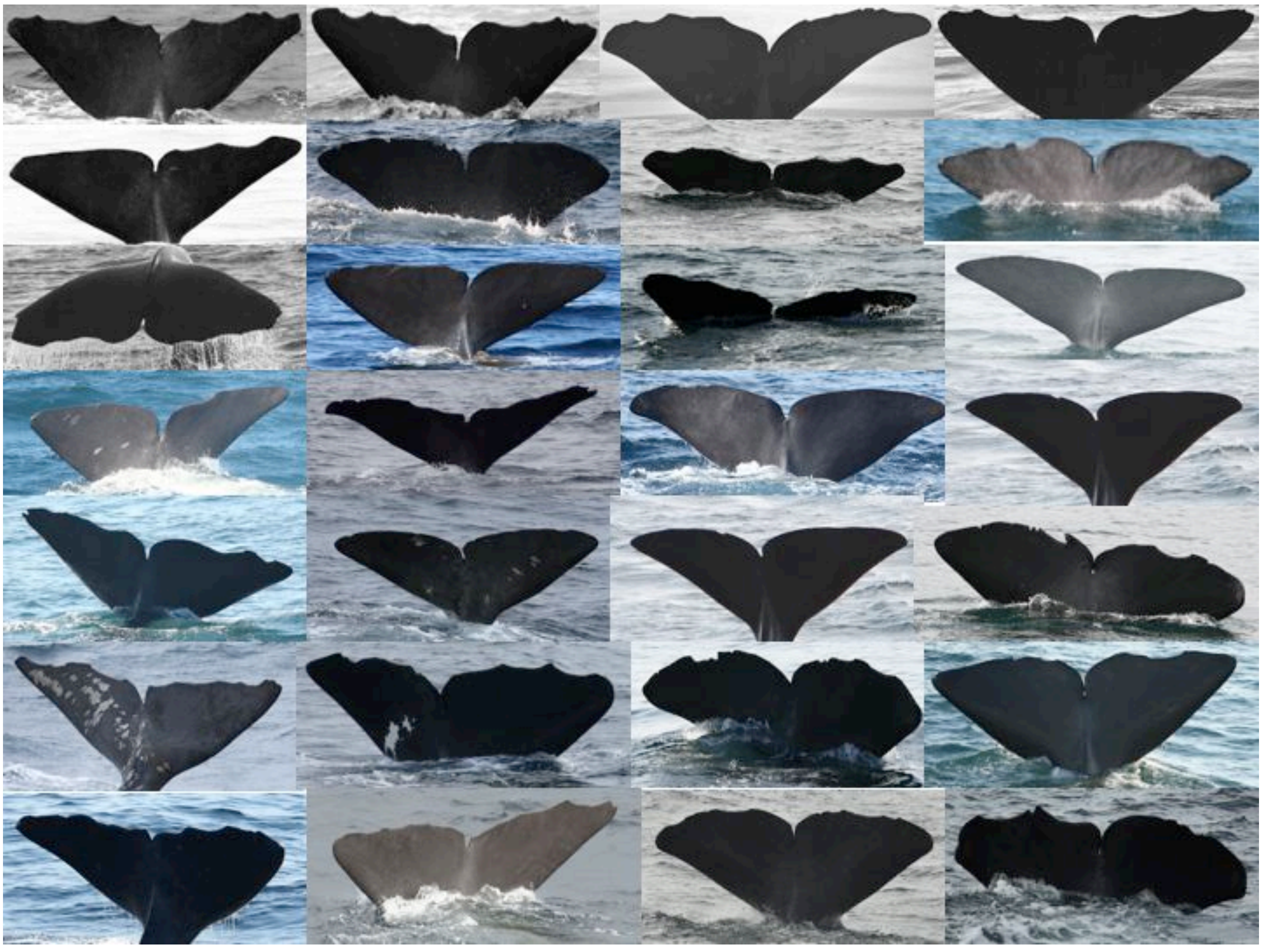
POPULATION ESTIMATION OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) FROM BLEIK CANYON, NORWAY



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PREFACE

Growing up in Ålesund on the west coast of Norway, I actually did not find the sea that special.
It was not until I moved to Oslo that I realized how much the sea really means to me, and how much I miss the salty air, the crushing sound of waves and almost being able to go fishing from my bedroom window. During my biology studies at the University of Oslo, I have come to realize that everything is so much more interesting when it lives in the sea. Even plants get my attention when submerged in seawater, and that is quite spectacular! So when the time to decide the future came, choosing marine biology was one of the easiest things I have ever done, and after some searching I found the perfect project for my thesis, which had all the important features: a lot of field work, a lot of ocean and a huge study animal – the sperm whale.
I did not know anything about sperm whales when I started this thesis, but thanks to all the people working at Whalesafari Andenes in 2009 and 2010, I have learned so much about sperm whales, about the ocean and about people – thank you all for that!

This work was supported by Whalesafari Andenes Research Department (Norway).
I especially want to thank the former guide coordinator Camilla Ilmoni for letting me come to Andenes and participate in the photo-ID project in the first place, and for lending me her copy of Whiteheads number one sperm whale book, which was my most protected item during my studies in Australia. I want to thank the current guide coordinator and research responsible, Daniele Zanoni, for all his great advice about photographs, sperm whales and on my thesis. I also want to thank Erland Lettevall for being a good consultant during my work and for sending me a copy of his thesis, which has been much in use. I want to send a special thanks to all the researchers from the previous years back to 1987 for your efforts, skills and devoted work, without you this thesis would not exist; Morten Lindhardt, Hanne Strager, Erland Lettevall, Daniele Zanoni, Tuula Skarstein, Vivi Fleming, Luca Lamoni, Marta Acosta, Camilla Ilmoni, Montserrat Domingo, Lara Polo, Luca Tassara and all the other people who has contributed in making this one of the largest sperm whale catalogues in the world!

I also want to thank my supervisors Stein Fredriksen at the University of Oslo and Arne Bjørge at the Institute of Marine Research for all the advice they have given me during these two hectic years, and for encouraging me in my work. Thanks to Tore Schweder at the University of Oslo for giving me valuable insight to statistics, and to all my friends and colleagues at the Biological Department at the University in Oslo for their support, advice, smiles and valuable comments to my thesis. Finally, I want to thank my friends and family for encouraging me to follow my heart in choosing my future, and to you, Magnus Viddal, for always being there for me. The thought of being finished as a student is a little less scary when I know that you will be there, as well as my dear Tonje Gladheim!

Elisabeth Støhle Rødland
Oslo, June 1st, 2011

1 INTRODUCTION

1.1 Purpose of this investigation

The sperm whale is one of the most widely distributed species on the planet. Migrating males are found in all deep oceans between the Arctic and Antarctic ice edges (Rice, 1989). Genetical analyses have not documented strong differences between sperm whales in various parts of the world oceans (Lyrholm, 1999; Lyrholm, 1998; Dillon, 1996), and animals from the same ocean differ even less (Dufault, 1999). This indicates an extended rate of migration.

In the Norwegian Sea, previous studies (Øien, 2009) have shown that the sperm whales have almost a uniform distribution south of 73°N. The presence of sperm whales in Bleik Canyon off Lofoten in northern Norway is one of the closest aggregations near land, and there have been several previous studies including acoustics (Møhl *et a*l., 2000; Madsen 2002; Teloni *et al*., 2008, Lamoni 2011) and photo-identification (Ciano and Huele, 2001; Lettevall, 2003; Zanoni, 2004), on these sperm whales. Analysis of the photo-identifications indicated that the group of sperm whales in Bleik Canyon formed an open group with a few individuals present for many years and a large group of exchanging males, mainly younger adults. The annual number of individuals has been estimated to range between 31 and 149 individuals in the period 1988-1999 (Lettevall, 2003). Zanoni (2004) estimated a maximum of 35 different individuals in Bleik Canyon during the 2002 season, and about 1/3 of them were replaced every two weeks.

My investigation was designed to be a continuation of previous studies on photo-identification in Bleik Canyon. I had access to ID-photos for the years 1987-2010, with the exception of 1998 and 2001. Due to the results of previous studies, I expected to find a movement of young mature males into the Bleik Canyon water. I also expected there to be a certain flux out of this pool due to mortality and movement either to the southern latitudes for mating or to the higher latitudes in search of other feeding grounds.
The aim of this project is to update the current knowledge of the feeding aggregation of sperm whales off the coast of northern Norway. Two hypotheses were selected for this study:

1. The number of sperm whales in Bleik Canyon has fluctuated without a trend
2. The sperm whales in Bleik Canyon form a loose feeding aggregation

1.2 General biological background

The sperm whale (*Physeter macrocephalus* Linnaeus, 1758) is the largest living member of the toothed whales (Odontoceti) and belongs to the family Physeteridae as the only living species. The sperm whales separated from the rest of the toothed whales about 20-30 million years ago, and their closest relatives belong to the family Kogiidae, the pygmy and dwarf sperm whales. As well as being the largest of the odontocetis, it is also the most sexually dimorphic of all cetaceans in both body length and weight (Whitehead, 2003). The largest sperm whales recorded by Rice (1989) was 11,0 m in length and 24,0 tons for females, and 18,1 m and 57,1 tons for males. However, a few individuals have been recorded to be longer from snout to tail (females: 12,5 m; males: 18.3 m). The dimorphic differences between the sexes in sperm whales are almost entirely due to the large size difference. The body proportions are the same for all body parts, except a slightly shorter head in females compared to males. The sperm whales have a quite distinct body shape (Figure 1), due to its large barrel-shaped head. The head is in fact about one-third of the total body weight and one-quarter of the body length (Clarke, 1978)

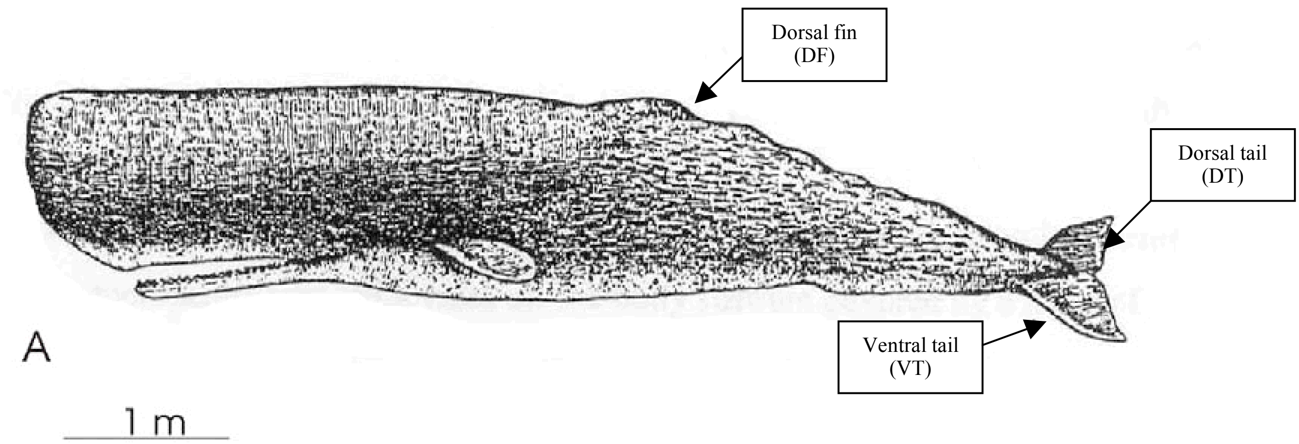


Figure 1: Full body morphology of a sperm whale (Madsen, 2002)

Females usually reach sexually maturity much earlier than males, starting at 7-13 years. After this, the growth will steadily decrease until they cease growing when they reach physical maturity (25-45 years old) (Rice, 1989). Males usually reach full sexual maturity at the age of 18-21 years (Rice, 1989). They have a delayed physical maturity, which means that they will continue to grow at a constant or even higher rate after reaching sexual maturity, and cease growth much later than females (from 35-60 years old) (Rice, 1989). Males use their large body size to compete for female attention, and are therefore usually not able to reproduce until they are well over 20 years old.

The female sperm whales are usually observed at latitudes below 40° N and S, mainly restricted by a sea surface temperature above 15ºC (Whitehead, 2003). Females gather in groups with other females and their calves. The young females usually stay in the same group as their mother for the rest of their lives (Best *et al*., 1984). The females are also rarely found in waters shallower than 1 km deep. Males, on the other hand, lead completely different lives. Most of them will leave the female group they were born into even before they reach puberty at the age of 7-11 years (Rice, 1989) and can often be found in "bachelor groups": loose aggregations of males of about the same age. As they grow older, these groups get smaller and move closer towards the ice edges (Whitehead 2003).

The largest aggregations of adult males are in areas of deep water, often called "grounds" (Rice, 1989), from a few hundred meters to several thousand meters deep, although they are also found in quite shallow waters such as close to shore off British Colombia and South Africa (Best, 1999; Gregr et al., 2000). These grounds are usually, but not always, associated with areas of high primary and secondary production. Recent studies have tried to observe the distribution of sperm whales on different scales, both spatial and temporal (Jaquet and Whitehead, 1996; Jaquet *et al*., 1996; Griffin, 1999; Biggs *et al*., 2000). These studies have shown that biological or oceanographical features alone cannot explain all the variability in their distribution. As the sperm whale diet includes mainly deep-water species of squid, cephalopods and fish (Kawakami, 1980; Rice, 1989), a lag in both time and space will be expected when comparing the sperm whale distribution to peaks in chlorophyll concentrations (Jaquet 1996a). It is therefore difficult to relate the sperm whale distribution to the traditional measures of high primary production. When looking at smaller spatial scales, like the "grounds", it is observed that the depth and topography have no influence on the distribution and the whales seem to be equally present in both shallow and deep areas (Jaquet and Gendron, 2002).

2 MATERIALS AND METHODS

2.1 Study Area

The study area for this master thesis was the Bleik Canyon (Bleiksdjupet) (Figure 2) in the Norwegian Sea, which is also referred to as the Andøya Canyon because it is situated about 15 km northwest of Andenes, Andøya (69°25′N 15°45′E). The canyon is about 40-50 km long (Lettevall, 2003), has a maximum width of 20 km between the canyon shoulders and a maximum depth of about 3000 m at the mouth of the canyon (Laberg *et al*., 1999).

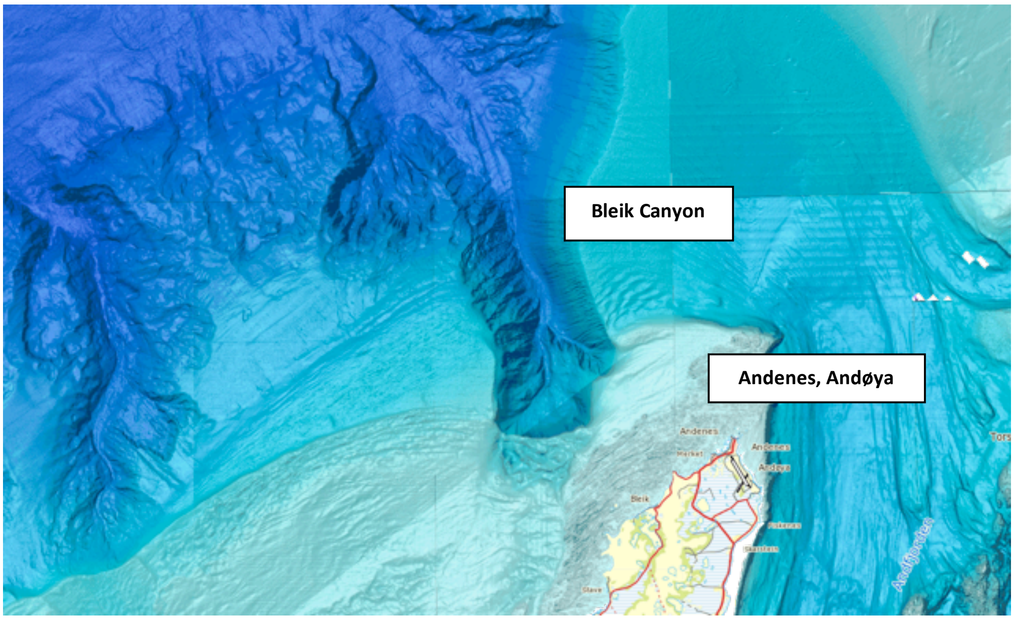


Figure 2: Map of the location of Bleik Canyon in relation to Andenes, Andøya. (http://www. MAREANO.no)

The canyon is the starting point of the Lofoten Basin Channel, which is the down slope continuation of the Bleik Canyon (Laberg *et al*., 1999). This system was possibly created before the Quaternary period, and the Bleik Canyon has not been active in terms of sediment transportation on a large scale since the Holocene (Laberg *et al*., 1999). The shelf topography off northern Norway is dominated by a large number of small shallow banks separated by troughs, and this topography has great influence on the Coastal currents circulation (Sundby, 1984). The Bleik Canyon has quite steep sides, filled with cracks and slide scars, which makes the area quite complex (Figure 3; Laberg *et al*. 1999, 2007).

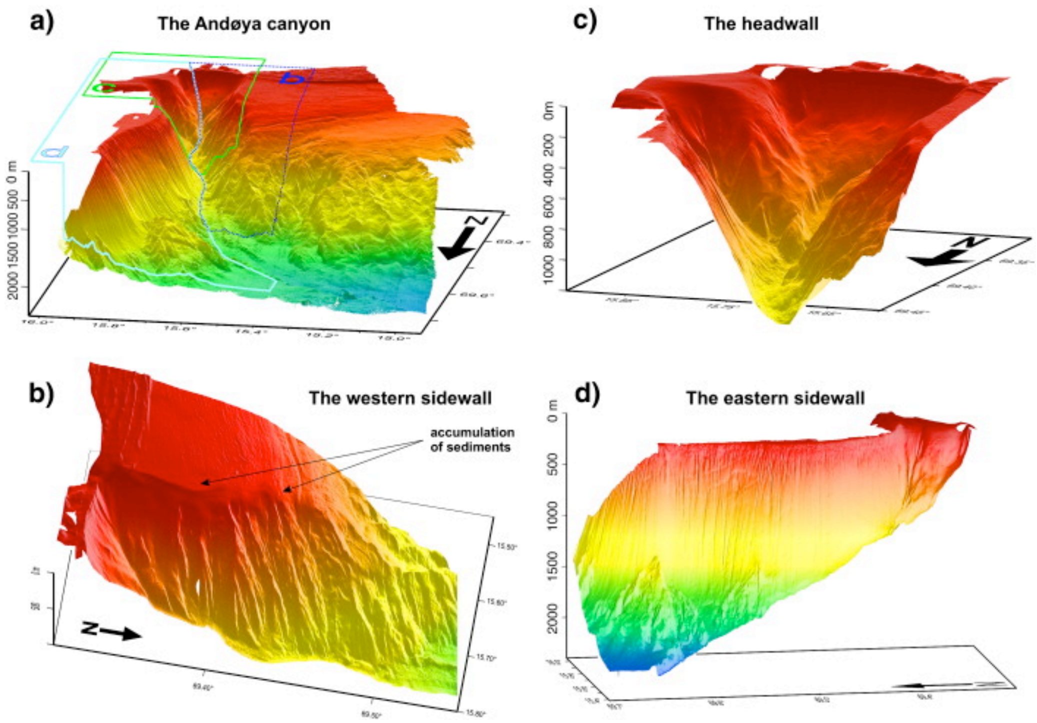


Figure. 3 Graphical presentation of the morphology of Bleik Canyon (From Laberg et al. 2007)

The canyon is highly productive because it induces upwelling in the current system (Blindheim, 1985; Sundby, 1984). There is a large production of both zooplankton and fish (Brander and Hurley, 1992), and they attract larger fish, cephalopods, sea birds and marine mammals (Skjoldal, 2004). These waters also attract sperm whales since fish and deep-sea cephalopods form an important part of their diet (Kawakami, 1980). The area is also especially suited for whale research because the Bleik Canyon is so close to land that daily observation expeditions are possible. Collaboration with the commercial whale watching company Whalesafari Ltd., makes it possible to collect data throughout the whale watching season. Figure 4 shows the area in the canyon covered on our surveys in 2009 and 2010.

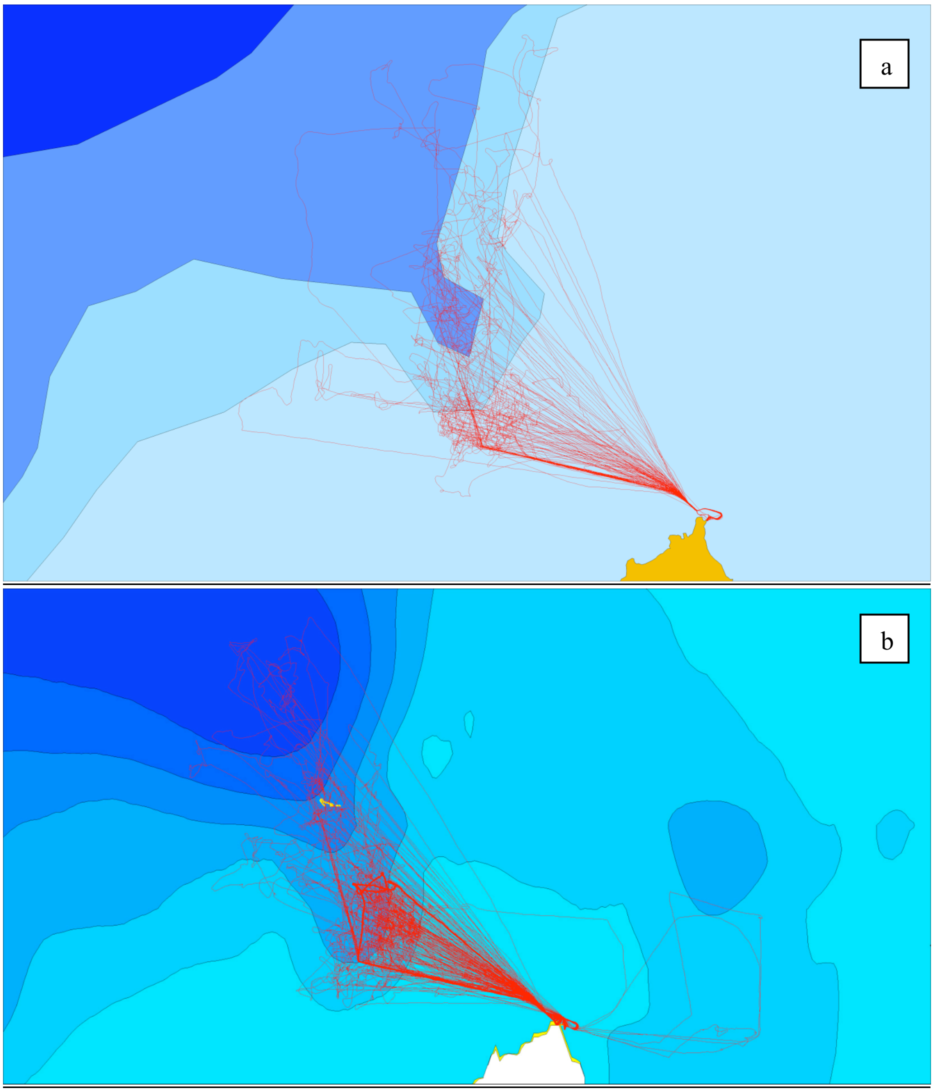


Figure 4: GPS routes of the area sampled by MS Reine and MS Maan Dolphin for a) 2009 (01.07-29.07.) (Luca Lamoni) b) 2010 (29.05-11.09.) (Luca Tassara).

2.2 Data collection

The data set for this investigation consisted of photo-ID pictures of sperm whales taken from Bleik Canyon, Andøya, in the period 1987-2010. In 2009 and 2010, I participated in the sampling of material from Bleik Canyon myself. Sampling was done during the whale-watching season, which starts about 15th of May and may last until about 15th of September, depending on the weather and amount of tourists. The material was sampled from whale watching vessels of Whalesafari Andenes Ltd., and the sampling rate was closely linked to the number of trips possible per day. In the period mid-June to July and mid-August to September, there was usually a minimum of one trip per day, and in the high season (July-August) there might be up to three trips per day per boat. For the sampling, at least one person per boat was needed to take the photographs and collect all the data possible. For every trip, data collection sheets (Appendix 1) were used where the observer notes the position and time of every observation, as well as other notes considered important for identifying the specific individuals. The observer did also take notes on behavior that could help to identify an individual before physical features were recognized, or simply for other studies than photo-identification.

During the high seasons in 2009 and 2010 Whalesafari Andenes Ltd. had two boats in use, and both were available for photo-ID sampling. MS Reine (Figure 5a), which was an old sealing vessel, and MS Maan Dolphin (Figure 5b), a catamaran cruise ship. On both vessels hydrophones were used to locate the sperm whales when they were beneath the surface and to follow them until they resurfaced for air. Additionally, the horizon was searched for spouts to locate the whales that were on the surface.

Figure 5: The Whale Watching vessels of Whalesafari Andenes Ltd. (a) MS Reine, (b) MS Maan Dolphin (Photo: Whalesafari Andenes Ltd.)

When a sperm whale was spotted, the boat was positioned behind the whale (Figure 6a), so it was easy to see the whole fluke when the whale started a dive. The whale does not stay still on the surface, but slowly swim while it is refilling its oxygen stores. The whales can be scared off if the boat comes too close or makes loud noises. Therefore the boat kept its distance and carefully followed the whale until it submerged. The best time to take a photo-ID picture is when the fluke of the whale is completely vertical (Figure 6b) because then the whole fluke contour can be seen.

Figure 6: Observing ID-192 in 2010. (a) Tourists on board the Whalesafari vessel MS Maan Dolphin. (b) ID-192 in vertical position and ready to disappear under surface (Photo: Elisabeth Rødland, Whalesafari Andenes Ltd).

2.3 Equipment

In 2009 and 2010 a GPS Garmin Extrex H was used to get the correct position of each sighting, as well as tracking the route of the boat on every trip (Figure 4). In previous seasons the coordinates of the sightings have been written down from the GPS located in the steering house on the boat.

Different cameras have been used in previous seasons; all mainly analogue cameras. In 2009 and 2010, two digital cameras were used, a Canon Eos 5D (body) and a Canon Eos 1000D (body) with two types of lenses, Canon EF lens 100-400 mm and Canon EF lens 70-300 mm.

2.4 Categorization of pictures

All data were continuously organized. The observation logs were transferred from the data collecting sheets to excel files stored at the station. The pictures were uploaded and renamed to have all the information needed to categorize the pictures. To avoid using too much space and to make the Photo-ID work easier, only pictures of the dorsal fin (DF), dorsal tail (DT), and ventral tail (VT) if possible, were kept. If the animal was already known and pictures of all the markings needed already existed, only the best picture of this observation was kept (often the VT).

The pictures were renamed according to a filing system that comprised date, boat and trip number, observation number and picture category. Example: 100724-RE1-023VT.
100724 is the date (year-month-day), RE1 is the first trip with MS Reine that particular day, 023 the observation number and VT is the category. All sperm whale encounters where there was a picture of a DF, DT or VT were given an observation number. The observation nr start on 001 and each boat has its own observation numbers. So RE1-001 is the first observation made onboard MS Reine in the given year, and MD1-004 is the fourth observation made onboard MS Maan Dolphin. From each date, the best ID-picture of all the observations was extracted and organized into individual folders, named according to when they were first seen (ID_year). So the 01_10 would be the individual first observed in 2010. After the season was over, all pictures were matched again to make sure that there were no duplicates and then the new ID-numbers for the ID-catalogue were given to all new individuals.

2.5 Matching of the individuals

Markings on the tail/fluke were used for the identification of individual sperm whales.
These markings (Figure 7) were either skin pigmentation (birth marks, scar tissue) or different types of marks where parts of the fluke were missing. Whitehead (1990) defined 7 different mark types for identification; nicks, distinct nicks, scallops, waves, holes, tooth mark scars and missing portions. Also the shape of the fluke can be used for identification, distinguishing between an open or closed fluke notch (Whitehead, 1990). We also used markings on other places of the body if such occurred.

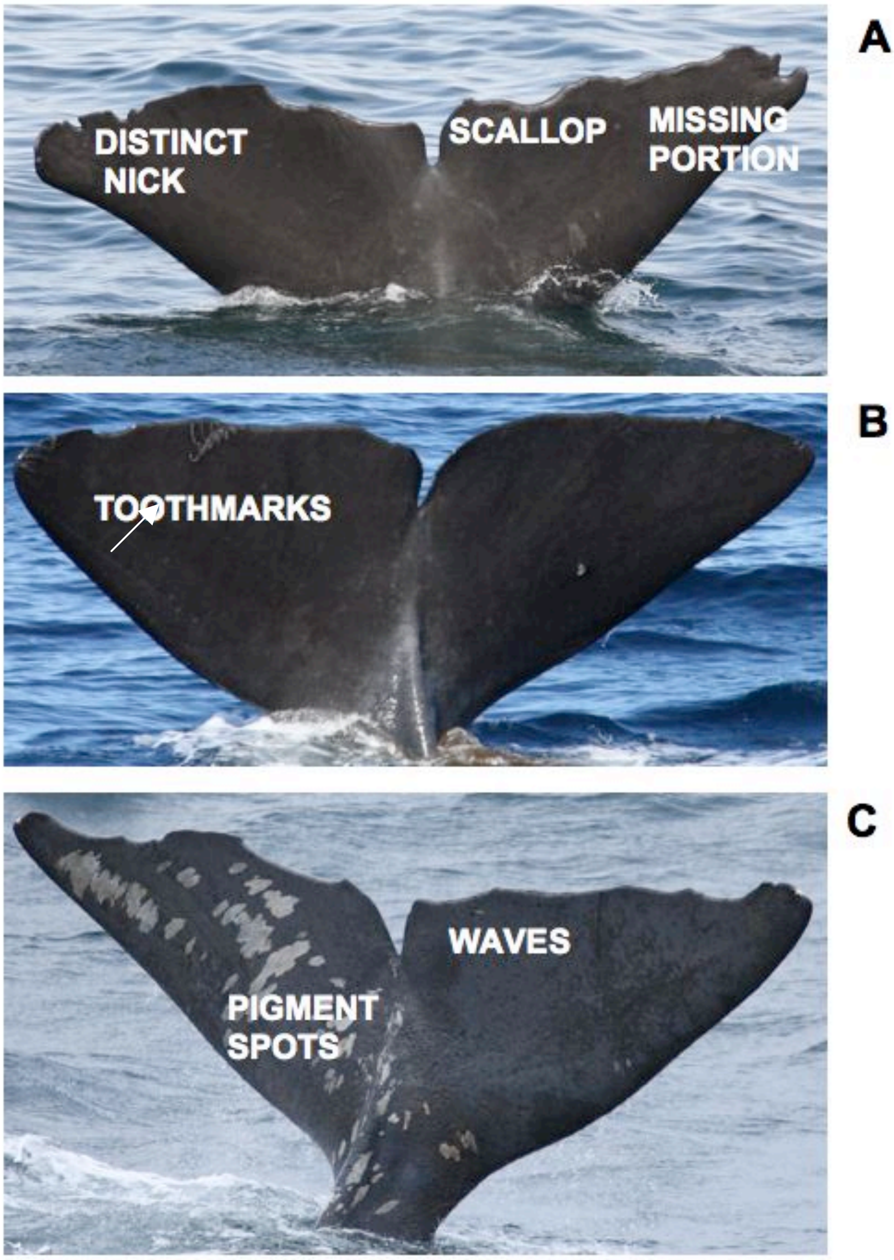


Fig. 7 (A-C): Examples of the different types of markings used to identify sperm whale individuals (Photo: Whalesafari Andenes AS)

2.6 The datasets

The first dataset, D1, comprises all 22 seasons in one dataset, and includes the encounter histories of all the individuals seen throughout the study. The encounter histories are in a 101010-format, where the animal is scored 1 if it is seen that season and 0 if it is not. The advantage of using this dataset is that one can get a good overview of the number of years an individual has been seen in the canyon, which individuals are present in which year and the how this changes radically after only a few years. However, this dataset also has its flaws. It does not tell us anything except which year an individual was seen, as multiple sampling occasions of the same individual during a season is ignored. Information about how many days they are seen during this season is not available in this dataset and therefore leaves out a lot of valuable information that may be helpful in making a better estimation. This information can however, be found in the additional datasets, D2-D17, one dataset for each season. Due to inconsistent sampling effort and missing data, seasonal datasets was not available from the years 2001 to 2007. In the seasonal datasets, each season was divided into smaller periods of 3-4 days, which was the mean number of days individuals were seen in the canyon in 2008-2010. The encounter histories of the individuals were scored in the same way as for D1. A total of 3856 ID photographs were taken during the study (Table 1). The number of photographs discarded on the basis of quality was uncertain for many of the seasons and therefore not included.

Table 1: Number of ID photographs taken each season and in total. The table also shows the number of discarded photographs, for all years available.

Year	No. of photos	Discarded photos
1987	25	
1988	39	
1989	93	
1990	173	
1991	178	
1992	185	
1993	294	
1994	188	
1995	252	
1996	426	
1997	460	
1999	96	
2000	58	
2002	259	41
2003	105	
2004	113	19
2005	58	63
2006	35	
2007	27	1
2008	172	16
2009	305	24
2010	315	16
Total	3856	180

2.7 Mark-recapture abundance estimation

For the statistical analysis of the sighting records, a mark-recapture approach was found most appropriate. Mark-recapture methods have been used for describing animal populations since the early 1900s (Petersen, 1889; Dahl, 1917; Lincoln, 1930) and is today one of the most important methods in population ecology. Several software programs have been developed to handle mark-recapture estimation (Otis *et al*., 1978; White *et al*., 1978; White and Burnham, 1999; Efford *et al*., 2004). Previous sperm whale studies from Bleik Canyon (Lettevall *et al*., 2003) have used the program MARK (White & Burnham, 1999), and this program was therefore chosen for this study as well.

Generally, the idea of mark-recapture methods is to estimate the size of a population by marking a subset of the population, releasing them and then sample a new subset and thus calculate the proportion of marked animals that was recaptured. Mark-recapture methods are based on sampling and resampling of individuals in a certain area, and therefore provide estimates of the number of animals using this area, rather than the total population size (Boyd *et al*., 2010). Information about individual capture histories is required for mark-recapture estimation.

The simplest way of estimating the total population size (N) is using the Peterson estimator, which only utilize a single capture occasion and one single recapture occasion. In the capture occasion, n_1 individuals are captured, marked and released back into the population. In the recapture occasions, n_2 individuals are captured of which m_2 are marked. Under the assumption of random mixing, the proportion of marked animals in the recapture occasion will be the same as the proportion of marked animals in the population, so

$$\frac{m2}{n2} = \frac{n1}{N}$$

Hence the size of the population is estimated as

$$N = \frac{n1n2}{m2}$$

and the capture probability (p) is estimated as the proportion of marked animals captured:

$$\frac{m2}{n2} = p$$

so the population estimator may be written as

$$N = \frac{n1}{p1} = \frac{n1m2}{m2}$$

This basic estimator may be extended to multiple sampling occasions. In each sampling occasion except the first, both the number of recaptures and new captures can be estimated. The length of this study is crucial with regard to the influence of changes in the population caused by factors like births, deaths, immigration and emigration (Boyd *et al.*, 2010). If these factors are negligible, the population is defined as closed. If not, it is defined as open. The program MARK allows exploration of both assumptions (Cooch and White, 2010).

Closed model with multiple sampling occasions

Assuming that the aggregation of male sperm whales in Bleik Canyon is closed during the investigation period, it is possible to use closed mark-capture models to estimate the size of the aggregation (the modification of adding 1 is motivated by avoiding the huge numerical dominance of small recapture in the denominator).

$$N = \frac{(n1+1)(n2+1)}{(m2+1)} - 1$$

The assumptions of the closed population (from Cooch and White, 2010) are:

i) There is no immigration, emigration, births or deaths
ii) Marks are not lost or overlooked
iii) All individuals have the same probability of being captured (p) and recaptured (c)

Only 'closed-capture' models where the abundance was conditioned in the likelihood (Otis et al., 1978) was included in this study. Four closed models were explored; two of which were based on the 'closed capture' models of Otis *et al.* (1978) and the second two were based on the slightly different parameterization 'closed captures with heterogeneity', in which two or more mixture groups can be incorporated to deal with heterogeneity in the capture and recapture probability amongst individuals. For this study, two mixture groups were applied, representing the observed presence of transients and residents in Bleik Canyon. Details on these models can be found in Appendix 2.

Open population models (Jolly-Seber)

Assuming that the aggregation of male sperm whales in Bleik Canyon does not follow the assumptions of a closed population, a range of open models based on the original Jolly-Seber model can be applied. The general idea of open models is that permanent emigration and immigration may occur during the sampling period, as well as deaths and births.

The assumptions of the Jolly-Seber models are (from Cooch and White, 2010)

i) Marks are not lost or overlooked
ii) All individuals have the same probability of being captured (p) and recaptured (c) during each sampling occasion
iii) The study area is constant

Open population models are very flexible and can provide estimates for survival (φ), recruitment and population growth as well as estimates of abundance. In this study, the POPAN formulation of the Jolly-Seber models, by Schwarz and Arnason (1996) was used. This formulation is a parameterization of the original Jolly-Seber model, where a metapopulation (Ni) is assumed to exist. All animals observed in the study population would then belong to this metapopulation. It uses the same parameters p_i and φ_i as the original Jolly-Seber model, but also includes the parameters b_t (β) which represents the probability that an animal from the metapopulation would enter the study population between t and t_{+1}. Assuming that all animals have the same probability of being captured during each sampling occasion is one of the most crucial assumptions for the Jolly-Seber models. Having assumed equal probability of capture for all the individuals, original Jolly Seber models are unable to take into account individual heterogeneity that might occur in the datasets. Details on the models used can be found in the Appendix.

The equations used in the POPAN models can be described as followed:

The number of animals in the study population at occasion 1 is estimated by

$$N1 = \beta 0 \ x \ N$$

The number of new animals (by births, B) entering population before occasion i is estimated by

$$Bi = \beta i \ x \ N$$

The size of the metapopulation (Ni) on occasion 1 is estimated by

$$Ni = (N(i-1) - loss\ on\ capture)\ x\ \varphi(i-1) + Bi$$

3 RESULTS

3.1 Sightings and resightings

3856 fluke photographs from Bleik Canyon contained a total of 411 individually identified male sperm whales. With only two years missing in the period of 1987 to 2010, this study has 22 years of seasonal sampling and therefore one of the most comprehensive photo-ID databases for sperm whales. The seasonal identification rate (the total number of identifications (n) divided on the total number of ID-photographs) varied between seasons; from 0.07 to 0.56 with a mean of 0.26 (SD ± 0.10) (Figure 8, Appendix 6). The ratio of new individuals also varied a lot between seasons; from 0.09 to 0.89 with a mean of 0.46 (SD ± 0.22) (Figure 9, Appendix 3).

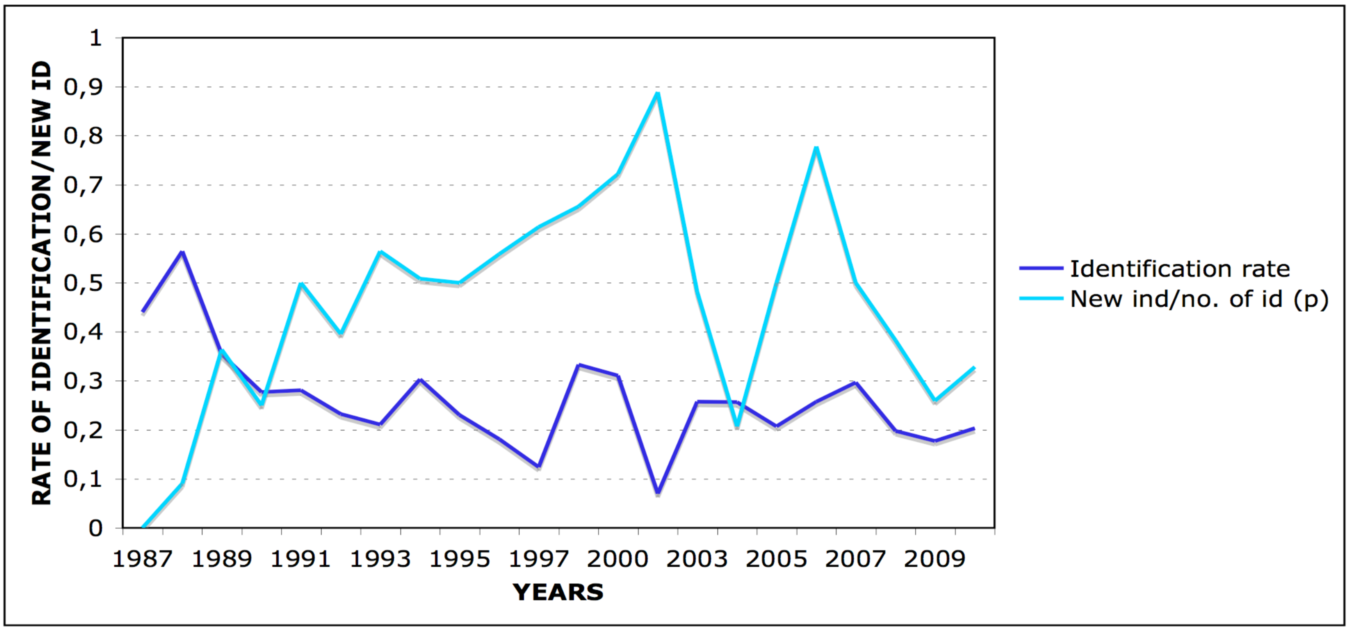


Figure 8: Identification rate, which is the total number of identifications (n) divided on the total number of ID-photographs, and the rate of new individuals against the total number of individual (n).

The number of individuals spotted each season varied a lot (Figure 9, Table 2). The total number of individuals seen the very first year of the study was quite low; only 11 individuals. However, the number of sightings gradually increased in the following years, until it reached a peak in 1996; with a total of 67 individuals recorded. After 1996, the sightings decreased, and from 1999 to 2006 the number of sightings was very low compared to the previous years. 2007 has the record of the lowest number of individuals seen in a season so far, with only 8 individuals recorded. In 2008, the number of sightings increased again, and continued to increase in 2009 and 2010. The number of resighted animals increases from 2 animals in 1988, which is the first year of resightings, and up to 38 resighted individuals in 1996.

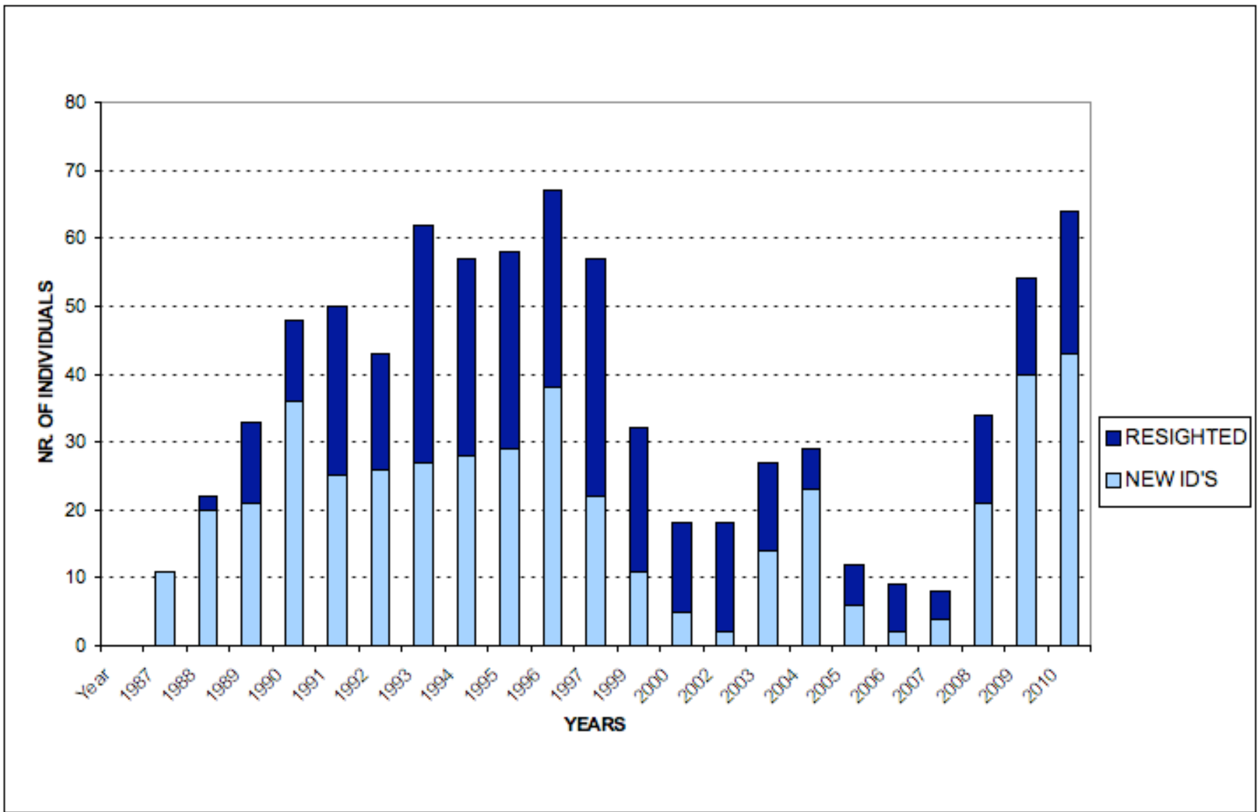


Figure 9: Number of individuals sighted and resighted in Bleik Canyon in the period 1987-2010

Table 2 includes a simple estimation of the seasonal abundance ($N_t = M_t/\alpha_t$), which varied from 27 to 197 individuals, as well as the survival rate (probability for surviving to the next sampling period) for each seasons ($\Phi t = (M_{t+1})/(M_t+(s_t-m_t))$), which varied from -0.07 to 37,7.

More details on these calculations can be found in Table 2.

Table 2: Summary statistics for the complete study period from 1987-2010, including a simple estimation of the seasonal abundance (Nt) and the survival rate (Φt)

n_t: the number of animals captured at the season t, both marked and unmarked animals.

m_t the number of marked animals in the total captured at season t

u_t: the number of unmarked animals in the total captured at season t

s_t: the number of animals released back into the population after season t, which would be the same as variable n_t in this study because we are not actually capturing the animals

R_t: the number of animals in s_t that were caught again in a later season.

Z_t: the number of animals that were marked before season t, not captured in season t, but captured in a later season

α_t: the proportion of animals marked in season t (m_{t+1}/n_{t+1})

M_t: the total number of marked animals in the population in season t ($((s_{t+1})*Z_t)/(n_{t+1}) + m_t$)

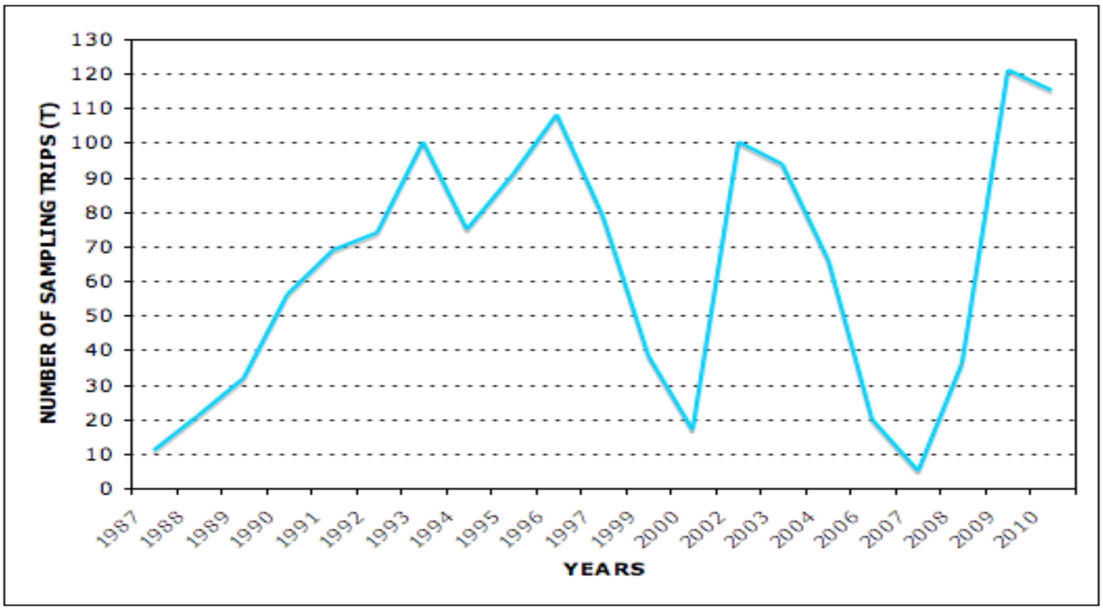
N_t: estimated number of animals in the population at season t (M_t/α_t)

Φ_t: estimated survival rate for season t, the probability of an individual surviving from season t to season t+1. ($(M_{t+1})/(M_t+(s_t-m_t))$)

SEASON	nt	mt	ut	st	Rt	Zt	αt	Mt	Nt	Φt
1987	11	0	11	11	7					12
1988	20	2	20	20	14	3	0,14	6,20	43,40	21,27
1989	32	12	21	32	23	6	0,39	20,25	51,40	21,88
1990	48	12	36	48	31	17	0,27	38,03	143,35	37,72
1991	50	25	25	50	28	23	0,51	65,45	128,38	26,33
1992	41	17	26	41	20	35	0,43	87,00	203,00	24,73
1993	60	35	27	60	35	17	0,59	63,81	108,11	26,37
1994	53	29	28	53	24	27	0,56	87,32	157,18	24,77
1995	50	29	29	50	31	24	0,59	67,25	114,33	22,07
1996	67	38	29	67	29	15	0,57	72,00	125,54	29,99
1997	55	35	22	55	19	13	0,64	71,40	111,07	20,54
1999	24	21	11	24	13	10	0,88	38,86	44,16	3,95
2000	15	13	5	15	7	12	0,88	37,00	42,29	2,79
2002	15	16	2	15	10	9	1,06	29,09	27,38	-0,07
2003	27	13	14	27	9	5	0,50	27,00	54,00	15,70
2004	29	6	23	29	8	12	0,23	46,00	197,14	23,57
2005	12	6	6	12	6	11	0,54	26,43	49,08	7,40
2006	9	7	2	9	3	12	0,80	37,00	46,25	2,41
2007	8	4	4	8	7	10	0,56	15,25	27,45	5,49
2008	34	13	21	34	17	5	0,40	22,72	56,81	22,45
2009	56	14	40	56	14	5	0,26	33,00	125,40	
2010	63	21	43	63						

Simple abundance index

Since these data are based on photo-ID pictures from opportunistic surveys, the appropriate index for the number of animals should be modified by the sampling effort measured as the number of sampling trips (Figure 10a). A simple abundance index is then obtained as the number of sighted whales (n) divided by the number of sampling trips (T) (Figure 10b). As seen in Figure 11a, the number of sampling trips in each year appears to fluctuate without a trend; from 11 trips in 1987 to 121 trips in 2010. 12 out of 22 seasons had over 60 sampling trips in total.



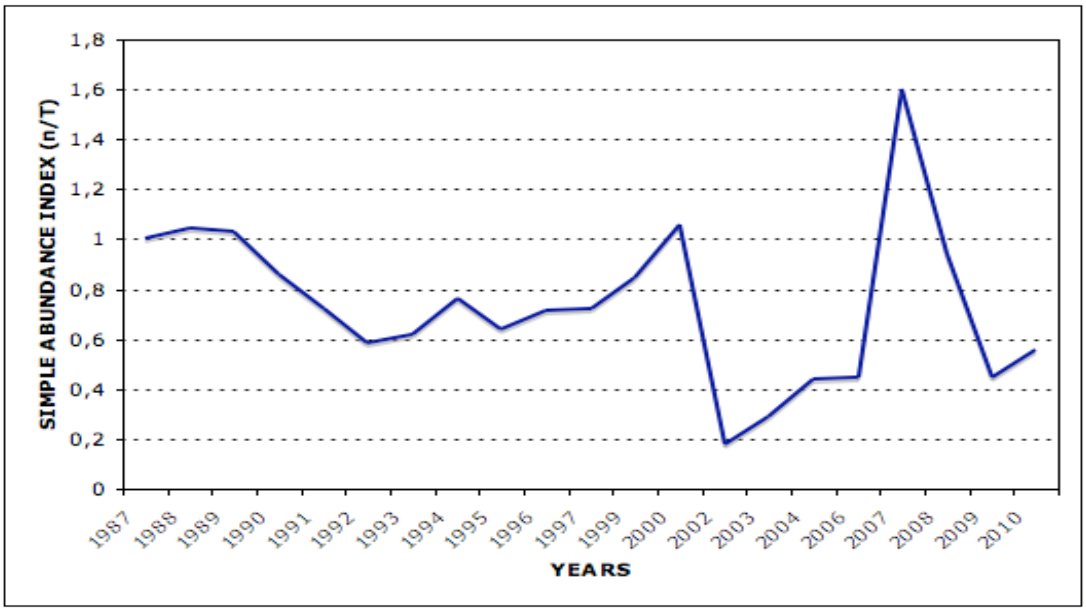


Figure 10: a) Number of sampling trips made each season of the study **b)** Simple abundance index of the sperm whales of Bleik Canyon: number of individuals sighted (n) divided on number of sampling trips (T)

However, only five days of sampling was recorded for 2007. The simple abundance index (Figure 10b) for each season is also fluctuating without a trend. For 16 out of 22 seasons, the abundance index is less than 1. This means that the number of sampling trips (T) is higher than the number of individuals seen (n). The lowest index was found in 2002 (0.18), where 100 sampling trips were performed, but only 18 individuals were sighted. The abundance index is close to 1 for seasons 1987 (1), 1988 (1.05), 1989 (1.03), 2000 (1.06), which means that the number of individuals seen is almost equal to the number of sampling trips. The highest abundance index was in 2007, the only year where the abundance index was higher than 1 (1.6). This means that the number of individuals sighted was higher than the number of sampling trips.

Relationship between individuals sighted and number of sampling trips

A strong covariance between the number of sampling trips (T) and the number of individuals sighted (n) is observed. A generalized linear model in the program R formally analyzed this covariance. A quasi-poisson distribution was found to describe the dataset best. The output from this analysis can be found in Appendix 4. The analysis found no significant ($P < 0.1$) yearly trend in the number of sperm whales sighted when the number sampling trips was taken into consideration. A test for covariability was also performed by simple linear regression (Figure 11), where the number of sampling trips (T) was plotted against the number of individuals sighted (n). The number of sampling trips described 57,5% of the variability in the sighting record ($P < 0.00001$; see Appendix 5), which supports the results of the covariance analysis.

On the basis of the simple abundance index, the covariance analysis and the covariability test, hypothesis 1 of this study can be considered confirmed on; there is no visible trend in the sperm whale abundance of Bleik Canyon.

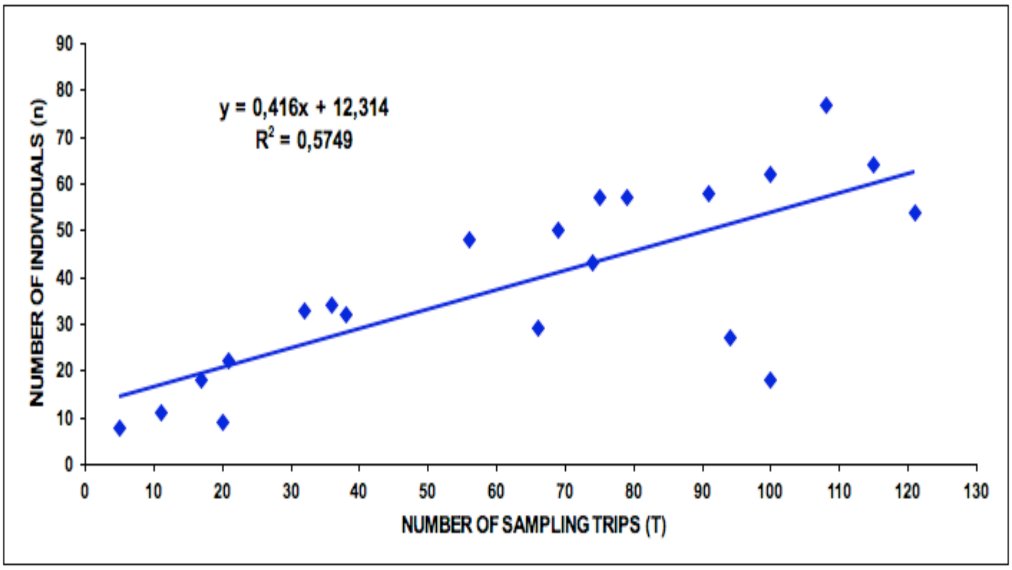


Figure 11: Scatterplot of individuals sighted (N) against the number of sampling trips (T) for the period 1987-2010.

3.2 Residency

Of the 411 individuals in this study, 251 (61 %) were only seen once during the 22 years. About 1 of 5 (78 individuals; i.e. 19 %) was seen in the canyon more than three years. Five individuals clearly have a stronger preference for the area than the other individuals since they were sighted 14 of the 22 years (Figure 12).

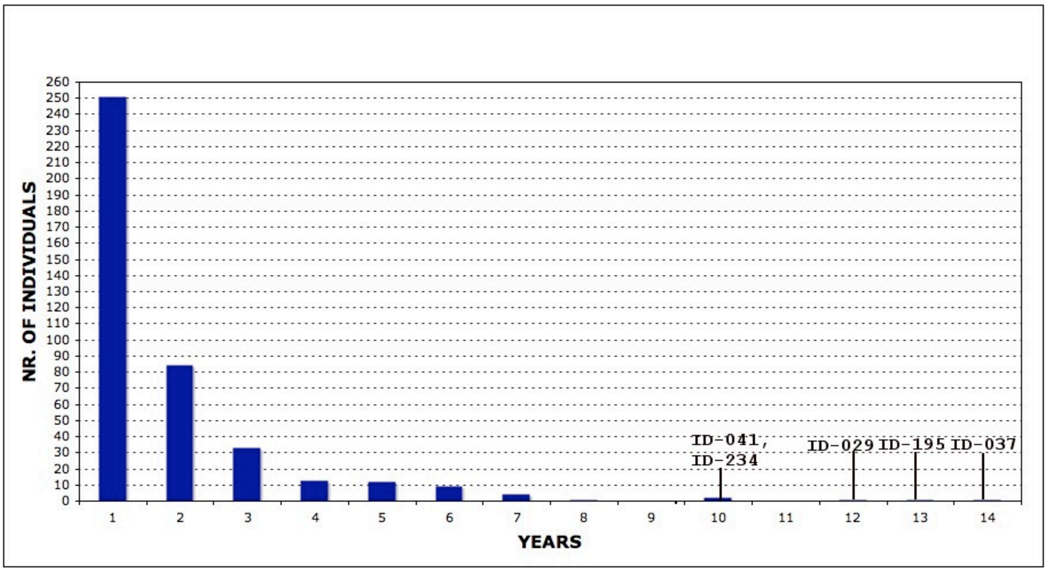


Figure 12: Number of individuals sighted in a particular number of years over Bleik Canyon in the period 1987-2010. Only five individuals were seen 10 or more years (ID-041, ID-234, ID-029, ID-195, ID-037)

On the basis of this, it does appear that the population in Bleik Canyon comprises both long-term residents and short-time visitors, or transients. A simple residency time was calculated as mean number of days observed in the canyon. Including all individuals observed from 1987 to 2010, the number of days observed was between 1 and 18 days, with a mean of 2.26 days. However, if we consider the individuals seen more than 3 days to be seasonal residents, and the individuals seen 3 days or less to be seasonal transients, then the mean number of days sighted was 1.53 days and 6.66 days for each group respectively (Appendix 7). The proportion of seasonal residents was quite low for nearly all years, between 0.00 and 0.29. However, in seasons 1990, 1991 and 1994 the proportion of seasonal residents was very large; 0.89, 0.79 and 0.87 respectively (Appendix 5).

Looking closer into the observations made in 2008, 2009 and 2010 (Figure 13), the residency seems to follow the same pattern as in Figure 12. A high percentage of the individuals are only seen on one single day in all three years (2008: 46%, 2009: 57%, 2010: 63%), and only a few individuals are seen more than ten days (2008: 6%, 2009: 6%, 2010: 3%). The most frequently observed individuals for all three years together were ID-195 (56 days), ID-192 (30) and ID-427 (24 days), ID-234 (19 days), (Table 3). Both ID-195 and ID-192 were first seen in 1993/1994, and ID-195 has been seen 12 years after this. It is therefore one of our most observed whales, both on year to year-basis and during the summer season. ID-234 was first seen in 1995 and is also one of the most observed males in Bleik Canyon, with 10 years of sightings in total. ID-427 is on the other hand one of the newcomers in the area, with first appearance in the dataset in 2008.

The small proportion of residents seen in consecutive years combined with the high proportion of transients suggests that the sperm whales of Bleik Canyon do not constitute a population of its own, but rather a loose feeding aggregation. On the basis of these observations, hypothesis 2 of this study can be considered confirmed.

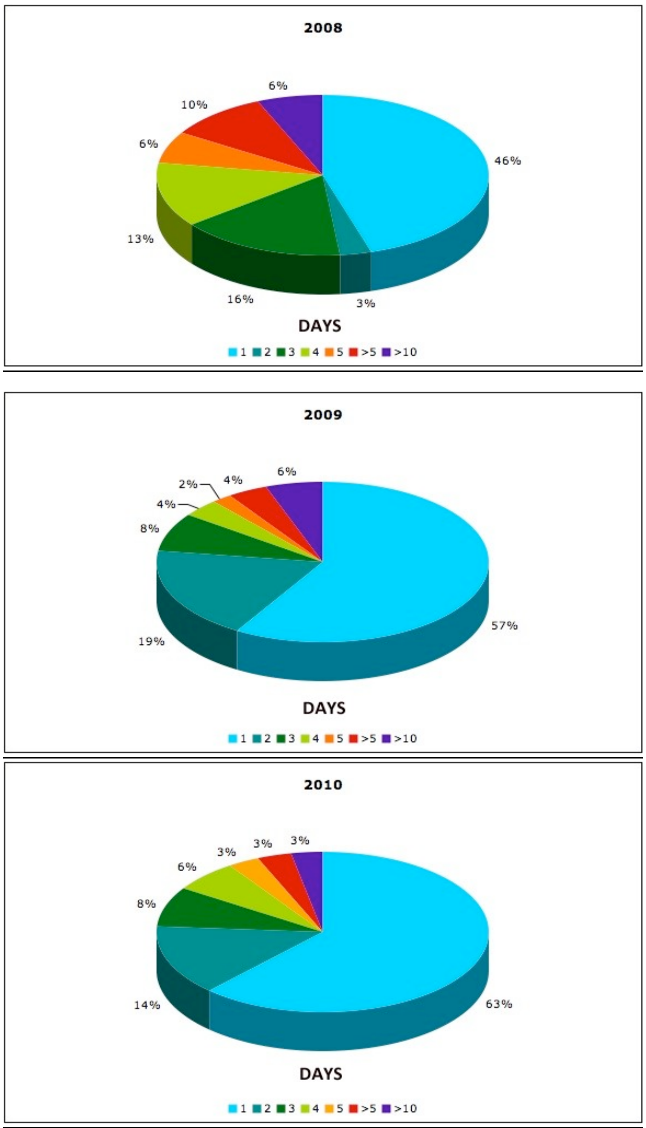


Figure 13: The percentage of individuals seen only one day or several days in the canyon. A high percentage of the individuals are only seen on one single day in all three years (2008: 46%, 2009: 57%, 2010: 63%), and only a few individuals are seen more than ten days (2008: 6%, 2009: 6%, 2010: 3%).

Table 3: The top four most seen individuals in Bleik Canyon in 2008, 2009 and 2010

ID	**2008**	**2009**	**2010**
195	11	26	19
234	13	5	1
192	5	2	23
427	8	11	5

3.3 Abundance estimation

For each dataset, Akaike's Information Criterion (AIC) was used to determine the most parsimonious model, based on a trade-off between the best model fit and the number of parameters used (Boyd *et al.*, 2010). In this section, the most parsimonious model of both the closed and the open models are presented.

Closed population models

Table 4 gives a summary of the estimates based on the closed population models for the seasonal datasets. Model M0 was the most appropriate model for seasons 1987-1989, 1999, 2000 and 2008. Model Mh was the most appropriate model for seasons 1990-1992, 1994-1997 and 2009-2010. Model Mth was the most appropriate model for the 1993 season. For detailed description of the models, see Appendix 2.

Figure 14 illustrates the estimated abundance of sperm whales in Bleik Canyon from the closed capture models. The seasonal estimates varied from 10 to 209 individuals, with a mean of 89 (± 95% CI = 33) individuals. The estimated abundance was especially high in 1990 (209 individuals), 1991 (182 individuals) and 1994 (255 individuals) in comparison to the other seasons.

The capture probability (p) was calculated for each season, and for the heterogeneity models, the two mixture groups had different capture probabilities. For the seasons estimated with a general model (M0), the capture probability ranged from 0.10 to 0.42, with a mean of 0.19.
For seasons estimated with heterogeneity models, the capture probability for the first mixture group ranged from 0.30 to 0.55 (mean = 0.40) and the capture probability of the second mixture group ranged from 0.02 to 0.10, with a mean of 0.05. Overall, the seasons estimated with a heterogeneity model had a slightly higher capture probability, and the animals that belong to the first mixture group also have a higher capture probability than the animals belonging to the second group.

Table 4: The abundance estimates (EST), standard errors (SE) and capture probability (P) from the most parsimonious models of each season using closed population models of dataset D2-D17. For heterogeneity models (Mh/Mht) capture probability of both mixtures are presented (P1, P2)

YEAR	EST	SE	P1	P2	Model
1987	10,76	1,58	0,42		M0
1988	46,25	16,34	0,11		M0
1989	68,94	15,94	0,10		M0
1990	209,26	198,89	0,26	0,02	Mh
1991	182,33	117,54	0,30	0,01	Mh
1992	53,48	13,24	0,55	0,10	Mh
1993	77,84	8,85	0,45	0,07	Mht
1994	255,28	359,53	0,30	0,01	Mh
1995	70,08	9,97	0,39	0,07	Mh
1996	72,39	9,28	0,32	0,07	Mh
1997	69,50	11,65	0,30	0,06	Mh
1999	33,50	5,68	0,14		M0
2000	23,33	6,44	0,18		M0
2008	46,17	17,70	0,21		M0
2009	95,97	14,85	0,55	0,06	Mh
2010	121,73	21,90	0,53	0,05	Mh

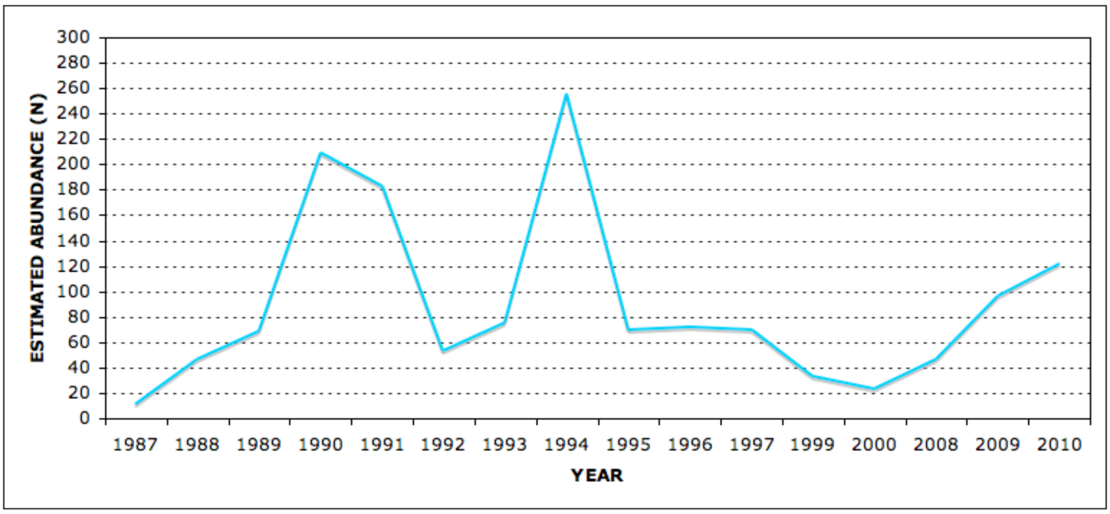


Figure 14: The estimated seasonal abundance of sperm whales in Bleik Canyon using closed capture models. The figure shows the estimates for each season with a horizontal line.

Open population models (Jolly-Seber)

Table 6 shows the estimates of the open population model using the complete 22-year dataset (D1). The presented estimates are from the most parsimonious model for this dataset, which was the M1-model. The estimated seasonal abundance ranges from 31 to 186 individuals, with a mean of 101 (± 95% CI = 22) individuals. The estimates are also plotted in Figure 15 to get a better overview of the seasonal abundance estimates from this model. In the M1 model, the capture probability (p) is assumed constant over the complete sampling period, and it is estimated to be 0.35.

Table 6: The abundance estimates (EST), standard errors (SE) and capture probability (p) from most parsimonious models of each season using open population models of dataset D1

YEAR	EST	SE	p	Model
1987	31,33	9,50	0,35	M1
1988	58,70	12,55	0,35	M1
1989	79,75	13,914	0,35	M1
1990	143,06	15,84	0,35	M1
1991	137,39	16,79	0,35	M1
1992	142,66	17,37	0,35	M1
1993	150,63	17,86	0,35	M1
1994	161,15	18,82	0,35	M1
1995	137,91	16,65	0,35	M1
1996	174,09	18,13	0,35	M1
1997	138,81	17,97	0,35	M1
1999	58,57	10,49	0,35	M1
2000	48,76	9,75	0,35	M1
2002	36,62	7,65	0,35	M1
2003	69,94	12,24	0,35	M1
2004	91,28	14,31	0,35	M1
2005	44,46	9,20	0,35	M1
2006	33,76	7,99	0,35	M1
2007	31,04	7,51	0,35	M1
2006	83,50	14,13	0,35	M1
2009	186,55	18,01	0,35	M1
2010	186,55	18,01	0,35	M1

Table 7 shows the estimates of the open population model using the seasonal datasets (D2-D17). The estimates presented are from the most parsimonious models from each dataset. The estimated seasonal abundance ranges from 11 to 116 individuals, with a mean of 69 (± 95% CI = 14) individuals. These estimates have also been plotted in Figure 16. In both model M1 and M2, the capture probability is assumed constant during each season. The capture probability (p) for the 1996 season, using model M1, was 0.34. The capture probabilities for the rest of the seasons, using model M2, ranged from 0.13 to 0.69, with a mean of with a mean of 0.36.

Table 7: The abundance estimates (EST), standard error (SE) and capture probability (p) from most parsimonious model of the open population models of dataset D2-D17

YEAR	EST	SE	p	Model
1987	11,55	1,89	0,69	M2
1988	49,02	18,77	0,13	M2
1989	90,58	23,74	0,29	M2
1990	100,53	18,85	0,26	M2
1991	87,31	13,47	0,27	M2
1992	51,77	5,90	0,43	M2
1993	82,64	8,03	0,32	M2
1994	75,20	9,57	0,36	M2
1995	71,08	7,21	0,34	M2
1996	87,99	10,44	0,34	M1
1997	67,71	6,81	0,25	M2
1999	38,87	7,10	0,53	M2
2000	30,06	10,22	0,28	M2
2008	43,43	5,74	0,50	M2
2009	109,80	16,13	0,41	M2
2010	116,81	87,89	0,31	M2

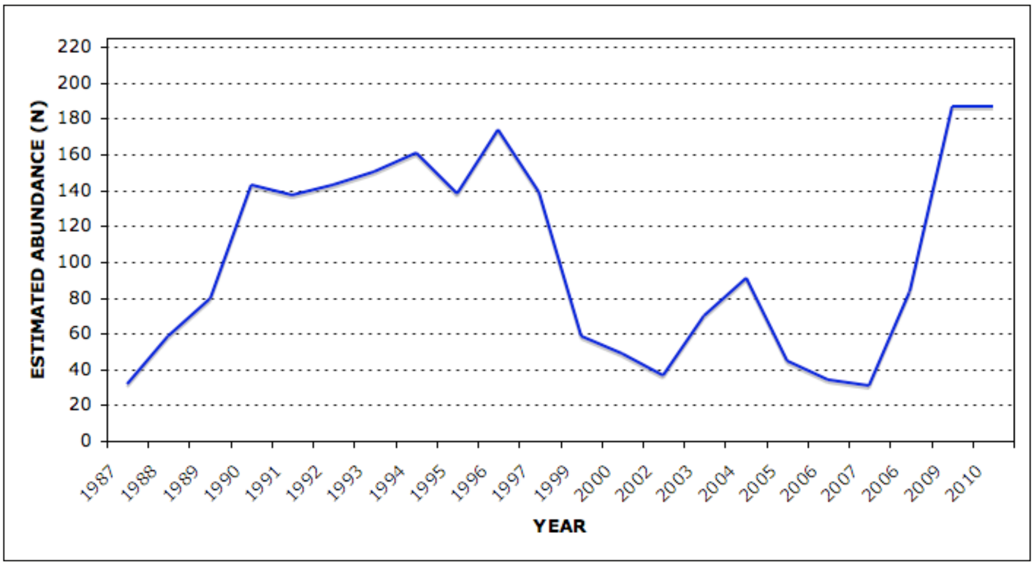


Figure 15: The estimated abundance of sperm whales in Bleik Canyon using open population models for dataset D1.

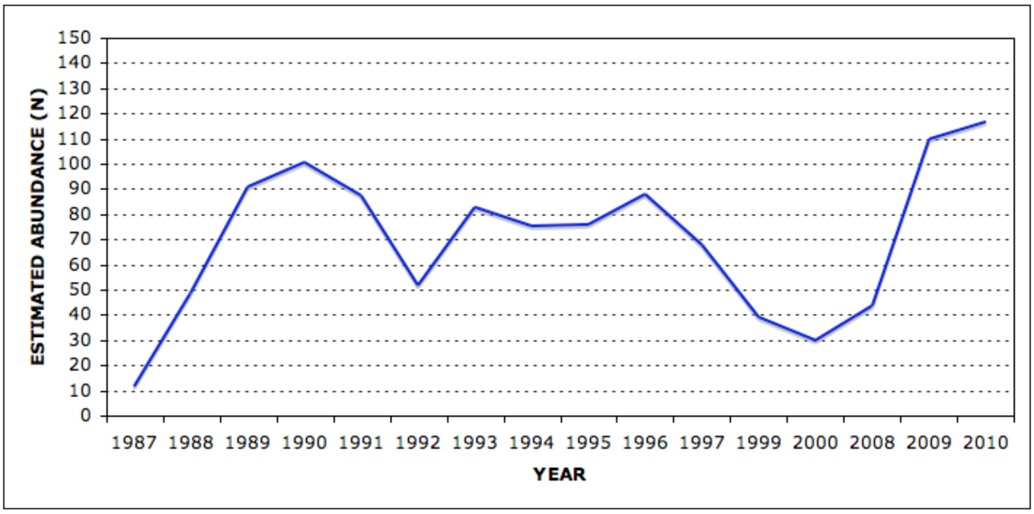


Figure 16: The estimated abundance of sperm whales in Bleik Canyon using open population models for the seasonal datasets D2-D17.

Using the seasonal datasets, the open models also provided abundance estimates for all sampling periods during each seasons. These estimates are summarized in Table 8. The number of sampling days in each period is summarized in Table 9. The estimated abundance (N) seems to fluctuate through the summer seasons (Table 8). The average estimates seems to be lowest in the first and second half of June (14 and 17 individuals), and in the second half of August (17 individuals) and the first half of September (18 individuals). The average estimated abundance seem to be highest in the second half of July (23 individuals), followed by the first half of July and the first half of August (both 21 individuals). The average number of sampling days was lowest in the first and second half of June (6 and 7 days) and in the second half of August and first half of September (7 and 4 days). The average number of sampling days was highest in the first and second half of July (7 and 9 days) and the first half of August (8 days).

Relationship between estimated abundance and number of sampling days

To examine the effect number of sampling days might have on the estimated abundance; a test for covariability was also performed by simple linear regression (Figure 17). The number of sampling days was plotted against the average estimated abundance (N). No significant linearly trend was found ($P = 0.12$, Appendix 4). This suggests that the number of sampling days did not have a significant affect on the estimated number of sperm whales present in the area. There should therefore be other factors influencing the number of sperm whales present in the different periods of the summer season.

Table 8: The half-monthly abundance estimates of the open population models using dataset D2-D17. In some seasons, certain periods have not been sampled and are therefore not available (NA)

ESTIMATES	JUNE.1	JUNE.2	JULY.1	JULY.2	AUG.1	AUG.2	SEPT
1987	NA	NA	NA	4,17	8,02	6,38	NA
1988	NA	25,92	40,54	40,54	31,46	32,45	NA
1989	NA	NA	13,02	34,62	18,37	24,92	NA
1990	NA	14,49	22,86	30,48	18,11	16,65	21,61
1991	13,80	19,89	29,97	30,53	27,96	22,72	NA
1992	18,49	18,49	18,61	15,83	19,69	13,78	NA
1993	15,09	19,93	24,37	24,00	27,78	21,24	18,08
1994	12,74	12,32	22,20	23,13	22,06	10,92	NA
1995	23,30	15,41	20,68	23,95	19,70	15,28	NA
1996	15,39	18,39	19,27	22,76	27,77	17,38	15,02
1997	14,64	23,31	30,94	32,19	34,20	29,76	20,55
1999	NA	3,53	6,49	8,06	9,92	11,10	NA
2000	NA	NA	NA	18,29	14,91	12,48	NA
2008	NA	NA	15,91	14,62	23,71	16,60	NA
2009	2,76	9,44	12,36	23,22	19,42	15,03	14,86
2010	10,81	24,43	15,66	16,75	22,95	23,26	21,54
AVERAGE	14,11	17,13	21,30	23,23	21,08	17,90	18,61

Table 9: Number of sampling days used to estimate the half-monthly abundance in the open population models using dataset D2-D17. In some seasons, certain periods have not been sampled and are therefore not available (NA)

DAYS	JUNE.1	JUNE.2	JULY.1	JULY.2	AUG.1	AUG.2	SEPT
1987	NA	NA	NA	NA	5	2	NA
1988	NA	3	3	4	4	4	NA
1989	NA	NA	3	8	8	7	NA
1990	NA	4	8	12	8	8	4
1991	2	8	4	8	12	8	NA
1992	6	5	16	10	10	10	NA
1993	4	8	12	12	12	8	7
1994	8	4	8	16	8	3	NA
1995	12	12	8	12	8	7	NA
1996	8	8	8	16	12	8	3
1997	4	12	12	12	12	8	3
1999	NA	4	4	8	8	8	NA
2000	NA	NA	NA	3	6	3	3
2008	NA	NA	6	12	12	8	NA
2009	8	12	8	12	4	8	4
2010	8	8	12	8	12	9	5
TOTAL	64	92	110	149	137	113	29
AVERAGE	6,40	7,08	7,86	9,93	8,56	7,06	4,14

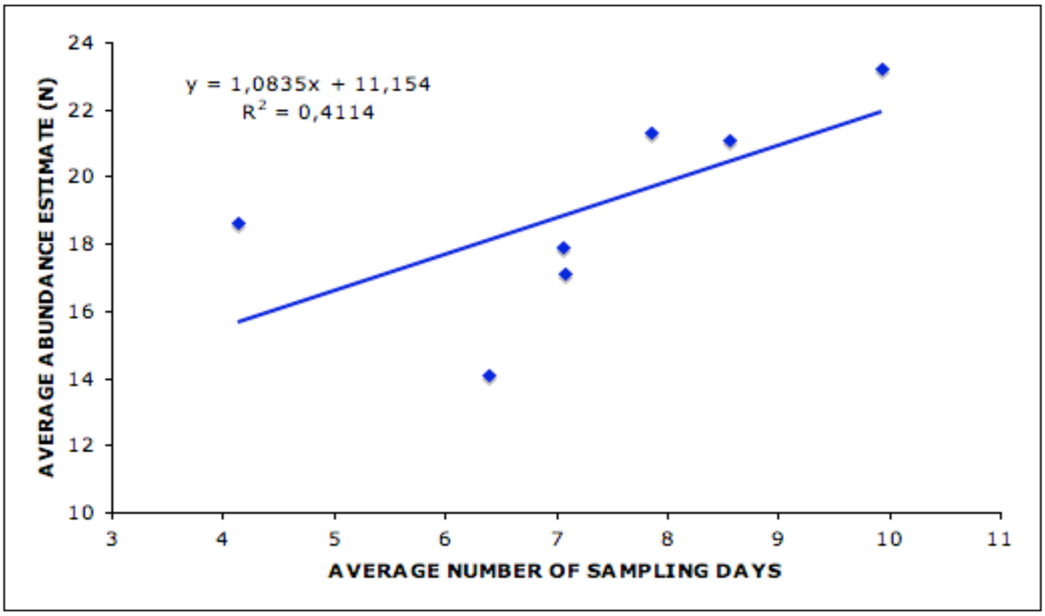


Figure 17: Scatterplot of the average abundance estimate (N) against the average number of sampling days

4 DISCUSSION

4.1 Sightings and resightings

This study shows that male sperm whales have been present in Bleik Canyon from 1987 to 2010 during the summer months from May to September. The mean ratio of new individuals observed was relatively high (0.54 ± 0.22), although it fluctuated between years (Appendix 6).

Over half of the individuals observed through the 22 years of study were only seen during one season. These individuals fit the description of transient individuals; male sperm whales passing through the area on their way to the polar feeding grounds or on their way south to the mating sites. Only one out of five individuals was seen more than three years, so the number of possible residents is quite low. The presence of transient and resident sperm whale in Bleik Canyon is described in several studies (Ciano and Huele, 2001; Lettevall *et al*., 2002; Zanoni, 2004; Lamoni 2011), and for other sperm whale aggregation sites (Childerhouse *et al*., 1995; Jaquet *et al*. 2000; Whitehead and Weilgart, 2000; Lettevall *et al*., 2002).

Relationship between number of individuals and number of sighting trips

The observed number of sperm whales fluctuated between years with no visible trend (Figure 11, Figure 12, Appendix 4), confirming the findings of Lettevall (2003). Similar results for seasonal residents was reported from Kaikoura, New Zealand by Childerhouse *et al*. (1995), and also found in the Gully, Nova Scotia (in Lettevall *et al*. 2003). A significant linear relationship between number of sightings and number of sampling trips was found (Figure 12). This is, however, logical. The more you sample an area, the more you will observe and the more individuals you will identify. However, as this linearly trend was not perfect, and only described 57% of the variation in number of sightings. There must therefore be other factors causing the number of sperm whales to fluctuate between seasons, and one of these factors might be the effect of killer whales (*Orcinus orca*) in present the area.

After the ban on whaling, killer whales have been the main predators on sperm whales (Whitehead, 2003). There have been several observed attacks of killer whales on sperm whales (Jefferson *et al*. 1991; Pitman *et al*., 2001; Dufault and Whitehead, 1998) although in most cases the sperm whales seem to defend themselves successfully. It also seems that the killer whales attack mainly calves, probably because they are an easier target than an adult male sperm whale.

Nevertheless, it has been observed during my study that whenever killer whales are present in the area where we usually observe sperm whales, the sperm whales move to the outermost parts of the canyon. As the killer whales move on to other areas, they quickly return and can be observed as normal the next couple of days. It would be interesting to examine whether male sperm whales would show a stronger tendency of grouping (e.g. decreasing the spatial scale of the aggregation) as a response to the presence of killer whales. In recent years, there have been an increased number of observations of killer whales in Bleik Canyon. The killer whales of Northern Norway primarily feed on the Norwegian spring spawning (NSS) stock of herring (*Clupea harengus*) and have been found to follow the migration pattern of the NSS stock (Foote *et al*., 2010). Areas that have been known to have a high abundance of killer whales, such as Tysfjorden, now only have a few observations during the year. Both observations suggests that the herring has changed its migration pattern, and with the herring so has the killer whales. This increased presence of killer whales might have a stronger effect on future studies, if their presence in Bleik Canyon should be more permanent. This may lead to a changed distribution pattern of the sperm whales, or they might ignore the killer whales if they become more permanent inhabitants, as they do not have any reasons to be afraid of them as adults.

Pilot whales (*Globicephala* spp.) have also been observed to harass or attack sperm whales (Weller *et al*., 1996). In the study of Madsen *et al*. (2002), sperm whales in Bleik Canyon were observed in the outermost parts of the canyon at the same time as a large pod of long-finned pilot whales were observed in the innermost part of the canyon. Dolphins have also been suggested to harass sperm whales. However, one day in 2010, a white-sided dolphin was observed close to a male sperm whale on several occasions in Bleik Canyon. The dolphin, however, did not seem to have any effect on the sperm whale, and may have been looking for companionship rather than harassing the sperm whale.

Another explanation may be that the distribution and abundance of prey is not constant for the whole study period. If the distribution of prey changes from one part of the canyon to another, the distribution of sperm whales may follow and as we do not observe this change we continue to visit the same part of the canyon and may observe fewer sperm whales than other years. It is found that cephalopods often aggregate when spawning and different species spawn at different times (Clarke, 1980). This may cause shifts in the distribution of sperm whales in the canyon, as different cephalopod species have different habitat and depth preferences (Gardiner and Dick, 2010).

4.2 Residency

The number of days any individuals was seen in the period 1987 to 2010 was between 1 and 18 days, with a mean of 2.3 days (Appendix 7). In seasons 2009 and 2010, over half of the individuals was observed only one single day (Figure 13). Seasonal transients (e.g. observed 3 days or less) have an even lower residency time (mean = 1.53 days). This indicates that the transients visiting Bleik Canyon does not stay in the canyon for long. The proportion of seasonal residents (e.g. observed more than 3 days) was very low, and only accounted for one fifth of the individuals seen in seasons 2009 and 2010. They also had a much higher residency time (mean = 7.14 days).

Studies on other male sperm whale aggregation sites, such as Kaikoura, New Zealand (Dawson *et al*., 1995) and the Galapagos Island (Christal, 1998) both found considerably higher values (mean residence time of 42.0 days). This corresponds to the high number of residents found at Kaikoura (Jaquet *et al*., 2000). Male sperm whales are also present at Kaikoura all year round, and are sampled both during the summer season and the winter season (Jaquet *et al*., 2000). As there is no photo-ID material gathered in Bleik Canyon during the winter, we may only speculate on whether the sperm whales are present all year round or if they leave the area during the winter months. Local fishermen have confirmed that sperm whales are present in the canyon also during winter, but we have no data on the abundance are or which individuals these are. However, if a large proportion of the aggregation does leave the area during winter, the chances of them leaving for another feeding site and not returning to Bleik Canyon the following year should be higher than if they are present all year round, and it might explain why we observe so few resident males in Bleik Canyon. Perhaps are these transients males on their way to the ice edges and polar fronts in the north, or they might be on their way to the females in the south, and only use Bleik Canyon as a feeding stop on the way.

Both whaling data from 1925-1971 (Christensen *et al*., 1992) and previous sighting surveys (Øien 1990, 2009) from the Norwegian Sea has suggested that Bleik Canyon is a significant sperm whale aggregation site during summer months. A sperm whale aggregation is defined as an assembly of more than 20 males over an area of more than 20 km across for several days or more. Lettevall et al. (2002) described the aggregation of male sperm whales in Bleik Canyon as strongly associated with the bathymetry of the canyon and found that the density of sperm whales decreased away from the canyon. The study found that there were a mean number of 15 individuals present in the canyon at any time over an area that was 10 to 30 km across. This corresponds to the findings of this study, with mean of 14 to 23 individuals present from June to September. Similar results have been found at other study sites (Lettevall, 2003). The reason why the male sperm whales are found so widely distributed in the canyon may be that the food distribution is predictable (Whitehead and Weilgart, 2000; Lettevall, 2003), and the prey species are also widely distributed in the canyon.

4.3 Abundance estimation

Violation of assumptions

Several different approaches have been used to describe the seasonal abundance of sperm whales in Bleik Canyon in this study (Figure 18). Estimating the seasonal abundance of a feeding aggregation with a large proportion of transient animals is not an easy task, and there are several assumptions to each model that needs to be met for the estimates to be reliable. From my observations, it is clear that the aggregation of male sperm whales in Bleik Canyon is not a closed population. The estimated survival rate (Table 2) is low and the proportion of transients is high; both suggesting that the loss of animals from one season to the next is high. This may be due to death or emigration, though migration out of the study area is a more likely explanation as the lifespan of these animals are close to 80 years (Rice 1989). Another assumption of closed models is the assumption of equal capture probability for all animals in the population. The presence of seasonal residents must be considered a violation of this assumption, as they will have greater chances of being captured than those that spend less time in the canyon. However, using a closed model where heterogeneity is taken into account can solve this. The third assumption of closed models, which also applies to open models, is that marks are not lost or overlooked. This is discussed further in detail in 4.5.

The parameterized Jolly-Seber models do not assume closure, which would seem to fit my dataset better. On the other hand, to use this model a greater number of the parameters must be estimated and the model becomes more uncertain. They are also unable to account for any individual heterogeneity in capture probability, which as stated above, does occur in this dataset. The study area for an open model must be constant, which can be a problem studying a pelagic animals. However, as seen in Figure x, the same area of the canyon is sampled in both 2009 and 2010, and also reported as the study area for previous studies in Bleik Canyon (Ciano and Huele, 2001; Lettevall, 2003, Zanoni, 2004).

Comparison between models

The two open Jolly-Seber models (POPAN) seem to follow a similar fluctuating trend in the abundance estimates. However, the models using dataset D1 gave a relatively higher seasonal estimate than the models using the seasonal datasets D2-D17. The reason for this might be that since dataset D1 lacks the information about residency time, it overestimates the abundance, as it is unable to differentiate between seasonal residents and seasonal transients. On the other hand, sampling without replacement (e.g. excluding multiple sampling occasions within one year) has been suggested to be less biased to unequal capture probabilities caused by seasonal residents and transients (Childerhouse, 1995), and might therefore be closer to the true abundance of the aggregation than the open model using seasonal dataset.

The second models type used was the 'closed capture' model. This model gives almost exactly the same estimates as the open model using seasonal datasets for all seasons except 1990, 1991 and 1994. The sampling period used for the seasonal datasets are quite short (3-4 days) and the similar results found between the open and closed model indicates that there might not be any significant immigration or emigration during these short sampling periods. Another explanation may be that the aggregation only appears to be closed due to low sampling effort. This may be true for the years 1987, 1988 and 2000, where less than 25 days were sampled (Figure 11a). The closed model estimates of seasons 1990, 1991 and 1994 are clearly different from both of the open models, with a very high estimated abundance and large standard errors (Table 4). All three seasons were estimated with models where individual heterogeneity was expected, and since it was observed a high proportion of seasonal residents in all three seasons (Appendix 8), the open models may have underestimated the abundance as they are not able to include any heterogeneity in capture probability. However, the high proportion of residents may also have influenced the estimates from the closed model, as this causes the estimates to deviate from a normal distribution. This is indicated by high standard errors of the estimates of these years.

A simple estimation model (Table 2) was also included. This model seems to follow a similar trend as the open model using dataset D1 and has almost the same abundance estimates for seasons 1990, 1993 and 1995. This similarity may be due to the fact that both models were sampling without replacement. However, the estimates for seasons 1988, 1999, 2000, 2008, 2009 and 2010 are closer to the open model using the seasonal datasets.

From the comparison between all models, the most realistic model is suggested to be the open model using the seasonal datasets. No trend was found in the number of sightings that could be linked to the large abundance estimates of the other models, and it is for instance questionable that over 250 animals visited the canyon in 1994 (estimate from closed capture model), and only 53 of them was sighted by Whalesafari Andenes Ltd. Also, the estimates from the open model with multiple seasonal sampling occasions are similar to the estimates from the other models for several years of the study, which indicates that it is close to the true abundance of sperm whales found in Bleik Canyon in these years.

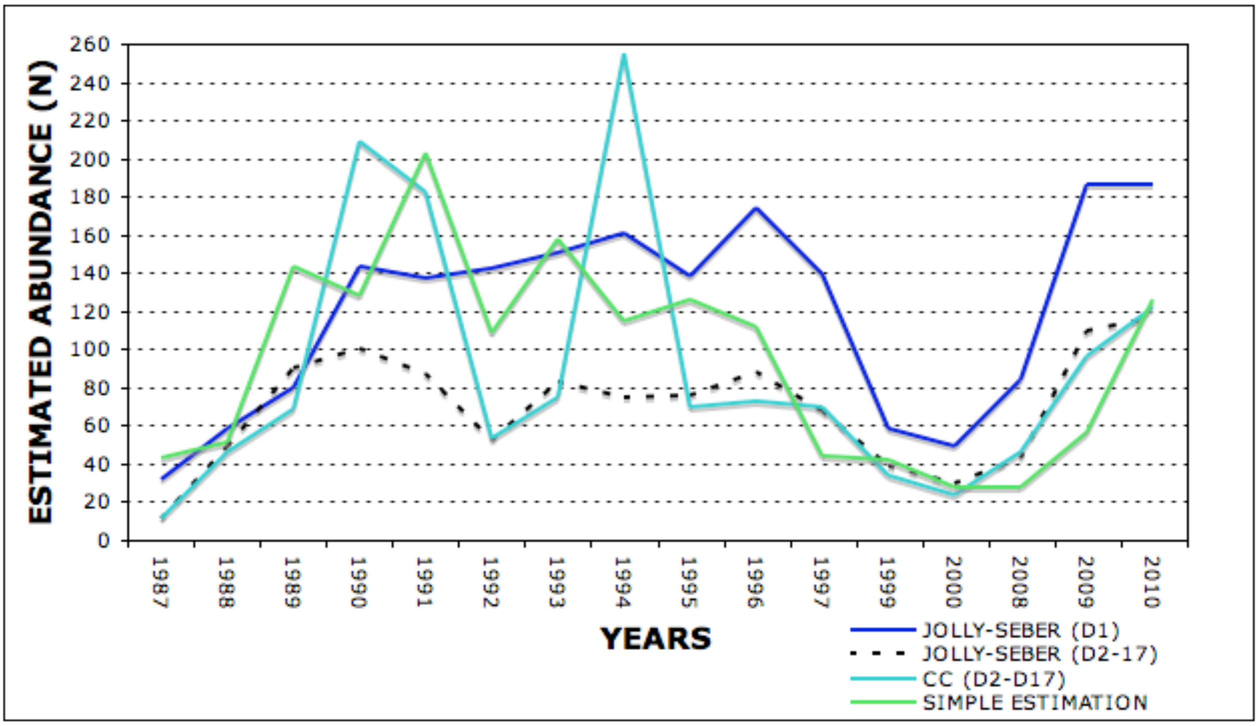


Figure 18: Comparison between the estimates of the two open models, the closed model and the simple estimation model

Comparison with previous abundance estimates from Bleik Canyon

The closed and open model estimates of this study were also compared to the model estimates from the study of Lettevall (2003) of the same years (e.g. 1987 to 2000). The closed model of this study estimated a higher abundance than what was estimated by Lettevall (2003) in the years 1988 to 1991 and in 1994, and a lower abundance in the years 1992 to 1993 and 1995 to 2000. Overall, the closed model by Lettevall (2003) estimated that the size of the aggregation fluctuated between 12 and 129 individuals, with an average of 70 individuals. In this study, the closed model estimated that the seasonal abundance fluctuated between 10 and 255 individuals, with a mean of 89 individuals.

The estimates from the open Jolly-Seber models also differed between this study and the study of Lettevall (2003). The estimates from Lettevall (2003) were generally higher for all seasons except 1989, 1991 and 1993. With the open model, Lettevall (2003) estimated that the size of the aggregation fluctuated between 75 to 214 individuals, with a mean of 153 individuals. In this study, the seasonal estimates fluctuated between 31 to 186 individuals (mean = 101 individuals) with dataset D1 and 11 to 116 individuals (mean = 69 individuals) with dataset D2-D17. The reasons for the different estimates might be that the updated version of the program MARK (White and Burnham, 1999) used in this study has been changed in the way it estimates the parameters compared to the previous version used by Lettevall (2003). Another reason for the different abundance estimates may be that the models chosen as the most parsimonious model was not the same on both studies for most of the years. Only in 1987, 1988 and 1992 did both studies use the same model for the estimations.

Ciano and Huele (2001) investigated the sightings of sperm whales in Bleik Canyon for the season 1998. As this material was not made available for this study, it has not been possible to compare the data from this year to later seasons. However, they compared the findings of 1998 with the findings of previous years in Bleik Canyon, and these results are similar to the results found in this study. They found that a large proportion of the individuals had been sighted in previous seasons (32/61 individuals), and that most individuals were only seen between one and three years (23/61), which is consistent with the findings of this study. They calculated the residency time as the time interval between the first and the last sighting, which is not comparable to the calculations of this study. However, they did observe that a large proportion (43%) of the animals were only seen once during the season, which is also consistent with the high number of seasonal transients found in this study.

For the seasons 2002 to 2007, there was not sufficient data available to create seasonal datasets. However, using dataset D1, the seasonal abundance in these years could also be estimated. Zanoni (2004) estimated the abundance in the 2002 season using an open Jolly-Seber approach, and estimate that there as between 6 and 32 individuals present in the canyon during the summer with all individuals included, and between 8 and 34 individuals present when excluding one individuals that observed throughout the season and assumed to cause heterogeneity in the capture probability. This estimate corresponds well to the estimates of this study, where it was estimated a mean of 36 individuals (SE = 7,65) for the whole season (Figure 15).

Capture probabilities

In this study, the capture probabilities using a closed model varied between seasons, with a range between 0.10 and 0.55. This is to be expected when there is heterogeneity in the capture probability among individuals. The capture probability estimated in the open model also varied a lot for the same reason as above, and was between 0.13 and 0.69 for the seasonal dataset and assumed constant at 0.35 for dataset D1. Menkens and Anderson (1988) advised against using the open model approach by Otis et al. (1978) when the capture probability is low and the sample size is less than 100. In this study, only years 1988 to 1991, 1997 and 2000 had capture probabilities below 0.30 and the estimates of these years may be biased as an effect of the low capture probabilities.

Relationship between the estimated abundance and the number of sampling days

The lack of covariability between estimated abundance and sampling effort on a seasonal basis (Figure 18) might be explained by the low number of seasonal residents observed in the area (Figure 13, Appendix 7) and the unpredictable movement pattern of the sperm whales. The reason why a significant linear trend was found between number of animals and number of sampling trips and not when using the seasonal estimates may be that the seasonal estimates are much more sensible to the distribution of prey in the canyon and to the possible influence of killer whales.

4.4 Sampling issues

The sampling for this study was mainly done onboard the whale watching vessels of Whalesafari Andenes Ltd. (see Materials and Method section for details), and was therefore opportunistic and not statistically randomized. This is one of the pitfalls when using a tourist-based sampling platform. Because the main goal of the whale safari is to find whales for the tourists, the crew will start the search in areas where they have found whales before and only search in new areas if the whales are not found at these known areas. As seen in Figure 4, this study mainly covers the eastern and innermost part of the canyon and only on rare occasions move to the more western parts of the canyon. The whole area of Bleik Canyon is never covered, so in fact we are sampling a subset of the animals that may be present in Bleik Canyon. Also, when a whale has been found, either beneath or above surface, the boats tend to stay in close vicinity of this sighting to make sure they can see this individual again if no other individuals appear. This is a reassurance for the operators as well as for the tourists, but less of an advantage for the scientist, who then will resight the same animal in the same area over a short period of time. Having randomly chosen sampling areas or line transect of the whole canyon instead of tourist-based platforms would be better, but as this is far more expensive and time-consuming, the latter is an efficient and affordable solution.

The number of sampling occasions was also a variable in this study. Weather and number of tourists booked influence how many trips are made during a season. Both in the start of the season (May) and in the end of the season (September), the weather at sea is quite unpredictable, and many potential sampling days are lost because the weather is too rough to take the tourists out at sea. It is also hard to find the sperm whales when the weather is bad, as white-tipped waves makes it difficult to see any spouts and the noise from waves smashing into the boats makes it difficult to hear them beneath the surface. The number of sampling occasions was also dependent on the presence of an ID photographer on the boats. In some seasons, only a few weeks were sampled because there was nobody onboard dedicated to take the photos the rest of the season. This latter issue is by far the easiest to control and making sure that the whole season is covered is one of the most important goals of the future.

4.5 Natural markings for photo-identification

The marks used in this study are natural markings on the sperm whale's fluke. These are marks made by other sperm whales or by killer whales, sharks or cephalopods (Best *et al*., 1984; Arnbom, 1987). Photo-identification studies are subject to two types of matching errors; mismatching two individuals as one (False positives) or mismatching one individual as two individuals, e.g. duplicates (False negative) (Whitehead, 2003). To minimize the risk of matching errors, only pictures of good quality were used, and the opinion of a second person was asked when in doubt. 'Good quality' implies that the picture was taken when the fluke was vertical and the whole contour of the fluke could be seen. This would then result in either a picture f the DF or the VT (see Materials and Methods for details). Individuals without any distinct marks on the trailing edges of their fluke were discarded because they would be difficult to reidentify and may cause either false positives of false negatives. False negatives could also appear if markings changes from one capture to the next.

Arnbom (1987) suggested that tooth marks and other skin damages may be lost over time, and may therefore not be very stable mark for long-term studies. Marks on the fluke, however, are usually missing portions of the fluke of different shapes and sizes (Figure 7). These might be considered more stable and more useful for long-term studies, as they would need to be either regenerated or taken away by an even larger missing portion to be lost. Dufault and Whitehead (1995) confirmed that the gain rates were higher than the loss rates for all mark types in sperm whales, except tooth marks. However, most of the observed changes due to gain of marks were small and did not change the overall pattern of the fluke. It would therefore still be possible to reidentify an individual even though new marks have been gained. Only in rare occasions would the new marks cause such a major change in the fluke pattern that an animal can not be reidentified.

Also in this study, gain of new marks was observed, as illustrated in Figure 19.
ID-431, first observed in 2008, was observed with new tooth marks in seasons 2009. It might have gained this mark from struggles with a squid or from another sperm whale. It might also have gained it from shark attacks if the individual had been visiting the southern latitudes between the 2008 and 2009 season.

Figure 19: Sperm whales can also have distinct changes in fluke pattern as adults (a) ID-431 seen on August 11th, 2008, (b) ID-431 seen on August 27th, 2009, now with new markings pointed out by the arrows.
(Photo: Whalesafari Andenes Ltd.)

4.6 Future studies

As we have observed that only a small proportion of the observed animals are seen in the canyon for more than one year, it would be very interesting to see if these animals actually stay in the area the whole year or if they leave in the end of the summer and comes back the next summer. This has not been an option using the whale safari as a platform because there are so few tourists during winter and too harsh weather conditions to arrange whale safaris in Bleik Canyon during winter. To do this it would be useful to have a boat that was entirely dedicated to scientific purposes. It would then also be possible to perform line transects and randomized observation sites of the whole Bleik Canyon. This way the abundance estimates would be more representative for the animals using the Bleik Canyon.

Another important goal of the future would be to compare the complete dataset of Bleik Canyon with other similar datasets of male sperm whales around the world. Especially interesting would be to compare the Photo-ID records of Bleik Canyon to the records in the Azores, as it is highly possible that males observed in Bleik Canyon will migrate to the waters around the Azores for mating. Collaboration between Arctic Sea Cruises in Tromsø and Whale Watch Azores (Steiner *et al.*, submitted 2011) have already given results, and found 3 matches between the sites. All animals had first been photographed in the Azores and then later seen at the Tromsø study site Malangsdjupet (69°43’: 69°50′N, 16°18’: 16°36′E). This indicates that these animals were all young individuals that may have been born at the mating grounds of the Azores and later migrated north. It is possible that these individuals also visited Bleik Canyon on their way to Malangsdjupet and matching of the complete ID-catalogue of Bleik Canyon to both the complete ID-catalogue of the Azores would therefore be very interesting. In the same study they also presented a match between one individual last seen in Bleik Canyon in 1992 and one individual found stranded on Ireland in 1997. This is also interesting, as it may give indications on the migration pattern of the male sperm whales moving between the high latitude feeding areas and the southern mating grounds

There have also been confirmed 7 matches between Malangsdjupet and Bleik Canyon from sightings from 2008, confirming that individuals do move between those two areas. The complete results from this study will be presented at the 2011 SMM Biennial Conference in Florida. This may indicate that there are several feeding areas like the Bleik Canyon in the Northern Atlantic, and that the male sperm whales do move between them. However, in the study of Steiner *et al*. (submitted 2011) no matches was found between Malangsdjupet or the Azores to the catalogues of Iceland, Nova Scotia, Greenland, Dominica, Guadeloupe, Gulf of Mexico or the Mediterranean. As the ID-catalogue of Bleik Canyon comprises a much larger dataset (1987 to 2010) than the catalogue of Malangsdjupet (2005 to 2008), it is possible that matches will be found if this dataset is included in future studies. It may also be that no matches are found because the sperm whales found at the eastern part of the North Atlantic has a different migration route than the animals found at the western part, though lack of sufficient data leaves only speculations.

5 CONCLUSIONS

In summary, this study supports the results from previous studies and confirms the presence of both transient and resident male sperm whales in Bleik Canyon as a loose feeding aggregation. The total residence time varied between one day and 14 years, although most individuals were only seen one or two years (Figure 12). The number of sighted whales fluctuated between years, and no trend was found. The number of sampling trips only explained about half of the varying number of sightings, and presence of killer whales, pilot whales and a variable food distribution was proposed as other influencing factors. The estimated abundance also fluctuated between years without any trend. The open model with multiple seasonal sightings (D2-D17) is suggested to be the most realistic model for the abundance estimates. The presence of male sperm whales in Bleik Canyon is not unique for the Norwegian Sea, as several matches have been found between Bleik Canyon and Malangsdjupet. However, it is unique to have such a high abundance of sperm whales so close to land, which is of great importance for the tourism of this area. Further investigations is needed to reveal the whereabouts of these male sperm whales during winter and whether or not the individuals sighted in Bleik Canyon also has been sighted at other important sperm whale locations, such as the mating grounds of the Azores.

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APPENDIX

Appendix 1: Log sheets used on the boats on all sampling trips

BOAT LOG	Page: ___/___	Boat: ❑ Reine ❑ Dolphin	Date: ___-___-201__	Photographer: ____________			Recorder: _______________	
Weather	Air temp: ___°C	Wind speed: ___ Kt	Wind direction: _____	Start: ____:____	Hydrophones	ON:____:____	69:_____:_____	15:_____:_____
	Cloud cover: ___/8	Rain: ❑ yes ❑ no	Sea (Beaufort): ____/12	End: ____:____	Record ON	Time:____:____	69:_____:_____	15:_____:_____
					Record OFF	Time:____:____	69:_____:_____	15:_____:_____

Time	Latitude	Longitude	Species	No. Animals	Notes	Click time	Blows	Other boats
___:___	69:____:____	15:____:____						
:	69: :	15: :						
:	69: :	15: :						
:	69: :	15: :						
___:___	69:____:____	15:____:____						
:	69: :	15: :						
:	69: :	15: :						
:	69: :	15: :						
___:___	69:____:____	15:____:____						
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:	69: :	15: :						
:	69: :	15: :						

Species: SW sperm whale - KW killer whale - PW pilot whale - MW minke whale - HB humpback whale - HP harbour porpoise - WBD white beaked dolphin - FW fin whale

DF:dorsal fin - DT:dorsal tail - VT: ventral tail | WS: whalesafari boats - FB fishing boats - Tourist boats - Other:________ |) white sided dolphin - Other________

Appendix 2: Description of the models used to estimate the abundance of sperm whales in Bleik Canyon

Closed capture models:

Parameters used in the models

p: probability of first capture

ci: probability of recapture, given that the individuals has been captured before

N: population abundance

Model	**M**	**Description**
N, p = c	M0	Constant capture (p) and recapture (c) probability
N, $p_t = c_t$	Mt	Time-dependent capture (p) and recapture (c) probability
N, π, pa = ca, pb = cb	Mh	Constant capture (p) and recapture (c) probability in each mixture group
N, π, $pa_t = ca_t$, $pb_t = cb_t$	Mht	Time-dependent capture (p) and recapture (c) probability in each mixture group

Model M0 is the generalized model, and both capture and recapture probabilities are assumed constant over time. In the Mt model, both capture and recapture probability is time-dependent.
In model Mh, the two mixture groups have their own capture and recapture probability, which is assumed constant over time. In model Mht, the two mixture groups still have their won capture and recapture probabilities, but these are time-dependent.

Open population (Jolly-Seber) models:

Parameters used in the models

p: probability of first capture

Φ_i: Survival rate from occasion i to i +1

β_i: Probability of an individual from the superpopulation entering the study population

Models	**M**	**Description**
p_t, Φ_t, β_t	M0	Time-dependent capture probability, survival rate(Φ) and entry probability (β)
p, Φ_t, β_t	M1	Constant capture probability, time-dependent survival rate (Φ) and entry probability (β)
p, Φ, β_t	M2	Constant capture probability and survival rate(Φ), , time-dependent entry probability (β)

Model-M0 is a generalized model, where encounter probability (p), survival probability (Φ) and the probability of an individual from the meta-population entering the study population (β) are all set time-dependent. The other two models are both relaxed in various ways from the generalized M0-model. In model-M1 the encounter probability is set constant over the complete study period and in model-M2 both the encounter probability and the survival probability are set constant over the time of the study.

Appendix 3: Covariance analysis between the number of sampling trips and the number of sightings. Table below gives the output from the analysis in R.

```
glm(formula = INDIVIDUALS ~ YEAR + offset(log(TRIPS)), family = quasipoisson)

Deviance Residuals:
    Min       1Q    Median       3Q      Max
-4.9058  -0.8569   0.1437   2.2019   4.3022

Coefficients:
             Estimate  Std. Error  t value  Pr(>|t|)
(Intercept) 50.48825   26.53014   1.903    0.0723 .
YEAR        -0.02559    0.01328  -1.927    0.0691 .
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for quasipoisson family taken to be 6.26657)

Null deviance: 130.12  on 20  degrees of freedom
Residual deviance: 106.16  on 19  degrees of freedom
AIC: NA

Number of Fisher Scoring iterations: 4
```

Appendix 4: Covariability test for 1987-2010, dataset D1

SOURCE	SS	df	MS	F	crit 5%	P
TRIPS	4724,20	1	4724,202828	25,7	4,4	6,81006E-05
RESIDUAL	3492,749553	19	183,8289238			
TOTAL	8216,95	20				

Appendix 5: Covariability test for seasonal data, datasets D2-D17

SOURCE	SS	df	MS	F	crit 5%	P
DAYS	23,15088383	1	23,15088383	3,5	6,6	0,120524365
RESIDUAL	33,12737977	5	6,625475954			
TOTAL	56,28	6				

Appendix 6: Summary table of number of new individuals, number of resighted individuals, total number of individuals sighted, number of photographs, identification rate and rate of new individuals divided on total number of individuals (p)

Year	Nr. of new ids	Nr. of resighted	Total no. of ids (n)	No. of photographs		Identification rate	New ind / no. of id (p)
1987	11	0	11	25		0,44	1,00
1988	20	2	22	39		0,56	0,91
1989	21	12	33	93		0,35	0,64
1990	36	12	48	173		0,28	0,75
1991	25	25	50	178		0,28	0,50
1992	26	17	43	185		0,23	0,60
1993	27	35	62	294		0,21	0,44
1994	28	29	57	188		0,30	0,49
1995	29	29	58	252		0,23	0,50
1996	34	43	77	426		0,18	0,44
1997	22	35	57	460		0,12	0,39
1999	11	21	32	96		0,33	0,34
2000	5	13	18	58		0,31	0,28
2002	2	16	18	259		0,07	0,11
2003	14	13	27	105		0,26	0,52
2004	23	6	29	113		0,26	0,79
2005	6	6	12	58		0,21	0,50
2006	2	7	9	35		0,26	0,22
2007	4	4	8	27		0,30	0,50
2008	21	13	34	172		0,20	0,62
2009	40	14	54	305		0,18	0,74
2010	43	21	64	315		0,20	0,67
					Mean	0,26	0,54
Total				3856	± SD	0,10	0,22

Appendix 7: Mean number of days of sighting of all individuals, and divided in residents (seen more than 3 days) and residents (seen less than 3 days)

YEARS	ALL INDIVIDUALS	RESIDENTS	TRANSIENTS
1987	1,9	NA	NA
1988	1,38	NA	NA
1989	1,43	5,00	1,32
1990	1,73	5,20	1,30
1991	2,21	6,00	1,32
1992	2,92	7,75	1,45
1993	2,84	8,09	1,56
1994	2,30	8,17	1,44
1995	2,80	7,17	1,38
1996	2,51	5,75	1,60
1997	2,96	6,57	1,51
1999	2,21	4,60	1,58
2000	1,4	NA	NA
2002	NA	NA	NA
2003	NA	NA	NA
2004	NA	NA	NA
2005	NA	NA	NA
2006	NA	NA	NA
2007	NA	NA	NA
2008	3,13	7,13	1,68
2009	2,15	7,13	2,43
2010	2,25	8,00	1,35
AVERAGE	2,26	6,66	1,53