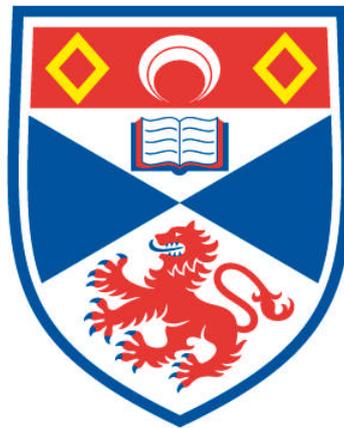


**POPULATION DYNAMICS AND DISTRIBUTION OF  
NORTHERN NORWEGIAN KILLER WHALES IN  
RELATION TO WINTERING HERRING**

**Sanna Kuningas**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St Andrews**



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Population dynamics and distribution of northern Norwegian killer whales  
in relation to wintering herring

Sanna Kuningas



University of  
St Andrews

This thesis is submitted in partial fulfilment for the degree of PhD

at the

University of St Andrews

December 2013



Killer whales encountered in Vestfjord, in November 2006.

**Candidate's declarations:**

I, Sanna Kuningas, hereby certify that this thesis, which is approximately 60,500 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in January 2007 and as a candidate for the degree of Doctor of Philosophy in January 2007; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2013

Date 11<sup>th</sup> December 2013

Sanna Kuningas

**Supervisor's declaration:**

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Ph.D. in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date 11<sup>th</sup> December 2013

Prof. Philip D. Hammond

Date 11<sup>th</sup> December 2013

Dr. Jens Christian Holst

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Sanna Kuningas

Prof. Philip S. Hammond

Dr. Jens Christian Holst

## Collaboration statement

### Collaborations and related publications

Some aspects of the work in this thesis involved collaborations and have resulted in publications.

Publications:

1. Kuningas S, Similä T & Hammond PS. 2013. Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986-2003. - Journal of Marine Biological Association of the United Kingdom. doi:10.1017/S0025315413000933.
2. Kuningas S, Kvadheim P, Lam F-PA & Miller PJO. 2013. Killer whale presence in relation to naval sonar activity and prey abundance in northern Norway. - ICES Journal of Marine Science. doi:10.1093/icesjms/fst127.

The work in Chapter 2 was conceived by Hammond and Similä. Data collection in 1986-2004 was by Similä and colleagues. Data collection in 2005-2013 was by Kuningas. All data analysis was done by Kuningas. The thesis chapter and the resulting publication were written by Kuningas. Hammond and Similä commented on drafts of the chapter and publication.

The work in Chapter 5 was conceived by Miller and Kvadsheim with early input from Kuningas. The fieldwork involved all four authors. Kuningas compiled the used whale-watching dataset. Table 2 in the publication was a result of combined ("blind folded") effort of Kuningas, Kvadsheim and Miller. Figure 2 in the publication was done by Lam. All other data analysis was done by Kuningas. The thesis chapter and the resulting publication were written by Kuningas. Miller, Kvadsheim and Lam commented on drafts of the publication.

## ABSTRACT

The northern Norwegian killer whale (*Orcinus orca*) is an important predator but little is known about its population dynamics, particular in response to changes in its main prey, the highly dynamic Norwegian spring spawning (NSS) herring (*Clupea harengus*). The main aims of this thesis were to estimate killer whale population parameters, to explore the future viability of the population, and to explore the response of this predator to changes in distribution and abundance of its main prey over the last 25 years. Population size was estimated as ~ 700 individuals, taking heterogeneity of capture probabilities into account and correcting for unmarked animals. Apparent survival rates of 0.974 (SE = 0.006) for adult males and 0.984 (SE = 0.006) for adult females were estimated accounting for temporary emigration, transience and trap-dependency. Temporary emigration was greater for males than females. Calving intervals ranged from 3 to 14 years (mean = 5.06); equivalent to 0.197 calves per mature female per year. Future viability of the killer whale population was evaluated under various plausible scenarios. The baseline scenario using the best available information predicted a viable population and indicated that the population may be increasing size. Analysis of data on naval sonar activity, killer whale sightings and herring abundance showed that naval sonar activity appeared to have a negative effect on killer whale presence during a period of low prey availability. A time lag of four years was found between the first sign of NSS herring changing its distribution and reduced killer whale presence inside the fjord system. Analysis of energy budgets showed that killer whales spent more time travelling/foraging in 2005/06 than the 1990s. The fjord system was inferred to be a preferred habitat for killer whales when there was a higher density of NSS herring in this area compared to offshore area.

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# CHAPTER 1

## General introduction

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### **1.1 Conservation and management of marine mammals**

Over the last few decades, particularly since the 1960s, the attitude to and interest in wildlife has experienced a marked change from exploitation to preservation (Reeves & Reijnders 2002; Reeves 2009). This change has been particularly clear with respect to cetaceans (whales, dolphins and porpoises), with which there has been a marked change of focus, from large scale whaling operations and live capture of animals for human displays (Øien 1988; Sigurjónsson & Leatherwood 1988; Reeves et al. 2003), to strong attitudes against whaling and even attempts to release captive animals back into the wild (Wells et al. 1998; Simon et al. 2009). Conservation of populations and preserving biodiversity have become the overarching themes regarding nature and wildlife. The term “conservation” can be interpreted in various ways, e.g. as preserving biodiversity or wild populations (Reeves & Reijnders 2002; Reeves 2009) or critical resources (Mangel 1996), or as preventing extinctions of populations or species (Begon et al. 1996).

Several factors can threaten the viability of marine mammal populations, most of them as a consequence of human activities. One of the most direct threats, that also has received a lot of public attention, is the removal of animals either to obtain consumables or food products, i.e. hunting, or for controlling the population size of certain species, i.e. culling (Øien 1988; Clapham et al. 2007). Probably the first marine mammal species that was hunted to extinction was the Steller’s sea cow (*Hydrodamalis gigas*) (Anderson & Domning 2009). Industrial scale whaling of cetaceans, initially of the large slow moving species but later of all large whales, lead to serious depletion and risk of extinction of many species, e.g. the North Atlantic right whale (*Eubalaena glacialis*) and blue whale (*Balaenoptera musculus*) (Clapham & Baker 2009). Whaling operations have declined markedly since the International Whaling Commission (IWC) “moratorium” in the mid-1980s and whaling is currently not considered a threat to any species (IWC 2012). However, the effect of previous whaling can still be seen in low population numbers of certain species, e.g. blue and northwest Pacific gray whales

(*Eschrichtius robustus*) (Bradford et al. 2008; Clapham & Baker 2009). In addition to hunting and culling, some species of marine mammals are live captured for human displays in aquariums (Bigg & Wolman 1975; Sigurjónsson & Leatherwood 1988; Reeves et al. 2003).

Ever increasing fishing effort on a global scale is arguably the major threat to marine mammals generally. Bycatch (i.e. the incidental capture of non-target marine mammals in fishing gear) and other interactions with fisheries are a risk for all species of marine mammals (Lewison et al. 2004; Read et al. 2006; Reeves et al. 2013), due in part to the overlap in distribution of many marine mammal populations and commercial fishing stocks. The greatest risk results from the use of passive gill-net fisheries (Read et al. 2006; Reeves et al. 2013). For example, the vaquita (*Phocoena sinus*) is currently considered as the most endangered small cetacean in the world with a serious risk of extinction due to bycatch in gillnets (Rojas-Bracho et al. 2006; Jaramillo-Legorreta et al. 2007). Other types of fishing gear, such as purse seines, trawls and long-lines, can all kill cetaceans and seals through bycatch (Lewison et al. 2004; Northridge 2009). Fisheries may also have an indirect effect on marine mammals. Increasing fishing effort and overexploitation has led to the depletion of many fish stocks around the world, leading to lowered food availability for marine mammals (Pauly et al. 1998; DeMaster et al. 2001; Pauly et al. 2002; Myers & Worm 2003). However, prey availability can also fluctuate through natural variation in biomass and thus negatively impact the viability of predator species (Toreisen & Østvedt 2000; Ford et al. 2010; Williams et al. 2013).

Another cause of direct mortality of marine mammals is ship strikes, which has become an increasing threat as marine traffic continues to increase globally (Laist et al. 2001). Two examples of this are the cases of Florida manatee (*Trichechus manatus latirostris*) and western North Atlantic right whale populations where concerns have been raised about the viability of these species due to vessel collisions (Knowlton & Kraus 2001; Nowacek et al. 2004).

As well as the direct threats described above, there is a range of indirect threats to marine mammals resulting from ever expanding human impact on the marine environment, which can cause disturbance to marine mammals in their preferred habitats. Increasing noise in the marine environment is receiving increased attention (Southall et al. 2007; Wright et al. 2007). Underwater, marine mammals rely mostly on their hearing to locate prey, to navigate and to communicate with one another (Ketten 1991). Therefore any anthropogenic noise added to the marine environment has the potential to impact the hearing and communication ability of marine mammals and may also lead to displacement of individuals from important

habitat, with a consequent negative impact on their fitness (Morton & Symonds 2002; Southall et al. 2007; Goldbogen et al. 2013).

Noise in the marine environment comes from various sources; e.g. from shipping, from the use of echo-sounders and sonar, from seismic surveys and from construction of marine developments (Richardson et al. 1995; Nowacek et al. 2007; Southall et al. 2007; Nabe-Nielsen et al. 2011; Miller et al. 2012). Active military sonar sources that transmit powerful sound to the marine environment are used for marine warfare purposes and may be a serious risk for marine mammals (Richardson et al. 1995; Southall et al. 2007; Miller et al. 2012). In extreme cases, naval exercises have caused strandings of e.g. beaked whales (Frantzis 1998; D'Amico et al. 2009). The continuous demand for oil and gas leads to exploration of increasingly wider areas, including most recently to Arctic waters (Gautier et al. 2009). As mentioned above, seismic surveys introduce high levels of sound into the marine environment in the search for locations of these reserves (McCauley et al. 2000; Southall et al. 2007). Construction of renewable energy sites (e.g. offshore wind-farms) or coastal developments increase, at least temporarily, noise in these locations and may displace marine mammals and/or could alter their habitat, e.g. causing changes in the distribution of important prey species (Tougaard et al. 2009; Bailey et al. 2010; Brandt et al. 2011).

Whale-watching activities are popular and profitable businesses in many locations around the world and have undoubtedly increased the public awareness of marine mammals (Cisneros-Montemayor et al. 2010). However, the increased number of vessels taking tourists to see marine mammals have been shown to impact some species in some locations (Williams et al. 2002; Lusseau & Bejder 2007). For example, Williams et al. (2006) showed that the presence of boats reduced the amount of time that killer whales (*Orcinus orca*) in the northeast Pacific spent on feeding activities, which may have an effect on the condition of the individuals through decreased energy intake.

The high levels of contaminants (e.g. DDT and PCB), generated as by-products of human activities, that have been recorded in the tissue of many marine mammal species, such as harbour (*Phoca vitulina*) and grey (*Halichoerus grypus*) seals, belugas (*Delphinapterus leucas*) and killer whales, can also have a negative effect on health and reproductive rates (Reijnders 1980; Reijnders 1986; De Guise et al. 1995; Bergman 1999; Ross et al. 2000; Hickie et al. 2007; Wolkers et al. 2007; Cullon et al. 2009; Reijnders et al. 2009). Oil production platforms and the transport of oil in the marine environment presents a risk of contamination via oil spills, which may have a harmful impact on the viability of marine mammal populations

(Jenssen 1996; Matkin et al. 2008). The effects of synthetic marine debris is also causing some concern (Williams et al. 2011a; de Stephanis et al. 2013).

At a much larger scale, and increasingly, climate change is also considered a risk to the viability of marine mammal populations. For example, this could be a result of species distribution range shifts across the entire food chain and due to loss of suitable habitat (Kovacs & Lydersen 2008; MacLeod 2009; Forcada et al. 2012). Prediction of effects is difficult but it is expected that species with limited habitat preference, especially those dependent on ice, are at greater risk of extinction due to the significant potential for habitat degradation (Learmonth et al. 2006; Stirling & Derocher 2012).

Generally, small populations are at higher risk of extinction than larger populations and are particularly vulnerable to low genetic variability, inbreeding depression or to sudden catastrophic events (Gilpin & Soulé 1986; Allendorf & Ryman 2002). K-selected species, including large mammals, have high survival rates and low reproductive rates and thus have a higher risk of extinction because of their slow population growth rate and limited potential for recovery (Pianka 1970; Boyce 1984; McKinney 1997).

Conservation effort focussed on a particular species is usually initiated after the realization of a population decline or a presence of a threat to that species or a population. This was the case for example with observed decline of the Steller sea lion (*Eumetopias jubatus*) population in Alaska, which was later linked to a decline in the availability of suitable prey (Trites & Larkin 1996; Trites & Donnelly 2003). The initial recognition of a problem is typically followed by an attempt to understand the potential reasons for a decline and/or the particular threat(s) and its effect on the population in question. To achieve this, it is important to have information on survival and reproductive rates (Hammond et al. 1990). As population parameters may vary between geographical locations even for the same species, it is valuable to estimate vital rates for each population (Olesiuk et al. 1990; Poncelet et al. 2010; see Chapters 2 and 3). For marine mammals, population specific parameters (including abundance) are usually investigated using mark-recapture methodology, line-transect sampling or direct counts (Hammond et al. 1990; Buckland et al. 2001).

This information can be used to parameterise a population viability analysis (PVA) in which future population size and extinction risk can be evaluated, incorporating the potential sources of threat (Gilpin & Soulé 1986; Akçakaya & Sjögren-Gulve 2000; Harwood 2000; Beissinger & McCullough 2002). Critical interpretation of the results provided by a PVA can be very useful for setting more informed population specific management goals (Coulson et al. 2001; Ralls et al. 2002; Taylor et al. 2002). For many species and populations, obtaining the

necessary population parameters for a population viability analysis is not possible, due to limited data. If particular factors are recognised to pose a threat to a population, efforts can be made to minimize these risks, e.g. reducing bycatch by using fishing equipment designed to lower the risk of entanglement (Larsen et al. 2007; Dawson et al. 2013).

Scientific research is needed to gather the information on population status and threats possessing risk to its viability. However, minimizing any type of threat also requires the involvement of decision makers to mitigate the impacts of harmful activities and at governmental or international level (e.g. European Union) to ensure enforcement of changes to existing legislation. Conservation action should then be followed by continued monitoring of a population to evaluate if limiting a threat has had the desired effect of increasing population size and viability (Evans & Hammond 2004). Conservation efforts may also include designating defined marine protected areas to maintain sustainability of a particular population, species or a certain type of important habitat (Kelleher 1999; Wilson et al. 2004; Ashe et al. 2010; Gormley et al. 2012; IWC 2012).

Several regional and international agreements or organisations, e.g. the North Atlantic Marine Mammal Commission (NAMMCO) and the International Whaling Commission (IWC), have been established to work towards favourable conservation status and management of marine mammals by using the latest available scientific knowledge as guidance for their management plans. The International Union for the Conservation of Nature (IUCN) is the largest international conservation organisation, and acts as an information channel to other organisations. Through the Red List, IUCN provides information on, e.g. species status assessments, extinction probabilities and conservation priorities (Baillie et al. 2004; Rodrigues et al. 2006). Within Europe, the EU Habitats Directive (Council Directive 92/43/EEC, adopted in 1992 (EU 1992)) acts as an important conservation driver, with the main aim to promote the maintenance of biodiversity and favourable conservation status of wild fauna and flora. Within Europe, family *Phocidae* is protected under Annex II and all cetacean species are protected under Annex IV (Council Directive 92/43/EEC (EU 1992)).

## **1.2 Ecosystem approach to management**

The majority of conservation and management efforts are focused on single species (Simberloff 1998). However, increasing attention is being focussed on conservation and management of holistic ecosystems, because individual species are interlinked with the surrounding environment and with other species within that ecosystem. This framework is called the ecosystem approach to management (Christensen et al. 1996). Driven by concerns

about overfishing, this approach was first considered in the context of fisheries management (Botsford et al. 1997; Brodziak & Link 2002), but nowadays there is increasing interest in applying it more generally (Leslie & McLeod 2007; Murawski 2007). Generally this concept means an integrated management of all human activities to achieve sustainable use of resources and conservation of species in an ecosystem which includes all biological and physical components (Christensen et al. 1996; Larkin 1996). The ecosystem approach to management has been agreed as the way forward on many levels, both nationally and internationally, e.g. in EU Marine Strategy Framework Directive (EU 2008) and in United Nations Environment Programme (UNEP 2008). In 2002, the Norwegian government adopted the ecosystem approach to management of the Norwegian Sea (Miljøverndepartementet 2002; Skjoldal 2004).

In practice, ecosystem modelling faces multiple difficulties. A comprehensive report on available ecosystem models, their advantages and challenges was compiled by Plagányi (2007). The ecosystem approach to management requires combining large-scale datasets of each component which in many parts are unavailable (DeYoung et al. 2004; Plagányi 2007). Also, co-operation of multiple scientists and institutions at an international level is required to bring all the needed information together. Regarding marine mammals, information on population distribution, prey requirements and abundance are necessary because this information could also feed into ecosystem models to allow evaluation of their impact on and role in the ecosystem (Pauly et al. 2000; Plagányi 2007). Progress towards ecosystem based management has been made by implementing multi-species models fitted to predator-prey datasets with some species e.g. killer whale and Steller sea lion in the Aleutian Islands (Guénette et al. 2007) and minke whale and its prey species in the Barents Sea (Lindstrøm et al. 2009).

### **1.3 Predator-prey interactions**

Marine mammals are abundant, widely dispersed, and have a large body size requiring a high energy intake and are thus considered to have a major impact on marine ecosystems (Bogstad et al. 1997; Bowen 1997; Estes et al. 2011). As top predators, they may play an important role in shaping the behaviour and life history of their prey species and also have both direct and indirect effects on other species of the marine food web (Bowen 1997; Estes et al. 1998; Morissette et al. 2006; Trites et al. 2006; Heithaus et al. 2008; Estes et al. 2011; Morissette et al. 2012).

Some evidence for top-down effects of cetaceans as predators comes from the studies of killer whales in the NE Pacific. A decrease in sea otter (*Enhydra lutris*) abundance caused an

increase in sea urchin density and consequently de-forestation of kelp beds (Estes et al. 1998), and this has resulted in a debate about the possible causes. The hypothesis that the reduction in populations of large whales through industrial whaling could have forced killer whales to change their prey species from these large cetaceans to smaller marine mammals and thereby cause declines especially in seal, sea lion and sea otter abundance has been a topic of some disagreement among researchers (Springer et al. 2003; Whitehead & Reeves 2005; DeMaster et al. 2006; Trites et al. 2007; Springer et al. 2008; Wade et al. 2009).

Another topic of wide interest has been the fish consumption by marine mammals and its possible negative effect on fish stocks from the perspective of the fishing industry and fisheries management (Trites et al. 1997; Yodzis 2001; Matthiopoulos et al. 2008; Morissette et al. 2012). Marine predators and fisheries share the capability to reduce the biomass and influence the life histories of prey species. However, fisheries can take harvests that go well beyond the capabilities of marine mammals (Trites et al. 1997; Pauly et al. 2002; Trites et al. 2006; Morissette et al. 2012), as shown for Norwegian spring spawning herring (*Clupea harengus*) in the late 1960s (Dragesund et al. 1997; Toresen & Østvedt 2000). Additionally, on a global scale marine mammals largely consume fish species that are not targeted by fisheries, thereby limiting direct competition (Trites et al. 1997; Morissette et al. 2012).

The ecologic role of marine mammals and their importance to marine ecosystems has been studied by estimating the consumption of different prey species (Bogstad et al. 1997; Sigurjónsson & Víkingsson 1997; Williams et al. 2004; Morissette et al. 2006; Bolt et al. 2007; Overholtz & Link 2007). This requires knowledge of abundance, diet composition and of energy requirements of the predator species (Pauly et al. 1998; Nøttestad & Olsen 2004; Williams et al. 2004; Williams et al. 2011b). Marine mammals are the largest predatory component of the Norwegian Sea ecosystem, with an estimated total biomass of 700,000 tonnes (Nøttestad & Olsen 2004). Most studies on marine mammal food consumption in the Norwegian Sea and Barents Sea have investigated consumption by minke whales (*Balaenoptera acutorostrata*) (Olsen & Holst 2001; Tjelmeland & Lindstrøm 2005; Smout & Lindstrøm 2007; Lindstrøm et al. 2009). The quantitative data available on direct feeding of minke whales indicate an annual consumption of 16,700 tonnes of herring in the Norwegian Sea (Olsen & Holst 2001). There is no information on food consumption of killer whales from Norwegian waters.

As discussed above, predators can have a major impact on their prey species. However, predator-prey interactions are a two-way process in which the abundance and distribution of prey also affects the life histories and distribution of predators. For example, in the NE Pacific Chinook salmon (*Oncorhynchus tshawytscha*) abundance has been shown to

have an effect on the reproductive and survival rates of resident killer whales (Ward et al. 2009; Ford et al. 2010). More generally, the patchy distribution of prey, both temporally and spatially, results in an aggregative response by predators in areas with high food concentrations, and movement between the locations of prey (Similä et al. 1996; Stevick et al. 2002).

The first studies on large whale migration involved the use of Discovery marks, which were individual numbered tags shot into a whale and later recovered when the whale was killed in whaling operations (Brown 1978). More recently, cetacean migration and movement has been studied by advanced tagging methods such as satellite telemetry, passive acoustics, genetic tagging and photo-identification methods (see e.g. Similä et al. 1996; Palsbøll et al. 1997; Similä et al. 2002; Stevick et al. 2002; Johnson & Tyack 2003; Mate et al. 2007; Andrews et al. 2008). Information on year-round distribution of many cetacean species is still lacking because of the difficulties in following animals through all seasons.

Despite its importance and some research focus, the ecological role of marine mammals in the marine ecosystem is not well understood (Bowen 1997; Sigurjónsson & Víkingsson 1997; Williams et al. 2004; Morissette et al. 2006). One of the reasons is that collection of the necessary data is logistically difficult and expensive. Predator-prey interactions occur at different spatial and temporal scales and so reliable long-term datasets on distribution and abundance of both predator and prey are needed to study the ecological role of a predator. Such long-term datasets are extremely rare at least for most marine mammal species. One of the longest datasets available for a cetacean species is for the northeast Pacific resident killer whales (Bigg 1982; Olesiuk et al. 1990; 2005). Some of the studies on these populations have also investigated the predator-prey interactions between killer whales and salmon (Ward et al. 2009; Ford et al. 2010). The study presented in this thesis used two long-term datasets both on predator and prey: 1) a long-term photo-identification dataset of the northern Norwegian killer whale population and 2) a long-term acoustic survey dataset on the Norwegian spring spawning herring stock.

#### **1.4 Study species - Killer whale (*Orcinus orca*, Linnaeus 1758)**

##### **1.4.1 Distribution and ecotypes**

The killer whale as a species has a world-wide distribution and is found in all major oceans (Matkin & Leatherwood 1986; Forney & Wade 2007). Locally though, specific prey preferences, behaviours and adaptations of different populations have led to the formation of different “ecotypes” of killer whales, which can be distinguished morphologically and/or genetically

(Hoelzel et al. 2007; LeDuc et al. 2008; Foote et al. 2009; Morin et al. 2010; Pilot et al. 2010; Foote et al. 2011). In the North Pacific, three sympatric types of killer whale are documented: fish-eating resident, mammal-eating transient and potentially fish-eating offshore (Bigg 1982; Bigg et al. 1987; Ford & Ellis 1999; Ford et al. 2000). In Antarctic waters three types have been identified: mammal-eating A and B, and fish-eating C (Pitman & Ensor 2003; Pitman et al. 2007), but information is still limited from this large area and possibly some other types also exist (Olson et al. 2012). A type D killer whale has been reported from sub-Antarctic waters, possibly feeding on fish (Pitman et al. 2011). Two different types: fish-eating type 1 and potential mammal-eating type 2 have been identified in the North Atlantic (Foote et al. 2009). Fish-eating killer whales in the North East Atlantic form three different populations; herring-feeding A, mackerel-feeding B and tuna-feeding C (Foote et al. 2011). The killer whale population in northern Norway represents type 1 and population A (Foote et al. 2009; 2011). There is current discussion regarding the designation of certain killer whale ecotypes as species based on morphological and ecological differences and due to reproductive isolation (Pitman & Ensor 2003; Pitman et al. 2007), and also based on results from mitochondrial genome analysis (LeDuc et al. 2008; Morin et al. 2010). Despite location-specific differences between killer whale populations globally, a common trait for all killer whale ecotypes is the tight social structure based around mothers and their offspring, a unit called the matrilineal group (Bigg et al. 1987; 1990) from which the individuals seldom separate.

#### **1.4.2 Diet**

Global dispersal of killer whales is possible through the generalist foraging habits of this species. However, the diet of different populations varies locally from various fish species, e.g. herring, salmon and tuna, to large baleen whales (Heimlich-Boran 1988; Guinet 1991; Baird & Dill 1995; Similä et al. 1996; Ford et al. 1998; Saulitis et al. 2000; Pitman & Ensor 2003; Burdin et al. 2004; Ford & Ellis 2005; Herman et al. 2005; Tarasyan et al. 2005; Guinet et al. 2007; Krahn et al. 2007; Matkin et al. 2007; Higdon et al. 2011; Ford et al. 2011; Reisinger et al. 2011a; Pitman & Durban 2012). These location-specific prey resources have resulted in population-specific behavioural traits influencing group size (Bigg et al. 1990; Baird & Dill 1996; Ford et al. 1998; Higdon et al. 2011), acoustic behaviour (Barrett-Lennard et al. 1996; Deecke et al. 2005; Samarra et al. 2010) and feeding techniques (see e.g. Guinet 1991; Similä & Ugarte 1993; Baird & Dill 1995; Ford et al. 1998; 2005).

The northern Norwegian killer whale population mainly feeds on Norwegian spring spawning herring (Jonsgård & Lyshoel 1970; Christensen 1988; Similä & Ugarte 1993; Similä et

al. 1996). The list of prey species reported also includes mackerel (*Scomber scombrus*), saithe (*Pollachius virens*), cod (*Gadus morhua*), eider duck (*Somateria molissima*) (Similä et al. 1996) and Atlantic salmon (*Salmo salar*) (Vester & Hammerschmidt 2013). Additionally some evidence suggests that certain pods of killer whales may feed on seals (Similä et al. 1996; Vongraven & Bisther in press).

### 1.4.3 Morphology and life history

The body length of killer whales varies to some extent between different ocean basins; males have been recorded reaching a maximum length of 9 m and females 7 m (Matkin & Leatherwood 1986; Ford et al. 2000). In northern Norway, killer whales on average reach a length of about 7 m, and females are normally closer to 6 m long (Jonsgård & Lyshoel 1970; Christensen 1984; Stenersen & Similä 2004).

Killer whales are long-lived mammals with a maximum age of 70 years for males and 80 years for females, but with a mean life expectancy at birth of 30 years for males and 50 years for females (Olesiuk et al. 1990; Ford et al. 2000; Olesiuk et al. 2005). The killer whale is a slowly reproducing species (Olesiuk et al. 1990; Ford et al. 2000; Olesiuk et al. 2005). Males reach sexual maturity between 10.5-17.5 years and 50% of males are estimated to be sexually mature at the age of 14.8 years (Olesiuk et al. 1990). Males reach physical maturity and the dorsal fin is fully grown at a mean age of 21 years (Olesiuk et al. 1990, Ford *et al.* 2000). Most female killer whales give birth to their first viable calf at 12-17 years of age (Olesiuk et al. 1990; 2005). The gestation period of killer whales lasts on average 17 months (varying between 15-18 months) (Walker et al. 1988; Duffield et al. 1995). Killer whale females demonstrate a rare phenomenon of reproductive senescence, and it has been recorded that around the age of 40 female killer whales no longer reproduce (Olesiuk et al. 1990; 2005). In addition to killer whales, reproductive senescence has also been recorded for pilot whales (*Globicephala macrorhynchus* and *G. melas*) (Kasuya & Marsh 1984; Marsh & Kasuya 1986; Martin & Rothery 1993).

Most information on killer whale population parameters comes from studies conducted off the Pacific coast of North America (Olesiuk et al. 1990; Olesiuk et al. 2005; Zerbini et al. 2007; Matkin et al. 2012). In southern and northern resident killer whale populations in waters of Washington State, USA and British Columbia, Canada, all individuals have been catalogued and monitored (Ford et al. 2000; Olesiuk et al. 2005). Recent information on population size and survival rates of killer whales has been produced from the Crozet Archipelago (Poncelet et al. 2010) and the Gulf of Alaska (Matkin et al. 2012) and on

abundance from Marion Island (Reisinger et al. 2011b). Estimated annual survival rates for NE Pacific resident killer whales vary between 0.91–0.99 (Olesiuk et al. 1990; 2005). Alaskan transients were estimated to have an average apparent annual survival of 0.98–0.99 (Matkin et al. 2012). Killer whales from the Crozet Archipelago were estimated to have lower apparent annual survival of 0.90–0.94 (Ponzelet et al. 2010). Survival rates have not been estimated for the northern Norwegian killer whale population prior to this thesis.

Calving intervals of 2 to 14 years have been recorded for the NE Pacific resident killer whales, with a mean fecundity rate of 0.177-0.205 calves per year (Olesiuk et al. 1990; 2005). Reproductive rates for the northern Norwegian killer whale population were unknown prior to this thesis.

#### **1.4.4 Status and threats**

In the current IUCN Red List, the killer whale as a species globally is listed as “Data Deficient” (Taylor et al. 2012). Some local populations are considered to have a critical status, i.e. the population resident to the Strait of Gibraltar (Cañadas & de Stephanis 2006) and the southern resident killer whale population in the NE Pacific (Krahn et al. 2004; Reynolds et al. 2009). The population of ten killer whale individuals in the West coast of Scotland has been proposed as a separate management unit for conservation (Beck et al. 2013). The northern Norwegian killer whale population is currently considered neither to be under immediate threat nor to be at risk of extinction.

As described earlier, the range of human-induced pressures and threats to the continued viability of killer whale populations come from multiple sources. Fisheries interactions have been recorded as a cause of concern in the Crozet Archipelago (Ponzelet et al. 2010; Tixier et al. 2010). Only a few lethal interactions between fisheries and killer whales are known from northern Norway (see Chapters 2 & 4). Offshore developments, oil exploration, military activities, increased shipping and the consequent increase in noise in the oceanic environment can displace killer whales from preferred locations and lead to lowered viability (Erbe 2002; Morton & Symonds 2002; Williams et al. 2006; Southall et al. 2007; Matkin et al. 2008; Lusseau et al. 2009; Miller et al. 2012; see Chapter 5). Killer whales have also been reported from many locations to carry extremely high levels of contaminants, something that could affect survival and reproductive rates (Ross et al. 2000; Hickie et al. 2007; Wolkers et al. 2007; Cullon et al. 2009; Noël et al. 2009). Killer whales were previously subject to large catches in Norway and the NE Pacific (Christensen 1982; Øien 1988; Olesiuk et al. 1990), which could have had an effect on their status. Currently catches are not considered to be a threat to

any killer whale population. However, small numbers of killer whales are hunted in the waters of e.g. Greenland and Japan (Reeves et al. 2003) and live-captured in Kamchatka Russia (Burdin et al. 2007). Changes in prey availability have been shown to have an effect on both survival and reproductive rates of killer whales, and changes in prey availability can seriously affect the viability of killer whale populations (Ward et al. 2009; Ford et al. 2010).

#### **1.4.5 Previous studies of killer whales in Norway**

The long-term study of killer whales in northern Norway was initiated in 1986 (with some material dating back to 1983) (Lyrholm 1988; Similä 1997a), and includes consistent collection of photo-identification data, following the methodology introduced by Bigg (1982) and Bigg et al. (1986) for the killer whale in the NE Pacific.

Studies of the behavioural ecology of these killer whales included investigation of seasonal occurrence patterns (Similä et al. 1996) and studies of social organisation (Similä 1997a; Ugarte 2001). Some major findings included the description of a unique co-operative feeding behaviour of northern Norwegian killer whales, called “carousel feeding”, where a tight ball of herring is forced close to the surface by the hunting whales, which then use tail slaps to stun the herring for easy consumption (Similä & Ugarte 1993; Similä 1997b). The results of a satellite tagging study in 2000 and 2001 revealed interesting movement behaviour of killer whales between the fjord system and offshore during winter months (Similä et al. 2002; Stenersen & Similä 2004), and this is discussed further in Chapters 3 and 6 in this thesis.

Vocal behaviour has been studied in the context of call repertoires (Strager 1995), production of ultrasonic whistles (Samarra et al. 2010) and during different behavioural stages (Van Parijs et al. 2004; Van Opzeeland et al. 2005; Simon et al. 2007). The effect of exposure of killer whales to naval sonar has also been studied in northern Norway and has been shown to have the potential to displace killer whales from their preferred location and to interrupt important behaviours like feeding (Miller et al. 2012).

Studies of the genetic structure of killer whale populations, including the Norwegian population, have suggested that three significantly different populations exist in the NE Atlantic (Foote et al. 2011). Wolkers et al. (2007) revealed that the northern Norwegian killer whales carry very high levels of contaminants, making them the most polluted animals in the Arctic.

Information on population parameters of the northern Norwegian killer whale population has previously been very limited. Christensen (1988) estimated that at least 1,500 killer whales were present in coastal waters of Norway when the herring was in this area

during January to March. The North Atlantic Sighting Survey (NASS) estimated 7,000 killer whales in Norwegian waters (Øien 1993) in summer 1989. However, these whales are likely to belong to a number of different populations and this estimate does not give a separate population size estimate for the northern Norwegian population. Previous mark-recapture analysis of the data specifically from northern Norway has produced estimates of about 490-550 killer whales in the Norwegian spring spawning herring wintering areas during October-January 1990-1993 (Similä & Christensen 1992; Similä 1997a). However, this analysis did not take into account likely heterogeneity in capture probabilities. As mentioned above, estimates of survival and reproductive rates for this killer whale population have not been made prior to this thesis.

### **1.5 The Norwegian spring spawning herring (*Clupea harengus*, Linnaeus 1758)**

The Norwegian spring spawning herring (hereon referred to as NSS herring) is a streamlined silver coloured fish growing to the maximum length of 40 cm and to a maximum age of 20 years, and feeds on zooplankton, such as copepods (*Calanus finmarchicus*) (Holst et al. 2004). However, during winter months the NSS herring does not feed and this period is defined by predator avoidance. The NSS herring is a pelagic schooling fish and forms the largest herring stock in the world and the largest fish stock in the NE Atlantic (Holst et al. 2004; ICES 2013). This herring stock is of major economic importance, and countries fishing on this stock include Norway, Iceland, Russia and many EU countries (ICES 2013; Pilling et al. 2009). The NSS herring is also an important prey species in the NE Atlantic ecosystem; species feeding on this stock include cod, saithe, many species of sea birds and whales (Similä & Ugarte 1993; Pitcher et al. 1996; Nøttestad 1998; Axelsen et al. 2001; Nøttestad & Similä 2001; Olsen & Holst 2001; Nøttestad et al. 2002; Tjelmeland & Lindstrøm 2005). The killer whale follows the yearly migration pattern of the NSS herring stock (Christensen 1988; Similä et al. 1996; Stenersen & Similä 2004).

The NSS herring stock has gone through major changes in its biomass within the last century. A record high spawning stock biomass of 16 million tonnes was reported in 1945 (Toresen & Østvedt 2000). Following heavy exploitation due to improved fishing methods, the stock collapsed at the end of the 1960s to as low as 50 000 tonnes (Dragesund et al. 1997; Toresen & Østvedt 2000). From the late 1980s, stock numbers increased again due to recruitment of large year classes to the spawning stock in 1983, 1991 and 1992, reaching a new high of spawning stock biomass of approximately 6 million tonnes in the late 1990s (Toresen & Østvedt 2000; Orellana 2006; ICES 2013).

The NSS herring stock is highly dynamic and undertakes large-scale seasonal migrations over thousands of kilometres between coastal and offshore waters, and is known to alter this migration pattern at uneven intervals (Dragesund et al. 1997; Huse et al. 2002; Holst et al. 2002; 2004). Considerable changes in the wintertime location of NSS herring have taken place since the 1950s, from offshore to coastal and sheltered fjord areas (Dragesund et al. 1997; Huse et al. 2010). Since 1986, the adult and adolescent NSS herring started wintering in Vestfjord (see Figure 1.1), expanding to the branching fjords of Tysfjord and Ofotfjord in 1987 between October and January (Holst et al. 2002; Orellana 2006; Huse et al. 2010). Throughout the 1990s, the whole spawning stock of NSS herring was concentrated in Tysfjord, Ofotfjord and Vestfjord areas in winter. Since 2002, part of the NSS herring stock started to winter in a new area outside the fjord system in offshore waters of the Norwegian Sea between 69°-73°N (Huse et al. 2010; see Chapter 6). This change in wintertime distribution was caused by a relatively strong recruitment to the NSS herring stock in 1998 and 1999, and these year-classes no longer entering the fjord system in wintertime (Holst et al. 2004; Huse et al. 2010). By 2006, only a fraction of the spawning herring stock was found wintering inside the fjord system, with the main part of the stock distributed in offshore areas of the Norwegian Sea (Huse et al. 2010).

### **1.6 Study sites**

The main study site from where data were collected and results presented in this thesis was the so-called “fjord system” comprising the three connecting fjords of Vestfjord, Ofotfjord and Tysfjord. This fjord system is located in northern Norway, north of the Arctic Circle (see Figure 1.1), at latitude 67°50'N-68°32'N. The maximum depth of 897 meters is in Tysfjord, making this fjord the second deepest in Norway. Photo-identification data of killer whales presented in this thesis were collected from this area during 1986-2008.

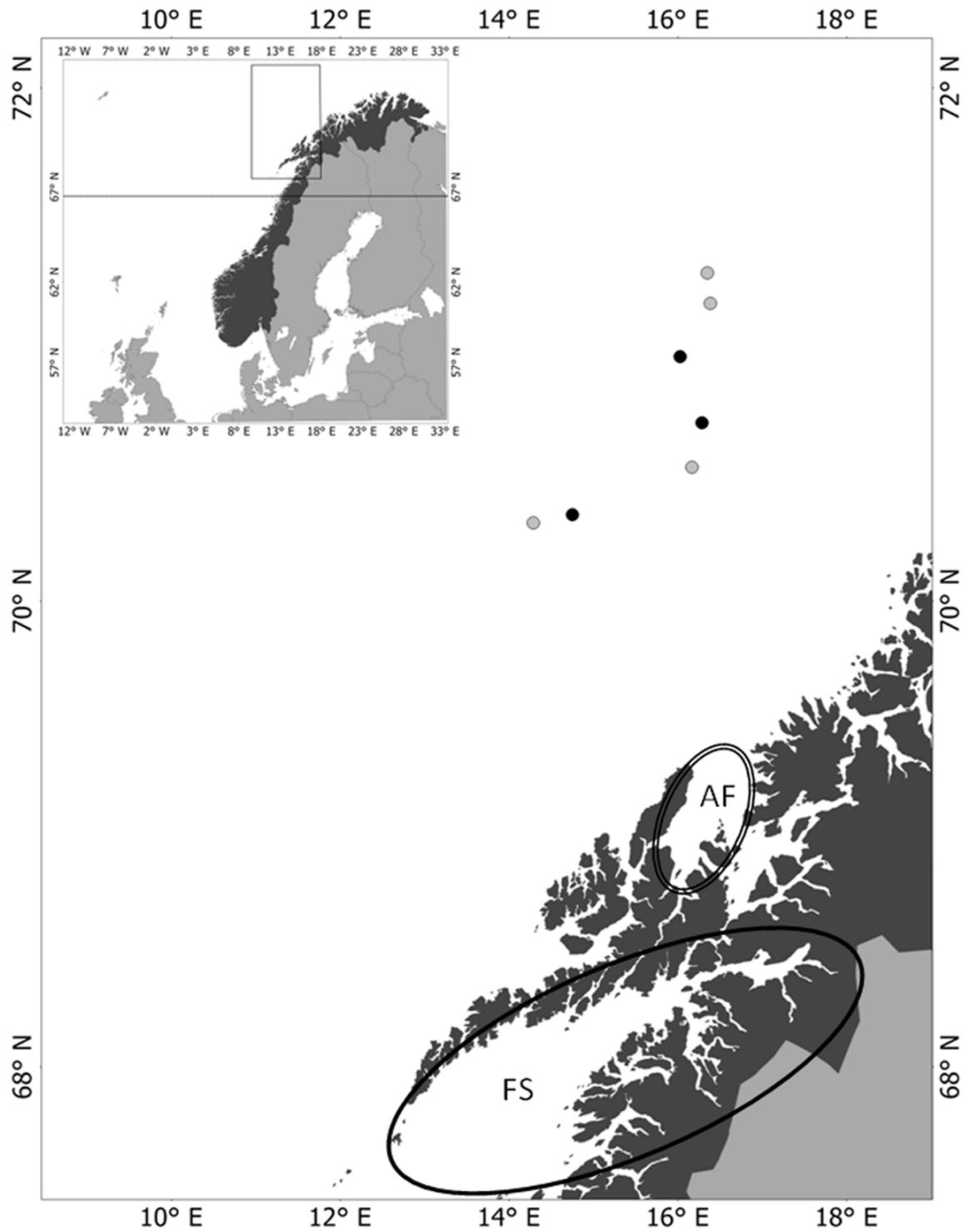


Figure 1.1 - Norway is indicated with dark grey colour on the smaller map, with the dark horizontal line representing the Arctic Circle. The larger map includes the three fieldwork areas where killer whale photo-identification data were collected; 1) the fjord system (FS) 2) offshore locations where killer whales were encountered are indicated with dots (black dots indicating photo-identification positions), and 3) Andfjord (AF).

The offshore area that became the main wintering area for the NSS herring since 2002 (Huse et al. 2010) is located in the Norwegian Sea between latitudes 68°N and 73°N. The NSS herring has been widely dispersed in this area and the distribution has varied annually to some extent in the area, with the distribution to the east following the 1000 meter bathymetric contour. Attempts were made to collect photo-identification data in this offshore area in December 2007 and November 2008. Photo-identification data were also collected in Andfjord (see Figure 1.1) in January 2013.

All of these study sites suffer from a serious lack of daylight during wintertime (October-January). The daylight diminishes from approximately 11 hours on 1 October to 24 hour dawn or darkness in late December. This has caused major challenges for the photo-identification methods used to study the killer whale population in these areas.

The NSS herring survey data collected by the Norwegian Institute of Marine Research (IMR) that were used in this thesis were collected in the fjord system during 1986-2006 and in the offshore areas during 2002-2007.

### **1.7 Thesis overview**

Information on killer whale population parameters are best known for the northern and southern resident killer whales of the NE Pacific (Olesiuk et al. 1990; 2005). Population-specific differences are expected in these parameters, and inferring these parameters between populations is unlikely to be justified. There has been a complete lack of information on survival and reproductive rates of the northern Norwegian killer whale population. In Chapter 2, I use photo-identification and mark-recapture methods to estimate survival and reproductive rates for the northern Norwegian killer whale population for the first time. Additionally, annual total population size is estimated with a long-term dataset, taking into account heterogeneity of capture probabilities and the proportion of identifiable individuals in this population.

With the attempt to obtain more accurate adult survival rate estimates, in Chapter 3 the estimation of survival rates is explored in more detail to account for so-called temporary emigration (Pollock 1982; Kendall et al. 1995; 1997); i.e. that not all the individuals in the population are available to be captured each year due to some individuals being temporarily out of the study area. The estimates of survival rate from Chapters 2 and 3, and the differences found between different killer whale populations are discussed. Results indicating the existence of temporary emigration of killer whales from the fjord system and the potential reasons behind it are also discussed.

With the newly obtained population parameter estimates from Chapters 2 and 3, I then build a population viability model in Chapter 4 to assess future population size and extinction risk of this killer whale population under different potential scenarios. Possible future declines in NSS herring prey resources are evaluated and discussed. Additionally, an attempt is made to model the previous catches from this killer whale population in a retrospective way.

The impact of anthropogenic sound exposure in underwater environments is a current concern (Nowacek et al. 2007; Southall et al. 2007). Military sonar exposure in the study site of the fjord system has previously led to fears that killer whales have been displaced from their preferred location (WWF-Norway 2001; Miller et al. 2012), something that might also have implications for the mark-recapture methods used in Chapters 2, 3 and 6. In Chapter 5, a whale-watching sighting dataset from 2002-2008 indicating the presence of killer whales, in addition to dedicated research effort on killer whale presence in 2006 are correlated to known naval sonar activity in the fjord system. The potential displacement of killer whales due to naval sonar exposure under certain environmental conditions is discussed.

In Chapter 6, I describe the large-scale distribution change of the NSS herring stock that started in 2002, using the Norwegian Institute of Marine Research (IMR) herring survey data. With the long-term photo-identification data (1986-2008 & 2013) of killer whales, I evaluate the observed response of a top predator to this major distribution change of its prey species. Additionally, I discuss the potential habitat preference of this population of killer whales and the plasticity of killer whales to change in the distribution and abundance of their prey.

## CHAPTER 2

### Abundance, survival and reproductive rates of northern Norwegian killer whales in 1986-2003

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#### ABSTRACT

A long-term photo-identification study of killer whales in northern Norway was initiated in 1986, when their prey the Norwegian spring-spawning herring started to winter in a complex fjord system. The aim of this work was to estimate population size and apparent survival rates in this killer whale population using photo-identification and mark-recapture techniques with data collected during October-December 1986-2003. Mark-recapture analysis was done using program MARK. Total population size was estimated to be highest in 2003: 731 individuals (SE = 139, 95% CI = 505-1059), using a model taking heterogeneity of capture probabilities into account. Apparent survival of adult males and adult females was estimated using the Cormack-Jolly-Seber model as 0.971 (SE = 0.008) and 0.977 (SE = 0.009), respectively. Calving intervals ranged from 3 to 14 years (mean = 5.06, SE = 0.722). These are the first estimates of northern Norwegian killer whale population parameters, allowing their dynamics to be investigated and comparisons to be made with killer whale populations globally.

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## 2.1 INTRODUCTION

Killer whales (*Orcinus orca*) have an important role in the marine environment as top predators. Information on their distribution, abundance and population dynamics is necessary to be able to evaluate their impact on the marine ecosystem, and knowledge of their status is crucial to monitor their population specific viability for conservation purposes (Boyd et al. 2006). Killer whales have a global distribution and are found in all major oceans (Matkin & Leatherwood 1986; Forney & Wade 2007). World-wide dispersal is possible through the generalist foraging habits of this species, their diet varying from various fish species, e.g. herring and salmon, to large baleen whales (Heimlich-Boran 1988; Guinet 1991; Baird & Dill 1996; Similä et al. 1996; Ford et al. 1998; Saulitis et al. 2000; Pitman & Ensor 2003; Burdin et al. 2004; Ford & Ellis 2005; Herman et al. 2005; Tarasyan et al. 2005; Guinet et al. 2007; Krahn et al. 2007; Matkin et al. 2007; Higdon et al. 2011; Ford et al. 2011; Reisinger et al. 2011a; Pitman & Durban 2012).

Local adaptations, behaviours and specific prey preferences have led to the formation of different “ecotypes” of killer whales that can be distinguished morphologically and/or genetically (Hoelzel et al. 2007; LeDuc et al. 2008; Foote et al. 2009; Morin et al. 2010; Pilot et al. 2010; Foote et al. 2011). In the North Pacific, three sympatric types of killer whale are documented; fish-eating resident, mammal-eating transient and potentially fish-eating offshore (Bigg 1982; Bigg et al. 1987; Ford & Ellis 1999; Ford et al. 2000). In Antarctic waters three types have been identified; mammal-eating A and B, and fish-eating C (Pitman & Ensor 2003; Pitman et al. 2007), but information is still limited from this large area and possibly some other types also exists (Olson et al. 2012). A type D killer whale has been reported from sub-Antarctic waters, possibly feeding on fish (Pitman et al. 2011). Two different types; fish-eating 1 and potential mammal-eating 2 have been identified in the North Atlantic (Foote et al. 2009). Fish-eating killer whales in the North East Atlantic are forming three different populations; herring-feeding A, mackerel-feeding B and tuna-feeding C (Foote et al. 2011). The killer whale population in northern Norway represents type 1 and population A (Foote et al. 2009; 2011).

The main prey of killer whales in northern Norwegian waters is the Norwegian spring-spawning herring (*Clupea harengus*) (hereafter called NSS herring) (Jonsgård & Lyshoel 1970; Christensen 1988; Similä & Ugarte 1993; Similä et al. 1996). The NSS herring stock conducts large-scale seasonal migrations over thousands of kilometres between coastal and offshore waters, and is known to alter this migration pattern at uneven intervals (Dragesund et al. 1997; Huse et al. 2002; Holst et al. 2002; 2004). Considerable changes in the wintertime location of

NSS herring have taken place since the 1950s, from offshore to coastal and sheltered fjord areas (Dragesund et al. 1997; Huse et al. 2010). The NSS herring stock has also gone through major changes in its abundance within the last six decades, the last stock collapse happening at the end of the 1960s (Dragesund et al. 1997; Toresen & Østvedt 2000).

The distribution and local abundance of killer whales in northern Norway is associated with the presence of this dynamic NSS herring stock (Jonsgård & Lyshoel 1970; Christensen 1982; 1988; Øien 1988; Similä et al. 1996). Since 1986, the adult and adolescent NSS herring started wintering in Vestfjord, north of the Arctic Circle (Figure 2.1a & 2.1b), expanding to the tributary fjords of Tysfjord and Ofotfjord in 1987 between October and January (Holst et al. 2002; Orellana 2006; Huse et al. 2010).

A long-term study on killer whales in this accessible area was initiated in 1986 (with some material dating back to 1983) (Lyrholm 1988; Similä 1997a). Throughout the 1990s, the whole spawning stock of NSS herring was concentrated in Tysfjord, Ofotfjord and Vestfjord areas in winter. The very strong NSS herring year-classes in 1991 and 1992 contributed to this stock and the biomass of spawning NSS herring stock reached about 6 million tonnes in the late 90s (Toresen & Østvedt 2000; Orellana 2006). Since 2002, part of the NSS herring stock started to winter in a new area outside the fjord system in offshore waters of the Norwegian Sea between 69°-73°N (Huse et al. 2010). This change in wintertime distribution was caused by a relatively strong recruitment to the NSS herring stock in 1998 and 1999, and these herring year-classes no longer entering the fjord system in wintertime (Holst et al. 2004; Huse et al. 2010).

Most information on killer whale population parameters and social organization comes from studies conducted off the Pacific coast of North America (Bigg et al. 1990; Olesiuk et al. 1990; Matkin et al. 1999; Ford et al. 2000; Olesiuk et al. 2005; Ward et al. 2011; Zerbini et al. 2007). In southern and northern resident killer whale populations in waters of Washington State, USA and British Columbia, Canada, all individuals have been catalogued and monitored (Ford et al. 2000; Olesiuk et al. 2005). Killer whales are a long-lived (maximum 70 years for males and 80 years for females) and slowly reproducing species (Olesiuk et al. 1990; Ford et al. 2000; Olesiuk et al. 2005). Most female killer whales give birth to their first viable calf at 12-17 years of age (Olesiuk et al. 1990; 2005). The gestation period of killer whales lasts on average 17 months (varying between 15-18 months) (Walker et al. 1988; Duffield et al. 1995). Males reach sexual maturity between 10.5-17.5 years and 50% of males are estimated to be sexually mature by the age of 14.8 years (Olesiuk et al. 1990). Males reach physical maturity and the dorsal fin is fully grown by a mean age of 21 years (Olesiuk et al. 1990; Ford et al. 2000).

Recent information on population size and survival rates of killer whales has been produced from the Crozet Archipelago (Poncelet et al. 2010) and the Gulf of Alaska (Matkin et al. 2012) and on abundance from Marion Island (Reisinger et al. 2011b). Estimated survival rates for NE Pacific resident killer whales vary between 0.91 - 0.99 (Olesiuk et al. 1990; 2005). Alaskan transients were estimated having average apparent survival of 0.98 – 0.99 (Matkin et al. 2012). Killer whales in Crozet Archipelago were estimated to have lower apparent survival of 0.90 – 0.94 (Poncelet et al. 2010). Previous work in northern Norway has produced estimates of about 490-550 killer whales in the NSS herring wintering areas during October-January 1990-1993 (Similä & Christensen 1992; Similä 1997a). No previous survival or calving rate estimates exist for northern Norwegian killer whales.

Analysis in this study used individual recognition data of northern Norwegian killer whales, collected during 1986-2003 between October-December each year from the NSS herring wintering ground inside the fjord system (see Vestfjord, Tysfjord and Ofotfjord in Figure 2.1). The dataset was limited in earlier years and variable through years. The nature of the dataset was such that no particular mark-recapture model had all the assumptions met. Therefore a number of models were investigated, and their performance and results compared in order to make the most of the data and to draw the most robust conclusions. This 18 year dataset was used to estimate a time series of population size taking into account those individuals in the population that were insufficiently marked to include in mark-recapture analysis. For estimating population size, a simple closed two-sample Chapman estimator was used for pairs of years and multi-sample closed capture models were used for each year. An open population model was also explored to estimate population size. Apparent survival rates were estimated with Cormack-Jolly-Seber models for adult males and adult females, and for sub-adults where possible. Robust design models estimating apparent survival and population size taking into account temporary emigration are explored in Chapter 3. Calving rates were calculated using data from 1989-2002.

The results of this study add substantially to the knowledge of population parameters of killer whales and allow comparison with different killer whale populations world-wide. The results can be used to inform future monitoring of the status and viability of the northern Norwegian killer whale population. Information on its population dynamics is also valuable for projects implementing an ecosystem approach to management; the results could be used to evaluate the role of killer whales as top predators in the northeast Atlantic ecosystem, by estimating prey consumption rates and thereby their importance as predators, e.g. on economically important fish species like the NSS herring.

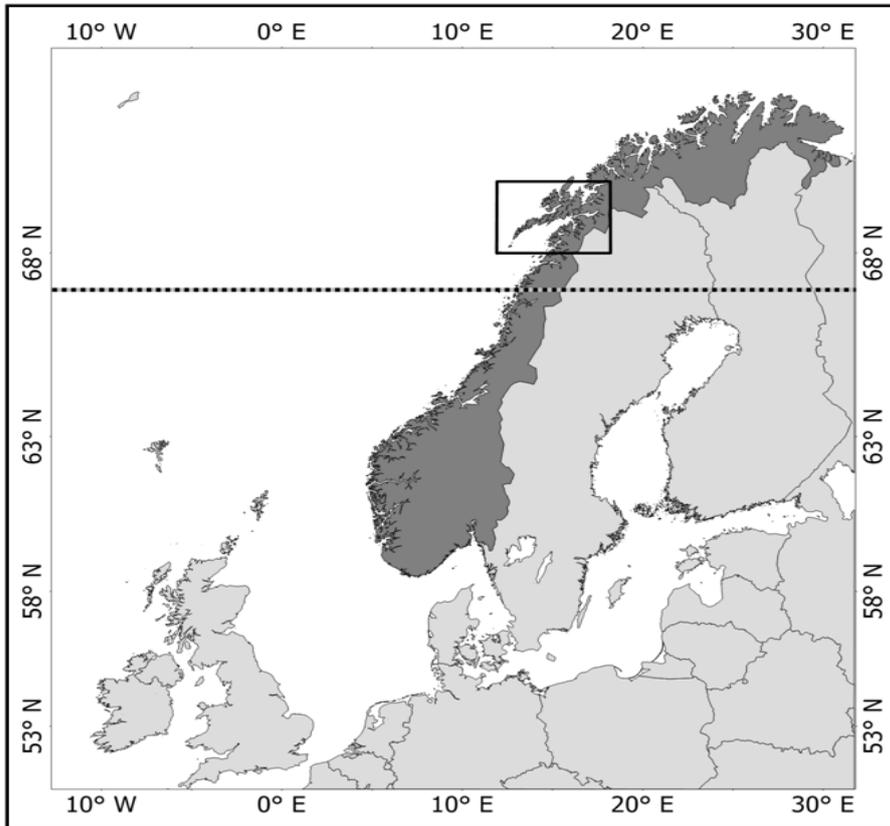


Figure 2.1a - The research area (dark square) located in northern Norway above the Arctic Circle (dashed line).

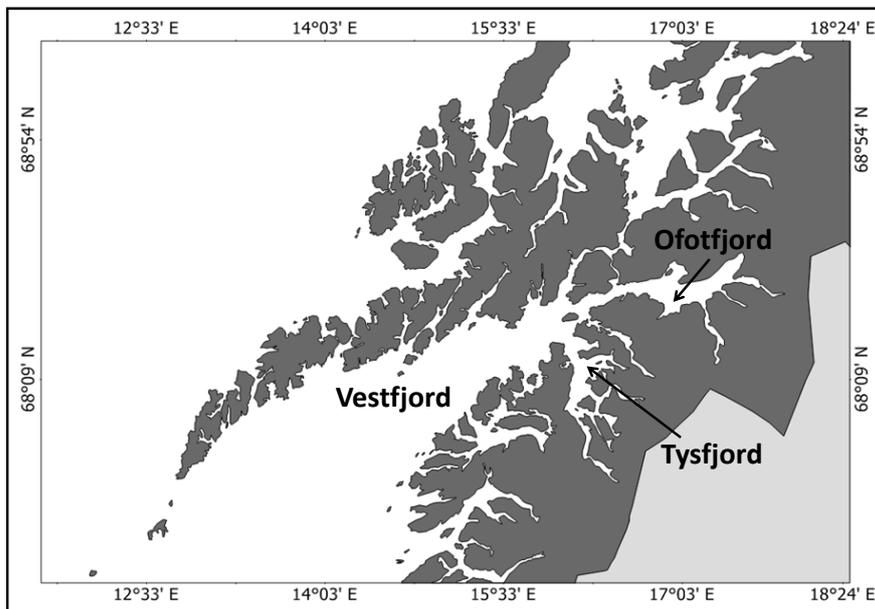


Figure 2.1b - The research areas of Vestfjord, Tysfjord and Ofotfjord in northern Norway.

## **2.2 METHODS**

### **2.2.1 Data collection**

The research area is located above the Arctic Circle in the waters south of the Lofoten islands in northern Norway (Figure 2.1a). The data were collected in Ofotfjord, Tysfjord and Vestfjord (Figure 2.1b) between October and January at a time of very limited daylight. The field season shifted later over the years because of herring entering the fjords later each year. For consistency throughout the study, the data collected between October and December 1986-2003 were selected for analysis.

Killer whales were searched for opportunistically, aided by information from the crew of ferries, whale-watching boats and fishing vessels. When killer whales were encountered the size of the pod and/or group was estimated and, when possible, the number of adult males, adult females, sub-adults, juveniles and calves was recorded. Throughout, the term pod refers to a matrilineal family unit of killer whales whereas the term group refers to a cluster of killer whales including individuals from different pods.

Identification photographs were taken, with preference for the left side of the animal, using the method described by Bigg (Bigg 1982; Bigg et al. 1986; 1990). An effort was made to photograph as many of the individuals as possible in an encounter and all individuals equally, regardless of their degree of identifiability, e.g. adult males with fully grown dorsal fins. In 1986 -2000 pictures were taken with SLR cameras equipped with 200 or 300 mm lenses. The majority of images were taken with KODAK T MAX 400 ASA film pushed to 1600 ASA. From 2001, images were taken using digital cameras with 200 or 300 mm lenses.

### **2.2.2 Data processing**

The films were inspected using a stereoscopic microscope and the digital images were viewed in Adobe Photoshop. Individuals were identified by the shape of the dorsal fin and the grey saddle patch behind the dorsal fin and by natural markings in these areas (Bigg 1982). The identified individuals were divided into different categories: males, females/sub-adults and juveniles (see below). The best picture of each individual from each encounter was compared to pictures in the identification-catalogue (of pictures taken in earlier years), which held 585 identified individuals from northern Norway by the end of the study.

Each individual was given a letter-number code, e.g. N-100, where N is for Norway and 100 is the number of the individual. Where possible the individual whales were assigned to pods based on stable associations with other individuals and thereby also given a pod-

associated identification-code, e.g. NB-20, where N is for Norway, B is the pod ID and 20 is the number of the individual within that pod.

The quality of each picture was evaluated for contrast and focus, using a scale from 1 to 4 (1 being the best). Additionally the angle of the picture was evaluated from 1 to 3, angle 1 being parallel, 2 being with a slight angle from behind and 3 being with a slight angle from front. The amount of the saddle patch seen in the picture was measured on a scale 1 to 3, 1 being the top 1/3, 2 being the top 2/3 and 3 when saddle patch was seen fully. From these, the overall quality of the picture was assessed. Only good quality left-hand-side photographs of identifiable individuals were used for further analysis.

Encounter histories of identifiable individuals were built through 18 years and used for estimating population size and survival rates using mark-recapture analyses. Weeks were used as sampling occasions within the years for estimating population size with yearly models. For calculating calving rates, a calf was assigned to a specific female based on close proximity, swimming in the echelon position (Mann & Smuts 1999; Noren et al. 2008) and the calf needed to be seen on at least two days with the same female to be assigned to that specific female.

#### ***2.2.2.1 Determining sex and age-class***

Adult male killer whales can be identified correctly as male from the first sighting based on their tall dorsal fin (Bigg 1982). Females do not have such clear morphological evidence of physical maturity, so other methods were used to determine sex. When an individual non-calf killer whale that is not an adult male is encountered the first time, it could be an adult female, a sub-adult female or a sub-adult male. To identify adult females in northern Norway, several years of encounters would be needed to determine sex correctly.

A multistep process was conducted to determine the sex of each identifiable individual from northern Norway. Initially the information on how individuals were divided in the ID-Catalogue was used; adult males vs. females/sub-adults. Those individuals seen in close and consistent association with a calf were assigned as adult females. The sighting history data of each killer whale individual was used to determine the number of years an individual was encountered and especially the years between the first and the latest sighting.

A protocol was then created to determine the age of each identifiable individual with the information from the encounter histories. Calves were categorised to be 1-2 years old, juveniles 3-6 years and sub-adults 6+ years old. If a calf, juvenile or sub-adult was only seen in one year throughout the sighting history data, it was assigned as a calf, juvenile or sub-adult, respectively. If an individual was first seen as a calf, only if it was still seen after 15 years was it

assigned as an adult female or an adult male. An individual first seen as a juvenile needed to have been encountered 13 or more years to be assigned as an adult female or an adult male. Individuals first seen as a sub-adult could be assigned as an adult female or an adult male after observations of 9 or more years. Individuals that could not be categorised into any sex/stage specific groups were omitted from analysis. Stage refers here to different age groups, e.g. sub-adult or adult individuals.

### **2.2.3 Data analysis**

#### **2.2.3.1 Analytical assumptions**

Assumptions about the data when using natural or tag markings for mark-recapture analysis are that marks should be unique, permanent and need to be correctly recorded to minimize the risk of false positive or negative matching (Hammond 1986; 2010). To minimize violating these assumptions, only natural markings known to be identifiable and permanent on killer whales (Similä & Lindblom 1993) were used and only good quality photographs were selected (see above) for any analysis because decreased photographic quality leads to an increase in false matching (Stevick et al. 2001; Friday et al. 2008).

In basic mark-recapture models it is assumed that all individuals have an equal chance of being captured in each sampling occasion (Hammond 1986; 2010). This is often not the case and failure to fulfill the assumptions of equal capture probability leads to heterogeneity of capture probabilities and downward bias in estimates of population size, survival and underestimation of variance (Hammond 1995). The assumption of equal capture probability can be violated due to individual differences in behaviour, e.g. some individuals might tend to avoid the research vessel and therefore have a lower probability of being photographed. Although it is unlikely that actual trap-dependency (Pradel 1993; Pradel & Sanz-Aguilar 2012) would occur on marine mammals that are not physically handled in photographic capture, the unequal capture probabilities between individuals can be manifested as “trap-shyness” or “trap-happiness” due to differences between individual’s and/or pod’s behaviour.

Individual differences in capture probabilities can also be caused by transient individuals (Pradel et al. 1997). Transients are defined as individuals that are photographically captured only once in the study area during the study period, as after the first capture they permanently emigrated from the area. These transient individuals are then never recaptured, thereby violating the assumption of equal capture probability and potentially leading to biased estimates of population size and survival rate. Transient individuals are not to be confused

with the transient killer whale ecotype of the NE Pacific. Differences in behaviour were attempted to be taken into account in selected mark-recapture models.

Killer whales live in pods and are not sighted as independent individuals but in these larger aggregations of individuals (Bigg 1982; Lyrholm 1988; Similä & Christensen 1992; Similä 1997a), which violates the assumption of equal probability of sighting (Hammond 1986). Some individuals and pods may have area preferences and so may not be encountered randomly. It was assumed that all killer whale individuals used the whole research area.

The assumption of equal capture probability can also be violated by inadequate implementation of the methodology. There should be sufficient time between the sampling occasions so that all individuals can be assumed to have mixed and thereby have equal chance of being captured during the next sampling occasion (Hammond 1986). There was sufficient time (at least 1 day) between weekly sampling occasions to allow all individuals/pods to mix within the research area. Poor weather conditions on some days determined which area could be accessed. All individuals should also be recorded equally to minimize the heterogeneity of capture probability. Effort was made to photograph all individuals in an encounter, regardless of their distinctiveness.

Goodness of fit tests were used to explore the data with a set of models to try to find the best fitting model accounting for heterogeneity of capture probabilities, thus minimizing bias and maximizing precision. The population of killer whales was considered to be closed to births, deaths and permanent emigration and immigration during each field season and so closed capture methods were used to estimate population size in each year. This can be assumed to be true in the case of long-lived mammal species like killer whale and when the sampling is done over a short period of time, e.g. months (Hammond 1986; Nichols 1992; Hammond 2009).

This northern Norwegian killer whale population has a bigger range than the one selected as a research area (Similä et al. 2002; Stenersen & Similä 2004). Therefore, the potential for some individuals not being available within the research area during sampling but being temporarily out of the study area and thereby violating the assumption of closure was explored with open population and robust design models (see Chapter 3).

In addition to other assumptions mentioned above, open population Cormack-Jolly-Seber models assume that all animals have an equal chance of survival from one sampling occasion to another and that marking does not affect the probability of survival (Cormack 1964; Pledger et al. 2003). Models accounting for trap-dependency and transience were used

in analysis of apparent survival to account for unequal capture probabilities (Burnham & Overton 1978; Otis et al. 1978; Pollock 1982; Pradel 1993; Pradel et al. 1997).

### **2.2.3.2 Number of identifiable animals in population**

Photo-identification data from October-December 1986-2003 were first used to estimate the number of identifiable individuals ( $\hat{N}$ ) for pairs of years using a simple two-sample closed population Chapman estimator (Chapman 1951; Borchers et al. 2002):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

where  $n_1$  and  $n_2$  are the number of individuals captured in each of the two years, and  $m_2$  is the individuals captured in both years. Variance was estimated as:

$$\text{Var}(\hat{N}) = \frac{(n_2 + 1)(n_1 + 1)(n_2 - m_2)(n_1 - m_2)}{(m_2 + 1)^2(m_2 + 2)}$$

To explore the likely occurrence of heterogeneity in capture probabilities, population size of identifiable individuals was estimated independently for each year by fitting multi-sample closed capture models in program CAPTURE implemented within program MARK (Otis et al. 1978; Pollock et al. 1990; Chao & Huggins 2005; Cooch & White 2012). Weeks were used as sampling occasions within years. The most likely fitting models in program CAPTURE can be selected based on the Model Selection Criterion (MSC), which is based on the results of hypothesis tests run in program CAPTURE to investigate the support for models with different forms of variation in capture probability. No unique Goodness of Fit test exists for closed capture models, so the actual fits of the models to the data were not possible to test.

An exploratory analysis was also conducted in program MARK to estimate the number of identifiable individuals using multi-sample closed capture models (Otis et al. 1978) and Pledger mixture models that take heterogeneity of capture probabilities into account (Pledger 2000; Cooch & White 2012). In all years, except 1990, 1992 and 1995, the mixture model accounting for heterogeneity gave lower estimates of population size than the model that did not include heterogeneity. This indicated that modelling heterogeneity as a mixture was not the appropriate way to estimate population size with this dataset because accounting for heterogeneity should remove negative bias. Therefore results of this analysis are not presented here.

### 2.2.3.3 Proportion of identifiable individuals

Data on the proportion of identifiable individuals ( $\hat{\theta}$ ) in the population were used to derive estimates of total population size. The total number of individuals and the number of identifiable individuals were known for 20 killer whale groups encountered during 1992-2003. From these data, six groups from 1992-1995 were used to calculate the proportion of identifiable individuals to correct population estimates for 1990-1996. Fourteen groups from 1997-2003 were used for estimates for these years.

### 2.2.3.4 Total population size

Total population size was then estimated as:

$$\hat{N}_{total} = \frac{\hat{N}}{\hat{\theta}}$$

where  $\hat{N}_{total}$  = estimated total population size,  $\hat{N}$  = estimated number of identifiable individuals in the population and  $\hat{\theta}$  = proportion of identifiable individuals in the population. Variance was estimated directly from the data on proportions of identifiable individuals, using R (version 2.15.2) as:

$$V\hat{a}r(\hat{N}_{total}) = \hat{N}_{total}^2 \left( \frac{V\hat{a}r(\hat{N})}{\hat{N}^2} \right) + \left( \frac{V\hat{a}r(\hat{\theta})}{\hat{\theta}^2} \right)$$

This method is the same as in Wilson et al. (1999) but with variance estimation accounting for sampling variability.

### 2.2.3.5 Apparent survival rates

For the estimation of apparent survival, the data were organised into four datasets: 1) adult males, adult females and sub-adults together (dataset MFS); 2) adult males and adult females together (dataset MF); 3) adult males only; and 4) adult females only.

#### 2.2.3.5.1 Investigating goodness of fit

Goodness of fit of the CJS model was assessed using Program U-CARE (version 2.3.2) (Choquet et al. 2009). Program U-CARE performs directional chi-square tests (3.SR, 3.SM, 2.CT & 2.CL) to assess different aspects of model fit to evaluate potential issues with assumed equal survival and capture probabilities e.g. possible transience and trap-dependency (Choquet et al. 2005).

U-CARE also performs a global chi-squared test of the general goodness of fit which combines the statistics of the directional tests.

The global goodness of fit test in program U-CARE showed significant departures from adequate model fit for dataset MFS, dataset MF and for adult males and adult females separately ( $p < 0.001$ , see Appendix 2.1).

For the directional tests, the subtest within Test 3.SR with adult males showed an indication of transience ( $p = 0.001$ ) but its influence was not substantial resulting in the overall 3.SR test being supported ( $p = 0.305$ , see Appendix 2.1). However, a time-since-first-marking model (also known as an “age-class” model) was built in program MARK to account for the potential issue with transience in adult male data. Model was built in such way that the first period of marking (“1<sup>st</sup> age-class”) was different compared to following periods (“2<sup>nd</sup> age-class”), separating the transient individuals that were only seen in that first period. Ignoring the transience in the data could lead into negatively biased estimates of survival due to the permanent emigration of transient individuals from the study area.

Test 2.CT showed a highly significant ( $p < 0.001$ ) result for trap-dependency for adult males (see Appendix 2.1). Test 2.CT also gave a significant ( $p < 0.001$ ) result for trap-dependency for adult females, but this resulted from only two years of the dataset showing significance. Trap-dependency in all cases was “trap-happiness”, meaning that recapture probability in subsequent years of initial capture was higher than expected by chance. A mark-recapture model was built in program MARK to account for the trap-dependency with the adult male and adult female datasets (Sandland & Kirkwood 1981; Pradel 1993). None of the results of the directional tests were significant for sub-adults.

In addition, the goodness of fit of models to the data was explored using tests in program RELEASE within program MARK (White & Burnham 1999; Cooch & White 2012). The assumptions tested in program RELEASE were equal probability of recapture (TEST2) and equal probability of survival (TEST3). TEST 1 was performed to check for potential differences of equal probabilities of survival between different sex/stages: adult males, adult females and sub-adults.

RELEASE TEST3 was non-significant for datasets MFS and MF and also for adult males and adult females separately ( $p > 0.151$ , see Appendix 2.2). TEST2 was significant ( $p < 0.003$ ) for all datasets. These results are in line with the U-CARE test results indicating violation of the assumptions of equal capture probabilities. TEST1 for dataset MFS was significant ( $p < 0.001$ ) indicating a difference between the sex/stages. The need to separate sub-adults was confirmed with the non-significant TEST1 result for dataset MF ( $p = 0.462$ ).

### **2.2.3.5.2 Investigating over-dispersion**

The amount of over-dispersion in the data was investigated with the variance inflation factor  $\hat{c}$ , with  $\hat{c} = 1$  indicating no over-dispersion (Anderson et al. 1994; Cooch & White 2012). This was calculated within program U-CARE by dividing the chi-square statistic by the degrees of freedom. For comparison, over-dispersion was also evaluated in program RELEASE again by dividing the chi-square statistic by the degrees of freedom.

Additionally a parametric bootstrap goodness of fit test was used to measure over-dispersion in two ways in program MARK. Firstly, the estimates from the model being evaluated were used to simulate encounter histories, from which a  $\hat{c}$  was calculated. The number of simulations used was 100. The estimate of  $\hat{c}$  from the actual data was then divided by the mean of the simulated values of  $\hat{c}$ . Secondly, the “median- $\hat{c}$ ” approach was used, in which the best estimate of  $\hat{c}$  was determined to be the value where the observed model  $\hat{c}$  fell halfway in the distribution of all simulated  $\hat{c}$  values. The number of replicates used was again 100. A detailed description of the methods to estimate  $\hat{c}$  with a parametric bootstrap goodness of fit test can be found in Cooch & White (2012). Results of different methods to measure  $\hat{c}$  were compared.

For dataset MFS, U-CARE estimated  $\hat{c} = 1.65$  (see Appendix 2.3). For dataset MF, U-CARE estimated  $\hat{c} = 2.03$ , and for adult males and adult females separately, 2.21 and 1.79, respectively. Program RELEASE estimated  $\hat{c} = 1.63$  for dataset MFS,  $\hat{c} = 1.82$  for dataset MF and  $\hat{c} = 2.07$  and  $\hat{c} = 1.52$  for adult males and adult females separately.

Calculations by bootstrap for dataset MFS gave a  $\hat{c}$  of 1.20. The “median- $\hat{c}$ ” for dataset MFS was 1.18. These values of  $\hat{c}$  for dataset MF were 1.44 and 1.18, respectively. For adult males the bootstrap  $\hat{c}$  was 1.19 and the “median- $\hat{c}$ ” was 1.18 and for adult females the corresponding values were 1.63 and 1.29.

Overall,  $\hat{c}$  varied between 1.18 – 1.65 for dataset MFS, between 1.18 – 2.03 for dataset MF, 1.18 – 2.21 for adult males and between 1.29 – 1.79 for adult females. Over-dispersion in the data was thus not sufficient to cause any unacceptable lack of model fit ( $\hat{c} < 3$ ) (Lebreton et al. 1992; Burnham & Anderson 2002).

### **2.2.3.5.3 Cormack-Jolly-Seber models**

Cormack-Jolly-Seber (hereafter called CJS) open population models (Cormack 1964; Jolly 1965; Seber 1965) implemented in program MARK were used to estimate apparent survival ( $\varphi$ ) rates for sex/stage specific groups: adult males, adult females and sub-adults. Apparent survival

includes death and permanent emigration. Capture probabilities ( $p$ ) are also estimated by the CJS models.

Of the 18 years of data (1986-2003), the data in the 1980s were limited due to small sample size but were sufficient for analysis with the CJS models. The data from 1990-2003 were more substantial, and were subsequently also used to estimate apparent survival with Robust Design models (hereafter called RD), which can take into account potential temporary emigration (Pollock 1982; Pollock et al. 1990; Kendall et al. 1997) – see Chapter 3.

Initially, adult males, adult females and sub-adults were all analysed together (dataset MFS). CJS models assume that all individuals have the same probability of survival from one sampling occasion to another (Cormack 1964; Schwarz & Seber 1999; Pledger et al. 2003). However, sub-adults were likely to have lower apparent survival compared to adult individuals, so a second analysis included only adult males and adult females (MF). A third analysis estimated apparent survival separately for adult males and for adult females.

Several CJS models were constructed (Table 2.1), including models that allowed apparent survival and capture probabilities to be constant or to vary by time or by group (i.e. sex/stage). The interaction model  $\varphi(t) p(t*m)$  was built to account for the trap-dependency ( $m$ ) (Sandland & Kirkwood 1981; Pradel 1993), identified by the U-CARE goodness of fit tests (see section 2.2.3.5.1). This model estimated probability of capture as a function of time, trap-dependency and the interaction of time and trap-dependency. Ignoring trap-dependency can lead into underestimation of apparent survival rates (Pradel 1993; Pradel & Sanz-Aguilar 2012). To reduce the number of parameters in the model, an additive model where the interaction between time and trap-dependency was removed was also implemented  $\varphi(t) p(t+m)$ . An “age-class model”  $\varphi(a2)$  was built to account for the transience in the adult male data (Pradel et al. 1997), identified by the U-CARE goodness of fit tests (see section 2.2.3.5.1). This model estimated apparent survival separately for individuals identified as transients and for killer whales sighted regularly in the study area. Without excluding transients as a separate cohort, apparent survival of adult males could be underestimated (Pradel et al. 1997).

Model selection was based on the Quasi-likelihood Akaike’s Information Criterion (QAICc) (Anderson et al. 1994; Burnham & Anderson 2002), which is the AIC adjusted for small sample size and incorporating the appropriate  $\hat{c}$  value to account for the degree of over-dispersion in the data. The model having the lowest QAICc was considered to be the best model. Different models having  $\Delta$ QAIC of less than 2 were considered to have similar support from the data.

To obtain more precise estimates, the model averaging procedure based on the normalised Akaike weights was applied to take account of model uncertainty (Burnham & Anderson 2002; Cooch & White 2012).

Table 2.1 - Description of the CJS model variables used to estimate apparent survival and recapture probabilities.

<b>Probability of survival</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\varphi(.)$	Constant survival throughout years
Time	$\varphi(t)$	Time varying survival
Group	$\varphi(g)$	Survival varying among groups
"Age class"	$\varphi(a2)$	Survival accounting for transience

<b>Probability of recapture</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\rho(.)$	Constant recapture probability throughout years
Time	$\rho(t)$	Time varying recapture probability
Group	$\rho(g)$	Group varying recapture probability
Trap dependency	$\rho(t*m)$	Probability of recapture acc. for trap-dependency - interaction model
Trap dependency	$\rho(t+m)$	Probability of recapture acc. for trap-dependency - additive model

### **2.2.3.6 Calving rates**

Calving intervals and calving rates were calculated from individual capture histories of identifiable females over a period of 14 years (1989-2002), including whether or not each females had a calf born that year. Not all of the females were encountered every year. Individual encounter histories that had a minimum of nine years between first and last sighting and had no more than two years in which the female was not seen were included in the analysis.

## 2.3 RESULTS

Survey effort and encounter rates were variable during 1986-2003. The fieldwork season shifted from October towards November and the beginning of December over the period of study (Table 2.2). For the 18 years investigated, a total of 573 encounters, revealing 513 identified individuals and 31 pods with good quality photographs were recorded (Table 2.2 & 2.3). Most of the identified killer whale pods were encountered in the fieldwork area on multiple years during the period of 18 years, showing a high degree of return to the same location (Table 2.3).

Table 2.2 - Dates when photo-identification photographs were obtained during October-December on each year with the number of days when whales were photographed (whale days), number of total encounters per year, number of pods identified per year and number of identified individuals with good quality photographs used in analysis for each year.

Year	Dates	Whale days	Encounters	No of Pods	No of Ind.
1986	2.10. - 23.10.	12	13	3	18
1987	10.10. - 19.10.	5	7	3	12
1988	20.10.	1	3	4	15
1989	16.10. - 15.11.	4	4	2	12
1990	16.10. - 28.11.	27	56	20	159
1991	7.10. - 18.11.	32	73	22	136
1992	8.10. - 20.11.	33	64	23	228
1993	16.10. - 11.11.	18	37	18	109
1994	17.10. - 22.11.	19	25	14	60
1995	20.10. - 19.11.	20	35	20	108
1996	30.10. - 27.11.	12	21	15	97
1997	14.10. - 19.11.	8	14	13	52
1998	14.10. - 12.11.	15	22	16	96
1999	21.10. - 15.11.	13	19	14	94
2000	31.10. - 12.11.	7	15	13	46
2001	19.10. - 1.12.	18	18	13	39
2002	23.10. - 7.12.	36	77	25	141
2003	18.10. - 5.12.	35	70	22	164

Table 2.3 - Killer whale pod ID's and number of years seen during 1986-2003.

Pod	Years seen	Pod	Years seen	Pod	Years seen
NE	16	KA	10	ND	4
NG	15	NV	9	NS	4
NQ	15	Nc	8	Ne	3
NB	14	NU	8	Ng	3
NC	13	Nf	7	Na	2
NP	13	NX	7	Ni	1
NY	13	NÄ	6	NL	1
NA	12	NN	6		
NÅ	12	NR	6		
NO	12	NZ	6		
NT	12	Nb	5		
NW	12	NØ	5		

The number of killer whale pods and individuals encountered per year varied (Table 2.2, Figure 2.2 & 2.3). The number of days with whales was highest in 1990-1992 and 2002-2003 resulting in more pods and individuals encountered. In some of the years, e.g. 1994, effort was relatively high but the encounter rate and number of identified individuals recorded was relatively low.

The cumulative number of identified individuals increased sharply in the early 1990s with the increased fieldwork effort and levelled out towards the early 2000s (Figure 2.3). In 2002 and 2003 a large number of new identifiable individuals were photographed. The discovery curve of the cumulative number of identified killer whale individuals against the cumulative number of killer whales encountered is shown in Figure 2.4. The number of identified pods (31) has stayed the same from 1996 onwards (Figure 2.2).

A total of 187 identifiable individuals were only seen once during the study (Figure 2.5) and 97 of these were new individuals identified for the first time in either 2002 or 2003. The remaining 326 individuals (63.5%) were seen two or more times during the period of 18 years.

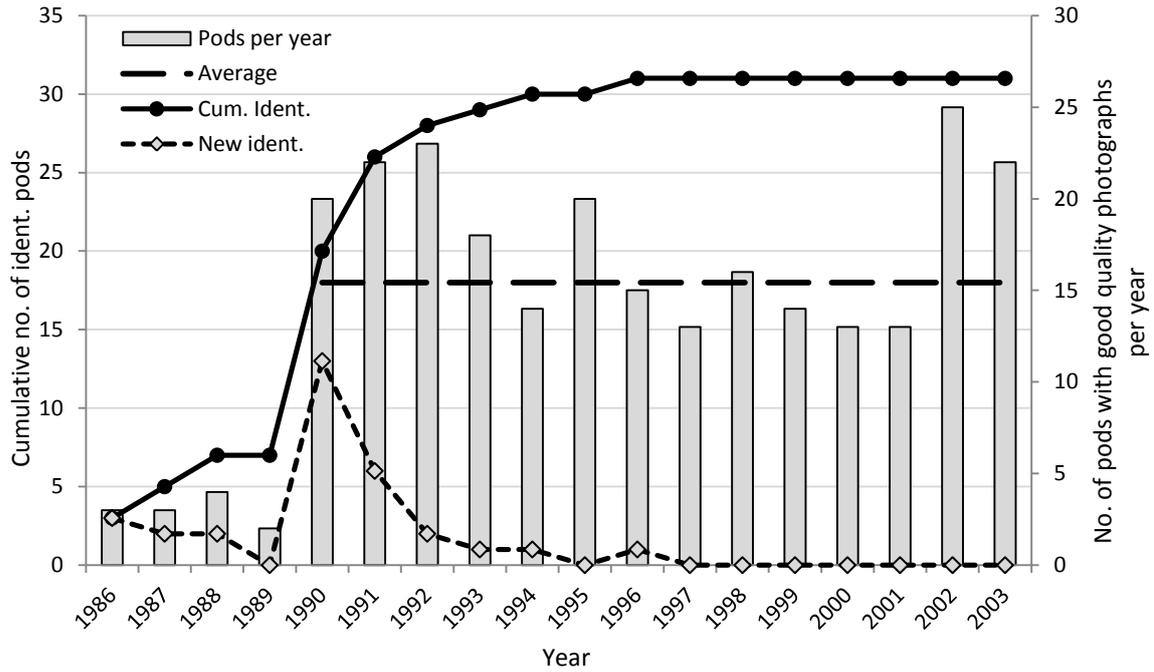


Figure 2.2 - Cumulative number of identified killer whale pods (black line), number of newly identified pods per year (dotted line) and number of killer whale pods encountered per year with good quality photographs (gray bar). The horizontal dashed line is the annual average of the number of killer whale pods encountered in 1990-2003.

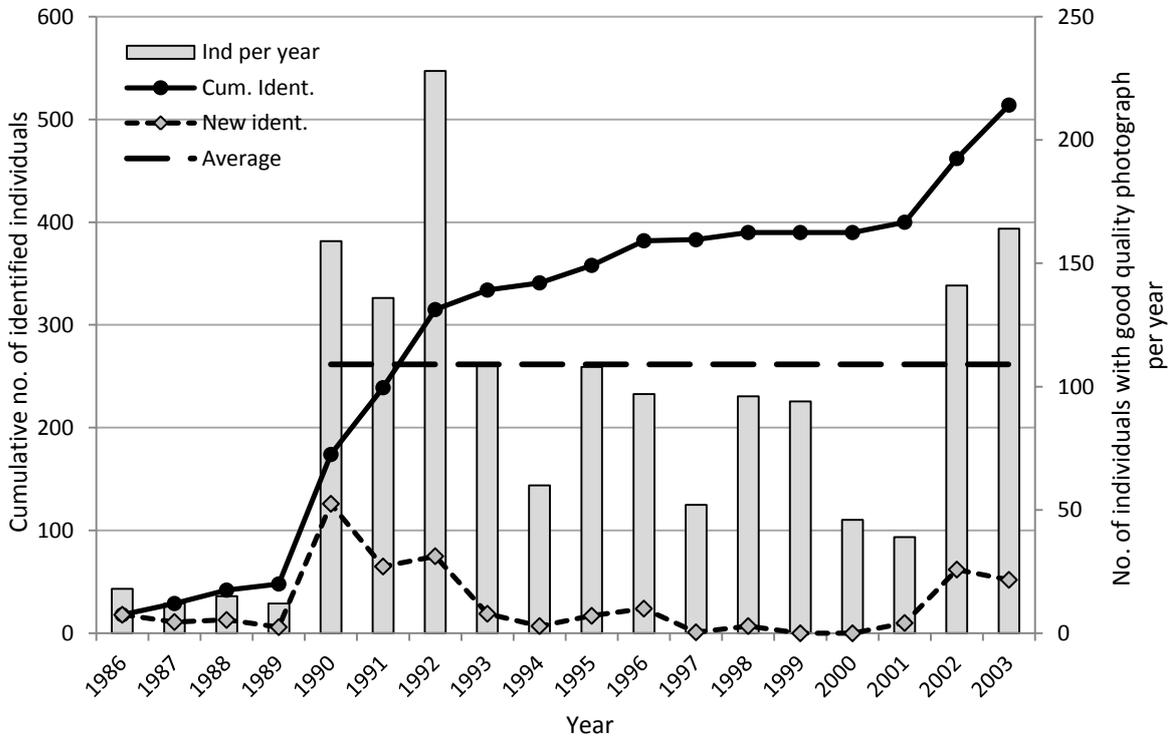


Figure 2.3 - Cumulative number of identified killer whale individuals (black line), number of new identified individuals per year (dotted line) and number of identifiable killer whale individuals encountered per year with good quality photographs (gray bar). The horizontal dashed black line is the annual average of the number of killer whale individuals encountered in 1990-2003.

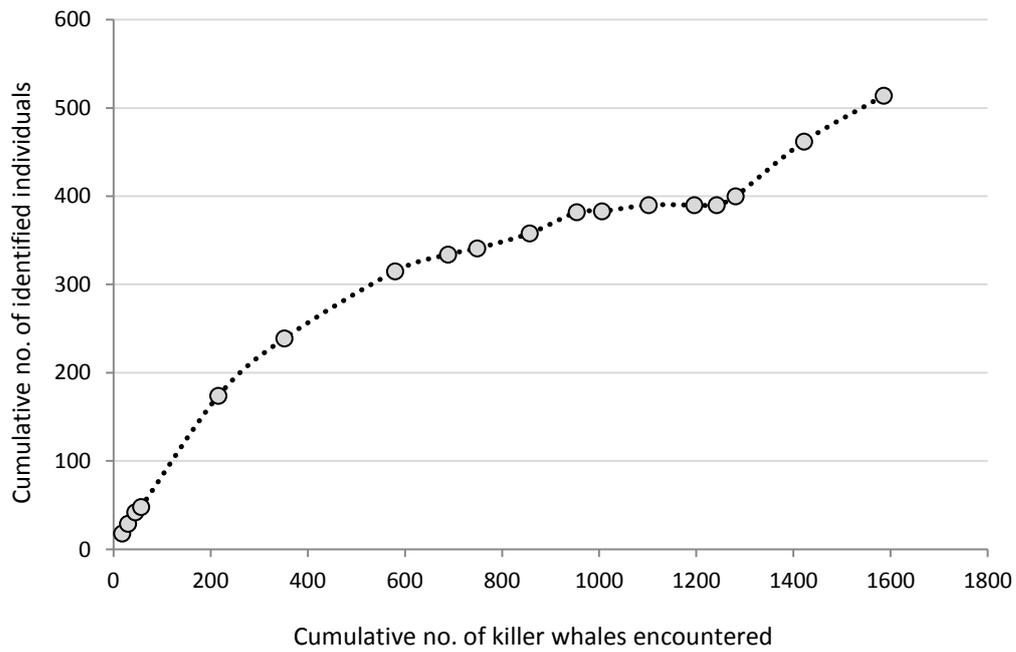


Figure 2.4 - Cumulative number of identified killer whale individuals against the cumulative number of killer whales encountered during 1986-2003.

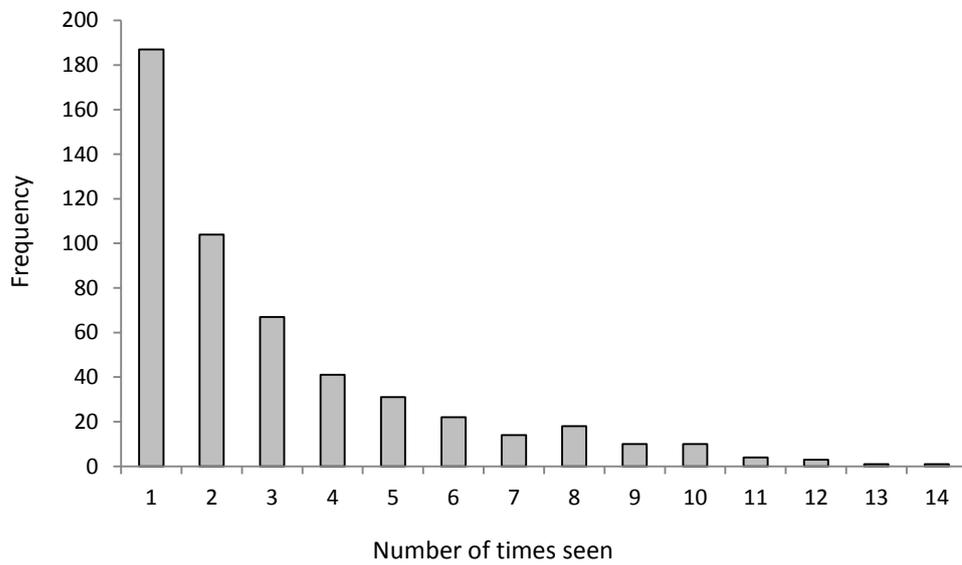


Figure 2.5 - Sighting frequency of killer whale individuals (including juveniles and calves) with good quality photographs during 1986-2003.

### 2.3.1 Estimates of population size

Sample sizes prior to 1990 were insufficient to obtain reliable estimates of population size with either the Chapman two-sample model or the annual multi-sample closed capture models and so all the results for population size are for 1990-2003.

The number of identifiable individuals in the population estimated from the Chapman two-sample model varied between 178 (SE = 21) in 1999-2000 and 567 (SE = 143) in 2001-2002 (Table 2.4). The standard errors for the population size estimates in 2000-2001 and 2001-2002 are very high. The number of identified individuals per year was lowest in 2000 and 2001 (Table 2.2) and these low sample sizes resulted in low precision of the estimated abundance. In 2002-2003 the estimated number of identifiable individuals was 403 (SE = 33).

Table 2.4 - Chapman two-sample estimates of the number of identifiable individuals ( $\hat{N}$ ) and total population size ( $\hat{N}_{total}$ ). 95% CI calculated assuming estimates are log-normally distributed.

Years	$\hat{N}$	SE	95% CI	$\hat{N}_{total}$	SE	95% CI
1990-1991	317	20	280-359	570	65	456-712
1991-1992	310	12	287-334	557	57	457-680
1992-1993	318	15	289-349	572	61	465-704
1993-1994	185	16	156-220	334	43	260-429
1994-1995	236	28	188-298	426	64	317-572
1995-1996	395	55	300-518	710	120	512-986
1996-1997	235	33	179-310	423	72	304-589
1997-1998	223	30	171-289	339	49	256-449
1998-1999	199	15	172-231	304	28	254-364
1999-2000	178	21	142-223	271	34	211-347
2000-2001	375	136	189-746	571	209	285-1144
2001-2002	567	143	349-922	864	222	526-1419
2002-2003	403	33	344-472	614	59	509-741

Based on  $\chi^2$  tests run within program CAPTURE, taking heterogeneity into account is important (see Appendix 2.4). For the multi-sample closed model estimates within years, two models were chosen by MSC to estimate yearly population size of identifiable individuals; 1) model  $M(th)Chao$  that allows capture probability to vary by time and individual and 2) model  $M(t)Chao$  allowing capture probabilities to vary by time (Chao et al. 1992; Chao 2001). Model  $M(th)Chao$  was selected as a better model nine times out of fourteen years based on MSC compared to model  $M(t)Chao$ . Model  $M(th)Chao$  generated higher estimates of population size than model  $M(t)Chao$  for all years indicating that not taking heterogeneity into account

was likely causing a negative bias. For consistency, estimates of the number of identifiable individuals from model  $M(th)Chao$  are considered as best estimates for all years and are presented in Table 2.5. The estimated number of identifiable individuals varied between 108 (SE = 22) in 1994 and 480 individuals (SE = 88) in 2003.

Table 2.5 - Estimates of the number of identifiable individuals ( $\hat{N}$ ) and total population size ( $\hat{N}_{total}$ ) within years using the closed model  $M(th)Chao$ .

Year	$\hat{N}$	SE	95% CI	$\hat{N}_{total}$	SE	95% CI
1990	297	37	241-391	535	84	394-725
1991	202	21	172-258	364	51	277-478
1992	348	28	305-417	626	78	492-798
1993	388	110	242-695	698	209	394-1239
1994	108	22	81-174	194	44	126-300
1995	262	54	187-409	472	107	304-731
1996	232	51	163-372	418	100	263-663
1997	121	31	82-213	184	48	111-305
1998	263	70	173-462	401	109	238-675
1999	318	99	193-605	484	153	265-886
2000	133	47	78-282	203	72	103-400
2001	182	97	82-517	277	148	104-742
2002	284	47	218-408	433	75	309-606
2003	480	88	349-703	731	139	505-1059

### 2.3.1.1 Total population size

The proportion of identifiable individuals in the population was estimated to be 0.556 (SE = 0.052) for 1990-1995 and 0.656 (SE = 0.034) for 1997-2003.

Estimates of total population size using the estimates of the number of identifiable individuals for pairs of years are given in Table 2.4. These estimates varied between 271 (SE = 34) in 1999-2000 and 864 (SE = 222) in 2001-2002. Again the standard errors are high for the estimates for 2000-2001 and 2001-2002.

The within-year estimates from the  $M(th)Chao$  model with the correction of the proportion of identifiable individuals give estimates of total population size between 184 (SE = 48) in 1997 and 731 (SE = 139) in 2003 (Table 2.5, Figure 2.6). These results represent the estimate of the number of animals in the population using the fjord system in any given year.

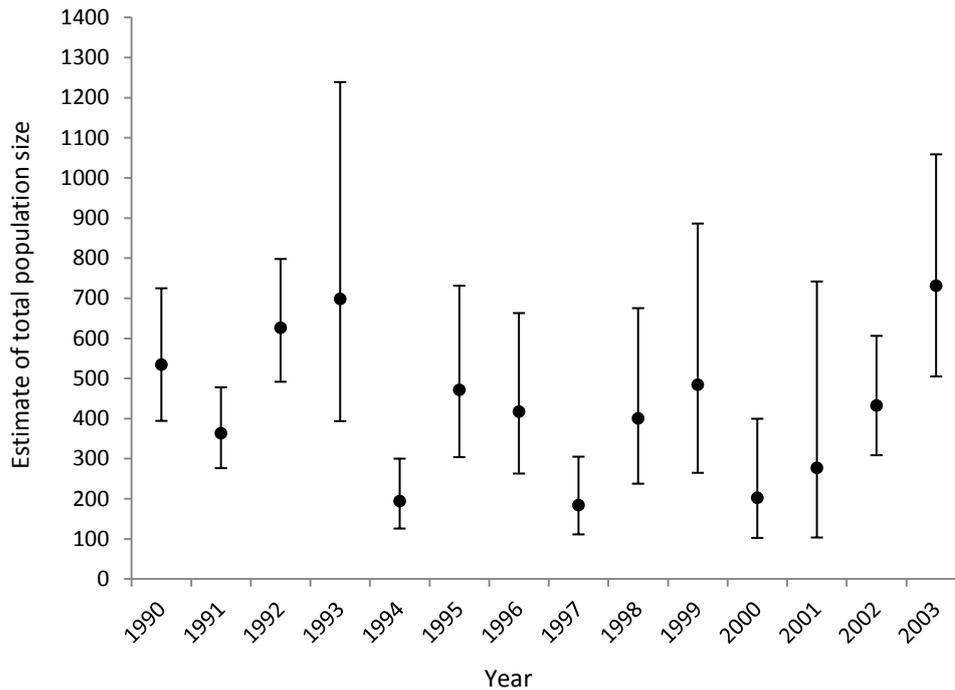


Figure 2.6 - Total population size estimates using model  $M(th)Chao$  with 95% confidence intervals.

## 2.3.2 Survival

### 2.3.2.1 Model selection

Model diagnostics including QAICc for adult males, adult females and sub-adults together (dataset MFS), adult males and adult females together (dataset MF) and for adult males and adult females separately using the 1986-2003 data are presented in Tables 2.6, 2.7, 2.8 and 2.9, respectively.

For the MFS dataset, the best support was given to model  $\varphi(g) p(t)$  estimating apparent survival as constant for each sex/stage and with time varying capture probability (Table 2.6). The best model for dataset MF estimated constant apparent survival for both sexes together and accounted for variation in group and time and trap-dependency in capture probabilities (model  $\varphi(.) p(g+t+m)$ ) (Table 2.7). Model  $\varphi(.) p(t+m)$  also received good support from the data.

For adult males the best model was the “age-class” model  $\varphi(a2) p(t+m)$  (Table 2.8). The second best model  $\varphi(.) p(t+m)$  also had high support ( $\Delta QAICc = 0.5$ ). Both of these models accounted for trap-dependency in capture probabilities.

The best model for adult females was the model estimating apparent survival as constant accounting for trap-dependency in capture probabilities with the additive model ( $\varphi(.) p(t+m)$ ) (Table 2.9).

Table 2.6 - Model selection diagnostics for CJS models of apparent survival and capture probabilities of dataset MFS. The model with lowest QAICc, highest QAICc Weight and Likelihood value was considered as the best one. Difference between models was compared with  $\Delta$ QAICc which is the difference between the QAICc of the model compared to lowest QAICc.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(g) p(t)$	2574.6	0	1	1	20	1383.0
2	$\varphi(g) p(g^*t)$	2607.9	33.3	0	0	54	1344.4
3	$\varphi(.) p(g^*t)$	2608.3	33.7	0	0	52	1349.1
4	$\varphi(.) p(t)$	2624.8	50.2	0	0	18	1437.4
5	$\varphi(t) p(g^*t)$	2634.5	59.9	0	0	67	1342.5
6	$\varphi(t) p(t)$	2650.1	75.5	0	0	34	1429.4
7	$\varphi(g^*t) p(t)$	2652.7	78.1	0	0	67	1360.7
8	$\varphi(g^*t) p(g^*t)$	2694.5	119.9	0	0	99	1329.8
9	$\varphi(g) p(g)$	2720.6	146.0	0	0	6	1557.6
10	$\varphi(.) p(g)$	2724.6	150.1	0	0	4	1565.7
11	$\varphi(g) p(.)$	2733.1	158.5	0	0	4	1574.1
12	$\varphi(t) p(g)$	2737.4	162.8	0	0	20	1545.9
13	$\varphi(.) p(.)$	2784.2	209.7	0	0	2	1629.3
14	$\varphi(t) p(.)$	2789.1	214.6	0	0	18	1601.7
15	$\varphi(g^*t) p(g)$	2789.2	214.6	0	0	54	1525.7
16	$\varphi(g^*t) p(.)$	2799.2	224.6	0	0	52	1540.0

Table 2.7 - Model selection diagnostics for CJS models of apparent survival and capture probabilities of dataset MF.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(.) p(g+t+m)$	2583.8	0	0.4560	1	35	2543.1
2	$\varphi(.) p(t+m)$	2584.7	0.9	0.2936	0.6439	18	2546.1
3	$\varphi(g) p(t+m)$	2586.6	2.8	0.1134	0.2486	19	2545.9
4	$\varphi(.) p(t^*m)$	2587.0	3.2	0.0920	0.2017	18	2521.3
5	$\varphi(g) p(t^*m)$	2589.0	5.1	0.0353	0.0774	19	2521.1
6	$\varphi(t) p(t+m)$	2592.4	8.6	0.0063	0.0139	34	2541.3
7	$\varphi(t) p(t^*m)$	2593.6	9.8	0.0034	0.0075	34	2515.1
8	$\varphi(.) p(t)$	2626.2	42.3	0	0	18	2589.6
9	$\varphi(g) p(t)$	2628.0	44.1	0	0	19	2589.3
10	$\varphi(.) p(g^*t)$	2642.7	58.9	0	0	35	2570.6
11	$\varphi(g) p(g^*t)$	2644.5	60.6	0	0	36	2570.2
12	$\varphi(t) p(t)$	2649.7	65.9	0	0	34	2581.8
13	$\varphi(t) p(g^*t)$	2667.8	83.9	0	0	51	2563.5
14	$\varphi(g^*t) p(t)$	2676.6	92.8	0	0	51	2570.1
15	$\varphi(g^*t) p(g^*t)$	2698.7	114.8	0	0	68	2556.8
16	$\varphi(.) p(g)$	2795.2	211.3	0	0	3	2789.2
17	$\varphi(.) p(.)$	2796.8	213.0	0	0	2	2792.8
18	$\varphi(g) p(g)$	2797.2	213.4	0	0	4	2789.2
19	$\varphi(g) p(.)$	2798.5	214.7	0	0	3	2792.5

20	$\varphi(t) p(g)$	2808.0	224.2	0	0	19	2769.4
21	$\varphi(t) p(.) P$	2808.8	225.0	0	0	18	2772.3
22	$\varphi(g^*t) p(.)$	2834.2	250.3	0	0	35	2762.1
23	$\varphi(g^*t) p(g)$	2834.3	250.5	0	0	36	2760.1

Table 2.8 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult males.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(a2) p(t+m)$	1423.6	0	0.5319	1	20	1382.4
2	$\varphi(.) p(t+m)$	1424.1	0.5	0.4116	0.7740	19	1385.1
3	$\varphi(t) p(t+m)$	1428.2	4.6	0.0537	0.1010	25	1376.4
4	$\varphi(a2) p(t)$	1435.4	11.8	0.0014	0.0027	19	1396.4
5	$\varphi(.) p(t)$	1436.6	13.0	0.0008	0.0015	18	1399.7
6	$\varphi(a2) p(t^*m)$	1438.4	14.8	0.0003	0.0006	33	1369.3
7	$\varphi(.) p(t^*m)$	1439.1	15.6	0.0002	0.0004	32	1372.2
8	$\varphi(t) p(t^*m)$	1443.3	19.7	<0.0001	0.0001	38	1363.1
9	$\varphi(t) p(t)$	1461.2	37.6	0	0	33	1392.0
10	$\varphi(.) p(.)$	1514.5	90.9	0	0	2	1510.5
11	$\varphi(t) p(.)$	1534.0	110.5	0	0	18	1497.1

Table 2.9 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult females.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(.) p(t+m)$	1117.7	0	0.8608	1	17	1082.4
2	$\varphi(.) p(t)$	1122.3	4.7	0.0832	0.0966	18	1084.9
3	$\varphi(t) p(t+m)$	1123.3	5.6	0.0516	0.0600	22	1077.1
4	$\varphi(.) p(t^*m)$	1128.2	10.6	0.0044	0.0051	29	1066.4
5	$\varphi(t) p(t^*m)$	1137.9	20.2	<0.0001	0	35	1062.3
6	$\varphi(t) p(t)$	1152.9	35.2	0	0	34	1079.6
7	$\varphi(.) p(.)$	1190.8	73.1	0	0	2	1186.7
8	$\varphi(t) p(.)$	1209.2	91.5	0	0	18	1171.7

### 2.3.2.2 Estimates of apparent survival

RELEASE Goodness of Fit TEST1 showed that adult individuals should not be pooled together with the sub-adults (see Appendix 2.2). Sub-adults had a constant apparent survival of 0.768 (SE = 0.04, 95% CI = 0.682 – 0.837) with the best model  $\varphi(g) p(t)$  (Table 2.6). For adults only (dataset MF), the two models with similar support from the data both gave a constant apparent survival for adult males and adult females together as 0.981 (SE = 0.006, 95% CI = 0.965 – 0.990).

For adult males, the best fitting model gave an estimate of apparent survival excluding the transients of 0.980 (SE = 0.009, 95% CI 0.952 – 0.991) and an estimate of apparent survival of 0.923 (SE = 0.034, 95% CI 0.823 – 0.969) for the transients. The second best model gave constant apparent survival of 0.971 (SE = 0.008, 95% CI = 0.950 – 0.983). The model averaged estimate of adult male apparent survival (excluding transients) varied between 0.964 (SE = 0.056, 95% CI = 0.525 – 0.998) and 0.977 (SE = 0.011, 95% CI = 0.943 – 0.991).

For adult females, the best model gave a survival estimate of 0.977 (SE = 0.009, 95% CI = 0.951 – 0.989), slightly higher than for adult males with the same model.

### 2.3.2.3 Capture probabilities 1987-2003

Estimated capture probabilities varied greatly between years (Figure 2.7). The best CJS model based on QAICc with dataset MF, model  $\varphi(.) p(g+t+m)$ , gave capture probabilities of 0.037 – 0.778 for adult males and 0.031 – 0.744 for adult females in the time period 1987-2003. Adult females had always slightly lower capture probabilities compared to adult males.

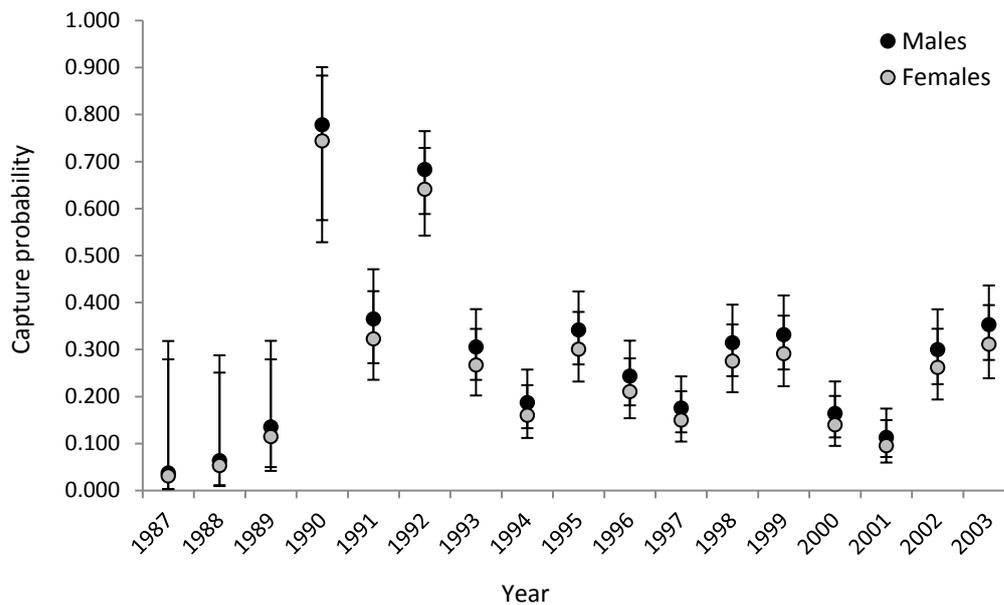


Figure 2.7 - Capture probabilities of adult males and adult females 1987-2003 estimated from dataset MF and model  $\varphi(.) p(g+t+m)$  and 95% CI.

### 2.3.3 Calving rates

Data from 10 identifiable females were used to estimate calving rates with individual encounter histories in 1989-2002. In total 25 calves were recorded for these females. Calving intervals ranged from 3 to 14 years (mean = 5.06, SE = 0.722, Figure 2.8).

Females in northern Norway were calculated to have an average fecundity rate of 0.197 calves per year (range 0.07-0.31, SE = 0.065).

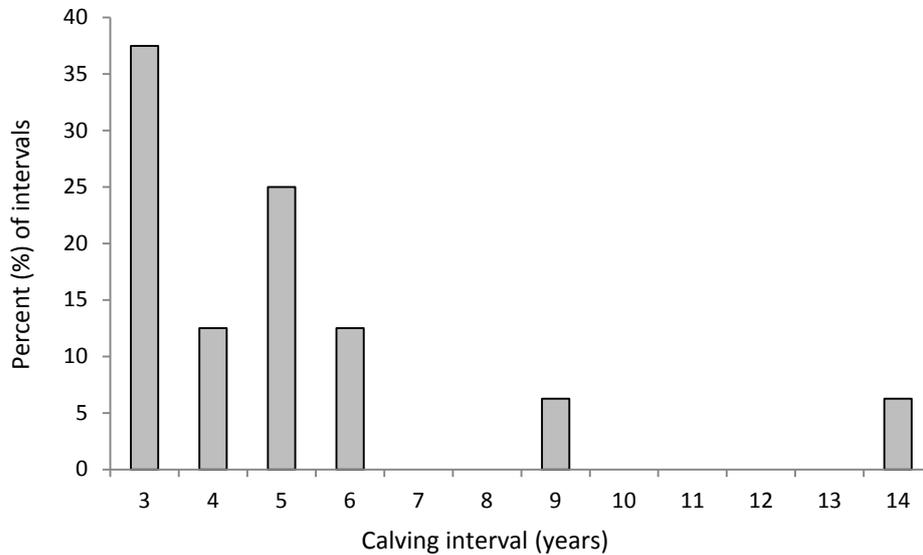


Figure 2.8 - Observed calving intervals as a percentage of all intervals during 1989-2002.

## 2.4 DISCUSSION

### 2.4.1 Model selection and analysis

Goodness of fit tests showed that adult males and adult females were subject to heterogeneity of capture probabilities, more specifically significant trap-dependency which in all cases was “trap-happiness”, i.e. increased capture probability after first capture. It is unlikely that actual trap-dependency occurs as killer whales are not physically handled in photographic capture but more likely it is a proxy for something else, e.g. indicating differences in sighting probabilities (Sandland & Kirkwood 1981; Pradel 1993; Pradel & Sanz-Aguilar 2012).

Killer whales live in stable family pods and are thereby encountered as groups rather than as independent individuals, violating the assumption of equal sighting probability. Additionally, variability in the behaviour of different pods exists, e.g. some pods are less disturbed by surrounding boats and are easier to approach for photographing, further compromising the equal capture probabilities. Different killer whale pods might also have area preferences within the study area and as some areas were surveyed more often, it is possible that some pods and individuals were captured more often than by chance. The sampling methodology itself might also have caused heterogeneity in sighting probabilities. All these issues might lead to trap-dependency showing in the dataset. Guided by the U-CARE test

results, trap-dependency was taken into account in appropriate models within the CJS analysis, as has been done with some other studies on marine mammals, e.g. manatees, blue and humpback whales (Langtimm et al. 1998; Ramp et al. 2006; 2010). Results showed that for adult males and adult females, incorporating trap-dependency improved the models. In most cases, incorporating trap-dependency in addition to time gave the best fit. The issue of temporary emigration, a phenomenon that could imitate trap-dependency, is addressed in Chapter 3.

Goodness of fit tests also indicated some evidence of transience in the data for adult male killer whales. In analysis, an age-class model improved the model fit. The estimate of apparent survival for adult males was higher when excluding the transients (0.980) than when they were not excluded (0.971). There was no evidence of transience in the data for adult females. It is understandable that transience did not show for females because they need to be encountered for several years before assigning them as adult females compared to adult males which can be assigned as a male on first sighting based on their tall dorsal fin. It has also been suggested that some of the males in northern Norway have a nomadic lifestyle rather than living in stable family pods (Bisther & Vongraven 1995), which could be perceived as transience in the goodness of fit tests. These nomadic males could have previously been part of a pod, but be separated from the rest of the pod after their mother died. Whether or not these nomadic individuals have a different range from the individuals living in pods and whether or not they are more occasional visitors in the study area is not known.

It was shown based on TEST1 in program RELEASE that sub-adult individuals could not be pooled together with adult individuals due to their probability of survival being unequal from one occasion to another compared to adult individuals. Apparent survival of juveniles and calves could not be estimated as there were limited data of these sex/stages. Also with the very limited information, there was difficulty specifying their age correctly and assigning them to the correct stage-groups.

#### **2.4.2 Population size**

Killer whales are found all along the coast of Norway with concentrations in Lofoten, Møre and Finnmark (Christensen 1982). Christensen (1988) estimated that at least 1500 killer whales were present in coastal waters of Norway when the herring was in this area during January to March. The North Atlantic Sighting Survey (NASS) estimated 7000 killer whales in Norwegian waters (Øien 1993) in summer 1989. However, these whales are likely to belong to a number of different populations. About 490-550 killer whales were previously estimated in the NASS herring wintering areas during October to January based on photo-identification data and

mark-recapture analysis during the years 1990–1993 (Similä & Christensen 1992; Similä 1997a).

The highest total population size estimate for an individual year presented in this study was, in 2003, about 700 individuals (model  $M(th)Chao$ , SE = 139, 95% CI = 505-1059). The analysis for pairs of years gave the highest estimate of total population size in 2001-2002, about 860 individuals, but the standard error for this estimate was very high. In this analysis information of the proportion of identifiable individuals was incorporated, thereby generating higher estimates of population size compared to previous estimates. However, the size of the population that used the fjords may still be underestimated.

A high number of new identifiable individuals were recorded during 2002 and 2003. As killer whales become individually identifiable by natural markings after about the age of three, it can be assumed that these new killer whale individuals were born sometime in the late 1990s. This period corresponds to a very high NSS herring spawning stock biomass of about 10 million tonnes inside the fjords (Toresen & Østvedt 2000; Orellana 2006). It is possible that the increased food abundance led to an increase in killer whale fecundity at this time. This would be interesting to study further, as also suggested by Ward et al. (2009) and Ford et al. (2010) with respect to resident killer whales and the high abundance of Chinook salmon in the NE Pacific.

Photographic methodology changed from film to digital in 2001 and it is also possible that the change in methodology has had the effect of increased number of new identified individuals in 2002 and 2003. The number of photographs taken is greater with digital cameras, a greater proportion of digital photographs can be suitable for analysis compared to film photographs and the quality of photographs can be better (Markowitz et al. 2003). The new identified individuals in 2002 and 2003 represented a range of sex/stage groups from juveniles to adult individuals. This implies that the large number of new identifiable individuals cannot fully be explained by the increased food hypothesis. Changes in data collection methods may therefore at least partly explain the high number of new identified individuals in 2002 and 2003, whereby digital photography might have increased the potential to identify more individuals.

Estimates of annual total population size varied substantially among years. These results represent the number of individuals estimated to have used the study area in a particular year, and do not necessarily indicate the size of the total northern Norwegian killer whale population. This kind of variation from year to year would be expected if the whole

population was not present in the fjords every year but was spread out over a larger area during the fieldwork season.

As shown by the satellite tagging experiments in 2000 and 2001 (Similä et al. 2002; Stenersen & Similä 2004) some killer whales emigrated temporarily from the fjord area, probably to keep track of the NSS herring distribution. This would lead to a situation where not all individuals were available to be captured in the study area. It was noted during some years that the number of killer whale sightings was low, despite comparable effort to other years. This may be in response to changes in NSS herring abundance and resulting variation in distribution inside the fjord system (see Chapter 6) and/or higher temporary emigration rates in a particular year (see Chapters 3 and 6).

Annual Norwegian Navy exercises (called FLOTEX), using active high intensity anti-submarine sonar, conducted inside the fjords during November might also have displaced some killer whales, leading to decreased sightings in some of the years (Kvadsheim et al. 2007). These naval exercises were previously blamed for reduced numbers of killer whale sightings and herring catches inside the fjords (WWF-Norway 2001). The retrospective data comparison between killer whale sightings and FLOTEX experiments is explored in Chapter 5.

### **2.4.3 Survival**

The apparent survival rate estimates presented here are the first ones for northern Norwegian killer whales. Compared to resident killer whales in the northeast Pacific, adult males in northern Norway had higher estimated survival rates (Table 2.10). The highest apparent survival for northeast Pacific adult male killer whales was estimated with both cropped (previously exploited) and non-cropped pods together to be 0.9610 (SE = 0.0076) (Olesiuk et al. 1990). This analysis had southern and northern residents combined, compared to analysis for northern residents only in Olesiuk et al. (2005). Including the previously exploited pods in the analysis might result in the estimated survival rate being higher as a result of density dependent effects due to recovery from previous removals from the population. However, no evidence was found in the study by Olesiuk et al. (1990) that life history parameters would have been affected by previous exploitation.

When comparing results between adult females, the northern Norwegian killer whales had lower apparent survival rates than those in the northeast Pacific (Table 2.10). In 1996-2004, Olesiuk et al. (2005) estimated apparent adult female survival to be 0.9705 (SE = 0.0072) for all age-classes combined which was closest to the estimate of adult female survival in northern Norwegian killer whales. In the Norwegian data, adult females included both

reproductive and post-reproductive females. Mortality has been recorded to increase with the start of reproductive senescence in killer whale females around the age of 40 (Olesiuk et al. 2005) and combining both reproductive and post-reproductive aged females does not account for differences in age-specific survival.

Table 2.10 - Estimates of apparent survival for adult male and adult female killer whales from northern Norway, northeast Pacific (Olesiuk et al. 1990; 2005) and the Crozet Archipelago (Ponzelet et al. 2010).

<b>NORWAY</b>			
<b>1986-2003</b>	$\varphi$	SE	95% CI
Males ( $\varphi(\cdot) p(t+m)$ )	0.971	0.008	0.950-0.983
Females ( $\varphi(\cdot) p(t+m)$ )	0.977	0.009	0.951-0.989
<b>NE PACIFIC</b>			
<b>Olesiuk et al. 1990 – Southern &amp; northern KWs</b>	$\varphi$	SE	95% CI
Males	0.9610	0.0076	-
Females	0.9886	0.0033	-
<b>Olesiuk et al. 2005 – Northern KWs</b>	$\varphi$	SE	95% CI
Males (1973-1996)	0.9590	0.0081	-
Females (1973-1996)	0.9836	0.0039	-
Males (1996-2004)	0.9089	0.017	-
Females (1996-2004)	0.9705	0.0072	-
<b>CROZET ARCHIPELAGO</b>			
<b>Ponzelet et al. 2010</b>	$\varphi$	SE	95% CI
Males (1977)	0.935	-	0.817-0.979
Males (2002)	0.895	-	0.746-0.961
Females (1977)	0.942	-	0.844-0.980
Females (2002)	0.901	-	0.742-0.966

Differences in estimated survival rates between Atlantic and Pacific killer whale populations are potentially due to location specific ecological features and/or differences in human induced pressures, e.g. noise (Erbe 2002; Morton & Symonds 2002), traffic (Lusseau et al. 2009) or contaminants (Ross et al. 2000; Wolkers et al. 2007; Cullon et al. 2009). Killer whales are highly specialised predators (Guinet 1991; Similä et al. 1996; Ford et al. 1998; Reisinger et al. 2011a) and the difference in diet between these locations could lead to differences seen in population parameters. Killer whales in the Pacific have been recorded to respond to changes in their prey abundance with changes in their survival rate (Ford et al. 2010; Ward et al. 2011), indicating that prey availability plays an important part in determining survival rates. The datasets also differ between locations, as in northern Norway only a

proportion of the individuals in the population are identified compared to resident killer whale populations in the NE Pacific where all individuals are identified and catalogued. This could cause differences in the results between these two locations.

Comparison of apparent survival rates between northern Norway and the Crozet Archipelago (Poncelet et al. 2010) shows that both adult males and adult females in Norway had higher estimated apparent survival rates (Table 2.10). Human impacts on killer whales in Crozet Archipelago due to lethal interactions with the long-line fisheries are causing concern about the viability of the decreasing population (Poncelet et al. 2010; Tixier et al. 2010). Killer whales in Crozet Archipelago have a very different diet, varying from fish to marine mammals (Guinet 1991), compared to Norwegian fish-eating killer whales. Additionally a decline in the elephant seal population in Crozet Islands (Guinet et al. 1999) may have influenced the low estimated survival rates as this is an important prey species for killer whales in this area. These location specific variables likely explain the difference in estimates of apparent survival rates between Norway and Crozet Archipelago.

A consistent result among northern Norway, northeast Pacific and Crozet Archipelago was that adult male killer whales had lower apparent survival compared to adult females. These differences were smaller within the northern Norwegian population than differences between males and females in the northeast Pacific (Olesiuk et al. 1990; 2005). Killer whales as a long-living species follow the typical mammalian U-shaped mortality curve, where the very youngest and oldest individuals have the highest mortality rates (Caughley 1966; Olesiuk et al. 1990). Sex-specific differences are expected in this curve because male killer whales have a shorter expected lifespan compared to females (Ford et al. 2000; Olesiuk et al. 2005) leading to the mortality curve being narrower. Killer whale females go through a period of extremely low mortality during their reproductive phase (Olesiuk et al. 2005), differentiating them from male life history.

The increased information on population parameters from locations around the world contributes to current knowledge of killer whales as a species and can help to better understand the influences that different ecological or manmade pressures have on killer whale populations and to guide making more informed management decisions. The new results for the survival rate of northern Norwegian killer whales add to this existing knowledge of population parameters and are a key component in monitoring the status of this particular Norwegian population.

Previous work on satellite tagged killer whales in northern Norway showed that killer whales from this population occasionally left the study area to track and follow their herring

prey during winter (Similä et al. 2002; Stenersen & Similä 2004). This kind of movement in and out of the study area could cause negative bias in survival rate estimates (Fujiwara & Caswell 2002). This issue of temporary emigration and its potential effect on apparent survival estimates is addressed in Chapter 3.

Based on the Norwegian Institute of Marine Research surveys, part of the NSS herring stock started to winter in a new area offshore in the Norwegian Sea from 2002 onwards leading to the abundance of NSS herring inside the fjords declining thereafter (Orellana 2006; Huse et al. 2010). Whether or not this large scale change in distribution of this killer whale population's main prey has negatively affected survival by increasing killer whale travelling time and decreasing time spent foraging and socialising is unknown. The abundance of NSS herring might also play a role in survival rates of killer whales in northern Norway in a similar way that Chinook salmon availability has been found to affect Chinook salmon feeding killer whale survival in the northeast Pacific (Ford et al. 2010; Ward et al. 2011). However, the decrease of NSS herring abundance was due to changes in distribution rather than to a decline in the total NSS herring biomass. Potential changes that could be seen in apparent survival due to changes in NSS herring wintertime distribution are further addressed in Chapters 3 and 6.

Killer whales in northern Norway feed using a method called carousel feeding (Similä & Ugarte 1993; Similä 1997b). This behaviour decreased towards the end of the 1990s and at beginning of the 2000s, at the same time as the commercial NSS herring fishery rapidly increased, including in the fjord area (pers. comm. Similä; Pilling et al. 2009). The total NSS herring landings peaked in 1997; up to 1.5 million tonnes were caught annually (Pilling et al. 2009; Det Norske Veritas 2011). Killer whales were found more often towards the end of this time period feeding around the fishing boats (e.g. purse seine vessels) catching the fish falling from the nets and vessels. At the same time the number of new nicks on identifiable killer whale individuals increased, potentially due to increased contact with the fishing gear. This is supported by the 10% increase in the estimated proportion of identifiable individuals in the population in this study during the same time period (see Results). There have been only a few recorded incidents of killer whales becoming entangled in the fishing gear in this area. However, this increased interaction with fisheries could potentially negatively affect survival. Interactions between killer whales and fisheries are reported from Prince William Sound in Alaska (Matkin et al. 2008) and from Possession Island (Poncelet et al. 2010). However, in these locations interactions have been with long-lines rather than nets.

Killer whales in northern Norway carry extremely high levels of contaminants (Wolkers et al. 2007), making them the Arctic mammal species with the highest recorded contaminant

levels. These high contaminant levels could potentially have a negative effect on the health and survival rates of killer whales (Cullon et al. 2009; Ward et al. 2011). Sex and age of an individual influence the amount of contaminants accumulated, reproductive females usually having lower contaminant levels compared to adult males and juveniles due to transferring part of their contaminant load to their calves through gestation and lactation (Ross et al. 2000; Hickie et al. 2007; Krahn et al. 2009). Juvenile individuals might be at particular risk for health effects with high concentrations of contaminants during the time of rapid development (Krahn et al. 2009). The estimated survival rates for the northern Norwegian adult male killer whales are the highest reported among killer whale populations globally, indicating that the Norwegian population is currently potentially coping with this pressure. Only long-term future monitoring will determine whether or not the contaminant load on these animals might affect survival in years to come.

#### 2.4.4 Calving rates

The calving rates presented here are the first ones for the northern Norwegian killer whale population. Calving intervals for northern Norwegian killer whales varied between 3 to 14 years, with a mean interval of 5.06 years, which was closest to the calculation for unexploited resident killer whales in the northeast Pacific (Olesiuk et al. 1990). For northeast Pacific resident killer whales, Olesiuk et al. (1990) calculated calving intervals similar to Norwegian killer whales, ranging between 2-12 years (mean = 5.86) for previously exploited pods and 2-10 years (mean = 5.02) for unexploited pods (Table 2.11). Using a much longer dataset including only northern resident killer whales, the calving interval was estimated to be between 2-14 years (mean = 4.88 using a model with unrestrained population growth and mean = 5.53 using a model with no net population change) (Olesiuk et al. 2005).

Table 2.11 - Comparison of reproductive rates between northern Norway and NE Pacific killer whales.

	Calving interval			Calves per year		
	Range	Mean	SE	Range	Mean	SE
Norway	3 to 14	5.06	0.722	0.08-0.33	0.22	0.078
NE Pacific Residents (exploited)*	2 to 12	5.86		-	0.177	-
NE Pacific Residents (non-exploited)*	2 to 10	5.02		-	0.203	-
NE Pacific Residents (unrestrained growth) <sup>1</sup>	2 to 11	4.88	0.793	-	0.205	-
NE Pacific Residents (no net change) <sup>1</sup>	2 to 14	5.53	1.103	-	0.180	-

\*Olesiuk et al. 1990 (Northern & southern residents 1973-1987)

<sup>1</sup>Olesiuk et al. 2005 (Northern residents 1973-2004)

The average fecundity rate was 0.22 calves per year (SE = 0.078) in northern Norway, which is comparable to the estimates for the northeast Pacific resident killer whales (0.18-0.21) (Olesiuk et al. 1990; 2005).

There have been relatively recent removals from this Norwegian killer whale population. Catches through the 1930s – 1980s in the Lofoten area totalled 662 individuals with the majority of catches taken in 1978-1981. In 1979 alone, 219 individuals were taken in the Lofoten area (Christensen 1982; Øien 1988) from the population under study in this thesis. There is no population size estimate of the northern Norwegian killer whales from that time. If population size were similar to that estimated for 2003 in this study (~700 individuals), the catch in 1979 would have represented approximately 30% removal from the population in one year.

In the NE Pacific during 1962-1977, a total of 68 killer whales were live-captured from the resident population for display in dolphinariums, reducing southern resident community to 70% of its original size (Olesiuk et al. 1990). These kinds of removals could be expected to change the sex and age composition of the population, as was reported for southern resident community after live-capture catches (Olesiuk et al. 1990). Catches could therefore affect reproductive potential (Ward et al. 2009), especially if individuals of reproductive age have been removed. Density dependent responses to a reduction in population size would be expected to lead to a recovery in population size. This could be through an increase in survival and fecundity rates, or as a decrease in age at first reproduction (Fowler 1984; Eberhardt 2002). Such detailed information on the nature of density dependence is very difficult to obtain for long-living marine mammal species and requires very long datasets. Study on resident killer whales in the NE Pacific has shown that killer whales would response to density dependency through changes in the reproductive rates (Olesiuk et al. 1990). The data from this study on the Norwegian killer whale population were not detailed enough to investigate age specific fecundity, change in the age at maturity or changes in fecundity rates.

For calculating calving rates there were some data limitations. Sighting histories were incomplete when females were not seen every year, meaning that some calves might have been missed from the analysis. This limitation can potentially lead to underestimation of the fecundity rate due to overestimating the calving interval. The dataset used might be too short to investigate calving rates in a long-lived, slowly reproducing mammal species like the killer whale as calving intervals might be left incomplete, something that could lead to underestimating calving interval. Also the number of females that spent sufficient time within the study period to be included into the analysis was small (10 individuals). A longer dataset

and a larger number of females with more complete sighting histories included in the analysis would increase the reliability of the result.

#### **2.4.5 Conclusions**

This work represents the first estimates of apparent survival and calving rates for the northern Norwegian killer whale population, and new estimates of total population size from a long-term dataset. These results will be an important part in building up an ecosystem level picture of the northeast Atlantic and the role of killer whales as top predators in this marine system. The NSS herring has recently gone through a large-scale change in its migration route and wintertime distribution, putting the killer whale population through a highly altered habitat change, with impacts that we cannot predict with certainty. Human caused pressures like noise and contaminants create threats to the viability of this killer whale population. The knowledge of the population parameters is therefore very valuable as a baseline from which to monitor the status of this killer whale population in the future.

Globally the results presented in this study are useful for continued comparison of killer whale population parameters from different locations and help build up a picture of the range of survival and calving rates for this species. With increased knowledge it becomes possible to try to evaluate how location specific ecological or man-made pressures affect different killer whale populations through changes in population parameters. This information could be used for better informed management decisions.

Further work in this thesis estimates apparent survival incorporating temporary emigration (Chapter 3) and expands the use of individual recognition data (Chapter 4) and conducts similar analysis as presented here for the years 2004-2006 (Chapter 6). Additional work examines the impact of the wintertime distribution change of the NSS herring on this northern Norwegian killer whale population distribution (Chapter 6).

## CHAPTER 3

### Survival estimates of adult killer whales incorporating temporary emigration, transience and trap-dependency: a 14 year study

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#### ABSTRACT

Killer whales (*Orcinus orca*) in northern Norway are known to follow their migrant and dynamic prey species, the Norwegian spring-spawning herring (*Clupea harengus*), between and during seasons. To explore how this behaviour may affect estimates of population parameters, a mark-recapture analysis was conducted to estimate adult male and adult female survival with a long-term dataset (1990-2003), accounting for temporary emigration, transience and trap-dependency. Analysis was carried out with Cormack-Jolly-Seber (CJS) and robust design models in program MARK. Constant annual apparent survival rate for adult males and adult females were estimated with a CJS model that incorporated trap-dependency to be 0.968 (SE = 0.008) and 0.978 (SE = 0.011), respectively. Overall, incorporating age-class and trap-dependency into the CJS models improved the fit. The best robust design model estimated constant annual apparent survival rate as 0.974 (SE = 0.009) for adult males and 0.976 (SE = 0.008) for adult females. Thus, not accounting for temporary emigration in the CJS models caused survival rate to be underestimated for adult males. Temporary emigration of adult females was random and constant 0.269 (SE = 0.053). For adult males, the probability of temporary emigration was Markovian and variable among years 0.067 (SE = 0.188) – 0.539 (SE = 0.105). These results show that the range of this population in wintertime exceeds the sampled area and that temporary emigration needs to be taken into account to be able to obtain unbiased estimates of population parameters. Differences in the pattern of temporary emigration between adult males and adult females reflect sex-specific differences in behaviour, either in the way they search for the migrant food resources or possibly the existence of nomadic males in this population.

### 3.1 INTRODUCTION

Estimated survival rates of a population not only increase knowledge and understanding of the life history of a species, they provide valuable information for conservation purposes by being one of the key components needed to assess the future viability of a population and can also reflect changes in environmental conditions that could threaten a population's viability (Lebreton et al. 1992; Morris & Doak 2002; White et al. 2002). Several studies on marine mammals have contributed to management and conservation planning of the populations through estimating survival rates, e.g. the study on Gulf of St Lawrence blue whales (Ramp et al. 2006) and the study on the critically endangered population of gray whales in the western Pacific (Bradford et al. 2006). Some studies on marine mammals have also used estimated survival rates in population models to assess potential reasons behind population declines and to examine extinction probabilities. Examples of such studies include those on Steller sea lions (Winship & Trites 2006), bottlenose dolphins in New Zealand (Currey et al. 2009) and on critically endangered North Atlantic right whales (Caswell et al. 1999). In this thesis, estimates of survival rate were incorporated into a population model in an attempt to evaluate the viability of northern Norwegian killer whales (*Orcinus orca*) (see Chapter 4).

Mark-recapture methods are commonly used for estimating population parameters such as survival rates, both for terrestrial and aquatic species (Schwarz & Seber 1999). Mark-recapture methods use tags or natural markings for identifying individuals for subsequent recaptures (Hammond 1986; 2010). For cetaceans, which spend their entire life at sea and mainly underwater, the use of natural markings for photographic capture and mark-recapture models are a widely used method for monitoring populations in all parts of the world (Hammond et al. 1990).

The killer whale is a marine top predator, found in all oceans across the world (Matkin & Leatherwood 1986; Forney & Wade 2007), feeding on a wide range of prey from multiple fish species, e.g. herring and salmon to large baleen whales (Heimlich-Boran 1988; Guinet 1991; Baird & Dill 1996; Similä et al. 1996; Ford et al. 1998; Saulitis et al. 2000; Pitman & Ensor 2003; Burdin et al. 2004; Ford & Ellis 2005; Herman et al. 2005; Tarasyan et al. 2005; Guinet et al. 2007; Krahn et al. 2007; Matkin et al. 2007; Higdson et al. 2011; Ford et al. 2011; Reisinger et al. 2011a; Pitman & Durban 2012). The main prey of the northern Norwegian killer whale population is the Norwegian spring-spawning herring (hereafter referred to as NSS herring, *Clupea harengus*) (Jonsgård & Lyshoel 1970; Christensen 1988; Similä & Ugarte 1993; Similä et al. 1996). The NSS herring is a highly important commercial fish species; it is the largest herring

stock in the world with annual catches reaching up to 1.5 million tonnes in the Norwegian Sea (Pilling et al. 2009; Det Norske Veritas 2011). The NSS herring stock is highly dynamic, both in terms of its annual migration route and with major fluctuations in stock size. The yearly migration route of the NSS herring has gone through major changes at uneven intervals, the wintertime distribution changing between coastal and offshore areas (Dragesund et al. 1997; Holst et al. 2002; 2004). The latest distribution change was recorded by the Norwegian Institute of Marine Research from 2002 onwards, when the distribution changed from fjordic to offshore area (Huse et al. 2010; see Chapter 6). The NSS herring stock has also gone through major fluctuations in its biomass within the last six decades with the last stock collapse happening at the end of the 1960s (Dragesund et al. 1997; Toresen & Østvedt 2000). The spawning stock had recovered to very high levels by 2009 with biomass up to 8.5 million tonnes (Pilling et al. 2009; ICES 2013).

Both the NSS herring and its killer whale predator were concentrated in a confined fjord system of Tysfjord, Vestfjord and Ofotfjord in northern Norway (see Figure 2.1 in Chapter 2) between October and January for two decades (Similä et al. 1996; Holst et al. 2002; Orellana 2006; Huse et al. 2010, see Chapter 6). A photo-identification study of the killer whales was initiated in this area in 1986 (Lyrholm 1988; Similä 1997a). Mark-recapture estimates of population parameters, using the long-term photo-identification data, showed that the size of the killer whale population associated with the NSS herring in wintertime was ~700 individuals (see Chapter 2, Kuningas et al. 2013a). This study also provided the first estimates of apparent survival rates for killer whales in the North Atlantic, estimating the constant apparent annual survival rate over 18 years (1986-2003) for adult males and adult females as 0.971 (SE = 0.008) and 0.977 (SE = 0.009), respectively (see Chapter 2, Kuningas et al. 2013a).

Estimates of survival rates also exist for killer whale populations in the Northeast Pacific and Indian Ocean (Olesiuk et al. 1990; 2005; Poncelet et al. 2010; Matkin et al. 2012), providing an opportunity to compare location specific variation in survival rates and consider the potential causes for differences between populations. The consistent result between the killer whale populations from different ocean basins is the higher estimated survival rate for adult females compared to adult males (Olesiuk et al. 1990; 2005; Poncelet et al. 2010, Kuningas et al. 2013a, see Chapter 2), which is expected given the known life history for the different sexes in this species (Ford et al. 2000; Olesiuk et al. 2005).

In this Chapter, estimation of survival rates is explored in more detail to account for so-called temporary emigration (Pollock 1982; Kendall et al. 1995; 1997); meaning that not all the individuals in the population are available to be captured in each sampling occasion (year)

because some are temporarily out of the study area. The reason to investigate the effects of temporary emigration was partly motivated from the knowledge that the whole population of killer whales was not necessarily available within the study area during the sampling period (October-December). A satellite tagging study conducted in 2000 and 2001 of this killer whale population during wintertime showed that killer whales make so-called “scouting trips”, moving away from main NSS herring resource in the fjords to outside areas apparently to keep track of their migratory prey species (Similä et al. 2002; Stenersen & Similä 2004). The reasons for these scouting trips may be to monitor the timing of the herring migration to spawning grounds and also the general distribution of herring, which is known to alter its migration routes (Holst et al. 2002; Stenersen & Similä 2004). The satellite tracked killer whales were within the NSS herring wintering grounds inside the fjords most of the time, but there were 2-25 day trips to outside areas, with 78-1537 km in distance (Similä et al. 2002; Stenersen & Similä 2004). Additionally, as shown in Chapter 2, incorporating trap-dependency improved the models estimating apparent survival rates, a phenomenon that could indicate the existence of temporary emigration. Therefore, due to the likely existing temporary emigration, there was a clear need to investigate evidence for temporary emigration in the data and to explore whether this needed to be taken into account to avoid bias in estimates of survival rates.

## **3.2 METHODS**

### **3.2.1 Data collection**

The research area is located above the Arctic Circle in the waters south of the Lofoten islands in northern Norway. The data were collected in Ofotfjord, Tysfjord and Vestfjord (see Figure 2.1b in Chapter 2) between October and January at a time of very limited daylight. The field season shifted later over the years because of herring entering the fjords later each year. The data collected between October and December 1990-2003 were selected for analysis in this Chapter to meet the data requirements of the robust design analysis.

Killer whales were searched for opportunistically, aided by information from the crew of ferries, whale-watching boats and fishing vessels. When killer whales were encountered, the size of the pod and/or group was estimated and, when possible, the number of adult males, adult females, sub-adults, juveniles and calves was recorded. Throughout, the term pod refers to a matrilineal family unit of killer whales, whereas the term group refers to a cluster of killer whales including individuals from different pods.

Identification photographs were taken, with preference for the left side of the animal, using the method described by Bigg (Bigg 1982; Bigg et al. 1986; 1990). An effort was made to photograph as many of the individuals as possible in an encounter and all individuals equally regardless of their degree of identifiability, e.g. adult males with fully grown dorsal fins are highly identifiable. In 1990-2000 pictures were taken with SLR cameras equipped with 200 or 300 mm lenses. The majority of images were taken with KODAK T MAX 400 ASA film pushed to 1600 ASA. From 2001, images were taken using digital cameras with 200 or 300 mm lenses.

### **3.2.2 Data processing**

The films were inspected using a stereoscopic microscope and the digital images were viewed in Adobe Photoshop. Individuals were identified by the shape of the dorsal fin and the grey saddle patch behind the dorsal fin and by natural markings in these areas (Bigg 1982). Initially, the identified individuals were divided into different categories: males, females/sub-adults and juveniles. The best picture of each individual from each encounter was compared to pictures in the identification-catalogue (of pictures taken in earlier years), which held 585 identified individuals from northern Norway by the end of the study.

Each individual was given a letter-number code, e.g. N-100, where N is for Norway and 100 is the number of the individual. Where possible the individual whales were assigned to pods based on stable associations with other individuals and thereby also given a pod-associated identification-code, e.g. NB-20, where N is for Norway, B is the pod ID and 20 is the number of the individual within that pod.

The quality of each picture was evaluated for contrast and focus, using a scale from 1 to 4 (1 being the best). Additionally the angle of the picture was evaluated from 1 to 3, angle 1 being parallel, 2 being with a slight angle from behind and 3 being with a slight angle from front. The amount of the saddle patch seen in the picture was measured on a scale 1 to 3, 1 being the top 1/3, 2 being the top 2/3 and 3 when saddle patch was seen fully. From these, the overall quality of the picture was assessed. Only good quality left-hand-side photographs of identifiable individuals were used for further analysis.

Data selected for the analysis in this Chapter included the years 1990 – 2003 (a total of 14 years). The data from the 1980s were not included as they were insufficient for the robust design analysis. Sub-adults, juveniles and calves were not included in the analysis because of limited data on these sex/stage groups.

Encounter histories of identifiable individuals were built through the 14 year period and used for estimating the probabilities of capture, apparent survival and temporary

emigration using mark-recapture analyses with CJS and robust design models. Data used in the mark-recapture analysis in this Chapter, with good quality photographs, included 235 adult males and 133 adult females.

### ***3.2.2.1 Determining sex and age-class***

A multistep process was conducted to determine the sex and age-class of each identifiable individual from northern Norway. For details, see section 2.2.2.1 in Methods in Chapter 2.

## **3.2.3 Data analysis**

### ***3.2.3.1 Analytical assumptions***

The open population CJS models (Cormack 1964; Jolly 1965; Seber 1965) make several assumptions: 1) marks used for individual identification are permanent, are not lost and are correctly recorded, 2) all individuals have the same probability of being captured within a sampling occasion, 3) all individuals have the same probability of survival from one sampling occasion to another and 4) marking is instantaneous and does not have an effect on an individual's capture or survival probability (Cormack 1964; Pollock et al. 1990; Pledger et al. 2003).

In addition to these assumptions, for the secondary sampling occasions in robust design models, the assumptions of closed population models additionally apply, meaning no birth, death, emigration or immigration occurring within the sampling period (Kendall et al. 1995). This can be assumed to be true in the case of long-lived mammal species like killer whale and when the sampling is done over a short period of time, e.g. months, as was the case here (Hammond 1986; Nichols 1992; Hammond 2009).

To minimize violating these assumptions, only natural markings known to be identifiable and permanent on killer whales (Similä & Lindblom 1993) were used and only good quality photographs were selected (see section 3.2.2) for any analysis because decreased photographic quality leads to an increase in false matching (Stevick et al. 2001; Friday et al. 2008).

Failure to fulfil the assumptions of equal capture probability leads to heterogeneity of capture probabilities and can lead to downward bias in estimated population parameters and underestimation of variance if not accounted for (Hammond, 1995, 2010; Kendall et al. 1995; 1997; Pledger & Efford 1998). The assumption of equal capture probability can be violated by inadequate implementation of the methodology. There should be sufficient time between the sampling occasions so that all individuals can be assumed to have mixed and thereby have

equal chance of being captured during the next sampling occasion (Hammond 1986). In this study, there was sufficient time (at least 1 day) between weekly secondary sampling occasions to allow all individuals/pods to mix within the research area. All encountered individuals should also be recorded equally to minimize the heterogeneity of capture probability; effort was made to photograph all individuals within a group, regardless of their distinctiveness.

The assumption of equal capture probability can also be violated due to individual differences in behaviour; this could occur in several ways. First, some individuals might tend to avoid the research vessel and therefore have a lower probability of being photographed, resulting in individual differences in capture probabilities.

Second, behavioural differences among individuals and/or groups of animals may lead to unequal capture probabilities as a result of so-called trap-dependency (Pradel 1993; Pradel & Sanz-Aguilar 2012), where capture probability changes once an animal has been captured. Although actual trap-dependency is unlikely for animals captured by photo-identification, it may be important to account for it because it may indicate some other underlying issue and lead to biased estimation of capture probabilities and thus population size and survival rates (Sandland & Kirkwood 1981; Pradel 1993; Pradel & Sanz-Aguilar 2012).

Third, unequal capture probability may be caused by so-called transience, whereby some individuals, referred to as transients, are captured only once, after which they permanently emigrate from the study area, thereby violating the assumption of equal capture probability and potentially leading to biased estimates of survival rate (Pradel et al. 1997). Transient individuals are not to be confused with the transient killer whale ecotype of the NE Pacific.

Finally, a specific focus of this chapter, some animals may emigrate temporarily from the study area, meaning that they are unavailable to be sampled in one or more sampling occasions thus affecting capture probability. In the case of killer whales in northern Norway, such absence from the study area may be because they were making “scouting trips”, as described in section 3.1.

Differences in behaviour were attempted to be taken into account in selected mark-recapture models (see below). Models accounting for temporary emigration, trap-dependency and transience were used in analysis to estimate apparent survival rates with CJS and robust design models to account for unequal capture probabilities (Burnham & Overton 1978; Otis et al. 1978; Pollock 1982; Pradel 1993; Pradel et al. 1997).

### **3.2.3.2 Cormack-Jolly-Seber models**

For estimating probabilities of capture and apparent survival with the CJS models (Cormack 1964; Jolly 1965; Seber 1965) for 1990-2003, the data were organised into three datasets: 1) adult males and adult females together (dataset MF); 2) adult males only; and 3) adult females only.

#### **3.2.3.2.1 Investigating goodness of fit**

Goodness of fit of the CJS model was assessed using Program U-CARE (Version 2.3.2) (Choquet et al. 2009). Program U-CARE performs four directional chi-square tests to assess different aspects of model fit to evaluate potential issues with assumed equal survival (3.SR and 3.SM) and capture probabilities (2.CT & 2.CL), e.g. possible transience and trap-dependency (Choquet et al. 2005). Test 3.SR evaluates transience in the data and test 3.SM compares when previously and newly marked individuals were seen. Test 2.CT identifies trap-dependency and 2.CL evaluates the difference in the expected time of next recapture among individuals. U-CARE also performs a global chi-squared test of the general goodness of fit which combines the statistics of the directional tests.

The global goodness of fit test in program U-CARE showed significant departures from adequate model fit for dataset MF and for adult males and adult females separately ( $p < 0.001$ , see Appendix 3.1). For the directional tests, the subtest within Test 3.SR with adult male data showed an indication of transience ( $p = 0.001$ ) but its influence was not substantial resulting in the overall 3.SR test being supported ( $p = 0.258$ , see Appendix 3.1). However, as a cautious approach a time-since-first-marking model (also known as an “age-class” model) was built in program MARK to account for the potential issue with transience in adult male data. This model was built in such way that the first period of marking (“1<sup>st</sup> age-class”) was different compared to all following periods (“2<sup>nd</sup> age-class”), thus separating the transient individuals that were only seen in that first period. Ignoring the transience in the data could lead into negatively biased estimates of survival due to the permanent emigration of transient individuals from the study area.

Test 2.CT showed a highly significant ( $p < 0.001$ ) result for trap-dependency for adult males (see Appendix 3.1). Test 2.CT also gave a significant ( $p < 0.001$ ) result for trap-dependency for adult females, but this resulted from only two years of the dataset showing significance. Trap-dependency in all cases was “trap-happiness”, meaning that recapture probability in subsequent years of initial capture was higher than expected by chance. A mark-

recapture model was built in program MARK to account for the trap-dependency with the adult male and adult female datasets (Sandland & Kirkwood 1981; Pradel 1993).

In addition, the goodness of fit of models to the data was explored using tests in program RELEASE within program MARK (White & Burnham 1999; Cooch & White 2012). The assumptions tested in program RELEASE were equal probability of recapture (TEST2) and equal probability of survival (TEST3). RELEASE TEST3 was non-significant for dataset MF and also for adult males and adult females separately ( $p > 0.145$ , see Appendix 3.2). TEST2 was significant ( $p < 0.002$ ) for all datasets. These results are in line with the U-CARE test results indicating violation of the assumptions of equal capture probabilities.

### **3.2.3.2 Investigating over-dispersion**

The amount of over-dispersion in the data was investigated with the variance inflation factor  $\hat{c}$ , with  $\hat{c} = 1$  indicating no over-dispersion (Anderson et al. 1994; Cooch & White 2012). This was calculated within program U-CARE by dividing the chi-square statistic by the degrees of freedom. For comparison, over-dispersion was also evaluated in program RELEASE again by dividing the chi-square statistic by the degrees of freedom.

Additionally a parametric bootstrap goodness of fit test was used to measure over-dispersion in two ways in program MARK. Firstly, the estimates from the model being evaluated were used to simulate encounter histories, from which  $\hat{c}$  was calculated. The number of simulations used was 100. The estimate of  $\hat{c}$  from the actual data was then divided by the mean of the simulated values of  $\hat{c}$ . Secondly, the “median- $\hat{c}$ ” approach was used, in which the best estimate of  $\hat{c}$  was determined to be the value where the observed model  $\hat{c}$  fell halfway in the distribution of all simulated  $\hat{c}$  values. The number of replicates used was again 100. A detailed description of the methods to estimate  $\hat{c}$  with a parametric bootstrap goodness of fit test can be found in Cooch & White (2012). Results of different methods to measure were  $\hat{c}$  compared.

For dataset MF, U-CARE estimated  $\hat{c} = 2.24$ , and for adult males and adult females separately, 2.31 and 2.15, respectively (see Appendix 3.3). Program RELEASE estimated  $\hat{c} = 1.91$  for dataset MF and  $\hat{c} = 2.09$  and  $\hat{c} = 1.71$  for adult males and adult females separately.

Calculations by bootstrap for dataset MF gave a  $\hat{c}$  of 1.18. The “median- $\hat{c}$ ” for dataset MF was 1.35. For adult males the bootstrap  $\hat{c}$  was 1.52 and the “median- $\hat{c}$ ” was 1.18 and for adult females the corresponding values were 1.83 and 1.18.

Overall,  $\hat{c}$  varied between 1.18 – 2.24 for dataset MF, between 1.18 – 2.31 for adult males and between 1.18 – 2.15 for adult females. Over-dispersion in the data was thus not

sufficient to cause any unacceptable lack of model fit ( $\hat{c} < 3$ ) (Lebreton et al. 1992; Burnham & Anderson 2002).

### **3.2.3.2.3 Model construction and selection**

CJS open population models implemented in program MARK were used to estimate capture probabilities ( $p$ ) and apparent survival rates ( $\varphi$ ) for adult males and adult females. Apparent survival includes death and permanent emigration.

Initially, data for adult males and adult females were analysed together (dataset MF). A second analysis estimated apparent survival separately for adult males and for adult females. Several CJS models were constructed (Table 3.1), including models that allowed apparent survival and capture probabilities to be constant or to vary by time or by sex. The interaction model  $\varphi(t) p(t*m)$  was built to account for the trap-dependency ( $m$ ) (Sandland & Kirkwood 1981; Pradel 1993) in the data, identified by the U-CARE goodness of fit tests (see section 3.2.3.2.1). This model estimated probability of capture as a function of time, trap-dependency and the interaction of time and trap-dependency. To reduce the number of parameters in the model, an additive model where the interaction between time and trap-dependency was removed was also implemented  $\varphi(t) p(t+m)$ . An “age-class model”  $\varphi(a2)$  was built to account for the transience in the adult male data (Pradel et al. 1997), identified by the U-CARE goodness of fit tests (see section 3.2.3.2.1). This model estimated apparent survival for individuals identified as transients separately from killer whales sighted at least twice in the study area.

Model selection was based on the QAICc (Anderson et al. 1994; Burnham & Anderson 2002), which is the AIC adjusted for small sample size and incorporating the appropriate  $\hat{c}$  value to account for the degree of over-dispersion in the data (see section 3.2.3.2.2). As a cautious approach, the highest  $\hat{c}$  values were chosen to account for the slight over-dispersion in each datasets. The model having the lowest QAICc was considered to be the best model. Different models having  $\Delta$ QAIC of less than 2 were considered to have similar support from the data. To obtain more precise estimates, the model averaging procedure based on the normalised Akaike weights was applied to take account of model uncertainty (Burnham & Anderson 2002; Cooch & White 2012).

Table 3.1 - Description of the CJS model variables used to estimate apparent survival and recapture probabilities.

<b>Probability of survival</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\varphi(.)$	Constant survival throughout years
Time	$\varphi(t)$	Time varying survival
Group	$\varphi(g)$	Survival varying between sexes
2 blocks	$\varphi(2blocks)$	Constant survival for each of two time periods, 1990-1997 & 1998-2003
"Age class"	$\varphi(a2)$	Survival accounting for transience

<b>Probability of recapture</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$p(.)$	Constant recapture probability over all years
Time	$p(t)$	Time varying recapture probability
Group	$p(g)$	Recapture probability varying between sexes
Trap dependency	$p(t*m)$	Probability of recapture acc. for trap-dependency - interaction model
Trap dependency	$p(t+m)$	Probability of recapture acc. for trap-dependency - additive model

### 3.2.3.3 Robust design models

To explore the effect of temporary emigration from the main study site inside the fjords and to estimate annual survival rates for adult male and adult female killer whales, robust design models implemented in program MARK (Kendall et al. 1997; Cooch & White 2012) were used in the analysis presented in this Chapter. The robust design combines closed population models (Otis et al. 1978) for estimation of abundance using secondary sampling occasions (within each primary sampling occasion) with open population models to estimate survival and temporary emigration probabilities between primary sampling occasions (years in this case). Temporary emigration can be modelled as either a random process (i.e. the probability of emigration is equal for all individuals, leading to equal capture probabilities in each primary sampling occasion) or Markovian (i.e. the probability of emigration is dependent on the state in the previous primary sampling occasion, either available or temporarily unavailable to be sampled) (Kendall et al. 1997; Kendall 1999). If temporary emigration exists and is random, the models can result in biased estimates of capture probabilities and population size, while estimates of survival are unbiased (Kendall et al. 1997). If temporary emigration is Markovian, estimates of all parameters can be biased. If either type of temporary emigration exists,

random or Markovian, the precision of estimates of all parameters is decreased (Kendall et al. 1995; 1997).

The data between October-December 1990-2003 were organised into 14 primary sampling occasions (years) and 72 secondary sampling occasions (weeks within years) (Table 3.3). The data for adult males and adult females were analysed separately in robust design models.

For the closed models within years, the Huggins closed capture model (Huggins 1989; 1991) that does not include an estimate of population size ( $\hat{N}$ ) in the likelihood was used to estimate model parameters. The Pledger mixture model (Pledger 2000) was not used because it was shown in previous analyses (see section 2.2.3.2 in Chapter 2) that modelling heterogeneity as a mixture was not the appropriate way to estimate population size. Pledger mixture models also had the potential of over-parameterization.

Within secondary periods the probability of capture ( $p$ ), recapture ( $c$ ) and true capture probability ( $p^*$ ) were estimated (Kendall 2012). Estimated parameters between primary periods were apparent survival rate ( $\varphi$ ), apparent encounter probability ( $P$ ), probability of temporary emigration ( $\gamma''$ ) and immigration ( $1 - \gamma'$ ). In the random emigration model ( $\gamma'' = \gamma'$ ) the probability of emigration is independent of the previous state, whereas in the Markovian emigration model ( $\gamma'' \neq \gamma'$ ) the probability of emigration is conditional on the previous state (Kendall et al. 1997).

In the first stage of modelling, the no-emigration model ( $\gamma'' = \gamma' = 0$ ) was used as a start-up model to test the effects of constant ( $.$ ), session ( $s$  = variation in capture probabilities within primary period) and the interaction of session and time variation ( $s*t$ ) on capture probabilities (Table 3.2). Additionally survival was estimated, both for adult males and adult females, as constant ( $.$ ), time varying ( $t$ ) and with two time intervals (1990-1997 & 1998-2003) to investigate potential change in survival rates between time periods (*2blocks*).

In the second stage of modelling, the random ( $\gamma'' = \gamma'$ ) and Markovian emigration ( $\gamma'' \neq \gamma'$ ) were incorporated into the best selected model from first stage. This followed estimating survival again with the other remaining options. Appropriate constraints were set on the last two  $\gamma''$  and  $\gamma'$  parameters when modelling survival as time varying, to avoid the issue of otherwise confounding the last two  $\varphi$  and  $\gamma''$  parameters. Due to evidence of a behavioural response indicated by the U-CARE results (see section 3.2.3.2.1), capture probability and recapture probability were then set to be unequal in the best selected models.

Table 3.2 - Description of the RD model variables used to estimate apparent survival, capture and temporary emigration probabilities.

<b>Probability of survival</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\varphi(.)$	Constant survival throughout years
Time	$\varphi(t)$	Time varying survival
2 blocks	$\varphi(2blocks)$	Constant survival for two time periods, 1990-1997 & 1998-2003
<b>Probability of capture</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$p(.) = c(.)$	Constant capture=recapture probabilities
Session	$p(s) = c(s)$	Capture=recapture probabilities varying within primary periods
Time*session	$p(s*t) = c(s*t)$	Capture=recapture probabilities varying within and between primary periods
<b>Temporary emigration</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
No emigration	$\gamma'' = \gamma' = 0$	No temporary emigration/immigration
Random	$\gamma'' = \gamma'$	Probability of emigration/immigration being random
Markovian	$\gamma'' \neq \gamma'$	Probability of emigration/immigration dependent on the previous state

No goodness of fit test is available for robust design and thereby assessing the model fit was not possible (for comparison, see goodness of fit testing for CJS models in section 3.2.3.2.1). Equally the variance inflation factor  $\hat{c}$  was not able to be estimated and thereby model selection was done by using Akaike's Information Criterion (AICc) (Anderson et al. 1994; Burnham & Anderson 2002). Different models having  $\Delta AICc$  of less than 2 were considered to have similar support from the data.

### 3.3 RESULTS

Survey effort and killer whale encounter rates were variable during 1990-2003 (Table 3.3). For the 14 years investigated, a total of 546 encounters, revealing 368 identified adult killer whale individuals and 29 pods with good quality photographs were recorded. 90 individuals were encountered only once during the 14 years (Figure 3.1), 65 of these being new adult individuals identified in 2002 and 2003 (Table 3.3). The remaining 278 individuals were encountered two or more times, resulting in a re-sighting rate of 75.5% for adult individuals. Details of cumulatively identified pods and all identifiable individuals up until year 2003 can be found in Figures 2.2 & 2.3 in Chapter 2.

Table 3.3 - Dates when photo-identification photographs were obtained during October-December (secondary period) in each year (primary periods) with the number of days when whales were photographed (whale days), number of total encounters per year, number of pods identified per year, number of identified adult individuals with good quality photographs used in analysis for each year and the number of new adult individuals identified per year.

Year (primary period)	Dates (secondary period)	Sampling occasions (weeks)	Whale days	No of encounters	No of pods	No of adult ind.	New adults identified
1990	16.10.-28.11.	6	27	56	20	143	
1991	7.10.-18.11.	7	32	73	22	123	59
1992	8.10.-20.11.	7	33	64	23	186	49
1993	16.10.-11.11.	4	18	37	18	91	11
1994	17.10.-22.11.	6	19	25	14	54	6
1995	20.10.-19.11.	5	20	35	20	96	12
1996	30.10.-27.11.	5	12	21	15	77	13
1997	14.10.-19.11.	4	8	14	13	48	1
1998	14.10.-12.11.	4	15	22	16	83	3
1999	21.10.-15.11.	4	13	19	14	86	0
2000	31.10.-12.11.	3	7	15	13	43	0
2001	19.10.-1.12.	3	18	18	13	34	6
2002	23.10.-7.12.	7	36	77	25	115	43
2003	18.10.-5.12.	7	35	70	22	124	22

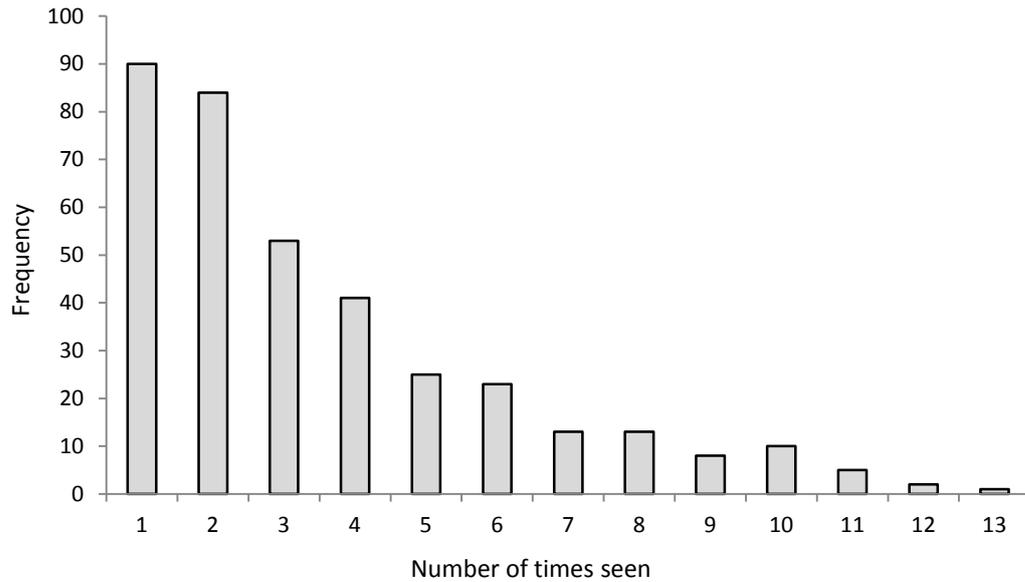


Figure 3.1 - Sighting frequency of adult killer whale individuals with good quality photographs during 1990-2003.

### 3.3.1 Cormack-Jolly-Seber model (CJS)

#### 3.3.1.1 Model selection

Model diagnostics for datasets MF, adult males and adult females using the 1990-2003 data are provided in Tables 3.4, 3.5 and 3.6, respectively. For the MF dataset, the model estimating apparent survival as constant for both sexes together and accounting for trap-dependency  $\varphi(.)$   $p(t*m)$  was selected as the best model based on QAIC (Table 3.4). The second best model estimating sex specific constant apparent survival had  $\Delta$ QAIC of 2 showing similar support from the data compared to the best model.

For adult males the best model was the “age-class” model  $\varphi(a2)$   $p(t+m)$  (Table 3.5). Two second best models, one estimating apparent survival as constant and other with two time periods, had  $\Delta$ QAIC < 2.2 showing similar support. All these three best models estimated probability of capture including trap-dependency with the additive model.

Table 3.4 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for dataset MF. The model with lowest QAICc, highest QAICc Weight and Likelihood values was considered as the best one.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(.) p(t^*m)$	2273.4	0	0.7346	1	14	2245.1
2	$\varphi(g) p(t^*m)$	2275.5	2.0	0.2652	0.3611	15	2245.0
3	$\varphi(.) p(t+m)$	2290.0	16.6	0.0002	0.0003	14	2261.6
4	$\varphi(t) p(t^*m)$	2293.6	20.2	< 0.0001	0	26	2240.4
5	$\varphi(.) p(g+t+m)$	2314.4	40.9	0	0	27	2259.0
6	$\varphi(.) p(t)$	2324.0	50.6	0	0	14	2295.6
7	$\varphi(g) p(t)$	2326.0	52.6	0	0	15	2295.6
8	$\varphi(2blocks) p(t)$	2327.6	54.2	0	0	17	2293.1
9	$\varphi(.) p(g^*t)$	2336.4	63.0	0	0	27	2281.1
10	$\varphi(g) p(g^*t)$	2337.8	64.4	0	0	28	2280.4
11	$\varphi(t) p(t)$	2343.2	69.8	0	0	26	2290.0
12	$\varphi(t) p(g^*t)$	2356.8	83.4	0	0	39	2276.0
13	$\varphi(g^*t) p(t)$	2361.7	88.2	0	0	39	2280.9
14	$\varphi(g^*t) p(g^*t)$	2380.3	106.8	0	0	52	2271.4
15	$\varphi(.) p(g)$	2449.5	176.1	0	0	3	2443.5
16	$\varphi(.) p(.)$	2450.9	177.5	0	0	2	2446.9
17	$\varphi(g) p(g)$	2451.4	178.0	0	0	4	2443.4
18	$\varphi(g) p(.)$	2452.8	179.4	0	0	3	2446.8
19	$\varphi(2blocks) p(g)$	2454.2	180.7	0	0	6	2442.1
20	$\varphi(2blocks) p(.)$	2455.0	181.6	0	0	5	2444.9
21	$\varphi(t) p(g)$	2458.2	184.8	0	0	15	2427.8
22	$\varphi(t) p(.)$	2458.7	185.3	0	0	14	2430.4
23	$\varphi(g^*t) p(.)$	2477.5	204.1	0	0	27	2422.2
24	$\varphi(g^*t) p(g)$	2477.7	204.2	0	0	28	2420.3

The best model for adult females was the model estimating apparent survival as constant accounting for trap-dependency in probability of capture with the additive model  $\varphi(.) p(t+m)$  (Table 3.6). With adult female data, four models had  $\Delta$ QAIC < 2.1. The second best model estimated apparent survival as constant and capture probability varying with time. Two models estimating apparent survival over two time periods also had reasonable support based on QAIC. In all datasets, incorporating trap-dependency improved the model fit. In the adult male dataset, including the “age-class” model for estimating apparent survival also improved the model fit.

Table 3.5 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult males.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(a2) p(t+m)$	1426.1	0	0.4645	1	16	1393.3
2	$\varphi(.) p(t+m)$	1426.5	0.4	0.3751	0.8077	15	1395.8
3	$\varphi(2blocks) p(t+m)$	1428.3	2.2	0.1584	0.3411	16	1395.5
4	$\varphi(a2) p(t)$	1438.3	12.2	0.0011	0.0023	15	1407.6
5	$\varphi(.) p(t)$	1439.5	13.4	0.0006	0.0012	14	1410.9
6	$\varphi(2blocks) p(t)$	1441.4	15.3	0.0002	0.0005	15	1410.7
7	$\varphi(a2) p(t*m)$	1444.2	18.1	0.0001	0.0001	27	1388.0
8	$\varphi(.) p(t*m)$	1445.0	18.9	< 0.0001	0.0001	26	1391.0
9	$\varphi(2blocks) p(t*m)$	1446.6	20.5	< 0.0001	0	27	1390.5
10	$\varphi(t) p(t*m)$	1451.2	25.1	0	0	32	1384.2
11	$\varphi(t) p(t)$	1457.6	31.5	0	0	25	1405.7
12	$\varphi(.) p(.)$	1512.7	86.6	0	0	2	1508.7
13	$\varphi(a2) p(.)$	1513.7	87.6	0	0	3	1507.7
14	$\varphi(2blocks) p(.)$	1514.6	88.5	0	0	3	1508.6
15	$\varphi(t) p(.)$	1526.5	100.4	0	0	14	1497.9

Table 3.6 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult females.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(.) p(t+m)$	861.5	0	0.3708	1	14	830.5
2	$\varphi(.) p(t)$	861.7	0.2	0.3343	0.9015	14	832.8
3	$\varphi(2blocks) p(t+m)$	863.5	2.0	0.1366	0.3683	15	830.3
4	$\varphi(2blocks) p(t)$	863.7	2.1	0.1285	0.3464	15	832.6
5	$\varphi(t) p(t+m)$	866.6	5.1	0.0295	0.0794	26	826.9
6	$\varphi(.) p(t*m)$	876.2	14.6	0.0003	0.0007	14	820.9
7	$\varphi(2blocks) p(t*m)$	878.2	16.7	0.0001	0.0002	15	820.7
8	$\varphi(t) p(t)$	882.1	20.6	< 0.0001	0	26	829.1
9	$\varphi(t) p(t*m)$	885.0	23.4	0	0	26	818.3
10	$\varphi(.) p(.)$	899.0	37.4	0	0	2	894.9
11	$\varphi(2blocks) p(.)$	899.9	38.4	0	0	3	893.9
12	$\varphi(t) p(.)$	912.4	50.9	0	0	14	883.5

### 3.3.1.2 Estimates of apparent survival rate

For dataset MF, the best fitting model  $\varphi(.) p(t+m)$  estimated constant apparent survival for all adults together as 0.978 (SE = 0.007, 95% CI = 0.959 – 0.988). The second best model estimating apparent survival for adult males and females separately also had similar support, QAICc = 2 (Table 3.4).

For adult males, the best fitting model  $\varphi(a2) p(t+m)$  gave an estimate of apparent survival excluding the transients of 0.977 (SE = 0.009, 95% CI = 0.949 – 0.990) (Table 3.7) and an estimate of apparent survival of 0.920 (SE = 0.035, 95% CI = 0.820 – 0.966) for the transients. The second best model  $\varphi(.) p(t+m)$  had similar support (QAICc = 0.4) (Table 3.5), but as this model did not exclude transients the estimated apparent survival was lower (Table 3.7). Model averaged apparent survival for adult males varied between 0.969 (SE = 0.016, 95% CI = 0.918 – 0.989) and 0.972 (SE = 0.010, 95% CI = 0.944 – 0.987).

For adult females, the best model  $\varphi(.) p(t+m)$  gave an apparent survival estimate of 0.978 (SE = 0.011, 95% CI = 0.943 – 0.992) (Table 3.8), higher than for adult males with the same model. Model averaged apparent survival for adult females varied between 0.964 (SE = 0.061, 95% CI = 0.470 – 0.999) and 0.978 (SE = 0.014, 95% CI = 0.928 – 0.994).

Table 3.7 - Estimated apparent survival rates for adult males, based on the three best fitting models ( $\Delta$ QAIC < 2.2).

CJS model	$\varphi$	SE	95% CI
$\varphi(a2) p(t+m)$	0.977	0.009	0.949 - 0.990
$\varphi(.) p(t+m)$	0.968	0.008	0.946 - 0.981
$\varphi(2blocks) p(t+m)$ 1991-1997	0.971	0.010	0.943 - 0.986
$\varphi(2blocks) p(t+m)$ 1998-2003	0.952	0.026	0.865 - 0.984

Table 3.8 - Estimated apparent survival rates for adult females, based on the four best fitting models ( $\Delta$ QAIC < 2.1).

CJS model	$\varphi$	SE	95% CI
$\varphi(.) p(t+m)$	0.978	0.011	0.943 - 0.992
$\varphi(.) p(t)$	0.976	0.011	0.944 - 0.990
$\varphi(2blocks) p(t+m)$ 1991-1997	0.981	0.013	0.932 - 0.995
$\varphi(2blocks) p(t+m)$ 1998-2003	0.960	0.048	0.674 - 0.996
$\varphi(2blocks) p(t)$ 1991-1997	0.979	0.012	0.934 - 0.994
$\varphi(2blocks) p(t)$ 1998-2003	0.954	0.046	0.730 - 0.994

Analysing apparent survival with two blocks of time for adult males and adult females with model  $\varphi(2blocks) p(t+m)$  had good support based on QAIC results for both sexes (Tables 3.5 & 3.6) and showed slightly decreased apparent survival in the second time block (Tables 3.7 & 3.8).

### 3.3.1.3 Capture probabilities

Estimated capture probabilities varied between years (Figure 3.2). Model averaged estimates of capture probabilities for adult males were 0.135 (SE = 0.038) – 0.709 (SE = 0.061) and for adult females 0.092 (SE = 0.042) – 0.672 (SE = 0.072) in the time period 1991-2003 (Figure 3.2). Capture probabilities for adult females were in most cases lower compared to adult males.

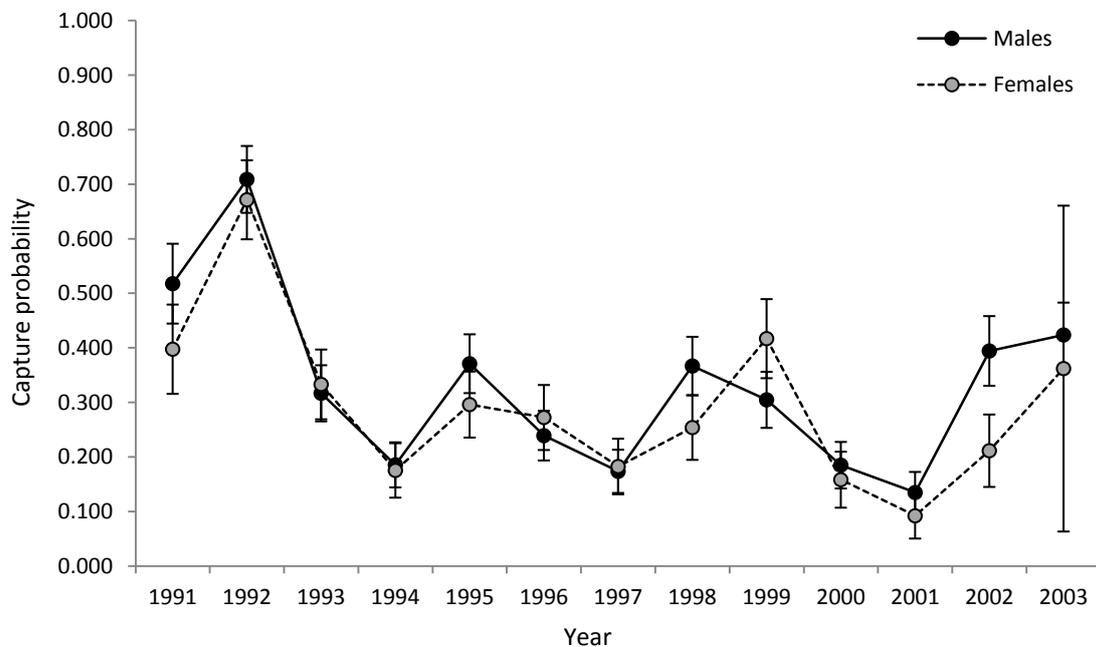


Figure 3.2 - Capture probabilities of adult males and adult females 1991-2003 estimated from the model averaged CJS models with standard errors.

## 3.3.2 Robust design

### 3.3.2.1 Model selection

The best model from the first stage of modelling the adult male data included survival estimate as constant and the interaction of session and time variation in capture and recapture probabilities  $\varphi(.) y''=y'=0 p(s*t)=c(s*t)$  (model 8, Table 3.9). After including random and Markovian emigration models in this best selected model and fitting two other effects on survival, the model with constant survival and Markovian emigration with time variation was

selected as the best model  $\varphi(.) y''(t) y'(t) p(s^*t)=c(s^*t)$  based on AIC comparison (model 1, Table 3.9). The second best model with survival estimated with two time periods also got good support based on  $\Delta AICc < 1$  (model 2, Table 3.9). Including behavioural response in capture probabilities did not improve the models.

The model selected as the best based on AICc comparison for adult female data in the first stage of modelling also included constant survival and the interaction of session and time variation in capture and recapture probabilities  $\varphi(.) y''=y'=0 p(s^*t)=c(s^*t)$  (model 6, Table 3.10), the same as for adult males. After the second stage of modelling, fitting the random and Markovian emigration to the best selected model from the previous stage and including the time varying and two time blocks on survival, the best model based on AIC comparison was  $\varphi(.) y''(.)=y'(. ) p(s^*t)=c(s^*t)$  (model 1, Table 3.10). This model estimated survival as constant and emigration as a random with constant parameters. The second best model estimating survival with two time periods also got reasonable support,  $\Delta AICc = 2.38$  (model 2, Table 3.10). Again, setting capture and recapture probabilities unequal to account for behavioural response did not improve the models.

Table 3.9 - Model selection diagnostics for robust design models of apparent survival, capture and emigration probabilities for adult males. The model with lowest AICc, highest AICc Weight and Likelihood values was considered as the best one.

#	Model	AICc	$\Delta AICc$	AICc Weight	Likelihood	Num. Par	Deviance
1	$\varphi(.) y''(t) y'(t) p(s^*t)=c(s^*t)$	6369.86	0	0.584	1	98	8879.1
2	$\varphi(2blocks) y''(t) y'(t) p(s^*t)=c(s^*t)$	6370.82	0.96	0.361	0.619	97	8882.4
3	$\varphi(.) y''(. ) y'(. ) p(s^*t)=c(s^*t)$	6374.58	4.72	0.055	0.095	75	8937.7
4	$\varphi(t) y''(t) y'(t) p(s^*t)=c(s^*t)$	6388.82	18.97	0	0	108	8873.8
5	$\varphi(.) y''(t)=y'(t) p(s^*t)=c(s^*t)$	6401.69	31.84	0	0	86	8939.3
6	$\varphi(.) y''(.)=y'(. ) p(s^*t)=c(s^*t)$	6419.59	49.73	0	0	74	8985.0
7	$\varphi(.) y''(t) y'(t) p(s^*t) c(s^*t)$	6432.38	62.53	0	0	156	8805.0
8	$\varphi(.) y''=y'=0 p(s^*t)=c(s^*t)$	6456.36	86.50	0	0	73	9024.1
9	$\varphi(2blocks) y''=y'=0 p(s^*t)=c(s^*t)$	6458.30	88.44	0	0	74	9023.7
10	$\varphi(t) y''=y'=0 p(s^*t)=c(s^*t)$	6474.24	104.38	0	0	85	9014.2
11	$\varphi(.) y''(t) y'(t) p(s) c(s)$	6721.17	351.31	0	0	54	9331.6
12	$\varphi(.) y''=y'=0 p(s)=c(s)$	6821.34	451.49	0	0	15	9514.8
13	$\varphi(.) y''=y'=0 p(.)=c(. )$	6916.68	546.83	0	0	2	9636.5

Table 3.10 - Model selection diagnostics for robust design models of apparent survival, capture and emigration probabilities for adult females.

#	Model	AICc	$\Delta$ AICc	AICc Weight	Likelihood	Num. Par	Deviance
1	$\phi(.) y''(.)=y'(. ) p(s^*t)=c(s^*t)$	4019.39	0	0.628	1	74	5341.9
2	$\phi(2blocks) y''(.)=y'(. ) p(s^*t)=c(s^*t)$	4021.77	2.38	0.191	0.304	75	5341.7
3	$\phi(.) y''(t) y'(t) p(s^*t)=c(s^*t)$	4022.85	3.46	0.111	0.177	98	5282.0
4	$\phi(.) y''(t)=y'(t) p(s^*t)=c(s^*t)$	4023.78	4.39	0.070	0.111	86	5315.2
5	$\phi(t) y''(.) y'(. ) p(s^*t)=c(s^*t)$	4033.60	14.21	0.001	0.001	87	5322.4
6	$\phi(.) y''=y'=0 p(s^*t)=c(s^*t)$	4036.08	16.69	0	0	73	5361.1
7	$\phi(2blocks) y''=y'=0 p(s^*t)=c(s^*t)$	4037.79	18.40	0	0	74	5360.3
8	$\phi(t) y''(.)=y'(. ) p(s^*t)=c(s^*t)$	4043.76	24.38	0	0	86	5335.2
9	$\phi(t) y''=y'=0 p(s^*t)=c(s^*t)$	4058.59	39.21	0	0	85	5352.7
10	$\phi(.) y''(.)=y'(. ) p(s^*t) c(s^*t)$	4068.90	49.51	0	0	130	5234.7
11	$\phi(.) y''(.)=y'(. ) p(s) c(s)$	4193.04	173.65	0	0	30	5619.3
12	$\phi(.) y''=y'=0 p(s)=c(s)$	4206.68	187.30	0	0	15	5665.2
13	$\phi(.) y''=y'=0 p(.)=c(.)$	4297.21	277.83	0	0	2	5782.4

### 3.3.2.2 Estimates of survival

The adult male constant survival was estimated as 0.974 (SE = 0.009, 95% CI = 0.951 – 0.986) (model 1, Table 3.9). Survival estimated with two time periods showed a decrease in survival, from 0.981 (SE = 0.009, 95% CI = 0.952 – 0.993) in 1991-1997 to 0.937 (SE = 0.020, 95% CI = 0.885 – 0.967) in 1998-2003. The model averaged estimate of adult male apparent survival varied between 0.962 (SE = 0.024, 95% CI = 0.877 – 0.989) and 0.978 (SE = 0.010, 95% CI = 0.945 – 0.991).

The constant survival for adult females was estimated as 0.976 (SE = 0.008, 95% CI = 0.956 – 0.987) (model 1, Table 3.10). Estimated survival showed a decrease between the two time periods from 0.978 (SE = 0.009, 95% CI = 0.951 – 0.991) to 0.965 (SE = 0.028, 95% CI = 0.841 – 0.993), smaller than for males. The model averaged estimate of survival for adult females varied between 0.975 (SE = 0.016, 95% CI = 0.917 – 0.993) and 0.977 (SE = 0.008, 95% CI = 0.953 – 0.989).

### 3.3.2.3 Temporary emigration and capture probabilities

Robust design analysis of both adult male and adult female datasets provided evidence for temporary emigration from the main NSS herring wintering area, as shown by the no-emigration models being discarded in favour of random or Markovian emigration models (Tables 3.9 & 3.10).

For adult males the best fitting model had Markovian emigration with time variation in both  $\gamma''$  and  $\gamma'$  parameters (model  $\varphi(.) y''(t) y'(t) p(s*t)=c(s*t)$ , Table 3.9). The probability of temporary emigration ( $\gamma''$ ) was 0.067 (SE = 0.188) – 0.539 (SE = 0.105). The probability of remaining outside the sampling area ( $\gamma'$ ) was 0.209 (SE = 0.251) – 0.974 (SE = 0.058). The derived return rate of temporary emigrants ( $1-\gamma'$ ) was 0.026 – 0.791, and the probability of remaining inside the sampling area ( $1-\gamma''$ ) was 0.461 – 0.933.

For adult females the best fitting model had random emigration with constant  $\gamma''$  and  $\gamma'$  parameters (model  $\varphi(.) y''(.)=y'(.)$   $p(s*t)=c(s*t)$ , Table 3.10). The probability of temporary emigration or remaining outside the sampling area was 0.269 (SE = 0.053). The derived return rate and probability of remaining inside the sampling area was 0.731.

Capture probabilities varied within and between years. For adult males capture probability varied between 0.005 – 0.488, and for adult females between 0.010 – 0.450.

### 3.4 DISCUSSION

#### 3.4.1 Model selection and analysis

Goodness of fit tests conducted in programs U-CARE and RELEASE showed that adult males and adult females were subject to heterogeneity of capture probabilities. Significant trap-dependency was shown, by the goodness of fit results of U-CARE, which in all cases was “trap-happiness”, i.e. increased capture probability after first capture (Pradel 1993; Pradel & Sanz-Aguilar 2012). Based on directional test 2.CT, trap-dependency was considered to be an issue with adult male data for most of the years in the dataset, however with adult females the issue was related only to a couple of the years in the dataset.

It is unlikely that actual trap-dependency occurs as killer whales are not physically handled in photographic capture but more likely it is a proxy for something else, e.g. indicating differences in sighting probabilities (Sandland & Kirkwood 1981; Pradel 1993; Pradel & Sanz-Aguilar 2012). These differences may have one of several causes, for example killer whales being encountered as groups of individuals rather than independent individuals or differences in the behaviour among pods and/or individuals. Such variable behaviour among individuals could be caused by temporary emigration, which would lead to some individuals being recaptured more often than others. Pods and/or individuals could also have unique preferences for certain areas within the study area. Additionally sampling methodology itself could cause sighting probabilities to vary. All these issues might lead to trap-dependency, i.e.

“trap-happiness”, showing in the dataset, which overall could be a result of certain individuals and/or pods having a higher probability of capture for one reason or another and those individuals and pods being captured sooner on average and thereafter more often than the other individuals and pods with lower capture probabilities.

Guided by the U-CARE test results, trap-dependency was taken into account in appropriate models within the CJS analysis, as has been done with some other studies on marine mammals, i.e. manatees, blue and humpback whales (Langtimm et al. 1998; Ramp et al. 2006; 2010). Based on QAICc comparison between the CJS models, for adult males, including trap-dependency clearly improved the model fit. For adult females, incorporating trap-dependency improved the model fit but not as much as for adult males. The results from the robust design analysis may provide an explanation for this difference between sexes. Males were best described by Markovian temporary emigration and females by random temporary emigration. This may indicate that the trap-dependency apparent in the data was partially a result of temporary emigration.

Goodness of fit tests in program U-CARE also indicated some evidence of transience (Pradel et al. 1997) in the data for adult male killer whales and in analysis with the CJS models, an age-class model improved the model fit. There was no evidence of transience in the data for adult females. It is understandable that transience did not show for females because they need to be encountered for several years before assigning them as adult females, whereas adult males can be assigned as a male on first sighting based on their tall dorsal fin. If there was an individual which was in the initial capture categorised as a sub-adult/female and was never recaptured, it was excluded from the analysis in this study (see section 2.2.2.1 in Chapter 2). The transience found to be an issue only for adult males could indicate sex-specific differences in how adult males and adult females use their total range. Alternatively, individuals that for some reason have lower capture probabilities could be perceived as transients due to lower probability of being recaptured.

The issues violating the assumption of equal capture probabilities are recognised in this study and were taken into account as far as possible during data collection and processing, and then additionally in data analysis by incorporating trap-dependency, transience and temporary emigration into the selected models. Over-dispersion of the data was found to be within acceptable limits. However, the measure of over-dispersion was incorporated into the model selection in CJS models to adjust for the lack of fit.

The annual fieldwork seasons (years) used within the robust design models were assumed to be closed to births, deaths, emigration and immigration so that closed models

could be used to analyse the secondary sampling occasions (weeks) (Kendall & Nichols 1995; Kendall et al. 1995). This is a reasonable assumption for a long-living, slowly reproducing species like the killer whale (Hammond 1986; Nichols 1992; Hammond 2009). With the adult female data showing random temporary emigration with the robust design analysis, the survival rate estimate is unbiased although the precision of the estimates can be reduced (Kendall et al. 1997; Kendall 1999). However, for adult males with Markovian temporary emigration, all the capture probabilities and population estimates could be biased (Kendall 1999). In this study, temporary emigration was incorporated with the robust design analysis to obtain survival rate estimates for adult individuals of both sexes that would be unbiased. The Pledger mixture model (Pledger 2000), which could account for unequal capture probabilities within years, was not used in this study as it was shown in previous analyses (see section 2.2.3.2 in Chapter 2) that modelling heterogeneity as a mixture was not the appropriate way to estimate population parameters and had the potential of over-parameterization.

#### **3.4.2 Survival rate**

The major contribution of this study is to present sex-specific adult killer whale survival rate estimated from a long-term dataset while taking into account temporary emigration, transience and trap-dependency, the first time this has been done for any killer whale population. The increased knowledge that these more precise estimates of survival rate provides is important to understanding the future viability of this northern Norwegian killer whale population.

Previous estimates of apparent survival for this killer whale population used a longer sighting dataset 1986-2003 with the CJS model (see Chapter 2, Kuningas et al. 2013a), but this analysis did not allow the possibility of temporary emigration, in part because of limited data for the years in the 1980s. Estimated apparent constant survival rates were similar between these two time series, 1986-2003 & 1990-2003, especially for adult females (Table 3.11). For adult males, a slightly lower estimate of survival rate was given by the CJS model compared to the robust design model for the 1990-2003 dataset. This is probably because the Markovian temporary emigration found to be important in the robust design model was not taken into account in the CJS model; unequal capture probabilities due to Markovian temporary emigration can bias survival rate estimates low (Kendall et al. 1997). This highlights the importance of taking temporary emigration into account when estimating population parameters, because ignoring this kind of variability in capture probabilities both reduces the precision and results in negatively biased estimates of population parameters (Kendall et al.

1995; 1997). The consistent result found between the two studies in Chapter 2 and Chapter 3 is the higher estimated survival rates for adult females compared to adult males (Table 3.11).

The results presented here also allow for more detailed comparison of survival rate estimates between different killer whale populations. Similarly to the findings in Chapter 2, when comparing the survival rate estimates between northern Norwegian killer whales and the resident killer whales from the northeast Pacific, adult males in Norway were estimated to have a higher survival rate (Table 3.11). In contrast, adult females in Norway were estimated to have lower survival rate compared to resident female killer whales in the NE Pacific. Estimated survival rate for resident female killer whales in the study of Olesiuk et al. (2005) for the later part of the time series, was the closest to the estimate of Norwegian female killer whales. Olesiuk et al. (2005) combined all age-classes of adult females together. Similarly, in the Norwegian data, adult females included both reproductive and post-reproductive females. Mortality has been recorded to increase with the start of reproductive senescence in killer whale females around the age of 40 (Olesiuk et al. 2005); combining both reproductive and post-reproductive aged females does not allow for such differences in age-specific survival to be explored.

Comparison between the estimates of survival from northern Norway and the Crozet Archipelago from the study by Poncelet et al. (2010) reveals that the survival estimates are higher for both adult males and adult females in the Norwegian population (Table 3.11).

The differences found in the estimated survival rates from these different killer whale populations living in different ocean basins, probably indicate location specific ecological variability. The killer whale populations compared here all have a very different diet: the Norwegian population mainly feeds on NSS herring (Similä et al. 1996), the resident killer whales in the northeast Pacific feed mainly on Chinook salmon (*Oncorhynchus tshawytscha*) (Ford et al. 1998) and the diet of the Crozet Archipelago killer whales varies from fish to marine mammals (Guinet 1991; Reisinger et al. 2011a). This kind of difference in diet between these locations could lead to the differences seen in survival rates.

Table 3.11 - Estimates of survival rates for adult male and adult female killer whales from northern Norway, northeast Pacific (Olesiuk et al. 1990; 2005) and the Crozet Archipelago (Poncelet et al. 2010). The details of the analysis with the Norway 1986-2003 dataset can be found in Chapter 2. CJS = Cormack-Jolly-Seber and RD = robust design.

<b>NORWAY</b>			
<b>1986-2003 CJS</b>	$\varphi$	SE	95% CI
Males $\varphi(.) p(t+m)$	0.971	0.008	0.950-0.983
Females $\varphi(.) p(t+m)$	0.977	0.009	0.951-0.989
<b>1990-2003 CJS</b>	$\varphi$	SE	95% CI
Males $\varphi(.) p(t+m)$	0.968	0.008	0.946-0.981
Females $\varphi(.) p(t+m)$	0.978	0.011	0.943-0.992
<b>1990-2003 RD</b>	$\varphi$	SE	95% CI
Males	0.974	0.009	0.951-0.986
Females	0.976	0.008	0.956-0.987
<b>NE PACIFIC</b>			
<b>Olesiuk et al. 1990</b>	$\varphi$	SE	95% CI
Males	0.9610	0.0076	
Females	0.9886	0.0033	
<b>1973-1996. Olesiuk et al. 2005</b>	$\varphi$	SE	95% CI
Males	0.9590	0.0081	
Female	0.9836	0.0039	
<b>1996-2004. Olesiuk et al. 2005</b>	$\varphi$	SE	95% CI
Males	0.9089	0.017	
Females	0.9705	0.0072	
<b>CROZET ARCHIPELAGO</b>			
<b>Poncelet et al. 2010</b>	$\varphi$	SE	95% CI
Males (1977)	0.935		0.817-0.979
Males (2002)	0.895		0.746-0.961
Females (1977)	0.942		0.844-0.980
Females (2002)	0.901		0.742-0.966

Resident killer whales in Pacific have been recorded to respond to changes in their salmon prey abundance with changes in their survival rate (Ford et al. 2010; Ward et al. 2011), indicating that prey availability plays an important part in determining survival rates. Most likely, similarly food abundance can affect the survival of the northern Norwegian killer whale population. Over the study period here, the abundance of NSS herring has reached top levels, up to 6 million tonnes (ICES 2013). The biomass of the NSS herring stock is known to have varied considerably over decades (Dragesund et al. 1997; Toresen & Østvedt 2000; Holst et al. 2004) and it can only be assumed that this has had an effect on population parameters of the

Norwegian killer whales. Decreasing fat reserves in northern Norwegian killer whales were recorded during the whale catches conducted between 1951 and 1968, at the same time as the NSS herring stock collapsed in the 1960s (Christensen 1982). The rapidly decreased herring prey resource likely then influenced the viability of the killer whale population. It is important to maintain the long-term monitoring of this northern Norwegian killer whale population in the future, to be able to document the fluctuations in the NSS herring biomass and their effect on killer whale population parameters (see Chapter 6).

Another location-specific reason for survival rates to be different among killer whale populations is human-caused pressures, e.g. vessel traffic (Lusseau et al. 2009), underwater noise (Erbe 2002; Morton & Symonds 2002), or contaminants (Ross et al. 2000; Wolkers et al. 2007; Cullon et al. 2009). Very high contaminant levels have been recorded for killer whales in northern Norway (Wolkers et al. 2007). High accumulation can occur especially in adult males, compared to females which through pregnancy and lactation pass on part of the toxic load to calves (Ross et al. 2000; Hickie et al. 2007; Krahn et al. 2009). Given the highest reported adult male survival rates for any killer whale population, it appears that the males in this northern Norwegian killer whales population are currently coping with this pressure.

Interactions with fisheries can also present a threat to some killer whale populations, as is the case with the Crozet Archipelago killer whales where lethal interactions with the long-line fisheries have been reported (Poncelet et al. 2010; Tixier et al. 2010), and can at least partly explain the low and decreasing survival rates for males and females in this location (Table 3.11). Increased interactions between killer whales and fisheries have also been reported for the northern Norwegian killer whale population, simultaneously with the increase in NSS herring biomass and consequent increase in fishing effort (Similä 2005), but only a few confirmed lethal interactions have been reported. The increase in interactions with the fishing gear is thought to have increased the proportion of well-marked individuals in this population (see Chapter 2, Kuningas et al. 2013a).

The datasets used in the analysis between these three different locations vary and this could also result in varying estimates of survival rate. The NE Pacific resident dataset is unique because all individuals in the small population are identified and regularly sighted across years (Ford et al. 2000; Olesiuk et al. 2005). In contrast, estimation of survival rates for the Norwegian population rely on mark-recapture methods of analysis because the population that used the fjord system over winter months in northern Norway is estimated to be more than 700 individuals (see Chapter 2, Kuningas et al. 2013a) and only a proportion of these

individual are identified, and the fieldwork season coincides with a time of very limited daylight and challenging fieldwork conditions in the winter.

As also described in the previous analysis (see Chapter 2, Kuningas et al. 2013a), a consistent result between northern Norway, the northeast Pacific and Crozet Archipelago was that adult male killer whales had lower apparent survival compared to adult females. These differences were smaller within the northern Norwegian population than differences in the northeast Pacific (Olesiuk et al. 1990; 2005). The killer whale is a long-living species and follows the typical mammalian U-shaped mortality curve, whereby the very youngest and oldest individuals have the highest mortality rates (Caughley 1966; Olesiuk et al. 1990). Sex-specific differences are expected because male killer whales have a shorter expected lifespan compared to females (Ford et al. 2000; Olesiuk et al. 2005), leading to the mortality curve being narrower. Additionally, killer whale females have been found to go through a period of extremely low mortality during their reproductive phase (Olesiuk et al. 2005), thus differentiating them from male life history.

Estimating constant apparent survival of adult males and adult females within two blocks of time with the 1990-2003 datasets got reasonable support from the data, both with CJS and robust design models. In CJS models capture probabilities were estimated including time (year) and trap-dependency and in robust design the capture probabilities varied by session (week) and time (year). Apparent survival for adult males and adult females was lower in the more recent time block with both CJS and robust design models, but the decrease in apparent survival was only between 1.3 – 2.1% for adult females and between 1.9 – 4.4% for adult males. However, if differences between the two time periods are compared with regards to the percentage change in mortality rates, the change for adult males was 66.7 – 231.7% and for adult females 60.8 – 111.3 %. If this reduction in survival rate (increase in mortality rate) is real, the explanation potentially lies with the NSS herring distribution change.

During the second block of time (1998-2003), large scale changes in the distribution of NSS herring were first recorded in 2002 as part of the NSS herring stock established a new wintering area offshore (Holst et al. 2004; Huse et al. 2010). Therefore a decline in apparent survival might simply indicate that fewer killer whale individuals were available to be encountered inside the fjord system because of increased temporary or permanent emigration towards the end of the time series. An increase in permanent emigration in the later part of the time series could be the reason for the decrease in apparent survival in the second time block. The decrease in estimated survival rates between the two time periods was larger for adult males than for adult females with the robust design model. This could be due to the

differences in the temporary emigration probabilities between sexes; adult males had a higher probability of temporary emigration and that temporary emigration was Markovian.

There have been relatively recent direct removals from this northern Norwegian killer whale population. The intention was to limit the numbers of killer whales because it was feared that the size of the killer whale population was not allowing the NSS herring to recover from the major stock collapse in the 1960s (Christensen 1982). Catches through the 1930s – 1980s in the Lofoten area totalled 662 individuals with the majority of catches taken in 1978–1981. In 1979 alone, 219 individuals were taken in the Lofoten area (Christensen 1982; Øien 1988) from the population under study in this thesis. In the northeast Pacific, the killer whale populations were subjected to live-capture catches in the 1960s and 1970s and these individuals were placed in aquarium exhibitions (Bigg 1982; Olesiuk et al. 1990). These kinds of removals from populations could be expected to have an effect on population parameters. Specifically, including data from previously exploited pods in analysis might result in higher estimated survival rates as a result of density dependent effects as the population recovered from previous removals. Unfortunately, the data for northern Norwegian killer whales were insufficient to be able to investigate the effect of these removals on the estimated survival rates. In the NE Pacific, no evidence was found by Olesiuk et al. (1990) that life history parameters had been affected by previous exploitation.

In addition to presenting new and more detailed results of the estimated survival rates for adult males and adult females for the northern Norwegian killer whale population, this study also clearly shows the need to incorporate temporary emigration into estimating survival rates. Understanding the unique behaviour of killer whale populations (such as scouting the unpredictable herring prey resources, see Stenersen & Similä 2004), and the need to incorporate temporary emigration from the study site to the mark-recapture analysis is clearly important to be able to obtain unbiased estimates of survival. Accounting for temporary emigration is especially important if emigration probabilities are Markovian, as this can cause negatively biased estimates of survival rate due to unequal capture probabilities (Kendall et al. 1997), as was seen for adult males in this study.

### **3.4.3 Capture probabilities**

Estimated capture probabilities varied between years and the number of individuals identified per year correlated with the estimated yearly capture probabilities, as expected. Capture probabilities for adult females were in most cases lower compared to adult males, which could be due to higher identifiability of adult males compared to adult females.

Methodological issue due to changing from film to digital photography from 2001 onwards could have increased the efficiency of capturing more individuals in the late part of this time series (Markowitz et al. 2003). A high number of new identifiable individuals was recorded in 2002 and 2003, which could be due to this change in photographic method. An additional explanation for the newly identified individuals could lie in the heavily increased biomass of NSS herring in the late part of 90s (Toresen & Østvedt 2000; Orellana 2006; ICES 2013), and the potential increase in the reproductive rates due to high food abundance (see Discussion in Chapter 2). The high abundance of Chinook salmon in the NE Pacific has been suggested to increase fecundity of the resident killer whales (Ward et al. 2009; Ford et al. 2010).

In this study transients among adult males and temporary emigration of both sexes were recorded introducing heterogeneity of capture probabilities. Markovian temporary emigration in adult males, indicated by the robust design models, violates the assumption of equal capture probabilities and lowers the capture probabilities obtained with the CJS model (Kendall et al. 1997; Kendall 1999). Random temporary emigration in adult females means that the estimated capture probabilities with the CJS models are also lower but unbiased (Kendall et al. 1997). Trap-dependency found in the goodness of fit test (Test 2.CT) in U-CARE, which could mimic temporary emigration from the study area, also causes the capture probabilities to vary among the individuals in the population.

#### **3.4.4 Emigration and immigration rates**

In this analysis, the probability of temporary emigration for adult males and adult females separately was taken account of for the first time when estimating population parameters for this, or any other, killer whale population. The results show that temporary emigration does exist, as was suspected given what was known about the results from the satellite tagging study conducted in 2000 and 2001 on this killer whale population (Stenersen & Similä 2004). For adult males the probability of temporary emigration varied with time (0.07-0.54) and was Markovian, indicating a pattern in the emigration and immigration probabilities. For adult females though, the probability of temporary emigration was constant (0.27) and random, meaning that individuals leave and return independently of their location in the previous sampling occasion. The return rate for adult males was low to high (0.03-0.79), while adult females showed a high constant return rate to the study area (0.73). Overall, adult females showed higher site fidelity to the fieldwork area compared to adult males.

One of the main reasons for movement of all marine mammal species is to locate their food resources, which are distributed in patches and can be unpredictably available (Stevick et al. 2002). The NSS herring abundance inside the fjords in wintertime has been variable and the distribution within the fjords has changed through the 14 years under study here (Orellana 2006; see Chapter 6), which could have contributed to the temporary emigration identified in the data, as it was not feasible to cover the entire fjord system in all years. An additional reason for temporary emigration of killer whales from the research area during wintertime could be due to the annual naval sonar exercises conducted in the fjord system during October and November (Chapter 5; Kuningas et al. 2013b). The use of active high intensity anti-submarine sonar on these exercises was blamed by the whale-watching community to have negatively affected killer whale abundance in the fjord system (WWF-Norway 2001). Avoidance of the sonar exercises could have resulted in some of the killer whales being temporarily out of the study area and thereby unavailable for photographic capture.

In general, the robust design analysis illustrated temporary emigration away from the research area, together with moderate to high probability of remaining away. These results indicate a larger distributional range for killer whales during wintertime than covered by the research effort. Therefore it is evident that in this study only a proportion of a larger population (superpopulation - Kendall et al. 1997) is captured during wintertime in the selected research area inside the fjords. Superpopulation refers to the total population of killer whales in northern Norway, of which only some of the individuals are available to be captured within the fjord system in a given time during winter. Additionally on the methodological side, the variable sampling effort between years likely has influenced the capture probabilities and thereby has affected the variable temporary emigration rates seen.

Comparing adult males and adult females, site fidelity was lower for adult males. Overall, adult males showed more dispersal behaviour from the study area. The differences found in temporary emigration probabilities between adult males and adult females in the Norwegian population are extremely interesting, especially given what is known about killer whales living in stable family pods, males staying with their mothers throughout their lives (Bigg 1982; Similä 1997) and their co-operative feeding behaviour (Similä & Ugarte 1993). The results of this study imply that those close family pods separate, at least for certain periods of time, as adult males and adult females have different probabilities of being available within the study area.

One potential reason could be in the way that killer whales search for their migrant and dynamic NSS herring prey. Potentially adult males conduct more of the scouting after the

NSS herring outside the fjord system compared to adult females. Adult killer whale males have a larger body size compared to adult females (Christensen 1984; Bigg et al. 1987; Stenersen & Similä 2004; Fearnbach et al. 2011), and this bigger body size with larger fat reserves could allow males to scout for herring over wider areas. Larger home ranges have been recorded for other male mammals (Greenwood 1980), including marine mammals e.g. harbour seals (Thompson et al. 1998), grey seals (Austin et al. 2004; Breed et al. 2006) and bottlenose dolphins (Connor et al. 2000; Krützen et al. 2004), but in these species individuals do not form lifelong mixed-sex family units, as killer whales do.

Additionally, the energetic cost of travel is higher for females, especially if accompanied by a calf, and might favour females staying inside fjords (Williams & Noren 2009). Due to larger body size, the daily energetic requirement is higher for adult males (Williams et al. 2004), something that could lead to different foraging strategies (Weise et al. 2010). Paradoxically though, it is curious that adult male killer whales in this northern Norwegian population would temporarily emigrate away from the highly abundant NSS herring resource inside the fjord system, given that the energy requirement to maintain the larger body size of adult males would predict males staying within the fjords together with the plentiful prey. Potentially being aware of the NSS herring distribution and any signs of prey migration may exceed the importance of staying with the highest prey abundance location at all times. Previous satellite tagging studies on killer whales, in Norway or elsewhere, do not reveal if there would have been differences in the movement patterns between males and females in terms of duration and/or distance (Similä et al. 2002; Stenersen & Similä 2004; Andrews et al. 2008; Durban & Pitman 2011; Matthews et al. 2011). The impression from the satellite tagging study conducted on killer whales in northern Norway is that the family pods temporarily emigrated away from the fjords together (pers. comm. Tiu Similä), although the sample size remains low and does not allow detailed analysis between sexes.

At a smaller spatial scale, males temporarily forage at a distance from the rest of the family pod, as has often been seen during feeding events in northern Norway, both during carousel feeding events and while feeding around purse seiners (Bisther & Vongraven 1995; pers. comm. Tiu Similä; observations by the author). Commonly, during an active feeding event a whole pod of killer whales is engaged in foraging, but later on females move away with calves, leaving adult males to continue feeding. Also, in the NE Pacific frequent periods of males feeding on their own have been recorded (Hoelzel 1993; Ford & Ellis 2005; Ford et al. 2011).

Another potential reason behind the differences between the temporary emigration probabilities between the sexes could be in reproductive strategies. Killer whale pods are formed by genetically closely related individuals (Bigg et al. 1990; Ford et al. 2000). Consequently, for reproductive benefit and to avoid inbreeding there is a need for adult males to separate from their family pod and to temporarily disperse to find adult females in other pods (Barrett-Lennard 2000; Hoelzel et al. 2007; Pilot et al. 2010). Dispersal from the family pod for reproductive reasons could therefore explain part of the higher dispersal of adult males, but it is not clear that adult males would move as far out as off the fjord system during wintertime in the search for potential mates. This kind of long distance dispersal is unlikely especially given that the main mating season of northern Norwegian killer whales is thought to be summer and autumn and not during wintertime, which is the peak calving time after the gestation period of ~17 months (Christensen 1984; Walker et al. 1988; Duffield et al. 1995; Similä 1997a). Additionally, mating is thought to take place more commonly during brief periods of time when different family pods come together, without male dispersal (Barrett-Lennard & Ellis 2001; Pilot et al. 2010).

It has also been suggested that some of the adult males in northern Norway have a nomadic lifestyle rather than living in stable family pods (Bisther & Vongraven 1995). Nomadic or solitary males have been reported also from other killer whale populations (Matkin et al. 1999; Baird & Whitehead 2000; Burdin et al. 2007; Ivkovich et al. 2009; Pilot et al. 2010). Such nomadic individuals within the adult male data could be perceived as transient individuals, as was shown by goodness of fit tests. The nomadic males in the Norwegian population could have previously been part of a family pod, but be separated from the rest of the pod after their mother died due to natural mortality. It is also likely that a large number of family pods disintegrated during the intense years of killer whale catches in the 1970s and 1980s (Christensen 1982; Øien 1988), leaving behind many solitary males that could have been later encountered as nomadic males. Whether or not these nomadic individuals have a different range from the individuals living in pods and whether or not they are more occasional visitors in the study area is not known.

The robust design framework has previously been used in other studies to estimate abundance and survival rates of bottlenose and Guiana dolphins (Silva et al. 2009; Cantor et al. 2012; Daura-Jorge et al. 2012; Nicholson et al. 2012) and western Pacific gray whales (Bradford et al. 2006; Bradford et al. 2008). However, none of these studies have been able to estimate sex specific survival or temporary emigration rates, due to difficulties of correctly identifying males and females. A maximum likelihood model presented by Whitehead (1990) was used to

estimate temporary emigration rates of transient killer whales in the Northeast Pacific, but did not specify sex-specific probabilities of temporary emigration (Ford et al. 2007). Therefore, to my knowledge, the study presented here is currently the only one estimating temporary emigration rates for adult males and adult females separately for any cetacean species.

### 3.5 CONCLUSIONS

This study presents the first estimates of sex-specific survival rates for any killer whale population while accounting for temporary emigration, transience and trap-dependency. The results of this long-term study have allowed more detailed comparison of survival rates between killer whale populations and consideration of location specific ecological traits that might affect survival.

It was clear, based on the results between models, that the implementation of robust design accounting for temporary emigration to estimate population parameters is highly useful. It was shown here that ignoring Markovian emigration can result in negatively biased estimates of survival. Also, taking transience and trap-dependency into account improved the model fit and allowed some of the issues that violated the assumption of equal capture probabilities to be taken into account.

Differences in temporary emigration probabilities between sexes indicate higher dispersal behaviour of adult males. This is probably due to different strategies on how to keep track of the migrant NSS herring prey. The existence of nomadic males is recorded for this killer whale population and these nomadic males could show different movement and ranging behaviour.

The continuation of the long-term study of this killer whale population is highly recommended to monitor population parameters and the viability of the population in the changing Norwegian Sea ecosystem. The NSS herring stock is highly dynamic in its changing distribution and biomass (Dragesund et al. 1997; Toresen & Østvedt 2000; Holst et al. 2004; Huse et al. 2010; see Chapter 6), which, together with larger scale changes in the ecosystem, could affect the population parameters of killer whales substantially. A large decrease in the NSS herring stock is again predicted to take place during the next few years due to collapsing plankton biomass (pers. comm. Jens Christian Holst). This prediction highlights the importance of the results presented in this study on survival rates and the need for close monitoring of this killer whale population in the future.

## CHAPTER 4

### Assessment of the future viability of the northern Norwegian killer whale population

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#### **ABSTRACT**

The future viability of a population can be evaluated by assessing a population's risk of extinction and population size projections with a given timeframe. Program Vortex is a commonly used tool for this kind of analysis and was applied here to assess the future viability of the northern Norwegian killer whale (*Orcinus orca*) population and the factors that might lead to reduced viability. Estimates of population size, survival and reproductive rates obtained from Chapters 2 and 3, together with other parameters derived from studies of the northeast Pacific resident killer whale populations, were used in the analysis. Future viability was evaluated under various scenarios, which investigated the effect of reduced reproductive rates and increased mortality rates that could result from different environmental stressors. An attempt was made to evaluate retrospectively the effect of previous catches from this population. The effect of a potential future decline in NSS herring biomass was investigated through two different scenarios. The baseline scenario using the best available information predicted a viable killer whale population and indicated that this population may be increasing in size. However, a reproductive rate of less than 16% of adult females breeding (calving interval longer than 6.25 years) predicts a decline in the population size. Removal of eight or more individuals per year also turned the growth rate negative and the removal of 15 individuals per year (the previous catch level) would lead to a serious risk of extinction after 50-60 years. Both scenarios evaluating the effects of future decline in the NSS herring biomass indicated that the final population size after 100 years would be approximately 50% lower than the baseline scenario. This work presents the first evaluation of the future viability of the northern Norwegian killer whale population and provides information that could be useful for future conservation efforts.

## 4.1 INTRODUCTION

Assessment of a population's potential risk of extinction and projections of its future population size are needed to be able to evaluate the viability of a population (Gilpin & Soulé 1986; Shaffer 1990; Beissinger & McCullough 2002). This population viability analysis (PVA) and an associated sensitivity analysis can also be a valuable way to explore the factors threatening the future viability of a population and, therefore, provide guidance towards potentially needed specific conservation and management measures (Akçakaya & Sjögren-Gulve 2000; Beissinger & McCullough 2002; Mills & Lindberg 2002). Population viability analysis provides an opportunity to investigate the effects of deterministic processes (e.g. harvest, loss of habitat and pollution), and the effects of demographic, environmental, catastrophic and genetic stochastic events on a given population (Lacy 1993; Beissinger & McCullough 2002; Miller & Lacy 2005). Generally, small populations are at higher risk of extinction than larger populations and are particularly vulnerable to low genetic variability, inbreeding depression or to sudden catastrophic events (Gilpin & Soulé 1986; Allendorf & Ryman 2002). K-selected species, such as many large mammals, have high survival rates and low reproductive rates and thus have a higher risk of extinction because of their slow population growth rate and limited potential for recovery (Pianka 1970; Boyce 1984; McKinney 1997).

Population viability analysis has been subjected to some criticism and debate (Harwood 2000; Coulson et al. 2001; McCarthy et al. 2001; Beissinger 2002; Ellner et al. 2002; Reed et al. 2002; Taylor et al. 2002; McCarthy et al. 2003) due to uncertainty in the estimates of population parameters used for future viability predictions and due to the uncertainty of predicting extinction as an event. A retrospective analysis by Brook et al. (2000) showed previous PVA predictions to have been quite accurate, although this analysis was also not without criticism (Coulson et al. 2001). A key part of a reliable population viability analysis is good quality input data for the demographic rates used to predict future viability (Coulson et al. 2001; Ralls et al. 2002). The analysis also needs to reflect the life history of the target species and is usually best suited for long-living species such as mammals with late age of maturity and low fecundity rates (Miller & Lacy 2005). In addition, the timeline used for predictions needs to be meaningful and not too long (Coulson et al. 2001; Ralls et al. 2002). Finally, one needs to be realistic and careful when drawing conclusions from the predictions (Beissinger 2002; Ralls et al. 2002).

Population viability analysis has been used for many species, including marine mammals e.g. manatee (Castelblanco-Martínez et al. 2012), Hector's dolphin (Martien et al. 1999; Burkhart & Slooten 2003), bottlenose dolphin (Thompson et al. 2000; Gaspar 2003; Fortuna 2006; Currey et al. 2009) and also on northeast Pacific resident killer whales (Taylor & Plater 2001). With marine mammals the population growth has been found to be more sensitive to changes in adult survival than reproductive rates.

The northern Norwegian killer whale (*Orcinus orca*) population, associated with the migratory Norwegian spring-spawning herring stock (hereafter referred to as NSS herring) (Christensen 1988; Similä et al. 1996), is currently considered neither to be under immediate threat nor to be at risk of extinction. In the past, the population was subjected to whaling during the period 1930s -1980s with a total of 662 individuals taken (Christensen 1988; Øien 1988). The magnitude of the previous catches probably affected the demographic rates of this population, although the analyses presented in Chapters 2 and 3 were not able to tease out any specific influence of the effects of the catches.

Previous work on this killer whale population has resulted in a population size estimate of ~700 individuals and did not indicate any population decline (see Chapter 2, Kuningas et al. 2013a). In the current IUCN Red List, the killer whale as a species globally is listed as "Data Deficient" (Taylor et al. 2012). The motivation of the study presented here was to explore the future viability of this northern Norwegian killer whale population with the newly obtained population parameters (see Chapters 2 & 3), and to consider the factors that might potentially lead to a population decline.

This population of killer whales is known to have accumulated a high level of contaminants (Wolkers et al. 2007), which carries a risk of reduced viability and reproductive rates through toxicological effects (Reijnders 1986; De Guise et al. 1995; Cullon et al. 2009). Another current threat to this population is potential entanglement in fishing gear (see sections 2.4.3 & 3.4.2 in Chapters 2 & 3, respectively). Individuals of this killer whale population are known to feed around the purse-seiners targeting the large NSS herring stock and occasionally to become entangled in the fishing gear. This kind of feeding behaviour around the fishing vessels was reported to have increased since the late 1990s when the NSS herring fishing fleet rapidly increased in size (see Chapter 2; Similä 2005; Pilling et al. 2009). Additional human-induced pressure comes from increasing oil exploration and shipping in the Norwegian Sea. Yearly military active sonar exercises by the Norwegian Navy or multinational navies, conducted within the range of this killer whale population, have also raised concern, because the powerful sound transmitted to the ocean environment could displace killer

whales from their preferred habitat (see Chapter 5; WWF-Norway 2001; Miller et al. 2012; Kuningas et al. 2013b).

The main prey of this killer whale population is the NSS herring (Jonsgård & Lyshoel 1970; Christensen 1988; Similä et al. 1996). This highly dynamic NSS herring stock has gone through major changes both in its annual biomass and migration route over the last seven decades (Dragesund et al. 1997; Toresen & Østvedt 2000; Huse et al. 2010). The most recent major collapse in the NSS herring stock took place in the late 1960s after a period of heavy fisheries exploitation (Dragesund et al. 1997; Toresen & Østvedt 2000). After a period of fisheries closure, from the late 1980s onwards, the NSS herring stock started to grow rapidly and had increased to an historically high spawning stock biomass of 8.5 million tonnes by 2009 (ICES 2013). A new crash in the biomass of the NSS herring stock has been predicted to take place soon, due to a rapid decline in their plankton food under pressure of predation from very large fish stocks (pers. comm. Jens Christian Holst).

In the population viability analysis presented in this Chapter, estimates of population size, survival and reproductive rates obtained from Chapters 2 and 3, together with other parameters derived from studies of the northeast Pacific resident killer whale populations, were used to assess the future viability of this northern Norwegian killer whale population. A commonly used tool for conducting PVA is the program Vortex (Lacy 1993; Lacy 2000), which is most applicable to species with low fecundity rates and long life-spans; this software was selected for analysis here. Projections of future population size and estimates of extinction risk were evaluated under various scenarios, which investigated the effect of reduced reproductive rates and increased mortality rates. Investigation of the effect of previous catches from this population was attempted in a retrospective way. The effect of a potential future decline in the NSS herring biomass was investigated through two different scenarios.

## **4.2 MATERIALS & METHODS**

Program Vortex (version 9.99c) (Lacy 1993; 2000; Miller & Lacy 2005), an individual-based simulation model that uses user-specified population parameters, was chosen to conduct population viability analysis. In Vortex, mortality rates, reproductive rates and sex ratio are modelled as binomial distributions and environmental variability is modelled as a normal distribution (Miller & Lacy 2005). Where possible, the population parameters used in analysis were taken from work done on the northern Norwegian killer whale population (see Chapters

2 and 3). Other parameters were derived from the two most-studied killer whale populations, the northern and southern resident killer whales of the northeast Pacific (Olesiuk et al. 1990; 2005).

#### 4.2.1 Model parameters

Parameters relating to the reproductive system, mate monopolization and initial population size were the same for all modelled scenarios (Table 4.1). Reproduction was specified as being polygynous (Dahlheim & Heyning 1999). The mean age of first reproduction (age at which the first viable calf was born for females) was set to 15 years for both females and males (Olesiuk et al. 1990; 2005). Reproductive senescence was specified to occur at 40 years of age, giving an overall reproductive period of 25 years (Olesiuk et al. 1990; 2005; Taylor et al. 2007).

Table 4.1 - Parameters used as input to program Vortex for the “Baseline” scenario. EV – environmental variability. Derived parameters from the resident killer whale populations from the NE Pacific are indicated with superscripts: 1) Dahlheim & Heyning 1999, 2) Olesiuk et al. 1990, 3) Olesiuk et al. 2005 and 4) Taylor & Plater 2001.

Parameter	Values reported	Value used	Source
Reproductive system	Polygynous	Polygynous	1
Age of first reproduction (yr)			
Males	15 <sup>2</sup> , 13-15 <sup>3</sup> , 16 <sup>4</sup>	15	2, 3, 4
Females	12-16 <sup>2</sup> , 14.1 - 15.4 <sup>3</sup> , 16 <sup>4</sup>	15	2, 3, 4
Age of senescence (yr)	38-46 <sup>2,3</sup>	40	2, 3
Sex ratio at birth (%)	50 <sup>3</sup> , 57 <sup>4</sup>	50	3, 4
Males in breeding pool (%)	~50 <sup>3</sup> , 42 <sup>4</sup>	50	3, 4
Maximum no. of broods/year	1	1	2
Maximum no. of progeny/brood	1	1	2
% adult females breeding	20	20	Chapter 2
EV in breeding (%)	n.a.	7	Chapter 4
Mortality rates (%)			
Calves (0-1yr)	3 - 9 <sup>2,3</sup>	9	2, 3
Calves (1-3yr)	2 - 3 <sup>2,3</sup>	2	2, 3
Juveniles (3-6yr)	2 - 7 <sup>2,3</sup>	7	2, 3
Sub-adults (6-10yr)	1 - 2 <sup>2,3</sup>	1	2, 3
Sub-adults (10-15yr)	1 - 2 <sup>2,3</sup>	2	2, 3
Adult females	1 - 4 <sup>2,3</sup>	2	Chapter 3
Adult males	1 - 5 <sup>2,3</sup>	3	Chapter 3
Initial population size	731	731	Chapter 2

Sex ratio at birth and the percentage of adult males in the breeding pool were both set to 50% (Olesiuk et al. 2005). The initial population size estimate of 731 individuals was taken from the mark-recapture analysis conducted in Chapter 2 (see also Kuningas et al. 2013a), and the age distribution was set to be stable.

Density dependence in the reproductive rates was ignored in the analysis because no evidence has been found for this in killer whale populations, likely because populations are well below their potential carrying capacities (Olesiuk et al. 1990; Ward et al. 2009). Inbreeding is not considered to be an issue with this population and was therefore ignored here. Environmental variability (EV) was set to be concordant between reproduction and survival under the assumption that good years of reproduction are also good years for survival (Ford et al. 2010). The reproductive and mortality rates used in the baseline model are given in Table 4.1. The percentage of adult females breeding was set to be 20%, based on the mean calving interval of ~5 years (Chapter 2; Kuningas et al. 2013a). The standard deviation due to EV in adult females breeding was calculated as:

$$\sigma_{EV} = \sqrt{\sigma_{EV}^2} = \sqrt{\sigma_{TOT}^2 - \overline{\sigma_{DS}^2}}$$

where  $\sigma_{TOT}^2$  is the total variance across the data and  $\overline{\sigma_{DS}^2}$  is the mean sampling binomial variance across individual rates (Miller & Lacy 2005). The EV in breeding was calculated to be 7%. Reproductive rate was assumed to be normally distributed.

Estimated sex-specific mortality rates for adult females and adult males were taken from the analysis in Chapter 3 incorporating temporary emigration in the estimates (Table 4.1). The sub-adult mortality rate estimated in Chapter 2 was very high and was considered unreliable and therefore ignored here. For more reliable values, the estimates of sub-adult mortality rates were derived from Olesiuk et al. (1990; 2005) for NE Pacific resident killer whales. Similarly, due to lack of data on calf and juvenile mortality from the Norwegian population, these values were also obtained from Olesiuk et al. (1990; 2005). Values of EV were not included for the mortality rates due to lack of data and/or information.

#### 4.2.2 Modelling and scenarios

The number of iterations used in all simulations was 1000. The population size projection and probability of extinction were evaluated over the period of 50 and 100 years. Extinction was defined as occurring when individuals of only one sex survived. Carrying capacity was set to

1000 individuals, except in the scenario “Herring – prey depletion” (Table 4.2), which took into account the potential NSS herring decline through a reduced carrying capacity.

Five scenarios were initially run in program Vortex (Table 4.2), including the “Baseline” scenario, which was set up with the most likely estimated population parameters (Tables 4.1 and 4.2). In the “Worst case” scenario, the highest estimated mortality rates and the lowest estimated fecundity rates were used. In the “Harvest” scenario, the baseline parameters of reproductive and mortality rates were used but a removal of one individual per year taken due to bycatch entanglement with fishing gear was also included (see Discussions in Chapters 2 and 3). This was done by setting the removal to be one female and one male harvested with an interval of every second year (Table 4.2).

Table 4.2 - Specifications and parameter values used in the five initial scenarios modelled in program Vortex. Variations from the Baseline scenario are given in bold.

Scenario Name		Baseline	Worst case	Harvest	Herring - prey depletion	Herring - Catastrophe
Mortality Rates	Calves 0-1	9	<b>9</b>	9	9	9
	Calves 1-3	2	<b>3</b>	2	2	2
	Juveniles 3-6	7	<b>7</b>	7	7	7
	Sub-adults 6-10	1	<b>2</b>	1	1	1
	Sub-adults 10-15	2	<b>2</b>	2	2	2
	Females	2	<b>4</b>	2	2	2
	Males	3	<b>5</b>	3	3	3
Catastrophes	NSS herring decline/crash	no	no	no	no	<b>yes</b>
	Frequency %	no	no	no	no	<b>2</b>
	Severity - Reproduction %	no	no	no	no	<b>-50</b>
	Severity - Mortality	no	no	no	no	<b>double</b>
% Adult females breeding		20	<b>7</b>	20	20	20
Carrying capacity		1000	1000	1000	<b>500</b>	1000
Harvest	First year of harvest	no	no	<b>1</b>	no	no
	Last year of harvest	no	no	<b>100</b>	no	no
	Interval (years) between harvests	no	no	<b>2</b>	no	no
	Number of individuals harvested	no	no	<b>2</b>	no	no

The potential future NSS herring stock crash was attempted to be taken into account in the future viability predictions of this killer whale population by modelling potential prey decline in two ways. Firstly, in the “Herring crash – prey depletion” scenario, the carrying capacity was adjusted to 500, simulating that a smaller population could be maintained due to

the depleted prey resource (Table 4.2). Secondly, the NSS herring decline was modelled as a likelihood of a catastrophe occurring with a 2% chance per year within the 100 year time period in the scenario “Herring crash - Catastrophe”. The severity of the catastrophe was set to be with an impact of 50% decline in reproductive rate and with a doubling of mortality rate.

#### **4.2.3 Sensitivity to reproductive rate and harvest**

In addition to the above scenarios, the effect of a declining reproductive rate, which could result from a heavy contaminant load on this population (Wolkers et al. 2007), was investigated in a stepwise manner. This was done by evaluating future viability with scenarios that set the percentage of adult females breeding to 16, 13, 10 and 7%. The lowest percent of adult females breeding (7%) corresponds to the longest calving interval reported, 14 years, for this killer whale population (see Chapter 2).

The effect of the magnitude of the annual “harvest” was evaluated by increasing the number of individuals removed per year, and these results were compared to the “Baseline” scenario. These scenarios run were with 4, 8, 10 and 15 killer whale individuals taken per year. The 15 individuals taken per year correspond to the mean number of killer whales taken per year during the period of catches in 1930s-1980s (Christensen 1988; Øien 1988).

### **4.3 RESULTS**

#### **4.3.1 Initial scenarios**

The “Baseline” scenario estimated a population growing at a mean rate of 0.8% per year and zero probability of extinction after 50 and 100 years (Table 4.3, Figure 4.1). The generation time for adult females and adult males was calculated to be 26.1 years and 25.6 years, respectively.

The “Worst case” scenario, with the lowest reproductive and highest mortality rates, predicted a population decline estimated as -4.4% per year (Table 4.3, Figure 4.1). The probability of extinction was estimated as 8.6% in 100 years time, with a mean time to first extinction of 94 years (Figure 4.2).

Table 4.3 - Results of the population viability analysis for the five initial scenarios, with deterministic growth rate (det-r) and stochastic growth rate (stoc-r) together with standard error (SE) and annual rate of change ( $\lambda$ ). Extinction probability (% ext-risk) and the total population size (N) were assessed after 50 years and 100 years.

Scenario	det-r	stoc-r (SE)	$\lambda$	% ext-risk 50 yr	N 50 yr (SE)	% ext-risk 100 yr	N 100 yr (SE)
Baseline	0.008	0.008 (0.019)	1.008	0	981 (32)	0	988 (18)
Worst case	-0.042	-0.044 (0.057)	0.959	0	89 (25)	8.6	11 (7)
Harvest	0.008	0.007 (0.019)	1.008	0	969 (47)	0	988 (20)
Herring – prey depl.	0.008	0.008 (0.021)	1.008	0	492 (12)	0	493 (11)
Herring – Catastrop.	-0.002	-0.006 (0.105)	0.998	0	610 (308)	0.3	458 (307)

The “Harvest” scenario, assuming removal of one individual per year due to fisheries interactions, predicted mean population growth to be 0.7% per year (Table 4.3, Figure 4.1). The probability of extinction was estimated to be zero after both 50 and 100 years. Overall, the “Harvest” scenario gave a very similar prediction compared to the “Baseline” scenario, indicating that the removal of one individual per year did not alter future viability of the population (Figure 4.1).

The scenario, “Herring crash – prey depletion”, evaluating the impact of a future NSS herring decline by a reduced killer whale carrying capacity predicted a mean population growth of 0.8% per year (Table 4.3, Figure 4.1). The estimated probability of extinction was zero after both 50 and 100 years and mean final population size was predicted to be just below the new carrying capacity, 493 individuals.

The other scenario modelling the future viability of the killer whale population in response to a potential NSS herring decline as a catastrophe, “Herring crash - Catastrophe”, predicted a population decline with an estimated mean rate of -0.6% per year. The probability of extinction was estimated as 0.3% after 100 years (Table 4.3, Figure 4.2). In both the scenarios predicting the effects of NSS herring decline, the change in final population size compared to the “Baseline” scenario was approximately -50%.

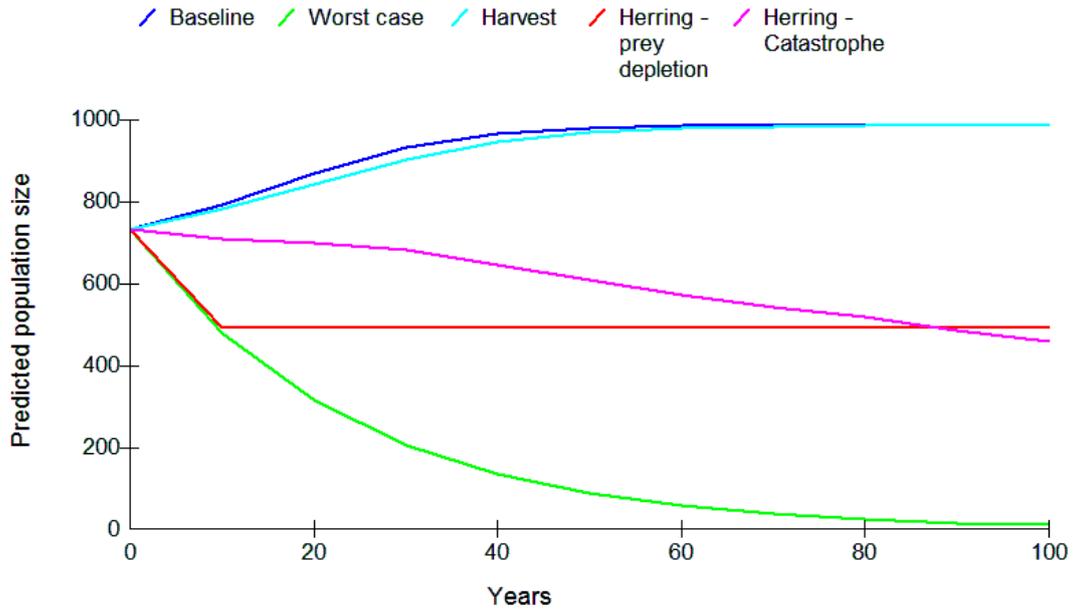


Figure 4.1 - Predicted population sizes for the five initial scenarios, over a 100 year period.

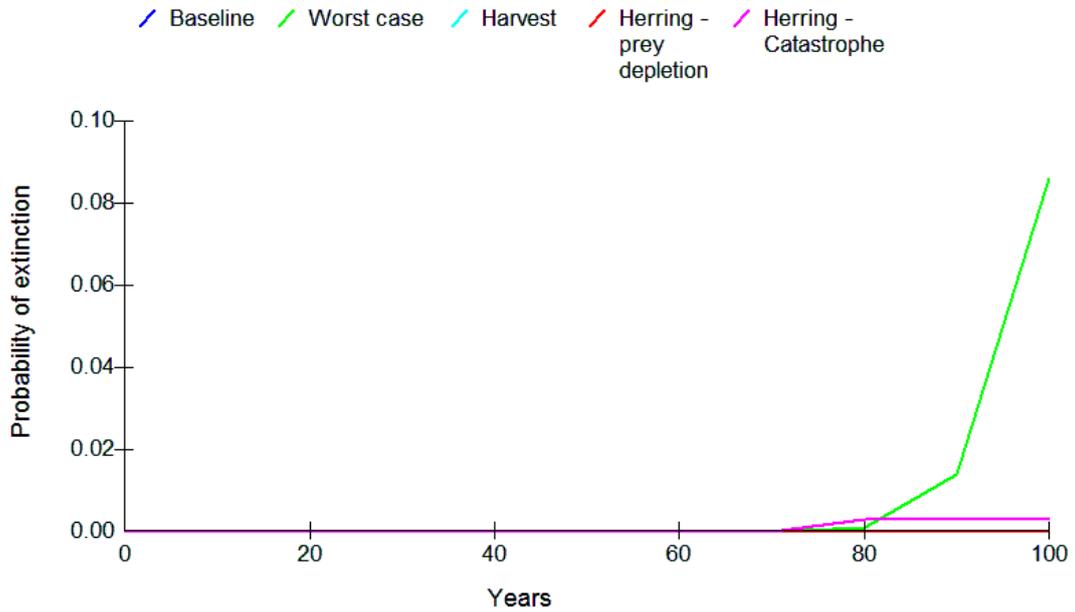


Figure 4.2 - Extinction probabilities predicted for the five initial scenarios, over a 100 year period.

### 4.3.2 Sensitivity to change in reproductive rate and harvest

A change in the percentage of females breeding annually, from 20% to 16%, resulted in the prediction that the population growth came to a halt; the stochastic growth rate was estimated at 0% per year (Table 4.4). The population size was predicted to remain similar to the initial population size of 731 over the whole 100 year period (Figure 4.3); this represented a decrease of 27% in final population size compared to the "Baseline" scenario (Table 4.5).

The scenario with 13% of adult females breeding predicted a decline in population growth of -0.8% per year. The change in the percentage of females breeding annually from 20% to 7% gave a predicted annual growth rate of -3.2%, indicating a clearly declining population (Figure 4.3); this represented a decrease of 96% in final population size compared to the "Baseline" scenario. 7% of adult females breeding would correspond to a calving interval of 14 years. None of these scenarios of reduced percentage of females breeding annually predicted extinction after 50 or 100 years (Table 4.4) but a reproductive rate of lower than 16% was predicted to lead to a declining population size (-66% to -96% change in final population size) and thereby to lowered population viability (Figure 4.3).

The scenario with a harvest of four individuals per year still maintained positive growth in the population, with a mean estimated stochastic growth rate of 0.4% per year (Table 4.4, Figure 4.4). The final population size showed only a 4% decrease compared to the "Baseline" scenario (Table 4.5). A harvest of eight individuals per year led to a declining population, with an estimated growth rate of -0.4% per year, but did not predict extinction after either 50 or 100 years. However, a harvest of eight individuals per year was predicted to lead to a population decline. The final population size was predicted to be 45% lower compared to the "Baseline" scenario prediction (Table 4.5).

With the scenario of a harvest of ten individuals per year, the estimated growth rate was -1.8% per year and within the timeframe of 100 years the predicted extinction risk was estimated to be 1% (Table 4.4, Figure 4.5). Mean time for first extinction was predicted to be 95.3 years.

The scenario with the highest harvest rate, 15 individuals per year, predicted a population decline with a rate of -6.8% per year and a 67% decrease from the initial population size after 50 years. The probability of extinction was very high, 100% after 100 years (Table 4.4, Figure 4.5). The mean time to first extinction was estimated to be 73.4 years.

Table 4.4 - Results with scenarios of declining percent of adult females breeding and increased harvest per year. Results include the deterministic (det-r) and stochastic (stoc-r) growth rate with standard error (SE). Probability of extinction was evaluated as extinction risk in 50 and 100 years time (%). Total population size (N) was assessed after 50 and 100 years.

Scenario / parameter	det-r	stoc-r	SE(r)	% ext-risk 50 yr	N 50 yr (SE)	% ext-risk 100 yr	N 100 yr (SE)
Baseline model	0.008	0.008	0.019	0	981 (32)	0	988 (18)
<b>Reproductive rates</b>							
Adult F breeding 16 %	0.000	0	0.021	0	727 (96)	0	721 (132)
Adult F breeding 13 %	-0.008	-0.008	0.024	0	493 (78)	0	332 (81)
Adult F breeding 10 %	-0.018	-0.018	0.030	0	304 (57)	0	126 (39)
Adult F breeding 7 %	-0.030	-0.032	0.043	0	160 (41)	0	35 (16)
<b>Mortality</b>							
Harvest 4/yr	0.008	0.004	0.019	0	875 (93)	0	949 (73)
Harvest 8/yr	0.008	-0.004	0.020	0	646 (101)	0	543 (195)
Harvest 10/yr	0.008	-0.018	0.044	0	514 (95)	1	215 (167)
Harvest 15/yr	0.008	-0.068	0.123	0	240 (87)	100	0.04 (0.8)

Table 4.5 - Percentage change in the input values, predicted extinction risks and final population sizes (N) between "Baseline" scenario and reduced percentage of adult females breeding and number of individuals harvested per year.

Scenario / parameter	% change in input	% ext-risk 100 yr	% change in ext-risk 100 yr	N 100 yr (SE)	% change in N 100 yr
Baseline model	n.a.	0	n.a.	988 (18)	n.a.
<b>Reproductive rates</b>					
Adult F breeding 16 %	-20	0	0	721 (132)	-27
Adult F breeding 13 %	-35	0	0	332 (81)	-66
Adult F breeding 10 %	-50	0	0	126 (39)	-87
Adult F breeding 7 %	-65	0	0	35 (16)	-96
<b>Mortality</b>					
Harvest 4/yr	300	0	0	949 (73)	-4
Harvest 8/yr	700	0	0	543 (195)	-45
Harvest 10/yr	900	1	1	215 (167)	-78
Harvest 15/yr	1400	100	100	0.04 (0.8)	-100

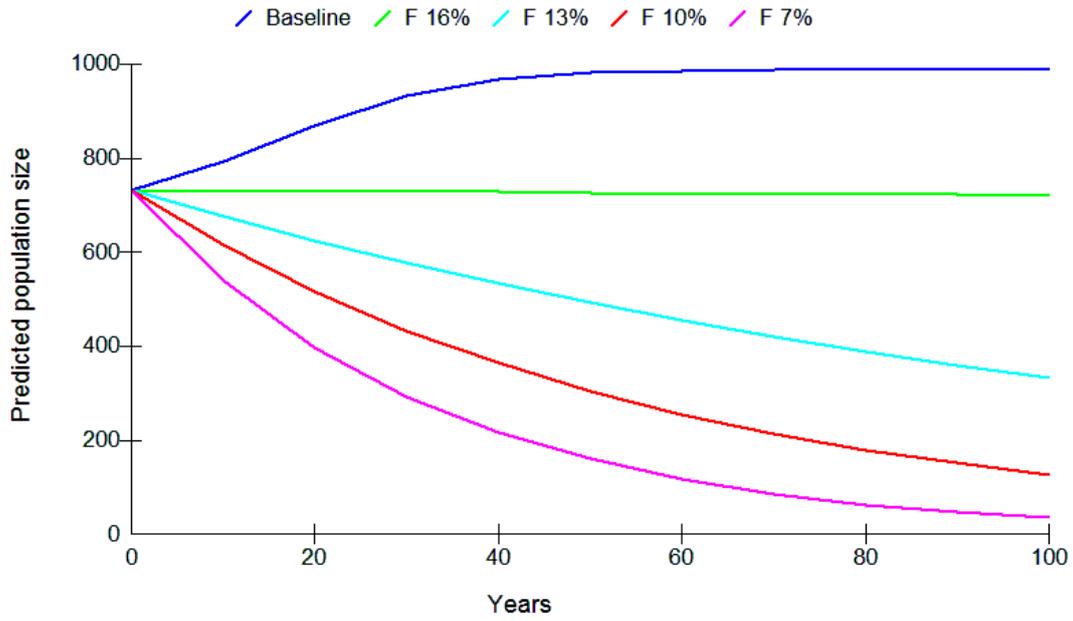


Figure 4.3 - Predicted population sizes given by the Baseline scenario and scenarios comparing the effect of reducing the percentage of adult females breeding annually from 20% (Baseline) to 16, 13, 10 and 7%, over a period of 100 years.

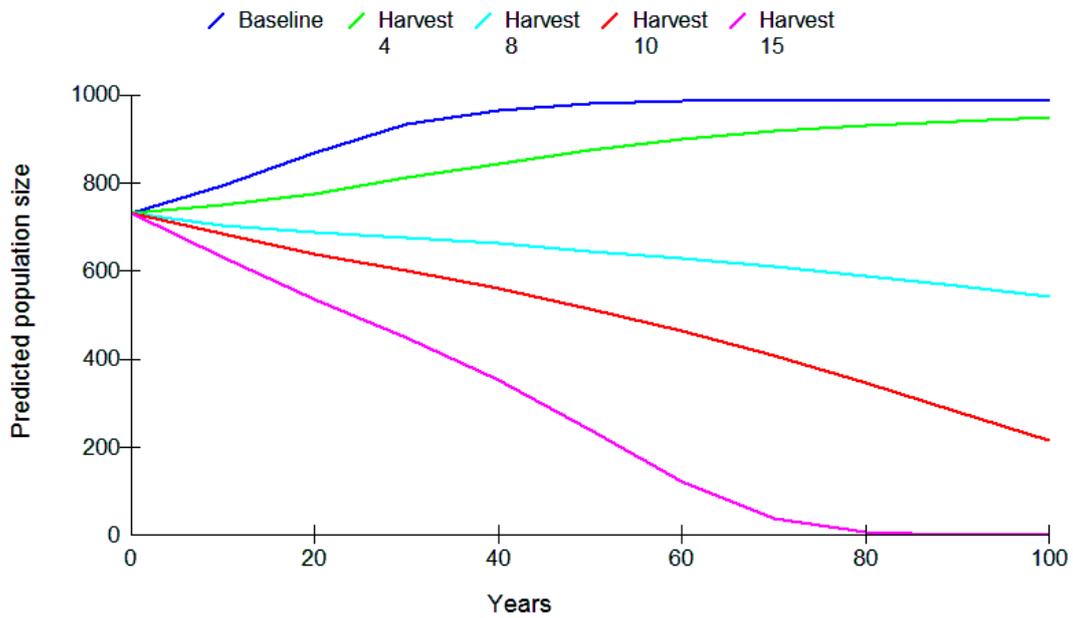


Figure 4.4 - Predicted population sizes given by the Baseline scenario and scenarios comparing the effect of increased number of individuals harvested from the population with scenarios of 4, 8, 10 and 15 individuals harvested per year.

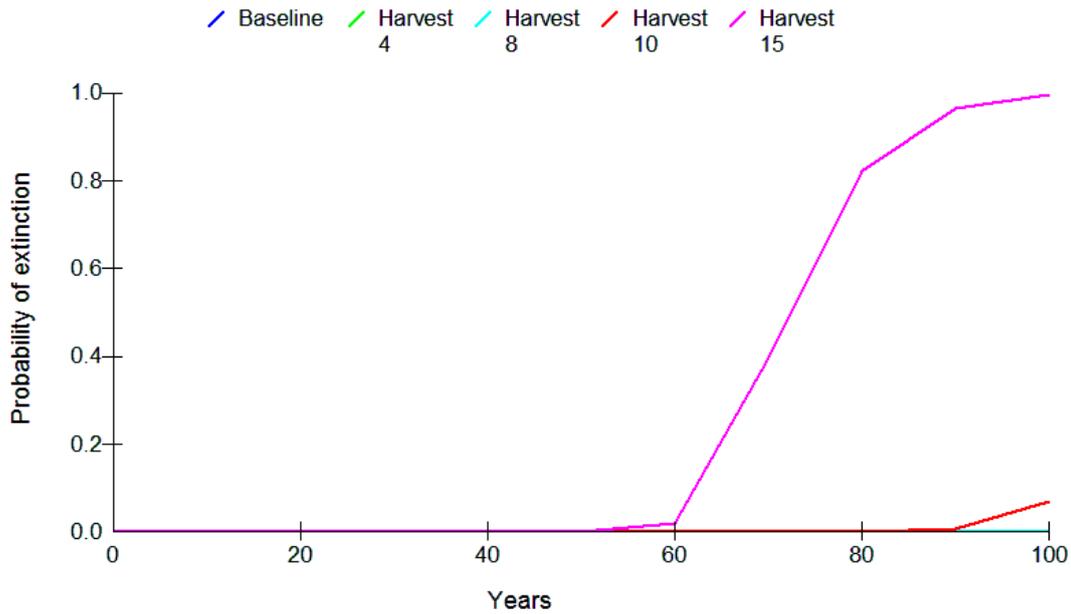


Figure 4.5 - Probability of extinction predicted, by the population viability analysis, for the different scenarios of increased number of individuals harvested (4, 8, 10 and 15 per year) over a 100 year timeline.

#### 4.4 DISCUSSION

The “Baseline” scenario predicted a viable killer whale population both in 50 and 100 years time, with a mean growth rate of 0.8% per year. For comparison, the predicted population growth rate for northern resident killer whales in the NE Pacific was 0.5% in the period of 1996-2004 (Olesiuk et al. 2005). These results indicate that with the newly acquired estimates of population parameters for this killer whale population, with the associated assumptions met (see Chapters 2 & 3), the northern Norwegian killer whale population can be considered to be viable under the “Baseline” scenario. It is also shown that this population may be increasing in size.

##### 4.4.1 Fisheries interactions and previous catches

The harvest of one individual per year, the likely current situation in relation to fisheries interactions, did not change the overall positive future prediction. The simulation with four individuals removed per year slowed down the growth rate by 50% compared to the “Baseline” scenario but still resulted in a growing population. Removal of eight or more individuals per year turned the growth rate negative and the removal of 15 individuals per year lead to a serious risk of extinction around after 50-60 years of harvest.

This northern Norwegian killer whale population was previously hunted through 1938 – 1981, with catches taken in the waters around the Lofoten Islands (Christensen 1982; Øien 1988). Catching killer whales in Norwegian waters ceased in 1982 (Christensen 1988). A total of 662 individuals were taken over the 44 years of whaling from the area under study here (Øien 1988), resulting in approximately 15 individuals taken per year. Results of the population viability analysis presented here indicate that a removal of 15 individuals per year from this killer whale population would lead to a serious risk of extinction. The size of the northern Norwegian killer whale population when the killer whale harvest began in the 1930s is unknown. However, the size of the NSS herring stock in 1930s was of a similar magnitude as in early 2000s (Toresen & Østvedt 2000), and therefore it can be assumed that the population size of killer whales was within the similar range as estimated in Chapter 2 for 2003 and set as the initial population size of 731 individuals in the analysis here. This is a reasonable assumption given that killer whales are top predators and their prey abundance is likely to be the main factor affecting their demographic rates (Ward et al. 2009; Ford et al. 2010).

Treating the analysis presented here as a type of a retrospective analysis of the impact of previous whaling may provide some insight into what happened to this northern Norwegian killer whale population in terms of its population size due to previous catches. The analysis with a harvest of 15 individuals per year shows a predicted population size of 352 individuals after 40 years from the start of the harvest and 240 individuals remaining 50 years after the start of the harvest. Accordingly, the population size could have been approximately 300 individuals by the time the whaling came to an end in 1982 after 44 years of whaling.

The results of Olesiuk et al. (1990) indicated the level of total sustainable population harvest of the resident killer whales of the NE Pacific to have been 3.17% during the live-capture fisheries in the 1970s and 1980s. The simulated harvest of 15 individuals per year from an initial population size of 731 represented an initial harvest proportion of 2.01% and would lead to rapid population decline and ultimately to the extinction of the northern Norwegian killer whale population. The catches made in northern Norway were at a much larger scale, catches taken over 44 years compared to 16 years in the NE Pacific (Christensen 1988; Øien 1988; Olesiuk et al. 1990). Additionally, the mean number of individuals taken per year from the NE Pacific resident populations was 4.25, whereas in northern Norway the mean annual catch was 15 individuals.

The existence of nomadic, solitary males without a connection to any specific family pod has been reported for this northern Norwegian killer whale population (Bisther & Vongraven 1995). It has been speculated that these nomadic males represent individuals that,

after the extensive years of catches, got separated from their maternal family pods, after their mothers were killed during whaling operations. The simulation of the removal of 15 individuals per year from this killer whale population and the result indicating a rapid decline in population size visualizes how it is very likely that many individuals did indeed get separated from family units due to whaling. A study by Williams & Lusseau (2006) simulated the previous live-capture catches of resident killer whales of the NE Pacific and showed that these kinds of targeted removals are likely to break the important social networks into isolated groups.

It is not known if this northern Norwegian killer whale population has fully recovered from previous whaling and reached its potential carrying capacity. The carrying capacity level used in the analysis here is speculative and represents the upper limit of the estimated population size (see Chapter 2). However, the best estimates of current reproductive and mortality rates predict that this population is currently increasing.

#### **4.4.2 Other human impacts on this killer whale population**

Other factors affecting this population's viability in the area could lead to losses of individuals. The area around Lofoten Island is under increased interest for oil exploration and expanding coastal development plans, both of which would lead to additional negative impacts on this killer whale population due to increased shipping, and seismic air gun and construction noise (Southall et al. 2007). Certainly military sonar exercises have previously been blamed to have displaced killer whales from their preferred location due to the use of active high intensity underwater sonar by the navy (see Chapter 5; WWF-Norway 2001; Miller et al. 2012; Kuningas et al. 2013b). Displacement due to disturbance from a habitat that represents an important feeding, breeding or socializing environment, can lead to lowered viability of a population (Williams et al. 2006; Lusseau et al. 2009). The planned developments in the Lofoten area would also increase the risk of serious oil spills in the area. The "Exxon Valdez" oil spill in Alaska in 1989 resulted in two groups of killer whales suffering losses of individuals and in a situation where neither group has recovered to pre-oil spill levels (Matkin et al. 2008). Another potential threat that could lead to increased mortality rates could be an outbreak of a disease (Gaydos et al. 2004), although so far no such event has been reported for this killer whale population.

This killer whale population has been shown to carry a very high load of contaminants making them the Arctic mammal species with the highest recorded contamination levels (Wolkers et al. 2007). This high contaminant load has the potential to have a negative effect on health and reproductive rates (Reijnders 1986; De Guise et al. 1995; Ross et al. 2000; Hickie et

al. 2007; Cullon et al. 2009). The estimated survival rates in Chapters 2 and 3 showed that at least for now this population seems to be able to cope with this pressure, given that the survival rates of adult males are the highest estimated anywhere (Olesiuk et al. 1990; 2005; Poncelet et al. 2010; Kuningas et al. 2013a). The potential of the contaminant load affecting fecundity rate was simulated here by stepwise reduction of the percentage of adult females breeding annually. Results showed that a reduction of 20% in the reproductive rate, equivalent to a calving interval of 6.25 years, was sufficient to reduce population growth to zero. A reduction of 35% (calving interval of seven years) or more in reproductive rate led to a population decline.

#### **4.4.3 Future decline in the NSS herring stock**

The highly dynamic NSS herring stock has gone through major changes in its biomass over the last seven decades (Dragesund et al. 1997; Toresen & Østvedt 2000; Huse et al. 2010) and is predicted to experience a new collapse within the next few years (pers. comm. Jens Christian Holst). Such a major decline in prey abundance could have a strong impact on killer whale population viability. Ford et al. (2010) found survival rates of the NE Pacific resident killer whales to be highly correlated with the abundance of their main prey, the Chinook salmon (*Oncorhynchus tshawytscha*). Results of that study showed that a decline in Chinook salmon abundance led to an increased mortality of killer whales with a lag of one year. Ward et al. (2009) also showed that reproductive success of killer whales was correlated with the abundance of Chinook salmon, with a 50% difference in the probability of a female calving between the low and high salmon abundance years.

An attempt was made to model the potential future NSS herring stock decline in two ways. First the carrying capacity was set to 500 individuals, half of the “Baseline” scenario, as was done in the population viability analysis conducted with resident killer whales of the NE Pacific in relation to a decline in prey abundance (Taylor & Plater 2001). Secondly, the future NSS herring crash was modelled as a catastrophe that could be expected to occur twice within the timeframe of 100 years. This is a reasonable assumption given what is known of the historical NSS herring stock dynamics and the NSS herring stock going through the previous major collapse in the late 1960s (Dragesund et al. 1997; Toresen & Østvedt 2000). Results show that neither one of the NSS herring crash scenarios predicted extinction within the 100 years timeframe, but did indicate a 50% decline in final population size with both scenarios predicting it to be below 500 individuals. On the “Herring crash - prey depletion” scenario

however, as the carrying capacity was set to 500, population size could not increase above it since the initial decline.

Given the highly dynamic nature of the NSS herring stock, it is likely that this northern Norwegian killer whale population has adapted to the changes taking place with its main prey, at least in terms of its distribution (see Chapter 6; Similä et al. 1996; Stenersen & Similä 2004). The satellite tagging study in 2000 and 2001 showed that killer whales followed the migration of the NSS herring through winter and spring (Similä et al. 2002; Stenersen & Similä 2004). This was expected given the previous knowledge of the relationship between NSS herring and killer whales (Christensen 1982; Similä et al. 1996). The satellite tagging study also showed that during winter killer whales additionally moved away from the abundant NSS herring stock inside the fjord system, to the other parts of herring range, potentially to keep track of the distribution of NSS herring and by doing so to be aware of the first signs of any change taking place (Similä et al. 2002; Stenersen & Similä 2004). The analysis presented in Chapter 3 showed that killer whales did temporarily emigrate from the fjord system during winter and also indicated that adult males and adult females might have different strategies regarding this ranging behaviour. These studies show that this population of killer whales may have mechanisms in place to be able to predict changes in the distribution of their main prey (Similä et al. 2002; Stenersen & Similä 2004; Chapters 3 & 6).

However, there is no previous information on how this killer whale population would cope with a strong decline in their herring prey. Studies started in the mid-1980s and the NSS herring stock has been growing ever since then (Lyrholm 1988; Toresen & Østvedt 2000). Nor is it known if these killer whales could rely on other food sources during a time of low abundance of NSS herring. Killer whales can be highly specialized predators but also show a remarkable variation in foraging techniques and diet around the world (Guinet 1991; Similä et al. 1996; Ford et al. 1998; Pitman & Ensor 2003; Matkin et al. 2007). This kind of specialization enables killer whales to occupy a range of habitats and have made it one of the most widespread species, occupying all major oceans (Matkin & Leatherwood 1986; Forney & Wade 2007). This high level of food specialization might cause inflexibility on changing prey species (Ford et al. 2010). Another potential prey for killer whales in the northern Norwegian Sea might be mackerel (*Scomber scombrus*) (Luque et al. 2006) but this stock may also experience a similar decline as the NSS herring in the near future due to collapsing plankton resources in the Norwegian Sea (pers. comm. Jens Christian Holst).

#### **4.4.4 Criticism and recommendations for future work**

The use of population viability analysis is controversial and has been widely criticised (Coulson et al. 2001; McCarthy et al. 2001; Beissinger 2002; Ellner et al. 2002; Reed et al. 2002; Taylor et al. 2002; McCarthy et al. 2003). However, it provides a useful tool to predict population viability of a species, given good quality input data. In particular, sensitivity analysis using different scenarios offers the possibility to investigate the parameters most strongly affecting model outcomes. Sensitivity analysis allows evaluation of the relative difference in the future prediction results between baseline and other future scenarios, and therefore can provide guidance in drawing the appropriate final conclusions for management and conservation plans.

There were some data limitations with the analysis presented here. Some of the parameters needed are not known for this northern Norwegian killer whale population and needed to be inferred from studies of NE Pacific resident killer whale populations, and this therefore leads to uncertainty because the parameters drawn from other populations might not be representative of this population. There is also uncertainty around the reproductive values used in this analysis because of limited data to calculate reproductive rates (see Discussion in Chapter 2). However, effort was made to take this into account by investigating different scenarios of lowered fecundity rates. Also the parameters used from Chapters 2 and 3 are derived from data 1986-2003 and do not necessarily represent the current situation in 2013. Environmental variation was not possible to be taken into account in most of the parameters. This information was lacking especially for the mortality rate estimates and this could introduce potential bias and underestimate variability in the future viability predictions due to ignoring the annual variation in demographic rates resulting from environmental variation.

Program Vortex also has some limitations. Cetaceans have unique breeding with varying inter-birth intervals, long gestation and lactation periods, and program Vortex might not be the best tool to incorporate all this detail. There was also an inability to model the NSS herring decline in a dynamic way. It would be expected that after some time the NSS herring stock would start increasing again, as it did after the previous stock collapse, and thereby the carrying capacity of the killer whale population would also rise but this could not be modelled in Vortex. One potential way around this could be a development of a specific purpose written software to model this particular population, but was beyond the scope of this study. Overall, the results presented here should be considered as plausible outcomes but subject to potential bias.

Continuation of the long-term photo-identification study of this population of killer whales is strongly recommended to be able to continue monitoring the viability of this population, especially over the next few years if the NSS herring stock does experience a strong decline. It would also be very valuable to estimate the survival rates of this population with more recent data and to fill in the gaps where information from this population is still lacking, especially on calf and juvenile survival rates. Additionally, obtaining more data to calculate reproductive rates is recommended (see Discussion in Chapter 2). The next few years can provide a unique situation to study the population dynamics of an ocean top predator within a highly dynamic environment and provide valuable information on adaptation of a predator to changes in its prey resource.

## CHAPTER 5

### Killer whale presence in relation to naval sonar activity and prey abundance in northern Norway

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#### ABSTRACT

The effect of anthropogenic sound exposure on cetaceans is a global concern but remains poorly understood. In this study, retrospective data on naval sonar activity and prey abundance were correlated with killer whale (*Orcinus orca*) sightings within a fjord basin in northern Norway in 2002-2008. In addition, passive acoustic and visual marine mammal surveys were conducted before, during, and after a specific navy exercise in 2006. The killer whale presence data were modelled using generalised linear models (GLM) with respect to available covariate data to explore the key factors explaining their presence. Herring abundance was the main factor affecting killer whale presence. Naval sonar, either operational navy sonar exercises (Flotex) or experimental sonar activity (CEE) alone, did not explain killer whale occurrence. However, naval sonar activity during a period of low prey availability seemed to have had a negative effect on killer whale presence. It is concluded that the level of reaction to sonar can be influenced by multiple factors, including availability of prey.

## 5.1 INTRODUCTION

Knowledge of the impact of anthropogenic sound (e.g. vessel traffic noise, seismic airguns, pile driving, military sonar) on cetaceans is limited but currently increasing and indicating avoidance reactions that may have negative biological consequences (Richardson et al. 1995; Nowacek et al. 2007; Miller et al. 2012). Reactions vary from change in travel/swim direction and change in swim speed to alterations from one behavioural stage to another (Richardson et al. 1995; McCauley et al. 2000; Nowacek et al. 2004; Lusseau et al. 2009; McCarthy et al. 2011; Tyack et al. 2011; Miller et al. 2012). Disturbance to animals' normal behaviour can have negative impacts on their viability because of increased stress (Romano et al. 2004), disruption of feeding (Nowacek et al. 2004; Lusseau et al. 2009), increased energetic cost of locomotion due to avoidance (Nowacek et al. 2004), interference to communication among individuals (Clark et al. 2009; Miller et al. 2012), habitat loss (Morton & Symonds 2002) and, in extreme circumstances, by stranding (Frantzis 1998; Cox et al. 2006; D'Amico et al. 2009; Filadelfo et al. 2009). Anthropogenic sound exposure can also cause physical trauma, e.g. in the form of temporary threshold shift in hearing (Nowacek et al. 2007; Southall et al. 2007). Military sonar exposure and its effects have received special attention over the last years due to its impact on cetaceans (Parsons et al. 2000; Evans & Miller 2003; Filadelfo et al. 2009; McCarthy et al. 2011; Tyack et al. 2011; Miller et al. 2012). Duration and intensity of a sonar exposure and the behavioural context in which it is presented determines the severity of the reaction (Ellison et al. 2012). Negative impacts not only affect the cetaceans themselves but might have larger ecological consequences in the marine ecosystem. Immediate impacts affecting humans could include disruption to economically important whale-watching operations (Cisneros-Montemayor et al. 2010) if cetaceans become locally unavailable to be seen due to sonar activity.

The killer whale (*Orcinus orca*) population in northern Norway used to concentrate in a confined fjord system comprising Vestfjord, Tysfjord and Ofotfjord, during October to January (Similä et al. 1996) (see Chapter 6), whilst their main prey, the Norwegian spring-spawning herring (*Clupea harengus*) (hereafter called NSS herring) stock wintered in this area during this time (Toresen & Østvedt 2000; Holst et al. 2002; Orellana 2006; Huse et al. 2010). Killer whales are known to follow the large-scale migration of NSS herring (Jonsgård & Lyshoel 1970; Christensen 1988; Similä et al. 1996). The NSS herring stock has experienced considerable fluctuations in stock biomass over the decades. During peak years in the late 1990s the biomass of the NSS herring stock wintering inside the fjord system was approximately 6 million

tonnes (Toresen & Østvedt 2000; Orellana 2006; ICES 2013). Whale-watching focusing on sighting whales during these winter months in the fjords has been an active business since 1992.

Active military sonar sources transmit powerful sound to the marine environment and are used for marine warfare purposes (Richardson et al. 1995; Southall et al. 2007; Ainslie 2010). Low-frequency (LFAS) and mid-frequency active sonar (MFAS) are used by the military, typically with a frequency range of 1-10 kHz and there is evidence to suggest that killer whale hearing is more sensitive in the mid-frequency range (Szymanski et al. 1999; Ainslie 2010). The Flotex Silver operational sonar exercises are a yearly often multi-national fleet exercise, which on many occasions has overlapped with the whale-watching area and season in northern Norway. In 2000 and 2006 there were public complaints and allegations that naval sonar activity had affected the NSS herring and killer whale abundance in this area, resulting in a negative impact on the fishing fleet and on the whale-watching companies (WWF-Norway 2001) due to the use of active high intensity anti-submarine sonar. Several studies later showed that, whereas herring are not severely affected by naval sonar activity (Doksæter et al. 2009; 2012; Sivle et al. 2012), killer whales can respond to sonar activity at relatively low received sonar levels by avoiding the sonar source (Miller et al. 2012).

Another incident similar to the Flotex Silver exercise involved the U.S. Navy vessel *USS SHOUP* which took part in an active sonar exercise in the waters of Washington State, U.S.A. and Haro Strait in Canadian waters (NMFS 2005), also causing public concern. The use of active mid-range sonar altered the natural behaviour of killer whales near San Juan Island. A pod of killer whales was documented to have clustered into a tight formation and to have changed its course several times while the *USS SHOUP* was approaching. The estimated received sound levels for the killer whale pod was between 150 – 180 dB<sub>RMS</sub> re 1µPa (NMFS 2005). These kind of navy exercises have the potential to displace killer whales temporarily from their preferred location and food resources, and thereby have a negative effect on their wellbeing (Richardson et al. 1995; Morton & Symonds 2002; Nowacek et al. 2007).

Controlled sonar exposure experiments (CEE) on killer whales were conducted in northern Norway in 2006 – 2009 (Miller et al. 2011; 2012), with an aim to study dose-response thresholds of killer whale responses to sonar that could be used for mitigation measures. Prolonged avoidance behaviour of killer whales was recorded for the majority of the experiments, showing increased swimming speeds and changes of travel direction away from the path of the approaching sound source (Miller et al. 2012). Reactions to sonar included an event where a group of killer whales abruptly stopped feeding and changed to highly

directional, high speed travel away from the sonar source towards offshore waters for an extended period of time, ultimately leaving the fjord area (Miller et al. 2012). An event where a calf became separated from the rest of the family pod for a period of time was also documented to be a result of sonar exposure. Avoidance response thresholds at root mean square sound pressure levels between 92 – 163 dB re 1  $\mu$ Pa, with a mean received levels of 129 dB prior to the onset of avoidance behaviour were recorded for killer whales (Miller et al. 2012). The dose-response curves arising from the study by Miller et al. (2012; in review) differ significantly from the one used currently by the U.S. Navy (US Navy 2008; 2012). They show behavioural responses to sonar at very low received levels and imply that in a real world naval exercise killer whales could be displaced from large areas (Miller et al. 2012). A key question is to what extent the experimental data can be used to extrapolate to an actual sonar exercise. This chapter explores such a real world scenario.

To investigate the potential temporary displacement of killer whales due to real sonar activity, the killer whale sightings dataset 2002 – 2008 of the whale-watching company “Orca Tysfjord”, was used to retrospectively build up a picture of killer whale presence in the fjords and to analyse presence in relation to known naval sonar activity during this period. Additional information was used from extensive visual and acoustic observations of killer whales during a full-scale navy Flotex exercise conducted in Vestfjord and Ofotfjord in 2006.

## 5.2 MATERIALS & METHODS

### 5.2.1 Whale-watching and navy datasets

For the analysis of whale-watching sightings relative to sonar activity in the fjord system, consistent records from 2002-2008 made by the whale-watching company “Orca Tysfjord” were used to identify days with and without sightings of killer whales. Sighting location was recorded at the scale of a fjord (Tysfjord, Ofotfjord or Vestfjord). “Orca Tysfjord” made intensive efforts to sight whales within the fjord system on most days, if weather permitted. “Orca Tysfjord” operated between October and January each year but, for consistency, the period 25<sup>th</sup> October – 30<sup>th</sup> November was chosen from their daily log for further analysis in each year to correspond with the navy Flotex exercise times. Within this period, a day was categorized as a “*whale day*” if killer whales were sighted, a “*no-whale day*” if no killer whales were sighted or a “*no effort day*” if “Orca Tysfjord” did not look for killer whales, based on

their log. If weather conditions made killer whale sightings difficult a day was also categorized as a “*bad weather day*”, again based on records of the log.

Data on operational sonar exercises in the area were based on naval planning documents (EXOPLANs) and ships’ logbooks, which were made available by the Royal Norwegian Navy and the Naval Museum. The most commonly used sonar system on Norwegian Navy anti-submarine warfare ships operated in the 6 – 8 kHz band at source levels ranging from 215 to 227 dB re 1 $\mu$ Pa m depending on operational mode, but occasionally also other sonar systems would have been in use if foreign naval vessels participated in the exercise. Two to seven days of operational naval sonar activity were confirmed to have occurred each year 2002-2006 in Vestfjord and/or Ofotfjord between late October and November. No naval sonar exercise was carried out during 2007-2008 inside the fjord system. Based on the naval documents, days were scored to be a “*sonar day*” or a “*no-sonar day*”. In 2006, additional confirmation of operational naval sonar activity was received from the visual and acoustic records of a research team monitoring killer whale presence before, during and after the Flotex Silver 2006 (13<sup>th</sup> – 16<sup>th</sup> November) exercise. Observational records of the research team confirm the navy records for that particular year, providing additional confidence in the reliability of the navy documents of earlier years.

### **5.2.2 *In situ* observations of sonar activity in 2006**

To assess how a real sonar exercise might impact killer whale presence, killer whales were extensively searched for both visually and acoustically before, during and after (5<sup>th</sup> – 30<sup>th</sup> November 2006) the 2006 Flotex Silver exercise (13<sup>th</sup> – 16<sup>th</sup> November 2006) (Kvadsheim et al. 2007). Searching was carried out in Vestfjord, Tysfjord and Ofotfjord from FFI R/V *HU Sverdrup II* and R/V *Nøkken*. Daytime visual observers searched for killer whales from both platforms during the 6 - 8 hour daylight period. In addition, information on sightings of killer whales was received from a network of local contacts working at sea. A towed single 54-meter line hydrophone array (*Delphinus*) was used for 24-hour acoustic detection from R/V *HU Sverdrup* (Kvadsheim et al. 2007). The *Delphinus* contained 18 hydrophones with a frequency range of 10 – 40 kHz.

A multi-purpose towed acoustic source called *Socrates I* (developed by Netherlands Organisation for Applied Scientific Research) was used for CEEs on schools of NSS herring and tagged killer whales during November 2006 (Kvadsheim et al. 2007). CEE activity included transmissions of authentic naval sonar signals but usually for shorter durations than during navy exercises. Source levels up to 209 dB re 1 $\mu$ Pa m, and frequencies of 1 – 2 kHz (LFAS) and 6

– 7 kHz (MFAS) were used. This experimental use of sonar (CEE) was also considered naval sonar activity and scored as “*sonar day*” in the analysis.

Sonar activity and whale sightings were recorded at a spatial scale of a fjord (Tysfjord, Ofotfjord or Vestfjord) and a temporal scale of days (24-hours). This means that overlap between sightings and sonar activity is examined at a distance scale of < 10-40 km.

### 5.2.3 Data analysis

The relationship between killer whale presence and naval sonar activity in the fjord system was explored with binomial generalised linear models (GLM) (Nelder & Wedderburn 1972), using R version 2.15.2 (R Development Core Team 2012). A link function describes how the mean response is linked to the covariates through the linear predictor (Faraway 2006). Three different link functions available for binomial GLM (“logit”, “probit” and “complementary log-log”) were explored to investigate the best way to formulate the model itself, determined by the Akaike’s Information Criterion (AIC) (Burnham & Anderson 2002). Covariates included *Herring* (yearly herring biomass inside the fjords<sup>1</sup>), *Year*, *Sonar* (whether or not there was sonar activity during a 24-hour day), *SonarType* (separating naval sonar activity to operational Flotex exercises and experimental CEE activity), *SonarLag* (to investigate a 24-hour time-lag after sonar activity), *Weather* (bad weather conditions recorded based on the “Orca Tysfjord” log) and *JulianDay* (Table 5.1). Collinearity, i.e. some covariates being highly correlated, can cause the model being unstable and standard errors being inflated (Fox 2008). Candidate covariates were thereby assessed for collinearity by using generalized variance inflation factor (GVIF) (*vif* function in R). The acceptable limit was selected to be GVIF < 5. Where significant collinearity was observed, the covariate that was poorer in explaining the observed relationship was removed in favour of the better predicting covariate. *Herring*, *Year* and *JulianDay* were continuous covariates and thereby smoothed terms were fitted for these covariates manually using B-splines (effectively thereby running a manual GAM) (Table 5.1). All other covariates were included as factors. The interaction term *Herring*\**Sonar* was also explored. Serial autocorrelation in the data was not considered to be a concern because the data were collected at a 24-hour scale.

Models were compared with AIC, the lowest AIC indicating the best model (Burnham & Anderson 2002). The relative importance of covariates in the best model was assessed by considering the deviance explained by each covariate. Analysis included data from years 2002-

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<sup>1</sup> Acoustic estimate (Norwegian Institute of Marine Research (IMR)), November-December 2002-2007. Supplied by Jens Christian Holst (IMR)

2007. Year 2008 was excluded because of a lack of NSS herring biomass data from inside the fjords from that year.

Table 5.1 - Candidate covariates used in GLM models, the fitted effects (bs = B-splines, f = factor) and the data range/level used.

<b>Covariate</b>	<b>Effect</b>	<b>Data range/level</b>	<b>Details</b>
<i>Herring</i>	bs	0.02-2.2	Acoustic biomass estimate (IMR)
<i>Year</i>	bs/f	2002-2007	—
<i>Sonar</i>	f	1	Sonar activity within 24-hour day
<i>SonarType</i>	f	3	Separating navy and CEE sonar
<i>SonarLag</i>	f	1	24-hour time-lag after sonar activity
<i>Weather</i>	f	1	Bad weather conditions specified by "Orca Tysfjord"
<i>JulianDay</i>	bs	298-334	—

## 5.3 RESULTS

### 5.3.1 2002-2008

Whale-watching sightings data together with visual and acoustic observations of killer whale presence during the 2006 Flotex exercises indicate that killer whales were regularly sighted from 25<sup>th</sup> October to 30<sup>th</sup> November from 2002 to 2006, including many days with sonar activity (Figure 5.1). The entire study period had a total of 30 days with naval sonar activity. Killer whales were sighted in the same sub-fjord (Vestfjord) as sonar activity on 21 days. On four days of sonar activity, killer whales were seen in a different sub-fjord. In 2004, on one day (1<sup>st</sup> November) operational navy sonar activity was recorded with no killer whales sighted inside fjords (red cell in Figure 5.1). In 2006, there were four days recorded with no whales detected during sonar activity, three of these being consecutive days (16<sup>th</sup> – 18<sup>th</sup> November) following the Flotex Silver exercise carried out in Vestfjord and Ofotfjord (13<sup>th</sup> – 16<sup>th</sup> November).

Based on the "Orca Tysfjord" whale-watching records, during 2002-2005, killer whales were sighted on 97-100% of days of searching and in 2006 on only 59% of days (Figure 5.1 & 5.2). During 2007 and 2008 killer whale sighting rate decreased markedly from previous years to 37% and 30% of days seen, respectively. No operational naval sonar exercise or other sonar experiments were carried out inside the fjord system during 2007 or 2008. In 2008 the operational sonar exercises were moved to offshore waters.

	October							November																															
	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
2002	Green	Green	Black	Green	Green	Green	Black	Green	Yellow	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green							
2003	Green	Green	Black	Black	White	Green	Green	Green	Green	Green	Green	Green	Yellow	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
2004	Green	Green	White	Yellow	Yellow	Green	White	Red	Green	Yellow	Yellow	Yellow	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
2005	Green	Green	Yellow	Yellow	Yellow	Green	Green	Green	White	Yellow	Yellow	Green	Green	Yellow	Yellow	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green
2006	White	White	White	Green	White	Green	Green	White	White	White	White	Red	White	Green	Green	Yellow	Green	Green	Yellow	Yellow	Yellow	Yellow	Red	Red	Red	Green	Green	Green	Yellow	Yellow	Green	Yellow	Green	Green	Green	Yellow	White	White	
2007	Black	Black	Black	Black	Black	Black	Black	White	White	Green	White	White	Green	White	White	Green	Green	White	Green	White	Green	White	White	White	White	White	White	White	Green	Green	White	White	Green	Green	White	White	White	White	White
2008	Black	Black	Black	Black	Black	Black	White	White	White	White	White	Green	Green	Green	White	White	White	White	White	Green	Green	White	Black	Green	White	White	Green	White	White	White	Green	White	Green	White	White	White	White	White	White

	"Sonar day"	"No sonar day"
"No-whale day"	Red	White
"Whale day"	Yellow	Green
"No effort day"	Grey	Black

Figure 5.1 - Whale-watching (Orca Tysfjord) sightings of killer whales during October-November 2002-2008 in relation to all naval sonar activity with a key to colours. Sonar activity includes both operational sonar exercises and experimental CEE activity in 2006.

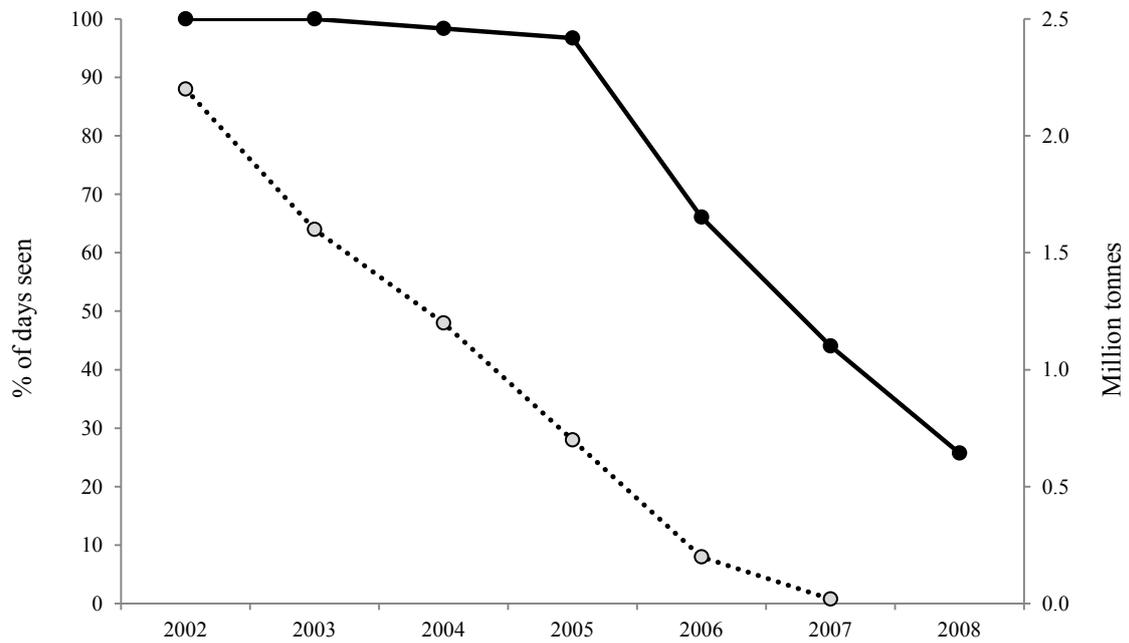


Figure 5.2 - Percentage of days that killer whales were encountered by the whale-watching company (Orca Tysfjord) during October-November 2002-2008 (black circles with black line), and the abundance of NSS herring in millions of tonnes (data courtesy of Norwegian Institute of Marine Research<sup>1</sup>) inside fjords (grey circles with dotted line).

<sup>1</sup>Acoustic estimate (IMR), November-December 2002-2007. Supplied by Jens Christian Holst (IMR)

### 5.3.2 2006 observations

The navy Flotex Silver and CEE sonar activity days are shown in Figure 5.3. The Flotex Silver exercise was conducted 13<sup>th</sup> – 16<sup>th</sup> November 2006 and CEE activity was carried out on a total of 11 days and/or nights during November 2006. On 5<sup>th</sup> November, CEE activity was a result of *Socrates I* equipment testing. One low-frequency active sonar (LFAS) experiment and one mid-frequency active sonar (MFAS) experiment on killer whales were carried out on 13<sup>th</sup> and 23<sup>rd</sup> November, respectively. Other CEE activities were the experiments carried out on the NSS herring.

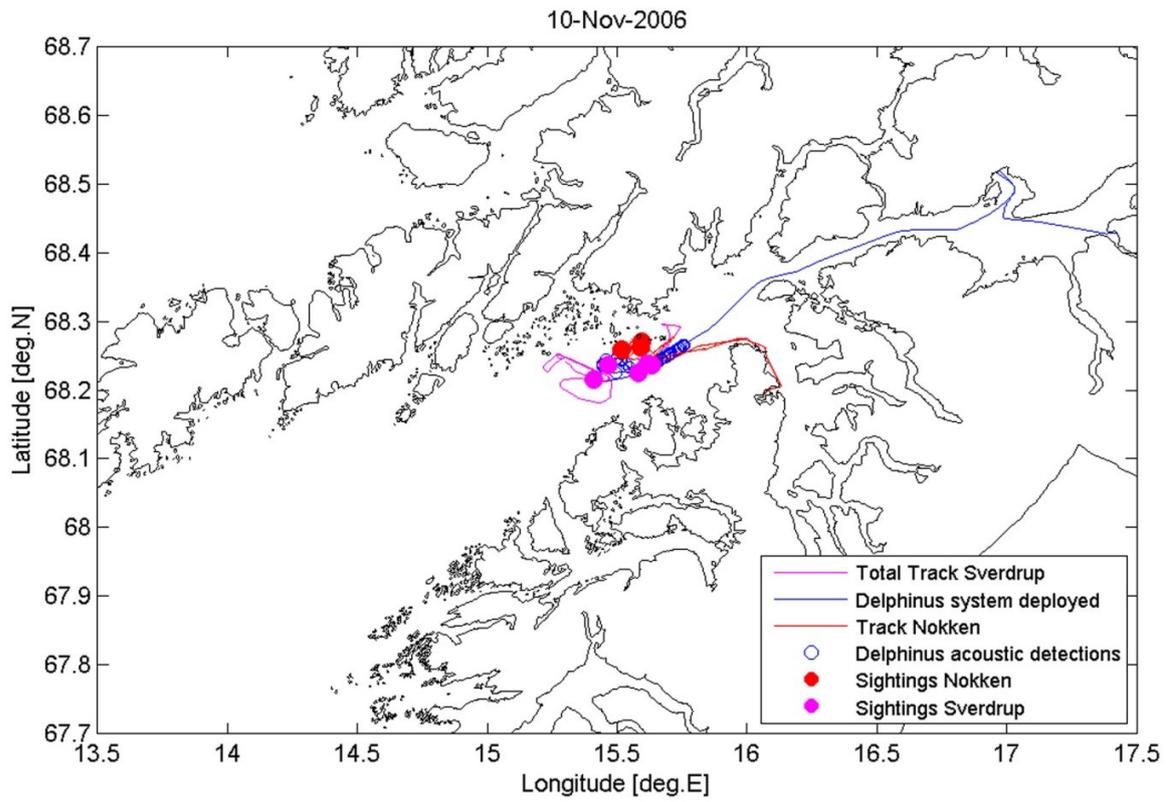
In monitoring of killer whale presence in relation to the 2006 Flotex Silver exercise and CEE, it was found that killer whales were present every day in Vestfjord/Ofotfjord from 7<sup>th</sup> – 15<sup>th</sup> November (Figure 5.3) (Kvadsheim et al. 2007). A herring CEE sonar experiment was carried out on the evening of 9<sup>th</sup> November. On the following day (10<sup>th</sup> November) killer whales were found close to the CEE site in Vestfjord (Figure 5.4a). It was estimated that 50-80 killer whales were present in multiple subgroups on 13<sup>th</sup> November in Vestfjord during the day before the start of operational naval sonar use in the Flotex exercise later in the evening. The number of whales sighted dropped sharply after the first night of operational naval sonar exercise to approximately 10 animals within a single group encountered on 14<sup>th</sup> November in Vestfjord. Following a second night of operational sonar exercise, only four adult males were seen during 15<sup>th</sup> November in Vestfjord. Despite exhaustive searching, no killer whales were encountered either by intensive visual or acoustic efforts by the research team, the whale-watching company or any local contacts in the area from 16<sup>th</sup> – 18<sup>th</sup> November (Figure 5.3 & 5.4b). The Flotex Silver trial ended on 16<sup>th</sup> November. Killer whales were reported by whale-watch companies to be back in Vestfjord again on 19<sup>th</sup> November on a day the research team was on land for maintenance. The research team encountered killer whales again in the fjords every day between 20<sup>th</sup> - 29<sup>th</sup> November 2006 (Figure 5.3 & 5.4c). Visual effort was not possible on 11<sup>th</sup>, 17<sup>th</sup> and 18<sup>th</sup> November due to bad weather conditions.

	November																													
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30				
<b>WW sightings</b>	Black	Black	Green	Green	Green	Green	Green	Green	Green	Green	Green	Black	Black	Black	Black	Green	Green	Green	Green	Green	Green	Black	Green	Green	Green	Green	Black			
<b>Visual</b>	Grey	Black	Green	Green	Green	Green	Grey	Green	Green	Green	Green	Black	Grey	Grey	Grey	Green	Green	Green	Green	Green	Green	Green	Black	Green	Green	Green	Black			
<b>Acoustic</b>	Grey	Black	Green	Green	Green	Green	Green	Green	Green	Green	Green	Black	Black	Black	Black	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green	Green			
<b>Sonar activity</b>	Yellow	White	White	White	Yellow	White	White	Yellow	Yellow	Red	Red	Red	Yellow	Red	Yellow	Yellow	White	White	White	Yellow	Yellow	White	White	White	White	White	Yellow			

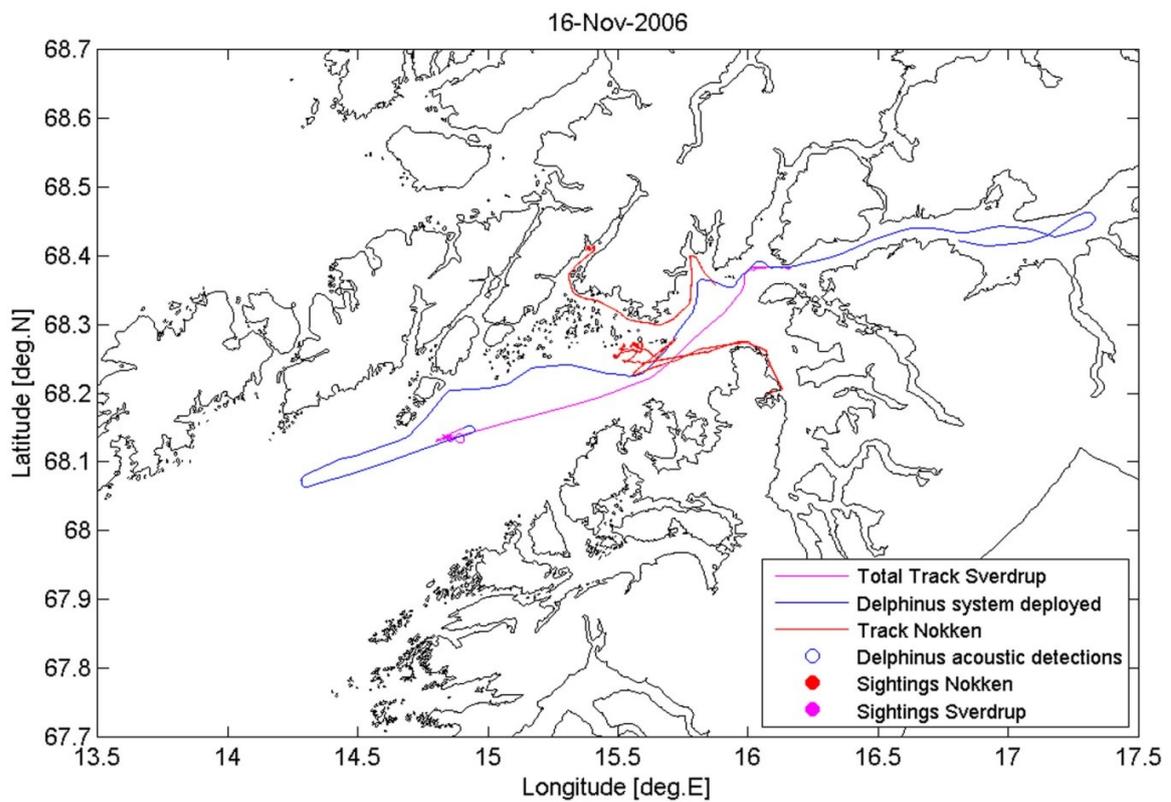
	Colour
<b>Detections</b>	Green
<b>No detections</b>	Black
<b>No effort</b>	Grey
<b>Navy sonar</b>	Red
<b>CEE sonar</b>	Yellow

Figure 5.3 - Killer whale sightings recorded by the whale-watching (WW) company (Orca Tysfjord), visual and acoustic detections of killer whales by the research team and naval sonar activity days within the fjord system in November 2006, with a key to colours.

a



b



c

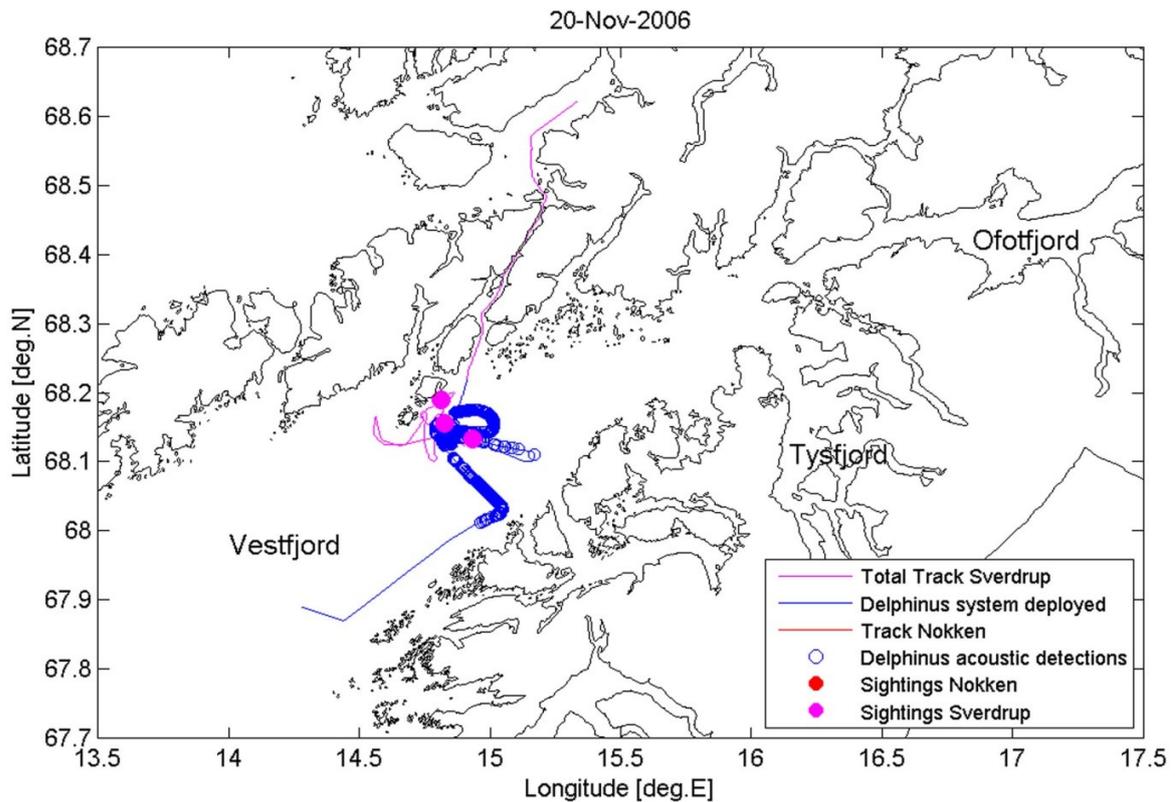


Figure 5.4 - Tracks of R/V *H.U. Sverdrup II* and R/V *Nøkken* with visual and acoustic (*Delphinus* array) detections of killer whales before (10<sup>th</sup> November (a)), during (16<sup>th</sup> November(b)) and after (20<sup>th</sup> November (c)) the Flotex 2006 exercise in the fjord system (Vestfjord, Ofotfjord, Tysfjord).

### 5.3.3 Statistical analysis

The “probit” link function was selected as the best one based on AIC and was thereby used. The three best models all had similar support from the data, as shown by the AIC difference < 2 (see Table 5.2). Covariates retained in these top three models were *Herring*, *Year*, *SonarType*, *Weather* and *JulianDay*. In model 2, *Year* was included instead of *Herring*, but based on AIC *Herring* was the better explaining covariate of killer whale presence and was thereby retained in the best model. In model 3, *SonarType* was taken out of the best selected model 1 and see if excluding *SonarType* was a better model. In models 4 and 5, *SonarType* was replaced with *SonarLag* and *Sonar*, respectively.

The best GLM model to explain killer whale presence based on AIC included *Herring*, *SonarType*, *Weather* and *JulianDay* as covariates (Figure 5.5, Table 5.2 & 5.3). *Herring* was significant ( $p = 0.001$ ) in explaining variability in the killer whale sightings in the fjords, as was *Weather* ( $p = 0.001$ ) and *JulianDay* ( $p = 0.001$ ) (Table 5.3). Based on the deviance explained, *Herring* was the most important explanatory variable, followed by *Weather* and *JulianDay*.

Killer whale presence was higher when herring biomass was larger and later on in November. Good weather conditions improved the detectability of killer whales.

In none of the models did operational sonar exercise itself statistically-significantly affect the presence of killer whales. However, a weak but significant relationship was identified between the type of sonar used and killer whale presence. There is some evidence to suggest ( $p = 0.1$ ) that the level or duration of sonar activity caused by the combination of operational sonar exercise and experimental CEE activity in 2006 negatively impacted killer whale presence (Figure 5.5, Table 5.3). The limited dataset and the low sample size of days with sonar activity leads to wide confidence intervals around the results.

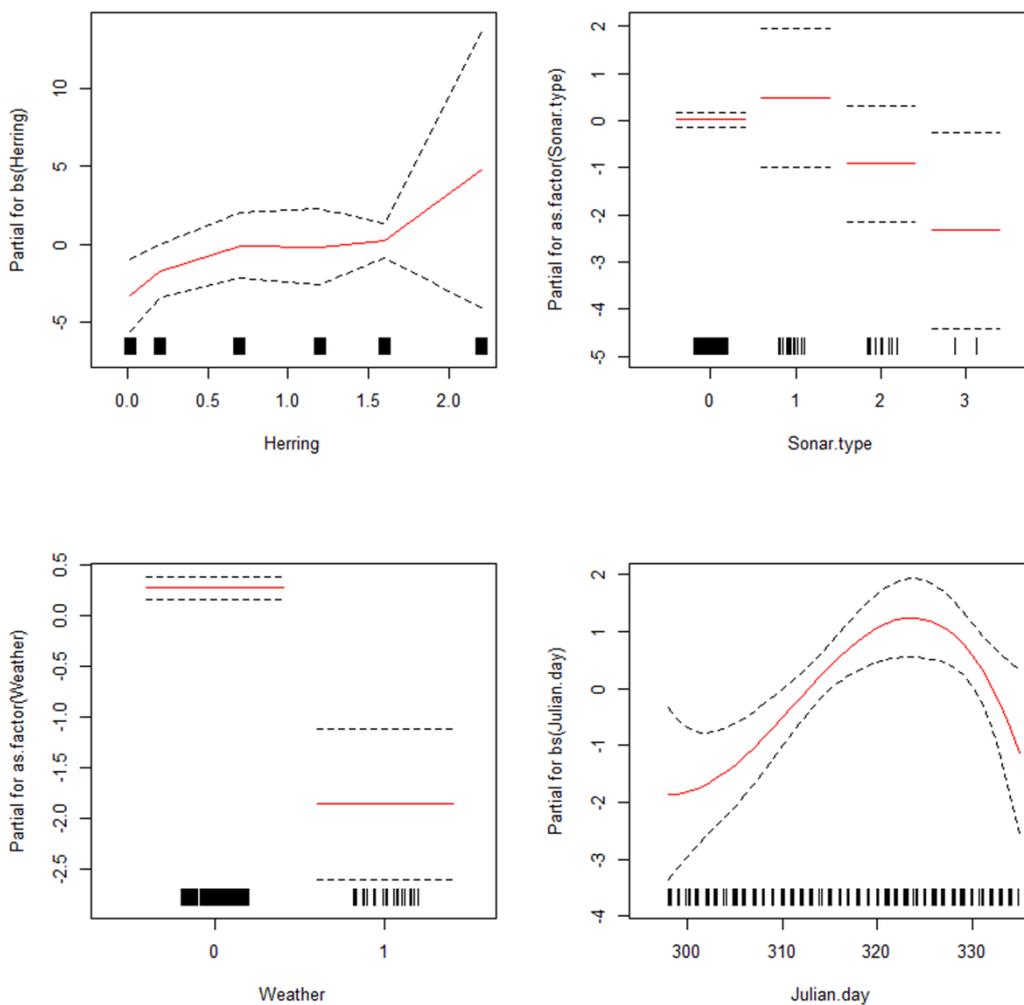


Figure 5.5 - Relationship of killer whale presence against the covariates (red line) selected in the best GLM model (based on AIC); *Herring* (biomass in million tonnes), *SonarType* (0 = no sonar, 1 = navy sonar exercise, 2 = CEE, 3 = navy sonar exercise & CEE), *Weather* (0 = good weather, 1 = bad weather) and *JulianDay* with 95% CIs (dotted line).

Table 5.2 - Model selection diagnostics with AIC for GLM models run with “probit” link function, including residual deviance and degrees of freedom. Fitted covariate effects included bs = B-splines and f = factor.

#	Model variables	AIC	Residual deviance	df
1	<i>bs(Herring)+f(SonarType)+f(Weather)+bs(JulianDay)</i>	97.38	75.4	200
2	<i>bs(Year)+f(SonarType)+f(Weather)+bs(JulianDay)</i>	97.82	75.8	200
3	<i>bs(Herring)+f(Weather)+bs(JulianDay)</i>	97.87	81.9	203
4	<i>bs(Herring)+f(SonarLag)+f(Weather)+bs(JulianDay)</i>	99.66	81.7	202
5	<i>bs(Herring)*f(Sonar)+f(Weather)+bs(JulianDay)</i>	101.50	77.5	199

Table 5.3 - Covariates in the best selected GLM model, ordered by the deviance explained indicating the importance of the covariates, degrees of freedom and p-values. \*The combination of operational navy sonar exercise and CEE activity in 2006.

Covariate	Deviance explained	df	p
<i>Herring</i>	57.2	3	0.001
<i>Weather</i>	33.4	1	0.001
<i>JulianDay</i>	23.3	3	0.001
<i>SonarType</i>	6.5	3	0.1*

## 5.4 DISCUSSION

On site observations of killer whale presence before, during and after the Flotex Silver 2006 naval exercise clearly indicate that sonar activity within the fjord system could have caused whales to leave the area and be unavailable for whale-watching while the exercise was on-going as claimed by the whale-watching community and an NGO for an earlier exercise (WWF-Norway 2001). This result is also consistent with controlled sonar exposure experiments showing killer whale avoidance to sonar transmission at relatively low received levels (Miller et al. 2012), indicating avoidance range around operational naval sonar between 20-39 km depending on frequency, source level and propagation conditions (Miller et al. in review).

In 2006 it was observed that the number of whales sighted decreased markedly for two days after the start of an operational Flotex Silver exercise, from up to 80 killer whales seen in Vestfjord to only four adult males encountered on 15<sup>th</sup> November. The lack of other age-sex classes in this latter sighting is notable because killer whales normally are encountered in mixed age-sex matrilineal pods (Similä 1997a). This was followed by no whales encountered for three days despite intensive search both visually and acoustically. The sudden drop in numbers and ultimate disappearance of killer whales were also observed by the whale-

watching community. These fjords are also populated areas and sightings information from a network of local contacts working at sea also confirmed the impression that killer whales had left the entire fjord basin (Vestfjord, Ofotfjord and Tysfjord), but returned three days after the operational navy sonar activity ceased. The CEEs conducted in 2006 added to the naval sonar activity level, and could have contributed to the disappearance of killer whales, as indicated by the statistical analysis, creating a combined disturbance together with operational navy exercise in that particular year. However, the small sample size on the sonar days and of the different types of sonar available to be used in the models leads to uncertainty in the results.

The retrospective data are less conclusive. During the years before 2006, killer whales were sighted many times in the same sub-fjord during days with operational sonar exercise. It is possible that animals were disturbed by the navy sonar activity that occurred in 2002-2005, but that the reactions were not of sufficient magnitude to make all animals in the area leave and thus become unavailable as subjects for whale-watching. Prior to 2006, navy sonar exposure of the Vestfjord and/or Ofotfjord was for a maximum of three days in a row, whereas in 2006 naval sonar activity was carried out for four days. In addition, experimental CEE sonar activity was carried out in 2006, which extended the total sonar activity period for seven consecutive days. It is worth noting that both the navy operational sonar source level (up to 227dB) and exposure length (days) differ significantly from the ones used in the CEEs (max 209dB and max 2h, respectively) (Doksæter et al. 2009; Miller et al. 2012) and can therefore be expected to have a more severe impact on the behaviour of killer whales.

The strongest trend in the whale-watching sighting record is a clear decline of killer whale sightings from 2005 to 2008, despite no sonar activities after 2006, when the Flotex exercises were moved to offshore waters. This dramatic decline in killer whale sightings is thought to result from a strong offshore shift in the distribution of the over-wintering NSS herring, resulting in the biomass of NSS herring declining inside the fjord system (Orellana 2006; Huse et al. 2010). The first signs of the NSS herring distribution change were recorded by the Norwegian Institute of Marine Research (IMR) in 2002 (Huse et al. 2010). As a result, far fewer killer whales were present inside the fjord system and on fewer days after 2005 due to the offshore shift in the distribution of their prey. In November 2007 and 2008, large numbers of killer whales were observed associated with the NSS herring fishing fleet in offshore waters of the Norwegian Sea north of 70°N (see Chapter 6). Killer whales previously sighted inside Tysfjord, Ofotfjord and Vestfjord were photo-identified in these offshore waters (see Chapter 6).

Therefore, as the number of killer whales inside the fjord system was greater prior to 2006, it is possible that some of the killer whales were displaced during sonar activity in earlier years but not all of them and so killer whales were still found in other parts of the fjords. The sheer number of killer whales present inside the fjords in earlier years, more than 700 individuals (Chapter 2, Kuningas et al. 2013a), could have meant that some whales were always present inside fjords despite navy sonar activity, because of the very high prey abundance. After 2005, as the NSS herring biomass inside fjords decreased, the number of killer whales using the area also decreased. The sonar activity inside fjords in 2006, when prey abundance and killer whale numbers were much lower, could have caused the remaining killer whales to leave the fjords. Additionally, in earlier years killer whales were regularly sighted with plenty of NSS herring inside Tysfjord, an area which was never used for navy exercises. Therefore, exercises taking place in Vestfjord and/or Ofotfjord did not necessarily result in killer whales leaving the overall fjord system.

The estimated number of killer whales using the fjord system in a given year until 2003 varied among years (Chapter 2, Kuningas et al. 2013a). This could partly be due to inter-annual variation in wintering NSS herring biomass and/or distribution (Orellana 2006). Based on a satellite tagging study conducted in 2000 and 2001, killer whales in northern Norway are known to conduct “scouting trips” outside the fjord system with the likely purpose to keep track of the distribution of their migrant NSS herring prey (Stenersen & Similä 2004). This kind of movement represents a naturally occurring temporary emigration from the fjord system, compared to naval sonar exposure representing an unnatural cause of displacement of killer whales. It is possible that in a particular year under a certain biological setting regarding the NSS herring biomass and distribution inside the fjords together with variable rate of temporary emigration (see Chapter 3), killer whales could have been more susceptible to leave a fjord during a naval sonar exercise, as might have been the case in 2000 (WWF-Norway 2001).

Unfortunately, there were no data available to investigate the Flotex incidence of year 2000, after which allegations were made by an NGO that killer whales were chased away by navy sonar activity (WWF-Norway 2001). With this limited dataset, it is not possible to strongly conclude that the naval sonar transmissions were the sole cause of killer whales temporarily disappearing from the fjords, as was claimed by the whale-watching community.

A number of factors likely influence how killer whales react to use of sonar, and variability in responding to a certain level of sound exposure depends of the context in which animals are being exposed (Ellison et al. 2012; Southall et al. 2007). A high level of variation in response threshold has been recorded for killer whales, with some behavioural responses to

sonar observed at very low received levels (less than 120 dB re 1  $\mu$ Pa, Miller et al. 2012). This indicates that killer whales might be especially sensitive to sonar exposure, responding with lower sound pressure levels compared to long-finned pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*) (Miller et al. 2012). Miller et al. (2012) also found that killer whales responded to lower source levels of mid-frequency active sonar than of low-frequency active sonar, which is noteworthy as navy sonar mainly operates at the mid-frequency bandwidth. Killer whales remaining inside fjords may have been more likely to leave in response to sonar in 2006 when less of their NSS herring prey was present within the fjord system, making the area lower quality for them than during 2002-2005 with higher food abundance (Frid & Dill 2002; Orellana 2006). Based on the statistical analysis, NSS herring abundance was the most important covariate explaining killer whale presence. It is possible that a critical threshold exists for the killer whales not to abandon the fjords during sonar exposure in terms of a sufficient amount of their prey being available. Or at least there was a sufficient amount of prey available before 2006 in another fjord to move there while the exercises was taking place in another one of the fjords, making it unnecessary to move to offshore areas. During a much lower NSS herring biomass inside the fjords in 2006, when killer whales were mostly encountered in Vestfjord, in the same fjord where the operational sonar exercises and CEE were taking place, there were three days without killer whale sightings after the active operational sonar exposure.

This study shows that under some conditions naval sonar activity has the potential to displace killer whales from a whale-watching area that encompasses a large basin. It also illustrates that the consequences of actual sonar activity for affected animals and human stakeholders in the marine environment can be difficult to predict solely from controlled dose-response experiments, but that the combination of results from long-term sightings data, controlled experiments and observations during real sonar exercises provide a stronger indication of the influence of sonar than one of them alone (Tyack et al. 2011). Other factors such as density and distribution of prey, and fitness of the exposed individuals might strongly influence the reaction of killer whales to sonar exposure (Bejder et al. 2006; Ellison et al. 2012).

## CHAPTER 6

### Large-scale change in the distribution of wintering Norwegian spring spawning herring: implications for killer whales

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#### ABSTRACT

Top predators have an important role in their ecosystem and may influence the abundance of their prey species. However, the distribution and population dynamics of a predator may also be strongly affected by the availability of their prey. The Norwegian spring spawning (NSS) herring (*Clupea harengus*) is the largest fish stock in the northeast Atlantic and is important as prey for multiple species in this ecosystem. The NSS herring is the main prey for killer whales (*Orcinus orca*) in northern Norway, which follow the annual migration of the NSS herring stock. Migration of the NSS herring is highly dynamic, characterised by unpredictable large-scale shifts particularly in its wintering areas. Here, parallel long-term data series for both the NSS herring and killer whales (a rare situation for a marine top predator and its prey) were used: 1) to describe the presence of the wintering NSS herring stock and killer whales inside a fjord system in northern Norway over more than two decades (1986-2008); 2) to document the large-scale change in the distribution of the wintering NSS herring stock from the fjord system to offshore waters during 2002-2006; and 3) to evaluate the response of killer whales to this large-scale change in the distribution of their prey. A time lag of four years was recorded between the first sign of the NSS herring stock changing its wintering distribution in 2002 and reduced killer whale presence inside the fjord system in 2006. Reduced herring abundance inside the fjord system altered the daytime activity budget of killer whales, increasing their time spent travelling/foraging, compared to a previous study during high NSS herring abundance. Higher probabilities of adult killer whales being temporarily away and lower probabilities of remaining in the fjord system were recorded compared to previous analysis (Chapter 3). The fjord system likely represented a preferred habitat for killer whales due to the higher density of NSS herring in this area compared to the offshore area until 2006.

## 6.1 INTRODUCTION

Due to their large body size, marine mammals have a high energy intake and are considered to have a major impact on marine ecosystems (Bogstad et al. 1997; Bowen 1997; Estes et al. 2011). As top predators, they may play an important role in shaping the behaviour and life history of their prey species and also have both direct and indirect effects on other species in the marine food web (Bowen 1997; Estes et al. 1998; Morissette et al. 2006; Trites et al. 2006; Heithaus et al. 2008; Estes et al. 2011; Morissette et al. 2012). However, top-marine predators are also influenced by bottom-up processes due to the availability and ecology of their prey (Trites & Donnelly 2003; Frederiksen et al. 2006; Trites et al. 2006). The abundance of a prey species can affect the life history and distribution of a predator (Similä et al. 1996; Ward et al. 2009, Ford et al. 2010). The patchy distribution of prey, at both temporal and spatial scales, results in an aggregative response by predators in areas with high food concentrations, and movement between these prey concentrations (Similä et al. 1996; Stevick *et al.* 2002; Worm et al. 2003).

Long time series of data on the distribution and abundance of both a predator and its prey are needed to study the interaction between them. Such long-term datasets are rare, at least for most marine mammal species, because collection of the necessary data at sea is logistically difficult and expensive. One of the longest data series on a cetacean species is from the extensively studied population of northeast Pacific resident killer whales (*Orcinus orca*) (Bigg et al. 1990; Olesiuk 1990, 2005). The study presented here uses two parallel long-term datasets of a prey and a predator, to describe a large-scale change in the wintering distribution of the prey and to examine the consequences of that change for the predator.

The Norwegian spring spawning herring (*Clupea harengus*, hereafter referred to as NSS herring) stock is the largest herring stock in the world and the largest fish stock in the NE Atlantic (Holst et al. 2004; ICES 2013). This herring stock is of major economic importance with fisheries catches sometimes reaching more than 1.5 million tonnes annually. Countries fishing on this stock include Norway, Iceland, Russia, Faroes, Denmark, UK, Ireland, Sweden, Germany and The Netherlands (ICES 2013; Pilling et al. 2009). The NSS herring is an important prey species in the NE Atlantic ecosystem; species feeding on various life stages of this herring stock include cod (*Gadus morhua*), saithe (*Pollachius virens*), many species of sea birds and whales (Similä & Ugarte 1993; Pitcher et al. 1996; Nøttestad 1998; Axelsen et al. 2001; Nøttestad & Similä 2001; Olsen & Holst 2001; Nøttestad et al. 2002; Tjelmeland & Lindstrøm 2005).

The NSS herring stock is highly dynamic, and its distribution and abundance have both undergone large fluctuations during the last 100 years (Dragesund et al. 1997; Toresen & Østvedt 2000). A major collapse in the stock biomass was experienced in the late 1960s due to heavy pressure from fisheries and unfavourable climatic conditions, followed by a long stock recovery period (Dragesund et al. 1997; Toresen & Østvedt 2000). From the late 1980s the stock biomass started to increase due to high recruitment levels particularly from the strong year-classes of 1983, 1991, 1992, 1998, 1999, 2002 and 2004 and the stock peaked in 2009 with a spawning stock biomass of 8.5 million tonnes (ICES 2013). Today, the biomass of NSS herring is again decreasing rapidly due to a lack of strong year-classes after 2004 (ICES 2013), possibly combined with increased natural mortality after 2009 (pers. comm. Jens Christian Holst).

The NSS herring stock undertakes large-scale seasonal migrations over thousands of kilometres between coastal and offshore waters between the spawning, feeding and wintering areas, and is known to alter this migration pattern at uneven intervals (Dragesund et al. 1997; Huse et al. 2002; Holst et al. 2002; 2004). In particular, it is characterized by unpredictable large-scale shifts in wintering areas between coastal and offshore waters (Dragesund et al. 1997; Huse et al. 2010). Considerable changes in the recorded wintering location of NSS herring have taken place since the 1950s and about six major shifts have been described since then (Dragesund et al. 1997; Huse et al. 2010). The shifts in wintering areas have been connected with large year-classes recruiting into the spawning stock resulting in a high ratio between younger and older year-classes (Huse et al. 2010). Around 1986 a new shift was observed when the 1983 year-class started wintering in the Vestfjord area after its Barents Sea juvenile period (Holst et al. 2002; Orellana 2006; Huse et al. 2010). Following this shift the spawning stock of NSS herring wintered in the Tysfjord-Ofotfjord-Vestfjord area (hereafter referred to as the fjord system, see Figure 6.1) up until the period 2002-2006 when a new shift occurred to an offshore wintering area (Huse et al. 2010).

The distribution of killer whales has been reported to follow the distribution of the adult (and adolescent) NSS herring (Christensen 1982; Similä et al. 1996; 2002; Stenersen & Similä 2004). The NSS herring is the main prey for killer whales in northern Norwegian waters, at least during wintertime (Jonsgård & Lyshoel 1970; Christensen 1988; Similä & Ugarte 1993; Similä et al. 1996), and killer whales have adapted to feeding on herring with an advanced hunting technique known as carousel feeding (Similä & Ugarte 1993; Similä 1997b). A long-term photo-identification study of this population started in the 1980s, when killer whales arrived in the sheltered fjord system following the NSS herring into its new wintering area

(Lyrholm 1988; Similä 1997a). The large NSS herring spawning stock inside the fjord system during wintertime supported approximately 700 killer whales in this area (see Chapter 2; Kuningas et al. 2013a). The presence of killer whales in the fjord system also provided multiple whale-watching companies great opportunities for profitable business during these years.

The study presented here describes the presence of the NSS herring stock and killer whales inside the fjord system over more than two decades, the large-scale change in distribution of the wintering NSS herring stock from the fjord system to offshore waters since 2002, and evaluates the response of the killer whales to this change. This is achieved using two parallel long-term datasets on the NSS herring and killer whales in northern Norway over a time frame of 1986-2013. Additionally, this study explores the presence of other NSS herring predators: the herring fishery, cod and saithe, in relation to the large-scale change in distribution of the NSS herring stock.

## **6.2 MATERIALS & METHODS**

### **6.2.1 Study areas**

The main research area was the fjord system (Vestfjord, Tysfjord and Ofotfjord) located north of the Arctic Circle east of the Lofoten islands, and the offshore area north and northwest off Vesterålen in northern Norway (Figure 6.1).

The Norwegian Institute of Marine Research (IMR) conducted annual acoustic trawl surveys of the NSS herring stock for management advice and general research purposes. These surveys were carried out in October-December in the fjord system NSS herring wintering areas during 1986-2006, and in the new oceanic NSS herring wintering areas during 2002-2007.

The killer whale photo-identification data were collected in the fjord system between October and January 1986-2008. In addition, killer whale photo-identification data were collected in offshore areas in December 2007 and in November 2008, see Figure 6.1. Photo-identification data were also collected in January 2013 in Andfjord which is part of the new NSS herring wintering area.

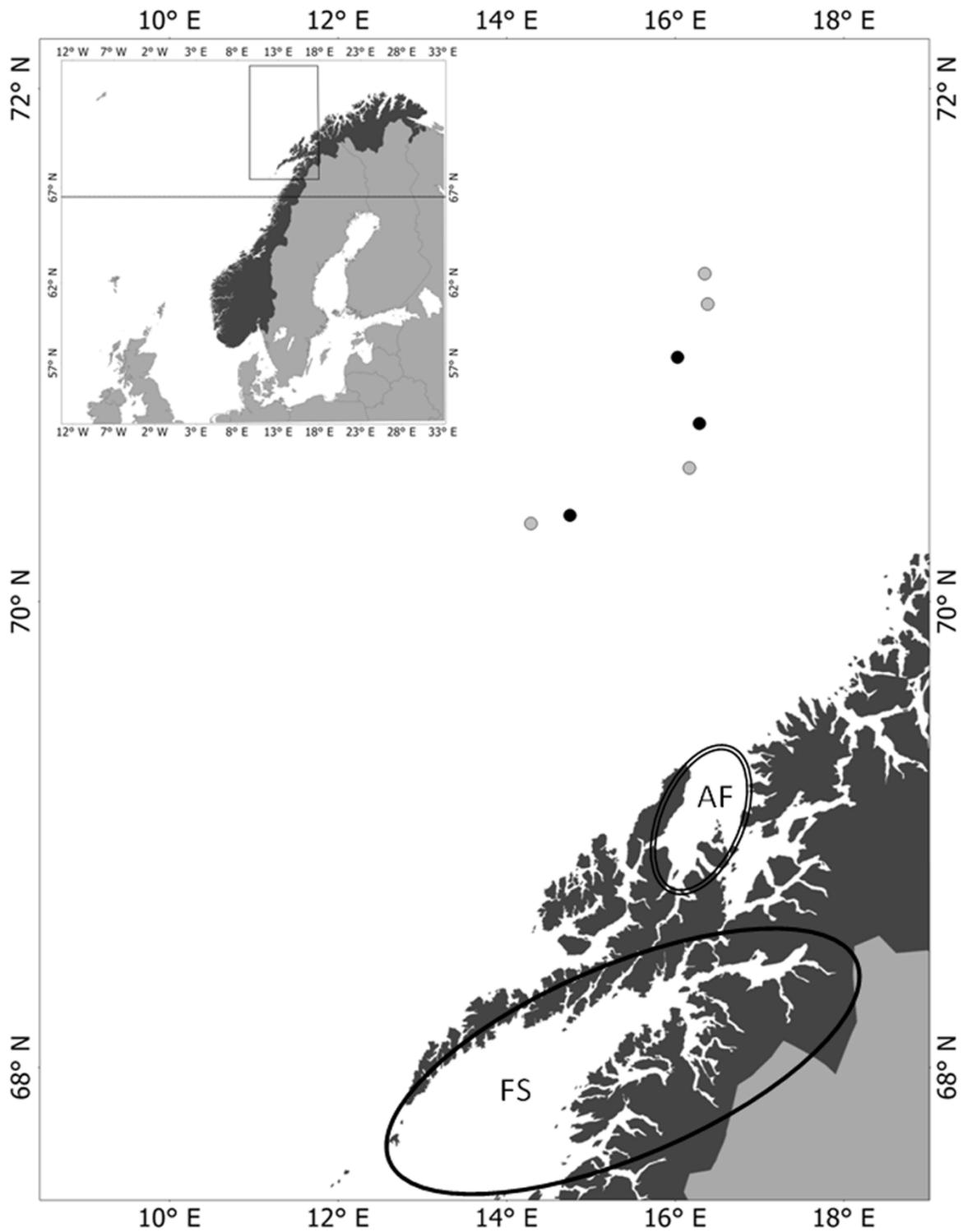


Figure 6.1 - Data collection areas in northern Norway: fjord system (FS) comprising Ofotfjord, Tysfjord and Vestfjord where killer whale photo-identification data were collected in 1986-2008 and NSS herring surveys were conducted in 1986-2006; and offshore positions where killer whales were encountered in 2007 and 2008 (indicated with dots; black dots are locations where photo-identification was attempted), and Andfjord (AF) where killer whales were photographed in January 2013.

### **6.2.2 The NSS herring survey data and analysis**

The IMR's survey data included maps of the distribution and estimates of the biomass, age- and length composition of the NSS herring during 1986-2007 (for methodological details see Foote et al. 1997). The 2002 offshore mapping came about *ad hoc* as an extension of the fjord system survey, because a large amount of herring of the 1998 and 1999 year-classes were missing in the survey done in the fjord system (pers. comm. Jens Christian Holst). The offshore coverage in 2002 therefore lasted only for some hours but confirmed the presence of these year-classes north and west of Vesterålen. Thereafter, during the period 2003-2007, the survey was planned and conducted with full coverage also in the offshore areas. The wintertime survey series ceased after 2007 as the survey variance was considered too large to be used for stock assessment purposes.

The survey dataset was used to investigate the distribution of the NSS herring inside the fjord system during 1986-2006 and the shift to an offshore distribution during 2002-2007. Further, the NSS herring dataset was used to describe the changes in abundance of NSS herring inside the fjord system and offshore during 1988-2013. Two sources of NSS herring biomass were used: 1) The spawning stock estimates as given in International Council for the Exploration of the Sea Advice 2013 (ICES 2013; ICES Advice 2013) for 1988-2013 and 2) the IMR's survey biomass estimates from the wintering areas for 2001-2007.

Mean densities of wintering herring in the fjords and offshore were obtained by dividing the spawning stock estimates given by ICES (ICES 2013) by the area inhabited by herring, as judged from positive acoustic values assigned to herring during the trawl acoustic herring surveys. The size of the areas inhabited by herring by year were obtained from planimetric measurements of herring distributions plotted using Surfer (Golden Software).

### **6.2.3 Killer whale photo-identification data and analysis**

Sections 2.2.1 and 2.2.2 in Chapter 2 give details on killer whale photo-identification data collection and processing, respectively. The killer whale sightings data collected between October and December during 1986-2008 in the fjord system were selected for analysis in this Chapter. Encounter histories of identifiable individuals were built through 23 years inside the fjord system. These data were used to calculate the number of identifiable individuals and pods encountered each year. Photo-identification data for December 2007 and November 2008 from the offshore area and for January 2013 from Andfjord were used to investigate the continued presence of individuals that were previously encountered in the fjord system.

Mark-recapture analyses presented in Chapters 2 and 3 were extended in this Chapter to estimate the total population size of the killer whale population. Additionally, analyses to estimate adult male and female survival rates and temporary emigration probabilities were extended with three more years of data (to 1990-2006) to evaluate the potential change seen in these population parameters due to the offshore shift of the NSS herring. Details of the methods and results of this mark-recapture analysis are given in Appendix 6.1. For details on how sex and age-classes of each identifiable individual were determined, see section 2.2.2.1 in Chapter 2.

#### **6.2.4 Focal follow data**

Focal follow data for killer whales were collected in November 2005 and November 2006 in the fjord system. After an individual killer whale within a pod was tagged with a suction cup tag (Dtag, Johnson & Tyack 2003), the pod of killer whales associated with this tagged individual became a focal group that was followed and their behaviour documented once every two minutes (more details in Shapiro 2008). The selected focal group was followed as long as environmental conditions (e.g. sea state and light conditions) allowed. A reasonable distance (~100 m) from the animals was maintained to avoid influencing their natural behaviour. Initially these data were collected with the purpose of investigating killer whale behaviour in relation to their acoustics and underwater movement (Shapiro 2008). In the study presented here, the focal follow data were used to calculate the proportion of time spent in different behavioural states.

The behavioural state of the focal group was organised into four categories: 1) travelling/foraging, 2) feeding, 3) playing/socializing and 4) resting, following similar work previously done on this population (Similä 1997a). Activity budgets calculated in 2005 and 2006 were compared to those presented in Similä 1997a, which were based on focal follow data collected during 1990-1993.

#### **6.2.5 Whale-watching data**

The whale-watching company Orca Tysfjord has operated whale-watching tours in the fjord system since 1992. For each day spent at sea, the team of Orca Tysfjord consistently recorded killer whale sightings (date and location) made in the fjord system. These data were available for the period 2002-2008 and were used to investigate changes in the locations of encounters among the three fjords: Tysfjord, Vestfjord and Ofotfjord.

### **6.2.6 Fisheries catch data**

Fisheries catch data for NSS herring, cod and saithe were provided by the Directorate of Fisheries (Fiskeridirektoratet) in Norway for the catch areas of the fjord system (code 00) and offshore (codes 05, 27, 37 and 39) over the period 1988-2010 (see Appendix 6.2). Catches were recorded as tonnes of fish landed per month. Data between October-December were selected for analysis.

The fisheries catch data were used to investigate the development of NSS herring fisheries during 1988-2010 inside the fjord system and offshore. Catches of cod and saithe were used from the fjord system. These data were used to investigate how these other predators responded to changes in the distribution and abundance of NSS herring.

### **6.2.7 Index of predator abundance and predator-prey ratio**

An index of relative abundance of killer whales inside the fjord system was calculated by dividing the number of different individuals and pods encountered each year by the total number of different individuals (228) and pods (25), respectively, observed during the period 1988-2008.

Similarly the NSS herring catch for each year was divided by the maximum catch (in 1999). These indices of the relative abundance of killer whales and relative magnitude of the fishery inside the fjord system were used to compare differences in the use of the fjord system in relation to NSS herring abundance in this area during 1988-2008.

Additionally, the number of killer whale pods and individuals encountered per year and the fisheries catch per year were all divided by the estimated annual NSS herring biomass present in the fjords. These values were used to investigate changes in the predator-prey ratio during 1990-2006 inside the fjord system.

## **6.3 RESULTS**

### **6.3.1 The NSS herring distribution**

In 1986, the strong NSS herring year-class of 1983 started wintering in Vestfjord (Figure 6.2) thus initiating the creation of a new wintering area for the stock (Røttingen 1990). In 1987 between October and January the herring stock expanded to the branching fjords of Tysfjord and Ofotfjord (Røttingen 1990; Holst et al. 2002; 2004; Huse et al. 2010). Up until 2001, the NSS herring spawning stock was resident in this area during wintertime. The distribution of herring inside the fjord system varied to some extent between years throughout the period (as

indicated in Figures 6.3 and 6.4), typically linked with fluctuations in stock size. At lower abundance the main wintering areas were Tysfjord and Ofotfjord while at higher abundance the herring also populated the inner Vestfjord.

In 2002, the first signs of the NSS herring altering its wintertime distribution were recorded by the IMR's NSS herring autumn survey (Figure 6.5). The main part of the stock was still wintering inside Tysfjord and Ofotfjord this year, but 1.6 million tonnes were estimated to be wintering offshore, west and north of Vesterålen and Andøya (Figure 6.5a, Figure 6.9). It was mainly the large 1998 and 1999 year-classes that were about to enter the spawning stock which did not appear as expected in the fjord system at that time.

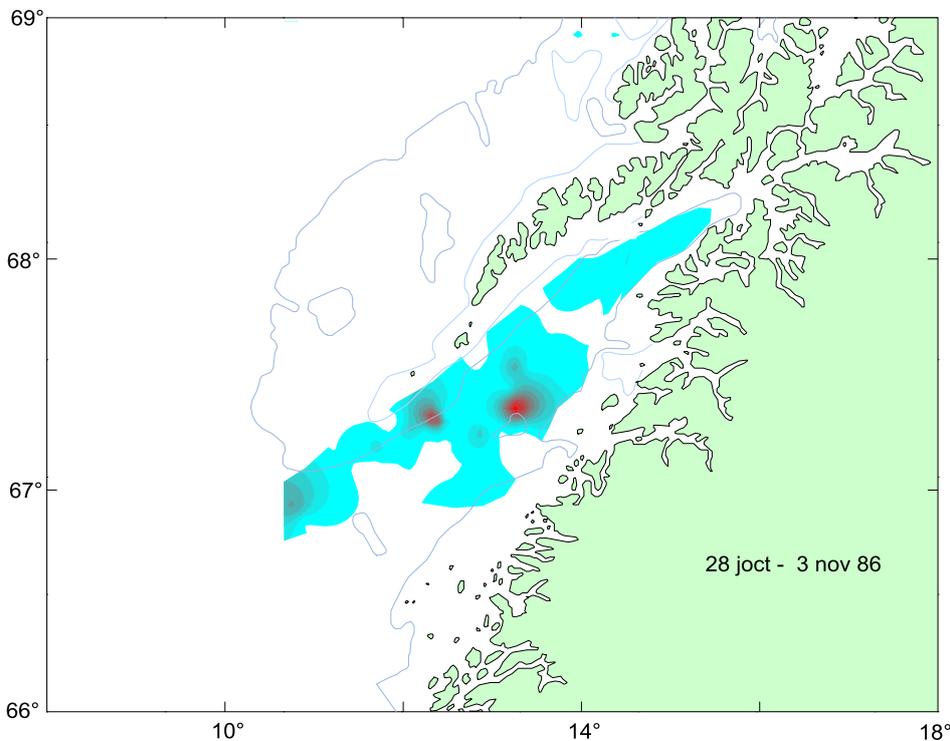


Figure 6.2 - The NSS herring distribution in Vestfjord based on the IMR survey during October-November 1986. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

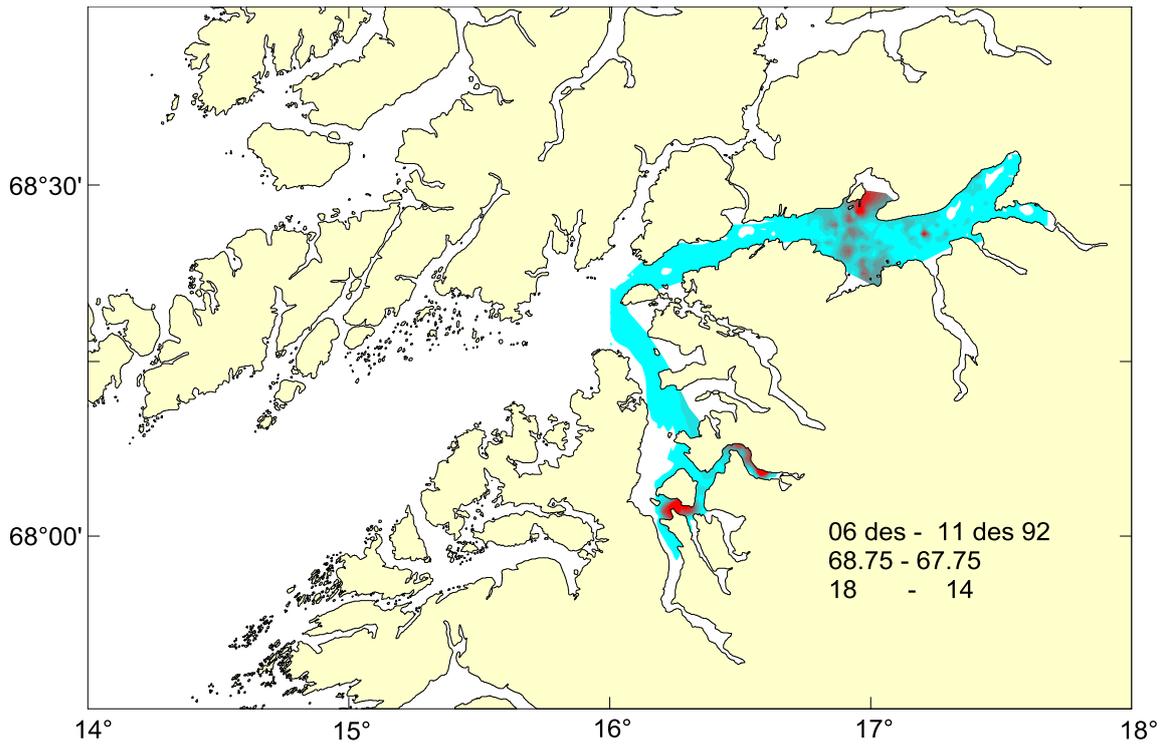


Figure 6.3 - The NSS herring distribution in the fjord system based on the IMR survey during December 1992. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

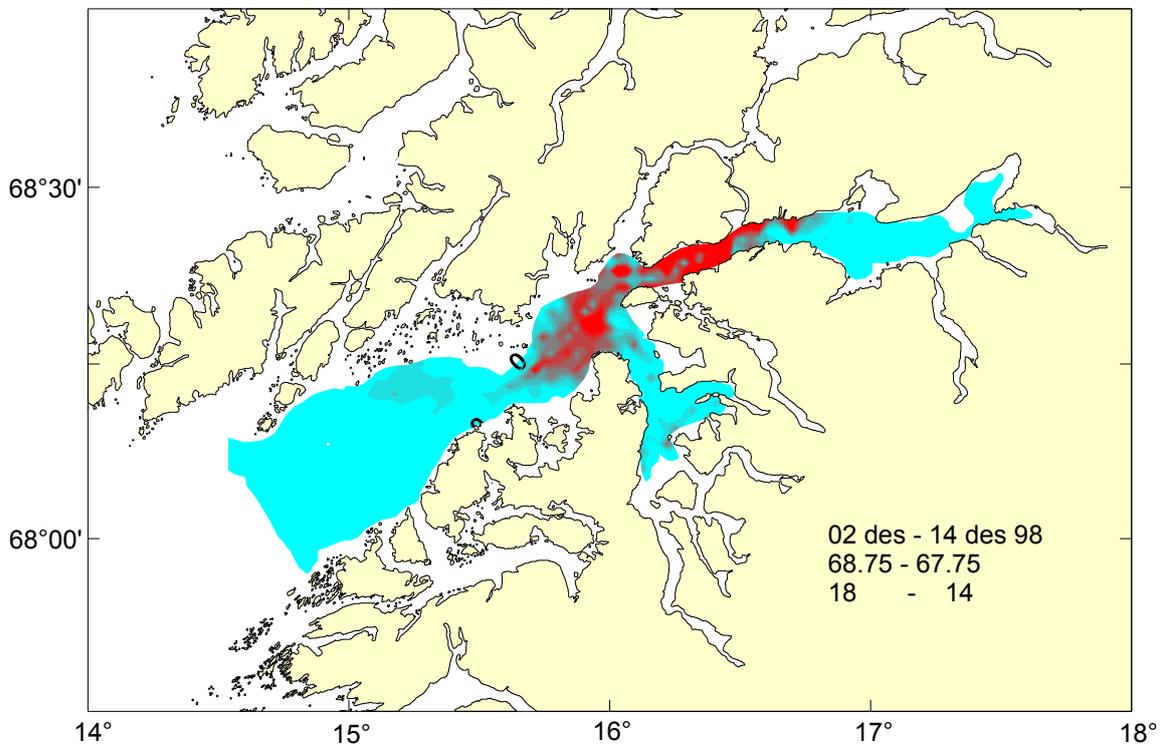
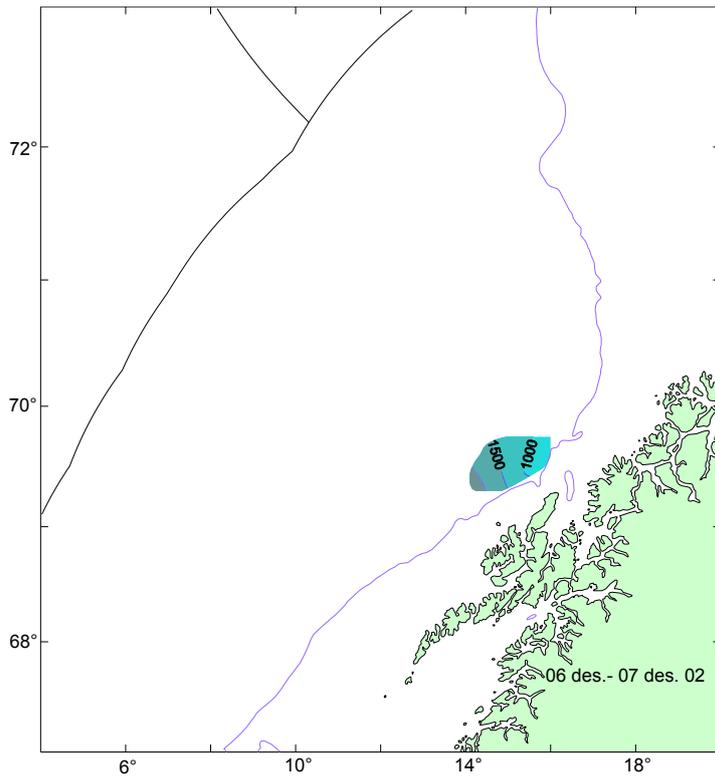
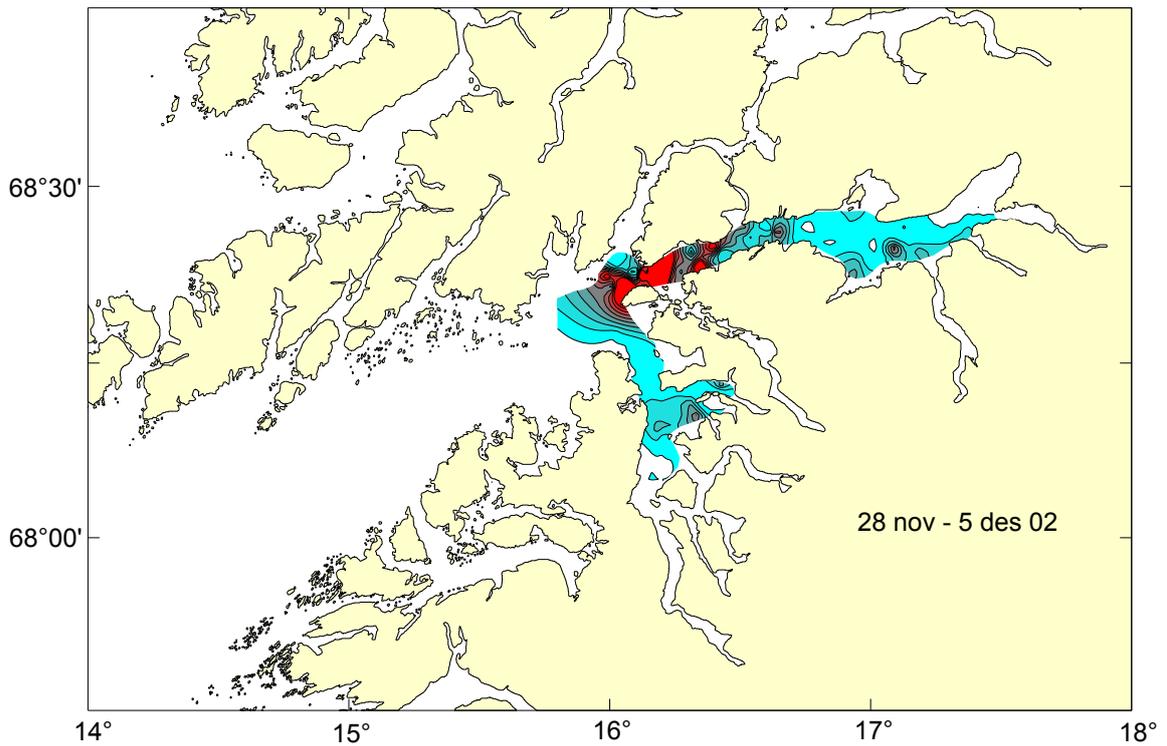


Figure 6.4 - The NSS herring distribution in fjord system based on the IMR survey during December 1998. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.



a)



b)

Figure 6.5 - The NSS herring distribution based on the IMR survey during November-December 2002 a) offshore (note that the offshore coverage is incomplete) and b) inside fjord system. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

In 2003 the offshore component was estimated to be larger than the fjord system component, which was concentrated inside Tysfjord and Ofotfjord (Figure 6.6).

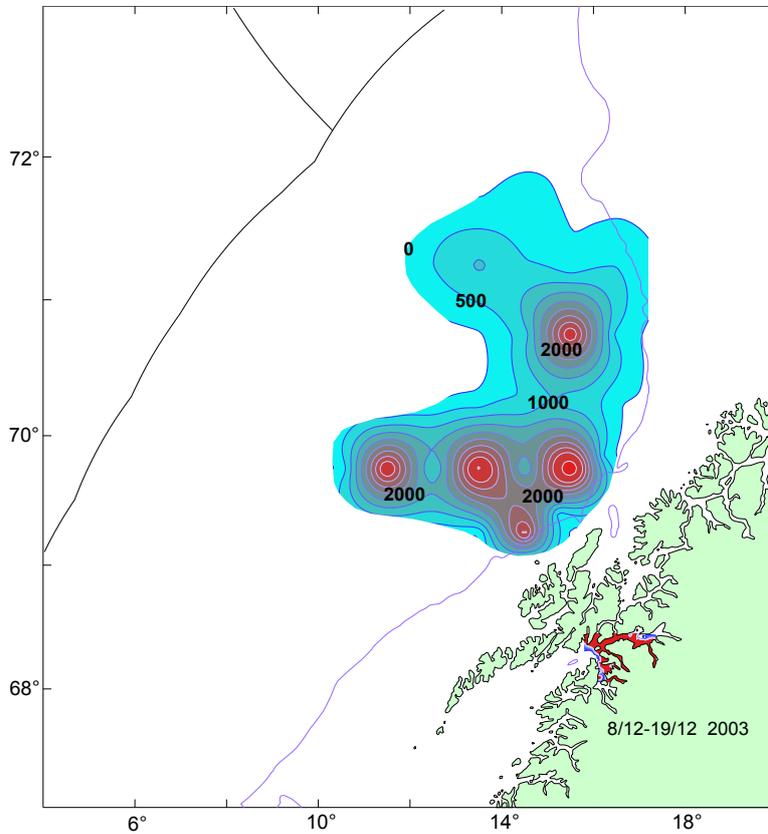


Figure 6.6 - The NSS herring distribution based on the IMR survey during December 2003 inside fjord system and offshore. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

Herring biomass in the fjord system continued to decline in 2004, 2005 and 2006, as the main part of the NSS herring stock wintered northwest of Lofoten, Vesterålen and Andøya (Figure 6.7). The fjordic NSS herring component was very small by this time and only some scattered schools were found in the Vestfjord area during the 2006 survey. In 2007, the entire spawning stock of the NSS herring wintered offshore in the Norwegian Sea between 70° and 73° N (Figure 6.8). The eastern border of the herring distribution was approximately at the 1000 m depth contour.

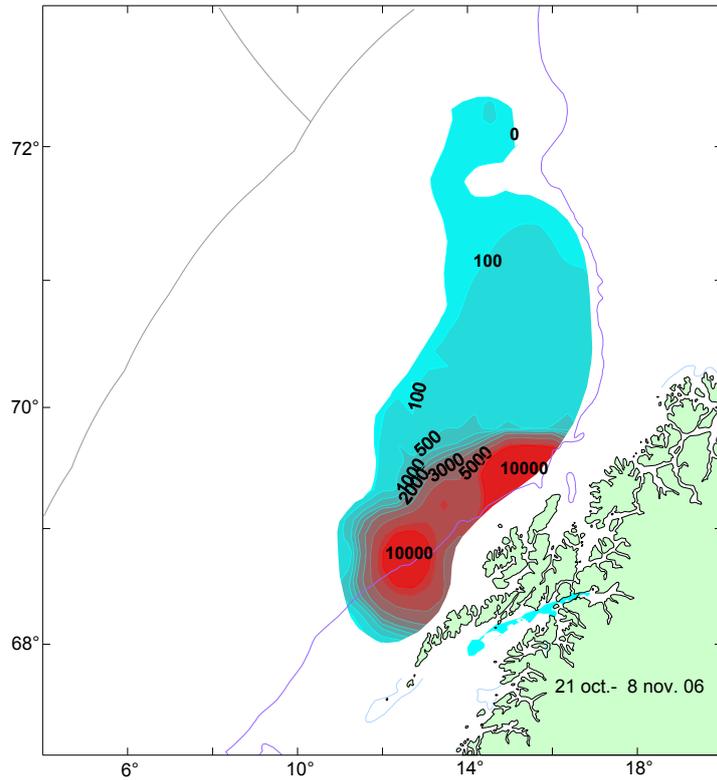


Figure 6.7 - The NSS herring distribution based on the IMR survey during October-November 2006 inside fjord system and offshore. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

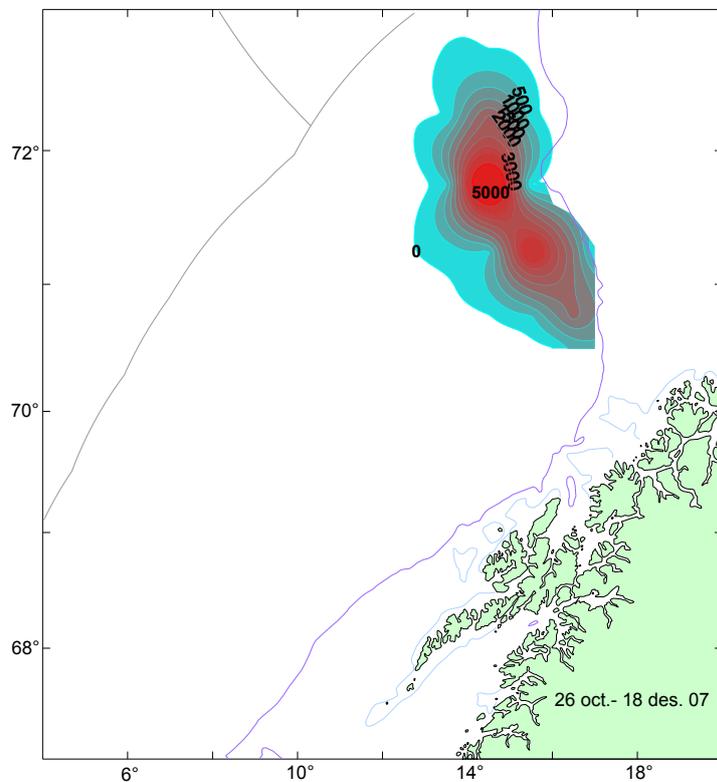


Figure 6.8 - The NSS herring distribution based on the IMR survey during October-December 2007 offshore. Blue and red colours indicate the overall distribution, and the red area a higher density of NSS herring.

### 6.3.2 NSS herring abundance and density

The total spawning stock biomass (SSB) of NSS herring increased from 1988 to 1999 (Figure 6.9). The early rise from 1988 to 1990 was due to the recruitment of the strong 1983 year-class while the two large year-classes of 1991 and 1992 contributed to a major part of the increase during 1996-1999. These years were followed by smaller year-classes and as a result the spawning stock decreased between 2000 and 2002. Other later strong year-classes were 1998, 1999, 2002 and 2004 which contributed to a record high SSB in this cycle of 8.5 million tonnes in 2009 (ICES 2013). From 2010 onwards the spawning stock of NSS herring has been decreasing due to poor recruitment but possibly also due to increased natural mortality in the stock (pers. comm. Jens Christian Holst).

An estimated 100% of the NSS herring spawning stock wintered in the Vestfjord system during 1988-2001. The biomass of herring inside the fjord system decreased after 1999, partly due to a decline in the overall NSS herring stock size during this period and partly due to the offshore distribution shift from 2002 (Figure 6.9). A steep decline in the percentage of NSS herring wintering inside the fjord system occurred between 2002 and 2006. In 2005, only 0.7 million tonnes of NSS herring was estimated to be wintering inside the fjord system, and in 2006 only 70,000 tonnes of NSS herring was estimated still to winter in the fjord system, representing 1% of the SSB.

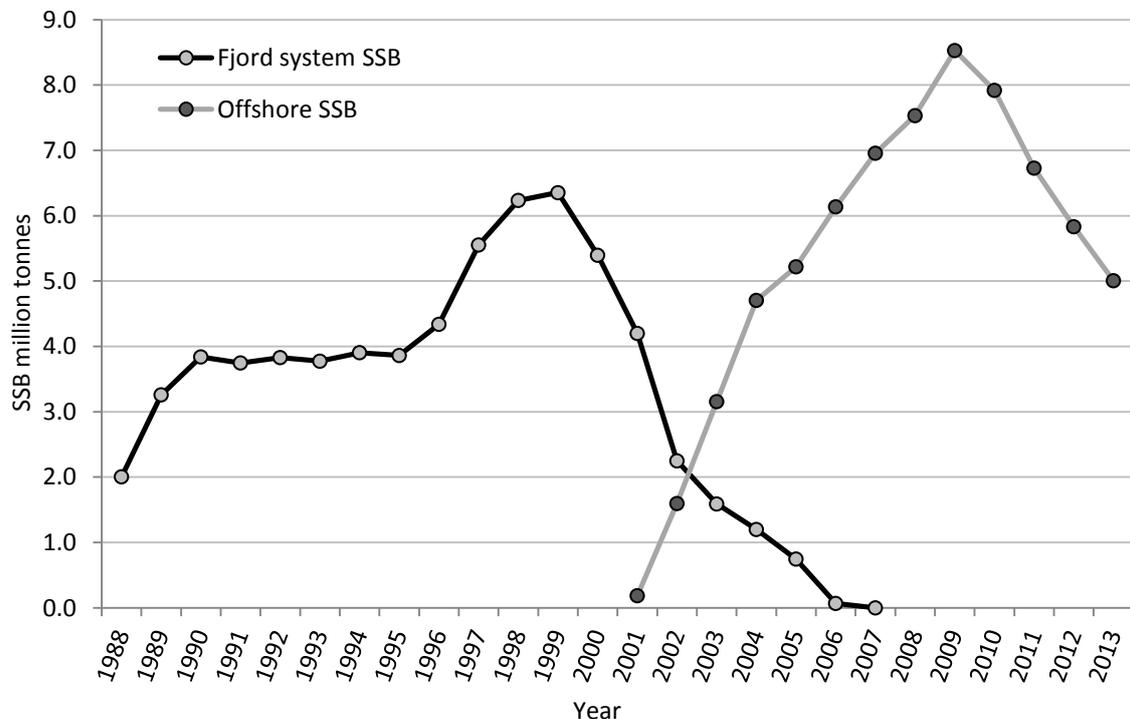


Figure 6.9 - The estimated NSS herring spawning stock biomass (SSB) in millions of tonnes inside the fjord system and offshore in 1988-2013.

The estimated density of herring inside the fjord system was higher compared to offshore in 1998-2005 (Figure 6.10). The density inside the fjords varied between years and was higher in 2002 and 2003 compared to 1999-2001. This change in density was mainly due to changes in the herring distribution inside the fjords (see Figures 6.5 and 6.6 compared to Figure 6.4). The mean density of herring offshore remained low through 2003-2007 despite the large amount of herring wintering in this area due to wide dispersal over this area. In 2006, the densities of NSS herring both inside the fjord system and offshore were estimated to be approximately the same, 0.6 thousand tonnes of NSS herring per square nautical mile.

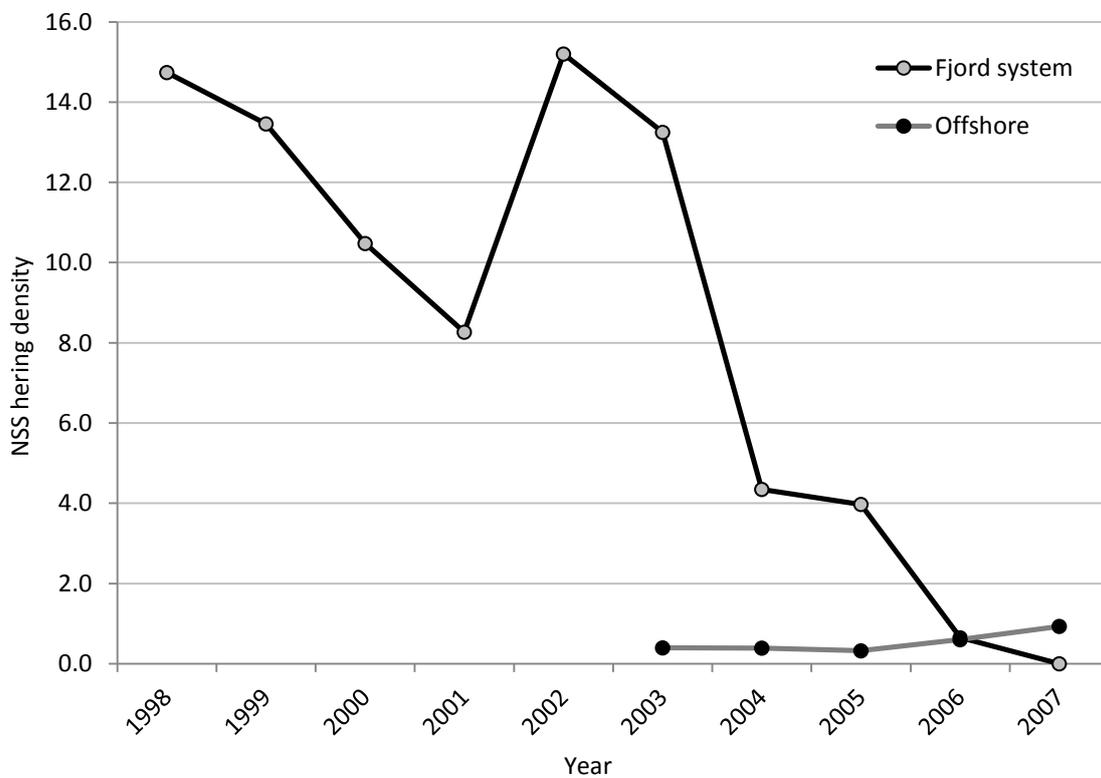


Figure 6.10 - NSS herring density (thousands of tonnes/nmi<sup>2</sup>) inside the fjord system and offshore during 1998-2007.

### 6.3.3 Killer whale individuals and pods

Survey effort and encounter rates of killer whales were variable during 1986-2013 (Table 6.1). For the 23 years investigated inside the fjord system, a total of 656 encounters, revealing 584 identified individuals and 31 pods from good quality photographs were recorded. Most of the identified killer whale pods were encountered in the fjord system area in multiple years during the period of 23 years, showing a high degree of return to the same location (Table 6.2). The identification-catalogue held 686 identified killer whale individuals from northern Norway by the end of the study in 2013.

Table 6.1 - Dates when photo-identification photographs were obtained during October-December in each year (primary sampling occasions) with the number of secondary sampling occasions (weeks) used in the robust design analysis (see Appendix 6.1). Also given are the number of days when whales were photographed (whale days), total number of encounters per year, number of pods identified per year, number of identified adult individuals with good quality photographs used in analysis for each year and the number of new adult individuals identified per year. Location of data collection: FS = fjord system, OF = offshore and AF = Andfjord.

Year (primary sampling occasion)	Dates	No. of sampling occasions (weeks)	Photo-ID collected in	Whale days	No of encounters	No of pods	No of adult ind.	New adults identified
1986	2.10.-23.10.	n.a.	FS	12	13	3	18	18
1987	10.10.-19.10.	n.a.	FS	5	7	3	12	11
1988	20.10.	n.a.	FS	1	3	4	15	13
1989	16.10.-15.11.	n.a.	FS	4	4	2	12	6
1990	16.10.-28.11.	6	FS	27	56	20	159	126
1991	7.10.-18.11.	7	FS	32	73	22	136	65
1992	8.10.-20.11.	7	FS	33	64	23	228	75
1993	16.10.-11.11.	4	FS	18	37	18	109	19
1994	17.10.-22.11.	6	FS	19	25	14	60	7
1995	20.10.-19.11.	5	FS	20	35	20	108	17
1996	30.10.-27.11.	5	FS	12	21	15	97	24
1997	14.10.-19.11.	4	FS	8	14	13	52	1
1998	14.10.-12.11.	4	FS	15	22	16	96	7
1999	21.10.-15.11.	4	FS	13	19	14	94	0
2000	31.10.-12.11.	3	FS	7	15	13	46	0
2001	19.10.-1.12.	3	FS	18	18	13	39	10
2002	23.10.-7.12.	7	FS	36	77	25	141	62
2003	18.10.-5.12.	7	FS	35	70	22	164	52
2004	19.10.-19.11.	3	FS	8	14	9	39	7
2005	5.11.-8.12.	5	FS	20	37	15	90	29
2006	8.11.-29.11.	5	FS	12	19	13	61	29
2007	9.11.-9.12.	n.a.	FS / OF	6 / 3	10 / 3	3 / 0	7 / 0	1 / 0
2008	8.11.-26.11.	n.a.	FS / OF	3 / 1	3 / 1	2 / 2	9 / 12	4 / 10
2013	20.1.-30.1.	n.a.	AF	6	17	1	2	n.a.

The pods encountered in 2007 inside the fjord system represented three killer whale pods (NA, NE and NW) that were commonly encountered in this area in previous years (Table 6.2). During the final field season in the fjord system in 2008, two pods were identified visiting the fjord system in search of herring. One (NB) has been encountered in the fjord system regularly, while the other (NØ) was only occasionally encountered.

Table 6.2 - Killer whale pod ID codes and number of years seen during 1986-2008 inside the fjord system. The pods still seen in 2007 are highlighted in dark grey and the pods seen in 2008 in light grey.

Pod ID	Years seen	Pod ID	Years seen	Pod ID	Years seen
NE	19	NO	14	NØ	6
NG	18	KA	10	Nb	5
NQ	18	NU	10	ND	4
NB	16	NN	9	NS	4
NC	16	NV	9	Ng	4
NA	15	NX	8	Ne	3
NP	15	Nc	8	Na	2
NT	15	Nf	7	Ni	1
NW	15	NR	7	Nj	1
NY	15	NZ	7	NL	1
NÅ	14	NÄ	6		

The number of killer whale individuals and pods encountered per year was quite variable (Table 6.1, Figures 6.11 & 6.12). The number of days with whales and the number of encounters were highest in 1990-1992 and 2002-2003 resulting in more pods and individuals identified (Table 6.1, Figure 6.13). In some of the years, e.g. 1994 and 2006, effort was high but the encounter rate and number of identified individuals recorded was relatively low.

The cumulative number of identified individuals increased sharply in the early 1990s with increased fieldwork effort and levelled out towards the early 2000s (Figure 6.14). In 2002 and 2003 many new identifiable individuals were photographed, and this trend of identifying new individuals continued in the final years of the photo-identification work. The number of identified pods (31) has stayed the same from 1996 onwards (Figure 6.14) partly due to lack of work on social structure and the consequent inability to assign individuals to family pods since the late 1990s.

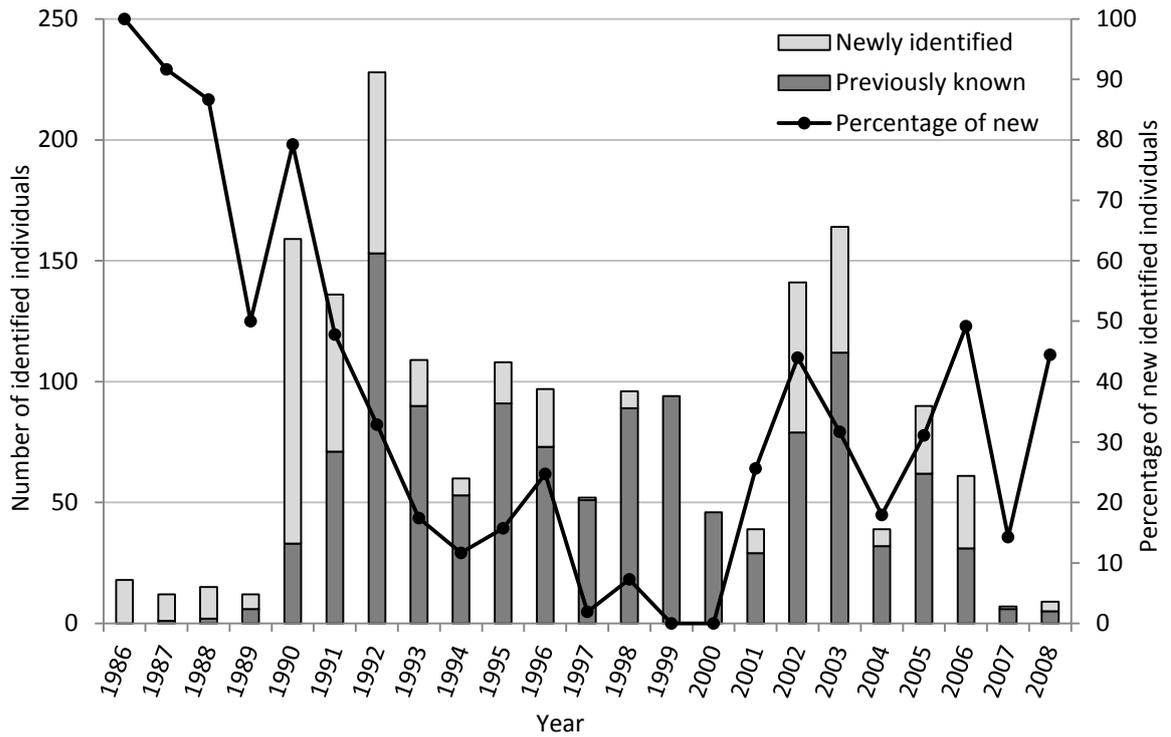


Figure 6.11 - Number of individuals identified per year (whole bars), with the new identified individuals (light grey bar) and the percentage of new individuals identified in the fjord system (black line) 1986-2008.

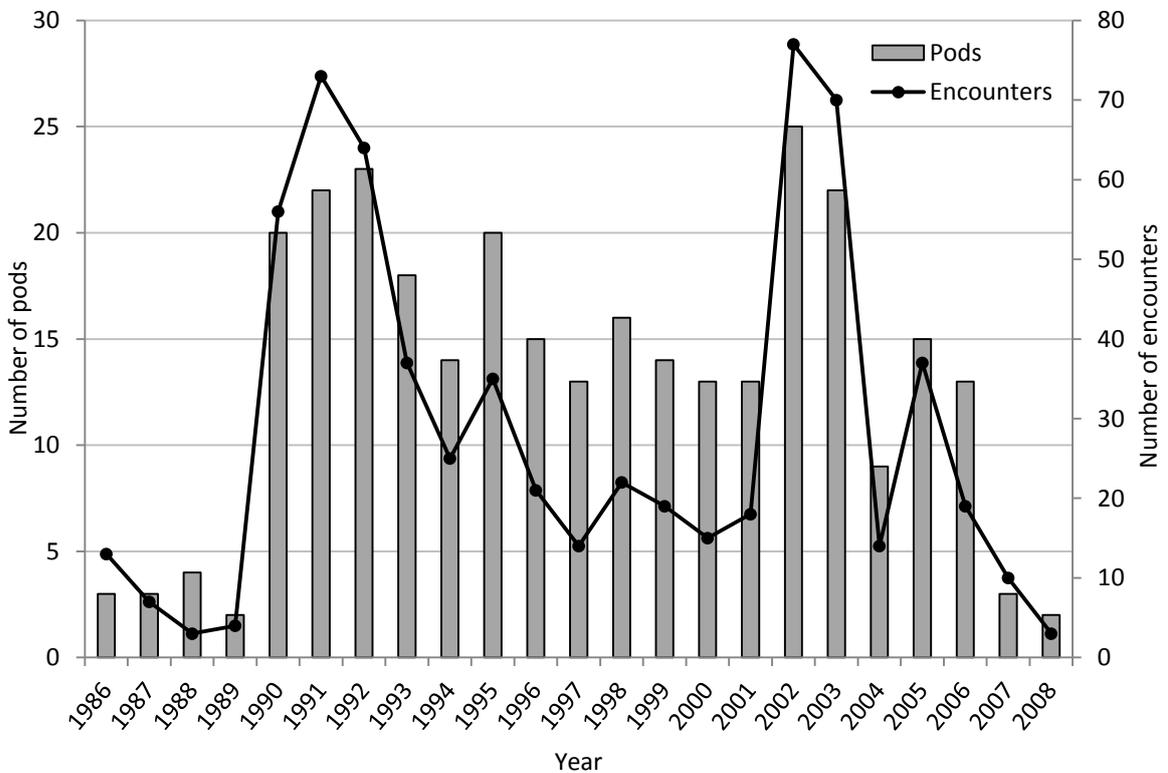


Figure 6.12 - Number of pods identified per year, with the number of encounters per year in the fjord system 1986-2008.

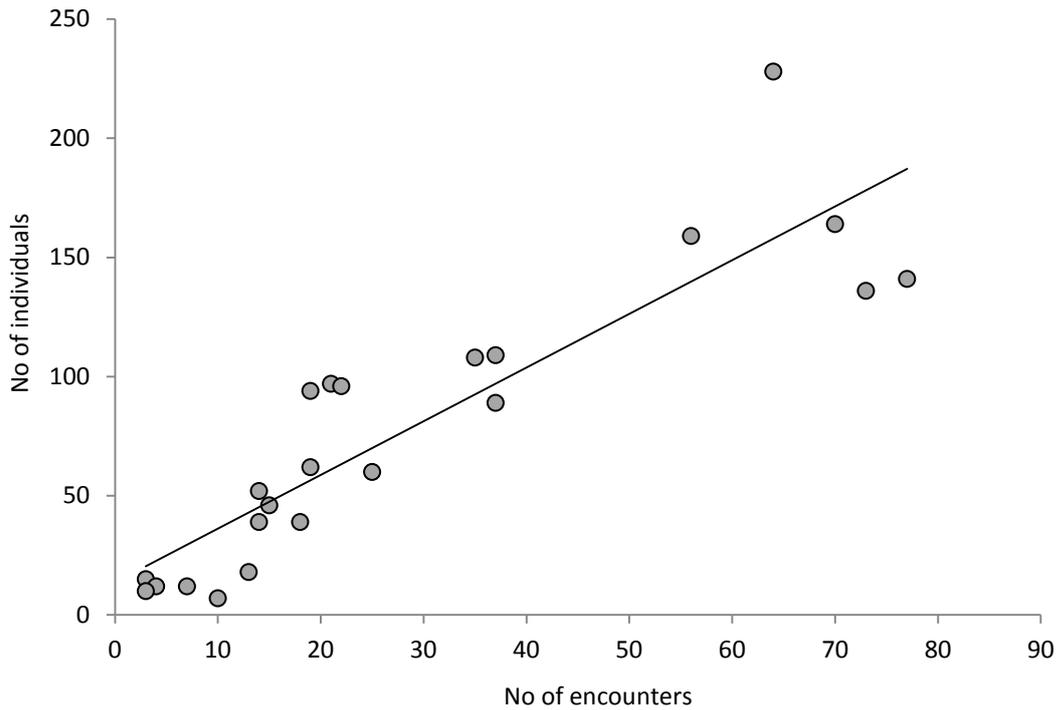


Figure 6.13 - Number of individuals identified plotted against the number of encounters.

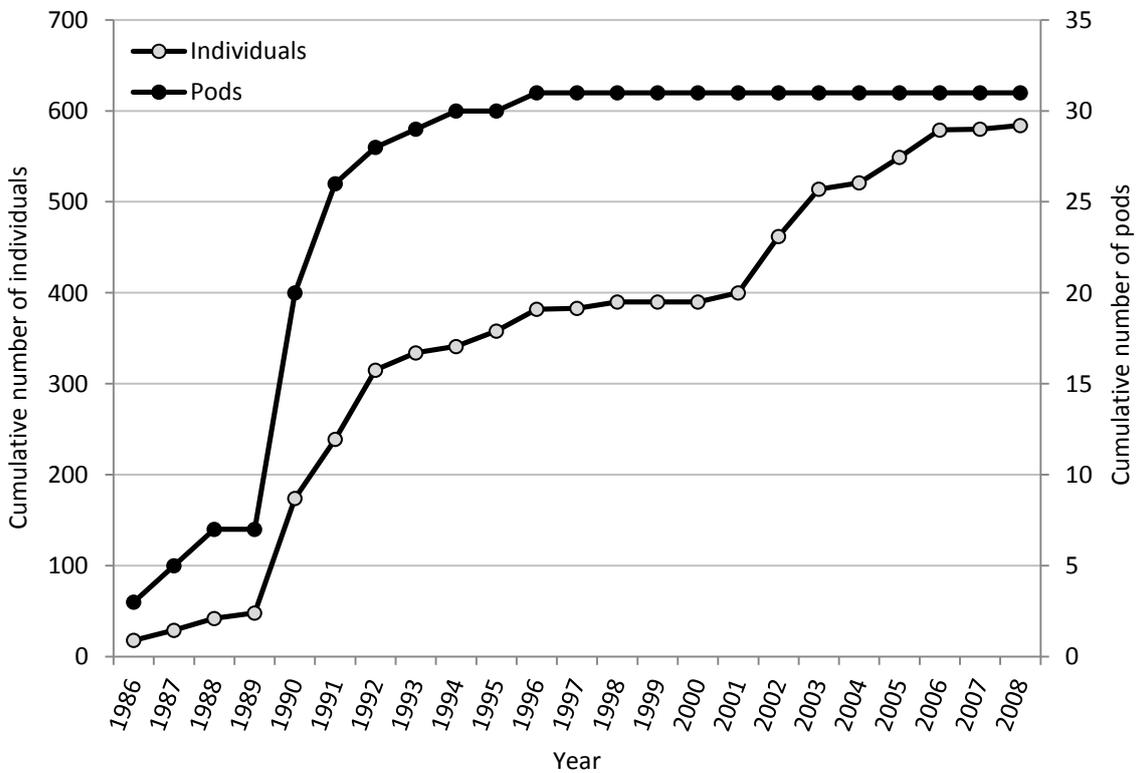


Figure 6.14 - Cumulative number of identified killer whale individuals (grey circles) and pods (black circles) inside the fjord system during 1986-2008.

A total of 231 identifiable individuals were only seen once during the study inside the fjord system (Figure 6.15) and 138 of these were new individuals identified for the first time since 2001. The remaining 356 individuals (60.8%) were seen two or more times during the period of 23 years inside the fjord system.

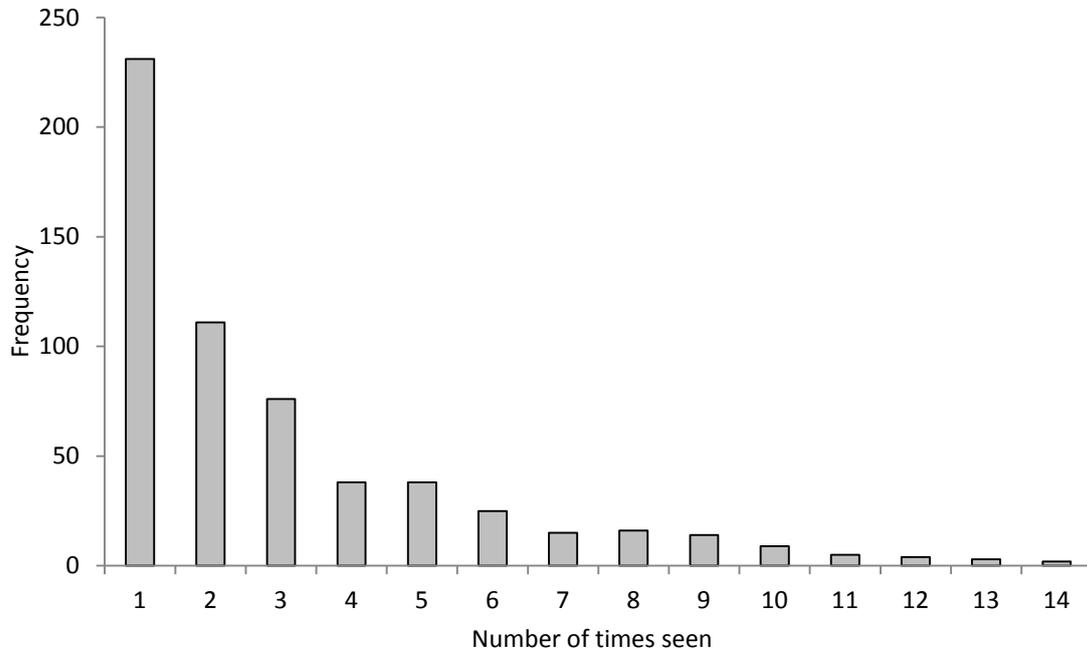


Figure 6.15 - Sighting frequency of killer whale individuals (including sub-adults, juveniles and calves) with good quality photographs during 1986-2008 inside the fjord system.

#### 6.3.4 Killer whale activity budget

The activity budgets of killer whales in northern Norway varied considerably between the early 1990s, 2005 and 2006 (Figure 6.16). Time spent travelling/foraging in the early 90s was 40% (Similä 1997a); this increased by 60% to 64% (SE = 2%) in 2005 and to 74% (SE = 6%) in 2006, a further increase of 16%.

Time spent feeding experienced little change; 25% in the early-90s and 26% (SE = 6%) in 2006. Time spent playing/socializing declined markedly from 17% in the early-90s to 4% (SE = 1%) in 2005, a 76% decline in this behaviour. In 2006, the time spent in this behaviour was 0%.

A similar change was apparent in time spent resting. In the early-90s killer whales spent 18% of their daytime resting (Similä 1997a), but in 2005 this had declined to only 13% (SE = 1.6%), a decline of 28%, which declined further to 0% in 2006.

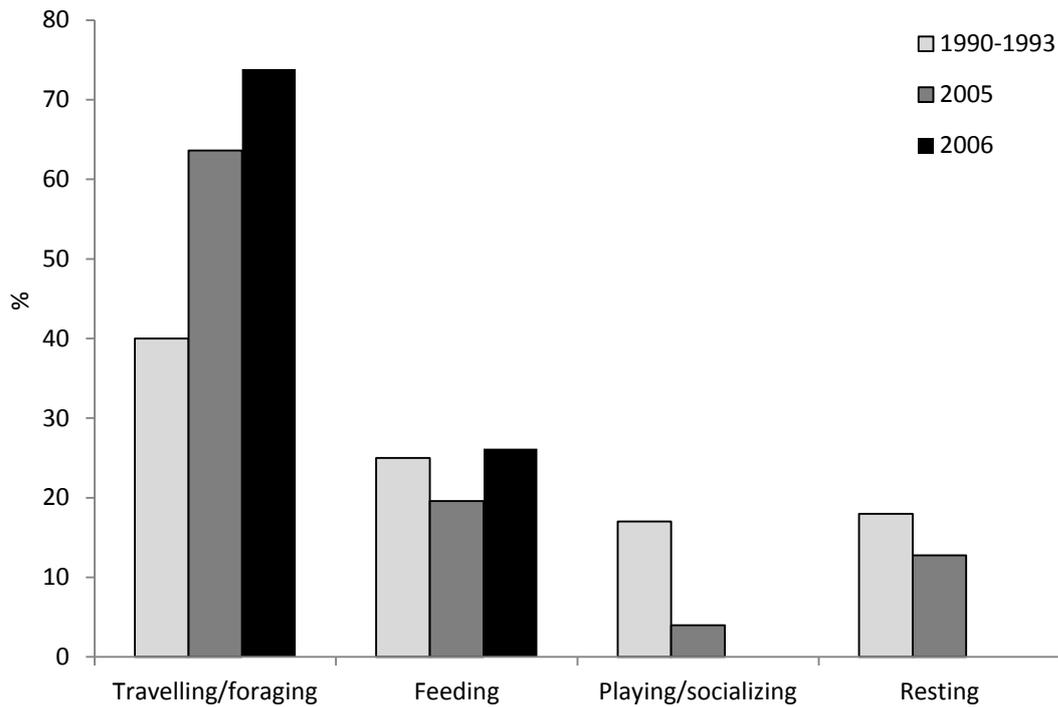


Figure 6.16 - Activity budget of killer whales in 2005 and 2006, compared to results from the previous study of Similä (1997a) using data from 1990-1993.

### 6.3.5 Distribution of killer whales inside the fjord system

The whale-watching sighting records of Orca Tysfjord indicated that killer whale sightings were mostly made inside Tysfjord between 2002 and 2005, declining steadily from 78% to 66% of days (Figure 6.17). A marked change was seen in 2006 when killer whales were seen inside Tysfjord on only 21% of days but were encountered in the Vestfjord area on 66% of days. A similar pattern was seen in 2007 and 2008.

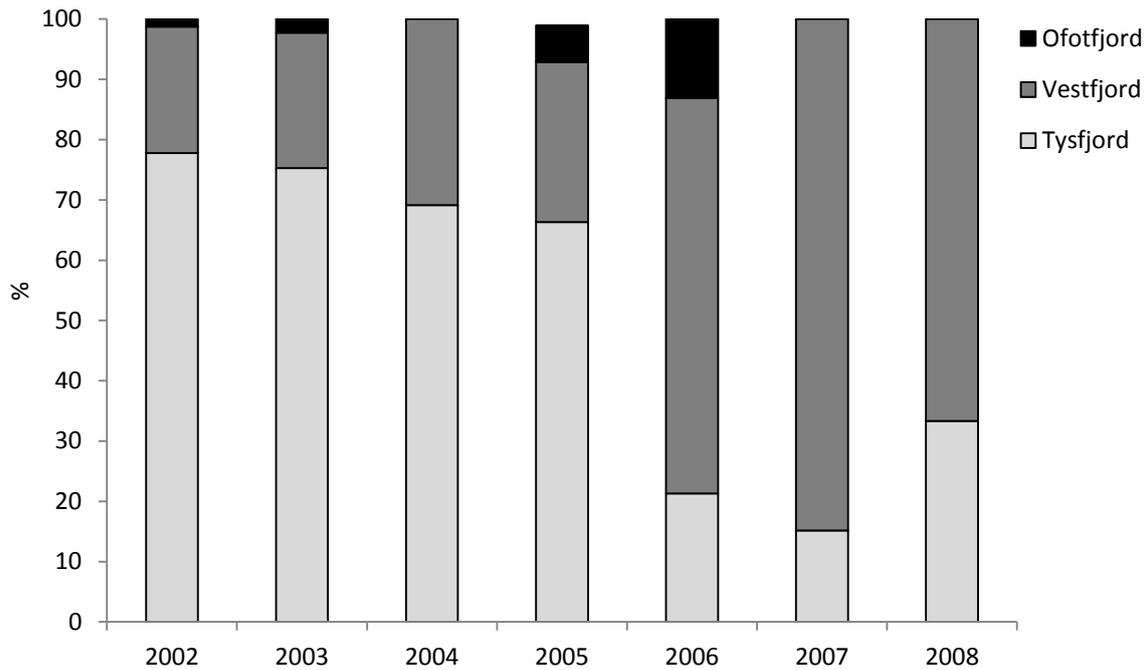


Figure 6.17 - Percentage of killer whale sightings made in Tysfjord, Vestfjord and Ofotfjord by the whale-watching company Orca Tysfjord in 2002-2008.

### 6.3.6 Fisheries and other predators of NSS herring

The NSS herring fisheries catches increased inside the fjord system during 1988-1999 (Figure 6.18). From 2000 onwards these catches decreased steadily until a major decrease in 2006. By 2007 the fjordic catches were taken only by small scale local fishing effort and were mainly composed of Norwegian autumn spawning herring (Husebø et al. 2005) and small local stocks.

In contrast, catches of NSS herring in the offshore area were small during 1991-2004 but increased rapidly in 2005 and 2006 to approximately 120,000 tonnes landed in 2005 and ~280,000 tonnes landed in 2006, the year in which fjordic catches dropped to ~63,000 tonnes (Figure 6.18). Since 2006, the large majority of wintertime catches have been taken in the offshore areas off Vesterålen.

Catches of other species showed an increase in fjordic catches of cod until 1995 (Figure 6.19), with ~5,900 tonnes landed in that year. From 1996, the annual catch of cod decreased and stabilized at 270 - 490 tonnes landed during 2006-2010 from the fjord system. Catches of saithe showed a similar increase until 1995. However, after three years with lower catches, the catches of saithe increased again from 1999, reaching the highest catch in 2002 with ~9,100 tonnes landed. From 2003, the catches of saithe decreased in the fjord system, to between 1,000 and 2,000 tonnes landed annually in 2007-2010.

Chapter 6 – NSS herring distribution change

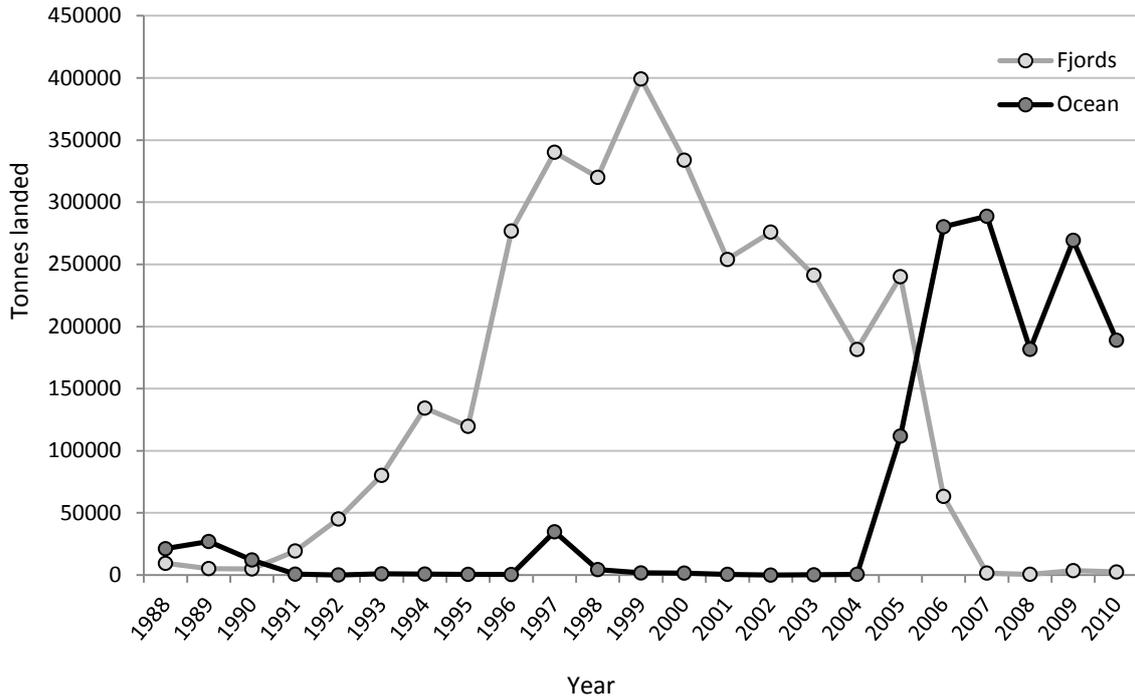


Figure 6.18 - The NSS herring fisheries catches in the fjord system and offshore in 1988-2010 based on records of the Directorate of Fisheries.

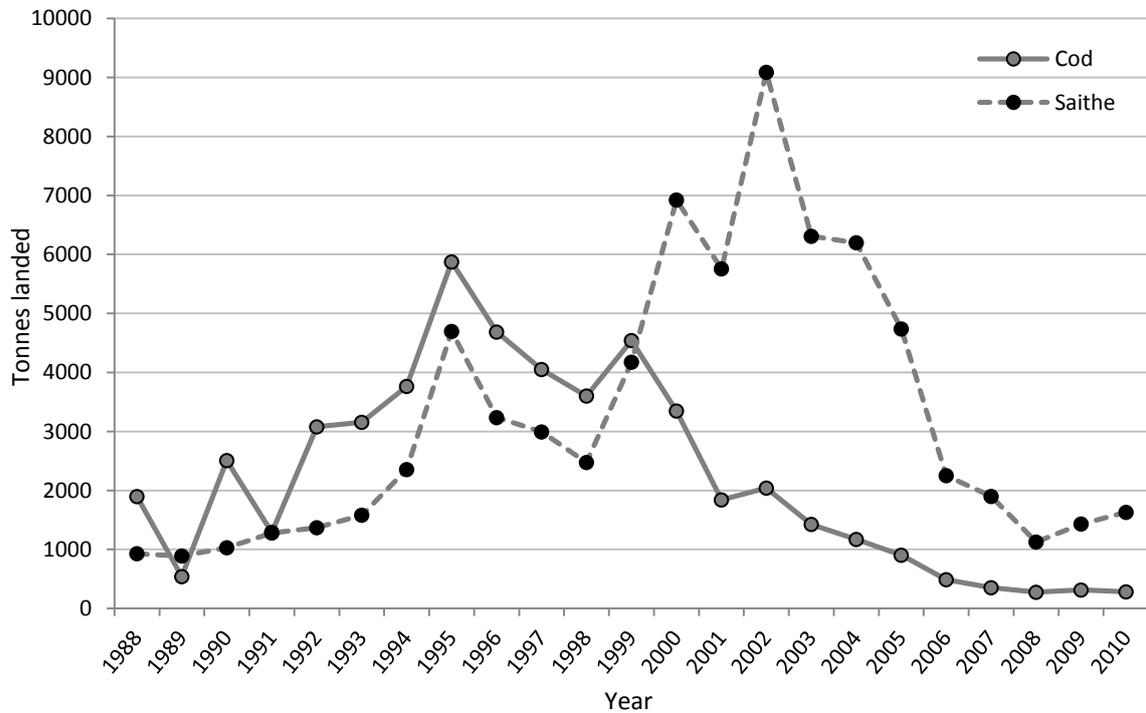


Figure 6.19 - Catch records of cod and saithe inside the fjord system in 1988-2010 based on records of the Directorate of Fisheries.

### 6.3.7 Predator abundance and predator-prey ratio

The indices of killer whale pod and individual abundance indicate the arrival of killer whales to the fjord system in large numbers from 1990 onwards (Figure 6.20). The highest number of killer whale encounters was in 1992 and the highest number of pods was in 2002. Since 2003, the indices of killer whale pods and individuals declined. The index of herring fisheries catches gradually increased during the 1990s, reaching a peak in 1999 (Figure 6.21). From 2000, herring catches decreased inside the fjords. Fisheries seemed to leave the fjords earlier than the killer whales, as between 2005 and 2006 the fisheries index decreased strongly from 0.60 to 0.16. At the same time, there was a smaller decrease in killer whale pod and individual indexes. A marked decrease in killer whale pod and individual indexes took place between 2006 and 2007.

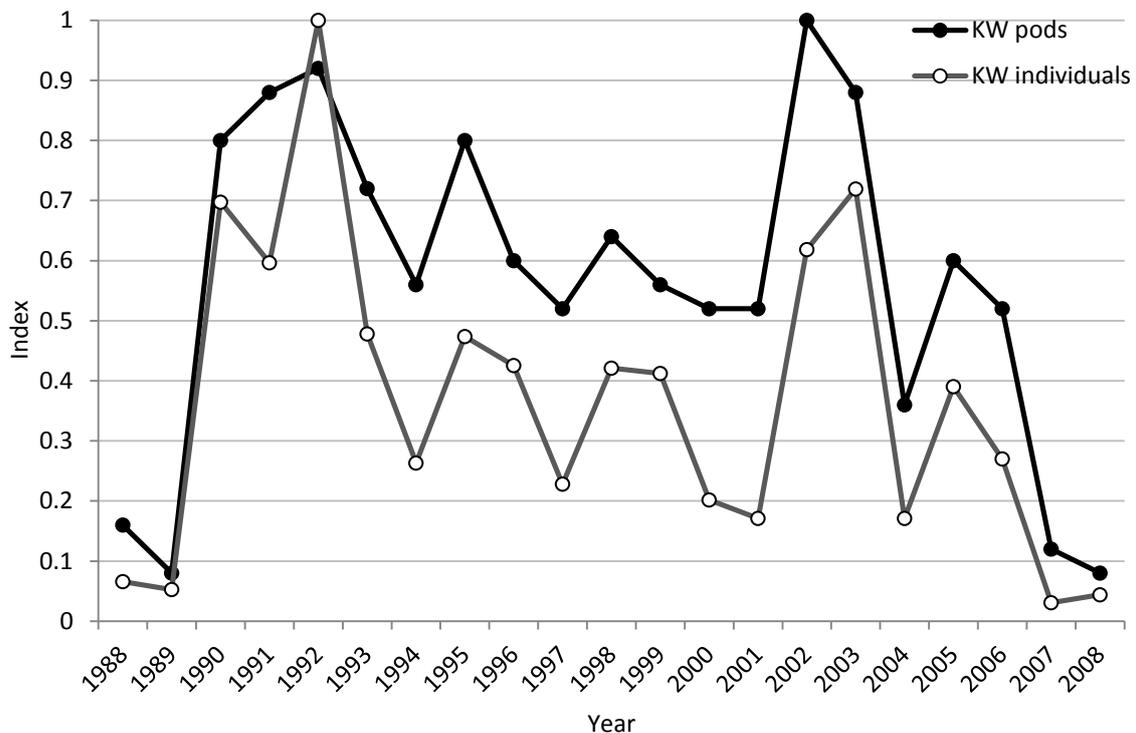


Figure 6.20 - Indices of killer whale pod and individual abundance (encounters per year/max encountered) during 1988-2008 inside the fjord system.

The percentage of NSS herring catch taken inside the fjord system of the total NSS herring catch taken in Norwegian waters (ICES Advice 2013), shows that during 1991-1995, when the fjord system catch was low, it represented 46-91 % of all the NSS herring catch made (Figure 6.21). The percentage of NSS herring catch taken inside the fjord system stayed high

until 2004. In 2005, it declined to 48% and declined further to 14% in 2006. Only 5% and 1% of NSS herring catches were made inside the fjord system in 2007 and 2008, respectively.

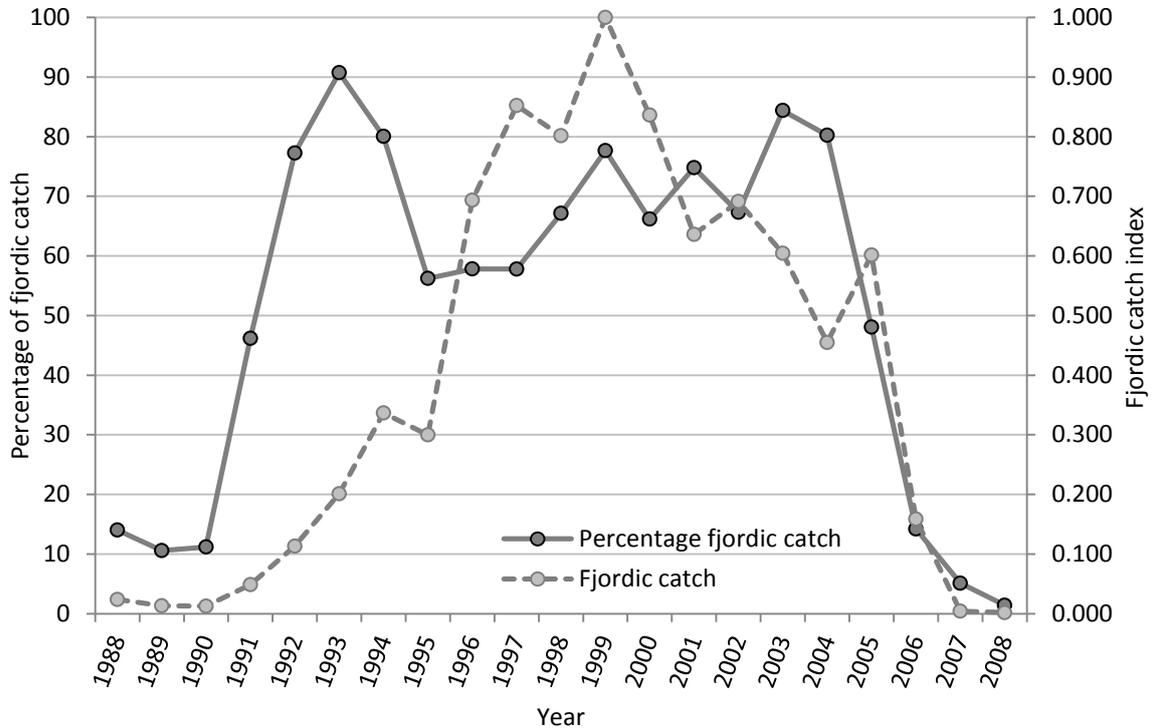


Figure 6.21 - Fisheries index (annual catch/maximum catch) and percentage of fjord system catch of total NSS herring catch in Norwegian waters during 1988-2008 inside the fjord system.

The number of killer whale pods encountered in relation to NSS herring biomass inside the fjord system remained fairly stable (slight decline) during 1990-2001 (Figure 6.22). From 2002, a general positive trend was established in this index and in 2006 it increased markedly. The number of killer whale individuals in relation to NSS herring biomass shows a comparable trend to that of pods.

The fisheries catches in relation to NSS herring biomass showed an increasing trend during the period 1990 to 1996, were stable from 1996 to 2001, and then increased again from 2001 to 2006. There was an increase in 2005 and a marked increase in 2006.

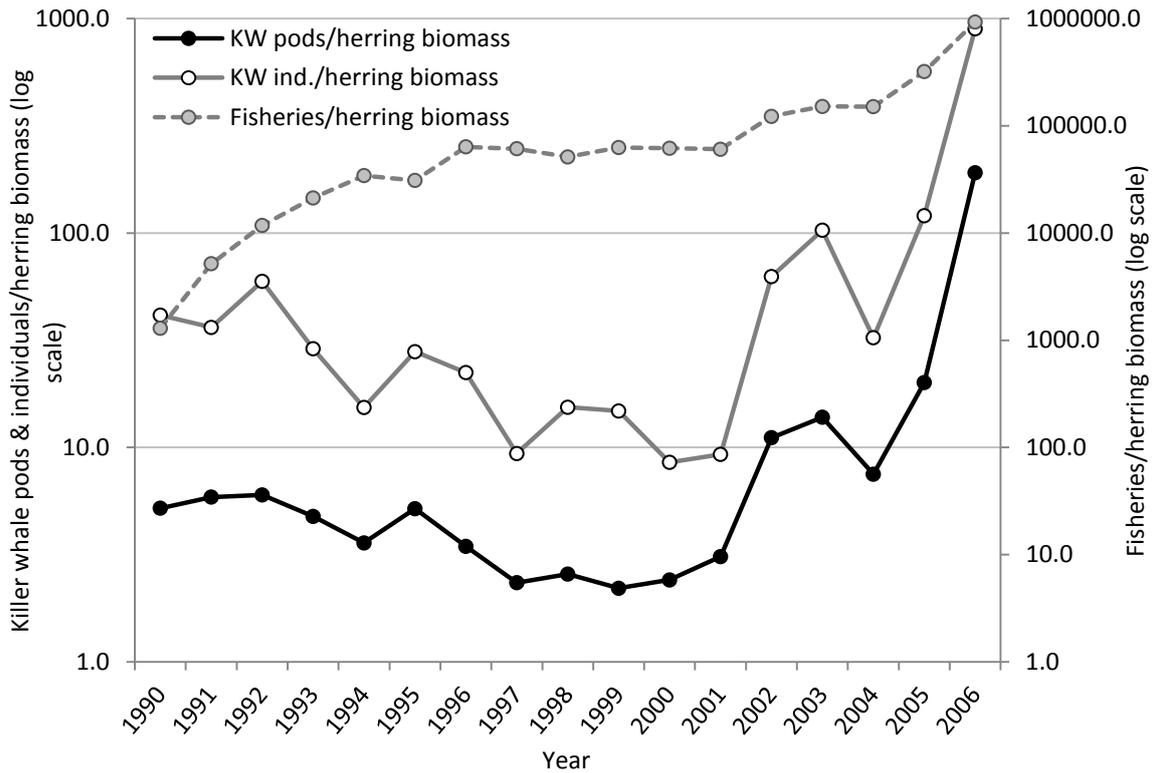


Figure 6.22 - Number of killer whale pods, individuals and fisheries catches divided by the NSS herring biomass inside the fjord system during 1990-2006. Note that the vertical axes are on a log scale.

### 6.3.8 Killer whale individuals identified offshore and in Andfjord

The offshore areas were visited on three days in December 2007 and on four days in November 2008. In 2007, only poor quality photographs were obtained during two days of photo-identification effort, from which four individuals previously encountered inside the fjord system were identified. One of these individuals was a member of pod NG. In 2008, one day of photo-identification effort yielded good quality photographs, which revealed two individuals previously identified inside the fjord system belonging to pods Nc and NG. Poorer quality photographs revealed three other previously known individuals belonging to pods NC, NG and NX.

A large number of killer whales were encountered in Andfjord during 20-30 January 2013. On days with good visibility, up to six different killer whale groups were seen in the area at the same time. These killer whales were observed feeding on the NSS herring found in this area by driving herring against the shore line and also by using the carousel feeding method (Similä & Ugarte 1993). The dominant categories of behaviour observed in this area were travelling/foraging and feeding. Only on a few occasions were killer whales observed resting or socializing. Photo-identification photographs of killer whales were obtained on six days in

Andfjord in January 2013 (Table 6.1). Good quality photographs were taken on three of these days but only two individuals previously known from the fjord system were identified, one of which was identified as belonging to pod NØ.

## 6.4 DISCUSSION

### 6.4.1 Wintertime distribution of NSS herring

The importance of migration generally is understood as a way of maximizing fitness and as an adaptation to exploiting patchily distributed resources for feeding and reproductive purposes (Corkeron & Connor 1999; Stevick et al. 2002). Migration between locations can also be beneficial to avoid predation and therefore increase survival (Corkeron & Connor 1999). The NSS herring stock has been documented to alter its migration route due to numerical changes resulting from variable year-class sizes, overfishing or due to changes in climate (Holst et al. 2004; Sissener & Bjørndal 2005; Huse et al. 2010). In the situation when the younger NSS herring year-classes dominate and do not follow the migration pattern of the older NSS herring, an opportunity to learn the route to previous (potentially beneficial) wintertime location is lost and a new wintertime area is formed (Huse et al. 2010).

Wintertime is a very different kind of time for NSS herring compared to the spawning and feeding seasons. During winter the herring does not feed or reproduce (Slotte 1999; Nøttestad et al. 2004) but needs to conserve energy, which is done by limiting movement and by using a specialized “rise and glide” strategy (Huse & Ona 1996). Wintertime is also characterized by predator avoidance (Nøttestad 1998; Huse et al. 2010). The NSS herring migrates vertically in deep water during daytime and also displays a number of anti-predator schooling formations and gas-bubble release to avoid predation (Huse & Ona 1996; Nøttestad 1998; Nøttestad et al. 2002).

The importance of location in wintertime for NSS herring is unclear. Given that winter is the time for NSS herring to conserve energy, avoid predators and survive to the spawning period, it is possible that the fjords could offer certain benefits for NSS herring. The bathymetry of the fjords can potentially help the formation of denser schools of herring. The density of the herring was much higher inside the fjord system compared to offshore between 2003-2005, even when the abundance of NSS herring was much higher at offshore. Being part of a dense school is a type of predator avoidance strategy because it reduces the risk of an individual herring being eaten (Nøttestad et al. 2004). From the predatory aspect, the fjord

system provided more protection from predation compared to the offshore area because the fjord system lacked the large baleen whale predators. In Andfjord, large numbers of humpback whales (*Megaptera novaeangliae*) and some fin whales (*Balaenoptera physalus*) were observed to be present and feeding on the abundant NSS herring stock in addition to large number of killer whales (observations by the author), increasing the natural mortality of the NSS herring compared to the situation observed in the fjord system.

It is evident that the NSS herring stock works as a driving force in this Norwegian Sea ecosystem, due to its large stock biomass and wide distribution in the northeast Atlantic. A number of predators, including killer whales, cod and saithe, react to these changes in the distribution of this prey species. Prey distribution also affects seasonal occurrence and distribution of predators in other locations around the world. Interactions between resident killer whales feeding on Chinook salmon (*Oncorhynchus tshawytscha*) in the NE Pacific (Ford et al. 2000) and long-beaked common dolphins (*Delphinus capensis*) feeding on South African sardine (*Sardinops sagax*) off the east coast of South Africa (O'Donoghue et al. 2010) have been studied.

#### **6.4.2 Number of killer whale individuals and pods inside the fjord system**

The number of identified individuals and pods inside the fjord system was high during 1990-2006 but, despite the research effort being very high in 2007 and 2008, very low numbers were encountered inside the fjord system in these years. Individuals encountered in the fjord system in the final fieldwork years represented a mixture of well-known and other individuals. At the same time, fishermen reported large numbers of killer whales in the offshore area. The killer whales pods encountered inside the fjord system in 2007 and 2008 were different family pods, and therefore there was no indication of particular pods using the fjord system more systematically and for an extended period of time.

In 2007 and 2008, more adult females were encountered than adult males, compared to the opposite pattern in earlier years. This could be due to females showing higher site fidelity to the fjord system compared to adult males, as was shown by the robust design analysis (see Appendix 6.1). The potential reasons for females showing higher site fidelity to the fjord system are further discussed in section 3.4.4 in Chapter 3 and in section 7.3 in Chapter 7. Other studies implementing the robust design framework e.g. on bottlenose and Guiana dolphins (Silva et al. 2009; Cantor et al. 2012; Daura-Jorge et al. 2012; Nicholson et al. 2012) and transient killer whales (Ford et al. 2007) have not been able to estimate sex-specific temporary emigration rates.

Each year since 2001, newly identified individuals were recorded. New individuals could have been identified for various reasons: normal recruitment into the population, a change from film to digital photography in 2001 (Markowitz et al. 2003), or a potentially increased reproductive rate following the increase in prey abundance throughout the 1990s. The reproductive rate of resident killer whales was shown by Ward et al. (2009) to increase during years of high salmon abundance. For more discussion on this see section 2.4.2 in Chapter 2. At the same time as new individuals were identified, the number of pods has remained the same since 1996. This is a result of a lack of studies on social structure after the late 1990s (Similä 1997a) resulting in no more pods being able to be assigned.

A consistent detailed record of annual photo-identification effort is lacking. If effort data had been available, it would have been possible to make an attempt to take it into account when comparing the variable number of individuals and pods identified across years.

#### **6.4.3 Change in distribution of killer whales**

Tysfjord was the main area where killer whale sightings were made in 2002-2005 based on the whale-watching company records. Before 2002, killer whales were also mostly sighted in Tysfjord (pers. comm. Per Ole Lund). In 2006, there was a sharp decrease in whale-watching sightings made inside Tysfjord, with most of the sightings in the Vestfjord area. A change in killer whale presence and area in 2006 was also evident for the research team and locating killer whales was a greater challenge compared to previous years. The IMR's herring surveys found that the NSS herring remaining in the fjords was distributed in Vestfjord in 2006, which corresponds with the killer whale observations in this area. This change in the area where whales were sighted also coincides with the decrease in NSS herring density, which in this year was the same in the fjord system as offshore.

Killer whale sightings were increasingly reported by fishermen in the offshore area since 2006. Due to logistical challenges associated with the offshore area during winter (wind, swell and light), these areas were not able to be consistently covered for photo-identification work, creating a lack of data from this area and also a gap in the long-term photo-identification dataset for the killer whale population.

In January 2011-2013, killer whales were reported in the Andfjord area. While the NSS herring stock had mostly dispersed into a wide area offshore, a part of this stock remained in the fjords east of Andøya. Dedicated photo-identification work on killer whales was conducted in Andfjord in January 2013, but only two individuals were identified as previously known from the fjord system.

One potential reason behind the difficulties to identify individuals encountered in Andfjord is the six year gap (between November 2006 and January 2013) in dedicated photo-identification effort. As discussed above, new identified individuals were assigned each year since 2001. Assuming a similar rate of new individuals during years lacking photo-identification data, approximately 70 new identifiable individuals would have been present in the population in January 2013. During the gap in the dataset, it is likely that younger individuals (that previously were not identifiable) were now grown to be identifiable adult individuals. The NSS herring stock biomass also remained high and could have positively affected killer whale reproductive rates (Ward et al. 2009; Ford et al. 2010) and resulted in an increase in new individuals born into the population. In this context, the population viability analysis presented in Chapter 4 indicated an increasing population under the baseline scenario. It is also possible that due to the distribution of killer whales changing from the fjord system to offshore, mixing with other killer whale populations present in the Norwegian and Barents Seas has or will occur. Foote et al. (2009) identified two sympatric killer whale types in the NE Atlantic. Sympatric killer whale populations also occur in the Pacific (Bigg et al. 1987; Ford et al. 2000) and in Antarctic waters (Pitman & Ensor 2003; Olson et al. 2012).

Many killer whale pods were observed in Andfjord, together with numerous humpback whales also feeding on the NSS herring present in this fjord. Additionally, sightings were made daily of fin whales passing through the fjord and feeding on NSS herring. This was a unique situation with both killer and humpback whales using the same area and feeding side by side on the NSS herring. It was unclear if one or the other of killer whales or humpback whales initiated feeding and the other species then opportunistically fed on the herring. Predation attempts by killer whales on humpback whales have been recorded, including in the North Atlantic (Jefferson et al. 1991; McCordic et al. 2013). Foote et al. (2009) also described a type 2 killer whale in the North Atlantic that feeds on minke whale (*Balaenoptera acutorostrata*). However, aggressive behaviour between the two species was not recorded in Andfjord. The very abundant herring prey likely favours killer whales targeting this species. Killer whales attacking humpback whales has not been described in Norwegian waters (Jefferson et al. 1991).

#### **6.4.4 Altered activity budget**

A change in the killer whale activity budget inside the fjord system was recorded during 2005 and 2006 compared to previous work done in the early 1990s (Similä 1997a). The time spent travelling/foraging increased to 64% and 74% of time spent in this behaviour during 2005 and

2006, respectively, compared to 40% of time spent on this behaviour in 1990-1993 (Similä 1997a). This likely was due to reduced biomass and density of herring found inside the fjords. As a result there was a need for killer whales to search for scarce prey in a much larger area and to increase their time spent travelling/foraging. In the study by Similä (1997a) made on the activity budget of killer whales in the offshore area during summer, it was found that 60% of daytime activities of killer whales were travelling/foraging. These results suggest that during the time when herring is more dispersed, as was the case in the fjord system in 2005-2006 and in the offshore area, killer whales increase their time spent in this behaviour.

Time spent playing/socializing experienced a marked decrease in 2005, and was completely absent in 2006. Similarly, time spent resting decreased in 2005 compared to the early 1990s and was not observed within the fjord system during daytime in 2006. It is possible that socializing or resting activities took place during the hours of darkness but this could not have been observed. Both activity budget datasets, in the early 1990s and 2005-2006, were collected during daylight hours.

Time spent feeding was the behavioural state that experienced the least change. The least time spent feeding for this population has been recorded during summer in the area outside fjords; 15% of daily activity budget (Similä 1997a). Limited variability in this behavioural state could result from daily energetic requirements of killer whales (Williams et al. 2004; 2011b). Comparison with the activity budget of the resident killer whales from the NE Pacific was not feasible due to activity states being categorised differently (Williams et al. 2006; Lusseau et al. 2009).

It is worth noting that the dataset available to calculate the activity budget for 2005 and 2006 was limited compared to the dataset used by Similä (1997a). In addition, during 2005 and 2006 focal groups included an individual that was tagged with a suction cup tag (Dtag). Therefore, the focal groups' behaviour could have been influenced during the tagging effort. However, the behaviour of killer whales is reported to return to normal quickly after tagging effort ceases. The impact of suction cup tags on behaviour is considered to be minor, very short lived and not to affect the behavioural state following tagging (Baird 1998; Baird et al. 2005). As behavioural state was recorded only after the tagging effort ceased, it is assumed that the behaviour of the killer whales was natural.

In 2007 and 2008, the overall impression was that killer whales came into the fjord system occasionally, travelled quickly through the area in search of the remaining NSS herring and left the fjord system within a few days. It is possible that killer whale behaviour observed in these final years was mirroring the "scouting behaviour" previously described for this killer

whale population during 2000 and 2001 (Similä et al. 2002; Stenersen & Similä 2004). The satellite tagging work by Similä et al. (2002) highlighted a situation where killer whales travelled temporarily away from the fjord system containing the whole spawning stock of NSS herring to the offshore areas with the assumed objective to keep an eye on the movements of the dynamic NSS herring stock. It is possible that killer whales continue to use this method of scouting in an area previously known to be abundant with prey even when the main wintering area of the NSS herring has changed.

#### **6.4.5 Habitat preference of killer whales**

Killer whales were observed in the fjord system in large numbers since 1990, immediately after the whole spawning stock of the NSS herring started wintering in this area. In the later part of the time series, however, there was a time lag of four years between first signs of NSS herring distribution change (in 2002) and reduced killer whales presence (in 2006). Furthermore, it took one more year for the fjords to be only seldom visited by the killer whales. This indicates that killer whales preferred to stay inside the fjords longer than the biomass of NSS herring present inside fjords would suggest.

Some abiotic factors, such as the bathymetry of the fjords, tide and daylight at this latitude, could potentially influence the preference of killer whales to use the fjord system compared to the offshore area. The bathymetric properties of the fjord system, with several shallow areas present along the shoreline of the fjords, could have provided killer whales with an opportunity to more easily herd the NSS herring into tight balls for carousel feeding events (Similä & Ugarte 1993), and the shallow areas also prevented the herring from escaping to depth. The studies of Similä (1997a; b) showed that killer whale feeding behaviour was mostly observed in these shallow areas of the fjords, in waters less than 200 m deep. Feeding in shallower waters can potentially also save energy by avoiding the need to dive into deeper waters (Similä 1997b; Williams et al. 1999). Similä (1997a) also recorded that feeding behaviour was positively correlated with the rising tide, and that this potentially also helped to drive the herring close to these shallow waters areas. Additionally more daylight is available in the fjord system (68°N) compared to the offshore area (70°-71°N). The presence of daylight allows visual cues for killer whale while herding herring (White et al. 1971; Similä 1997b). The white ventral colouring of killer whales can also work as a visual scaring effect to the herring during daylight close to the surface and therefore aids the herding of herring (Similä & Ugarte 1993).

The density of the NSS herring stock was calculated to have been higher inside the fjord system compared to offshore until 2006, when the mean densities were estimated to be about the same in both areas. This was because the NSS herring located offshore, even when at higher biomass, was very widely dispersed in the open ocean. It is likely that the density of the NSS herring played a major role in killer whales choosing their wintertime location. A marked change in killer whale sighting rate inside the fjords was experienced only in 2006, when the densities of NSS herring was the same in both areas.

Based on the robust design mark-recapture analysis, adult female killer whales showed a higher site fidelity to the fjord system compared to adult males (see Chapter 3 and Appendix 6.1). Several reasons might explain the higher dispersal behaviour of adult males, e.g. searching for prey from larger area and the energetic cost of travel being higher for females due to their smaller body size (Williams & Noren 2009). Wintertime has also been reported to be the peak season for killer whales for calving (Christensen 1984) which may increase the importance of the sheltered fjord system habitat for females with calves during winter.

#### **6.4.6 Plasticity of killer whales to change**

In this study, it was observed that killer whales changed their distribution according to a change in their prey distribution, indicating the capability to alter their use of habitat. The satellite tagging study conducted in 2000 and 2001 showed that tagged killer whales were keeping track of the distribution of NSS herring by temporarily visiting the known herring spawning and feeding areas outside the fjord system (Similä et al. 2002; Stenersen & Similä 2004). This shows a remarkable adaptation to the natural behaviour of their prey species, which historically is known to alter its migration route at uneven intervals (Dragesund et al. 1997; Huse et al. 2010).

It was also shown in this study that killer whales sighted inside the fjord system in lower food abundance years in 2005 and 2006, increased their time spent travelling/foraging compared to the years of high food abundance in early 90s (Similä 1997a). Therefore, killer whales adapted their activity budget based on the availability of prey. Behaviour of killer whales inside the fjord system has also been reported to change in relation to feeding method. During the 1990s, killer whales were encountered more and more feeding around the purse seine vessels fishing on NSS herring, instead of being engaged to active carousel feeding behaviour (see Chapter 2). This presents an adaptation for the feeding behaviour with least energetic cost.

The previous major stock collapse of the NSS herring took place in the late 1960s (Dragesund et al. 1997; Toresen & Østvedt 2000). At this time there was no research conducted on killer whales in the Norwegian Sea and it is not known how killer whales adapted to the very low NSS herring abundance years. In periods of low availability of the NSS herring, it is probable that killer whales are able to switch to feeding on other available prey species. Another potential prey species for killer whales in northern Norway is mackerel (*Scomber scombrus*) (Similä et al. 1996). The spawning stock biomass of mackerel was estimated as 2.46 million tonnes in 2012 (likely strongly underestimated) and is widely distributed in the northeast Atlantic (ICES 2013). Additionally killer whales are reported to have fed on saithe, cod, eider duck (*Somateria molissima*) (Similä et al. 1996) and on Atlantic salmon (*Salmo salar*) (Vester & Hammerschmidt 2013). Some evidence also suggests that certain pods of these killer whales may feed on seals (Similä et al. 1996; Vongraven & Bisther in press).

Prey switching has been suggested for transient killer whales in the NE Pacific. Commercial catching of large whales during 1940s-1970s caused a decline in large whale abundance. It has been claimed that, as a result, transient killer whales changed from feeding on large whales to smaller marine mammals, consequently causing declines especially in seal, sea lion and sea otter abundance (Estes et al. 1998; Springer et al. 2003; Whitehead & Reeves 2005; Trites et al. 2007; Wade et al. 2009). Switching from a preferred prey species to another can potentially lead to lowered body condition and ultimately lead to a decline in predator abundance due to changes in the nutritional quality of the prey. The so called “junk-food hypothesis” has been suggested for the decline of Steller sea lions which happened after a decline in the variability of their diet (Rosen & Trites 2000). The NSS herring has a high lipid content, which is particularly high after the feeding period spent in offshore waters (Slotte 1999). A decline in the abundance of the nutrient rich NSS herring could be expected to result in changes in survival and reproductive rates of killer whales. Resident killer whales in the NE Pacific have been recorded to respond to changes in their salmon prey abundance with lowered survival and reproductive rates (Ford et al. 2010; Ward et al. 2011), indicating that prey availability plays an important part in determining population viability. Low prey availability has also been shown to negatively influence the body condition and reproductive rate of fin whales in the North Atlantic (Williams et al. 2013).

A decline in the biomass and the wide dispersal of NSS herring in the offshore area is expected to increase the time that killer whales need to search for suitable prey. A change in activity budget of killer whales was linked to reduced herring prey abundance inside the fjord system. Increased time spent travelling and searching for suitable prey increases the energetic

cost to the predator. The cost of travelling can be particularly high for females, which have a smaller body size than males, and especially costly for females accompanied by a calf (Williams & Noren 2009). Longer foraging trips have been reported to lead to reduced reproductive success of Antarctic fur seals (Costa et al. 1989; Boyd et al. 1994).

#### **6.4.7 Distribution change reflected in temporary emigration rates**

The results of the mark-recapture analysis indicated higher probabilities of adult male and female killer whales emigrating temporarily from the fjord system and lower probabilities of remaining in the fjord system when the longer time series of data was analysed (Appendix 6.1 and Chapter 3). This reflects the increased emigration from the fjord system to offshore area and the resulting decreased site fidelity to the fjord system due to the change in distribution of the NSS herring stock to offshore waters. In general, adult females showed higher site fidelity to the fieldwork area compared to adult males.

#### **6.4.8 Fisheries and other NSS herring predator's adaptation to change**

Based on the fisheries catch index, the fisheries targeting the NSS herring inside the fjord system increased gradually from 1991, in comparison to the rapid arrival of killer whales after the NSS herring stock became present in the area. However, the fisheries catches were related to annual quotas and are also driven by the market price of the fish; they are not solely dependent on the presence of the herring. In addition, the percentage of the catch inside the fjord system was high from 1992 until 2004. Overall, the NSS herring fisheries followed the pattern of NSS herring abundance inside the fjord system.

The fisheries catch index declined sharply between 2005 and 2006 and the killer whale indices declined between 2006 and 2007, potentially indicating a difference of one year in response to the change in distribution of the herring. Fisheries with large vessels are not tied to a particular habitat in the similar way as killer whales are regarding their catching method. The offshore location however is much more exposed to extreme weather conditions and especially limits the ability of small vessels to fish in this area.

An asynchronous pattern was observed between the catches of cod and saithe. More cod was caught until 1999 compared to saithe. In comparison, saithe catches were dominant in the later part of the time series. In general, both cod and saithe catches followed the overall pattern of the abundance of NSS herring inside the fjord system. These catch records lack catch-per-unit-effort details, and could be related to quota and bycatch regulations. However, local fishermen confirmed the patterns seen in the catch records, and that cod was more

abundant in the beginning and saithe in the later part of the time series (pers. comm. Åge Tjeldnes<sup>1</sup>).

#### **6.4.9 Future directions**

The concentration of both the NSS herring and killer whales inside the fjord system for nearly two decades provided a unique opportunity to study both species and their interactions in this easily accessible area. Working in the offshore location entails greater logistical challenges that need to be taken into account when planning continued work on these species.

Predation on the NSS herring stock has been suggested to have increased in the offshore wintering area due to the presence of large baleen whales in addition to the killer whales, as compared to the described situation in the fjord system. Obtaining improved quantitative knowledge on the variation in natural mortality of the NSS herring stock could improve the quality of the future management of the stock.

Future work is encouraged to estimate the consumption rates and energy requirements of killer whales in this population to be able to evaluate more fully their importance as predators of herring in the Norwegian Sea. Information obtained from the mark-recapture analysis presented here together with information on the consumption rate, energy requirements and NSS herring survey data could feed into multi-species models and aid progress towards a more holistic ecosystem based management.

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<sup>1</sup> Professional cod and saithe fisherman based in Lødingen, fishing in the fjords during the period of 1988-2006.

## CHAPTER 7

### General discussion

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#### **7.1 Thesis synthesis**

Understanding the role of a species in its environment requires knowledge of population dynamics, as determined by survival and reproductive rates, and of distribution and abundance. This information is also fundamentally important for assessing the viability of a population and for informing conservation and management plans. Although the distribution, abundance and life history parameters of some killer whale populations have been well-studied (Olesiuk et al. 1990; 2005), until now there has been a complete lack of information on the survival and reproductive rates of northern Norwegian killer whales.

In Chapters 2, 3 and 6, I presented the first estimates of survival rates for adult male and adult female killer whales for the northern Norwegian population. I also extended the survival rate analysis to account for temporary emigration, i.e. that not all the individuals in the population are available for capture each year because they may be temporarily out of the study area. The results show that killer whales did exhibit temporary emigration away from the fjords where this study mainly took place, and that the probabilities of being temporarily away from the fjords were higher for adult males than for adult females, indicating a sex-specific difference in ranging behaviour. The constant survival rate was estimated as 0.974 (SE = 0.006, CI = 0.960 – 0.983) for adult males, and as 0.984 (SE = 0.006, 95% CI = 0.965 – 0.993) for adult females, with the robust design model using data from 1990-2006. In Chapter 2, I also present the first estimates of reproductive rates for this killer whale population, with calving intervals ranging from 3 to 14 years (mean = 5.06, SE = 0.722), equivalent to a fecundity rate of 0.197 calves per mature female per year.

Previous mark-recapture analysis of photo-identification data has produced population size estimates of about 490-550 killer whales in the NSS herring wintering areas during October-January 1990-1993 (Similä & Christensen 1992; Similä 1997a). In Chapter 2, I expanded this analysis with ten more years of data and the total annual population size was estimated taking into account heterogeneity of capture probabilities and the proportion of

identifiable individuals in this population. This new analysis indicates a larger population with approximately 700 killer whales using the fjord system during 1990-2003.

Using the newly estimated population parameters, I then explored a population viability analysis in Chapter 4 to forecast the rate of population change and to evaluate the risk of extinction under various scenarios. The baseline scenario using the best available information predicted a viable population that may be increasing in size. The use, for the first time, of such population models provides a good framework within which to consider the future monitoring of this killer whale population.

The northern Norwegian killer whale population faces a number of potential threats from anthropogenic activities. These include a heavy contaminant load (Wolkers et al. 2007), expanding exploration and transportation of oil and gas in their environment (Gautier et al. 2009; Hasle et al. 2009), and also the use of active sonar for military training purposes (WWF-Norway 2001; Miller et al. 2012; Kuningas et al. 2013b). The annual operational Navy sonar exercises, which on many occasions have overlapped with the killer whales wintertime habitat, have caused concern and complaints from fishermen and the whale-watching community (WWF-Norway 2001). In Chapter 5, sightings from a whale-watching dataset from 2002-2008, and observations from dedicated research effort in 2006 were correlated to known naval sonar activity in the fjord system. Naval sonar activity during a period of low prey availability seemed to have had a negative effect on killer whale presence. It was also concluded that the level of reaction to sonar can be influenced by multiple factors, including the availability of prey.

The main prey species of the northern Norwegian killer whale population is the NSS herring (Jonsgård & Lyshoel 1970; Christensen 1988; Similä et al. 1996), and killer whales follow the annual migration of this stock (Similä et al. 1996; 2002). The NSS herring stock is highly dynamic in terms of its abundance and distribution, and the migration pattern has changed substantially over the last 100 years (Dragesund et al. 1997; Huse et al. 2002; Holst et al. 2002; 2004; Huse et al. 2010). The latest change in wintertime distribution took place starting in 2002 (Huse et al. 2010). This event provided a unique opportunity to investigate a large-scale change in distribution of a prey species and to evaluate the subsequent response of a top predator. The results of this study (Chapter 6) show that killer whales adapted to this change after a time-lag of four years. The whales showed a preference for remaining in the fjord system but eventually abandoned it when the density of herring in the fjord system fell below that in the offshore area. The killer whales were also found to have changed their daytime activity budget between high and low abundance years of the NSS herring, increasing

the proportion of time spent travelling/foraging during the time when herring abundance declined.

## **7.2 Response of killer whales to NSS herring dynamics**

This study benefitted from a rare opportunity to use long-term datasets of a predator and a prey species; killer whales and NSS herring. These data were used to describe a large-scale change in distribution of the wintering NSS herring stock from the fjord system to offshore waters of the Norwegian Sea and the response of killer whales to this change.

The NSS herring is the largest herring stock in the world and the largest fish stock in the NE Atlantic (Holst et al. 2004; ICES 2013), with widespread influence in the Norwegian Sea both as a predator itself (feeding on zooplankton such as *Calanus* sp. and krill) and as prey for multiple species, including humans. The NSS herring stock undertakes large-scale seasonal migrations over thousands of kilometres between coastal and offshore waters between spawning, feeding and wintering areas, and is characterized by unpredictable large-scale shifts particularly in its wintering areas (Dragesund et al. 1997; Huse et al. 2002; Holst et al. 2002; 2004; Huse et al. 2010). The latest large scale change in herring distribution and the response of killer whales and predatory fish described in Chapter 6 show the major role that the NSS herring stock has in this ecosystem, driving the distribution of multiple predator species.

The role of NSS herring in the NE Atlantic is similar to that of key species in other ecosystems that are known to exert a strong influence on the distribution and abundance of predator species. For example, the Antarctic krill (*Euphausia superba*) in the Southern Ocean waters experiences fluctuations in its biomass and distribution that are reflected in the presence, population size and reproductive rates of its predator species (Reid & Croxall 2001; Reid et al. 2006). Sandeels (*Ammodytes marinus*) in the North Sea represent an important prey species for many top predators, including many species of seabirds, seals and cetaceans, and also show variability in distribution and abundance, resulting in changes in predator abundances (Camphuysen et al. 2006; Enstipp et al. 2006).

Killer whales in northern Norway, which mainly feed on NSS herring, could be expected to have mechanisms in place to adapt to the distribution changes in their primary prey. Similä et al. (2002) and Stenersen & Similä (2004) showed how killer whales travelled temporarily away from the fjord system containing the wintering spawning stock of NSS herring to the offshore areas with the inferred objective to check for changes in the distribution of this dynamic stock. The satellite tracked killer whales were within the NSS herring wintering grounds inside the fjords most of the time, but there were 2-25 day

“scouting” trips to outside areas covering 78-1,537 km (Similä et al. 2002; Stenersen & Similä 2004). This indicates a remarkable behavioural adaptation of the killer whales in this population in response to the dynamic migration pattern of the NSS herring. The results presented here (Chapters 3 and 6) also show that killer whales in this population have a wider range than the fjord system and that whales emigrated temporarily from the fjord system between years, something that could also be a consequence of the need to locate prey in a wider area.

Killer whales responded to the large-scale distribution change and to the reduced abundance of their main prey species inside the fjord system in various ways. A change in the daytime activity budget of killer whales inside the fjord system was found in 2005 and 2006 compared to the early 1990s (Similä 1997a). The proportion of time spent travelling/foraging increased as herring abundance and density declined inside the fjord system, indicating a need to allocate more time to searching for prey. The proportion of time spent socializing/playing and resting decreased markedly between the two time periods, likely as a direct result of the increased time spent travelling/foraging. Similä (1997a) found that the time killer whales spent travelling/foraging in summertime in offshore waters was higher compared to wintertime, likely reflecting the lower density of prey in this area. Saulitis et al. (2000) found that the activity budgets of transient and resident killer whales were different, with transient killer whales spending more time travelling and foraging, as a result of different feeding specializations. Changes in the behaviour of Antarctic fur seals (*Arctocephalus gazella*), represented by increased time spent travelling or variability in diving activity, has been recorded in response to reduced food availability and the need to search for prey over a larger area (Costa et al. 1989; Boyd et al 1994; Lea et al. 2002).

Increased time spent travelling/foraging is expected to increase the energy requirement for killer whales (Noren 2011), especially females because their smaller body size makes swimming more energetically costly than for adult males (Williams & Noren 2009). In addition, female energetic requirements are higher during lactation (Noren 2011) and swimming in the echelon position with a calf can also increase energy requirements (Noren 2008). A change in the time spent feeding could have direct consequences for the condition and fitness of an animal (Williams et al. 2006; 2013). However, in this study the time spent feeding changed little, indicating that the killer whales were still finding sufficient prey in the fjord system in 2005 and 2006.

The density of NSS herring was higher inside the fjord system than in the offshore area until 2006. This and the favourable bathymetric properties in the fjords for capturing herring

(Similä 1997a; Similä 1997b) likely explain the preference of the killer whales for the fjords even after the herring started to stay offshore in 2002. Up until 2006, the fjords offered a better habitat for killer whales under the theory of optimal foraging (MacArthur & Pianka 1966). The whales spent less time and energy locating and capturing herring inside the fjord system than they would have done offshore. In addition, the energy content of herring was likely higher inside the fjord system because it was the older larger herring that remained in this area (Slotte et al. 2000). Thus, killer whales could maximise energy intake and minimise the cost of foraging inside the fjord system until 2006. When the density of herring became the same in the fjord system and offshore in 2006, a decrease in killer whale presence inside the fjord system was observed and in 2007 and 2008, when the abundance and density of herring was higher offshore compared to the fjord system, killer whales were only rarely encountered in the fjord system. Benoit-Bird et al. (2013) showed that the distribution of three predator species, black-legged kittiwakes (*Rissa tridactyla*), thick-billed murre (*Uria lomvia*) and northern fur seals (*Callorhinus ursinus*), was driven primarily by prey density, and that the horizontal prey patch size did not predict the presence of these predators, a result that reflects with the findings of this study (Chapter 6).

The NSS herring is an exceptional stock because of its large-scale annual migration and particularly because of the unique feature of this migration pattern to change at uneven intervals (Dragesund et al. 1997; Holt et al. 2004; Huse et al. 2010). Killer whales feeding on this NSS herring stock have a mechanism in place to track the distribution and movement of herring stock (Similä et al. 2002), indicating an adaptation to the behaviour of their main prey. Large scale changes in distribution of marine mammals have been observed elsewhere. Hammond et al. (2013) documented a major shift in harbour porpoise distribution in the North Sea between 1994 and 2005, the most likely reason for which was believed to be changes in prey distribution. Varying oceanographic conditions resulting from El Niño and La Niña events affect the distribution of cetaceans, such as common dolphins and Pacific white-sided dolphins, along the Californian coast and in the eastern tropical Pacific driven by changes in the availability of prey (Benson et al. 2002; Keiper et al. 2005). These distribution changes due to El Niño and La Niña events appear to be mostly driven by the large scale changes in oceanographic conditions which then have a bottom up effect on the distribution of prey and predator species.

The NSS herring stock has been declining since 2009 due to low recruitment in recent years (ICES 2013) and possibly due to increased natural mortality (pers. comm. Jens Christian Holst). What consequences might this decline in herring biomass have on the killer whale

population? The previous major collapse in the NSS herring stock took place in the late 1960s due to overfishing (Dragesund et al. 1997; Toresen & Østvedt 2000) but no studies were conducted on killer whales at that time and therefore it is not known how killer whales responded to this major decline in prey abundance. In periods of low availability of the NSS herring, it seems likely that killer whales are able to switch to feeding on other available prey species, such as mackerel (Similä et al. 1996). Additionally killer whales are reported to have fed on saithe, cod, eider duck (Similä et al. 1996) and on Atlantic salmon (Vester & Hammerschmidt 2013). Some evidence also suggests that certain pods of killer whales may feed on seals (Similä et al. 1996; Vongraven & Bisther in press). Spitz et al. (2012) investigated the metabolic cost of living and the quality of diets in eleven cetacean species in the North Atlantic, and found that those cetaceans with a high metabolic cost of living need to feed on prey species with high energetic content. Therefore, the need to change to feeding on a secondary prey species might have negative consequences for the predator. For northern Norwegian killer whales, changing from energy rich herring, the preferred prey, to lower quality prey might result in poorer body condition, as has been found with Steller sea lions and fin whales (Rosen & Trites 2000; Williams et al. 2013).

Variation in prey availability has been shown to have a marked impact on the fitness of killer whales in the NE Pacific. Ford et al. (2010) found survival rates of southern and northern resident killer whales to be highly correlated with the abundance of their main prey, the Chinook salmon (*Oncorhynchus tshawytscha*), and that a decline in Chinook salmon abundance led to increased mortality of killer whales with a lag of one year. Ward et al. (2009) showed that reproductive success of killer whales was also correlated with the abundance of Chinook salmon, with a 50% difference in the probability of a female calving between low and high salmon abundance years. During periods of low prey abundance, many mammal species respond with reduced reproductive rates (e.g. Lunn et al. 1994; Pitcher et al. 1998; Ward et al. 2009).

However, generally, the high survival rates of large long-lived mammals are possible because of the capability to tolerate variability in prey abundance, at least if the predator is able to utilize a variety of prey species (Pianka 1970; Fowler 1981; McKinney 1997). Reduced survival rates of resident killer whales in the NE Pacific and killer whales in the Crozet Archipelago have been linked to declines in their prey species abundance (Ford et al. 2010, Poncelet et al. 2010). Could the feeding specialization shown by killer whales in many areas represent a risky strategy? If the main prey abundance declines, a limited ability to adapt to this change could reduce fitness. The viability of a population can also potentially be further

compromised in the presence of human-caused stressors, as contaminants or due to added anthropogenic noise in their environment (Ross et al. 2000; Morton & Symonds 2000; Lusseau et al. 2009).

The northern Norwegian killer whale population is specialized on feeding on the highly dynamic NSS herring (Similä et al. 1996), that includes large scale changes in distribution and abundance (Toreisen & Østvedt 2000; Huse et al. 2010). Killer whales in this population have a behavioural strategy in place to track the movement of this dynamic herring stock (Similä et al. 2002). It is possible that the killer whales in this population are also flexible to changes taking place in the NSS herring abundance. In contrast, if the prey species is characterised by very predictable presence, like in the case of Chinook salmon in the NE Pacific (Ford et al. 2000; Hanson et al. 2010), killer whale as a predator might be limited in the ability to change its behaviour. As a result, a population might be in a higher risk of lowered viability once the main prey abundance declines.

Several other species feed on the NSS herring in the Norwegian Sea, including cod, many bird species and whales (Similä & Ugarte 1993; Pitcher et al. 1996; Nøttestad 1998; Axelsen et al. 2001; Nøttestad & Similä 2001; Olsen & Holst 2001; Nøttestad et al. 2002; Tjelmeland & Lindstrøm 2005). It is not known how increased competition between different species feeding on NSS herring during low herring biomass years would affect the viability of the killer whale population. The current and predicted future decline in herring abundance presents an opportunity to study this in the future.

### **7.3 Sex-specific temporary emigration**

One of the most noteworthy results in this thesis is the estimation of sex-specific survival rates for the first time for any killer whale population while also accounting for temporary emigration. The robust design analytical framework has previously been used in studies of other marine mammal species to estimate abundance and survival rates of bottlenose and Guiana dolphins (Silva et al. 2009; Cantor et al. 2012; Daura-Jorge et al. 2012; Nicholson et al. 2012) and western Pacific gray whales (Bradford et al. 2006; Bradford et al. 2008). However, none of these studies was able to estimate sex specific survival or temporary emigration probabilities, due to difficulties in correctly identifying males and females. A maximum likelihood model presented by Whitehead (1990) was used to estimate temporary emigration rates of transient killer whales in the Northeast Pacific, but did not specify sex-specific probabilities of temporary emigration (Ford et al. 2007). This study is therefore the first to

estimate temporary emigration probabilities for adult males and adult females separately for any cetacean species.

The importance of this result is that the probabilities of being temporarily out of the study area were found to be different for adult males and adult females. For adult males the probability of temporary emigration varied with time and was Markovian, indicating a pattern in the emigration and immigration probabilities. For adult females, the probability of temporary emigration was constant and random, meaning that individuals leave and return independently of their location in the previous sampling occasion. Overall, adult females showed higher site fidelity to the fjord system than adult males. High probabilities of temporary emigration indicate a larger distributional range for killer whales during wintertime than the fjord system alone and only a proportion of a larger population (so-called superpopulation - Kendall et al. 1997) was therefore present during wintertime inside the fjord system.

The sex-specific difference in temporary emigration probabilities could be caused by adult males conducting more of the scouting trips to follow the NSS herring outside the fjord system compared to adult females. Adult killer whale males have a larger body size compared to adult females (Christensen 1984; Bigg et al. 1987; Stenersen & Similä 2004; Fearnbach et al. 2011), and this bigger body size with larger fat reserves could allow males to scout for herring for longer and over wider areas.

An alternative reason for sex-specific differences in temporary emigration probabilities could be differences in energy requirements and costs. The higher daily energetic requirement for adult males (Williams et al. 2004) could lead to different foraging strategies between males and females, and males foraging more widely (Weise et al. 2010). In addition, the higher energetic cost of travel for females, especially if accompanied by a calf (Williams & Noren 2009), might favour females using the fjord system. Larger home ranges have been recorded for other male mammals (Greenwood 1980), including marine mammals e.g. harbour seals (Thompson et al. 1998), grey seals (Austin et al. 2004; Breed et al. 2006) and bottlenose dolphins (Connor et al. 2000; Krützen et al. 2004), but in these species individuals do not form lifelong mixed-sex family units, as in killer whales. It is not clear how these sex-specific differences in temporary emigration fit in with the current understanding of stable family units of killer whales.

Sex-specific differences in temporary emigration probabilities could be related to reproductive strategies. Studies of killer whales in the NE Pacific have shown that pods are composed of genetically closely related individuals (Bigg et al. 1990; Ford et al. 2000).

Consequently, for reproductive benefit and to avoid inbreeding there is a need for adult males to separate from their family pod and to temporarily disperse to find adult females in other pods (Barrett-Lennard 2000; Hoelzel et al. 2007; Pilot et al. 2010). Dispersal from the family pod for reproductive reasons could therefore explain part of the higher dispersal of adult males. However, it is not clear why adult males would move out of the fjord system during wintertime in the search of potential mates.

It has been suggested that some of the adult males in northern Norway may have a nomadic lifestyle rather than living in stable family pods (Bisther & Vongraven 1995). Nomadic or solitary males have also been reported in other killer whale populations (Matkin et al. 1999; Baird & Whitehead 2000; Burdin et al. 2007; Ivkovich et al. 2009; Pilot et al. 2010). As well as a possible explanation for higher temporary emigration rates, such nomadic males could also explain the evidence for transient individuals in mark-recapture model goodness of fit tests (Chapter 3 and 6). Whether or not these nomadic individuals have a different range from the individuals living in pods and whether or not they are more occasional visitors to the fjord system is not known.

The results described in Chapter 5 showed that under certain biological conditions the use of naval sonar has the potential to displace killer whales from the fjord system. It is not known if the annual naval sonar exercises in previous years resulted in more killer whales being unavailable to be encountered, and consequently affected the probability of killer whales being temporarily away from the fjord system. During 2002-2005, while the herring prey was still available in the fjord system, 17 naval sonar days were reported. On only one of these sonar activity days (representing 6%) were killer whales not encountered in the fjord system. Additionally, the results of the GLM modelling showed that killer whale presence inside the fjord system was not explained by sonar activity. Therefore, it can be concluded that naval sonar activity did not markedly alter the estimated probability of temporary emigration of killer whales in this study.

### **7.4 Conservation issues and aid for management**

In 2007, the International Whaling Commission's Scientific Committee encouraged the collection of demographic information on killer whales from all locations around the world (IWC 2007). This thesis has responded by producing the first estimates of survival and reproductive rates (Chapters 2, 3 and 6) for the northern Norwegian killer whale population. Updated and improved estimates of total population size have also been generated (Chapters 2 and 6).

In the context of conservation, these estimated parameters have been used to evaluate the future viability of this population under various plausible scenarios (Chapter 4). The results increase knowledge of the status of killer whales, currently considered to be “Data deficient” on the IUCN Red List (Taylor et al. 2012), by showing that the northern Norwegian killer whale population is viable, potentially increasing in size and not considered to be under an immediate threat. In contrast, a population viability analysis conducted for the southern resident killer whale population in the NE Pacific predicted a much more negative future with extinction likely within 100 years (Taylor & Plater 2001). Despite the positive future prediction for the Norwegian population, the population viability analysis conducted in this thesis also showed that a reproductive rate of less than 16% of adult females breeding annually (calving interval longer than 6.25 years) predicted a decline in population size. Additionally, removal of eight or more individuals per year also turned the growth rate negative.

The population of killer whales in northern Norway faces a number of threats from human activities that could result in reduced reproductive rates or increased mortality. These include anthropogenic noise from various sources, including active military sonar operations. In Chapter 5, it was shown that sonar activity within the fjord system could have caused killer whales to leave the area, confirming that the whales may have been unavailable for whale-watching while the exercise was on-going as claimed for an earlier exercise by the whale-watching community and an NGO (WWF-Norway 2001). This result is consistent with controlled sonar exposure experiments showing killer whale avoidance of sonar transmission at relatively low received levels (less than 120 dB re 1  $\mu$ Pa) (Miller et al. 2012), indicating an avoidance range around operational naval sonar of 20-39 km depending on frequency, source level and propagation conditions (Miller et al. in review). Miller et al. (2012) also found that killer whales might be especially sensitive to sonar exposure, responding to lower sound pressure levels compared to long-finned pilot whales (*Globicephala melas*) and sperm whales (*Physeter macrocephalus*).

Being exposed to anthropogenic noise or another form of disturbance can lead to individuals being displaced from their preferred habitat (Morton & Symonds 2002; Lusseau et al. 2009; Brandt et al. 2011). Displacement from a habitat that represents an important feeding, breeding or socializing environment, can lead to lowered viability of a population (Bejder et al. 2006; Williams et al. 2006; Lusseau et al. 2009). Given the results presented in Chapter 5, it could be assumed that killer whales in the Norwegian population might be temporarily displaced from a location due to anthropogenic noise, but be mainly driven by the abundance and presence of their herring prey. Potential serious risk to the killer whale

population might result if a high level of anthropogenic noise is continuously present in an area where herring prey is concentrated.

The area outside Lofoten is under on-going interest for oil exploration and expanding coastal development plans, both of which could lead to additional negative impacts on this killer whale population due to increased shipping, seismic air gun and construction noise (Southall et al. 2007; Gautier et al. 2009). Given the present new distribution of killer whales in offshore area year around, the potential negative effect from these anthropogenic sources might have increased. Planned developments in the Lofoten area would increase the risk of serious oil spills or releases in the area. The “Exxon Valdez” oil spill in Alaska in 1989 resulted in two groups of killer whales suffering losses of individuals and neither group has recovered to pre-oil spill levels (Matkin et al. 2008).

High levels of contaminants (e.g. PCBs) have been recorded for the northern Norwegian killer whale population (Wolkers et al. 2007), similar to other marine mammal top predators: e.g. seals, belugas and Pacific killer whales (DeGuise et al. 1995; Bergman 1999; Wolkers et al. 2007). These high contaminant levels could potentially have a negative effect on the health and survival rates of killer whales (Cullon et al. 2009; Ward et al. 2011). Comparison of estimated survival rates between killer whale populations, indicate that the Norwegian population is currently likely coping with this pressure, given that the survival rates of adult males in Norway are the highest estimated anywhere (Olesiuk et al. 1990; 2005; Poncelet et al. 2010; Kuningas et al. 2013a; Chapter 2 and 3). However, an exploration in the population viability analysis (Chapter 4), in which reproductive rate was reduced by 20% to mimic the possible effects of a high contaminant load, showed that the resulting calving interval of 6.25 years was sufficient to reduce population growth to zero.

Prey depletion, from overfishing or natural fluctuation in NSS herring stock biomass, could potentially impact the viability of the northern Norwegian killer whale population through changes in survival and reproductive rates, as has been shown elsewhere (Ward et al. 2009; Ford et al. 2010; Williams et al. 2013). As discussed above, it is likely that Norwegian killer whales can switch to alternative prey during times when herring abundance is low but such changes in prey may potentially alter population viability (Rosen & Trites 2000; Williams et al. 2013). Given the likely future declines in the NSS herring stock biomass, it is strongly recommended that this killer whale population be monitored in the future.

Conservation of top predators, such as killer whales, is important because of their vital role in the marine environment (Boyd et al. 2006; Heithaus et al. 2008; Baum & Worm 2009). Removal of top predators has been shown to have wide consequences on the productivity of

the ocean, downgrading ocean ecosystems through shortened food chains through the removal of top-down control (Heithaus et al. 2008; Baum & Worm 2009; Estes et al. 2011). A well-known example of this is the decrease in sea otter (*Enhydra lutris*) abundance that caused an increase in sea urchin density and consequently de-forestation of kelp beds in Alaska (Estes et al. 1998).

The killer whale is a widely distributed top predator found in all major oceans and, as a species, is not considered to be under threat or at risk of extinction (Matkin & Leatherwood 1986; Forney & Wade 2007; Taylor et al. 2012). However, some local populations are considered to have a critical status, i.e. the population resident to the Strait of Gibraltar (Cañadas & de Stephanis 2006) and the southern resident killer whale population in the NE Pacific (Krahn et al. 2004; Reynolds et al. 2009). Regarding conservation and management plans for any killer whale population, it would be highly relevant to consider and take into account, not only the population specific population parameters and the abundance of prey, but the potential for adaptation of a predator to changes in its environment. Small populations are generally at higher risk of extinction (Gilpin & Soulé 1986). If a small population is highly specialized on certain prey species and with a low potential to adapt, it is likely to be at a high risk of extinction if changes take place in a previously stable environment.

Killer whale populations around the world are subject to a range of anthropogenic stressors, e.g. fisheries interactions, vessel traffic and contaminants (Morton & Symonds 2002; Wolkers et al. 2007; Tixier et al. 2010; Miller et al. 2012), that need to be considered in conservation and management plans. Single species conservation plans might offer effective ways forward (Simberloff 1998). Alternatively, more holistic ecosystem management approaches could offer a better possibility to integrate conservation objectives for killer whales with the management of, for example, fisheries. Ecosystem modelling however is limited by the requirement for large-scale datasets of each component, which are unavailable in many situations (DeYoung et al. 2004; Plagányi 2007).

### **7.5 Recommendations for future work**

Continuation of the dedicated photo-identification work on this population of killer whales in northern Norway is highly encouraged so that monitoring the viability of this population can continue in the future. The study presented here suffered from a lack of systematically recorded fieldwork effort data, and it is recommended that in future studies effort data would be recorded while in the field.

Estimating survival rates for this population with more recent data and to fill in the gaps where information from this population is still lacking, i.e. calf, juvenile and sub-adult survival rates, is also encouraged. Extending this analysis could shed light on the question of whether the current offshore distribution and potential future decline of NSS herring might impact survival rates of the killer whales. New and improved information on population parameters would also allow the further development of population viability analysis and the generation of predictions with greater reliability.

Collecting more data to improve and extend estimates of reproductive rates for the northern Norwegian killer whale population is also recommended. In this study, there were limited data on calves, limiting the inferences that could be drawn about reproductive rates. More data would also improve the reliability of population viability analysis and could be used to evaluate changes in reproduction in response to future fluctuations in prey availability.

This population has currently been evaluated to be viable, but the threats in their ecosystem, e.g. prey depletion and high level of contaminants, might alter this positive situation. The predicted future decline in the NSS herring stock highlights the importance of the results presented in this study on population parameters and the need for monitoring this killer whale population in the future. Reduced herring abundance may reduce survival and reproductive rates. The next few years provide a rare opportunity to study the population dynamics of an ocean top predator within a highly dynamic environment with the promise of valuable new insight into the adaptation of a marine predator to changes in its prey resource.

Future work is also encouraged to estimate consumption rates and energy requirements of killer whales in this population to be able to evaluate more fully the importance of killer whales as predators in the Norwegian Sea. Information obtained from the mark-recapture analyses presented in this thesis, together with information on consumption rates and energy requirements and abundance of prey, would be valuable input into more holistic ecosystem based management.

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Appendix 2.1 - U-CARE Goodness of fit test (Global test & Directional tests) results with dataset 1986-2003. Directional test 3.SR examines the potential transience, 3.SM the probability of equal survival, 2.CT the trap-dependency and 2.CL the equal capture probabilities in the dataset.

<b>Global test</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
Males, females & sub-adults	141	232.17	1.65	< 0.001
Males & females	108	218.88	2.03	< 0.001
Males	61	134.54	2.21	< 0.001
Females	47	84.34	1.79	< 0.001

<b>Directional tests</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
<b>Males</b>				
<b>3.SR</b>	10	11.71	1.17	0.305
<b>3.SM</b>	14	23.44	1.67	0.054
<b>2.CT</b>	15	64.36	4.29	< 0.001
<b>2.CL</b>	22	35.03	1.59	0.038
<b>Females</b>				
<b>3.SR</b>	8	14.72	1.84	0.065
<b>3.SM</b>	9	3.33	0.37	0.950
<b>2.CT</b>	14	36.98	2.64	< 0.001
<b>2.CL</b>	16	29.31	1.83	0.022
<b>Sub-adults</b>				
<b>3.SR</b>	9	1.0092	0.11	0.999
<b>3.SM</b>	6	3.11	0.52	0.795
<b>2.CT</b>	10	5.17	0.52	0.879
<b>2.CL</b>	8	3.99	0.50	0.858

Appendix 2.2 - RELEASE Goodness-of-Fit results for dataset 1986-2003. TEST3 examines the probability of equal survival, TEST2 the equal capture probabilities and TEST1 differences between groups.

<b>M&amp;F&amp;S</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	49	47.11	0.96	0.550
TEST2	96	189.72	1.98	< 0.001
TEST3+TEST2	145	236.83	1.63	< 0.001
TEST1	48	141.19	2.94	< 0.001
<b>M&amp;F</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	39	46.48	1.19	0.191
TEST2	86	181.05	2.11	< 0.001
TEST3+TEST2	125	227.53	1.82	< 0.001
TEST1	30	30.07	1.00	0.462
<b>Males</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	23	29.93	1.30	0.151
TEST2	45	111.01	2.47	< 0.001
TEST3+TEST2	68	140.94	2.07	< 0.001
<b>Females</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	16	16.55	1.03	0.415
TEST2	41	70.04	1.71	0.003
TEST3+TEST2	57	86.59	1.52	0.007

Appendix 2.3 - Estimates of over-dispersion (indicated with the variance inflation factor  $\hat{c}$ ) investigated with program U-CARE, RELEASE and Parametric bootstrap for 1986-2003.

<b>U-CARE</b>		
<b>Global test</b>	$\hat{c}$	
Males, females & sub-adults	1.65	
Males & females	2.03	
Males	2.21	
Females	1.79	

<b>RELEASE TEST3+TEST2</b>		
	$\hat{c}$	
Males, females & sub-adults	1.63	
Males & females	1.82	
Males	2.07	
Females	1.52	

<b>Parametric Bootstrap</b>		
<b>C of observed model/mean c of simulated values</b>	$\hat{c}$	
Males, females & sub-adults	1.20	
Males & females	1.44	
Males	1.19	
Females	1.63	
<b>"Median c"</b>	$\hat{c}$	<b>95% CI</b>
Males, females & sub-adults	1.18	1.16 - 1.19
Males & females	1.18	1.16-1.19
Males	1.18	1.16-1.19
Females	1.29	1.25-1.32

Appendix 2.4 - Model assumption  $\chi^2$  test results examining the fit of models  $M(t)$  and  $M(h)$  within program CAPTURE.

<b>Year</b>	<b>Model</b>	<b><math>\chi^2</math></b>	<b>df</b>	<b>p</b>	<b>Year</b>	<b>Model</b>	<b><math>\chi^2</math></b>	<b>df</b>	<b>p</b>
1990	$M(t)$	158.33	115	0.004	1990	$M(h)$	54.68	5	< 0.001
1991	$M(t)$	97.10	78	0.069	1991	$M(h)$	117.12	6	< 0.001
1992	$M(t)$	160.32	144	0.167	1992	$M(h)$	192.90	6	< 0.001
1993	$M(t)$	53.40	38	0.050	1993	$M(h)$	32.17	3	< 0.001
1994	$M(t)$	56.82	45	0.111	1994	$M(h)$	68.14	5	< 0.001
1995	$M(t)$	124.45	84	0.002	1995	$M(h)$	67.55	4	< 0.001
1996	$M(t)$	58.02	50	0.2034	1996	$M(h)$	44.13	4	< 0.001
1997	$M(t)$	Test not performed.			1997	$M(h)$	20.02	3	< 0.001
1998	$M(t)$	34.90	27	0.140	1998	$M(h)$	17.25	3	< 0.001
1999	$M(t)$	47.53	34	0.062	1999	$M(h)$	17.39	3	< 0.001
2000	$M(t)$	Test not performed.			2000	$M(h)$	7.61	2	0.0223
2001	$M(t)$	Test not performed.			2001	$M(h)$	5.69	2	0.0581
2002	$M(t)$	82.10	83	0.512	2002	$M(h)$	43.74	6	< 0.001
2003	$M(t)$	80.29	73	0.264	2003	$M(h)$	116.88	6	< 0.001

Appendix 3.1 - U-CARE Goodness of fit test (Global test & Directional tests) results with dataset 1990-2003.

<b>Global test</b>	<b><i>df</i></b>	<b><i>chi</i><sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b><i>p</i></b>
Males, females & sub-adults	116	204.64	1.76	< 0.001
Males & females	85	189.99	2.24	< 0.001
Males	47	108.37	2.31	< 0.001
Females	38	81.62	2.15	< 0.001

<b>Directional tests</b>	<b><i>df</i></b>	<b><i>chi</i><sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b><i>p</i></b>
<b>Males</b>				
<b>3.SR</b>	9	11.26	1.25	0.258
<b>3.SM</b>	9	9.37	1.04	0.404
<b>2.CT</b>	11	55.25	5.02	< 0.001
<b>2.CL</b>	18	32.49	1.81	0.019
<b>Females</b>				
<b>3.SR</b>	7	17.99	2.57	0.012
<b>3.SM</b>	7	2.24	0.32	0.945
<b>2.CT</b>	11	32.67	2.97	< 0.001
<b>2.CL</b>	13	28.72	2.21	0.007
<b>Sub-adults</b>				
<b>3.SR</b>	9	1.9	0.99	0.992
<b>3.SM</b>	6	3.11	0.52	0.795
<b>2.CT</b>	9	6.58	0.73	0.680
<b>2.CL</b>	7	3.06	0.44	0.880

Appendix 3.2 - RELEASE Goodness of fit results for 1990-2003.

<b>M&amp;F&amp;S</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	42	37.11	0.88	0.685
TEST2	85	180.55	2.12	< 0.001
TEST3+TEST2	127	217.66	1.71	< 0.001
TEST1	40	138.78	3.47	< 0.001
<b>M&amp;F</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	32	35.85	1.12	0.293
TEST2	76	170.47	2.24	< 0.001
TEST3+TEST2	108	206.31	1.91	< 0.001
TEST1	24	28.67	1.19	0.233
<b>Males</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	18	16.29	0.90	0.573
TEST2	39	102.79	2.64	< 0.001
TEST3+TEST2	57	119.07	2.09	< 0.001
<b>Females</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	14	19.56	1.40	0.145
TEST2	37	67.68	1.83	0.002
TEST3+TEST2	51	87.24	1.71	0.001

Appendix 3.3 - Estimates of over-dispersion with U-CARE, RELEASE and Parametric bootstrap for 1990-2003.

<b>U-CARE</b>		
<b>Global test</b>	$\hat{c}$	
Males, females & sub-adults	1.76	
Males & females	2.24	
Males	2.31	
Females	2.15	

<b>RELEASE TEST3+TEST2</b>		
	$\hat{c}$	
Males, females & sub-adults	1.71	
Males & females	1.91	
Males	2.09	
Females	1.71	

<b>Parametric Bootstrap</b>		
<b>C of observed model/mean of simulated values</b>	$\hat{c}$	
Males, females & sub-adults	1.21	
Males & females	1.18	
Males	1.52	
Females	1.83	

<b>"Median c"</b>	$\hat{c}$	<b>95% CI</b>
Males, females & sub-adults	1.18	1.16-1.19
Males & females	1.35	1.30-1.40
Males	1.18	1.16-1.19
Females	1.18	1.16-1.19

## **A.6.1 INTRODUCTION**

Mark-recapture analyses presented in Chapters 2 and 3 were extended in this Chapter to estimate the total size of the northern Norwegian killer whale population using data covering the period 1986-2006. In addition, analyses estimating adult male and female survival rates and temporary emigration probabilities were extended with data from three more years (to 1990-2006) to evaluate the potential change seen in these population parameters due to the offshore shift of the NSS herring.

## **A.6.2 METHODS**

### **A.6.2.1 Analytical assumptions of mark-recapture models**

Details of the analytical assumptions of mark-recapture models are given in Chapters 2 and 3 in sections 2.2.3.1 and 3.2.3.1, respectively.

### **A.6.2.2 Number of identifiable animals in population**

Photo-identification data from October-December 1990-2006 were first used to estimate the number of identifiable individuals ( $\hat{N}$ ) for pairs of years using a simple two-sample closed population Chapman estimator (Chapman 1951; Borchers et al. 2002). Details are given in section 2.2.3.2 in Chapter 2.

An attempt was made to explore the likely occurrence of heterogeneity in capture probabilities while estimating population size of identifiable individuals independently for years 2004-2006 by fitting multi-sample closed capture models in program CAPTURE implemented within program MARK (Otis et al. 1978; Pollock et al. 1990; Chao & Huggins 2005; Cooch & White 2012). This analysis was done following the methodology presented in Chapter 2, section 2.2.3.2. However, due to the limited data and number of recaptures within the years 2004-2006, these models failed to give reliable estimates of population size.

An exploratory analysis was also conducted using program MARK to estimate population size using an open population POPAN model (Schwarz & Arnason 1996) with the 1986-2008 dataset. RELEASE TEST2 and TEST3 used to investigate the goodness of fit of the open population model to the data were rejected ( $p < 0.0001$ ), and also reported several times that there were insufficient data to conduct these tests. In addition, on many occasions where

the models were run the survival and probability of entry parameters were not able to be estimated. Therefore results of this analysis are not presented here.

#### **A.6.2.3 Proportion of identifiable individuals**

Data on the proportion of identifiable individuals ( $\hat{\theta}$ ) in the population were used to derive estimates of total population size. The total number of individuals and the number of identifiable individuals were known for 20 killer whale groups encountered during 1992-2003. From these data, six groups from 1992-1995 were used to calculate the proportion of identifiable individuals to correct population estimates for 1990-1996. Fourteen groups from 1997-2003 were used for estimates for 1997-2006.

#### **A.6.2.4 Total population size**

Total population size was then estimated following the method presented in section 2.2.3.4 in Chapter 2.

#### **A.6.2.5 Cormack-Jolly-Seber models**

For estimating probabilities of capture ( $p$ ) and apparent survival ( $\varphi$ ) with the Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965) for 1990-2006, the data were organised into two datasets: 1) adult males (274 individuals) and 2) adult females (136 individuals). For details on how the sex and age-class of each identifiable individual were determined, see section 2.2.2.1 in Chapter 2.

##### ***A.6.2.5.1 Investigating goodness of fit***

Goodness of fit of the CJS models was assessed using Program U-CARE (Version 2.3.2) (Choquet et al. 2009). Details are given in section 3.2.3.2.1 in Chapter 3.

The global goodness of fit test in program U-CARE showed significant departures from adequate model fit for adult male and adult female datasets ( $p < 0.001$ ) (Table A.6.1). For the directional tests, the subtests which compose the Test 3.SR showed an indication of transience ( $p < 0.001$ ) for adult male data, resulting in the overall 3.SR test being significant ( $p = 0.017$ ). Therefore, a time-since-first-marking model (also known as an “age class” model) was built in program MARK to account for the potential issue with transience in adult males. This model was built in such way that survival probability in the first period of marking (“1<sup>st</sup> age-class”) was different compared to all following periods (“2<sup>nd</sup> age-class”), thus separating survival for the transient individuals that were only seen in that first period. Ignoring the transience

evident in the data could lead to negatively biased estimates of survival due to the permanent emigration of transient individuals from the study area.

Table A.6.1 - U-CARE Goodness of fit test (Global test & Directional tests) results with dataset 1990-2006.

<b>Global test</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
Males	64	135.14	2.11	< 0.001
Females	49	102.75	2.10	< 0.001

<b>Directional tests</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
<b>Males</b>				
<b>3.SR</b>	12	24.58	2.05	0.017
<b>3.SM</b>	14	12.97	0.93	0.529
<b>2.CT</b>	14	63.23	4.52	< 0.001
<b>2.CL</b>	24	34.35	1.43	0.079
<b>Females</b>				
<b>3.SR</b>	8	18.98	2.37	0.015
<b>3.SM</b>	10	1.96	0.20	0.997
<b>2.CT</b>	14	43.06	3.08	< 0.001
<b>2.CL</b>	17	38.75	2.28	0.002

Test 2.CT showed a highly significant ( $p < 0.001$ ) result for trap-dependency for both adult males and adult females. Trap-dependency in all cases was “trap-happiness”, meaning that recapture probability in years subsequent to initial capture was higher than expected by chance. A mark-recapture model was built in program MARK to account for the trap-dependency in adult males and adult females (Sandland & Kirkwood 1981; Pradel 1993); for more details see section 3.2.3.2.3 in Chapter 3.

In addition, the goodness of fit of models to the data was explored using tests in program RELEASE within program MARK (White & Burnham 1999; Cooch & White 2012). The assumptions tested in program RELEASE were equal probability of recapture (TEST2) and equal probability of survival (TEST3). TEST3 was non-significant for both adult males and adult females ( $p > 0.090$ ). TEST2 was significant ( $p < 0.001$ ) for both datasets (Table A.6.2). These results are in line with the U-CARE test results indicating violation of the assumptions of equal capture probabilities.

Table A.6.2 - RELEASE Goodness of fit results for 1990-2006.

<b>Males</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	24	33.69	1.40	0.090
TEST2	54	117.72	2.18	< 0.001
TEST3+TEST2	78	151.41	1.94	< 0.001
<b>Females</b>	<b>df</b>	<b>chi<sup>2</sup></b>	<b><math>\hat{c}</math></b>	<b>p</b>
TEST3	17	20.89	1.23	0.231
TEST2	47	91.55	1.95	0.001
TEST3+TEST2	64	112.44	1.76	0.002

#### **A.6.2.5.2 Investigating over-dispersion**

The amount of over-dispersion in the data was investigated with the variance inflation factor  $\hat{c}$ , with  $\hat{c} = 1$  indicating no over-dispersion (Anderson et al. 1994; Cooch & White 2012). For methodological details, see section 3.2.3.2.2 in Chapter 3.

For adult males, U-CARE estimated  $\hat{c} = 2.11$  and for adult females  $\hat{c} = 2.10$  (Table A.6.3). Program RELEASE estimated  $\hat{c} = 1.94$  for adult males and  $\hat{c} = 1.76$  for adult females. For adult males the bootstrap  $\hat{c}$  was 1.20 and the “median- $\hat{c}$ ” was 1.18 and for adult females the corresponding values were 1.48 and 1.18.

Overall,  $\hat{c}$  varied between 1.18 and 2.11 for adult males and between 1.18 and 2.10 for adult females. Over-dispersion in the data was thus not sufficient to cause any unacceptable lack of model fit ( $\hat{c} < 3$ ) (Lebreton et al. 1992; Burnham & Anderson 2002).

Table A.6.3 - Estimates of over-dispersion with U-CARE, RELEASE and Parametric bootstrap for 1990-2006.

<b>U-CARE</b>		
<b>Global test</b>	$\hat{c}$	
Males	2.11	
Females	2.10	
<b>RELEASE TEST3+TEST2</b>		
	$\hat{c}$	
Males	1.94	
Females	1.76	
<b>Parametric Bootstrap</b>		
<b>C of observed model/mean of simulated values</b>	$\hat{c}$	
Males	1.20	
Females	1.48	
<b>"Median c"</b>	$\hat{c}$	95% CI
Males	1.18	1.16-1.19
Females	1.18	1.16-1.19

#### **A.6.2.5.3 Model construction and selection**

CJS open population models implemented in program MARK were used to estimate recapture probabilities ( $p$ ) and apparent survival rates ( $\phi$ ) for adult males and adult females. Apparent survival includes death and permanent emigration. Several CJS models were constructed (Table A.6.4). Analysis was conducted using the same methods as presented in section 3.2.3.2.3 in Chapter 3.

Model selection was based on the QAICc (Anderson et al. 1994; Burnham & Anderson 2002), which is the AIC adjusted for small sample size and incorporating the appropriate  $\hat{c}$  value to account for the degree of over-dispersion in the data (see section 6.2.4.5.2). As a cautious approach, the highest  $\hat{c}$  values were chosen to account for the slight over-dispersion in each dataset. The model having the lowest QAICc was considered to be the best model. Different models having a  $\Delta$ QAIC of 2 or less were considered to have similar support from the data. Model averaging based on the normalised Akaike weights was applied to take account of model uncertainty (Burnham & Anderson 2002; Cooch & White 2012).

Table A.6.4 - Description of the CJS model variables used to estimate apparent survival and recapture probabilities.

<b>Probability of survival</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\varphi(.)$	Constant survival over all years
Time	$\varphi(t)$	Time varying survival
2 blocks	$\varphi(2blocks)$	Constant survival for each of two time periods: 1990-2001 & 2002-2006
"Age class"	$\varphi(a2)$	Survival accounting for transience

<b>Probability of recapture</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$p(.)$	Constant recapture probability over all years
Time	$p(t)$	Time varying recapture probability
Trap dependency	$p(t*m)$	Probability of recapture acc. for trap-dependency - interaction model
Trap dependency	$p(t+m)$	Probability of recapture acc. for trap-dependency - additive model

#### A.6.2.6 Robust design models

To explore the effect of temporary emigration from the main study site inside the fjords and to estimate survival rates for adult male and adult female killer whales, robust design models were implemented in program MARK (Kendall et al. 1997; Cooch & White 2012) in this Chapter using the 1990-2006 dataset. This extended the analysis using the 1990-2003 dataset presented in Chapter 3 (see section 3.2.3.3), to investigate whether the estimates differed due to the offshore shift in the NSS herring distribution since 2002.

The data from October-December 1990-2006 were organised into 17 primary sampling occasions (years) and 85 secondary sampling occasions (weeks within years) (see Table 6.1 in Chapter 6). The data for adult males and adult females were analysed separately. Analysis was conducted the same way as described in Chapter 3. For details of the robust design models and the modelling procedure, see section 3.2.3.3 in Chapter 3. Table A.6.5 shows the different effects modelled in the estimation of probabilities of survival, temporary emigration and capture.

No goodness of fit test is available for robust design models and therefore assessing model fit was not possible. Equally the variance inflation factor  $\hat{c}$  cannot be estimated and therefore model selection was done using Akaike's Information Criterion (AICc) (Anderson et al. 1994; Burnham & Anderson 2002). Different models having a  $\Delta AICc$  of 2 or less were considered to have similar support from the data.

Table A.6.5 - Description of the Robust Design model parameters used to estimate apparent survival, capture and temporary emigration probabilities.

<b>Probability of survival</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$\varphi(.)$	Constant survival throughout years
Time	$\varphi(t)$	Time varying survival
2 blocks	$\varphi(2blocks)$	Constant survival for two time periods: 1990-2001 & 2002-2006

<b>Probability of capture</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
Constant	$p(.) = c(.)$	Constant capture=recapture probabilities
Session	$p(s) = c(s)$	Capture=recapture probabilities varying within primary periods
Time*session	$p(s*t) = c(s*t)$	Capture=recapture probabilities varying within and between primary periods

<b>Temporary emigration</b>		
<b>Effect</b>	<b>Parameter</b>	<b>Description</b>
No emigration	$\gamma'' = \gamma' = 0$	No temporary emigration/immigration
Random	$\gamma'' = \gamma'$	Probability of emigration/immigration is random
Markovian	$\gamma'' \neq \gamma'$	Probability of emigration/immigration dependent on the previous state

## A.6.3 RESULTS

### A.6.3.1 Estimates of population size

The number of identifiable individuals in the population estimated from the Chapman two-sample model varied between 178 (SE = 21) in 1999-2000 and 796 (SE = 255) in 2005-2006 (Figure A.6.1). The proportion of identifiable individuals in the population was estimated to be 0.556 (SE = 0.052) for 1990-1995 and 0.656 (SE = 0.034) for 1997-2006 (see Chapter 3). Estimates of total population size using the estimates of the number of identifiable individuals for pairs of years are shown in Figure A.6.1. These estimates varied between 271 (SE = 34) in 1999-2000 and 1,226 (SE = 395) in 2005-2006. The standard error of estimated population size for 2005-2006 was large, due to the very small number of recaptures between these years so this estimate should be interpreted with caution. If the estimate for 2005-2006 is ignored, there seems to be a decline in population size from 2001-2002. However, given that the 95%

confidence intervals for the 2004-2005 and 2005-2006 estimates do not overlap, it is likely that population size was higher in 2005-2006 than in 2004-2005.

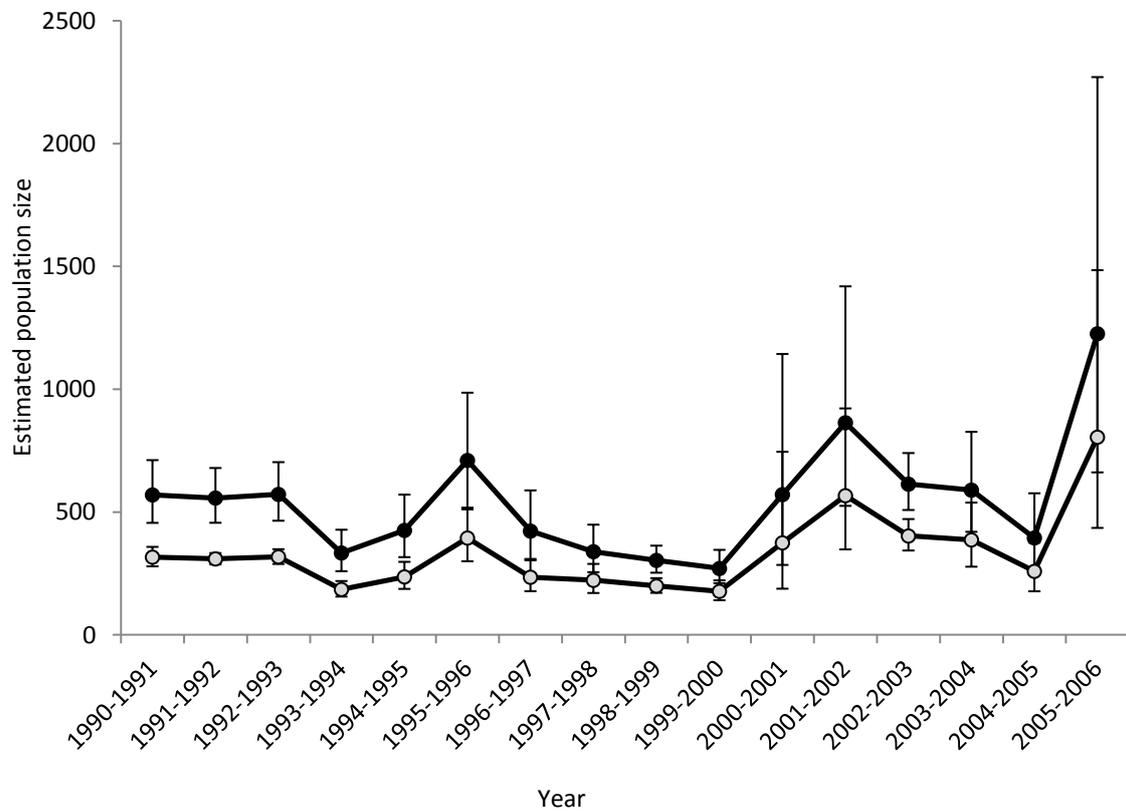


Figure A.6.1 - Chapman two-sample estimates of the number of identifiable individuals ( $\hat{N}$ ) (grey circles) and total population size ( $\hat{N}^{total}$ ) (black circles) between pairs of years 1990-2006. 95% CI are calculated assuming estimates are log-normally distributed.

### A.6.3.2 Cormack-Jolly-Seber (CJS) models

#### A.6.3.2.1 Model selection

Model diagnostics for adult males and adult females using the 1990-2006 data are given in Tables A.6.6 and A.6.7, respectively. For adult males the best model was the “age-class” model  $\varphi(a2) p(t+m)$  (Table A.6.6). Other models with  $\Delta QAIC \leq 2$  were the model estimating survival with two time periods  $\varphi(2blocks) p(t+m)$  and the model estimating constant survival  $\varphi(.) p(t+m)$ . All of these models estimated probability of capture including trap-dependency with the additive model. The best model for adult females estimated survival as constant accounting for trap-dependency in probability of capture with the additive model  $\varphi(.) p(t+m)$  (Table A.6.7). With adult female data, four models had a  $\Delta QAIC \leq 2$ . The top four models had

either constant or two time blocks for survival and either time varying or trap dependent capture probability.

Table A.6.6 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult males.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(a2) p(t+m)$	1314.9	0	0.4585	1	18	1276.0
2	$\varphi(2blocks) p(t+m)$	1316.0	1.1	0.2609	0.5690	18	1279.2
3	$\varphi(.) p(t+m)$	1316.2	1.3	0.2338	0.5100	17	1279.4
4	$\varphi(a2) p(t)$	1320.5	5.6	0.0273	0.0595	18	1283.7
5	$\varphi(.) p(t)$	1322.4	7.5	0.0108	0.0234	17	1287.7
6	$\varphi(t) p(t+m)$	1324.0	9.2	0.0047	0.0102	32	1274.7
7	$\varphi(2blocks) p(t)$	1324.4	9.5	0.0040	0.0088	18	1287.6
8	$\varphi(.) p(t^*m)$	1338.4	23.5	0	0	17	1271.9
9	$\varphi(t) p(t)$	1347.3	32.5	0	0	32	1283.1
10	$\varphi(t) p(t^*m)$	1348.7	33.8	0	0	32	1267.1
11	$\varphi(t) p(.)$	1400.4	85.6	0	0	17	1365.7
12	$\varphi(.) p(.)$	1411.2	96.3	0	0	2	1407.2

Table A.6.7 - Model selection diagnostics for CJS models of apparent survival and capture probabilities for adult females.

#	Model	QAICc	$\Delta$ QAICc	QAICc Weight	Likelihood	Num. Par	QDeviance
1	$\varphi(.) p(t+m)$	867.3	0	0.3973	1	17	830.0
2	$\varphi(2blocks) p(t+m)$	868.3	0.9	0.2506	0.6307	18	828.8
3	$\varphi(.) p(t)$	868.7	1.4	0.1993	0.5018	17	833.5
4	$\varphi(2blocks) p(t)$	869.3	2.0	0.1488	0.3745	18	832.0
5	$\varphi(t) p(t+m)$	876.5	9.2	0.0040	0.0100	32	826.2
6	$\varphi(.) p(t^*m)$	887.5	20.2	0	0.0001	17	821.6
7	$\varphi(t) p(t^*m)$	892.0	24.7	0	0	32	817.0
8	$\varphi(t) p(t)$	894.8	27.5	0	0	32	828.9
9	$\varphi(t) p(.)$	914.4	47.1	0	0	17	879.2
10	$\varphi(.) p(.)$	916.0	48.7	0	0	2	912.0

#### A.6.3.2.2 Estimates of apparent survival

For adult males, the best fitting model  $\varphi(a2) p(t+m)$  gave an estimate of apparent survival excluding the transients of 0.981 (SE = 0.008, 95% CI = 0.956 – 0.992) and 0.910 (SE = 0.041, 95% CI = 0.793 - 0.964) for the transients. The second best model  $\varphi(2blocks) p(t+m)$  estimated survival for the first time period as 0.971 (SE = 0.008, 95% CI = 0.949 - 0.984). Survival for the

second time period hit the upper bound ( $\varphi = 1$ , SE = 0, 95% CI = 0 -1). The third best model  $\varphi(.) p(t+m)$  estimated constant survival as 0.973 (SE = 0.008, 95% CI = 0.952 - 0.985). Model averaged apparent survival for adult males varied between 0.942 (SE = 0.043, 95% CI = 0.779 – 0.987) and 0.984 (SE = 0.013, 95% CI = 0.923 – 0.997).

For adult females, the best model  $\varphi(.) p(t+m)$  gave an apparent survival estimate of 0.988 (SE = 0.010, 95% CI = 0.941 – 0.998), higher than for adult males with the same model. The third best model also estimated constant survival  $\varphi(.) p(t)$  but without taking trap-dependency into account as 0.984 (SE = 0.010, 95% CI = 0.948 - 0.995). The second and fourth best models estimated survival for two time periods. The second one estimated probability of capture including trap-dependency with the additive model and gave an estimate of 0.992 (SE = 0.010, 95% CI = 0.920 -0.999) for the first time period and 0.850 (SE = 0.110, 95% CI = 0.511 - 0.969) for the second time period; note the large SE. The fourth model estimated capture probability as time varying and gave estimates of apparent survival rate of 0.988 (SE = 0.010, 95% CI = 0.942 - 0.998) for the first time period and as 0.842 (SE = 0.099, 95% CI = 0.552 - 0.959) for the second time period; note again high the large SE for the second time period. Model averaged apparent survival for adult females varied between 0.930 (SE = 0.102, 95% CI = 0.385 – 0.996) and 0.988 (SE = 0.010, 95% CI = 0.936 – 0.998).

#### **A.6.3.2.3 Capture probabilities**

Estimated capture probabilities varied among years (Figure A.6.2). Model averaged estimates of capture probabilities for adult males varied between 0.079 (SE = 0.029) – 0.716 (SE = 0.070) and for adult females 0.050 (SE = 0.049) – 0.648 (SE = 0.078) in the time period of 1991-2006. Capture probabilities for adult females were in most cases lower compared to adult males.

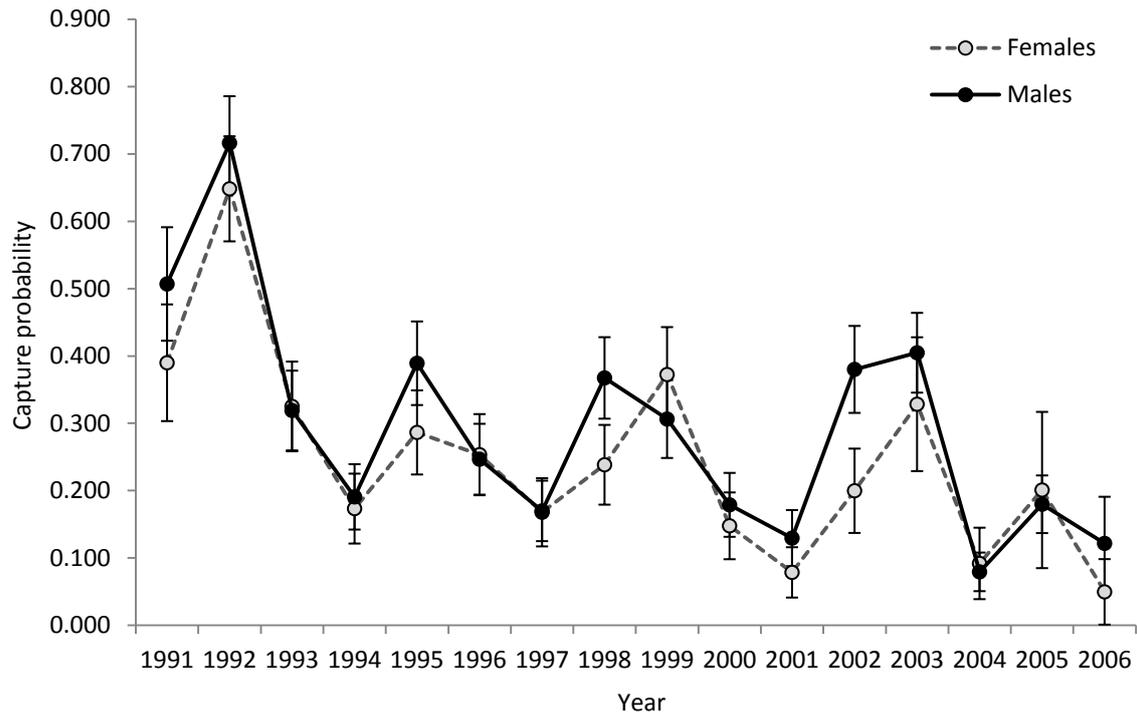


Figure A.6.2 - Capture probabilities of adult males and adult females 1991-2006 estimated from the model averaged CJS models with standard errors.

### A.6.3.3 Robust design models

#### A.6.3.3.1 Model selection

The model with constant survival, Markovian emigration with time variation and the interaction of session and time variation in capture/recapture probabilities was selected as the best model  $\varphi(.) y''(t) y'(t) p(s*t)=c(s*t)$  for adult males (Table A.6.8). The second best model with survival estimated with two time periods also had quite good support ( $\Delta AICc = 2.16$ ; model 2, Table A.6.8).

The best model for adult females included constant survival, emigration as random and constant, and the interaction of session and time variation in capture/recapture probabilities  $\varphi(.) y''(.)=y'(.) p(s*t)=c(s*t)$  (Table A.6.9). The second best model that estimated survival with two time periods also had good support,  $\Delta AICc = 1.04$  (Table A.6.9).

Appendix 6.1 - Mark-recapture analysis

Table A.6.8 - Model selection diagnostics for robust design models of apparent survival, capture and emigration probabilities for adult males. The model with lowest AICc, highest AICc Weight and Likelihood values was considered as the best one.

#	Model	AICc	ΔAICc	AICc Weight	Likelihood	Num. Par	Deviance
1	$\varphi(\cdot), y''(t) y'(t), p(s^*t)=c(s^*t)$	7435.22	0.00	0.747	1	117	10248.6
2	$\varphi(2blocks), y''(t) y'(t), p(s^*t)=c(s^*t)$	7437.39	2.16	0.253	0.339	118	10248.4
3	$\varphi(\cdot), y''(\cdot) y'(\cdot), p(s^*t)=c(s^*t)$	7457.54	22.31	< 0.001	0	88	10339.4
4	$\varphi(t), y''(\cdot) y'(\cdot), p(s^*t)=c(s^*t)$	7458.20	22.97	< 0.001	0	103	10305.1
5	$\varphi(2blocks), y''(\cdot) y'(\cdot), p(s^*t)=c(s^*t)$	7459.84	24.61	0	0	89	10339.4
6	$\varphi(t), y''(t) y'(t), p(s^*t)=c(s^*t)$	7459.90	24.68	0	0	130	10241.5
7	$\varphi(\cdot), y''(t)=y'(t), p(s^*t)=c(s^*t)$	7465.52	30.29	0	0	102	10314.7
8	$\varphi(t), y''(t)=y'(t), p(s^*t)=c(s^*t)$	7489.24	54.02	0	0	117	10305.1
9	$\varphi(t), y''(\cdot)=y'(\cdot), p(s^*t)=c(s^*t)$	7501.32	66.10	0	0	102	10350.6
10	$\varphi(\cdot), y''(t) y'(t), p(s^*t) c(s^*t)$	7515.65	80.42	0	0	185	10162.6
11	$\varphi(t), y''=y'=0, p(s^*t)=c(s^*t)$	7539.50	104.28	0	0	101	10391.1
12	$\varphi(2blocks), y''=y'=0, p(s^*t)=c(s^*t)$	7547.83	112.61	0	0	87	10432.0
13	$\varphi(\cdot), y''=y'=0, p(s^*t)=c(s^*t)$	7548.55	113.32	0	0	86	10435.0
14	$\varphi(\cdot), y''(t) y'(t), p(s) c(s)$	7831.28	396.06	0	0	66	10762.9
15	$\varphi(\cdot), y''=y'=0, p(s)=c(s)$	7956.09	520.87	0	0	18	10990.4
16	$\varphi(\cdot), y''=y'=0, p(\cdot)=c(\cdot)$	8131.60	696.38	0	0	2	11198.4

Table A.6.9 - Model selection diagnostics for robust design models of apparent survival, capture and emigration probabilities for adult females.

#	Model	AICc	ΔAICc	AICc Weight	Likelihood	Num. Par	Deviance
1	$\varphi(\cdot), y''(\cdot)=y'(\cdot), p(s^*t)=c(s^*t)$	4421.27	0	0.625	1	87	5842.9
2	$\varphi(2blocks), y''(\cdot)=y'(\cdot), p(s^*t)=c(s^*t)$	4422.32	1.04	0.371	0.594	88	5841.3
3	$\varphi(\cdot), y''(t) y'(t), p(s^*t)=c(s^*t)$	4431.76	10.48	0.003	0.005	117	5771.4
4	$\varphi(2blocks), y''(t)=y'(t), p(s^*t)=c(s^*t)$	4434.32	13.04	0.001	0.002	103	5813.2
5	$\varphi(2blocks), y''=y'=0, p(s^*t)=c(s^*t)$	4443.33	22.06	< 0.001	0	87	5864.9
6	$\varphi(\cdot), y''=y'=0, p(s^*t)=c(s^*t)$	4443.99	22.71	< 0.001	0	86	5868.2
7	$\varphi(t), y''(\cdot)=y'(\cdot), p(s^*t)=c(s^*t)$	4451.90	30.63	0	0	102	5833.5
8	$\varphi(t), y''=y'=0, p(s^*t)=c(s^*t)$	4472.89	51.62	0	0	101	5857.2
9	$\varphi(\cdot), y''(\cdot)=y'(\cdot), p(s^*t) c(s^*t)$	4544.21	122.94	0	0	149	5786.9
10	$\varphi(\cdot), y''(\cdot)=y'(\cdot), p(s) c(s)$	4603.62	182.34	0	0	36	6147.8
11	$\varphi(\cdot), y''=y'=0, p(s)=c(s)$	4612.91	191.63	0	0	18	6196.0
12	$\varphi(\cdot), y''=y'=0, p(\cdot)=c(\cdot)$	4755.19	333.92	0	0	2	6371.3

**A.6.3.3.2 Estimates of survival**

Adult male constant survival was estimated as 0.974 (SE = 0.006, 95% CI = 0.960 – 0.983) (model 1, Table A.6.8). Survival estimated with two time periods gave estimates of 0.972 (SE = 0.007, 95% CI = 0.955 – 0.983) for 1991-2001 and 0.999 (SE = 0.049, 95% CI = 0 – 1) for 2002-2006. The estimate for the second time period was very close to the upper bound and the confidence interval was uninformative. The model averaged estimate of adult male apparent survival varied between 0.973 (SE = 0.006, 95% CI = 0.958 – 0.983) and 0.980 (SE = 0.0127, 95% CI = 0.759 – 0.999).

Constant survival for adult females was estimated as 0.984 (SE = 0.006, 95% CI = 0.965 – 0.993) (model 1, Table A.6.9). Estimated survival showed a decrease between the two time periods from 0.988 (SE = 0.007, 95% CI = 0.965 – 0.996) to 0.901 (SE = 0.063, 95% CI = 0.694 – 0.973). The model averaged estimate of survival for adult females varied between 0.953 (SE = 0.056, 95% CI = 0.632 – 0.996) and 0.986 (SE = 0.007, 95% CI = 0.964 – 0.996).

**A.6.3.3.3 Temporary emigration**

Robust design analysis of both adult male and adult female datasets provided evidence for temporary emigration from the main NSS herring wintering area, as shown by the no-emigration models being discarded in favour of random or Markovian emigration models (Tables A.6.8 & A.6.9).

For adult males, the best fitting model had Markovian emigration with time variation in both  $\gamma''$  and  $\gamma'$  parameters (model  $\varphi(.) y''(t) y'(t) p(s*t)=c(s*t)$ , Table A.6.8). The probability of temporary emigration ( $\gamma''$ ) was 0.055 (SE = 0.117) – 0.856 (SE = 0.058). The probability of remaining outside the sampling area ( $\gamma'$ ) was 0.149 (SE = 0.257) – 0.971 (SE = 0.063). Thus, the derived return rate of temporary emigrants into the study area ( $1 - \gamma'$ ) was 0.029 – 0.851, and the probability of not emigrating temporarily ( $1 - \gamma''$ ) was 0.144 – 0.945.

For adult females the best fitting model had random emigration with constant  $\gamma''$  and  $\gamma'$  parameters (model  $\varphi(.) y''(.)=y'(.) p(s*t)=c(s*t)$ , Table A.6.9). The probability of temporary emigration and of remaining outside the sampling area was 0.303 (SE = 0.051). The derived return rate and probability of remaining inside the sampling area was 0.697.

## **A.6.4 DISCUSSION**

### **A.6.4.1 Most appropriate models**

Both adult males and adult females were subject to heterogeneity of capture probabilities in the form of trap-dependency, which in all cases was manifested as “trap-happiness”, i.e. increased capture probability after first capture (Pradel 1993; Pradel & Sanz-Aguilar 2012). Including trap-dependency improved model fit. Section 3.4.1 in Chapter 3 discusses the occurrence of trap-dependency in detail. There was also some evidence of transience (Pradel et al. 1997) for adult males and, in analysis using CJS models, incorporating transience as “age-class” improved the model fit. There was no evidence of transience for adult females.

Additionally, a robust design analysis was implemented to account for any bias due to temporary emigration in survival estimates for adults of both sexes. The random temporary emigration shown for adult females should mean that the CJS survival rate estimate is unbiased, although the precision of the estimates can be reduced (Kendall et al. 1997; Kendall 1999). For adult males with Markovian temporary emigration, estimates of capture/recapture and survival probabilities could be biased if not accounted for (Kendall 1999).

Issues leading to violation of the assumption of equal capture probabilities were recognised and taken into account as far as possible during data collection and processing, and then additionally in data analysis by incorporating trap-dependency, transience and temporary emigration into the selected models. Model selection issues are discussed further in section 3.4.1 in Chapter 3.

### **A.6.4.2 Abundance estimates**

The highest estimated total population size from the two-sample models of 1,226 (SE = 395) in 2005-2006 has a very high standard error and needs to be considered critically. If this estimate is ignored, the apparent decline in population size since 2001-2002 could potentially be a result of the offshore shift of the wintering NSS herring stock since 2002. However, estimated annual population size has varied over the period 1990-2005 and therefore strong inferences cannot be made. The number of killer whales that used the fjord system during wintertime was previously estimated as ~700 individuals (see Chapter 2; Kuningas et al. 2013a). Individuals still encountered using the fjords in the final years were a random selection of individuals (meaning that no particular individuals showed a higher preference to the area) with a very low recapture rate, as reflected in the large standard error of the estimates for the final years.

#### **A.6.4.3 Survival rates**

Comparison of the survival rates estimated from the CJS models presented in Chapter 3 and in this Chapter show higher estimated survival for both adult males (+0.5%) and for adult females (+1%) for analyses of the longer time series. This result is likely due to re-sightings of some individuals previously not seen in the later years of the shorter time series of data analysed in Chapter 3. In addition, there was a high number of new individuals identified in 2002 and 2003 (the final years of the data analysed in Chapter 3) and some of these individuals were recaptured in the analysis extending the time series with three more years.

The robust design models gave the same survival estimate for adult males (0.974) for the two different time series (see section 3.3.1.2 in Chapter 3). For adult females, however, the estimated survival rate with the robust design model in this Chapter was slightly higher (+0.8%).

Overall, the CJS and robust design models run on the extended dataset presented in this Chapter generated very similar estimates of survival rate for both adult males (0.973-0.974) and adult females (0.984-0.988). Comparison with killer whale survival estimates from other locations around the world show a higher adult male survival rate in northern Norway but a comparable survival rate for adult females (Olesiuk et al. 1990, 2005; Poncelet et al. 2010, section 3.4.2 in Chapter 3).

#### **A.6.4.5 Emigration and immigration rates**

In this Chapter, analyses were conducted on a longer time series than analysed in Chapter 3 to evaluate the influence of decreasing prey availability inside the fjord system. Overall, the models selected were the same in this Chapter as in Chapter 3 but there were differences in the estimated parameters.

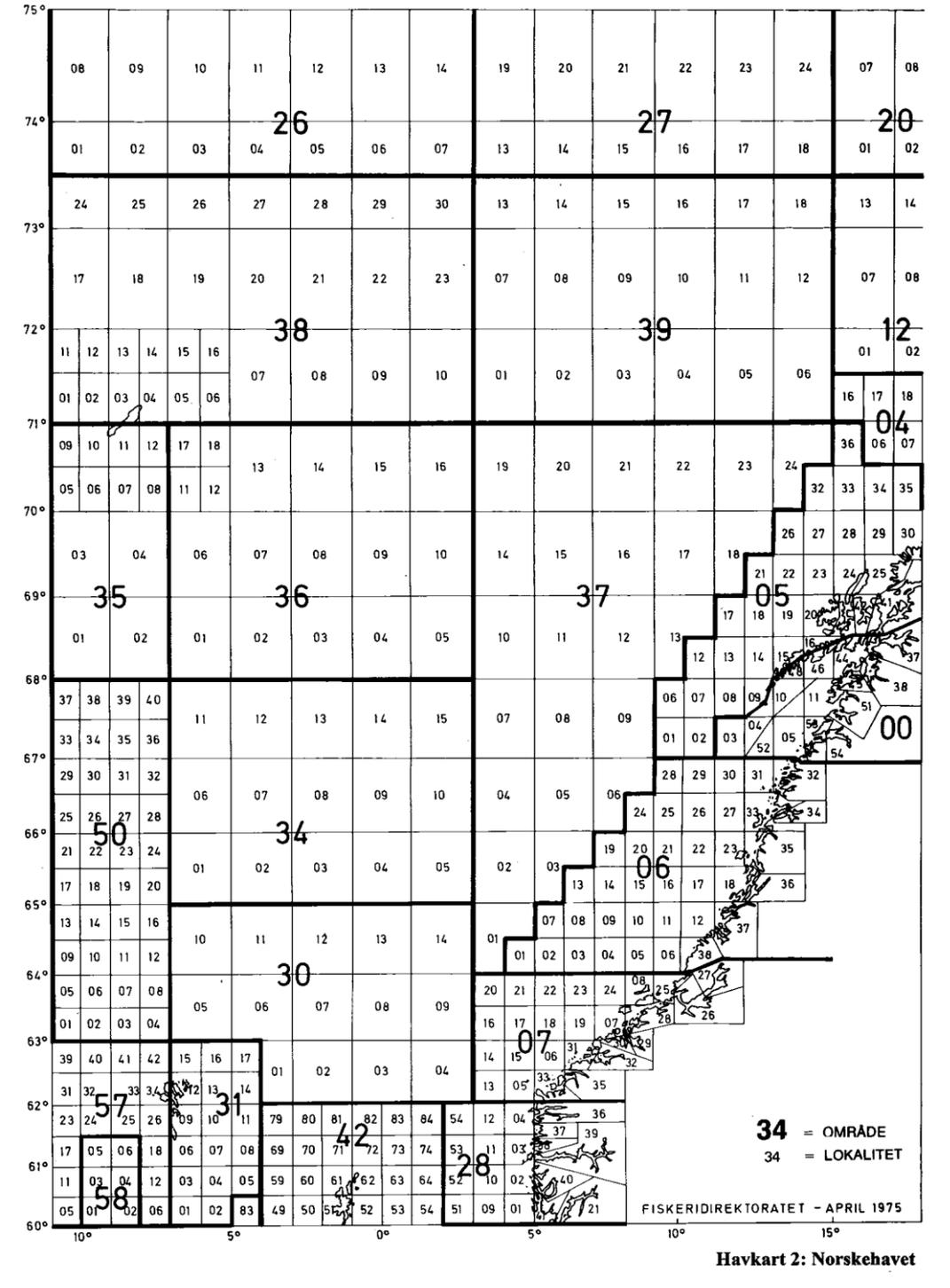
For adult males, the probability of adult males temporarily emigrating was on average 59% higher in this Chapter compared to Chapter 3. For adult females, the probability of adult females temporarily emigrating was 13% higher here compared to Chapter 3. The probability of remaining inside the study area decreased for adult males by 69% in the lower end of the range of probabilities compared to Chapter 3. For adult females the high probability of remaining in the study area decreased by 5% compared to Chapter 3. Overall, the analyses in this Chapter confirmed the higher site fidelity of adult females compared to adult males seen in Chapter 3 (more details are given in section 3.4.4 in Chapter 3).

Overall, the results presented in this Chapter from analyses of the longer time series indicate higher probabilities of adult killer whales being temporarily away from the fjord

system and lower probabilities of remaining in the fjord system. This likely reflects the increased emigration from the fjord system to the offshore area, and consequent decreased site fidelity to the fjord system, due to the change in distribution of the NSS herring stock to offshore waters.

Appendix 6.2 - Catch areas

Appendix 6.2 - The NSS herring catch areas in the Norwegian Sea specified by the Norwegian Directorate of Fisheries. Data on NSS herring catches were provided for the areas 00 (fjord system), 05, 27, 37 and 39 in the offshore area for the period 1988-2010.



## Appendix 7

Population size, survival and reproductive rates of northern Norwegian killer whales (*Orcinus orca*) in 1986–2003

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## Appendix 8

Killer whale presence in relation to naval sonar activity and prey abundance in northern Norway.

Kuningas, S., Kvadsheim, P. H., Lam, F-P. A., and Miller, P. J. O.

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