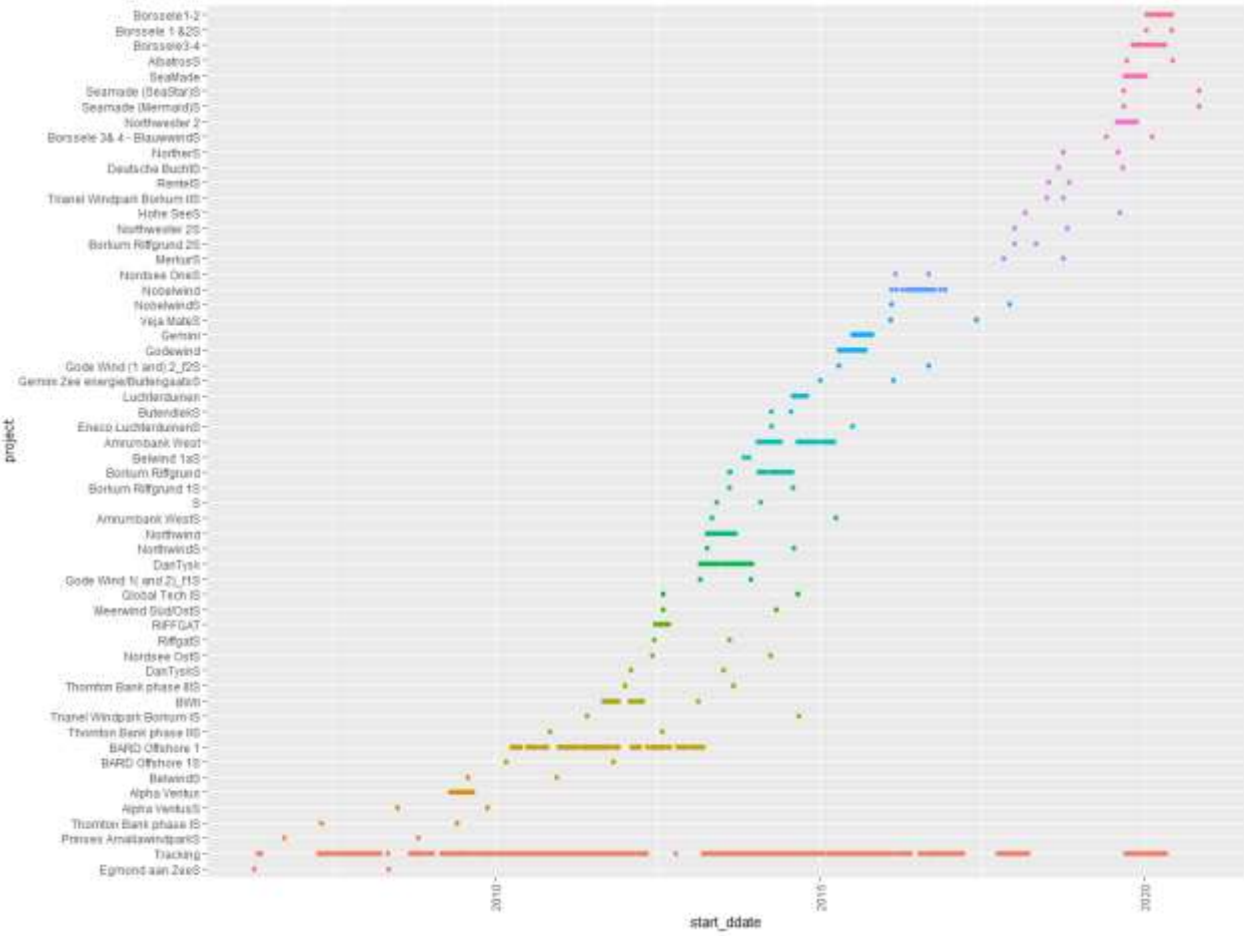


Figure 4.1. *Timeline of construction of windfarms in the Southern North Sea compared to the seal tracking data of WMR (Wageningen Marine Research) (orange line below). Start and end of the construction is indicated by a dot. When detailed data on piling of individual windmills is known, this is indicated by a series of dots. On the x-axis time (2005-2022) is indicated. On the y-axis, every row represents one windfarm (project). Windpark names followed by capital S represent those with summary data about the start and end of construction. For some parks, both summary data and detailed piling logs are available, and these parks appear twice in the figure.*

4.2 Methods

Precise details on the methodology can be found in the manuscript Appendix 3. Here we provide additional information on methodological steps that deviate from those presented in the manuscript.

4.2.1 Pile driving data

Data on the construction of the following wind parks were provided: Alpha Ventus, BARD offshore I, BWII, Riffgat, DanTysk, NorthWind, Borkum Riffgrund, Amrumbank West, Luchterduinen, Godewind, Gemini, Nobelwind, Northwester 2, SeaMade, Borssele 1-2, and Borssele 3-4. See Figure 4.2. Most pile driving data contained information on the location of the monopile (or tri-pole/tripod), the start and end of piling, the number of strikes, whether a seal scarer was used, and whether noise mitigation (bubble curtains) was in place. For some Dutch parks, like Gemini and Luchterduinen more detailed information on the piling logs was available. This allowed us to separate piling events in two or more pile driving events when there were large gaps in pile driving, e.g., due to malfunctioning of the hammer. For most German and Belgium parks, only information on the start and end of piling was available, and hence we had to assume continued piling took place within this period, though interruptions in piling cannot be excluded.

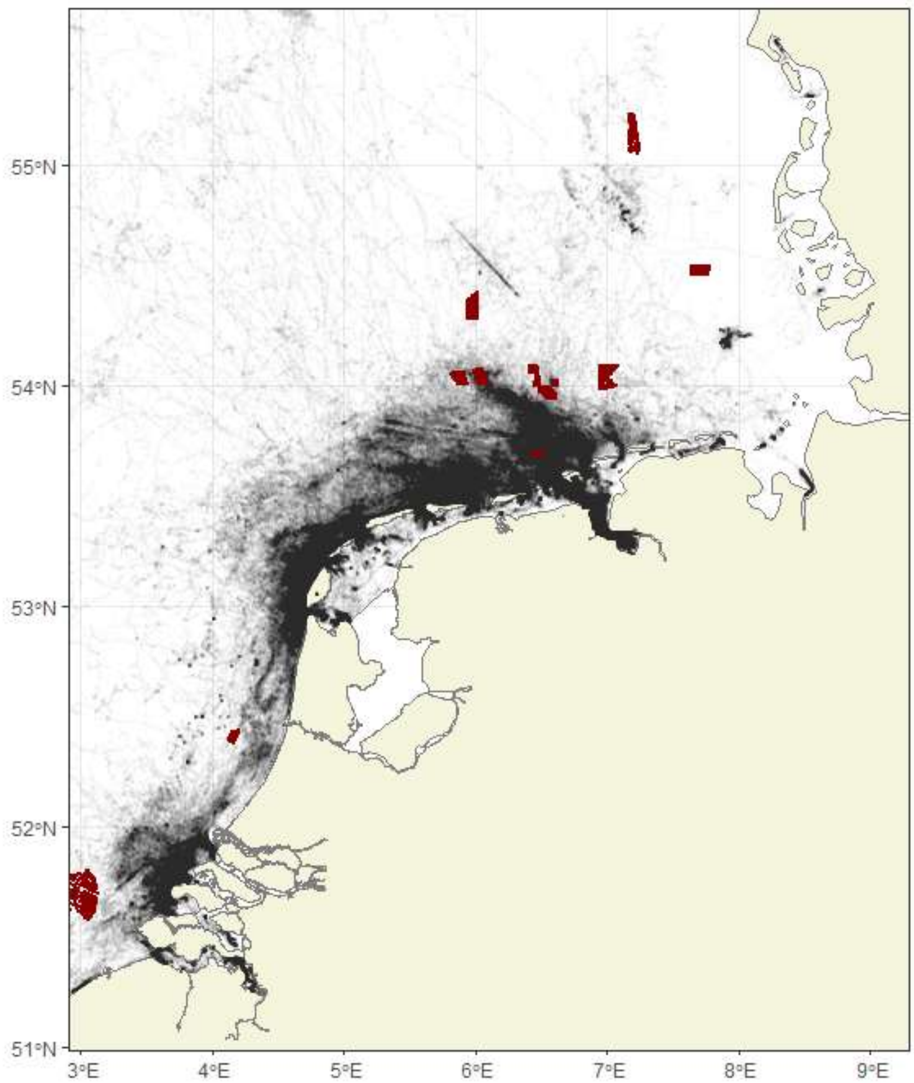


Figure 4.2. *Map of windfarm locations (red) for which there was detailed construction data. Black points indicate locations of tracked seals (2007-2019)*

4.2.2 Seal tracking data

For this study all available seal tracking data were used: 253 harbour seals, and 99 grey seals. however, not all tracking data overlapped with pile-driving. Any instance in which a seal was tracked during a specific piledriving event was considered an exposure. Though large numbers of tracked harbour and grey seals were exposed to pile-driving events for which we had information on the start and end of pile-driving, but many exposures were at large distances (several tens of kilometres). And it was unlikely for the seals to be measurably affected by pile-driving, particularly when pile driving noise was mitigated. Figure 4.3 shows the frequency of exposures event as a function of distance to pile driving for grey (a) and harbour seals (b).

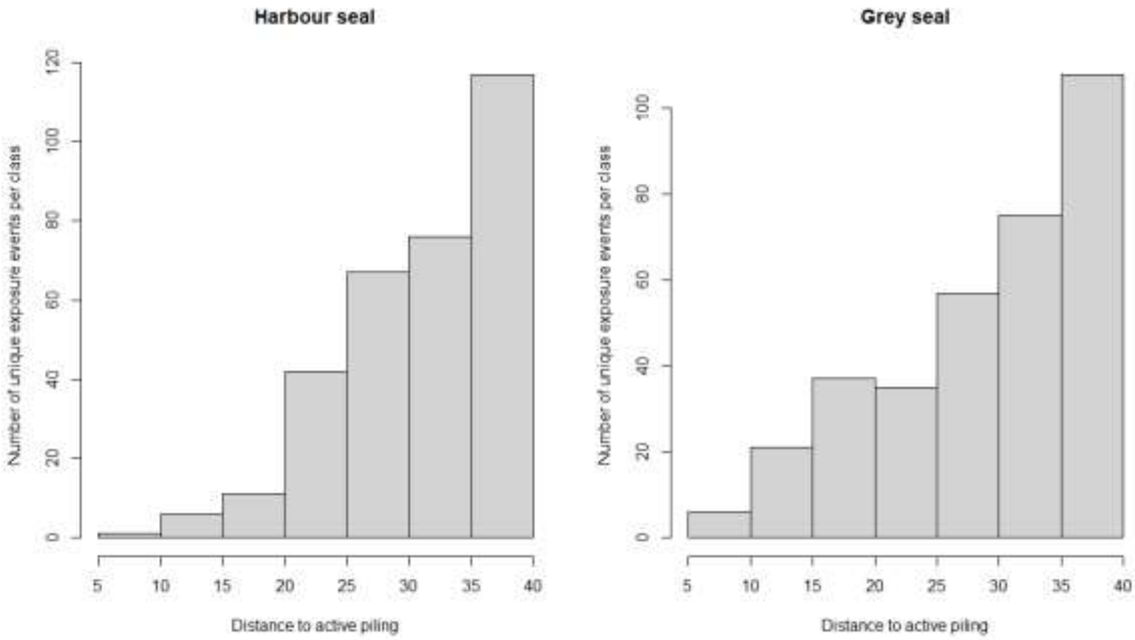


Figure 4.3. *Frequency of exposures event as a function of distance to pile driving up to 40 km.*

4.2.3 Statistical analysis

Detailed analyses are described in appendix 3. But a summary is provided here. For each dive, the vertical descent speed was calculated. For the most recent dive data (where the dives were recorded in 23 or 25 depth bins), the descent speed was calculated between the depth at 1% of the dive and the first depth point were depth exceeded 80% of the maximum dive depth. For some of the older tracking data, the dive data were only recorded into 9 depth bins (i.e., at 10%, 20%, ...90% of the dive). Often a seal would reach the bottom well before the first dive depth point (i.e., at 10% of the time), and hence this may lead to an underestimate of the dive speed. For these older data, the descent speed was calculated as the average speed between time=0 (when the seal dives below 1.5m) and the first 10% quantile of the dive.

For each exposure event (the period where the seal was within 50km of the nearest active pile driving site), a model was fitted to the series of descent speeds, with the periods prior, during and after pile-driving included as factor variables. The model also included a temporally correlated auto-regressive term to capture residual correlation in the descent speed. When pile-driving significantly changes the descent speed during the pile-driving, the parameter associated with the "during pile-driving" factor variable should be (significantly) smaller than zero.

The parameters describing the effect of "pile-driving" for all exposure events were combined and modelled as a smooth function (using a generalized additive model) of distance to the pile-driving location. If on average, pile driving leads to decrease in overall descent speed, we would expect low parameter values at close distance to pile-driving, and no effect (parameters close to 0) at large distances.

4.3 Results

There was a large variability in the observed behaviour. In some cases, a change in movement direction was observed when pile-driving started (See Figure 4.4; seal pv39-84-11). In this instance, the seal was initially swimming Northwards (green dots), and when pile driving commenced, it turned around and swam away from the construction site (indicated as a large blue dot). Also, a rapid decline in descent speed was observed in some instances. This occurred particularly when exposed to unmitigated events, i.e., Luchterduinen and Gemini. One example is shown in Figure 4.5. In this instance, seal number hg43LZ-Z066-14 showed high vertical descent speeds (indicative of foraging), but when pile driving started, it decreased descent speed to values well below 0.5 m/s, which is indicative of more horizontal displacement (i.e., lower vertical speed). Later during the pile-driving event, the vertical descent speed increased again to pre-piling values. In many other instances, no clear change in dive behaviour was apparent, even at short distances (See e.g., Figure 4.6). For example, seal pv39-84-11 (same seal as described above, but during another exposure event) was within 12km of the construction site and revealed no clear changes in the dive profiles. Finally, during some exposures, no behavioural response was apparent at the onset of pile-driving (as recorded in the data), but changes in dive behaviour were visible well into the pile-driving event (Figure 4.7). These behavioural changes could be unrelated to pile-driving, or they might be the result of imprecise records on pile driving. For example, intensive hammering might have only started late into the pile-driving event. Since no detailed piling log data were available, this could not be validated or disproved.

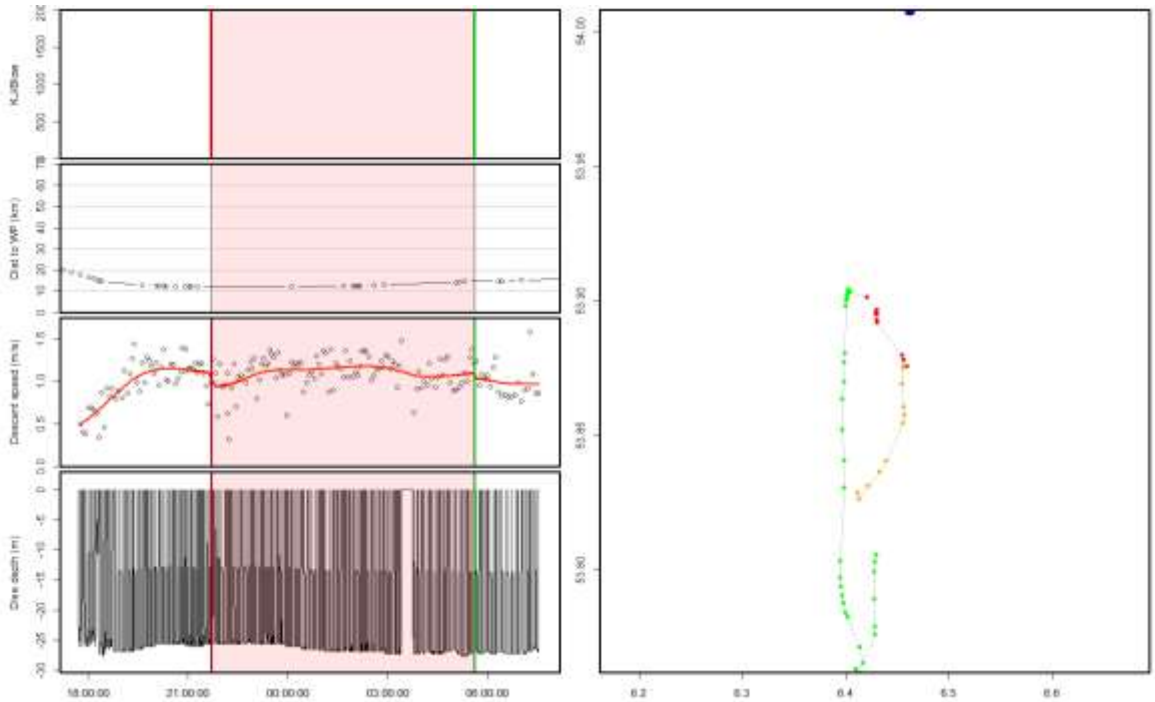


Figure 4.4. *Example of a typical response to pile driving: seal pv39-84-11, approximately 12 km away from Windfarm BWII (Monopole DE 213, unmitigated). Just prior to the commencement of pile-driving (1st panel, left), the seals' vertical descent speed decreased slightly, with an apparent increase in variability (3rd panel, left). The right figure indicates the movement of the seal in relation to pile-driving site (blue dot). The colours represent locations prior (green), during (red) and after (orange) pile-driving. In this example, the seal appears to turn around when pile-driving commenced.*

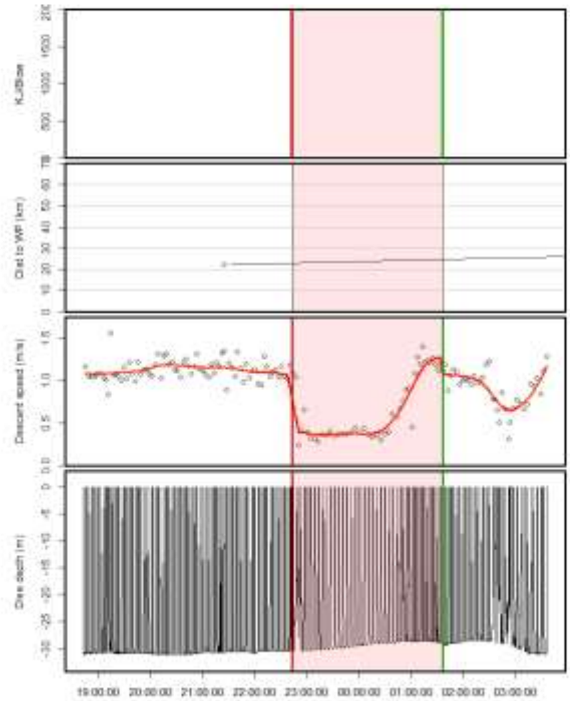


Figure 4.5. *Example of a typical response to pile driving: grey seal hg43LZ-Z066-14, approximately 23 km away from Borkum Riffgrund (Monopole DE 610, unmitigated), revealed a rapid decline in descent speed when pile-driving commenced (3rd panel, left). During the last phase of pile-driving the, the descent speed returned to presumably normal levels. Note that very few GPS location fixes are available, insufficient to plot the track of the seal before, during and after pile driving.*

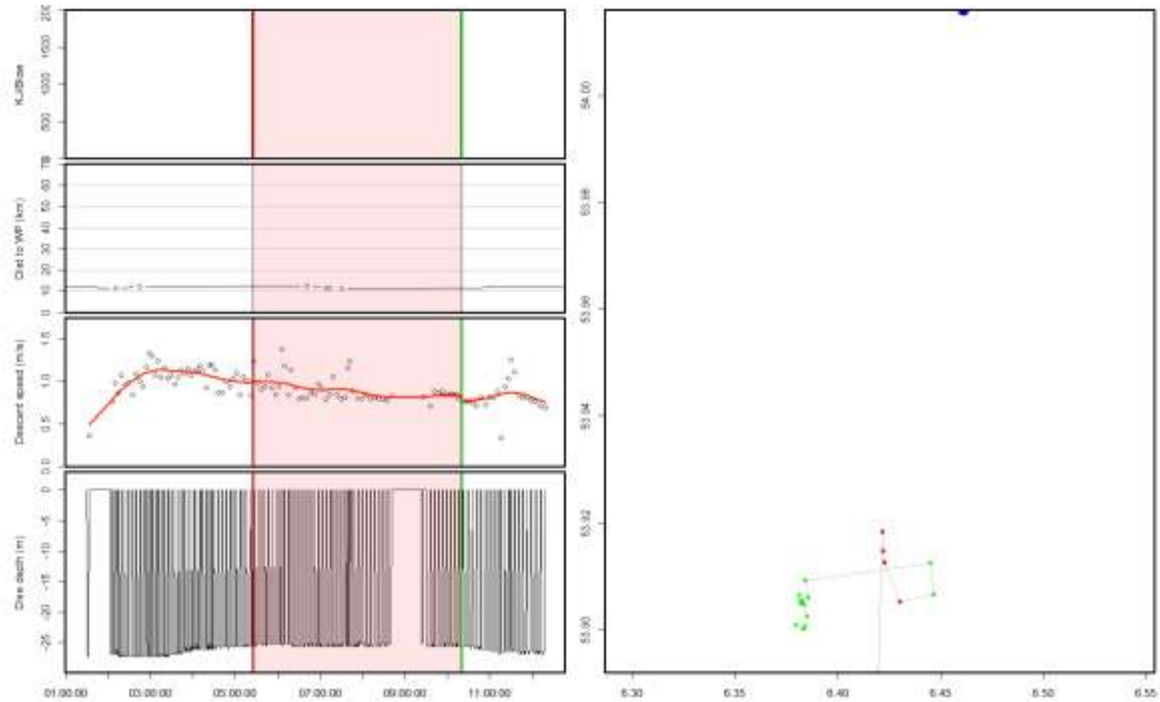


Figure 4.6. *Example of no obvious response to pile driving: harbour seal pv39-84-11 was approximately 12 km away from BWII (Monopole DE 212, mitigated) when pile-driving commenced, but did not reveal a clear change in behaviour, and even moved slightly towards the pile-driving location, when pile driving commenced.*

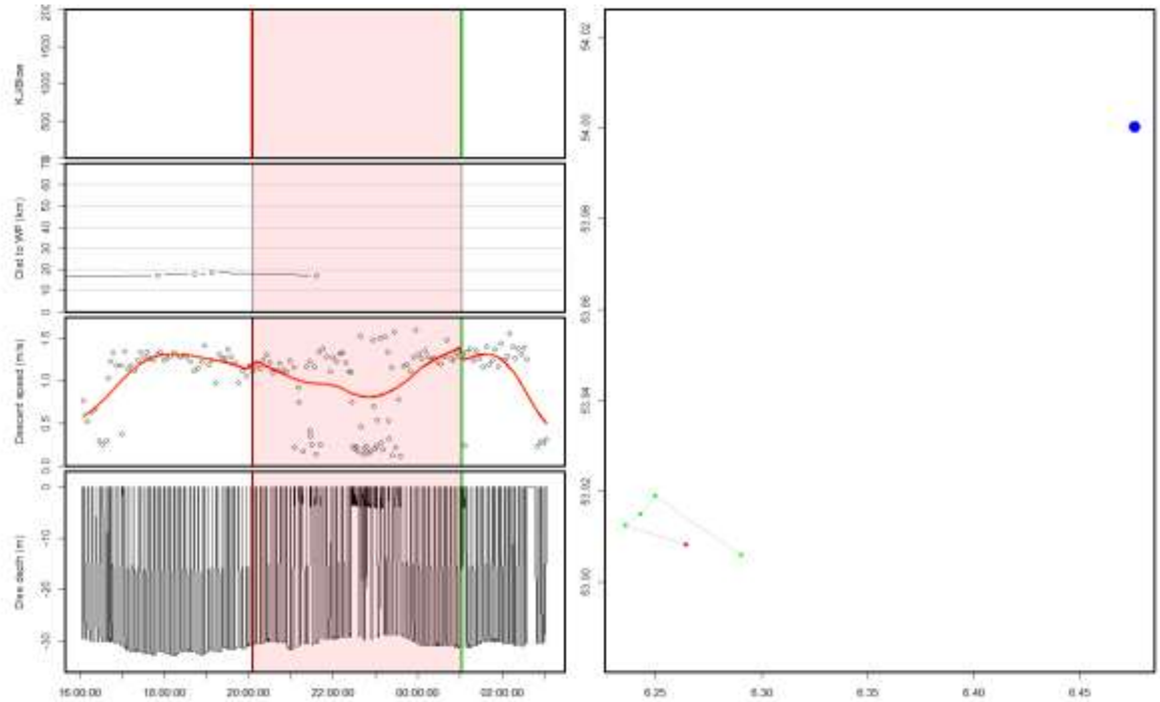
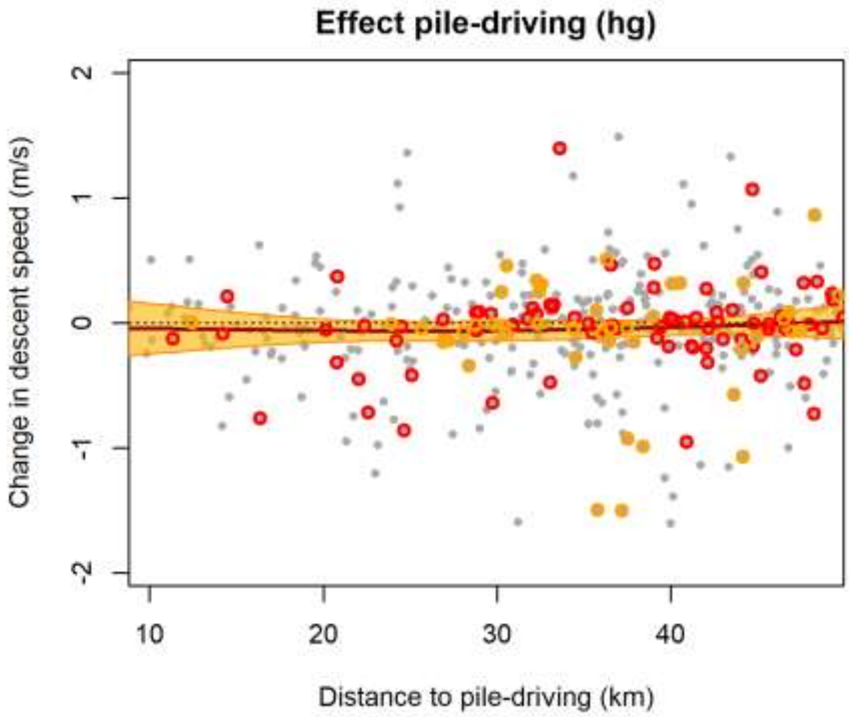


Figure 4.7. *Example of changes in diving behaviour during the pile driving session: harbour seal pv39-95-11 was approximately 18 km away from BWII (Monopole DE 223, mitigated) when pile-driving commenced, but did not reveal a clear change in behaviour. However, later during the pile-driving session (lasting approximately 5 hours), a rapid decrease in descent speed is apparent. Since no detailed information on hammer-intensity was available, these changes could be related to sudden increase in hammer intensity.*

When all exposure events are combined, no clear effect of distance to pile-driving is observed for both grey seals and harbour seals (Figure 4.8). Note however, that the vast majority of pile driving events were mitigated (grey dots), except for the Luchterduinen and Gemini windpark (red points) and some pile-driving events in the other German or Belgium parks (orange points). For Luchterduinen and Gemini (no noise mitigation), significant behavioural changes were observed beyond 30km.

Also note that very few pile driving exposures were within 10km from the pile driving site, which seems to suggest that seals avoid the vicinity of the construction site even when no pile driving activity is going on (as was also observed for the Borssele windpark region, Brasseur *et al.,* 2022). It might also be possible that seals were sometimes in the vicinity of the construction site, but when they are disturbed and rapidly swimming away from the site, this may limit the time the seal is at the surface and no GPS location fix may be established.



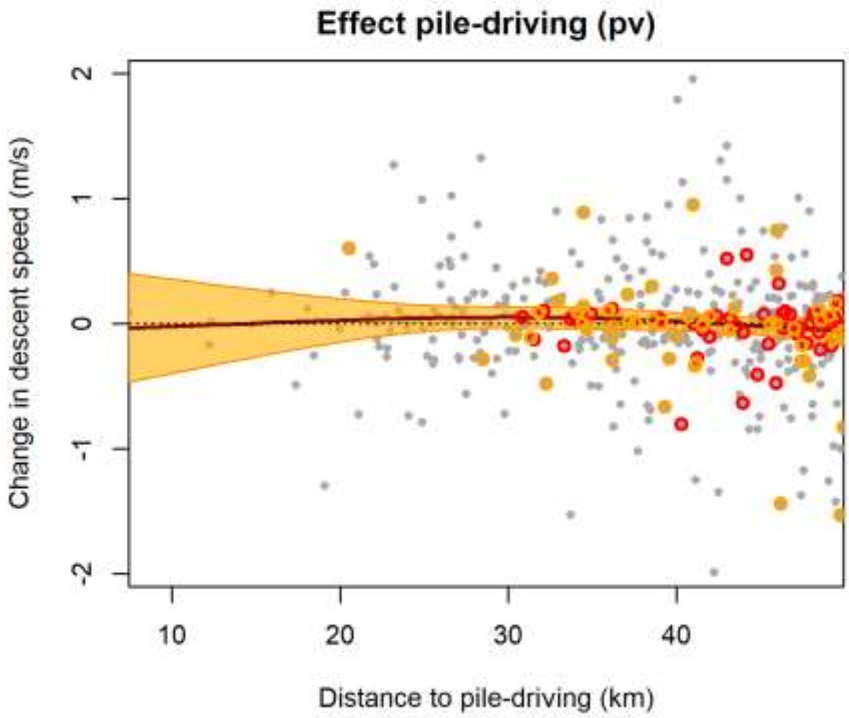


Figure 4.8. *Changes in descent speed of grey (top) and harbour seals (bottom) in relation to the distance to pile driving events (km). Grey dots represent every exposure, red dots data from Gemini and Luchterduinen and orange dots represent pile-driving events with no mitigation in place (excluding Gemini and Luchterduinen).*

4.4 Discussion

4.4.1 Disruption of diving behaviour in response to unmitigated pile driving

This and previous studies showed that grey seals in the vicinity of unmitigated pile-driving near Luchterduinen and Gemini reduced descent speed (presumably diving more diagonally as they attempt to swim away) and reduced their bottom time during pile-driving events. There was significant evidence this happened when within 36 km from the pile-driving, but occasionally behavioural responses were observed at distances well beyond this (See Appendix 3). Grey seals are generally benthic feeders (Thompson *et al.,* 1991), so a reduction in bottom time has a direct effect on their food intake and this means the individuals would need to work harder to gain required resources during times when there was no pile-driving, or forage elsewhere. For harbour seals there were too little occasions where they were close enough to measure such effect.

When studying the effect of pile-driving on the diving behaviour of grey and harbour seals using the construction data from all parks combined, no significant changes in diving behaviour were visible. However, all these parks (except Luchterduinen and Gemini) were constructed using either mitigation measures or using tripod structures, except for some individual monopiles. Since mitigation can reduce the noise-level substantially, this could explain not detecting significant effects on behaviour. Since harbour seals also did not venture in close vicinity of the construction site (<10km), this meant we had insufficient data to study the behavioural response of harbour seals to pile driving, one of the major goals of this study and the motivation of using piling data from parks constructed in German and Belgium waters.

4.4.2 Lacking precise data on human activities

Seals live in an environment with a multitude of environmental stressors, some of which are natural, but many are also anthropogenic in nature. These anthropogenic activities include shipping, fishing, seismic surveys and maintenance or construction work of offshore installations, like wind farms. Since unmitigated pile-driving is one of the loudest sound sources in the North Sea, it is expected to see some behavioural responses in relation to pile-driving, particularly at close range. For the tracked harbour and grey seals, there is precise data on their diving behaviour (continuous records of diving behaviour up to 4 second time resolution). For the construction of some wind farms, like Gemini, Luchterduinen and Borssele also detailed piling logs were available. Assuming the recorded times were correct, and the time-zone was well defined, this allowed us to investigate the behavioural responses. In this and previous studies we did indeed found variable but evident behavioural responses to pile driving, even at distances beyond 30km.

Unfortunately, for many of the German and older Belgium parks, such detailed data were unavailable. Only the start and end time of the pile-driving was recorded. It was unknown whether other loud noise producing activities (like installation of the pile-hammer) took place prior to the defined start times. Furthermore, it was not known whether there were extended periods with no hammer activities. Particularly during the earlier installations (2010-2015), hammering of monopiles tend to last much longer (often up to 6hours or longer), and likely there were periods of non-hammering in-between.

Close inspection of the diving seals' diving behaviour often revealed disrupted diving behaviour during pile driving, but also before the recorded pile-driving started. The question is whether this disruption of diving behaviour prior to pile driving was due to natural processes (e.g., full stomach), or whether it was due some anthropogenic activity related or unrelated to pile-driving? Without detailed sound measurements and interpretation of these measurements, it is challenging to answer this question. Also, seals were almost never seen at very close range (<10km) from the construction site during the construction period.

4.4.3 Effectiveness of noise mitigation

Very few clear changes in behaviour were observed in response to the pile driving of most of the German parks analysed in this study, most of which were constructed with at least some noise mitigation in place (e.g., Bubble screen or Hydro-Hammer). This is a probable one explanation for the low number of the apparent behavioural responses. When mitigation measures were not in place, often some change in behaviour was visible, as exemplified in Figure 4.4 and Figure 4.5. This suggests reasonable effectiveness of noise mitigation. However, there also appears an overall avoidance of the wind park, with very few exposures at small distances <10km. This was also observed during the windfarm construction in the Borssele area (Brasseur *et al.,* 2023). It is not unlikely that seals avoid these areas, either because of pile-driving, but perhaps also due to other activities, like shipping that is taking place within and near the offshore wind park.

4.4.4 Future directions

Given the high noise levels produced during pile-driving, it is presumed in most impact studies that this activity has the highest impact on marine mammals, including seals. In previous research, we demonstrated that, based on a detailed analysis of the diving behaviour, seals' behaviour changed once pile-driving began. This has been demonstrated for both Luchterduinen and Gemini, which lacked noise mitigation. In contrast, in the study associated with the construction of the Borssele wind farm and German parks, where sound mitigation was implemented, mitigation seemed effective in reducing the distance at naïveh behavioural changes in diving could be observed. Despite the mitigation during pile-driving, there is however mounting evidence that seals continue to avoid the general vicinity of the construction site. This indicates that they are aware of the ongoing activities and may be disturbed by the piling or other construction-related activities, such as shipping. Typically, these activities take much longer than the piledriving alone, and the entire construction phase, including the laying of cables and installation of the turbines, can last months or a year. There are very few, if any, studies that measure the effects of these activities or the operation of wind farms, particularly when multiple wind farms cover larger areas. Future research should ideally focus on potential effects on both a larger spatial scale (including adjacent activities as described above, operation, and multiple wind farms) and a larger temporal scale (if and when seals return to the wind farm areas, and examining effects on individual health and survival as well as population level effects).

5 Development of Agent Based Model

In this chapter we report on the construction of the ABM AgentSeal. Based on the information gathered in previous studies and this study, and in collaboration with an international team, an Agent Based Model for harbour seal (AgentSeal) was developed, and this model was subsequently adapted for seals in the Netherlands. The estimation of the effect of absolute prey availability (for which estimates are currently lacking) on fitness was given special consideration.

5.1 AgentSeal

Lead by St. Andrews University, and in collaboration with Cromarty Lighthouse (Aberdeen University), Aarhus University and Wageningen Marine Research, an agent-based model for seals has been developed: *AgentSeal*. In summary, the model simulates the movement of seals at sea, considering a whole suite of variables and processes related to the main agents (i.e., harbour seals), including movement characteristics, cognition, energy use and intake, and other physiological requirements (e.g., the need to rest and perform skin maintenance on land). *AgentSeal* also considers features of the landscape, like the distribution of known haul-out sites, the 'seascape' in which the seals move, and the quality of habitat which defines the prey intake rate, but also how seals move (i.e., richer habitats lead to slower movement and higher sinuosity). All details can be found in appendix 6. Initially, the model was developed for harbour seals on the East coast of Scotland (Chudzinska *et al.,* 2021).

5.2 *AgentSeal*-NL methodology

In this study, the *AgentSeal* model is adapted to seals using the Dutch Wadden Sea and adjacent North Sea. This required the re-construction of different input variables, which are described below.

5.2.1 Seascape and distance to haul-out

The Dutch study area was defined as a regular grid of 1km spatial resolution. The geographic projection of the grid was UTM 31N, WGS84. Based on the Emodnet bathymetry grid, all areas shallower than -1.5m were defined as land. Hence, several intertidal areas within the Wadden Sea were treated as land, as seal tracking data shows that they rarely cross these intertidal mudflats (although they may forage and rest along the edges). This seascape grid was also used to calculate the distance to each haul-out cluster. The outer edges of the landscape (Figure 5.1) were treated as hard boundaries, seals could not cross. This is to prevent seals from being 'lost' from the simulation.

5.2.2 Haul-out clusters

The locations of haul-out sites were based on the survey counts collected on 21 August 2017. This survey date was chosen because it coincides with surveys carried out in Germany and Denmark, which would allow for future extensions to the international Wadden Sea. Survey locations were clustered spatially in groups using the function *point.clustering* (package SHAModels), with minimum distance of 5km. See Figure 5.1.

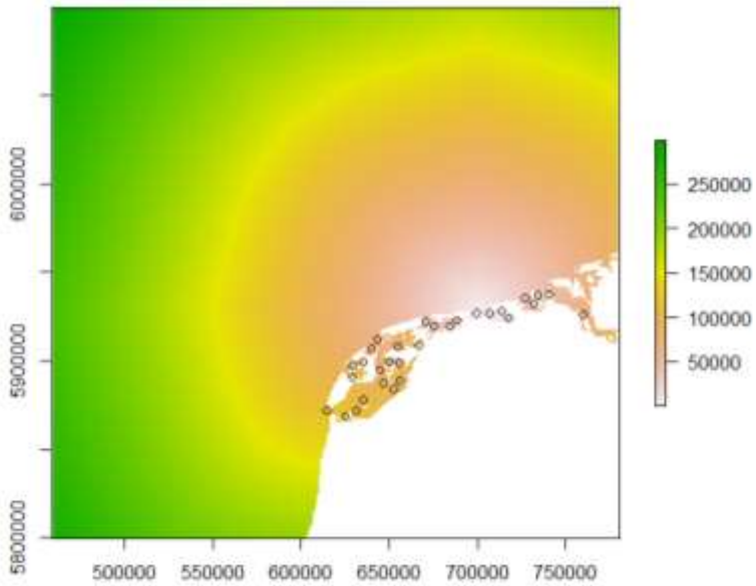


Figure 5.1*. Distance to one of the haul-out cluster location (in m). All white areas are treated as land that could not be crossed by the seals.*

5.2.3 Prey quality landscape

Ideally, a prey landscape is used by the ABM to define the distribution of their prey. Unfortunately, such high-resolution data on prey are not available (see also 2.2). Therefore, following the UK version of *AgentSeal* (Chudzinska *et al.,* 2021) as well as the DEPONS model for porpoises (Nabe-Nielsen *et al.*, 2018), we use marine mammal distributions (in this case seal) based on tracking data as proxy for habitat quality. Future studies might be able to rely on direct estimates of fish abundance. For this we refitted the habitat distribution model as outlined in (Aarts *et al.*, 2016) but removed the effect of distance to the haul-out (see Figure 5.2). The motivation is that this distance-effect is unrelated to habitat quality, but mostly the result of accessibility constraints (i.e., seals having to move from the haul-out sites to the foraging areas). This accessibility constraint will be captured by the simulation of movement of seals.

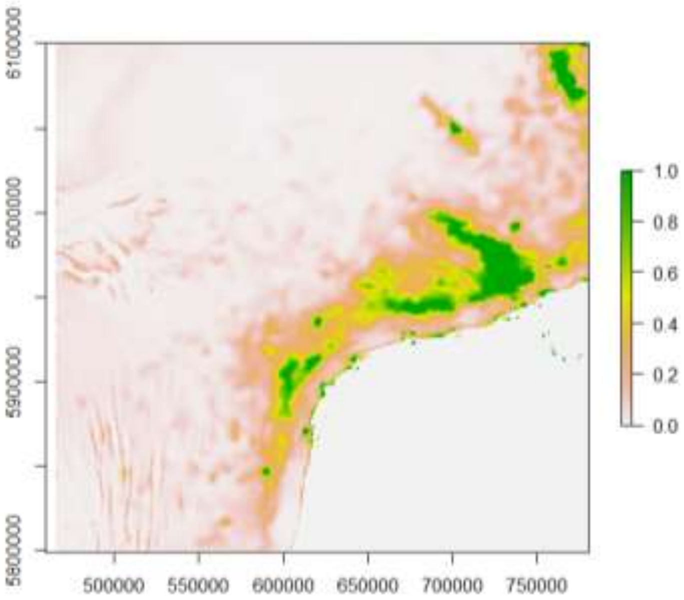


Figure 5.2. *Habitat suitability index. Note the effect of distance to the haul-out site is excluded. The habitat suitability index map is scaled by first setting all habitat suitability values > 99% quantile to that quantile and subsequently dividing by the maximum habitat suitability.*

5.2.4 Model calibration

AgentSeal contains many model parameters, all of which will have an influence on the model outcome (See Figure 5.3 for a screenshot). Most model calibration has been carried out in the development of the *AgentSeal*-UK model. These are explained in the Trace document (supplement of Chudzinska *et al.*, 2021). For this study we have only varied the fish-NAÏVE-multiplier which was applied to the whole study region. This parameter is important because it regulates how habitat suitability relates to absolute prey intake rate. If this parameter is too high, the prey capture rate is over-estimated leading to seals rapidly building op energy reserve, a high haul-out probability, and survival of almost all seals. If this parameter is too low, it leads to loss of energy reserve and eventually all seals dying of starvation. The *AgentSeal* model simulates naïve pups that gradually develop knowledge of their environment. Therefore, most seals should initially lose energy reserves (due to lack of information on suitable foraging sites to visit), with some dying of starvation. Eventually seals should be able to build-up energy reserves, returning to favourable sites. When setting a value of 0.1 for this fish-naïve-multiplier mortality estimates closest to what was expected for the harbour seal population.

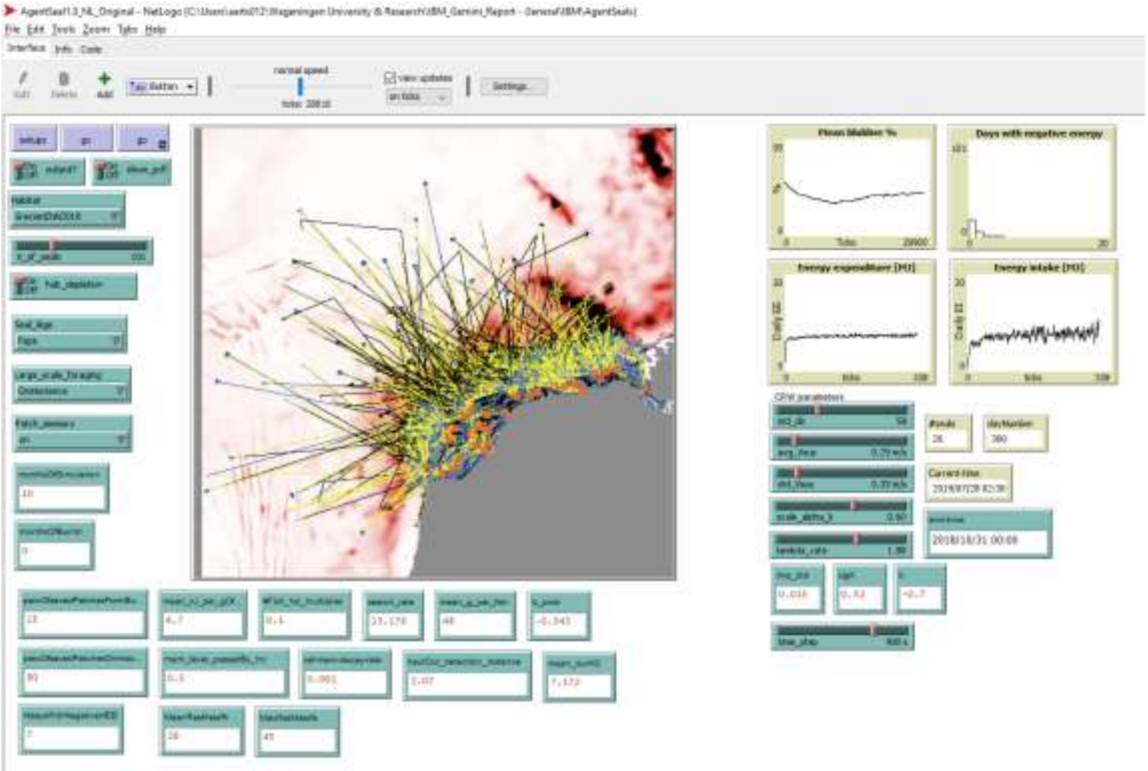


Figure 5.3. *Screenshot of AgentSeal as developed by Chudzinska et al., 2021 applied to the Dutch coast. The left part shows several model parameters (input). The right part all emerging variables (output).*

5.2.5 Scenario simulations

One of the initial objectives was to simulate the effect of the construction of the Gemini Windfarm area on harbour seal populations. However, since this study was unable to estimate the effect distance of pile driving for harbour seals, and very few seals venture in the vicinity of Gemini Windpark, a different scenario simulation was chosen. Instead, we explore the effect of declines in catch-rate on survival of naïve harbour seals. In other words, for example, if seals become 10% less effective in catching fish (e.g., due to anthropogenic disturbance or a decline in prey availability), how does this translate into changes in body condition (% blubber) and vital rates (survival probability)? For this we varied the scale parameter fish-naïve-multiplier between 0.05 and 0.25 by steps of 0.025. For these different scenarios we present their spatial distribution, changes in (surviving) population size, and haul-out probability.

5.3 Results

5.3.1 Baseline simulation

The simulation was run for 100 naïve seals, for 300 days (10 months), with the fish-naïve-multiplier set to 0.1. Some of the emerging variables are shown in Figure 5.4. At the onset of the simulation, when most seals are located within the Wadden Sea, and still naïve regarding their surroundings, the energy intake is low, and average body condition (expressed as mean blubber %) is declining. However, approximately half-way through the simulation (after 4-5 months), the mean blubber % slowly increases. This is also reflected in the energy intake rate. During the first 20 days, the energy intake rapidly increases (mostly due to seals leaving the Wadden Sea, where food is scarce), and continues to increase slowly throughout the simulation. The energy expenditure is relatively constant and only increases due to the increasing size of the seal.

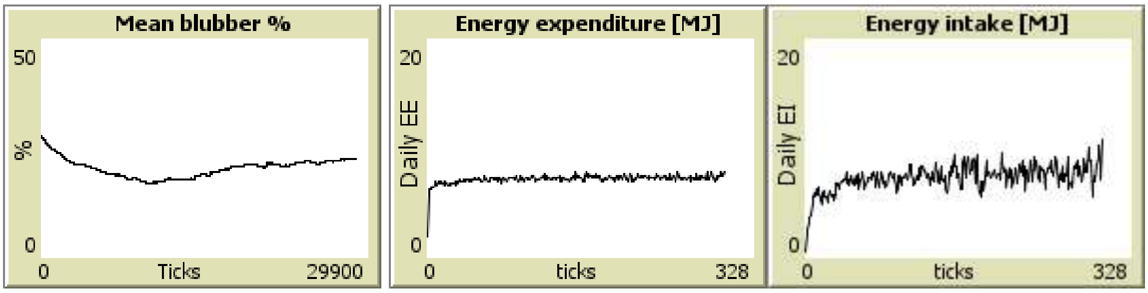


Figure 5.4. *Physiological variables emerging from AgentSeal. The mean blubber mass as percentage of total body mass (left), the daily energy expenditure (middle) and daily energy intake (right). Note the unit of time is 15 minutes in the left figure and in days in the right two figures. The (small) variability in energy expenditure is caused by variation in activities (e.g., resting or foraging). The variability in energy intake rate is mostly explained by variation in prey encounter rate.*

Figure 5.5. shows the emerging distribution of the modelled seals. Note that despite the fact that the underlying habitat suitability model excluded the effect of distance to haul-out sites and revealed low values near haul-out sites, the actual emerging distribution of seals is high near haul-out sites. As seals strive to minimize the distance they must swim to feed, this is to be expected. Also note that the emerging seal distribution is high along the southern edges of the highly suitable habitats (the green areas in Figure 5.5), but much lower further North within those same highly suitable regions.

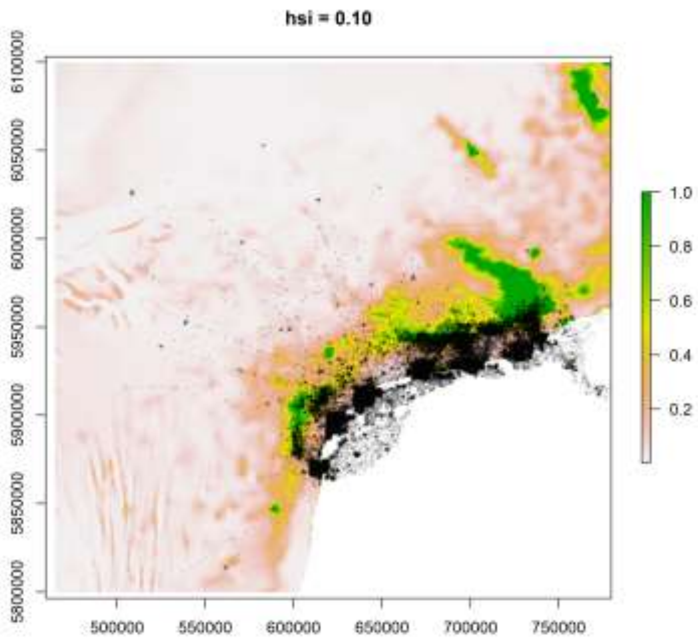


Figure 5.5. *Emerging distribution of 100 seals simulated in AgentSeal. Note the relative low density of seals in the Wadden Sea and high use of seals near the haul-out site on the outer-edges of the Wadden Sea. This is partly caused by the presence of suitable foraging areas near these haul-out sites (see also Figure 5.2)*

5.3.2 Varying effect prey catch rate

To investigate the effect of changes in catch rate (the amount of prey a seal can acquire per unit of area), on spatial distribution, survival, and behaviour, we varied the fish-naïve-multiplier (denoted by 'naïve') between 0.05 (low catch rate) and 0.25 (high catch rate). The emerging distributions are shown in Figure 5.6. When naïve is small, this low catch rate leads to more large-scale foraging trips. The model initiates these large-scale foraging trips when seals have a negative energy balance for 7 days. Note the overall higher usage further away from the haul-out sites. When naïve increases (i.e., leading to higher prey capture rates), the number of large-scale foraging trips decreases, and most seals remain within the vicinity of the haul-out sites.

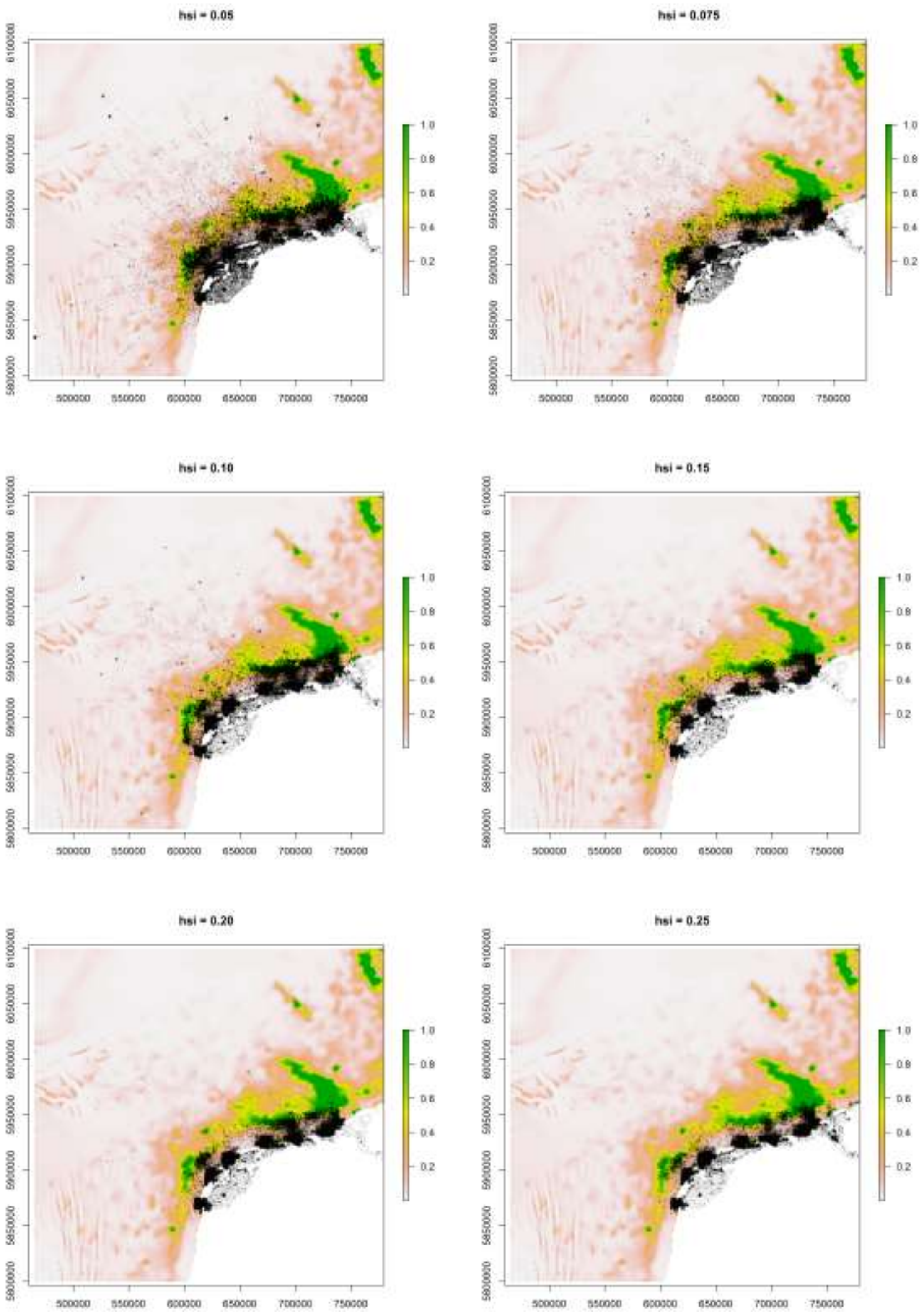


Figure 5.6. *Emerging spatial distribution (100 simulated seals) for different values for the fish-naïve-multiplier (denoted by 'naïve'). The coloured map shows the habitat suitability map used to define the distribution of prey and is equal for all scenarios.*

Not only the distribution, but also the percentage of surviving juvenile seals varies greatly between the different model scenarios (Figure 5.7). When the prey capture rate is high (e.g. naïve = 0.25), most seals survive. When the prey catpure rate is low, all seals die of starvation. The changes in surival probability does not vary linearly with changes in prey capture rate. When the fish-naïve-multiplier declines from 0.15 to 0.10 (a 33% reduction), this leads to a decline of survival from 82% to 27%, a drop of 55%.

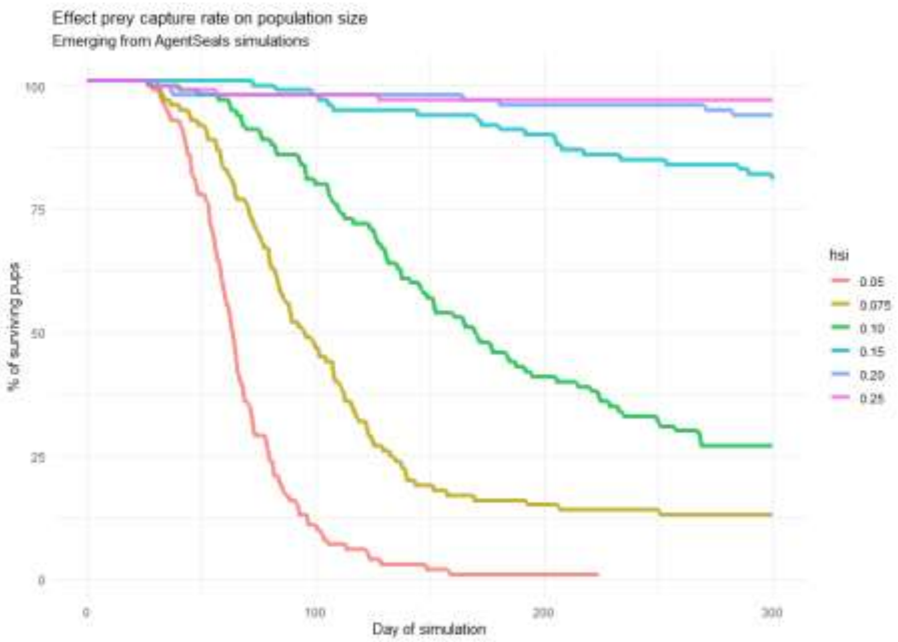


Figure 5.7. *Percentage of surviving seals as function of day of the simulation. Higher prey capture rate (high 'naïve' values), lead to high survival probability, while declines in prey 44apture rates below naïve = 0.15 rapidly leads to increased mortality of naïve seals.*

The changes in the prey capture rate also has an influence on the proportion of time spent in each of behavioural classes (Figure 5.8). When prey capture rate is low (low naïve-values), seals spend more time foraging and less time hauled-out on land, but also, less time long-resting at sea. The latter might be caused by having lower intake and hence lower required digestion.

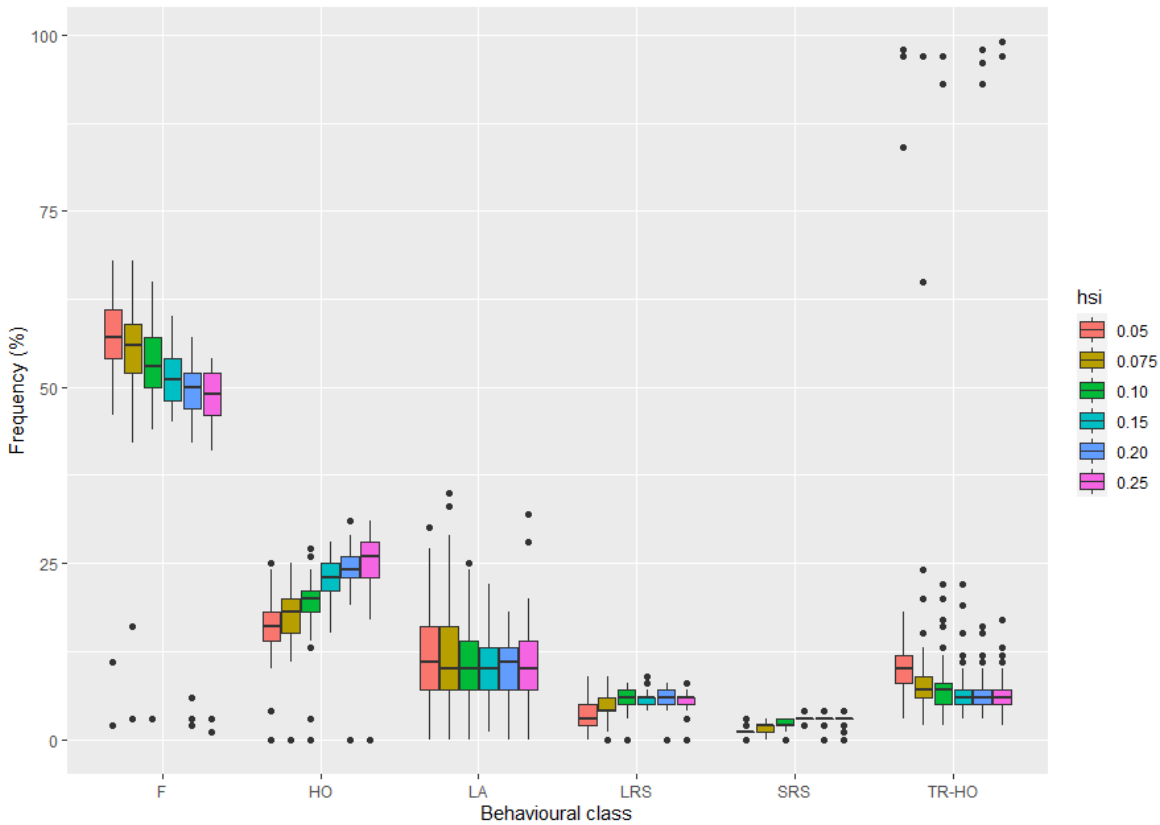


Figure 5.8*. Frequency of behavioural class as function of variation in prey capture rate (naïve values). F = Foraging, HO = Haul-Out, LA = Land Avoidance, LRS = Long Resting at Sea (digestion), SRS = Short Resting at Sea (empty stomach) and TR-HO = Travel to Haul-Out.*

5.4 Discussion

5.4.1 AgentSeal: A digital twin of seals

The ABM AgentSeal was developed for harbour seals living along the East-coast of Scotland. Most model parameters were tuned based on a limited harbour seal tracking data set from that region. In this study we used the same model, but changed the necessary input variables (e.g., habitat suitability maps). The emerging results of *AgentSeal*-NL appear similar to what has been observed in wild seals. For example, the model predicts that seals spend approximately 15-25% hauled out, which is similar to field observations (Aarts *et al.*, 2016).

There are however also a few discrepancies between the emerging model output and recent tracking data from naïve seals released from captivity (3.3). First, the tracked harbour seals released from captivity appear to be much more explorative and spending longer periods of time at sea (Figure 5.9). For example, seal pv79-122-22 is often out at sea for 1-2 weeks in a row (Figure 5.10). There might be different explanations for this discrepancy in distribution. One cause could be a mis-specification of the ABM. For example, the model's current rules for returning to haul-out for skin maintenance or digestion are based on adult seals (from Scotland) and those return-rules may be less stringent or may not apply to weaned pups. In other words, the ABM might force seals to go back to land more quickly, relative to what weaned pups would do. An additional misspecification of the ABM could be that the current ABM does not accurately capture density-dependent processes that may occur in the wild. These processes could lead to local food depletion near the colonies (known as Ashmole's halo), causing seals to forage further offshore (see also the section on density-dependent effects below).
It is also possible that the tracking data collected from seals released from captivity are not representative of seals in the wild. Seals in captivity are fed different prey species (such as mackerel, herring, and even salmon) and have a more consistent and energy-dense diet. According to the marginal value theorem, as a result, they may have a very low giving up (food) density. In other words, when these seals are released into the environment and come across a foraging patch, they could judge it to be of poor quality and move on to the next patch. This could potentially prolong the "keep-searching" mode for a released captive seal. Although these individuals released from captivity travelled quite a distance, it appears that young animals in the wild also make lengthy journeys. This could be due to age, as juvenile animals must be more exploratory because they are unfamiliar with their environment, or the season. Future research should investigate these observed variations further.

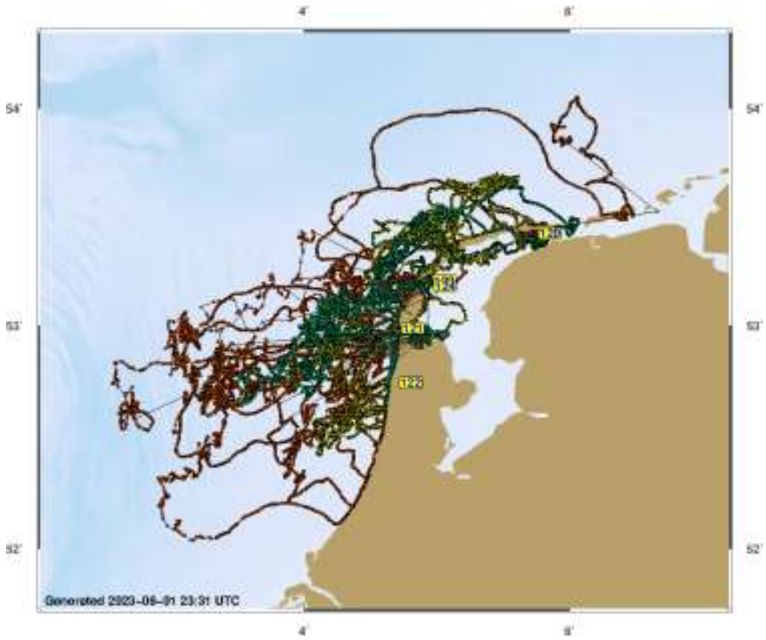


Figure 5.9. *Observed distribution of 5 GPS tracked juvenile seals released from captivity. See accelerometry chapter for more details.*

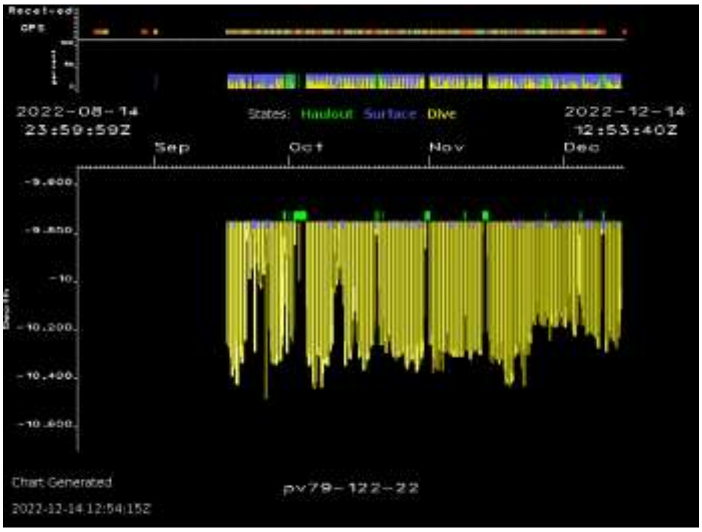


Figure 5.10. *Summary of dive data and behavioural state (haulout, surface and dive) of one seal pv79-122-22. Green blocks represent haul-out periods. Note the long at-sea periods.*

5.4.2 Prey encounter rate

While numerous studies in recent years have focused on refining dynamic energy budget models (how energy is allocated) for various species (REF), we believe that the role of absolute prey availability and catchability has been neglected. The inclusion of prey capture rate (i.e., the quantity of prey captured per unit of time) is one of the most difficult tasks in AgentSeal. Capturing prey is contingent on the local prey density, spatial heterogeneity (i.e., patchiness), the area per unit of time that can be searched, the capture probability once prey is encountered, and the capturing and handling time. The majority of these processes have unknown parameter values, and it is unlikely that they will become available in the near future. Running the simulation and tracking the energy intake, blubber percentage, and survival rate of seals can provide some useful information. In an ideal scenario, naïve seals should first decline in health (due to their lack of knowledge of the area), with some seals succumbing, and then, as they gain experience, some seals should rebuild their energy reserves. This was accomplished in the simulation described above by modifying a scaling parameter (fish-naïve-multiplier). This parameter's value (and thus the prey capture rate) has a significant effect on the fitness and vital rate of seals. An attractive feature of an ABM is that it can be used to mechanically link short-term behaviour and prey ingestion rate to longer-term vital rate parameters, such as survival, and eventually to population changes. In this study, the effect of variation in the aggregate prey capture rate on pup survival was investigated. This relationship is non-linear, as revealed by the model. Declining prey capture rate in a food-rich environment may have little effect on survival probability, but once prey capture rate falls below a certain threshold, a large number of seals may perish. This observation is significant because it suggests that under favourable conditions, environmental alterations (such as anthropogenic disturbance) may have little effect on seals. In harsher conditions, however, such as when seals are nutritionally stressed, minor variations in their hunting efficiency may have a significant effect on their survival. While we may not be able to mechanically deduce the absolute prey capture rates, the model could be refined in future research using population demographic data to fine-tune these parameters.

5.4.3 Density dependent processes

One observation is that many simulated seals remain in close proximity to the haul-out site, and if they do venture further out, they frequently forage near the edge of the nearest suitable habitat patch. Assuming seals maximize foraging efficiency (which is an inherent characteristic of AgentSeal), they are expected to forage close to their haul-out site when there is a suitable patch, regardless of its size. Under normal conditions, foraging would lead to a decrease in prey density, and this would eventually make it more advantageous to move further offshore to non-depleted foraging areas that are further away. This is currently not the happening, and as a result, the emerging distribution of simulated seals does not match that of the tracked seals. This suggests a lack of density-dependent processes, which is to be expected given that the simulation was only run for 100 seals, whereas the Dutch Wadden Sea is home to approximately 10,000 harbour seals. Inclusion of density-dependent processes may also have a significant effect on population development. In the current AgentSeal simulation, seals are released into a non-depleted landscape. When seal density is high, it is expected that seals will create a food landscape where food density is, on average, low near haul-out sites and high further offshore. This appears to be supported by the fact that the North Sea's prey density is also higher further offshore (Aarts *et al.,* 2021). Young seals must therefore not only compensate for their lack of hunting experience, but also face the difficult task of locating rich patches further offshore, which may result in a high mortality rate. This could be one (of the many) explanation for the current population development, where it appears that few pups survive to become adults (Galatius *et al.,* 2022).

5.4.4 Future directions

The ultimate goal of an agent-based model from a policy perspective is to predict the effects of environmental changes such as anthropogenic activities on the species in question. As highlighted in this report, AgentSeal is the only tool capable of linking behavioural changes directly to population-level consequences, such as changes in survival, for seals. Currently, the model is run with 100 individuals/agents; however, if density-dependent processes are to be considered, additional animals should be included. To realistically simulate the movement and level of depletion of the entire harbour seal population, it appears feasible to increase the sample size to 1,000 individuals and increase the individual-level depletion by a factor of 10. For this, however, the model requires additional refinement, particularly regarding how naïve pups move through the landscape, as well as the potential addition of seasonal variation. The ongoing research project 'sandeels and seals' should provide some of the necessary information for more accurate prey abundance estimations.

6 Conclusions

6.1 Integration

The purpose of this research was to fill critical knowledge gaps. The studies addressing these knowledge gaps were conducted independently. In this section, we attempt to summarise how all these factors inter-connect and affect the ABM.

Seals travel out to sea in search of and to capture prey. In chapter 2, the dominant prey base has been identified in this study. Moreover, we have compiled data from fisheries surveys in order to estimate the abundance and distribution of their prey. Ideally, these prey-field data should be included in the ABM. However, the spatial resolution of the fish survey data is currently inadequate. In addition, there was insufficient data concerning essential prey species such as sandeel. The 'sandeel and seal' project was designed to address this knowledge gap. Estimating the energy landscape with more precise data on sandeel and other small demersal fish species (as Ransijn *et al.*, did) is one of the anticipated future outcomes. In the future, such a landscape of prey-energy could directly feed AgentSeal.

To bridge the gap between food density and actual prey intake rate, information on prey detection and capture probability is required. What is the seal's search area, and what is the likelihood that it will capture a prey once it is encountered? In chapter 3, we have developed accelerometery methods to measure such prey capture attempts. Iorio-Merlo *et al.*, 2021 eloquently illustrate the potential of accelerometery data. We argue that prey capture probability is one of the most neglected aspects of an ABM. This significance is exemplified by the fact that varying the fish-NAÏVE-scaler results in drastically different population survival rates. Understanding the role of prey capture probabilities is also important in the context of climate change, given that the swim speed and escape abilities of fish (relative to that of its predator) are highly temperature-dependent. As the temperature rises, the capture probability decreases. This is the most likely reason why there are so few seals in tropical waters. In the North Sea, where water temperatures are rising at an unprecedented rate due to climate change, seals may be less able to capture prey. By combining the fish energy landscape, accelerometery studies, and AgentSeal, it should be possible to estimate not only the effect of anthropogenic activities, but also the effect of climate change.

In Chapter 4 we looked at the effect of pile-driving, using all pile-driving available to us. When we know more precisely how seals respond, and at what distance from the piling-locations, these behavioural changes could be incorporated into AgentSeals. However, the German wind parks (for which we had information available on the start and end of piling) were mostly build with mitigation measures in place. Therefore, it was unfortunately not possible to accurately estimate how seals respond and we were unable to include this into AgentSeals. In the study for Borssele wind park area, there was evidence for general avoidance. Also here, very few seals venture into the vicinity of the wind parks. Refitting a habitat distribution model based on all parks under construction, was beyond the scope of this study, but this could hopefully be a topic of investigation in future analysis. Once these avoidance distances are properly defined, such temporary avoidance areas could be included into AgentSeals.

6.2 Recommendations

The anticipated expansion of human activities in the North Sea could have an impact on the recovery of marine mammal populations and even pose a threat in the near future. In response to the perceived risks, research could be conducted to determine whether and how such human activities impact the species in question. Despite the policy relevance of these questions, such research attention may not provide the answers when knowledge on the ecological mechanisms and life-history of the species is lacking. For instance, in chapter 5 we have demonstrated that the food landscape and emerging intake rate can have a significant impact on the viability of a population. In the end, the degree to which animals are nutritionally stressed will ultimately determine the impact of any non-lethal human activity. Any study that intents to conduct an impact assessment but disregards the role of the natural environment is therefore incomplete.

The challenge is determining which research questions to pursue in light of limited financial and time resources. Here is where an Agent Based Model could prove especially valuable. Not so much to answer the question at hand (e.g., impact assessment), but rather to highlight the pathways through which seals could be affected. This project's objective was to help fill in some of the gaps in the knowledge that could lead to a well-functioning ABM. Based on the findings of this study, we now propose several knowledge gaps or research avenues that could potentially be pursuit in future research endeavours.

From habitat selection to habitat quality

An important component of the ABM is the habitat suitability index (NAÏVE) map. It determines how seals move (by altering speed and sinuosity as a function of NAÏVE), the prey intake rate, and the points of attraction, i.e., the regions that seals are drawn to. These NAÏVE maps are derived from variations in seal density. It is assumed that high-density areas are more suitable. However, it does not fully explain *why* some areas are suitable (or unsuitable). Is it due to a high prey density, favourable environmental conditions for prey capture, or low disturbance (e.g., from shipping)? To answer these questions, it is necessary to define the quality of a habitat and how it determines the local population size, going beyond the concept of suitability. The first step in addressing this issue is to estimate how a specific habitat configuration affects local population numbers. For instance, by defining for each haul-out region the area at sea where those seals forage, also known as the 'Hinterland'. Next, the number of seals on haul-out sites can be correlated with the overall habitat suitability within the Hinterland. Once such a relationship has been established, this habitat selection model could be expanded to incorporate the effect of human activities at sea, such as shipping, sand extraction, seismic surveys, and the construction of offshore wind farms. Potentially, this would reveal not only whether the distribution of seals in the North Sea is affected by these human activities, but also the effect of these activities on population size.

Incorporating density dependent competition

The current ABM used in this study does not include density dependent competition. Future studies should include more individuals in the simulations, that deplete the food landscape. This will have important consequences for the emerging results of the model: Seals will tend to eventually move further offshore due to depletion near the haul-out site, the overall distribution should become more homogenized because of depletion of the highest quality food patches, and likely spatial segregation between colonies will arise, due to density dependent competition. The ABM currently already can include prey depletion. However, what is first needed is proper estimates of *absolute* prey density. Such data are currently collected in the sandeels and seal project. Once these results are available, density dependent competition could be included into AgentSeal, and this should considerably improve the emerging properties of the ABM.

Individual variation

As a result of the short suckling period (less that a month) young seals are left to discover their environment alone. This leads to a great variation in behaviour and potential reaction to environmental or anthropogenic changes. Understanding this variation will be key to perfectioning an ABM that reflects the challenges a population might face correctly.

Accelerometery tracking of (young) harbour and grey seals.

During the recovery phase of both harbour and grey seal population size, the population growth rate often exceeded 10% per year. Currently, the growth rate is close to zero and might even be negative, despite continued reproduction. This suggests that substantial mortality is taking place, and most likely during the first year of the seals' life, when it must gain experience in catching prey and locating favourable foraging areas. This study was the first occasion trackers were deployed on naïve seals, and indeed the tracking results seem to reveal the development of spatial memory: more apparent spatial exploration to regions further offshore. However, the sample size was low, and trackers were deployed on seals from captivity, which may behave different from those in the wild. To understand where and how seals find and catch prey, more accelerometery trackers on harbour and grey seals would be recommended.

Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

References

Aarts, G., M. MacKenzie, B. McConnell, M. Fedak, and J. Matthiopoulos. 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31:140–160.

Aarts, G., Brasseur, S., Poos, J.J., Schop, J., Kirkwood, R., Kooten, T.V., Mul, E., Reijnders, P., Rijnsdorp, A.D., Tulp, I., 2019a. Top-down pressure on a coastal ecosystem by harbor seals, Ecosphere 10 1.

Aarts, G., Brasseur, S., Geelhoed, S., van Bemmelen, R., Leopold, M., 2013a. Grey and harbour seal spatiotemporal distribution along the Dutch West coast, Report / IMARES Wageningen UR, C103/13 IMARES Wageningen UR, IJmuiden, p. 63.

Aarts, G., Fieberg, J., Brasseur, S., Matthiopoulos, J., 2013b. Quantifying the effect of habitat availability on species distributions. Journal of Animal Ecology 82, 1135-1145.

Aarts, G., Brasseur, S., Rindorf, A., Smout, S., Dickey-Collas, M., Matthiopoulus, J., 2011. Spatial selection of sandeel (Ammodytes marinus) by grey seals (Halichoerus grypus), ICES Council Meeting 2011.

Aarts, G., Brasseur, S., Winter, E., Kirkwood, R., 2015- unpublished. Persistent maximum swim speed of harbour porpoise, harbour seal and grey seal.

Adams, L., 1965. Progress in ecological biotelemetry. BioScience, 83-86.

Arcadis, 2012. Passende Beoordeling windparken en kabeltracé Gemini, Arcadis report 076496519: A – Definitief, 19 oktober 2012.

Baum, J.K. and Worm, B., 2009. Cascading top-down effects of changing oceanic predator abundances. Journal of Animal Ecology, 78: 699-714. https://doi.org/10.1111/j.1365-2656.2009.01531.x

Brasseur, S., Kirkwood, R., Aarts, G., 2018a. Seal monitoring and evaluation for the Gemini offshore windfarm: Tconstruction - 2015 report, Wageningen Marine Research, Yerseke.

Brasseur, S., Schop, J., Cremer, J., Aarts, G., 2018b. Harbour seal monitoring and evaluation for the Luchterduinen offshore windfarm : Final report, Wageningen Marine Research, Texel.

Brasseur, S.M.J.M., Aarts, G.M., Meesters, H.W.G., Polanen-Petel, T.v., Dijkman, E.M., Cremer, J.S.M., Reijnders, P.J.H., 2010. Habitat preferences of harbour seals in the Dutch coastal area: analysis and estimate of effects of offshore wind farms, IMARES, Texel, p. 55.

Brasseur, S.M.J.M., Polanen Petel, T.v., Aarts, G.M., Meesters, H.W.G., Dijkman, E.M., Reijnders, P.J.H., 2009. Grey seals and Offshore Wind Farms, Den Helder, The Netherlands.

Brasseur, S.M.J.M., Reijnders, P.J.H., 2000. Radio tracking of seals - behaviour and habitat use of free ranging harbour seals, In: Hutterer, C.M.-C.R. (Ed.), Deutsche Gesellschaft für Säugetierkunde und Vereniging voor Zoogdierkunde en Zoogdierbescherming, gemeinsame Tagung, ; Kurzfassungen der Vorträge un Posterdemonstrationen. Jena (Germany), , p. 10, Urban & Fischer, 2000, Groningen.

Brasseur, S.M.J.M., Reijnders, P.J.H., 2001. Zeehonden in de Oosterschelde, fase 2; effecten van extra doorvaart door de Oliegeul, Alterra, Wageningen.

Brasseur, S.M.J.M., Reijnders, P.J.H., Cremer, J., Meesters, E., Kirkwood, R., Jensen, L.F., Jeβ, A., Galatius, A., Teilmann, J., Aarts, G., 2018c. Echoes from the past: Regional variations in recovery within a harbour seal population. PLOS ONE 13, e0189674.

Brasseur, S.M.J.M., van Polanen Petel, T.D., Gerrodette, T., Meesters, E.H.W.G., Reijnders, P.J.H., Aarts, G., 2015. Rapid recovery of Dutch gray seal colonies fueled by immigration. Marine Mammal Science 31, 405-426.

Brasseur, S.M.J.M., Schop J., Aarts, G.M. 2022. Measurement of effects of pile driving in the Borssele wind farm zone on the seals in the Dutch Delta area- version II: Changes in dive behaviour, haul-out and stranding of harbour and grey seals, including sound modelling. Wageningen Marine Research Report C059/22, Den Helder, The Netherlands

Burggraaf-van den Berg, I., Argiolu, R., Verlinde Y. 2012. MER Windparken Gemini Deel A. Arcadis report 076707817, Arnhem, The Netherlands

Christensen, A., M. Butenschön, Z. Gürkan & I.J. Allen, 2013. Towards an integrated forecasting system for fisheries on habitat-bound stocks. Ocean Science, 9: 261-279.

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., McConnell, B., 2021. AgentSeal: Agent-based model describing movement of marine central-place foragers. Ecological Modelling 440, 109397.

Daan, N., Bromley, P.J., Hislop, J.R.G., Nielsen, N.A., 1990. Ecology of North sea fish. Netherlands Journal of Sea Research 26, 343-386.

Dannenberger, D., Möller, R., Westphal, L., Moritz, T., Dähne, M., Grunow, B., 2020. Fatty Acid Composition in Blubber, Liver, and Muscle of Marine Mammals in the Southern Baltic Sea. Animals 10, 1509.

de la Vega, C., Lebreton, B., Siebert, U., Guillou, G., Das, K., Asmus, R., Asmus, H., 2016. Seasonal Variation of Harbor Seal's Diet from the Wadden Sea in Relation to Prey Availability. PLOS ONE 11, e0155727.

Duffill Telsnig, J.I., Jennings, S., Mill, A.C., Walker, N.D., Parnell, A.C., Polunin, N.V.C., 2019. Estimating contributions of pelagic and benthic pathways to consumer production in coupled marine food webs. Journal of Animal Ecology 88, 405-415.

Engelhard G.H., J.L. Blanchard, J.K. Pinnegar, J. van der Kooij, E.D. Bell, S. Mackinson, D.A. Righton 2013. Body condition of predatory fishes linked to the availability of sandeels. Mar. Biol. 160: 299-308.

Engelhard, G.H., Peck, M.A., Rindorf, A., C. Smout, S., van Deurs, M., Raab, K., Andersen, K.H., Garthe, S., Lauerburg, R.A.M., Scott, F., Brunel, T., Aarts, G., van Kooten, T., Dickey-Collas, M., 2014. Forage fish, their fisheries, and their predators: who drives whom? ICES Journal of Marine Science: Journal du Conseil 71, 90-104.

Foo, D., Semmens, J.M., Arnould, J.P.Y., Dorville, N., Hoskins, A.J., Abernathy, K., Marshall, G.J., Hindell, M.A., 2016. Testing optimal foraging theory models on benthic divers. Animal Behaviour 112, 127-138.

Galatius A., B.S., Carius F., Jeß A., Meise K., Meyer J., Schop J., Siebert U., Stejskal O., Teilmann J., Thøstesen C. B., 2022. Survey Results of Harbour Seals in the Wadden Sea in 2022, In: Common Wadden Sea Secretariat, W., Germany. (Ed.)

Gilles, A., S. Viquerat, E.A. Becker, K.A. Forney, S.C.V. Geelhoed, J. Haelters, J. Nabe-Nielsen, M. Scheidat, U. Siebert, S. Sveegaard, & F.M. Beest, 2016. Seasonal habitat-based density models for a marine top predator, the harbor porpoise, in a dynamic environment. Ecosphere, 7: e01367.

Hall, A.J., Engelhard, G.H., Brasseur, S.M.J.M., Vecchione, A., Burton, H.R., Reijnders, P.J.H., 2003. The immunocompetence handicap hypothesis in two sexually dimorphic pinniped species - there a sex difference in immunity during early development? Developmental and Comparative Immunology 27, 629-637.

Härkönen, L., Dietz, R., Reijnders, P.J.H., Teilmann, J., Harding, K., Hall, A., Brasseur, S.M.J.M., Siebert, U., Goodman, S.J., Jepson, P.D., Rasmussen, T.D., Thompson, P., 2006. A review of the 1988 and 2002 phocine distemper virus epidemics in European harbour seals. Diseases of Aquatic Organisms 68, 115-130.

Härkönen, T., Heide- Jørgensen, M.P., 1991. The Harbor Seal *Phoca vituli*na as a Predator in the Skagerrak. Ophelia 34, 191-207.

Iorio-Merlo, V., Graham, I.M., Hewitt, R.C., Aarts, G., Pirotta, E., Hastie, G.D., Thompson, P.M., 2022. Prey encounters and spatial memory influence use of foraging patches in a marine central place forager. Proceedings of the Royal Society B: Biological Sciences 289, 20212261.

Madgett, A.S., Yates, K., Webster, L., McKenzie, C., Moffat, C.F., 2019. Understanding marine food web dynamics using fatty acid signatures and stable isotope ratios: Improving contaminant impacts assessments across trophic levels. Estuarine, Coastal and Shelf Science 227, 106327.

McConnell, B.J., M.A. Fedak, P. Lovell, & P.S. Hammond, 1999. Movements and foraging areas of grey seals in the North Sea. J. of Appl. Ecol. 36: 573-590.

Kavanagh, A.S., Cronin, M.A., Walton, M., Rogan, E., 2010. Diet of the harbour seal (Phoca vitulina vitulina) in the west and south-west of Ireland. J Mar Biol Assoc Uk 90, 1517-1527.

Moore, S. E., 2008. Marine Mammals as Ecosystem Sentinels. Journal of Mammalogy, Volume 89, Issue 3, 5 534–540, https://doi.org/10.1644/07-MAMM-S-312R1.1

Nabe-Nielsen, J., van Beest, F.M., Grimm, V., Sibly, R.M., Theilmann, J., Thompson, P.M. (2018) Predicting the impact of anthropogenic disturbances on marine populations. Conservation Letters.

O'Boyle, R., Sinclair, M., 2012. Seal–cod interactions on the Eastern Scotian Shelf: Reconsideration of modelling assumptions. Fisheries Research 115–116, 1-13.

Pierce, G.J., Boyle, P.R., 1991. A Review of Methods for Diet Analysis in Piscivorous Marine Mammals. Oceanography and Marine Biology 29, 409-486.

Pinnegar J.K., J. van der Kooij, G.H. Engelhard, J.L. Blanchard, K.J. Warr, D. Righton 2006. Small-scale variability in fish diet and whether or not this reflects local patterns of prey availability. ICES CM 2006/F:06.

Reay, P.J., 1970. Synopsis of biological data on North Atlantic sandeels of the genus Ammodytes: A. tobianus, A. dubius, A. americanus, and A. marinus. FAO Fish Synop 82, 1-52.

Reijnders, P.J.H., 1985. On the extinction of the Southern Dutch harbour seal population. Biological Conservation 31, 75-84.

Reijnders, P.J.H., 1986. Reproductive failure in common seals feeding on fish from polluted coastal waters. Nature 324, 456-457.

Reijnders, P.J.H., van Dijk, J., Kuiper, D., 1995. Recolonization of the dutch Wadden Sea by the grey seal Halichoerus grypus. Biological Conservation 71, 231-235.

Reynolds, J.E. III , Marsh, H., Ragen, T.J., 2009. Marine mammal conservation. Endangered Species Research 7:23-28. https://doi.org/10.3354/esr00179

Rindorf, A., S. Wanless, M.P. Harris, 2000. Effects of changes in sandeel availability on the reproductive output of seabirds. Mar. Ecol. Prog. Ser. 202: 241–252.

Ross, T.R., Thiemann, G.W., Young, B.G., Ferguson, S.H., 2022. Complementary diet analyses reveal intraspecific and temporal variation in ringed seal (Pusa hispida) foraging in the Canadian high arctic. Polar Biology.

Russell, D.J.F., Brasseur, S.M.J.M., Thompson, D., Hastie, G.D., Janik, V.M., Aarts, G., McClintock, B.T., Matthiopoulos, J., Moss, S.E.W., McConnell, B., 2014. Marine mammals trace anthropogenic structures at sea. Current Biology 24, R638-R639.

Santos, M.B., Pierce, G.J., 2003. The diet of harbour porpoise (Phocoena phocoena) in the northeast Atlantic. Oceanography and Marine Biology, Vol 41 41, 355-390.

Scharff-Olsen, C.H., Galatius, A., Teilmann, J., Dietz, R., Andersen, S.M., Jarnit, S., Kroner, A.-M., Botnen, A.B., Lundström, K., Møller, P.R., Olsen, M.T., 2018. Diet of seals in the Baltic Sea region: a synthesis of published and new data from 1968 to 2013. ICES Journal of Marine Science 76, 284-297.

Siniff, D.B., Tester, J.R., 1965. Computer analysis of animal-movement data obtained by telemetry. Bioscience 15, 104-108.

Sørlie, M., Nilssen, K.T., Bjørge, A., Freitas, C., 2020. Diet composition and biomass consumption of harbour seals in Telemark and Aust-Agder, Norwegian Skagerrak. Marine Biology Research 16, 299-310.

Smout, S., Rindorf, A., Hammond, P.S., Harwood, J., Matthiopoulos, J., 2013. Modelling prey consumption and switching by UK grey seals. ICES Journal of Marine Science 71, 81-89.

Stewart, C., Lang, S.L.C., Iverson, S., Bowen, W.D., 2022. Measuring repeatability of compositional diet estimates: An example using quantitative fatty acid signature analysis. Ecol Evol 12, e9428.

Temming, A., S. Götz, N. Mergardt, & S. Ehrich 2004. Predation of whiting and haddock on sandeel: aggregative response, competition and diel periodicity. J. Fish Biol., 64: 1351-1372.

Thomas, A.C., Deagle, B., Nordstrom, C., Majewski, S., Nelson, B.W., Acevedo-Gutiérrez, A., Jeffries, S., Moore, J., Louden, A., Allegue, H., Pearson, S., Schmidt, M., Trites, A.W., 2022. Data on the diets of Salish Sea harbour seals from DNA metabarcoding. Scientific Data 9, 68.

Thompson, D., Hammond, P.S., Nicholas, K.S., Fedak, M.A., 1991. Movements, Diving and Foraging Behavior of Gray Seals (Halichoerus-Grypus). Journal of Zoology 224, 223-232.

Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C., Racey, P.A., 1996a. Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE Scotland. Journal of Applied Ecology 33, 1572-1584.

Thompson, P.M., Tollit, D.J., Greenstreet, S.P.R., Mackay, A., Corpe, H.M., 1996b. Between-year variations in the diet and behaviour of harbour seals Phoca vitulina in the Moray Firth; causes and consequences. Aquatic predators and their prey, 44-52.

Trites, A.V.C.D.P., 1997. competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J.Northw.Atl.Fish.sci. 22, 173-187.

Trites, A.W., Spitz, J., 2018. Diet, in: Würsig, B., Thewissen, J.G.M., Kovacs, K.M. (Eds.), Encyclopedia of Marine Mammals (Third Edition), Academic Press, pp. 255-259.

Vance, H.M., Hooker, S.K., Mikkelsen, L., van Neer, A., Teilmann, J., Siebert, U., Johnson, M., 2021. Drivers and constraints on offshore foraging in harbour seals. Scientific Reports 11, 6514.Van de Vijver, K.I., Hoff, P., Das, K., Brasseur, S., Van Dongen, W., Esmans, E., Reijnders, P., Blust, R., DE Coent, W., 2005. Tissue distribution of perfluorinated chemicals in harbor seals (Phoca vitulina) from the Dutch Wadden Sea. Environ Sci Technol 39, 6978-6984.

Wanless, S., P. Wright, M. Harris, & D. Elston, 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Mar. Ecol. Prog. Ser., 279:237–246.

Wanless, S., M.P. Harris, P. Redman & J.R. Speakman 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. Mar. Ecol. Prog. Ser., 294:1-8. Wilson, L.J., Hammond, P.S., 2016. Harbour seal diet composition and diversity. Marine Scotland Science.

Wilson, L.J., Hammond, P.S., 2019. The diet of harbour and grey seals around Britain: Examining the role of prey as a potential cause of harbour seal declines. Aquatic Conservation: Marine and Freshwater Ecosystems 29, 71-85.

Young, B.G., Ferguson, S.H., 2014. Using stable isotopes to understand changes in ringed seal foraging ecology as a response to a warming environment. Marine Mammal Science 30, 706-725.

Justification

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Approved: Steve Geelhoed
Researcher

Signature: 

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Date: 11-09-2023

Appendix 1 e-DNA

This manuscript is work in prep and will be replaced by the (open-access) publication once completed.

eDNA and Hard parts : Diet analyses of seals: a comparison between methods and species

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Abstract

Diet is key to understanding an animals' requirements and its role in the ecosystem. In this study we investigated methods to infer the diet composition of two seal species common in the North Sea and Wadden Sea, the harbour seal *Phoca vitulina* andgrey seal *Halichoerus grypus*, based on their faecal remains. Traditional methods are mostly based on the visual identification of prey remains recovered from stomach contents, regurgitates or faeces. Hard part analysis is unique to determine prey size, it is, however, both labour intensive and inefficient in detecting species when hard parts are worn by digestion or only soft parts are ingested. Recent development in molecular analysis enables to identify multiple prey taxa in one run. This method, (E-DNA) targeting fragmented DNA of consumed prey, may give an additional, broader insight into the seals' diets. In this study we used frozen faecal samples collected in the wild (2011 - 2018) along the Dutch coast. Different methods were used to dissolve faecal samples and extract the genetic material: Ethanol followed by freeze-drying and phosphate-buffered saline (PBS). PBS was a better solvent, as Ethanol seemed to react with the faecal material, creating a paste which strongly adhered to hard parts complicating morphological identification. The Qiagen Fast DNA Stool Kit was used to extract DNA. To identify prey DNA, a ~75 base pair fragment of the 16S mtDNA was used. This fragment targets many chordate species, including seals. therefor a blocking primer was added to block the seal DNA. Next Generation Sequencing was used to sequence all amplified faeces DNA. Faecal samples were washed and remaining hard parts were examined and brought to species level. By comparing the analysis of hard parts with that of DNA, we were able to obtain a (more) complete insight into the diet of harbour and grey seals living in the North Sea and Wadden Sea.

Keywords: molecular scatology, diet, grey seal, *Halichoerus grypus*, harbour seal, *Phoca vitulina*, phosphate buffered saline (PBS), hard-part analysis, non-invasive, Next Generation Sequencing

Appendix 2 Top-Down Pressure

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esa ECOSPHERE

Top-down pressure on a coastal ecosystem by harbor seals

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Abstract. Historic hunting has led to severe reductions of many marine mammal species across the globe. After hunting ceased, some populations have recovered to pre-exploitation levels and may have regained their prominent position as top predator in marine ecosystems. Also, the harbor seal population in the international Wadden Sea grew at an exponential rate following a ban on seal hunting in 1960s, and the current number ~38,000 is close to the historic population size. Here we estimate the impact of the harbor seal predation on the fish community in the Wadden Sea and nearby coastal waters. Fish remains in fecal samples and published estimates on the seal's daily energy requirement were used to estimate prey selection and the magnitude of seal consumption. Estimates on prey abundance were derived from demersal fish surveys, and fish growth was estimated using a Dynamic Energy Budget model. GPS tracking provided information on where seals most likely caught their prey. Harbor seals hauling-out in the Dutch Wadden Sea fed predominantly on demersal fish, for example, flatfish species (flounder, sole, plaice, dab), but also on sandeel, cod, and whiting. Although harbor seals acquire the majority of prey further offshore in the adjacent North Sea, and only spend 14% of their diving time in the Wadden Sea, seal predation was still estimated to cause an average annual mortality of 43% of the remaining fish in the Wadden Sea and 60% in the nearby shallow coastal waters (<20 m). There were however large sources of uncertainty in the estimated impact of seals on fish, including the migration of fish between the North Sea and Wadden Sea, and catchability estimates of the fish survey sampling gear, particularly for sandeel and other pelagic fish species. Our estimate suggested a considerable top-down pressure by harbor seals on demersal fish. However, predation by seals may also alleviate density-dependent competition between the remaining fish, allowing for increased fish growth, and partly compensating for the reduction in fish numbers. This study shows that recovering coastal marine mammal populations could become an important component in the functioning of shallow coastal ecosystems.

Appendix 3 Accelerometry

This manuscript is work in prep and will be replaced by the (open-access) publication once completed.

OBJECTIVE SEPARATION OF BODY MOTION AND ORIENTATION IN ACCELEROMETRY DATA

Geert Aarts, Manon den Haan, Sophie Brasseur, Phil Lovell, Paul Thompson & Rory Wilson

ABSTRACT: Animal-borne accelerometers can provide detailed information on animal behavior, including three-dimensional movement, prey-capture attempts and measures of energy expenditure. Accelerometers measure the tri-axial total g-force. One component is the gravitational force divided among the three orthogonal dimensions, which changes with the animal's body orientation relative to the Earth's gravitational field. The other component reflects dynamic acceleration or deceleration of the animal. Since changes in body orientation and the resulting changes in the direction of the gravitational force are generally more gradual compared to the dynamic component, separating body motion and orientation is generally achieved by applying a smoother or frequency filter to the raw accelerometer measurements. However, currently, no objective method exists for selecting the best filter or smoother to extract the animals' behavior and movement from accelerometry data.

Since the vectorial sum of the gravitational components of all three orthogonal axes combined should equal 1*g* (=9.81 ms^{-2}), we propose that the best approximation of the gravitational component is found when the size of the smoothing window or cut-off frequency yields an estimated total gravitational component closest to 1*g*. This method is tested on simulated data and applied to measured accelerometry data from six different species, with a main focus on harbor seals (*Phoca vitulina)*.

For the simulated data, where the best smoothing window and cut-off filter frequency is known *a-priori*, the proposed methodology selects the optimal smoothing window and cut-off filter frequency closely, except in the presence of large centrifugal forces. In actual accelerometer measurements, the value of optimal smoothing or filtering is shown to vary between species and between types of behaviors.

Appendix 4 Prey encounters

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Research

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Prey encounters and spatial memory influence use of foraging patches in a marine central place forager

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Given the patchiness and long-term predictability of marine resources, memory of high-quality foraging grounds is expected to provide fitness advantages for central place foragers. However, it remains challenging to characterize how marine predators integrate memory with recent prey encounters to adjust fine-scale movement and use of foraging patches. Here, we used two months of movement data from harbour seals (*Phoca vitulina*) to quantify the repeatability in foraging patches as a proxy for memory. We then integrated these data into analyses of fine-scale movement and underwater behaviour to test how both spatial memory and prey encounter rates influenced the seals' area-restricted search (ARS) behaviour. Specifically, we used one month's GPS data from 29 individuals to build spatial memory maps of searched areas and archived accelerometery data from a subset of five individuals to detect prey catch attempts, a proxy for prey encounters. Individuals were highly consistent in the areas they visited over two consecutive months. Hidden Markov models showed that both spatial memory and prey encounters increased the probability of seals initiating ARS. These results provide evidence that predators use memory to adjust their fine-scale movement, and this ability should be accounted for in movement models.

Appendix 5 Sound exposure

This manuscript is work in prep and will be replaced by the (open-access) publication once completed.

OPPORTUNISTIC SOUND EXPOSURE EXPERIMENTS:

BEHAVIOURAL REACTIONS OF WILD GREY SEALS TO PILE-DRIVING

Geert Aarts, Sophie Brasseur & Roger Kirkwood

ABSTRACT: Marine mammals rely on underwater sound for social interaction, communication, navigation, predator avoidance and foraging. Pile-driving during the construction of offshore windfarms produces high energy, broad spectrum sound that can be detected by marine mammals, potentially causing injury or changes in behaviour that could ultimately reduce body condition, survival or reproductive output. Grey seals (Halichoerus grypus) are abundant predators in the North Sea, but their responses to anthropogenic sounds are still largely unknown. To examine if pile-driving could influence their movement and diving behaviour, grey seals were tracked during the construction of two offshore windfarms in 2014 and 2015. Reactions of the grey seals to the pile driving were diverse, and included: altered surfacing or diving behaviour, and changes in swim direction. Also, during a large number of exposures, seals did not appear to change their diving behaviour or movement. The change in behaviour most often observed in response to pile-driving was a decline in the descent speed, which suggests a transition from foraging (diving straight down to the bottom), to more horizontal movement. The decline in speed were on average larger and occurred more frequent at smaller distances from the pile driving events (statistically significantly different up to 36km). Occasionally, seals displayed a change in diving behaviour at larger distances. For example, during one instance a grey seal at 48 km from pile-driving significantly reduced its descent speed and average dive depth when pile-driving started, and immediately after pile-driving ceased, continued to pre-piling behaviour. In addition to changes in dive behaviour, also changes in movement were recorded. On average, grey seals within 33 km were more likely to swim away from the pile-driving. This was however only the case for one windfarm, where pile driving intensity was higher and GPS location estimates were more frequent. Often individual tracks did show changes in direction, but not always away from pile-driving. This suggests that seals might not always be able locate the location of pile-driving accurately.

Appendix 6 AgentSeal

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AgentSeal: Agent-based model describing movement of marine central-place foragers

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ABSTRACT

Understanding why animals move as they do when searching for resources is a central question in ecology, and a prerequisite for the development of predictive process-based models for conservation and management. Many species are central-place foragers (CPF). While several models for CPFs have been proposed, they often assume well-defined return rules to the focal point (like breeding). For some CPFs, however, the decisions to return to central sites are governed by multiple interactions between environmental and physiological factors.

We present AgentSeal, a behaviour- and physiology-based, spatially explicit, agent-based model. We use harbour seals, a marine CPF, as a case study and focus on individuals outside their breeding and moulting seasons to capture general fine- and large-scale movements and drivers behind CPF. We model movement decisions based on optimal foraging strategy, cognitive and physiological processes in a realistic landscape, coupled with realistic prey distribution and tuned to a range of behavioural and physiological patterns observed at different scales and levels of organisation (pattern-orientated modelling, POM).

The model can reproduce energetic, movement and other behavioural patterns such as net energy balance, at-sea and on land site fidelity, daily activity budgets and trip extents. The model reveals the crucial elements needed to model return-trips of CPFs including movement characteristics that vary as a function of local environmental conditions, cognitive mapping of foraging areas as points of attraction in subsequent foraging trips, and physiological requirements defining switches between resting and foraging.

We discuss potential applications and extensions of the model, including investigations of fundamental questions in foraging ecology: how spatial distribution and aggregation of resources affect movement of marine CPFs; what are the main drivers behind their at-sea site-fidelity to foraging patches? We also discuss applied objectives such as improving our understanding of population-level consequences of anthropogenic disturbances and ultimately evolving AgentSeal into a practical management tool.

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