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

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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. We 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 we 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 40 600 MJ.day⁻¹. Based on available energy density and mass data, we 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 – 100 000s). Conversely, the smaller populations (100s – 1 000s) of Antarctic fur seals and southern elephant seals are sensitive to predation, particularly the latter as they have a high energy content (ca. 2 000 – 9 000 MJ). Populations of these seals are currently increasing or stable and we 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, we are better able to concentrate future efforts on plausible predation effects.

KEYWORDS

Orcinus orca; top-down control; predator-prey interactions; elephant seal; fur seal; penguin; apex predator

RUNNING HEAD

Impact of killer whales on pinnipeds and penguins

INTRODUCTION

Due to their size, mobility and energy requirements, large predators can have marked effects on ecosystems despite their relative rarity (e.g., Terborgh, 1990). However, 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). Investigations of the predatory role of killer whales (*Orcinus orca*) have thus 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 & 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 whale predation has been suggested as a major factor in the southern elephant seal (*Mirounga leonina*) declines at least at the Subantarctic Prince Edward Islands (PEIs) and Îles Crozet (Condy, van Aarde & Bester, 1978; Guinet, Jouventin & Weimerskirch, 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, de Bruyn & Bester, 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.

The Southern Ocean ecosystem has undergone large-scale changes brought about by top predator removals (Laws, 1977), commercial fishing (Ainley & Blight, 2009) and climate change (Weimerskirch *et al.*, 2003). To suggest that the PEIs marine ecosystem is pristine would be symptomatic of “shifting baseline syndrome” (Pauly, 1995). Nevertheless, to critically assess the role of killer whales in the PEIs marine ecosystem, a “model system” with broad relevance for the Subantarctic (Chown & Froneman, 2008), we quantified the potential predatory impact of killer whales on pinniped and penguin populations based on the theoretical energy requirements of killer whales. Our 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, we aim to assess whether top-down control of pinniped and penguin populations at the PEIs is broadly plausible currently, following an eliminatory approach. We 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 (296km²; 46°54'S, 37°45'E) and, approximately 19km to the north east, the smaller Prince Edward Island (45km²; 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 & Lutjeharms, 2005), sustaining the food web that supports the numerous mammal and bird species that breed there (Table 1). While penguins and seals forage tens to thousands of kilometres from the PEIs, we assumed throughout this study that the only predators they had were killer whales inshore at the PEIs.

Killer whale population size, structure and seasonal occurrence

From 2006 to 2009, 37 individuals were identified (19 adult females, 3 lactating adult females with calves, 7 adult males and 5 individuals of unknown age-sex class; Reisinger, de Bruyn & Bester, in review). Killer whales occurrence inshore at the PEIs peaks in April-May and September-December (Reisinger *et al.* in press). Killer whales were sighted on 80 days.year⁻¹ in 2006-2009 (MRI unpublished data).

Killer whale energy requirements

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

$$FMR = 19.65M_b^{0.756} \quad \text{Equation 1}$$

Where *FMR* is field metabolic rate in Watts and *M_b* is body mass in kilograms.

We 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.

$$M_b = 8.6791 L^{3.2769} \quad \text{Equation 2}$$

Where *L* is length in meters.

We used average lengths of 7.26m (males) and 6.42m (females), obtained from killer whales taken during Southern Hemisphere whaling operations (excluding "dwarf" individuals; Mikhalev *et al.*, 1981). The resulting energy requirements were adjusted upwards for an assumed assimilation efficiency (metabolisable energy) of 84.7% (Williams *et al.*, 2004), giving the energy killer whales would need to ingest to meet basic energetic demands. These energetic requirements are for adult killer whales and assumed no growth or reproductive costs. However, we 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.

Prey energy content

The energy density (energy content per mass) and average mass of prey consumed by killer whales at the PEIs was obtained from published and unpublished data – energy density was multiplied by the average mass of a prey type to give the prey type’s average energy content (Table 3).

Prey consumed

To calculate the number of seals and penguins consumed, we 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. (*cf.* Baird & Dill, 1996). Partial consumption of select portions of certain prey types (e.g., Pitman & 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. To predict the “worst case scenario” or maximum predatory impact for each prey type, we initially assumed that killer whales consumed each prey type exclusively (1). Based on these daily consumption rates we calculated the proportion of available prey (i.e., the percentage of the total prey population at the PEIs) consumed over time. We 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).

We 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 (*Arctocephalus gazella*) pups, Antarctic fur seals and elephant seal pups (see Results, Fig. 1). We 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), we 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

We calculated average masses of 5 750kg and 3 843kg for adult males and females, respectively (using Equation 2). Adult males and females were thus predicted (using Equation 1) to have field metabolic rates of 13 667W and 10 078W, respectively, requiring the ingestion of 1 394MJ.day⁻¹ and 1 028MJ.day⁻¹ (Table 2). 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 2), particularly those for free-ranging killer whales. Expanding these requirements to the entire known population (37 individuals), killer whales at the PEIs would need to ingest 40 600MJ.day⁻¹. Energy densities for PEIs prey were comparable to those estimated for similar prey in other studies (Table 3).

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. 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 Fig. 1a. Other prey types experience relatively little predation pressure nearshore around the PEIs. When each prey type is assumed to comprise an equal proportion of killer whale diet (11% each; Fig. 1b) predation 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 (Fig. 1c), each prey type experiences identical, low predation pressure. If diet is assumed to comprise prey proportions relative to their abundance (Fig. 1d), rockhopper (*Eudyptes chrysocome*) and macaroni penguins (*E. chrysolophus*) 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 (Fig. 1e), elephant seal pups experience relatively high predation pressure due to their small population size and high energy content and elephant seal adults and Antarctic fur seal pups experience moderate predation pressure.

The results of varying prey population size on predation mortality (Fig. 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 (Fig. 2a), for Antarctic fur seal pups below 500 pups (Fig. 2b), and for Antarctic fur seals below 1 000 individuals (Fig. 2c).

Due to their high energy content (Table 3) and small population size (Fig. 2a) elephant seal pups are likely most sensitive to killer whale predation. We therefore present the potential impact of killer whale predation on elephant seal pups on a small temporal scale (Fig. 3), given their short availability as prey. Assuming that killer whales meet their energy needs by preying exclusively on elephant seal pups, Fig. 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 - 2 months after weaning, the predation levels required to produce the observed 40% first year mortality would be 50% - 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 predating 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. Fig. 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.

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 (Fig. 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 (*A. tropicalis*) 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 (*Aptenodytes patagonicus*) at the Îles Crozet have survival rates of 90% (Saraux *et al.* 2011), and could thus support killer whales for 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 the occurrence, behaviour and growth rate (or its potential) of these prey taken into account, this indicates that prey mortality rates cannot escalate enough to cause population declines. However, various factors will affect diet composition. 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 (*Phoca vitulina*), harbour porpoises (*Phocoena phocoena*) and Steller sea lions (*Eumetopias jubatus*) 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 Fig. 1a assume that killer whales prey exclusively on a certain prey type – an assumption we know to be incorrect from observations at the PEIs and studies elsewhere (e.g, Condry *et al.*, 1978; Guinet, 1992, Ford *et al.*, 1998). 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 Fig. 1 (b-e). The dietary composition of killer whales at the PEIs is unknown, but Reisinger *et al.* (in press) report killer whales preying on Subantarctic fur seals, elephant seals, king penguins and macaroni penguins.

Predatory impact

Despite the apparent magnitude of the predation rates (Fig. 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).

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 we logically assume that *currently* killer whale predation pressure is not sufficient to cause declines in prey populations, although Fig. 1 certainly demonstrates the potential to do so for some species, and continued long-term monitoring of predator and prey populations is required.

When considering the effects of prey population size changes on predation mortality (Fig. 2a-c), 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 would, however, depend on the total response (numerical and functional response [Solomon, 1949]) of killer whales to changes in prey density. We have assumed no total response in Fig. 2 but

killer whales are unlikely to show strong numerical responses to changes in prey abundance although functional responses have been suggested (Barrett-Lennard *et al.*, 1995). It is 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]).

Fig. 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 4 additional elephant seal pups daily, first year mortality in elephant seals could realistically double (Fig. 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 & 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 not causing population declines, however, predation mortality certainly 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 much stronger adverse population effects (*cf.* Cooper & 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; Reisinger *et al.*, in review), and; fur seal abundance must continue to be monitored and demographic studies should be initiated. Moreover, data describing any changes in seal and penguin diets, as well as the risks these animals take to acquire food, are necessary. Given the paucity of data concerning killer whale diet and predation at the PEIs, we have taken an

extremely simple approach to assessing their predatory impact. Despite this, we 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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TABLES

Table 1. Population sizes of seals and penguins at the Prince Edward Islands.

Species	Pup production	Total population	Breeding pairs	Reference
Subantarctic fur seal	>30 000	150 000	-	^{a, b}
Antarctic fur seal	>1 500	5 800	-	^{a, b}
Southern elephant seal	>560	>2100	-	^{c, d}
King penguin	-	-	67 000	^e
Gentoo penguin	-	-	>1 100	^e
Macaroni penguin	-	-	302 000	^e
Rockhopper penguin	-	-	80 000	^e

^aHofmeyr *et al.*, 2006; ^bBester, Ryan & Visagie, 2009; ^cBester & Hofmeyr, 2005; ^dRyan & Bester, 2008; ^eCrawford *et al.*, 2009.

Table 2

Energy requirements of different age-sex classes of killer whales estimated by various studies (including this study).

Study	Age-sex class ^a	Mass (kg)	Energy requirement		AE ^b (%)	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 ^c	-	-	-	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 <i>et al.</i> , 1995	-	-	-	-	-	921.10	-	25% upward adjustment of Kriete's (1995) estimates applied to free-ranging mammal-eaters
Williams <i>et al.</i> , 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 <i>et al.</i> 's (2004) allometric regression
	AF	3 843	870.76	0.23	84.70	1 028.05	0.27	

^aAM – adult male, AF – adult female, SA – subadult, C – calf; ^bAssimilation efficiency; ^cMass accounts for the additional energetic requirements of the lactating mother.

Table 3

Energy density, average mass and energy content of killer whales' pinniped and penguin prey occurring at the Prince Edward Islands, with other prey included for comparison.

Prey type	Energy density (MJ.kg ⁻¹)	Average mass (kg)	Energy content (MJ)	Notes
<i>Seals</i>				
Antarctic fur seal pup	8.24 ^a	11.24 ^b	92.66	
Antarctic fur seal adult female	10.59 ^a	30.6 ^b	324.05	
Subantarctic fur seal pup	-	12.70 ^b	104.62	Assuming Antarctic fur seal pup energy density
Subantarctic fur seal adult female	-	36.5 ^b	386.54	Assuming Antarctic fur seal adult female energy density
Elephant seal pup	20.2 ^c	116.46 ^b	2 352.54	
Elephant seal		437 ^d	8 827.40	Assuming elephant seal pup energy density. Average mass of adult females and subadult males
<i>Penguins</i>				
King penguin adult	11.16 ^e	14.3 ^f	159.59	Average of pre-moult and pre-breeding energy density; mass of incubating males from Crozet
Macaroni penguin adult	9.6 ^c	5.36 ^g	51.46	
Rockhopper penguin adult	-	3.14 ^g	30.14	Assuming macaroni penguin energy density
<i>For comparison</i>				
Sea otter adult	7.58 ^h	-	-	
Steller's sea lion pup	10.97 ^h	-	-	
Northern fur seal	10.47 ⁱ	-	-	
Ringed seal	14.86 ^j	-	-	
Harbour seal pup	17.05 ^k	-	-	
Harbour seal adult female	12.94 ^k	-	-	
Gentoo penguin	10.0 ^c	-	-	

^aArnould, Boyd & Speakman, 1996; ^bMRI unpublished data; ^cForcada *et al.*, 2009; ^dde Bruyn *et al.*, 2009b;

^eCherel, Charrassin & Handrich, 1993; ^fHalsey *et al.*, 2008; ^gCrawford *et al.*, 2006; ^hWilliams *et al.*, 2004;

ⁱStansby, 1976; ^jStirling & McEwan, 1975; ^kBowen *et al.*, 1992.

Table 4

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.

Prey type	Adult males	Adult females	Unknown	Calves	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

FIGURES

Fig. 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.

Fig. 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).

Fig. 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.