

Department of Arctic and Marine Biology

## Hungry during migration? Humpback whale movement from the Barents Sea to a feeding stopover in northern Norway revealed by photo-ID analysis

#### **Theresia Ramm**

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## Abstract

In the last nine winters, a humpback whale feeding aggregation has been observed in the nearshore waters and fjords of northern Norway. This seasonal humpback whale occurrence is presumably driven by a shift in the overwintering distribution of Norwegian spring spawning (NSS) herring into these coastal areas. Eastern North Atlantic humpback whales feed during summer in relative remote regions in offshore waters. Their new proximity to a populated coast allowed to monitor this fairly understudied population in Norwegian waters. The North Norwegian Humpback Whale Catalogue (NNHWC) was established in the first winter of their nearshore occurrence and contains identification-photographs from both dedicated surveys and public submissions. The Norwegian Sea is thought to be used as a migration corridor during the seasonal movement of eastern North Atlantic humpback whales between the Arctic summer feeding ground in the Barents Sea and wintering grounds at low latitudes. The fjord systems of northern Norway are located roughly en route of this movement and could constitute a feeding stopover area for whales feeding in the Barents Sea. The main aim of this study was therefore to investigate the migratory connectivity between these two regions by comparing photo-identification data from both areas. The photo-identification material further allowed for a detailed description of this new Norwegian winter-feeding area with respect to site fidelity and the length of stay. A total of 342 individual humpback whales from the Barents Sea and 866 individuals from northern Norwegian coastal waters have now been identified between 2010-2019. The photographic comparison between these two regions yielded 39 individual matches. Among these were 17 within-season re-sightings, which demonstrate that the Norwegian fjords indeed constitute a stopover early in the southward breeding migration. The seasonal return (site fidelity) to this new feeding stopover area progressively increased throughout the nine years of study and remained between 60 and 80% in the last four years. Re-sightings within a season in northern Norway revealed that individuals occupied the area between two days and 15 weeks, on average 27.5 days (SD = 11.5). Although it is not clear whether humpback whales foraged on NSS-herring offshore before they entered the fjord-systems, the results indicate that humpback whales are capable of a flexible migration strategy, integrating feeding stopovers when prey is available.

**Key words:** *Megaptera novaeangliae*, humpback whale, stopover, Barents Sea, eastern North Atlantic, Norway, site fidelity

## **1** Introduction

Every year, animals undertake extensive round-trips between their breeding and feeding sites (Greenberg & Marra, 2005; Dingle & Drake, 2007). In many of these animals, migratory movements are commonly responsive to seasonal variation in the resources needed for survival and reproduction. Migrants thus spend different phases of their annual cycle in geographically separate regions to benefit from temporally available resources at each location (Dingle and Drake 2007; Ramenofsky and Wingfield 2007; Jonzén et al. 2013). Annual migrations are synchronized with other biological events that occur over the course of a year and may be structured into distinct stages: preparation (e.g. increased feeding), movement, stopovers (e.g. refuelling) and arrival (e.g. breeding) (Sapir et al. 2010; Jonzén et al. 2013). These different stages are inseparably linked, as the events and conditions in one season can influence an individual's performance in another season (Webster and Marra 2005; Harrison et al. 2011).

Among mammals, baleen whales (mysticetes) are known for their extensive annual journeys, travelling thousands of kilometres within ocean-basins (Corkeron and Connor 1999). Among these, humpback whales (*Megaptera novaeangliae*) perform remarkable long-distance migrations between low-latitude breeding grounds and high-latitude productive waters for feeding (Dawbin, 1966; Stone et al., 1990). Humpback whales are found in all oceans, but genetic data suggests limited inter-oceanic exchange, dividing the species into three major populations or sub-species, each located in the North Atlantic, North Pacific and Southern Hemisphere (Baker et al. 1993; Jackson et al. 2014). Despite the potential for dispersal, humpback whales show high degrees of natal philopatry to breeding grounds (Baker et al. 2013) and maternally driven fidelity to feeding grounds (Palsbøll et al. 1995; Larsen et al. 1996; Baker et al. 2013). The migratory destinations are presumed to be culturally transmitted from mothers to their calves whilst completing the first annual migration together during the calf's first year (Baker et al. 1990; Clapham 1996). This early experience results in the migratory returns of individual whales to specific regions and promotes population genetic structuring at the ocean basin scale (Kershaw et al. 2017).

Many of the migratory destinations of humpback whales have been identified from their natural individual markings on the ventral side of the fluke using photo-identification (Katona and Beard 1990). This is a powerful, non-invasive tool to monitor the species in their known

breeding and feeding grounds, as well as to unravel migratory connectivity between these sites (Katona and Beard 1990).

Within the North Atlantic, the majority of humpback whales are believed to overwinter and reproduce in the West Indies, an area ranging from Cuba to northern Venezuela with a very high concentration of whales off the Dominican Republic (Mattila et al. 1994; Stevick et al. 2003b; Bettridge et al. 2015). The second recognized breeding population is found on the eastern margin of the North Atlantic around the Cape Verde Islands (Bettridge et al. 2015). During summer, these humpback whales segregate into several distinct feeding aggregations with little observed interchange between the regions: the Gulf of Maine, eastern Canada, western Greenland, Iceland and subarctic/arctic Norway (Katona and Beard 1990; Christensen et al. 1992; Stevick et al. 2006). Genetic analysis indicates population separation between western and eastern feeding aggregations occurs as a result of long-term feeding ground fidelity (Palsbøll et al. 1995; Valsecchi et al. 1997). The wide-spread area around the West Indies is utilized by individuals of all feeding grounds, yet is considered as one breeding population (Stevick et al. 2003b; Bettridge et al. 2015). However, whales foraging during summer in the central and eastern North Atlantic (Iceland and Norway) tend to occupy predominantly the south-eastern Caribbean (Stevick et al. 2018). Moreover, humpback whales arrive in the south-eastern Caribbean significantly later than individuals breeding in the heavily used waters off the Dominican Republic (Stevick et al. 2018). The Cape Verde Islands are used by a very small population, with the most recent study reporting only 267 photographically identified humpback whales (Wenzel et al. 2020). The largest number of photographic recaptures for this second breeding population were to Norway and Iceland, and no matches were found to the western feeding groups (Wenzel et al. 2020). Although the Cape Verde Islands and the south-eastern Caribbean are separated by more than 4000 kilometres, humpback whales return to both breeding areas at similar times (Stevick et al. 2018). The later arrival of eastern whales may be related to their longer migratory distances from high-latitude feeding grounds to these tropical wintering areas (Stevick et al. 2003b, 2016, 2018; Wenzel et al. 2020). The easternmost feeding ground in the North Atlantic is found off the northern Norwegian coast and in the higharctic waters of the Barents Sea (Bettridge et al. 2015). Humpback whales travel in some instances more than 8000 kilometres from their breeding grounds to arrive in this remote northern feeding area (Stevick et al. 2016; Whaletrack 2018).

Within their known northern feeding grounds, prey abundance may vary in different locations throughout a season and between years (Stevick et al. 2006). In response, movement patterns of humpback whales are driven by spatial and temporal availability of prey and its predictability (Stevick et al. 2006). High concentrations of their preferred prey are often associated with oceanographic features and include euphausiids, sand lance (*Ammodytidae spp.*), Atlantic herring (*Clupea haerengus*) and capelin (*Mallotus villosus*) in the North Atlantic (Ingebrigtsen 1929; Hain et al. 1982; Christensen et al. 1992; Hazen et al. 2009; Davoren 2013; Nøttestad et al. 2013; Ressler et al. 2015). In the western North Atlantic, whales commonly perform small-scale movements with tens and hundreds of kilometres between prey aggregations. In contrast, eastern humpback whales cover much larger foraging distances with movements of up to 2000 kilometres between food resources (Stevick et al. 2006).

Early in the feeding season (spring/early summer), eastern humpback whales pass through the Norwegian Sea which is thought to be used as a migration corridor between the Tropics and the Barents Sea (Nøttestad et al. 2013). Their distribution in the Norwegian Sea is mainly located around Jan Mayen and Bear Island, overlapping with the presence of euphausiids, amphipods and Norwegian spring spawning herring (hereafter termed as NSS-herring) (Ingebrigtsen 1929; Christensen et al. 1992; Nøttestad et al. 2013). Later in the summer, humpback whales may proceed into the northern Barents Sea, where capelin is believed to become their main forage-species next to euphausiids (Ingebrigtsen 1929; Stevick et al. 2006; Skern-mauritzen et al. 2011; Ressler et al. 2015). Here, they can fuel their bodies in preparation for their expected southbound journey in autumn or early winter.

Since 2010, a seasonal humpback whale feeding aggregation has been observed in nearshore waters of northern Norway, driven by adult wintering NSS-herring (Jourdain and Vongraven 2017; Rikardsen 2019; Broms 2020). This forage fish unexpectedly started to partly overwinter in fjords and coastal areas; first in the northern part of the Vesterålen (Andøya and Senja), then also around Kvaløya outside Tromsø and later further north in the fjord-system off Skjervøya (Jourdain and Vongraven 2017; Rikardsen 2019; Broms 2020). Each winter, the highly migratory NSS-herring gathers in dense concentrations from October to February before embarking southwards for spawning (Huse et al. 2010; Huse 2016). During this overwintering period, separate areas might be utilized concurrently by the spawning stock and can include near and offshore waters (Huse et al. 2010). Since the 1950s, the NSS-herring overwintering sites repeatedly shifted, although the coastal and offshore waters of northern Norway have been utilized for several decades (Huse et al., 2010; Shuter et al., 2013).

However, there are no reported observations of humpback whales before the winter season in 2010. Historical records of Norwegian whalers document that the last winter sightings in northern Norway were indeed almost 100 years ago (Ingebrigtsen 1929). However, in recent years, large numbers of humpback whales have been re-visiting this high latitude feeding area. Meanwhile, the NSS-herring aggregations partly shifted their wintering area slightly northwards along the Norwegian coast and were followed by their predators (Rikardsen 2019). During the humpback whales' southbound migration from the Barents Sea to the Tropics, the fjord systems of northern Norway are located roughly en route. Therefore, these nearshore waters, occupied by high herring densities could provide a final opportunity to acquire additional energy needed for the long-distance movement, breeding activities and nursing.

Visser et al., (2011) reported the use of a migratory stopover around the Azores during the northbound journey towards the feeding grounds. Refuelling during spring-migration might be especially relevant due to depleted body reserves after breeding activities. The findings of Cucuzza et al., (2015) suggest that the occurrence of humpback whales and duration of stay in the Azores is a function of seasonal productivity and prey availability. They furthermore identified the island group as a stopover between the Cape Verde Islands and the Barents Sea. The only documented stopover point during southbound migration in the eastern North Atlantic is located around the British Isles (Ryan et al. 2013; O'Neil et al. 2019). Recently, humpback whales were sighted between January and March in the Firth of Forth in Scotland. Although only four individual whales have been so far identified in this region, one of them was re-sighted west of Svalbard in the Barents Sea (O'Neil et al. 2019). For humpback whales using this apparently new stopover area in northern Norway, their summer feeding locations before arrival and return rates to northern Norway are still unknown.

The sudden seasonal humpback whale aggregation in northern Norwegian fjords provided the unique opportunity for large-scale photo-identification to monitor the species in Norwegian waters. This was initiated in the first year of their winter occurrence in 2010 and has since led to the establishment of the North Norwegian Humpback Whale Catalogue (NNHWC). The NNHWC consists of identification photographs from dedicated surveys in this new winterfeeding area and submitted fluke photographs from the public, also including some sightings from the high arctic Barents Sea and Svalbard (hereafter termed as the Barents Sea). In addition, a research cruise was conducted in September 2018 leading into the Barents Sea,

east of the Svalbard Archipelago with the intention to satellite tag humpback whales, obtain biopsy-samples and collect fluke identification photographs (Whaletrack, 2018).

Using fluke photographs from both surveys and citizen scientists would allow photographic comparison between the Barents Sea and northern Norway as well as to explore patterns of site fidelity in northern Norway.

Therefore, the main aim of this study was to increase understanding of the migratory behaviour of eastern North Atlantic humpback whales. The specific objectives were to:

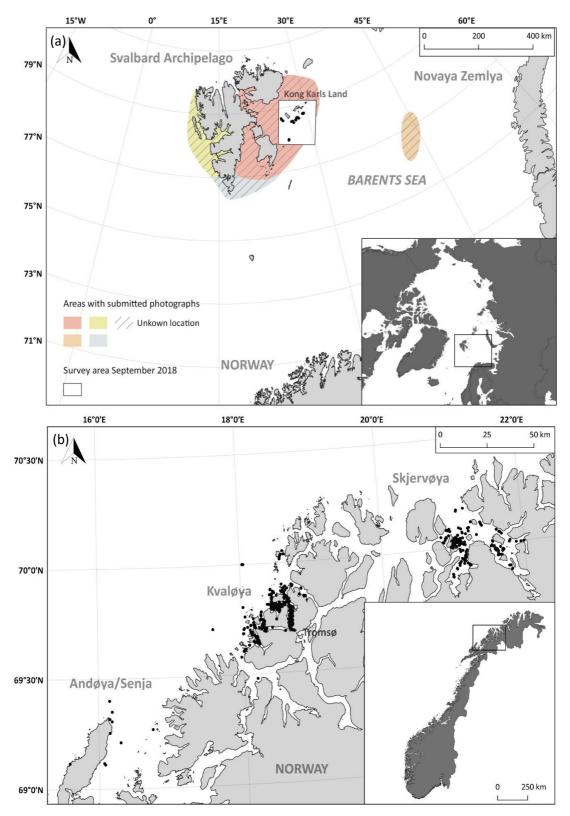
- investigate the relationship between the Barents Sea feeding aggregation and the seasonal winter occurrence of humpback whales in northern Norway using photoidentification material from both regions, and
- (2) to describe the use of this new Norwegian winter-feeding area over the last nine years, with respect to site fidelity and the length of stay using the photographic sighting history of individual humpback whales.

## 2 Materials and Methods

## 2.1 Study areas and data collection

#### 2.1.1 Barents Sea

The Barents Sea, a highly productive shelf sea, is situated off the coast of northern Norway and northwest Russia with the Norwegian Sea representing the border to the west, Franz Josef's Land to the north-east and Novaya Zemlya to the east (Wassmann et al. 2006). Photoidentification data of humpback whales was collected during a research cruise between the 3rd and 11th of September 2018. The cruise was conducted in cooperation between the Institute of Marine Research (IMR Bergen, Norway) and UiT – The Arctic university of Norway (UiT, Tromsø, Norway), surveying an area east of the Svalbard, close to the island group of Kong Karls Land (**Fig. 1a**). The timing and survey area were chosen based on a priori information on humpback whale occurrence originating from annual joint Norwegian/Russian ecosystem surveys in the Barents Sea and adjacent waters (IMR, Norway/PINRO, Russia). When humpback whales were sighted, a small boat was launched to allow closer approaches. Fluke photographs were taken from both the small boat and the larger research vessel using DSLR cameras (one camera with built-in GPS module). In addition to the survey, photographs from incidental humpback whale encounters around Svalbard and the Barents Sea were submitted by various contributors (2012 to 2019) (**Fig. 1a**).



**Figure 1.** The Barents Sea/Svalbard with coloured areas (submitted fluke photographs) representing approximate humpback whale (*Megaptera novaeangliae*) locations and black dots in the survey area referring to exact GPS points (a). The three main locations (Andøya/Senja, Kvaløya, Skjervøya) within the northern Norwegian winter-feeding area with exact humpback whale locations (b).

#### 2.1.2 Northern Norway

Identification photographs of humpback whales were collected in several northern Norwegian fjords and coastal areas mainly during late October and into February from the winter season of 2010/11 to 2018/19 (**Fig. 1b**). The study sites included waters around Andøya/Senja (2010 to 2012), Kvaløya (2012 to 2017) and Skjervøya (2017 to 2019), located in the counties of Nordland and Troms og Finnmark. Surveys were conducted by the UiT and founder of the NNHWC (see below) throughout the period of seasonal humpback whale occurrence. Photographic sampling was mainly conducted opportunistically using small vessels and was dictated by weather and light conditions. During the darkest month of the polar night (December), sampling was therefore normally restricted to a few hours around midday. However, on some surveys a flash system was used to allow sampling to continue in low light conditions. The survey effort differed between years and study sites (**Table 1**).

In the winter of 2010 to 2011, the first humpback whale sightings were reported around Andøya/Senja (69° 10' N, 15° 55' E) which offered the initial opportunity to obtain photoidentification material and led to the establishment of the NNHWC founded by Fredrik Broms. In the following seasons, leading up to the winter of 2016 to 2017, the fjords around Kvaløya outside Tromsø (69° 40' N, 18° 43' E) experienced high numbers of humpback whales, as well as killer whales from the 2012/2013-season. The main sampling site was therefore located in the fjords of Kvaløya, especially in Kaldfjord, a narrow 16 km long fjord. The fjords geography offered good conditions to survey a large area and its location is easily accessible. The other sampling sites around Kvaløya included Vengsøyfjord, Grøtfjord, Skarsfjord, Kvaløyvågen, Sandøya, Sessøyfjord and Ersfjord. The proximity of the UiT and Tromsø allowed surveys to occur on a weekly basis in this area. During the winter of 2016 to 2017, first humpback whales were also sighted further north in the less accessible Kvænangen fjord off Skjervøya (70° 1' N, 20° 58' E). In the following season (2017/18), the NSS-herring stopped entering the fjords of Kvaløya and from observations, it appeared most feeding activity had shifted to Skjervøya (Rikardsen, 2019). Since then, the sampling effort was therefore focused in this area until the winter of 2018 to 2019. This larger (72 km) and more exposed fjord than Kaldfjord, branches into two main fjords with several smaller arms (Fig. **1b**). The sampling effort in the first winter off Skjervøya totaled less days than the mean effort in Kvaløya but is comparable in the following winter of 2018 to 2019 (Table 1). The sudden seasonal aggregation of whales in northern Norway also led to the establishment of

**Table 1.** Combined table of effort-based surveys and non-effort-based data collection for each location within the winter-feeding area off northern Norway (2010/11 to 2018/19). Surveys were conducted by the UiT and the founder of the NNHWC (effort-based). Other records (non-effort-based) represent days in which fluke identification photographs were submitted by various contributors. The period depicts the first and last humpback whale fluke capture in a winter and days indicate the length of the feeding season in northern Norway. IDs represent the number of individuals identified per day by surveys in each winter season.

	Andøya	/Senja	Kvaløya		Skjerv	/øya			
Winter season	Effort survey (days)	Other records (days)	Effort survey (days)	Other records (days)	Effort Survey (days)	Other records (days)	Period	Days	IDs per day (effort)
2010/11	2	1					27 Dec- 19 Jan	23	2
2011/12	1	3	2				06 Dec- 29 Jan	54	2.7
2012/13		15	19	25			03 Nov- 11 Feb	100	5.4
2013/14		33	22	35			07 Nov- 06 Feb	91	6.4
2014/15		14	39	44			28 Oct- 15 Feb	110	7.8
2015/16		12	29	51			29 Oct- 24 Feb	118	9.7
2016/17			18	27		5	23 Oct- 24 Jan	93	3.9
2017/18					10	5	10 Nov- 13 Jan	64	11
2018/19					28	26	26 Oct- 28 Jan	94	3.4
Total	3	78	129	182	38	36		747	
Mean	1.5	13	21.5	36.4	19	12		83	5.8

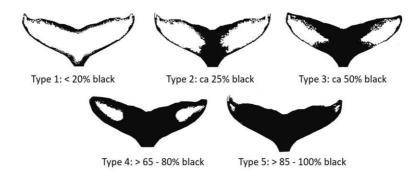
Note: Humpback whale fluke photographs (other records) submitted from the winter of 2012 /13 to 2015/16 off Andøya/Senja were taken during January and sometimes February.

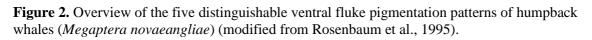
a whale watching industry, invited locals for recreational boating and attracted the attention of researchers from various institutes. Therefore, the integration of the public and other researchers played a vital role in data collection and was facilitated by an interactive online web-portal for the submission of fluke photographs, established in 2015 (hvalid.no).

## 2.2 Photo-identification

### 2.2.1 Data processing and photographic matching

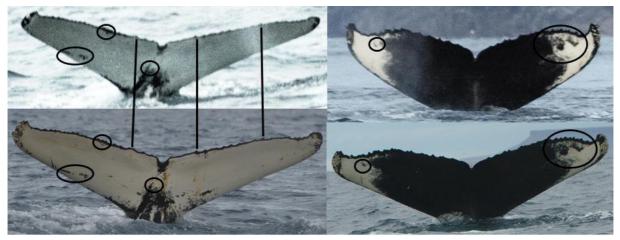
The collaborative NNHWC combines fluke photographs from more than 190 contributors. Before this study, a total of 808 individual humpback whales was already identified off northern Norway and 83 individuals in the Barents Sea/Svalbard region. In addition, humpback whales identified during the last two winter seasons off Skjervøya (2017/18 and 2018/19) and the Barents Sea cruise in September 2018 were included in this study, thereby updating the catalogue.





The most commonly used features to identify individual humpback whales are their unique patterns on the ventral side of the fluke and the distinctive serration pattern along the trailing edge (Katona et al., 1979). All fluke photographs were sorted by their percentage of black pigmentation and classified into one of five fluke types (**Fig. 2**) (Rosenbaum et al. 1995). Once the unique fluke pattern of an individual whale was identified, photographs of each encounter were gathered to compile a sighting history for that individual (date, location, exact GPS if available). Its fluke pattern was then compared to the current collection using a double screen to inspect the photographs visually (**Fig. 3**). Afterwards, the photograph was either added to the sighting history of an already existing whale, added as a new whale to the catalogue or recorded as unidentifiable. Each new identification was accepted as a match or as a new individual after second confirmation by the founder of the NNHWC. The highest

quality photograph of each individual was selected to represent it within the catalogue. A high picture quality required a clear distinctiveness of the fluke pattern (through black and white pigmentation) and/or trailing edge, a nearly perpendicular angle and a nearly sharp focus (Friday et al. 2000). The sighting history of each individual was used to clarify whether it had been sighted in the Barents Sea and northern Norway to investigate the movement between these two regions. Thereby, within-season re-sightings were also identified.



**Figure 3.** Matching process examples. Upper humpback whale (*Megaptera novaeangliae*) flukes were registered in northern Norway and were re-sighted in the Barents Sea (lower fluke photographs). Lines indicate identification by shape of trailing edge and circles mark unique fluke patterns.

## 2.2.2 Site fidelity in northern Norway

The seasonal return of individual humpback whales to the winter-feeding area in northern Norway was assessed using the sighting history of individuals registered for this region between the 2010/11 and 2018/19. Re-sightings between seasons were investigated with respect to their subsequent and first and last sightings by counting sighting intervals. These intervals were also counted between the first and last sightings of individuals within a season to obtain frequencies which indicate the length of stay. The rate of annual return describes site fidelity on a population level and was calculated as the number of photographically recaptured individuals in the year, divided by the total number of individuals sighted in that year (Clapham 1993).

# 3 Results

## 3.1 Photographic collection

Between 2010 and 2019, a total of 5320 fluke identification photographs of 1169 unique humpback whales were collected and registered in the NNHWC. The catalogue covers a latitudinal range from 67° to 80° N and contains sighting records of individual humpback

whales throughout the year with summer and autumn sightings mainly focused in the Barents Sea (**Table 2**). 70% of all fluke photographs were collected during surveys and the other 30% were submitted by various contributors (**Appendix S1**).

**Table 2.** Summary of total registered humpback whale (*Megaptera novaeangliae*) sightings in the NNHWC from 2010 to 2019. Numbers of fluke photographs and identified whales are given per month and by region. Individual whales that have been encountered in multiple months and/or regions are listed in each of them. Totals in bold represent the number of unique humpback whales identified by region.

	Northern Nor	wegian fjords	Barents Sea			
Month	No. photos	No. whales	No. photos	No. whales		
January	976	505	0	0		
February	182	130	0	0		
March	0	0	0	0 0		
April	1	1	0			
May	0	0	1	1		
June	9	9	11	8		
July	6	5	29	23		
August	1	1	59	54		
September	2	1	1950	266		
October	43	37	0	0		
November	1202	474	0	0		
December	848	447	0	0		
Total	3270	866	2050	342		

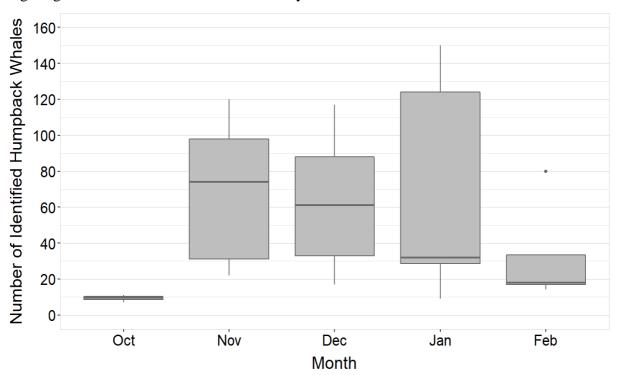
#### 3.1.1 Barents Sea

In the Barents Sea, humpback whale sightings are registered from May to September (**Table 2**). In total, 2050 fluke photographs of 342 individual whales were collected in this region. Most identification photographs (95%) were obtained during a research cruise surveying waters east of the Svalbard Archipelago in early September 2018. One week of sampling resulted in the identification of 264 individual whales. All other fluke photographs (5%) originated from incidental humpback whale encounters between 2012 and 2019 and were submitted. These photographs resulted in the identification of 83 individuals. In total, five between-season re-sightings were found within the Barents Sea.

#### 3.1.2 Northern Norway

Between 2010 and 2019, a total of 3270 fluke photographs of 866 individual humpback

whales were collected in northern Norway with 58 of them identified during the last two seasons off Skjervøya (Table 2). Humpback whales were sighted throughout the year, however summer sightings accounted for only 1% of all identifications. During surveys (October to February), 54.7% of all fluke photographs were obtained. The other 45.3% originated from various contributors and included all summer sightings. Throughout nine years of collecting data, there was a total of 170 days of dedicated photo-identification survey effort, with considerably less effort during the first two winters seasons (**Table 1**). The annual survey effort across all winter seasons averaged 17 days (SD = 13.1) and 23.6 days (SD = 9.4) without the first two seasons. Additionally, fluke photographs that were submitted by various contributors reported humpback whale sightings on 296 days from October to February. The survey effort combined with submitted fluke captures resulted in the identification of 856 unique humpback whales during the autumn and winter months, while 10 individuals were identified at other times of the year. The total number of photo-identified humpback whales per winter ranged from a minimum of six individuals in the first year off Andøya/Senja to a maximum of 408 individuals in the 2015/16 season off Kvaløya (Table 3). The total number of individual whales registered per month showed great variation between winter seasons (Fig. 4). Aside from the exception of the first two winters (2010/11 and 2011/12), the peak in sightings occurred from November to January.

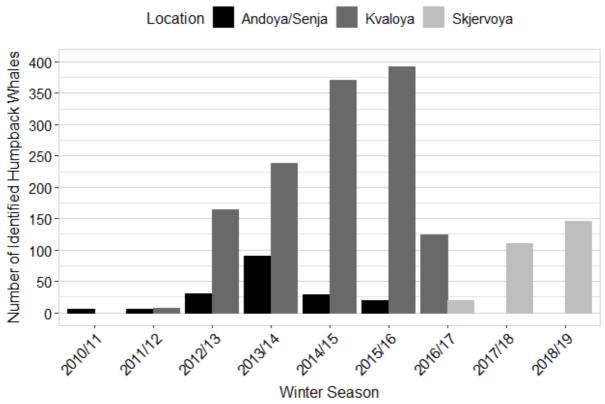


**Figure 4.** Total number of individual humpback whales (*Megaptera novaeangliae*) registered per month during the winter-feeding season in northern Norway from 2012/13 to 2018/19. Lines in boxes correspond to medians and vertical lines represent minimum and maximum numbers of identified whales per month.

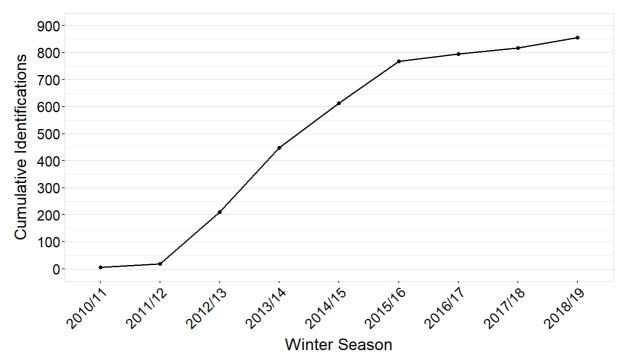
**Table 3.** Total number of humpback whales (*Megaptera novaeangliae*) photo-identified each winter season as well as new and re-sighted individuals from 2010/11 to 2018/19. Within-season re-sightings are given in bold. Year of initial sight corresponds to new IDs and year of later re-sight depicts their photographic recapture.

				Year of later re-sight								
Year of initial sight	New IDs	Re-sights	Total IDs (% new)	2010/11	2011/12	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19
2010/11	6	0	6 (100)	0	0	0	0	0	1	1	0	0
2011/12	13	0	13 (100)		0	3	5	7	5	1	1	0
2012/13	191	3	194 (98)			51	82	94	91	31	23	26
2013/14	238	87	325 (73)				117	128	96	43	27	31
2014/15	165	229	394 (42)					192	60	21	15	17
2015/16	155	253	408 (38)						180	20	13	16
2016/17	26	117	143 (18)							71	9	8
2017/18	23	88	111 (21)								45	9
2018/19	39	107	146 (27)									83

In the first two winter seasons (2010/11 and 2011/12), 19 unique humpback whales were identified off Andøya/Senja (n = 12) and Kvaløya (n = 7, second winter) (**Fig. 5**). In the following winter (2012/13), the observed main feeding activity shifted into the fjords around Kvaløya and the total number of photo-identified individuals increased by one order of magnitude (n = 194). Greater numbers of humpback whales were identified in the following feeding seasons (2013/14, n = 325; 2014/15, n = 394) until 2015/16. During the last occurrence off Kvaløya in 2016/17, the total of identified individuals notably declined in comparison to the previous year (2015/16, n = 408; 2016/17, n = 143) (**Table 3, Fig. 5**). Concurrently, 2016/17 represented the first winter, humpback whale sightings were reported off Skjervøya (n = 20). The total number of individually identified whales per winter in Skjervøya (2017/18, n = 111; 2018/19, n = 146) were comparable to the last winter occurrence off Kvaløya. The cumulative curve of identifications began to plateau after the winter of 2015/16 but showed a slight increase in the last year of study (**Fig. 6**).



**Figure 5.** Total number of individual humpback whales (*Megaptera novaeangliae*) identified by location in each winter-feeding season in northern Norway (2010/11 to 2018/19).



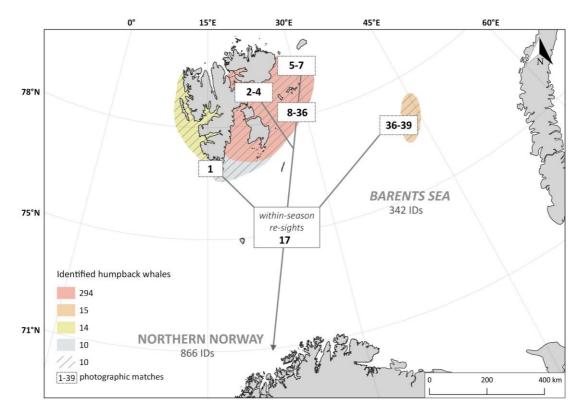
**Figure 6.** Cumulative curve of photo-identified humpback whales (*Megaptera novaeangliae*) in a winter-feeding area in northern Norway (2010/11 to 2018/19).

# 3.2 Photographic matching between the Barents Sea and northern Norway

The photographic comparison between the Barents Sea and northern Norway yielded 40 matches of 39 individual humpback whales. One individual (**Fig. 7, No. 36**) was seen in two different years in the Barents Sea and re-sighted in both off northern Norway during winter. All individuals were re-sighted during the autumn and winter months in northern Norway (**Appendix S2**). The summer feeding location of these 40 humpback whales ranged as far west as Hornsund in Svalbard, as far north as Hinlopen strait and the border to Russia marked the eastern most sighting (**Fig. 7**). Among these 40 matches, 17 within-season re-sightings of 16 individuals were found (**Table 4**).

**Table 4.** Total number of humpback whales (*Megaptera novaeangliae*) identified per summer season by submitted fluke photographs (2012 to 2019) and survey effort (2018) in the Barents Sea. Withinseason re-sightings between the Barents Sea and northern Norway are given in bold. Animals encountered in multiple years in the Barents Sea are listed in each year.

Year	2012	2013	2014	2015	2016	2017	2018	2019
No. of individuals	15 ( <b>3</b> )	2 (1)	19 ( <b>2</b> )	23 ( <b>2</b> )	12	7	267 ( <b>9</b> )	2



**Figure 7.** Identified humpback whales per location and photographic matches of 39 individuals between northern Norway and the Barents Sea are shown. Within-season re-sightings are indicated by the arrow. **Note:** Individual 36 was observed in two different years in the Barents Sea and is listed in both observed locations. Diagonal grey lines represent unknown location.

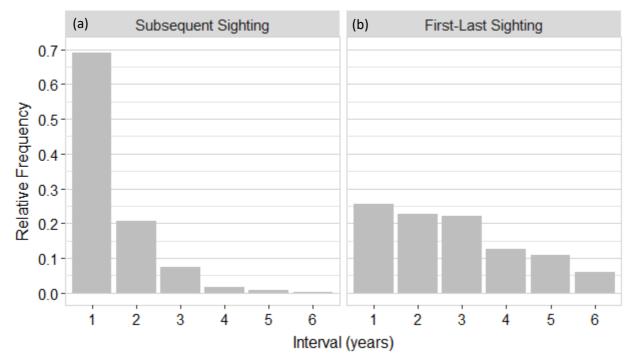
## 3.3 Site fidelity in northern Norway

#### 3.3.1 Between season re-sightings

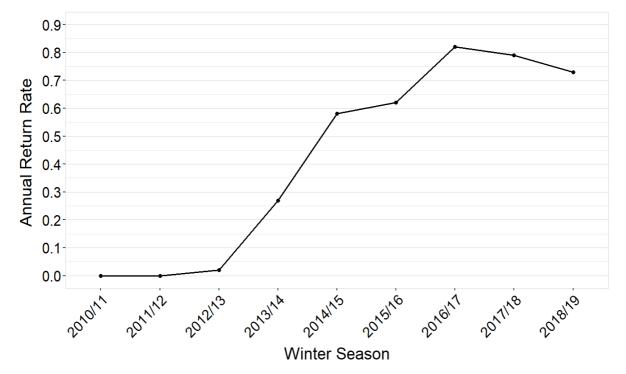
Between the winter of 2010/11 and 2018/19, a total of 856 individual humpback whales were sighted in northern Norway. While 46.6% (n = 399) of them were sighted in only one season, 53.4% (n = 457) of these individuals were photographed in two or more winters. Most of the whales were seen in two (n = 202), three (n = 131) or four (n = 83) different years. Seven years was the longest period an individual was re-sighted (n = 1; NNHWC-368). Re-sightings between seasons occurred most frequently in sequential years (69.4%), followed by two-year intervals (20.6%) (**Fig. 8a**). The interval between the first and last photographic capture of an individual humpback whale varied between one and six years (**Fig. 8b**).

In each winter season, new individual humpback whales were photo-identified. Until the winter of 2013/14, new fluke captures accounted for more than 70% of the total number of whales identified in a season. In all following winters, the number of re-sightings was higher than first captures, on average 70.9% (SD = 10.5). The rate of annual return progressively increased until the 2016/17 season (the last winter season off Kvaløya), when it reached the

overall maximum of re-sightings (81.8%) (**Fig. 9**). During the two winter seasons off Skjervøya, the number of re-sightings remained between 70 and 79%.



**Figure 8.** Between season intervals (a) and intervals between first and last sighting (b) of humpback whales (*Megaptera novaeangliae*) feeding off northern Norway during winter (2010/11 to 2018/19).

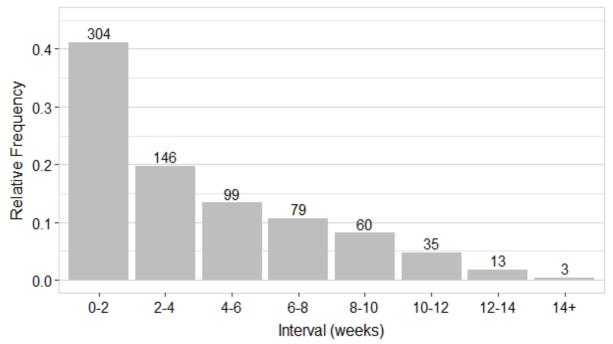


**Figure 9.** Annual return rate of humpback whales (*Megaptera novaeangliae*) to a winter-feeding area in northern Norway (2010/11 to 2018/19).

As described above, re-sightings between seasons were commonly observed between different locations. For instance, the individual NNHWC-368 was seen in seven consecutive winters, foraging in four seasons off Kvaløya and three seasons off Skjervøya, including the winter of 2016/17 before the observed main feeding activity shifted to Skjervøya. It is one of 151 individuals that were first photographically captured off Kvaløya and had future sightings in Skjervøya. In addition, another three whales were first encountered off Andøya/Senja and were later observed in Skjervøya. Numerous re-sightings also occurred bidirectionally between Andøya/Senja and Kvaløya (n = 142). In total, 40 individual humpback whales were observed in all three locations.

#### 3.3.2 Within-season re-sightings

Within-season re-sightings occurred for the first time in the third year of study (2012/13) and then became increasingly common (**Table 3**). On average 43.2% (SD = 10.1) of the whales were seen more than once within a season. The time interval between within-season resightings ranged from a minimum of 2 days to a maximum of 15 weeks, on average 27.5 days (SD = 11.5) (**Fig. 10**). In several winters, humpback whales were observed in two locations in the same season. Between Andøya/Senja and Kvaløya, a total of 56 within-season resightings were found (2012/13, n = 8; 2013/14, n = 23, 2014/15, n = 14, 2015/16, n = 11). All of them were first observed off Kvaløya and were later re-sighted in January and sometimes



**Figure 10.** Within-season re-sighting intervals between first and last sighting of humpback whales (*Megaptera novaeangliae*) feeding off northern Norway during winter (2012/13 to 2018/19). Numbers on top of bars correspond to absolute frequencies.

February off Andøya/Senja. In the winter of 2016/17, humpback whales occurred off Kvaløya and Skjervøya, but no within-season matches were found.

## 4 Discussion

#### Humpback whale movement from the Barents Sea towards northern Norway

The present study shows that over the course of the last nine years, a few northern Norwegian fjords systems used as a wintering habitat of Norwegian spring spawning (NSS) herring have become a migratory feeding stopover for humpback whales during their southbound breeding migration. Several humpback whales stopped during their movement from the summer feeding ground in the Barents Sea to the winter breeding grounds at low latitudes. This is also the first study that demonstrates the connectivity between northern Norway and the Barents Sea. Although, the breeding ground connectivity was not investigated in this study, there is evidence that humpback whales continue their breeding migration due to tracking data and photo-identification analysis (Broms et al. 2017; Whaletrack 2018; Kettemer et al. 2019).

The northern Barents Sea, in particular the area east of the Svalbard archipelago seems to represent an important foraging area for humpback whales late in the season (late summer/autumn) based on the results from annual joint Russian/Norwegian ecosystem surveys that frequently report humpback whales in this region (Anon. 2009; Prokhorova 2013; Van der Meeren and Prozorkevich 2018). To date, 342 humpback whales are registered in the North Norwegian Humpback Whale Catalogue (NNHWC) for the Barents Sea with most of them photographed during one week of sampling (n = 264) in September 2018, east of Svalbard. All other whales were identified in diverse locations around the Svalbard archipelago and Barents Sea by public fluke submission (2012-2019). The high encounter rate during the survey east of Svalbard, further indicates the importance of this area as a main foraging ground. However, since humpback whale distribution appears to consistently overlap with capelin and euphausiids in the Barents Sea, distribution shifts may occur in concert with changes in abundance and availability of this forage species (Christensen et al. 1992; Anon. 2009; Skern-mauritzen et al. 2011; Ressler et al. 2015; Prozorkevich and Sunnanå 2016; Van der Meeren and Prozorkevich 2018, 2019). During the sampling period in 2018, capelin was mainly distributed along the western edge of the Great Banks and overlapped nicely with the area in which humpback whales were encountered (Van der Meeren and Prozorkevich 2019).

From old whaling records it can be inferred that their occurrence in the northern Barents Sea during the late feeding season has been known for a long time (Ingebrigtsen 1929). Since the commercial hunting ban for humpback whales in the North Atlantic in 1955, the number of whales have seemingly increased in this area (Best 1993; Øien 2001; Stevick et al. 2003; Leonard and Øien (in press)). Although, there is no recent abundance estimate for the whole Barents Sea in particular, the entire eastern North Atlantic humpback whale population was estimated at 10,708 (95% CI = 4906-23,370) between 2014 and 2018 (Leonard and Øien (in press)). The highest abundance was estimated for the area east of the Svalbard archipelago at 3684 (95% CI = 624-21,747) (Leonard and Øien (in press)).

Over the last seven years 11.4% (39 out of 342) of the identified whales in the Barents Sea have been re-sighted foraging in the stopover area in northern Norway. In general, a total of 39 matches appears to be low, but by comparing the number of identified whales in the Barents, particularly east of Svalbard (n = 294) to the abundance estimate in this area (3684; 95% CI = 624-21,747), it shows that only a small proportion (<10%) was available for the matching process. The highest number of whales were identified in the year of the Barents Sea cruise in September 2018, with 3.4% of them visiting northern Norwegian fjords the following winter. Because it is not expected that all humpback whales were photographed in the fjords, this percentage clearly represents a minimum estimate of movement between these two regions. Considering, that most re-sighted individuals in northern Norway were photographed in the area east of Svalbard, a re-sighting rate of 3.4-11.4% of the estimated abundance in this area (not taken the large confidence interval into account) approximately matches the number of whales identified in a stopover season (range = 111-408). Moreover, it was possible to follow the migratory southward movement of eight humpback whales due to satellite-tagging efforts during the Barents Sea survey in 2018 (Whaletrack 2018). While none of them was observed entering the stopover area, one individual lost its tag very close to the coast moving towards a potential stopover. Unfortunately, there was no fluke photoidentification material obtained of this animal while tagging. Therefore, it was not possible to verify whether it entered the fjords, assuming it would have been photographed. If it did perform a stopover, it would show that 12.5% (1 out of 8) of the tagged whales might have utilized this stop-over point. This is surprisingly close to the percentage of total re-sightings (11.4%). All other whales with transmitting tags moved from the Barents Sea towards the breeding grounds, foregoing a stopover in northern Norway. We therefore conclude that it is

highly likely that a large fraction of the identified humpback whales performing a winter stopover originate from the summer feeding ground in the Barents Sea.

#### Northern Norway, a migratory feeding stopover point

Northern Norway became apparent as a stopover point for humpback whales when the abundant wintering NSS-herring gathered in dense concentrations in northern Norwegian fjords in 2010 (Rikardsen, 2019). Although, the first observations of humpback whales during winter were reported in 2010, it cannot be ruled out that the whales foraged on this prey species before that in offshore and less accessible regions. Baleen whales have been described as 'sentinels of ecosystem change' as their adaptive search behaviour ensures them to find dense concentrations of ephemeral prey (Nøttestad et al. 2015; Moore et al. 2019). The herrings overwintering site was located offshore the Vesterålen (70°N) a few years before 2010 (Huse et al. 2010), roughly en route the humpback whales southwards movement. It is therefore likely that they detected this food source in this region. However, the NNS-herring is known to conduct diel vertical migrations, staying deep during day (130-400m) and moving into shallower waters during night-time (range 30-50m) (Huse and Korneliussen 2000). Therefore, the NSS-herring might have been too deep to forage efficiently during daytime. Between dusk and dawn however, the NSS-herring probably became more accessible and Ochoa Zubiri (2017) reported that humpback whales feed on this schooling fish during nighttime within the stopover area. Therefore, some humpback whales may have been feeding on overwintering NSS-herring in offshore locations before the wintering herring aggregation also occupied the fjords in northern Norway in 2010.

In northern Norway, 866 individual humpback whales were identified across the last nine years (2010/11 to 2018/19). The number of encountered whales progressively increased each winter season until it reached its maximum in the 2015/16 season in which 408 individuals were photographed. In the consecutive winter in 2016/17, the number of photo-identified whales suddenly dropped to 143 individuals and remained comparable low since. There can be several possible explanations for this sudden seasonal humpback whale feeding aggregation in northern Norwegian fjords since 2010 and some of them might work in concert. Firstly, the NSS-herring was gathering in dense concentrations in relatively narrow fjords which 'compresses' the aggregation. This might have facilitated predation by humpback whales, as they commonly force the herring towards the shoreline as one of the feeding strategies (A. Rikardsen, pers. com.). Secondly, the overwintering in narrow and

shallow fjords that rarely exceed 250 m might have limited predator avoidance reactions of herring like dispersal or downward movement (Doksæter et al. 2009) which furthermore facilitated predation. Finally, the high biomass of herring in the fjords could have exceeded a foraging threshold that made it profitable to feed (Holling 1965; Piatt and Methven 1992; Huse 2016; ICES 2019). For example in a study in Newfoundland, baleen whales, including humpback whales did only aggregate when capelin abundance passed a certain threshold per km<sup>2</sup> (Piatt and Methven 1992).

NSS-herring shows varying recruitment patterns resulting in infrequent strong year classes, often with several years or even decades in-between (Dragesund et al. 1980; ICES 2019). A strong year class occurred in 2004 (Huse 2016). When this NSS-herring joined and outnumbered the older fish of the spawning stock, the recruitment potentially contributed to the establishment of a new wintering habitat in nearshore waters in 2010/11 (Huse et al. 2010). Since then high densities of NSS-herring occupied the coastal areas and fjords, first off Andøya/Senja and later off Kvaløya (Rikardsen 2019). Interestingly, the present study identified re-sightings of humpback whales between Kvaløya and Andøya within the same season. All these whales were first photographed off Kvaløya in November and December and then at Andøya in January and sometimes February. These re-sightings could therefore indicate that humpback whales followed the herrings spawning movement as parts of stock may have begun their migration. In the winter of 2016/17, considerably less humpback whales were encountered in the known stopover area around Kvaløya, and the first individuals were sighted in Kvænangen off Skjervøya. In the consecutive winter, the fjords around Kvaløya were deserted and the observed feeding-activity had shifted to Skjervøya. This may relate to new NSS-herring recruitment of the 2013 year class to the spawning stock (Slotte et al. 2017) which possibly utilized novel wintering sites offshore and in the fjordsystem off Skjervøya. Parts of this year class already joined the stock in 2016/17, while they were the most abundant in the adult stock in 2017/18 (Slotte et al. 2017, 2018).

The lower numbers of identified whales since 2016/17 may have several reasons. It seems that NSS-herring aggregated in several wintering habitats concurrently (the 2013 year class predominantly north of 67°N, and older fish further south), including offshore areas (Slotte et al. 2017, 2018). Therefore, humpback whales might have distributed accordingly. While photo-identification efforts could only cover coastal areas, whales potentially foraging and remaining offshore were not photographed in these years. Another important aspect is the decrease in the NSS-herring biomass. In general, the NSS-herring stock experienced poor

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recruitment since the strong 2004 year class resulting in a decline of the stock size from approximately 7 million tonnes in 2009 to 4.5 million tonnes in 2016 and a further reduction to 4 million tonnes in 2019 (ICES 2019). The 2013-year class that occupied areas off Skjervøya led to the stability of the total herring biomass in 2018 but was not comparable to the much stronger 2004 year class (Slotte et al. 2018; ICES 2019). Therefore, the potentially lower biomass in the fjords might have attracted less whales. In addition, the fjord-system off Skjervøya is wider and larger than the fjords around Kvaløya. This might have impacted search efficiency and the animal densities encountered within surveys.

#### Rate of return to stopover areas in northern Norway

While site fidelity of humpback whales has been shown in breeding and feeding grounds, there are no earlier information on return movement to a known migratory feeding stopover for this species (Stevick et al. 2006; Baker et al. 2013; Wenzel et al. 2020). The present study is therefore the first to report this. From the establishment of this feeding stopover area in 2010, the rate of annual return progressively increased and for the last four years has remained between 60% and 80%. This high site fidelity is comparable to what has been observed in their main known feeding grounds (Clapham 1993; Calambokidis et al. 1996). Although some of the NSS-herring overwintering sites shifted slightly northwards during the study period, the same fjords and coastal areas were repeatedly utilized over several years (Rikardsen 2019). Humpback whale return movement therefore occurred within tens of kilometres while the NSS-herring occupied the same region, and hundreds of kilometres when the NSS-herrings wintering site shifted. Although this feeding stopover activity might be an elusive and non-lasting event (depending on the NNS-herring movement), this study has proven long-term site fidelity in these coastal areas since 2010. More than half the whales identified across the nine years of study returned with 27% of them performing this feeding stopover over a period longer than three years. Furthermore, humpback whales most often visited this stopover point in sequential years. Therefore, it seems, since they discovered this food-source along the migratory route, it became a habit to re-visit the area where they "expected" to find the prey aggregations. Stopovers have been shown to be essential to the ecology of other species as well. For examples, fuel loading in birds at identified areas along their migratory route can increase reproductive output (Sapir et al. 2010). The identification of Northern Norway as a foraging area for migrating humpback whales evokes questions; how important are these feeding opportunities for humpback whales? Does feeding along the

migratory route occur simply opportunistically or are foraging stopovers as essential as shown in birds?

#### Relevance of a feeding stopover, length of stay

The use of a migratory feeding stopover could be of varying importance for individual whales and may be related to sex, reproductive status, or age (Craig and Herman 1997). Length of stay in the stopover area may provide an indication for the differing needs of individuals. The results suggest that the majority of whales utilized this winter-feeding area for a period longer than two weeks. Whales occupied the area on average for about one month and stayed a maximum of over three months. However, while interpreting re-sighting intervals it is important to consider the variability of photographic "catchability". This is highly influenced by the size of the survey area, weather exposure, number of photographers, varying fluking behaviour of whales, or varying response behaviour of whales towards survey vessels (Fisheries et al. 2014). Combined, all this could have biased the sampling results. Therefore, the here reported residence time represents a minimum estimate of the length of stay. Despite this, the length of stay observed in northern Norway far exceeds previously reported residence times at other stopover points. For example, Visser et al. (2011) reported that whales stayed up to only two weeks around the Azores when suitable prey was available. The relatively long residency in northern Norway might be explained by continuous and stable prey availability over 3-4 months, as the seasonal humpback whales occurrence reflects the overwintering period of the NSS-herring (Huse 2016).

Differences in the length of stay between individuals may represent varying energetic demands (Craig and Herman 1997). The feeding opportunity, these whales experience in northern Norway during winter might be especially valuable for adult females as they are either pregnant, accompanied by a calf or rest one to three years between subsequent pregnancies (non-lactating, non-pregnant) (Chittleborough 1958; Clapham 1996; Weinrich 1998). Pregnancy and lactation are energetically highly demanding and while resting, females restore sufficient body reserves to allow future reproduction (Oftedal 2000; van der Hoop et al. 2017). In general, pregnant females are reported to depart last from feeding grounds and arrive latest at breeding areas (Chittleborough 1958; Dawbin 1966). This group could therefore dominate the late winter-feeding season in northern Norway. Old whaling logs that report humpback whale captures during winter in northern Norway around 100 years ago, may provide support to this theory. These logs document that the majority of caught mature

female humpback whales were pregnant with foetuses measuring a length between 12 to 14 feet (3.6 to 4.2 metres), which is close to the mean birth length (4.5 metres) of a humpback whale calf (Ingebrigtsen 1929; Clapham and Mead 1999). A female bias during feeding stopovers was reported for Southern Hemisphere humpback whales while migrating towards the feeding grounds (Barendse et al. 2010). Owen et al. (2015) reported a prey dependent sex bias with males stopping for schooling fish and females preferring krill in Australia, again on their movement towards the feeding grounds. Yet there is comparatively little information on sex-ratios during foraging events along the migratory route.

A full year tracking data of one tagged animal in the stopover area in northern Norway revealed that it undertook a second stopover in southeast Iceland before continuing towards the breeding ground (Kettemer et al. 2019). This individual stopped at the same area off Iceland on the way north again, before migrating to the northern Barents Sea. It then re-occurred the next stopover season in northern Norway, accompanied by a calf and thus was pregnant in the winter of tagging. During the present study, several whales were identified as females by the presence of calves, but photo-identification data was not sufficient to include a sex-ratio into this analysis. Therefore, it would be interesting to complement photo-identification data with genetic methods and hormone measurements to investigate sex-ratios at different times of the feeding season (October to February) with respect to the reproductive status of mature females (with dependent calf, pregnant, resting). This would provide inside into the length of stay and timing of migratory departure for both sexes and if any group dominates the late feeding season.

#### Northern Norway, more than a stopover?

Despite the general belief that humpback whales migrate annually, there is growing evidence that not all individuals complete this long-distance movement every year (Swingle et al. 1993; Brown et al. 1995; Barendse et al. 2010; Víkingsson et al. 2015). For example, at the winter breeding grounds, a sex-bias towards males appears to be consistent worldwide (Smith et al. 1999; Rosenbaum et al. 2009; Herman et al. 2011; Ryan et al. 2013; Franklin et al. 2018; Steel et al. 2018). In addition, a male-biased sex-ratio was found along the migration route in Southern Hemisphere humpback whales (Brown et al. 1995). Although, a longer breeding ground residency of males partially explains this bias, it may also suggests that females do not complete or forego migration to breeding grounds in some years (Clapham 2018). Pregnant females could potentially give birth along the migration route and females resting between

pregnancies may remain in the feeding grounds throughout the winter because the movement costs (approximately 25% of annual energy budget) might outweigh the benefits (Barlow and Clapham 1997; Barendse et al. 2010, Kettemer et al., 2019). In addition, juvenile humpback whales were reported to occur throughout the winter (January to March) in nearshore waters of Virginia in the North Atlantic (Swingle et al. 1993). Swingle et al. (1993) suggested that immature individuals may not complete a full migration and rather continue feeding during winter and spring. This might be the case for some humpback whales in northern Norway, as Aniceto et al. (2019) detected humpback whale calls to continue until mid-April along the shelf break in northern Norway which was occupied by high herring densities using passive acoustic detection. Humpback whales were also observed to feed on spawning capelin during April on the banks outside Tromsø in northern Norway (A. Rikardsen, pers. com.). Víkingsson et al. (2015) reported a similar picture in Icelandic waters where humpback whales follow the spawning migration of capelin throughout the winter. Therefore, in northern Norway, some individuals may stay throughout the winter. Consequently, these animals forego a migratory movement towards winter breeding grounds but for now it is unknown whether they are juveniles and/or females.

## 5 Conclusion

The present study confirms that northern Norway constitutes a feeding stopover for humpback whales migrating from the summer feeding ground in the Barents Sea to lower latitudes. The results further indicate that this winter stopover may be dominated by individuals of the Barents Sea feeding aggregation, although some individuals may also originate from other areas. In addition, the results suggest that just a fraction of the Barents Sea feeding aggregation undertakes this stopover, while the majority probably migrates directly towards breeding areas. This evokes the question, for which individuals additional fuel accumulation might be beneficial. Therefore, further studies should focus on estimating sex ratios throughout the period of seasonal occurrence with respect to the pregnancy status of mature females. This would provide an insight into group composition and might clarify for which group a stopover could be most relevant. This study also documented a high annual return rate to the stopover area and fairly long feeding periods of some individuals. These findings suggest that this winter-foraging activity has become an important annual event for individual humpback whales. Therefore, future work should aim to understand which drivers might influence the decision to stop and whether these stopovers influence the overall fitness of individual whales.

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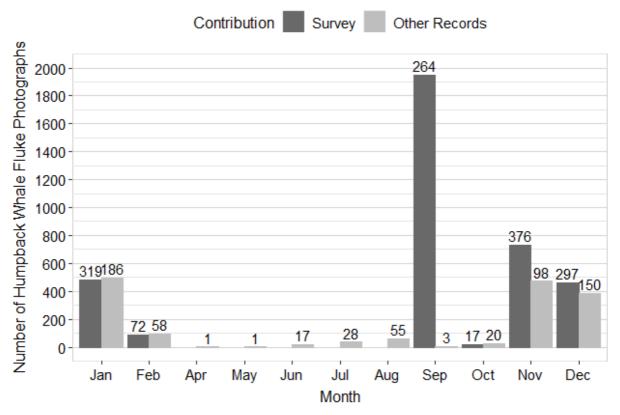
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# Appendix

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**S 1.** Total number of NNHWC fluke photographs registered per month and by contribution from 2010 to 2019. Survey (dark-gray) represents effort-based data collection. Other records (light-gray) represent non effort-based data submission by various contributors. Numbers on top of bars correspond to the total number of individual humpback whales identified per month. Individuals identified by surveys were not listed again in other records.

	Summer feeding Barents Se	Winter feeding area northern Norway								
ID	Location	Date	2012/13	2013/14	2014/15	2015/16	2016/17	2017/18	2018/19	Within-season re-sighting
1	Hornsund	28/08/2018			K				S	
2	Hinlopen strait	12/07/2013	K	K	K					
3	Hinlopen strait	07/07/2014		Κ	Κ	Κ	Κ		S	
4	Hinlopen strait	07/07/2014		Κ	Κ	K	K			
5	NE- Svalbard	19/07/2012	K							
6	NE- Svalbard	25/08/2012	K		K; A	Κ	Κ			
7	NE- Svalbard	25/08/2012	K							
8	Olga strait	03/09/2018		K						
9	Olga strait	03/09/2018				K		S	S	
10	Kong Karls Land	04/09/2018		K						
11	Kong Karls Land	04/09/2018				Κ	Κ			
12	Kong Karls Land	04/09/2018							S	
13	Kong Karls Land	05/09/2018	K	K; A	K	Κ	Κ			
14	Kong Karls Land	05/09/2018	K							
15	Kong Karls Land	05/09/2018	K	Κ	K		K	S		
16	Kong Karls Land	05/09/2018	K	Κ		K				
17	Kong Karls Land	05/09/2018	K; A							
18	Kong Karls Land	05/09/2018		K	K	K				

**S 2.** Photographic sighting history of 39 individual humpback whales matched between the Barents Sea and northern Norway. Individual 36 was observed twice in both regions. A = Andøya, K = Kvaløya, S = Skjervøya represent the three locations within the winter feeding area in northern Norway. Seventeen within-season re-sightings are shaded in dark-gray.

19	Kong Karls Land	05/09/2018		K	K				S	
20	Kong Karls Land	05/09/2018			Κ	Κ		S	S	
21	Kong Karls Land	05/09/2018				K				
22	Kong Karls Land	05/09/2018				K				
23	Kong Karls Land	05/09/2018							S	
24	Kong Karls Land	08/09/2018		K; A	Κ	K; A		S	S	
25	Kong Karls Land	08/09/2018			Κ		Κ			
26	Kong Karls Land	08/09/2018			А	K				
27	Kong Karls Land	09/09/2018	Κ	Κ						
28	Kong Karls Land	09/09/2018	А	К						
29	Kong Karls Land	09/09/2018		K						
30	Kong Karls Land	09/09/2018			K	Κ				
31	Kong Karls Land	09/09/2018			K	Κ		S		
32	Kong Karls Land	09/09/2018			K					
33	Kong Karls Land	09/09/2018	Κ							
34	Kong Karls Land	09/09/2018				K				
35	Kong Karls Land	09/09/2018							S	
36	Kong Karls Land	08/09/2018		А	K; A	Κ		S	S	
36	Border to Russia	08/08/2015								
37	Border to Russia	08/08/2015			Κ	Κ				
38	Border to Russia	08/08/2015		А	А					
39	Barents Sea (unkown)	19/06/2019		К						

