



UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

Human impact on highly mobile cetaceans: the use of biotelemetry data to inform ocean management

Evert Mul

A dissertation for the degree of Philosophiae Doctor – September 2020



Cover photo: Evert Mul

Killer whales feeding near a herring fishing vessel.

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UiT, the Arctic University of Norway - Tromsø
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VISTA

A collaboration between the Norwegian
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Summary

The human presence in the world's oceans is increasing, in response to the growing demand for marine resources. This expansion of human activities will increase pressure on marine ecosystems and demands a responsible ocean management, to ensure the sustainable use of marine resources. Highly mobile marine top predators, such as cetaceans (whales, dolphins and porpoises) are exposed to a multitude of anthropogenic activities, as they frequent various habitats. This highlights the need to evaluate the cumulative impacts of multiple human activities on these species. However, studying these animals can be challenging, as they spend most of their time under water and travel over long distances, often in remote offshore regions. In this thesis, biotelemetry data is used to assess the influence of human activities on two marine top predators in the Norwegian and Barents Sea, humpback whales and killer whales. Humpback whales are seasonal migrants in the study area, primarily in the Barents Sea, and transit through the coastal regions of northern Norway. In contrast, killer whales reside in Norwegian waters throughout the year, often in coastal regions where the concentration of human pressure is high. This difference in life strategy is likely to influence how these species overlap and interact with human activities.

Biotelemetry is recognised as a valuable tool in the analysis of animal behaviour. To evaluate how this tool can be used to study human impact, 41 killer whales (*Orcinus orca*) and 30 humpback whales (*Megaptera novaeangliae*) were tagged with Argos satellite devices between 2014 and 2019 in the Norwegian and Barents Sea. As both species are associated with winter herring aggregations in the fjords of northern Norway, most of the tags were deployed during the herring overwintering. In addition, some humpback whales were instrumented during the late summer in the Barents Sea, and some killer whales were instrumented during the spring off the coast of western Norway. Since Argos tags can only transmit data when they are above the surface, tag placement on the animal might influence the quality and the quantity of location estimates. To test the influence of tag placement, two tags were deployed at different heights on the dorsal fin of a single killer whale. The tag that was placed higher up the dorsal fin generated more and higher quality location estimates. This could influence the results and conclusions of biotelemetry studies, in terms of area usage and association with specific oceanographic or anthropogenic features. For example, we found that correlations to environmental characteristics can either be missed or falsely identified at a spatial resolution of less than a few kilometres. These results demonstrate that tag placement should be considered when interpreting biotelemetry data, in particular when comparing the movement of multiple individuals. Alternatively, increasing the spatial resolution of the analysis can reduce the influence of tag placements on the interpretation of biotelemetry studies.

We studied how one anthropogenic activity influences the movement of a highly mobile marine predator. To test if killer whales are attracted to fishing vessels, we used biotelemetry data from 25 killer whales from two consecutive years. Killer whales may be drawn to fishing activity, for example because of escaped or discarded fish, or by picking fish from the nets. Here we selected a spatial scale that would be largely impervious to variation in tag performance, based on the outcome of the first part of this thesis. A hidden Markov model indicated that most of the killer whales were attracted to fishing activity. Almost 80% of the locations from some individuals were identified as "attracted to fishing activity" by the model. Our model showed that whales were more likely to be attracted when they were within 20 km of the nearest fishing activity. This could explain why attraction occurred primarily in the fjords. Herring leaves the fjord at the end of the winter to migrate to their spawning

grounds along the Norwegian coast. Although both killer whales and fishers appeared to follow the herring, perhaps the killer whales were often too far from fishing vessels to react.

In the final step of this thesis, all the data were combined, in order to develop and test a new framework for dynamic cumulative impact assessment for highly migratory top predators. This framework was tested on humpback and killer whales in the Norwegian and Barents Sea, by evaluating all the major human activities and by calculating a cumulative impact index. We found that areas of high impact were strongly influenced by seasonal variations in the distribution of cetaceans. In this case study, we identified an area of high impact in the northern Barents Sea during the summer. Here, foraging humpback whales overlapped with shipping and fishing activities. During the autumn, winter and spring, high impact areas were identified primarily along the coast of northern Norway. Between winter and spring, a clear southwards shift can be recognised in the high impact area, which appears to coincide with the migration of Norwegian Spring Spawning herring (*Clupea harengus*). The concentration of human activities in this area is generally higher than in the Barents Sea, which demonstrates that humpback whales are exposed to various intensities of anthropogenic activities, while killer whales are exposed to high intensities throughout the year. Although the distribution of human activities also varies throughout the year, in this study, animal distribution appeared to be the main factor influencing the areas of high impact. With this study, we have demonstrated that this framework can be used to identify areas of high cumulative impact and that seasonal variation in animal distribution should be considered in cumulative impact assessments for highly mobile top predators. Biotelemetry data provides a powerful input for a dynamic cumulative impact assessment, in particular if animal data can be collected throughout the year.

Cumulative impact assessments require knowledge on detailed animal responses to individual anthropogenic activities. Unfortunately, this knowledge is often lacking, which indicates the need for biotelemetry studies that focus on the interaction between a species and a human activity. The proposed framework for dynamic cumulative impact assessments is suitable to evaluate how multiple anthropogenic activities affect highly mobile marine top predators along their migration routes. This approach can identify dynamic areas of high cumulative overlap that may require conservation priority. Future studies can build on this framework to develop dynamic cumulative impact assessments for other species or ecosystems. Especially considering climatic and anthropogenic changes in the Arctic in the near future, there is a strong need for evaluation on human impacts on species, ecosystems and habitats, including highly mobile marine predators.

List of papers

- Paper 1: Mul, E., Blanchet, M.-A., Biuw, M. & Rikardsen, A. (2019) ‘Implications of tag positioning and performance on the analysis of cetacean movement’, *Animal Biotelemetry*, 7(1), p. 11. DOI: 10.1186/s40317-019-0173-7.
- Paper 2: Mul, E., Blanchet, M.-A., McClintock, B. T., Grecian, W. J., Biuw, M. & Rikardsen, A. (2020) ‘Killer whales are attracted to fishing activity’, *Marine Ecology Progress Series* (in press), DOI: 10.3354/meps13481.
- Paper 3: Mul, E., Hausner, V. H., Blanchet, M.-A., Biuw, M., Dietz, R., Olsen, M. T. & Rikardsen, A. (manuscript) ‘Cumulative impact assessment for dynamic management of marine top predators’, intended journal: *Conservation Biology*

Contributions

	Paper 1	Paper 2	Paper 3
Concept and idea	EM, AR, MAB, MB	EM, AR, MAB, MB	EM, MAB, AR
Study design and methods	EM, MB, MAB	EM, BMC, WJG, MB, MAB	EM, VHH, MAB
Data gathering and interpretation	EM, AR	EM, AR, MB	EM, AR, MB, RD, MTO
Manuscript preparation	EM, AR, MAB, MB	EM, MAB, BMC, WJG, MB, AR	EM, VHH, MAB, AR, MB, RD, MTO

EM = Evert Mul

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MAB = Marie-Anne Blanchet

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RD = Rune Dietz

MTO = Morten Tange Olsen

1 Introduction

As the demand for resources grows, the world's oceans are currently looked upon to drive the expansion of marine industries (Hodgson, Essington, *et al.*, 2019; Jouffray *et al.*, 2020). As a result, marine ecosystems are under increased pressure from anthropogenic activities (Dailianis *et al.*, 2018; Halpern *et al.*, 2019). Responsible ocean management requires a clear understanding of the potential impacts these activities can have on marine organisms and ecosystems. Currently, the impact of anthropogenic activities on wildlife and ecosystems is insufficiently considered in the development of marine industries (Harris *et al.*, 2018). Human activities are primarily concentrated near coastal regions. However, due to recent technological developments in e.g. shipping and navigation, remote off-shore regions have become accessible and human activities at sea are no longer limited to coastal regions (Jouffray *et al.*, 2020). The Arctic in particular is becoming increasingly accessible to maritime operations, due to declining sea-ice (Pizzolato *et al.*, 2016; Kozmenko *et al.*, 2018; Ng *et al.*, 2018). As a result, pressure on Arctic ecosystems and wildlife is likely to increase (Andersen *et al.*, 2017; Halliday *et al.*, 2017), which highlights an urgent need for impact assessment studies to address potential consequences of increased pressure on marine ecosystems and wildlife in the Arctic.

Highly mobile marine predators such as marine mammals, seabirds, sharks and turtles often travel over long distances. As they encounter various habitats, including coastal areas, these animals are exposed to a multitude of anthropogenic pressures (Block *et al.*, 2011; Maxwell *et al.*, 2013; Avila *et al.*, 2018). Human activities can affect these animals in various ways. For example, every year, many marine mammals, seabirds, and turtles become entangled and drown in fishing gear (Read *et al.*, 2006; Carretta *et al.*, 2019). Cetaceans often bear scars from propellers or direct strikes from small vessels, while collisions with larger cargo vessels can have a lethal outcome. Vessel noise may mask communication (Holt *et al.*, 2009), while seismic activity, military exercises and offshore construction can cause hearing damage (Erbe *et al.*, 2000), or possibly even death (Jepson *et al.*, 2003), as many cetaceans rely on echolocation to find and capture prey. Human activities can also generate beneficial consequences for marine top predators. Seabirds and marine mammals can be attracted to fishing activity, as this provides them with beneficial foraging opportunities (Esteban *et al.*, 2016; Pirota *et al.*, 2018). Some populations of seabirds now depend entirely on discards from fishing activity (Tew Kai *et al.*, 2013). However, this attraction may also increase the risk of entanglement and ship strikes, in the case of cetaceans.

Cetaceans and other marine predators play an important role in marine ecosystems, as they form crucial links between various energetic paths in the food web (Blanchet *et al.*, 2019). Therefore, evaluation of potential impacts of anthropogenic activities on these species has been recognised as a key element of ocean management (Maxwell *et al.*, 2013; Harris *et al.*, 2018). It is particularly valuable to identify to which pressures they are exposed during various stages of their migration. Human impact can be studied by observing changes in animal behaviour or movement. However, studying the movement of cetaceans is often challenging, as they are often difficult to follow over longer periods of time. They spend most of their time under water, they can travel fast and over long distances, and they may occur in remote areas. Electronic animal tracking devices (biotelemetry tags) are a valuable tool to address this issue. These devices can be deployed on animals to collect information about the location of the animal, or about environmental characteristics (Box 1).

Many cetaceans migrate over large distances between breeding and foraging areas and they may encounter various intensities of anthropogenic activities throughout their migration routes. For example, the density of activities in coastal areas is often higher than in remote offshore regions (Jouffray *et al.*, 2020). In addition, cetaceans are seldom confronted with a single type of activity. They may experience multiple anthropogenic activities simultaneously, particularly in coastal regions. Evaluation of human pressure on these animals should therefore be based on the cumulative effects of multiple human activities (Hodgson & Halpern, 2019). Currently, conservation studies often focus on singular anthropogenic activities, thereby disregarding interacting pressures from multiple human activities at variable intensity (Holsman *et al.*, 2017; Hodgson & Halpern, 2019). Cumulative effects describe changes to an animal, ecosystem or environment that are caused by a human action in combination with other human actions that are occurring, have occurred or will occur in the foreseeable future (Judd *et al.*, 2015). Spatially explicit mapping of cumulative impacts can help to localise impact hotspots to wildlife populations, which can be used to assign conservation priorities (Avila *et al.*, 2018). Although cumulative impact assessments are recognised as a valuable tool for marine management and conservation, a clear framework is currently lacking (Judd *et al.*, 2015; Jones, 2016; Murray *et al.*, 2020). In particular, cumulative impact assessments often ignore seasonal variation in the distribution of either the animals or the anthropogenic activities. Due to seasonal variation in cetacean distribution, ocean management actions in certain areas might only be applied seasonally. Some human activities, such as fisheries and tourism are also subject to seasonal variation, while yet other activities, such as construction work, seismic surveys or military exercises can change throughout the year without a clear seasonal pattern. Assessment of cumulative impacts on cetaceans and other highly mobile marine species therefore needs to include temporal dynamics of both the animals and the human activities (Maxwell *et al.*, 2015; Welch *et al.*, 2019).

In this thesis, animal tracking data from 41 killer whales (*Orcinus orca*) and 30 humpback whales (*Megaptera novaeangliae*) in the Barents and Norwegian Sea was used to investigate the impact of multiple human activities on their movement. These two species have different distribution patterns in space and time. While killer whales reside in Norwegian waters throughout the year (Jourdain *et al.*, 2019), humpback whales commonly migrate between foraging areas in the Barents Sea and breeding areas in the Caribbean or near the Cape Verde islands (Wenzel *et al.*, 2009; Stevick *et al.*, 2018). Consequences of overlap with human activities have been reported for both species. For example, both humpback whales and killer whales have been caught in fishing gear, although this appears to be more common for humpback whales than for killer whales (Robbins *et al.*, 2004; Reeves *et al.*, 2013). Both species rely heavily on communication which can be masked or obstructed by various types of human activity (Holt *et al.*, 2009; Frankel *et al.*, 2017). Little is known about their overlap with and their reaction to human activities in Norwegian waters. In this thesis, these knowledge gaps are addressed by exploring how biotelemetry data can be used to inform ocean management.

After the objectives of this thesis have been defined (section 2), an overview of the study area and species is presented (section 3). The use of the study area is diverse and dynamic, both for human activities and for the two study species. For this reason, the biology of humpback and killer whales is also briefly described here. Because of its role as one of the main drivers behind the (winter) distribution of humpback and killer whales, the biology of Norwegian Spring Spawning herring (*Clupea harengus*) is presented in this section, despite not being a study species in its own right. Section 4 describes how the data for this thesis were collected and processed, and which methods for inferring behaviour and distribution from biotelemetry data were used. A brief introduction to

biotelemetry data in general is also presented in Box 1, in order to illustrate the challenges of marine mammal biotelemetry data. The results are presented in section 5 and discussed in section 6. Finally, a brief discussion of how this work contributes to the evaluation of human impacts on highly mobile marine top predators and what could be done in future work is given in section 7.

2 Objectives

The main goal of this thesis was to investigate how animal tracking data can be used to evaluate human impact on humpback and killer whales in Norwegian waters.

Specifically, the aims of this thesis were:

1. To explore how the positioning of a tag on a whale influences the tag performance, and how this affects common animal movement analyses (paper 1)
2. To study fine-scale behavioural responses of killer whales to fishing activity along the coast and in fjords of northern Norway (paper 2)
3. To map and estimate dynamic cumulative impacts of anthropogenic activities on humpback and killer whales in the Norwegian and Barents Seas (paper 3)

3 Study area & species

3.1 Study area

The study area is located primarily in the Arctic and covers the coastal region of the Norwegian Sea and part of the Barents Sea between mainland Norway and Svalbard (Figure 1). Currently, the Arctic is facing rapid changes, both in environmental conditions and in a growing human presence (Wassmann *et al.*, 2011; Ng *et al.*, 2018). Due to disappearing sea-ice, shipping has intensified in the last decades and will likely continue to do so (Eguíluz *et al.*, 2016). This area is rich in natural resources, such as fish, oil and gas (Dore, 1995; Bachiller *et al.*, 2016; Eriksen *et al.*, 2018), which attract a variety of marine industries (Michalsen *et al.*, 2013; Olsen *et al.*, 2016). Compared to the coastal region of the Norwegian Sea however, the Barents Sea can be considered relatively pristine, as human activities are commonly concentrated near coastal regions (Jouffray *et al.*, 2020). The high productivity in this area also attracts many migratory animals, including cetaceans (Skern-Mauritzen *et al.*, 2011; Leonard *et al.*, 2020). Some of these species use the study area to forage during the summer before they embark on long migrations to breeding areas (Stevick *et al.*, 2018), while others reside in Norwegian waters throughout the year (Jourdain *et al.*, 2019). Different use of the Barents and Norwegian Sea are likely to cause differences in the exposure of anthropogenic activities. The impacts of present and future anthropogenic activities in this study area are currently insufficiently considered in marine management and conservation.

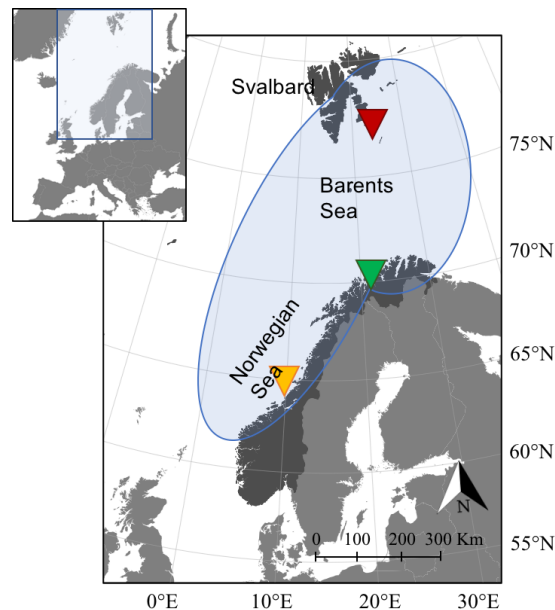


Figure 1 – Map of the study area, which covers part of the Barents Sea and the Norwegian Sea. Norway is marked in dark grey. The inset shows a map of Europe. The triangles represent the tagging areas, the Barents Sea (red), several fjords in northern Norway (green) and off the coast of western Norway (yellow).

3.2 Norwegian Spring Spawning herring

Herring is an important prey species for both killer whales and humpback whales (Jourdain *et al.*, 2017). Therefore, a brief description of the Norwegian Spring Spawning (NSS) herring distribution is given even though it is not a study species of this thesis. During the summer, adult NSS herring is widely distributed throughout the Norwegian Sea (Toresen *et al.*, 2019). However, during the winter, NSS herring form dense overwintering aggregations. Ever since the collapse of the herring stock in the

late 1970s, part of the population overwinters in relatively small fjord systems, or near the coast of Northern Norway (Huse *et al.*, 2010). Every decade or so, a new dominant age class selects a new area to overwinter. These aggregations attract the attention of killer whales and in recent years also humpback whales. In addition, fishers, tourists, and whale researchers are drawn to this winter spectacle (Rikardsen, 2019). Since 2011, the herring resided primarily in fjords near the city of Tromsø, and in 2017 the herring moved to a new fjord, approximately 100 km to the east. Herring spawns during the spring off the western coast of Norway (Toresen *et al.*, 2019).

3.3 Killer whales

Killer whales are a marine top predator with a global distribution (Ford, 2009). They are the largest member of the oceanic dolphin family (Delphinidae) and among the largest toothed whales (odontocetes). The current abundance of the northeast Atlantic population (including Norwegian waters) is estimated to be approximately 15.000 (Leonard *et al.*, 2020). In Norway, their distribution is strongly associated with NSS herring (Similä *et al.*, 1996; Kuningas *et al.*, 2013; Vogel, 2020), or Atlantic Mackerel (*Scomber scombrus*) (Nøttestad *et al.*, 2014). A part of the population in Norway appears to have a seasonal preference for other prey beside herring, such as pinnipeds (Jourdain *et al.*, 2020). Killer whales are distributed throughout the Norwegian Sea and are infrequent visitors near Svalbard (Jourdain *et al.*, 2019). They occur both near the coast (Similä *et al.*, 1993; Jourdain *et al.*, 2017) and offshore (Nøttestad *et al.*, 2014). Killer whales are affected by various anthropogenic activities. For example, vessel noise can mask killer whale communication (Erbe, 2002; Holt *et al.*, 2009), induce avoidance behaviour (Williams *et al.*, 2014), or disrupt foraging behaviour (Lusseau *et al.*, 2009). Killer whales are also known to interact with fisheries throughout the world, as the fishing activities provide them with beneficial foraging conditions (Kock *et al.*, 2006; Peterson *et al.*, 2013; Esteban *et al.*, 2015; Lennert *et al.*, 2017). This often leads to depredation; when killer whales take fish from a fishing line or a net (e.g. Dalla Rosa *et al.*, 2007; Escalle *et al.*, 2015). In the north east Atlantic, killer whales have been observed scavenging around mackerel (*Scomber scombrus*) and herring trawlers (Couperus, 1994; Luque *et al.*, 2006), and near herring fishing vessels in Norway (Van Opzeeland *et al.*, 2005; Kuningas *et al.*, 2014). These interactions can lead to long term consequences, such as population-level behavioural changes or increased reproduction output (Tixier *et al.*, 2015).

3.4 Humpback whales

Humpback whales (*Megaptera novaeangliae*) are a globally distributed species of baleen whales (mysticetes). The abundance of the northeast Atlantic population (including Norwegian waters) is estimated to be approximately 11.000 (Leonard *et al.*, 2020) and appears to have stabilised after an increase in the last decade of the 20th century. This population is part of a larger population that breeds in the Caribbean or the Cape Verde islands (Smith *et al.*, 2009; Wenzel *et al.*, 2009; Stevick *et al.*, 2018). During the summer, a part of this population feeds on euphausiids (krill) and small schooling fish species, such as capelin (*Mallotus villosus*) in the Barents Sea (Stevick *et al.*, 2003; Smith *et al.*, 2009; Skern-Mauritzen *et al.*, 2011; Ramm, 2020). In recent years, humpback whales have been attracted to large aggregations of overwintering herring in fjords of Northern Norway (Jourdain *et al.*, 2017; Rikardsen, 2019). Their association with herring during the winter can be regarded as a stop-over on their southwards migration to the breeding areas (Ramm, 2020). During their migration between the Barents Sea and breeding areas further south, they use the Norwegian sea as a migration corridor. However, these migration patterns are subject to change and individual variation (Nøttestad

et al., 2015). While the Barents Sea is relatively pristine, the humpback whales are confronted with high concentrations of human activities as they migrate along the Norwegian coast. Attraction to overwintering herring in north Norwegian fjords will likely increase the time they spend in these coastal waters. Humpback whales are affected by various anthropogenic activities. For example, they can become entangled in a variety of fishing gear (Robbins *et al.*, 2004; Johnson *et al.*, 2005; Neilson *et al.*, 2009; Rikardsen, 2019) and they can be affected by the noise of shipping traffic or seismic activities (McCauley *et al.*, 2000; Blair *et al.*, 2016). Overlap between humpback whales and human activities has been studied in other areas (Rosenbaum *et al.*, 2014), but little is known about such overlap in Norwegian waters.

Box 1. Cetacean biotelemetry: studying the movement of whales

Studying the movement of cetaceans is challenging, as they spend most of their time under water. Biotelemetry and biologging devices (tags) can be used to gather information about their movement or about the environment (Cooke, 2008). Biologging devices, or archival tags, record information about animal movement or about the environment (McIntyre, 2014). Some biologging tags are able to transmit data via cell phone networks in coastal areas, or via a satellite link. However, data from additional sensors is often too large to be transmitted, which is why most biologging devices need to be recovered, so that this data can be retrieved (Cooke, 2008). Biotelemetry devices (tags) typically do not store information. Instead they transmit messages that can be used to estimate locations. Most cetacean studies rely on satellite-linked devices, as these devices can be used anywhere on earth. Other types, such as VHF, GSM or acoustic radio transmitters may be used, but are less common for cetaceans.

Satellite-linked tags can be used to estimate whale locations over time (Dujon *et al.*, 2014). However, since satellite connections can only be established through air, tags can only attempt communication during the brief moment when cetaceans come to the surface to breathe. As a result, locations may be inaccurate and are often irregular in time (Kuhn *et al.*, 2009). There are two approaches for location estimation through a satellite link. In this thesis, we used Argos satellite tags, which transmit small identification messages to a receiver on a single passing satellite (Vincent *et al.*, 2002). The position of the tag can be estimated, based on the known trajectory of the satellite, and the Doppler shift between the received messages. The second approach is Fastloc GPS (www.wildlifecomputers.com), which generates more accurate locations estimates than Argos tags (Patterson *et al.*, 2010). Fastloc GPS tags receive information from passing satellites. Messages from three or more satellites can be used to calculate the position of the tag (Dujon *et al.*, 2014). However, this information needs to be transmitted through the Argos system or stored to be retrieved when the device is recovered. As these tags are more advanced, they are generally more expensive, which is why Argos tags are still a popular instrument for many cetacean studies.

Tags for cetaceans can be attached via suction cups (Sivle *et al.*, 2012), bolted onto the dorsal fin (Pavlov *et al.*, 2007), or deployed into the blubber layer with an air-powered rifle or a crossbow (Reisinger *et al.*, 2014). Suction cup attachment is often used for high-resolution storage tags and normally last for several hours, up to a few days. Tags that are bolted to the dorsal fin or dorsal ridge can remain on the animal for a long time, but for this purpose the animal needs to be captured and constrained. In this thesis, tags were deployed using an air-powered rifle.

4 Methods

4.1 Data collection

In total, 41 killer whales and 30 humpback whales were equipped with SPOT 5, SPOT 6 or SPLASH Argos satellite tags (www.wildlifecomputers.com). These tags were attached transdermal in the blubber layer of humpback whales or in the connective tissue layers of killer whale dorsal fins (Figure 2) (Andrews *et al.*, 2015). Tags were deployed using an air-powered rifle (www.restech.no) from 24-26 ft open motorboats at a distance of 5-10 m (Figure 2A). During the data collection period (2014-2019), the herring changed their overwintering areas. Both humpback and killer whales were primarily tagged in the two herring overwintering fjord systems in northern Norway (Figures 1 & 3). In addition, humpback whales were tagged in the Barents Sea east of Svalbard in September (figures 1 & 3). Some killer whales were tagged during the early spring in herring spawning areas of the coast of western Norway (Figures 1 & 3). To study the influence of tag positioning on the performance of the tag, two Argos satellite tags were deployed on a single male killer whale. One tag was placed at the base of the dorsal fin, while the other was placed approximately halfway up the dorsal fin, 33 cm higher. The two tags were deployed approximately one day apart.

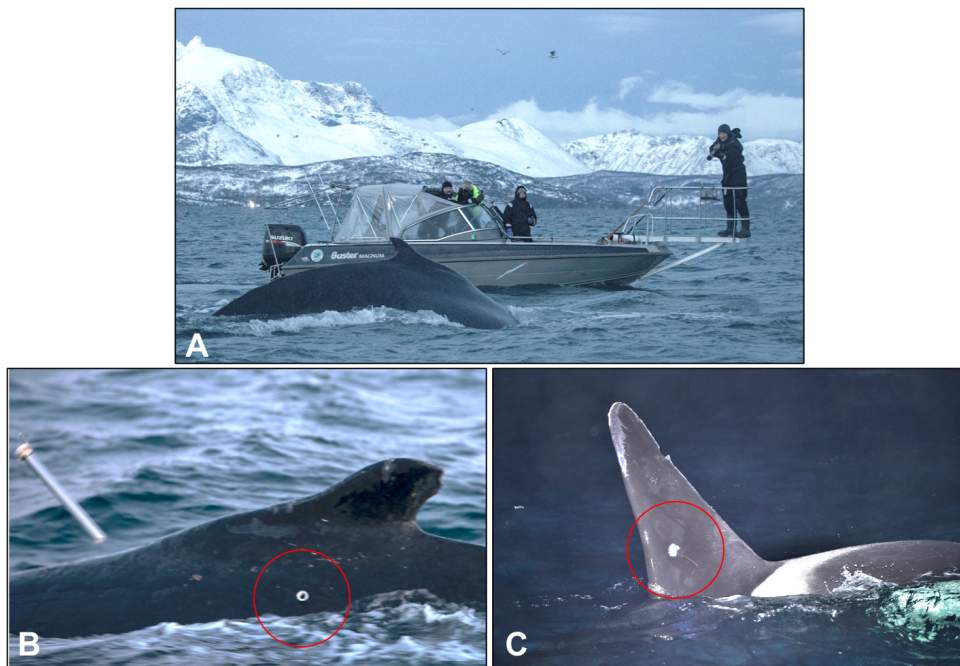


Figure 2 – A) the instrumentation process, B) instrumented humpback whale and C) instrumented killer whale. The tags are deployed from a high vantage point on the bow of the vessel (A), using an air-powered rifle. The carrier that is used to shoot the tag can be seen in pictures A & B. The carrier is retrieved after each tag deployment. Humpback whales are instrumented under the dorsal fin and killer whales either in the dorsal fin or at the base of the dorsal fin. Photos: Evert Mul

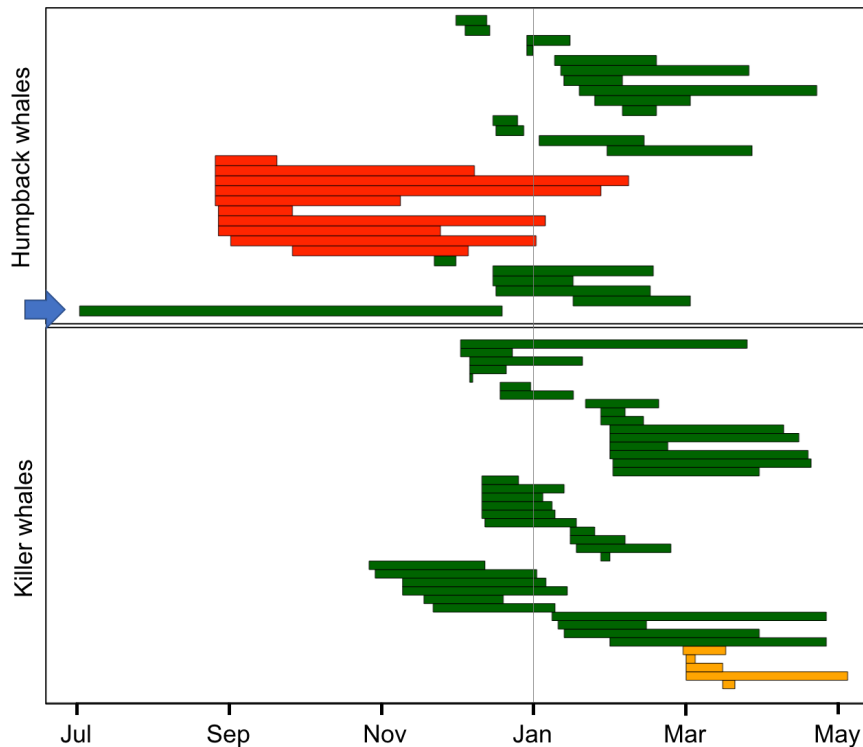


Figure 3 – Tagging periods and retention time of the Argos satellite tags. The colors represent the tagging locations: Green = North Norwegian coast and fjords (herring overwintering areas), Red = Northern Barents Sea, Orange = Northwest coast of Norway (herring spawning grounds). The humpback whale that is marked with a blue arrow was tagged the year before and returned to Norwegian waters after a migration to the Caribbean in July. Humpback whale tracks were limited to Norwegian waters. The tags were deployed between 2014-2019, primarily during the winter.

Spatial data for several anthropogenic activities and installations that occur in the study area were also obtained: Fishing, shipping (including tourism), oil and gas facilities and pipelines, seismic surveys, aquaculture facilities, telecommunication cables, and main ports. Most datasets were obtained from open access sources, with the exception of the herring fishery data, which was obtained through the Norwegian Directorate of Fisheries (www.fiskeridir.no).

4.2 Data processing

Since satellite tags can only transmit or receive signals when the antenna is above the water surface, location estimates are often irregular in time, and may be subject to large spatial error (Box 1). The Argos system uses information from previous location estimates to improve the accuracy and the quantity of location estimates. This method assigns a quality class to each location, but also estimates an error ellipse to indicate the uncertainty of the location (McClintock *et al.*, 2015). Due to this uncertainty, raw and unprocessed Argos data might not provide a realistic representation of the true animals' path. A simple method to filter Argos locations uses the maximum speed of an animal to estimate which locations are unrealistic (McConnell *et al.*, 1992; Freitas, Lydersen, *et al.*, 2008). These locations are then filtered from the dataset. Irregularity in time can be solved by linear extrapolation (Calenge, 2006). A downside of this method is that part of the locations is removed, while the remaining locations are assumed to be accurate and the estimated error is ignored. An alternative approach is to model movement parameters from which a path can be reconstructed (McClintock, 2017; Jonsen *et al.*, 2020). This method involves a continuous-time state space model that estimates the unobserved state (the animal's true locations), based on the observed state (the raw animal

locations) (Johnson *et al.*, 2008). A correlated random walk model is fitted, based on the estimated error ellipse around each raw location (McClintock *et al.*, 2015). Filtering methods are sometimes used in preparation for a movement model (Jonsen *et al.*, 2020). State space models estimate time-regular locations with estimated error ellipses, which can be incorporated in subsequent analyses. In the first paper, pseudo-tracks were calculated from the estimated error around a reconstructed path. In the second paper, a different approach was found, which draws multiple imputations from a movement model, rather than one “best” reconstructed path (McClintock, 2017). Analyses were performed with all the pseudo-tracks or imputations and the results were averaged to create one set of values per animal.

4.3 Behavioural analyses

Animal tracking data can be used to evaluate animal behaviour (Aarts *et al.*, 2008; Patterson *et al.*, 2008; Handcock *et al.*, 2009). The speed and the angle between locations reflect the underlying behaviour. Using these movement parameters, animal tracks can be segmented to indicate habitat use (Edelhoff *et al.*, 2016). For example, area restricted movement can highlight areas that are of particular importance to the animal, such as foraging areas. Movement models can be used to assign behavioural states (e.g. “transit” or “area restricted movement”) to each data point, which are characterized by a combination of movement parameters (Langrock *et al.*, 2012). Identified behaviour can be linked to environmental variables and human activities, to identify drivers behind changes in behaviour (Grecian *et al.*, 2018; Pirota *et al.*, 2018).

4.3.1 First Passage Time

First Passage Time (FPT; Fauchald *et al.*, 2003) aims to identify area restricted behaviour from whale tracking data, which can indicate foraging behaviour. FPT refers to the time an animal spends within a circle of a specific radius around each location (Freitas, Kovacs, *et al.*, 2008; Byrne *et al.*, 2012). In order to identify the spatial scale at which animals concentrate their search effort, the variance of the log-transformed FPT is plotted (Fauchald *et al.*, 2003). A peak in the variance illustrates a distinguishable spatial scale, but if no peak is found, there might not be sufficient variation in the dataset for this method to be effective.

4.3.2 Hidden Markov models

The main tool to distinguish between different types of animal behaviour in this thesis was the hidden Markov model (HMM, e.g. Langrock *et al.*, 2012). Like other state space models, HMMs estimate the latent, or “hidden” state of a process (such as the behavioural state of an animal), based on the associated observable state, such as speed and turning angle (Figure 4, Jonsen *et al.*, 2005; Dragon *et al.*, 2012a). HMMs differ from other SSMs, as they are used to identify a discrete, rather than a continuous latent state (Langrock *et al.*, 2012). To assess the effect of tag placement, we compared the results of a simple HMM, based on input from two tags that were placed on one animal. The HMM distinguished between behaviour that was associated with “transiting” or “searching” behaviour. The movement parameters that were used to identify these behavioural states were “step length” and “turning angle”. Step length refers to the length between locations. In the case of time-regularized locations, this is synonymous with speed. The turning angle for a location refers to the angle to the next location, relative to the angle from the previous location. HMMs can be used to identify biased movement to an attractor (Pirota *et al.*, 2018). This principle was applied to examine the degree to which killer whales are attracted to fishing vessels. A model was fitted with three behavioural states:

“traveling” movement, “area restricted” movement, and “attraction” to the nearest fishing activity. Here, traveling movement was modelled as a correlated random walk, with longer step lengths and lower turning angles (compared to area restricted movement). The attraction state was modelled as a biased random walk, with a bias towards the nearest fishing activity. HMMs can also test the influence of environmental covariates on the transition probability between states (Figure 4) (McClintock, 2017; Grecian *et al.*, 2018). To evaluate the effect of distance to the nearest fishing vessel on the transition probability between behavioural states, this distance was included as a covariate in the model.

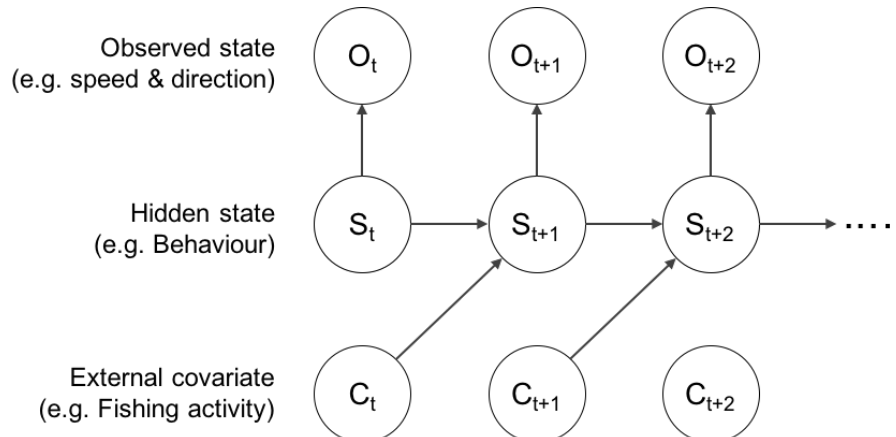


Figure 4 – Schematic representation of a hidden Markov model, based on an example used in this thesis. Unobserved or hidden states (S) at particular time (t), such as foraging or traveling are estimated based on observed states (O), such as specific combinations of speed (step length) and direction (turning angle). External covariates (C) might influence the probability that the individual shifts between behavioural states.

4.3.3 Environmental relationships

Animal movement is often driven by environmental factors (Aarts *et al.*, 2008; Handcock *et al.*, 2009). Identifying correlation with environmental variables is therefore an important aspect of studying animal movement. In the first paper, the relationship between two killer whale distributions and a series of simulated environmental variables was tested, using GLMs. Since the two distributions were based on two tags that were deployed on one animal, any relation with one of the distributions should be detectable by using the other distribution. The environmental variables were simulated as a set of resources that were placed on top of one of the killer whale distributions (high correlation).

Relating other movement parameters to environmental conditions can shed light on the behaviour of an animal, without differentiating between discrete behaviours. One such method is the study of move persistence, which depends on an animals’ speed and changes in direction (Jonsen *et al.*, 2019). Move persistence can be analysed in a mixed effects model to evaluate individual variation. Although this method was ultimately not included in the papers of this thesis, it has been used for an MSc thesis that describes the relationship between killer whales and the distribution of herring in the Norwegian Sea (Vogel, 2020).

4.4 Distribution estimation

Impact assessments of anthropogenic activities requires knowledge of the animals’ spatial distribution (Maxwell *et al.*, 2013). Animal distributions describe the probability of animal occurrence along a gradient (Horne *et al.*, 2019). They can be calculated for one individual animal, or for a population. Home ranges and core areas of high usage can be estimated from the distribution by calculating probability contours (Samuel *et al.*, 1985; Fieberg *et al.*, 2005). For example, the 50% probability

contour is sometimes used to describe core areas. This means that 50% of the probability of occurrence happened in this contour. In other words, the animal spent 50% of its time in this area. Core areas of high usage can be used to calculate overlap between the occurrence of species, between species and environmental variables or between species and human activities. Various methods can be used to analyse animal space use and distribution, based on tracking data (Aarts *et al.*, 2008; Dragon *et al.*, 2012b; Patterson *et al.*, 2017).

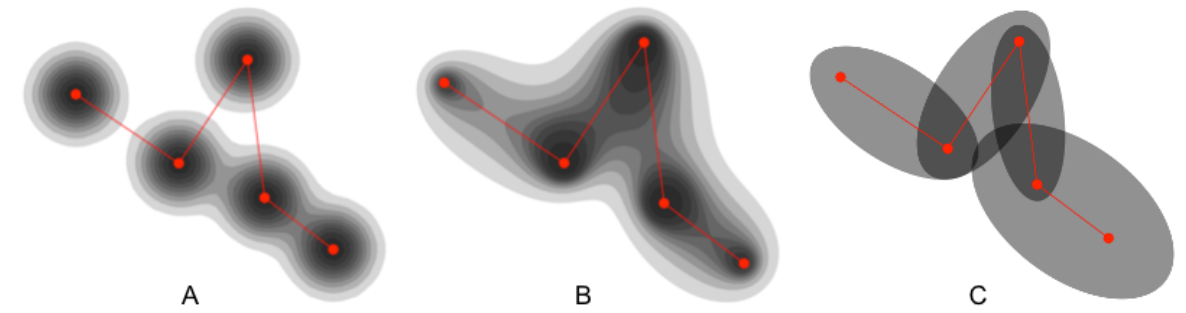


Figure 5 – The three methods that are used in this thesis to estimate the density distribution of an animal, based on hypothetical animal locations (red points). The red line represents the trajectory of the animal. A) kernel density, B) Brownian motion, C) Potential Path Area. The gradient indicates where the likelihood of animal presence is highest, at any point in time.

4.4.1 Kernel density

Kernel density methods estimate probability densities, such as an animals' home range, based on a series of locations (Worton, 1989). To estimate a kernel density of a series of data points, a kernel is placed over each point (Figure 5A). The average of all kernels forms the overall density estimate (Horne *et al.*, 2019). A key step in this approach is to select an appropriate kernel width or smoothing parameter (h), which can be challenging (J. Long *et al.*, 2015; Walter *et al.*, 2015). Methods to estimate the smoothing parameter, such as Least Squares Cross Validation (LSCVh) or Likelihood Cross-Validation (CVh) (Horne *et al.*, 2006), are based on statistical characteristics of the dataset, rather than on biologically interpretable values. Kernel density estimation is an appropriate method when data points are not auto-correlated, i.e. when the points are independent (Horne *et al.*, 2019). This method was therefore selected to identify core areas for the fishery, which is based on independent locations of fishing activities. Core areas were calculated as the 50% contour of the fisheries distribution.

4.4.2 Brownian motion

In contrast to the fishing locations described above, the locations in animal tracking data (or reconstructed paths) are spatially and temporally auto-correlated (Aarts *et al.*, 2008). Kernel density methods do not consider the movement between correlated locations (Figure 5A). More appropriate methods to estimate animal distributions based on tracking data rely on movement processes that explicitly account for the order and the time between locations (Kranstauber *et al.*, 2012; Walter *et al.*, 2015). Brownian motion is a movement process that estimates a distribution between successive locations (Figure 5B) (Kranstauber *et al.*, 2012). The variance parameter that is used to estimate this distribution is based on the mobility of an animal, and can be estimated from the animal tracking data (Horne *et al.*, 2007). Although Brownian bridge movement models can account for location error as a single parameter, they can't incorporate the full information of the error ellipses as estimated by path reconstruction methods. We included location error only when the uncertainty around each location

was addressed by predicting multiple alternative paths (imputations) rather than one reconstructed path. In this case, the uncertainty around each imputation was implemented in the Brownian bridge movement model, by taking the average of the estimated x-axis error and the y-axis error. Core areas of high usage were estimated as 50% contours of the distributions that were calculated with Brownian Bridge movement models.

4.4.3 Potential path area

Potential Path Areas (PPA) represent a potential area in which an animal could have been during particular time intervals, based on their maximum swimming speed (Long *et al.*, 2012; J. A. Long *et al.*, 2015). This method makes no assumptions regarding the most likely movement between two successive locations. Instead, the PPA estimates an ellipse that encompasses all possible routes at maximum swimming speed between two points (Figure 5C). As a result, PPAs do not generate a probability distribution, but rather the contour of a home range (J. Long *et al.*, 2015). A PPA indicates where an animal could have been during a particular time. Therefore, overlap between PPAs indicate an area where an animal could have been for a longer period, or more often. In this area, the overall probability of animal presence is higher, as the animal spent more time here (Figure 5C). This can be used to generate an alternative distribution on a large scale. Combining PPAs of multiple animals can indicate areas of high usage. PPAs are parameterised based on biological assumptions (maximum animal speed), rather than by statistical characteristics of the data, as is the case for other methods (Horne *et al.*, 2019), which makes them easier to interpret. Estimated error ellipses around locations are not taken into account. However, PPAs likely overestimate the ‘home range’, since it is based on the animals’ maximum speed. Location uncertainty is likely masked by this overestimation. This method can be useful because it is easy to interpret, and requires much less computational time, compared to the previously described alternative methods. It is particularly useful when studying animal distribution at a relatively large scale.

4.5 Cumulative Impact Assessment

Studying the cumulative impact of multiple activities can identify areas of high impact that might not be identified when individual impacts are studied separately (Avila *et al.*, 2018). The assessment of human impact on wildlife requires knowledge on: 1) the distribution of animals, 2) the distribution of anthropogenic activities, and 3) the impact an activity can have on an animal (Halpern *et al.*, 2008). Since cetaceans are highly mobile species, their distributions change throughout the year. Therefore, temporal dynamics of both cetaceans and anthropogenic activities should be considered when studying cumulative impacts (Maxwell *et al.*, 2015; Welch *et al.*, 2019). We estimated seasonal cetacean distributions using PPAs, based on reconstructed whale paths that were divided per season. Spatial information on each anthropogenic activity in the Barents and Norwegian Seas was re-scaled to a 10 km² resolution. Given the large spatial scale of this project, this relatively large resolution is a compromise between precision and the required computational time. This resolution was sufficient to indicate areas of high usage and areas of high impact in the Barents and Norwegian Seas. A key component of cumulative impact assessments is to identify impact weights for each anthropogenic activity (Halpern *et al.*, 2007), which is often done by expert evaluations. In paper 3, the weighing process was largely based on literature research. It was scored on eight different factors: Severity of impact, Frequency of impact, Spatial & Temporal scale of impact, Functional impact (impact on one whale or multiple whales), Direct or indirect impact on the whales, Whale recovery time, and the Certainty of the assessment.

5 Main findings

Implications of tag positioning and performance on the analysis of cetacean movement (paper 1)

Of the two tags that were placed on the dorsal fin of a killer whale, the tag in the top position (hereafter: top tag) resulted in twice the amount of location estimates during the same period (approximately two weeks), compared to the lower placed tag (bottom tag).

The location estimates generated by the top tag were also of better quality. Less than 50% of the locations were assigned to Argos quality class B (the poorest quality), compared to 90% for the bottom tag.

The reconstructed path based on the top tag was 1.5 times longer than the other path, which also resulted in a higher average speed. The maximum distance between the two paths was 31 km at any point in time.

The core area that was based on the top tag was 17% smaller than the core area that was based on the bottom tag, and 20% of this core area was not covered by the bottom tag core area.

Due to the large estimated error around the reconstructed path for the bottom tag, a First Passage Time analysis was unable to identify a spatial scale at which searching effort was focussed.

Transitions between behavioural states, assigned by an HMM, occurred at different points in time between the two datasets.

A GLM only identified a correlation between the bottom tag and a simulated environmental variable that was based on the top tag data at a spatial resolution of 4 km or higher.

Killer whales are attracted to fishing activity (paper 2)

Spatial overlap between killer whales and fisheries was indicated by 53% and 93% overlap (first and second study period respectively) between core areas of killer whales and fisheries.

Overall, individual killer whales spend up to 34% of their time within 3 km of fishing activity.

When killer and fishing activity occurred within 3 km of each other, killer whales arrived after the start of the fishery more than 60% of the time.

Attraction between killer whales and fisheries was identified by an HMM. Up to 79% of the locations of individual animals were assigned to 'attraction', provided that there was a fishery within 100 km to which the killer whale could be attracted. The overall number of locations assigned to 'attraction' accounted for 44% of the locations.

Nine killer whales (total = 25) were attracted more than 50% of their time, while two individuals were not attracted to any fishery, which implicates strong individual variation in behaviour.

Killer whales were most likely to be attracted if they were within 20km of the fishing activity.

Cumulative impact assessment for dynamic management of marine top predators (paper 3)

We developed a framework for a dynamic cumulative impact assessment for highly mobile species. This method follows four steps: 1) estimation and mapping of seasonal distribution of anthropogenic activities in a study area, 2) estimation and mapping of seasonal distributions for one or more species in the study area, 3) weight assessment for individual anthropogenic activities on the study species and 4) identify areas of spatiotemporal overlap between species and activities, and apply the weighing factor to identify areas of high impact, that might require conservation priority.

The case study on humpback and killer whales and human activities in the Norwegian and Barents Seas showed strong seasonal variation in the distribution of some anthropogenic activities, such as fisheries, shipping and seismic activities.

We also found strong seasonal variation in the distribution of both species, but particular for the humpback whales. During the summer and autumn, humpback whales occurred in the northern Barents Sea. Some animals began their migration to southern breeding areas from the Barents Sea, but others migrated first to the coast of northern Norway. Here they spent the winter, foraging on aggregated herring, before they started their migration during the spring. At the start of this migration, they transited along the coast of northern Norway.

Killer whales appeared to use the coastal areas of northern Norway throughout the year, although no data was collected for this study during the summer. During the autumn and winter, their distribution was concentrated near the fjords where herring overwinter, but in spring they were dispersed along the coast, and offshore into the Barents Sea.

The highest impact weights were assigned to fishery and shipping activities, and main ports. Main factors were noise and risk of entanglement.

An area of high cumulative impact for humpback whales was identified in the Barents Sea during the summer. The main activities that contributed to the cumulative impact in this region were shipping and fishery. Throughout the autumn, winter and spring, the main area of high cumulative impact for both species was along the coast of northern Norway. This area is shifted slightly to the south between the winter and the spring.

This framework was successful for humpback and killer whales in the Norwegian and Barents Sea, and can be adapted to fit other species or regions.

6 Discussion

Identifying animal behaviour from biotelemetry data (papers 1 & 2)

The Argos tags that were used in this thesis are a common choice for researchers that study marine mammals and other marine top predators. We have demonstrated that the precision of locations and the number of locations per unit of time is influenced by tag placement on the animal. Currently, tag placement is rarely discussed in biotelemetry studies, even though results could be influenced by the quality and quantity of the data. To filter the uncertainty around location estimates, raw Argos data were processed using movement models, based on continuous-time correlated random walks (McClintock, 2017; Jonsen *et al.*, 2020). The output of these models can be used to infer detailed information about animal behaviour (Durban *et al.*, 2012). We used the step length (speed) and turning angles (direction) between killer whale locations to identify “foraging” associated behaviour and “transit” associated behaviour. The results of this analysis were affected by tag placement, which influenced tag performance. This problem was addressed by using multiple imputations per whale track to account for uncertainty around the reconstructed path (McClintock, 2017).

Animal behaviour in relation to human activities or environmental variables (paper 2)

Reconstructed paths can also be used to identify influences from environmental variables or human activities on animal behaviour (Grecian *et al.*, 2018; Towers *et al.*, 2019). This process, however, can be influenced by tag placement. At spatial resolutions of less than 4 km, we were unable to indicate a correlation using a regression model. To reduce the influence of tag placement on the identification of correlations with the environment, we adjusted the spatial scale when studying the interaction between killer whales and fishing activity. For example, we used a 3 km radius around fishing activity to classify killer whales as being “nearby” the fishery. In addition, fishing vessels that were active simultaneously within a 4-km radius were grouped together. Here, the two-state behavioural model that was used to evaluate tag placement was modified, by including a third behavioural state “attraction to fishing activity” (e.g. Pirotta *et al.*, 2018). This model showed that killer whales were attracted to fishing activity, and that this attraction was influenced by the distance to the nearest fishing activity. Within 20 km of the nearest fishing activity, killer whales were most likely to be attracted. Attraction between cetaceans and fishery has been reported throughout the world (Luque *et al.*, 2006; Thode *et al.*, 2007; Esteban *et al.*, 2015; Towers *et al.*, 2019). The fishing activity likely provides beneficial foraging conditions (Esteban *et al.*, 2016), for example by aggregating and immobilizing the fish. In Norway, killer whales appear to change their foraging behaviour in close proximity (Van Opzeeland *et al.*, 2005; Kuningas *et al.*, 2014). This could indicate that they can adopt a foraging strategy at lower energetic costs, when they are feeding near fishing vessels. Attraction to fishery can have long-lasting effects on reproduction rate and population dynamics (Tixier *et al.*, 2015, 2017), which can affect other levels of the ecosystem (Newsome *et al.*, 2015). Attraction to fishery can also increase the risk of entanglement in fishing gear (Jourdain *et al.*, 2019). Killer whale entanglements have occurred in Norway (Kuningas *et al.*, 2014; Jourdain *et al.*, 2019), although no further information was found regarding the details, the frequency and the outcome for the animals involved. In general, killer whale entanglements are considered to be rare (Reeves *et al.*, 2017). Interaction between fisheries and cetaceans can also have adverse consequences for the fishery, such as loss of catches (Hanselman *et al.*, 2018; Tixier *et al.*, 2020). It is unlikely that this is the case for the Norwegian purse-seine herring fishery, as the killer whales do not appear to reduce the fishers’ catch. However, negative consequences for the fishers should be further investigated in Norway. Most attraction occurred in the fjords of northern Norway, where human pressure from e.g. shipping,

fishing, aquaculture and tourism is relatively high. This region was also identified as the area with the highest cumulative impact.

Identifying animal distributions from biotelemetry data (papers 1, 2, 3)

Knowledge about a species' distribution in space and time is crucial in order to identify areas of high human impact (Maxwell *et al.*, 2013). Biotelemetry can be used to estimate an animals distribution (e.g. Walter *et al.*, 2015). To analyse the fine-scale killer whale distribution in relation to human activity in coastal areas, we used Brownian bridge movement models (Horne *et al.*, 2007). For the third paper, we used a Potential Path Area approach (Long *et al.*, 2012), because it is easy to interpret, and particularly suitable for studies at a large spatial scale. The estimated distributions were then used to calculate core areas (Samuel *et al.*, 1985). The size and accuracy of core areas was affected by tag placement. This should be considered and discussed in papers that compare overlap between core areas of two individual animals. It is less relevant however, when a core area is calculated from a distribution that was based on several animals. Killer whale core areas were relatively small, compared to the entire distribution of the 25 killer whales. This indicates a high concentration of movement, most likely related to foraging efforts. Animal distributions, calculated from biotelemetry data, are dependent on the number of individual animals. Animal biotelemetry identifies in much detail the presence of an animal, but it does not provide any information regarding the absence of an animal. Therefore, animal distributions that are based on biotelemetry data should be regarded as a minimum distribution for the overall population. In this thesis, the distributions of killer whales and humpback whales contain some level of bias, which is the direct result of where animals were instrumented. The conclusions that are drawn only apply to the animals that were instrumented, as other individuals might behave differently and might have different distributions. For example, killer whales in Norway may have seasonal preferences of prey species (Jourdain *et al.*, 2020). These individual differences might indicate individual foraging strategies (Patrick *et al.*, 2015) that differ from the animals that were instrumented for this study. This problem can be addressed by instrumenting animals at different locations and during different periods. In addition, the likelihood of capturing different individual strategies increases with the number of instrumented individuals.

Seasonal variation in animal distributions (paper 3)

After the winter aggregations in fjords of northern Norway, NSS herring migrates southwards towards spawning grounds (Huse *et al.*, 2010). The killer whales appear to follow this migration, which is reflected in their reconstructed paths. However, no temporal component was implemented in the calculation of the killer whale core areas. As a result, the killer whale core areas were possibly biased towards the distribution during the winter. Temporal variation is commonly ignored in the calculation of animal distributions, home ranges, core areas and other measures of general space use (J. A. Long *et al.*, 2015). For highly mobile marine species, such as most cetaceans, it might be more suitable to incorporate a temporal component to seasonal distributions (Hückstädt *et al.*, 2020). Therefore, we developed a dynamic approach to estimate seasonal distributions of humpback and killer whales, which identified large seasonal variations. While the killer whales appeared to be associated with the Norwegian coast throughout most of the year, their distribution moved southwards during the spring. This is likely a response to the NSS herring migration (Kuningas *et al.*, 2013; Vogel, 2020). The distribution of humpback whales also varied throughout the year. During the summer, they forage in the Barents Sea (Stevick *et al.*, 2003; Smith *et al.*, 2009; Skern-Mauritzen *et al.*, 2011). While some individuals migrate from the Barents Sea to the breeding grounds during the autumn or winter (paper 3), a large portion of the population migrates first to the herring overwintering areas in the fjords of

northern Norway (Ramm, 2020). These humpback whales continue their migration to the breeding grounds during the spring.

Spatial overlap between animal distributions and human activities (papers 2 & 3)

The coast of northern Norway is used for a variety of human activities, such as fishery, shipping, aquaculture and main ports. The distribution of both humpback and killer whales is concentrated largely in this area during the autumn, winter and spring. We also studied this area in more detail, to identify overlap between killer whale core areas and herring fishery core areas. Killer whales are also associated with coastal regions of other countries, where the overlap with human activities is potentially high (Visser, 1999; Olsen *et al.*, 2018). This indicates that some killer whale populations are exposed to higher concentrations of human activities, compared to populations in remote areas. In Norway, killer whales are distributed along the coast throughout the year. In contrast, humpback whales only use this area during the winter, in order to feed on herring (Rikardsen, 2019; Ramm, 2020). During the summer, the humpback whale distribution is concentrated in the Barents Sea, where they are exposed to lower intensities of anthropogenic activities. However, human activity in the Arctic is likely to increase, as a consequence of climate change, technological developments and a growing demand (Lam *et al.*, 2016; Myllylä *et al.*, 2016; Ng *et al.*, 2018). Humpback whales will therefore likely be increasingly exposed to human activity during the summer. Identifying spatial overlap between human activities and marine mammals is an essential first step in the assessment of human impact (Rosenbaum *et al.*, 2014; Andersen *et al.*, 2017; Aschettino *et al.*, 2020; Chou *et al.*, 2020).

Dynamic cumulative impact assessment (paper 3)

The framework for a dynamic cumulative impact assessment for highly mobile marine predators, that was developed in paper 3, successfully captured seasonal variation in the distribution of animals. This framework could therefore be implemented in other regions, provided that biotelemetry data is available for mobile species in these regions. As such, it could be a powerful tool in the management of marine activities and in marine wildlife conservation in general (Maxwell *et al.*, 2013; Lewison *et al.*, 2015; Hazen *et al.*, 2018). The cumulative impact assessment of multiple human activities on humpback and killer whales, identified a large seasonal difference between areas of high impact. The main area of high impact during the summer was in the Barents Sea, and is the result of spatial overlap between humpback whales, fisheries and shipping activities. These two activities were also identified as having the highest impact on these cetaceans, due to a combination of noise, collision risk, and entanglements (e.g. Neilson *et al.*, 2009; Guzman *et al.*, 2013; Basran, 2014; Dunlop, 2016). The intensity of these activities in the Barents Sea was relatively low, compared to the coastal region of the study area, but it is likely to increase (Eguíluz *et al.*, 2016). Oil and gas facilities also occur in the Barents Sea, but little evidence was found that under normal use, these activities have a strong impact on the behaviour or distribution of cetaceans. This can change in case of an accident (Jarvela Rosenberger *et al.*, 2017), but since this is not considered “normal operation”, the risk for accidents, such as oil spills were not implemented in this impact assessment. During the autumn, winter and spring, the coast of northern Norway was identified as a high impact area for both species. Here, almost all of the anthropogenic activities were present, often in high concentrations. Particularly in this area, the consequences of spatial overlap between cetaceans and marine activities should be further investigated, to evaluate whether conservation action is required. A particular benefit of the dynamic Cumulative Impact Assessment that is presented here, is that it likely estimates smaller areas of high impact, compared to conventional methods (Lewison *et al.*, 2015; Hazen *et al.*, 2018). This

could make the implementation in ocean management more efficient. In addition, in some areas, seasonal conservation actions could be sufficient to relieve pressure on highly mobile species. This would contribute to an efficient balance between the increasing need for anthropogenic activities at sea, and the need to reduce the impact on highly mobile species.

7 Conclusions and future perspective

Conclusion

The main goal of this thesis was to investigate how biotelemetry data can be used to evaluate human impact on humpback and killer whales in Norwegian waters. Biotelemetry data can be used to reconstruct the detailed movements of individual animals. Based on these reconstructed paths two analytical pathways are addressed in this thesis to investigate human impact. First, a behavioural model, such as an HMM can evaluate the movement parameters of a reconstructed path, in order to differentiate between two or more behavioural states. The impact of a human activity on the transition probability between states can be tested, or attraction to human activities can be included as a behavioural state in the model. This approach identifies how individual animals respond to a single human activity. The second pathway addresses the spatial distribution of an animal, rather than the movement. This approach is particularly suitable for studies on a large spatial scale, or which address the combined effects of multiple activities. The spatial distribution of an animal, or multiple animals, is estimated from the reconstructed paths and is based on the uncertainty around the locations. Three different methods were described in this work: kernel density, Brownian bridge and potential path areas, which may be selected based on the spatial scale of the study area. To evaluate areas of high overlap, spatial distributions between animals and human activities can be compared. Cumulative impact assessments are based on this principle but have one additional step. The potential impact of each human activity can be weighted, to identify areas of high (potential) cumulative impact. Here, behavioural studies can be used to help to evaluate the potential impact of an activity. Areas of high cumulative impact are valuable to ocean management and conservation, as these are areas on which conservation actions should be concentrated. To increase the efficiency of this method for highly mobile species, a dynamic framework is proposed. The spatial distribution of highly mobile species often varies over time and should therefore be estimated for specific periods. Similarly, the distribution of dynamic human activities should also be estimated for specific periods. Based on this approach, ocean management can be focussed on smaller areas, that may only require seasonal actions.

In conclusion, animal biotelemetry can contribute to ocean management, as it can help to identify behavioural responses to individual human activities on a fine scale. Furthermore, biotelemetry data can be used to estimate animal distributions that have a seasonal component, which can be compared to seasonal distributions of multiple human activities in dynamic cumulative impact assessments.

Future perspective

As human presence at sea is increasing, especially in the Arctic, cumulative impact assessments are more valuable than ever before. Dynamic ocean management should be based on a clear understanding of human impact on species, ecosystems and habitats. The pathway that is proposed in this thesis consists of 1) the evaluation of the impact of individual human activities on the behaviour or movement of a species and 2) combining this knowledge from multiple human impacts on a species in a dynamic cumulative impact assessment. Current knowledge is lacking in both elements. Impact studies for individual pressures are often performed on species that can be studied under controlled conditions, such as benthic species, (commercially valuable) fish species, shellfish and plankton, which makes these species easier to study. However, since marine top predators are difficult to study, few studies have addressed the influence of human activities on the fine-scale movement of these species. Therefore, there is a need for biotelemetry studies to investigate how various human activities

influence the movement of species. For example, in this thesis we investigated the interaction between killer whales and fisheries. A similar study would be relevant for humpback whales, which are also often observed feeding near fishing vessels. Following a similar study structure, the impact of other activities, such as shipping can be investigated for humpback and killer whales. Shipping noise is known to affect both species (Holt *et al.*, 2009; Tsujii *et al.*, 2018), but these studies often rely on real-time visual or acoustic observations or on short term biologging data. Biotelemetry studies could be used to study how these species respond to shipping activity over longer periods of time. It is particularly important to compare the influence of human activities during different seasons and at different locations. For example, do humpback whales respond the same to fishing or shipping activity at their summer feeding areas in the Barents Sea, compared to when they migrate along the coast of northern Norway? In killer whales, the attraction to fishing vessels might be stronger during the winter, compared to other seasons. This implicates that behavioural responses to human activities can be affected by other factors, such as the migration and behavioural patterns of prey.

The second element that is addressed in this thesis concerns the cumulative impact of human activities. This is an emerging topic that is currently recognised as an essential tool to inform ocean management (e.g. Hodgson & Halpern, 2019). An essential component of a cumulative impact assessment is information on the spatial distribution of species. Although this type of data can be collected in different forms (e.g. surveys), other methods generally lack the level of (temporal) detail of biotelemetry data. However, the number of animals that are tagged has direct influence on the estimation of animal distribution. The accuracy of the estimated distribution as a representation of the real distribution will increase with the number of tagged individuals. In addition, data needs to be collected throughout the year, in order to fully account for seasonal variations. Data that is collected in different years can be combined, as we have done in this thesis. However, environmental changes, such as changes in the distribution of prey, can affect patterns in the seasonal distribution of animals. For example, every decade or so, herring switches to a new overwintering location. Data that was collected prior to such a change might indicate that an area is of importance to cetaceans, even if this is no longer the case for that particular area. On a larger scale however, this shift might have little influence on the identification of high impact areas.

Ultimately, knowledge on the (cumulative) impact of human activities on a species can be used to parameterize Agent Based Models (ABMs, Beltran *et al.*, 2017). These models can be used for example to predict population-level effects of human activities (Railsback *et al.*, 2011). Parameterizing such a model requires knowledge on long term effects on individuals, such as reproduction rate and mortality. In combination with knowledge on the distribution of a species in space and in time, population effects can be estimated via ABMs. What makes this type of models particularly valuable is their ability to simulate future scenarios. For example, with this approach, population-level effects of potential future shipping intensity could be estimated. Multiple impacts could be included in an Agent Based Model, to estimate effects of future scenarios of human activities on wildlife in the Norwegian and Barents Sea. Due to their relative simplicity, these models are valuable additions to cumulative impact assessments in order to estimate animal distributions and population dynamics under future scenarios.

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Papers

Paper 1

Implications of tag positioning and performance on the analysis of cetacean movement

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TELEMETRY CASE REPORT

Open Access



Implications of tag positioning and performance on the analysis of cetacean movement

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Abstract

Background: Satellite-linked animal-borne tags enable the study of free-ranging marine mammals. These tags can only transmit data while their antenna is above the surface for a sufficient amount of time. Thus, the position of the tag on the animal's body will likely influence the quality and the quantity of location estimates. We explored the effects of tag placement and tag performance on the analysis of cetacean movement, by deploying two identical Argos tags 33 cm apart on the dorsal fin of a male killer whale in Norway in January 2017.

Results: The highest placed (top tag) generated 540 location estimates, while the lowest placed tag (bottom tag) generated 245 locations. In addition, the top tag generated locations of higher quality, with less than 50% of the location estimates in Argos class B (the class with the highest estimated uncertainty), compared to the bottom tag (90% Argos class B locations). The distance between two reconstructed paths ranged from 81 m to 31 km. The path based on the top tag was 1.5 times longer, yielding a higher average speed and more extreme turning angles. The estimated uncertainty around the top track was smaller than that of the bottom track. Switches between searching and travelling behaviour, based on data from the top and the bottom tags, occurred at different positions and times. A significant relationship between core utilization areas and a simulated environmental variable was detectable at a finer spatial scale using data collected by the top tag compared to the bottom tag. A literature search yielded no evidence that tag performance or tag placement is commonly discussed in killer whale telemetry articles.

Conclusions: The differences in quality and quantity of location estimates from our two tags had a substantial effect on derived movement metrics, behavioural inferences and significance of a simulated environmental variable. These differences in tag performance are likely linked to the height difference in tag placement of 33 cm. We suggest that tag positioning on free-ranging marine mammals and tag performance should be considered as a covariate in telemetry studies, especially at a fine scale.

Keywords: Marine mammal, Telemetry, Killer whale, Animal movement, Tag placement, Argos tags, Core areas, Animal behaviour, Tag performance

Background

Movement data are crucial to understanding how animals interact with their environment. The collection of these data may be challenging, particularly in the case of elusive animals that inhabit remote areas or roam over large ranges. Animal-borne instruments (hereafter:

tags) have become widely used in various environments and in animal ecology for a variety of taxa from insects to large megafauna [1, 2]. Technological advances in biotelemetry have led to fundamental discoveries in ecology, providing insight into the horizontal and vertical movements of animals and their physiological state (see [1] for a review). Two main types of tags exist: data loggers that record and store data and need to be recovered, and data transmitters that transmit data to a remote platform [3]. Although different methods exist

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for the transmission of data, most of them do not work underwater, because seawater is opaque to radio waves, and signals cannot pass the water–air barrier. Satellite-based transmission forms a viable option for aquatic animals that often use entire ocean basins [4]. However, this mode of transmission requires tag antenna exposure to air for a sufficient duration in order to communicate with a satellite. Satellite communication serves two purposes in telemetry studies: location estimation and data transfer. In the case of the Argos system, messages used solely for location estimation require a transmission of at least 360 ms, while messages containing data collected by sensors on the tag require a transmission of 920 ms [5]. The quantity and quality of estimated locations depend on the number of received messages, the satellite constellation and the temporal pattern of the messages transmission. Location estimation is therefore directly influenced by the amount of time the antenna is exposed to air [4]. Marine mammals present a significant challenge for satellite telemetry as they spend most of their time underwater and are only briefly at the surface to breath. Satellite-linked tags must be placed strategically on the body of a marine mammal in order to maximize the antenna surface exposure while taking into account the animal's potential discomfort to the tag, its drag and the attachment method. In odontocetes, tags can be mounted onto or below the dorsal fin or on the dorsal ridge [6]. For some species, however, the large size of the dorsal fin allows for substantial inter-individual vertical variation in the placement of the tag. This is the case with killer whales (*Orcinus orca*) and especially males, as the dorsal fin of a male killer whale can grow up to 1.8 m in height [7]. This means that tags may be deployed within a potential vertical range of more than one metre, while at the surface, the upper part of the dorsal fin is exposed to air longer and more frequently than the lower part. Thus, the frequency and duration of tag-satellite communication depend on the vertical placement of the tag on the dorsal fin.

In this study, we explore the differences in data collected by two identical tags that were placed at different vertical positions on the dorsal fin of a male killer whale. We discuss how these differences influence various analytical steps, and we discuss the potential consequences for ecological inferences.

Results

Tag performance and location estimation rate

The tag that was positioned the highest on the dorsal fin (hereafter: top tag, Fig. 1a) was transmitting for 430 h, while the lowest placed tag (hereafter: bottom tag) was

transmitting for a total of 448 h. We restricted these datasets to the 423 h during which both tags were operational simultaneously. During this time, the top tag generated more than twice as many location estimates compared to the bottom tag, respectively, 540 and 245 Argos location estimates. This yields a rate of 1.28 location estimates per hour for the top tag, and a rate of 0.58 location estimates per hour for the bottom tag. The top tag transmitted the percentage dry time on 10 days (out of 19 days), while the bottom tag transmitted the percentage dry time only on 2 days. The reported average percentage dry time per hour by the top tag was higher than that of the bottom tag, 4.8% versus 3.0%, respectively.

The quality of the location estimates, as shown by the distribution of Argos classes, differed between the two tags, with the top tag producing higher-quality location estimates (Fig. 2a). Half of the location estimates from the top tag were assigned to class B, the Argos class associated with the largest measurement error, compared to 90% of the location estimates from the bottom tag. The time intervals between consecutive location estimates were shorter for the top tag (Fig. 2b, median 44.5 and 70.5 min for the top tag and bottom tag, respectively).

Path reconstruction

The total cumulative length of the track based on the top tag (hereafter: top track) was 1.5 times longer than the track based on the bottom tag (hereafter: bottom track), respectively, 1338 km versus 896 km. This yields an average speed for the top track of 3.16 km/h versus 2.12 km/h for the bottom track. The distances between the first and the last locations of both reconstructed paths were similar (Fig. 3a, top track: 127.6 km, bottom track: 138.5 km). Distances between locations of both tracks with the same time stamp, measured as distances between paired hourly locations of the two tracks, ranged from 81 m to 31 km (Fig. 3b) with a median distance of 5 km. The turning angles for the top track were more extreme, with a wider distribution around 0 (Watson's two-sample test, test statistic: 3.4681, p value < 0.001, Fig. 3c). The step lengths (distance per hourly locations) were greater for the top track than those for the bottom track (top: mean = 3.16, sd = 2.35, bottom track: mean = 2.35, sd = 1.77—two-sample Kolmogorov–Smirnov test: $D = 0.26714$, p value = $7.763e-14$, Fig. 3d).

The estimated standard errors in longitude and latitude associated with the two modelled tracks were smaller for the track based on the top tag compared the bottom one (Wilcoxon rank-sum test latitude: $W = 42,763$, p value < $2.2e-16$, longitude: $W = 50,280$, p value < $2.2e-16$, Additional file 1: Fig. S1).

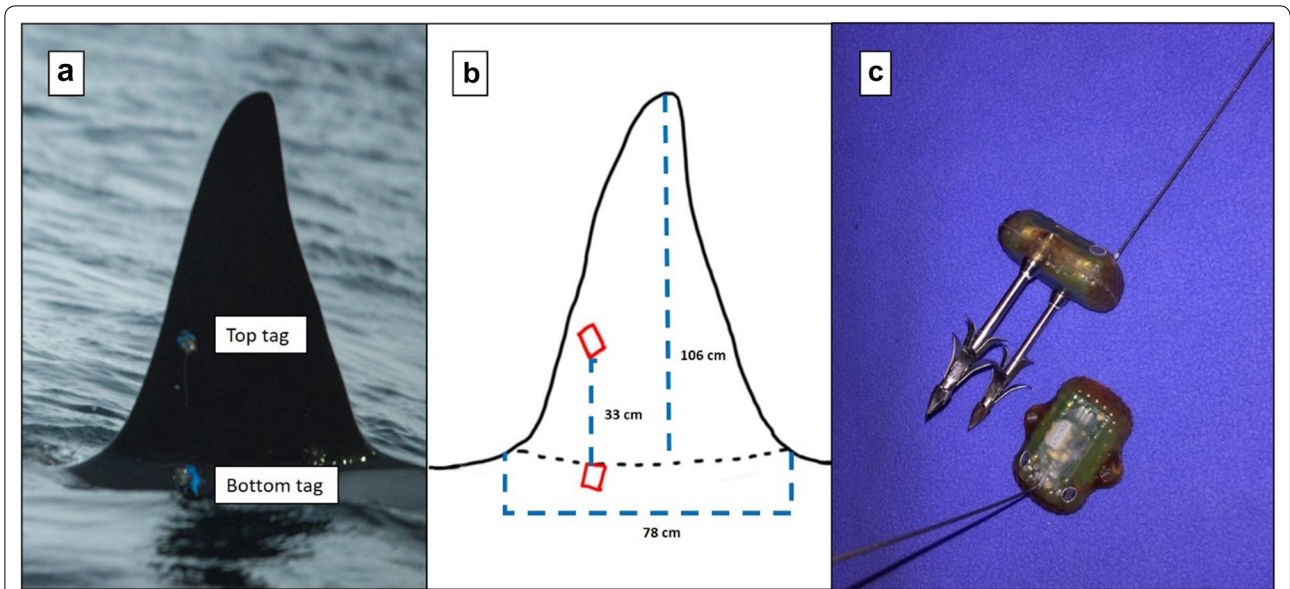


Fig. 1 **a** Photograph of the two tags on the male killer whale instrumented on 9–10 January 2018 in Northern Norway. **b** Schematic of the dorsal fin of the instrumented animal. The estimated measurements of the dorsal fin and the distance between the tags are based on the known dimensions of the tags. **c** Photograph of the type of tags used in this study

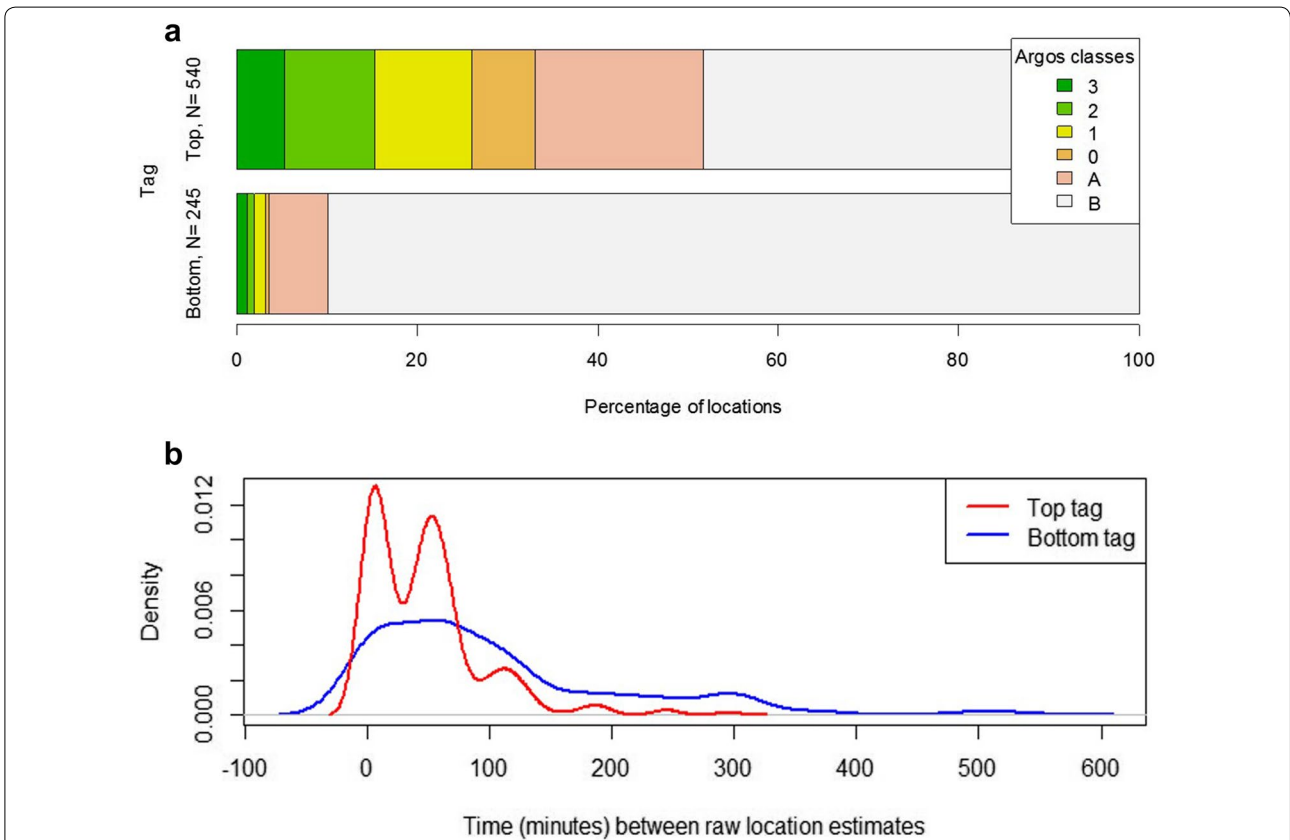
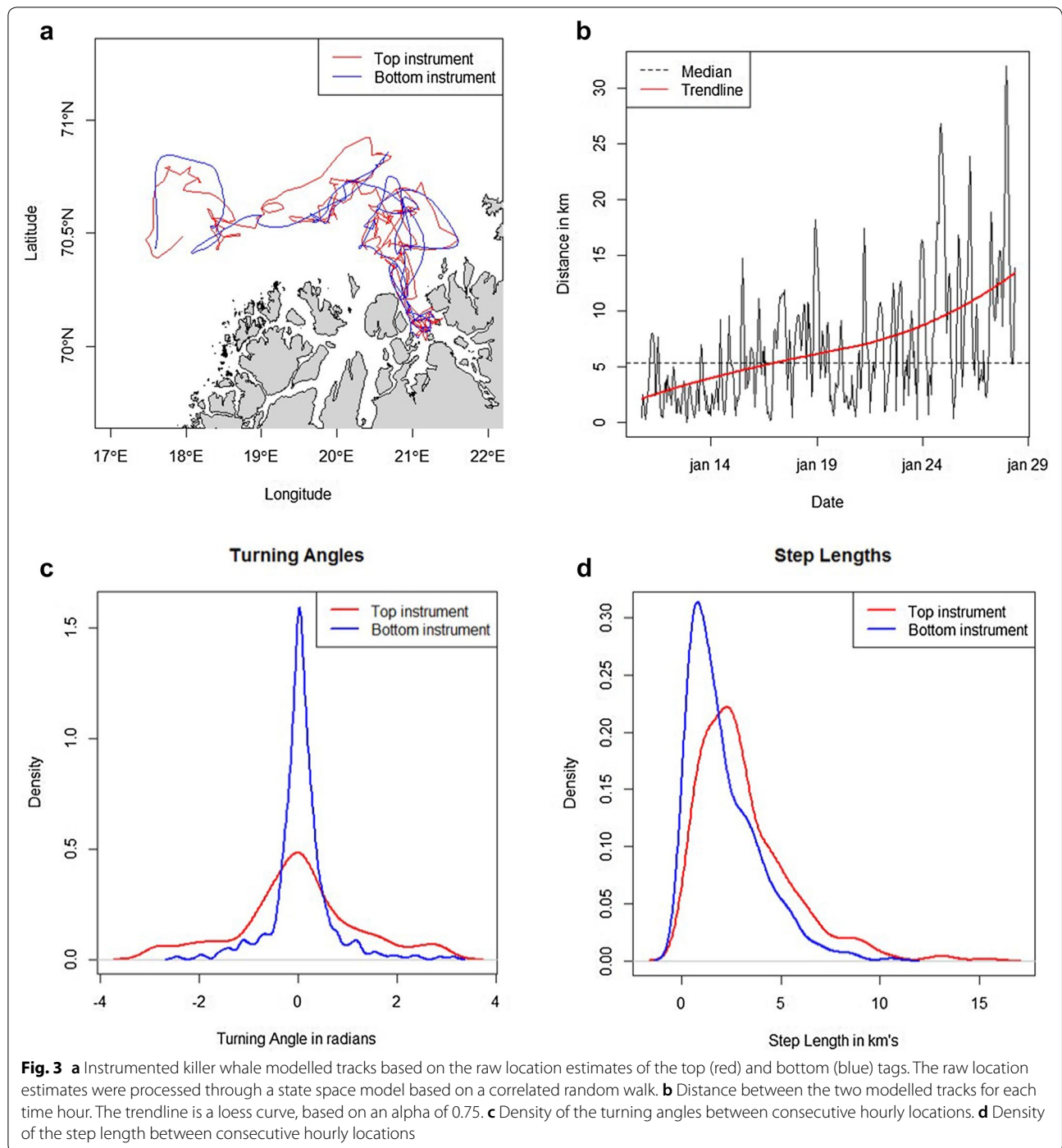


Fig. 2 **a** Proportion of Argos classes associated with the raw location estimates from the two tags. Location classes are colour-coded based on the estimates associated with the smallest positional error (class 3) to the largest (class B). **b** Density plot of the time intervals between two consecutive raw location estimates acquired by the top (red) and bottom (blue) tags



Core area of high utilization

We define the area of high utilization (hereafter: the top or bottom core area, respectively) as the 95% contour of the utilization distribution (UD, hereafter top or bottom UD, respectively). The top core area was approximately 17% smaller than the bottom core area (5399 km² vs. 6293

km², Fig. 4a, b). Eighty per cent of the top core area was included in the bottom core area.

Behavioural analysis

First passage time (FPT)

The variance of log(FPT) based on the top track showed a distinct maximum at 12 km, indicating that the animal was concentrating its search effort within a 12 km radius

(Additional file 2: Fig. S2A). The maximum of the bottom track falls within the error range of estimated error around each location. This means that it cannot be properly interpreted. Any other peak in the graph may be caused by the artificial tortuosity around the track, as a result of the estimated error (Additional file 2: Fig. S2B).

Hidden Markov model (HMM)

We distinguished two behavioural states, “searching” and “transit” along each of the modelled tracks, using a hidden Markov model (Fig. 4a, b). The total number of the

424 locations assigned to either behavioural states was similar for the modelled tracks resulting from both tags (top tag: 234 searching and 190 transit, bottom tag 232 searching and 192 transit). However, these behavioural states did not occur at the same locations nor at the same time. Thirty per cent of the paired locations were not assigned to the same behavioural state (Fig. 4c).

Relationship to environmental variables

We studied whether an environmental variable that is associated with the top track would also be associated

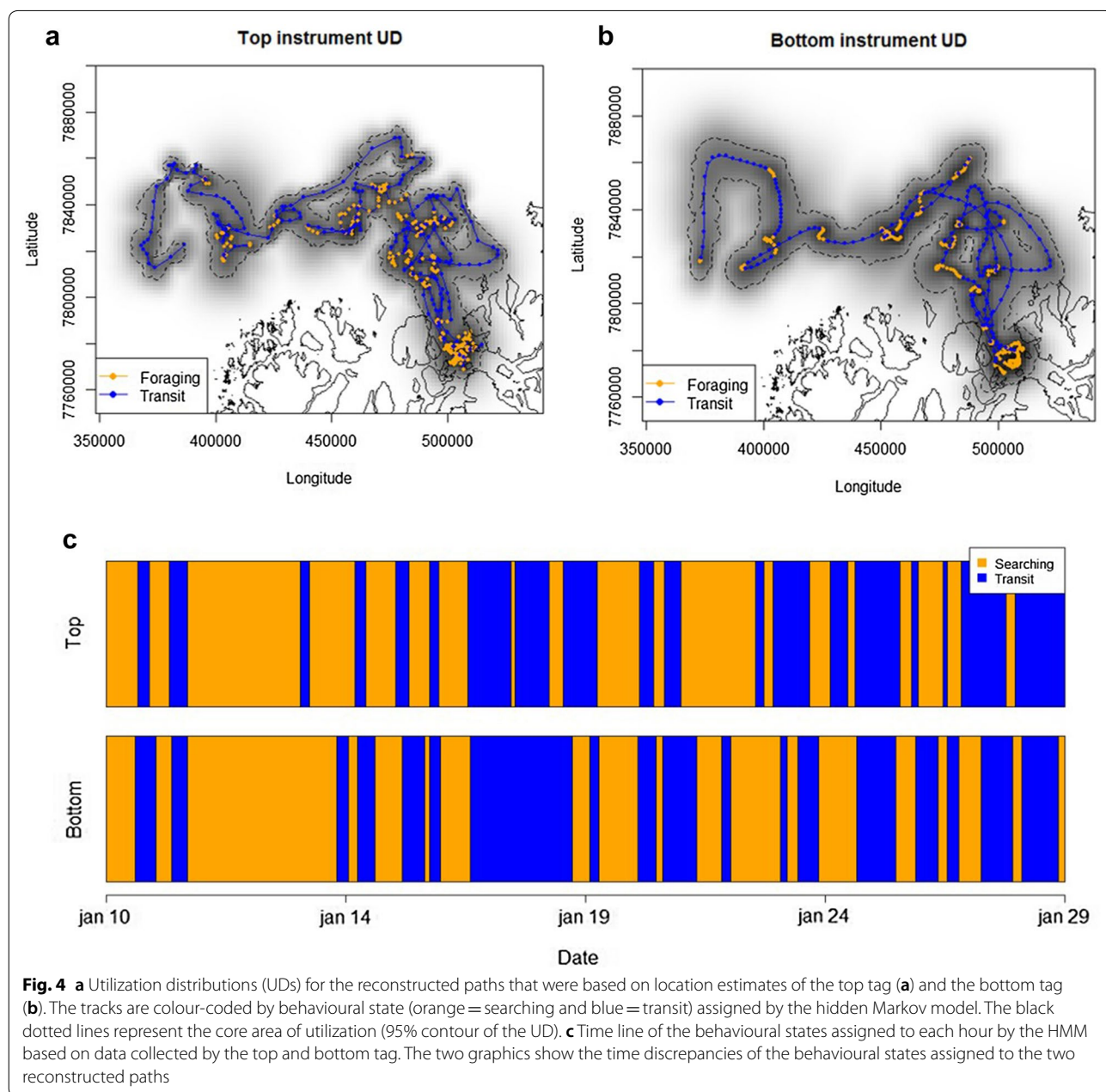


Fig. 4 a Utilization distributions (UDs) for the reconstructed paths that were based on location estimates of the top tag (a) and the bottom tag (b). The tracks are colour-coded by behavioural state (orange = searching and blue = transit) assigned by the hidden Markov model. The black dotted lines represent the core area of utilization (95% contour of the UD). c Time line of the behavioural states assigned to each hour by the HMM based on data collected by the top and bottom tag. The two graphics show the time discrepancies of the behavioural states assigned to the two reconstructed paths

with the bottom track, and the influence of the size of environmental structures on these relationships. To incorporate the uncertainty around each track, we used the UD's rather than the tracks themselves. The bottom track was only significantly related in one scenario: the scenario without any level of randomness, and with an environmental structure radius of 4 km (Fig. 5). In contrast, the top track was significantly related to environmental variables with environmental structure radii of 2 km or more and with up to 50% randomness added to the environmental variable.

Literature review

The tag model that was used in our study has been deployed on 307 animals and 18 species, including killer

whales, between 2006 and 2015 [6]. We focused on (male) killer whales because they represent an extreme example of potential variety in tag placement, due to the size of their dorsal fin. We found no evidence that the influence of tag performance or tag placement on the quality of data output is commonly discussed as an influential factor on the analysis of killer whale data.

Three studies used 12, 19 and 37 instrumented killer whales, respectively, but did not specify the tag positions on the animals [8–10]. Two other studies using two and five killer whales reported tag positions either on the dorsal fin [11], at the base of the dorsal fin or near the saddle patch [12]. Three studies used both females and males [8, 9, 11], while in [12] the animals were identified as either adult females or sub-adult males. One study did

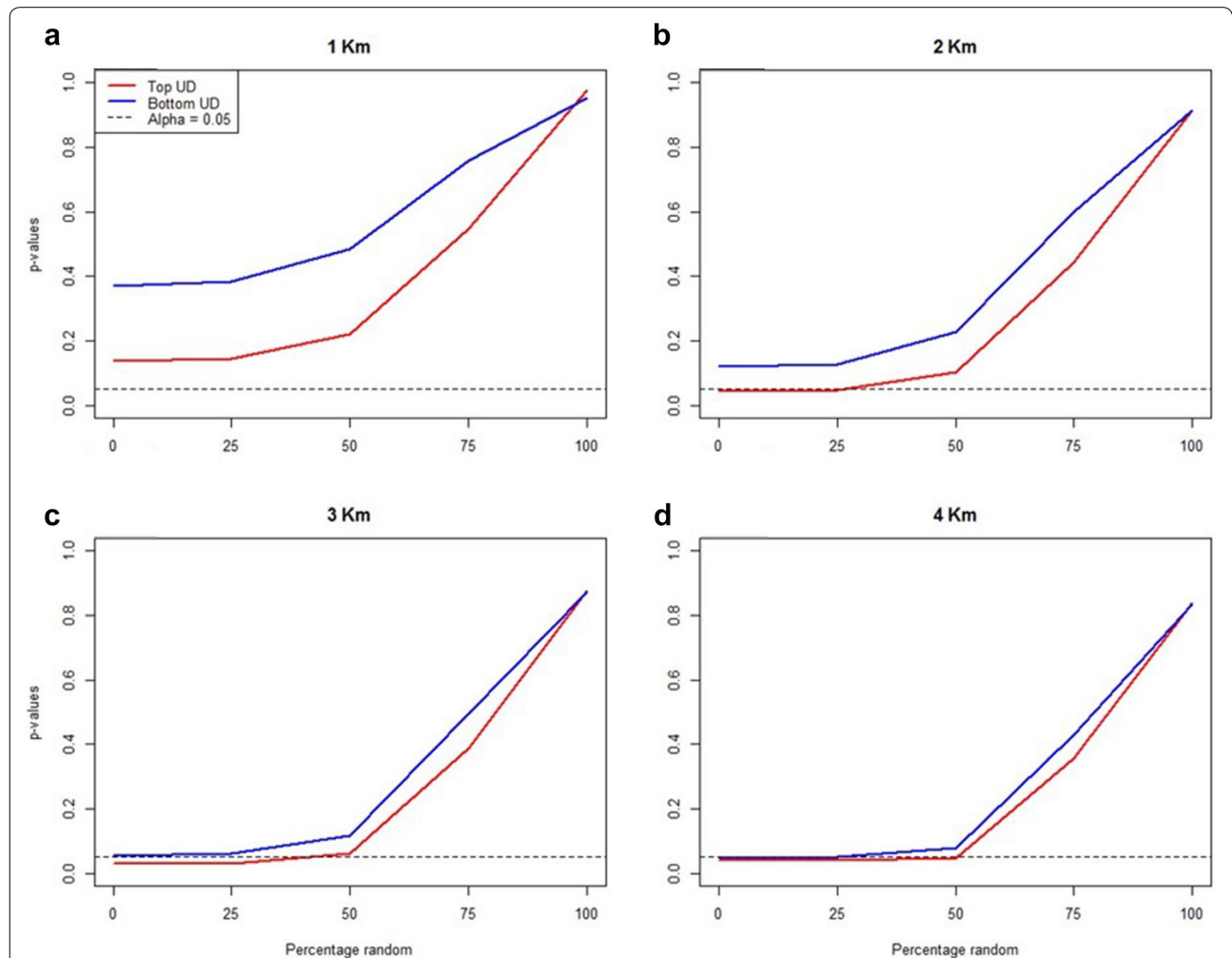


Fig. 5 Relationships between the top (red line) and bottom utilization distributions (blue line) and a range of hypothetical environmental variables. The four plots represent four different scales, expressed as radii of environmental structures. The y-axes show the *p* values from generalized linear models, while the x-axes represent a range of environmental variables, ranging from highly associated to the top track (0% random) to a completely random scenario (100%). The black dotted line represents a threshold value of 0.05

not specify sex [10]. While tag performance was mentioned in three studies (as location estimates per day, in some cases only an average was given for all animals), it was not discussed or taken into account in the analyses [8–10]. One study reported an average of four location estimates of Argos class 1 or better throughout the study [9], while [8, 10] reported averages of between 10 and 20 locations per day, or approximately 0.4 and 0.8 locations per hour.

Discussion

This double-tagging experiment on a male killer whale has allowed us to explore how tag performance influences movement metrics associated with a free-ranging animal's path and the behavioural and ecological inferences. In the present study, these differences are most likely caused by a small vertical difference of 33 cm in tag placement. Aquatic animals that spend long periods submerged are problematic for satellite-linked techniques due to the instrument's reliance on signal transmission through air and real-time communication with satellites [13]. In addition, the location estimates provided by the satellite are prone to measurement error giving an approximation of an animal's real locations. More locations of higher quality should increase the accuracy (how close is the estimated location to the real location) and precision (how large is the uncertainty around an estimated location) of the reconstructed path and associated metrics [14]. To obtain more and better location estimates, the air exposure time of the tag antenna must be maximized. A tag that is exposed to air longer and more often than another tag, is likely to generate more and higher-quality location estimates. This is because it is more likely to send a message while satellites are passing. In addition, it is less likely that messages are interrupted by water splashing on the conductivity sensor. Indeed, we have shown that the placement of an Argos-linked tag on a male killer whale affects the quality and the quantity of collected data with the less exposed bottom tag providing less and lower-quality location estimates compared to the top tag. These differences were significant even though the vertical distance between both tags was just 33 cm. The performance of the bottom tag, expressed in location estimations per hour, is comparable to tag performance described in the literature, while the top tag generated more location estimates per hour. However, since tag performance is most commonly described only briefly and as an average of multiple tags, the range that we found is only a crude approximation of the actual range of location estimates per unit of time. Percentage dry time was only transmitted during some days, and more often by the top tag, presumably because the top tag was exposed to air for longer stretches of time. The transmission of

data messages takes at least 920 ms, during which the antenna must be dry. Therefore, the length of time a tag is exposed to air, and not affected by waves is even more important for data messages which require longer transmission time. Tag performance may also have been influenced by the repetition rate with which the tags transmit. After each transmission, the tag would wait 45 s before re-transmission, which means that it is unlikely that a single surfacing event from the killer whale would have allowed for multiple transmissions from either tag. Both tags were restricted to sending 15 messages per hour, which could cause one or both of the tags to transmit all 15 messages within the first part of each hour. However, we found no indications that the location estimates were clustered to the beginning of each hour.

Based on the differences in raw data, tag placement appears to affect both the accuracy and the precision of the reconstructed paths and identification of behaviour. The two reconstructed paths were noticeably different. The distance between the two tracks, ranging from 81 m to 31 km, indicates a clear difference in accuracy. We assume the top track to be more accurate, as it is based on location estimates of better quality and quantity, compared to the bottom track. The top track was also more precise, with smaller error estimates around the locations compared to the bottom track. The distance between the two tracks appears to increase over time (Fig. 3b). This is most likely caused by the animal's behaviour. Based on the HMM output, the animal is transiting more towards the end of both reconstructed paths, thus spending less time at the surface. This means that consecutive locations of the reconstructed paths are further apart. Slight discrepancies between the two reconstructed paths may thus be amplified, resulting in an increase in distance between the reconstructed path towards the end of both recordings.

Movement metrics, calculated from reconstructed paths, such as travel distances and average velocity, are approximations of 'true' metrics. The length of a reconstructed path can be longer than the real path the animal has taken. The error around location estimates can artificially inflate the track length. However, if path reconstruction is based on relatively few raw location estimates per hour, the model is likely to underestimate the track length, as there is not enough information to accurately reconstruct the meandering movement of the animal. We argue that this is the case for our reconstructed paths, which are based on either 0.58 or 1.28 raw Argos location estimates per hour (bottom or top track, respectively). Since the bottom track is based on fewer raw Argos locations, it is likely missing more of the animals' fine-scale movement. This explains why the bottom reconstructed path is 1.5 shorter than the top reconstructed path.

Metrics that are calculated from track length, such as average speed, are therefore also likely to be underestimated if the rate of location estimation is low. Given the rate of location estimations reported in the literature, we argue that track length and associated metrics are often underestimated.

These metrics are commonly reported metrics in killer whale studies [8, 11, 12]. However, the effect of tag placement or tag performance on these metrics is not commonly taken into account.

Understanding which environmental features are important for an individual or a species and which behaviours are realized in a certain area can help decision-making processes, for example, in the development of marine protected areas. However, we have shown that the precision and accuracy of a modelled track and associated areas of high utilization affect inferences about how a free-ranging animal interacts with its environment. First, the placement of the tags led to different conclusions from behavioural analyses. We found a spatial scale on which the animal concentrated its search effort, based on locations generated by the top tag. The detection of such a spatial scale can, for example, be used to mitigate human activities in a certain place or during a particular period. We could not reach the same conclusion based on locations generated by the bottom tag. This might be caused by the reduced level of detail in the bottom track, which is a direct result of the relatively low quality and quantity of the locations generated by the bottom tag. While we did detect a similar amount of switches between search-related behaviour and travel-related behaviour along both tracks, these switches occurred at different times along both tracks. This could easily lead to misinterpretation of an animal behaviour at a certain time and place. Second, we have shown that tag placement affects the scale on which animal behaviour can be related to environmental conditions. The top track was significantly related to environmental variables with radii of 2 km or more, while the bottom track was only significantly related when the radius of environmental structures was 4 km. Since both tracks represent the same animal path, this difference is an indication that tag performance influences the spatial scale at which relationships with environmental variables may be detected. This can be explained by the uncertainty around the reconstructed path, which is translated into the size, shape and concentration of the UD. A track with a high level of certainty results in a highly concentrated and relatively narrow UD, while a large uncertainty around the track leads to a larger UD where the values are spread out. This level of uncertainty is the reason why the top track was not significantly related to a very fine scale (environmental structure radius 1 km) environmental

variable, even though one scenario of the environmental variable was directly based on the top track. Since the uncertainty around the reconstructed bottom track is larger than around the top track (e.g. the bottom core area is 17% larger), the values of the UD are also more spread out, which makes it less likely small-scale environmental variable are significantly related. There is a bias in the detectability of the relationships, as one scenario of the environmental variable is directly based on the top track. Our two UD's provide two slightly different representations of the animal's true distribution. Neither of these can be completely accurate, but in this analysis we treat one of them (the top UD) as a more accurate representation. This is because the top UD is based on more and higher-quality raw Argos locations. While it is unlikely that the "true" distribution of the killer whale is identical to the top UD, it is likely more closely associated with the top UD than with the bottom UD.

Tag placement and tag performance are most important for fine-scale movement analysis. Studies of large-scale migrations over long periods might be less dependent on high-quality data. The authors of [8] studied killer whale migration on such a large scale that it is unlikely that tag performance affected the conclusions. [10–12] focused on smaller scales, where tag performance may potentially have affected the results.

We focused on killer whales, as the size of their dorsal fins allows for potential variation in tag placement, which may influence tag performance. We showed the effects of a vertical difference in tag position of 33 cm. Similar vertical differences in tag placement may also occur in female killer whales, or in other cetacean species. For example, pilot whales and false killer whales also have relatively large dorsal fins, although not as extreme as male killer whales. Humpback whales and other large whales are typically tagged under their dorsal fin. Due to their large size, substantial height variation in tag placement may occur in the tagging of these species as well.

Conclusions

We have shown that tag performance can be influenced dramatically by the vertical placement of a tag. A tag placed relatively high on the dorsal fin yields location estimates of higher quality and quantity, since the frequency and duration of the tag's surface are higher compared to a tag placed at the base of the dorsal fin. Tag positioning can be controlled to some extent during deployment, in contrast to other factors that may influence tag performance, such as technical malfunction, individual variation between tags and satellite availability. Furthermore, movement metrics, calculated from reconstructed paths, such as travel distances and average velocity, may be underestimations, specifically when location estimation

rate is relatively low. Tag performance and tag placement can also lead to misinterpretation of behaviour, or misidentification of the occurrence of particular behaviour in space or time. The effect of tag performance and tag placement on inferences about behaviour or the environmental relationships is scale dependent. Conclusions in small spatial scale studies are more likely to be affected by tag performance, especially with regard to fine-scale environmental variation, for example, in coastal waters. We found that the effect of tag placement on the quality or quantity of data and the potential influence of tag performance are not commonly taken into account. It is likely that variation in vertical tag placement, or variation in tag performance, may also occur in other cetacean species. Our study focuses on killer whales as an extreme example of potential variability in tag placement; however, general tag performance regardless of the reason should be discussed in telemetry studies of any species. We advocate that tag placement on a free-ranging animal should be carefully considered prior to tagging and that relative tag performance should be considered as a covariate in telemetry studies, especially at a fine scale.

Methods

Tag and instrumentation procedure

We deployed two identical Argos tags (Limpet spot 6/240) [15] on a male killer whale in Kvænanen fjord, Northern Norway (Fig. 6), in January 2018. The tags measured $54 \times 46 \times 20$ mm (Fig. 1a) and were surface-mounted with two sub-dermal 68-mm titanium anchors [6]. A 15-cm-long antenna of flexible material is mounted on the top of the tag (Fig. 1c). When the tag is placed on the dorsal fin of a killer whale, the antenna is positioned horizontally. Due to the flexibility of the antenna material, the antenna might point downwards (Fig. 1a). Both tags were programmed to transmit up to 15 messages per hour. The standard repetition rate or minimum time between transmissions for this type of tag is 45 s. The SPOT 6 tags operate via an internal clock, rather than a 24-h timer that starts at zero once activated. Argos tags instantly transmit 3-bit messages for location estimation when the dry-wet sensor detects that the tag is dry. The dry-wet sensor is sampled every 0.25 s. Therefore, there is a potential delay of up to 0.25 s when the animal surfaces before the message is sent. Since the transmission

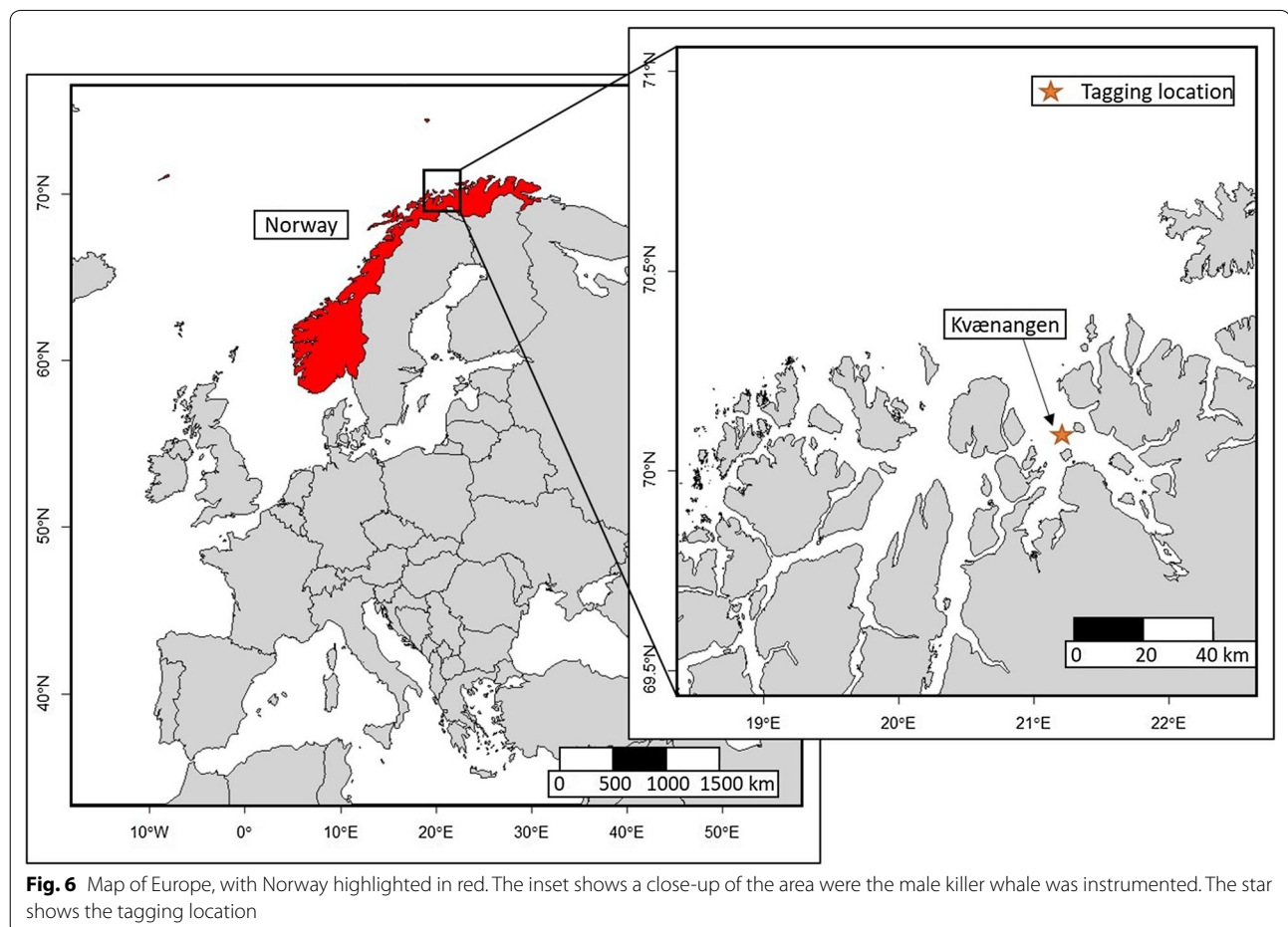


Fig. 6 Map of Europe, with Norway highlighted in red. The inset shows a close-up of the area where the male killer whale was instrumented. The star shows the tagging location

time of a standard location message is 0.36 s, the potential required time for one successful location transmission is 0.51 s. During the transmission, at least 10% of the antenna needs to be above the surface [16, personal communication].

The animals were approached from a 26-ft open RIB boat while they were feeding in groups of 30–150 animals in the vicinity of purse-net herring fishing vessels. The tags were deployed with an ARTS tag applicator (using a pressure of 8 bar at a distance < 10 m), similar to the tag applicator described in [17] and the anchors were cleaned with 70% alcohol prior to the deployment. The bottom tag was deployed at the base of the dorsal fin (Fig. 1a) on 9 January 2018 at 11:55, while the top tag was deployed at approximately 60 cm from the tip of the dorsal fin on 10 January 2018 at 15:51. The vertical distance between the two tags was estimated to be 33 cm. We estimated the dorsal fin to be 106 cm in height, and 78 cm at the base, based on the known dimensions of the tags (Fig. 1b).

The placement of two tags on one individual male was not a planned event and precautions were taken during this study to minimize the risk of tagging the same individual twice: (1) the target animal was always followed prior to the tagging event in order to manoeuvre the boat in a proper position facilitating the tag placement, (2) tagged animals were identified, based on characteristics of the dorsal fin and the saddle patch and photographed, (3) all animals were tagged on the same side of the dorsal fin, and (4) tags were only deployed from a distance of less than 15 m. However, light and weather conditions during the winter in Northern Norway can be challenging. In this particular tagging event, the first tag was placed at the base of the dorsal fin and was poorly visible when the animal was at the surface. Upon the discovery that we double tagged an animal, the Norwegian Food Safety Authority (Mattilsynet) was contacted immediately. This body is the responsible authority for animal research in Norway. After investigation, Mattilsynet decided that all required precautions had been taken and that our methods were in line with our tagging permit. Mattilsynet agreed that although unplanned, this event could benefit marine mammal research by providing insight into the functioning of electronic tags that are placed at different heights on the body of a cetacean. They fully support the present study and granted permission to double tag one animal a posteriori.

No reaction was observed during either tagging occasion, and the animal continued to feed with the other animals from its group, alongside the fishing boats. Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under the permit: FOTS-ID 14135, and evaluated by an accredited veterinarian (Mattilsynet Report nr. 2017/279575).

Raw data and path reconstruction

We restricted the analysis to data recorded between 10 January 2018 17:00 and 28 January 2018 08:00 (423 h), when both tags transmitted simultaneously. The Argos system provides irregular location estimates associated with an error ellipse, depending on the location quality class [18, 19]. Argos location estimates are classified into 6 quality classes: 3, 2, 1, 0, A and B. The classes 3–0 associated with the highest accuracy have an estimated error ranging from < 100 m (class 3) to > 1500 m (class 0). The classes A and B do not have an estimated error, since they are based on less than 4 Argos messages. We compared the number of location estimates, the quality class distributions, the time intervals between locations, the number of location estimates per hour and the transmitted percentage dry time (recorded as average per hour) between the tags. The hourly percentages dry time are transmitted 10 times for each day, to increase the chance the message is recorded by a passing satellite. All data preparation, comparison and analysis were performed in R [20].

In order to obtain an estimate of the most probable path taken by the animal, we fitted a continuous-time correlated random walk (CRW), based on a state space model framework (SSM), on the raw Argos locations [21]. The CRW is an extension of a Random Walk and assumes that the movement rate at a location is correlated with the movement rates at previous locations [22]. Path reconstruction using a CRW does not require the exclusion of any location but takes into account the error associated with each ARGOS location estimate. The model also provides an estimated error around the track [23]. We used the “ssmTMB” package in R [24], and we computed location estimates at 1-h intervals.

We calculated summary metrics of the reconstructed paths based on the data from the two tags [25]. We used total displacement, cumulative track length, average speed, hourly speed step lengths and turning angles. Step length refers to the straight distance between hourly location estimates, while turning angles refer to the changes in direction between two consecutive location estimates. We compared the cumulative distribution functions (CDF) of the step lengths for both modelled tracks with a Kolmogorov–Smirnov test. The distributions of the turning angles were compared using a Watson’s two-sample test of homogeneity. In addition, an unpaired two-sample Wilcoxon test was used to compare the distributions of the standard errors that were estimated by the CRW model for latitude and longitude for the two modelled tracks. Finally, we calculated the distance between the two reconstructed paths at each hourly time step.

Identification of areas of high utilization

To incorporate the error around the reconstructed paths, as estimated by the CRW, we developed a modified version of a utilization distribution (UD). A UD can be described as the distribution of animal locations over a period of time [26]. We selected 20 locations from the standard error ellipse (based on the CRW output) around each location, creating 20 sets of locations for each track. Around each of these sets, we estimated the probability of occurrence across a regularized raster (1069×825 m resolution) using Brownian bridges, following a similar procedure as [21, 27]. The resulting 20 distributions were then combined into one average UD by taking the mean value for each raster cell. This approach generates an average UD for each of the two reconstructed paths (hereafter: top UD and bottom UD) that accounts for the estimated uncertainty around each reconstructed path. In order to compare the two areas of utilization, we used the 95% contours of the top and bottom UDs to create a core area of high utilization. We compared the size of the core areas, and we calculated the percentage overlap.

Identification of behavioural states

We used the first passage time (FPT) method and a hidden Markov model (HMM) in order to partition each track according to two behavioural states [21, 28–32]. The FPTs, the time an animal spends within a circle of a specific radius centred at each hourly location, were calculated along the two modelled tracks. We calculated the variance of the log (FPT) at radii that ranged from 0 to 30 km at 1-km intervals. The radius for which the variance of the log(FPT) is at a maximum provides an estimate of the spatial scale within which the search effort of an animal is concentrated [33]. We used the R package *adehabitatLT* [34].

We used a state space model to infer the behavioural state of the killer whale based on its movements, e.g. [30, 35]. An SSM estimates model parameters to predict different states (e.g. searching and travelling behaviour). These states themselves are unknown, but they are described by a process model, which is fitted to observed data (e.g. movement metrics) [23]. Hidden Markov models (HMMs) are a special case of SSM, which predict discrete, rather than continuous states (see [36] and references therein). In this study, we used an HMM to predict parameter estimates for step lengths and turning angles of two discrete behavioural states “searching” and “transit”, following the approach by [21]. We fitted the two modelled tracks separately in a HMM, using the *momentuHMM* package [37]. We used the Viterbi algorithm to assign behavioural states to predicted locations of the reconstructed paths. A Viterbi algorithm estimates the most likely sequence of states, based on the parameter

estimates from the HMM, where the behavioural state is dependent on the previous state [37].

Relationship with environmental variables

Animal movement and distribution studies often develop models assessing the importance of one or several environmental characteristics, e.g. [38, 39]. However, the statistical significance of the relationship between environmental variable and animal movement depends on their resolution and the accuracy of the estimated tracks. We aimed to test if an environmental variable that was associated with one track would also be associated with the other track. Second, we aimed to study how the relationship between the environmental variable and the animal tracks was affected by changing the radius of environmental structures.

A range of environmental variables was created for this analysis, based on a number of environmental structures. We define the term environmental structure as an area that influences killer whale movement. This may include a school of fish, but it may also represent, for example, an area with a specific surface temperature. Each environmental variable consisted of 30 structures; the number 30 is arbitrary. First, we varied the locations of the environmental structures. Second, we varied the radius of the structures, between 1 and 4 km. For the first step, we created two scenarios with different environmental structure locations. We also created intermediate scenarios by taking the weighted means of these two scenarios (0.25–0.75, 0.5–0.5, 0.75–0.25). The first scenario was created by randomly selecting 30 locations from the same grid that was used to create the UDs. In the second scenario, one of the two reconstructed paths is treated as a more accurate representation of the animals true path. We selected the top track for this role, since it is based on more, and more accurate location estimates than the bottom track. This scenario was created by selecting 30 locations from the highest values of the top UD, which can be interpreted as the top track with the uncertainty around it.

For the second step, we varied the radius of the environmental structures. We used a multivariate distribution to distribute 10,000 points around the locations of the scenarios that we created in the previous step. We then varied the radius of all the structures between 1 and 4 km at 1-km intervals. We then summed the number of points in each grid cell, using the same grid cell that was used to create the UDs. These summed values per grid cell were normalized so that we could compare the values of the different structure radius variants.

The relationship between both tracks and each variation of the environmental variable was tested in a series

of simple GLMs. We used the UD to represent each track and the uncertainty around it in the following model structure: GLM (UDs grid cell values ~ environmental variable). The *p* value of each model was recorded and compared with the *p* values of the other models (Additional file 3: Fig. S3).

Literature review

We conducted a literature search to study whether researchers take tag placement into account in their analysis. We focused on published, peer-reviewed articles using the search engines Google Scholar and Biological Abstracts, using various combinations of the keywords: “killer whale”, “telemetry”, “satellite”, “tag”, “PTT”, “Argos”, “transdermal”. We looked for information on the placement of killer whale tags in these studies and whether tag performance (number of location estimates per unit of time) was evaluated or taken into account during the analysis. We focused on killer whale literature and tag models that were similar to the SPOT 6 tags that we used. The focus on killer whales was directed by the size of their dorsal fin and the potential vertical variation in tag placement.

Additional files

Additional file 1: Fig. S1. Latitude (A) and Longitude (B) of the reconstructed paths.

Additional file 2: Fig. S2. Variance of the log-transformed first passage time.

Additional file 3: Fig. S3. Simulated environmental variables.

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Authors' contributions

EM and AR conducted the fieldwork, and AR deployed the tags. EM, MAB and MB analysed the data. EM, MAB, MB and AR wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

Ethics approval

The placement of two tags on one individual male was not a planned event and precautions were taken during this study to minimize the risk of tagging the same individual twice: (1) the target animal was always followed prior to the tagging event in order to manoeuvre the boat in a proper position facilitating the tag placement, (2) tagged animals were identified, based on characteristics of the dorsal fin and the saddlepatch and photographed, (3) all animals were tagged on the same side of the dorsal fin, (4) tags were only deployed from a distance of less than 15 m. However, light and weather conditions during the winter in Northern Norway can be challenging. In this particular tagging event, the first tag was placed at the base of the dorsal fin and was poorly visible when the animal was at the surface. Upon the discovery that we double tagged an animal, the Norwegian Food Safety Authority (Mattilsynet) was contacted immediately. This body is the responsible authority for animal research in Norway. After investigation, Mattilsynet decided that all required precautions had been taken and that our methods were in line with our tagging permit. Mattilsynet agreed that although unplanned, this event could benefit marine mammal research by providing insight into the functioning of electronic tags that are placed at different heights on the body of a cetacean. They fully support the present study and granted permission to double tag one animal a posteriori. No reaction was observed during either tagging occasion, and the animal continued to feed with the other animals from its group, alongside the fishing boats. Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet), under the permit: FOTS-ID 14135, and evaluated by an accredited veterinarian (Mattilsynet Report nr. 2017/279575).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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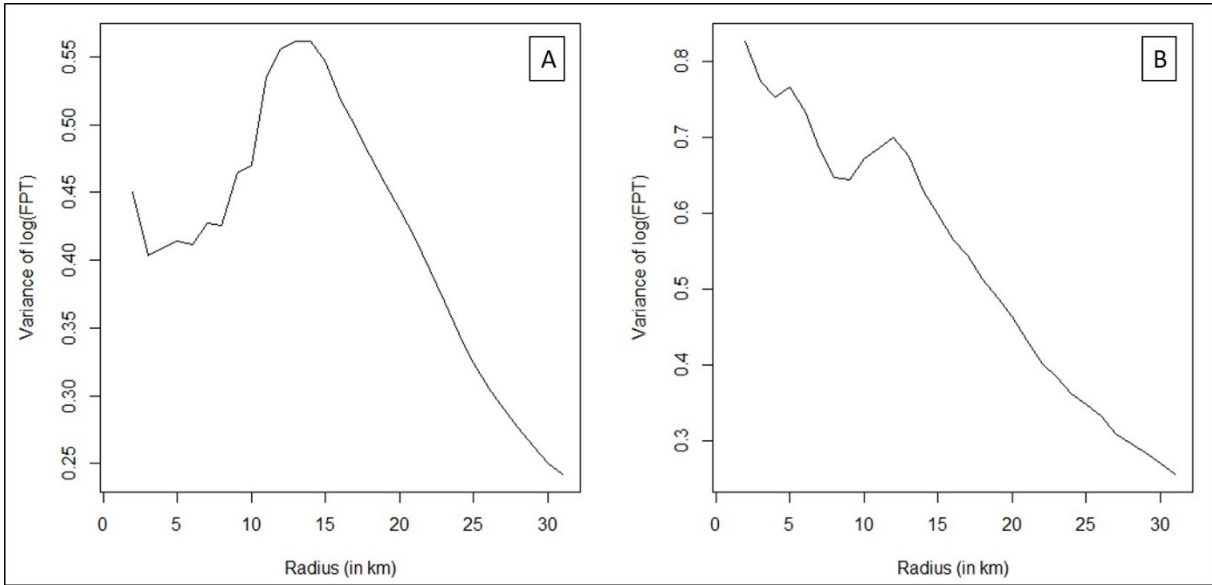
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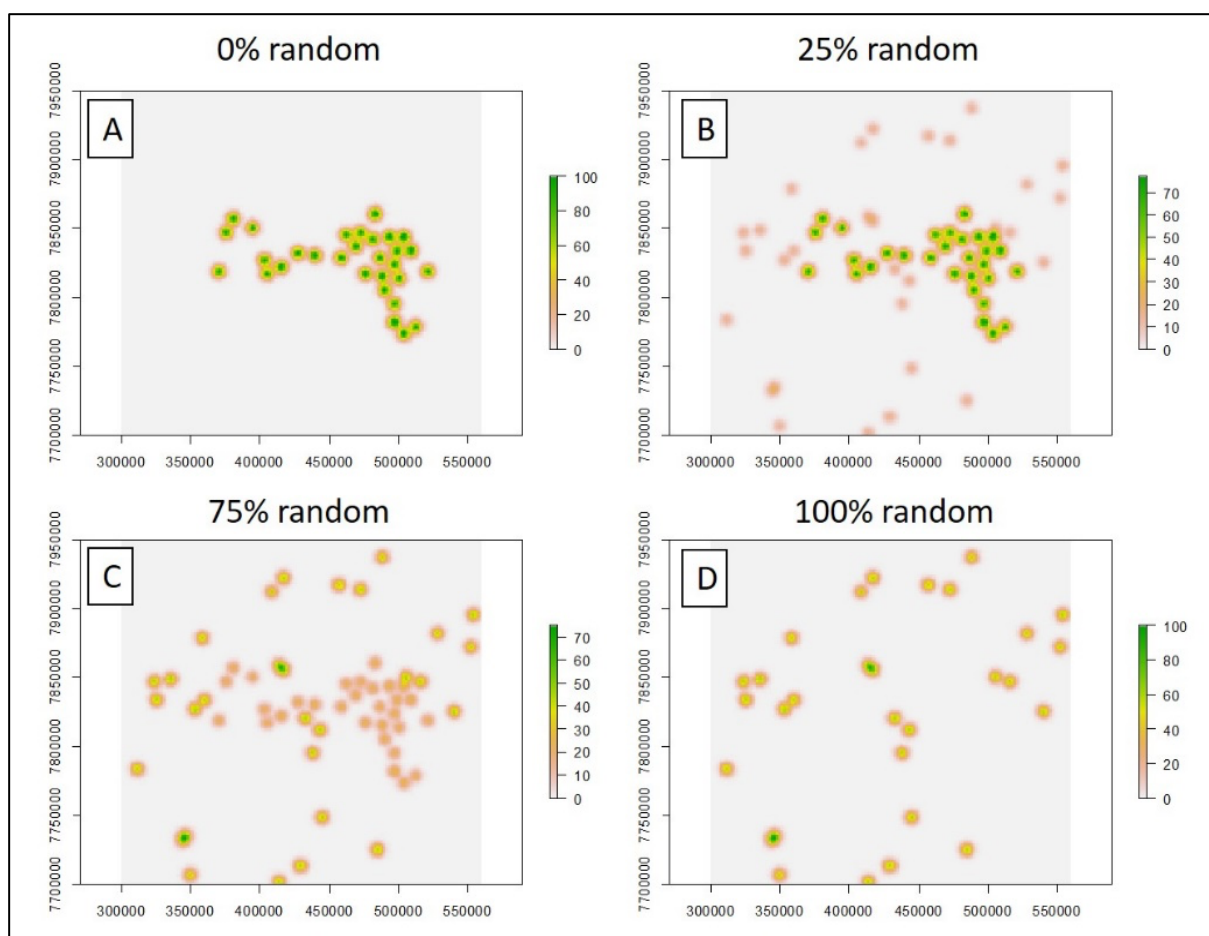


Additional figure 1 is missing, because it is a moving image (gif). It can be found via the DOI of the paper:

<https://doi.org/10.1186/s40317-019-0173-7>



Additional file 2: Fig. S2 – Variance of the log-transformed First Passage Time of the top track (A) and the bottom track (B). The top FPT shows a maximum at 12 km, while the bottom FPT does not show a clear maximum.



Additional file 3: Fig. S3 – Simulated environmental variables, ranging from a variable that is highly associated to the top UD (A) to a completely random environmental variable (D). In the analysis we varied the radius of each environmental structure between 1 and 4 km.

Paper 2

Killer whales are attracted to fishing activity

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1 **Killer whales are attracted to herring fishing vessels**

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15

KILLER WHALE ATTRACTION TO FISHING ACTIVITY

1 **Abstract:**

2 Marine mammals and fisheries often target the same resources, which can lead to operational
3 interactions. Potential consequences of operational interaction include entanglements, damaged or
4 reduced catches, but also enhanced foraging opportunities, which can attract marine mammals to
5 fishing vessels. A responsible fisheries management therefore requires detailed knowledge of the
6 impact of these interactions. In northern Norway, killer whales (*Orcinus orca*) are frequently observed
7 in association with large herring aggregations during the winter. We use a combination of biotelemetry
8 and fisheries data to study if, to what extent, and at what distance killer whales are attracted to fishing
9 activity. Twenty-five satellite transmitters were deployed on killer whales at herring overwintering and
10 spawning grounds, often near fishing vessels. Over 50% of the killer whale's core areas of high usage
11 overlapped with the fisheries' core areas, and individual whales spent up to 34% of their time close to
12 active fishing. We used a three-state hidden Markov model (HMM) to assess whether killer whale
13 movements were biased towards fishing activities. Fifteen percent (CI = 11% – 21%) of the overall
14 whale movements were biased towards fishing activities, with marked heterogeneity among
15 individuals (0% – 57%). During periods of active fishing, whale movements were biased towards
16 fishing events 44% (CI = 24% – 66%) of the time, with individual percentages ranging from 0% to
17 79%. Whales were more likely to be attracted when they were within 20 km. This information can be
18 used in fishery management, in order to consider potential consequences for fishers and whales.

19

20 *Keywords: fishery interactions, killer whales, Orcinus orca, herring fishery, behaviour, hidden*

21 *Markov model, momentuHMM, attraction*

22

1 **1 Introduction:**

2 Commercial fisheries are present in all the world's oceans and can affect marine wildlife and
3 ecosystems in various ways (Botsford 1997). Marine top predators, such as marine mammals,
4 seabirds, sharks and sea turtles, often inhabit the same regions and share resources with a variety of
5 fisheries. As a result, their movements overlap temporally and spatially, leading directly to operational
6 interactions, which are defined as direct contacts with operational fishing gear (Northridge 1991, Read
7 et al. 2006, Read 2008). Over the last decades, increasing fishing activities have caused increased
8 operational interactions between fisheries and marine top predators (Read et al. 2006, Read 2008,
9 Northridge et al. 2017).

10 Consequences of these interactions can be neutral (no effect), positive, or negative for either
11 the animals, the fisheries, or for both. Top predators may benefit from fisheries, as fishing activity may
12 provide good foraging opportunities by immobilizing or aggregating prey, or by relocating prey to the
13 surface. Predators can either take fish that has been captured by the fishers (depredation), or they
14 might target discarded or escaped fish, or fish that aggregates around a fishing net (Söffker et al. 2015,
15 Tixier et al. 2019). As a result, some species are attracted to fishing activity. Similarly, fishers may
16 also be attracted to top predators, which might lead them to commercially important prey species
17 (Escalle et al. 2015). However, operational interactions can also have adverse consequences. Fisheries
18 may lose revenue due to depredation or competition, lost or damaged fishing gear, or increased
19 operation time (Kock et al. 2006, Güçlüsoy 2008, Tixier et al. 2019). A wide range of seabirds, sea
20 turtles, sharks and marine mammals die in various fishing gears around the world as a result of
21 operational interactions (Moore et al. 2009, Abdulqader et al. 2017, Northridge et al. 2017, Carretta et
22 al. 2019). The foraging benefits near fishing activity can provide long-term effects for the killer whale
23 population, such as increased calving rate (Tixier et al. 2015). Ultimately, these effects can cascade
24 through the ecosystem in which the killer whales are the top predator. Studying the short-term
25 behavioural response of killer whales to fisheries can help to identify long-term consequences that
26 fisheries may have on killer whales in Norway. Little is known about the mechanisms behind
27 interaction between fisheries and marine mammals and how animal behaviour is influenced by the

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1 presence of fishery activity (Richard et al. 2020). Studying the interaction between fisheries and
2 marine mammals requires fine-scale animal movement data, which can be used to detect changes in
3 the movement that may be induced by the fisheries (Mathias et al. 2012, Straley et al. 2014, Towers et
4 al. 2019, Richard et al. 2020).

5 Killer whales (*Orcinus orca*) are highly mobile, globally distributed predators. In Norway,
6 killer whales interact with industrial purse seine herring fisheries by feeding around the nets (Similä
7 2005, Rikardsen 2019). A recent estimate suggests 15 056 killer whales (CV=0.293, CI 95% 8 423 –
8 26 914) inhabit the North east Atlantic (Leonard & Øien 2020), with more than 1 100 known
9 individuals in Norwegian waters (<https://www.norwegianorca-id.no>). Killer whale movements in
10 Norway have been associated with their primary prey species: Norwegian spring spawning herring
11 (NSS), which is the largest herring (*Clupea harengus*) stock in the North east Atlantic (Dragesund et
12 al. 1980, Similä et al. 1996, Kuningas et al. 2014, Jourdain et al. 2019). A large portion of the NSS
13 herring stock often overwinters close to the Norwegian coast (Nøttestad & Axelsen 1999, Huse et al.
14 2010, Rikardsen 2019). These winter aggregations have attracted large numbers of killer whales since
15 the 1980s and humpback whales (*Megaptera novaeangliae*) since 2011 (Similä et al. 1996, Jourdain &
16 Vongraven 2017). After the winter, the herring migrates southwards to spawn off the coast of western
17 Norway (Huse et al. 2010). NSS herring is also an important commercial species, with a quota of
18 400 000 t in 2020. Purse seine fishing vessels congregate in the fjords during the winter (November –
19 January) and overlap with killer whales and other top predators (Rikardsen 2019). However, little is
20 known about the level of overlap and the nature of interactions between killer whales and herring
21 fishing activity in Northern Norway. The killer whales appear to be attracted to the fishing activity
22 during the winter herring aggregations, but to what extent, how often, and from what distances
23 remains unclear. Such knowledge should be considered when managing coastal fisheries.

24 The main objective of this study was to describe and quantify fine-scale overlap between
25 herring fisheries and killer whale movements in northern Norway during and after winter herring
26 aggregations, based on killer whale satellite tags and fishing vessel data. More specifically, our aims
27 were: (1) to identify areas of overlap between fishing activities and killer whales; (2) to explore in
28 detail the level of overlap in the fjords during the winter, and offshore during the spring; and (3) to

1 investigate to what extent killer whales are attracted to fishing vessels, how often they are attracted,
2 and from which distances.

3 **2 Materials and methods**

4 *2.1 Killer whale instrumentation:*

5 We equipped 25 killer whales with Argos satellite tags (Limpet SPOT 6/240, Wildlife Computers Inc,
6 USA). The tags measured 54×46×20 mm and were surface-mounted with two sub-dermal 68-mm
7 titanium anchors. Tags were specifically deployed close to the middle of the dorsal fin, as this position
8 yields better position data, compared to a lower placed tag (Mul et al. 2019). All killer whales were
9 adult males, with the exception of one adult female. We used a 26 ft open RIB and an ARTS tag
10 applicator (<https://restech.no>) with 7-10 bar pressure at a distance of about 5-10 m. The tags were
11 programmed to transmit 14-15 messages per hour for the first 40-45 days. The number of
12 transmissions was reduced to 8-10 per hour for the following 35-45 days, and to 55 transmissions per
13 day for the remaining lifespan of the battery. We deployed 11 tags between 02-12-2017 and 20-01-
14 2018 (hereafter: first study period), and 10 tags between 26-10-2018 and 23-01-2019 (hereafter:
15 second study period) in Kvænangen fjord in northern Norway (Fig. 1A, Table 1). In addition, four tags
16 were deployed between 16-02-2019 and 17-02-2019 off the coast of the Møre county in the western
17 part of Norway (Fig. 1A, Table 1). Killer whales were tagged in different locations, in different social
18 groups and around different fishing vessels, in order to avoid tagging multiple animals in the same
19 social group. The techniques used in this study have previously been shown to have little or no long-
20 term effect on the demography and behaviour of the killer whales (Reisinger et al. 2014). Tagging
21 procedures were approved by the Norwegian Food Safety Authorities (<https://www.mattilsynet.no>,
22 permit: FOTS-ID 14135) and evaluated in the field by an accredited veterinarian (Mattilsynet Report
23 nr. 2017/279575).

24

25 *2.2 Fisheries data:*

26 Electronic catch diaries from the fishing vessels were reported to the Norwegian directorate of
27 fisheries (<https://www.fiskeridir.no>). We obtained these data with masked vessel identification,

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1 through the Institute of Marine Research (<https://www.hi.no>). In this study, we focussed only on purse
2 seine herring fishing vessels. NSS herring is caught throughout the year, but with a peak winter season
3 between October and January. According to our data, 189 purse seine vessels made approximately
4 3 500 fishing trips in 2017. The fleet consists primarily of small vessels that are between 20 and 40
5 meters in length, and large vessels that are between 60 and 80 meters in length. The latter operated
6 primarily offshore. We only obtained fishery data that overlapped in time with the killer whale
7 tracking data (Fig. 1B). The data consisted of fishing locations, start and end times of each fishing
8 event, and the catch size. A fishing event is defined as starting when the nets are set and ending the
9 nets are completely hauled onto the fishing vessel. However, based on communication with fishers and
10 with the directorate of fisheries, there is some variation amongst fishers regarding the reporting of
11 these events. In addition, fish finding efforts and on-site pre and post fishing preparations were not
12 included in the reported start and end time. In order to include all the potential cues that may attract
13 the whales to the fishing site, we added two hours before the start and after the finish of each fishing
14 activity. We based this decision on personal observations in the field. NSS herring is caught with
15 circling and closing purse-seine nets. Since fishing vessels remained relatively stationary when
16 hauling the net, we assigned each fishing event to one location corresponding to the start of the fishing
17 event. Therefore, fishing events within a 3 km radius of each other and less than 4 hours apart, were
18 grouped together. These threshold values were based on field observations in the study area. Grouped
19 fishing activities were assigned to the mean latitude and longitude coordinates, the summed catch size,
20 the earliest start time and the latest end time of all the fishing events.

21

22 2.3 Data processing:

23 To account for both location uncertainty (e.g. Kuhn et al. 2009) and time-irregularity in the killer
24 whale Argos locations, we fitted a correlated random walk using a continuous-time state-space model
25 (Johnson et al. 2008) based on the location class and error ellipse estimates (McClintock *et al.*, 2015).
26 This method is based on a Kalman filter and estimates movement parameters, from which one or
27 several animal paths, or imputations, can be reconstructed (McClintock 2017). We used 30
28 imputations for each killer whale track, rather than one “best fit” path reconstruction, to account for

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1 the uncertainty and error around the raw Argos locations. Locations were estimated at a 1 h time
2 interval as a reasonable representation of the raw Argos data (range: 0.3–1.5 locations per hour, Table
3 1). We fitted the model using the “crawl” package (Johnson & London 2018) via a wrapper function
4 from the “momentuHMM” package (McClintock & Michelot 2018). All results based on the 30
5 realizations of each track were pooled using standard multiple imputation formulae (e.g. Rubin 1987).
6 All data processing and analyses were performed with R statistical computing software, version 4.0.0
7 (R Core Team 2019).

8

9 *2.4 Large-scale overlap between whale movements and fishing activity:*

10 We calculated the size of the areas of overlap between whales and fisheries distributions for each
11 study period separately by identifying areas where killer whales and fishing events were more likely to
12 occur. These Core Areas (CAs) were estimated by calculating the 50% contour of the utilization
13 distribution (UD) for fishing events and killer whales. The UD is an estimation of the probability
14 density of an animals' occurrence in space (Samuel et al. 1985). The fisheries UD's were calculated for
15 each study period, based on a least-squared cross validation kernel method (Worton 1989, Horne &
16 Garton 2006), using the “adehabitatHR” package in R (Calenge 2006). Since the killer whale data
17 were based on consecutive locations, rather than independent points such as the fishery data, we used a
18 Brownian bridge method to calculate killer whale UD's (Horne et al. 2007). We first calculated the UD
19 for each of the 30 imputations for each whale over a 1x1 km grid, using the “BBMM” package in R
20 (Nielson et al. 2013). We then calculated an average individual UD and finally a cumulative UD per
21 study period, by summing individual UD's. The spatial overlap between herring fisheries and whale
22 movements was calculated as the percentage of the killer whale CA that overlapped with the fisheries
23 CA. In addition, we calculated percentages of fisheries catches and fishing events within the killer
24 whale CA for each study period.

25

26 *2.5 Fine-scale overlap between killer whales and fishing activity:*

27 Overlap between whale movements and fishing activity on a finer scale was quantified by combining
28 spatial overlap and temporal overlap. We calculated how many killer whale locations were within

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1 detection range of fishing activity and how many of these locations were in close proximity to fishing
2 activity. The maximum detection range was defined as 100 km. This distance is an overestimation of
3 the maximum distance at which killer whales can either detect fishing activity, or react to it. An event
4 at a distance of 100 km is unlikely to trigger an attraction response because it would take a killer
5 whale 10 hours to reach it at a maximum sustained speed of $10 \text{ km} \cdot \text{h}^{-1}$ (Williams and Noren 2009). In
6 addition, killer whales were most likely unable to detect audible cues from fishing activity at a
7 distance of 100 km. For example, Erbe (2002) found that small whale watching motorboats were only
8 audible to killer whales at distances up to 16 km. We defined ‘close proximity’ to fishing activity as
9 any location that was within 3 km of fishing activity, in order to account for the uncertainty in the
10 whale locations and because fishing events within 3 km were grouped.

11 To assess when killer whales arrived relative to the start of the fishing activity, we calculated
12 the percentage of close encounters where whales arrived after the start of the fishing activity. If killer
13 whales are attracted to fishing activity, they should not respond before the start. However, in some
14 cases, a fishing vessel might have been present at the fishing location even before the reported start of
15 the fishing activity. For example, searching time and preparations for the fishery were not included in
16 the reported fishing time. It is possible that killer whales have learnt to associate these activities with
17 an upcoming fishing activity, and they may therefore be attracted to the fishing location even before
18 the reported start of the fishery. For this reason, we performed this analysis twice; once with the
19 reported start of the fisheries and once with the reported start minus two hours.

20

21 2.6 *Whale behaviour*

22 The effect of fishing activity on whale behaviour was assessed with a hidden Markov model (HMM).
23 HMMs are discrete state-space models that can be used to identify an unknown underlying state, such
24 as a behavioural mode, based on indirect measures such as turning angle and Euclidean distance (step
25 length) between consecutive locations (Langrock et al. 2012). Whale behaviour was categorised by the
26 HMM into $N = 3$ states: “travelling” movement (state 1), “area restricted” movement (state 2), and
27 “attraction” to the nearest fishing activity (state 3). Area restricted movement was modelled as a
28 simple random walk, travelling movement as a correlated random walk with longer step lengths

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1 (relative to area restricted movements) and attraction as a biased random walk (with bias directed
 2 towards the nearest fishing activity). We used a gamma distribution to describe the step lengths and a
 3 von Mises distribution to describe the turning angles, using the distance and angle towards the nearest
 4 fishing activity as covariates on the parameters. Given the wide range of distances to fishing activity
 5 (< 1 km to 100 km), all distances were scaled by subtracting the mean and dividing by the standard
 6 deviation. The state transition probability of the underlying state process was expressed as a function
 7 of the nearest distance to a fishing vessel (x_t):

$$8 \quad \gamma_{tij} = \frac{\exp(a_{ij} + x_t \beta_{ij})}{\sum_{j=1}^N \exp(a_{ij} + x_t \beta_{ij})}, \quad \text{Equation 1}$$

9 where γ_{tij} is the transition probability from state i at time t to state j at time $t + 1$, and a_{ij} and β_{ij} are
 10 logit-scale intercept and slope parameters, respectively. This allowed us to assess the importance of
 11 the covariate on the probability of switching between states (Towner et al. 2016, Leos-Barajas et al.
 12 2017, Grecian et al. 2018). To avoid overparameterization while allowing constraints to be imposed on
 13 switches to the attraction state, we set $a_{11} = \beta_{11} = a_{22} = \beta_{22} = a_{32} = \beta_{32} = 0$ for $i = j$. State
 14 transitions to the attraction state were prohibited when there was no fishing activity or the nearest
 15 fishing activity exceeded the maximum detection range (i.e. $\gamma_{ti3} = 0$ if no fishing or $x_t > 100$ km).
 16 We similarly included linear and quadratic effects of the Euclidean distance between locations and the
 17 nearest fishing activity on the turn angle concentration parameter of the von Mises distribution for the
 18 attraction state (κ_3) in order to investigate potential distance effects on the strength of bias towards
 19 fishing activity:

$$20 \quad \kappa_3 = \exp(\alpha_0 + \beta_1 x_t + \beta_2 x_t^2). \quad \text{Equation 2}$$

21 Models were fitted by maximum likelihood using the R Package “momentuHMM” version
 22 1.5.1 (McClintock & Michelot 2020). We specified weakly informative Normal(0,100) prior
 23 constraints on a_{ij} and β_{ij} , in order to improve the numerical stability of the optimization in the event
 24 any of the state transition probability estimates fell near a boundary. Movement parameters were
 25 independently estimated for each of the 30 imputations and then pooled. We used Akaike’s
 26 Information Criterion (AIC; Burnham & Anderson 2002) to evaluate the strength of evidence for
 27 distance effects on the strength of bias across the 30 imputations. Since changing the transition

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1 probability formula would result in different prior constraints, we were not able to use AIC to compare
2 models with different structures for the state transition probabilities. For the best supported model, we
3 used global state decoding (based on the Viterbi algorithm) to infer the most likely sequence of states.
4 Stationary probabilities were used to assess overall state probabilities as a function of any covariates.
5 Goodness of fit for the best supported model was assessed by visually examining pseudo-residual
6 plots.

7 **3 Results**

8 *3.1 Tagging and fishing data:*

9 Tag retention time varied between two and 93 days (Table 1) with an average duration of 21 days
10 during study period one (sd = 14 days) and 44 days in period two (sd = 26 days). Cumulative length of
11 individual paths varied from 146 km to over 10 000 km (mean = 3 673 km \pm 2 997) accounting for a
12 mean daily distance of 105 km \pm 31 (Table 1). The time between the first and last transmission was 72
13 days for the first study period, and 167 days for the second study period. The 11 killer whales
14 instrumented during the first period accounted for a total of 5 465 hourly locations and the 14
15 instrumented animals during the second period yielded a total of 14 791 hourly locations. During
16 period one, a total of 97 952 t of herring were caught in 566 fishing activities. During period two,
17 278 735 t of herring were caught in 1 172 fishing activities. Fishery events lasted between four and 18
18 h, with a mean of 6.55 h (sd = 1.67) or 6.72 h (sd = 1.70) for the first and second study period
19 respectively. Reported single catch sizes varied between one and 2 442 t, with a median of 140 t.

20

21 *3.2 Large-scale overlap between whale distribution and fishing activity:*

22 During both periods, the main killer whale CA was located in K enangen fjord; the main tagging area.
23 In addition, smaller offshore areas were included in the northern and southern part of Norway
24 including off the M ore county where four individuals were tagged (Fig. 1 & 2). During the first and
25 second study period, 53% and 93% of the whale CAs overlapped with the fisheries respectively. In
26 these areas of overlap, 16% and 32% of the total herring catches were fished representing 30% and
27 38% of the fishing events for each period.

1

2 *3.3 Fine-scale overlap between killer whales and fishing activity:*

3 Thirty-three percent of the killer whale locations were within 100 km of active fishing events, and 8%
 4 of all whale locations were within 3 km of the nearest fishing activity (Table 1). On average,
 5 individual whales spent 36% of their time (range: 0% – 74%) within 100 km of the nearest active
 6 fishing event and 9% (range: 0% – 34%) within 3 km of fishing activity. Averaged over the 30
 7 imputations per individual, 23% (sd = 0.3%) of the fishing events that took place during the study
 8 periods were approached (3 km) by one or more killer whales. One whale never ventured within 100
 9 km of any fishery, while another did so only once (Table 1). These two animals also had the shortest
 10 tracks (45 and 80 hours). Ten killer whales spent at least 10% of their time within 3 km of the nearest
 11 fishing activity. Of all the locations within 3 km of the nearest fishing activity, only 4.4% were not in
 12 or near Kvænangen fjord.

13 In 65% (range: 61% – 68%) of the fishing events where a whale was within 3 km of a fishing
 14 activity, the whale arrived at the fishing location after the reported start of the fishery. If we accounted
 15 for the vessel searching time prior to the start of the fishery, whales were not yet present at the
 16 locations in 73% of the cases (range: 70% – 75%). Fig. 3 shows an example of killer whale movement
 17 relative to the start of a fishing event. A more extensive example is provided as an animation in the
 18 supplementary files (supplementary Fig. 1).

19

20 *3.4 Whale behaviour*

21 Based on average AIC weights across all 30 imputations (supplementary Table 1), the best supported
 22 model included linear and quadratic terms for the effect of distance to the nearest vessel on the turn
 23 angle concentration parameter for the attraction state ($\alpha_0 = 0.87$, CI = $-0.75 - 2.48$; $\beta_1 =$
 24 -3.02 , CI = $-10.42 - 4.39$; $\beta_2 = -7.26$, CI = $-14.17 - -0.34$). When the nearest fishing activity
 25 was farther away (10 – 20 km), attraction towards the fishery was more directed as the distance
 26 decreased. However, at shorter distances (<10 km) the movements became less directed (Fig. 4).
 27 Distance had a weak positive effect on the state switching probability from area restricted movement

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1 to travelling movement ($\beta_{21} = 1.39, CI = -0.86 - 3.63$), a weak negative effect on the probability of
2 switching from area restricted movement to the attraction state ($\beta_{23} = -2.15, CI = -6.16 - 1.86$)
3 and a negative effect on the probability of remaining in the attraction state ($\beta_{33} = -10.76, CI =$
4 $-21.23 - -0.30$) (supplementary Fig. 2).

5 Global state decoding by the Viterbi algorithm assigned 15% (CI = 11% - 21%) of the overall
6 1 hr time steps to the attraction state, 47% (CI = 40% - 54%) to the area restricted movement state,
7 and 37% (CI = 27% - 49%) to the travelling movement state. Between 0% and 57% of the locations
8 for individual whales were assigned to the attraction state. During periods of active fishing within a
9 100 km radius, 44% (CI = 24% - 66%) of the whale movements were assigned to the attraction state,
10 with individual percentages ranging from 0% to 79% (Table 2). Without fishing activity within a 100
11 km radius, the percentage of state assignments to travelling movement was 49% (CI = 36% - 62%)
12 and the percentage of area restricted movement was 51% (CI = 38% - 64%). When fishing activity
13 was within 100 km, the stationary probability of travelling movement appeared to increase with the
14 distance to the nearest fishing activity, while the probability of attraction appeared to decrease
15 (supplementary Fig. 3). Twenty-three of the whales were attracted $\geq 10\%$ of the time they were within
16 100 km of the nearest fishing activity and 9 whales were attracted $\geq 50\%$ (Table 2). Two whales had
17 respectively zero or one location within 100 km of the nearest fishing activity, and could therefore not
18 have been attracted to any fishing activity.

19 Plots of the pseudo-residuals indicated that the model fitted the data well (supplementary Fig. 4).

20 There appeared to be some lack of fit in the step lengths, which could be attributable to a small amount
21 of periodicity in the data and/or by unexplained variation in the step length distributions that appears
22 to be largely attributable to one or two individuals, which had relatively short or relatively long step
23 lengths compared to the overall average.

24 **4 Discussion**

25 Our results reveal a strong spatial and temporal overlap between killer whale (*Orcinus orca*)
26 distribution and herring (*Clupea harengus*) fishing activity in northern Norway during the winter. All
27 but two of the tagged whales encountered fishing activity at close proximity, primarily in Kvænangen

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1 fjord (Fig. 2). The start of fishing activity triggered a change of behaviour and killer whale movements
2 were biased towards herring purse-seiners, suggesting that killer whales were sometimes attracted to
3 fishing activity.

4 Killer whales are attracted to fisheries around the world (Luque et al. 2006, Peterson et al.
5 2013, Escalle et al. 2015, Söffker et al. 2015, Towers et al. 2019), because fishing activities offer
6 beneficial foraging opportunities (Tixier et al. 2015, Esteban et al. 2016). The fishing events in our
7 study aggregated large quantities of herring at the surface in the purse-seine nets. This allowed killer
8 whales to feed on the aggregated, stunned and disorganised herring outside of the net, or they may
9 pick individual fish through the mesh of the net. The killer whales appeared to gather around the edges
10 of the fishing net as soon as it was set, even before the herring was pumped into the vessel. They
11 stayed near the edges of the net, until the net was hauled out of the water and the last fish dispersed
12 (personal observations). Some killer whales were caught inside the nets, but most of them either
13 escaped or were released successfully by the fishers. Although deaths have occurred, no official
14 numbers have been published (Rikardsen 2019). In the absence of fishing vessels, killer whales often
15 herd the herring towards the surface into a tight ball (carousel feeding), before they immobilize
16 individual or several herring with a fluke slap (Similä & Ugarte 1993). Carousel feeding is an
17 elaborate cooperative feeding technique that comes at a relatively high energetic cost, compared to
18 feeding on discarded herring from fishing activity. Earlier studies found that in the vicinity of herring
19 fishing vessels, killer whales changed their foraging behaviour (Van Opzeeland et al. 2005) and
20 carousel feeding was observed less frequently (Kuningas et al. 2014). It is unclear to what cues killer
21 whales respond, and how they detect the fishing activity. Sperm whales appear to respond to acoustic
22 cues from long-line fishing gear (e.g. winching), or from propellor or engine sounds that indicate
23 changes in speed (Thode et al. 2007, Mathias et al. 2012). Killer whales and sperm whales can follow
24 long-line fishing vessels for hundreds of km (Towers et al. 2019), suggesting that they respond to
25 vessel specific acoustic signals. It is possible that the killer whales in Norway also respond to acoustic
26 cues from the fishing gear or fishing operation itself, such as winching, pumping, or the setting of the
27 nets.

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1 Our results show that overlap and attraction occurred primarily in and near the overwintering
2 herring in the fjords. This might be due to the fact that most of the recorded locations were inside
3 Kväenangen fjord where most of the tags were deployed. However, the core areas of the four whales
4 that were instrumented off the coast in southern Norway overlapped less with active fishing activity.
5 Whales that left the fjords also overlapped less often with fisheries, compared to when they were still
6 in the fjords. This suggests that outside of the fjord, the whales might not react as strongly to fishing
7 activity. Outside of the fjord, the herring and the fishing activities are distributed over a larger area
8 (Huse et al. 2010). Fishing activity may occur at distances too large for killer whales to either detect,
9 or respond to.

10 Herring is a keystone prey species for killer whales in Norway (Similä et al. 1996, Jourdain et
11 al. 2020). However, the importance of herring in the whales' diet varies among individuals, as some
12 animals occasionally switch to other prey species (Jourdain et al. 2020). Therefore, some individuals
13 may be less attracted to the herring overwintering grounds. In addition, inter-individual differences in
14 foraging behaviour among herring-eating killer whales may cause differences in the utilisation of
15 fisheries. Such differences in fisheries interaction has been observed in seabirds (Patrick et al. 2015).
16 In our study, some individuals did not interact with fishing activity, even though they were tagged in
17 areas with a high herring density. Perhaps these individuals were attracted to herring, but not to fishing
18 activity. Finally, there may be gender-associated differences in the attraction to fishing activity, as
19 there are gender-related differences in feeding behaviour (Baird et al. 2005). However, we observed
20 both females and males in large numbers around the fishing vessels.

21 Our hidden Markov model indicated attraction between killer whales and fisheries and an
22 effect of distance on the strength of bias towards the nearest fishing vessel. At very close range, the
23 strength of attraction tended to decrease, suggesting that the animals began to switch towards area
24 restricted movement (possibly foraging) near the fishing vessels. Another possibility for the
25 decreasing strength of attraction in close proximity to fishing events might be that the herring density
26 in the general area of the fishing event may be relatively high and therefore attractive to killer whales.
27 Area restricted movement and attraction therefore became difficult to distinguish within close range of
28 the fisheries based solely on step lengths and turn angles. Additional model structure or data streams,

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1 such as dive activity data, accelerometer data, or mandible movement (e.g. van Beest et al. 2019),
2 would likely improve the ability of our model to distinguish between possible foraging and weaker
3 attraction within close range of the fisheries. The effect of distance to the nearest vessel on the state
4 transition probabilities was subject to large uncertainties, but the transition probabilities to the
5 attraction state appeared to be negatively affected by distance. A confounding factor might have been
6 the number of co-occurring fishing activities, and the relatively close proximity between them. In our
7 model, only the nearest fishing activity was considered as a potential attractor. However, killer whales
8 could have been attracted to other fishing activities farther away. As a result, it is likely that the
9 occurrence of attraction, as identified by the HMM, is an underestimation of the real occurrence of
10 attraction. Other studies may not have had this issue (e.g. Pirotta et al. 2018), since there were fewer
11 vessels operating at the same time.

12 Interactions between killer whales and fisheries may come at a cost. For example, killer whale
13 entanglements have been reported for this area (Rikardsen 2019), although deadly entanglements are
14 considered to be rare (Reeves et al. 2017). Interaction may also lead to a predator-dependency on the
15 fishery (Tew Kai et al. 2013). In some fisheries, depredation by marine mammals results in reduced
16 revenues (Hanselman et al. 2018, Tixier et al. 2020). Killer whales that were feeding near fishing
17 vessels mostly targeted the fish outside the net (personal observations), which does not impact the
18 catch size for the fishers. The number of fishes that was taken from the nets appeared to be low and the
19 effect on the catch size may have been insignificant. Still, if a whale entered a purse-seine net, the
20 fishers had to attempt to release the whale, which would take time and could potentially mean the loss
21 of (part of) the catch.

22 Our results indicate that whales indeed benefit from feeding in close vicinity to fishing activity, which
23 suggest these activities provide a substantial resource subsidy to the whales. Resource subsidies to
24 predators can lead to an increase in the abundance of the predator, changes in the dietary preferences,
25 changes in survival, reproduction or sociality, and changes in home ranges or behaviour (Oro et al.
26 2013, Newsome et al. 2015). These changes can further affect prey or other species that interact with
27 killer whales. We have shown that killer whales are attracted to fishing activities during the
28 overwintering of the herring in the fjords. However, it is unclear if, and to what extent killer whales

1 interact with other types of fisheries, and during the rest of the year. Further research is required to
2 determine the long-term effect of the herring fishery and potential other fisheries on killer whales in
3 Norway.

4 **5 Conclusion**

5 This study provided novel insight into fine-scale interactions between killer whales and herring
6 fisheries in northern Norway. Herring forms an important part of the diet for killer whales in Norway,
7 and fishing activity provide easy foraging opportunities specifically targeted by killer whales.

8 Decreased foraging costs might decrease their overall energy budget and these foraging opportunities
9 might be important for the growth of the Norwegian killer whale population (e.g. Halpern et al. 2019).

10 Although there have been few reports of negative consequences that herring fisheries may have on
11 killer whales, it is important to consider cumulative effects from increasing anthropogenic activities, in
12 order to understand the overall impact of anthropogenic activities on killer whales in Norway.

13 Furthermore, if the interaction between whales and fishery increases and becomes a challenge for the
14 fishery, mitigation actions need to be taken to reduce the risk of negative outcomes both for the fishery
15 and whales.

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13 Studies', *Ecology*, 70(1), pp. 164–168. doi: 10.2307/1938423.

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KILLER WHALE ATTRACTION TO FISHING ACTIVITY

1 **Figures and tables**

2 *Table 1 – Detailed overview of raw killer whale data, tag performance and the reconstructed whale tracks (based on a*
 3 *correlated random walk). The last two columns represent the number of locations that are within 100 km and within 3 km of*
 4 *the nearest fishing activity.*

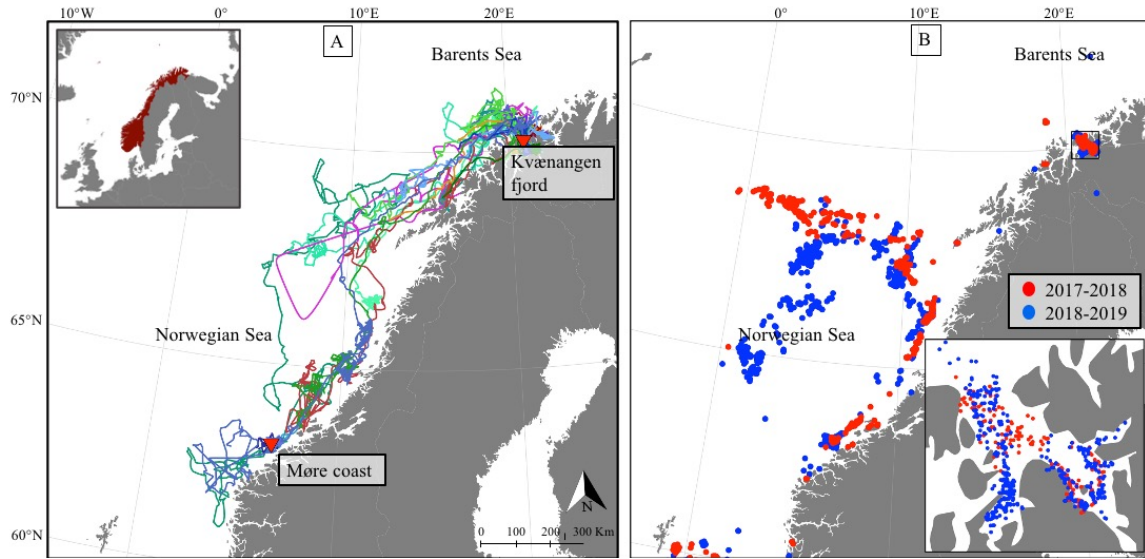
Period	Location	Raw locations				Reconstructed paths				
		Whale ID	Tagging Date	Locations	Tracking duration (days)	Average Locations per hour	Hourly locations	Cumulative distance in km	Locations < 100 km of active fisheries	Locations < 3 km of active fisheries
Period 1	Kvænangen	47572	02/12/2017	240	12	0.8	287	810	205	97
		47580	02/12/2017	1269	37	1.4	881	4129	135	54
		47590	02/12/2017	404	19	0.9	468	1364	310	135
		47592	02/12/2017	523	23	0.9	555	2596	272	90
		47594	02/12/2017	680	34	0.8	827	3013	363	60
		47582	03/12/2017	317	40	0.3	954	5023	272	77
		47581	10/01/2018	212	8	1.1	188	570	59	28
		47587	10/01/2018	542	18	1.3	431	1753	73	19
		47577	12/01/2018	811	31	1.1	751	3384	75	15
		47573	20/01/2018	24	2	0.6	44	146	0	0
		47574	20/01/2018	35	3	0.4	79	614	1	0
Period 2	Kvænangen	54013	26/10/2018	681	38	0.7	914	3176	571	145
		53561	28/10/2018	1041	53	0.8	1277	6134	566	57
		53559	06/11/2018	1112	57	0.8	1366	5180	605	141
		54011	06/11/2018	1267	64	0.8	1539	5260	687	175
		83761	13/11/2018	557	26	0.9	629	2317	465	92
		83760	16/11/2018	866	40	0.9	964	3712	462	7
		53557	04/01/2019	1615	93	0.7	2239	9698	412	147
		83764	06/01/2019	498	29	0.7	689	2742	366	111
		83756	08/01/2019	1301	64	0.8	1531	8846	339	93
		83768	23/01/2019	1358	71	0.8	1696	10262	72	8
		Møre	83755	16/02/2019	116	14	0.4	329	1291	128
	83752		17/02/2019	46	3	0.8	61	311	39	7
	83754		17/02/2019	176	12	0.6	287	1308	106	22
	179032		17/02/2019	1122	53	0.9	1270	8182	118	17

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KILLER WHALE ATTRACTION TO FISHING ACTIVITY

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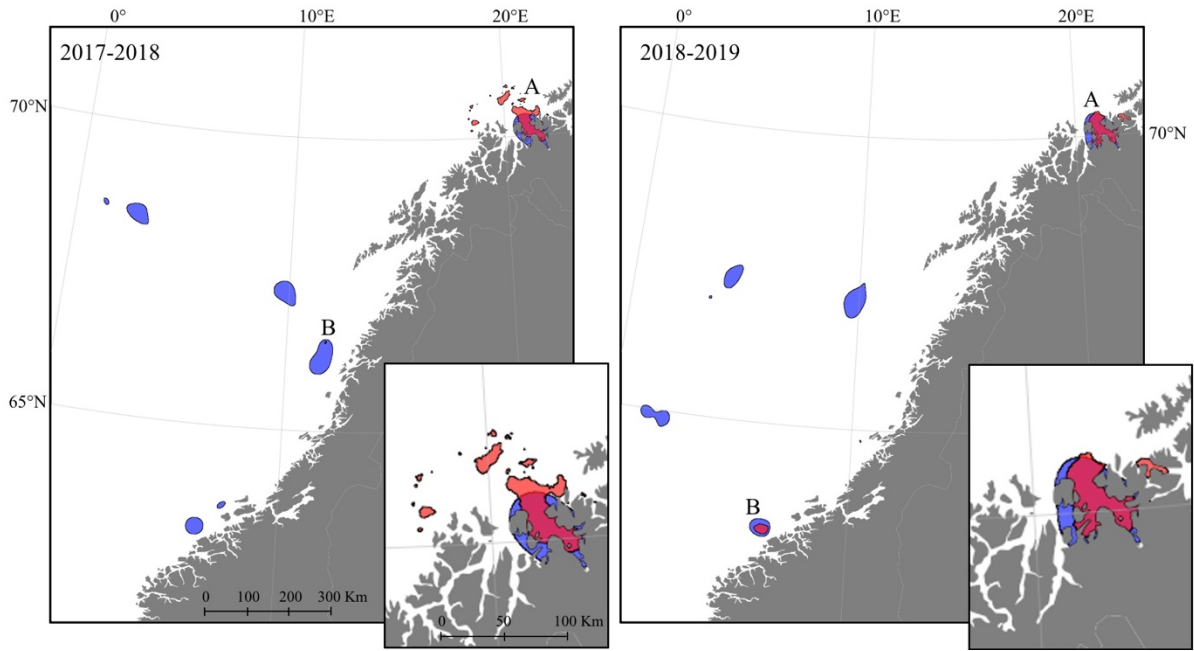
7

Figure 1 – A) Map of Northern Europe with the two tagging locations in Norway (red triangles). During the winter of 2017/2018, 11 killer whales were tagged in Kvænangen fjord. During the winter of 2018/2019, ten killer whales were tagged in Kvænangen fjord, and four whales were tagged near the coast of Møre. The inset shows Norway in a larger geographical extent. B) Herring fisheries locations in 2017/2018 and in 2018/2019, during the periods when killer whale tags were in operation. The inset shows Kvænangen fjord.

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KILLER WHALE ATTRACTION TO FISHING ACTIVITY

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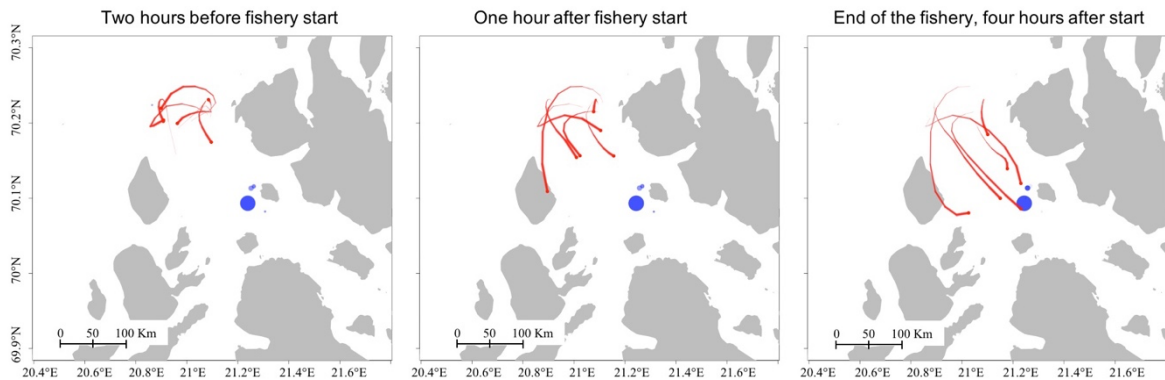
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Figure 2 – Core areas of the killer whales (red) and fishery (blue), for the first and second study period. The core areas are based on a 50% contour of the utilization distribution. The core areas that overlap with fisheries are marked with A and B. The insets show the largest killer whale core areas (A) in more detail. Note that in both study periods the core areas are located near the tagging locations.

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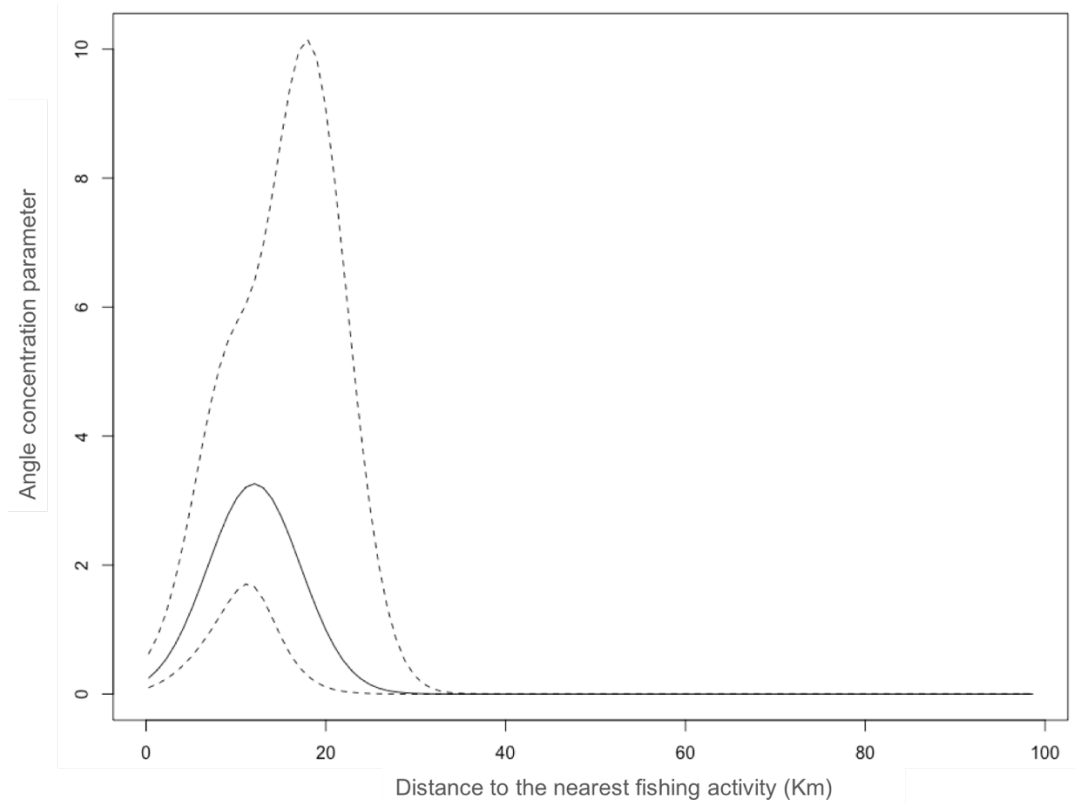
Figure 3 – An example of the attraction between killer whales (red lines) and fisheries (blue dots). The killer whale tracks are based on one imputation of a reconstructed path, and each frame represents a three-hour interval. The tail indicates the historical path of the whale and fades out after 10 hours. The fishery start-time and end-time represent the time the net is set until the time the net is retrieved. Note that there may be some fishing associated search activity prior to the reported start of the fishery.

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KILLER WHALE ATTRACTION TO FISHING ACTIVITY

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Figure 4 – The estimated effect of distance to the nearest fishing activity (in Km) on the turn angle concentration parameter of the von Mises distribution for the attraction state (κ_3). This figure shows that the strength of attraction to the nearest fishery is greatest at a distance of approximately 10 km.

KILLER WHALE ATTRACTION TO FISHING ACTIVITY

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2 *Table 2 Percentage of time steps assigned to each state, for locations that were within 100 km of the nearest fishing activity.*
 3 *The values between brackets are the standard errors of the percentages. States were assigned by global state decoding of the*
 4 *hidden Markov model. Whale “47573” did not have locations within 100 km of an active fishery.*

Animal id	Locations	Traveling movement	Area restricted movement	Attraction to the nearest Fishing activity
47572	205	0% (0%)	21% (23%)	79% (23%)
47580	135	16% (16%)	23% (19%)	61% (22%)
47590	310	0% (0%)	28% (19%)	72% (19%)
47592	272	15% (7%)	27% (21%)	58% (19%)
47594	363	14% (7%)	49% (10%)	37% (8%)
47582	272	19% (8%)	32% (15%)	50% (15%)
47581	59	0% (0%)	27% (21%)	73% (21%)
47587	73	2% (2%)	49% (12%)	49% (12%)
47577	75	11% (15%)	51% (14%)	38% (12%)
47573	0	NA	NA	NA
47574	1	100% (0%)	0% (0%)	0% (0%)
54013	571	1% (3%)	49% (13%)	50% (14%)
53561	566	50% (17%)	33% (16%)	16% (7%)
53559	605	8% (3%)	49% (12%)	44% (13%)
54011	687	3% (2%)	49% (11%)	48% (11%)
83761	465	4% (4%)	57% (8%)	39% (9%)
83760	462	10% (6%)	80% (24%)	10% (20%)
53557	412	3% (5%)	33% (20%)	64% (21%)
83764	366	4% (5%)	38% (20%)	58% (18%)
83756	339	24% (14%)	29% (15%)	47% (17%)
83768	72	68% (14%)	15% (12%)	17% (8%)
83755	128	1% (4%)	58% (12%)	41% (12%)
83752	39	85% (13%)	5% (9%)	10% (11%)
83754	106	11% (6%)	48% (15%)	42% (14%)
179032	118	88% (10%)	3% (5%)	8% (8%)
OVERALL	6701	13% (4%)	42% (11%)	44% (11%)

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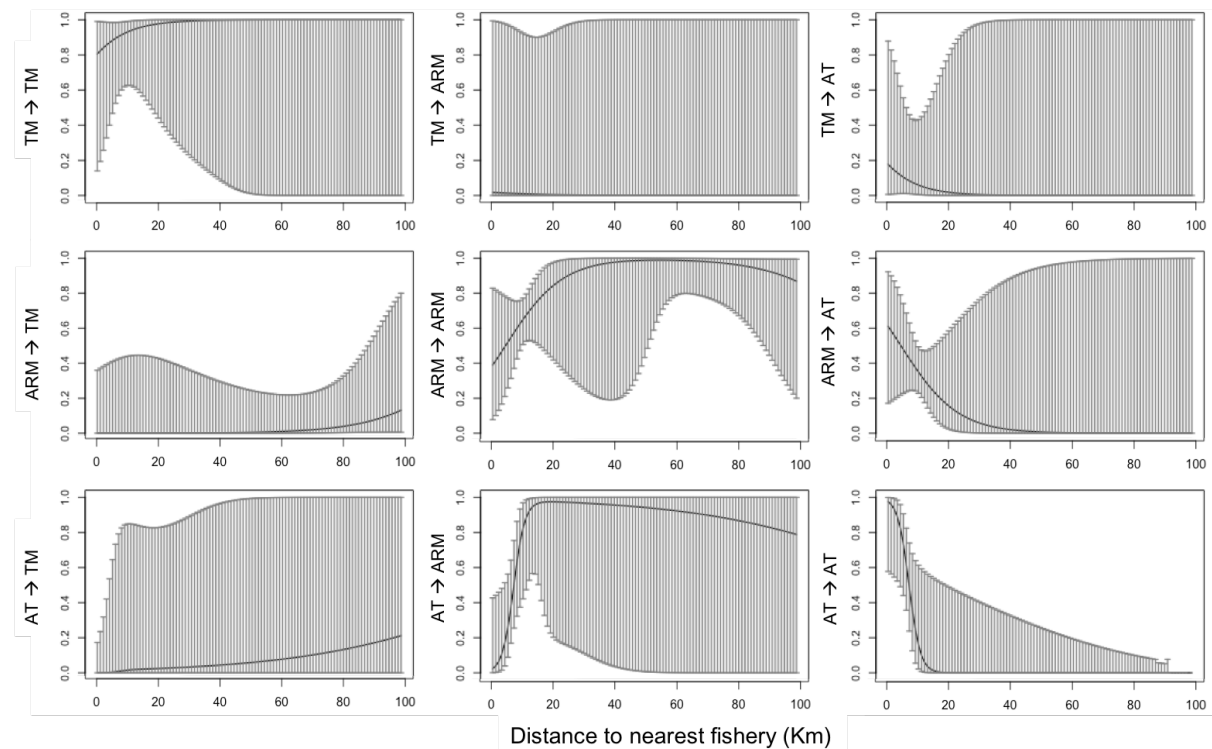
Supplementary figures and tables

Supplementary table 1 – Comparison of AIC weights between a model with and without the distance to the nearest fishing activity as a covariate on the turn angle concentration parameter for the attraction state. Comparisons are based on the mean and standard deviation of AIC weights across 30 imputations.

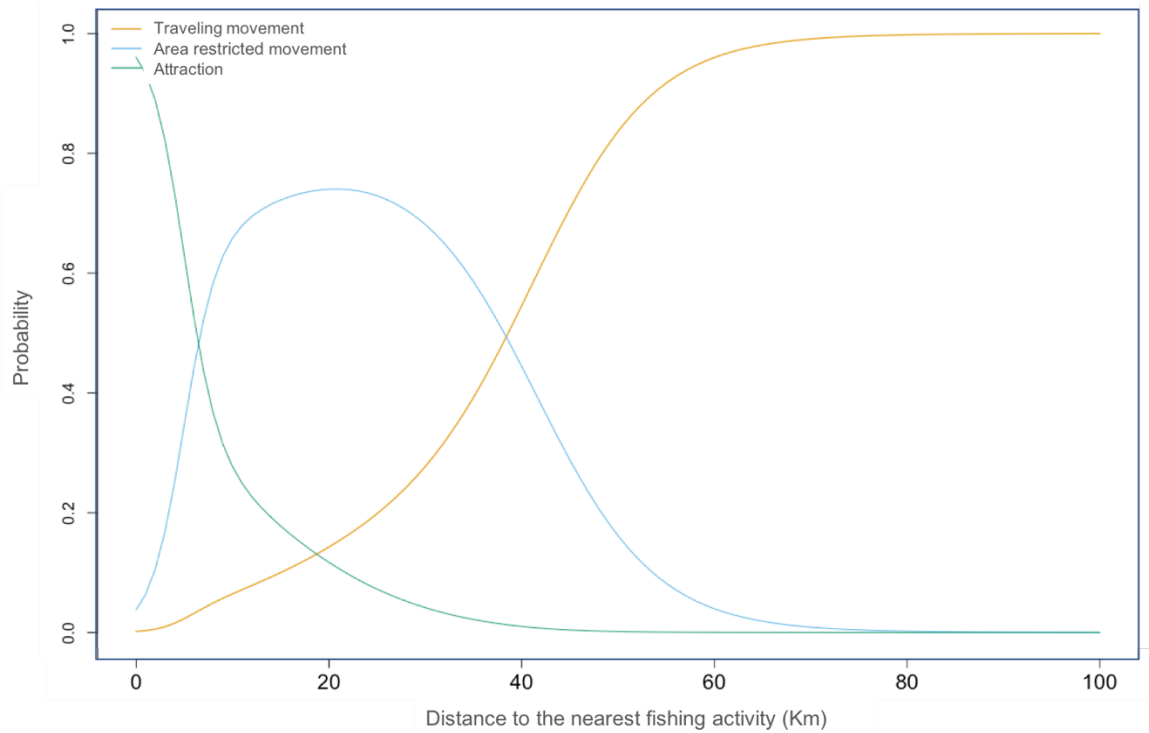
Covariate on angle concentration parameter	Weight	Sd
Distance to the nearest fishing activity	0.941	0.223
No covariate	0.059	0.223

(NB. moving image added separately)

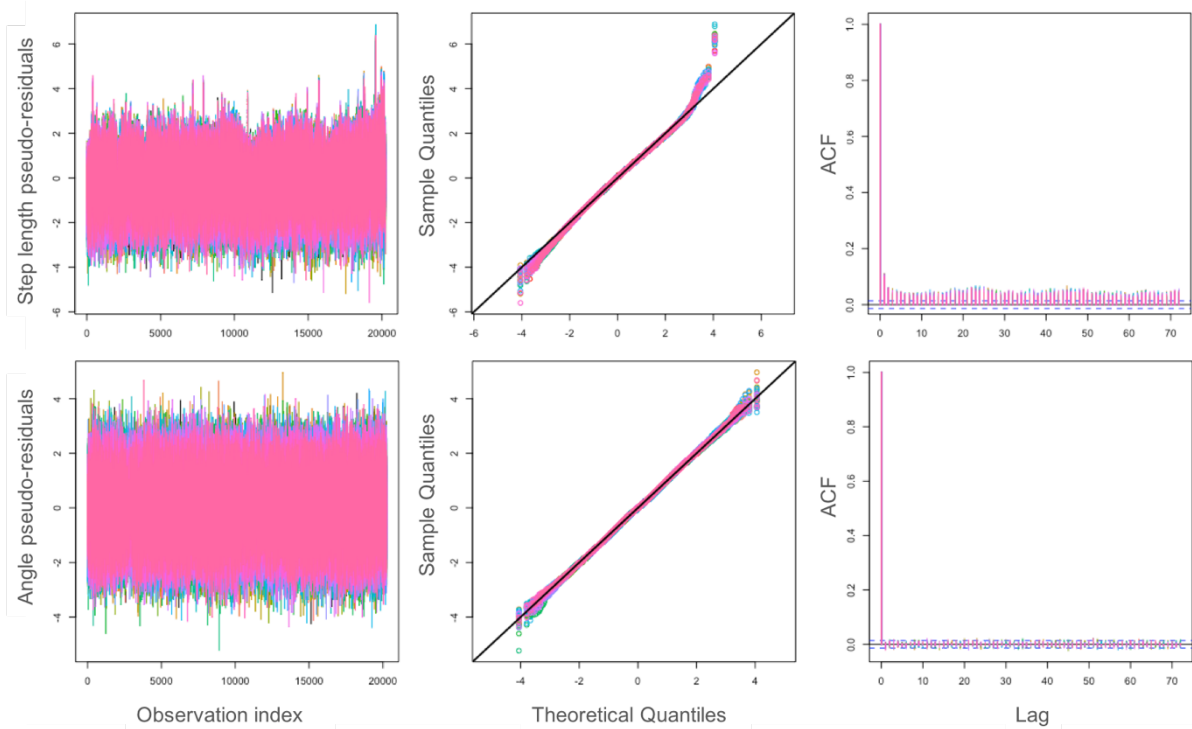
Supplementary figure 1 – Animation of one week of killer whale movement, relative to fishing activity. Killer whales are represented by red lines, while the fishing activity is represented by blue dots. Each frame represents one hour.



Supplementary figure 2 – Transition probabilities between the three behavioural states of our HMM, based on the distance to the nearest fishery. These probabilities apply to whale locations that are within 100 km of the nearest fishing activity. The three states are: Traveling movement (TM), Area restricted movement (ARM) and Attraction to the nearest fishing activity (AT).



Supplementary figure 3 – Stationary probabilities of the three behavioural states at different distances to the nearest fishing activity when a fishing activity was present with a radius of 100 km. Large confidence intervals for this figure were omitted, as the figure became unreadable.



Supplementary figure 4 – Time series, qq-plot and sample ACF plots of the pseudo-residuals for step lengths and for turning angles for each HMM fitted on 30 imputations.

Paper 3

Cumulative impact assessment for dynamic management of marine top predators

Mul, E., Hausner, V. H., Blanchet, M.-A., Biuw, M., Dietz, R., Olsen, M. T. & Rikardsen, A.

Manuscript, intended journal: Conservation Biology

1 Cumulative impact assessment for dynamic 2 management of marine top predators

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16

17 **Abstract:**

18 Cumulative impact assessments are a valuable method to evaluate the potential impact of
19 multiple anthropogenic activities on wildlife. However, current methods often insufficiently account
20 for temporal variation in the distribution of either animals or anthropogenic activities. In this study,
21 we developed a dynamic cumulative impact assessment framework that can be used to estimate the
22 impact of human activities on highly mobile top predators. We tested this framework on killer whales
23 and humpback whales in the Norwegian and Barents Seas and identified high variability in the spatial
24 distribution of cumulative impacts as a result of animal movement and seasonal variation in human

25 activities. We identified high potential impact for humpback whales during the summer in the
26 Barents Sea, and along the coast of Northern Norway for both species during the rest of the year.
27 Shipping and fishing activities had the highest potential impact weight and had the strongest
28 spatiotemporal overlap with the movement of the whales. Our results confirm the need for dynamic
29 management of human impacts on highly mobile marine top predators. We propose the
30 implementation of animal tracking data to implement time-accurate estimations of dynamic
31 cumulative impact assessments.

32

33 **Introduction**

34 The world's oceans are currently looked upon as the new economic frontiers driving the expansion of
35 both existing and new marine industries (Hodgson et al. 2019, European Commission 2020, Jouffray et al.
36 2020). This growth in the "blue economy" has been endorsed without sufficient consideration of the
37 potential threats these variety of ocean development activities poses to marine wildlife and their habitats
38 (Avila et al. 2018, Harris et al. 2018). Conservation science has to date primarily focused on singular
39 threats to species and habitats, thereby disregarding the multiple and interacting pressures that act at
40 multiple spatial and temporal scales (Holsman et al. 2017, Hodgson & Halpern 2019).

41 Cumulative impacts assessments are not consistently defined in the literature and there are no
42 agreed upon procedures for analysing the impacts of multiple human activities (Judd et al. 2015, Jones
43 2016, Murray et al. 2020). Most legal instruments recognize the need to address the impact of human
44 activities/actions in concert with past, present and foreseeable future actions that may incrementally
45 contribute to significant impacts on wildlife and ecosystems (Judd et al. 2015). The most common
46 approach for assessing cumulative impacts of multiple human activities is to I) map the density
47 distribution of each human activity, II) map the density distribution of the species, habitat or ecosystem,
48 III) identify and apply vulnerability weights predicting the potential impact of a specific human activity,
49 and IV) summarize all the singular scores into one map of cumulative impact scores (Halpern et al. 2008).

50 Spatial explicit mapping of cumulative impacts is valued for the possibility to include numerous human
51 activities and to localize risk hotspots of the threat to wildlife populations in specific locations (Avila et al.
52 2018). Such data can be used to assign conservation priorities and to establish marine protected areas
53 that preserve core habitats of marine mammals, but can fail to protect highly mobile or migrating marine
54 species. Cumulative impact assessment for highly mobile marine species is also challenging due to
55 seasonal variations in anthropogenic activities such as fisheries and shipping. Assessment of cumulative
56 impacts on highly mobile marine species therefore need to include temporal dynamics of species of
57 conservation concern and the multiple human activities that affect these species (Maxwell et al. 2015,
58 Welch et al. 2019).

59 Marine animal tracking data provides new avenues for including such temporal data into cumulative
60 impact assessments and for developing conservation tools that can effectively manage threats to mobile
61 species in space and time (Hays et al. 2019, Lennox et al. 2019). Here, we use animal tracking data to
62 investigate the cumulative impact of various human activities on humpback whales (*Megaptera*
63 *novaeangliae*) and killer whales (*Orcinus orca*). We study how cumulative impact changes depending on
64 seasonal distributions and variation in the multiple human activities in the Norwegian - and the Barents
65 Sea. While both species are highly mobile, their range and migration patterns differ. Humpback whales
66 migrate thousands of km to breed in warmer regions of the Atlantic (Stevick et al. 2003, Wenzel et al.
67 2009), while killer whales reside primarily in Norwegian waters (Jourdain et al. 2019). This study area
68 represents a sharp contrast between coastal regions with high densities of anthropogenic activities and
69 relatively pristine areas in the Barents Sea. However, as a result of the blue economy boom, human
70 activities are likely to increase in the Barents Sea, as a result of climate change, and emerging
71 opportunities in the Arctic (Lam et al. 2016, Myllylä et al. 2016).

72 In this paper, we aim to develop a cumulative impact assessment framework for dynamic
73 management of migratory species under pressure from blue growth. We implement this framework in
74 a case study on two common cetacean species from the Norwegian Sea and Barents Sea. Specifically, we
75 1) estimate the distribution of a range of static and dynamic anthropogenic activities, II) use animal
76 tracking data to estimate the distribution of two species of whales, III) allocate potential impact weights

77 to each anthropogenic activity, and IV) estimate overall cumulative dynamic impact, and how this varies
78 over time. Finally, we discuss the importance of dynamic cumulative impact assessments for marine
79 management and conservation, and the value updated information on the distribution of either whales or
80 anthropogenic activity in a cumulative impact assessment framework.

81 **Methods**

82 **Data collection:**

83 We collected data on the distribution of 24 main anthropogenic activities (Table 1) in eight
84 categories; shipping, fishery, seismic, aquaculture, oil & gas, telecommunication cables and main
85 ports. Shipping data of 13 different vessel types was obtained from the European Marine
86 Observation and Data Network (EMODnet, www.emodnet-humanactivities.eu), which is an initiative
87 from the European Commission Directorate-General for Maritime Affairs and Fisheries (DG MARE).
88 Shipping data was downloaded as vessel density maps, which are based on data from vessel
89 automatic identification system (AIS). Vessel density was calculated as the number of shipping hours
90 per month per km² (Falco et al. 2019). Shipping data was downloaded both as average per month,
91 and averaged over the entire year. We downloaded vessel density maps for the year 2018, to
92 represent yearly variation in shipping of any year. This is also the year with the most whale satellite
93 tag deployments. Most fishery data were obtained through the BarentsWatch information system
94 (www.barentswatch.no), which is an initiative by the Norwegian Ministry of Foreign Affairs and the
95 Ministry of Fisheries and Coastal Affairs and executed by the Norwegian Coastal Administration
96 (www.kystverket.no). This portal combines input from 27 Norwegian research institutes and state
97 agencies. We obtained data on passive fishing gear from this portal (gillnets, long lines and crab
98 pots), as well as data from purse seine fisheries. The Norwegian Directorate of Fisheries
99 (<https://www.fiskeridir.no>) collects electronic catch diaries from the fishing vessels, including trawler
100 vessels. We obtained these data with masked vessel identification from the Institute of Marine
101 Research (<https://www.hi.no/>). Seismic data was also obtained through the BarentsWatch portal.

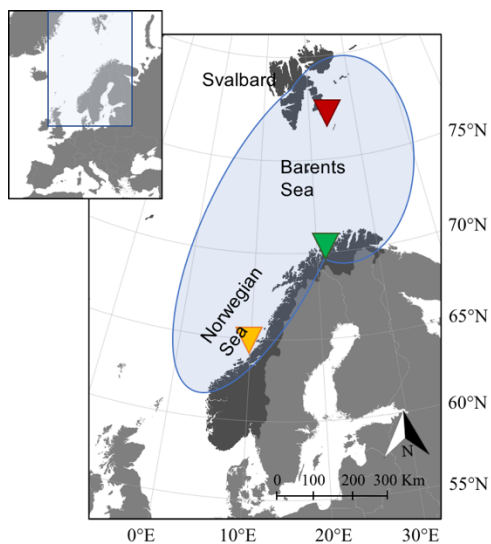
102 Locations from aquaculture facilities were downloaded from the Norwegian Directorate of Fisheries
 103 and is publicly accessible (Table 1). The Norwegian Petroleum Directorate (www.npd.no) provides
 104 open access data on the locations of oil and gas facilities and we downloaded locations of pipelines
 105 from the EMODnet portal. Finally, spatial information on telecommunication cables and main ports
 106 was also obtained through the EMODnet portal. All datasets used here are openly accessible, with
 107 the exception on the trawler fisheries dataset available upon request to, the Norwegian Directorate
 108 of Fisheries website.

109 **Table 1 - Anthropogenic activities with their sources and the assigned impact weight factor.**

	Anthropogenic activity	Sub-categories	Obtained from	Weight
1	Shipping	Cargo	EMODnet	21
2		Dredging or Underwater ops		20
3		High Speed Craft		21
4		Fishing		21
5		Military and Law Enforcement		22
6		Passenger		21
7		Pleasure Craft		19
8		Sailing		13
9		Service		19
10		Tanker		21
11		Tug and Towing		19
12		Other		20
13		Unknown		20
14	Fishery	Gillnet	BarentsWatch	21
15		Long line		16
16		Crab pots		20
17		Purse seine		17
18		Trawler		Norwegian Directorate of Fisheries
19	Seismic		BarentsWatch	19
20	Aquaculture		Norwegian Directorate of Fisheries	17
21	Oil and gas	Facility locations	Norwegian Petroleum Directorate	17
22		Pipelines		EMODnet
23	Telecommunication cables		EMODnet	18
24	Main ports		EMODnet/BarentsWatch	20

110

111 We equipped 41 killer whales and 30 humpback whales with SPOT 5, SPOT 6 or SPLASH Argos
112 satellite tags (<https://wildlifecomputers.com>). We deployed the tags using an ARTS tag applicator
113 (<https://restech.no>) with 7-10 bar pressure, from a 26 ft open RIB at distance of 5-10 m. Tagging
114 occurred at four different locations in northern Norway between 2014 and 2019. Both humpback –
115 and killer whales were tagged during the winter months near the coast of Northern Norway to feed
116 on large aggregations of overwintering Norwegian Spring Spawning (NSS) herring (*Clupea harengus*).
117 In addition, humpback whales were also tagged in the Barents Sea during the early autumn, whereas
118 killer whales were also tagged further south along the coast of Norway during the spring (Fig. 1).
119 Tagging procedures were approved by the Norwegian Food Safety Authorities (Mattilsynet, permit: FOTS-
120 ID 14135).



121
122 **Figure 1 – The three tagging locations. Both killer- and humpback whales were tagged in north Norwegian fjords during**
123 **the winter (green triangle), humpback whales were tagged east of Svalbard during the summer (red triangle) and killer**
124 **whales were tagged during the spring near the coast of western Norway (orange triangle). All tags were deployed**
125 **between 2014 and 2019.**

126 **Distributions of anthropogenic activities and whales**

127 All data preparations, analyses and calculations were performed in “R” (R Development Core
128 Team 2020). Human activity data consisted of spatial data, which was converted to spatial
129 distributions by summarizing data for individual activities over an array of 10*10 km cells. Values for

130 each separate activity were log-transformed and rescaled, using min-max normalization. All
131 anthropogenic activities were then summed to form an anthropogenic density index.

132 Whale data consisted of time-irregular Argos positioning data. For this study, we only used
133 whale data that consisted of more than 10 locations. Fewer than 10 locations indicate a problem
134 with either the placement or the functioning of the tag. Since this study is focussed on the
135 Norwegian and Barents Sea, we removed all estimated whale locations outside this region. Individual
136 whale tracks were split in two when time intervals between consecutive locations exceeded 48
137 hours. Any location estimates from before the time the tag was deployed on the whale were
138 removed. Finally, if time intervals of more than 24 hours occurred within the first five or last five
139 locations, the locations before or after the time interval were also removed. To account for the
140 uncertainty and time irregularity of the whale locations, we used a correlated random walk approach
141 in the foieGras package to filter the data (Jonsen & Patterson 2019). We used three-hour time
142 intervals between consecutive locations. The distribution of humpback whales and killer whales was
143 calculated from the filtered location data, using a Potential Path Area approach (PPA, Long & Nelson
144 2012). A PPA describes the potential area where an animal could have occurred, given a set of
145 locations, the time interval between them, and the species' maximum speed. This method calculates
146 an ellipse around each consecutive pair of locations, without specifying the probability of occurrence
147 within the ellipse. However, if a location is encompassed by more than one ellipse, one may argue
148 that the location has a higher potential of being visited by a whale than a location that was only
149 encompassed by one ellipse. Therefore, a proxy for density distribution can be calculated from PPAs,
150 by calculating the number of overlapping ellipses in each 10*10 km grid cell. The resulting whale
151 distributions were also log-transformed and rescaled.

152

153 **Dynamic distributions**

154 Based on preliminary analysis, we divided the whale data and the anthropogenic activities
155 data in four periods: Summer: July & August, Autumn: September & October, Winter: November –
156 January, and Spring: February – April. Note that these periods do not represent a full year, as no
157 whale data was obtained during the months May and June. The same separation of periods was used
158 for dynamic anthropogenic activities, such as shipping and active or passive fishing activities. Other
159 anthropogenic installations and activities, such as pipelines, oil and gas facilities, aquaculture
160 facilities, main ports and telecommunication cables were considered static and were thus not
161 separated by season.

162

163 **Potential impact weight**

164 Each activity was assigned a weight factor, which represented the potential severity of the
165 effect the activity on humpback whales or killer whales. This weight is constructed from multiple
166 scores addressing the impact of an activity on whales and is largely based on (Halpern et al. 2007),
167 who designed a ranking system that has become a standard for assessing the impact on an
168 ecosystem. We adapted this ranking system to calculate impacts specific to the two whale species
169 (Table 2). In this study, we focussed on the “normal” performance of human activities. We did not
170 include accidents or other potential impacts that can be considered rare. For example, while we did
171 include potential entanglements in fishing gear, we did not include oil spills. Entanglements can
172 occur during regular fishing operations, while oil spills should not occur during regular oil exploitation
173 operations. Similarly, collisions between vessels and whales can occur during normal operations,
174 while potential consequences of shipwrecking or other vessel-related accidents (e.g. spilling) are not
175 considered regular events. We also did not include potential effects of ghost fishing gear, because
176 discarding fishing gear is illegal, and therefore not part of “normal” operations. We evaluated all
177 potential impact of each human activity, regardless of whether this impact was adverse or beneficial
178 for the whales.

179 The potential impact of human activities was scored based on eight factors: **Severity** of the
180 impact. To what degree does an activity affect the health or behaviour of whales? The highest
181 severity means the activity result in the death of one or more animals. **Frequency**, does the activity
182 occur frequently or rarely? **Spatial scale & Temporal scale**, at what spatial scale could the activity
183 influence whales and how long is the activity present? For example, a seismic explosion is relatively
184 short, while a gillnet might be present for several days. **Functional impact**, does the activity affect a
185 single individual animal (e.g. ship strike), a group of animals (e.g. noise), or potentially all animals in
186 the region (e.g. chemical or biological structural change in the environment or ecosystem)? **Direct or**
187 **indirect**, does the activity have a direct impact on whales themselves, on their food sources, or on
188 another tropic level? This factor was adopted from Maxwell et al. (2013). **Recovery time**, how long
189 does it take for the animal to recover from the activity? **Certainty of the assessment**, how much
190 empirical data exists to support the assessment of a particular activity? All factors in the ranking
191 system are scored resulting in a potential maximum score of 32 (Table 2). The full impact weight
192 assessment of human activities is addressed in supplementary note one.

193 **Table 2 – Weight assessment table for each human activity**

FACTOR	RANK	DESCRIPTION
Severity	1	No significant change in health or behaviour
	2	Temporary behavioural change or small health impact
	3	Severe injury or long-term health impact, or long-term behavioural change
	4	Death
Frequency	1	Rare
	2	Occasional
	3	Regular
	4	Persistent/constant
Impact spatial scale	1	< 1 km ²
	2	1 – 10 km ²
	3	10 – 100 km ²
	4	100 – 1000 km ²
	5	> 1000 km ²
Impact temporal scale	1	< 1 hour
	2	1 – 6 hours
	3	6 – 24 hours
	4	1 day – 1 week
	5	> 1 week
Functional impact	1	One animal
	2	Multiple animals

Direct or indirect	3	All animals in the region
	1	Impact on trophic levels that influence the whales' prey species
	2	Impact on the whales' prey species
	3	Impact on the whales
Recovery time	1	< 1 hour
	2	1 – 24 hours
	3	1 day – 1 year
	4	> 1 year
	5	No full recover (permanent injury or death)
Certainty	1	Very little or no empirical data
	2	Some empirical work exists
	3	Extensive amount of empirical work exists

194

195

196 **Cumulative impact index**

197 A Cumulative Index of Utilization and Impact (CIU) was calculated for each period by
 198 multiplying the weighted cumulative distribution of anthropogenic activities with the distributions of
 199 humpback whales and killer whales. CIU was calculated for each 10 km². This approach is based on
 200 (Halpern et al. 2008, Maxwell et al. 2013):

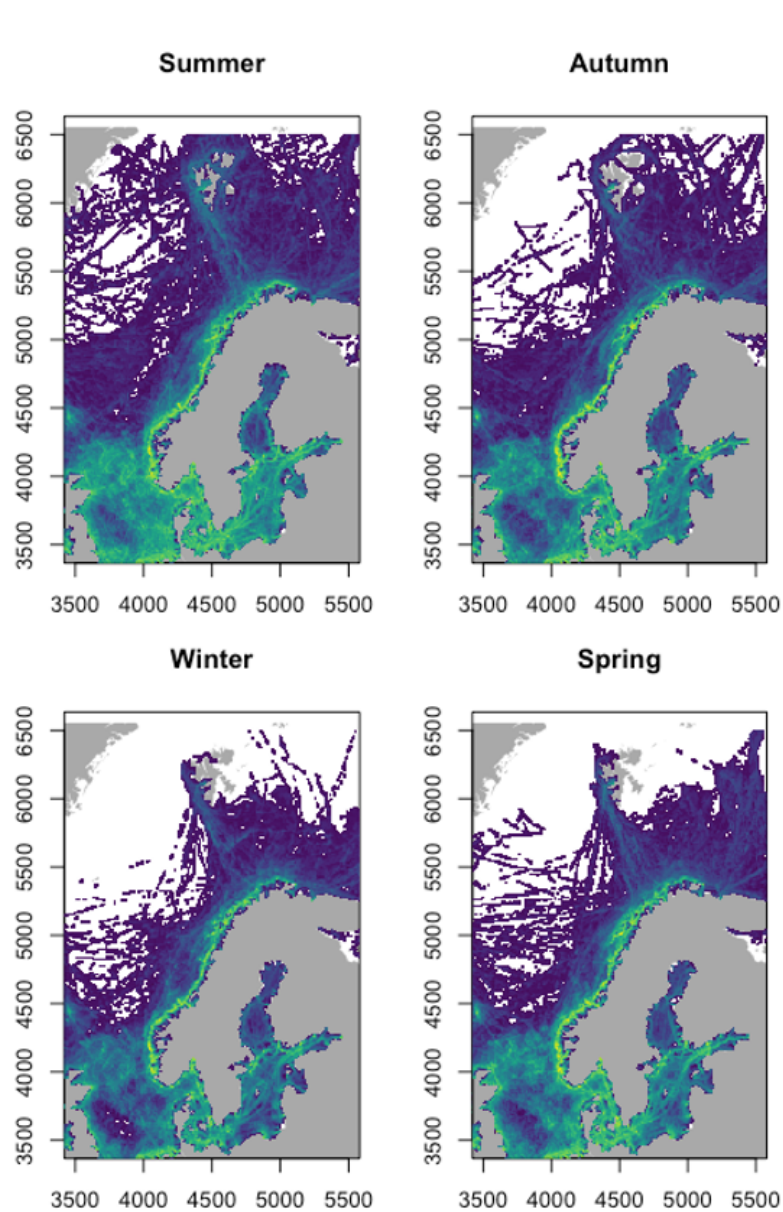
$$201 \quad CIU = \sum_{i=1}^n \sum_{j=1}^m D_i \times S_j \times u_{i,j}$$

202 Where D_i is the density of anthropogenic activity i ($n=24$), S_j is the probability of occurrence for
 203 species j ($m=2$), $u_{i,j}$ is the estimated impact weight of stressor i on species j .

204 **Results**

205 **Distribution human activities**

206 Human activities were distributed throughout the Norwegian Sea and Barents Sea. The overall
 207 density was highest along the Norwegian coast (Fig 2). There was seasonal fluctuation, as human
 208 activities were reduced during the wintertime, particularly in the Barents Sea. However, areas with
 209 the highest intensity of human activities remained relatively stable throughout the year.



210

211 **Figure 2 - Seasonal distribution of 24 anthropogenic activities combined**

212 The main human activities is shipping especially in the Barents Sea. Combined shipping activities
 213 have the highest density of the 24 human activities, as well as the widest distribution (supplementary
 214 Fig 1). Shipping activity is particularly high along the coast of Norway and between mainland Norway
 215 and the west coast of Svalbard. During the winter and spring, the shipping intensity is considerably
 216 lower in the northern part of the Barents Sea and the north western part of the Norwegian Sea,
 217 compared to the summer. Fishing activities are restricted to the Barents Sea and along the
 218 Norwegian coast, except for the summer, when fishing activities also occur further west of the coast

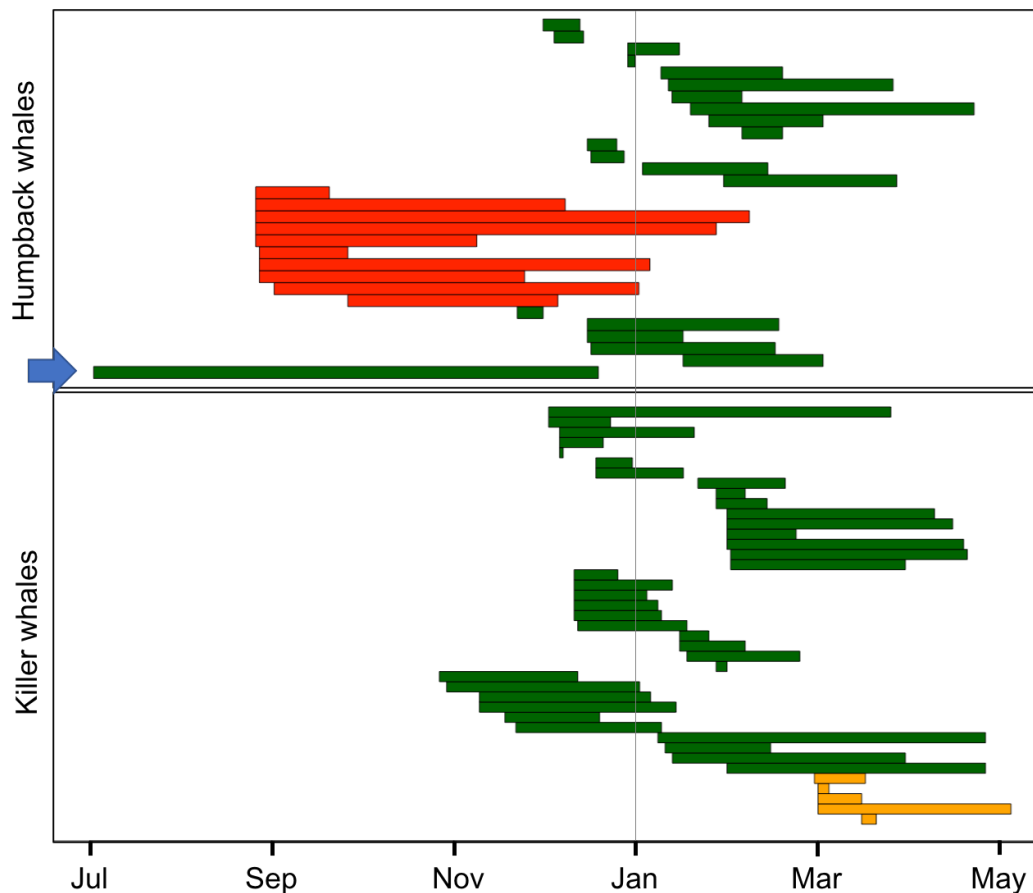
219 of Norway (supplementary Fig 2). Fishing intensity is highest in northern Norway and between
220 Norway and eastern Svalbard, in particular during the autumn and winter. During the spring, fishing
221 activities appear to be less widely spread, and primarily concentrated around the Lofoten area, to
222 the west of northern Norway. During the summer, the spread of fishing activity is highest. No seismic
223 activity was reported during the spring of the sampling year, 2018. In the Barents Sea, activity
224 primarily took place during the summer. Activity of the west coast of Norway was reported in the
225 summer, autumn and winter (supplementary Fig 3). Some seismic activity occurred just north of
226 Norway during the winter. Oil and gas facilities, cables and pipelines, main ports and aquaculture
227 were considered to be non-dynamic, and do not change throughout the year. In general, there are
228 more oil and gas facilities, cables and pipelines in the southern part of Norway, but some can be
229 found in the Barents Sea (supplementary Fig 4). Oil and gas facilities and pipelines largely coincide
230 with seismic activity. One major telecommunication cable runs through the Barents Sea, as it
231 connects Svalbard to mainland Norway. This cable overlaps with a shipping route between mainland
232 Norway and Svalbard. Aquaculture and main ports appear to be relatively equally distributed along
233 the Norwegian coast.

234

235 **Seasonal whale distribution**

236 The dataset that was used in this study consisted of 30 humpback whale tracks and 41 killer
237 whale tracks. The reconstructed paths, regularized at three-hour time intervals consisted of 12 242
238 humpback whale locations, and 11 483 killer whale locations. Whale locations in Norwegian waters
239 (after filtering) occurred between July and April. In the remaining months (May and June), some
240 humpback whale tags were transmitting, but the whales had left the Norwegian and Barents Sea. No
241 killer whale tags lasted past April. Most humpback whale locations occurred between September and
242 January, with a slight peak in January (Fig 3). Killer whale locations occurred primarily between
243 November and March, with a peak in December. Note that this distribution of location estimates is

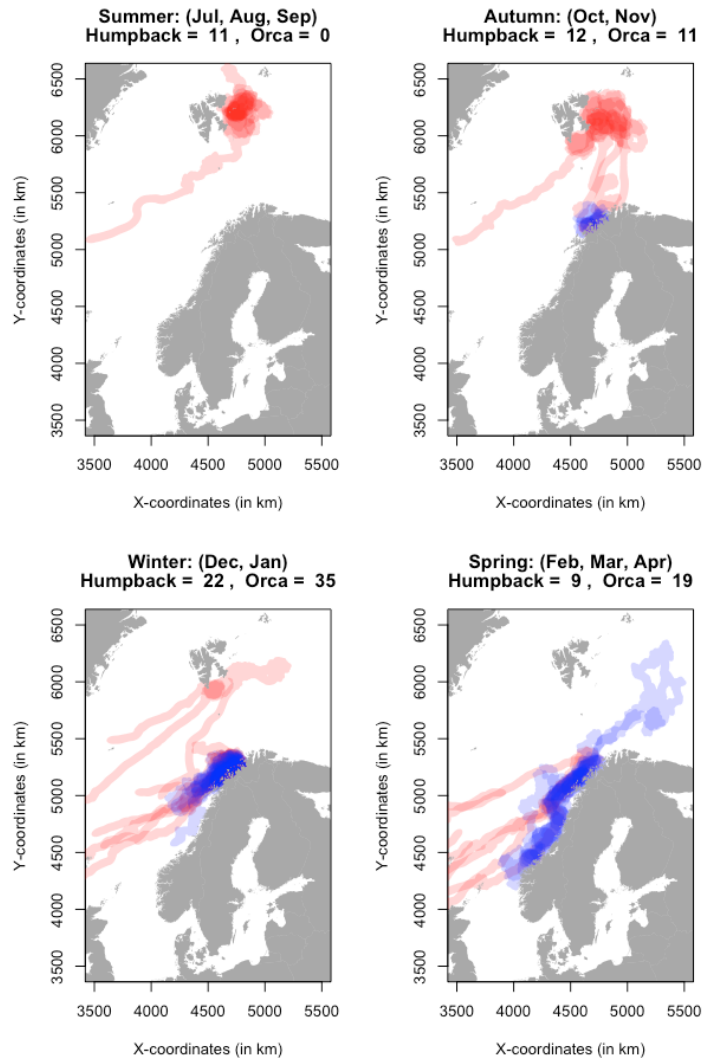
244 related to the tagging periods for both species, and not necessarily to the occurrence of these
 245 species in Norwegian waters. The humpback whale data for July comes from a single animal that re-
 246 entered Norwegian waters in July.



247
 248 **Figure 3 – Tagging periods and retention time of the Argos satellite tags. The colors represent the tagging locations:**
 249 **Green = North Norwegian coast and fjords (herring overwintering areas), Red = Northern Barents Sea, Orange =**
 250 **Northwest coast of Norway (herring spawning grounds). The humpback whale that is marked with a blue arrow was**
 251 **tagged the year before and returned to Norwegian waters after a migration to the Caribbean in July. Some of the**
 252 **humpback whale tags are cut off when the whales left Norwegian waters. The tags were deployed between 2014-2019,**
 253 **primarily during the winter.**

254 The distribution of both whale species changes drastically throughout the year. Humpback
 255 whale density appears to be highest in the Barents Sea during Summer and Autumn, and near the
 256 coast of northern Norway during the winter (Fig 4). During the Summer, one animal that was tagged
 257 one-year prior returned to the Barents Sea after passing Iceland. In the Autumn, the first animal

258 started its migration in the opposite direction, followed by others in the Winter. However, most of
259 the tagged individuals did not migrate directly from the Barents Sea to the breeding areas, instead,
260 they first travelled to the coast of northern Norway to prey on herring during the Winter. The last
261 remaining humpback whales in this study left Norwegian waters during the Spring. The killer whales
262 generally were closer to the coast of mainland Norway. They are spread out during the spring along
263 the entire northern Norwegian coast. No killer whale locations were collected during the summer.
264 During the spring, the killer whale distribution is widely spread, with some animals venturing far into
265 the Barents Sea, while the rest of the population is spread along the coast of Norway.

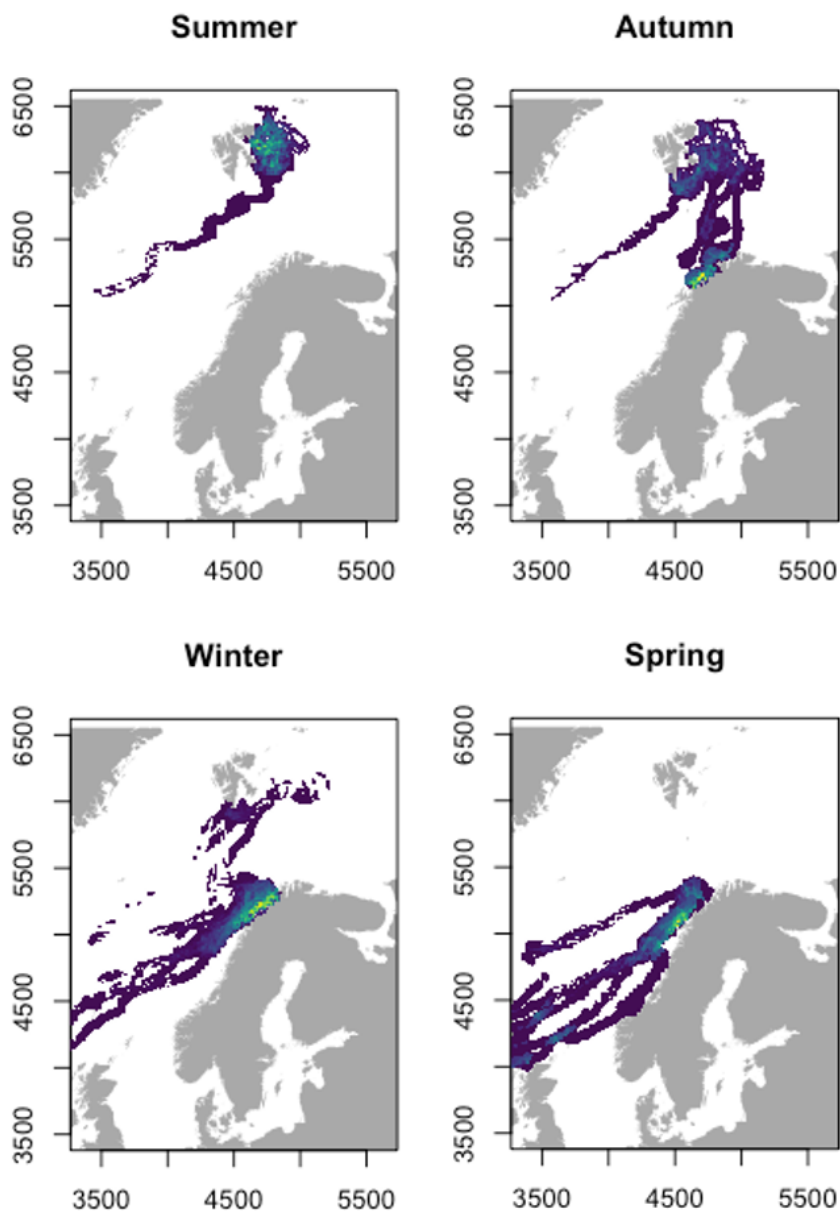


266

267 **Figure 4 - Seasonal distribution of 30 humpback whales (red) and 41 killer whales (blue), based on the animals that were**
 268 **tagged for this study between 2014 and 2019. The number of tagged individual animals is reported for each panel. The**
 269 **animals were tagged between the Summer and the Spring.**

270 **Cumulative impact index**

271 The potential cumulative impact differs substantially between the four seasons. In general,
 272 the highest cumulative impact occurs in coastal areas, but it is subject to great seasonal variation.
 273 During the summer, overlap solely takes place east of Svalbard, since no animals were tracked near
 274 the coast of Norway during this time (Fig. 5).



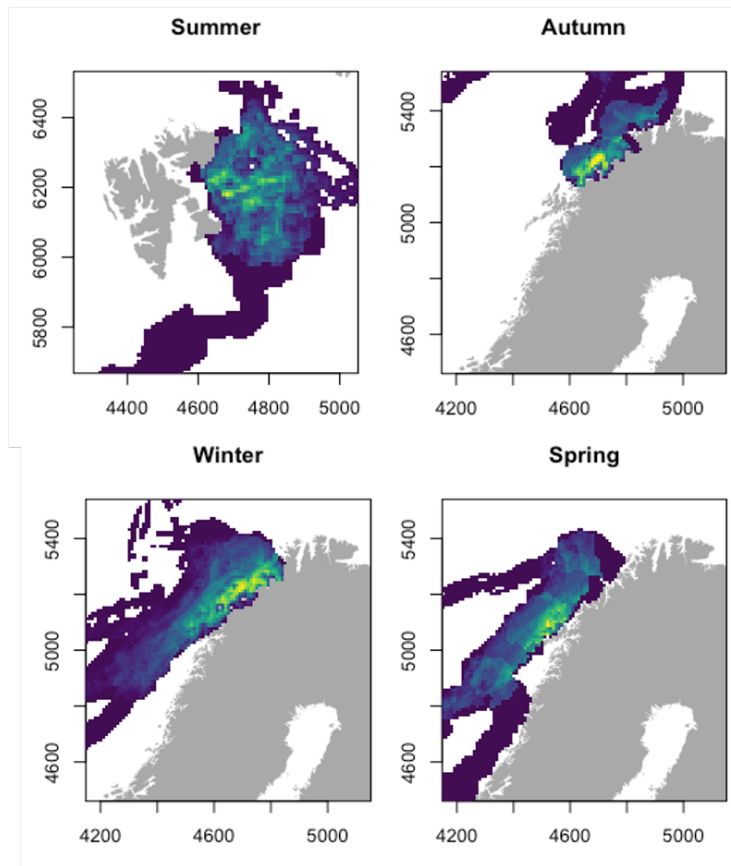
275

276 **Figure 5 – Seasonal cumulative impact index for all anthropogenic activity and 41 killer whales and 30 humpback whales**
 277 **combined for the period between 2014 and 2019.**

278 Based on the cumulative intensity of all human activities combined (Fig. 2), the intensity of
 279 human activities in this area is relatively low, compared to the intensity along the coast of Norway.
 280 However, the activities that do occur in this area have the highest impact weights (Table 1). The
 281 overlap during the summer describes the overlap between foraging humpback whales and shipping
 282 or fishing activities. During the autumn the humpback whales that leave for the breeding areas in

283 warmer regions of the Atlantic encounter only low intensities of shipping, although they have to pass
284 the relatively intense shipping lane and the telecommunication cable to Svalbard. However, the
285 humpback whales that move towards the coast of Northern Norway are confronted with a much
286 higher intensity of shipping, fishing, oil and gas operations, as well as with ports and aquaculture
287 facilities. At this point in the spring, the cumulative impact is much higher near the coast of northern
288 Norway, compared to the eastern part of Svalbard. Killer whales are confronted with the same
289 intensity of human activities. During the winter and the spring, we see a shift from north to south-
290 west. Humpback whales are leaving Norwegian waters, but they pass high intensity areas near the
291 north-western coast of Norway (Fig 6). Many of the humpback whales move southwards along the
292 coast of Norway, where the potential for human impact is high. Killer whales appear to be more
293 concentrated, compared to the humpback whales during the autumn and the winter as they are
294 tightly associated with the herring concentrations during this period. They also encounter high
295 concentrations of human activities along the coast of Norway (Fig 6). With the exception of the
296 spring, killer whales appear to favour the coastal regions over the open ocean, despite the high
297 concentrations of human activities. However, it is unknown how they are distributed during the
298 summer, when the herring is dispersed over the Norwegian and Barents Sea. Areas of concern
299 include the northern part of the Barents Sea during summer, the region between the northern
300 Barents Sea and northern Norway, and a dynamic region along the coast of north and north-western
301 Norway. This dynamic region is centred around the northern tip of Norway during the autumn and
302 the winter, and is shifted to the north-western coast of Norway during the spring.

303



304

305 **Figure 6 – Close up of the seasonal cumulative impact index for all anthropogenic activity and killer whales and**
 306 **humpback whales combined.**

307 **Discussion**

308 We developed a cumulative impact assessment framework that can be used for highly
 309 mobile top predators under pressure from multiple human activities. We applied the framework on
 310 killer whales and humpback whales, and found the spatial distribution of cumulative impacts to differ
 311 considerably with respect to season and species. Our results confirm the need for dynamic
 312 management of threats to these species taking into account the shifts in temporal distribution of
 313 large migratory species. Humpback whales represent migratory predators, while killer whales
 314 represent relatively stationary predators. The study area highlights the contrast between a heavily
 315 used coastal region and a relatively pristine environment in the Barents Sea. Anthropogenic activities
 316 overlap with the whales' distribution all-year round but is subject to seasonal and spatial variability.
 317 We identified high potential impact for humpback whales during the summer in the Barents Sea, and

318 along the coast of Northern Norway for both species during the rest of the year. Shipping and fishing
319 activities had the highest potential impact weight and had the strongest spatiotemporal overlap with
320 the movement of the whales.

321 Cumulative impact assessment provides managers and policymakers with essential
322 information regarding the most urgent pressures for wildlife and ecosystems, and on which areas to
323 focus conservations measures (Halpern et al. 2015). However, most marine management approaches
324 focus on stationary areas (Maxwell et al. 2015), which might not be efficient for highly mobile marine
325 top predators. Managerial or conservation actions can be tailored to better fit the dynamic
326 distribution of these animals, by implementing a time component (Siders et al. 2016). For example,
327 dynamic fishery closure areas can be smaller than conventional closure areas (Lewison et al. 2015,
328 Hazen et al. 2018). We have adapted the cumulative impact assessment framework by using animal
329 tracking data to inform the variable animal distribution. Animal tracking data has been recognised as
330 a valuable tool in the management of marine activities (Hays et al. 2019, Lennox et al. 2019), since it
331 provides information about changes in animal distribution over time. Combined with seasonal
332 information on the distribution of human activities, this provides a highly accurate cumulative impact
333 assessment over a specific period of time. A sufficient amount of animal tracking data can be used to
334 parameterise a dynamic cumulative impact assessment, which can be updated with additional animal
335 tracking data. Continuously or regularly adding new whale tracking data and human activity data will
336 generate an impact assessment that can be used to identify high-risk areas in near real-time (Halpern
337 et al. 2015, Sequeira et al. 2019). Cumulative impact assessments require knowledge on the
338 distribution of human activities. Distributions of static activities, such as oil facilities, pipelines, main
339 ports can directly be included in a dynamic cumulative impact assessment. However, distributions of
340 dynamic activities, such as fishery, shipping or seismic should be matched temporally with the animal
341 tracking data, in order to identify accurate overlap.

342 The cumulative impact assessment for whales in Norwegian waters demonstrated a large
343 variety in the distribution of whales and high-impact areas. The movements of humpback whales and
344 killer whales in our data are in line with general movement patterns described in previous studies.
345 Between the autumn and the spring, the killer whale distribution is primarily coastal, as they are
346 highly associated with the herring migration (Similä et al. 1996, Huse et al. 2010, Kuningas et al.
347 2014). Humpback whales cross through the Barents Sea during the spring and autumn, as part of
348 their migration to and from breeding areas (Stevick et al. 2003, 2018, Wenzel et al. 2009, Nøttestad
349 et al. 2015). They frequent the coast of Norway during the winter in pursuit of herring. As a result,
350 one area along the coast of northern Norway in the winter and spring was identified as a high-impact
351 area for both humpback and killer whales, despite the stark contrast in their migration patterns.
352 Therefore, any management or conservation actions for this region during this time could benefit
353 both species. The temporal component in our cumulative impact assessment clearly shows how the
354 area of high impact moves southwards between the autumn and spring. Another high-impact area
355 can be identified east of Svalbard in the Barents Sea, which is only relevant during the summer.
356 Management actions in this region should therefore be limited to the summer. The main activities in
357 this area consist of fishery and shipping activities, while the high-impact area in the other seasons
358 includes almost all of the human activities included in this study. Therefore, seasonal management
359 actions during the summer can be tailored specifically to fishing and shipping actions. Examples
360 might include dynamic fishing closures or vessel speed reductions (Hays et al. 2019). Due to their
361 long-range migration, humpback whales are not only affected by human activities in Norwegian
362 waters, but they are also affected by activities along their migration route, or in their breeding areas.
363 Therefore, cumulative impact assessments in one area might need to be performed in tandem to
364 identify potential impacts in both areas. The distribution of human activities is based on a single year,
365 2018, because this year overlaps with the majority of the active whale transmitters. There might be
366 inter-annual variation in the distribution of these activities, but for most activities we argue that the
367 variation is small.

368 **Conclusion**

369 Conservation and marine management for many marine top predators can be difficult, due
370 to the large temporal variation in their distribution. Animal tracking data can be used to identify this
371 variation. Incorporating animal tracking data in cumulative impact assessments can help to ensure
372 efficient and accurate identification of seasonal areas of high impact. It can also identify high-
373 impacting anthropogenic activities throughout the year. Therefore, we conclude that dynamic
374 cumulative impact assessments can be a valuable tool of dynamic ocean management and
375 conservation focussing on highly mobile marine top predators.

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487

Supplementary note

Impact weights

Shipping

Whales are impacted by human activities in various ways, depending on the type of activity. Possibly the most severe threat of shipping activity to humpback whales is collision (Neilson *et al.*, 2012; Guzman *et al.*, 2013; García-Cegarra *et al.*, 2019; Aschettino *et al.*, 2020), often with lethal consequences. Although vessel collisions with killer whales have also been described (Van Waerebeek *et al.*, 2007), vessel noise may pose a more eminent threat for killer whales. High levels of vessel noise potentially mask killer whale communication (Erbe, 2002; Lusseau *et al.*, 2009; Williams *et al.*, 2014; Veirs *et al.*, 2016; Cominelli *et al.*, 2018). Vessel noise may also affect humpback whale communication (Blair *et al.*, 2016; Dunlop, 2016; Frankel *et al.*, 2017; Tsujii *et al.*, 2018). The risk of vessel collision is related to vessel tonnage and vessel speed (Guzman *et al.*, 2013), although small vessels can also have a high collision rate in some areas (Neilson *et al.*, 2012). Therefore, cargo vessels, passenger vessels, tankers and high-speed vessels are therefore assigned to high impact weight factor, due to the relatively high risk of collision. Vessel noise can affect whales in a number of ways. For example, killer whales may avoid areas with high vessel traffic (Williams *et al.*, 2014), or they may need to increase the volume of their calls (Holt *et al.*, 2009). Similarly, humpback whales may temporarily cease vocalizations, as large passenger vessels pass by (Tsujii *et al.*, 2018). Behavioral reactions to vessel noise are likely to affect the animals energy budget (Lusseau *et al.*, 2009; Blair *et al.*, 2016). In extreme situations, animals may suffer from temporary or permanent reduction of hearing sensitivity, injury, or even death (Simmonds *et al.*, 2014). A special case of noise pollution might be presented by military vessels and military operations. Naval sonar and other military operations can have severe effects on the behavior or the wellbeing of many cetaceans (Parsons *et al.*, 2000; Kuningas *et al.*, 2013). Military activity at sea has been linked to abrupt changes in the dive behavior of killer whales and other cetaceans (Sivle *et al.*, 2012), but also to animal strandings (Reynolds, 2008). Fishing vessels may abandon, lose or discard fishing gear, in which case it forms a long-term risk to many marine organisms, including whales (Gilman, 2015; Stelfox *et al.*, 2016). Ghost fishing occurs in all the world's oceans, including in Norwegian waters (Humborstad *et al.*, 2003). We therefore included this threat as a weight factor for fishing vessels. Dredging activities can also affect marine mammals, although direct effects are not considered dramatic (Todd *et al.*, 2015). Instead, dredging might affect benthic organisms and potentially other lower tropic levels.

Fishery

Entanglement might be the primary threat related to fishing activity. More than half of the humpback whales in the Gulf of Maine, and almost half of the humpbacks studied near Iceland showed signs of entanglement in fishing gears (Johnson *et al.*, 2005; Basran, 2014). Gillnets and (crab) pots appear to be most common fishing gear involved in entanglements (Ryan *et al.*, no date; Johnson *et al.*, 2005; Reeves *et al.*, 2013), although entanglements involving hook-and-line gear and seine nets are also mentioned (Basran, 2014; Rikardsen, 2019). Killer whales are less often involved in entanglements, but it does occur (Reeves *et al.*, 2013; Jourdain *et al.*, 2019). Risk of entanglement, vessel collision and other negative effects of fishing-associated activities are further stimulated by the notion that killer whales, and humpback whales to a lesser extent, are attracted to fishing activity (Similä, 2005; Luque *et al.*, 2006; Peterson *et al.*, 2013; Escalle *et al.*, 2015; Söffker *et al.*, 2015).

Seismic activity

Seismic activity can dramatically influence the behaviour of marine mammals including humpback whales and killer whales (McCauley *et al.*, 2000; Stone *et al.*, 2006; Weir, 2008; Dunlop *et al.*, 2017). Although strandings have been attributed to seismic surveys (Engel *et al.*, 2003), spatial displacement, increased breathing rate and interrupted vocalizations are the most commonly reported (Gordon *et al.*, 2003; Stone *et al.*, 2006; Dunlop *et al.*, 2017). Seismic activity can affect whale behaviour at distances of more than 10 km (McCauley *et al.*, 2000), or even more (Gordon *et al.*, 2003). Compared to smaller odontocetes, the response of killer whales and humpback whales to seismic surveys may be more localized (Stone *et al.*, 2006). The main threat from seismic activity comes from the use of air guns, which produce noise between 1 and 100 Hz of 205-255 dB re. 1 μ Pa at 1 m (Hückstädt *et al.*, 2020). This study indicated that seismic activity is likely to affect the behaviour of humpback whales and other baleen whales, although the nature of behavioural responses is not yet determined (Hückstädt *et al.*, 2020). The behaviour of male fin whales (*Balaenoptera physalus*) was drastically impacted by a seismic survey, in that they stopped vocalisations (Weilgart, 2013). This is likely to affect the reproduction of this population, at least temporarily. Similar effects can be expected for humpback whales.

Aquaculture

Aquaculture facilities pose threats to cetaceans and other wildlife, for example in the form of entanglement, litter ingestion, and noise or chemical pollution (Baker, 2005). In addition, shipping activities that are associated with aquaculture facilities increase the pressure on wildlife, particularly in the areas between the aquaculture and ports (Baker, 2005). Some facilities use acoustic harassment devices (ADH) to prevent marine mammal predation (Milewski, 2000). As a result of these devices, local numbers of killer whales were reduced near a salmon farm in Canada, and killer whale appeared to avoid the area in general (Milewski, 2000). The same study suggested high noise levels might impact humpback whales and other baleen whales, although this was not tested. Entanglements of baleen whales have been reported for shellfish farms (Young, 2015), and may also be relevant for other types of aquaculture. Similar to fishery, aquaculture facilities might attract cetaceans, which increases exposure to the previously mentioned threats (Callier *et al.*, 2018). In Norway, humpback whales can become entrapped inside the salmon farms (Fiskeridirektoratet, 2019), although little is known about the frequency of these encounters. In general, not much is known about cetacean interactions with, and responses to aquaculture.

Stationary facilities

We address oil and gas facilities, pipes and telecommunication in one section, since literature on the effects of these activities is scarce. It is well known that oil spills have a large negative impact, not only on whales, but on the entire food web on which whales rely (Matkin *et al.*, 2008; Jarvela Rosenberger *et al.*, 2017; Takeshita *et al.*, 2017). However, these extreme events were not incorporated in this study. Impacted water quality, pollution and generated noise by oil and gas facilities have been identified as common threats to marine mammals (Burek *et al.*, 2008; Chou *et al.*, 2020). Spatial overlap between whales and oil & gas facilities have been reported for other areas (Rosenbaum *et al.*, 2014), and is likely to also affect cetaceans in the Norwegian and Barents Sea. Risk of entanglement in

Telecommunication cables appears to be low (Wood *et al.*, 2008), although it has been reported in Norway at least once (Rikardsen, 2019). Other potential influences of telecommunication and power cables include: heat and electromagnetic field emissions (Taormina *et al.*, 2018). Other effects might be associated with the commissioning of these cables, but we regard these events as a separate human activity. Potential influences on the communication of marine mammals are still unknown (Jurdana *et al.*, 2014).

Main ports

Although no literature was found that explicitly addressed the impact of main ports on marine mammals, it is likely that much of the impacts that are mentioned for the other human activities also apply for the areas near main ports. Especially the exposure to noise, chemical pollution, potential for ship strikes and entanglement are high in these areas. In Norway, both humpback whales and killer whales have been observed near, or inside harbours, particularly during overwintering herring aggregations in fjords with adjacent ports (Rikardsen, 2019).

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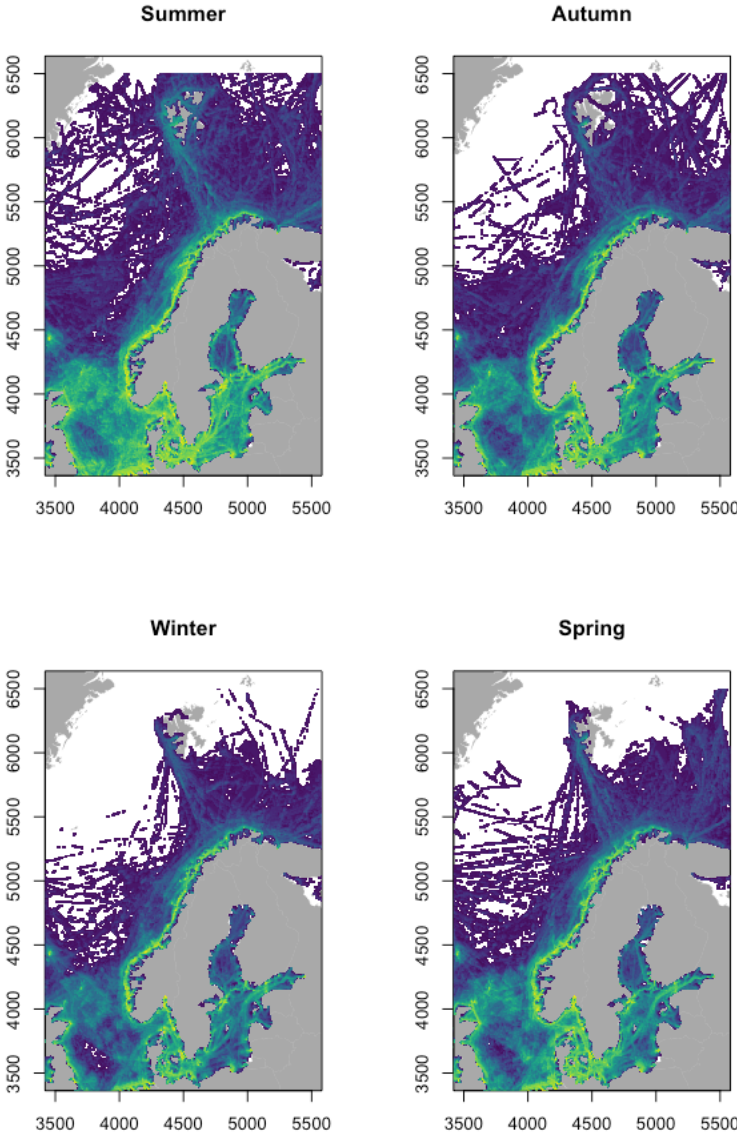
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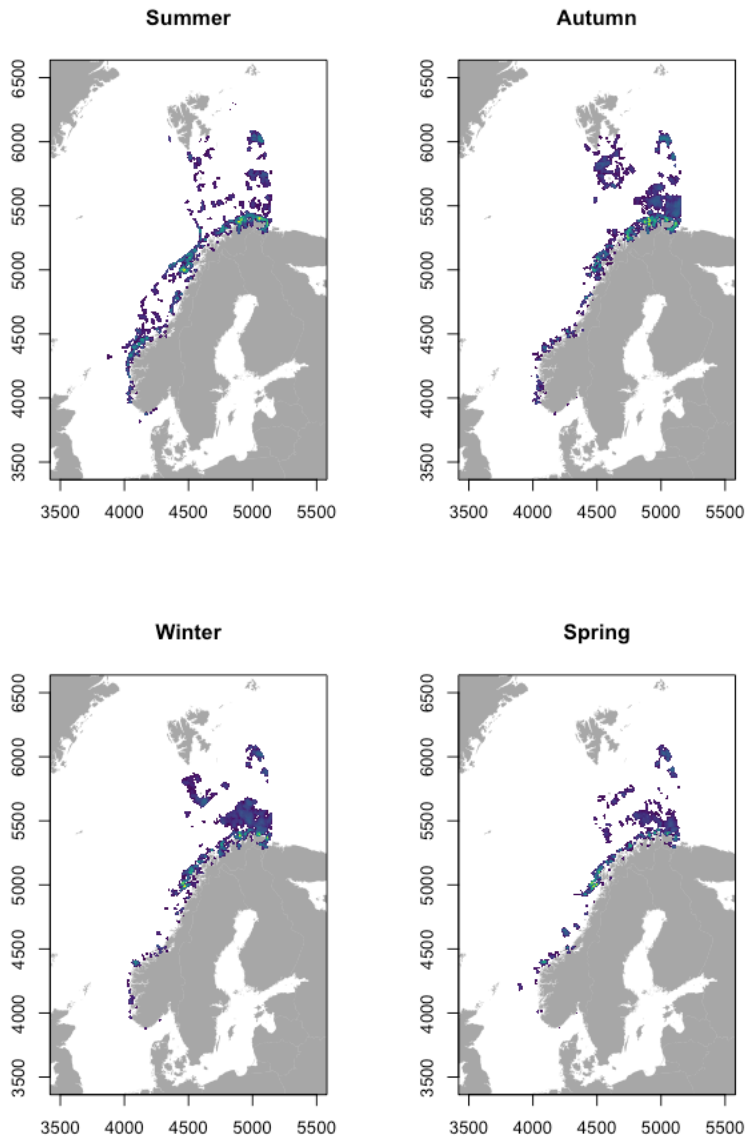
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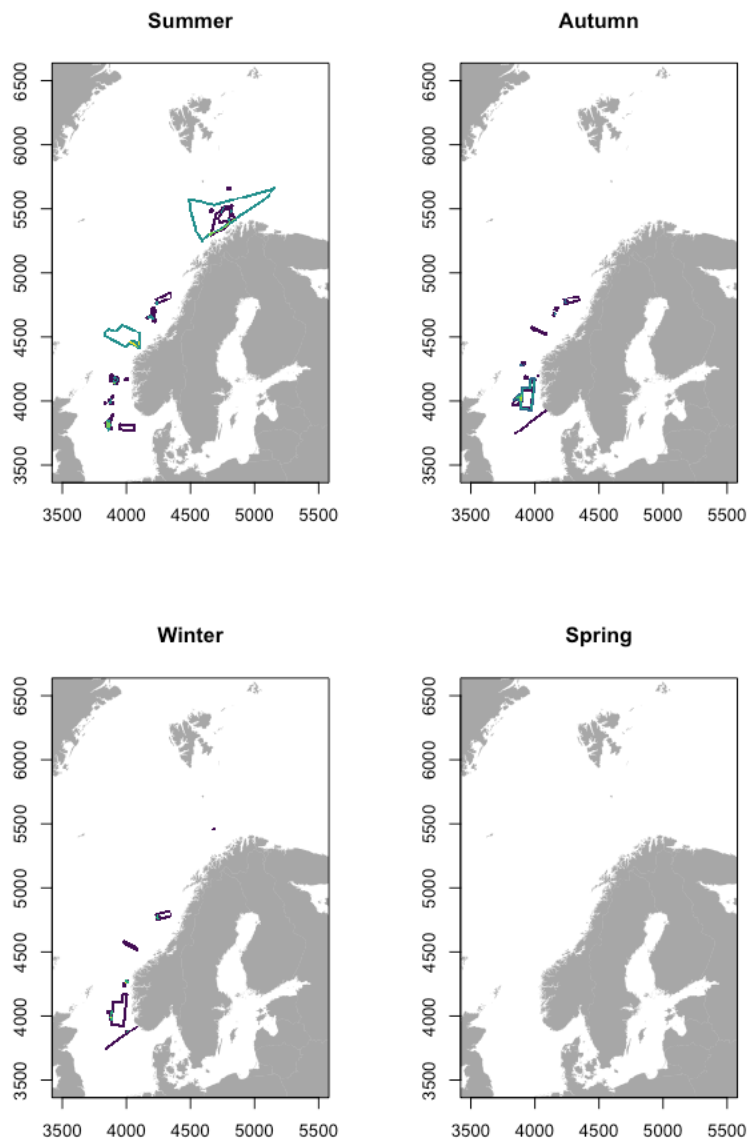
Supplementary figures



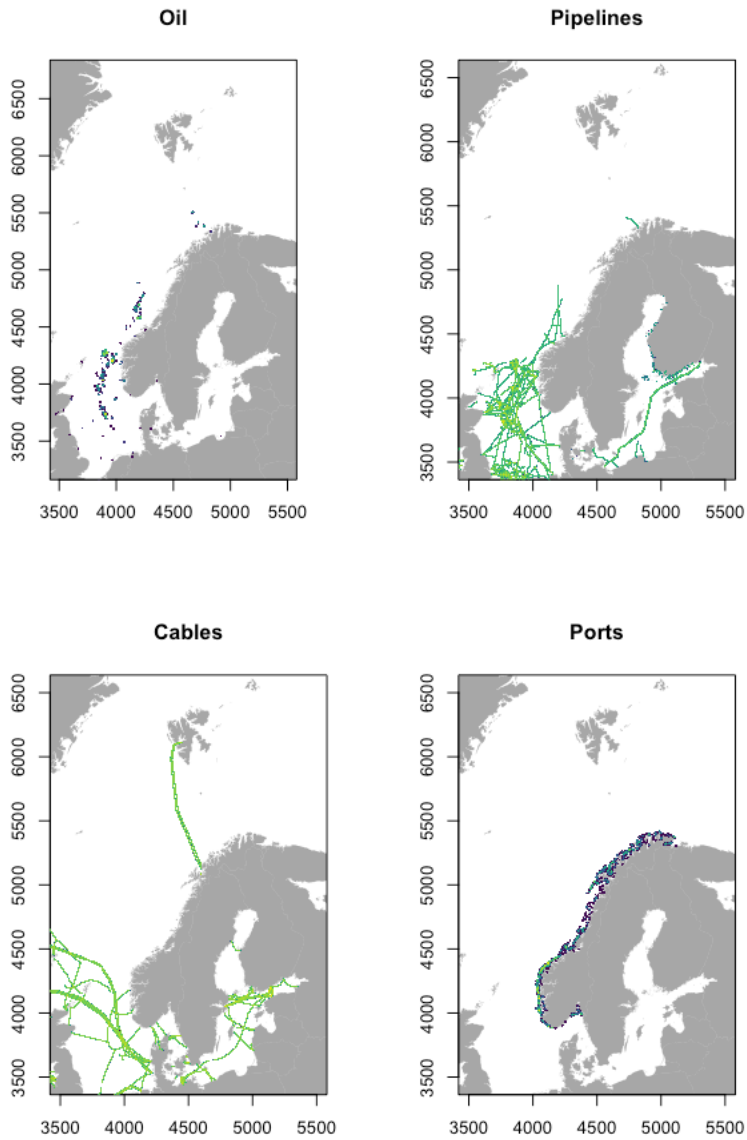
Supplementary figure 1 – Seasonal distribution of combined shipping activities. All values are standardized. Bright green indicates a high concentration, while blue indicates a low concentration.



Supplementary figure 2 – Seasonal distribution of combined fishing activities. All values are standardized. Bright green indicates a high concentration, while blue indicates a low concentration.



Supplementary figure 3 – Seasonal distribution of seismic activities. All values are standardized. Bright green indicates a high concentration, while blue indicates a low concentration. No seismic activities occurred during the spring during the sample year of 2018.



Supplementary figure 4 – Distribution of static activities; oil and gas facilities, pipelines, telecommunication cables and ports. All values are standardized. Bright green indicates a high concentration, while blue indicates a low concentration.



Humpback whale breaching in the polar night. Photo: Evert Mul

