Abundance and predatory impact of killer whales at Marion Island

by

Ryan Rudolf Reisinger

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Declaration

I, Ryan Rudolf Reisinger, declare that the dissertation, which I hereby submit for the degree MSc (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature:

Date:

Summary

Title: Abundance and predatory impact of killer whales at Marion Island

Student: Mr. R.R. Reisinger
Supervisors: Prof. M.N. Bester
Dr. P.J.N. de Bruyn
Degree: MSc (Zoology)
Department: Zoology and Entomology, University of Pretoria

Abstract: Killer whales are the oceans' apex predator and are known to have important effects on ecosystems. At Subantarctic Marion Island, southern Indian Ocean, they have only been studied opportunistically, resulting in limited knowledge of their ecosystem impact here. This dissertation describes the prey and seasonal abundance, estimates the population size and assesses the predatory impact of killer whales on seals and penguins at Marion Island, using dedicated and opportunistic shore-based observations and photographic identification, from 2006 to 2009.

During 823 sightings of killer whales at Marion Island (2006 to 2009) 48 predation events were recorded; in only 10 cases could prey be identified. Killer whales fed on fur seals, elephant seals and penguins. Constant effort (dedicated) observations (259 hours, 2008 to 2009) showed that killer whale abundance, which peaked in September to December with a secondary peak in April to May, is linked to the abundance of seals and penguins.

Mark-recapture analyses were performed using nearly 10 000 photographs taken from 2006 to 2009. Following careful quality control criteria 37 individuals were identified and a population size of 42 (95% CI = 35-50) individuals estimated using the open population

POPAN parameterization in the software program MARK. The analytical approach is more rigorous than that used in any previous population size assessment at Marion Island.

Finally, the above data were integrated to assess whether top-down control of seal and penguin populations at Marion Island is generally plausible using a simple process of elimination. Based on published data I predicted the energetic ingestion requirements of adult male and female killer whales as 1 394 MJ.day^{-1} and 1 028 MJ.day^{-1}, respectively. Expanding these requirements to the 37 killer whales photographically identified at Marion Island, the population requires 40 600MJ.day^{-1}. Based on available energy density and mass data, I predicted the energy content of available seal and penguin prey and calculated the rates at which killer whales would consume these prey in various scenarios. Penguins and Subantarctic fur seals are relatively insensitive to killer whale predation owing to their large population sizes (10 000s to 100 000s), conversely, the smaller populations (100s to 1 000s) of Antarctic fur seals and southern elephant seals are sensitive to predation, particularly the latter as they have a high energy content (approximately 2 000 to 9 000 MJ). Populations of these seals are currently increasing or stable and I conclude that presently killer whale predation is not driving population declines, although they clearly have the potential for regulation of these smaller populations. Thus, if population sizes were reduced by bottom-up processes, if killer whale diet shifted, or if prey availability changed, top-down control by killer whales could become significant.

This study provides baseline information for the informed management and conservation of killer whales at Marion Island, identifies avenues for further research, and provides a foundation for the continuation of structured and dedicated killer whale research at Marion Island.

Key words: apex predator; diet; foraging; killer whale; Marion Island; occurrence cycle; *Orcinus orca*; penguin; photo-ID; population size; predator-prey interactions; program MARK; seal; Southern Ocean; Subantarctic; top-down control

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Contents

CHAPTER 1

General introduction

CHAPTER 2

Prey and seasonal abundance of killer whales at Marion Island

CHAPTER 3

Mark-recapture abundance estimates of killer whales at Marion Island

CHAPTER 4

Predatory impact of killer whales on pinniped and penguin populations at the Prince Edward Islands: fact and fiction

CHAPTER 5

General conclusion

APPENDIX A

APPENDIX B

List of tables

List of figures

Manuscripts

Chapters 2, 3 and 4 of this dissertation have been prepared for publication as separate manuscripts. The reader will therefore have to bear a fair amount of repetition, especially in the Methods sections, for which I apologise.

Prey and seasonal abundance of killer whales at Subantarctic Marion Island
RR Reisinger, PJN de Bruyn, CA Tosh, WC Oosthuizen, NT Mufanadzo, MN Bester
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Abundance estimates of killer whales at Subantarctic Marion Island
RR Reisinger, PJN de Bruyn, MN Bester
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Aquatic Biology

CHAPTER 1

General introduction

"BIG FIERCE ANIMALS" IN ECOSYSTEMS

It is a truism that predators must eat other organisms in order to sustain themselves and predator-prey interactions are consequently among the most conspicuous of species interactions. The direct effects of predation are limited to impacts on prey populations but the role of predators in shaping and structuring communities and ecosystems depends as much on the indirect effects of predation (Estes et al. 2001). For decades ecologists have debated whether bottom-up (resource limitation) or top-down (predation) processes regulate populations and structure communities (Hairston et al. 1960, Hunter and Price 1992). Although the relative roles and interactions of these processes and their various strengths at different spatio-temporal scales are now being emphasised, rather than each paradigm as an absolute (e.g., Hunter and Price 1992, Sinclair et al. 2003, Hunt and McKinnell 2006, Frank et al. 2007), the role of predators in ecosystems is increasingly being recognised. Due to their size, mobility and energy requirements, large predators can have great effects on ecosystems despite the fact that "big fierce animals" (Colinvaux 1979) naturally are rare and are becoming more so as anthropogenic change sweeps across the planet (Terborgh 1990, Seidensticker and McDougal 1993, Gittleman and Gomper 2005, Steneck 2005). Their extirpation from many ecosystems, rarity, mobility and often cryptic behaviour makes large predators difficult to study and examples of their effects are often sparse. "Considerable empirical and theoretical research supports the thesis that large predators *can* affect community structure and biodiversity. It is less well known under which conditions predators *do* exert, or could exert, major influences on the structure and function of ecosystems." (Steneck 2005:9).

Studies of the dynamical interactions of predators and their prey do not only have heuristic value for the understanding of predator-prey ecology, a topic of considerable theoretical interest (e.g., Barbosa and Castellanos 2005), but are of critical conservation and management importance (e.g., Soulé et al. 2005, Sinclair and Byrom 2006). Ecosystems cannot be effectively managed and conserved without knowledge of their function and the forces that structure them. Top predators are often employed as conservation tools, acting as surrogate species for the conservation of ecosystems, yet the efficacy of this approach cannot be gauged without understanding and evaluating the role of predators in ecosystems (Boyd et al. 2006, Sergio et al. 2008). Further, modelling approaches to management require information about predator-prey interactions (e.g., Guénette et al. 2006, Rayfield et al. 2009).

The potential role of killer whales (*Orcinus orca*) in ecosystems has been highlighted by the intensely debated "sequential megafaunal collapse hypothesis" (Estes et al. 1998, Springer et al. 2003). This hypothesis posits that the depletion of great whale stocks in the North Pacific Ocean during post World War II industrial whaling forced killer whales to "fish down" the ecosystem (*sensu* Pauly et al. 1998), or sequentially switch to smaller/less abundant marine mammal prey species, in response to the loss of their great whale prey, causing declines in pinniped and then sea otter populations. An analogous mechanism was proposed to explain declines in southern elephant seal (*Mirounga leonina*) populations in the Southern Ocean (Barrat and Mougin 1978) following the depletion of great whales in the Southern Hemisphere during 20th century whaling operations (Clapham and Baker 2002). Killer whale predation was speculated to be a factor in local population size changes of elephant seals and penguins (Condy et al. 1978, Guinet et al. 1992, Keith et al. 2001, Ainley et al. 2010), but only a single study has quantitatively addressed this issue, albeit at an ocean wide scale (Branch and Williams 2006). This dissertation focuses on the predatory role of killer whales at the Prince Edward Islands (PEIs; Figure 1.1), southern Indian Ocean, and has been stimulated to a large degree by the speculation and debate surrounding the role of killer whales in ecosystems. As an expansion of the ongoing pinniped monitoring programme at Marion Island, initiated in 1976 (Bester 1988, de Bruyn et al. 2008) this dissertation aims to improve our understanding of the dynamics of upper trophic level interactions and to provide information for future conservation and management endeavours at the PEIs (e.g., Lombard et al. 2007).

KILLER WHALES – FORAGING SPECIALIZATIONS

"Indeed, they may be regarded as marine beasts, that roam over every ocean; entering bays and lagoons, where they spread terror and death among the mammoth balaenas and the smaller species of dolphins, as well as pursuing the seal and walrus, devouring, in their marauding expeditions up swift rivers, numberless salmon or other large fishes that may come in their way." Scammon 1874:89

Orcinus orca is the largest member of the Delphinidae and is currently recognised as a single cosmopolitan species. The most widely distributed non-human mammal (Ford 2002), killer whales occur in all oceans and most seas, although they appear to be more common in areas of high ocean productivity, temperate nearshore environments and at high latitudes (Heyning and Dahlheim 1988, Ford 2002, Forney and Wade 2006, Jefferson et al. 2008). The language used to describe killer whales may have tempered somewhat since Captain Scammon's days, but it remains true that killer whales are the oceans' apex predators. As a species, they prey on a wide variety of taxa including cephalopods, bony and cartilaginous fishes, reptiles, birds, and mammals (Hoyt 1990, Jefferson et al. 1991). Members of all marine mammal families except the river dolphins and manatees have been recorded as prey and attacks have been observed on at least 35 species of marine mammal (Jefferson et al. 1991). Numerous fish species are included in their diet (at least 22 in the eastern North Pacific alone), notably salmon (*Oncorhyncus* spp.), herring (*Clupea harengus*), cod (*Gadus* spp.), tuna (*Thunnus* spp.) and various elasmobranchs (Ford et al. 1998, Dahlheim and Heyning 1999, Saulitis et al. 2000, Visser 2005). Despite this generally eclectic diet, dietary specialization is one of the most striking among the extensive morphological, genetic and ecological differences that have been described between various killer whale populations. These differences have prompted several workers to propose different species or subspecies of killer whales (Mikhalev et al. 1981, Berzin and Vladimirov 1982, 1983, Baird 1994, Pitman et al. 2007, Morin et al. 2010), albeit without general consensus, and a revision of killer whale taxonomy is imminent (Jefferson et al. 2008). Currently killer whales should at least be considered a species complex (Whale and Dolphin Conservation Society 2002, Barrett-Lennard and Heise 2006).

The most intensively studied killer whale populations occur in the eastern North Pacific Ocean where three distinct, sympatrically occurring "ecotypes" have been described (Bigg et al. 1987, Ford et al. 2000). *Transient* killer whales feed mainly on marine mammals, but also include seabirds in their diet, while *resident* killer whales feed exclusively on fish and squid (Ford et al. 1998, Saulitis et al. 2000). *Offshore* killer whales are less well known, but their diet likely comprises bony and cartilaginous fishes (Dahlheim et al. 2008). These ecotypes also differ in a number of other aspects, including morphology (Bigg et al. 1987, Baird and Stacey 1988, Ford et al. 2000, Dahlheim et al. 2008), acoustic behaviour (Barrett-Lennard et al. 1996), genetics and social organization (Hoelzel et al. 1998, Barrett-Lennard 2000, Baird and Whitehead 2000). The socio-biological isolation of these ecotypes may have evolved due to their foraging specializations (Baird and Whitehead 2000, Ford 2002). Similarly, in the Antarctic at least three killer whale ecotypes have been identified, based mainly on morphological differences, but also on their differing group sizes and apparently differing dietary and habitat preferences, and there is some evidence that the three ecotypes are reproductively isolated (Pitman and Ensor 2003, Pitman et al. 2007, LeDuc et al. 2008, Morin et al. 2010). *Type A* killer whales feed mainly on Antarctic minke whales (*Balaenoptera bonaerensis*), *Type B* mainly feed on pinnipeds but also take penguins (Pitman and Durban 2010) and *Type C* are piscivorous (Krahn et al. 2008). These regions present the most studied examples of sympatric population differentiation in killer whales, but studies in other regions are revealing similar patterns. In the North Atlantic, for example, morphological traits, nitrogen stable isotope ratios, tooth wear and mitochondrial DNA divergence point to divergent killer whale ecotypes: a large dietary generalist, and a smaller dietary specialist (Foote et al. 2009).

Despite the description of killer whale ecotypes in Antarctic waters, killer whales are comparatively poorly studied in the Southern Ocean and surrounding oceans. At Punta Norte, Argentina, photographic identification studies were initiated in 1975 and have identified a small population (~30 individuals) that ranges along the Patagonian coast. A core group within this population returns to Punta Norte seasonally to hunt pinnipeds, often capturing them by intentionally stranding themselves ashore, although penguins and fish are also included in their diet (Iñíguez et al. 2002). Associations between individuals appear relatively stable, and three pods have been identified in the core group (Lopez and Lopez 1985, Hoelzel 1991, Iñíguez 2001). At the Îles Crozet, southern Indian Ocean, opportunistic photographic identification has been carried out since 1964 (Guinet 1991); 70 killer whales were identified from 1988 to 1989, and 32 from 1998 to 2000. Mark-recapture analyses indicate a population size of 37 individuals for the latter period, and highlight a worrying decline in population size and survival, possibly due to low prey stocks and lethal interactions with fisheries (Poncelet et al. 2010). Killer whales at the Îles Crozet include elephant seals (which they often capture by intentional stranding), whales, penguins and fish in their diet (Guinet 1992). At least 18 pods have been identified, typically composed of a single matriarchal unit (Guinet 1991), as is common in other populations (e.g., Bigg et al. 1990, Baird and Whitehead 2000, Ivkovich et al. 2010).

The few studies of killer whales at the PEIs comprise opportunistic data collected since the early 1970s when Condy et al. (1978) described killer whales attacking southern elephant seals, king penguins (*Aptenodytes patagonicus*) and rockhopper penguins (*Eudyptes chrysocome filholi*) close inshore. They linked the seasonal abundance of killer whales to the haulout patterns of elephant seals and penguins. Observations from 1973 to 1996 confirmed the seasonal occurrence of killer whales inshore, with a peak evident between October and December, and 26 individuals were identified from photographs, 11 of which recurred at the island (Keith et al. 2001). Based on observations from a single day, Pistorius et al. (2002) described the local movement of killer whales along the island's east coast and estimated the population size to be 25 to 30 individuals. Most recently, Tosh et al. (2008) described non-random associations between individuals in a preliminary analysis of social structure based on photographic identification data from a single year. No study has taken a dedicated sampling approach to collecting photographic identification and observational data and, consequently, the above studies have drawn very limited conclusions about the population characteristics and predatory role of killer whales at the PEIs.

THE PRINCE EDWARD ISLANDS AND THEIR MARINE SURROUNDS

The Subantarctic PEIs comprise Marion Island and Prince Edward Island, two volcanic outcrops in the Indian Ocean sector (half of the area between 30° and 60° South) of the vast Southern Ocean (Chown and Froneman 2008; Figure 1.1). Marion Island (46°54'S, 37°45'E) is the larger of the PEIs with an area of around 300 km^2 (Meiklejohn and Smith 2008) and an approximately 90 km coastline. Prince Edward Island (46°38'S, 37°57'E), 19 km to the

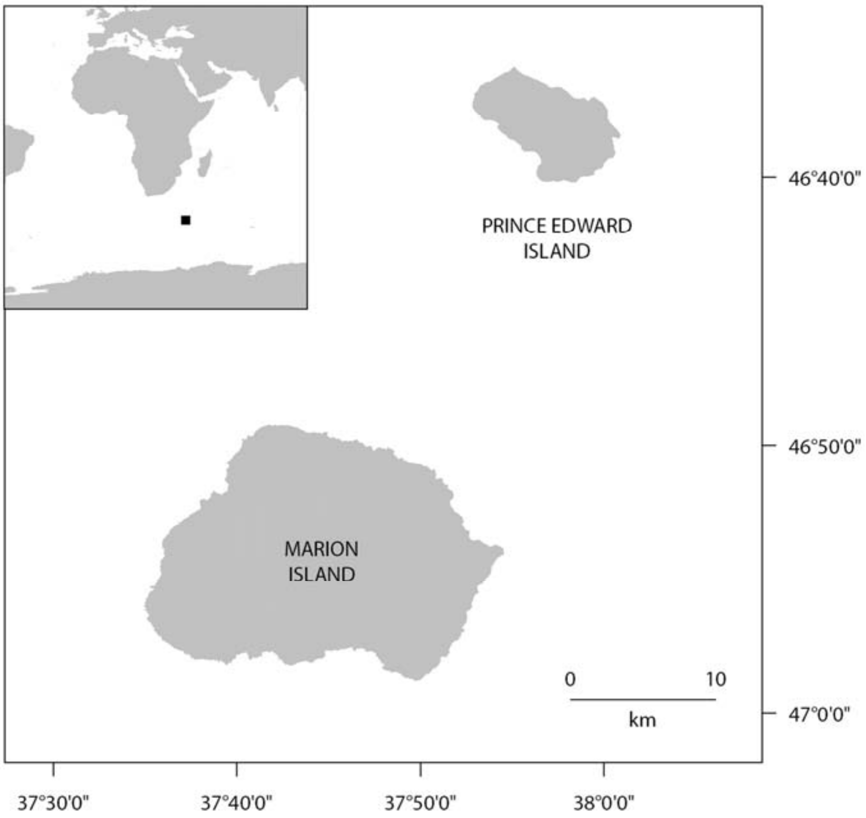

FIGURE 1.1 The Prince Edward Islands group, southern Indian Ocean. The inset shows the islands' position in relation to Africa and Antarctica.

northeast, has an area of about 46 km^2 and an approximately 30 km coastline. The islands are located ~2 000 km southeast of South Africa and ~2 000 km north of the Antarctic continent, but their nearest landfall is the Île aux Cochons of the Îsles Crozet, 950 km to the east (Lutjeharms and Ansorge 2008).

The PEIs lie in the path of the eastward flowing Antarctic Circumpolar Current (ACC) and are situated in the Polar Frontal Zone (PFZ), bounded to the north by the Subantarctic Front (SAF) and to the south by the Antarctic Polar Front (APF; Lutjeharms and Valentine 1984, Belkin and Gordon 1996) both of which show high degrees of latitudinal variability in this region (Lutjeharms 1990). The two islands lie on a pinnacle that rises from about 5 000 m depth and are separated by a shallow (40 to 200 m deep) saddle (Ansorge and Lutjeharms 2002). The major bathymetric feature in the region is the South-West Indian Ridge which lies to the immediate west of the islands, extending south-west to north-east. While the general oceanographic environment of the PEIs is mostly similar to other Subantarctic islands, influenced by the ACC and associated fronts, the PEIs lie in a region of high mesoscale variability (Lutjeharms and Ansorge 2008) characterised by eddies which are generated particularly at the Andrew Bain fracture zone in the South-West Indian Ridge. Here the ACC is constrained through a narrow gap, picking up speed and generating mesoscale turbulence (Ansorge and Lutjeharms 2003, 2005). These eddies may be warm, (anti-cyclonic) or cold (cyclonic), depending on their origin, and include organisms from their region of origin so that the surrounding waters of the PEIs have a diverse biota (Bernard et al. 2007, Ansorge et al. 2010). The increased primary productivity and prey abundance associated with fronts and eddies is exploited by top predators (reviewed by Bost et al. 2009) and the PEIs support large terrestrially breeding populations of 3 seal species, 4 penguin species, 5 albatross species, 14 petrel species and 5 other seabird species, totalling several million individuals (Ryan and Bester 2008). The oceanographic and biological oceanographic features that provide food to support this superabundance of top predators has been termed the PEIs' "life support system" (Pakhomov and Froneman 1999, Pakhomov and Chown 2003, McQuaid and Froneman 2004).

Marion Island's rugged coastline comprises cliffs interspersed with rock, boulder or pebble beaches. The west coast consists mainly of vertical cliffs rising directly from the sea, with few, rocky beaches. Conversely, the leeward east coast has more numerous beaches with gentler topography and boulder and pebble substrate, which provide breeding sites for elephant seals and king penguins. Subantarctic fur seal (*Arctocephalus tropicalis),* macaroni penguin (*Eudyptes chrysolophus*) and rockhopper penguin rookeries are distributed along the entire coast, whereas Antarctic fur seal (*Arctocephalus gazella*) colonies are restricted to the south and east coasts. Large beds of bull kelp (*Durvillea antarctica*) are a ubiquitous feature of the islands' shallow inshore waters (<100 m from shore), while giant kelp (*Macrocystis pyrifera*) forms a second "ring" around the islands in the deeper waters further offshore (>500 m from shore). Mean sea surface temperature (SST) at Marion Island (1949 to 1998) was 5.3 °C with mean monthly SSTs ranging from 4.3 °C (September) to 6.4 °C (February; Mélice et al. 2003). Mean annual air temperature (5.7 °C) matches SST closely and the hyperoceanic climate is further characterized by strong wind, (wind speeds greater than 54 km.h^{-1} on >100 days.year^{-1}), high precipitation (~2 000 mm.year^{-1}), high humidity (average 80%) and low incident radiation (25 to 30% of possible sunshine; Smith and Steenkamp 1990, le Roux 2008).

DISSERTATION AIMS AND STRUCTURE

The direct effect of a predator on populations of its prey will depend on the predator's diet, abundance and per-capita consumption rate, the latter dictated by metabolic rate and prey quality (Williams et al. 2004). As an initial step in assessing the role of killer whales in the PEIs ecosystem – the overall aim of this dissertation – I have addressed two of these factors (diet and abundance), and synthesised the information to evaluate the possible effects of killer whales on their prey populations.

Chapter 2 describes predation and temporal abundance of killer whales at the PEIs based on observations. Specifically I answer the questions:

a) What species of pinnipeds and penguins do killer whales prey on?
b) When are killer whales most abundant in the inshore waters of Marion Island?
c) Are any temporal abundance patterns of killer whales related to the phenology of their prey species?

In **Chapter 3** I compile a photographic identification catalogue of killer whales at Marion Island (**Appendix A**) and perform mark-recapture analyses of these data to estimate the abundance of killer whales at Marion Island. The key questions answered are:

a) What is the age-sex class composition of the population?
b) Do killer whales return annually to Marion Island?
c) What is the size of the killer whale population?
d) How do these aspects compare to similar killer whale populations elsewhere?

In **Chapter 4**, I use the above information, with published data on the energy requirements of killer whales and the energy content of their prey, to assess the potential direct effects of killer whale predation on pinniped and penguin populations. I use a process of elimination to assess the impact that different predation scenarios may have on prey populations. In so doing I attempt to eliminate least likely scenarios, and identify most probable predation scenarios to focus future work on. Specifically, I ask the following key questions:

a) How much energy does the killer whale population at the PEIs require?
b) How many individuals of each prey species are required to meet the energy requirements of the killer whale population?

c) Does this represent a considerable proportion of the population of any prey species?
d) What predation scenarios (prey composition) would result in regulation of prey populations and are these scenarios biologically realistic?
e) What is the impact of killer whales on smaller prey population sizes?
f) Are killer whales a likely regulator of the southern elephant seal population at these islands?

Finally, I summarize in **Chapter 5**, and identify relevant avenues for further research.

Additionally, I aimed to establish a long-term dedicated observational framework, focussed on regular and systematic photographic identification of individuals, for the continued study of various aspects of killer whale ecology at the PEIs (**Appendix B**). This study therefore not only aims to answer the above key questions – representing a valuable contribution to our understanding of the killer whale population at the PEIs and their management – but aims to provide baseline information and impetus to future studies.

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CHAPTER 2

Prey and seasonal abundance of killer whales at Marion Island

ABSTRACT

To understand the role of killer whales in marine ecosystems, descriptions of their diet are vital, yet this aspect is poorly known in Subantarctic killer whales. During 823 sightings of killer whales at Subantarctic Marion Island (2006 to 2009) 48 predation events were recorded; in only 10 cases could prey be identified. Killer whales fed on fur seals, elephant seals and penguins. Constant effort (dedicated) observations (259 hours, 2008 to 2009) showed that killer whale abundance, which peaked in September to December with a secondary peak in April to May, is linked to the abundance of seals and penguins.

INTRODUCTION

Killer whales (*Orcinus orca*) exhibit wide variation in foraging ecology throughout their range (and even locally), with distinct populations specializing on certain prey types (reviewed by Baird 2000). They are apex predators and their documented prey include a variety of taxa including cephalopods, bony and cartilaginous fishes, reptiles, birds, and mammals (Hoyt 1990, Jefferson et al. 1991). As such, killer whales can have important top-down effects on marine ecosystems (Bowen 1997; see also Springer et al. 2003) and the diversity of their prey means they can potentially influence ecosystem structure and function at various levels (Ford and Ellis 2006).

In the southern Indian and Atlantic oceans, killer whales have been poorly studied. At the Îles Crozet killer whales were observed feeding on seals, penguins, fish and large cetaceans (Guinet 1992) and at Punta Norte, Argentina, killer whales are frequently observed attacking seals, but also to some extent feed on penguins and fish (Lopez and Lopez 1985, Hoelzel 1991, Iñíguez et al. 2002). At Marion Island, opportunistic studies have investigated killer whale population structure, local movements and social structure (Condy et al. 1978, Keith et al. 2001, Pistorius et al. 2002, Tosh et al. 2008). A population size of 42 animals was recently estimated using mark-recapture methods and 37 individuals were photographically identified (Chapter 3, Appendix A). As at the Crozet Islands and Punta Norte (situated at similar latitudes), killer whales are sighted year-round at Marion Island, but their abundance peaks in the austral summer, arguably as a function of the seasonal haul-out of elephant seals (*Mirounga leonina*) and certain penguin species (Condy 1978, Keith et al. 2001). Seasonal co-occurrence with potential prey species is speculative and has not been verified using dedicated observational sampling techniques. Opportunistic observations of killer whale predation at Marion Island (Condy et al. 1978, Keith et al. 2001) suggest that they include a combination of seals and penguins in their diet.

Marion Island supports increasing populations of both Subantarctic (*Arctocephalus tropicalis*) and Antarctic fur seals (*A. gazella*) with total pup productions of 16 045 and 759, respectively, in 2004 (Hofmeyr et al. 2006). The elephant seal population appears to be increasing and current pup production is approximately 520 (de Bruyn 2009, McMahon et al. 2009). King penguins (*Aptenodytes patagonicus*) numbered 65 000 breeding pairs in

2008; gentoo penguins (*Pygoscelis papua*), macaroni penguins (*Eudyptes chrysolophus*) and eastern rockhopper penguins (*E. chrysocome filholi*) numbered 1 100, 290 000 and 42 000 breeding pairs, respectively, in 2008 (Crawford et al. 2009). Clearly, these large populations provide substantial potential prey for top-predators such as killer whales.

This study aims to describe the diet of killer whales at Marion Island, based on direct observation, and to investigate their seasonal abundance at the island in relation to known prey species that occur in this region.

METHODS

Study site

Subantarctic Marion Island (46°54'S, 37°45'E, Figure 2.1) is the larger (300 km^2) of a pair of islands comprising the Prince Edward Islands (PEIs) group. It is situated in the southern Indian Ocean with the nearest landmass being the Îles Crozet (950 km to the east) in practically the same latitude. The interplay between the Antarctic Circumpolar Current and the prominent bottom topography of the South West Indian Ridge results in productive turbulent water masses around the PEIs (Ansorge and Lutjeharms 2005), sustaining the numerous mammal and bird species that breed there.

Field methods

Land-based, opportunistic sightings of killer whales at Marion Island were recorded between April 2006 and April 2009. For each sighting, location, group size and age- and sex-class composition of the group, as well as direction of movement was recorded. Sex was determined based on size and shape of the dorsal fin, relative body size and close association with calves (adult females). Distance from shore was recorded following Condy et al. (1978): zone 1: within 5 m of shore; zone 2: 5 to 100 m from shore, usually extending to the first kelp belt (*Macrocystis* sp.); zone 3: 100 to 500 m from shore, usually extending to the second kelp belt; zone 4: beyond 500 m from shore. As many individuals as possible were photographed at each sighting and notes were made regarding the animals' behaviour. Predation events were noted when killer whales were seen with prey in their jaws, or

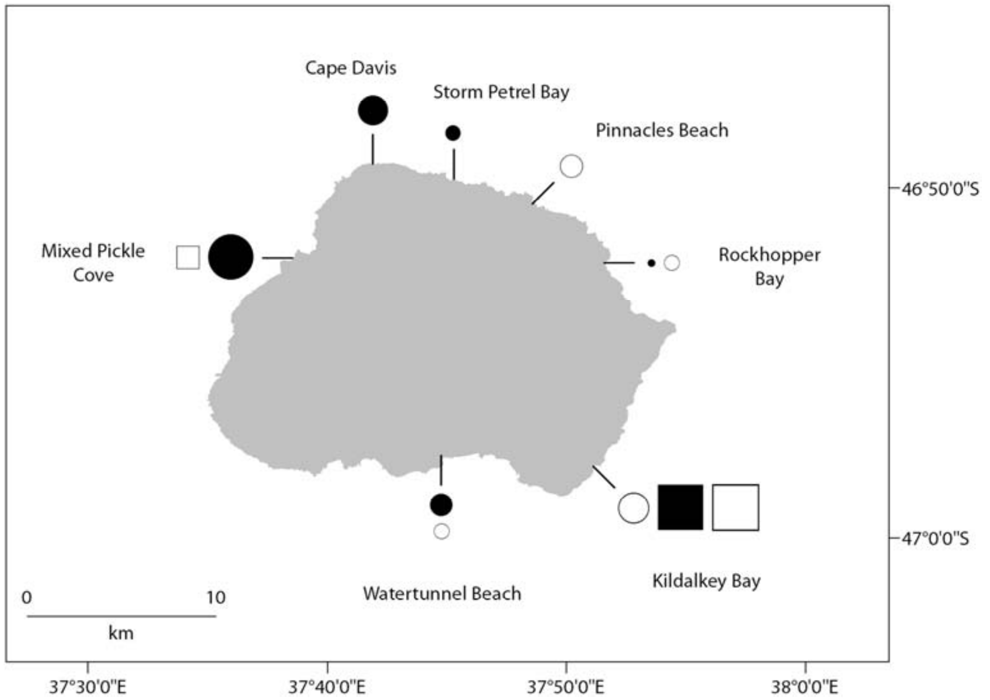

FIGURE 2.1 Map of Marion Island, southern Indian Ocean, showing the locations (Mixed Pickle Cove, Cape Davis, Storm Petrel Bay, Pinnacles Beach, Rockhopper Bay, Kildalkey Bay and Watertunnel Beach) where dedicated killer whale observations were made and the breeding population sizes of fur seals (●), elephant seals (○), king penguins (■) and macaroni penguins (□) at these locations. Symbol sizes represent relative population sizes.

when prey remains were visible at the sea surface immediately following killer whale observation (usually giant petrels [*Macronectes* spp.] fed on these).

Additionally, land-based "dedicated observation sessions" were performed between May 2008 and April 2009, during which one of two trained observers remained at set observation points and visually searched for killer whales for a pre-determined length of time. The same data were recorded as for opportunistic sightings, as well as Beaufort sea state. Figure 2.1 shows the distribution and relative population sizes of fur seals (Hofmeyr et al. 2006), southern elephant seals (de Bruyn 2009), king penguins (Crawford et al. 2003a) and macaroni penguins (Crawford et al. 2003b) at dedicated observation sites. Rockhopper penguins are distributed relatively evenly along Marion Island's coast (Crawford et al. 2003c) and gentoo penguins nest in small colonies (on average, less than 40 pairs) at few locations (Crawford et al. 2003d). Observation locations were thus sited at certain breeding colonies of all seal and penguin species. Short-term (one day) observations of the inshore movements of killer whales at Marion Island (Pistorius et al. 2002) suggest that groups of killer whales patrol large sections of the coast, and that they are active at all (daylight) hours (Keith et al. 2001), increasing the likelihood of sighting animals from single observation points.

Observation sessions were of two types:

1) In order to investigate the seasonal abundance of killer whales, between May 2008 and April 2009, 93 short (2 to 3 hours) observation sessions were performed from the same point at Rockhopper Bay, Marion Island (Figure 2.1), totalling 249 hours (approximately the same effort monthly, except for April 2009; Table 2.1). Observation sessions were performed at regular intervals throughout each month, and at approximately the same time of day. Because the probability of sighting killer whales far from shore was potentially influenced by sea state, we limited our analysis to sightings of groups within 100 m from shore (zones 1 and 2). We considered the probability of sighting groups at this distance not to be influenced by sea state. Repeat sightings of a group during a session were also eliminated. These were identified by the group size and composition, and direction of movement.
2) 46 long (10 hours - uninterrupted) observation sessions were performed at various points (Figure 2.1) around the island more than once a week between August 2008 and April 2009, totalling 460 hours.

RESULTS

Predation

Between April 2006 and April 2009, a total of 823 killer whale sightings were made during opportunistic and dedicated observations. Forty eight predation events were recorded. For 38 events the prey could not be identified, but in 10 instances the prey was unequivocally identified from photographs. Penguins (unknown sp.) were killed by killer whales on three occasions, several (>4) king penguins were killed and eaten on one occasion (Figure 2.2a) and a macaroni penguin on one occasion. Elephant seals were killed twice (one a subadult, the other a subadult or adult female; Figure 2.2b) and Subantarctic fur seals were killed on three occasions (all pups; Figure 2.2c). Killer whales unsuccessfully pursued a

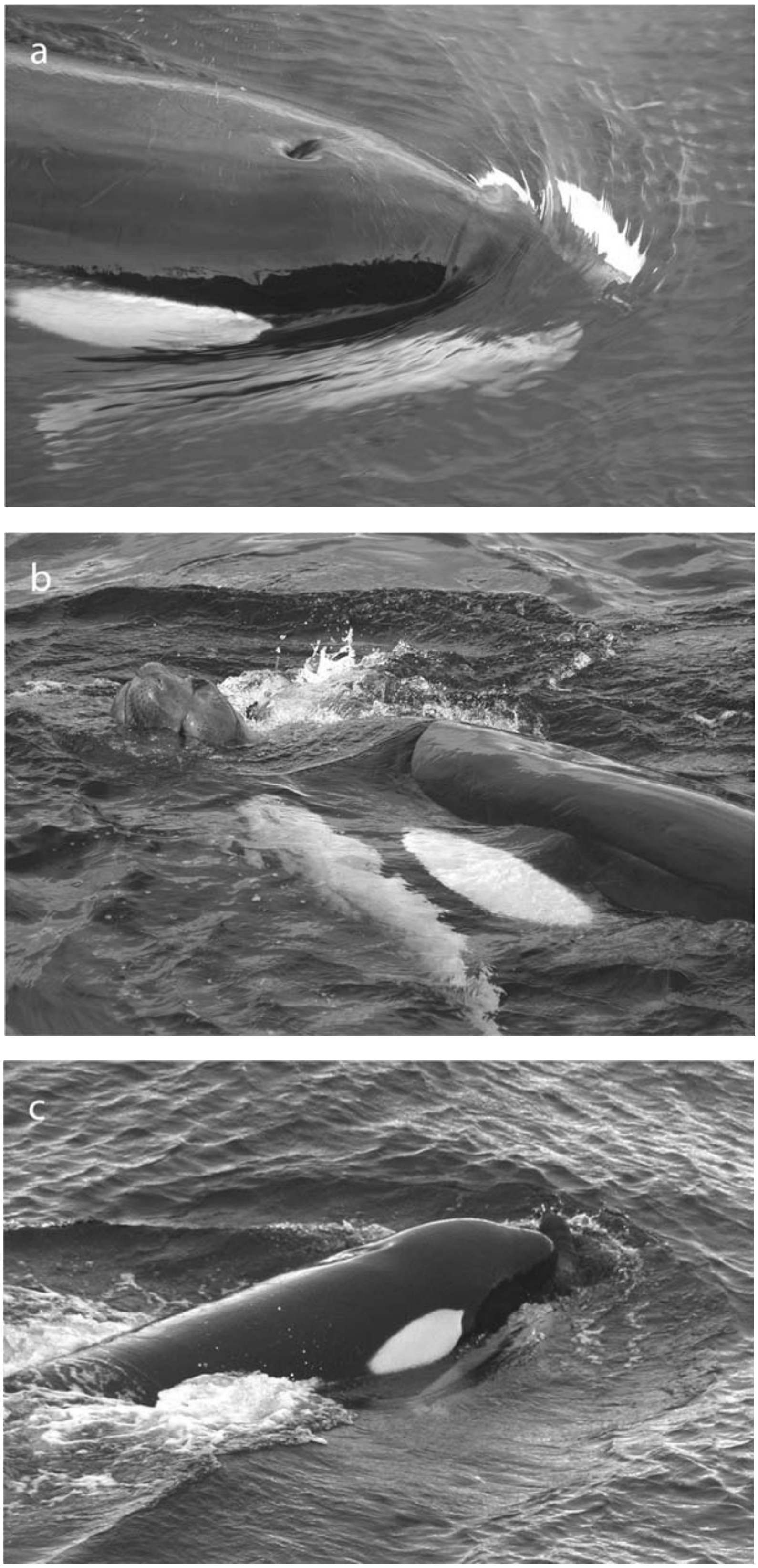

FIGURE 2.2 Photographs showing killer whales predating on (a) a king penguin, (b) an elephant seal, and (c) a Subantarctic fur seal pup at Marion Island. Actual feeding followed these observations. Photographs by PJN de Bruyn, RR Reisinger and C Eadie.

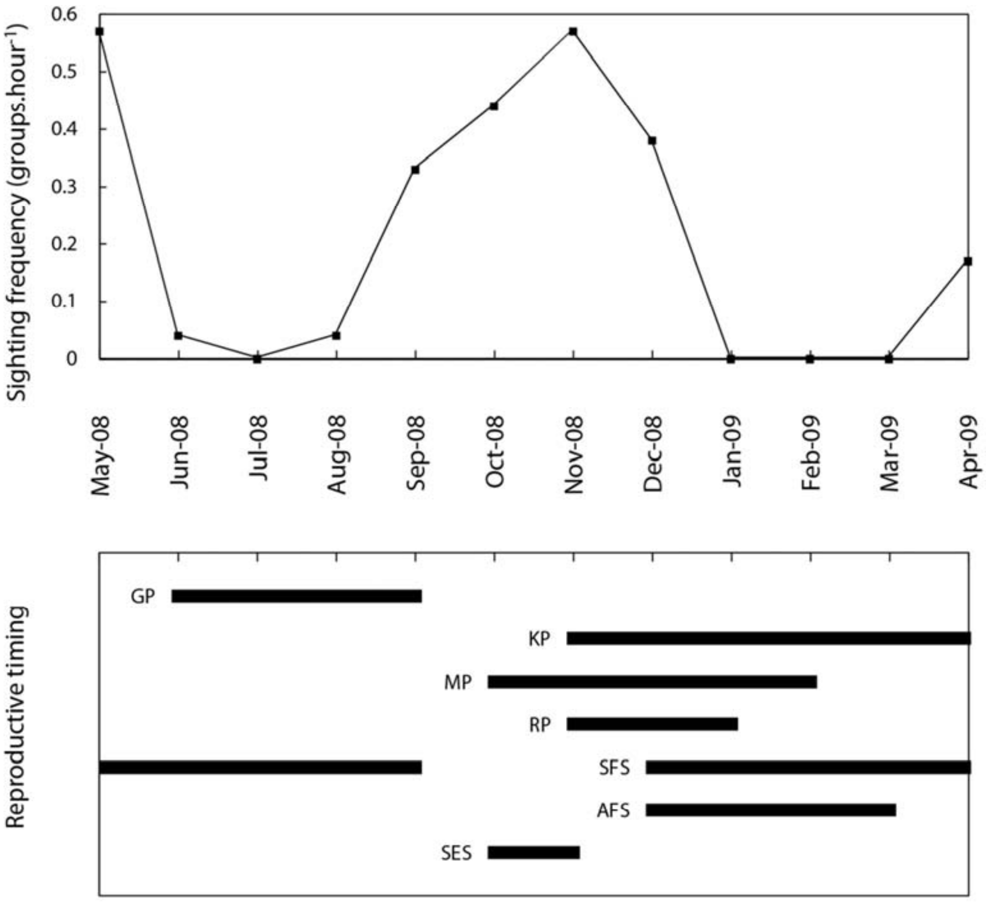

FIGURE 2.3 Monthly sighting frequency (groups.hour^{-1}) of killer whales at Rockhopper Bay, Marion Island, between May 2008 and April 2009, as well as the reproductive timing (median arrival to median crèching date for penguins and median pupping to median weaning date for seals) of gentoo penguins (GP; Crawford et al 2003d), king penguins (KP; du Plessis et al. 1994), macaroni penguins (MP; Crawford et al. 2003b), rockhopper penguins (RP; Crawford et al. 2003c), Subantarctic fur seals (SAFS; Hofmeyr et al. 2007), Antarctic fur seals (AFS; Hofmeyr et al. 2007) and southern elephant seals (SES; Kirkman et al. 2004).

subadult elephant seal as well as an adult female Subantarctic fur seal. While killer whales were not directly observed predating on Antarctic fur seals, unknown prey was consumed at Watertunnel Beach (Figure 2.1), the site of the largest Antarctic fur seal breeding colony on the island, on more than one occasion. Three observations were made of killer whales interacting with large cetaceans (a southern right whale, humpback whales and a group of unidentified whales): on each occasion the killer whales moved towards the whales and swam alongside or around them, but presumably (as could be observed) did not make physical contact with the whales.

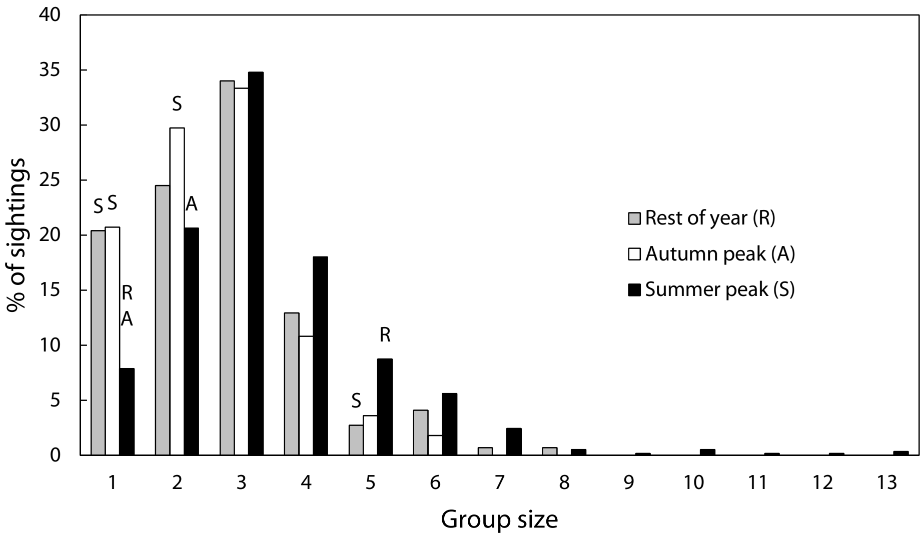

FIGURE 2.4 Group size frequency distribution of killer whales at Marion Island between April 2006 and April 2009. "Rest of year" represents sightings from January to March and June to August; "Autumn peak" represents sightings from April to May; and "Summer peak" sightings from September to December. Letters above a bar indicate a significant difference (*p* < 0.05) between the group size sighting frequency in that period and the period corresponding to the letter.

Year	Month	Effort (hours)
2008	May	14
	June	25
	July	24
	August	24
	September	27
	October	18
	November	21
	December	24
2009	January	24
	February	15
	March	27
	April	6

TABLE 2.1 Monthly observational effort for killer whales at Rockhopper Bay, Marion Island.

Seasonal abundance

During 93 dedicated observation sessions at Rockhopper Bay (April 2008 to May 2009), killer whales were sighted 49 times (repeat sightings per session excluded; zone 1 only). The maximum number of sightings per month was 12 (November 2008) and no killer whales were sighted in July 2008 and January, February and March 2009. Maximum sighting frequency was 0.57 groups.hour^{-1}, during May and November 2008 (Figure 2.3) and mean monthly sighting frequency was 0.21 groups.hour^{-1}. Overall, monthly sighting frequencies differed significantly (Kruskal-Wallis test, $p < 0.01$) Killer whale sighting frequency showed a clear peak in May 2008 and between September and December 2008; Mann-Whitney pair-wise comparisons are shown in Table 2.2. For all sightings from April 2006 to April 2009, group size ranged from 1 to 13 individuals with a modal group size of 3. Group size frequency distribution of killer whales sighted in the summer peak of sighting frequency (September to December), autumn peak (April to May) and the rest of the year (January to March and June to August) is shown in Figure 2.4. A Kruskal-Wallis test showed slight significant ($p = 0.03$) difference between the frequency distribution of the three periods (Figure 2.4). Two-sample tests for equality of proportion showed significant ($p < 0.05$) differences in four of the 39 pair-wise period-group size frequency comparisons (Figure 2.4), but only highly significant differences ($p < 0.01$) between the sighting frequency of one individual in the summer and autumn peaks and between the summer peak and the rest of the year.

DISCUSSION

Predation

Killer whales were observed preying on two of the three seal species occurring at Marion Island and two of the four penguin species and these observations are similar to data for *transient* killer whales in the eastern North Pacific and seemingly similar to populations at the Îles Crozet and Punta Norte. It is unknown whether killer whales at Marion Island include fish and cetaceans in their diet.

In the eastern North Pacific foraging observations and stomach content analyses show that *transient* killer whales feed primarily on harbour seals (*Phoca vitulina*) but include a variety of other pinnipeds, cetaceans (including large whales) and seabirds in their diet (Ford et al.

	May-08	Jun-08	Jul-08	Aug-08	Sep-08	Oct-08	Nov-08	Dec-08	Jan-09	Feb-09	Mar-09
Jun-08	0.0168										
Jul-08	**0.0024**	0.3384									
Aug-08	0.0282	0.9383	0.2616								
Sep-08	0.5839	**0.0056**	**0.0004**	0.0102							
Oct-08	0.9344	0.0149	**0.0025**	0.0346	0.6196						
Nov-08	0.8832	**0.0082**	**0.0013**	0.0186	0.4099	0.8840					
Dec-08	0.8420	0.0185	**0.0027**	0.0393	0.9594	0.7881	0.5931				
Jan-09	0.0116	0.4555	...	0.3816	**0.0026**	0.0121	**0.0072**	0.0126			
Feb-09	0.0420	0.5896	...	0.5271	0.0129	0.0439	0.0298	0.0444	...		
Mar-09	**0.0078**	0.4214	...	0.3458	**0.0016**	**0.0080**	**0.0046**	**0.0085**	...	...	
Apr-09	0.3810	0.2720	0.0247	0.3485	0.4344	0.4890	0.3696	0.5839	0.0801	0.2059	0.0594

TABLE 2.2 Post-hoc Mann-Whitney pair-wise comparisons for significant differences between monthly sighting rates of killer whales at Rockhopper Bay, Marion Island. *p* values shown. Grey shading indicates $p < 0.05$, bold type indicates $p < 0.01$.

1998). Iñíguez et al. (2002) reported that killer whales in Northern Patagonia feed mainly on southern sea lions (*Otaria flavescens*) (85.7%) but also on elephant seals (3.9%), Magellanic penguins (*Spheniscus magellanicus*) (3.9%) and fish (6.1%). In southern Africa the 26 stomachs of killer whales examined (mainly from animals taken during whaling operations) contained primarily marine mammal remains (84.6% of stomachs) followed by fish (23.1%), squid (3.8%) and seabirds (3.8%; Best 2010). While seabirds may not represent an important food source in the eastern North Pacific or South African waters (Williams et al. 1990, Ford et al. 1998), penguin populations in the Southern Ocean – often locally numbering several hundred thousand birds – may be more important for killer whales at these localities. Antarctic *Type B* killer whales apparently feed mainly on seals but also take penguins (Pitman and Ensor 2003, Pitman and Durban 2010).

Killer whales in the vicinity of Marion Island (i.e., outside the fisheries exclusion zone of 8 to 12 nm around the PEIs [de Villiers and Cooper 2008]) are frequently observed depredating Patagonian toothfish (*Dissostichus eleginoides*) during demersal longlining operations (Kock et al. 2006, Williams et al. 2009) and further photographic identification investigation should be directed at determining whether these individuals also feed on seals and penguins close inshore. Equivocal interactions were observed with large cetaceans and it is unclear whether killer whales prey on large cetaceans at Marion Island as they do at the adjacent (950 km) Îles Crozet, directly to the east of Marion Island (Guinet 1992, Guinet et al. 2000).

Unfortunately, describing the diet of killer whales based on observations of predation events has important limitations: such observations are relatively rare, observations include mainly larger prey consumed at or near the surface, reflect dietary habits only in the area where observations are made (in this study, near inshore), it may be difficult to distinguish prey killed and consumed from prey killed and left, and the dietary habits observed may be short term (Ford et al. 1998, Krahn et al. 2008).

Seasonal abundance

Structured dedicated observation sessions (this study) confirm the previously shown peak in killer whale occurrence at Marion Island between September and December (Condy et al. 1978, Keith et al. 2001), and link it to the breeding timing of seals and penguins at the island

(Figure 2.3). The dedicated observations confirm a secondary peak during April to May, linked to the occurrence of fur seal pups in inshore waters, and without the potential effects of observer effort bias present in previous studies. The occurrence and distribution of killer whales has been linked to the abundance of prey resources before (e.g., Nichol and Shackleton 1996, Similä et al. 1996) and to seasonal breeding in seals (Hoelzel 1991, Iñíguez 2001, Bolt et al. 2009).

Elephant seals have a median haulout date of 15 October (Kirkman et al. 2004) at Marion Island and give birth within a week after arrival (Laws 1956). Pups wean at an age of 21 days and swim close to shore before dispersing in November and December (Wilkinson and Bester 1990). Weaned elephant seal pups are presumably profitable prey for killer whales as they would be relatively easy to catch and safe to handle, with up to 25% of weaned pups taken off a particular beach at Îles Crozet (Guinet et al. 1992). The median arrival date of king penguin adults at colonies is in November (du Plessis et al. 1994), macaroni penguin median arrival is in mid-October (Crawford et al. 2003b), rockhopper penguin arrival in early November (Crawford et al. 2003c) and gentoo penguin in late June (Crawford et al 2003d). The first three species breed in large numbers (Crawford et al. 2003) and their densities in inshore waters are high as they arrive to breed at Marion Island. Their timing of breeding coincides with the peak occurrence of killer whales. Gentoo penguins are present in relatively small numbers (Crawford et al. 2003), and likely do not represent an important prey source for killer whales at this site. Antarctic fur seals and Subantarctic fur seals have median parturition dates of 6 and 18 December, respectively (Hofmeyr et al. 2007) and thus prior to this, large numbers of fur seals arrive to breed, providing prey for killer whales. Antarctic fur seal pups wean at an age of 112 days and Subantarctic fur seal pups at approximately 300 days (i.e., in March and October of the following year, respectively; Kerley 1985), whereafter they disperse. Pups of both species start swimming close to shore especially in February (Kerley 1983). The availability of large numbers of fur seal pups inshore likely explains the secondary peak in occurrence of killer whales in April to May.

The observed group sizes (Figure 2.4) of killer whales at Marion Island are consistent with earlier observations for the island (Condy et al. 1978, Keith et al. 2001, Tosh et al. 2008), as well as for populations of pinniped-eating killer whales elsewhere. This is likely an optimal group size for maximizing energy intake in such populations (Baird and Dill 1996). The modal group size observed (3 individuals) is comparable to average group sizes of 4.2 (Condy et al. 1978), 3.6 (Keith et al. 2001) and 3.4 (Tosh et al. 2008) reported previously at Marion Island, and 3.2 (modal group size of 2) at Punta Norte (Lopez and Lopez 1985) and modal group size of 3 at Vancouver Island, British Columbia (Baird and Dill 1996). Larger group sizes are reported for piscivorous populations (e.g., Bigg et al. 1990, Pitman and Ensor 2003, Dahlheim et al. 2008) and Burdin et al. (2007) showed significant differences between group sizes of mammal- and fish-eating killer whales in the Russian Far East. The largest groups observed at Marion Island included identified individuals which were mostly observed separately on other occasions (Mammal Research Institute, unpublished data), indicating temporary interactions of smaller groups, likely for socializing and perhaps cooperative hunting (Baird and Dill 1996). This illustrates that, albeit for killer whales in different habitats and aquatic ecosystems, a stable group size occurs in predominantly pinniped-eating populations, governed by the energetic limitations of foraging on marine mammal prey (Baird and Dill 1996). The highly significant differences between sighting frequencies of single individuals during the summer sighting peak, autumn peak and the rest of the year, are likely related to the social role of “roving” males as identified in British Columbia (Baird and Whitehead 2000). Such males disperse from their maternal pod and appear to spend some of their time alone, occasionally associating with groups that contain potentially reproductively receptive females. Such associations may be more common at certain times of the year in the Marion Island population, explaining the change in sighting frequency of solitary killer whales.

CONCLUSIONS

Killer whales at Subantarctic Marion Island predate on elephant seals, fur seals and penguins but it is unknown whether other prey species, such as cetaceans and fish, may be included. Their temporal abundance at the island is linked to the near-/onshore temporal abundance of the observed prey species. My findings are similar to those for killer whales at the Subantarctic Crozet Islands and Punta Norte, Argentina. Despite the limitations of the current study, it provides systematically collected information about the diet of a poorly known population of killer whales.

For the informed management and conservation of killer whale populations as well as their prey, attempts to elucidate the diet of killer whales at Marion Island should continue, employing the current observational methods (which are neither costly nor invasive) as well as methods such as fatty acid and stable isotope analysis (e.g., Herman et al. 2005). Of particular interest is the frequency of occurrence of particular prey types and the potential impact of killer whales on populations of their prey, especially seals. Future research should also be directed at the large-scale movements of killer whales, using continued photographic identification at various localities and satellite telemetry (e.g., Andrews et al. 2008), as well as their stock structure in the region, using genetic methods (e.g., Hoelzel et al. 1998).

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CHAPTER 3

Mark-recapture abundance estimates of killer whales at Marion Island

ABSTRACT

Killer whales (*Orcinus orca*) are apex predators known to have important effects on marine ecosystems. A fundamental step towards understanding their role in ecosystems, and vital for their informed management and conservation, is the rigorous estimation of abundance. Studies concerning this species have used mark-recapture analytical techniques to estimate abundance, but enumeration of identifiable individuals is more common. This study estimated the abundance of killer whales occurring inshore at Subantarctic Marion Island. Mark-recapture analyses were performed using nearly 10 000 photographs taken from 2006 to 2009. Using careful quality control criteria we identified 37 individuals and by using the open population POPAN parameterization in the software program MARK estimated a population size of 42 (95% CI = 35-50) individuals. These results are comparable to recent abundance estimates for the neighbouring Îles Crozet Archipelago (~950 km due east). Previously no rigorous approach was used to estimate the abundance of killer whales at Marion Island. Despite the acknowledged limitations of this estimate, it provides a foundation for further research related to the sociality and potential ecological impact of this population of killer whales in the Southern Ocean.

INTRODUCTION

Killer whales (*Orcinus orca*) are cosmopolitan (Heyning and Dahlheim 1988) apex predators with different populations preying on a variety of taxa including cephalopods, bony and cartilaginous fishes, reptiles, birds, and mammals (Hoyt 1990, Jefferson et al. 1991, Ford 2009). As apex predators they potentially have important effects on marine ecosystems (e.g., Estes et al. 1998, Williams et al. 2004) and the diversity of their prey means they can influence ecosystems at various levels and intensities (e.g., Springer et al. 2003, Ford and Ellis 2006). In the Southern Ocean, southern elephant seals (*Mirounga leonina*) underwent a population decline between the 1950s and 1990s throughout most of their breeding range (McMahon et al. 2005) and killer whale predation has been suggested as one of the causes of this decline at two breeding locations: Marion Island (Condy et al. 1978) and the Îles Crozet (Guinet et al. 1992).

A critical step towards understanding the role of killer whales in ecosystems, however, and necessary for quantitatively evaluating the effects of killer whales in ecosystems, is the estimation of their abundance. Moreover, abundance estimates are vital for the informed management and conservation of cetaceans (e.g., Karczmarski et al. 1999, Keith et al. 2002, Parra et al. 2006) and trends in the abundance of marine top predators may be useful in detecting environmental changes in marine ecosystems (Weimerskirch et al. 2003, Boyd et al. 2006).

Forney and Wade (2007) reviewed worldwide killer whale abundance, estimating a minimum global population size of 50 000, but abundance data are poor for many regions and the authors identified the need for further estimates. Regional abundance estimates for the Southern Ocean, based on line-transect surveys, indicate that killer whales are relatively common in these waters. Hammond (1984) estimated 38 278 (CV = 0.63) killer whales in the Indian Ocean sector of the Southern Ocean, Kasamatsu and Joyce (1995) estimated 80 400 (CV = 0.15) individuals in the Southern Ocean with uncorrected abundance estimates for the Indian Ocean sector totalling 12 093 (CVs ranging from 0.44-0.96) and most recently Branch and Butterworth (2001) estimated 24 790 (CV = 0.23) killer whales south of 60°S.

In the southern Indian Ocean rigorous local population size estimates are only available for Île de la Possession (Îles Crozet). Poncelet et al. (2010) used mark-recapture (MR) methodology to estimate the population size at 98 animals between 1988 and 1989, (95% CI = 70-156) and 37 individuals between 1998 and 2000 (95% CI = 32-62). Their analyses show a worrying decline in population size and survival rates, which the authors speculate is due to changes in prey availability (southern elephant seals and large whales) and lethal interactions with illegal Patagonian toothfish (*Dissostichus eleginoides*) fisheries (see also Tixier et al. 2010). At Marion Island no rigorous population size estimates have been produced. Keith et al. (2001) identified 26 individual killer whales from 159 photographs taken opportunistically from 1975 to 1989 and based on simultaneous island wide observations on a single day, Pistorius et al. (2002) approximated the population size at 25 to 30 individuals.

At Île de la Possession, Poncelet et al. (2010) used mark-recapture methodology to estimate the population size at 98 animals between 1988 and 1989, (95% CI = 70-156) and 37 individuals in the subsequent 1998 to 2000 period (95% CI = 32-62). Their analyses also show a worrying decline in survival rates of the population, which the authors speculate is due to changes in prey population sizes (southern elephant seals and large whales) and lethal interactions with illegal Patagonian toothfish (*Dissostichus eleginoides*) fisheries. At Marion Island no rigorous population size estimates have been produced. Keith et al. (2001) identified 26 individual killer whales from 159 photographs taken opportunistically from 1975 to 1989 and Pistorius et al. (2002) used simultaneous island wide observations on a single day to estimate the population size at 25 to 30 individuals. Furthermore, killer whales at Marion Island were only studied opportunistically at a population level, and local movements as well as social structure have been preliminarily analyzed (Condy et al. 1978, Keith et al. 2001, Pistorius et al. 2002, Tosh et al. 2008).

MR analyses of photographic identification data have been used to estimate population size in killer whales (Kuningas et al. 2007, Williams et al. 2009, Poncelet et al. 2010, Durban et al. 2010) but this approach has generally been necessitated by logistical constraints (e.g., large populations where individuals are encountered infrequently, or large and/or remote areas) or financial constraints (see Williams et al. 2009, Durban et al. 2010). More commonly the abundance of small, well-studied killer whale populations is determined by a count of known individuals (e.g., Dahlheim et al. 1997, Matkin et al. 1999, Ford et al. 2000).

To provide information required for the assessment of the ecological role of killer whales at Marion Island, and to furnish baseline information for their management and conservation there and in the broader southern Indian Ocean, I used MR analyses of photographic identification data collected from 2006 to 2009 to estimate the abundance of killer whales at Marion Island. The study also establishes a photographic identification catalogue of individuals at the island and compares enumeration of the population using this catalogue to MR population size estimates.

METHODS

Marion Island

Subantarctic Marion Island (46°54'S, 37°45'E) is the larger (300 km^2) of a pair of islands comprising the Prince Edward Islands group. It is situated in the southern Indian Ocean with the nearest landmass being the Îles Crozet – approximately 950 km to the east at similar latitude. The interplay between the Antarctic Circumpolar Current and the prominent bottom topography of the South-West Indian Ridge results in productive turbulent water masses around the Prince Edward Islands (Ansorge and Lutjeharms 2005), sustaining the large breeding populations of seals and seabirds.

Field methods

Land-based sightings of killer whales at Marion Island were recorded from April 2006 to April 2009. Small-vessel based surveys are impossible due to logistic and safety concerns regarding the isolation of Marion Island and the very poor weather and sea conditions (Prince Edward Islands Management Plan Working Group 1996). Sightings were of two types: *Opportunistic* observations were recorded from April 2006 to April 2009 while observers were engaged in various field activities, mostly systematic pinniped monitoring (see de Bruyn et al. 2008 for further pinniped monitoring details); *dedicated* observation sessions were conducted at various points on the north, east and south coast of the island (Figure 2.1) from May 2008 to April 2009. I consider these locations a representative inshore sampling/survey area as killer whales patrol mainly beaches along the east coast

(Keith et al. 2001, Pistorius et al. 2002). During these sessions a trained observer would remain at a point and visually search for killer whales for a predetermined length of time. Such *dedicated* observation sessions were of two types:

1) Short (2 to 3 hours) observation sessions were performed 93 times at Rockhopper Bay (Figure 2.1), totalling 249 hours (approximately the same effort monthly, except for April 2009), at regular intervals throughout each month, and at approximately the same time of day;
2) Long (10 hours uninterrupted) observation sessions were performed 46 times at various points (Figure 2.1) more than once per week from August 2008 to April 2009, totalling 460 hours.

For all types of observations, the location, group size and age-sex class composition of the group, as well as direction of movement, was recorded for each sighting. Distance from shore was recorded following Condy et al. (1978): zone 1: within 5 m of shore; zone 2: 5 to 100 m from shore, usually extending to the first kelp (*Macrocystis* sp.) belt; zone 3: 100 to 500 m from shore, usually extending to the second kelp belt; zone 4: beyond 500 m from shore. As many individuals as possible were photographed using an 8 megapixel Canon 350D with a Canon 75-200 mm f4.5-5.6 lens or a 10.2 megapixel Nikon D200 with either a Nikon 80-200 mm f 2.8 lens or a Nikon 80-400 mm f4.5-5.6 lens. To minimize capture heterogeneity observers made a conscious effort to direct equal photographic effort at all individuals, independent of any noticeable marks on the individuals. Observers continued to take photographs as long as a group was within photographic range, irrespective of whether all individuals were photographed.

Treatment of photographs

Photographs were carefully examined and assigned a quality (*Q*) score from 1 (unusable for MR analyses) to 5 (excellent), independent of the distinctiveness of the individual represented. The *Q* score took into account the size of the dorsal fin in the photograph, focus, lighting, exposure, the angle of the dorsal fin to the photographer and the proportion of the dorsal fin obscured by water. Photographs of *Q*4 and *Q*5 were well-exposed and lit, in focus and the dorsal fin was sufficiently large in the photograph, relatively perpendicular to the photographer and not obscured by water. While photographs of *Q*1 to *Q*5 were considered for the catalogue of identifiable individuals (Appendix A), only photographs of *Q*4 and *Q*5 were considered for MR analyses (Friday et al. 2000).

Individuals were identified based on natural markings of the dorsal fin and saddle patch (Bigg et al. 1987), mainly the pattern of nicks, notches and mutilations along the trailing edge of the dorsal fin. Individuals which were considered recognizable were assigned a unique numeric identifier and included in a catalogue to which all subsequent photographs were compared (Appendix A, also Tosh et al. 2008). Both left and right side images of dorsal fins were used, as they could reliably be matched to the same individual. Catalogued individuals were not rated according to their distinctiveness, rather all catalogued individuals were considered reliably identifiable from photographs of *Q*4 and *Q*5, other than calves, which were excluded from MR analyses.

For all photographs of *Q*4 and *Q*5, a ratio was calculated relating the number of dorsal fins that could be reliably identified (excluding calves) to the total number of photographed fins. This calculation was performed for each sighting, and subsequently an overall ratio was calculated representing the proportion of identifiable individuals (θ).

Analyses

MR analyses of the sighting histories of recognizable individuals were performed using the software program MARK (White and Burnham 1999), which uses Maximum Likelihood models to estimate population parameters (Cooch and White 2009). Per-sighting captures were pooled into monthly capture events, thus a single calendar month constituted a sampling occasion. Due to the length of the study and the strongly seasonal occurrence of killer whales around Marion Island (Condy et al. 1978, Keith et al. 2001, Reisinger et al. in press), population closure was not a reasonable assumption (three births were recorded during the study period, see Results). Population parameters were estimated using the open-population POPAN parameterization (Schwarz and Arnason 1996, 2009) which includes the parameter N, denoting the size of a superpopulation. N can be thought of as either the total number of animals available for capture at any time during the study, or, alternatively, as the total number of animals ever in the sampled area between the first and last occasion of the study (Nichols 2005). The parameter Φ represents apparent survival rate, p is the probability of capture and b denotes the probability that an animal from the superpopulation enters the sub-population (sub-population referring to the animals occurring in the study area). In model notation, the subscripts t and **.** represent time-dependent and constant parameters, respectively (after Lebreton et al. 1992). The initial analysis is based on the fully time-dependent/Cormack-Jolly-Seber (CJS) model $\{\Phi_t\ p_t\ b_t\}$. The first step in the analysis involves Goodness-of-Fit (GOF) tests for the CJS model using the program RELEASE GOF to validate model assumptions. Models were constructed for combinations of time-dependence and consistency for Φ and p, and seasonal (s) variation was allowed for p. Based on the seasonal abundance of killer whales at Marion Island (Reisinger et al. in press), October to December of each year was considered "peak" occurrence while January to September was considered "low" abundance. The most appropriate model was selected using the small sample corrected Akaike Information Criterion (AIC_c; Burnham and Anderson 1998). AIC weighs the deviance (quality of fit) and the precision (via number of estimable parameters) to select a model that best describes the data (Lebreton et al. 1992). Based on the GOF results of TEST 2 + TEST 3 in program RELEASE a post-hoc variance inflation factor ($\hat{c}$) may be estimated to adjust for extra-binomial variation in the data, resulting in a quasi-Akaike Information Criterion (QAIC). Median $\hat{c}$ and bootstrap GOF are not available in the POPAN parameterization. The MR abundance estimates apply only to the population of marked animals (excluding calves) and these estimates were expanded to include the entire population (including calves) by dividing N by the proportion of identifiable individuals (θ), yielding total abundance (N_{total}). Variance was estimated using the delta method as

$$\text{var}(N_{\text{total}}) = N_{\text{total}}^{2}\left(\frac{\text{var}(N)}{N^2} + \frac{1-\theta}{n\theta}\right) \qquad \text{Equation 3.1}$$

where n is the total number of dorsal fins from which θ was calculated. Confidence intervals for N_{total} assumed the same error distribution as the MR estimates (Wilson et al. 1999).

RESULTS

From April 2006 to April 2009 (inclusive), killer whales were sighted 846 times at Marion Island and 9,724 photographs were taken. Table 3.1 shows the number of sightings per year, the numbers of photographs taken in various categories and the number of photo-

Period	Sightings		Photographs		Identifications		Unique individuals sighted	New individuals identified
	All	Photographic	(Q1 to Q5)	(Q4 and Q5)	(Q1 to Q5)	(Q4 and Q5)		
2006-2007	239	83	334	49	190	21	21	21
2007-2008	166	94	1 334	86	299	54	21	10
2008-2009	441	209	8 056	1 446	4 075	1 283	30	6
2006-2009	**846**	**386**	**9 724**	**1 581**	**4 564**	**1 374**	**37**	**37**

TABLE 3.1 Sightings of killer whales at Marion Island, photographic effort, number of identifications and individuals identified, April 2006 to April 2009.

graphic identifications in various categories. Killer whales were regularly observed close inshore; 50 % of sightings included sightings in zone 1 and 65% of sightings included sightings in zone 2. Group size ranged from 1 to 13 individuals (Figure 3.1) and the proportion of individuals photographed in each group per occasion ranged from 0% to 100%. In total, 37 individuals were identified, of which 7 were classified as adult males, 22 as adult females, 5 as unknown age-sex class and 3 as calves (born during the study period and identified by their colouration, relative size, close association with an adult female and previous absence from groups). Left and right side dorsal fin images were available for 30 individuals; the remaining 30 were photographed from one side only. Only 30 animals were included in the mark-recapture analyses, the remaining 7 were calves (3 animals) or were not identified in photos of *Q*4 and *Q*5 (4 animals). Figure 3.2 shows the sighting frequency distribution of these animals and Figure 3.3 shows the discovery curve – or cumulative number of identified individuals – as well as photographic effort monthly (both figures used *Q*4 and *Q*5 only and calves excluded).

Of the six biologically sensible model combinations tested, one did not reach numerical convergence. Parameters for each occasion were often inestimable due to sparse data. Based on the result of TEST 2 + TEST 3 in program RELEASE GOF (Table 3.2), a variance inflation factor of $\hat{c} = 1.30$ was estimated and applied, indicating only slight overdispersion in the data (Cooch and White 2009). Only TEST 2 was rejected (Table 3.2), however RELEASE reported insufficient data to perform tests for a number of occasions. According to the QAIC_c scores, model $\{\Phi_{.}\ p_s\ b_t\}$ (constant survival, probability of capture varies seasonally and probability of entry varies with capture occasion) was the most parsimonious. Model choice criteria as well as abundance estimates and parameter estimates are shown in Table 3.3. No models had a ΔQAIC_c (difference between the QAIC_c of the model in question and that of the top ranked model; Table 3.3) less than 2 units, which would have indicated that they were also likely descriptors of the data (Burnham and Anderson 1998). The proportion of identifiable individuals was 0.77 (SE = 0.34), and based on model $\{\Phi_{.}\ p_s\ b_t\}$'s estimate, total abundance was estimated at 42 individuals (SE = 3.83, 95% CI = 35-50) for the superpopulation, *N*.

DISCUSSION

The observed group sizes (Figure 3.1) of killer whales at Marion Island are consistent with earlier observations for the Island (Condy et al. 1978, Keith et al. 2001, Tosh et al. 2008), as well as for populations of pinniped-eating killer whales elsewhere, likely an optimal group size for maximizing energy intake in such populations (Baird and Dill 1996). The most frequent group size observed (3 individuals) is comparable to average group sizes of 4.2 (Condy et al. 1978), 3.6 (Keith et al. 2001) and 3.4 (Tosh et al. 2008) reported previously at Marion Island, and 3.2 (modal group size of 2) at Punta Norte (Lopez and Lopez 1985) and modal group size of 3 at Vancouver Island, British Columbia (Baird and Dill 1996). The largest groups observed at Marion Island included identified individuals which were mostly observed separately on other occasions (Tosh et al. 2008, Mammal Research Institute unpublished data), indicating that large groups formed temporarily during interactions of smaller groups, likely for socializing and perhaps cooperative hunting (Baird and Dill 1996). This illustrates that, albeit for killer whales in different habitats and aquatic ecosystems, a stable group size aligned with the energetic constraints of predation on marine mammals has evolved (e.g., Baird and Dill 1996).

The number of individuals identified in this study is substantially larger than the number of individuals identified by Keith et al. (2001) but the proportion of adult females in the current catalogue (59%) is almost identical to that in Keith et al.'s study (58%) although the proportion of adult males differs markedly (19% in the present study compared to 35%). The opportunistic nature of Keith et al.'s (2001) study may have meant that males were more likely to be observed due to their much larger dorsal fins, potentially explaining the higher proportion of males in that study. The number of individuals identified here is similar to photographic identification studies at Punta Norte (30 individuals in 1975 to 1997; Iñíguez 2001) and Île de la Possession (32 individuals in 1998 to 2000; Poncelet et al. 2010). The sighting frequency distribution (Figure 3.2) suggests a population of regularly occurring animals; only 4 animals were seen during one month only and the majority of animals were seen in a number of months during the study period. The presence of a large proportion of transient (not to be confused with the eastern North Pacific killer whale ecotype) or migratory animals is therefore unlikely. Further, there is no suggestion of separate populations of transient/migratory and resident (again, not to be confused with the

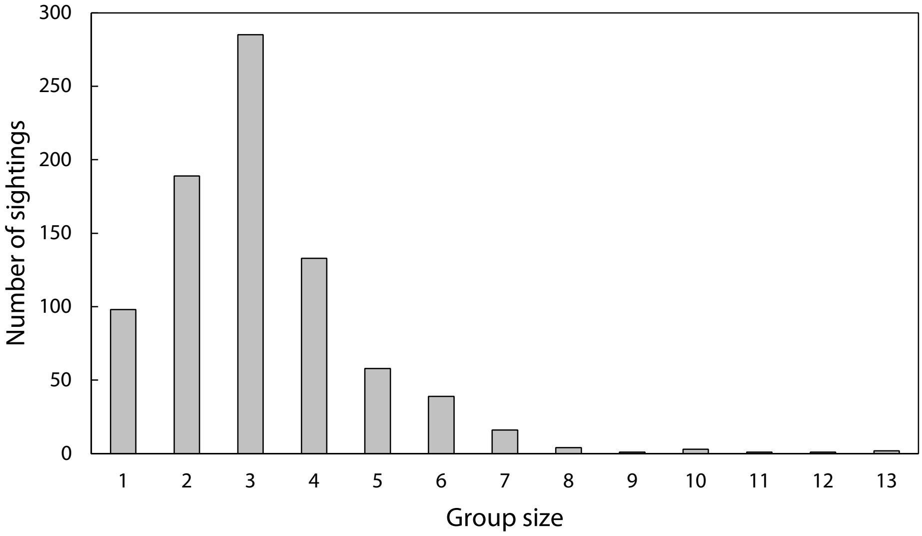

FIGURE 3.1 Frequency distribution of group sizes of killer whales sighted at Marion Island, April 2006 to April 2009.

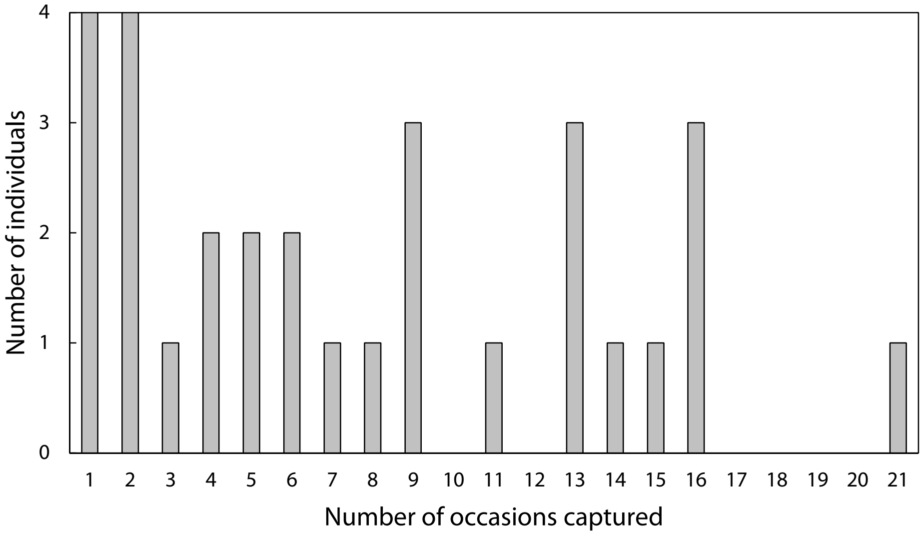

FIGURE 3.2 Sighting frequency distribution of identifiable killer whales at Marion Island from April 2006 to April 2009 (photographs of Q4 and Q5 only, calves excluded).

eastern North Pacific killer whale ecotype) animals as sighting frequencies are relatively evenly distributed without clear clustering.

The discovery curve (Figure 3.3) shows the expected rapid initial increase in 2006 to 2007 and 2007 to 2008, but despite the far greater photographic effort in 2008 to 2009 (Table 3.1) and the increasing number of identifications, appears to level off. This asymptotic tendency in the discovery curve indicates that most individuals in the population have been identified, however, only continuation of the photographic MR effort in a structured protocol can confirm this (e.g., Wilson et al. 1999, Baker et al. 2006).

Assumptions: validation and violations

Validation of the assumptions underlying MR methods is critical in providing relatively unbiased estimates of population parameters (Begon 1983). The natural characteristics used to identify killer whales have proven to be long-lasting, allowing individuals to be recognized for years in long term studies (e.g., Bigg et al. 1987, Bigg et al. 1990, Baird and Whitehead 2000, Parsons et al. 2009, Ivkovich et al. 2010). This makes killer whales conducive to MR analysis following rigorous photographic surveying and I therefore considered mark loss in this study as being negligible. Sampling was instantaneous, and sampling effort was consciously similarly distributed between marked and unmarked animals, although heterogeneous capture probabilities due to differences in the behaviour of individuals are unavoidable in most photographic identification MR studies (e.g., Hammond 1986, see also Baird and Dill 1995). Any further violations of equal capture probabilities were minimized by imposing careful photographic quality criteria, however capture heterogeneity is evident in this study (see below).

TEST 2 and TEST 3 in program RELEASE are useful for identifying lack-of-fit in the data. TEST 2 and TEST 3 examine the assumptions of equal capture probabilities and survival, respectively (Cooch and White 2009). The result of TEST 2 + TEST 3 (Table 3.2) indicates little overdispersion in the data. If $\hat{c} \leq 3$, the lack-of-fit is acceptable and models can be confidently corrected with such an inflation variance factor (Lebreton et al. 1992). Of the component tests (Table 3.2) only TEST 2 (capture heterogeneity) is rejected, which could be expected, as capture heterogeneity seems unavoidable in MR studies of cetaceans, especially given the differences in behaviour of individuals (Hammond 1986). Also, given that this is

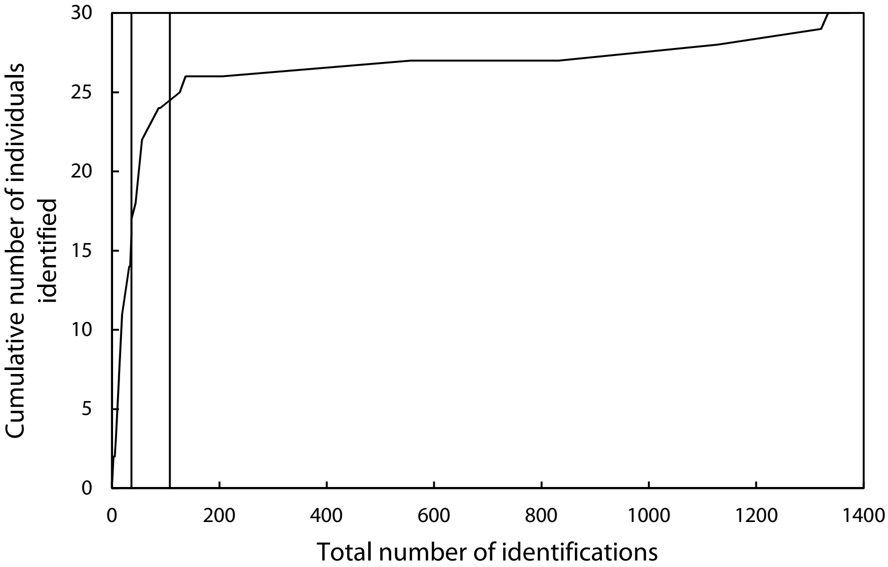

FIGURE 3.3 Discovery curve, or cumulative number of individuals identified, for killer whales at Marion Island, April 2006 to April 2009 (only Q4 and Q5 photographs; calves excluded). Vertical lines indicate study years (2006 to 2007, 2007 to 2008 and 2008 to 2009).

Test	$\hat{c}$	X^2	*df*	*p* value
TEST 2 + TEST 3	1.30	41.58	32	0.12
TEST 2	2.11	40.12	19	0.00
TEST 3	0.11	1.46	13	1.00
TEST 3.SR	0.08	0.53	7	1.00
TEST 3.SM	0.17	0.94	6	0.99

TABLE 3.2 Program RELEASE goodness-of-fit results for the fully time-dependent/Cormack-Jolly-Seber model tested in a mark-recapture analysis of individual sighting histories of killer whales at Marion Island, April 2006 to April 2009, using the open population POPAN parameterization in program MARK.

Model	Model choice criteria						Abundance estimates								Parameter estimates					
							Marked population				Total population									
	$QAIC_c$	$\Delta QAIC_c$	W	Likelihood	NP	Q Dev	N	SE	LCL	UCL	N_{total}	SE	LCL	UCL	Φ	SE	p	SE	b	SE
$\Phi(.)p(s)b(t)$	353.06	0.00	1.00	1.00	18	156.36	33	2.91	27	38	42	3.83	35	50	0.99	0.01	0.31	0.09	0.10	0.16
$\Phi(.)p(t)b(t)$	371.37	18.30	0.00	0.00	30	138.92	33	3.13	27	39	43	4.11	35	51	0.99	0.01	0.33	0.10	0.16	0.11
$\Phi(.)p(.)b(t)$	407.88	54.81	0.00	0.00	15	219.01	31	1.70	28	34	40	2.29	36	45	0.99	0.01	0.34	0.03	0.07	0.13
$\Phi(t)p(t)b(t)$	438.92	85.86	0.00	0.00	48	134.56	33	3.40	26	40	43	4.46	34	52	0.98	0.04	0.31	0.11	0.19	0.09
$\Phi(t)p(.)b(t)$	463.08	110.02	0.00	0.00	36	209.54	32	2.33	27	36	41	3.09	35	47	0.97	0.03	0.36	0.03	0.07	0.12
$\Phi(.)p(.)b(s)$	2,483.91	2,130.85	0.00	0.00	8	2,311.88	33	2.85	27	38	43	3.75	35	50	0.99	0.01	0.37	0.03	0.20	0.06
$\Phi(.)p(.)b(.)$	2,517.95	2,164.89	0.00	0.00	3	2,356.87	61	10.23	41	81	79	13.34	53	105	0.90	0.03	0.69	0.02	-	-
$\Phi(t)p(.)b(s)$	2,523.58	2,170.52	0.00	0.00	28	2,297.64	40	7.26	26	55	52	9.46	34	71	0.96	0.03	0.39	0.03	0.20	0.06

TABLE 3.3 Abundance estimates for killer whales at Marion Island, April 2006 to April 2009, produced using the POPAN parameterization in Program MARK. Model choice criteria for each model, as well as average parameter estimates are also shown. Models are listed by $QAIC_c$ rank.

$QAIC_c$ – small sample corrected Quasi-Akaike Information Criterion; $\Delta QAIC_c$ – difference between the $QAIC_c$ of the model in question and that of the top ranked model; W model weight; NP – number of estimable parameters in model; N – estimated number of individuals; SE – standard error; LCL – lower 95% confidence limit; UCL – upper 95% confidence limit; Φ – monthly apparent survival; p – monthly probability of capture; b – monthly probability of entry. Text in brackets refers to subscripts in model notation.

an open population, slight temporary emigration is biologically sensible and may result in such heterogeneity. Capture heterogeneity biases abundance estimates downwards, but survival estimates are more robust (Pledger and Efford 1998). Only recently have likelihood based open-population models for abundance estimation incorporating heterogeneity of capture been developed (Pledger et al. 2010).

Mark-recapture problems and comparisons with catalogue counts

Beyond the careful consideration of the assumptions underlying MR models, MR population size estimates should always be issued with appropriate caveats and interpreted cautiously. As a consequence of sparse data and capture heterogeneity in this study, I advise caution when interpreting my estimates. Simply applying the proportion of identifiable individuals (θ) to the number of individuals included in the MR analyses (30 animals), yields a population size of 39 animals – very close to the number of individuals in the catalogue (37 animals) and the MR estimate (42, 95% CI = 35-50), although the latter is likely negatively biased. This agreement, combined with the sighting frequency pattern (Figure 3.2) and the asymptotic tendency of the discovery curve (Figure 3.3), indicates that most of the identifiable proportion of the population have been included in the catalogue, and lends confidence to the catalogue size (complete enumeration over time) as a rigorous abundance estimate free of the assumptions underlying MR estimates. While the catalogue may also be subject to some bias, it is more precise than MR estimates. My estimate is based on only three years of data, and continued study is undoubtedly required and may resolve problems with the MR analyses. The thorough establishment of a photographic identification catalogue and the continuation of the photographic identification study will be of future use to investigate various questions related to population parameters, social ecology and movement of individuals.

Comparison with other studies and defining the "population"

This study's catalogue size should not be compared to Keith et al.'s (2001) catalogue size with the view of identifying abundance trends because of the highly opportunistic nature of that study. In broad terms, my most parsimonious population size estimate of 42 animals (95% CI = 35-50, Table 3.3) is similar to the most recent estimate at Île de la Possession (37 animals, 95% CI = 32-62; Poncelet et al. 2010). Although the Île de la Possession population has undergone a marked decline, no comparable data are available for Marion

Island. The birth of at least three calves at Marion Island during 2008 to 2009 may suggest a higher fecundity than that reported at Possession (Guinet and Bouvier 1995).

This begs the question as to what the “population” is. In terms of the MR methodology, the “population” refers to individuals available to be captured during the study and thus refers to any animals which may occur in the inshore area. The POPAN parameterization, specifically assumes the existence of a superpopulation of animals available to be sampled (Schwarz and Arnason 2009). I have discussed why it is unlikely that such a population includes a large proportion of transient animals and can broadly refer to the population in this case as those animals which occur, at least seasonally, inshore at Marion Island (however it should be noted that there may be differences among groups in the use of inshore areas, Baird and Dill 1995). This population likely includes animals occurring at neighbouring Prince Edward Island. Prince Edward Island is only 19 km from Marion Island, a much smaller distance than the more than 40 km of coastline included in our survey area, and the only photograph available of a killer whale at Prince Edward Island (provided by R. Tarr[1]) was reliably identified as an individual included in the Marion catalogue.

Because my data are completely biased to killer whales occurring inshore, I cannot exclude the existence of a separate population of offshore animals (as exists in the eastern North Pacific; Dahlheim et al. 2008), and my abundance estimate would not apply to such a population. No studies have been conducted on the medium- and large-scale movement of killer whales at Marion Island, but inshore abundance data (Reisinger et al. in press, also Condy et al. 1978, Keith et al. 2001) indicate potential seasonal movement offshore, or increased ranging, both of which may be accompanied by a potential diet switch (e.g., Mikhalev et al. 1981).

Future research

While my abundance estimate is a novel and critical step in elucidating the role of killer whales in the Marion Island marine ecosystem — as well as being valuable for any conservation and management decisions in the region and for comparisons with other

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[1] Oceans and Coasts, Department of Environmental Affairs, Private Bag Roggebaai, 8012, South Africa

killer whale populations — the current photographic identification study should continue. Future research investigating the population structure and spatio-temporal distribution of killer whales at Marion Island can now be initiated in the context of this rigorous abundance estimate.

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CHAPTER 4

Predatory impact of killer whales on pinniped and penguin populations at the Prince Edward Islands: fact and fiction

ABSTRACT

Killer whales are the oceans' apex predators and their potential effects on ecosystems have been demonstrated. In the Southern Ocean the role of killer whale predation in population declines of southern elephant seals remains largely speculative. I aimed to assess whether top-down control of pinniped and penguin populations at the Subantarctic Prince Edward Islands is generally plausible using a simple process of elimination. Based on published data I predicted the energetic ingestion requirements of adult male and female killer whales as 1 394 MJ.day^{-1} and 1 028 MJ.day^{-1}, respectively. Expanding these requirements to the 37 killer whales photographically identified at the Prince Edward Islands, the population requires 40 600MJ.day^{-1}. Based on available energy density and mass data, I predicted the energy content of available pinniped and penguin prey and calculated the rates at which killer whales would consume these prey in various scenarios. Penguins and Subantarctic fur seals are relatively insensitive to killer whale predation owing to their large population sizes (10 000s to 100 000s), conversely, the smaller populations (100s to 1 000s) of Antarctic fur seals and southern elephant seals are sensitive to predation, particularly the latter as they have a high energy content (approximately 2 000 to 9 000 MJ). Populations of these seals are currently increasing or stable and I conclude that presently killer whale predation is not driving population declines, although they clearly have the potential for regulation of these smaller populations. Thus, if population sizes were reduced by bottom-up processes, if

killer whale diet shifted, or if prey availability changed, top-down predation by killer whales could become significant. By eliminating the possibility of some predation scenarios, future efforts can be better concentrated on plausible predation effects.

INTRODUCTION

Whether bottom-up (resource limitation) or top-down (predation) processes structure communities and regulate populations has engendered decades of debate among ecologists (Hairston et al. 1960, Hunter and Price 1992). However, the problem remains an artificial dichotomy in some respects and more recently investigators focussed on the relative roles and interactions of these processes and their various strengths at different spatio-temporal scales (Hunter and Price 1992, Menge 1992, Power 1992, Sinclair et al. 2003, Hunt and McKinnell 2006, Suryan et al. 2006, Frank et al. 2007).

Due to their size, mobility and energy requirements, large predators can have marked effects on ecosystems despite their relative rarity (Terborgh 1990, Seidensticker and McDougal 1993, Gittleman and Gomper 2005, Owen-Smith and Mills 2008). The most obvious of these effects is the direct consumption of other animals. Yet, there are a wide range of potential indirect effects, including trophic cascades, where the altered abundance of a predator's prey due to predation changes the abundance of organisms at lower trophic levels (Carpenter et al. 1985). Additionally, the behavioural effects of predation risk can alter prey life histories and abundance (Lima 1998, Brown et al. 1999). There is ample evidence for top-down effects in ecosystems (e.g., Pace et al. 1999, Shurin et al. 2002, Baum and Worm 2009) and the potential effects of large carnivores on ecosystems are being demonstrated in a growing number of studies (e.g., Berger et al. 2001, Ripple et al. 2001, Terborgh et al. 2001, Myers et al 2007, Owen-Smith and Mills 2008). In marine ecosystems, traditionally considered as being mainly regulated by bottom-up processes (e.g., Cushing 1975, Aebischer et al. 1990, Verity and Smetacek 1996, Steele 1998, Chavez et al. 2003, Ware and Thompson 2005, Chassot et al. 2007), such examples are scarcer (reviewed in Baum and Worm 2009) – possibly because this aspect has been little studied and is difficult to assess in ocean ecosystems (Hunt and McKinnell 2006, Baum and Worm 2009). However, a now "textbook" example (albeit nearshore) of the role of large predators in ecosystems is the cascading effects of killer whales (*Orcinus orca*) and sea otters (*Enhydra lutris*) in the kelp forests of the Aleutian archipelago, North Pacific Ocean (Estes et al. 1998). Sea otters were hunted to near extinction as a consequence of the fur trade, but following protection in the early 1900s the species underwent spatially disjunct recovery. Sea otters are keystone predators and promote the growth and maintenance of kelp forests and their associated communities by preying on sea urchins. The loss of sea otters result in increased sea urchin abundance and consequent extensive overgrazing of kelp forests that increase habitat homogeneity and decrease faunal richness (Estes and Duggins 1995). The precipitous and widespread declines in sea otter populations in the region during the 1990s (and resulting sea urchin ecosystem effects) have been attributed to increased predation on sea otters by killer whales with as few as four killer whales hypothesised to have caused the observed declines of sea otters (Estes et al. 1998). In an extension of this hypothesis, Springer et al. (2003) suggested that the depletion of great whale stocks in the North Pacific Ocean during post World War II industrial whaling forced killer whales to "fish down" the ecosystem (*sensu* Pauly et al. 1998), or sequentially switch to smaller/less abundant marine mammal prey species, in response to the loss of their great whale prey, causing declines in harbour seal (*Phoca vitulina*), northern fur seals (*Callorhinus ursinus*), Steller sea lions (*Eumetopias jubatus*) and then sea otter populations. This "sequential megafaunal collapse hypothesis" (Springer et al. 2003) sparked fierce debate (most recently, Estes et al. 2009, Kuker and Barrett-Lennard 2010) and detractors argue that killer whales never preyed heavily on great whales, great whale biomass removal was not substantial and declines were not sequential (e.g., DeMaster et al. 2006, Mizroch and Rice 2006, Wade et al. 2007). Nutritional stress and climate change have been proposed as alternative mechanisms (e.g., Trites and Donnelly 2003, Trites et al. 2007).

Notwithstanding any shortcomings, the sequential megafaunal collapse hypothesis does illustrate the potential influence of killer whales on marine ecosystems. They are the oceans' apex predator and, as a species, have an extremely diverse diet, including cephalopods, bony and cartilaginous fishes, reptiles, birds, and mammals (Hoyt 1990, Jefferson et al. 1991). Assessing the roles of large carnivores in an ecosystem is difficult due to their rarity and mobility (Williams et al. 2004) and can be even more difficult for marine mammals which often hunt at depth (Davis et al. 1999). Thus a number of investigations of the predatory role of killer whales have utilized energetic analyses to determine the strength of their top-down effects (Barrett-Lennard et al. 1995, Estes et al. 1998, Williams et al. 2004, Branch and Williams 2006, Williams 2006); incorporating information about their abundance, diet and per capita ingestion rate (which is determined by their metabolic rate and prey energetic content [Williams et al. 2004]).

Killer whales in the Southern Ocean have been comparatively poorly studied except for long-term photographic identification studies at the Îles Crozet, southern Indian Ocean, (Poncelet et al. 2010) and Punta Norte, Argentina (Iñíguez 2001). At the Subantarctic Prince Edward Islands (PEIs), southern Indian Ocean, killer whales have been studied opportunistically at a population level, and local movements as well as social structure were preliminarily analyzed (Condy et al. 1978, Keith et al. 2001, Pistorius et al. 2002, Bester et al. 2002, Tosh et al. 2008). Killer whales have been observed preying on southern elephant seals (*Mirounga leonina*), Subantarctic fur seals (*Arctocephalus tropicalis*), king penguins (*Aptenodytes patagonicus*) and macaroni penguins (*Eudyptes chrysolophus*) and occur year-round at the PEIs but their inshore abundance peaks in September to December and April to May, linked to the abundance of seals and penguins (Reisinger et al. in press). A population size of 42 animals was estimated using mark-recapture methods (Chapter 3). No evaluation of predation effect on prey exists for PEI killer whales, despite hypotheses (resulting from observable predatory events) alluding to their potential role in diminishing prey numbers (e.g., Condy et al. 1978, Keith et al. 2001). Observed high intensity predation of elephant seals at nearby Îles Crozet (Guinet et al. 1992) and the North Pacific sequential megafaunal collapse hypothesis, in particular, have sparked ideas of prey regulation by locally abundant killer whales at the PEIs (McMahon et al. 2003, de Bruyn 2009). However, such hypotheses for the PEIs predator-prey system remain speculative.

Southern elephant seal population sizes increased after the cessation of their commercial harvesting, but subsequently population sizes decreased throughout their breeding range between the 1950s and 1990s. Comparable to Springer et al.'s (2003) sequential megafaunal collapse hypothesis, Barrat and Mougin (1978) suggested that killer whale predation may have played a role in these declines following the depletion of great whales in the Southern Hemisphere during 20th century whaling operations (Clapham and Baker 2002). Killer whale predation has been suggested as a major factor in the elephant seal declines at least at the PEIs and Îles Crozet (Condy et al. 1978, Guinet et al. 1992) and several authors have alluded to the top-down influences of killer whales on pinniped populations at the PEIs (Keith et al. 2001, Pistorius et al. 2002, Tosh et al. 2008, de Bruyn 2009, de Bruyn et al. 2009a). However, only a single study has followed a quantitative approach to this question, albeit at a regional scale. Branch and Williams (2006) found it plausible that declines in elephant seals and southern sea lions (*Otaria flavescens*) in the Southern Ocean were due to increased predation by killer whales following the depletion of their preferred great whale prey.

As a first step towards critically assessing the role of killer whales in the PEIs marine ecosystem, a "model system" which has broad relevance for the Subantarctic (Chown and Froneman 2008), I quantified the potential predatory impact of killer whales on pinniped and penguin populations based on the theoretical energy requirements of killer whales. My intention is not to test any specific hypothesis of predation pressure explicitly, given the relative paucity of data on killer whales at this locality. Instead, I aim to assess whether top-down control of pinniped and penguin populations at the PEIs is broadly plausible, following an eliminatory approach. I suggest that this approach of eliminating scenarios on a scale of "presumably unrealistic to probable," can be broadly applicable for predator-prey studies to better isolate key aspects for future research focus.

METHODS

The Prince Edward Islands

The Subantarctic PEIs comprise Marion Island (300 km^2; 46°54'S, 37°45'E) and, approximately 19 km to the north east, the smaller Prince Edward Island (45 km^2; 46°38'S, 37°57'E). The PEIs are situated in the southern Indian Ocean with the nearest landmass being the Îles Crozet (950 km to the east) at similar latitude. The interplay between the Antarctic Circumpolar Current and the prominent bottom topography of the South-West Indian Ridge results in productive turbulent water masses around the PEIs (Ansorge and Lutjeharms 2005), sustaining the numerous mammal and bird species that breed there.

The PEIs support increasing populations of both Subantarctic and Antarctic fur seals with total pup productions at Marion Island of 16 045 and 759, respectively, in 2004 (Hofmeyr et al. 2006). Pup production of these species at Prince Edward Island was estimated as 14 130 and 810, respectively, in 2008 (Bester et al. 2009). The PEIs support total populations of approximately 150 000 Subantarctic fur seals and 5 800 Antarctic fur seals (Hofmeyr et al. 2006). The southern elephant seal population at Marion Island numbered about 1 764 in 1999, with a pup production (at weaning) of 434 (Ryan and Bester 2008) while the population at Prince Edward Island numbered about 410 in 2004, with a pup production of

130 (Bester and Hofmeyr 2005). The elephant seal population appears to be increasing and current pup production is approximately 520 at Marion Island (McMahon et al. 2009, de Bruyn 2009). King penguins numbered 67 000 breeding pairs in 2008; gentoo penguins (*Pygoscelis papua*), macaroni penguins and rockhopper penguins (*Eudyptes chrysocome filholi*) numbered >1 100, 302 000 and 80 000 breeding pairs, respectively, at the PEIs in 2008 (Crawford et al. 2009).

I have restricted my treatment to the inshore waters of the PEIs. While penguins and seals do forage pelagically, tens to thousands of kilometres from the PEIs (Adams and Wilson 1986, Adams 1987, Brown 1987, Jonker and Bester 1998, de Bruyn et al. 2009a), their distribution and density at sea, as well as the abundance of killer whales pelagically, is unknown. Penguins and seals must return to land to breed and moult, doing so relatively synchronously (per species), and then represent a concentrated nearshore prey source for killer whales and other species (Keith et al. 2001, Bester et al. 2002, de Bruyn et al. 2007). I assume unchanged (current) predation pressure by other predators in the local system (de Bruyn et al. 2007). Importantly, I have confident estimates of the number of killer whales occurring regularly in the inshore waters of the PEIs as well as the number of penguins and seals breeding at the PEIs. This information is vital for the evaluation of killer whales' predatory impact. As penguins and seals have strong seasonal occurrence at the PEIs, dictated by their breeding and moulting cycles, and killer whale temporal occurrence is linked particularly to the breeding patterns of their prey (Reisinger et al. in press), I necessarily also restrict the "system" temporally.

Killer whale population size and structure

Killer whales were studied at Marion Island (2006 to 2009) using photographic identification methodology, where individuals are identified based on natural markings of their dorsal fin and saddle patch (Bigg et al. 1987). Killer whales were sighted on 823 occasions and nearly 10 000 images were taken from which 37 individuals were identified, including 19 adult females, 3 lactating adult females with calves, 7 adult males and 5 individuals of unknown age-sex class (the latter may be subadult males or adult females). Mark-recapture analyses of these data estimated a population size of 42 (95% CI = 35-50) individuals (Chapter 3).

Killer whale energy requirements

To predict the energetic requirements of adult, free-ranging killer whales at the PEIs I used Williams et al.'s (2004) allometric field metabolic rate regression determined from the measured field metabolic rate of smaller marine mammals.

$$FMR = 19.65M_b^{\ 0.756} \qquad \text{Equation 4.1}$$

Where FMR is field metabolic rate in W and M_b is body mass in kg.

Williams et al. (2004) used average male and female killer whale body masses from Dahlheim and Heyning (1999), however since these masses were representative of the largest individuals weighed in an unknown region, and killer whales show marked morphological variation through their range (Heyning and Dahlheim 1988, Jefferson et al. 2008), I calculated likely masses for male and female killer whales at the PEIs using Best's (2007) length-mass regression for killer whales from the southern African subregion.

$$M_b = 8.6791\, L^{\ 3.2769} \qquad \text{Equation 4.2}$$

Where L is length in m.

I used average lengths of 7.26 m (males) and 6.42 m (females), obtained from killer whales taken during Southern Hemisphere whaling operations between 1961 and 1979 (excluding "dwarf" individuals; Mikhalev et al. 1981). The resulting energy requirements were adjusted upwards for an assumed assimilation efficiency (or metabolisable energy) of 84.7% (Williams et al. 2004), giving the energy killer whales would need to ingest to meet basic energetic demands. Carnivores usually assimilate about 90% of ingested food (Gordon et al. 1982). For seals placed on fish diets assimilation efficiencies ranged from 80.3% to 91.6% (Costa and Williams 1999) and captive killer whales on a fish diet showed assimilation efficiencies of 82% (Kriete 1995). These energetic requirements are for adult killer whales and assumed no growth or reproductive costs. However, I incorporated the additional energy requirements of lactating females (following Baird 1994) not by adjusting their energy requirements, but by assuming that calves were of equivalent mass to their mothers (and thus had equivalent energetic requirements). This is because unweaned calves gain all their energy by suckling and accounts for the up to 100% increase in energy required by lactating female killer whales (Kriete 1995). Daily per-capita energy (ingestion) requirements were multiplied by the population size and composition to determine the daily population energy (ingestion) requirements. The inability to distinguish between adult females and subadult males in some cases, resulting in classification as unknown age-sex class, allows the reasonable assumption that such animals are of similar mass to adult females, and are thus assumed to have the same energy requirements as adult females.

Prey energy content

The energy density (energy content per mass) of prey consumed by killer whales at the PEIs was obtained from published data. Sources calculated energy density from the measured body composition of prey (Cherel et al. 1993, Arnould et al. 1996) or from body composition data published in other sources (Forcada et al. 2009). For species where I did not have estimates of energy density, I used values for the same age class of the most closely related species. I did not have an estimate of the energy density of adult elephant seals, and used the energy density of pups, which is an overestimate. The average mass of prey was obtained from published and unpublished data. For seals at the PEIs, average masses of pups at weaning and average masses of adults (and subadult male elephant seals) captured for telemetry deployments were used (de Bruyn et al. 2009a, 2009b, Mammal Research Institute, unpubl. data). Elephant seal pups lose about 30% of their mass before dispersing (Wilkinson and Bester 1990), and weaning masses are thus an overestimate. For macaroni and rockhopper penguins at the PEIs, masses upon arrival for breeding were used (Crawford et al. 2006). Average king penguin mass at the PEIs was unavailable and thus mass from a study at the Îles Crozet (Halsey et al. 2008) was used. Energy density was multiplied by the average mass of a prey type to give the prey type's average energy content.

Prey consumed

To calculate the number of seals and penguins consumed, I divided the killer whale population's total energetic requirement by the calculated average energy content of each prey type, assuming the entire prey item was consumed. In 136 attacks on marine mammals in the eastern North Pacific remains larger than 1% of the estimated body size of the prey were observed on only four occasions although very large prey may not be consumed entirely (Baird and Dill 1996). However, partial consumption of select portions of certain prey types (e.g., Pitman and Durban 2010) could presumably result in underestimation of the number of prey killed, and while this serves as a precaution when drawing conclusions, observational data to account for this do not exist. Assuming whole prey item consumption, and in order to predict the "worst case scenario" or maximum predatory impact for each prey type, I initially assumed that killer whales consumed each prey type exclusively (1). Based on these daily consumption rates I calculated the proportion of available prey (i.e., the percentage of the total prey population at the PEIs) consumed over time. I then considered more realistic scenarios: (2) killer whale diet comprised equal proportions (energetically) of each prey type, (3) killer whale diet comprised proportions of available prey type relative to their proportional energetic biomass in the PEIs system, (4) diet comprised prey proportions relative to their abundance, and (5) diet comprised prey proportions according to their energy content (i.e. preference for prey was based on its energy content relative to that of other prey).

I then assessed predatory impact at various prey population sizes of the three prey types identified (above) to be most sensitive to killer whale predation: Antarctic fur seal pups, Antarctic fur seals and elephant seal pups (see Results, Figure 1). I assumed killer whales preyed exclusively on each prey type and predation mortality was 10%, 20% and 40% of the current prey population size. Keeping the absolute rate of predation constant (i.e., assuming that killer whales showed no total response to changing prey abundance; see Discussion), I varied prey population size to broadly predict at what population size predation mortality would become unsustainable, causing the prey population to decline markedly or be exterminated.

RESULTS

Using Mikhalev et al.'s (1981) average lengths for Southern Hemisphere killer whales in Equation 4.2 I calculated average masses of 5 750 kg and 3 843 kg for adult males and females, respectively. Adult males and females were thus predicted (using Equation 4.1) to have field metabolic rates of 13 667 W and 10 078 W, respectively, requiring the ingestion of 1 394 MJ.day^{-1} and 1 028 MJ.day^{-1} (Table 4.1). Despite the large body mass estimated for PEIs killer whales, per-animal and mass-specific energy (ingestion) requirements are comparable to estimates in previous studies (Table 4.1), particularly those for free-ranging

Study	Age-sex class	Mass (kg)	Energy requirement		AE (%)	Ingestion requirement		Notes on method
			Per animal (MJ.day^{-1})	Mass specific (MJ.kg^{-1}.day^{-1})		Per animal (MJ.day^{-1})	Mass specific (MJ.kg^{-1}.day^{-1})	
Baird (1994)	AM	5 600	-	-	-	1 453.66	0.26	Field estimation of ingestion rates for mammal-eaters
	AF	4 000	-	-	-	1 038.33	0.26	
	SA	2 000	-	-	-	519.16	0.26	
	C	4 000[1]	-	-	-	1 038.33	0.26	
Kriete (1995)	AM	3 750	-	-	-	753.62	0.20	Ingestion rates of captive fish-eaters
	AF	2 692	-	-	-	607.09	0.23	
Barrett-Lennard et al. (1995)	-	-	-	-	-	921.10	-	25% upward adjustment of Kriete's (1995) estimates applied to free-ranging mammal-eaters
Williams et al. (2004)	AM	4 733	1 019.49	0.25	84.70	1 203.00	0.25	Allometric regression of measured field metabolic rates
	AF	2 800	685.54	0.21	84.70	808.94	0.29	
This study	AM	5 750	1 180.84	0.21	84.70	1 394.15	0.24	Using Williams et al.'s (2004) allometric regression
	AF	3 843	870.76	0.23	84.70	1 028.05	0.27	

TABLE 4.1 Energy requirements of different age-sex classes of killer whales estimated by various studies (including this study). AM – adult male, AF – adult female, SA – subadult, C – calf; AE – assimilation efficiency. [1]Mass accounts for the additional energetic requirements of the lactating mother.

Prey type	ED (MJ.kg^{-1})	M (kg)	EC (MJ)	Notes
Seals				
Antarctic fur P	8.24[1]	11.24[2]	92.66	
Antarctic fur AF	10.59[1]	30.6[2]	324.05	
Subantarctic fur P	-	12.70[2]	104.62	Assuming Antarctic fur P ED
Subantarctic fur AF	-	36.5[2]	386.54	Assuming Antarctic fur AF ED
Elephant P	20.2[3]	116.46[2]	2 352.54	
Elephant		437[4]	8 827.40	Assuming elephant P ED. Average mass of AF and subAM
Penguins				
King	11.16[5]	14.3[6]	159.59	Average of pre-moult and pre-breeding ED; mass of incubating AMs from Îles Crozet
Macaroni	9.6[3]	5.36[7]	51.46	
Rockhopper	-	3.14[7]	30.14	Assuming macaroni ED
For comparison				
Sea otter	7.58[8]	-	-	
Steller sea lion P	10.97[8]	-	-	
Northern fur seal	10.47[9]	-	-	
Ringed seal	14.86[10]	-	-	
Harbour seal P	17.05[11]	-	-	
Harbour seal AF	12.94[11]	-	-	
Gentoo penguin	10.0[3]	-	-	

TABLE 4.2 Energy density (ED), average mass (M) and energy content (EC) of killer whales' pinniped and penguin prey occurring at the Prince Edward Islands, with other prey included for comparison. P – pup; AF – adult female; AM – adult male. [1]Arnould et al. (1996); [2]MRI unpubl. data; [3]Forcada et al. (2009); [4]de Bruyn et al. (2009b); [5]Cherel et al. (1993); [6]Halsey et al. (2008); [7]Crawford et al. (2006); [8]Williams et al. (2004); [9]Stansby (1976); [10]Stirling and McEwan (1975); [11]Bowen et al. (1992).

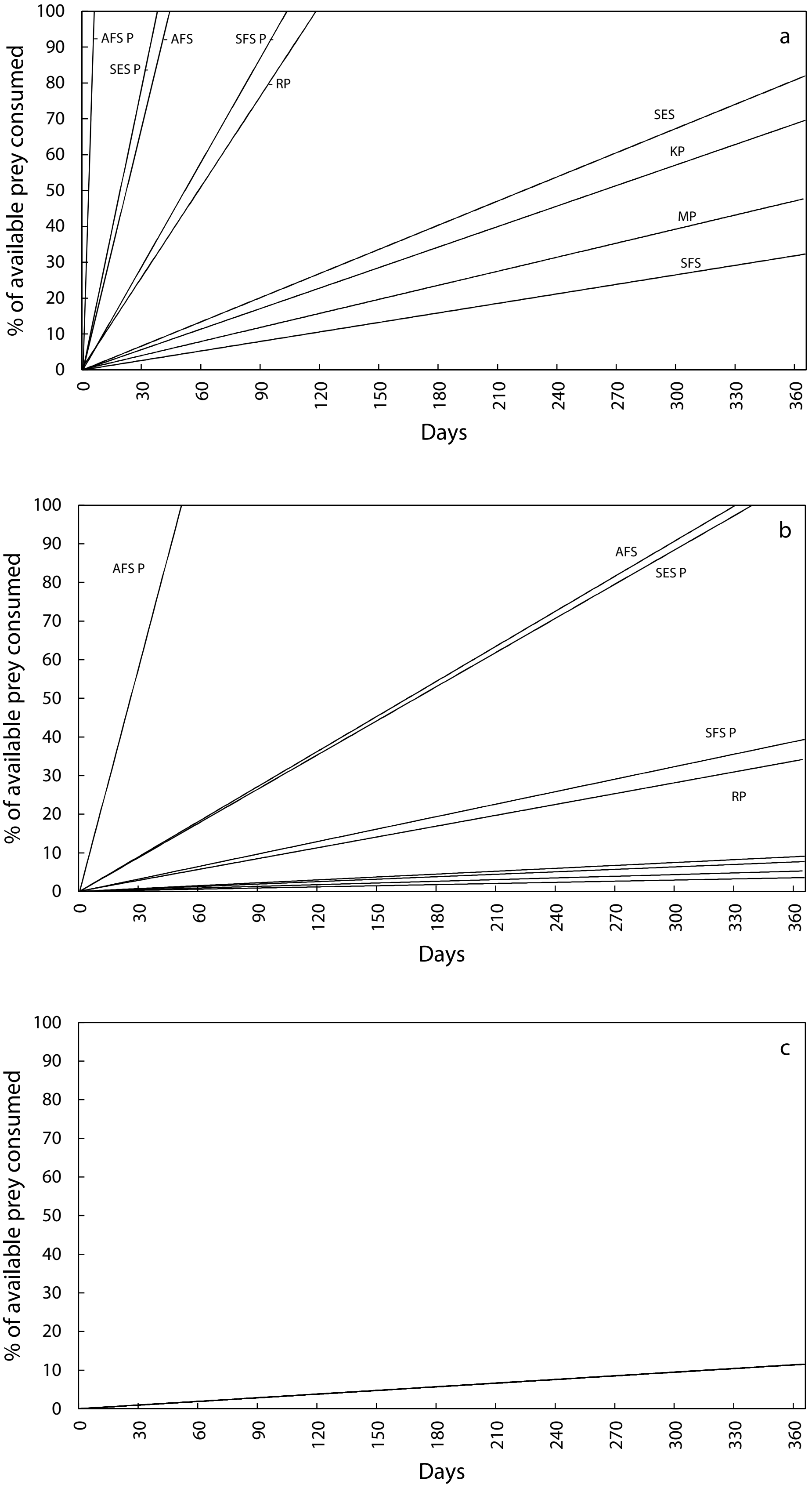
Prey type	AM	AF	U	C	Total population
Antarctic fur seal pup	105	244	55	33	438
Antarctic fur seal adult female	30	70	16	10	125
Subantarctic fur seal pup	93	216	49	29	388
Subantarctic fur seal adult female	25	59	13	8	105
Elephant seal pup	4	10	2	1	17
Elephant seal	1	3	1	0	5
King penguin	61	142	32	19	254
Macaroni penguin	190	440	100	60	789
Rockhopper penguin	324	750	171	102	1 347

TABLE 4.3 Number of various prey items required to meet the predicted daily energy requirements of the different age-sex classes of killer whales, as well as the total killer whale population, at the Prince Edward Islands. AM – adult male; AF – adult female; U – unknown; C – calf.

killer whales. Expanding these requirements to the entire known population (37 individuals), killer whales at the PEIs would need to ingest 40 600 MJ.day^{-1}.

The energy density of available prey ranged from 8.24 MJ.kg^{-1} for Antarctic fur seal pups to 20.2 MJ.kg^{-1} for elephant seal pups (Table 4.2). Penguins had energy densities comparable to those of fur seals, and king penguins owing to their relatively large body mass, have a relatively large energy content. Energy densities for PEIs prey were comparable to those estimated for similar prey in other studies (Table 4.2). Due to their comparatively massive body size and high energy density, elephant seals provided by far the most energy per prey item – an adult female or subadult male may have an energy content of nearly 9 000 MJ, although this is an average overestimate because I used pup energy density. Further, the entire carcass of such large prey is unlikely to be consumed (cf. Baird and Dill 1996).

The large numbers of prey required to sustain the PEIs killer whale population, assuming killer whales feed on each prey type exclusively, are shown in Table 4.3. Due to their high energy content, a small number of elephant seals is required to meet killer whales' energy requirements in contrast to other prey. When viewed as proportions of the available prey, Antarctic fur seal pups, Antarctic fur seal adults and elephant seal pups experience high relative predation pressure, as evidenced by the gradient of the respective lines in Figure 4.1a. For Antarctic fur seals, this high predation pressure is a result of their small


% of available prey consumed
100
90
80
70
60
50
40
30
20
10
0
0
30
60
90
120
150
180
210
240
270
300
330
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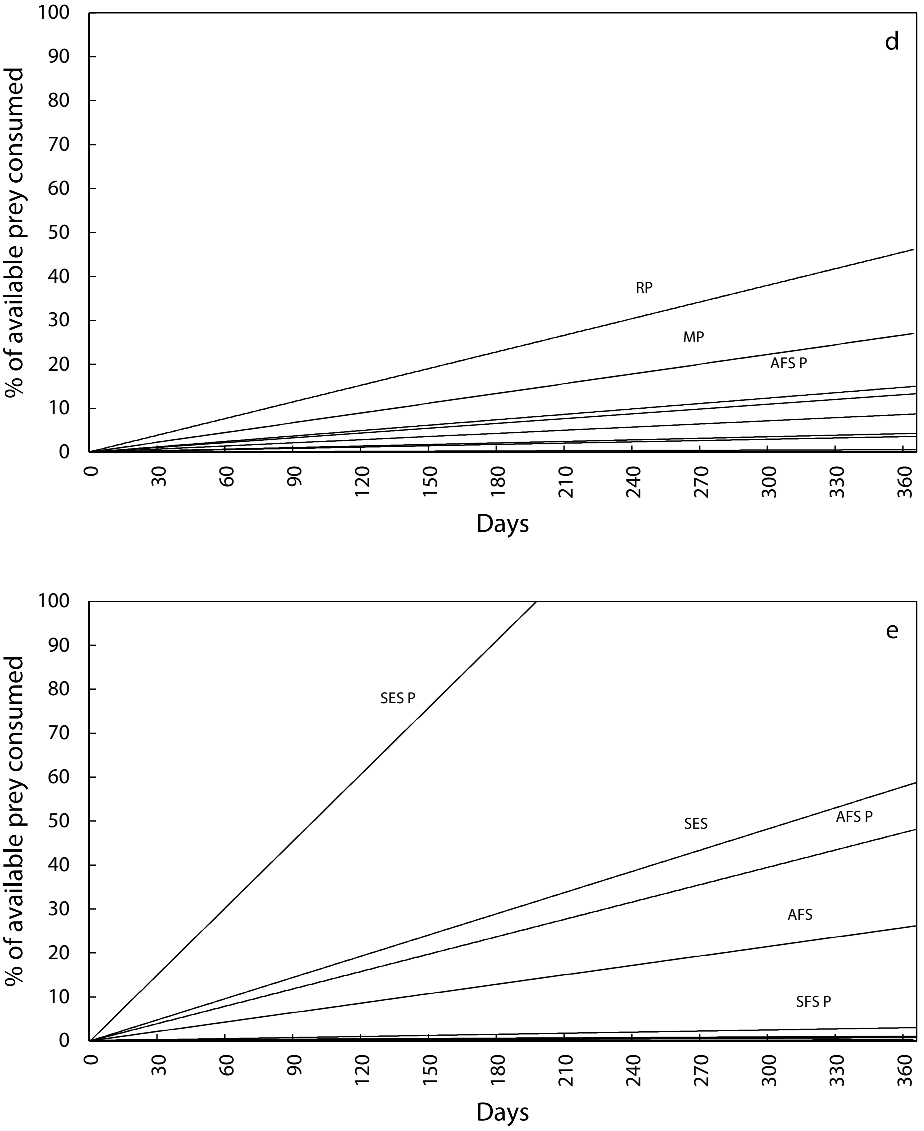

FIGURE 4.1 Proportion of available prey (i.e., percentage of the total prey population) necessary to meet the predicted energetic requirements of the killer whale population at the Prince Edward Islands, over time assuming: (a) killer whales prey exclusively on each prey type, (b) killer whale diet comprised equal proportions (energetically) of each prey type, (c) killer whale diet comprised proportions of prey type relative to their proportional energetic biomass in the Prince Edward Islands system, (d) diet comprised prey proportions relative to their abundance, and (e) diet comprised prey proportions relative to their energy content. AFS – Antarctic fur seal adults; AFS P – Antarctic fur seal pups; SFS – Subantarctic fur seal adults; SFS P – Subantarctic fur seal pups; SES – southern elephant seal adults; SES P – southern elephant seal pups; KP – king penguin; MP – macaroni penguin; RP – rockhopper penguin.

population size and relatively low energy content; for elephant seals high predation pressure (despite their high energy content) is a result of their small population size. Other prey types experience relatively little predation pressure. When each prey type is assumed to comprise an equal proportion of killer whale diet (11% each; Figure 4.1b) predation

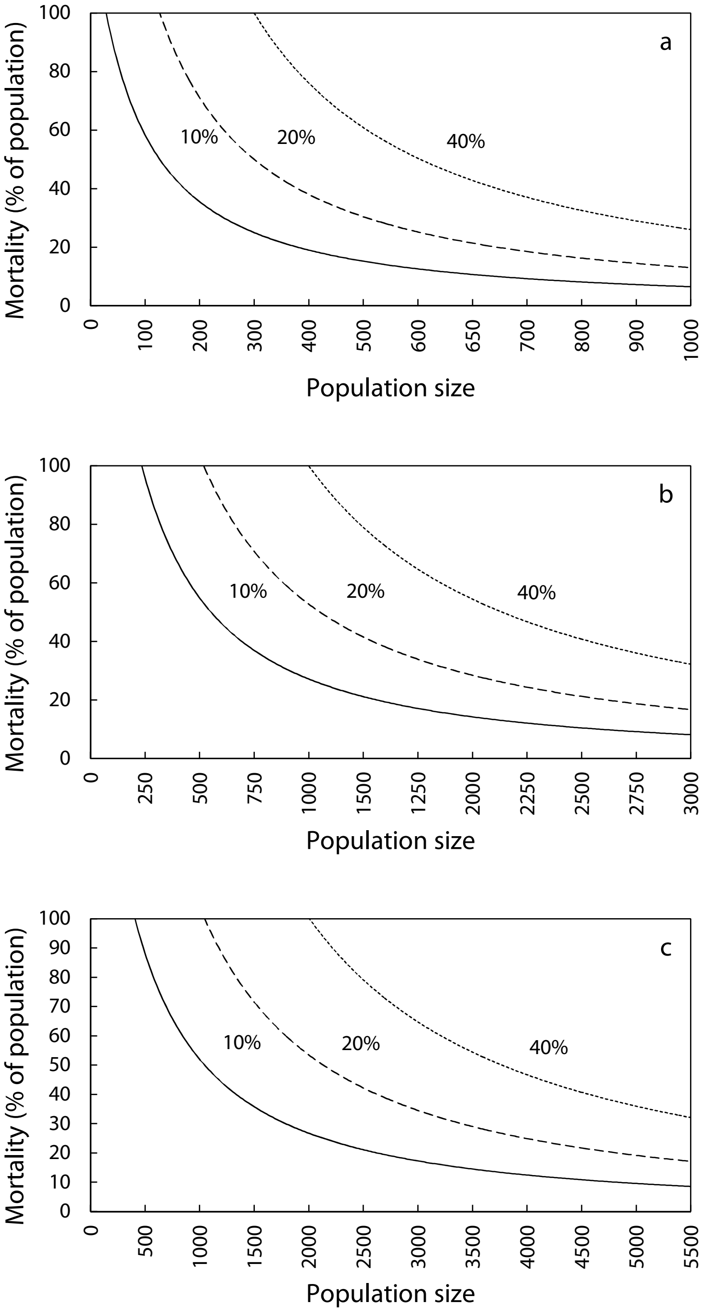

FIGURE 4.2 The effect of killer whale predation on different population sizes of (a) southern elephant seal pups, (b) Antarctic fur seal pups, and (c) Antarctic fur seal adults; assuming three different levels of predation pressure: predation mortality is 10% of current prey population size (solid lines), predation mortality is 20% of current prey population size (dashed lines), and predation is 40% of current prey population size (dotted lines).

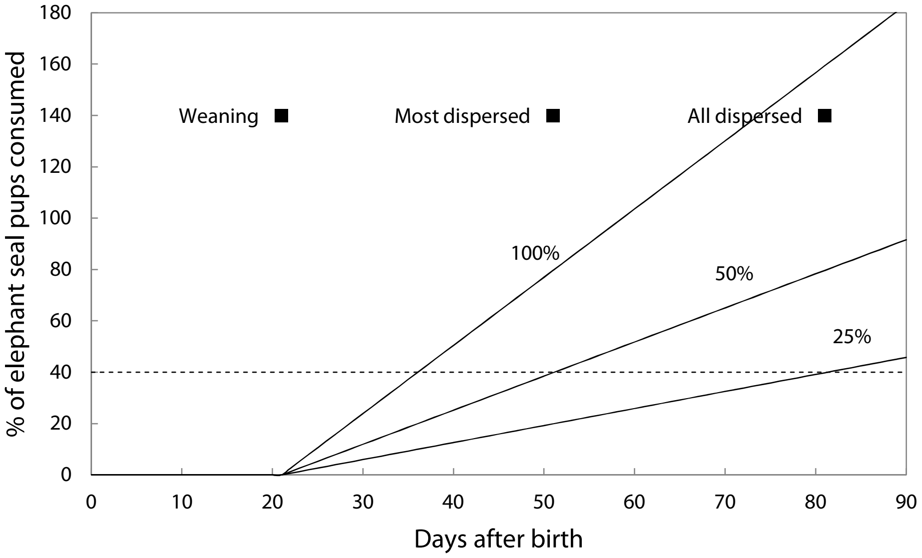

FIGURE 4.3 Potential predatory impact of the Prince Edward Islands killer whale population on southern elephant seal pups prior to their first trip to sea. Solid lines indicate predation assuming killer whales meet all their energy requirements by preying on elephant seal pups (100%), and 50% and 25% of this predation level. The dashed line indicates the currently observed first year mortality rate for elephant seals at Marion Island.

pressure on each prey type obviously decreases substantially, although Antarctic fur seal pups still experience relatively high predation pressure and Antarctic fur seals and elephant seal pups experience moderate pressure. Other prey types experience very little predation pressure in this scenario. If prey are assumed to comprise proportions of killer whale diet relative to their proportional energetic biomass in the PEIs system (Figure 4.1c), each prey type experiences identical, low predation pressure. If diet is assumed to comprise prey proportions relative to their abundance (Figure 4.1d), rockhopper and macaroni penguins experience moderate predation pressure due to their large population sizes but relatively low energy content, while other prey types experience low predation pressure. Finally, if diet is assumed to comprise prey proportions relative to their energy content (Figure 4.1e), elephant seal pups experience relatively high predation pressure due to their small population size and high energy content, and, in a similar fashion, elephant seals and Antarctic fur seal pups experience moderate predation pressure.

The results of varying prey population size on predation mortality (Figure 4.2) indicate that, at relatively low predation rates (10% predation mortality at current population size) seal populations would have to dwindle dramatically before predation mortality becomes unsustainable. A simple common sense calculation shows that populations would have to be literally decimated before predation mortality becomes 100%. For elephant seal pups, predation mortality becomes 80% below 100 pups (Figure 4.2a), for Antarctic fur seal pups below 500 pups (Figure 4.2b), and for Antarctic fur seals below 1 000 individuals (Figure 4.2c).

Due to their high energy content (Table 4.2), small population size (Figure 4.2a), and recently declining population size, elephant seal pups are likely most sensitive to killer whale predation. I therefore present the potential impact of killer whale predation on elephant seal pups on a small spatial scale (Figure 4.3), given their short availability as prey (see Discussion). Assuming that killer whales meet their energy needs by preying exclusively on elephant seal pups, Figure 4.3 shows that the currently observed first year mortality, ~40% (de Bruyn 2009), is reached two weeks after weaning, or about a month after birth. Assuming most pups disperse 1 to 2 months after weaning, the predation levels required to produce the observed 40% first year mortality would be 50% to 25% of the maximum rate (the rate where killer whales feed exclusively on elephant seal pups). These lower rates correspond, respectively, to the killer whale population taking approximately 9 and 13 fewer pups daily.

DISCUSSION

The predatory impact of killer whales at the PEIs is determined by what proportion of their prey populations they consume over time. Figure 4.1a illustrates the potential magnitude of killer whales' impact on their prey populations, showing that they can consume a substantial *number* of prey items, although this arguably only represents a considerable *proportion* of elephant seal pups, Antarctic fur seal pups, and Antarctic fur seal populations. Assuming exclusive predation, elephant seal pups would be exterminated in approximately 38 days, Antarctic fur seal pups in 6 days and Antarctic fur seals in 37 days. All other prey types could support killer whales for more than 100 days, assuming negligible non-predatory mortality levels of prey and unchanged predation pressure by other predators (e.g., de Bruyn et al. 2007).

First year survival for elephant seals at Marion Island is 58% and 63% for males and females, respectively, and adult survival is around 70% and 80% for males and females, respectively (de Bruyn 2009). Assuming this mortality is entirely due to predation, elephant seal pups would sustain killer whales for approximately 15 days, and adult elephant seals would sustain them for more than 100 days (Figure 4.1a). Demographic data are unavailable for fur seals and penguins at Marion Island but for Antarctic fur seals at Bird Island, South Georgia, first year survival was estimated at 65% and adult female survival at 90% (Payne 1977). Using these figures, Antarctic fur seal pups could support killer whales for little more than 1 day and adults for approximately 5 days. Subantarctic fur seals at Île Amsterdam, Indian Ocean, have a pup survival rate of 48% (Beauplet et al. 2005) and adult female survival is around 90% (Beauplet et al. 2006). Assuming these rates, Subantarctic fur seal pups could support killer whales for 54 days, and adults for more than 114 days. King penguins at the Îles Crozet have survival rates well over 90% (Olsson and van der Jeugd 2002), and could thus support killer whales for more than 53 days. Annual survival in macaroni penguins is approximately 77% (Williams 1995) and 84% in rockhopper penguins at Île Amsterdam and Île Saint Paul (Guinard et al. 1998), and these prey could thus support killer whales for 177 days and 20 days, respectively. Simply summing these figures (539 days) shows that there are sufficient prey resources to support killer whales at the PEIs annually assuming exclusive, sequential predation on each species. When viewed as a simple "available prey" scenario without prey occurrence and behaviour taken into account, this indicates that prey mortality rates cannot escalate enough to cause population declines. However, it is important to consider in such calculations factors affecting diet composition (discussed below). For comparison, in the Aleutian Islands the population of 170 killer whales, feeding exclusively on each prey species, would exterminate minke whales (*Balaenoptera acutorostrata*), harbour seals, harbour porpoises (*Phocoena phocoena*) and Steller sea lions within 6 to 12 months. Sea otters would be eliminated in two days. Together these species would sustain killer whales for three years. Dall's porpoises (*Phocoenoides dalli*) would be eliminated in three years (Williams 2006).

Diet composition and prey choice

The predation rates presented in Figure 4.1a assume that killer whales prey exclusively on a certain prey type – an assumption known to be incorrect from observations at the PEIs and studies elsewhere (e.g., Condy et al. 1978, Guinet 1992, Ford et al. 1998, Reisinger et al. in press). The predatory impact of killer whales at the PEIs will therefore be determined largely by what prey killer whales actually include in their diet, and in what proportions, more realistically reflected in one of the scenarios presented in Figure 4.1 (b to e).

The diet of killer whales at the PEIs is unknown aside from a small number of observations of predation events (Condy et al. 1978, Reisinger et al. in press), but killer whales in Northern Patagonia – a population similar to that at the PEIs (Reisinger et al. in press) – fed mainly on southern sea lions (85.71%) but also on elephant seals (3.89%), Magellanic penguins (*Spheniscus magellanicus*; 3.89%) and fish (6.06%; Iñíguez et al. 2002). In the eastern North Pacific, *transient* killer whales killed primarily harbour seals (55%) followed by cetaceans (18%), California (*Zalophus californianus*) and Steller sea lions (9%) and birds (6%; Ford et al. 1998). While birds may not be an important component in the diet of these populations, the abundance of penguins at the PEIs, and their energy content (Table 4.2) suggest they may be a comparatively more important food source for PEIs killer whales (also see Pitman and Durban 2010). I have not considered alternative prey in the diet of killer whales at the PEIs. They may include large cetaceans and fish in their diet, as killer whales at neighbouring Îles Crozet seem to do (Guinet 1992).

Killer whales' dietary composition is expected to be predicted largely by optimal foraging theory: the profitability of including prey in their diet will be influenced by the prey's energy content, traded off against the search time and handling time involved in capturing and consuming that prey (MacArthur and Pianka 1966, Stephens and Krebs 1986). Elephant seals represent a considerable energy resource (Table 4.2), and are likely to be targeted preferentially, yet the energetic costs of searching for and handling elephant seal prey relative to other prey are unknown. Fur seal adults also represent a good source of energy (Table 4.2). An important factor determining search costs will be the encounter rate of prey inshore, determined by their spatio-temporal density, and in these terms Subantarctic fur seals and penguins represent considerable energy resources owing to their abundance.

While all prey appear to be quite abundant at the PEIs, their inshore density and temporal attendance at the PEIs means their encounter rates will be highly variable – a critical factor limiting their profitable inclusion in killer whales' diet. Penguins and seals have highly synchronized breeding and will therefore represent an abundant but temporally limited prey source. Fur seals and penguins are income breeders, meaning that adults must undertake regular foraging trips to sustain themselves and their offspring during the breeding period, thus increasing inshore “traffic” as penguins and seals arrive and depart from the PEIs. Antarctic fur seal pups wean at an age of 112 days and Subantarctic fur seal pups at approximately 300 days, where after they disperse, although pups of both species start swimming close to shore at about two months of age (Kerley 1983). Elephant seals, on the other hand, are capital breeders and females do not leave the beaches until after their pups have weaned. Pups wean at an age of 21 days and swim close to shore before dispersing in the next month or two during which time they are apparently frequently available to killer whale predation (Wilkinson and Bester 1990), through likely crepuscular movement of older weaned pups to and from the sea (Lenglart and Bester 1982). At Îles Crozet, for example, up to 25% of elephant seal pups at a particular beach were taken by killer whales (Guinet et al. 1992). Elephant seals may thus experience relatively intense predation, but the short period of inshore availability before dispersing significantly dampens the predatory impact of killer whales (Figure 4.3).

Indeed, the results of Hoelzel’s (1991) study of killer whale predation at Punta Norte, where killer whales intentionally strand themselves to capture southern sea lions and elephant seals, is consistent with the predictions of optimal foraging theory. Despite the smaller size of sea lion pups (50 to 70 kg [Hoelzel 1991] compared to >100 kg for elephant seal pups [Table 4.1]) and expected lower energy content (compare the energy density of Steller sea lions to that of elephant seal pups in Table 4.1), killer whales directed the majority of their attacks (97%) at sea lions. Most (66%) of these attacks were directed at sea lion pups – the prey for which killer whales had the highest capture rate. Similarly, the predominance of harbour seals in *transient* killer whale diets (Ford et al. 1998, above) likely represents their year round abundance in the killer whales’ range, and their lower relative search and handling costs (Baird and Dill 1995, Ford et al. 1998). *Resident* killer whales in the eastern North Pacific Ocean have also been shown to be highly selective in their choice of salmon prey, preferring the largest species of available salmon, independent of relative salmon abundance (Ford and Ellis 2006).

Yet, in vertebrates, social influences can play an important role in foraging (Galef and Giraldeau 2001) and in killer whales foraging culture or tradition may be an important influence on dietary composition and should be taken into account when considering their impact on prey populations (Barrett-Lennard and Heise 2006). Killer whales exhibit marked foraging specializations through their range (see Baird 2000) with even sympatric populations having distinct diets (e.g., Ford et al. 1998). There is observational evidence suggestive of culture in killer whales (summarised in Rendell and Whitehead 2001) and cultural transmission or foraging traditions may have a strong influence on the dietary composition of killer whales. This is evident, for example, in the intentional stranding hunting technique of killer whales at Punta Norte and the Îles Crozet (Lopez and Lopez 1985, Guinet 1991, Guinet and Bouvier 1995), cooperative "carousel feeding" on herring in Norway (Similä and Ugarte 1993) and pod-specific foraging patterns of *transient* killer whales in the eastern North Pacific Ocean (Baird and Dill 1995).

Predatory impact

Despite the apparent magnitude of the predation rates (Figure 4.1), at the PEIs fur seal populations are increasing (Hofmeyr et al. 2006) after their near-extirpation by intensive commercial harvesting (King 1983), the elephant seal population is at least stable, likely increasing (de Bruyn 2009, McMahon et al. 2009), and the king penguin population appears stable (Crawford et al. 2009). Macaroni and rockhopper penguin populations are declining, but this is speculated to be due to mass disease outbreaks and altered food availability (Crawford et al. 2003, 2009). These trends are consistent with trends at many localities in the Southern Ocean and the Subantarctic and a large number of studies linked demographic changes in pinnipeds and seabirds to environmental changes and trophic effects in the Southern Ocean and surrounding oceans (Croxall 1992, Guinet et al. 1994, Barbraud and Weimerskirch 2001, Reid and Croxall 2001, Weimerskirch et al. 2003, Forcada et al. 2005, 2006, reviewed in Trathan et al. 2007).

Following an increase in population size after the cessation of their commercial harvesting, elephant seals underwent large population decreases throughout their breeding range between the 1950s and 1990s. Among the explanations for this decline (reviewed in McMahon et al. 2005), environmentally mediated changes in food abundance and availability (Burton 1986, McCann and Rothery 1988, Hindell 1991, Burton et al. 1997, Pistorius et al. 2004) seem the most plausible. However Barrat and Mougin (1978) proposed that killer whales may play a role in the elephant seal declines, in a manner equivalent to the hypothesised sequential megafaunal collapse in the North Pacific Ocean (Springer et al. 2003). Killer whale predation has been suggested as a major factor in the elephant seal decline at least at Marion Island and Îles Crozet (Condy et al. 1978, Guinet et al. 1992) and for small populations of northern elephant seals (*M. angustirostris*; Cooper and Stewart 1983). In the Southern Hemisphere more than two million whales were taken during commercial whaling operations in the 20th century (Clapham and Baker 2002). The removal of such a large biomass must certainly have had significant effects on Southern Hemisphere marine ecosystems (e.g., Ballance et al. 2006) and much focus has been placed on the "krill surplus hypothesis" (Laws 1977) which forwards that krill predators underwent competitive release after the removal of the great whales, allowing them to increase in abundance. However, these removals may have resulted in a significant shortfall of prey for killer whales, forcing them to switch to elephant seal prey, thus driving population declines by increased predation pressure. Branch and Williams (2006) tested this idea, and based on energetic and demographic analyses, found it plausible that even a relatively small dietary shift by killer whales in the Southern Hemisphere could have caused declines in elephant seals and southern sea lions. The results are similar to those of Estes et al. (1998) and Williams et al. (2004), who show that four to five killer whales could bring about the observed decline in sea otter populations in the eastern North Pacific Ocean; a presumed effect of the sequential megafaunal collapse. As I have highlighted in the above discussion of potential predation impacts at the PEIs, the real difficulty lies in evaluating the dietary composition of killer whales, upon which such scenarios hinge. In this case, there is a paucity of data about the diet, abundance and distribution of the at least two types of killer whales (Mikhalev et al. 1981; Pitman and Ensor 2003). Again, the plausibility of such scenarios underlines the potential for killer whales to significantly impact their prey populations, and highlights avenues for further research.

Bottom-up and top-down forces certainly both structure and affect ecosystems; accent must be placed on their relative roles and interactions. Because of the current trajectories of top predator populations at the PEIs I logically assume that *currently* killer whale predation pressure is not sufficient to cause declines in prey populations, although Figure 4.1 certainly demonstrates the potential to do so for some species, and continued long-term monitoring of predator and prey populations is required. I reiterate that this does not imply killer whales do not have a significant role in the structure and function of marine ecosystems.

Killer whale predation may have a significant dampening effect on vital rates. For example, Boveng et al. (1998) provided circumstantial evidence that leopard seals (*Hydrurga leptonyx*) limited population growth of Antarctic fur seals at the South Shetland Islands, Southern Ocean, by preying on pups. The number of pups counted at Elephant Island grew slowly (3.8% per annum) compared to rates as high as 11% at other locations in the South Shetland Islands with leopard seals taking up to 34% of the pup cohort at a particular locality.

When considering the effects of prey population size changes on predation mortality (Figure 4.2), it is apparent that reductions in population size of a few hundred animals are required before killer whale predation becomes a significant threat to the existence of such prey populations. However, if population sizes were to reach such low numbers, killer whale predation could certainly precipitate severe population declines. The nature of such interactions depends on the total response of killer whales to changes in prey density. I have assumed no total response in Figure 4.2 but, conceptually, the total response comprises the numerical and/or functional response of predators to such changes (Solomon 1949): in the former, predator numbers increase or decrease, in the latter, predators consume more or less prey per capita. Killer whales are unlikely to show strong numerical responses to changes in prey abundance (Barrett-Lennard et. al. 1995), particularly given their long lifespans (Olesiuk et al. 1990) and the wide variety of prey they could potentially exploit, although (Ford et al. 2010) have recently shown that population trends of eastern North Pacific Ocean *resident* killer whales are driven largely by changes in survival and that survival rates are strongly correlated with the abundance of their principal salmon prey. Numerical response may also result from migration of individuals. Classic functional responses (Holling 1959) are of three types: *Type I* in which the number of prey eaten per predator increases linearly with increasing prey density; *Type II* in which the number of prey eaten rises at a decreasing rate towards an asymptote; and *Type III* in which the number of prey taken is low at low prey densities and increases sigmoidally towards an asymptote. In a *Type III* response prey may find refuge from predation at low densities, and “break out” at high densities, but be caught in a “predator pit” of intense predation at intermediate densities. Barrett-Lennard et al. (1995) proposed a *Type III* response for *transient* killer whales preying on Steller sea lions in the eastern North Pacific Ocean based on observations that killer whales can specialize on other prey and sea lions can seek refuge by hauling out on land. Systems involving generalist predators or prey-switching can obscure predator-prey relationships (e.g., Mills et al. 1995, Murdoch et al. 2002). Paradoxically for such a generalist species, however, killer whales may be far more specialized foragers than currently suggested (see Ford et al. 2010 and discussion of social factors above) and novel prey preferences and foraging behaviours may actually arise slowly (Barrett-Lennard and Heise 2006). Further, simple models do not incorporate the complex dynamics of bottom-up and top-down interactions (e.g., Vucetich and Peterson 2004, Guénette et al. 2006) or competitive interactions related to same prey use by other predators (de Bruyn et al. 2007, van den Hoff and Morrice 2008). It is therefore difficult to predict the effects of predation on different prey population sizes at the PEIs, but it is reasonable to expect that small prey population will experience at least some increase in predation pressure (as shown in ecosystem simulations for predation on Steller sea lions in the North Pacific Ocean [Guénette et al. 2006]), possibly until the population finds refuge at low densities. The presence of secondary or alternative prey may have different effects. Prey may experience less predation by dilution of the functional response (Murdoch 1969) or prey may experience increased predation if the presence of alternate prey promotes a favourable numerical response in the predator (Holt 1977). The former situation could have allowed the recovery of elephant seal populations if the rapidly expanding fur seal population diluted killer whale predation but the latter situation may spell trouble for elephant seal populations if the expanding fur seal population elicits a numerical response in killer whales. If killer whales do show a numerical response it may most likely result from immigration of individuals to the PEIs.

Figure 4.3 shows how small changes in the number of elephant seal pups taken can result in large differences in mortality expressed as a percentage of the population. If the killer whale population at the PEIs were to take four additional elephant seal pups daily, first year mortality in elephant seals could realistically double (Figure 4.3). Small dietary shifts or changes in the availability of prey can thus have large impacts in small populations (as illustrated by Williams et al. 2004, Branch and Williams 2006).

In summary, the killer whale population at the PEIs can consume a substantial number of prey items, but this only represents a considerable proportion of elephant seal pups, Antarctic fur seal pups and Antarctic fur seal adults – and only if killer whales specialize on these prey. Populations of pinnipeds are increasing or stable at the PEIs, implying that killer whale predation is currently having no adverse effects on population size, however, predation mortality likely dampens population growth. If these populations became very small because of bottom-up processes, or if prey availability or killer whale diet changed, killer whales could have very significant adverse population effects (cf. Cooper and Stewart 1983).

To more accurately quantify the predation effects of killer whales at the PEIs and to move towards a better understanding of the PEIs marine ecosystem, further data are required: killer whale diets should be accurately described and the energy density of prey measured; their temporal abundance and movement patterns should be investigated; elephant seal and killer whale mark-recapture programmes must continue in order to describe any changes in abundance and vital rates (de Bruyn et al. 2008, Chapter 3), and; fur seal abundance must continue to be monitored and demographic studies should be initiated. Due to a lack of data concerning killer whale diet and predation at the PEIs, I have taken an extremely simplified approach to assessing their predatory impact. Despite this, I have shown that simple calculations using available data can be used to assess which prey may be sensitive to predatory impacts, and under what conditions. Eliminating unlikely scenarios allows the fruitful direction of the proposed future research and this approach is broadly applicable in large predator studies.

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CHAPTER 5

General conclusion

SYNTHESIS

Killer whales are the oceans' apex predators and have an eclectic diet including a variety of taxa, which means they can potentially influence marine ecosystems at a variety of levels (Ford and Ellis 2006). This is exemplified by the "sequential megafaunal collapse hypothesis" (Springer et al. 2003), which proposes that post World War II industrial whaling in the North Pacific Ocean depleted killer whales' great whale prey, forcing them to sequentially switch to smaller/less abundant marine mammal prey species, causing declines of seal and sea otter populations. A similar mechanism was proposed to explain the declines of southern elephant seals (*Mirounga leonina*) in the Southern Hemisphere (Barrat and Mougin 1978), following the depletion of great whales in the 20th century (Clapham and Baker 2002).

Despite speculation regarding the influence of killer whale predation on seal populations at the Prince Edward Islands (Condy et al. 1978, Keith et al. 2001, Pistorius et al. 2002, Tosh et al. 2008, de Bruyn 2009), no study has specifically addressed this issue. Indeed, killer whales have been poorly studied at the Prince Edward Islands, and, with one exception (Tosh et al. 2008), previous studies (Condy et al. 1978, Keith et al. 2001, Bester et al. 2002, Pistorius et al. 2002) have been based on opportunistically collected data.

Using observational and photographic identification data collected during opportunistic and dedicated observation sessions at Marion Island from 2006 to 2009, I attempted to assess the predatory impact of killer whales on seal and penguin populations.

In order to assess the impact of a predator on its prey populations, information is required about its diet and abundance.

Chapter 2 thus describes the observable diet of killer whales at Marion Island. During 823 sightings of killer whales 48 predation events were recorded, although prey could be indentified in only 10 cases. Killer whales fed on southern elephant seals, Subantarctic fur seals (*Arctocephalus tropicalis*), king penguins (*Aptenodytes patagonicus*) and macaroni penguins (*Eudyptes chrysolophus*). Constant effort observations revealed that killer whale abundance inshore peaked from September to December, with a secondary peak in April to May, a pattern linked to the phenology of their seal and penguin prey.

In Chapter 3 I estimated the abundance of killer whales occurring inshore at Marion Island by performing rigorous mark-recapture analyses using nearly 10 000 photographs taken from 2006 to 2009. Using careful quality control criteria I identified 37 individuals and estimated a population size of 42 (95% CI = 35-50) individuals using the open population POPAN parameterization in the software program MARK.

Finally, in chapter 4, I used the above information along with published predicted energy requirements of killer whales to predict the energy requirements of the killer whale population at the Prince Edward Islands: 40 600 MJ.day^{-1}. Based on available energy density and mass data, I predicted the energy content of available seal and penguin prey and calculated the rates at which killer whales would consume these prey in various scenarios. Penguins and Subantarctic fur seals are relatively insensitive to killer whale predation owing to their large population sizes (10 000s to 100 000s), conversely, the smaller populations (100s to 1 000s) of Antarctic fur seals and southern elephant seals are sensitive to predation, particularly the latter as they have a high energy content (approximately. 2 000 to 9 000 MJ). Populations of these seals are currently increasing or stable, leading to the conclusion that presently killer whale predation is not driving population declines, although they clearly have the potential for regulation of these smaller populations. Thus, if population sizes were reduced by bottom-up processes, if killer whale diet shifted, or if prey availability changed, top-down predation by killer whales could become significant.

This study provides a preliminary assessment of the potential predatory impact of killer whales at the Prince Edward Islands, and also provides valuable information for the conservation and management of killer whales and their prey. Further, this study provides a beachhead for future studies of killer whales at Marion Island, particularly through the establishment of regular photographic identification data collection and a catalogue of identifiable individuals.

FURTHER RESEARCH

This study has identified a number of areas for further research. Firstly, killer whale diet must be accurately described. Observational evidence for the inclusion of certain prey items remains important; however techniques such as fatty acid and stable isotope (e.g., Herman et al. 2005) analyses should be employed. Of particular interest is whether, and to what extent, fish and large cetaceans are included in the diet of Marion Island killer whales. Secondly, the movements of Marion Island killer whales should be investigated using satellite telemetry (e.g., Andrews et al. 2008), with particular emphasis on the whereabouts of killer whales when they are not observed at Marion island. Do they move offshore locally, and are thus unobservable from shore, or do they undertake larger scale seasonal migrations, as has been suggested (e.g., Mikhalev et al. 1981, Williams et al. 2009)? These studies will have independent heuristic value as well as improving further assessments of the predatory impact of killer whales at Marion Island (in conjunction with information about prey energy content and fur seal and penguin demography). Photographic identification data should continue to be collected as this will allow the eventual estimation of demographic parameters such as survival (e.g., Olesiuk et al. 1990) – essential information for management decisions. Continued photographic identification will also allow the description of social structure based on the association of identifiable individuals (e.g., Parsons et al. 2009, Ivkovich et al. 2010), but this should be complemented with genetic techniques (e.g., Pilot et al. 2010) which can also be used to infer regional stock structure (e.g., Morin et al. 2010).

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APPENDIX A

Photographic identification catalogue of killer whales at Marion Island

This appendix includes left and right side dorsal fin images of the 37 individual killer whales identified at Marion Island from 2006 to 2009. Individuals are assigned a unique alphanumeric identifier (e.g., MF001) where the first letter is always "M" (Marion Island) and the second letter corresponds to the individual's sex (M – adult male, F – adult female and U – unknown). The three digit identifier is unique, regardless of sex, and remains the same if an individual is assigned to a different sex class.

MF001 “Halfmoon”

MF002 “Linus”

MF003

MF004 “Dot”

MM005

MF006 “Harriet”

MM007 “Max”

MM008

MF009

MM010

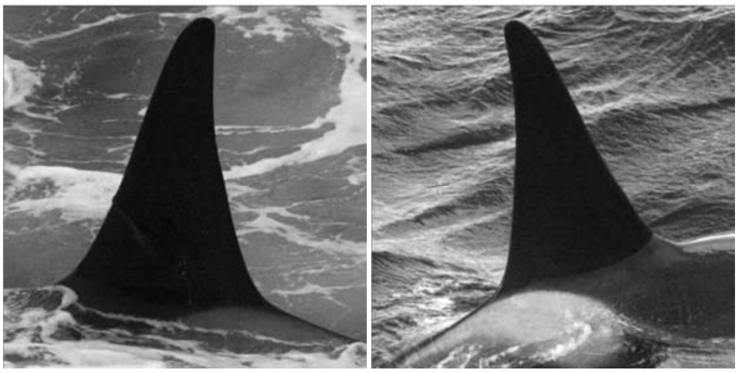
MM011

MF012

MF013

MF014 “Scratches”

MF015



MM016

MF017

MF018

MM019

MF020

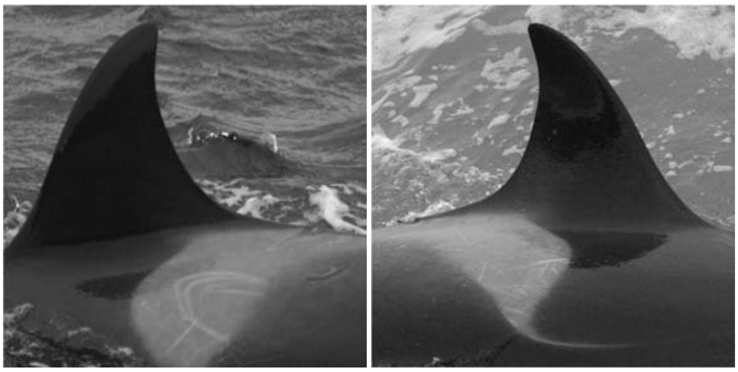
MU021

MF022

MF023

MU024 “David” – MF004’s calf, born in 2008

MU025



MU026 “O’Neill”

MU027 – MF002’s calf, born in 2008

MU028

MF029

MF030 “Top Notch”

MF031 “Bent”

MF032

MF033

MU034 – MF029's calf, born in 2008

MF035

MF036 "Rake"

MF037

APPENDIX B

Killer whale observation work plan

The text in this appendix is taken from the Marion Island Marine Mammal Programme work plan, which serves as a manual for overwintering marine mammal observers on Marion Island to continue various long-term monitoring projects on the island. Killer whale data collection at Marion Island is ongoing, and has been conducted according to these guidelines since 2008. I compiled these guidelines with the assistance of Nico de Bruyn and Chris Oosthuizen.

Killer whales are the most widespread cetaceans, but display great variation in their ecology throughout their range. Thus, despite being among the best-known cetaceans, studies at various localities are important and contribute new information to our knowledge of the species. Further, killer whales are poorly known in the Southern Ocean, making Marion Island a potentially very important study site.

Being so well-known, there is a large literature; selected papers can be found in the folder "Information and Literature" and relevant new papers will be e-mailed to you.

Only four papers, however, deal with killer whales at Marion Island:

Condy et al. (1978) Journal of Zoology 184:449-464
Keith et al. (2001) African Zoology 36:163-175
Pistorius et al. (2002) South African Journal of Wildlife Research 32:86-92
Tosh et al. (2008) Marine Mammal Science 24:929-940

Killer whale studies at Marion Island rely on shore-based observations and photographic identification of individuals. Observations are made:

- **a)** ***opportunistically*** **during other activities, or**
- **b)** **during** ***dedicated*** **killer whale observation sessions at various points around the island.**

For *any* observation (**a** or **b** above) the following should be recorded:

General data

1) The date.
2) The site (MM001 to MM068, see Beach Codes).
3) The number of animals in the pod (if you are unsure of the exact number, accurately estimate the range).
4) The number of adult males, adult females, subadults, calves and unidentified animals in the pod (first concentrate on accurately estimating the group size).

5) The direction they approach from and the direction they depart to.
6) Their time of arrival and departure (this will be the same unless the animals hang around for a while).
7) The distance that the animals are from shore (zone 1 to 4, see below).
8) Whether photographs were taken and if so, an estimate of the number of animals photographed (if possible, estimating this can be difficult sometimes).
9) Notes regarding behaviour (see below), distinctive animals, etc.
10) Name of the observer.

Dedicated observations

Dedicated observation sessions are divided into two duration categories – 3 hour and 10 hour:

Short sessions are conducted at Rockhopper Bay (**throughout the year**) and Mixed Pickle Cove (**during fur seal attendance observations**), and must last 3 hours. Try to distribute the sessions evenly between morning, midday and afternoon (e.g., 7:00 to 10:00, 11:00 to 14:00, 15:00 to 18:00; adjust as necessary in winter) around the fur seal attendance observations and through the week. Avoid conducting sessions on consecutive days.

Full day observations, must last 10 hours and should start between 07:00 and 08:00. However, 07:00 to 17:00 is ideal. These sessions need to be conducted at the following locations:

- Rockhopper Bay, Kildalkey, Watertunnel, Mixed Pickle, Pinnacles, Goney, Funk and Cape Davis beaches, and need to be spaced through time *roughly* as follows:
- *April to end August:* Cycle through *two* of – Rockhopper Bay, Kildalkey, Watertunnel and Cape Davis on each elephant seal census cycle (10 days). I.e., through four census cycles, each of these sites would have been covered twice. Try to do a north coast and south coast site simultaneously, rather than two from one side of the island.
- *May to mid August:* See TAPS schedule for Mixed Pickle killer observation details.
- *September to end December:* In alternating weeks, cover two of the following sites Kildalkey, Watertunnel, Pinnacles, Funk and Rockhopper Bay, simultaneously:

  - Week 1: One sealer – Kildalkey, other sealer – Watertunnel (on the same day).
  - Week 2: One sealer – Rockhopper, other sealer – Pinnacles (on the same day).
  - Week 3: One sealer – Kildalkey, other sealer – Funk (on the same day).
  - Week 4: One sealer – Rockhopper, other sealer – Goney (on the same day).
  - And then start the cycle again. These observations are focused on elephant seal predation.
- *January to end March:* Cycle through *two* of – Rockhopper Bay, Kildalkey, Watertunnel and Cape Davis on each elephant seal census cycle (10 days). I.e., through four census cycles, each of these sites would have been covered twice. Try to do a north coast and south coast site each time, rather than two from one side of the island.
- *Mid January – mid March:* See TAPS schedule for Mixed Pickle for details.

For these dedicated observations you should additionally (additional to *General data* – above) record:

1) The time you start and stop observing.
2) The sea state (see below; record this at the beginning of the session, and again if it changes).

During dedicated observation sessions you need to be alert (killer whales mostly arrive without warning, quickly appearing and disappearing) and keep watching the entire time. DON'T READ A BOOK DURING THIS TIME AS YOU WILL MISS THEM, rather get yourself an iPod to listen to. Choose a spot to sit where you have a good view, but you can react quickly to get as close to the animals as possible (spots will be suggested during Take-over). Continue watching the group once they have left, they may rest somewhere close where you can quickly and easily get to. Be sure to dress warmly; take a flask of coffee and some food as well as your sleeping bag and its outer cover. Fashion a protective covering for your camera (plastic bag or the like, for drizzly weather). Always take your binoculars with also.

When you are doing dedicated killer observations close to Base (e.g., Van den Boogaard/Rockhopper), take a radio with you. You can then radio the sealers (and others) at Base when you see killers that will pass by the point to augment extra observations on group size and enhance the opportunity to obtain good ID photographs. Carrying a radio may also be a useful strategy during your routine attendance pattern checks (for opportunistic killer observations).

Distance zones

Killers are observed:

1 Within 5 m of shore
2 5 to 100m from shore (usually to the first kelp belt)
3 100 to 500m from shore (usually to the second kelp belt)
4 Beyond 500m from shore

Sea state

Beaufort sea state	Observed sea surface condition	Sailor's term	Typical effects on (main)land	Typical wind speed (Knots)
0	Mirror smooth and glassy surface	Calm	Calm; smoke rises straight up	0
1	Small ripples or capillary waves on glassy surface	Light air	Smoke drifts with wind direction	1-3
2	Larger ripples or wavelets on glassy surface	Light breeze	Leaves begin to rustle; wind felt on face	3-6
3	Wavelets of irregular direction and shape; a few crests break on glassy surface	Gentle breeze	Small flags extend; leaves in constant motion	6-10
4	Small chop, defined direction; numerous whitecaps	Moderate breeze	Dust, leaves and loose paper move	10-16

5	Heavy chop; many white foaming crests; some spray	Fresh breeze	Small trees begin to sway	16-21
6	Larger surface waves form; whitecaps everywhere; more spray	Strong breeze	Large branches move, whistling heard in wires	21-27
7	Sea heaps up; white foam starts to blow in streaks along direction of wind; spindrift forms	Moderate gale	Resistance strong when walking	27-33
8	Moderately high waves, crests begin to break into spindrift; well marked streaks of foam	Gale	Twigs and small branches broken off trees	33-40
9	High waves, sea begins to roll; spray begins to reduce visibility; dense streaks of foam	Strong gale	Structural damage occurs especially to roofs	40-47
10	Sea mostly covered in white foam; visibility reduced; exceptionally large waves	Storm	Trees uprooted; considerable structural damage	>47
11-17	Concentrate on surviving!			

Estimating group size and identifying sex and age class

“Group” is a relatively loose term that refers to any animals in the same vicinity, moving in the same general direction, engaged in the same general activity. The definition and calculation of group size will be discussed with you in take-over. It is different from “pod” which is a more restricted term referring to a social unit. Animals in a group may be quite widely separated; often a single animal will travel/forage ahead of the rest, or the group may be split into pairs or trios travelling/foraging slightly separated (often some animals come in close to shore, while others are in zone 1 or 2 – these animals are still in the same group).

Therefore, watch carefully to be sure that you have sighted the whole group. Also remember that animals can travel long distances submerged, especially when foraging. A group may split and animals will travel in completely different directions – make a note of this. Conversely, two or more groups may join for some time. If you are uncertain of the group size, estimate the range.

Adult males are unmistakable: they have tall (up to 1.8 m), erect dorsal fins. Adult females have much smaller, falcate dorsal fins. Calves are noticeably smaller than adults (around 50 to 70% of their mother's length) and maintain close association with their mothers, often travelling right beside them. Subadults are difficult to identify. They may be slightly smaller than adults but do not obviously associate with a particular animal. In the field, adult females are indistinguishable from subadult males based on dorsal fin morphology – observe the associations between animals (e.g., cow-calf) for clues to sex and age class and use the "unknown" category if you have *any* uncertainty. A good approach is to identify adult males, identify calves and identify the animal they associate with as an adult female, and record the rest as "unknown".

Behaviour

It is useful to distinguish between activity state and surface behaviour. Activity state refers to what the animals are doing in a broad sense, such as foraging or socializing, while surface activity refers to short-term behaviour observable at the surface, such as spy-hopping or porpoising. Please record the activity state and any surface activities.

Surface activity may be discrete (can be counted, e.g., spy-hops, tail slaps) or continuous (cannot be counted, but duration can be recorded, e.g., porpoising)

Breach	Complete or nearly-complete leap from the water
Spy-hop	Bringing its head vertically out of the water
Porpoising	Leaping out of the water while moving at speed (At speed; not the usual surfacing while travelling)
Tail slap/lobtail	Slapping its tail on the water surface
Back-roll	Rolling on its back

A *lack of surface activity* (travelling long distances underwater) should also be noted.

Activity state can be broadly defined into four categories. Different animals may be engaged in different activities (e.g., calves may socialize while adults rest) and the activity state may change quickly:

Foraging/Travelling

This is the most commonly observed and will often be referred to as hunting, cruising or patrolling. The group's movement will be directed and animals will move relatively quickly, generally maintaining a surfacing order. Animals may stay submerged for some distance, patrolling an entire beach before surfacing (often at points on the coastline, presumably out of site of prey). If possible, note which animals travel ahead of the group, or whether different animals are in different zones.

Feeding

A large number of seabirds (particularly giant petrels) suddenly *landing on the water* is a sure sign of a kill. Remember that birds will often follow a group in hope of a kill (useful for sighting groups of killers; especially far out at sea). Also look for blood, fur, feathers, etc. at the water surface. When feeding, animals may mill in one spot, surfacing irregularly. Look for rapid changes in speed and direction (although this could also be socializing). Record any kills, indicating the prey species if known, or harassment (e.g., chasing fur seals or penguins).

Socializing

Socializing killers are in physical contact with each other, chasing each other, rolling together etc. or do things which seem playful, e.g., breaching, lifting their flukes. Generally few animals in the group will be socializing at the same time.

Resting

Resting groups will mill in the same spot, often for hours, maintaining their surfacing order and swimming in a regular pattern, or they will meander slowly (slower and less directed than foraging/travelling). Some animals may socialize and calves will often suckle from their mothers. Groups seem to rest in the same spots. Generally the animals will suddenly move on when they finish resting, often disappearing unseen (to continue foraging, presumably).

Photographic identification

Photographic identification (photo-ID) is an extremely powerful tool in cetacean studies, and has been applied to most species. Good photo-ID data can be used for a large number of research objectives and building a long-term identikit of individuals is one of the main aims of our study at Marion Island. In recent years (2006 to present) we have started to build an identikit, and you will be expected to build on this. Individual killer whales can be identified based on pigmentation, shape and scar pattern of the dorsal fin and saddle patch, as well as shape of the eye patch and other features.

When you sight killer whales, make an effort to photograph the dorsal fin, and any other markings, of all animals in the group.

Photo-ID is difficult, and even more so in field conditions such as those on Marion Island. What's more, you are land-based. Just do your best!

- The dorsal fin should be photographed as parallel as possible. Photograph the animal when it is parallel to you, and get low to the water (i.e., if you are on a high cliff, move down if it is possible and you have the time). If you are at the Point, you can move down the rope to sea level if weather conditions permit – just be careful! In general, photograph all the animals as soon as you see them and then reposition yourself if they hang around.
- Follow the animal underwater through the viewfinder and let the camera focus in the area that it will surface. Take a sequence of photographs as the animal surfaces and dives (just remember that digital cameras have a memory "buffer" which means they can only take a few photographs in a row – for the Canon EOS350D this is up to ~3 photos per second). This allows us to choose the clearest photograph of the dorsal fin and saddle patch.
- Make an effort to photograph *all* animals in the group, irrespective of how distinctive they are or how close they are to you; some animals will not appear

distinctive and will be "shy" and difficult to photograph. It is important that there is no bias against such individuals.

- Try and photograph the left and right side of each individual.
- Try and photograph calves with their mothers or directly before or after their mothers. You can record such information using the camera by taking an "indicator frame". For instance, if you want to show that the previous two animals you photographed are related, or if the animal you just photographed was travelling apart from the group, you could take a photograph of your backpack, or your hand. Just be consistent and record this in your notebook. Another example: sometimes individuals pass by one by one – separate individuals by photos of your hand, for example. Or, you may only be able to get two photos of two killers passing by quickly (one photo of each whale). Record this so that we know you took one photo of each whale – it makes it easier to try and identify them later on.
- Don't stop shooting; take as many pictures as possible!
- When the animals have left, record the information in your notebook and take a photograph of it, so that your sightings can easily be separated when you sort the photographs (this also serves as a backup if you lose your notebook).

Camera settings

For details, refer to the Canon 350D's User Manual in the "Literature and Information" folder.

- The images should be recorded in RAW ("Setting the image-recording quality" p. 52)
- You can use the camera in Programme AE mode ("Program AE" pp. 80-81). If this fails, switch to Full Auto mode ("Using Full Auto" pp. 44-45)
- Use the largest aperture possible (4.5-5.6, depending on zoom). This can be seen in the viewfinder ("Viewfinder information" p. 15) and adjusted using the Main Dial ("Nomenclature" p. 12).
- Shutter speed ("Viewfinder information" p. 15) should be as fast as possible. As a rule of thumb for sharp photographs, it should not be lower than twice the lens focal length (e.g., around 500 on the 200 mm lens).

- If the shutter speed is too low, increase the ISO ("Setting the ISO speed" p. 55). Just remember to decrease it again if possible as the greater the ISO, the "grainier" and less-detailed the photograph. For general work, leave it at 200 or 400.

For more information regarding photo-ID, refer to reviews such as Mazzoil et al. (2004) Aquatic Mammals 30:209-219.

Saving data in the database

1. *Opportunistic sightings* must be recorded on the form "Killer Whale Observations". Complete the paper copy and electronic copy. If you need more space for notes on behaviour, etc. make a .txt or MS Word file.

Name it:
YYYY_MM_DD_BeachCode_SightingNumber (e.g., 2008_12_20_MM067_1)

The sighting number refers to sightings made at the same beach on the same day (e.g., different groups of killers).

Save it in "KillerWhaleObs" – "Notes" and link it to the electronic copy.

2. *Dedicated observations* (**even if you don't see any killer whales!**) must be recorded on the form "Dedicated Killer Whale Observations".

The hard copy is scanned and saved as a .jpg in "KillerWhaleObs" – "Dedicated Observations".

Name the file:
DedicatedKW_2010-2011_page (e.g., DedicatedKW_2010-2011_01)

3. Save *photographs* from each sighting in their own folder in the "Killerpics" folder.

Name the folder:

YYYY_MM_DD_BeachCode_SightingNumber (e.g., 2008_12_20_MM067_1)

The sighting number refers to sightings made at the same beach on the same day (e.g., different groups of killers).

You will not be required to catalogue images or identify individuals, but please look through your images to:

- see if you recognize any animals from the existing catalogue,
- familiarize yourself with the animals you are sighting and
- see if and how you can improve your identification photographs.

Remember to delete/format the Compact Flash card after you have downloaded the photographs (*double check* that you have downloaded them).

Downloaded photographs should be backed up regularly with the rest of the Marine Mammal Programme to make sure we have a copy of all photographs.