

AN ECOSYSTEM STUDY OF THE PRINCE EDWARD ARCHIPELAGO

(SOUTHERN OCEAN)

by

LEIGH JOSEPHINE GURNEY

BSc, University of Cape Town, 1994
BSc, Honours Rhodes University, 1995
MSc, Rhodes University, 2000

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Abstract

This study brings together the wealth of data available for the Prince Edward Islands marine ecosystem and consolidates it into a network, mass-balanced model (using Ecopath). Biomass estimates for the land based top predators show penguins dominate the system for all three time periods assessed (1960s, 1980s and 2000s). The islands appear to have a carrying capacity which may be declining. A consumption model shows a change in prey for the land based top predators from one in which both crustaceans and myctophid fish were of equal importance in the 1960s, to one dominated by myctophids for the 2000s period. The contribution of the sources of primary production were assessed through the ecosystem model with open ocean productivity dominating at all but the smallest scale (shelf region), where the macrophyte production was important. The model describes the marine ecosystem for each of the above mentioned time periods at the scale of the Exclusive Economic Zone and, when compared to other subantarctic and Antarctic systems for which there are ecosystem models, the system was most similar to the neighbouring Kerguelen Islands. An investigation into the ecosystem boundary size was conducted, with all constituents able to satisfy their energetic requirements if considered at the scale of the EEZ. Using the dynamic temporal simulation approach (Ecosim), the model was able to successfully hindcast three past events: the fur seal exploitation, Patagonian toothfish fishery, and the effect of cat predation on small flying birds. In each instance the model performed well for the directly impacted groups. Potential ecosystem effects of climate change were explored through simulations of increasing and decreasing productivity. No single scenario was able to replicate observed patterns and a suite of drivers needs to be considered to reproduce observed patterns. The inclusion of energetic density of prey led to improvements in consumption rate estimates for the static models and should be incorporated into estimates to improve ecosystem model parameterization. The work constitutes the first ecosystem model for the PEIs that can be used as a tool for an ecosystem approach to marine resource management.

Preface

This work brings together two parts of my earlier professional development by linking field and research experience with the South African National Antarctic Programme, (1995 – 2000) with experience gained through my work at the Tasmanian Aquaculture and Fisheries Institute (2001 – 2004) and combining them in the construction of an ecosystem model, developed at the UBC Fisheries Centre. I was responsible for identifying and developing the research idea in consultation with my supervisor, Dr E. A. Pakhomov. Guidance through the program was provided by my supervisory committee. The work itself was completed solely by me, with advice and guidance in analysis and interpretation provided by my committee members in accordance with their area of expertise. Chapter 4 of this dissertation has been published as L.J. Gurney, E.P. Pakhomov and B.P.V. Hunt, (2011). Life-support system of the Prince Edward Archipelago: overview of local and advected resources. In: First symposium on The Kerguelen Plateau: Marine Ecosystem and Fisheries (Duhamel G. and Welsford D., eds), pp. 217-232. Paris: SFI. Initial formulation of the links in the food web were discussed by all three authors. The work itself was completed and written by me, with reviewing and editing contributions by the two co-authors. No other sections of the thesis have yet been published, though 4 sections have been presented at conferences (Chapter 5, Fisheries and Marine Ecosystems, Canada, 2006; Chapter 6, SCAR Symposium Russia, 2008; Chapter 7 Advances in Marine Ecosystem Modelling Symposium (AMEMR), Plymouth 2011; and Chapter 8, SCAR Symposium 2010, Argentina).

This work comprises a series of chapters tackling different aspects of the Prince Edward Islands marine ecosystem. The work did not follow a linear progression and in compiling the thesis, the structure has a number of sections which need to be clearly outlined.

Chapter 1 includes an introduction to the ecosystem approach to marine resources and ecosystem modelling which is followed by an overview of the study area: the Prince Edward Islands (PEIs) (Southern Ocean). Chapter 2 presents a full review of the PEI marine ecosystem and quantifies the system in terms of biomass estimates, for three time periods for which there are data (1960s, 1980s, 2000s), and illustrates the long term trends of seals and seabirds. In Chapter 3, the

biomass estimates from Chapter 2 are used in combination with local dietary data and a consumption model assesses the changes in consumption of broad prey categories for the land based top predators over the same three time periods (1960s, 1980s and 2000s). In Chapters 2 and 3, part of the data compilation that was necessary to construct the ecosystem models for the marine component of the PEIs was prepared, and forms the basis of the data behind all subsequent chapters.

The following three chapters (4,5 and 6) are static mass balanced models of the marine PEI ecosystem used to address different ecological questions. Chapter 4 is an assessment of the local and advected resources at the PEIs and was done in preparation for a workshop which was held in France in 2010, and subsequently published in the proceedings of the workshop. The model is unique, in that it was a simplified (collapsed) early version of the full model (has 21 functional groups), representing only one time period (1980s) and was focused on the primary producers at the islands. Data input for this model were slightly different from that used in all subsequent chapters. Although there is overlap with other sections of this thesis, the manuscript has been submitted here unaltered in text. The figures and tables have, however, been renumbered to fit in with the full document's structure.

The updated version of the PEI ecosystem model at the scale of the Exclusive Economic Zone (EEZ) includes a higher resolution of the model in terms of functional groups (37) as well as improvements in model parameterization across 3 time periods (1960s, 1980s and 2000s). This model is described in Chapter 5, and used in Chapter 6 to address the question of ecosystem boundary size of the land-based top predators based at the islands by investigating the spatial extent of these groups in the system through the resolution of their energetic requirements.

An improvement to the parameterization of the final model version involved important changes to the consumption estimates, and this work is presented as a standalone chapter, Chapter 7. The work focused on incorporating local energetic values of the prey when estimating consumption and helped to resolve model balancing issues that had proved challenging.

The ability to explore management options is often the goal of developing an ecosystem model. Before exploring future policy scenarios, it is useful to test if the model is capable of hind-

casting, with any degree of success, past known events for which there are data. It can also provide a useful tool for exploring future potential scenarios when developing risk assessments, associated management options and optimizing outcomes according to policy aims and objectives. With this in mind, Chapter 8 illustrates the models capability of hindcasting three known events (culling of fur seals, the Patagonian toothfish fishery and a demonstration of the deleterious effect of the cat infestation on the local small bird population). Chapter 9 demonstrates scenario testing of future potential climate change events at the islands.

A short summary of conclusions are presented in Chapter 10 to complete the work.

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Dedication

For Dorothy Anne Harris Gurney (nee Storie)

‘When one tugs at a single thing in nature, he finds it attached to the rest of the world’

- John Muir, Naturalist

(1838 – 1914)

Chapter 1 Introduction

1.1 Ecosystem approach to management of marine resources

Following the collapse of many fish stocks the world over, due at least partly to failure of traditional fisheries science management strategies to sustainably manage fisheries, a worldwide resolution to adopt a more holistic approach to management of marine resources has been made. Management strategies are turning to ecosystem studies to move from single species assessment models, to multi-species and ultimately to ecosystem based management. This approach comes with the recognition that resource management of marine ecosystems should incorporate a broader scope of variables and drivers including environmental, biological and socio-economic factors.

International meetings and conventions have played a role in highlighting the need for an ecosystem approach to marine resource management. These include: the 1972 Stockholm Conference on the Human Environment; the 1992 Conference on Environment and Development; the 1992 Convention on Biological Diversity; the 1995 Kyoto Declaration on Sustainable Contribution of Fisheries to Food Security; the 2001 Reykjavík Declaration; and the 2002 World Summit on Sustainable Development (Garcia et al. 2003; Shin and Shannon 2010). Policy has been changing globally with this new perspective and a push to include ecosystem considerations is being incorporated into operating procedures. This has created a need for the development of models that can be used for such an ecosystem approach, which currently range from individual based models through to ecosystem models (see overview in the following section, 1.2).

Ecosystem models for use in management are still in their early developmental phase but many management policies now require that ecosystem based models are used in assessing marine resources to address management options alongside traditional single stock assessments (Christensen and Walters 2011). Such models also provide the ability to test ‘what if’ scenarios, which can be useful in exploring ecosystem responses to change. Ecosystem models are time consuming to construct but provide a useful tool for managers to optimize for fisheries and/ or

societal benefits and/ or conservation objectives, while taking into consideration the ecosystem as a whole and not solely the targeted species. It was with this in mind that this ecosystem study was initiated for the Prince Edward Islands (PEIs). The main objective was therefore to create a model of the PEIs that can be used as a tool to explore a number of theoretical and applied ecological issues.

The PEIs are an archipelago situated in the southeast sector of the Southern Ocean and, like other Sub-Antarctic equivalents, are host to millions of seabirds (including penguins) and seals, which use the islands as a breeding ground and a refuge while moulting. Historically, seals were harvested at the islands and there is an on-going fishery for Patagonian toothfish (*Dissostichus eleginoides*). The islands host approximately 13% of the worldwide population of King penguins (*Aptenodytes patagonicus*) with the remaining three species of penguins making relatively small contributions to the world populations (Macaroni (*Eudyptes chrysolophus*) 4%, Southern Rockhopper (*Eudyptes chrysocome*) 5% (but 17% of the *filholi* race), and Gentoo (*Pygoscelis papua*) 0.5%) (Crawford and Cooper 2003; Ryan and Bester 2008). In terms of the conservation status, according to Birdlife International, the Gentoo penguin is classified as ‘Near Threatened’, both the Macaroni’s and Southern Rockhopper’s as ‘Vulnerable’, while the Kings are ‘Least Concern’ (IUCN Red List for birds (Downloaded from <http://www.birdlife.org> on 27/09/2011)). The islands therefore have both fisheries and conservation concerns. They fall under South African jurisdiction and are within the Conservation of Antarctic Marine Living Resources (CAMLRL) Convention Area (Areas 58.7, 58.6 and 58.4.4) (CCAMLR 2011). The Commission of the CAMLR has mandated that the PEIs must be managed using an ecosystem approach. Prior to this work no ecosystem model has existed for the archipelago.

1.2. Ecosystem models

The primary role of models in ecosystem science is to permit controlled exploration of a complex reality. Models in marine ecology have been developed for individuals through to ecosystems (Hollowed et al. 2000). A review of 20 models used to assess ecosystem approaches to fisheries by Plaganyi (2007) provided the framework for this assessment of modelling tools currently available. Individual based models (IBMs) track the fate of individuals through their life span with the assumption that the behaviour of an individual represents the population as a

whole. These models are usually single species but may be multi-species or represent an ecosystem, as for example OSMOSE (Shin et al. 2004). Dynamic multi-species models or Minimally Realistic Models (MRM) are restricted to those species most likely to have important interactions with the species of primary interest and are usually system specific, for example the original MRM (Punt and Butterworth 1995), ESAM (Extended Single-species Assessment Models (Hollowed et al. 2000)), MSVPA (Multi-Species Virtual Population Analysis), MULTSPEC (Tjelmeland and Bogstad 1998), BORMICON (Bjoernsson et al. 1998), SEASTAR (Tjelmeland and Lindstrøm 2005), GADGET (Taylor and Stefansson 2004), CCAMLR predator-prey models (e.g., Mori and Butterworth 2006), and Multi-species Statistical Models (Plaganyi 2007). Bioenergetic models, which are based on bioenergetics and allometric equations, have also been used. Examples include those of Yodzis and colleagues (Yodzis and Innes 1992; Yodzis 1998; Koen-Alonso and Yodzis 2005). Finally, whole ecosystem models, which take into consideration all trophic levels in a system, include Atlantis (Fulton et al. 2004a; Fulton et al. 2005) and the Ecopath with Ecosim (EwE) software (Christensen et al. 2008). The intention of this study was to create a whole ecosystem model, and therefore the discussion which follows focuses on these two models.

The Atlantis model was created through a series of amalgamations and developments from earlier models. The European Regional Seas Ecosystem Model (ERSEM) (Baretta et al. 1995) is a generic model, which focused on the lower trophic levels (plankton and regeneration cycle) and could be coupled to a physical model (e.g., Allen et al. 1998; Blackford et al. 2004; Sole et al. 2006; Siddorn et al. 2007). An updated version of this model (ERSEM II) was combined with the Port Phillip Bay integrated model (PPBIM) of Murray and Parslow (1999) to create the Integrated Generic Bay Ecosystem Model (IGBEM) (Fulton et al. 2004a). This model was later combined with Bay Model 2 (Fulton et al. 2004a) to create Atlantis (Fulton et al. 2005).

The EwE software developed from an ecosystem model (the original Ecopath) initially created by Polovina (1984). Christensen and Pauly (1991) developed this into a mass balanced ecosystem model (Ecopath II) which later incorporated developments from the independently developed ecosystem model (also based on Polovina 1984) called NETWRK by R.E. Ulanowicz (Ulanowicz 1986). Subsequent developments of the model include a temporal component

capable of simulations (Ecosim) (Walters et al. 1997) and a spatial component (Ecospace) (Walters et al. 1999), which enables exploration of changes in habitat. The model has been recognized as an important tool and was nominated by NOAA as one of the top ten scientific breakthroughs in their 200 year history (see <http://celebrating200years.noaa.gov/breakthroughs/ecopath/>).

The EwE model is rooted in ecosystem theory and has a user friendly Windows-based interface that enables a user with limited mathematical and programming skills to construct a useful model of an ecosystem (Shannon et al. 2004). This ease of access has been criticised because it can result in misuse (or insufficient depth of use) of the program (Plaganyi 2007). Other cautions regarding the use of EwE are that the default settings should not be used without careful consideration and alternative functional relationships should be considered (Plaganyi 2007) as these can produce markedly different model outputs (Koen-Alonso and Yodzis 2005). Ongoing software development for this model has allowed it to be the fore-runner in its field. EwE is the most widely used ecosystem model and capable of addressing the widest range of topical ecosystem approaches to fisheries research questions (Plaganyi 2007).

EwE and Atlantis both have the capacity to represent all trophic levels and are appropriate for addressing broad ecological questions. Both have the capability of including age structured functional groups and spatially resolved data, important considerations in models (Fulton et al. 2004b). Atlantis has a modular structure, which allows substitution of sub-models, a development now incorporated into EwE version 6 (Christensen et al. 2008), and one which will help with the transparency of the model and accessibility of the coding to allow for additional modules to be written and customised for particular ecosystems. For a summary of the strengths and weaknesses of each of these models, please refer to Plaganyi (2007).

Models of food webs aim to represent the links between predators and prey in an ecological community and as such are complex networks (Quince et al. 2005b). Important considerations in modelling include understanding the extent to which the model structure (Fulton and Smith 2004; Plaganyi 2007) and underlying model assumptions predetermine or have implications for the results obtained (Plaganyi and Butterworth 2004). This means that the models themselves need to be closely scrutinized to understand the extent to which these factors influence the model

outputs. The model structure (and even its development history) can have significant implications for the potential range of dynamics displayed (Fulton and Smith 2004; Plaganyi 2007). Important considerations for the development of ecosystem models include the effect of specific formulations on model outputs. Plaganyi (2007) gives three examples of this: feeding functional responses (Fulton et al. 2003b); predator-prey relationships (Yodzis 1994); and the structuring of competition (Rice 2000). The treatment of uncertainty and the feasible representation of biodiversity also need to be considered (Plaganyi 2007). There is current agreement that ideally more than one model should be used and outputs from different models should be compared (Shannon et al. 2004; Koen-Alonso 2005; Field et al. 2006; FAO 2008). For instance, in Aydin et al. (2005) three independent modelling assessment models (a NPZD model, Ecopath with Ecosim model and a bioenergetics model) were all used to investigate Pacific salmon in the Alaskan subarctic gyre ecosystem. It is important for models used to incorporate ‘top down’ as well as ‘bottom up’ forces in marine ecosystems (Reid et al. 2000; Aydin et al. 2005; Field et al. 2006; Christensen and Walters 2011).

Another issue that is important in developing a model is to determine the model complexity (Raick et al. 2006). From a practical standpoint it is not necessary to consider all the species to be found in a community as not all are equally important in determining the nature of the whole community. The major part of the energy flow involves a comparatively small number of species and we can learn much about communities and populations by concentrating on dominant populations in the major trophic levels (Odum and Odum 1959). Two issues arise when addressing the question of determining the nature of the community as a whole. The first is that with increasing model complexity (to represent biological realism) there is an associated increase in uncertainty and in scientific imprecision in estimates of the associated parameter values (Blackford et al. 2007; Plaganyi 2007). Secondly, it has been found that it is not necessary to include all of reality in terms of linkages as only a relatively small number of variables is often sufficient for effective models because “key factors” or “integrative factors” often govern or control a system (Odum 1971; Quince et al. 2005b). The conclusion, for model complexity, is that important groups should be focused on, and groups should only be added when there is good reason to look at those particular aspects in more detail. Those that only add noise to the system should be omitted (Shannon et al. 2004). Adding complexity for completeness does not

contribute anything if the resulting model is of poor quality and model comparisons have shown that intermediate model complexity results in optimal performance (Fulton et al. 2003a).

Typically there is a trade-off between the range in trophic levels considered and the corresponding detail with which each group is represented. Determination of which functional groups should be included in a model needs to be carefully assessed. Two suggested guidelines for aggregation of groups include guarding against aggregation of serially linked groups or combining groups (or age classes) that have rate constants that differ by 2 to 3 fold (Fulton et al. 2003a). Transgressions of these two suggested guidelines have been shown to decrease model performance (Fulton et al. 2003a). A suggestion of exclusion of feeding links that represent less than 10% of consumption, both by and of any species, has been shown to have minimal affect on model predictions, and this can amount to up to 44% of the links being removed as demonstrated by Yodzis (1998). Above this threshold for linkage strength the model predictions start to become unreliable. In a study on weak linkages by Pinnegar et al. (2005), it was found that, following a perturbation, models in which 'weak links' were aggregated into other groups created a more stable model output than models in which weak links were removed from the model completely. Implications of this suggest that considerations on whether weak links are removed by 'lumping' or 'chopping' may have very different system consequences (Pinnegar et al. 2005). An assessment of reducing model complexity through simplifying by aggregation found that even the simplest NPZD (nutrient, phytoplankton, zooplankton, detritus) models were able to recreate the global ecosystem features, however a greater degree of sophistication was required to simulate the various realistic behaviours (Raick et al. 2006). The findings of this study showed that a 9-compartment model that reduces functional groups but includes the bacterial loop and unbalanced algal growth performed best with respect to producing realistic behaviours (e.g., the phytoplankton competition, the potential carbon or nitrogen limitation of the zooplankton ingestion, the model trophic closure, etc.) (Raick et al. 2006).

The decision to use the EwE software to develop the first quantitative, network based ecosystem model of the Prince Edward Islands was based on a number of considerations, which were assessed at the start of the project: 1. The lack of a physical oceanographic model of the region meant that the capabilities of this component of the Atlantis model would be absent; 2. The lack

of accessibility to the Atlantis model code and absence of available documentation (pers comm. with B. Fulton); 3. The accessibility of the EwE software and supporting documentation (free download from www.ecopath.org) and training (graduate course followed at UBC); 4. The ease of access to the EwE software creators and developers, being based on UBC campus and; 5. The time required to develop an Atlantis model exceeds what was available for this study. A brief synopsis of the islands is provided below (Section 1.3), including information on background, history, geography, geology and oceanography. This is followed by a summary of the data collection for the marine ecosystem available for the construction of the model for which the guidelines outlined above were taken into consideration.

1.3. The Prince Edward Archipelago

1.3.1. Background and history

The Prince Edward Islands (PEIs) are a sub-Antarctic archipelago situated in the south-western Indian Ocean and are South African territory. Together with Crozet (France), Kerguelen (France), MacDonal (Australia) and Heard (Australia), these islands form the South Indian Ocean Province, one of three provinces of the Sub-Antarctic region (Hänel and Chown 1998). These islands, along with South Georgia (UK), Auckland (NZ), Campbell (NZ) and Macquarie (Australia), are all sub-Antarctic ecosystems (see Figure 1.1). The PEIs are found in a High Nutrient Low Chlorophyll zone (HNLC), and like other sub-Antarctic islands, are ‘hotspots’ with higher biological productivity in the vicinity of the islands than in the surrounding water. The islands are also host to millions of birds and seals, which use the islands as a refuge and breeding ground.

The Prince Edward archipelago consists of two islands: Marion (46° 54' S; 37° 45' E) and Prince Edward (46° 38' S; 37° 57' E) (Figure 1.1). Found approximately 1800 km southeast of Port Elizabeth (South Africa), 2300 km north of Lützow-Holm Bay (the closest point on the Antarctic continent) and 950 km west of the French Crozet Islands (Hänel and Chown 1998), the islands are remote. They were first sighted in 1663 by the Dutch East Indiaman, the Maerseveen, under the command of Barent Barentszoon Ham. No landing was made, but the names Maerseveen (Marion) and Dina (Dena/Denia) (Prince Edward) were given to each of the islands. Over a

hundred years later the French naval officer MM Marion du Fresne of the Frigate Le Mascarin passed the islands in 1772 and called them Isle of Hope (Marion) and Isle of Cavern (PE), but renamed them the Frigid Islands on leaving (Hänel and Chown 1998). In 1776 Captain James Cook renamed the islands again, calling both islands the Prince Edward Islands. Marion was later renamed in honour of the French naval officer from the earlier voyage. Initially, the islands were used as a stop off point for whaling ships en route to the Antarctic. In the 1800s sealing (for both elephant and fur seals) began at the islands. The last known visit by sealers was in the 1930s. The islands were annexed by South Africa in 1947/48 and a meteorological station was established. In the 1960s the station was expanded to include scientific research, which continues today. Terrestrial and marine research has been ongoing at the islands for over 50 years, with a resultant rich published literature (Hänel and Chown 1998).

1.3.2. Geology and geography

The two islands are the twin peaks of a coalescing shield volcano and are estimated to be less than 1 million years old (the oldest recorded lava on Marion is estimated to be 450 000 years old but most flows date between 15000 and 400 years) (Hänel and Chown 1998). The volcano is still active with the most recent eruptions recorded in 1980 (Verwoerd et al. 1981) and 2004 (pers. obs. by D.W. Hedding in Sumner et al. 2004). Glacial history is evident on Marion, with at least five glaciations having occurred during the Quaternary, along with evidence of a glacial event during the Late Pleistocene (Hänel and Chown 1998). Almost all of Marion Island was covered by ice at the last glacial maximum.

Marion is the larger of the two islands, 293 km² in size, with approximately 70 km of coastline (Beckley and Branch 1992). The highest peak on Marion is Mascarin, at a height of 1231 m. In the 1950s and 1960s this peak was covered in an 'ice plateau', which used to extend down to 1000 m, but now no longer exists due to rapid melting (Sumner et al. 2004). Prince Edward Island is smaller at 46 km², and its highest peak, Van Zinderen Bakker, is considerably lower at 672 m (Hänel and Chown 1998).

The terrain on the islands is wet and marshy, with many lakes and ponds. Slopes are generally fern-covered while hillsides and peaks of lava have no vegetation. The coastline is mostly cliff-

faced. Of the coves on Marion Island, most are boulder, rocky or pebble beaches, with only two categorized as sandy (Ship's Cove and a small beach at Goodhope Bay) (Hänel and Chown 1998). Prince Edward island has a more rugged coastline and fewer beaches (Hänel and Chown 1998).

1.3.3. Marine research

1.3.3.1. Oceanography

The PEIs lie east of the Southwest Indian ridge and southwest of the shallow Del Cano Rise, directly in the path of the Antarctic Circumpolar Current (ACC) (Deacon 1983; Lutjeharms 1985). Rising up from a depth of 3000m, Marion and PE are approximately 20km apart and separated by an inter-island shelf which varies between 45 and 260m depth (Pakhomov and Chown 2003). The islands fall in the Antarctic Polar Frontal Zone (APFZ) of the ACC between the Sub-Antarctic Front (SAF) in the north and the Antarctic Polar Front (APF) in the south. The SAF has been found between 45°15' S and 47°25' S (a range of 241 km) and has an average temperature of 7.0°C while the APF has been found between 49°39' S and 50°47' S (a range of 126 km) with an average temperature of 3.4°C (Lutjeharms and Valentine 1984). These fronts are also important biogeographic boundaries (Deacon 1983). Both fronts are consistent and well-defined oceanic thermal fronts (Deacon 1983; Lutjeharms 1985; Nowlin and Klinck 1986), however their position has been shown to be dynamic and variable (Lutjeharms and Valentine 1984; Duncombe Rae 1989a; Lutjeharms et al. 2002). The hydrodynamics in the vicinity of the islands are affected by the proximity of the SAF to the islands (Pakhomov et al. 2000a; Perissinotto et al. 2000; Ansorge and Lutjeharms 2002). Although the SAF is generally found to the north of the islands it has also been found south of the islands (Lutjeharms 1990), and on one occasion the SAF was found split into two branches, one passing north of the islands and the other to the south (Ansorge and Lutjeharms 2002). It is thought that when the SAF is close to the islands, increased current velocities associated with this front leads to a flow-through system between the islands (Pakhomov and Froneman 1999b; Ansorge and Lutjeharms 2000; Pakhomov et al. 2000a). When the SAF is further north the lower velocities of the inter-frontal zone result in water retention over the inter-island shelf and as a consequence little exchange of inshore/offshore waters over the inter island region occurs (Perissinotto and Duncombe Rae

1990). A number of other mechanisms for on shelf water retention have been postulated, including upwelling (Grindley et al. 1985), eddy formation (Allanson et al. 1985) and Taylor column formation (Perissinotto and Duncombe Rae 1990). Under conditions of water retention on the shelf, whatever the mechanism, phytoplankton blooms have been observed to occur between the islands (Allanson et al. 1985; Duncombe Rae 1989a; Perissinotto and Duncombe Rae 1990).

The oceanography in the area is complex because of the combination of the frontal features, the bathymetry and the interaction with the islands themselves (Ansorge and Lutjeharms 2002; Ansorge and Lutjeharms 2003; Ansorge and Lutjeharms 2005). Oceanographic surveys downstream of the islands have shown north-south meanders in the predominantly easterly flow which are thought to be the result of a wake downstream of the islands (Perissinotto et al. 2000). Both warm and cold-core mesoscale eddies have been observed upstream and downstream of the islands (Ansorge and Lutjeharms 2002; Ansorge and Lutjeharms 2003; Ansorge et al. 2004).

Water in the vicinity of the islands is generally Sub-Antarctic Surface Water (Deacon 1983) but both Subtropical and Antarctic Surface waters have been observed (Miller et al. 1984; Perissinotto et al. 2000). Nutrient levels in the Sub-Antarctic are relatively high and augmented in the vicinity of the islands by fresh water run-off that carries nutrients from guano and the feathers of moulting oceanic birds (Ismail 1990; Perissinotto and Duncombe Rae 1990). The concentrations of nutrients reported during different studies vary considerably but all lie within the range expected for Sub-Antarctic waters (Miller et al. 1984; Allanson et al. 1985; Ismail 1990; Perissinotto and Duncombe Rae 1990; Thomalla et al. 2011). Nitrogen, in both ammonia and urea forms, shows a concentration gradient spreading outwards and downstream from the islands to approximately 80 km off shore (Perissinotto et al. 2000).

1.3.3.2. Biology

Following annexation of the islands in 1947/48, a research station was established. Biological observations date back to the early 1950s and 1960s for many of the seal and seabird populations (Rand 1962; Van Zinderen Bakker Sr et al. 1971) with descriptions of the breeding populations of the land-based top predators described for the first time. In the 1970s oceanographic studies

on the pelagic system began (El-Sayed 1976) and resulted in the first comprehensive study of the phytoplankton and zooplankton of the area (El-Sayed et al. 1979a; El-Sayed et al. 1979b; Grindley and Lane 1979). These studies were followed by work done from the 1980s through to the early 2000s describing the community structure and variations in abundance related to oceanographic features in the vicinity of the islands (Miller et al. 1985; Boden and Parker 1986; Perissinotto 1989; Perissinotto and Boden 1989; Perissinotto and McQuaid 1992b; Hunt et al. 2001; Hunt et al. 2002; Bernard and Froneman 2003; Hunt and Pakhomov 2003; Hunt et al. 2008). It has been found that the islands do not have an endemic zooplankton community but species of subtropical, sub-Antarctic and Antarctic origin are all found (Pakhomov and Froneman 1999b; Pakhomov et al. 2000a; Pakhomov and Froneman 2000; Hunt et al. 2002) and the abundance and distribution of zooplankton groups varies on both temporal and spatial scales (Hunt et al. 2001; Hunt et al. 2002). Studies focused on particular zooplankton groups were also conducted through the late 1990s and early 2000s, including work on euphausiids (Gurney et al. 2001; Gurney et al. 2002; Bernard and Froneman 2006; Bernard et al. 2007), pteropods (Bernard 2006) and amphipods (Froneman et al. 2000b).

The benthic community was comprehensively studied in the 1980s using both dredging and diving surveys that produced a comprehensive list of species present and a review of the ecology of the community (Blankley 1984; Blankley and Branch 1984; Blankley and Branch 1985; Blankley and Grindley 1985; Arnaud and Branch 1991; Branch et al. 1991a; Branch et al. 1991b; Beckley and Branch 1992; Branch and Williams 1993; Branch 1994). The benthic community comprises approximately 550 species with seven benthic community groups. The benthic decapod *Nauticaris marionis* (Bate 1888), an endemic species, has the second highest crustacean biomass of the benthic community. It is believed that this species provides a link between the benthic production and the near-shore pelagic predators of the islands, and numerous studies have focused on this decapod because of its perceived key role in the ecosystem (Perissinotto and McQuaid 1990; Kuun et al. 1999; Pakhomov et al. 1999; Pakhomov et al. 2000c; Pakhomov et al. 2004).

Scientific sampling of marine fishes around the PEIs dates back to 1873 when the Challenger expedition visited the region and collected three species as new to science (Gunther 1880, in Gon

and Klages 1988). Almost 100 years passed before any further additions were made. Andriashev (1971) identified the few fish specimens brought back from the South African expedition in 1965/66 resulting in two new distributional records (Gon and Klages 1988). French scientists added to the species list considerably in 1976 when several trawls were made with the RV Marion-Dufresne during their Sub-Antarctic inter-island research cruise (Hureau 1979; Duhamel et al. 1983). The list of 33 species compiled by Gon and Klages (1988) was then extended by 36 new records to the area following the only fisheries independent survey in 2001 by the *MV Iris* (Pakhomov et al. 2006).

The only species to be targeted by a commercial fishery in the Exclusive Economic Zone of the islands, is the Patagonian toothfish *Dissostichus eleginoides*. Within 5 years of the fishery officially opening, the catch statistics indicated that the stocks were severely depleted (Brandao et al. 2002). A much reduced fishery is still ongoing today. The fishery is a long-line fishery and has in the past had serious impacts of by-catch on the sea bird population (Nel et al. 2002c; Nel et al. 2003), but data show that mitigation efforts have been successful and the by-catch significantly reduced (to zero) starting in the 2005/06 season (CCAMLR 2010).

The mesopelagic community has been neglected in studies to date. Very little data are available for this community in the vicinity of the islands. Studies that consider the abundance and/or diet of myctophid fish are rare (Perissinotto and McQuaid 1992b; Pakhomov et al. 1996) and no sampling has been targeted for studies of the cephalopod community. Data available for this important component of the ecosystem are lacking and currently limited to species lists established from the diet analyses of the seabirds and seals (Berruti and Marcus 1978; Adams et al. 1985; Cooper et al. 1988; Gartshore et al. 1988; Hunter and Klages 1989). Research on birds at the PEIs has been ongoing since the inception of the scientific research at the islands and there is a rich published literature on the birds of the islands, which provides a solid base of data for this important component of the ecosystem (Williams et al. 1975; Siegfried 1978; Williams et al. 1979; Cooper and Brown 1990; Crawford and Cooper 2003). Population dynamics of penguins (Crawford et al. 2003b; Crawford et al. 2003c; Crawford et al. 2003d; Crawford et al. 2009), albatross species (e.g., wandering and grey-headed) and other large birds (e.g., the northern and southern giant petrels) have been monitored with long term trends observed (Nel et al. 2002a;

Crawford et al. 2003d; Ryan et al. 2009). The effect of fisheries on marine birds is a worldwide concern (Tasker et al. 2000; Cury et al. 2011). Recent population declines have been linked to the increase in tuna long lining as well as recent large scale Illegal Unregulated and Unreported (IUU) long-line fishing for Patagonian toothfish (Nel et al. 2002b; Nel et al. 2003) though as already stated, recent mitigation measures have been successful.

Datasets for the mammals began with the earliest observations on populations recorded in Rand (1956) and Van Zinderen Bakker Sr et al. (1971). Following these, research on the breeding populations of the seals began in earnest (e.g., Condry 1977; Condry 1978a; Condry 1981) and has continued to today (Kerley 1983b; Wilkinson and Bester 1990a; Hofmeyr et al. 1997; Hofmeyr et al. 2006; Bester et al. 2009). In addition to these population studies, biological data on diet, foraging ranges and breeding have also been conducted and have resulted in a comprehensive dataset for the islands (Condry and Bester 1975; Klages and Bester 1998; Pistorius et al. 2001a; Pistorius et al. 2001b; Makhado 2002; Kirkman et al. 2003; Pistorius et al. 2008; de Bruyn et al. 2009).

1.4. Aims of the project

It is evident from the overview provided here that an ecosystem model of the Prince Edward Islands has the potential to provide a platform to collate the available biological data of the marine system, which can then be used to address ecological questions. With a model in place, there is the potential to use it in the future for practical management applications.

The overall aim of this study was to create the first ecosystem model of the PEIs marine system. The model will be based on the existing comprehensive biological and ecological dataset, and be used as a tool to explore a number of theoretical and applied ecological questions, specifically:

1. To describe and parameterize the food web of the marine component of the PEI ecosystem in terms of biomass (Chapter 2) and consumption (Chapter 3);
2. To characterise the ecosystem using a mass balanced ecosystem modeling approach (Ecopath) to:

- investigate the sources of productivity and their relative importance to the system at various spatial scales (Chapter 4); and
 - describe the ecosystem across a range of time periods (1960s, 1980s, 2000s) (Chapter 5);
 - determine the ecosystem boundary size of the top predators (Chapter 6)
3. To investigate the population dynamics at the PEIs using a dynamic temporal simulation approach (Ecosim) looking at past changes, which are directly related to human activity (Chapter 8) and potential effects of climate change (Chapter 9)

In the process of developing the ecosystem model for the PEIs, an investigation into the consumption rate estimates used in the model was initiated, which resulted in a revision of the available estimates. This work is presented in Chapter 7, and the methodology is included in all models.

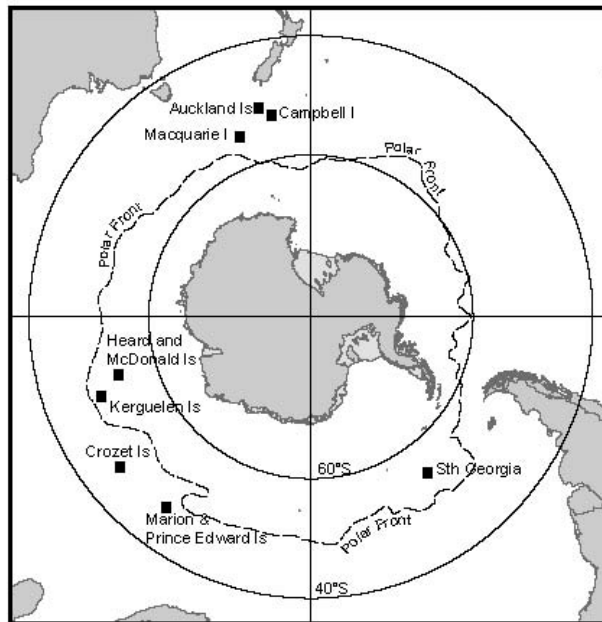


Figure 1.1. The Antarctic continent, the sub-Antarctic Islands and the approximate position of the Antarctic Polar Front (APF) (Australian Antarctic Division Data Centre, SCAR Map Catalogue, #13137)

Chapter 2 Review of the Prince Edward Island marine ecosystem: Quantifying the system in terms of biomass and highlighting long term trends

Introduction

An extensive published literature exists for the marine ecosystem of the Prince Edward Islands with many of the publications referred to in Chapter 1 of this dissertation. The aim of this section is to summarise the literature to provide the reader with a comprehensive overview of the ecosystem starting with the primary producers through to the top predators. This includes a summary of the pelagic components of the system (phytoplankton, zooplankton, nekton, fish), the benthos and the land-based vertebrates (seals and seabirds). A species list is provided in Table 2.1, which aggregates the marine ecosystem into 37 functional groups. Biomass estimates for the major components of the marine system have been quantified in preparation for construction of the ecosystem model, the spatial extent of which is the Exclusive Economic Zone (EEZ). Data for the islands exist in a variety of forms, dependent on the field of expertise / discipline of the original research. In many instances, raw data in the form of abundance estimates (in either absolute or relative terms) had to be converted into biomass estimates, which involved a number of conversion factors and assumptions. All conversion factors have been described and the final biomass estimates presented in absolute values (metric tonnes) or per unit area ($\text{t.km}^{-2}/\text{g.m}^{-3}$), whichever is more appropriate. (In general, biomass estimates for land based fauna are given in absolute terms while aquatic groups are given per unit area). Source data and derivations are explained in the text. Through this data compilation, where available, the long term changes in populations of the fauna of the marine ecosystem are illustrated and, finally, a note on the possibility of the islands having a ‘carrying capacity’ is discussed.

2.1. The marine ecosystem: A review and biomass estimates

2.1.1. Primary producers

Open ocean production

As described in the oceanography section of Chapter 1 (Section 1.3.3), the islands fall in the Antarctic Polar Frontal Zone of the Antarctic Circumpolar Current between the Sub-Antarctic Front (SAF) in the north and the Antarctic Polar Front (APF) in the south. The Sub-Antarctic water found to the south of the SAF, is cool (less than 10°C) and fresh with high nutrient concentrations but with low chlorophyll concentrations (Hempel 1985), known as HNLC waters. The open ocean phytoplankton is dominated by the nano- and picophytoplankton size fractions with the contribution of microphytoplankton to the whole phytoplankton community usually accounting for less than 20% of the total community (El-Sayed et al. 1979a; Froneman et al. 1998; Read et al. 2000; Thomalla et al. 2011). It has been frequently argued that in the Southern Ocean a lack of stability and deep mixing lead to light limitation and accounts for low chlorophyll biomass in this region (Mitchell-Innes 1967; Nelson and Smith 1991). However, Read et al. (2000) found the shallow layer (less than 25 m) of westward moving surface water had an adequate light environment and determined iron limitation to be the most probable cause for the absence of a diatom bloom in these surface waters. Beneath the surface layer, the observed sub-surface biomass maximum of small nanoplanktonic cells (less than 20 µm) is largely trapped in the layer 40-80 m between two density maxima, although low chlorophyll concentrations are found to depths of 120 m (Read et al. 2000).

Elevated production is associated with the frontal features (both the SAF and the APF) as they appear to have particularly pronounced vertical stability and are associated with enhanced upwelling of nutrients and leakage of nutrients across the front (Read et al. 2000). This observation for the fronts in the region of the PEIs, is also true of the eddies observed in the vicinity of the islands where shallow mixed layers and enhanced nutrients provide favourable conditions for phytoplankton growth (Lutjeharms et al. 1985; Pakhomov et al. 2000b; Ansorge et al. 2004). Elevated phytoplankton standing stock has also been observed downstream of the islands (approximately double the upstream observations), associated with a downstream wake

(Perissinotto et al. 2000). This increased productivity filters up through the food web to the higher trophic levels. For instance, at-sea distribution of Grey-headed albatross and King penguins have been shown to be closely related to frontal features (Bost et al. 1997; Guinet et al. 1997; Nel et al. 2001).

In situ data for the phytoplankton community of the PEIs is almost exclusively limited to the austral autumn because the SA Agulhas (the research and supply vessel used by the South African National Antarctic Programme) usually visits the islands just once a year to resupply the base. During this period, the marine surveys are conducted. Open ocean *in situ* measurements of chlorophyll-a (*chl-a*) in the vicinity of the PEIs range from $<0.1 - 0.8 \text{ mg.m}^{-3}$ (Froneman and Balarin 1998; Froneman et al. 2000a; Pakhomov et al. 2000b; Bernard and Froneman 2005; Hunt et al. 2008; McQuaid and Froneman 2008).

In an effort to increase both the spatial and temporal coverage of the dataset, remotely sensed ocean colour satellite data were analysed. The data used was at 1 km resolution over a six by six degree area centered over the islands (44°S to 50°S , and 35°E to 41°E) from SeaWiFS (1998 to 2004) and a two by two degree area (45.8°S to 47.8°S and 36.8°E to 38.8°E) from MODIS-Aqua (2005-2008) (see Figure 2.1).

For both instruments, daily Level-2 standard chlorophyll products were downloaded from the Ocean Color Web (Feldman and McClain 2007b) and mapped to a cylindrical coordinate system that retained the original 1-km spatial resolution. SeaWiFS standard chlorophyll (Reprocessing Version 5.1) was derived using the OC4v4 pigment algorithm (O'Reilly et al. 1998; O'Reilly et al. 2000). MODIS-Aqua standard chlorophyll (Reprocessing Version 1.1) was derived using the OC3 pigment algorithm (O'Reilly et al. 2000). Data from both instruments were derived using near real time meteorological and ozone data for atmospheric correction. Standard Level-2 quality flags were used to mask poor quality data (Feldman and McClain 2007a). The OC3 pigment algorithm is intended to yield MODIS-Aqua chlorophyll estimates that are directly comparable with chlorophyll estimates derived from the SeaWiFS instrument and the OC4v4 pigment algorithm (See for example: Franz 2005; Zhang et al. 2006).

Images of monthly composites are included in Appendix 1.A. of this thesis. Average annual *chl-a* values from the larger area and earlier period (1998 – 2004) from the SeaWiFS satellite ranged between 0.22 mg.m^{-3} and 0.26 mg.m^{-3} (mean $0.24, \pm \text{SD } 0.04 \text{ mg.m}^{-3}$), while data for the small area (and later time period 2005 - 2008) were lower with a range between 0.17 mg.m^{-3} and 0.21 mg.m^{-3} (mean $0.19 \pm \text{SD } 0.01 \text{ mg.m}^{-3}$) (Figure 2.2). An annual average of $0.22 \text{ mg chl-a.m}^{-3}$ was calculated from all years and is in agreement with historic *in situ* data (e.g. $0.22 \text{ mg chl-a.m}^{-3}$ (El-Sayed et al. 1979a); $0.2 \text{ mg chl-a.m}^{-3}$ (Boden 1988), $0.22 \text{ mg chl-a.m}^{-3}$ (Gurney et al. 2002)).

To convert the *chl-a* estimates to biomass, a *chl-a*:Carbon ratio of 32.25 was used (based on the relationship from Hewes et al. (1990): $C = 80 \text{ chl } a^{0.6}$, using the value of $0.22 \text{ mg chl-a.m}^{-3}$); a conversion factor of x 10 for Carbon to wet weight (Dalsgaard and Pauly 1997); and a euphotic depth of 120m (Read et al. 2000), resulting in an estimate of 8.51 t.km^{-2} (or a total of 3667929 t for the EEZ). This was divided into a microphytoplankton component (size $>20 \mu\text{m}$) of 1.70 t.km^{-2} (~20% of the total phytoplankton) and a nano and picophytoplankton component of 6.81 t.km^{-2} (~80% of the total phytoplankton) based on the relative contributions of these size fractions to the open ocean phytoplankton assemblages.

Island associated blooms

Since the earliest oceanographic studies at the islands, phytoplankton blooms in the vicinity of the islands have been observed. The perception of the blooms was that they were a relatively local phenomenon. With the advent of remote sensing of *chl-a* from satellite observations, it has become clear that the blooms extend away from the islands in various directions (see Appendix 1. A of images from SeaWiFS and MODIS-Aqua), and are therefore referred to here as ‘island associated blooms’.

Results from *in situ* measurements of *chl-a* from within the vicinity of the islands range from $0.01 - 2.8 \text{ mg chl-a.m}^{-3}$ (El-Sayed et al. 1979a; Miller et al. 1984; Allanson et al. 1985; Boden 1988; Duncombe Rae 1989a; van Ballegooyen et al. 1989; Perissinotto et al. 1990b; Froneman et al. 2000a; Perissinotto et al. 2000). Phytoplankton blooms are considered to occur when *chl-a* concentrations exceed 1.5 mg.m^{-3} (Boden 1988; Duncombe Rae 1989a). The blooms are

dominated by diatoms (Boden 1988). They occur seasonally and are usually the result of increased production of the chain-forming *Chaetoceros radiacans* (Boden et al. 1988), *Rhizoselena curvata*, and *Dictyocha speculum* (Perissinotto 1992) or *Fragilariopsis* spp. (McQuaid and Froneman 2008). They are thought to occur during periods of water retention in the vicinity of the islands, when reduced flow through results in a build-up of fresh water runoff carrying nutrients from the islands, and creating water column stability (Perissinotto and Duncombe Rae 1990; Perissinotto et al. 2000). Water retention needs to be prolonged (at least 14 days duration) to allow for phytoplankton build up (Perissinotto et al. 1990b). Under non-bloom conditions, *chl-a* concentrations range between 0.05 and 0.45 mg.m⁻³, with the composition dominated by nano- and/or picophytoplankton (Perissinotto et al. 2000; Bernard and Froneman 2002) similar to the open ocean phytoplankton composition.

The *in situ* data is limited in its temporal resolution (mostly austral autumn estimates). In an effort to increase the spatial and temporal resolution of the data, remotely sensed ocean colour satellite *chl-a* data at a 1km resolution from a subarea centred on the islands (46.5°S to 47.1°S and 37.5°E to 38.3°E) from 1998 to 2008 was processed (SeaWiFS data 1998 – 2004, MODIS data 2005-2008) (see Figure 2.1). Monthly averages peaked during the summer months and values of up to 1.4 mg *chl-a*.m⁻³ showed clear seasonal blooms in the vicinity of the islands. The annual averages for these data range between 0.18 and 0.42 mg *chl-a*.m⁻³, with the average *chl-a* for the sub-area 0.27 mg *chl-a*. m⁻³ (Figure 2.2). Therefore an increase of 0.05 mg *chl-a*.m⁻³ over and above the open ocean value of 0.22 mg *chl-a*.m⁻³, was attributed to the elevated production associated with the islands, contributing 20% to the productivity in the area in which it occurs. To convert the *chl-a* estimate to biomass: the value of 0.05 mg *chl-a*. m⁻³ was divided by 1000 to convert to g (from mg), then multiplied by 32.25 to convert from *chl-a* to carbon (see above), then multiplied by 10 to convert from carbon to wet weight (Dalsgaard and Pauly 1997) and multiplied by 25 based on the euphotic depth being approximated to be 25m (Knox 2007a). This resulted in an estimate of 0.403t.km⁻² for the area in which it occurs (assumed to be an area within a circle of radius 20nm, equivalent in size to the subarea of satellite data used), equating to an estimate of approximately 1737.47 t total (or 0.00403 t.km⁻² for the PEI EEZ).

Interestingly, zooplankton grazing studies during bloom conditions showed no evidence of grazing on microphytoplankton ($>20\ \mu\text{m}$) (the size fraction which dominates during such blooms), but grazing occurred in the nano- and pico- size fractions of the phytoplankton (Perissinotto 1992). This led to the theory that the production from the blooms falls out of the surface waters and provides a direct transfer of primary production from the pelagic to benthic subsystem. This has been confirmed by studies of stable isotope signatures in the pelagic and benthic communities (Kaehler et al. 2000).

Benthic macrophytes

Two kelp species, *Macrocystis laevis* and *Durvillaea antarctica* dominate the macrophyte biomass and, while the combined production per unit area of these two has been estimated to be greater than that of the phytoplankton production, it was thought to contribute less to the seas around the PEIs because of its limited spatial coverage (Attwood et al. 1991). *Macrocystis laevis* is endemic to the islands (Hay 1986) and occurs along the lee shore of the islands between 5 and 20 m depth (Attwood et al. 1991). This kelp has been found growing at a depth of 68 m in the open shelf area (Perissinotto and McQuaid 1992a) and the offshore limit is apparently controlled by availability of suitable rock substrata with the inshore limit apparently set by maximum height of storm-induced waves (Perissinotto and McQuaid 1992a). Quantitative estimates of the macrophytes made from photographs and from diving surveys conducted in the 1980s are 63 500 t for *M. laevis* (Attwood et al. 1991) and 3 300 t for *D. antarctica* (Haxen and Grindley 1985). Input from macrophyte production into the system by way of particulate or dissolved organic carbon through fragmentation was also thought to be limited as it was suspected that almost all of the production was exported to the open ocean pelagic environment (Attwood et al. 1991). This theory has subsequently been adjusted as evidence from stable isotope signatures has shown that the input of the macrophytes, particularly as particulate carbon, is substantial to the near shore benthic community (Kaehler et al. 2006).

2.1.2. Zooplankton

The islands do not have an endemic zooplankton community. Species of subtropical, sub-Antarctic and Antarctic origin are all found (Pakhomov and Froneman 1999b; Pakhomov and

Froneman 2000; Hunt et al. 2002). The abundance and distribution of zooplankton groups varies at both temporal and spatial scales (Hunt et al. 2001; Hunt et al. 2002). Zooplankton communities in the vicinity of the islands have been found to be associated with different water masses and water temperature, these factors accounting for as much as 69% of variation in community structure (Hunt et al. 2002). Elevated zooplankton densities are associated with the SAF region and within close proximity to the island plateau (Pakhomov and Froneman 1999a). Results from acoustic surveys suggest that large plankton and micronekton are mostly washed around rather than across the inter-island shelf region (Pakhomov and Froneman 1999a) with the shelf region generally characterised by low average zooplankton size and biomass (Hunt and Pakhomov 2003). Therefore, upstream, inter-island and downstream communities have been shown to have different characteristics with biomass estimates in the inter-island area being the lowest. While the community has been shown to be highly variable, euphausiids (*E. vallentini*, *E. longirostris* and *Nematoscelis megalops*), amphipods, fish, salps (*Salpa thompsoni*) and chaetognaths (*Sagitta gazellae*) often dominate the larger zooplankton size fraction (Miller 1982; Pakhomov and Froneman 2000). The mesozooplankton size fraction (and often the biomass on the whole) is dominated by copepods (Grindley and Lane 1979; Hunt et al. 2001; Bernard and Froneman 2002).

A review by McQuaid and Froneman (2008) estimated zooplankton biomass to range between 0.55 and 62.70 mg dry weight.m⁻³. Pakhomov and Froneman (1999) summarise an intermediary range of between 17 and 45 mg dry weight.m⁻³ and this estimate was used for the zooplankton biomass in this study. A dry weight to wet weight conversion of 5 (Cushing et al. 1958) with a depth integration to 200 m, divided by 1000 (mg to g) was used to convert from dry weight to integrated wet weight biomass. Therefore the range in g.m⁻² was equivalent to the above estimates quoted in mg dry wt.m⁻³. An intermediate value of 28 g.m⁻² was used and divided between three zooplankton groups with 5 g.m⁻² for large crustaceans, 16 g.m⁻² for small crustaceans and 7 g.m⁻² for other zooplankton (estimates are equivalent to t.km⁻²).

2.1.3. Benthic ecosystem

The benthic community comprises approximately 550 species with seven benthic community groups. There are 200 macrobenthic species, numerically dominated by polychaetes, crustaceans,

mollusks, nematodes and echinoderms. Biomass of the benthos has been found to increase with increasing depth (0.12 kg.m⁻² at 5 m, 0.34 kg.m⁻² at 10 m, 0.46 kg.m⁻² at 15 m) (Beckley and Branch 1992). Using an estimate of the shelf area from bathymetry data (Table 2.2, Figure 2.3; source GEBCO_08 Grid version 20100927; <http://www.gebco.net>), the area around the islands which falls within the 0 – 500 m is 887.37 km². Using the value at 15m depth (0.46 kg.m⁻²), an estimate for the model area (EEZ) would be approximately (408 190 t/ 431014 km² =) 0.947045 t. km⁻². Data from Perissinotto and McQuaid (1990), however, provide an estimate of approximately 6.4 g.m⁻² in the area where the benthic fauna occurs (bryozoa 4.5 g.m⁻², asteroidea 1.0 g.m⁻²; *Echinus* sp. 0.5 g.m⁻², ophiuroidea 0.2 g.m⁻², bivalves 0.1 g.m⁻², polychaetes 0.1g.m⁻²). This lower estimate results in a value of 0.013176 t.km⁻². For this study a biomass value of 0.5 t.km⁻² was used as the average of these two estimates.

Benthic decapod

Nauticaris marionis, the benthic decapod, has the second highest crustacean biomass and numerous studies have focused on this species because of its perceived key role in the ecosystem (Perissinotto and McQuaid 1990; Kuun et al. 1999; Pakhomov et al. 1999; Pakhomov et al. 2000c; Pakhomov et al. 2004). The decapod is consumed by some of the top predators on the islands (Brown et al. 1990) and therefore provides a link between benthic production and the higher vertebrates. It is widely distributed around both Marion and Prince Edward islands, but occurs mainly within the 200 m depth contours (Perissinotto and McQuaid 1990a). On the inter-island plateau the decapod occurs in a supra-benthic layer which extends 5-10 m above the bottom. The shallowest depth that it has been recorded at is between 30 – 33 m, while it has been found at depths as great as 606 m and 775 m (Perissinotto and McQuaid 1990a). Abundance estimates from dredge samples are as high as 25 ind.m⁻² but photographs of the bottom show much higher densities with a maximum of about 80 ind.m⁻² on the south-east coast of Marion Island and even this is considered to be a significant underestimate. Biomass estimates have been based on data from Branch et al. (1993) where abundance estimates of *N. marionis* are 20 ind.m⁻³. If swarms are considered 3.5m deep (or alternatively using a depth integrated estimate of 70 ind.m⁻²), with a wet weight biomass estimate of an individual equal to 226 mg. The average length of *N. marionis* is between 25-30mm, so 27mm was used, and the wet weight was

estimated at 266mg. Therefore the estimate of biomass was $(70 \text{ ind.m}^{-2} \times 0.266\text{g}) = 18.62 \text{ g.m}^{-2}$. Assuming the decapod is found in the area between 0 and 500m ($= 887.37 \text{ km}^2$; Table 2.2; Figure 2.3; GEBCO_08 Grid version 20100927; <http://www.gebco.net>), a total of 16 522 t of decapods may be found at the islands. The biomass estimate for the EEZ model is therefore $(16\,522/431014 \text{ t.km}^{-2}) = 0.0383 \text{ t.km}^{-2}$.

2.1.4. Cephalopods

The cephalopods are a key component of the marine ecosystem, yet no directed studies have focused on this important group, and no quantitative data on the cephalopods in the vicinity of the islands exists. Information on species composition comes largely from diet analysis of the top predators (Berruti and Harcus 1978; Cooper et al. 1990; Cooper et al. 1992; Cooper and Klages 1995) which has provided an extensive species list. Ashmole (1968) has suggested that surface feeding seabirds are essentially non selective with respect to the taxonomic affinities of their prey, and therefore suggest that species compositions from such diet analyses may be a true reflection of those in the vicinity of the islands (Berruti and Harcus 1978). Such an assumption however, may bias the species considered to the near surface species. Despite this potential issue, the prey of the two sooty albatrosses (*Phoebastria fusca* and *P. palpebrata*) at Marion Island, where 3 295 beaks were analysed (Berruti and Harcus 1978), along with other studies (Cooper and Klages 1995), were used to identify the most important cephalopod families, which were Onychoteuthidae, Histiotethidae, Chiroteuthidae and Cranchiidae. Of the 23 taxa found in the diets locally at the PEIs, *Kondakovia longimana* was identified as a key species in the diet of albatross species (Wandering and Grey-headed, (Cooper et al. 1992); Dark-mantled Sooty (Cooper and Klages 1995)) and penguins (Kings (Adams and Klages 1987); Macaroni and Rockhoppers, (Cooper et al. 1990)) with *Moroteuthis* species also important in Grey-headed albatross diets (Cooper et al. 1992) and recorded as the dominant cephalopod in the Patagonian toothfish diets (Pakhomov and Bushula 2003; Pakhomov et al. 2006).

Due to the lack of local data, biomass estimates for cephalopods were derived from information from models of other Subantarctic systems. For the Kuergelen Islands model a biomass estimate of 0.355 t.km^{-2} (Pruvost et al. 2005) was used, and for the Falklands model an estimate of 0.35 t.km^{-2} (for large cephalopods) (Cheung and Pitcher 2005). Because the PEI system is, in general,

less productive than both the Kerguelen and Falklands systems, the estimate has been approximated at one third of these and then partitioned between the small and large groups (approximately 0.1183 t.km^{-2} , divided between large 0.0650 t.km^{-2} and small 0.0450 t.km^{-2}). These estimates were adequate to supply the system needs and were a best approximation as no data exist.

2.1.5. Fish fauna

The two most important families in terms of the fish fauna considered at the islands are the Nototheniids and the Myctophids. At the PEIs the Nototheniids are found in a range of habitats including the inshore small demersal group, large demersals and large pelagics and are the dominant species in these habitats. The Myctophid fish, on the other hand, dominate the small pelagic biomass.

The Nototheniids are considered the most successful migrants to the waters of the Sub-Antarctic islands of the Indian Ocean both in terms of diversity and abundance (Gon and Klages 1988). *Gobionotothen marionensis* and *G. acuta* are found inshore, the Painted notie *Lepidonotothen larseni* is found on the continental slope, and the three larger demersal species, the Grey rockcod *Lepidonotothen squamifrons*, the Black rockcod *Notothenia coriiceps*, and the Marbled rockcod *N. rossii* are found in deeper water. In the pelagic domain, the smaller species *Paranotothenia magellanica* (previously known as *Notothenia macrocephalata*) is found, along with *Dissostichus eleginoides* (Patagonian toothfish) which dominates the large pelagic fish community, and for which there is an ongoing fishery. The only other species which has been identified as being of potential commercial value is the Nototheniid, the Grey rockcod (Duhamel et al. 1983; Pakhomov et al. 2006).

Myctophids are the most widely distributed and abundant pelagic fish in the Southern Ocean (Gjosaeter and Kawaguchi 1980; Kozlov 1995; Sabourenkov 1991), and at the PEIs 17 of the 35 species of small pelagic fish belong to this family. In Sub-Antarctic waters the four most abundant species are *Electrona carlsbergi*, *Electrona antarctica*, *Krefflichthys* (*Protomyctophum*) *anderssoni* and *Gymnoscopelus nicholsi*. Seasonality in the occurrence of myctophids has been observed in the diets of top predators at the islands, and this indirect

evidence suggests that there is seasonality in the occurrence of these species with different species dominating the diets during different times of the year. However, no pelagic trawling data exist for the islands.

The importance of the Nototheniids (particularly the Patagonian toothfish) is evidenced through the fishery. The key role of the myctophids in the system is clear through the diet composition of the vertebrate top predators (e.g., Adams and Klages 1987; Brown et al. 1990), as has also been shown for neighbouring systems (e.g., Crozet Islands (Cherel et al. 1993), Kerguelen Island (Lea et al. 2002)). The myctophids form an important component of the diet of the land based top predators, including the Sub-Antarctic fur seals (> 96% of the diet of Sub-Antarctic fur seals (Makhado 2002), as well as the penguins (e.g., King penguins - making up 86% of diet (Adams and Klages 1987; Brown et al. 1990; Cooper et al. 1990)). They also form an important part of the diet of other nekton (cephalopods) (Lipinski and Linkowski 1988) and fish species (e.g., Grey nototheniid, *Lepidonotothen squamifrons*) (Pakhomov and Bushula 2003; Pakhomov et al. 2006)).

Studies on Chondrichthys (sharks and rays) have not been conducted at the islands, though rays (*Bathyraja tuff*, *Rajella barnardi*, and another unidentified *Raja* sp.) were collected in the *MV Iris* survey (Pakhomov and Bushula 2003; Pakhomov et al. 2006). Along with these species, it is presumed that species described from the Kerguelen Islands are also present at the PEIs. Three species are described: the Greenland shark *Somiosus microcephalus*, Porbeagle *Lamna nasus*, and Lanternshark *Etmopterus granulosus* (Cherel and Duhamel 2004).

The only quantitative fisheries independent survey for the islands was conducted by the *MV Iris* in 2001. This trawl survey targeted predominantly demersal species with 54 trawls between 200 m and 1500 m made using a 100 mm mesh net (Pakhomov and Bushula 2003; Pakhomov et al. 2006). The results of the survey showed major shifts in fish community composition occurred at 500-600 m and 800-900 m, which was thought to be a result of physical and biological vertical zonation (Pakhomov et al. 2006). In terms of species, *Dissostichus eleginoides* was found to dominate at depths less than 500 m, *Lepidonotothen squamifrons* was found to dominate between 450 and 750 m, *Macrourus carinatus* at greater than 600 m and *Echiodon cryomargarites* between 600 and 1000 m (Pakhomov and Bushula 2003). The Commission for the Conservation

of Antarctic Marine Living Resources (CCAMLR) fisheries reports on catch data for the Patagonian toothfish fishery, for that portion of catch which falls within the area of CCAMLR, is reported annually in the CCAMLR report series. Estimates of by catch of fish and birds are also included in the reports, as are incidents of by catch of seabirds). Data on catch per unit effort (CPUE) for the Exclusive Economic Zone (EEZ) of the PEIs has been reported and estimates of landed catch as well as initial biomass estimates have been made (Brandao et al. 2002; Brandao and Butterworth 2009).

The paucity of data on the fish community at the PEIs made estimating quantitative biomass particularly challenging and highlighted the urgent need for more data on this community. The only quantitative estimates for the fish community are from the abundances recorded for the most common inshore species (Bushula et al. 2005) and data for the Patagonian toothfish, which has been derived from a combination of the fisheries independent survey from 2001 and fisheries catch data for the islands (Brandao et al. 2002; Brandao and Butterworth 2009). With the coefficient of variation around the estimate at 213%, the estimates are considered far from accurate. As no other data exist, relative abundances of the Patagonian toothfish estimates to other community groups from the *MV Iris* data (Pakhomov et al. 2006) were used to make estimates of this community. In addition, relative abundances of the different fish community groups from the neighbouring Kerguelen system (Duhamel and Hauteceur 2009) were used to assist in quantifying the biomass of contributions of the respective fish populations using the Patagonian toothfish as the reference quantity. The data from the Kerguelen Islands in particular proved useful (Duhamel and Hauteceur 2009), though as noted by Gon and Klages (1988), the fish fauna at the PEIs are inferior to that at the Kerguelen islands and do not support the same biomass, and this was taken into consideration. This has been attributed to the much larger shelf area of the Kerguelen plateau which supports larger populations of more species.

In preparation for constructing an ecosystem model for the PEIs, decisions on which species should be grouped together into functional groups had to be made. These decisions were based on fish size (large considered to be any fish greater than 50cm in length at maturity) and diets, with similar species being grouped together (Table 2.1). Biomass estimates for each of the functional groups for the fish fauna are outlined below. In all instances in this study where the

text refers specifically to a functional group and its input or output from the model, it is Capitalized and *italicized*. Where left in regular text, it refers to information or data that is not specific to the model, but to the species or group in any other capacity.

The large pelagic fish groups include the *Sharks and Rays*, *Large Pelagic Fish* and the *Patagonian Toothfish*. For the *Sharks and Rays*, catch rates for just one species from this group *Bathyrāja tuff* (Pakhomov et al. 2006) (in this paper as *taaf*) show very low occurrence of 0.02 ind.h⁻¹ out of 45.45 ind.h⁻¹ for deep demersals (in assemblage B of their study). The resulting estimate would be very low (at 0.843 t) for the system. A biomass estimate for two species of *Bathyrāja* at the Kerguelen islands found 28431 t, or 12% of the Patagonian toothfish biomass estimate (Duhamel and Hautecoeur 2009). Based on this, the estimate was determined as 0.00036 t.km⁻² (from 0.12*0.003; the most recent toothfish survey data from the PEIs). This is in contrast to the estimate of 0.001 t.km⁻² made in the Kerguelen model (Pruvost et al. 2005). Currently no estimates for the sharks exist, but the group remains so named in the hope that improvements to the model in future will allow for the inclusion of shark data in this functional group.

The biomass estimates for the *Large Pelagic Fish* group were made following the relative abundance of large pelagic fish in comparison to the local estimates made for the Patagonian toothfish (FPT) (Pakhomov et al. 2006). The value estimated is half the estimated biomass of the FPT stock and was set to 0.042t. km⁻², less than half of the estimate for the Kerguelen stock (0.0940 t.km⁻², model generated, Pruvost et al. 2005). For the FPT a biomass estimate of 1168 t with a coefficient of variation of 213% was estimated from the voyage of the *MV Iris* using swept area (Brandao et al. 2002). This amounts to a biomass of (1168/434101.4 =) 0.00271 t.km⁻² for the EEZ of the PEI for the 2000s time period. This biomass estimate is presumed to be a small percent of the original biomass that would have been in the system prior to the fishery crash of the mid 1990s. If the current estimate is 5% of original biomass (Brandao et al. 2002), estimated biomass prior to the start of the fishery is assumed to have been between 0.054196 t.km⁻² (or 23 359t) and 0.116004 t.km⁻² (or 49 999t). For the Kerguelen Islands, an estimate for the adults of this species was 0.129 t.km⁻² (approx 55 600t) (Pruvost et al. 2005), with a more recent estimate of current biomass higher at 0.288 t.km⁻² (124000 t), which is approximately half

of the estimated fish biomass for the Kerguelen Island system in total (245000 t, 0.57 t.km⁻²) (Duhamel and Hauteceur 2009).

Estimates for the mesopelagic fish community in the Southern Ocean are 4.5 t.km⁻² (Gjosaeter and Kawaguchi 1980), a figure later revisited for many regions but remaining unchanged for this area (Lam and Pauly 2005), which has been used for this study. Estimates for Myctophid fish in the Southern Ocean are generally in this range (e.g., Filin et al. 1991; Kozlov et al. 1991), though these estimates exceed those made by Pakhomov et al. (1996). Pakhomov et al.'s (1996) data were based on 5 voyages of the South African National Antarctic Program between 1985 and 1995 where dry weight estimates ranged from 0.01 to 1.1 g dry wt.m⁻² with an average of 0.138 g dry wt.m⁻². Using a dry to wet weight conversion of 5, the average biomass would be 0.69 t.km⁻², approximately six and a half times lower than that used in this model. However, the sampling gear used in Pakhomov et al.'s (1996) study was not ideal for sampling myctophids, and may account for the low estimate. There is an urgent need for further research of this particular group and the parameter used in this model should be revised once a comprehensive sampling of the area has been carried out.

Large demersal fish species were divided into two groups: a general *Large Demersal Fish* and a family specific *Large Nototheniid Demersal Fish* group. For the general *Large Demersal Fish* group, the data from the fisheries independent survey for all assemblages (Pakhomov et al. 2006) showed the Patagonian toothfish (FPT) *Dissostichus eleginoides* catch rate was 38.88 ind.hr⁻¹ compared to the rate for the general large demersal fish species (as categorized for this model) which was approximately 55.45 ind.hr⁻¹. Keeping in mind that the trawls were not targeting FPT, the toothfish were probably under represented. A recent trawl survey at Kerguelen showed the large demersal fish group to consist of approximately 50% of the FPT biomass and this estimate was used in combination with the local FPT data. The *Large Nototheniid Demersal Fish* were considered to be 12% of the FPT population, which leaves a remaining 38% to be classified as *Large Demersal Fish*. Using this approach with the pre-crash FPT data from the 1980s time period model (0.075t. t.km⁻²), the approximate value would be 0.0285 t.km⁻². This estimate is less than that for the Kerguelen model (0.5 t.km⁻²) (Pruvost et al. 2005) and Falklands model (>0.4t.km⁻²) (Cheung and Pitcher 2005). For estimating the biomass of the *Large Notothenid*

Demersal Fish group, the relative proportion of this group, compared to the FPT estimate, was used. *Lepidonotothen squamifrons* was caught at 4.53 and 1.45 ind.hr⁻¹, compared with 35.55 and 1.93 ind.hr⁻¹ for FPT in community assemblages A and B respectively (which represent different trawl depths) (Pakhomov et al. 2006). The relative contribution of *L. squamifrons* was therefore between 12 and 75 % of the toothfish biomass for these assemblages. The data for Assemblage A is similar to that found for the Kerguelen population (Duhamel and Hauteceur 2009) where *L. squamifrons* and *N. rossi* were found to have a biomass of approximately 10% of the FPT estimate. Using the lower estimate (12% of the FPT data) with the intermediate estimate of the FPT data (pre-crash) (0.075t.km⁻²) we get an estimate of 0.00955 t.km⁻², or 4119t.

The small demersal fish groups were divided into two: the *Small Continental Slope Demersal Fish* and the *Small Inshore Demersal Fish*. Of the *Small Continental Slope Demersals*, *Lepidonotothen larseni* occurs at a density of 0.2 ind.m⁻² and the mass varies in wet weight from 0.2 to 8 g (Bushula et al. 2005). If an average fish is considered to weigh 5 g, the biomass estimate would be 1 g.m⁻² (equivalent to t.km²). As this fish resides on the slope area there is a need to scale for this area only. Using bathymetry data (GEBCO_08 Grid version 20100927; <http://www.gebco.net>) from the vicinity of the islands, an estimate of the shelf area extending from the islands between the depths of 300 m to 1500 m is 1693.11 km² (see Table 2.2, Figure 2.3). If we presume that this one species is one third of the total for this group, the resulting biomass estimate is (1693.11km² x 3 t/km² =) 5079.33 t, or 0.01178 t.km⁻². Calculations for the *Small Inshore Demersals* were based on *Gobionotothen marionensis* as estimates were available for this species. Using an average weight for *G. marionensis* of 10 grams (midpoint of that found by Bushula et al. 2005), then the biomass estimate for this species is (0.2 ind x 10 g =) 2.0 g.m⁻² (equivalent to 2.0 t.km⁻²). To scale for the area in which this species occurs, bathymetry data (GEBCO_08 Grid version 20100927; <http://www.gebco.net>) from the islands was used to estimate the area from 0 m to 300 m depth (= 530.18 km²) (see Table 2.2, Figure 2.3). As *G. marionensis* is only one of the three species included in this group, the estimate for this group was made using the biomass estimate of this species (2.0 t km⁻² x 530.18 km²) multiplied by 3, equals 3181.08 t which equates to 0.007 t.km⁻² for the ecosystem (EEZ of PEIs).

2.1.6. Avian fauna

In excess of 2.5 million birds from 29 species are recorded as breeding at the Prince Edward Islands, only one of which is restricted to land (the Lesser sheathbill). There are four penguin species (King, Macaroni, Rockhopper and Gentoo) which currently dominate the avian biomass (between 92 and 96%) as well as the overall total land based top predator biomass (between 58% and 78%, depending on time period and method of calculation. See Table 2.3). Five albatross species (including Wandering, Yellow-nosed, Grey-headed, Light and Dark-mantled Sooty) breed at the islands, while numerous others are sighted in the area (Black-browed, Shy, Salvin's, Southern and Northern royal albatross) but are not considered resident. They contribute between 0.35 and 2.12 % of the avian biomass and less than 2% of the total biomass of the land based top predators. In addition there are three large flying birds at the islands, the Northern and Southern Giant petrels and Sub-Antarctic skuas. These are considered apex predators that feed mainly on seabirds and marine mammals during the breeding season (de Bruyn and Cooper 2005; de Bruyn et al. 2007). Fourteen small flying seabirds are found at the islands. These include the Fairy prion, Salvin's prion, Blue petrel, Great-winged petrel, Soft-plumaged petrel, Kerguelen petrel, Grey petrel, White-chinned petrel, Grey-backed petrel, Black-bellied storm petrel, South Georgian Diving petrel, Common Diving petrel, the Antarctic and Kerguelen terns. They make up between 2 and 6% of the avian biomass and between 1 and 5% of the total land based predator biomass (depending on time period and adjustments for time spent at the islands) (Table 2.3). Of these, the Salvin's prions and Blue petrels have by far the highest number of breeding pairs on the islands (population estimates for the two combined at 1 million birds) with hundreds of thousands of pairs of the remaining 12 species (9 petrels, 2 terns and 1 prion). The kelp gull, a predominantly coastal forager and the Crozet shag also breed on the islands.

A review of the known breeding cycles for the islands was completed by Cooper and Brown (1990), and the data from this study is presented in Table 2.4. In summary, King penguins and Wandering albatrosses have the longest breeding cycles, both of which are longer than one year. The Gentoo penguin, the Great-winged and Grey petrels are all winter breeders, while the remaining species are summer breeders. Most of the species are migratory and only spend the breeding portion of the year at the islands.

Of the birds found on the islands many are classified globally as ‘Near-Threatened’ (e.g. Gentoo penguin, Light-mantled Sooty Albatross) or ‘Vulnerable’ (Macaroni and Rockhopper penguins; Wandering, Grey-headed albatross) as well as ‘Endangered’ (Indian Yellow-nosed albatross and Dark-mantled Sooty albatross) by BirdLife International (2011) (IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 27/09/2011), and are a priority for conservation concerns at the islands.

Long term population trends, and corresponding biomass estimates have been summarised for this study (Figures 2.4.A - L) and the data provided (Appendix 2.A.). Average bird mass (summarised in Ryan and Bester 2008) was used with population estimates to construct biomass time series estimates. Descriptions for each group are given below.

Penguins

The four species of penguin (Kings, Macaronis, Southern Rockhoppers and Gentoos) dominate the seabird community making up approximately 95% of the biomass (Table 2.3). Extensive research on all aspects of their biology has been published on all four species and provides a comprehensive biological data set for this group at the islands (Williams 1982; Adams and Brown 1983; Lacock et al. 1984; Adams et al. 1985; Adams 1987; Adams and Klages 1987; Adams and Wilson 1987; Adams and Brown 1989; Adams and Klages 1989; Brown et al. 1990; Duplessis et al. 1994).

The most recent survey for King penguins sets the breeding population at 442000 individuals, and a corresponding total biomass of approximately 5000 t. This makes the species the single largest contributor to the biomass of the land based top predators at these islands. Population censuses for this species have not been conducted as regularly as those of the other three penguin species, but the data suggest that the population at the PEIs is stable to increasing (Figure 2.4.A, and Crawford et al. 2003d). Declines in populations are evident however for both the Macaroni and the Rockhopper populations. The most recent population estimate for the Macaroni population is approximately 600 000 individuals (Crawford et al. 2009). Between the 1980s and the early 2000s, the Macaronis showed a greater decline in the population on PE (50% decline) (Ryan et al. 2003) than the one on Marion (10-15% decline) (Crawford et al. 2003b), though data

from the most recent surveys show declines on both islands to be approximately 30% (Figure 2.4.B, data in Appendix 2.A, and Crawford et al. 2009). This equates to a decline in biomass from approximately 3883 t in the 1980s to 2778 t in 2009. The Southern Rockhoppers have declined even more than the Macaronis, from approximately 180 000 breeding pairs in 1994/5 to 67 000 pairs in 2002/3 (Crawford et al. 2003c), and down to 45 000 pairs in the last census (Crawford et al. 2009), which is one quarter of the 1994/5 population estimate (See Figure 2.4.C). In terms of biomass, decline was from approximately 1 140 t to 449 t over this time period. The Gentoo population is far smaller than those for the other penguins (contribute less than 0.4% of the penguin biomass for all time periods) with current estimates of breeding birds around 3500 individuals and historical fluctuations ranging between 1920 and 4235 individuals. The numbers of Gentoos declined from the mid 1990s, but show recent recovery (Figure 2.4.D, Appendix 2.A.) (Crawford et al. 2003a; Crawford et al. 2009), and have the lowest biomass of the four penguin species at between 15 t and 21 t.

It has been suggested that the relative success of the different species of penguins may be linked to the differences in their foraging ranges and hence their dependence on pelagic or near-island resources. King penguins are able to travel the furthest (Adams 1987) and this allows them to forage at the productive frontal systems, which may be some distance from the islands. The smaller penguins are, however, restricted in their foraging range and are therefore more dependent on the island ecosystem. Of the smaller penguins, the Macaroni travels the furthest (59 to 303km) (Brown 1987), followed by the Southern Rockhopper (4 to 157km) (Williams and Siegfried 1980; Brown 1987) and lastly the Gentoo (80% of all trips <40km, (Adams and Wilson 1987)). As both the Macaronis and the Rockhopper populations have been in decline, the reason may also be related to the food source of each of these species, as both have a predominantly crustacean diet, while the Kings and the Gentoos have a high contribution of fish to their diets (see section to follow on diets). The reduced breeding success that has been documented over the last decade for the Rockhopper penguins has pointed to the birds returning to the islands to breed in sub-optimal condition with lower recorded weights on arrival and sub-optimal conditions for feeding at the over-wintering grounds has been implicated in the breeding failure for these species (Crawford et al. 2008).

Breeding cycles of the four penguins species found at PE islands differ with both the Kings and Gentoos present year round while the Macaronis and Rockhoppers are summer breeders (see Table 2.4 (Rand 1955; Cooper and Brown 1990). Gentoos nest in winter, rearing chicks for a few months, while Kings lay eggs in mid-summer and rear chicks for 10 months. Rockhoppers and Macaronis arrive towards the end of October to breed then moult, leaving by the end of April, having spent between six and seven months at the islands (Rand 1955; Williams et al. 1975; Cooper and Brown 1990).

Large flying birds

As already mentioned, this group includes the five albatross species that breed at the islands (Wandering, Yellow-nosed, Grey-headed, and Light- and Dark-mantled Sooty albatross) as well as the Giant petrels (BGPs) (Northern and Southern) and the skuas. Together the albatross populations account for less than 1.65% of the total biomass of land based predators, and less than 2.2% of the total avian biomass. Population dynamics of albatross species (e.g. Wandering and Grey-headed) and other large birds (e.g., the Northern and Southern Giant petrels) have been monitored with long term trends observed (Nel et al. 2002a) and summarized here (Figures 2. 4. E-I, Appendix 2.A). Recent population declines have been linked to the increase in tuna long lining as well as large scale Illegal Unregulated and Unreported (IUU) long-line fishing for Patagonian toothfish (Nel et al. 2002b; Nel et al. 2002c; Nel et al. 2003), though following extensive mitigation measures the most recent estimates for by-catch of birds on the fishing vessels has been significantly reduced (CCAMLR report 2011). Biomass patterns, summarized in this study, show variability for the albatross species over the past decade, though all species show stable (to increasing) estimates. Feeding of these species is not limited to the islands themselves as their foraging ranges are extensive (Nel et al. 2001; Bost et al. 2009). Southern Giant petrels outnumber the Northern Giant petrels approximately 5:1 and species show variation in population sizes through the late 1990s with a general trend to higher populations from the first surveys (1970s) to the present (Williams et al. 1979; Cooper and Brown 1990; Ryan et al. 2009, Figures 2.4.J and K). In contrast the Subantarctic Skua numbers have shown a gradual decline over the same time period (Figure 2.4.L).

In terms of breeding patterns, the Wandering albatross are present year round, while all the remaining species may be considered summer breeders (summarized in Table 2.4, Cooper and Brown 1990), spending between 7 (Grey-headed) and 9.5 (Dark-mantled Sooty) months at the islands. Data on the Yellow-nosed albatross is limited as this species is only found on Prince Edward Island which is visited infrequently.

Small flying birds

Fourteen prion, petrel and tern species, as listed earlier, are included in the group. Population estimates for all species have been limited to broad ranges of 1000s, 10s of 1000s or 100s of 1000s, with only the most recent surveys providing more definitive estimates on the populations found at the islands. The biomass estimate calculated for this study is approximately 282 t, which is similar to that in the review by Ryan and Bester (2008) of around 300 t. The Salvin's prion, Blue petrel, Great-winged petrel and White-chinned petrel dominate the small flying seabirds in both population numbers (abundance) and also in biomass as together they constitute 89% and 85.7% respectively of these two estimates. The majority of these species are summer breeders with the two exceptions being the Great-winged and Grey petrels, which breed in winter (Table 2.4, from Cooper and Brown 1990).

2.1.7. Mammals

Ten cetacean species have been observed in the vicinity of the islands including three Mysticeti species (the Southern Right whale, Humpback whale and Blue whale), and six Odontoceti species (Sperm whales (*Physeter macrocephalus*), orcas (*Orcinus orca*) and various small cetaceans which include the Long-finned pilot whales (*Globicephala melas*), Hourglass dolphins (*Lagenorhynchus cruciger*), Dusky dolphins (*Lagenorhynchus obscuris*), Southern Right whale dolphins (*Lissodelphis peronii*) and the Strap toothed Beaked whale (or Layard's beaked whale) (*Mesoplodon layardii*). Of these, only the orcas are considered resident at the islands (Condy et al. 1978; Keith et al. 2001; Pistorius et al. 2002; Tosh et al. 2008).

A review of orca populations based on opportunistic observations from 1973 to 1996 shows the average pod size is 3.56 individuals and the maximum size is 28 individuals (Keith et al. 2001).

Populations peak October to December, decrease in January, and have a small increase in late April to early May after which killer whale sightings, during most years, decrease to almost nothing (Skinner et al. 1978; Keith et al. 2001; Pistorius et al. 2002; Tosh et al. 2008). No time series data on changes in the population have been documented for the islands. At any one time, if up to 28 individuals are present, the biomass can be as great as 63 t (using Trites and Pauly 1998) average weights, assuming a sex ratio of 1:1), though the biomass estimated for this study is considered to be around 11 t for the year.

The Pinnipeds that breed at the islands are the southern elephant seal (*Mirounga leonina*), the Subantarctic fur seal (*Arctocephalus tropicalis*) and Antarctic fur seal (*A. gazella*). Rare sightings of three additional pinnipeds have been made in the area (Leopard seal (Bester et al. 2006), Weddell seal and the South African fur seal)).

The largest of the three species of seal at the islands is the Southern elephant seal *Mirounga leonina*. Extensive research has been conducted on this seal population which comes to the islands to breed, moult and over-winter (Skinner et al. 1978; Bester and Pansegrouw 1992; Pistorius et al. 1999a; Kirkman et al. 2003; Pistorius et al. 2004). This species has been in decline at the Prince Edward Islands (PEIs) since the 1960s (See Fig 2.4.M). While early total population estimates of around 10 000 individuals (Rand 1962) are not considered accurate, decline rates were estimated at 69.5% of the population based on these earliest observations to 1977 (Pistorius and Bester 1998). Declines since 1977 have been well documented with a further decrease of 66.3% from 1977 to 2004 recorded (Condy 1977; Condy 1978a; Skinner et al. 1978; Condy 1981; Pistorius et al. 1999a; Bester and Hofmeyr 2005; Ryan and Bester 2008) (Appendix 2.B.).

The Southern elephant seal population at the PEIs is part of the Kerguelen stock, which includes populations at neighbouring Crozet and Kerguelen, and the population of this stock as a whole is in decline, as are the populations at other sub-Antarctic islands (McMahon et al. 2005). The reasons behind the declines are unknown but various hypotheses have been examined. In the past, Condy (1978) considered competition with man for fish in winter feeding grounds, predation by orcas at the islands, and competition for local food resources with fur seals to have led to the population decline. Competition with fisheries and human activity was discounted in

the late 1980s (Wilkinson and Bester 1988) but has since been cited as being a potential reason for the decline in population numbers at other Sub-Antarctic islands (e.g., Green et al. 1998; Goldsworthy et al. 2001). More recent studies suggest inter-specific competition and environmental change to be the most plausible explanations (McMahon et al. 2005).

For the PEIs, population a reproductive response to declining populations has been documented. Pistorius et al. (2001b) found that age at maturity declined and fecundity rates increased as the population declined, indicating a compensatory response. These authors propose that relative increase in food availability because of the population decline promoted earlier sexual maturity correlated with more rapid growth of juveniles when population abundance lowered (Pistorius et al. 2001b). The low pup mortality rate observed between 1990 and 1999 suggested that this was not the major population regulating agent at Marion (Pistorius et al. 2001a; Pistorius and Bester 2002).

Generating biomass estimates for this population involved a number of assumptions regarding the social structure of the elephant seal population. Total population estimates were made using female to pup ratios of 1.05 (Pistorius et al. 1999a) and population to pup ratios of 3.15 (Pistorius et al. 1999a), in contrast to other island populations where a value of 3.50 is traditionally used (Laws 1977) with census data of the respective groups from published literature (Rand 1962; Condry 1977; Condry 1978a; Skinner et al. 1978; Condry 1981; Pistorius et al. 1999a; Ryan and Bester 2008; See Appendix 2.B.). Because male to female ratios are known to vary, two biomass estimates were made using male to female ratios of 1:11 (Rand 1962; Condry 1978a) and 1:16 (Skinner and van Aarde 1983) (who provide adult sex ratios for each year between 1973 and 1982 and they range between 8.07 and 20 with the average = 16.42) combined with seal mass estimates (taking into account sex and maturity) from Ryan and Bester (2008). A third estimate was calculated using the 'average seal mass' (value of $353 \pm 137\text{kg}$) as determined by Condry (1981). All estimates from 1952 to 1999 compared favourably (2.4. M), with standard deviations within 4% of the average value of the three estimates. Population estimates for elephant seals on Prince Edward Island are scarce with estimates from 1970s and 2000s showing the population to be between 30 and 35% of that found on Marion (Condry 1978a; Ryan and Bester 2008) and a value of 32.6% was used to extend the Marion estimate to include the biomass on Prince

Edward. Estimates for the elephant seal biomass made in this study are lower (approximately 637 t for Marion and PE combined) than the biomass of 2500 t put forward by Ryan and Bester (2008), but the estimates here are in line with the rates of decline reported in the literature.

Elephant seals do not remain at the islands year round. For Marion, bulls arrive in mid August and cows follow in September. Maximum harem size is reached in mid October, and females leave 4 weeks later. Yearlings start the moult haul-out in mid November, are then joined by adult females from mid December to mid March, and by adult males from late December to mid April (Condy 1979). For the purposes of this study, Elephant seals are considered present at the islands for 8 months of the year.

Two species of fur seals are found on the islands, the Sub-Antarctic fur seal (*Arctocephalus tropicalis*) and the Antarctic fur seal (*A. gazelle*). Both were the target of a seal fishery through the 19th century and numbers are thought to be returning to pre-exploitation levels today. Sealing began at the islands in the early 1800s with the earliest recorded sealing activity in 1803, but by 1860 sealing was no longer economically viable. In 1909 an attempt to revive the industry was made without success and finally all sealing is believed to have stopped in the 1930s.

Populations have since increased exponentially, and numbers today are believed to be close to pre-exploitation figures. Early seal population estimates date back to the 1950s when the population was estimated at approximately 500 Subantarctic seals and less than 100 Antarctic fur seals (Rand 1956). Population increases have been well documented since (Condy 1981; Kerley 1983a; Wilkinson and Bester 1990a; Hofmeyr et al. 1997; Hofmeyr et al. 2006; Bester et al. 2009) with the Subantarctic seal population currently at ~150000 and still increasing at 5.2% per annum (half the rate of the 1950s – 2003/4 rate) (Hofmeyr et al. 2006). The Antarctic fur seals are less common at the islands (population estimate of ~5800) and are increasing at 17% per annum (Hofmeyr et al. 2006).

Biomass estimates of 4774 t for Subantarctic fur seal and 226 t for the Antarctic fur seal populations were made using the seal weights provided by Condy (1981), population estimates summarized in Bester et al. (2009), and conversion ratios of population numbers to pup numbers of 4.8 from Kerley (1983a). This results in a total biomass contribution for the fur seals of 5000

t as in Ryan and Bester (2008). The biomass trends over time for these two species are illustrated in Figure 2.4.N.

Along with the marine mammalian fauna found at the islands, a mention should be made of the presence of two land-based mammals introduced to the islands: the house mouse (*Mus musculus*) and the domestic cat (*Felis catus*). The mice are thought to have been introduced to the islands when the sealers visited the islands in the early 1800s. In the late 1940s, when South Africa set up the meteorological station, the base soon became infested with mice. As a solution to this problem, five cats were brought to Marion Island. Unchecked, these cats rapidly bred, resulting in a population estimated at in excess of 3000 cats by the late 1970s (Bester et al. 2000). The cats were found to have serious deleterious effects on the breeding populations of birds at the islands, resulting in local extinction of at least one species. Finally eradicated in the early 1990s, this historical effect of this alien invasion resulted in serious conservation issues for some of the breeding bird populations. These were ultimately resolved with the eradication of the cats, though not without long term implications, including the local extinction of one species.

2.2. 'Carrying capacity' for the islands?

The concept of 'carrying capacity' for an ecosystem can be described as the maximum biomass that can be sustained by the available resources (Odum 1983). It is interesting to note that the total top predator biomass that the islands have supported through the documented history has been similar through time (Table 2.3). Biomass estimates made in this study show total biomass at the islands of ~ 16 300 t in the 1950s and ~ 14 700 t in the 2000s, though the species composition has changed. Overall, the contribution of seals to the total biomass has increased from around 24% to up to 38%, although when these estimates are adjusted according to time spent at the islands, the contribution of the seal community for the islands remains at about 20% for the whole period. The penguins, as already noted, form the largest contribution to the overall biomass of top predators at the islands, though the percentage contribution initially increased from 71% to 74% between the 1960s to the 1980s but then drops to 58% in the 2000s. However, if reassessed using the adjusted biomass estimates for time spent at the islands, the contribution remains relatively constant (at around 75%). For all the top predators the most noticeable change between time periods is the change in the seal community from one dominated in terms of

biomass by the Southern elephant seals, to one which in 2010 was dominated by the fur seal population (Table 2.3 and Figure 2.5). The total seal biomass in the 1960s was quite similar to that in the 2000s, though the community has changed in composition. Declines in both the Macaroni and Southern Rockhopper biomass estimates are also clearly evident (Figure 2.5).

It is well documented that many of the top predators are not limited in their foraging range to the area around the islands, and many spend much of the year elsewhere when not breeding or moulting. However, it seems evident that the islands themselves appear to have a ‘carrying capacity’ of around 15 000t which can be supported. Whether this biomass limitation is from resources in terms of food or in terms of suitable habitat for breeding and moulting on land is not clear but further investigations of this phenomenon would be interesting to pursue. If one considers the data that have been adjusted to account for the time spent at the islands, there is a downward trend (from 11 980 to 9700) over the assessed time period (1960s to 2000s) in total biomass at the islands and it remains to be discovered if this pattern can be linked to particular drivers in the system.

Table 2.1. List of codes used to identify functional groups and the corresponding species names (or Phylum/Class/Order, whichever appropriate) included in this study of the marine ecosystem of the Prince Edward Islands.

#	CODE	Functional Group	Common names <i>Species name</i> OR Phylum/Class/Order for Invertebrates	no. of spp.
1	MOR	Orca	Orca <i>Orcinus orca</i>	1
2	MES	Southern Elephant Seal	Southern Elephant Seal <i>Mirounga leonina</i>	1
3	MAF	Antarctic Fur Seal	Antarctic Fur Seal <i>Arctocephalus gazella</i>	1
4	MSF	Subantarctic Fur Seal	Subantarctic Fur Seal <i>Arctocephalus tropicalis</i>	1
5	PKI	King Penguin	King Penguin <i>Aptenodytes patagonicus</i>	1
6	PMA	Macaroni Penguin	Macaroni Penguin <i>Eudyptes chrysolophus</i>	1
7	PSR	Southern Rockhopper Penguin	Southern Rockhopper Penguin <i>Eudyptes chrysocome filholi</i>	1
8	PGE	Gentoo Penguin	Gentoo Penguin <i>Pygoscelis papua</i>	1
9	AWA	Wandering Albatross	Wandering Albatross <i>Diomedea exulans</i>	1
10	AGH	Grey-headed Albatross	Grey-headed Albatross <i>Thalassarche chrysostoma</i>	1
11	AYN	Yellow-nosed Albatross	Yellow-nosed Albatross <i>Thalassarche carteri</i>	1
12	ALM	Light-mantled Sooty Albatross	Light-mantled Sooty Albatross <i>Phoebastria palpebrata</i>	1
13	ADM	Dark-mantled Sooty Albatross	Dark-mantled Sooty Albatross <i>Phoebastria fusca</i>	1
14	BGP	Giant Petrels	Southern Giant Petrel <i>Macronectes giganteus</i> ; Northern Giant Petrel <i>Macronectes halli</i>	2
15	BPP	Prions and Petrels	Fairy Prion <i>Pachyptila turtur</i> ; Salvin's Prion <i>Pachyptila salvini</i> ; Blue Petrel <i>Halobaena caerulea</i> ; Great-winged Petrel <i>Pterodroma macroptera</i> ; Soft-plumaged Petrel <i>Pterodroma mollis</i> ; Kerguelen Petrel <i>Lugensa brevirostris</i> ; Grey Petrel <i>Procellaria cinerea</i> ; White-chinned Petrel <i>Procellaria aequinoctialis</i> ; Grey-backed Storm Petrel <i>Garrodia nereis</i> ; Black-bellied Storm Petrel <i>Fregetta tropica</i> ; South Georgian Diving Petrel <i>Pelecanoides georgicus</i> ; Common Diving Petrel <i>Pelecanoides urinatrix</i> ; Antarctic tern <i>Sterna paradisae</i> ; Kerguelen tern <i>Sterna virgata</i>	14
16	FSR	Sharks and Rays	Southern lanternshark <i>Etmopterus granulosus</i> ; Skate/ray <i>Raja</i> sp.; Bighorn skate <i>Rajella barnardi</i> ; Greenland shark <i>Somniosus microcephalus</i> ; Skate <i>Bathyraja</i> sp (tuff); Porbeagle <i>Lamna nasus</i>	6
17	FLD	Large Demersal Fish	Slickhead <i>Alepocephalus</i> sp.; Blue antmora <i>Antimora rostrata</i> ; Southern seadevil <i>Ceratias</i> ; Finless flounder <i>Neoachirosetta milfordi</i> ; Longnose tapirfish <i>Polyacanthopus challenger tentaculatus</i> ; Unicorn icefish <i>Channichthys rhinoceros</i> ; Grenadier or rattail <i>Coryphaenoides</i> sp.; Slender codling <i>Halargyreus johnsonii</i> ; Abyssal halosaur <i>Halosaurus macrochir</i> ; Morid cod <i>Lepidion</i> sp.; Ridge scaled rattail <i>Macrourus carinatus</i> ; Bigeye grenadier <i>Macrourus holotrachys</i> ;	12
18	FLN	Large Nototheniid Demersal Fish	Grey Rockcod <i>Lepidonotothen squamifrons</i> ; Black Rockcod <i>Notothenia coriiceps</i> ; Marbled Rockcod <i>Notothenia rossii</i>	3
19	FSD	Small Continental Slope Demersal Fish	Messmate <i>Echiodon cryomargarites</i> ; Austral cod <i>Guttigadus kongi</i> ; Painted notie <i>Lepidonotothen larseni</i> ; Snailfish Liparididae gen. sp. ; Antarctic armless flounder <i>Mancopsetta maculata maculate</i> ; Marbled moray cod <i>Muraenolepis marmorata</i> ; Patagonian moray cod <i>Muraenolepis orangensis</i> ;; Cod & Haddock <i>Physiculus</i> sp.; Southern flounder <i>Pseudomancopsetta andriashevi</i> ; Antarctic horsefish <i>Zanclorhynchus spinifer</i>	10
20	FID	Small Inshore Demersals	Triangular Rockcod <i>Gobionotothen acuta</i> ; Lobe-lip notothen <i>Gobionotothen marionensis</i> ; South Georgia spiny plunderfish <i>Harpagifer georgianus</i>	3
21	FLP	Large Pelagic Fish	Short snouted lancetfish <i>Alepisaurus brevirostris</i> ; Daggertooth <i>Anotopterus pharaoh</i> ; Black dragonfish <i>Idiacanthus atlanticus</i> ; Barracudinas <i>Macroparalepis</i> sp.; Southern barracudina <i>Magnisudis prionosa</i> ; Barracudinas <i>Notolepis</i> sp.; Slender escolar <i>Paradiplosinus gracilis</i> ; Southern driftfish <i>Pseudoichthys australis</i> ; Smallscale waryfish <i>Scopelosaurus hamiltoni</i> ; Barracudinas <i>Stemonosudis</i> sp.	10
22	FPT	Patagonian toothfish	Patagonian toothfish <i>Dissostichus eleginoides</i>	1

Table 2.1. Continued. List of codes used to identify functional groups and the corresponding species names (or Phylum/Class/Order, whichever appropriate) included in this study of the marine ecosystem of the Prince Edward Islands.

#	CODE	Functional Group	Common names <i>Species name</i> OR Phylum/Class/Order for Invertebrates	no. of spp.
23	FSP	Small Pelagic Fish	Boulenger's snaggletooth <i>Astronesthes boulengeri</i> ; Deep-sea smelt <i>Bathylagus tenuis</i> ; Pearleyes <i>Benthalbella macropinna</i> ; Snaggletooth <i>Borostomias antarcticus</i> ; Sloane's viperfish <i>Chauliodus sloani</i> ; Smallhead flyingfish <i>Cheilopogon pinnatibarbus altipennis</i> ; Black swallower <i>Chiasmodon niger</i> ; Bristlemouth <i>Cyclothone</i> sp.; Rebains' portholefish <i>Diplophos rebainsi</i> ; Snaketooth <i>Dysalotus alcocki</i> ; Stoplight loosejaw <i>Malacosteus niger</i> ; Magellanic Rockcod <i>Paranotothenia magellanica</i> ; Silver lightfish <i>Phosichthys argenteus</i> ; Tubeshoulder <i>Platytrichtidae</i> gen. sp.; Crested bigscale <i>Poromitra crassiceps</i> ; Boa dragonfish <i>Stomias boa boa</i> ; Threelight dragonfish <i>Trigonolampa miriceps</i> ; Slender lightfish <i>Vinciguerria attenuata</i>	18
24	FMY	Myctophid Fish	Lanternfish <i>Diaphus</i> sp.; Electron subantarctic <i>Electrona carlsbergi</i> ; Rough lanternfish <i>Electrona subaspera</i> ; Lanternfish <i>Gymnoscopelus bolini</i> ; Lanternfish <i>Gymnoscopelus braueri</i> ; Lanternfish <i>Gymnoscopelus fraseri</i> ; False-midas lanternfish <i>Gymnoscopelus hintonoides</i> ; Nichol's lanternfish <i>Gymnoscopelus nicholsi</i> ; Lanternfish <i>Gymnoscopelus opisthopterus</i> ; Southern blacktip lanternfish <i>Gymnoscopelus piabilis</i> ; Lanternfish <i>Krefflichthys anderssoni</i> ; Diamondcheek lanternfish <i>Lampanyctus intricarius</i> ; Lantern fish <i>Nannobranchium achirus</i> ; Lanternfish <i>Protomyctophum bolini</i> ; Lanternfish <i>Protomyctophum choriodon</i> ; Norman's lanternfish <i>Protomyctophum normani</i> ; Lanternfish <i>Protomyctophum tenisoni</i>	17
25	CLA	Large Cephalopods	Cephalopods	>36
26	CLS	Small Cephalopods	Cephalopods	>36
27	BBE	Benthos	Arthropods (total 125): Cirripedia (1), Amphipoda (68), Isopoda (32), Tanaidacea (12), Decapoda (4), Reptantia (8); Brachiopods: Brachiopoda (3); Molluscs (total 94): Solenogastres (1), Bivalvia (35), Gastropoda (53), Polyplacophora (3), Scaphopoda (1), Cephalopoda (1); Pycnogonids (total 17): Pycnogonida (17); Echinodermata (total 69): Asteroidea (33), Ophiuroidea (22); Echinoidea (2); Holothuroidea (10); Crinoidea (2); Annelids: Polychaeta (89); Coelenterata: Hydrozoa (11); Bryozoa (19)	427
28	BBD	Benthic decapod	Benthic decapod <i>Nauticaris marionis</i>	1
29	ZLC	Large crustacean zooplankton	Arthropods: Euphausiids (14); Amphipods (18); Decapods (6)	38
30	ZSC	Small crustacean zooplankton	Arthropods (total 60): Calanoid copepods (48) Cyclopoid copepods (4), Harpacticoid copepods (2), Ostracods (6)	66
31	ZOT	Other zooplankton	Molluscs: Pteropods (8); Cephalopods (8); Annelids: Polychaeta (9); Ctenophores: Ctenophores (2); Cnidaria (total 11): Hydrozoa (10), Scyphozoa (1); Chaetognaths (2): <i>Eukrohnia hamat</i> , <i>Sagitta</i> spp.; Salps (3); Appendicularians (2): <i>Oikopleura</i> spp., <i>Fritillaria</i> spp.	45
32	POL	Open ocean large phytoplankton	>20um in size, predominantly diatoms	
33	POS	Open ocean small phytoplankton	<20um in size, nano- & picophytoplankton	
34	PIA	Island-associated blooms	Diatoms, predominantly <i>Chaetoceros radiicans</i> , <i>Rhizoselena curvata</i> , <i>Dictyocha speculum</i> or <i>Fragilariopsis</i> sp.	
35	PMA	Macrophytes	Predominantly <i>Macrocystis laevis</i> and <i>Durvillea antarctica</i>	
36	DMA	Macrophyte detritus		n/a
37	DGE	Detritus		n/a

Table 2.2. Area (in km²) considered to be between the contours between 0 and 1500m, as calculated using the GEBCO_08 Grid Version 20100927 from www.gebco.net

Contour	Area (km ²)
Islands	338.71
0-300m	530.18
300-500m	357.19
500-1000m	688.65
1000-1500m	647.37

Table 2.3. Total biomass (B, t) of all land based top predators for 3 time periods, including adjusted estimates for time spent away from the islands (BTA, t).

		Proportion of year at islands	Biomass (t)					
			B 1960	BTA 1960	B 1980	BTA 1980	B 2010	BTA 2010
Seals	Southern Elephant Seal	0.67	3759	2506	1008	672	637	425
	Antarctic Fur Seal	0.33	10	3	55	18.2	242	202
	Sub-Antarctic Fur Seal	0.83	129	108	1513	1260.7	4774	1591
Seal total (t)			3898	2617	2575	1951	5653	2218
Seal total %			23.9	21.8	19.2	18.7	38.4	22.8
Penguins	King Penguin	1.00	5286	5286	5286	5286	5304	5304
	Macaroni Penguin	0.58	4967	2881	3805	2207	2778	1611
	Southern Rockhopper Penguin	0.58	1459	846	933	541	449	260
	Gentoo Penguin	1.00	15	15	19	19	21	21
Penguin total (t)			11727	9028	10043	8053	8552	7197
Penguin total %			71.9	75.4	74.8	77.2	58.1	74.0
Albatross	Wandering Albatross	1.00	27.0	27	51	51.0	66	66
	Grey-headed Albatross	0.58	1.1	1	48	28.0	70	41
	Yellow-nosed Albatross	1.00	10.0	10	36	36	36	36
	Light-mantled Sooty Albatross	0.67	0.3	0	1	0.9	5	3
	Dark-mantled Sooty Albatross	0.79	5.1	4	14	11	15	12
Albatross total (t)			43	42	151	127	192	158
Albatross total (%)			0.3	0.3	1.1	1.2	1.3	1.6
Giant Petrels & Skuas	Giant Petrels and Skuas	0.55	18.1	10	34	19.0	33	18
Prions & Petrels	Prions and Petrels	0.46	615	283	615	283	282	130
Prions & Petrels (%)			3.8	2.4	4.6	2.7	1.9	1.3
Total biomass			16302	11980	13418	10433	14712	9720

Table 2.4. Breeding cycles for the seabirds at the Prince Edward Islands (adapted from Cooper and Brown 1990)

Species	% of year on islands (est.)	June	July	August	September	October	November	December	January	February	March	April	May	NOTES
King Penguin	100	Chicks	Chicks	Chicks	Chicks	Occ. & Chicks	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Chicks	Chicks	Chicks	(a)
Gentoo Penguin	100	Eggs	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Chicks	Chicks	Present	Present	Present	Present	
Macaroni Penguin	58					Present	Eggs	Eggs & Chicks	Chicks	Chicks	Moult	Moult		
Rockhopper Penguin	58					Start Mid Oct	Present	Eggs	Eggs & Chicks	Chicks	Chicks	Moult	Moult halfway	
Wandering Albatross	100	Chicks	Chicks	Chicks	Chicks	Chicks	Chicks	Chicks	Eggs & Chicks	Eggs & Chicks	Eggs & Chicks	Chicks	Chicks	
Grey-headed Albatross	58				Present	Present?	Present?	Present?	Chicks	Chicks	Chicks			(b)
Yellow-nosed Albatross	100													
Light-mantled Sooty Albatross	67					Eggs	Eggs	Eggs	Chicks	Chicks	Chicks	Chicks	Chicks	(c)
Dark-mantled Sooty Albatross	79			Mid Aug arrive	Present	Eggs	Eggs	Eggs	Chicks	Chicks	Chicks	Chicks	Chicks	
Southern Giant Petrel	58				Eggs	Eggs	Eggs & Chicks	Chicks	Chicks	Chicks	Chicks			(d)
Northern Giant Petrel	58			Eggs	Eggs	Eggs & Chicks	Chicks	Chicks	Chicks	Chicks				
Fairy Prion	42													
Salvin's Prion	42					Present	Eggs	Eggs	Chicks	Chicks				
Blue Petrel	63			Mid Aug arrive	Present	Eggs	Eggs	Chicks	Chicks					
Great-winged Petrel	67	Eggs	Eggs & Chicks	Chicks	Chicks	Chicks	Chicks					Present	Present	(d)
Soft-plumaged Petrel	38							Start mid Dec	Eggs	Eggs & Chicks	Chicks	Chicks		
Kerguelen Petrel	33					Eggs	Eggs	Chicks	Chicks					
Grey Petrel	46		Chicks	Chicks	Chicks	End mid Oct						Eggs	Eggs	
White-chinned Petrel	58				Mid month	Present	Eggs	Eggs	Eggs & Chicks	Chicks	Chicks	End mid month		
Grey-backed Storm Petrel	42													(d)
Black-bellied Storm Petrel	42													(d)
South Georgian Diving Petrel	42													(d)
Common Diving Petrel	42													(d)
Crozet Shag	100	Present	Present	Present	Present	Eggs	Eggs & Chicks	Eggs & Chicks	Chicks	Chicks	Chicks	Present	Present	
Sub-Antarctic Skua	50				Present	Present	Eggs	Eggs & Chicks	Eggs & Chicks	Chicks				
Kelp Gull	100	Present	Present	Present	Present	Present	Present	Eggs	Eggs & Chicks	Chicks	Chicks	Present	Present	
Antarctic Tern														
Kerguelen Tern														
Lesser Sheathbill	100	Present	Present	Present	Present	Present	Present	Eggs	Eggs & Chicks	Eggs & Chicks	Chicks	Moult	Moult	

Legend: Eggs Eggs & Chicks Chicks Occupation & Chicks Present Moult

Notes: (a) Offset from Macaroni penguins by half a month later; (b) Unknown: left as 100% of year; (c) Offset - half month earlier than Light Mantled Sooty; (d) No data: estimate 5 months

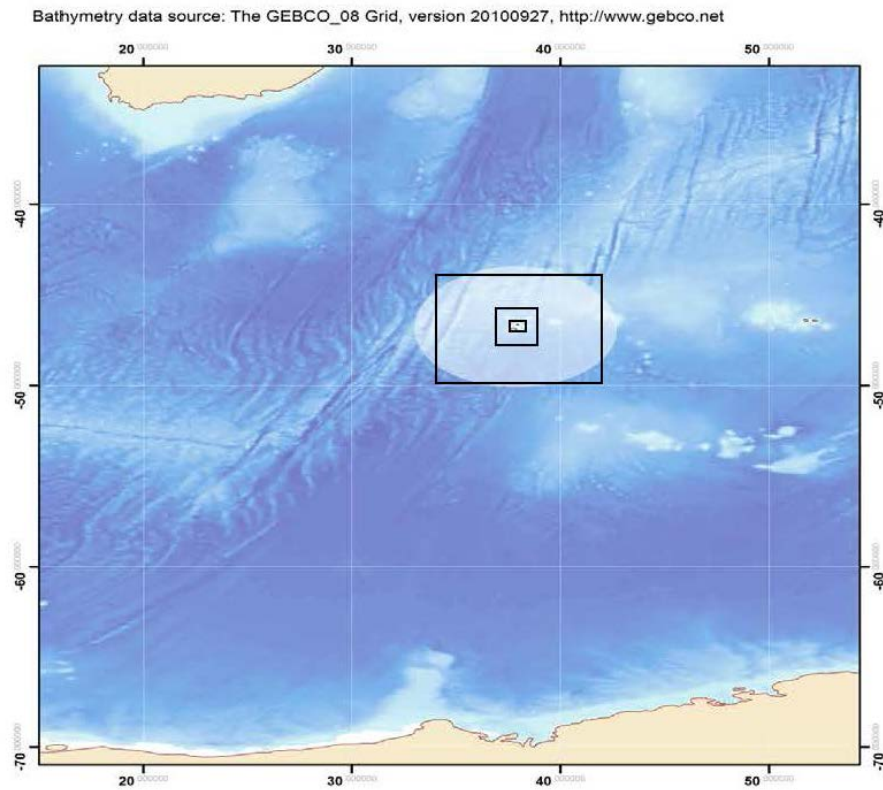


Figure 2.1. Satellite derived *chlorophyll-a* estimates from the region surrounding the Prince Edward Archipelago (Southern Ocean). Rectangles illustrate area from which satellite remote sensing data was extracted a) Large rectangle represents the 1km SeaWiFS LAC data extracted from January 1998 to December 2004, b) Medium rectangle represents the 1km MODIS LAC data extracted from January 2005 to December 2008; c) Smallest rectangle represents the 1km area LAC data extracted from SeaWiFS (Jan 1998 – Dec 2004) and MODIS (Jan 2005 – December 2008), used to quantify the island associated blooms.

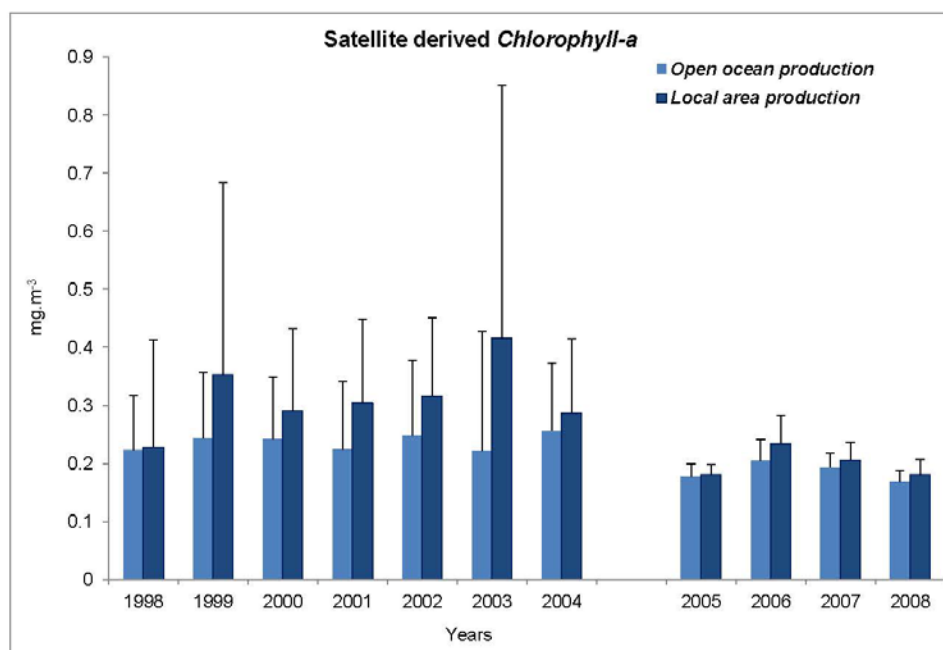


Figure 2.2. Summary of satellite derived *chlorophyll-a* data for the open ocean biomass and local area biomass in the vicinity of the Prince Edward Islands. Estimates for 1998 to 2004 were derived from the SeaWiFS Satellite, while estimates for 2005 to 2008 were derived from the MODIS Aqua satellite (see text for details). Error bars represent 1 standard deviation.

Bathymetry data source: The GEBCO_08 Grid, version 20100927, <http://www.gebco.net>

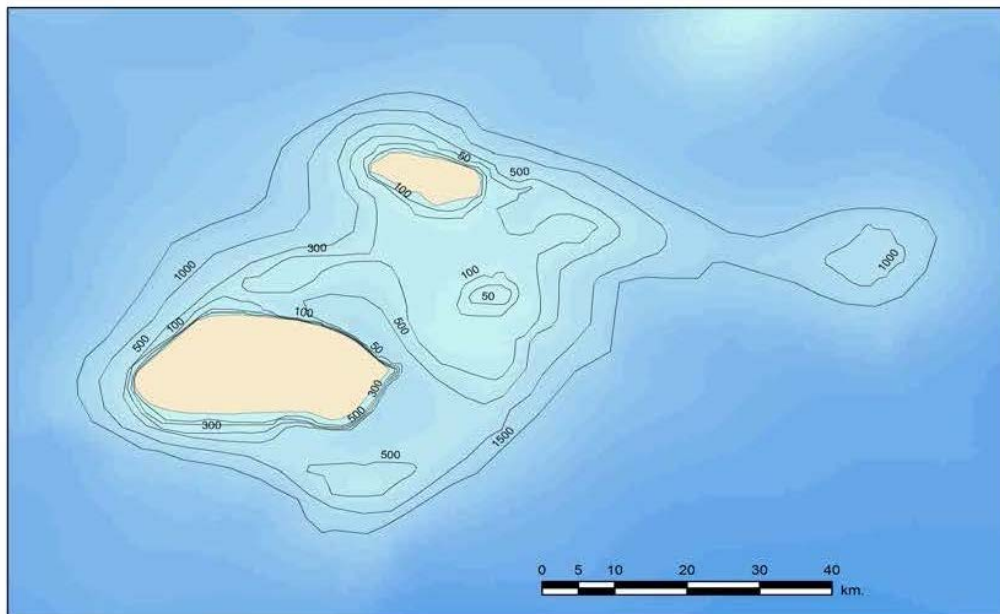


Figure 2.3. Bathymetry contour lines in the vicinity of the Prince Edward Islands estimated from the GEBCO_08 Grid Version 20100927 (www.gebco.net) bathymetry data.

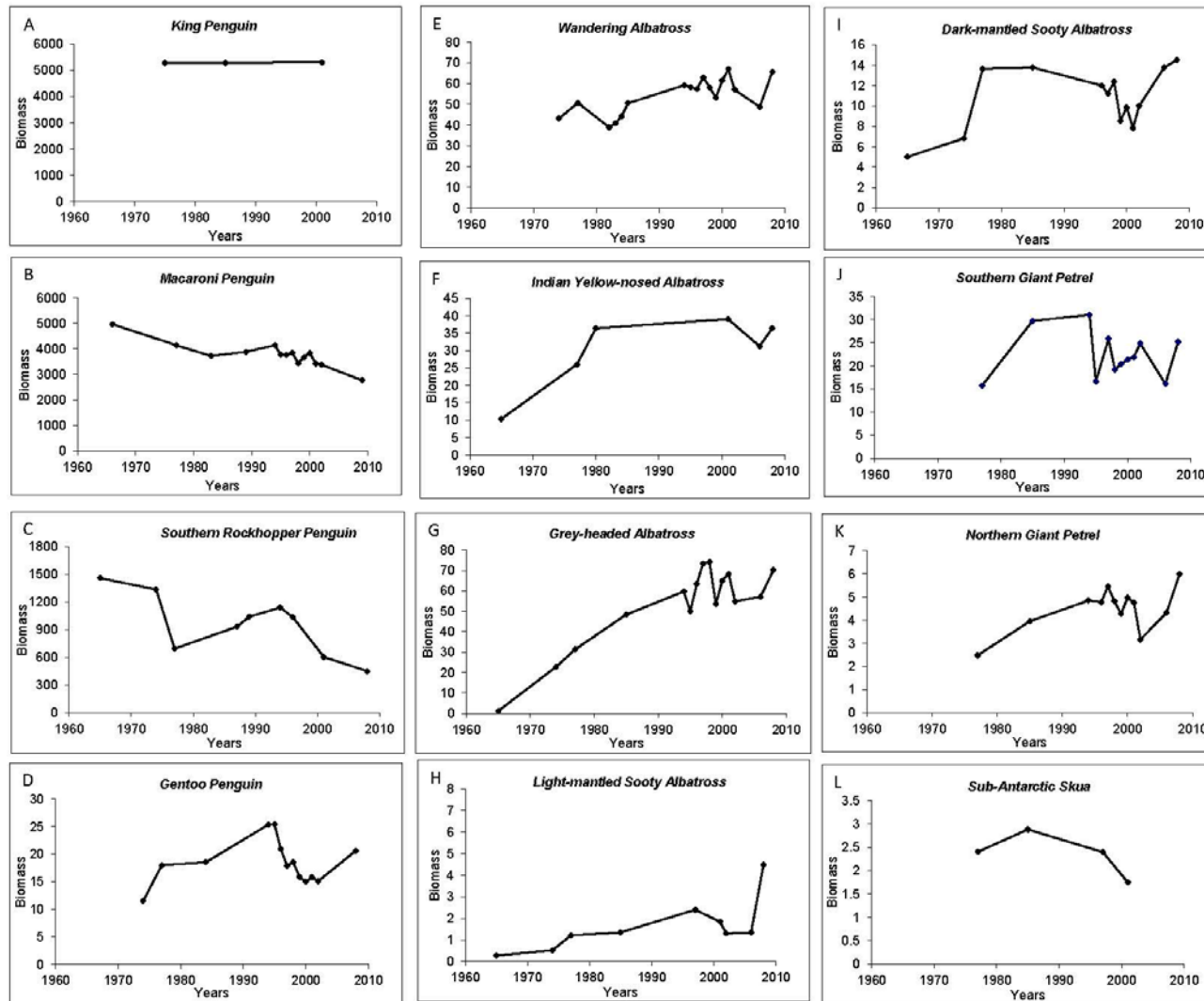


Figure 2.4.A-L. Figures illustrating bird biomass time series for penguins, albatross, Giant Petrels and Skua species at the Prince Edward Islands from the 1960s to 2010;

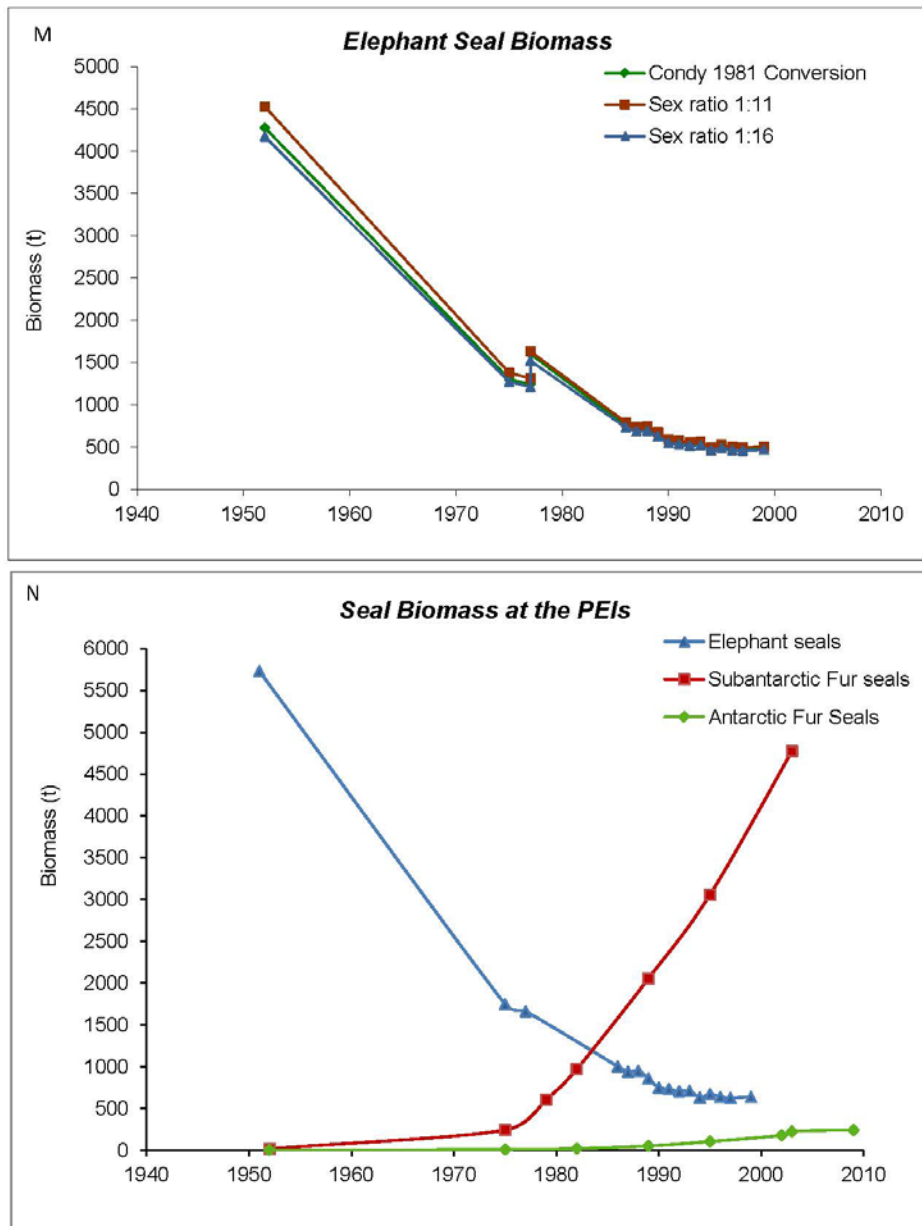


Figure 2.4.M-N. Figures illustrating seal biomass time series (M). Elephant seal biomass time series and (N). All seal biomass estimates for the Prince Edward Islands from 1950s to 2010.

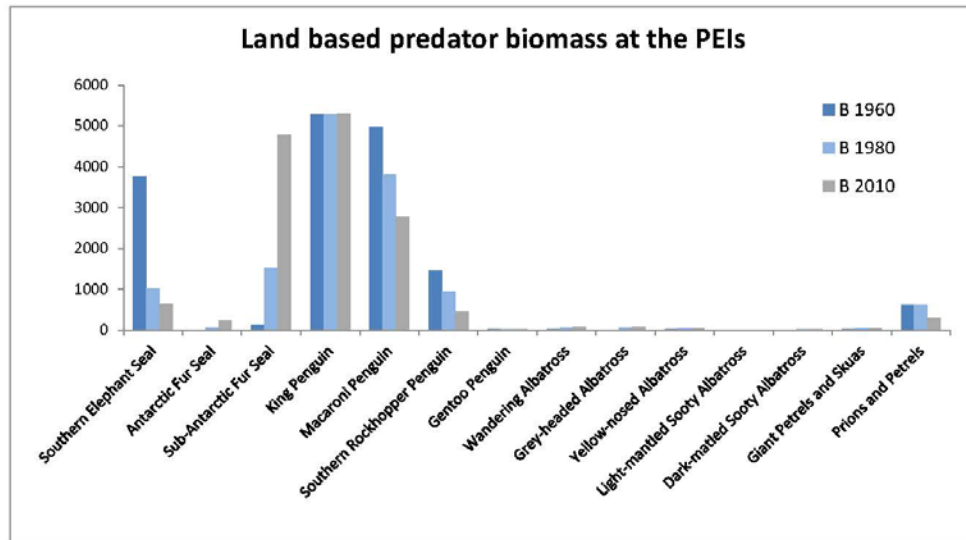


Figure 2.5. Land based predator biomass for three time periods (1960, 1980, 2000) for the Prince Edward Islands.

Chapter 3 Consumption estimates of marine resources by top predators at the Prince Edward Islands

3.1. Introduction

Population changes, as observed from long term monitoring programs, play a key role in the changes in consumption of marine resources (Guinet et al. 1996). Consumption estimates of birds and mammals have been made for many marine systems at regional (Sigurjónsson and Víkingsson 1997) and global scales (e.g., Karpouzi 2005; Karpouzi et al. 2007). Studies have been motivated in some instances by investigations of interactions between top predators and fisheries (e.g., Goldsworthy et al. 2001; Karpouzi et al. 2007). For instance, seal population recovery following the end of sealing in many systems has lead to the hypothesis that the return of the seal population has contributed to the decline or collapse of fisheries stocks. In systems where long term changes have been observed in resident populations of breeding seals and seabirds, the consideration of dietary overlap of species with fisheries, or between groups has been investigated (Goldsworthy et al. 2001). In order to assess the potential impacts that groups may have on each other, or that fisheries may have on groups, assessments of the consumption requirements for the studied groups are required. For this study, the diet composition of the top predators is summarised, and a consumption model put forward to estimate the consumption for the seabirds and seals at the islands. The data are compared between time periods, and with previous estimates of consumption at the islands.

In bioenergetic approaches to consumption estimates, detailed information is provided on population structure, differentiation of energetic requirements for different activities, as well as changes in dietary requirements depending on life stages and foraging patterns associated with such developments. Local diet information along with specific energetic content of prey is routinely incorporated into single species bioenergetic models (see Murie and Lavigne 1991; Adams et al. 1993; Perez and McAlister 1993; Boyd 2002; Mecenero et al. 2006; Halsey et al. 2008). When considering all species in an ecosystem, it is not feasible to construct such detailed assessments for each species in a system, but incorporation of the specific local diets and their

energetic density can be achieved relatively easily and the difference that this amendment can make to the consumption estimates can be significant (see Chapter 7).

For this section, a consumption model which takes into account local diet information is used. The consumption model adopted here is similar to that defined by the ICES Working Group on Seabird Ecology (ICES 2000) and is used in combination with the long term data of the land based top predator populations to provide insight into the change in the consumption of prey species between time periods.

3.2. Methods

Only species (or groups) that are considered resident at the island and are land based were included in this analysis. These included the three breeding seals (Southern elephant seal, the Antarctic fur seal and the Sub-Antarctic fur seal), four breeding penguins (Kings, Macaronis, Southern Rockhoppers and the Gentoos), five albatross (Wandering, Grey-headed, Indian Yellow-nosed, Light- and Dark-mantled Sootys) as well as the Giant petrels (the Northern and Southern Giant petrels considered together) and the small flying birds, here called the ‘Prions and Petrels’, which includes 14 species (as for section 2.1).

Consumption rates for individuals in terms of their energetic requirements were based on Field Metabolic Rates (FMR) for both the mammals and birds as summarised in Nagy et al. (1999, with amendments to selected equations from Ellis and Gabrielsen 2001) and provided in kJ.d^{-1} (Table 3.1.) In the case of the mammals the equation for ‘All mammals’ was used ($\text{FMR}=4.82\text{M}^{0.734} \text{ kJ.d}^{-1}$). For the bird species, order specific equations were used (penguins (Sphenisciformes $C=4.53\text{M}^{0.795} \text{ kJ.d}^{-1}$); albatross, Giant petrels, and prions and petrels (Procellariiformes $C=18.4\text{M}^{0.599} \text{ kJ.d}^{-1}$ – adjusted by Ellis and Gabrielsen 2001 to $C=17.9\text{M}^{0.6} \text{ kJ.d}^{-1}$) and for the two terns (Charadriiformes $C=8.13\text{M}^{0.77} \text{ kJ.d}^{-1}$ – adjusted in Ellis and Gabrielsen 2001 to $C=8.49\text{M}^{0.77} \text{ kJ.d}^{-1}$); Nagy et al. 1999). Estimates of body mass were taken from the literature. For the three seal species Condry’s (1981) ‘average seal mass’ was used, and for the bird species/groups data from Ryan and Bester’s (2008) summary of pelagic predators was used. In the two instances where more than one species was considered in a group (i.e. for the ‘Giant Petrels’ and ‘Prion and Petrel’ groups), mass estimates are provided based on

weighted contributions (according to population numbers) for each contributing species, and the consumption rates were estimated for each species individually, but the consumption estimates used for the group as a whole are calculated from weighted averages (of the biomass contributions) of all species considered in the group.

By dividing the daily individual consumption rates of energy required estimated above by the amount of energy in a gram of the diet, it is possible to convert the consumption rates from energy-based (kJ.d^{-1}) into mass-based estimates ($\text{g dry weight.d}^{-1}$). In order to do this, it is necessary to have the specific diets of each species/group under consideration, along with the energetic content of the prey, and the assimilation efficiencies of each consumer.

To achieve this, a literature review of the unique diets and assimilation efficiencies of species/groups from the islands was compiled. Following this, diet matrices for each species/group were collapsed into six broad prey group categories: vertebrate prey, general fish, mesopelagic fish (dominated by myctophids), cephalopods, crustaceans and a final group which incorporated all remaining prey categories (including benthos and other zooplankton) (Table 3.2). The energetic content of these six prey categories for the region was established from the literature and summarised (Appendix 3.B). An 'average' energetic value per gram of diet was calculated for each species/group using the relative contributions of the prey categories, weighted by their contribution to the energetic content of the diet (kJ.g^{-1} dry weight) (Table 3.2). Because a fraction of this energetic content is lost during digestion (i.e. not assimilated) the actual energetic value of each gram of diet is decreased in proportion to the assimilation efficiencies of each species/group (Table 3.2). The resulting reduced energetic content of the prey (in kJ.g^{-1} dry weight) was divided into the estimates of energetic requirements from the consumption estimates (kJ.d^{-1}), resulting in a consumption rate in terms of mass instead of energy ($\text{g dry weight.ind}^{-1}.\text{d}^{-1}$). In order to estimate the biomass consumed daily, a dry weight to wet weight conversion of 3.33 was used (water content of prey was assumed to be 70%; Nagy 1987; Nagy et al. 1999). The method described here is the same as the bioenergetic model created by the ICES Working Group on Seabird Ecology (ICES 2000) and used in Karpouzi et al. (2007):

$$DFI_i = \frac{ER_i}{\sum_{j=1}^G DC_{ij} \times ED_j} \times \frac{1}{AE_i}$$

Where DFI_i is the daily food intake for each species i (g.ind.d^{-1}), ER_i is the energy required for each i (kJ.d^{-1}), DC_{ij} is the fraction of prey item j in the diet of each i , ED_j is the mean energy density of each prey j (kJ.g^{-1}). AE_i is the mean food assimilation efficiency for each i , and G the total number of prey categories considered. In this study, the ER_i was based on the FMR equations of Nagy et al. (1999, with adjustments from Ellis and Gabrielson 2001) for mammals and birds, the composition of the diet (DC_{ij} , or fraction of the food prey item) was determined from a literature review of the diets of the top predators at the islands, and then consolidated into six principle prey groups (i.e. $G=6$). The mean energy density of each prey (ED_j) was determined from the literature as was the food assimilation efficiency (AE_i) for each consumer.

To extrapolate from individuals to consider the annual consumption of each species/group as well as the land based predators as a whole, data on population estimates along with the proportion of the year that each species/group spends at the islands is required. These calculations were completed for three time periods for which there are data (1960s, 1980s, and 2000s; see section 2.1) and values of total consumption (in metric tonnes) of each of the principle prey groups calculated.

3.3 Results

Daily energetic requirements as calculated from Nagy et al.'s (1999) FMRs with amendments as per Ellis and Gabrielsen (2001), for each of the land based top predators are provided in Table 3.1 along with a summary of average mass, the population estimates (details of estimates are provided in Chapter 2) and the percentage of time each species/group spends at the islands.

Diets

A full review of the diets for all top predators is provided in the Appendix 3.A. In summary, the Southern elephant seals consume a mix of fish and cephalopods, while both fur seal diets have diets dominated by myctophids. Of the penguins, two are principally fish eaters: the Kings with a diet dominated by myctophids and the Gentoos with a principally mixed fish diet, along with

some crustaceans, notably the benthic decapod. Both the Macaronis and the Rockhoppers have predominantly zooplankton diets. All albatross species have a mix of fish and squid. The *Giant Petrel* group have a diet dominated by vertebrates (mainly penguins) while the *Prions and Petrel* group diet is dominated by crustaceans with fish and cephalopods contributing. A summary of the diet composition of the land based top predator species/groups, summarised into 6 prey categories is provided (Table 3.2).

3.3.1. Assimilation efficiencies

The assimilation efficiency for all mammal groups was set to 0.90 (i.e. 0.1 is not assimilated) which was based on digestive efficiencies recorded in the literature for fur seals (93% Miller 1978, Mecenero et al. 2006) and juvenile Steller sea lions 92-96% (Rosen et al. 2000). These figures are similar to those found for harp seals which ranged between 93.5 and 96.6% (Lawson et al. 1997). It is noted that digestive efficiency may vary with age (Rosen and Trites 2000) but this is not considered for the purposes of this model. Assimilation efficiencies for the King penguins, Macaroni and Rockhopper penguins were all set to 76% based on a summary of assimilation efficiencies for other penguins (African penguins (previously ‘Jackass’ penguin) 74% on a diet of fish (Cooper 1977) and King penguins 81% on a cephalopod diet (Adams 1984), fish diet (75.5%) and squid diet (73%) (Adams 1984, and Adams unpublished, both in Adams et al. (1993)). For the Gentoo penguin a value of 80% was used based on Clark and Prince (1981) and Abrams (1985). For *Prions and Petrel* group, a value of 76% was used as in Brown (1989), which was based on a study of White-chinned petrels fed on crustaceans, squid and fish (Jackson 1986). A summary of assimilation efficiencies is given in Table 3.2.

3.3.2. Energetic content of prey

Six prey categories were nominated based on the difference in energetic density and their importance in the diets of the species/groups considered: vertebrate, general fish (all excluding small pelagic fish), mesopelagic fish (i.e. small pelagic, dominated by Myctophids), cephalopod, crustacean and other. A literature review of the energetic density of prey which occurs at the islands was conducted. The highest energetic content of prey (kJ.g^{-1} dry weight) was for vertebrate prey (30.7 kJ.g^{-1} dry weight) which was based on only two wet weight data values

(seal blubber, DW Doidge pers comm. and penguin carrion, Burger 1981; both in Hunter 1985). The next most energetically rich prey group considered is that of the mesopelagic fish (dominated by myctophids) at 27.4 kJ.g^{-1} dry weight ($n=17$). Data from Tierney et al. (2002) show that energetic content of myctophid fish from Macquarie Island ranges between $22.6\text{--}59.3 \text{ kJ.g}^{-1}$ dry weight, which suggests that this value may be an underestimate. A value for all other fish (excluding the mesopelagic fish) was based on much smaller data set ($n=5$), and a value of 21.3 kJ.g^{-1} was settled on. This value is in kJ.g^{-1} dry weight of fish, and is higher than values used in previous studies (Appendix 3.B.) which have a kJ of wet weight value of around 3.98 kJ.g^{-1} wet weight for fish (Croxall and Prince 1982) which when converted to dry weight (using a factor of 4, which from the literature appears to be most appropriate for this group; see Cherel and Ridoux 1992) gives a lower value of approximately 15.92 kJ.g^{-1} dry weight.

Cephalopods had the lowest energetic content at 10.3 kJ.g^{-1} dry weight, which was also based on wet weight estimates with conversion to dry weight values based on water content of 70%. Crustaceans were set to have an energetic value of 14.8 kJ.g^{-1} dry weight, calculated from a wet weight value of 4.45 kJ.g^{-1} assuming a wet to dry weight conversion of 3.33 (ie. water content 70%) and are in line with all estimates available (e.g., 4.35 kJ.g^{-1} for krill; Croxall and Prince 1982). All remaining diet categories were put together in a group named 'Other', which consisted of benthic prey along with non crustacean zooplankton, and arbitrarily given the energetic value of 12 kJ.g^{-1} dry weight. Using these data, in conjunction with the relative proportions (in terms of mass) that each prey category is found in the diet of each species/group, an average energetic value of a unit of mass of each diet for each species/group was calculated (Table 3.2). When dry weight estimates were available they were used, when unavailable wet weight conversions assuming 70% water content were used. A summary of the energetic content of prey for the six selected categories is given in Appendix 3.B.

Land based top predator community consumption

Using estimates for time spent at the islands based on the breeding seasons for all species/groups considered (Condy 1981; Cooper and Brown 1990), along with published population estimates (see Section 2.1), calculations were made for three time periods for which there are data (1960s,

1980s, and 2000s). An approximation of total consumption (in metric tonnes) by each of the land based predators of each of the principle prey groups was made and is provided in Table 3.3.

3.4. Discussion

The total consumption for the system was 589 601 t in the 1960s. This declined to 510 750 t in the 1980s and subsequently increased to 520 899 t in the 2000s (Table 3.3). In the 1960s the mesopelagic fish and the crustaceans were the two most important prey items representing 42.8% and 43.1% of the total consumption respectively. By the 2000s estimate, the mesopelagic fish dominate the consumption (56.2%) with the crustaceans reduced (31.7%). The ‘cephalopod’ contribution remained fairly constant through time (at ~ 11%), while the ‘vertebrate’, ‘general fish’ and ‘other’ groups all made low contributions to the overall consumption (less than 2%). The highest contributor to the change was the consumption of mesopelagic fish by the Subantarctic fur seals which increased exponentially in their population during this time (from about 4000 individuals in the 1960s to over 140 000 by the year 2000; see Table 3.1).

The most important component of the seabird consumption was the mesopelagic fish and the crustaceans. In the 1960s estimate the contribution from each of these two groups was approximately equal (43.4% and 45.1% respectively), but by the 2000s assessment the mesopelagic fish had a higher contribution to the overall consumption (Fig 3.1). This was a result of the decline in both the Macaroni and Rockhopper populations (predominantly crustacean eating) coupled with the steady King penguin population estimate (which had a diet dominated by mesopelagic fish).

For the seal consumption, the early estimates from the 1960s show cephalopods to be most important (51.5%), followed by mesopelagic fish (29.7%), and fish in general (19.8%), reflecting the Southern elephant seal diet. By the 2000s the mesopelagic fish were the most important prey group (93.6%), with the cephalopods decreased to 4.4% and the general fish group to 1.1%. These changes reflect the decline in the Southern elephant seal population and the recovery of the fur seal populations between 1960 and 2000 with the seal community consumption in 2000 reflecting the diet of the fur seals which is comprised predominantly of myctophid fish (see Table 3.2, Figure 3.1.B and Appendix 3.A). In terms of total consumption, the estimates for the

Southern elephant seals in the early period is around 24 125 t, which decreased to approximately 4 061 t by the 2000s. In contrast the consumption by the fur seals initially was low (1 660 t) but by the 2000s estimate reached around 59 555 t. Dietary overlap between these two groups is thought to be limited: both are believed to take myctophid fish, however, the contribution to the Southern elephant seal diet is considered to be limited (<10% of the diet) while this prey dominates the fur seal diets.

When all land based top predators are considered together, the pattern observed in the seabird community was clearly evident, which was due to the seabirds having the highest contribution to the overall biomass of this group. In the 1960s assessment, mesopelagic fish and crustaceans were equally important, but by the 2000s the mesopelagics dominated followed by crustaceans, a trend evidenced in the seabird analysis but emphasized by the changes in the seal community consumption as well. Cephalopods were the third most important prey item and remained between 10 and 12% of the overall consumption for all years.

Comparison to other estimates

An assessment of the consumption of penguins at the PEIs was made by Adams et al. (1993) for the 1980s period. Using a bioenergetic model, the total penguin consumption was estimated to be 880 000 t. In comparison, estimates from this study (considering only penguins for the same period) show the consumption to be approximately half of this estimate (at 442 083 t). The energetic content of prey, however, for this study was based on very similar energetic content of prey for all groups, excepting the fish, which were estimated to have a value of 3.97 kJ.g^{-1} wet weight, which is equivalent to 15.88 kJ.g^{-1} dry weight (just over half the value used in this study for myctophid fish, and also less than the value used for all other fish). Recalculating the consumption for the penguins using these data, the consumption for the 1980s increases to 649 778 t, an increase of 1.35 times the estimate in this study, but still 1.35 times less than the estimate from Adams et al. (1993). Differences in consumption between the two studies include a higher contribution of crustaceans to the diet of the penguin community in this study (38% versus 18% in Adams et al. 1993), and Adams et al. (1993) having a higher contribution of mesopelagic fish (70% versus 51% in this study). The contribution of cephalopods is similar

between studies (10% this study, 11% Adams et al. 1993) with all other groups less than 1.5% for both studies.

For the smaller birds found at the PEIs, food consumption estimates for Marion Island only had estimates for Whitechinned petrels at 5240 t; Great-winged petrels 12 576 t; Blue petrels 1798 t; and Salvin's prions 28 685 t with most of the consumption taking place in summer except for the Great-winged petrels which occur and feed at the islands in winter. The total consumption for these groups was estimated to be 48 299 t, which is higher than the estimate here of 35 304 t despite this estimate being for both Marion and Prince Edward Islands.

Seal consumption for the system was estimated here to be approximately 59 555 t per year for the Subantarctic fur seals, and 1 574 t for the Antarctic fur seals for the 2000s period. Makhado (2002) provided consumption estimates for the fur seal populations from the 1990s. Estimates of 185 986 t and 11 314 t per year for the Subantarctic and Antarctic fur seals respectively were found and far exceed the calculations done in this study. Differences in the assessments include that Makhado (2002) uses a different consumption equation (Nagy 1994 versus Nagy et al. 1999), an age structured model, and bases the calculations for the whole year (365, instead of pro-rata for time spent at the islands). The calorific content of the diet (particularly the myctophids as they dominate both fur seal diets) is similar in both studies (7.00 kJ.g^{-1} in Makhado 2002), though an attempt to recalculate the assessments of the model used in Makhado's (2002) study suggest that this value may have been used as a dry weight and not wet weight when converting from kJ required to grams consumed per day.

The accuracy of the estimates in this study is determined by the various input parameters, which include population estimates, diet matrices, energetic density of prey, assimilation efficiencies and the field metabolic rates. In bioenergetic studies, care is taken to consider the different energetic requirements needed for different phases of development (juvenile/adult, breeding/non-breeding) and these factors have not been taken into account in this study. No formal sensitivity test has been carried out on these results and therefore the uncertainty is not addressed. In previous studies on consumption rates of communities, population estimates and energetic requirements (existence metabolism values, flight or swimming activity levels and their energy costs) were found to have the greatest impact on the consumption estimates (Furness

1978, seabird community, Shetland Islands). The early population estimates for most of the groups, which were taken from the literature and used in this study, are not considered accurate, but more recent estimates may be considered more accurate. Regarding the estimates of energetic requirements, the estimates are made using widely accepted field metabolic rates (Nagy et al. 1999), though the study lacks the detail that would be included in bioenergetic assessments of single species. The objective is to provide an overview of the consumption of the community with the focus on the changes observed between time periods, therefore any assumptions are made across all time periods, providing some insight as to how the system has changed over time (as argued in Guinet et al. 1996).

3.5. Conclusions

In conclusion, the consumption estimates here are, in general, lower than earlier previous estimates (for the same time periods) which are due in part to a variety of reasons including, (a) the choice of consumption model, (b) use of a different calorific value of the prey, and (c) consumption estimates in this study including consumption only for the duration of the time spent at the islands. Future consultation to improve the population estimates and dietary habits for all the land based predators would improve the consumption assessment. Estimates from this study show that there has been a change from a system with both crustaceans and myctophid fish being equally important to one where myctophid fish are the dominant prey item for the land based top predators. This reflects the population changes with the increasing fur seal population (diet dominated by myctophids) and the declining Southern Rockhopper and Macaroni penguin populations.

Table 3.1. Species list (common names), average weight, field metabolic equations used, daily consumption rates for individuals (in terms of wet weight), population estimates for the 1960s, 1980s and 2000s and proportion of time spent at the islands.

Species	Average mass	FMR equation (dry mass)	Consumption (wet mass)	Population estimate			Time at islands
	kg	$\text{kJ} \cdot \text{ind}^{-1} \cdot \text{d}^{-1}$	$\text{g} \cdot \text{ind}^{-1} \cdot \text{d}^{-1}$	1960s #s	1980s #s	2000 #s	fraction of yr
Southern Elephant Seals	353	$C=4.82M^{0.734}$	12550.26	7900	2123	1330	0.67
Antarctic Fur Seals	46.92		1793.85	139	778	4810	0.50
Sub-Antarctic Fur Seals	33.67		1381.02	3843	44930	141778	0.83
King Penguins	12.0	$C=4.53M^{0.795}$	1395.81	440460	440460	442000	1.00
Macaroni Penguins	4.6		967.23	1080000	810000	744000	0.58
Southern Rockhopper Penguins	2.7		693.11	540000	345304	224000	0.58
Gentoo Penguins	6.0		1027.47	2500	3086	2638	1.00
Wandering Albatross	9.0	$C=17.9M^{0.6}$	1407.82	3000	5620	7438	1.00
Grey-headed Albatross	3.7		500.62	300	14000	18458	0.58
Yellow-nosed Albatross	2.6		409.45	4000	13074	15000	1.00
Light-mantled Sooty Albatross	2.8		458.88	100	482	658	0.67
Dark-mantled Sooty Albatross	2.5		466.50	2000	5510	3128	0.79
Giant Petrels	4.4		387.86	4114	7590	6050	0.58
Prions and Petrels	0.23	$C=17.9M^{0.6}$ & $C=8.49M^{0.77*}$	151.82	1199170	1199170	1199170	0.50

Table 3.2. Energetic content of six prey categories provided with summarised diet matrix, average energy density of diet and assimilation efficiencies for each species.

	PREY CATEGORIES						Average energy density of diet (kJ.g ⁻¹ dry weight)	Assimilation efficiency
Species	Vertebrate	Fish - general	Fish - mesopelagic	Cephalopods	Crustaceans	Other		
Energetic content of prey (kJ.g ⁻¹ dry weight)	30.7	21.3	27.4	10.3	14.8	12		
Southern Elephant Seals		0.200	0.250	0.550			16.78	0.90
Antarctic Fur Seals	0.005	0.006	0.948	0.040	0.001		26.68	0.90
Sub-Antarctic Fur Seals		0.006	0.982	0.010	0.002		27.17	0.90
King Penguins			0.850	0.140	0.010		24.88	0.76
Macaroni Penguins			0.180	0.070	0.750		16.75	0.76
Southern Rockhopper Penguins		0.001	0.069	0.020	0.810	0.100	15.31	0.76
Gentoo Penguins		0.590	0.000	0.010	0.370	0.030	18.51	0.80
Wandering Albatross	0.003		0.100	0.800	0.087	0.010	12.48	0.80
Grey-headed Albatross	0.004		0.586	0.350	0.030	0.030	20.59	0.80
Yellow-nosed Albatross			0.580	0.380	0.030	0.010	20.37	0.80
Light-mantled Sooty Albatross			0.500	0.460	0.030	0.010	19.00	0.80
Dark-mantled Sooty Albatross			0.410	0.550	0.030	0.010	17.46	0.80
Giant Petrels	0.911		0.035	0.054	0.001		29.49	0.80
Prions and Petrels			0.220	0.140	0.600	0.040	16.83	0.76

Table 3.3. Consumption (in t per year) of each species/group by prey category for A)1960s, B)1980s and C)2000s.

A

1960 Consumption		Prey (t)					
	t per year	Vertebrate	Fish general	Fish mesopelagic	Cephalopods	Crustaceans	Other
Southern Elephant Seals	24125.79	0.00	4825.16	6031.45	13269.19	0.00	0.00
Antarctic Fur Seals	45.51	0.23	0.27	43.14	1.82	0.05	0.00
Sub-Antarctic Fur Seals	1614.29	0.00	9.69	1585.24	16.14	3.23	0.00
King Penguins	224402.09	0.00	0.00	190741.78	31416.29	2244.02	0.00
Macaroni Penguins	221143.08	0.00	0.00	39805.75	15480.02	165857.31	0.00
Southern Rockhopper Penguins	79235.31	0.00	79.24	5467.24	1584.71	64180.60	7923.53
Gentoo Penguins	937.57	0.00	553.17	0.00	9.38	346.90	28.13
Wandering Albatross	1541.57	4.62	0.00	154.16	1233.25	134.12	15.42
Grey-headed Albatross	31.79	0.13	0.00	18.63	11.13	0.95	0.95
Yellow-nosed Albatross	597.80	0.00	0.00	346.72	227.16	17.93	5.98
Light-mantled Sooty Albatross	11.17	0.00	0.00	5.58	5.14	0.33	0.11
Dark-mantled Sooty Albatross	269.60	0.00	0.00	110.54	148.28	8.09	2.70
Giant Petrels	340.87	310.53	0.00	11.93	18.24	0.17	0.00
Prions and Petrels	35304.64	0.00	0.00	7767.02	4942.65	21182.79	1412.19
TOTAL	589601.08	315.51	5467.52	252089.17	68363.39	253976.49	9389.00

B

1980 Consumption		Prey (t)					
	t per year	Vertebrate	Fish general	Fish mesopelagic	Cephalopods	Crustaceans	Other
Southern Elephant Seals	6483.42	0.00	1296.68	1620.86	3565.88	0.00	0.00
Antarctic Fur Seals	254.70	1.27	1.53	241.46	10.19	0.25	0.00
Sub-Antarctic Fur Seals	18873.32	0.00	113.24	18533.60	188.73	37.75	0.00
King Penguins	224402.09	0.00	0.00	190741.78	31416.29	2244.02	0.00
Macaroni Penguins	165857.31	0.00	0.00	29854.32	11610.01	124392.98	0.00
Southern Rockhopper Penguins	50667.17	0.00	50.67	3496.03	1013.34	41040.41	5066.72
Gentoo Penguins	1157.33	0.00	682.83	0.00	11.57	428.21	34.72
Wandering Albatross	2887.87	8.66	0.00	288.79	2310.30	251.24	28.88
Grey-headed Albatross	1483.74	5.93	0.00	869.47	519.31	44.51	44.51
Yellow-nosed Albatross	1953.90	0.00	0.00	1133.26	742.48	58.62	19.54
Light-mantled Sooty Albatross	53.82	0.00	0.00	26.91	24.76	1.61	0.54
Dark-mantled Sooty Albatross	742.74	0.00	0.00	304.53	408.51	22.28	7.43
Giant Petrels	628.88	572.91	0.00	22.01	33.65	0.31	0.00
Prions and Petrels	35304.64	0.00	0.00	7767.02	4942.65	21182.79	1412.19
TOTAL	510750.95	588.78	2144.95	254900.03	56797.68	189704.99	6614.52

C

2000		Prey (t)					
Prey \ Predator	Consumption t per year	Vertebrate	Fish general	Fish mesopelagic	Cephalopods	Crustaceans	Other
Southern Elephant Seals	4061.68	0.00	812.34	1015.42	2233.93	0.00	0.00
Antarctic Fur Seals	1574.69	7.87	9.45	1492.80	62.99	1.57	0.00
Sub-Antarctic Fur Seals	59555.35	0.00	357.33	58483.36	595.55	119.11	0.00
King Penguins	225186.68	0.00	0.00	191408.68	31526.13	2251.87	0.00
Macaroni Penguins	152343.01	0.00	0.00	27421.74	10664.01	114257.26	0.00
Southern Rockhopper Penguins	32867.98	0.00	32.87	2267.89	657.36	26623.07	3286.80
Gentoo Penguins	989.32	0.00	583.70	0.00	9.89	366.05	29.68
Wandering Albatross	3822.06	11.47	0.00	382.21	3057.65	332.52	38.22
Grey-headed Albatross	1956.21	7.82	0.00	1146.34	684.67	58.69	58.69
Yellow-nosed Albatross	2241.74	0.00	0.00	1300.21	851.86	67.25	22.42
Light-mantled Sooty Albatross	73.47	0.00	0.00	36.74	33.80	2.20	0.73
Dark-mantled Sooty Albatross	421.65	0.00	0.00	172.88	231.91	12.65	4.22
Giant Petrels	501.28	456.67	0.00	17.54	26.82	0.25	0.00
Prions and Petrels	35304.64	0.00	0.00	7767.02	4942.65	21182.79	1412.19
TOTAL	520899.77	483.83	1795.69	292912.82	55579.22	165275.27	4852.94

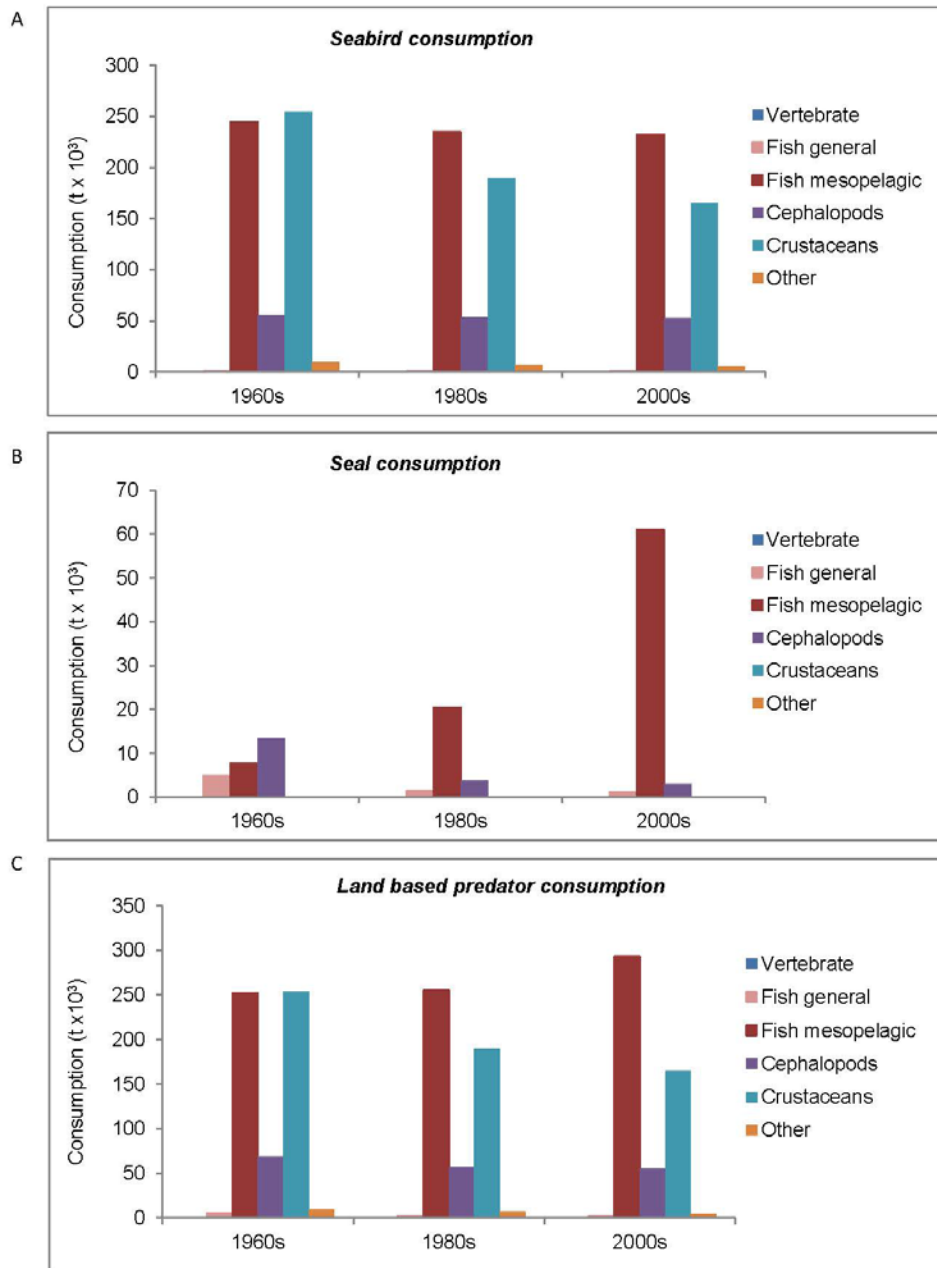


Figure 3.1. Community consumption estimates of the six prey categories for A) Seabirds, B) Mammals, C) All land based top predators

Chapter 4 Quantifying local and advected resources: Relative importance of the producers in the system at different spatial scales

4.1. Introduction

Oceanic islands are known to have an effect on the surrounding waters, resulting in increased productivity. This phenomenon is known as the ‘island mass effect’ (Doty and Oguri 1956). The Southern Ocean is, in general, characterised as a high nutrient, low chlorophyll (HNLC) region. However, many sub-Antarctic islands, including the Prince Edward Islands (PEI), are hotspots of biological productivity and are host to millions of seabirds and seals which use the islands as a breeding ground and refuge (Pakhomov and Chown 2003).

A conceptual model called the ‘Life Support System’ (LSS) has been created for the PEIs to describe how these islands are able to support the high biomass of top predators on the islands (Pakhomov and Froneman 1999b; Pakhomov and Chown 2003). The LSS as it stands now has ‘offshore’ and ‘inshore’ components that are named after the categories for the source of the supporting production. The ‘offshore’ component may be considered the allochthonous, or oceanic input, production that is advected into the system. This open ocean productivity is generally low (Hempel 1985; Pakhomov and Froneman 1999b). The ‘inshore’ component is the autochthonous production of the system and includes both island-associated phytoplankton blooms and near-shore macrophyte production. It is this production that is associated with the ‘island mass effect’.

Islands create the ‘island mass effect’ in a number of ways. It has been demonstrated that, in the HNLC Southern Ocean, input of iron from islands and their shallow shelves into the surrounding waters increases productivity (Atkinson et al. 2001; Blain et al. 2001; Blain et al. 2008). Islands also create a disturbance in the flow of the incident current, resulting in turbulence and mixing which may provide suitable conditions for elevated production associated with the islands, also known as ‘island stirring’ (Mann and Lazier 1996). At the neighboring Crozet archipelago (Atkinson et al. 2001; Bakker et al. 2007) and the Kerguelen plateau (Armand et al. 2008), as well as at the PEIs (Perissinotto et al. 2000), observed increases in productivity in the vicinity of, or downstream of the islands has been attributed to the ‘island mass effect’. Island shelf regions

provide substrata for near-shore macrophyte production, and runoff from the islands may carry nutrients from top predator populations that reside on the islands, aiding the benthic production and resulting in surface stratification, potentially enhancing local phytoplankton productivity as observed at the PEIs (Perissinotto and Duncombe Rae 1990).

The oceanography around the PEIs is complex because of a combination of the frontal features, the bathymetry and the interaction with the islands themselves (Ansorge and Lutjeharms 2002; Ansorge and Lutjeharms 2003; Ansorge and Lutjeharms 2005). Two frontal features are found in the vicinity of the islands: the Sub-Antarctic Front (SAF) to the north and the Antarctic Polar Front (APF) to the south (Deacon 1983; Lutjeharms 1985; Nowlin and Klinck 1986) (Figure 4.1). The position of these fronts is dynamic and variable (Lutjeharms and Valentine 1984; Duncombe Rae 1989a; Lutjeharms et al. 2002) and their proximity (the SAF in particular) is hypothesized to have a significant effect on the hydrodynamics at the islands. When the SAF is close to the islands, the increased current velocities associated with this front are predicted to lead to a flow-through system between the islands (Pakhomov and Froneman 1999a; Ansorge and Lutjeharms 2000) and advected sources of primary productivity dominate the system. Conversely, when the SAF is further north, lower velocities of the inter-frontal zone are predicted to result in water retention over the inter-island shelf and, as a consequence, little exchange of inshore/offshore waters over the inter-island region occurs (Perissinotto and Duncombe Rae 1990). Cross advection over the PEI shelf when the SAF is far to the north of the islands has been observed (Hunt et al. 2008), however there is little doubt that phytoplankton blooms can and do occur in the vicinity of the islands (Allanson et al. 1985; Duncombe Rae 1989b; Perissinotto and Duncombe Rae 1990). A number of mechanisms for on-shelf water retention have been postulated in the past, including upwelling (Grindley and David 1985), eddy formation (Allanson et al. 1985) and Taylor column formation (Perissinotto and Duncombe Rae 1990). However oceanographic data to support such findings are lacking. More recent studies have found mesoscale eddies up- and downstream of the islands (Ansorge and Lutjeharms 2002; Ansorge and Lutjeharms 2003; Ansorge et al. 2004; Durgadoo et al. 2010). Observed elevated phytoplankton production may be the result of the trapping of these eddies over the island shelf, as has been observed at other Southern Ocean islands, e.g., South Georgia (Whitehouse et al. 1999). A summary of knowledge points to the dynamics of frontal systems as the drivers of

shelf-water retention, and consequently of the relevant contributions of allochthonous and autochthonous phytoplankton (Perissinotto et al. 2000; Ansorge and Lutjeharms 2002).

The second form of autochthonous production is composed of benthic macrophytes. Two kelp species dominate the biomass, the endemic *Macrocystis laevis* (Hay 1986) and *Durvillaea antarctica* (Chamisso) (Hariot 1892). *Macrocystis laevis* occurs along the lee shore of Marion island, and is generally found between 5 and 20m depth (Attwood et al. 1991) but may be found at depths of up to 68m in areas where the substratum is favourable (Perissinotto and McQuaid 1992a). *Durvillaea antarctica* occurs in the infralittoral fringe of the islands (Beckley and Branch 1992).

The aim of this study was to quantify, for the first time, the relative importance of the three sources of primary production to the PEI food web. The relative contribution of each of the three primary production sources will differ, depending on the spatial scale at which the system is considered and we set out to test this by developing Ecopath models with four different boundary sizes. A preliminary investigation into the ecosystem boundary size, as determined by the centrally placed foragers, found that all energetic requirements for the inhabitants of the PEI could be met at the scale of the Economic Exclusion Zone (EEZ) (see Chapter 6). For this reason the EEZ i.e. a circular area of 200 nautical mile (nm) radius centred on the islands was chosen as the largest model considered, and a series of sequentially smaller models, the smallest of which was chosen to represent the island shelf area (radius of 20nm) was used. Using the top down approach of assessing consumer impacts on primary producers and ecosystem mass balance, we aimed to quantitatively evaluate the previous conceptual models of the PEI LSS.

4.2. Methods

The ecosystem model

A mass-balanced network model (Ecopath) was used to construct an ecosystem model of the Prince Edward Islands. The basic model is a closed system formulation of the functional groups in an ecosystem and the full methodology can be found in the user's guide (Christensen et al. 2004, Christensen et al. 2008). Each group (functionally related group or a single species) is

represented by their biomass and the groups are linked through their trophic interactions. The Ecopath model is based on two fundamental equations, one to describe the production term of the system:

Eq 1: Production = predation mortality + fishing mortality + biomass buildup + net migration + other mortality;

and another that satisfies the energy balance within each functional group:

Eq 2: Production = Consumption - Respiration - Unassimilated food.

Although the Ecopath model has the capability to include flows into or out of the system (Eq 1), for the purposes of this model, no net migration, biomass build-up, nor fishing was considered. The first equation deals with balancing the production terms between groups for the model while the second equation ensures that each group is balanced within. The equations are linked through the common production term. For a system with n groups, n linear equations can be written and a series of simultaneous equations are set up for each group and solved using a generalized method for matrix inversion, which is described by Mackay (1981). The routine solves for one of four parameters for each group, which are biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) or ecotrophic efficiency (EE), a measure of how much of a group's production is used within the system.

The data for the life-support system model

The ecosystem model was produced to represent the system in the 1980s. The dataset used for this study is an early version of the data and in condensed form (see section 3.1). Biomass estimates for all biota and rate measurements (production and consumption), along with diet compositions and assimilation rates, were made from the published literature of PEI and other sub-Antarctic systems. Trophic linkages were made from diet and stable isotope signatures. The 21 functional groups were divided into 15 consumers, 4 primary producers and 2 detrital groups. Where possible, data from the PEI were used; parameters were otherwise taken from ecosystem models of similar systems (Bradford-Grieve et al. 2003; Cheung et al. 2005; Pruvost et al. 2005).

Biomass estimates

The mammalian and avian top predators are represented by 5 groups, the seals (comprising the Southern elephant seal *Mirounga leonine* (Linnaeus 1758), sub-Antarctic fur seal *Arctocephalus tropicalis* (Grey 1872) and the Antarctic fur seal *Arctocephalus gazella* (Peters 1875)), the penguins (Kings, *Aptenodytes patagonicus* (Miller 1778), Macaroni *Eudyptes chrysolophus* (Brandt 1837), Southern Rockhopper *Eudyptes chrysocome filholi* (Hutton 1878) and Gentoo *Pygoscelis papua* (Forster 1781)), the albatross (Wandering *Diomedea exulans* (Linnaeus 1758), Grey-headed *Thalassarche chrysostoma* (Forster 1785), Yellow-nosed *T. carteri* (Rothschild 1903) and both Light-mantled Sooty *Phoebastria palpebrata* (Forster 1785) and Dark-mantled Sooty *P. fusca* (Hisenberg 1822)), the Giant Petrels (both Northern *Macronectes halli* (Mathews 1912) and Southern *M. giganteus* (Gmelin 1789)) and a group representing the majority of the small flying birds (Petrels and Prions) that breed at the islands (Appendix 4.A.). Kelp gulls *Larus dominicanus* (Lichtenstein 1823), Subantarctic skuas *Catharacta antarctica lonnbergi* (Lesson 1831), the Crozet shag *Phalacrocorax melangogenis* (King 1828) and the lesser sheathbill *Chionis minor marionensis* (Peters 1934) were not included in the model. Population estimates are available for breeding populations of the top predators on the islands and biomass estimates were based on published estimates from the 1980s (Hanel and Chown 1998). Adjustments in biomass estimates were made for all groups to account for the period of time that each group is considered resident at the islands (Condy 1979; Cooper and Brown 1990). Biomass estimates for mammalian groups include the full population, while for the avian fauna, only breeding populations are included.

The fish groups were divided into two demersal and two pelagic groups, with the separation between large and small fish based on the maximum length attained by each species (small groups total length <50cm, large groups total length >50cm). Two families are considered the most important at the islands, the nototheniids and the myctophids. The demersal groups include benthopelagic and demersal species. The large demersal fish group consists of 21 species. This group includes three nototheniid fish, (the grey rockcod *Lepidonotothen squamifrons* (Günther 1880), black rockcod *Notothenia coriiceps* (Richardson 1844) and the marbled rockcod *Notothenia rossii* (Richardson 1844)) all bathydemersal and benthopelagic species, as well as the

sharks and rays. The small demersal fish group consists of 13 species and incorporates the inshore and continental slope fish species. Important species in this group include inshore nototheniid species, the lobe-lip notothen *Gobionotothen marionensis* (Günther 1880) and *Gobionotothen acuta* (Günther 1880), as well as the painted notie (*Lepidonothen larseni* Lonnberg 1905), which is also found on the continental slope. The large pelagic group contains 11 species and is dominated by the nototheniid Patagonian toothfish *Dissostichus eleginoides* (Smitt 1898). The small pelagic fish are dominated by the Myctophidae family which comprise 17 of the 35 species. Myctophids are the most abundant pelagic fish in the Southern Ocean (Gjosaeter and Kawaguchi 1980; Sabourenkov 1991; Kozlov 1995) and are an important food source for many of the top predators (Adams and Klages 1987; Brown et al. 1990; Cherel et al. 1993; Lea et al. 2002).

Pelagic system biomass estimates for phytoplankton, zooplankton and for the pelagic fish groups were from the PEI, while biomass estimates for the small pelagic fish group and the cephalopods were taken from general Southern Ocean estimates. The PEI system is also notably different from many of the other sub-Antarctic islands in that it lacks a large shelf area as is, for instance, found at the Kerguelen archipelago. Macrozooplankton densities over the plateau at the Kerguelen Islands are higher (Hunt et al. 2011) and many of the top predator diets are dominated by zooplankton. While the PEIs do support locally high zooplankton biomass around the fringe of the islands, summaries of the diets of the most abundant predators indicate that myctophids are the most important prey species for the vertebrate predators found in the island system. Fish fauna studies carried out in the 1970s and 1980s (Gon and Klages 1988), along with the recent 2001 survey (Pakhomov et al. 2006), have provided a comprehensive list of species present at the islands but quantitative assessments are still lacking. Biomass estimates for all fish groups were made using CPUE data from Brandao et al. (2002) and Pakhomov et al. (2006). Similarly, species composition of cephalopods is known (largely from diet analysis of the top predators at the islands) but quantitative estimates of biomass are not known and estimates for the model were based on assessments from other sub-Antarctic systems.

The PEI have a rich benthic community and biomass estimates for the benthic components of the ecosystem were taken from the PEI data for all groups (Perissinotto and McQuaid 1990;

Attwood et al. 1991; Beckley and Branch 1992). Studies on the inter-tidal and benthic fauna of the islands were conducted in the 1980s, providing a comprehensive list of species present and a review of the ecology of the community (Blankley 1984; Blankley and Branch 1984; 1985; Blankley and Grindley 1985; Arnaud and Branch 1991; Branch et al. 1991a; Branch et al. 1991b; Beckley and Branch 1992; Branch and Williams 1993; Branch 1994). The benthic community comprises approximately 550 species with seven benthic community groups. *Nauticaris marionis* (Bate 1888), the benthic decapod, has the second highest crustacean biomass and numerous studies have focused on this benthic shrimp because of its perceived key role in the ecosystem (Perissinotto and McQuaid 1990; Kuun et al. 1999; Pakhomov et al. 1999; Pakhomov et al. 2000; Pakhomov et al. 2004). The decapod is consumed by some of the top predators on the islands, notably the penguins (Brown et al. 1990), and therefore provides a link between benthic autochthonous production and higher vertebrates. The benthic fauna are represented in this study by 2 functional groups, one that represents the benthic fauna as a whole, with a second one that represents the decapods.

An illustration of the spatial distribution of the three forms of primary production is given in Figure 4.2. The first comprehensive study of the phytoplankton and zooplankton of the area was conducted in the late 1970s (El-Sayed et al. 1979a; El-Sayed et al. 1979b; Grindley and Lane 1979). Of all the pelagic groups in the system, the zooplankton have received the most attention. Studies describing the zooplankton fauna through the 1980s (Miller 1985; Boden and Parker 1986; Perissinotto and Boden 1989) were followed by community assessments through the 1990s (Perissinotto 1989; Perissinotto and Boden 1989; Perissinotto and McQuaid 1992b) and early 2000s (Hunt et al. 2001; Hunt et al. 2002; Bernard and Froneman 2003; Hunt and Pakhomov 2003). For the purposes of this study, the zooplankton were divided into three functional groups: the large crustaceans (dominated by euphausiid biomass), small herbivorous crustaceans (dominated by copepods) and all remaining zooplankton.

The open ocean phytoplankton was divided into two groups, one to represent the microphytoplankton and one the nano- and pico phytoplankton. As summarized in chapter 2 *in situ* measurements of *chl-a* in the vicinity of the open ocean range from $<0.1 - 0.52 \text{ mg.m}^{-3}$ (4 studies) (Froneman and Balarin 1998; Froneman and Pakhomov 2000; Bernard and Froneman

2005; McQuaid and Froneman 2008). Remotely sensed ocean colour satellite data at 1 km resolution over a six by six degree area centered over the islands (44°S to 50°S, and 35°E to 41°E) from SeaWiFS (1998 to 2004) and a two by two degree area (45.8°S to 47.8°S and 36.8°E to 38.8°E) from MODIS (2005-2008) satellites show a total annual average value of 0.22 mg *chl-a*.m⁻³ using standard processing. This value was used in conjunction with a euphotic depth of 100m (Cheung et al. 2005), a *chlorophyll-a* to carbon ratio of 1:43.9 and a carbon to wet weight ratio of 1:9 (Christensen and Pauly 1995). A total biomass for open ocean primary producers was estimated to be 8.69 t.km⁻². A summary of the contribution of microphytoplankton to the whole phytoplankton community was estimated at approximately 20% (El-Sayed et al. 1979b; Froneman et al. 1998; Read et al. 2000). No explicit additional production associated with elevated productivity of the fronts was incorporated despite these features falling within the considered area.

The island-associated blooms are usually the result of increased production of diatoms (mainly the chain-forming *Chaetoceros radicans* (Schütt 1895) (Boden et al. 1988), *Rhizoselena curvata* (Zacharias 1905) and *Dictyocha speculum* (Ehrenberg 1837) (Perissinotto 1992) or *Fragilariopsis* spp. (McQuaid and Froneman 2008)). *In situ* studies of *chl-a* from within the vicinity of the islands range from 0.01 - 2.8 mg *chl-a*.m⁻³ (8 studies) (El-Sayed et al. 1979a; Miller et al. 1984; Allanson et al. 1985; van Ballegooyen et al. 1989; Perissinotto et al. 1990b; Froneman et al. 2000; Perissinotto et al. 2000). The phytoplankton blooms are dominated by diatoms and *chl-a* concentrations exceed 1.5 mg.m⁻³ (measurements of up to 2.8 mg.m⁻³ have been made) (Boden 1988; Duncombe Rae 1989b). Under non-bloom conditions, *chl-a* concentrations range between 0.05 and 0.45 mg *chl-a*.m⁻³ with the composition dominated by nano- and/or picophytoplankton (Perissinotto et al. 2000; Bernard and Froneman 2002). Remotely sensed ocean colour satellite *chl-a* data at a 1km resolution from a subarea centred on the islands (46.5°S to 47.1°S and 37.5°E to 38.3°E) from 1998 to 2008 were processed (SeaWiFS data 1998 – 2004, MODIS data 2005-2008). Monthly averages during summer months ranged between 0.4 and 1.4mg *chl-a*.m⁻³ showing clear seasonal blooms in the vicinity of the islands. The annual average concentration for the sub-area was 0.27 mg *chl-a*.m⁻³. An average annual increase of 0.05 mg *chl-a*.m⁻³ over and above the open ocean value of 0.22 mg

$chl-a.m^{-3}$ was attributed to the elevated production associated with the islands. A conservative euphotic depth of 20 m for the blooms was assumed (Perissinotto et al. 1990c).

Macrocystis laevis and *Durvillea antarctica* are the two macrophytes that dominate the system. Quantitative estimates of the macrophytes were made for Marion Island from both photographs and from diving surveys in the 1980s, with estimates of 63 500 t for *M. laevis* (Attwood et al. 1991) and 3 300 t for *D. antarctica* (Haxen and Grindley 1985). An extrapolation of these estimates to include macrophyte beds around Prince Edward island based on the percentage of the perimeter of Marion to Prince Edward, resulted in a total biomass of 87 495t for the system (Attwood et al. 1991).

Detritus estimates were made using the empirical equation of Pauly et al. (1993). Using a primary production estimate of $17.155 \text{ gC.m}^{-2}.\text{yr}^{-1}$ (lower estimate) (Pakhomov and Froneman 1999b), the annual estimate of detritus resulting from the open ocean phytoplankton productivity was 3.184 g.m^{-2} (equivalent to t.km^{-2}). Using a conversion of carbon to wet weight of 1:9, detrital input was estimated to be 28.7 t.km^{-2} .

Rate measurements

P/B data were taken from the published literature for the PEIs where possible or otherwise from similar systems. Open ocean production was estimated to be between $94 - 442 \text{ mgC.m}^{-2}.\text{d}^{-1}$ (Boden 1988; Balarin 2000). Island associated production ranged from 84 to $3000 \text{ mgC.m}^{-2}.\text{d}^{-1}$ (five studies) (El-Sayed et al. 1979b; Allanson et al. 1985; van Ballegooyen et al. 1989; Perissinotto et al. 1990b; Balarin 2000), resulting in P/B ratios for open ocean production of 150 yr^{-1} and for island-associated blooms of 200 yr^{-1} . Production rates for *M. laevis* were measured in both April and August and the mean productivity was $9.6 \text{ gC.m}^{-2}.\text{d}^{-1}$, which resulted in an estimated P/B of 5.22 yr^{-1} (based on a biomass of 11.5kg.m^{-2}) for macrophytes (Attwood et al. 1991).

Q/B data was estimated using empirical equations for all the top predators and based on energetic demands (Nagy et al. 1999), using the body mass of each group (Trites and Pauly 1998; Ryan and Bester 2008) and calorific content of diets (Burger 1981; Croxall 1984; Abrams 1985; Clarke 1985; Doidge and Croxall 1985; Brown and Klages 1987; Tierney et al. 2002),

with an assumption that water content was 70%, along with the specific diet for each group. Q/B data for fish were calculated using the empirical equation of Palomares and Pauly (1998) and taken from the literature for the benthic and zooplankton groups. Diet matrices and assimilation efficiencies used in the calculations were estimated from the literature and are presented in tables 4.1 and 4.2.

Nested models to assess primary production at different scales

Four models of different sizes were created. The areas for each model were calculated with four different radius lengths (200nm, 100nm, 50nm, 20nm), each of which was centered at the midpoint between the two islands that make up the archipelago (46°46'S, 37°51'E). For each of the four models, the biomass per unit area ($t.km^{-2}$) was scaled according to the size of each ecosystem i.e. higher biomass per unit area with smaller model size for all top predators as they were assumed to fill the entire area of each model (see Table 4.1). The estimates for all benthic components, including demersal fish, the benthic decapods, benthos, inter-island blooms and the macrophyte biomass, were scaled according to the area that their habitat occupied of the total area for each model i.e. higher biomass per unit area for each smaller model. Pelagic system biomass estimates were assumed to be uniformly distributed throughout the areas considered and therefore the biomass per unit area for all pelagic groups remained unchanged for each of the four models. Input data for all functional groups is presented in Table 4.1, and the diet matrix used for the model is presented in Table 4.2.

4.3. Results

The trophic linkages for the purposes of this model have been based on the available data for the island system and these relatively new trophic pathways have now been incorporated into this quantitative assessment, which is illustrated in Figure 4.3 at the scale of the EEZ. Only at this scale does the model balance, i.e. the energetic requirements for all the inhabitants are met. For the smaller size models, reductions in the land-based top predator biomass estimates are necessary for the models to balance. As none of these groups feed directly on the primary producers, the adjustments have no effect on how much of the production is directly used in the system, and for the purposes of this study, will not be considered further. The relative biomass

contributions of each of the producers at this scale are evident, with the open ocean nano- and picoplankton contributing the most per unit area (Figure 4.3, 4.4).

A quantitative assessment of the primary producers at the islands at each of the four scales considered clearly shows the increased productivity per unit area with proximity to the islands demonstrating the basic principle of the ‘island mass effect’ (Figure 4.4). The model constructed at the scale of the EEZ has a total producer biomass of 8.89 t.km^{-2} , while the smallest model has biomass contributions greater than three times this value at 29.395 t.km^{-2} . The open ocean production dominates at all but the smallest scale, where the macrophytes become important. Also evident from this assessment is the relatively small contribution the island associated blooms make to the system at all spatial scales. The greatest contribution of these blooms occurs in the smallest scale model, but even then contributes only 1.4% of the total primary producer biomass. If the assumption of the depth of the bloom is increased from 20 m to 120 m (Perissinotto et al. 1990), this contribution would have a maximum contribution of 7.5% at the smallest scale considered here.

These data provide an assessment of the biomass of the producers, but how much of this production is consumed within the system? The Ecopath routine, when provided with biomass, production and consumption rates, produces an Ecotrophic Efficiency (EE), given as a proportion, which is a measure of how much of each group is used within the system (Figure 4.5).

Of the two size fractions of open ocean phytoplankton production, the larger microphytoplankton portion is utilized the least. EEs for this group increase with decreasing model size, but all EEs are relatively low (maximum EE at the smallest model size of 0.14). The smaller open ocean phytoplankton size fraction (the nano and picoplankton) has consistently high EEs (between 0.84 and 0.87), suggesting that this source is well utilized in the system at all spatial scales.

As discussed, the contribution of the island associated blooms to the total production is low. However, of this production approximately 30% is consumed within the system. This EE is consistent because the consumers of this production are the benthic fauna, which are scaled with the model size, as are the blooms. This form of production is thought to enter the benthic sub-

system through fallout following the blooms. Such a detrital component has not been explicitly separated in this model, the inclusion of which would add to the relative importance of this input.

At the smallest scale, while the macrophytes contribute approximately 69.1% of the available primary producer biomass, much of the production is not directly consumed, as shown by the relatively low EEs (range 0.11 – 0.22). Even at the largest scale, relatively little of the macrophyte production is grazed on directly. Macrophyte detritus on the other hand is well used in the system: minimum EE of 0.60 in the smallest model and a maximum of 0.68 for the largest. This pattern is due to the diet of some of the pelagic components of the community consuming this form of detritus. The general detritus group follows the opposite trend, with increasing EE with decreasing model size (0.35 to 0.63), largely attributed to the benthic fauna which directly consumes the macrophyte detritus.

4.4. Discussion

Although the ‘island mass effect’ was recognised early on as a driving force behind enhanced local production at the PEI, the mode of operation and subsequent transfer of primary production up the PEI food web continued to be a subject of research and source of contention for a number of years. Since the earliest investigations at the PEI, the open ocean allochthonous production was found to be low (average approximately $0.2 \text{ mg chl-}a \cdot \text{m}^{-3}$) and studies were initially focussed on the autochthonous production, i.e. that of the island-associated blooms and the macrophyte production. During bloom conditions, *chl-a* concentrations were 5 to 10 times higher than average (between 1 and $2 \text{ mg chl-}a \cdot \text{m}^{-3}$) and this enhanced productivity was the result of seasonal blooms of diatom species (El-Sayed et al. 1979b; Boden 1988; Perissinotto et al. 2000). Studies through the 1990s that focussed on zooplankton grazing showed no evidence of feeding on this microphytoplankton size fraction ($>20 \mu\text{m}$), which dominates during such blooms, but grazing occurred in the nano- and pico- size fractions ($<20 \mu\text{m}$) (Perissinotto et al. 1990a). From these results, it appeared that the zooplankton community was adapted to consume the smaller size fraction, available year round, and likely did not make use of the seasonal blooms. Production from the blooms was therefore thought to sink out of the surface waters and provide a direct transfer of primary production to the rich benthic subsystem, with the pelagic community not directly benefiting from this form of production. A quantitative assessment of the

macrophyte production in the vicinity of the islands was made in the 1980s and found to be greater per unit area than that of the local phytoplankton production, as was to be expected (Mann 1973). However, this production was thought to contribute less to the seas around PEI because of its limited spatial coverage and because it was suspected that almost all of the macrophyte production was exported to the open ocean pelagic environment (Attwood et al. 1991).

At this point, the two forms of autochthonous production were thought to have different fates: the blooms providing input into the benthic community and the macrophyte production being exported from the system. The issue of scale was not directly addressed in these assessments, but publications at the time estimated the ecosystem to be delineated by a 300 km radius, thought to be the extent of the foraging distance of the island's top predators (Adams et al. 1993).

In the early 2000s, stable isotope studies conducted at the islands provided new insight into the trophic pathways in the PEI system. Unique carbon isotope signatures ($\delta^{13}\text{C}$) for each the three forms of production at the islands were identified (Kaehler et al. 2000) and allowed for an assessment of the relative importance of each of the producers to the system. Input from macrophyte production, primarily as particulate carbon, to the nearshore benthic community in particular was shown to be substantial (Kaehler et al. 2006), contradictory to earlier perceptions. Following from this, diet studies conducted in conjunction with stable isotope analysis (e.g., on euphausiids (Gurney et al. 2001), decapod *Nauticaris marionis* (Pakhomov et al. 2004) and the fish community (Bushula et al. 2005; Pakhomov et al. 2006)) contributed to a better understanding of the trophic pathways for many of the key consumers. Two co-occurring near-shore fish species, for instance, were found to have contrasting sources of production, one allochthonous and one autochthonous macrophytes (Bushula et al. 2005). These data provided new insights which were incorporated into the LSS model and allowed for a reassessment of the island system.

The relative importance of each of the producers is affected by the scale at which the system is assessed, a consideration seldom included in previous discussions of the PEI system. At all but the smallest spatial scale (where it contributes 23.8% to total available production), the small fraction (nano- and pico-) of the open ocean production dominates in terms of biomass per unit

area (between 78.7% and 58.3% of total available producer biomass). This allochthonous production is the most important of the three sources at the PEI and may be considered the driving force of the island ecosystem, particularly at the larger spatial scales. When the producers are assessed in terms of what is actually consumed at the islands (the biomass combined with the Ecotrophic Efficiency outputs from the Ecopath routine), this component contributes in excess of 92.0% of the production at all but the smallest scale, where it contributes 69.5%. When all first trophic level contributors are included in the assessment (i.e. the two detrital groups along with the primary producers), the general detrital group dominates and the contribution of the allochthonous small size fraction of the open ocean production is reduced to between 32 and 37% for the three larger models, and 21% for the smallest model.

Of the two autochthonous contributors, the macrophytes were found to contribute the most to the ecosystem. When the total biomass of the producers in the system was assessed, the macrophytes contributed, in decreasing order of model size, 2.3%, 8.5%, 27.1% and 69.1%. Direct consumption of the macrophytes, however, was limited. Therefore, even at the smallest scale considered, when the available macrophyte biomass dominated the system, the amount consumed directly was 26.4% of the total producers consumed. Detritus generated from this production was well utilized in the system at all spatial scales (Ecotrophic Efficiencies between 0.60 and 0.68), however in terms of its contribution to the system when all first trophic level contributors are assessed (all producers and detrital groups), it is greatest at the smallest spatial scale at 7.70% of the total, which is similar to the contribution of the macrophytes themselves at 7.98%. The combined consumption of these two groups is substantial (15.68%), though it ranks third in terms of what is used in the system behind the general detrital component (62.10%) and the small open ocean phytoplankton contribution (20.99%).

The absolute biomass of the island-associated blooms is small compared to all other contributors, even at the smallest scale (less than 2% for all models). Approximately 30% of this production was consistently consumed within the system and its contribution, particularly in its detrital form, could be important to the benthic community. Inclusion of this component through an explicit contribution of its detrital form may provide further insight into the fate of this production, but from this assessment it appears to be limited.

A weakness of this assessment is the omission of the microbial loop. Microbial studies on microheterotrophs in the PEI system have been conducted (Froneman and Balarin 1998; Froneman and Bernard 2004) and grazing impact of protists on phytoplankton may be between 47 and 71% of potential primary production per day (Froneman and Balarin 1998). Bradford-Grieve et al. (2003) produced an ecosystem model of a sub-Antarctic system (Southern Plateau, NZ) which paid close attention to the microbial loop with 5 functional groups of the 19 considered dedicated to this section of the food web. No account was made in their assessment of the macrophyte production, though its input, particularly through the detritus, was acknowledged (Bradford-Grieve et al. 2003). Inclusion of this important component of the food web will further redefine models of the system.

4.5. Conclusions

For the time period considered in this study (the 1980s), allochthonous production, in the form of nano- and picophytoplankton, should be considered the most important contributor to the PEI system, and the driver of the island food web at all but the smallest spatial scale. This production reaches the top predators of the PEI ecosystem via zooplankton and small pelagic fish. Elevated phytoplankton productivity associated with the ‘island mass effect’ at PEI was found to be of little importance, even at the smallest scale considered here. The alternate form of autochthonous production, the macrophyte production, was found to be utilized by both direct consumption and in its detrital form, and provides an important contribution to the system, particularly when considered at the smallest scale. The benthic fish populations and near-shore top predators (e.g., Gentoo penguins) are dependent on this autochthonous production; benthic-pelagic coupling (macrophyte production, benthic decapods and small demersal fish) thus represents an important trophic pathway in the system. Studies on the PEI ecosystem in the past decade have highlighted the importance of the autochthonous macrophyte contribution to the islands system. Indeed, we believe that this autochthonous component contributes towards a unique benthic habitat between the islands which warrants further detailed investigation. Overall, however, the findings of this study confirm previous perceptions that the system is largely reliant on pelagic allochthonous production. It was only when the model was considered at the scale of the PEI EEZ that the energy demands of the current population of PEI top predators was supported.

Table 4.1. Input parameter estimates for the four Life-Support System Models (P/B, Production to biomass ratio; Q/B, Consumption to biomass ratio; U/Q, Unassimilated consumption).

Model Size (radius length nm)	200	100	50	20	P/B	Q/B	U/Q
Model Size (km ²)	431014	107754	26938	4310			
Functional Group	B (t.km ²)				yr ⁻¹	yr ⁻¹	
Seals	0.0045	0.0180	0.0720	0.4500	0.09	14.25	0.10
Penguins	0.0213	0.0853	0.3412	2.1324	0.14	40.84	0.21
Albatross	0.0003	0.0012	0.0046	0.0290	0.02	41.34	0.20
Giant Petrels	0.00005	0.0002	0.0007	0.0045	0.07	57.26	0.20
Prions and Petrels	0.00033	0.0013	0.0053	0.0329	0.16	144.84	0.24
Large Demersal Fish	0.0154	0.0615	0.2459	1.5369	0.20	2.94	0.20
Small demersal fish	0.0130	0.0520	0.2080	1.3000	0.43	6.82	0.20
Large Pelagic Fish	0.09	0.09	0.09	0.09	0.16	1.92	0.20
Small Pelagic Fish	4	4	4	4	1.16	9.54	0.20
Cephalopods	0.11	0.11	0.11	0.11	3.44	13.94	0.20
Benthos	0.5	2	8	50	2.50	10.00	0.20
Benthic decapod	0.038	0.152	0.608	3.8	1.45	4.42	0.20
Large zooplankton crustaceans	6	6	6	6	5	14.00	0.20
Small zooplankton crustaceans	15	15	15	15	10	43.00	0.20
All other zooplankton	7	7	7	7	24	96.00	0.20
Open ocean large phytoplankton	1.69	1.69	1.69	1.69	150		
Open ocean small phytoplankton	7	7	7	7	150		
Interisland blooms	0.00405	0.0162	0.0648	0.405	200		
Macrophytes	0.203	0.812	3.248	20.3	5.22		
Macrophyte Detritus	0.037139	0.148556	0.594224	3.7139			
Detritus	28.66	28.66	28.66	28.66			

Denotes constant biomass per unit area as marine in origin and constant for all models

Table 4.2. Diet Matrix for the four Life-Support System models

Group #	Functional Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seals				0.06											
2	Penguins	0.00007	0	0.0023	0.781											
3	Albatross				0.00191											
4	Giant Petrels				0.001											
5	Prions and Petrels				0.02											
6	Large Demersal Fish	0.0298	0.0003				0.001									
7	Small Demersal Fish	0.0260	0.0007				0.005	0	0.004	0	0					
8	Large Pelagic Fish	0.0859	0				0.001	0	0.0233	0	0					
9	Small Pelagic Fish	0.6340	0.5528	0.4022	0.04	0.22	0.316	0	0.299	0	0.1773					
10	Cephalopods	0.2232	0.1058	0.5296	0.075	0.14	0.019	0	0.61	0	0.0591	0	0	0	0	
11	Benthos	0	0	0.0065			0.128	0.219	0	0.0088	0		0.1			
12	Benthic decapod	0.0006	0.0043	0			0	0.135	0	0	0	0.001	0.01			
13	Large zooplankton crustaceans	0.0006	0.1998	0.0302	0.022	0.2	0.095	0.1	0.0636667	0.3585	0.3127	0.05				
14	Small zooplankton crustaceans	0	0.1281	0.0192		0.4	0.069	0.319	0	0.3584	0.3045	0.08	0.05	0.4	0.1	
15	All other zooplankton	0	0.0082	0.01		0.04	0.090	0.154	0	0.2713	0.1464	0.08		0.2	0.2	
16	Open ocean large phytoplankton	0	0				0	0	0	0	0	0.05	0.05	0.1		
17	Open ocean small phytoplankton	0	0				0	0	0	0	0	0.05	0.05	0.3	0.6	0.7
18	Interisland blooms	0	0				0	0	0	0	0	0.05				
19	Macrophytes	0	0				0.2764	0.0731	0	0.0031	0	0.02				
20	Macrophyte Detritus	0	0				0	0	0	0	0	0.1	0.37			
21	Detritus	0	0				0	0	0	0	0	0.519	0.37		0.1	0.3
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

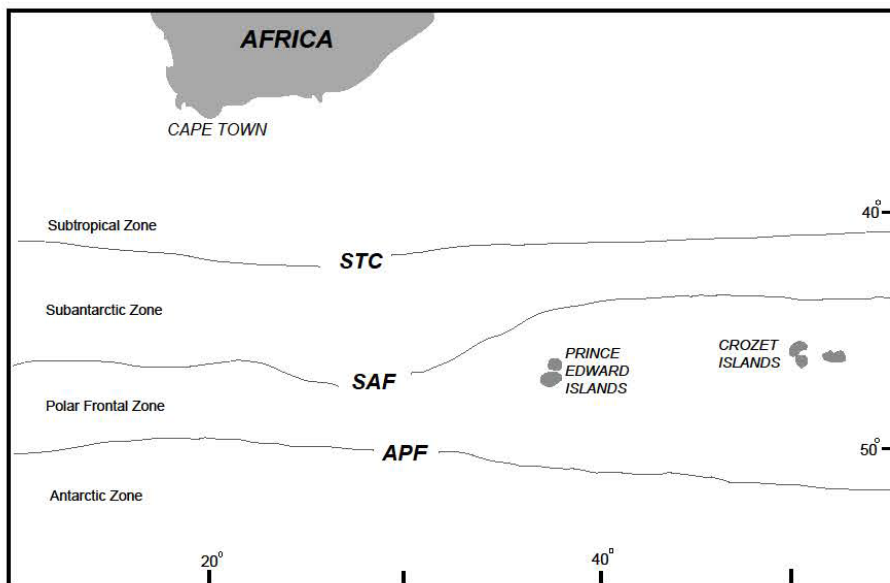


Figure 4.1. Map of the Indian sector of the Southern Ocean showing the position of the Prince Edward Islands and main frontal features (STC, Subtropical Convergence; SAF, Sub-Antarctic Front; APF, Antarctic Polar Front).

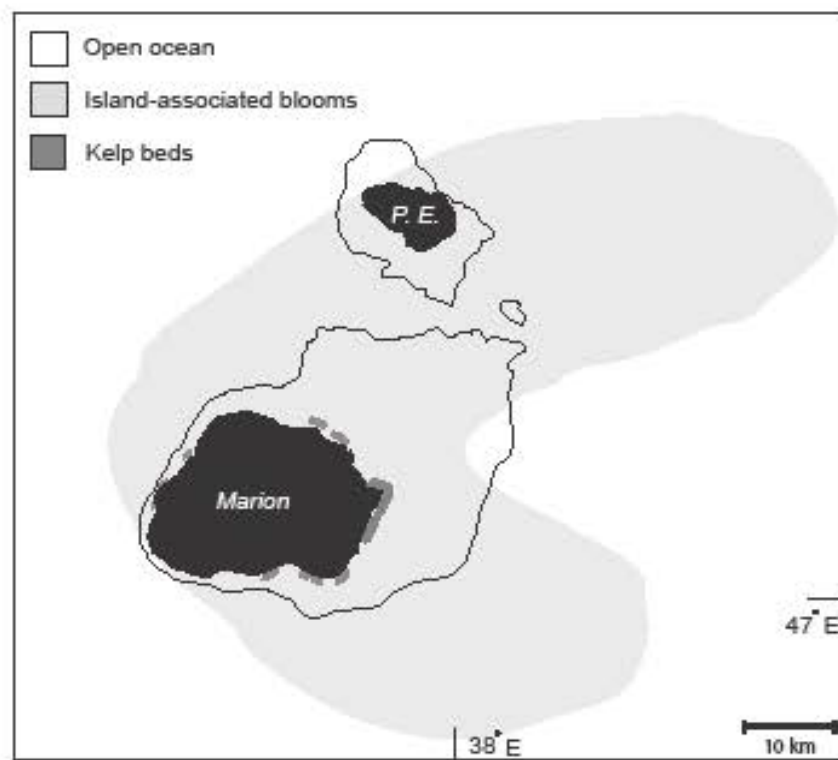


Figure 4.2. Map of the Prince Edward Islands, indicating the spatial distribution of the three primary producers.

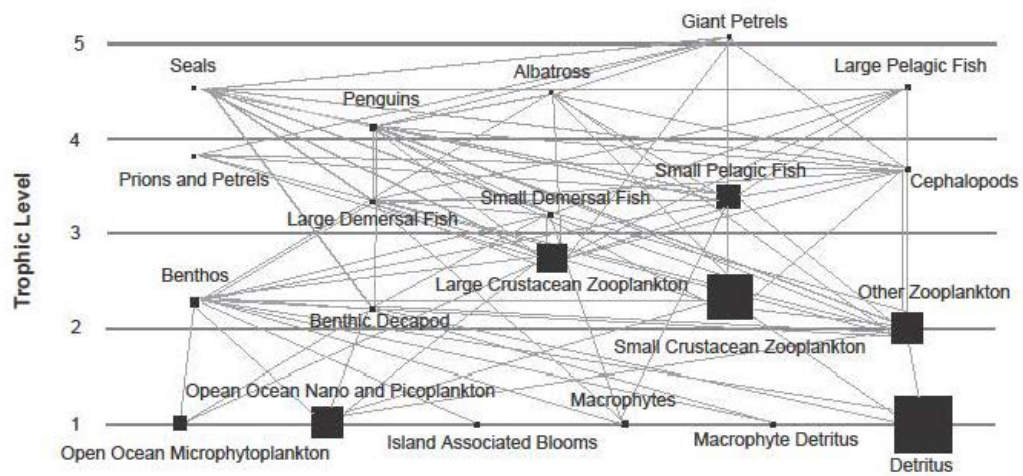


Figure 4.3. Flow diagram with relative importance of each primary producer at 200nm scale. Box size is proportional to the square root of the biomass of the functional group.

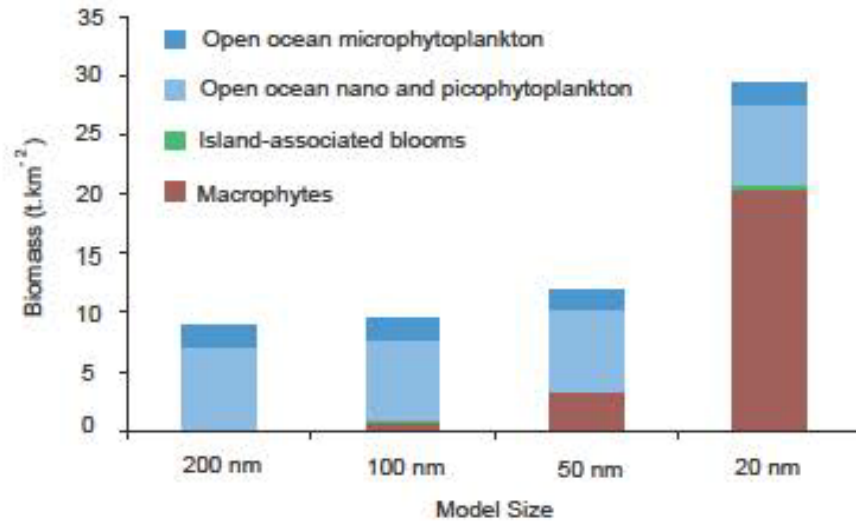


Figure 4.4. Relative biomass of each primary producer for the four model sizes (model sizes equivalent to circles with given radii).

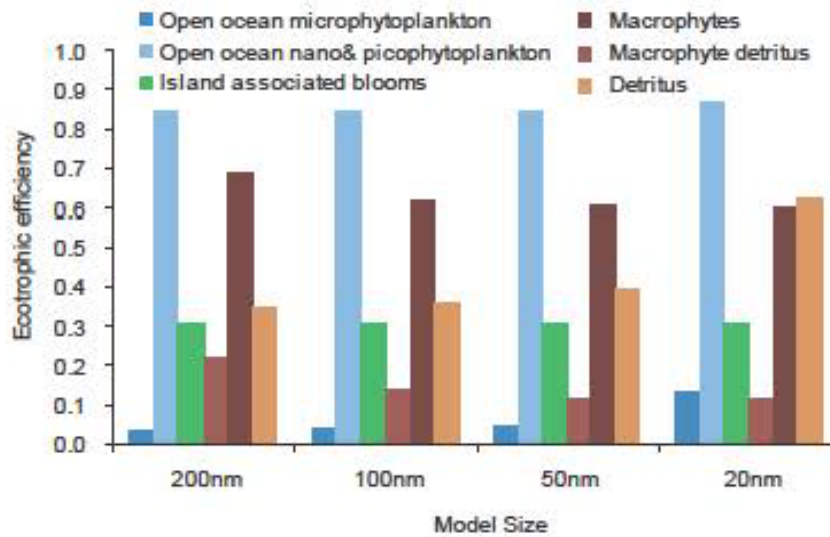


Figure 4.5. Ecotrophic efficiencies for functional groups of the first trophic level of the four 'Life-Support System' models.

Chapter 5 An ecosystem model of the Prince Edward Island Archipelago

5.1. Introduction

The Prince Edward Islands (PEIs), like all Sub-Antarctic islands, are hotspots of biological activity. The combination of the alteration of oceanographic dynamics by the interception of an island system and the provision of substrata for both land based top predators and benthic organisms combines to provide a site of elevated productivity in an otherwise relatively low productivity region (See Chapters 1 and 3). These islands are host to millions of seabirds and seals that use the islands as a seasonal breeding ground and refuge during moulting. The shelf areas around the islands are known to support increased levels of benthos and fish populations which aid in supporting the seasonal residents.

At the PEIs the population dynamics of many of the seabirds and seals have been well documented over the past 60 years. Disparate trends have been observed. In some instances the changes can be linked to known drivers. For instance, the Sub-Antarctic fur seals (*Arctocephalus tropicalis*) population increased exponentially from a few hundred individuals in the 1950s to over 150 000 by 2010 (Condy 1981; Kerley 1983a; Wilkinson and Bester 1990a; Hofmeyr et al. 1997; Hofmeyr et al. 2006; Bester et al. 2009), which is believed to be a population recovery following past exploitation. In other instances the changes, while studied, are not well understood. The Southern elephant seals (*Mirounga leonina*) have been in decline since the 1970s (Condy 1977; Condy 1978a; Condy 1981; Bester and Hofmeyr 2005) with no conclusive understanding of the reasons behind the decline, though interspecific competition, competition with fisheries and environmental changes have all been cited (Wilkinson and Bester 1990b; Green et al. 1998; Goldsworthy et al. 2001; McMahon et al. 2005). Population fluctuations for penguin species have also been shown, with the Southern Rockhopper penguins (*Eudyptes chrysocome filholi*) and the Macaroni penguins (*Eudyptes chrysolophus*) experiencing significant declines between 1994/5 and 2008/9 of 70% and 30%, respectively, (Crawford et al. 2009) raising conservation concerns.

Along with the land based top predators, the only fish species to be targeted by a fishery has also experienced a collapse in the population. The Patagonian toothfish (*Dissostichus eleginoides*) has

diminished to a fraction of its former population status following unsustainable catches being harvested from a pristine stock (largely taken illegally in the initial phase of the fishery in the 1990s) (Brandao et al. 2002; Brandao and Butterworth 2009; CCAMLR 2011). Fishery related by-catch of seabirds is documented as resulting in population related fluctuations for some of the albatross species (e.g. Wandering albatross, *Diomedea exulans*) that breed at the islands (Nel et al. 2002a; Nel et al. 2002c; Nel et al. 2003) though mitigation measures have been successful in reducing these events (CCAMLR 2011). Still, conservation concerns at the islands have been highlighted as all five of the populations of albatross that breed at the islands have been classified as having special status ('near-threatened, vulnerable or endangered') by BirdLife International (2011) (IUCN Red List for birds. Downloaded from <http://www.birdlife.org> on 27/09/2011). In addition, the presence of cats at the islands between 1949 and 1992 resulted in considerable predation on the breeding bird populations (Bester et al. 2000) adding to conservation concerns at the islands.

With the islands therefore having both fishery and conservation concerns, there is a need to develop a single platform from which these considerations can be assessed together. A search for a better understanding of the processes that underlie the observed changes and also the linkages between the various constituents of the foodweb is required. The construction of an ecosystem model provides such a framework where interactions between components of the ecosystem can be identified. The ecosystem state, structure and function in both past and present can be assessed and used to develop a better understanding of the ecosystem as a whole.

The wealth of scientific research that has been conducted at the PEIs provides a unique data set from which to build an ecosystem model. This work describes the first ecosystem model of the marine component of the PEIs. Through the construction of the model, a dataset has been compiled, providing a useful summary of existing data for the system as well as highlighting data gaps. This, combined with an assessment of data quality and model sensitivity provides a decision support platform for assessing where scientific research efforts should be focussed in future to improve the model parameters and thereby the quality and usefulness of the model. Finally, an assessment of the ecosystem in terms of its trophic structure, biomasses, flows through the food web and relevant ecosystem indicators is presented.

5.2. Methods

5.2.1. Study area

For the purposes of the creation of the model, the study area has been set to be the Exclusive Economic Zone (EEZ) of the Prince Edward Islands (See Figure 5.1). This area is demarcated with a circle with a radius of 200nm, centered between the two islands (46°46'S, 37°51'E). The total area is equal to 431015km².

5.2.2. Modelling approach

The approach used for this study is the mass balanced network model known as Ecopath (Christensen et al. 2008). The original 'Ecopath', first proposed by Polovina and Ow and developed by Polovina (Polovina 1984; Polovina and Ow 1985; Polovina 1986) combines a system of simultaneous linear biomass budget equations, which balance biomass production and loss. Since its original formulation (Christensen and Pauly 1992; Christensen and Pauly 1993) the model has been developed so that it no longer relies on a steady state, and it incorporates a network analysis component from theoretical ecology for detailed assessment of the trophic flows (Ulanowicz 1986; Christensen et al. 2004). These developments allow comparisons between ecosystems. Ongoing developments to the software have meant that this model is the fore-runner in its field. It has the capacity to represent all trophic levels. It is the most widely used ecosystem model and is appropriate for addressing broad ecological questions (Plaganyi 2007). A summary of the strengths and weaknesses of the model is discussed in Chapter 1.

In Ecopath, species can be considered individually, or pooled together into functionally related groups. Each group is represented by their biomass and the groups are linked through their trophic interactions. The basic Ecopath model is a closed system mass-balanced formulation of the functional groups in an ecosystem and the full methodology can be found in the user's guide (Christensen et al. 2008).

There are two principal equations in the Ecopath model, the first describing the production term within a group (i) (Eq 1) and the second describing the production term of the group (i) within the system (Eq 2).

Equation 1: Production = Consumption – Respiration – Unassimilated mass

$$P_i = Q_i - R_i - U_i$$

Equation 2: Production = Predation + Other mortality + Fishing mortality

$$P_i = B_i (M1_i) + B_i (M2_i) + M3_i$$

Where: P_i is the total production rate of i

Q_i is the consumption rate of i

R_i is the respiration rate of i

U_i is the rate of the unassimilated mass of i

B_i the biomass of i

$M1_i$ is instantaneous predation rate of i

$M2_i$ is the ‘other mortality’ rate of i

$M3_i$ is the total fishery catch rate of i

$M1_i$, the instantaneous predation rate of i , can be expressed as the sum of all n predator groups’ consumption rates (Q) on the prey (i) as:

$$M1_i = \sum_{j=1}^n Q_j (DC_{ji}) / B_i$$

Where Q_j is the consumption rate, in this instance for predator j , and DC_{ji} is the fraction of the prey i in the average diet of predator j .

Adjusting the equation to include the Q/B ratio for predator j results in

$$M1_i = \sum B_j (Q/B)_j (DC_{ji}) / B_i$$

Substitution of this into equation 2 gives:

$$P_i = \sum B_j (Q/B)_j (DC_{ji}) + B_i (M2_i) + M3_i$$

Ecopath uses the term 'Ecotrophic Efficiency' (EE), which is the proportion of the production of a group that is utilized in the system.

Substituting $M2_i$ (other mortality) with $P_i (1-EE_i) / B_i$ results in:

$$P_i - \sum B_j (Q/B)_j (DC_{ji}) - P_i (1-EE_i) - M3_i = 0$$

Adjusting the format of this equation to reflect production to biomass $(P/B)_i$ ratios, this equation can be expressed as:

$$B_i (P/B)_i - \sum B_j (Q/B)_j (DC_{ji}) - B_i (P/B)_i + B_i (P/B)_i (EE) - M3_i = 0$$

Or

$$B_i (P/B)_i (EE) - \sum B_j (Q/B)_j (DC_{ji}) - M3_i = 0$$

This equation indicates that the diet and consumption rate of a predator can be used to determine the predation mortality term for the prey. Or alternatively, if the mortality for a given prey is known then the equation can be used to estimate the consumption rates for one or more predators (Christensen and Walters 2004).

Based on the last equation, for a system with n groups, there are n linear equations. From the series of n simultaneous equations created (equivalent to the number of groups in the system), solutions for the equations are calculated based on the assumption of mass balance within the system using a generalised method for matrix inversion (see Christensen et al. 2008). The routine solves for one of four parameters for each group: biomass, production/biomass ratio (P/B) , consumption/biomass ratio (Q/B) or ecotrophic efficiency (EE). Three of the four parameters must be entered to calculate the one unknown. This means that the basic model parameters required include biomass estimates, diet compositions, assimilation efficiencies, catch rates

(where applicable) and three rate measurements (consumption, production and mortality). If all of these data are available, the EE of each group can be calculated by the model.

For the model as a whole, the energy input and output of all living groups must be balanced (Christensen et al. 2008). In Equation 2, only the production term of a group is included. To ensure balance within each group, Equation 1 is used. In Equation 1, respiration is the one term conventionally not measured and so it is left to the model to estimate (though if desired, this can be entered using an alternative input structure in Ecopath). The two master equations of Ecopath (Eq 1 and 2) can be considered filters for mutually incompatible estimates of flow with the result providing a possible picture of the energetic flows, the biomasses and their utilization (Christensen et al. 2008).

5.2.3. Data

Three models have been compiled for the PEIs to represent the ecosystem in three different decades: the 1960s, the 1980s, and the 2000s. Model parameter estimates were made to represent the island system for a time period of one year. Biomass (B), production/biomass ratio (P/B) (equivalent to the total mortality rate Z, (Allen 1971), consumption/biomass ratio (Q/B) (food consumed by a biomass unit of the group) as well as respective diet data were entered into the Ecopath framework and 'Ecotrophic Efficiencies' (EE) (how much is used within the system) were computed. Although Ecopath has the capability to consider flows into or out of the system (immigration, emigration, or biomass build up, see Chapter 4), for the purposes of this study the ecosystem was assumed to be in a steady state and closed. Seasonal migration into and out of the defined area was dealt with by adjusting the biomass of each group according to the proportion of the year that they spend at the islands.

For the purposes of the models, all major marine biological components were considered and the system was divided into 37 functional groups as described in Chapter 2 (Table 2.1). Species were aggregated into functional groups based on a combination of systematics, size, habitat, and diet preference. Groupings were also based on fishery or conservation considerations and were influenced by data availability. Guidelines for aggregation of groups were followed as recommended in the literature (Fulton et al. 2003a; Pinnegar et al. 2005; Quince et al. 2005a;

Raick et al. 2006). Overall the model incorporated four mammal groups, four penguin groups, seven flying bird groups, nine fish groups, two cephalopod groups, one all encompassing benthos group, a benthic decapod group, three zooplankton groups, four primary producers, and two detrital groups. The names of these functional groups are given in italics from here on throughout the text and 3 letter codes for each group provided for use in figures (see Table 2.1 in Chapter 2). Where italics are not used, the reference is to the species or groups in general and not specifically referring to the model functional group.

Data for all biological components of the marine ecosystem of the PEIs were collated from a full review of both the published and grey literature for the islands. The biological data available for the marine component of the PEI ecosystem is extensive and the model construction benefitted a great deal from the wealth of primary data that are available. For many of the required parameters, local data from population surveys, growth and reproduction studies, diet assessments as well as stable isotope analyses were found. In those instances where PEI ecosystem specific data could not be found, data from similar systems (Sub-Antarctic or Antarctic) were used. A simple overview of the data compilation for each of the primary parameters is described below, with a complete description given in Appendix 5.A.

Biomass estimates

For many of the mammals and seabirds, only abundance estimates were available, therefore assumptions were necessary to extrapolate these estimates to produce biomass estimates. For mammal population estimates, conversion factors included incorporating sex ratio estimates, female to pup ratios, pup ratios to population estimates, or males to population estimates. Population to biomass estimates were calculated using average weights for different components of the populations derived from Trites and Pauly (1998) or Condy (1981). Biomass estimates for the breeding bird populations were calculated from published data on population sizes and weight estimates provided in Ryan and Bester (2008). Adjustments of biomass estimates were also made to account for the proportion of time a group spends in the system in one year based on Cooper and Brown (1990). For all the seabird and seal groups, biomass estimates were reconstructed for each of the three different time periods selected for construction of the models.

Data on the fish fauna from the islands were limited due to the lack of reliable survey data. Biomass estimates were made by combining quantitative data from the commercial fishery with qualitative assessments made of the fish community from the PEIs (Brandao et al. 2002; Pakhomov et al. 2006; Brandao and Butterworth 2009) with additional information from the nearby Kerguelen (Duhamel and Hauteceur 2009). Broadly the fish were divided according to their habitat preference (benthic or pelagic) and divided by size into large and small groups (the division made at $L_{inf} = 50\text{cm}$). Within these divisions, groups perceived to be of particular importance to the system (for example the myctophid fish, the Patagonian toothfish, and a subset of three other Nototheniid species) were considered separately. The demersal fish were divided into three categories, Small Inshore Demersals, Small Continental Slope Demersals and Large Demersals. These divisions were made by taking known depth preferences into account. Sharks and rays were considered in a separate group.

The benthic community was lumped together into one primary group excluding the benthic decapod, which was considered separately because of its perceived importance in the island system. Three functional groups represent the relatively well studied zooplankton community. The primary producers were also considered in four separate groups. The open ocean phytoplankton was divided into a large size fraction, the microphytoplankton (greater than $20\mu\text{m}$) and a small size fraction, the nano- and picophytoplankton together (less than $20\mu\text{m}$), the plankton associated with the blooms that occur in the vicinity of the islands and the macrophyte community. Estimates for the open ocean productivity and the island associated blooms were made from remotely sensed satellite data (1997 to 2008). The macrophyte biomass estimate was based on *in situ* data from surveys at the islands in the 1980s. Two detrital groups were included, one representing all detritus generated in the system, and a separate one to account for the macrophyte detrital contribution.

Biomass estimates for the model were not made spatially explicit. The biomass estimates are entered as biomass per unit area calculated for the total EEZ. A detailed account of all estimates are provided in Appendix 5.A. Biomasses were estimated in absolute terms (tonnes), usually for land based or benthic groups, or in relative terms (per km^2) for all pelagic groups. Biomass input data provided in both formats are summarised in Table 5.1.

Across the three time periods, biomass estimates for the land based top predators, for which there are time series data available, have been provided. For all pelagic groups, excluding fish groups where data exist, the biomass estimates between time periods are unchanged due to lack of time series data availability.

Rate estimates (P/B; Q/B)

Production to biomass rate estimates were obtained using the Ecopath software guidelines (Christensen et al. 2008). For populations that have not been exploited, the production to biomass ratio was considered to be equivalent to total mortality (Z) (Allen 1971) and estimates were either taken from the literature or calculated using empirical equations. P/B for the fish groups in particular were calculated using the equation of Palomares and Pauly (1998). Rates remain unchanged for all groups for all years, excepting for the *Patagonian Toothfish*, which has a higher P/B estimate for the 2000s model, which is considered appropriate following its exploitation.

In ecosystem models the importance of food quality is often overlooked when the currency of the model is biomass. For consumption to biomass estimates of the mammals and seabirds used in this model, the food quality was incorporated in the estimates. Local diet preferences for each group were coupled with the local energetic content of prey items. Assimilation efficiencies were taken into consideration and water content of prey items was assumed to be 70%. Combining this information with annual energy requirements estimated by Nagy et al. (1999) from Field Metabolic Rates (FMR) (with adjustments as per Ellis and Gabrielsen (2001)), it was possible to provide Q/B estimates that take into consideration the food quality derived from the local diet preferences of these groups, a consideration not usually incorporated into such models. A full description of the methodology is provided in Chapter 7.

Incorporating the diet quality into the consumption estimates in such a way is valid and useful for the static models built here, but it is important to note that the consumption rate estimates in the model are not linked to the diet matrices as the calculations are done independently. Therefore, when the model is run in its temporally dynamic form (Ecosim), where prey switching is permitted to occur (linked to prey availability), the energetic value of the diet

content should be reassessed to ensure that the consumption estimates correspond to the new diet preferences. A future development of the ecosystem modelling software where this feature could be incorporated into the model would be beneficial.

All rate estimates are given in Table 5.1.

Diets

Trophic linkages were made from published information and included traditional data on diet as well as information on trophic linkages from stable isotope and fatty acid signatures (See Appendix 5.A). The input parameters for the proportion of the diet that is considered ‘Unassimilated’ are provided in Table 5.1. The input parameters for each functional group for the diets are provided in Table 5.2. Diets for different time periods for most functional groups were assumed to be the same. In instances, however, where the diet included a stipulated contribution from a broader group (for instance, the diet for *Orcas* was determined as being 40% of the higher vertebrates (seals and seabirds)), the diets for these groups were adjusted to represent consumption of the functional groups according to the contribution each group made to the total biomass of the ‘broader group’ for each specific time period. This approach was used for the diet matrices of *Orcas*, *Southern Elephant Seals* and for *Giant Petrels* for each of the three different time periods. This same approach of assigning relative proportions of a diet according to the available biomass was carried out in all instances where diet information was provided at a higher level than that of the functional group.

Data Quality

Pedigree

The EwE model provides a framework to assign a measure of data quality to the parameters used in the model: the ‘Pedigree’. Using this framework, each parameter is assigned a value to measure its perceived quality (Table 5.3.). A qualitative (descriptive) data pedigree was used to describe the data source for each parameter (Biomass, P/B and Q/B) for each functional group and thereby establish the model ‘Pedigree’.

Sensitivity Analysis

A sensitivity analysis to test which parameters were most important in terms of changing the outcome of the model was also performed on the data. (Due to the unavailability of this tool in the EwE version 6, the model was constructed in EwE version 5 for this analysis). In the sensitivity analysis, each input parameter (B, P/B, Q/B) for each functional group is changed in turn in 10% steps from -50% to 50% and the fourth parameter to maintain mass-balance then calculated. A table of the magnitude of the changes (as a percentage) of the fourth parameter for each functional group according to the change in the percentage of variation of the input parameter was extracted from Ecopath. The results of the sensitivity analysis were summarised by calculating a simple index of sensitivity per component following the methodology outlined in Olson and Watters (2003). The index is a count of all the parameters affected by $\pm 30\%$ or more for each component. This index was further modified in this study by removing all counts that were the result of the change in a parameter having an effect on itself.

Ecosystem Network Analysis

The Ecopath routine has incorporated in it a variety of indicators and a network analysis tool to summarise the system in terms of biomasses and flows (Lindeman 1942; Odum 1971; Finn 1976; Ulanowicz 1986; Christensen 1995b; Ulanowicz 1995). Transfer efficiencies estimated for each trophic level are calculated as the percentage of throughput entering a trophic level that is subsequently passed on to the next trophic level (or harvested) (Christensen and Pauly 1998). Biomasses and flows are also assessed and provided in the form of a Lindeman spine, which is a summary of the transfer efficiencies (TEs) and biomasses summarised by trophic level (TL). The mixed trophic impact (MTI), derived from economic theory (Ulanowicz and Puccia 1990), is provided and allows for the quantification of direct and indirect trophic interactions among groups with the positive and negative effect that a hypothetical increase in the biomass of one group would have on another. This index can be positive or negative, and from it, the relative total impact (RTI) can be calculated as an absolute overall effect (Libralato et al. 2006)

$$RTI = \sqrt{\sum_{j \neq i}^n MTI_{ij}^2}$$

where the effect on itself is not included (therefore MTI_{ii} is not included in the calculation).

Summary statistics include a summary of the consumption in the system, the total system throughput, the mean trophic level of the catch, the net primary productivity, the total primary production/ total respiration, the net system production, the total primary production/ total biomass, the total biomass estimate and the total biomass divided by the total throughput as well as the connectance index, and system omnivory index.

5.3. Results

5.3.1. Balancing the model

The balancing procedure for all three models was done manually without the aid of the automation feature available in Ecopath. Through the process of constructing the model many lessons were learned. One important factor, which contributed to easing the balancing process, was assigning the contribution of prey to predators based on the preys' local availability in instances where diet preferences were not specified at species/ functional group level, but at a higher level. An additional important step was the reassessment of the consumption rates. This issue was originally highlighted in the 1980s model where the *Giant Petrels'* (BGPs) high consumption rates, leading to high mortality rates on their prey (the penguins in particular) pushed the associated EEs of these groups over 1 and proved difficult to resolve. Initially, a 'dead penguin' functional group was created to feed the BGPs and balance the model. This solution was considered unsatisfactory by experts on the system (pers. comm. P. Ryan) and hence led to an in depth consideration of the consumption rates used. Initially, the investigation was solely for this group, but ultimately resulted in a reworking of the Q/B rates for all the mammal and bird functional groups. A review of the consumption rates traditionally used in ecosystem models was carried out, and the method used to estimate this parameter was revised to take local information into account. The inclusion of local diets and associated energetic content

of the prey into the consumption estimates made a significant contribution to the model parameterisation (see Chapter 7) for all three models for the different time periods. Following the inclusion of this adjustment, only relatively minor adjustments for a limited number of groups were required.

For the 1960s model, adjustments to the *Southern Elephant Seal* diet formulation had to be made. An initial run of the model highlighted that consumption by *Southern Elephant Seal* on both the *Large Pelagic Fish* and the *Patagonian Toothfish* was too high (EE of 1.07 and 1.65 respectively). An adjustment to increase the contribution of *Large Cephalopods* by 5%, combined with a reduction by 1% for *Large Pelagic Fish* and 4% for *Patagonian Toothfish* was able to resolve the model balancing procedure.

For all other time periods the contributions were left in proportion to their biomass contributions as originally assigned. An alternative solution would have been to increase the biomass of the fish groups, as biomass data for these groups are uncertain.

For the models of all three time periods (1960s, 1980s and 2000s) minor adjustments were also made for the diet matrix of the *Giant Petrel* group. The contribution of *Prions and Petrels* to the diet had to be reduced by 1% in the 1960s model, and by 5% in the 1980s and 2000s models to allow the model to balance. In each case diet was reassigned to the penguin contribution (weighted according to relative biomasses of the 4 species for each of the 3 time periods). The most logical explanation for this issue is related to the probable underestimate of the *Prions and Petrels* as the census results for these time periods are considered underestimates (Ryan and Bester 2008) and the effect of the cat predation on the on the small flying bird populations would also have played a role at these time periods. Population changes resulting from the cat predation are explored using temporal simulations of this model and discussed later in this work (see Chapter 8).

Finally, specific adjustments had to be made to the *Patagonian Toothfish* data. Initial biomass estimates for this group were derived from an estimate made from the data from the voyage of the *Iris*, using swept area, for the *Patagonian Toothfish* (Brandao et al. 2002). An estimate of 1168 tonnes, with coefficient of variation of 213%, was made. For the model area under

consideration here (the EEZ of the PEIs), this amounts to a biomass of $0.00271 \text{ t.km}^{-2}$. Considering the coefficient of variation of 213%, the upper limit of this estimate may be considered to be $0.00577 \text{ t.km}^{-2}$. This biomass estimate is presumed to be a small percent of the original biomass that would have been in the system prior to the fishery crash of the mid 1990s. If the current estimate is 5% of original biomass, estimated biomass for the 1960s and 1980s model are between 0.05420 and $0.11544 \text{ t.km}^{-2}$. In balancing the model, these ranges were taken into account and the values chosen from within this range to satisfy the system's requirements. The highest value of $0.09000 \text{ t.km}^{-2}$ was used for the 1960s model, which was required to meet the energetic requirements of the *Elephant Seal* population. An intermediate value of $0.07500 \text{ t.km}^{-2}$ was used for the 1980s model. This value was determined following simulations of the *Patagonian Toothfish* fishery and was the biomass estimate that produced the best fit to the available fisheries data (Chapter 8). A value of $0.00429 \text{ t.km}^{-2}$ was used for the 2000s model, which is just over twice the estimate from the survey data from that time period ($0.00271 \text{ t.km}^{-2}$). The final balanced model output data are provided in Table 5.1 with a flow diagram for the 1980s model provided in Figure 5.2.

5.3.2. Data quality

An assessment of the data quality for each parameter is provided in Table 5.3. For the mammal and bird biomass data that are derived from population estimates of land based groups, local sampling contributes to a relatively high estimate of data quality. For the *Orcas* and all the fish groups, approximate or indirect methods were used and the data are relatively poor in comparison. Exceptions are for the *Patagonian Toothfish*, where trawl survey data combined with fishery statistics improves the estimate of this group. Locally derived estimates for the small demersal fish groups are available and, although the estimates are considered to be of low precision, the quality of these estimates can be considered slightly better. No local quantitative data exist for the cephalopods for the islands system and all data were taken from other estimates of models from similar systems. All the biomass estimates for all invertebrate groups were obtained from local data with low precision, as well as for the primary producers. The quality of the open ocean phytoplankton data may be considered improved by the inclusion of the satellite derived biomass estimates.

Production to biomass ratio data for the mammals and birds were derived in almost all cases from values available for similar / the same species from similar / the same locality. Exceptions include the *Orcas*, for which an empirical equation was used, and the *Southern Elephant Seals* for which an estimate was made from local data. For all other functional groups the production to biomass ratio was taken from other models and does not receive a high pedigree index.

As already documented, much effort was put into improving the estimate of the consumption to biomass ratio for the mammals and bird functional groups. Even so the grading given to this parameter estimate was left as an empirical relationship (a relatively low ranking in terms of pedigree). For all other groups, the data were taken from other models and hence have even lower rankings in terms of pedigree.

The pedigree index calculated by the Ecopath routine for this model was 0.303. The range of pedigree indices for 50 models analysed was from 0.164 to 0.676 (Morissette 2007), and a value of 0.303 would place the pedigree for this model in the intermediate range. If the adjustments to the consumption rate estimates made in this model for the land based top predators are considered to be locally derived (they are still from an empirical equation, but have local data incorporated) the model pedigree improves to 0.402, considerably higher (and in the upper range for EwE models). In any event, much of data for many of the pelagic groups for these models is uncertain and an effort should be made to improve these estimates in particular.

Sensitivity analysis

A sensitivity analysis provides an assessment of which parameters have the greatest effect on the system. A summary of the counts of which of the three parameters were most important showed that changes in Biomass (t.km^{-2}) had the greatest effect for all three models (between 100 and 101 counts). Consumption to biomass (Q/B, yr^{-1}) ratios were found to be the second most important parameter with counts between 64 and 68, and production to biomass (P/B, yr^{-1}) rates had the fewest occurrences (34 – 37). When this sensitivity index was amended to exclude those occurrences where the change of a variable for a functional group affected the output of the same functional group, the counts contributing to the index for each parameter were reduced, with no

counts found for the P/B ratio. Biomass and Q/B ratios were found to be equally important, with counts ranging from 63 – 67 for the three models.

The sensitivity index is plotted in Figure 5.3 for the three models. Across all three time periods, the sensitivity tests highlight the importance of the estimates of the *Orcas* for all years. The second most important group identified in the sensitivity analysis was the *Giant Petrels*, with high counts in all years, with the 1980s period the highest (64 counts). The third most important group identified were the *Southern Elephant Seals*, though the counts decline through time, as does the biomass of this species. Across all the time periods, the *Small Pelagic Fish* are found to be important, along with the *Benthos* and both *Large* and *Small Crustacean Zooplankton* groups. These are followed by the *Myctophid Fish*. In the 1980s model, along with those already mentioned, the *Patagonian Toothfish* as well as the *Gentoo Penguins* are also found to be important.

5.3.3. Model output

Trophic level

The Ecopath routine provides an output of trophic level (TL). These are given as fractional outputs which have no units (Table 5.1). Trophic Levels are based on the relative contribution and the TL of the diet components. Primary producers and detritus groups are by default of TL 1. All consumers are TL 2 or higher, depending on their diets (see Christensen et al. 2008, pg 92). The TL outputs are based on diets that were identical between years for all functional groups excepting the *Orcas*, *Southern Elephant Seals* and the *Giant Petrel* groups. The difference in TL estimates between time periods for these three groups were minor, with differences in estimates less than 0.15 between all years.

Orcas have the highest TL at 5.11 for the 1960s model, with the *Giant Petrels* close behind at 5.10. The *Orcas* TL declines through the time periods to 5.09 in the 1980s model and 4.98 in the 2000s model. The *Southern Elephant Seals* show a similar trend of declining TL from 4.74 in the 1960s and 1980s models, to 4.67 in the 2000s estimate. In contrast the *Giant Petrels* increase from a TL of 5.10 in 1960s, to 5.15 in the 1980s and finally to 5.18 in the 2000s model.

All the seals occupied the 4th TL and ranged between 4.38 and 4.74, with the *Southern Elephant Seals* the highest (and ranging from 4.67 to 4.74 across time periods). Of the penguins, the *King Penguins* were the highest at 4.41 with the *Gentoo Penguins* next at 3.91. The relatively high values for these two species reflect their predominantly fish diets. Penguins eating mainly crustaceans, the *Macaroni Penguins* and the *Southern Rockhopper Penguins*, had lower TLs at 3.80 and 3.59 respectively. All albatross were similarly ranked, with trophic levels between 4.30 and 4.40. The TL of the small flying birds was estimated to be 3.78. The mean trophic level for these land based top predators was 4.38.

The highest trophic level calculated among the fish was for the *Patagonian Toothfish* at 4.63. *Sharks and Rays* followed at 4.56. *Large Pelagic Fish* were the only other functional group of the fishes to occupy the fourth trophic position with a value of 4.31. All the remaining fish groups (all large and small demersals, as well as the *Small Pelagic Fish* and *Myctophid Fish*) were ranked at the third order trophic level with TLs estimated at between 3.14 and 3.79. It should be remembered that individual fish species within each group may occupy higher or lower TLs, but the diet matrix that reflects the prey of the group as a whole was used and dictates the resulting TLs found here.

Large Cephalopods were ranked relatively high at 4.05, with *Small Cephalopods* at 3.27. All remaining groups, including the *Benthos* group (2.27), the *Benthic Decapod* (2.21), and the three zooplankton groups (*Large Zooplankton Crustacean* 2.73, *Small Zooplankton Crustacean* 2.33, and *All Other Zooplankton* 2.00) occupied the 2nd trophic level.

Ecotrophic Efficiencies

The Ecotrophic Efficiencies (EE) output of the models provided measures of how much of a group is used within the system (Figure 5.4). The results were as to be expected, with most of the top predators having EE values that were relatively low. Most of the seal and albatross groups were below values of 0.2, but the penguins and small flying birds had higher predation rates and therefore higher EEs. In many ecosystem models it is assumed that most of what is produced in the system is consumed and, when automated routines are adopted, values of 0.95 are suggested as being default EE estimates. In this construction, all EEs are estimated by the model as all

other parameters (B, P/B and Q/B) are entered. The result is that some of the EE estimates are less than might be expected and highlight areas where more information may be needed for the model construction. For instance, all the demersal fish have EEs at 0.6 or lower, which, particularly for the smaller sized demersal fish may be considered low. In terms of the *Patagonian Toothfish* the EE is high, at close to 1, for both the 1960s and the 2000s model, while for the 1980s this value is relatively low (0.3). The EE for the *Small Pelagic Fish* is too low (~0.2) for a group that is primarily a forage fish group and suggests that the biomass for this group should be reconsidered (reduced). In contrast, the *Myctophid Fish*, which trophically occupy the same niche as the *Small Pelagic Fish* have a high EE (between 0.9 and 1.0 for all three models) which is as expected. Partitioning of biomass between these two groups should be revised. Both the cephalopod groups have high EEs for the 1960s model, reduced through time in the later models. The EEs for the crustacean groups (both Large and Small) have EEs that are not as high as might be expected for groups which form such an important component of the diets of many predators. The patchy distribution of the zooplankton, both spatially and temporally, may be a contributing factor to the lack of direct consumption on these groups. Finally the low EEs of the *Large Open Ocean Phytoplankton* as well as the *Island-associated blooms* show that this production does not enter the system through direct consumption, but their contribution to the detrital food chain should not be overlooked. Explicit tracing of the contribution of these inputs to the detrital food chain would provide a way to quantify the importance of this production to the ecosystem and should be considered for future improvements of the model.

5.3.4. Ecosystem network analysis

Transfer efficiencies

For the system as a whole, the transfer efficiencies (TEs) averaged for the trophic levels (TLs) II – IV are approximately 11.2 % (range 10.7 to 11.7%) across all three time periods (Table 5.4). When the efficiencies are calculated from the primary producers only, the values are slightly lower (10.7 – 10.9%) than for the system when the transfer efficiency including the detritus is included in the calculations (11.6 – 11.7%). Assessed per trophic level, the lower trophic levels have relatively high TEs (between 15.8 (producer) to 19.4% (detritus)), decreasing with

increasing TL showing good coupling between the lower trophic levels and their predators. Interestingly, among the three models the TE differs with TLs IV and higher for the three time periods, with the highest TEs found in the early model (1960s), and declining efficiency in the coupling of the system in the subsequent two models.

The network analysis for the system is shown diagrammatically in the Lindeman Spine (Figure 5.5). The Lindeman Spine shows the consumption, predation, exports/catches, respiration and flow to detritus summarised for each trophic level (Baird and Ulanowicz 1993). The highest flows are in the lower trophic levels with minor differences between the time periods for trophic levels III, IV, and V owing to the differences in the biomasses of the top predators, also evident in the total system throughput. A summary of the biomass by TL is provided (Figure 5.6), clearly showing the highest biomass estimates are in TLs I – III with TL II having the greatest overall for all three time periods.

Model structure

Each of the balanced models constructed here is one of a number of possible models. To explore the basic structure of the model formulation, an assessment of the mixed trophic impact (MTI) provides a summary of the diet structure of all functional groups and assesses the impact each group has on all other groups. The impact can be positive (a prey has a positive impact on its predator) or negative (predation impact of predator on prey) and these patterns are seen in the data (Appendix 5.B). Interesting results include the effect of groups with relatively low biomass, which have impacts on other groups. These include the *Orcas* and *Giant Petrels*, which have both positive and negative effects on many of the land based mammals and birds. The *Gentoo Penguins*, despite their relatively low biomass contribution to the system as a whole, have a measureable effect on the demersal fish groups. *King Penguins*, with their relatively high biomass contribution to the system have a negative effect on most of the land based top predators, except for the *Giant Petrels*.

Along with the MTI, the Ecopath routine provides the relative total impact (RTI) which is an index of the trophic impact, consolidating the impact by removing whether it is negative or positive and considering only its magnitude. Results of this assessment are provided in Figure

5.7 and show that *Orcas*, *Southern Elephant Seals* and *Giant Petrels* are the vertebrate predators with the highest RTI. The *Orcas* consistently have the highest impact of 1. The *Southern Elephant Seals* also rate high at around 0.5, even in the 2000s model when the biomass for this group is substantially reduced, and they score higher than the *Sub-Antarctic Fur Seals*, even in the 2000s when their biomass estimates are far lower than that of the fur seals (less than 1000 t versus approximately 5000 t). The *Giant Petrels* are shown to have a high RTI. Following these groups, the *King Penguins* also consistently rank as a key group for all time periods with an intermediary biomass contribution to the system. As expected, the importance of the nekton groups (*Small Pelagic Fish*, *Myctophid Fish*, both cephalopod groups) are identified through the RTI and all have corresponding high biomass contributions. The *Patagonian Toothfish* is also identified, though this is only true for the two models prior to the start of the fishery (1960s and 1980s), following which the index becomes much reduced with the reduction in its biomass contribution. Finally, the *Benthos* and *Large Zooplankton Crustaceans* are also identified as having relatively high RTI scores highlighting the importance of these two groups in the system.

In this assessment it is useful to discuss what species might be termed ‘keystone’ in the ecosystem. A keystone species can be defined as a species that plays an important role in an ecosystem while at the same time making a relatively low biomass contribution to the ecosystem (Power et al. 1996). By plotting the RTI against biomass values for each of the functional groups, an indication of which species might be considered ‘keystone’ can be provided. In Figure 5.8 the plot of this index against each group’s relative biomass for all functional groups for the three time periods is provided. It highlights the findings noted above that, while some groups with high biomasses are found to have key roles in the foodweb (e.g. the nekton groups), the groups with low biomasses fit the description of ‘keystone species’. Those that can be highlighted as such (as defined here) in this ecosystem are the *Orcas*, *Southern Elephant Seals* and the *Giant Petrels* (labelled on the figure), with all three groups contributing less than 0.01% to the living biomass of the ecosystem as a whole yet having a high RTI. The *Gentoo Penguins* are also worth mentioning, as although the RTI for this group is not particularly high (around 0.2), its RTI is relatively high compared to the low contribution this group makes to the overall biomass.

5.3.5. Summary statistics

Statistics and flows of the three models constructed for this study are given in Table 5.5 along with the summary statistics of an additional 8 ecosystem models of other Sub-Antarctic and Antarctic systems for comparative purposes. The models include that of the Kerguelen Plateau (Pruvost et al. 2005), South Georgia (Hill et al. 2012), the South Shetlands (Bredesen 2003), the Falklands (Cheung and Pitcher 2005), three different assessments of the Antarctic Peninsula (Erfan and Pitcher 2005; Cornejo-Donoso and Antezana 2008; Hoover 2012), and the Southern Plateau (NZ) (Bradford-Grieve et al. 2003). The summary statistics provide an overview of the system, with information on the magnitude of the ecosystem and a summary of the flows within it. Comparisons of the summary statistics for the three different time periods constructed of the PEIs show minor differences between model formulations suggesting that, while the constituents of the system have changed over time, these elements are not captured in these metrics.

The net primary production of the system was estimated to be $1278 \text{ t.km}^{-2}.\text{yr}^{-1}$, with the total primary production divided by the respiration being 1.56. This indicator is an index of ecosystem maturity, with systems close to one being considered mature as the production and respiration tend to be balanced (Christensen et al. 1993; Christensen 1995a). For the PEI system, with the indicator greater than 1, more is produced than respired and this suggests that the system is intermediate in its maturity. The net system production was $459 \text{ t.km}^{-2}.\text{yr}^{-1}$ and total production/biomass, which may be considered an indirect measure of organism size, was 30.38. The total biomass (excluding detritus), which can be used as a measure of ecosystem size was 42.08 t.km^{-2} , indicating a relatively small system, while the total biomass/ total throughput of 0.012 yr^{-1} suggests a relatively complex system.

Regarding the fisheries and the metric provided to assess it, the data for the mean trophic level of the catch for the PEI 2000s model (the only model for which there is a fishery) shows a value of 4.63, which is most similar to that of the Southern Plateau model (4.48, Bradford-Grieve et al. 2003). In both instances, the Patagonian toothfish is the only fishery. For the other models summarised here, mixed fishery catches (South Georgia and South Shetlands) or principally krill catches (Antarctic Peninsula) result in lower trophic level of catches. The connectance and

omnivory indices for the PEI models were similar to the average of all systems summarised here and could be considered relatively low.

5.4. Discussion

This construction of a mass balanced model of the PEIs attempts to integrate many sources of scientific data. The model formulation is only one possible construction representing the ecosystem, and while the data search was extensive, improvements from consultation with experts for each parameter would certainly benefit the model estimates. It is hoped that the full transparency on the data preparation that is included here (see Appendix 5.A) will ease future contributions and improvements to the model construction.

It is evident from the compilation of data, and the assessment summarised in the pedigree index of the data quality, that many of the pelagic groups would benefit greatly from quantitative assessments. In particular, assessments of all the large fish groups (the *Patagonian Toothfish*, *Large Demersal Fish*, *Large Nototheniid Demersal Fish* and *Large Pelagic Fish*) are needed. With only one trawl survey of the fish population to date, a quantitative survey would greatly improve the data of these groups. Secondly, assessments of the nekton are almost entirely lacking with no dedicated sampling efforts having been applied to this group in the vicinity of the islands. Considering the importance of the nekton (small pelagic fish and cephalopod groups) to the ecosystem as a whole, they must be highlighted as requiring urgent attention in terms of data requirements. For rate estimates, attention should be focused on the lower trophic levels, the values for which have been derived in all instances from other models.

Future scientific data collection efforts should not only address the areas in which there are data gaps, but should also focus on those parameters that have the most impact on the system. The results of the sensitivity tests highlight groups that can be considered important. These range from the top trophic levels (*Orcas*, *Southern Elephant Seals*) through the middle order groups (*Small Pelagic Fish*, *Myctophid Fish*, *Benthos*) and also include some of the lower trophic levels (*Large Zooplankton Crustaceans* and *Small Zooplankton Crustaceans*) for all three models. In addition, for the 1980s time period, both the *Giant Petrels* and the *Patagonian Toothfish* were identified as having significant impacts on the system. The results of these sensitivity tests are

interesting as they highlight that, while some groups with high biomass contributions (e.g. the small pelagic fish and the crustacean groups) are identified as being important, this is not necessarily always the case (e.g. *Orcas*, *Southern Elephant Seals*). A range of TLs was represented by the species identified to be of importance through the sensitivity test, as was found by Olson and Watters (2003). In their study some low TL groups (primary producers, secondary consumers, epipelagic fish) and some high TL groups (marlins, sharks, toothed whales) along with some middle order TL groups (cephalopods) were all identified. In contrast, Allain et al. (2007) found that the results of the test identified the most important groups to be in the lower trophic levels only.

To assist in identifying where future efforts should be focussed, a qualitative summary of the relative urgency for attention has been compiled (Table 5.6). The table indicates which groups were highlighted, not only through the process of identifying data gaps/-data quality issues (Pedigree index), but also through an assessment of the impact the group had on the model (through the sensitivity index, mixed trophic index, relative trophic impact and the identification of 'Keystone' species). The *Orcas*, *Southern Elephant Seals* and *Giant Petrels* were identified through this assessment as being of primary importance. These groups were followed in rankings by the *Myctophid Fish*, *Small Pelagic Fish* groups and *Gentoo Penguins*. The *King Penguin* had the next highest ranking, equivalent to the cephalopod groups. Finally, all the large fish groups, benthic and pelagic and including the *Sharks and Rays* were identified. A noticeable omission from the species identified as having an impact on the system is the decapod shrimp, *Nauticaris marionis*. Numerous studies have identified this species as having a key role in the system and its absence in this assessment may be due to the scale of the system adopted here.

In summarising the data, are we able to capture the differences for the three separate time periods in the network analysis? Input data into the models for these different time periods differ only for the groups for which there are time series data. In total this is 15 of the 37 functional groups. Fourteen of these are mammal and seabird groups (the only land based top predator functional group without time series data is the *Prions and Petrels*). The only other group for which the biomass estimates are adjusted for each time period is the *Patagonian Toothfish*. In terms of the biomasses, all these groups combined count for less than 0.4% of the total consumer biomass for

the system. So, although the changes in the ecosystem are relatively significant for some of the functional groups (the reduction in the elephant seals, the increase in the fur seals, the changes in the penguin populations, the collapse of the Patagonian toothfish stock) they are not reflected in most of the metrics which capture the biomasses and flows for the system as a whole, showing only minor differences between periods. A challenge is how to capture these changes using the ecosystem indicators. One indicator that does reflect some differences is the TE for the higher TLs (greater than IV), which declines in each subsequent time period. One interpretation of the reduced TE in subsequent models may be related to a decline in the efficiency of the system following a perturbation. Christensen and Pauly (1998) refer to systems becoming 'leaky' following exploitation. Transfer between trophic levels becomes 'sloppy' and energetically the coupling declines. This finding is also illustrated here through the decline in the TEs for the higher trophic levels. Alternatively the decrease in efficiency may be linked to the decrease in biomass of the higher TLs resulting in less absolute transfer (fewer predators) and a lower TE.

Regarding the summary statistics for the ecosystem as a whole in comparison to the other 8 Southern Ocean/-Antarctic systems (Table 5.5), the PEI statistics were found to be most similar to those of the Kerguelen Islands (Pruvost et al. 2005) for most metrics (sum of consumption and production, flows, and total system throughput). The Southern Plateau model, with units of carbon (as opposed to biomass), is not directly comparable excepting for non-dimensional measures. In general, the Falklands, South Shetlands and South Georgia model ecosystems were found to have the highest values for most of the metrics, with the three Antarctic Peninsula models spread across the range of systems summarised here. As an example, the total biomass (excluding detritus), which can be considered an estimate of ecosystem size, was lowest for the PEI models (42 t.km^{-2}) with the Kerguelen Islands model twice as high (at 82.69 t.km^{-2}). The three Antarctic Peninsula models ranged from 156 to 557 t.km^{-2} and the Falklands, South Georgia and South Shetlands between 244 and 358 t.km^{-2} .

5.5 Conclusions

This work provides the first quantitative network model of the PEIs and highlights areas for which more research is needed to address data gaps while focusing on those elements of the system that have been identified to play an important role in the system. Through further

development and improvement this model can provide a platform for an ecosystem approach to marine resource management, where options for both fisheries and conservation objectives can be explored. The extension of the model to include temporal simulations through the fitting of time series data will allow for hindcasting of past populations dynamics (Chapter 8), as well as investigating forecasting using potential climate change scenarios (Chapter 9). Developing the model further to be spatially explicit will also allow assessment of policy options, such as the implications following the recent declaration of the PEI Marine Protected Area (April, 2013) (https://www.environment.gov.za/content/princeedwardislands_declaredmarineprotectedarea). Clarity of the data compilation will also provide a useful dataset for the development and use of other ecosystem models which can be constructed to compare and contrast management scenarios.

Table 5.1. Model parameters used for input for all three time periods. Includes Biomass (t or t.km⁻²) calculated for the Exclusive Economic Zone (EEZ) of the Prince Edward Islands (PEIs) for 1960s, 1980s and 2000s; Estimates of Production to Biomass (yr⁻¹); Consumption to Biomass (yr⁻¹) and Unassimilated Consumption (UC) is provided. Model outputs of Trophic Level (TL) and Production to Consumption rates (P/Q) given. Black text indicates the original estimates (done in t or t.km⁻², whichever was appropriate). Blue text is the conversion to relevant units (from the black text figures). * 0.08 for 1960s & 1980s models, 0.13 for 2000s model; **5.11 for 1960s, 5.09 for 1980s, 4.98 for 2000s; ***4.74 for 1960s & 1980s, 4.67 for 2000s; 5.10 for 1960s, 5.15 for 1980s, 5.18 for 2000s.

Data table	Input parameters						Output parameters				
	1960	1980	2000	1960	1980	2000	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	UC	All years TL	All years P/Q
Group name	B (t)	B (t)	B (t)	B (t.km ⁻²)	B (t.km ⁻²)	B (t.km ⁻²)					
Orcas	10.895	10.895	10.895	0.0000253	0.0000253	0.0000253	0.06	5.39	0.10	5.11	0.011
Southern Elephant Seals	2506	672	427	0.0058142	0.0015591	0.0009907	0.074	12.78	0.10	4.74	0.006
Antarctic Fur Seals	3.3	18.2	112.8	0.0000077	0.0000422	0.0002617	0.10	14.06	0.10	4.40	0.007
Sub-Antarctic Fur Seals	107.8	1260.7	3978.0	0.0002501	0.0029250	0.0092294	0.10	14.97	0.10	4.38	0.007
King Penguins	6343	6343	6343	0.0147164	0.0147164	0.0147164	0.125	42.46	0.24	4.41	0.003
Macaroni Penguins	2881	2207	1768	0.0066842	0.0051205	0.0041020	0.185	76.75	0.24	3.80	0.002
Southern Rockhopper Penguins	846	541	306	0.0019628	0.0012552	0.0007100	0.16	93.70	0.24	3.59	0.002
Gentoo Penguins	15	19	18	0.0000348	0.0000441	0.0000418	0.20	62.50	0.20	3.91	0.003
Wandering Albatross	27.0	51.0	61.5	0.0000626	0.0001183	0.0001427	0.04	57.10	0.20	4.52	0.001
Grey-headed Albatross	0.64	28.0	36.5	0.0000015	0.0000650	0.0000847	0.05	49.39	0.20	4.36	0.001
Indian Yellow-nosed Albatross	10	36	36	0.0000232	0.0000835	0.0000835	0.027	57.48	0.20	4.39	0.000
Light-mantled Sooty Albatross	0.2	0.9	3.0	0.0000005	0.0000021	0.0000070	0.027	59.82	0.20	4.30	0.000
Dark-mantled Sooty Albatross	4.0	11	11	0.0000093	0.0000255	0.0000255	0.027	68.11	0.20	4.36	0.000
Giant Petrels	10.0	19.0	17.5	0.0000232	0.0000441	0.0000406	0.07	32.24	0.20	5.10	0.002
Prions and Petrels	283	283	283	0.0006566	0.0006566	0.0006566	0.16	191.70	0.24	3.78	0.001
Sharks and Rays	155.17	155.17	155.17	0.000360	0.000360	0.000360	0.14	3.7	0.20	4.56	0.038
Large Demersals	12283.91	12283.91	12283.91	0.0285	0.0285	0.0285	0.19	1.98	0.20	3.79	0.096
Large Nototheniid Demersals	4116.19	4116.19	4116.19	0.00955	0.00955	0.00955	0.21	3.4	0.20	3.28	0.062
Small Continental Slope Demersals	5077.35	5077.35	5077.35	0.01178	0.01178	0.01178	0.502	7.33	0.20	3.14	0.068
Small Inshore Demersals	3017.10	3017.10	3017.10	0.007	0.007	0.007	0.32	6.0	0.20	3.28	0.053
Large Pelagics	18102.61	18102.61	18102.61	0.042	0.042	0.042	0.22	2.56	0.20	4.31	0.086
Patagonian toothfish	38791.30	32326.08	1840.431694	0.090	0.075	0.004	0.08	1.6	0.20	4.63	0.050
Small pelagics	484891.25	484891.25	484891.25	1.125	1.125	1.125	0.9	10.5	0.20	3.39	0.086
Myctophids	1454673.76	1454673.76	1454673.76	3.375	3.375	3.375	0.5	6.1	0.20	3.37	0.082
Large Cephalopods	28015.94	28015.94	28015.94	0.065	0.065	0.065	2.7	10.95	0.20	4.05	0.247
Small Cephalopods	19395.65	19395.65	19395.65	0.045	0.045	0.045	4.5	18.25	0.20	3.27	0.247
Benthos	215507.22	215507.22	215507.22	0.5	0.5	0.5	2.5	10	0.20	2.27	0.250
Benthic decapod	16378.55	16378.55	16378.55	0.038	0.038	0.038	1.45	4.42	0.20	2.21	0.328
Large zooplankton crustaceans	2155072.24	2155072.24	2155072.24	5	5	5	5	14	0.20	2.73	0.357
Small zooplankton crustaceans	6896231.17	6896231.17	6896231.17	16	16	16	10	43	0.20	2.33	0.233
All other zooplankton	3017101.14	3017101.14	3017101.14	7	7	7	24	96	0.20	2.00	0.250
Open ocean large phytoplankton	732724.56	732724.56	732724.56	1.70	1.70	1.70	150	-		1.00	
Open ocean small phytoplankton	2935208.39	2935208.39	2935208.39	6.81	6.81	6.81	150	-		1.00	
Island associated blooms	1736.99	1736.99	1736.99	0.00403	0.00403	0.00403	200	-		1.00	
Macrophytes	84047.82	84047.82	84047.82	0.195	0.195	0.195	5.22	-		1.00	
Macrophyte Detritus	16007.61	16007.61	16007.61	0.037	0.037	0.037	-	-		1.00	
Detritus	12499419.00	12499419.00	12499419.00	29	29	29	-	-		1.00	

Table 5.2. (A) Diet matrix for each functional group except *Orcas*, *Southern Elephant Seals* and *Giant Petrels* with contributions summing to 1 for all consumers for all three time periods (1960s, 1980s, and 2000s); (B) Diet matrix for *Orcas*, *Southern Elephant Seals* and *Giant Petrels* with unique diets provided for each time period (1960s, 1980s, and 2000s) (see text for details).

Table 5.2.A

Prey \ Predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31		
ALL YEARS	CODE	MOR	MES	MAF	MSF	PKI	PMA	PSR	PGE	AWA	AGH	AYN	ALM	ADM	BGP	BPP	FSR	FLD	FLN	FSD	FID	FLP	FPT	FSP	FMY	CLA	CLS	BBE	BBD	ZLC	ZSC	ZOT		
1 Orcas	MOR			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
2 Elephant Seals	MES			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
3 Antarctic Fur Seals	MAF			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
4 Sub-Antarctic Fur Seals	MSF			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
5 King Penguins	PKI			0.002	0	0	0	0	0	0.001	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
6 Macaroni Penguins	PMA			0.002	0	0	0	0	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0	
7 Southern Rockhopper Penguins	PSR			0.001	0	0	0	0	0	0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
8 Gentoo Penguins	PGE			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
9 Wandering Albatross	AWA			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
10 Grey-headed Albatross	AGH			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
11 Yellow-nosed Albatross	AYN			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
12 Light-mantled Sooty Albatross	ALM			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
13 Dark-mantled Sooty Albatross	ADM			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
14 Giant Petrels	BGP			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
15 Prions and Petrels	BPP			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
16 Sharks and Rays	FSR			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
17 Large Demersals	FLD			0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
18 Large Nototheniid Demersals	FLN			0.001	0.001	0	0	0	0.19	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19 Small Demersals	FSD			0.001	0.001	0	0	0	0.2	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0.006	0	0	0	0	0	0	0	0	0	0
20 Small Inshore Demersals	FID			0.001	0.001	0	0	0.001	0.2	0	0	0	0	0	0	0	0	0.05	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21 Large Pelagics	FLP			0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0.035	0	0	0	0	0	0	0	0	0	0
22 Patagonian toothfish	FPT			0.001	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23 Small pelagics	FSP			0.048	0.032	0.06	0.04	0.014	0	0.02	0.19	0.12	0.08	0.08	0.02	0.011	0.04	0.04	0	0	0.15	0.098	0	0	0.12	0	0	0	0	0	0	0	0	0
24 Myctophids	FMY			0.9	0.95	0.79	0.14	0.055	0	0.08	0.396	0.46	0.42	0.33	0.2	0.039	0.22	0.27	0	0	0.5	0.201	0.05	0	0.4	0	0	0	0	0	0	0	0	0
25 Large Cephalopods	CLA			0.03	0.005	0.07	0.04	0	0	0.4	0.1	0.11	0.01	0.1	0.02	0.44	0.19	0.01	0	0	0.1	0.41	0	0	0	0	0	0	0	0	0	0	0	0
26 Small Cephalopods	CLS			0.01	0.005	0.07	0.03	0.02	0.01	0.4	0.25	0.27	0.45	0.45	0.12	0.01	0	0	0	0	0	0.05	0.2	0	0	0.1	0	0	0	0	0	0	0	0
27 Benthos	BBE			0	0	0	0	0	0	0	0	0	0.02	0	0	0	0.2	0.16	0.14	0.2	0.25	0	0	0.07	0	0	0	0	0	0.1	0	0	0	0
28 Benthic decapod	BBD			0.001	0.001	0	0	0.05	0.15	0	0	0	0	0	0	0	0	0	0	0.05	0.27	0	0	0.001	0	0	0	0.001	0.01	0	0	0	0	0
29 Large zooplankton crustaceans	ZLC			0	0.001	0.005	0.45	0.5	0.15	0.05	0.02	0.02	0.02	0.02	0.2	0	0.15	0.07	0.1	0.1	0.2	0.05	0.242	0.35	0.24	0.1	0.05	0	0	0	0	0	0	
30 Small zooplankton crustaceans	ZSC			0	0	0.005	0.3	0.26	0.07	0.037	0.01	0.01	0.01	0.01	0.4	0	0.07	0.055	0.3	0.35	0	0	0.517	0.35	0.1	0.6	0.08	0.05	0.4	0.1	0	0	0	
31 All other zooplankton	ZOT			0	0	0	0	0.1	0.03	0.01	0.01	0.01	0.01	0.01	0.04	0	0.04	0.13	0.25	0	0	0	0.07	0.3	0.04	0.3	0.08	0	0.2	0.2	0	0	0	
32 Open ocean large phytoplankton	POL			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.1	0	0	0	
33 Open ocean small phytoplankton	POS			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0.05	0.3	0.6	0.7	0	
34 Interisland blooms	PIA			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0
35 Macrophytes	PMA			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.13	0.28	0.1	0.03	0	0	0.05	0	0	0	0.02	0	0	0	0	0	0
36 Macrophyte Detritus	DMA			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0.37	0	0	0	0	0
37 Detritus	DGE			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.6	0.37	0	0.1	0.3	0
Sum				1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 5.2.B

INPUT TABLE	CODE	MOR	1960 MES	BGP	MOR	1980 MES	BGP	MOR	2000 MES	BGP
1 Orcas	MOR									
2 Southern Elephant Seals	MES	0.07689		0.03351	0.02339		0.01206	0.01275		0.003
3 Antarctic Fur Seals	MAF	0.00010		0.00004	0.00063		0.00033	0.00337		0.001
4 Sub-Antarctic Fur Seals	MSF	0.00331		0.00144	0.04389		0.02262	0.11873		0.031
5 King Penguins	PKI	0.19462		0.50316	0.22082		0.58486	0.18932		0.632
6 Macaroni Penguins	PMA	0.08839		0.22854	0.07683		0.20350	0.05277		0.176
7 Southern Rockhopper Penguins	PSR	0.02596		0.06711	0.01883		0.04988	0.00913		0.030
8 Gentoo Penguins	PGE	0.00046		0.00119	0.00066		0.00175	0.00054		0.002
9 Wandering Albatross	AWA	0.00083			0.00178			0.00184		
10 Grey-headed Albatross	AGH	0.00002			0.00097			0.00109		
11 Yellow-nosed Albatross	AYN	0.00031			0.00125			0.00107		
12 Light-mantled Sooty Albatross	ALM	0.00001			0.00003			0.00009		
13 Dark-mantled Sooty Albatross	ADM	0.00012			0.00038			0.00033		
14 Giant Petrels	BGP	0.00031			0.00066			0.00052		
15 Prions and Petrels	BPP	0.00868		0.07600	0.00985		0.03600	0.00845		0.036
16 Sharks and Rays	FSR	0.00076	0.00038		0.00083	0.00041		0.00139	0.00070	
17 Large Demersals	FLD	0.06026	0.03013		0.06545	0.03272		0.11019	0.05509	
18 Large Nototheniid Demersals	FLN	0.02019	0.01010		0.02193	0.01097		0.03692	0.01846	
19 Small Demersals	FSD	0.02491	0.01245		0.02705	0.01353		0.04554	0.02277	
20 Small Inshore Demersals	FID	0.01480	0.00740		0.01607	0.00804		0.02706	0.01353	
21 Large Pelagics	FLP	0.08880	0.04440		0.09645	0.04822		0.16238	0.08119	
22 Patagonian toothfish	FPT	0.19028	0.09514		0.17223	0.08611		0.01651	0.00825	
23 Small pelagics	FSP	0.02500	0.06250	0.00875	0.02500	0.06250	0.00875	0.02500	0.06250	0.009
24 Myctophids	FMY	0.07500	0.18750	0.02625	0.07500	0.18750	0.02625	0.07500	0.18750	0.026
25 Large Cephalopods	CLA	0.05909	0.32500	0.03161	0.05909	0.32500	0.03161	0.05909	0.32500	0.032
26 Small Cephalopods	CLS	0.041	0.225	0.022	0.041	0.225	0.022	0.041	0.225	0.022
27 Benthos	BBE									
28 Benthic decapod	BBD									
29 Large zooplankton crustaceans	ZLC			0.000119			0.000119			0.000119
30 Small zooplankton crustaceans	ZSC			0.000381			0.000381			0.000381
31 All other zooplankton	ZOT									
32 Open ocean large phytoplankton	POL									
33 Open ocean small phytoplankton	POS									
34 Island associated blooms	PIA									
35 Macrophytes	PMA									
36 Macrophyte Detritus	DMA									
37 Detritus	DGE									
SUM		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 5.3. Index of Data Pedigree generated for each functional group based on the data quality of three input parameters (Biomass (B), Production to Biomass (P/B) and Consumption to Biomass (Q/B) estimates). Key for generating the index provided.

	Group name	Biomass	P/B	Q/B	Overall Index
1	Orcas	4	4	4	12
2	Southern Elephant Seals	6	8	4	18
3	Antarctic Fur Seals	6	3	4	13
4	Sub-Antarctic Fur Seals	6	3	4	13
5	King Penguins	5	7	4	16
6	Macaroni Penguins	6	7	4	17
7	Southern Rockhopper Penguins	6	5	4	15
8	Gentoo Penguins	6	7	4	17
9	Wandering Albatross	6	7	4	17
10	Grey-headed Albatross	6	7	4	17
11	Indian Yellow-nosed Albatross	6	5	4	15
12	Light-mantled Sooty Albatross	6	7	4	17
13	Dark-mantled Sooty Albatross	6	5	4	15
14	Giant Petrels	6	5	4	15
15	Prions and Petrels	5	6	4	15
16	Sharks and Rays	4	3	3	10
17	Large Demersals	4	3	3	10
18	Large Nototheniid Demersals	4	3	3	10
19	Small Continental Slope Demersals	5	3	3	11
20	Small Inshore Demersals	5	3	3	11
21	Large Pelagics	4	3	3	10
22	Patagonian toothfish	5	3	3	11
23	Small pelagics	4	3	3	10
24	Myctophids	4	3	3	10
25	Large Cephalopods	3	3	3	9
26	Small Cephalopods	3	3	3	9
27	Benthos	5	3	3	11
28	Benthic decapod	5	3	3	11
29	Large zooplankton crustaceans	5	3	3	11
30	Small zooplankton crustaceans	5	3	3	11
31	All other zooplankton	5	3	3	11
32	Open ocean large phytoplankton	5			
33	Open ocean small phytoplankton	5			
34	Island associated blooms	5			
35	Macrophytes	5			
36	Macrophyte Detritus				
37	Detritus				

Biomass	
1	Estimated by Ecopath
2	From Other Model
3	Guesstimate
4	Approximate or Indirect Method
5	Sampling locally, Low Precision
6	Sampling locally, High Precision

P/B and Q/B	
1	Estimated by Ecopath
2	Guesstimate
3	From Other Model
4	Empirical Relationship
5	Similar Species, Similar System, Low Precision
6	Similar Species, Same System, Low Precision
7	Same Species, Similar System, Low Precision
8	Same Species, Same System, Low Precision

Overall Index	
<11	Poor
11-15	Intermediate
16-20	Adequate
>20	Good

Table 5.4. Transfer efficiencies summarised by Trophic Level (TL) for flows from the producers, the detritus and all flows combined for all three time periods. A summary of the flows for TLs 2 to 4 for each case also provided.

Transfer efficiencies	Trophic level									Mean for TL II-IV
1960s	II	III	IV	V	VI	VII	VIII	IX	X	
Producer	15.8	8.6	9.6	6	4.6	2.8				10.9
Detritus	19.4	8.1	10.3	6.2	4.8	2.9				11.7
All flows	16.7	8.4	9.8	6.1	4.7	2.8	1.2	0.1		11.1
1980s										
Producer	15.8	8.5	9.4	5.6	3.7	1.9				10.8
Detritus	19.4	8.0	10.2	5.8	3.9					11.7
All flows	16.6	8.4	9.6	5.7	3.7	1.9	0.8	0.1		11.0
2000s										
Producer	15.8	8.5	9.2	5.1	2.7	1.6				10.7
Detritus	19.4	8.0	10.1	5.4	2.8					11.6
All flows	16.6	8.4	9.4	5.2	2.7	1.6	0.6	0.1		11.0

Table 5.5. Summary statistics of the Prince Edward Island model for each time period (1960s, 1980s and 2000s) as compared to 8 other Southern Ocean/Antarctic Ecopath models.

		Prince Edward Islands	Prince Edward Islands	Prince Edward Islands	Kerguelen Island	South Georgia	South Shetlands	Falklands	Antarctic Peninsula	Antarctic Peninsula	Antarctic Peninsula	Southern Plateau NZ
		This study 1960	This study 1980	This study 2000	Pruvost et al. 2005	Hill et al. 2012	Bredesen thesis 2003	Cheung and Pitcher 2005	Cornejo Donoso 2008	Erfan and Pitcher 2005	Hoover thesis 2012	*Bradford-Grieve et al. 2003
	Units	1960	1980	2000								
Sum of all consumption	t.km ⁻² .yr ⁻¹	1471.11	1470.89	1470.74	1689.16	7558.68	7975.66	4852.84	1955.08	414.80	4227.10	493.46
Sum of all exports	t.km ⁻² .yr ⁻¹	458.91	459.07	459.17	146.70	373.60	8250.29	27677.64	4248.34	1770.07	1164.75	101.76
Sum of all respiratory flows	t.km ⁻² .yr ⁻¹	819.42	819.25	819.15	926.91	3035.83	4704.35	2446.74	1025.66	173.18	1999.05	208.98
Sum of all flows into detritus	t.km ⁻² .yr ⁻¹	732.53	732.69	732.79	632.55	1901.43	9115.26	27727.69	4313.47	1879.36	1801.92	239.89
Total system throughput	t.km ⁻² .yr ⁻¹	3481.96	3481.91	3481.86	3395.31	12869.53	30045.55	62704.91	11542.55	4237.41	9192.83	1044.09
Sum of all production	t.km ⁻² .yr ⁻¹	1635.74	1635.74	1635.74	1498.02	5713.31	14630.57	31558.09	5812.40	1951.17	3736.16	496.53
Mean trophic level of the catch				4.63			3.16	3.73		2.10	2.41	4.80
Gross efficiency (catch/net p.p.)							6.02E-06	4.55E-06		5.58E-03	2.30E-05	6.28E-05
Calculated total net primary production	t.km ⁻² .yr ⁻¹	1278.32	1278.32	1278.32	1073.60	2702.19	12954.40	30122.55	5274.00	1792.50	3163.81	310.74
Total primary production/total respiration		1.56	1.56	1.56	1.16	0.89	2.75	12.31	5.14	10.35	1.58	1.49
Net system production	t.km ⁻² .yr ⁻¹	458.91	459.07	459.17	146.69	-333.64	8250.05	27675.81	4248.34	1619.32	1164.76	101.76
Total primary production/total biomass		30.38	30.39	30.44	12.98	6.82	53.09	83.95	9.46	11.48	16.61	48.56
Total biomass/total throughput	.yr ⁻¹	0.012	0.012	0.012	0.024	0.031	0.008	0.006	0.048	0.037	0.021	0.006
Total biomass (excluding detritus)	t.km ⁻²	42.08	42.06	41.99	82.69	396.29	244.02	358.80	557.68	156.13	190.48	6.40
Total catches	t.km ⁻² .yr ⁻¹						0.0780	0.1372		10.0000	0.0728	0.0195
Connectance Index		0.204	0.204	0.204	0.232	0.185	0.249	0.179	0.272	0.203	0.205	0.163
System Omnivory Index		0.220	0.210	0.200	0.165	0.405	0.157	0.277	0.161	0.152	0.178	0.294

**Italics* indicate values in units of Carbon as opposed to wet weight

Table 5.6. Qualitative assessment to highlight where scientific research efforts should be focussed in future.

#	CODE	Functional Group	Data Quality Poor	Sensitivity test result	Mixed Tophic Impact	Relative Total Impact	Keystone Species	Total Count
1	MOR	Orca		x	x	x	x	4
2	MES	Southern Elephant Seal		x	x	x	x	4
3	MAF	Antarctic Fur Seal						
4	MSF	Subantarctic Fur Seal						
5	PKI	King Penguin			x	x		2
6	PMA	Macaroni Penguin						
7	PSR	Southern Rockhopper Penguin						
8	PGE	Gentoo Penguin		x	x		x	3
9	AWA	Wandering Albatross						
10	AGH	Grey-headed Albatross						
11	AYN	Yellow-nosed Albatross						
12	ALM	Light-mantled Sooty Albatross						
13	ADM	Dark-mantled Sooty Albatross						
14	BGP	Giant Petrels		x	x	x	x	4
15	BPP	Prions and Petrels						
16	FSR	Sharks and Rays	x					1
17	FLD	Large Demersal Fish	x					1
18	FLN	Large Nototheniid Demersal Fish	x					1
19	FSD	Small Continental Slope Demersal Fish						
20	FID	Small Inshore Demersals						
21	FLP	Large Pelagic Fish	x					1
22	FPT	Patagonian toothfish		x		x		2
23	FSP	Small Pelagic Fish	x	x		x		3
24	FMY	Myctophid Fish	x	x		x		3
25	CLA	Large Cephalopods	x			x		2
26	CLS	Small Cephalopods	x			x		2
27	BBE	Benthos		x		x		2
28	BBD	Benthic decapod						
29	ZLC	Large crustacean zooplankton		x		x		2
30	ZSC	Small crustacean zooplankton		x		x		2
31	ZOT	Other zooplankton						
32	POL	Open ocean large phytoplankton						
33	POS	Open ocean small phytoplankton						
34	PIA	Island-associated blooms						
35	PMA	Macrophytes						
36	DMA	Macrophyte detritus						
37	DGE	Detritus						

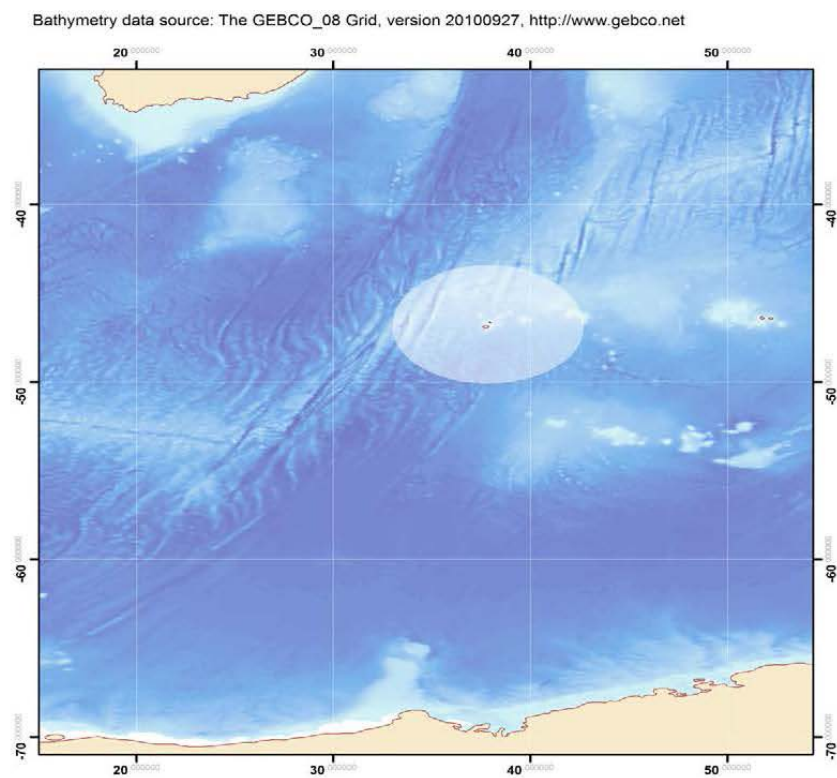


Figure 5.1. Study areas. Map showing the Exclusive Economic Zone (EEZ) of the Sub-Antarctic Prince Edward Islands situated southeast of South Africa.

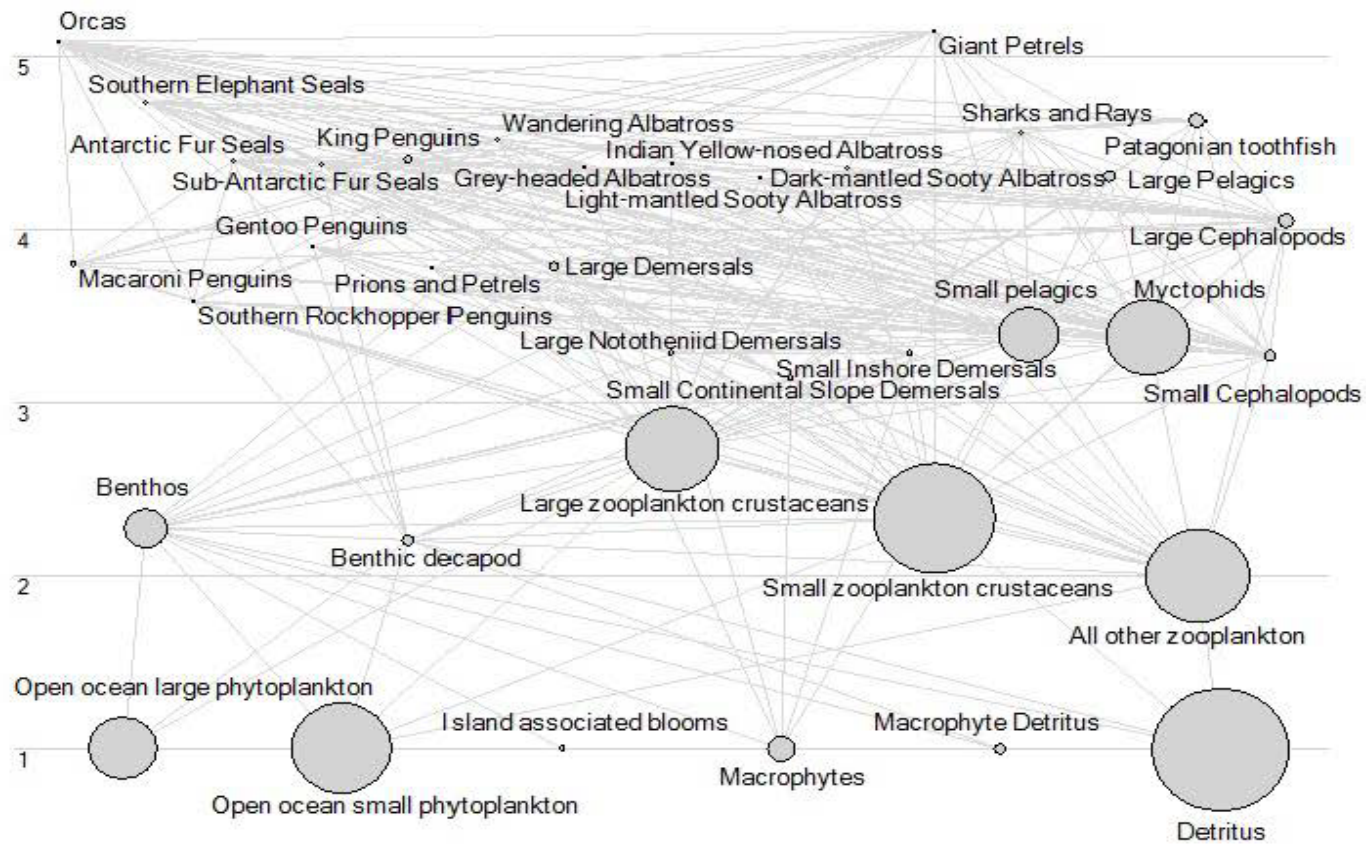


Figure 5.2. Schematic representation of the food web. Each functional group is represented by a circle which is scaled to the square-root of the biomass (t); groups are distributed with increasing Trophic Level (TL) on the y-axis and all trophic linkages indicated by grey lines.

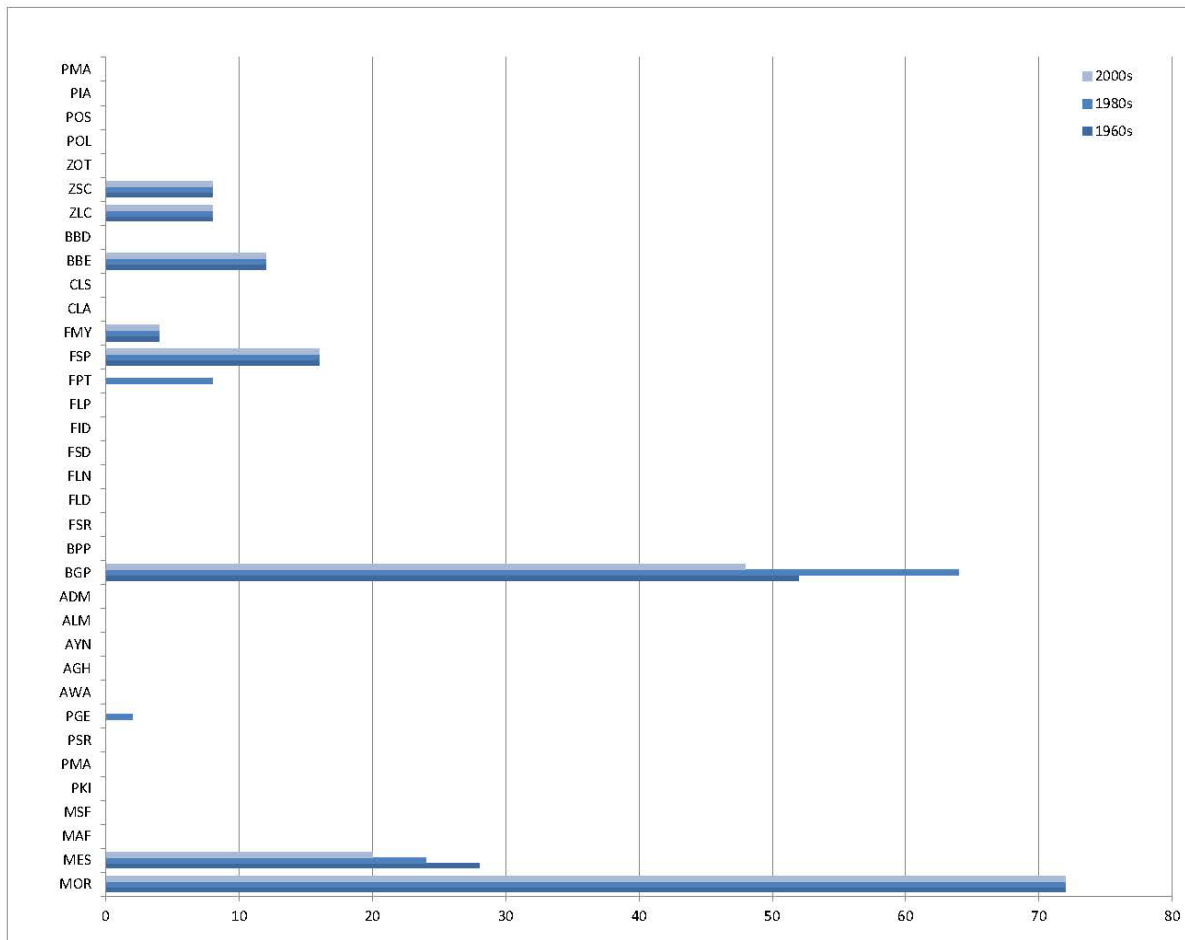


Figure 5.3. Results of the sensitivity analysis. The index is the count of estimated parameters of the model affected by at least 30%, given the changes (between -50% and 50%) in the input parameters of each functional group (listed on the y-axis). Effects within groups have been eliminated from the analysis.

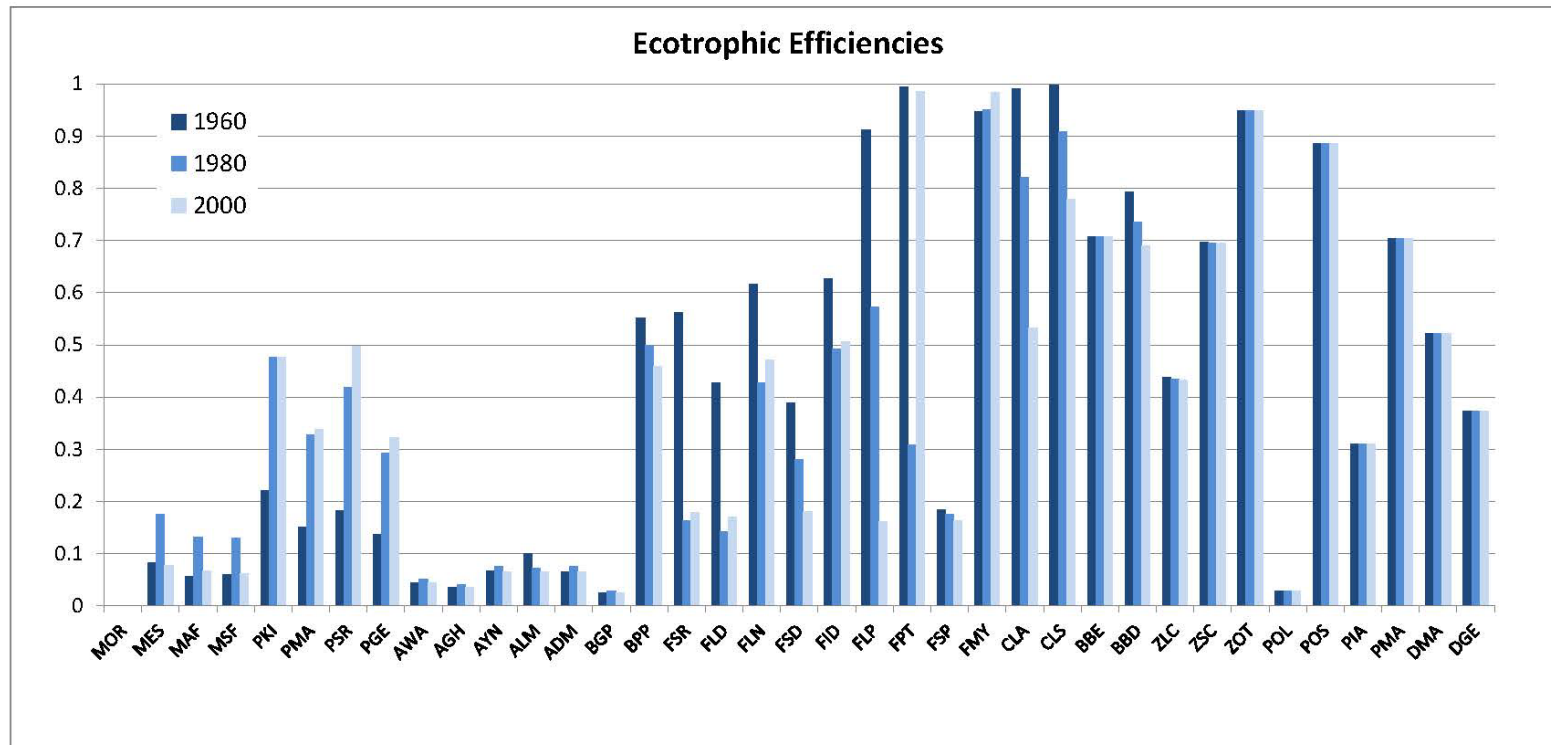


Figure 5.4. Plot showing the model results of the Ecotrophic Efficiencies (EE) (0-1), an index of how much of the production for each functional group is used in the system, for each of the three time periods (1960s, 1980s and 2000s).

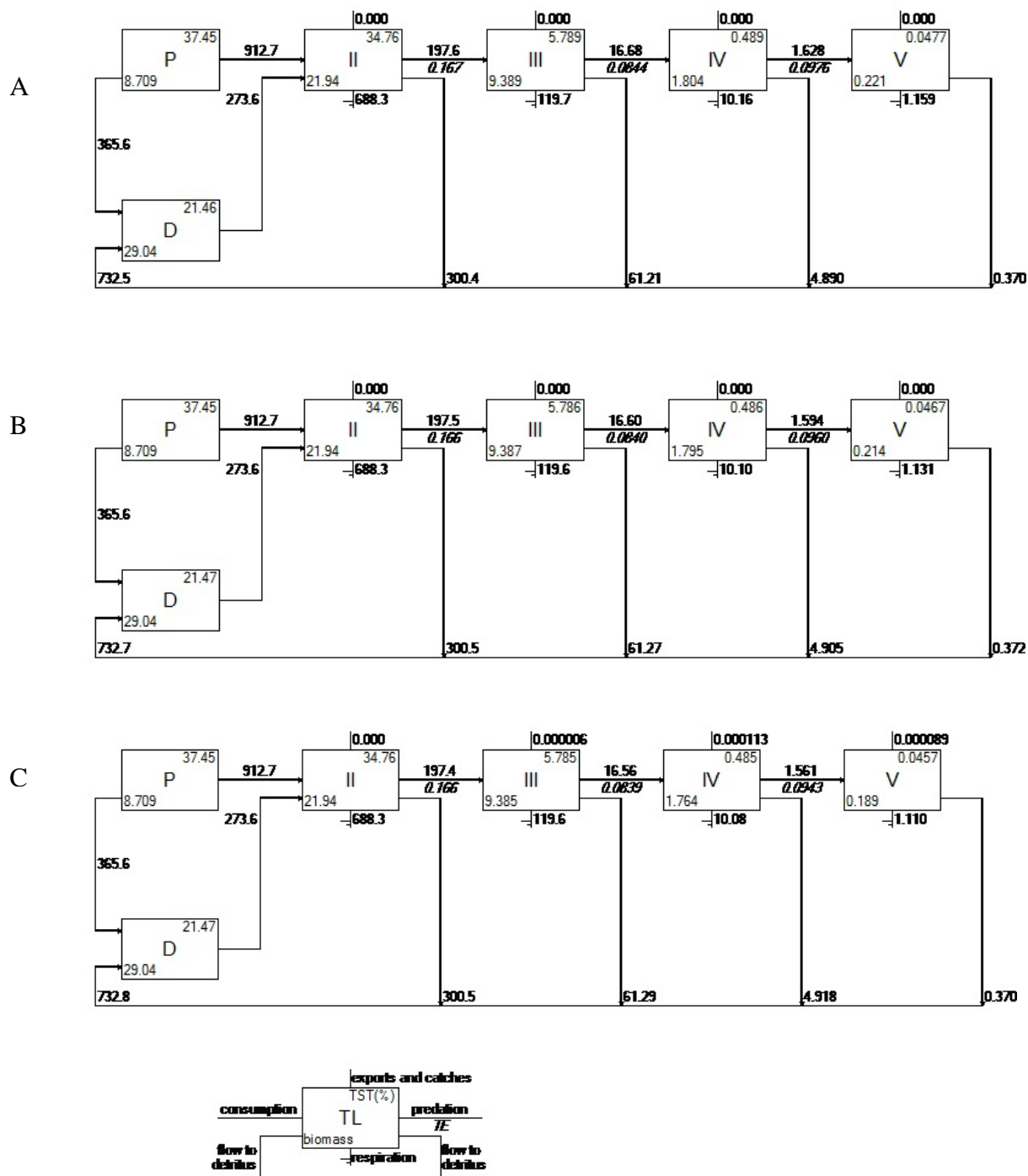


Figure 5.5. Diagram showing the trophic flows as summarised in the Lindeman spine for each of the three time periods for which models were constructed, A) 1960s, B) 1980s and C) 2000 (TST = Total System Throughput, TE – Transfer Efficiency).

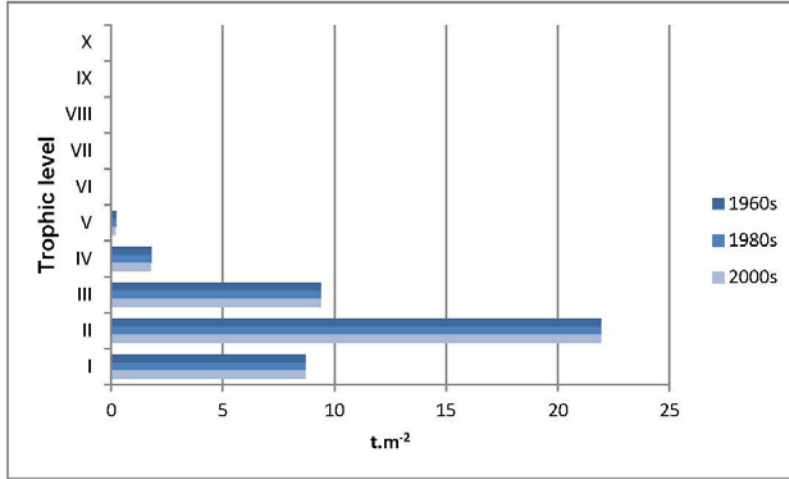


Figure 5.6. Bar plot showing the Biomass (B) by trophic level for each of the three time periods (1960s, 1980s, and 2000s).

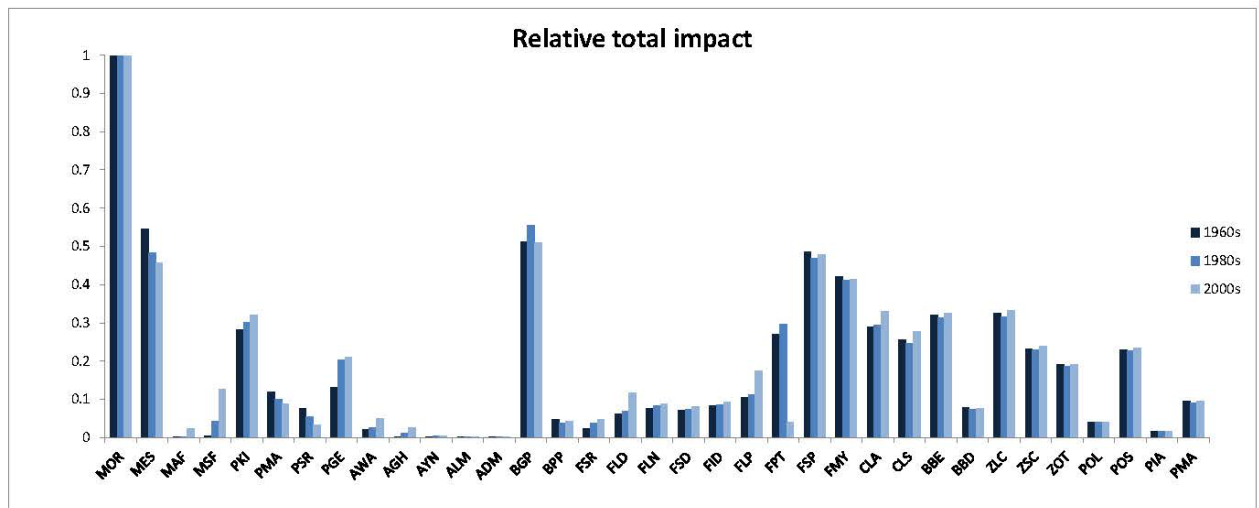


Figure 5.7. Plot showing the relative trophic impact (RTI) of each functional group for each time period (1960s, 1980s, and 2000s).

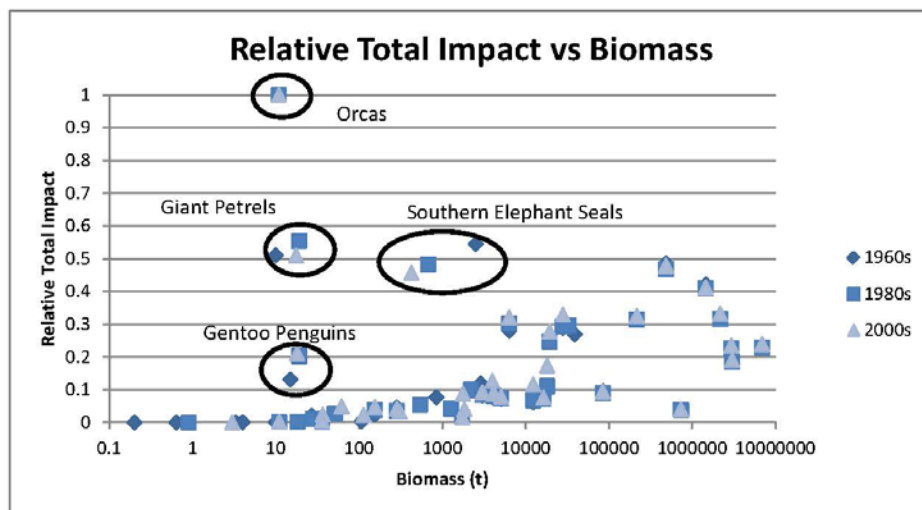


Figure 5.8. Scatter plot of the relative trophic impact (RTI) plotted against biomass (B), providing an indicator of 'keystone' species.

Chapter 6 Exploring ecosystem boundary size

6.1. Introduction

In ecological theory, an ecosystem is an area within which the energy flow between community production and consumption is balanced (Odum 1969). Such a statement suggests that there are boundaries to ecosystems, and therefore ecosystem boundaries are intrinsic to ecology theory. But setting the boundary for a marine ecosystem can be difficult because, unlike with terrestrial systems where physical boundaries may be obvious, in marine systems the transition between ecosystems is often not discrete. Exploring the boundary size of a marine ecosystem through energetic requirements can provide insight into the scale at which the system should be considered. An island-centered marine ecosystem provides a system that is easy to conceptualize for the exploration of ecosystem boundaries, particularly when many of the constituents of the ecosystem are bound, for one reason or another, to the island or island shelf. A study on the Privolov Islands (Cianelli et al. 2004) explored the issue of ecosystem boundary size through an energetic approach, where the boundary of the system was determined in terms of the balance between predatory demand and prey production. The study focused on the centrally placed foragers in the system and assessed at what extent the system should be considered. The Cianelli et al. (2004) study inspired this case study of the Prince Edward Islands (PEIs) to address the same question. Many of the top predators at the PEIs are island-based for the duration of their residency in the region considered here and the scale of the system can therefore be investigated through similar means.

In order to conceptualize an ecosystem as an entity around which to draw a boundary and consider the system of flows to be mass balanced, one has to assume that i) the system is closed, ii) the imports balance the exports, or iii) explicitly account for both the imports to and exports from the system using net migration and biomass accumulation/loss terms if required.

The scale of the formulation of the ecosystem model will depend on which option is selected. For the PEIs, it would not be appropriate to consider the system closed as it lies in an easterly flowing Antarctic Circumpolar Current with a 'conveyor belt' of open ocean production flowing into the system. At the same time, this flow-through environment means that the elevated

productivity, which is a direct result of the interaction of the oceanography and the islands themselves, also flows out of the system. The premise of the model used here is that the inflow and outflow of the imports and exports are in balance when the system is considered at the scale of the Exclusive Economic Zone (EEZ).

In the case of the PEIs, the pelagic system is a flow through system associated with the Antarctic Circumpolar current, flowing from west to east. For this model, the assumption is made that the pelagic imports and exports may be considered equivalent. Hypothetically, the predation impact of the top predators on the incoming pelagic resources (as has been documented by Hunt et al. (2001)) could be balanced by the increased pelagic production which is stimulated following the island mass effect, with the additional production associated with the islands resulting in downstream increases in pelagic productivity.

In addition to addressing the question of imports/ exports, in order to assume a ‘closed’ system one needs to adjust the parameters of the model to account for the residence time of the species that do not spend the entire year within the system. This can be relatively easily achieved by adjusting the biomass (t) of the respective groups according to the time they spend at the islands. This approach has been used in the formulation of the original PEI ecosystem model and is preferable to making adjustments to consumption and production rates (to achieve the same goal) as these rates are in many instances based on field based estimates associated with the biological demands of the life stage of the residents when based at the islands. For example, consumption rates measured for many of the land based top predators are derived from data collected during the breeding season, the only period in the year when the data are accessible. These consumption rates are higher than the rates for other times of the year due to the increased energetic demands associated with breeding, but as the model is attempting to capture the rates for the periods when the top predators are in the system, these elevated rates are appropriate for the model construction.

The objective of this study was to consider the Prince Edward Island ecosystem at various scales to investigate the size at which the energy requirements of all functional groups could be met, and explore the ecosystem boundary size at which the various functional groups should be considered.

6.2. Methods

The mass balanced Ecopath model of the ecosystem representing the EEZ of the Prince Edward islands (PEIs) for the 1980s time period was used (see Section 5.2). This model was then adjusted to create an additional three smaller models of the system. The areas for each model were calculated with four different radius lengths (the original remaining with a radius of 200nm; the additional models with radii of 100nm, 50nm and 20nm) (Table 6.1, Figure 6.1). Each model was centered at the midpoint between the two islands that make up the Archipelago (46°46'S, 37°51'E). Data for biomass, production and consumption rates as well as the diet matrices used are provided in Chapter 5 (see Table 5.2 and 5.3; Appendix 5A).

For each of the additional three models, the biomass per unit area (t.km^{-2}) was scaled according to the size of each ecosystem (i.e. higher biomass per unit area with smaller boundary size for all top predators, as they were assumed to fill the entire area of each model). Biomasses per unit area of pelagic groups, however, remained the same between models. Biomass estimates for the benthic components of the ecosystem (i.e. all demersal fish, the benthic shrimp, *Nauticaris marionis*, the 'Benthos', 'Macrophytes' and 'Macrophyte Detritus' groups) were scaled according to the area that the benthic component occupied of the total area for each model.

Following the calculation of the basic estimates for each of the output parameters of the model, the ecotrophic efficiencies (EEs, a measure of how much of each group is used in the system) and consumption mortalities were used to explore the ecosystem size. Finally, a balanced model was constructed by making the necessary adjustments to the parameters of the model to assess which of the above four models was most appropriate for each of the functional groups. For comparative purposes, the above exercise was then repeated for the 2000s model (Input parameters summarized in Section 5.2 and provided in Table 6.2).

6.3. Results

The results of the outputs following the basic estimate routine of the Ecopath model are provided in Table 6.3.

Model 1 (200 nm radius):

This model represents the PEI EEZ and balances without adjustment, as is described in Chapter 5 for the 1980s version of the model.

Model 2 (100 nm radius):

When the model is run, it does not balance. The ecotrophic efficiencies (EE) for 4 groups exceed 1, i.e. the production of each of these groups is not sufficient to supply the consumption. These groups are the *Patagonian Toothfish* (EE = 1.20), the *Myctophid Fish* group (EE = 2.11) and the two Cephalopod groups (*Large Cephalopods* EE = 2.25, and *Small Cephalopods* EE = 2.14). Ecopath provides a breakdown of the mortality estimates caused by each functional group on each functional group, and highlights which groups are ‘responsible’ for the over-consumption of the groups. The *Southern Elephant Seals* are identified as being the primary consumers of the *Patagonian Toothfish*, while the *King Penguins* are identified as the primary consumers of the *Myctophid Fish*. In the case of the two cephalopod groups, the greatest consumers of the *Large Cephalopods* are many of the land based top predators, including the *Southern Elephant Seals*, the *King Penguins*, and the *Macaroni Penguins*, and for the *Small Cephalopods* the *Prions and Petrels*. This result suggests that the foraging range for these groups is greater than the 100nm model constraint.

Model 3: 50 nm model

On the first run, the groups that had an EE >1 were the *Sharks and Rays* (EE = 2.63), *Large Pelagic Fish* (EE = 2.34), *Patagonian Toothfish* (EE = 4.77), *Small Pelagic Fish* (EE = 1.140), *Myctophid Fish* (EE = 6.74) and the *Large* and *Small Cephalopods* (EE = 7.96 and 7.01, respectively). Investigation into the predation mortalities showed that the *Southern Elephant Seals* were responsible for the consumption on the *Sharks and Rays*, the *Large Pelagics* and the *Patagonian Toothfish*. The *King Penguins* consumed the *Myctophid Fish* and the *Large* and *Small Cephalopods*, and finally the *Macaroni Penguins* and the *Prions and Petrels* consumed the *Cephalopods* (*Large* and *Small* respectively).

Model 4: 20 nm model

This model is the smallest one considered, and could never conceivably provide a balanced outcome with all the land based top predators constrained to feed in such a limited area. Accordingly, the ecotrophic efficiencies for the prey of these groups are greatly over consumed by up to 48 times (Table 6.3). The *Sharks and Rays* (EE = 16.434), *Large Pelagic Fish* (EE = 12.06), *Patagonian Toothfish* (EE = 29.74), the *Small Pelagic Fish* (EE = 6.54) *Myctophid Fish* (EE = 39.15) and *Large* (EE = 47.93) and *Small Cephalopods* (EE = 41.68) highlight this. In addition, some of the smaller prey were also over consumed: the *Large Zooplankton Crustaceans* (2.568), the *Small Zooplankton Crustaceans* (EE = 1.103) and the *Other Zooplankton* (EE = 1.21). Investigation into the mortality rates highlights the ‘culprits’ as the *Southern Elephant Seals* on the *Sharks and Rays*, the *Large Pelagic Fish*, the *Patagonian Toothfish* and the *Cephalopods* (both groups); the *Sub-Antarctic Fur Seals* on the *Myctophids Fish*; the *King Penguins* and *Macaroni Penguins* on the *Small Pelagic Fish*, *Myctophid Fish* as well as both groups of cephalopods; the *Rockhopper Penguins* on the *Small Cephalopods*; the *Wandering Albatross* on the *Cephalopods*; the *Prions and Petrels* on the *Myctophid Fish* and the *Large* and *Small Cephalopods*; and the *Large pelagic Fish* on the *Large Cephalopods*.

Model 5: Mixed Balanced Model (MBM)

For this model, an attempt was made to balance the model at the scale appropriate for each functional group from a top down perspective. Groups identified above were adjusted to see at what scale each group should be considered. Adjustments were made, in an iterative process, based on the information provided above. It is evident from Model 2 (100nm model) that many of the top predators could not satisfy their energetic requirements if restricted to prey inside this theoretical area. Using Model 2 as a starting point, the biomass per unit area for both the *Southern Elephant Seals* and the *King Penguins* were reset to their Model 1 (200nm model) values. When the model was rerun, it still did not balance, and a new ‘culprit’ was identified in the *Giant Petrels* which were then also reduced to biomass estimates reflecting the Model 1 values. Overconsumption of the *Patagonian Toothfish* and *Myctophid Fish* as well as both groups of *Cephalopods* was still evident (EEs for these groups > 1). Further adjustments to the fur seals (both groups) reduced the EEs to close to 1 (*Myctophid Fish* 1.07, *Large Cephalopods*

1.07, *Small Cephalopods* 1.27). With a reduction in biomass of the *Macaroni Penguins*, the model came close to balancing with only the *Myctophid Fish* and *Small Cephalopods* with EEs exceeding 1. A final adjustment of the *Prions and Petrels* to the Model 1 biomass estimate resulted in a balanced model.

When attempting to balance the model based on the Model 3 (50nm model) parameters, initial amendments were as before, adjusting those groups highlighted by the model to be causing the over-consumption (reflected in the EEs). They were the *Southern Elephant Seals*, *Fur Seals*, *King Penguins*, *Macaroni Penguins*, *Giant Petrels* and the *Prions and Petrels* which were all set to the biomass estimates for the largest model (Model 1). After attempting to balance this model, the *Orcas*, *Southern Rockhoppers*, *Large Demersal Fish* and *Large Nototheniid Demersal Fish* were all highlighted as being responsible for the continued overconsumption. Adjustments of the first three of these groups to biomasses from Model 2 (100 nm) were made. The *Large Nototheniid Demersal Fish* biomass estimate was set to be intermediary between Model 2 and 3 (with a value of 0.0440 t.km^{-2}). The albatrosses were then highlighted as being responsible for the unbalanced outcome, and only when these biomasses were reduced to the Model 1 estimates did they stop contributing to the overconsumption. Following these adjustments, to balance the model both the *Myctophid Fish* and the *Large Cephalopod* groups had to be increased by small amounts (*Myctophid Fish* from 3.38 to 3.40 t.km^{-2} ; *Large Cephalopods* from 0.065 to 0.060 t.km^{-2}) to enable the system to balance.

Finally, an attempt to balance the smallest model (Model 4) was made. The pattern of identifying those groups that were over-consumed in the model parameterization procedure and identifying the consumers was repeated. As before the biomass estimates for the Seal groups (*Southern Elephant*, *Antarctic Fur Seal* and *Sub-Antarctic Fur Seal*), two of the penguin groups (*King Penguin* and *Macaroni Penguin*), all the albatross groups, the *Giant Petrels* and the *Prion and Petrel* groups were reduced to reflect estimates used in the largest model (Model 1). Following this, the *Orcas* and the *Southern Rockhopper Penguin* groups were reduced to the Model 2 estimates and the *Large Demersal Fish* group to the Model 3 estimate. These adjustments brought the model close to balancing, with only 4 groups over-consumed (i.e. $EE > 1$): *Myctophid Fish* ($EE=1.49$), *Large Cephalopods* ($E=1.18$), *Large Zooplankton Crustaceans* ($E=1.49$) and *All*

Other Zooplankton (EE=1.19). Adjustments to the *Large Nototheniid Demersal Fish* (to 0.26 t.km⁻², a value between the Model 2 and 3 estimates) and the *Benthos* (to the Model 3 value of 8.0 t.km⁻²) brought the model very close to balancing with only the *Myctophid Fish* and *Large Cephalopods* still over-consumed (EEs of 1.12 and 1.05 respectively). Redistribution of biomass between the *Small Pelagic Fish* and the *Myctophid Fish* groups (increase of *Myctophid Fish* by 0.225t.km⁻² and decrease to *Small Pelagic Fish* of the same), along with an increase in the *Large Cephalopods* value from 0.065 to 0.070, brought the model to balance.

As is evident from the data supplied in Chapter 2, the composition of the top predators has changed significantly in the 20 years that separate the 1980s model description from that in the 2000s. In particular, the declines recorded in the *Southern Elephant Seal* population, the recovery of the fur seal populations as well as the collapse of the Patagonian toothfish stock would create a different scenario for this analysis. Therefore, the exercise was repeated for the dataset which represents the islands for the 2000s period, and the outcome showed some differences. In the first reduction in ecosystem size, only the *King Penguins* were identified to be responsible for over-consumption of the *Myctophids* resulting in the model not balancing. With a further reduction in ecosystem size (to the Model 3 size) the seals (both the *Southern Elephant Seals* and the *Sub-Antarctic Fur Seals*) and the *Macaroni Penguins* were identified as contributing to the over-consumption (on the *Sharks and Rays*, *Large Pelagics*, *Patagonian Toothfish*, *Myctophid Fish* and both *Large* and *Small Cephalopod* groups). On the final reduction in boundary size (Model 4) the *Wandering Albatross* and *Prions and Petrels* were added to the aforementioned groups and, along with the *Large Demersals*, were responsible for the model not balancing (due to over-consumption of the before mentioned groups and the *Small Pelagic Fish*).

A difference found between the two time periods was that only the *King Penguins* were identified as contributing to the overconsumption in the first model size reduction. The *Southern Elephants Seals*, the *Sub-Antarctic Fur Seals* and the *Macaroni penguins* are only identified in the subsequent reduction in model size, and finally the *Wandering Albatross*, *Prions and Petrels* and *Large Demersals* were identified in the smallest model. Another notable difference between the two time periods was that the *Southern Rockhopper Penguins* have no effect on the over-consumption for the 2000s time period while they are identified as being important to the

consumption in the 1980s model of the same size. This reflects the decline in the *Southern Rockhopper Penguin* population between these two time periods.

6.4. Discussion

Due to the scaling of the ecosystem models, the initial absolute biomass of the top predators and the benthic ecosystem effectively stayed the same in each model description, while the pelagic component became reduced with decreasing ecosystem size. Therefore the total absolute quantity of pelagic resources available within the system was dependant on the ecosystem size. In this exercise, with the decrease in ecosystem size, the pelagic resources were reduced. For those consumers that rely on the pelagic component to meet their consumption needs, the ecosystem boundary size would determine the population size that could be sustained.

It is apparent from the formulation of Model 1 (at the scale of the EEZ) that, if the system is considered to be in mass balance (in this instance with the assumption that imports and exports are equivalent), the energetic demands of the functional groups included in the model can be met. However, with each subsequent model that represented a reduction in size of the ecosystem (Models 2, 3 and 4), various functional groups could no longer be sustained within the system. In each instance the model was not able to achieve mass balance and groups that were over-consumed were highlighted (top-down approach). Investigation into those groups that were responsible for the over-consumption provided insight into the scale at which each group should be considered. For Model 2, the *Southern Elephant Seals* and the *King Penguins* were the first two groups to be identified as being responsible for the over consumption within the model. Following these two, the *Macaroni Penguins* and the *Prions and Petrels* were identified. This result was found in the Model 3 results. For the Model 4 (shelf model) results, in addition to the four functional groups already identified, the *Sub-Antarctic Fur Seals*, *Rockhopper Penguins*, and *Wandering Albatross* were also added to the list of top predators unable to satisfy their energetic demands at the smaller scale.

To gain a better understanding of the knock-on effects of adjustments to the models that would be required to balance the model, Model 5, a mixed balanced model, was constructed. The model provided a summary of the appropriate ecosystem size for the various groups of top predators

included in the assessment for the 1980s time period. The outcome of the balancing exercise suggested that the *Southern Elephant Seals*, the *Antarctic* and *Sub-Antarctic Fur Seals*, the *King Penguins*, *Macaroni Penguins*, *Giant Petrels*, albatross groups and *Prions and Petrels* should all be considered at the largest scale (Model 1, 200nm or EEZ). The *Orcas* and *Rockhopper Penguins* could be considered at a smaller scale (Model 2, 100nm) along with the *Large Demersal Fish* group. In addition, changes to the *Large Demersal Nototheniid Fish* (to a value of 0.26 which is intermediary between the Models 3 and 4) and a change in the *Benthos* group to the Model 3 value (of 8.0t.km⁻²) brought the model very close to balancing. The redistribution of biomass between the *Small Pelagic Fish* and the *Myctophid Fish* along with a small increase in the *Large Cephalopods* (from 0.065 to 0.070 t.km⁻²) resulted in a balanced model.

This exercise provided a routine that establishes the appropriate scale to consider the various groups of the model. At smaller ecosystem sizes the consumption needs of the larger predators could not be satisfied. The results tie in well with the foraging ranges of the top predators, which are considered to ultimately dictate the size at which particular functional groups should be considered to enable the ecosystem model to balance. Seals are known to have extensive foraging ranges, with the *Southern Elephant Seals* covering the largest distances (> 1 000km (~540nm) from Marion Island (Bester 1989; Bester and Pansegrouw 1992)). Of the penguins, the Kings travel the furthest (mean foraging range of adults with chicks during summer at Marion Island ranged between 225km (122nm) and 300km (162nm), depending on the size of their chicks (Adams 1987). These groups were identified as the first two to not be able to satisfy their energetic requirements in the reduced ecosystem size. Foraging range estimates for the Macaroni penguins have been recorded as being between 59 and 303 km (32 and 164nm) and between 4 and 157km (2.2 and 84.8nm) for Southern Rockhopper penguins (Brown 1987). In previous studies, the ecological extent of the PEIs system was considered to be an ocean area within a radius of approximately 300km (or 161 nm) from the islands, based on the foraging range of the seabirds nesting at the islands (Cooper pers. Comm. in Gon and Klages 1988). This estimate is similar to the finding in this model, where the energetic requirements of most of the avian fauna could not be met at the Model 2 (100nm radius) scale but were satisfied at the Model 1 (or EEZ) scale. The only land based top predator able to satisfy its energetic requirements in the smallest rendition of the model (Model 4) is the Gentoo penguin, and this concurs with its known

foraging range, which is thought to be less than 40km (21.6nm) and matches closely with the boundary of the smallest model (20nm radius).

While the outcome of this exercise is intuitive, it is encouraging to see that the model output supported the observations of the foraging distances of many of the top predators. The assumption is that each group would only travel as far as is necessary to satisfy the energetic demands for itself and its offspring. It would not make sense for these centrally placed foragers to travel great distances if the food availability within a smaller area was sufficient. However, in this exercise, there is no consideration of the heterogeneity of the system, temporally or spatially. The biomass estimates for example are assumed to be homogenous and spread evenly throughout the area under consideration which does not capture the reality of the often patchy environment. The question then arises whether an ecosystem model, without explicit spatial mapping, could provide insight into the foraging distances of these land based top predators. The results provide some confidence that despite the lack of explicit consideration in the spatial context of the ecosystem in the model construction (such as elevated productivity associated with oceanic fronts or shelf regions) the model is able to capture such patterns. Such patterns are, however, only evident when the groups considered are at their carrying capacity within the ecosystem, as when the numbers are below those that the ecosystem can support, the results are not clear. This is highlighted for example in the repeat of the exercise for the 2000s time period. The decline in the *Southern Elephant Seals* population resulted in this group only being picked up as needing a larger foraging range in the Model 3 configuration, a range well below the observed foraging range of this species. In addition, the *Southern Rockhopper Penguins* are not identified as requiring an increased foraging range due to their reduced population size during this time period.

Taking both considerations into account (the lack of spatial heterogeneity and the carrying capacity of the populations) the results of the exercise can provide insight into the minimum extent of the ecosystem boundary while the observed foraging distances of the system constituents might be considered the maximum extent as found in the Cianelli et al. (2004) study.

6.5. Conclusions

In the process of stepwise reduction of the size of the ecosystem, various groups were highlighted as being over consumed, and investigating the consumption rates of the predators allowed the consumers responsible to be identified. It is interesting to see that those groups that were identified are also the groups that have the greatest known foraging distances. This exercise was dedicated to assessing at what scale the model of the PEIs should be created. Is there a boundary size that is appropriate? The results show that the answer ultimately depends on the functional group in which one is interested. If considering the ecosystem as a whole with all the constituents without quantifying the imports/exports or biomass accumulation, the results here suggest that the formulation at the scale of the EEZ (Model 1) would be appropriate. If, however, the focus was to be on functional groups that do not utilize the resources of such a vast area, then, by making biomass adjustments to particular functional groups (reduction of groups that require larger area to satisfy their energetic demands) one can reduce the total area considered in the model and consider the ecosystem at a smaller scale.

Further development of the model to include spatial data could greatly improve this model. The EwE program currently has a habitat capacity model under development which will be able to include spatially explicit preferences for species movements associated with physical features (both spatially and temporally resolved) within the model framework. The use of the existing spatially resolved database generated from the Lombard et al. (2007) study would provide a platform from which the habitat capacity model could be run. This will provide an exciting avenue for exploring future management options with the inclusion of explicit spatial considerations in particular considering the recently (April 2013) declared Marine Protected Area at the Prince Edward Islands and associated management zones.

Table 6.1. Description of the model size according to the length of the radius (nm) used, area included in the model (km^2) and the proportion of each model that could be considered to represent the shelf region (as a percentage).

Model	Radius (nm)	Area (km^2)	Model Area = Shelf (%)
1	200	431014	1
2	100	107754	4
3	50	26938	16
4	20	4418	100

Table 6.2. Input parameters for each model. MBM = Mixed Balanced Model. B = Relative biomass (t.km^{-2}). P/B = Rate of production to biomass (yr^{-1}). Q/B = Rate of consumption to biomass (yr^{-1}). UC = Unassimilated consumption (between 0 and 1). Numbers in black = Pelagic associated groups. Numbers in grey = Land based or benthic associated groups. * = value = 0.08 for 1980s model and 0.13 for 2000s model.

Group name	1980					2000s						
	Model 1	Model 2	Model 3	Model 4	MBM	Model 1	Model 2	Model 3	Model 4	All models		
	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	B (t.km^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	UC (0-1)
Orcas	0.000025	0.000101	0.000404	0.002528	0.000101	0.000025	0.000101	0.000404	0.002528	0.06	5.39	0.1
Southern Elephant Seals	0.001559	0.006236	0.024946	0.155911	0.001559	0.000991	0.003963	0.015851	0.099069	0.074	12.78	0.1
Antarctic Fur Seals	0.000042	0.000169	0.000676	0.004223	0.000042	0.000262	0.001047	0.004187	0.026171	0.1	14.06	0.1
Sub-Antarctic Fur Seals	0.002925	0.011700	0.046799	0.292496	0.002925	0.009229	0.036918	0.147670	0.922939	0.1	14.97	0.1
King Penguins	0.014716	0.058866	0.235463	1.471644	0.014716	0.014716	0.058866	0.235463	1.471644	0.125	42.46	0.24
Macaroni Penguins	0.005120	0.020482	0.081928	0.512048	0.005120	0.004102	0.016408	0.065631	0.410195	0.185	76.75	0.24
Southern Rockhopper Penguins	0.001255	0.005021	0.020083	0.125518	0.005021	0.000710	0.002840	0.011359	0.070995	0.16	93.7	0.24
Gentoo Penguins	0.000044	0.000176	0.000705	0.004408	0.004408	0.000042	0.000167	0.000668	0.004176	0.2	62.5	0.2
Wandering Albatross	0.000118	0.000473	0.001893	0.011833	0.000118	0.000143	0.000571	0.002283	0.014269	0.04	57.1	0.2
Grey-headed Albatross	0.000065	0.000260	0.001039	0.006496	0.000065	0.000085	0.000339	0.001355	0.008468	0.05	49.39	0.2
Indian Yellow-nosed Albatross	0.000084	0.000334	0.001336	0.008352	0.000084	0.000084	0.000334	0.001336	0.008352	0.027	57.48	0.2
Light-mantled Sooty Albatross	0.000002	0.000008	0.000033	0.000209	0.000002	0.000007	0.000028	0.000111	0.000696	0.027	59.82	0.2
Dark-mantled Sooty Albatross	0.000026	0.000102	0.000408	0.002552	0.000026	0.000026	0.000102	0.000408	0.002552	0.027	68.11	0.2
Giant Petrels	0.000044	0.000176	0.000705	0.004408	0.000044	0.000041	0.000162	0.000650	0.004060	0.07	32.24	0.2
Prions and Petrels	0.000657	0.002626	0.010505	0.065659	0.000657	0.000657	0.002626	0.010505	0.065659	0.16	191.7	0.24
Sharks and Rays	0.00036	0.00036	0.00036	0.00036	0.00036	0.00036	0.00036	0.00036	0.00036	0.14	3.7	0.2
Large Demersal Fish	0.0285	0.114	0.456	2.85	0.114	0.0285	0.114	0.456	2.85	0.19	1.98	0.2
Large Nototheniid Demersal Fish	0.00955	0.0382	0.1528	0.955	0.26	0.00955	0.0382	0.1528	0.955	0.21	3.4	0.2
Small Continental Slope Demersal Fish	0.01178	0.04712	0.18848	1.178	1.178	0.01178	0.04712	0.18848	1.178	0.502	7.33	0.2
Small Inshore Demersal Fish	0.007	0.028	0.112	0.7	0.7	0.007	0.028	0.112	0.7	0.32	6	0.2
Large Pelagics	0.042	0.042	0.042	0.042	0.04	0.042	0.042	0.042	0.042	0.22	2.56	0.2
Patagonian Toothfish	0.075	0.075	0.075	0.075	0.075	0.00427	0.00427	0.00427	0.00427	*0.08	1.6	0.2
Small Pelagic Fish	1.125	1.125	1.125	1.125	0.9	1.125	1.125	1.125	1.125	0.9	10.5	0.2
Myctophid Fish	3.375	3.375	3.375	3.375	3.605	3.375	3.375	3.375	3.375	0.5	6.1	0.2
Large Cephalopods	0.065	0.065	0.065	0.065	0.07	0.065	0.065	0.065	0.065	2.7	10.95	0.2
Small Cephalopods	0.045	0.045	0.045	0.045	0.045	0.045	0.045	0.045	0.045	4.5	18.25	0.2
Benthos	0.5	2	8	50	8	0.5	2	8	50	2.5	10	0.2
Benthic Decapod	0.038	0.152	0.608	3.8	3.8	0.038	0.152	0.608	3.8	1.45	4.42	0.2
Large Zooplankton Crustaceans	5	5	5	5	5	5	5	5	5	5	14	0.2
Small Zooplankton Crustaceans	16	16	16	16	16	16	16	16	16	10	43	0.2
All Other Zooplankton	7	7	7	7	7	7	7	7	7	24	96	0.2
Open Ocean Large Phytoplankton	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	1.7	150	-	
Open Ocean Small Phytoplankton	6.81	6.81	6.81	6.81	6.8	6.81	6.81	6.81	6.81	150	-	
Island Associated Blooms	0.00403	0.01612	0.06448	0.403	0.403	0.00403	0.01612	0.06448	0.403	200	-	
Macrophytes	0.195	0.78	3.12	19.5	19.5	0.195	0.78	3.12	19.5	5.22	-	
Macrophyte Detritus	0.0371	0.1486	0.5942	3.7139	3.7140	0.0371	0.1486	0.5942	3.7139	-	-	
Detritus	29	29	29	29	29	29	29	29	29	-	-	

Table 6.3. Ecotrophic Efficiency output estimates for all Model sizes 1-4 for the 1990s and 2000s time period, as well as for the Mixed Balanced Model created for the 1980s. Ecotrophic Efficiency values that exceed 1 are printed in red text.

Group name	Ecotrophic efficiencies								
	1980s					2000s			
	Model 1 200nm	Model 2 100nm	Model 3 50nm	Model 4 20nm	MBM	Model 1 200nm	Model 2 100nm	Model 3 50nm	Model 4 20nm
Orcas	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Southern Elephant Seals	0.176	0.176	0.176	0.176	0.097	0.077	0.077	0.077	0.077
Antarctic Fur Seals	0.132	0.131	0.131	0.131	0.775	0.068	0.068	0.068	0.068
Sub-Antarctic Fur Seals	0.130	0.130	0.130	0.130	0.371	0.062	0.061	0.061	0.061
King Penguins	0.476	0.475	0.476	0.476	0.551	0.477	0.477	0.477	0.477
Macaroni Penguins	0.328	0.328	0.328	0.328	0.306	0.339	0.339	0.339	0.339
Southern Rockhopper Penguins	0.418	0.418	0.418	0.418	0.072	0.498	0.498	0.498	0.498
Gentoo Penguins	0.292	0.292	0.292	0.292	0.004	0.322	0.322	0.322	0.322
Wandering Albatross	0.051	0.051	0.051	0.051	0.212	0.044	0.044	0.044	0.044
Grey-headed Albatross	0.041	0.041	0.041	0.041	0.183	0.035	0.035	0.035	0.035
Indian Yellow-nosed Albatross	0.076	0.075	0.075	0.076	0.257	0.065	0.065	0.065	0.065
Light-mantled Sooty Albatross	0.072	0.076	0.073	0.072	0.907	0.065	0.065	0.065	0.065
Dark-mantled Sooty Albatross	0.075	0.075	0.075	0.075	0.256	0.065	0.065	0.065	0.065
Giant Petrels	0.029	0.029	0.029	0.029	0.092	0.025	0.025	0.025	0.025
Prions and Petrels	0.500	0.499	0.500	0.500	0.530	0.460	0.460	0.460	0.460
Sharks and Rays	0.164	0.657	2.629	16.434	0.292	0.180	0.718	2.874	17.960
Large Demersal Fish	0.143	0.133	0.131	0.130	0.059	0.170	0.161	0.159	0.158
Large Nototheniid Demersal Fish	0.427	0.401	0.396	0.394	0.968	0.470	0.445	0.439	0.437
Small Continental Slope Demersal Fish	0.280	0.180	0.156	0.148	0.095	0.180	0.167	0.163	0.162
Small Inshore Demersal Fish	0.493	0.470	0.465	0.464	0.270	0.507	0.484	0.479	0.477
Large Pelagic Fish	0.572	0.948	2.336	12.057	0.684	0.162	0.549	2.097	12.933
Patagonian Toothfish	0.308	1.200	4.767	29.738	0.053	0.986	2.329	7.702	45.313
Small Pelagic Fish	0.176	0.368	1.140	6.540	0.284	0.164	0.355	1.115	6.442
Myctophid Fish	0.951	2.106	6.736	39.145	0.995	0.984	2.282	7.473	43.809
Large Cephalopods	0.821	2.245	7.956	47.929	0.975	0.532	1.887	7.305	45.235
Small Cephalopods	0.908	2.143	7.085	41.680	0.983	0.779	1.962	6.692	39.806
Benthos	0.708	0.212	0.088	0.053	0.264	0.708	0.212	0.088	0.053
Benthic Decapod	0.735	0.574	0.534	0.523	0.343	0.690	0.529	0.489	0.478
Large Zooplankton Crustaceans	0.435	0.500	0.759	2.568	0.646	0.433	0.490	0.719	2.325
Small Zooplankton Crustaceans	0.696	0.708	0.758	1.103	0.760	0.696	0.707	0.754	1.080
All Other Zooplankton	0.948	0.956	0.988	1.211	0.999	0.948	0.956	0.988	1.208
Open Ocean Large Phytoplankton	0.028	0.032	0.044	0.129	0.046	0.028	0.032	0.044	0.129
Open Ocean Small Phytoplankton	0.885	0.887	0.891	0.912	0.891	0.885	0.887	0.891	0.912
Island Associated Blooms	0.310	0.313	0.313	0.310	0.050	0.310	0.310	0.310	0.310
Macrophytes	0.704	0.269	0.160	0.130	0.033	0.704	0.269	0.160	0.130
Macrophyte Detritus	0.522	0.211	0.184	0.177	0.079	0.522	0.211	0.184	0.177
Detritus	0.373	0.387	0.436	0.775	0.399	0.373	0.386	0.436	0.773

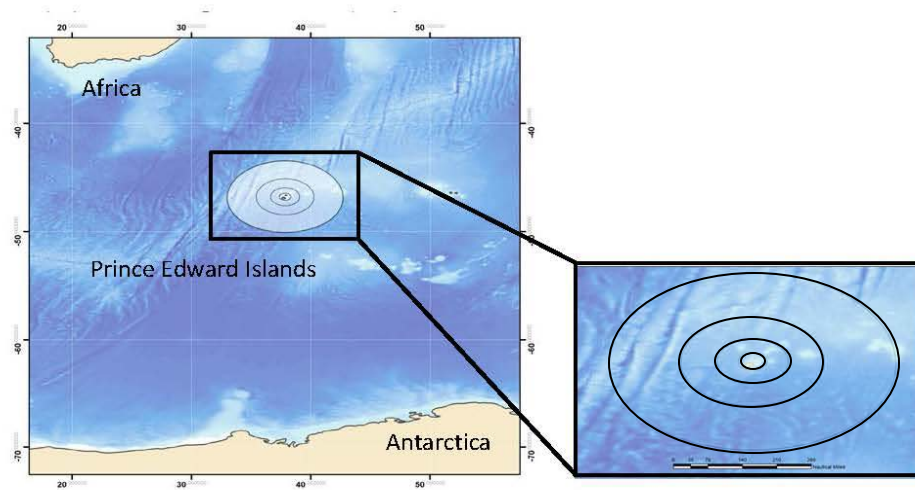


Figure 6.1. Illustration of the theoretical boundaries of each of the four models used in the study. The outermost ellipse represents Model 1 (an area equivalent to a circle with a radius of 200nm centered on the islands, representing the Exclusive Economic Zone of the Prince Edward Islands). The innermost ellipse represents Model 4 (an area equivalent to a circle with a radius of 20nm, representing the shelf region of the islands). Bathymetry data source: The GEBCO_08 Grid, version 20100927, <http://www.gebco.net>.

Chapter 7 The importance of incorporating diet quality into consumption rates for ecosystem modelling studies

7.1. Introduction

Ecosystem modelling approaches are becoming more popular as researchers endeavour to find practical solutions that can aid addressing marine resource management objectives to serve both conservation and exploitation needs. Parameterisation of ecosystem models is an important step in creating a model and can be time consuming to complete. Some parameters needed for ecosystem models are considered to be model specific, such as biomass estimates and the trophic linkages between groups (diet matrices), where data unique to the study area are compiled for each model. Other parameters, like production and consumption estimates, are generally considered transferable between systems and hence are often used across systems, without taking system specific considerations into account. These include the use of empirical equations for parameterisation of such rates. For production terms, species specific and site specific information is often incorporated into the estimates, which are calculated for each model (e.g. P/B rates estimated for fish using the equation of Palomares and Pauly (1998), which takes species specific information and local temperature into account). For consumption rates, however, it is common to transfer estimates between systems without taking local differences into consideration.

A variety of approaches to determine consumption rates are commonly used in ecosystem models for mammals and birds (Kleiber 1961; Laws 1977; Innes et al. 1987; Nagy 1987; Trites et al. 1997; Nagy et al. 1999; Ellis and Gabrielsen 2001; Knox 2007b). In some instances, consumption estimates are considered to be directly related to body mass, simply as a percentage of body mass consumed per day (Laws 1977; Pakhomov et al. 1996; Knox 2007b), and have been used to determine the consumption rates for invertebrates, fish and mammals. More commonly for higher vertebrates (birds and mammals), consumption estimates are based on allometric equations of body mass (M) $C = aM^b$, where C is consumption per day, and 'a' and 'b' are uniquely defined parameters for species or groups. In such empirical equations, consumption is calculated as being determined by the daily requirements of the individual (as estimated from

metabolic rates (basal metabolic rates (BMR) or field metabolic rates (FMR)) in terms of biomass of food ingested (kg.d^{-1}) e.g. Innes et al. (1987), or in terms of energy required (kJ.d^{-1}) e.g. Kleiber (1961), Nagy (1987) (which provides energetic equations with biomass conversions), Sigurjonsson and Vikingsson (1997), Trites et al. (1997), Nagy et al. (1999), Ellis and Gabrielsen (2001) or Karpouzi et al. (2007).

In general, when such allometric equations are provided based on biomass, assumptions of the energetic content of the prey are made without consideration of the system. In those instances where estimates of consumption are based on energy, the conversion from units of energy to biomass required per day (as necessary for the model) are usually done based on using generic conversion factors (based on the diet preference of the particular group; see Nagy 1987, Nagy et al. 1999) and part of the value of considering the consumption rate in terms of energy is lost. The lack of consideration of the energetic content of prey is a criticism that has been leveled at ecosystem models that use biomass as their currency (Plaganyi and Butterworth 2004), and addressing such issues would improve the parameterisation of such models.

Species specific bioenergetic models are a good starting point for examining how one might improve consumption rate estimates. In such models, detailed information on energetic requirements for the species concerned is provided, including differentiation of needs for different activities, as well as changes in dietary requirements depending on life stages and foraging patterns associated with such developments. These energetic requirements are matched with food requirements, which require information on diets, energetic density of the diet components as well as the digestive assimilation efficiency of the studied species. While it is not usually feasible to do such detailed compilations of data for each species in an ecosystem model, lessons that can be learned from species specific bioenergetic models can be relatively easily incorporated into parameters for ecosystem models. Estimates of energetic requirements from field metabolic rates in particular are widely used to estimate consumption rates for many of the birds and mammals in ecological studies and intrinsically incorporate in them the variety of activities that are undertaken. An important assumption in using such methods is that the daily energetic/food requirements are actually met. Keeping this assumption in mind, for the purposes of the ecosystem model, one can focus on the food requirements and improve the estimates by

incorporating local species specific information on diets along with specific energetic content of prey. This is routinely incorporated into single species bioenergetic models (see Murie and Lavigne 1991; Adams et al. 1993; Perez and McAlister 1993; Boyd 2002; Mecenero et al. 2006; Halsey et al. 2008) and has the potential to add value to consumption estimates used in ecosystem models.

For this study, it is proposed that the incorporation of local diet information, where it exists, in terms of composition, energetic content and assimilation efficiencies, should be used to improve the consumption rate estimates used in ecosystem models. In order to do this, a case study based on the data preparation for the ecosystem model of the Prince Edward Islands (PEIs) (Southern Ocean) is presented. A summary of commonly used empirical equations demonstrates the variation in consumption rates available to the ecosystem modeller for estimating consumption to biomass rates for mammals and birds (see Figure 7.1). For this study, the field metabolic rates of Nagy et al. (1999) (as amended by Ellis and Gabrielson 2001) for the bird species at the PEIs were used to demonstrate the difference that can be made by incorporating local diet related information (diets, energetic content of prey and assimilation efficiencies) into the consumption rate estimates and how the inclusion of such data can affect parameterization of the model.

7.2. Method

Four breeding penguin species (Kings, Macaronis, Southern Rockhoppers and the Gentoos), five albatross species (Wandering, Grey-headed, Indian Yellow-nosed, Light- and Dark-mantled Sootys) as well as the Giant Petrels (Northern and Southern) and Sub-Antarctic Skua, 14 species of small seabirds (including prions, petrels and terns), the kelp gull and the Crozet Shag (Species listed in Table 7.1) are included in this study.

Consumption rates for individuals in terms of their energetic requirements were based on field metabolic rates (FMR) for birds as summarised in Nagy et al. (1999, with amendments from Ellis and Gabrielsen 2001) and provided in kJ.d^{-1} . A full description of the method used is provided in Chapter 3. Consumption rates for each species of bird at the islands are given, with estimates of daily food intake (DFI) and Q/B rate estimates that were calculated by simply

multiplying the DFI values by 365 and dividing by the average mass of the species concerned (Table 7.1).

7.3. Results

Diets

A summary of the diet composition of the land based top predator species/groups, divided into six prey categories, is provided (Table 7.2). Two of the penguins are principally fish eaters: the Kings, with a diet dominated by myctophids, and the Gentoos, with a mixed fish diet with some crustaceans, notably the benthic decapod. Both the Macaronis and the Rockhoppers have predominantly zooplankton diets. All albatross species have a mix of fish and squid. The Giant Petrels have a diet dominated by vertebrates (mainly penguins) while the Prions and Petrels diet is dominated by crustaceans with fish and cephalopods contributing.

Assimilation efficiencies and energetic content of prey

A full description of the assimilation efficiencies and energetic content of prey is provided in Chapter 3. The relevant information required for this Chapter is provided in Table 7.2.

Consumption rates

Taking into consideration local diet preferences, prey energetic content and assimilation efficiencies (Table 7.2), field metabolic rate (FMR) estimates were used to establish the daily food intake (DFI; $\text{g.ind}^{-1}.\text{d}^{-1}$) and annual consumption to biomass rates (Q/B ; .y^{-1}) for all species (Table 7.1). Although the steps taken to incorporate the local diet are relatively simple, the results, as compared with estimates derived from standard processing, can be quite different. As shown in Figure 7.2, the incorporation of local diet information can alter the estimate of the Q/B rate by as much as 84% or -32% (significant in a paired 2 tailed t-test, $p < 0.0002$).

To illustrate this for the PEI ecosystem, a closer examination of the penguin group and the Giant petrels is appropriate. The amendments in the consumption rates for these groups were instrumental in resolving the balancing of the PEI ecosystem model (see Chapter 5). As already outlined, the King, Gentoo, Macaroni and Rockhopper penguins all co-exist at the PEIs. These

species vary in mass (see Table 7.1) and in their feeding preferences (Table 7.2). The diets vary between locations and between seasons, but in general the King penguin is an offshore feeder travelling great distances from the islands on which it occurs and consuming primarily myctophid fish. The Gentoo penguin is, by contrast, a near-shore feeder, and consumes a mix of both inshore fish and zooplankton. The Macaroni, while consuming a limited amount of fish, feeds predominantly on zooplankton, which is the primary source of food for the smaller Rockhopper (Figure 7.3.A). Usually, consumption rates within groups (for birds, it is usually considered at the level of Order) are calculated using a single equation with body mass affecting the difference between groups. However the differences in diet preference and the difference this makes to the energetic content of the prey for each species can and should be taken into account when calculating consumption rates. If a diet is nutritionally more valuable, the consumer will require less mass of the diet to satisfy their energetic requirements and using a standard uniform value for all species may be considered inappropriate. A comparison of what the energetic content is of a single gram of each of the available prey groups (Figure 7.3.B) and a single gram of the diet for each of these species when the local diet information is incorporated into the assessment (with and without the inclusion of the assimilation efficiency) as compared to standard processing (where a default value of 16.2kJ.g^{-1} dry weight is used, Nagy et al. 1999) is illustrated (Figure 7.3.C). From this summary, for all species, with the exception of the King penguin (where the high energetic content of the myctophid fish, which is the dominant species in the diet, results in a greater average energetic value), the energetic density of the diets within the species is estimated as being less than that for standard processing. This therefore translates into the consumption rate estimated for three of the four penguin species as being higher than when using standard processing, but lower for the King penguin.

Regarding the Giant petrel consumption estimates, the adjustment made to account for the energetic density of the local diets of these species decreased the original Q/B value by one third (from 47.33 to 31.79yr^{-1} and 49.62 to 35.62yr^{-1} for the Southern and Northern Giant petrels respectively). This is due to the relatively high energetic density of the Giant petrel diet, which is dominated by vertebrate prey. Until this amendment was made, there had been no satisfactory way found to resolve the energetic requirements of this group within the ecosystem model (see

Chapter 5) and the relative ease with which the model was able to be balanced following these adjustments was considered to be encouraging.

7.4. Discussion

When tasked with developing an ecosystem model there are a plethora of parameters that need to be collected (for example, considering only the biomass, consumption, production and diet matrix in the PEI model there are 1517 parameters to be entered for the static model). In general, the focus at the local scale is on preparing site specific species lists and diet matrices, which leaves little time for dedicated work on those parameters that are considered transferable between systems (e.g. consumption and production rates). When searching for transferable parameters, such as consumption rates, in other ecosystem models, there can be a lack of transparency in the parameterization of the model. In some instances the data source is referenced but the method of calculation is not explicitly stated (e.g. Cornejo-Alonso and Antenzana 2008) or, quite commonly, another model is cross-referenced (e.g. Erfan and Pitcher 2005, Cheung and Pitcher 2005) and a search for the original source ensues. In searching for consumption values for this work, a good illustration of the types of issues that arise can be found in the summary for the consumption rate estimates for the King penguins (See Appendix 5.A. for full documentation). A search in the literature returned a number of studies for consumption rates for this species. Some were based on consumption in weight per day and require subsequent estimates on how many days the birds spend at sea. For example, at the Iles Crozet, Putz and Bost (1994) found an average daily intake of food of $2.3 \text{ kg} \cdot \text{d}^{-1}$ from an average of 132 food ingestion events per day over a period of 125 days, which would give a Q/B ratio of 65 yr^{-1} (using Abrams (1985) average weight of 13.0 kg). Bost et al. (1997) calculated the average per day ingested was 2.4 kg resulting in an annual Q/B of 67.3 yr^{-1} (using mass of 13kg, Abrams 1985) or 73 yr^{-1} (using mass estimate of 12 kg, Ryan and Bester 2008) if the birds feed each day. For the Kerguelen model, a Q/B value of 67.9 yr^{-1} (from total prey biomass of $1.99 \text{ t} \cdot \text{km}^{-2}$) was calculated (Pruvost et al. 2005), but was considered too high, as was the estimate of 38.0 yr^{-1} (based on 1985 data) from Cherel et al. (2005). The value of 12.0 yr^{-1} from the Weddell Sea model (Jarre-Teichmann et al., 1991) was used for the Kerguelen model (Pruvost et al. 2005), which was considered to be in line with other similar systems (e.g. 18 year^{-1} for the

Southern Plateau, New Zealand; Bradford-Grieve et al., 2003). This is in contrast to the Falklands model which has a value of 80 yr^{-1} for Q/B for all penguins (Cheung and Pitcher 2005). It was following such issues that the search for a better estimate of Q/B for the PEI model was commenced. Nagy et al.'s (1999) field metabolic rate equation for penguins (Order: Sphenisciformes equation $C = 4.53M^{0.795} \text{ kJ.d}^{-1}$) with the average bird weight of 12.0 kg (Ryan and Bester 2008), taking into account diet preferences (see diet section) and energy content of prey, digestion efficiency of 76%, water content of diet assumed to be 70%, returns a Q/B estimate of 42.5 yr^{-1} . This compares well with calculations that result from Ellis and Gabrielson's (2002) equations of $Q/B = 40.9 \text{ yr}^{-1}$ and falls mid way in the range of rates outlined above (from 12 to 80 yr^{-1}).

There are instances in ecosystem models where allometric equations with species specific information are used, both with (e.g., Cianelli et al. 2004) and without (Shannon et al. 2003; Coll et al. 2006; Coll et al. 2007; Piroddi 2008) explicit consideration of the potential difference that local energetic content of prey of the diet might make. The work presented here is intended to raise the awareness of the effect such considerations may have on the output of the ecological models and an assessment of whether this is important for each system will need to be made. There is a large variation that is found in the various empirical equations that are available for the estimation of consumption rates for mammals and birds, as illustrated for these groups at the PEIs (Figure 7.1). Results from ecosystem models will vary depending on the method that is used and may be important to consider in instances when a species plays an important role in the ecosystem in terms of its biomass contribution or key role in the system.

7.5. Conclusions

This short communication provides an example of where the inclusion of local diet data can improve the assessment of consumption for the purposes of constructing a mass balanced ecosystem model. A simple sensitivity test (Chapter 5) of the PEI ecosystem model used in this case study highlighted the consumption to biomass rate estimates ($Q/B, \text{ yr}^{-1}$) to be as important as biomass estimates ($B, \text{ t.km}^{-2}$) and more important than production to biomass ($P/B, \text{ yr}^{-1}$) rate estimates in the model structure. Local diet assessments of prey and associated energetic density of the prey species can be important contributing factors when improving Q/B estimates. Global

datasets of species diet information are invaluable (e.g., Pauly et al. 1998 for mammals), and are heavily relied on for the construction of many ecosystem models. However, such datasets do not always provide information at the local scale and, while incorporation of the diet matrix in the consumption estimates improves the estimate and is appropriate for large scale studies (e.g., Karpouzi et al. 2007), further improvements can be made by using local diet information for evaluation of the energetic value of prey.

Using local diet information, the model parameters of the system were improved and the energetic requirements of the system were subsequently met with relatively minor adjustments. For future work, it is important to quantify the value and the impact such amendments make to the ecosystem model performance and to consider whether the adjustments are necessary in temporally and spatially dynamic models. This work demonstrates the issue of the energetic value of prey species can be incorporated into models that use biomass as their currency and can begin to address this issue that has been raised previously (Plaganyi and Butterworth 2004).

Table 7.1. Daily food ingestion rates ($\text{g.ind}^{-1}.\text{d}^{-1}$) and annual consumption to biomass rate estimates (yr^{-1}) of the species of birds found breeding at the Prince Edward Islands using Field Metabolic Rates (FMR) as defined by Nagy et al. (1999) (with amendments by Ellis and Gabrielson 2001) calculated using average mass estimates from Ryan and Bester (2008).

Species		Average mass	FMR equation	DFI Consumption	Q/B
Common names	Species names	kg	kJ.d^{-1}	$\text{g.ind}^{-1}.\text{d}^{-1}$	yr^{-1}
King Penguins	<i>Aptenodytes patagonicus</i>	12.0	$C=4.53M^{0.795}$	1395.81	42.46
Macaroni Penguins	<i>Eudyptes chrysolophus</i>	4.6		967.23	76.75
Southern Rockhopper Penguins	<i>Eudyptes chrysocome filholi</i>	2.7		693.11	93.70
Gentoo Penguins	<i>Pygoscelis papua</i>	6.0		1027.47	62.50
Wandering Albatross	<i>Diomedea exulans</i>	9.0	$C=17.9M^{0.6}$	1407.82	57.10
Grey-headed Albatross	<i>Thalassarche chrysostoma</i>	3.7		500.62	49.39
Yellow-nosed Albatross	<i>Thalassarche carteri</i>	2.6		409.45	57.48
Light-mantled Sooty Albatross	<i>Phoebastria palpebrata</i>	2.8		458.88	59.82
Dark-mantled Sooty Albatross	<i>Phoebastria fusca</i>	2.5		466.50	68.11
Southern Giant Petrel	<i>Macronectes giganteus</i>	4.50		390.46	31.67
Northern Giant Petrel	<i>Macronectes halli</i>	4.00		382.93	34.94
Fairy Prion	<i>Pachyptila turtur</i>	0.14		98.63	257.14
Salvin's Prion	<i>Pachyptila salvini</i>	0.17		115.01	246.93
Blue Petrel	<i>Halobaena caerulea</i>	0.20		119.56	218.19
Great-winged Petrel	<i>Pterodroma macroptera</i>	0.59		138.90	85.93
Soft-plumaged Petrel	<i>Pterodroma mollis</i>	0.31		94.37	111.12
Kerguelen Petrel	<i>Lugensa brevirostris</i>	0.35		112.89	117.72
Grey Petrel	<i>Procellaria cinerea</i>	1.00		220.47	80.47
White-chinned Petrel	<i>Procellaria aequinoctialis</i>	1.30		404.46	113.56
Grey-backed Storm Petrel	<i>Garrodia nereis</i>	0.03		40.79	496.30
Black-bellied Storm Petrel	<i>Fregetta tropica</i>	0.05		56.63	413.38
South Georgian Diving Petrel	<i>Pelecanoides georgicus</i>	0.11		89.13	295.74
Common Diving Petrel	<i>Pelecanoides urinatrix</i>	0.15		107.05	260.49
Crozet Shag	<i>Phalacrocorax melanogenis</i>	2.20	$C=4.54M^{0.844}$	1079.42	179.09
Sub-Antarctic Skua	<i>Catharacta antarctica</i>	1.60	$C=8.49M^{0.77}$	907.68	207.06
Kelp Gull	<i>Larus dominicanus</i>	1.00		656.17	239.50
Antarctic Tern	<i>Sterna vittata</i>	0.14		134.88	351.65
Kerguelen Tern	<i>Sterna virgata</i>	0.12		119.78	364.35

Table 7.2. Diet matrices of the breeding bird species of the Prince Edward Islands summarised into six prey categories, with energetic density of prey categories given, and average energetic density of diet (kJ.g⁻¹) and assimilation efficiency (as a fraction of the diet) for each bird species provided.

<i>Species</i>	PREY CATEGORIES						Average energy density of diet	Assimilation efficiency
	Vertebrate	Fish - general	Fish - mesopelagic	Cephalopods	Crustaceans	Other		
Energetic content of prey (kJ.g⁻¹)	30.7	21.3	27.4	10.3	14.8	12	kJ.g⁻¹	(fraction)
King Penguins			0.850	0.140	0.010		24.88	0.76
Macaroni Penguins			0.180	0.070	0.750		16.75	0.76
Southern Rockhopper Penguins		0.001	0.069	0.020	0.810	0.100	15.31	0.76
Gentoo Penguins		0.590	0.000	0.010	0.370	0.030	18.51	0.80
Wandering Albatross	0.003		0.100	0.800	0.087	0.010	12.48	0.80
Grey-headed Albatross	0.004		0.586	0.350	0.030	0.030	20.59	0.80
Yellow-nosed Albatross			0.580	0.380	0.030	0.010	20.37	0.80
Light-mantled Sooty Albatross			0.500	0.460	0.030	0.010	19.00	0.80
Dark-mantled Sooty Albatross			0.410	0.550	0.030	0.010	17.46	0.80
Southern Giant Petrel	0.904		0.055	0.04	0.001	0	29.69	0.80
Northern Giant Petrel	0.714		0.195	0.09	0.001	0	28.20	0.80
Fairy Prion			0.05	0.001	0.948	0.001	15.42	0.76
Salvin's Prion			0.09	0.22	0.66	0.03	14.86	0.76
Blue Petrel			0.16	0.21	0.59	0.04	15.76	0.76
Great-winged Petrel			0.9	0.04	0.06	0	25.96	0.76
Soft-plumaged Petrel			0.89	0.01	0.1	0	25.97	0.76
Kerguelen Petrel			0.7	0.06	0.24	0	23.35	0.76
Grey Petrel			0.709	0.28	0.001	0.01	22.45	0.76
White-chinned Petrel			0.17	0.57	0.24	0.02	14.32	0.76
Grey-backed Storm Petrel			0	0	0.999	0.001	14.80	0.76
Black-bellied Storm Petrel			0.1	0.35	0.549	0.001	14.48	0.76
South Georgian Diving Petrel			0.001	0.01	0.989	0	14.77	0.76
Common Diving Petrel			0.001	0	0.998	0.001	14.81	0.76
Crozet Shag		0.06	0.72	0.18	0.04	1	12.20	0.76
Sub-Antarctic Skua		0.001	0.001	0.001	0.997	1	12.02	0.76
Kelp Gull			0.25	0	0.75	1	11.58	0.76
Antarctic Tern				0.33	0.34	0.33	12.39	0.76
Kerguelen Tern				0.33	0.34	0.33	12.39	0.76

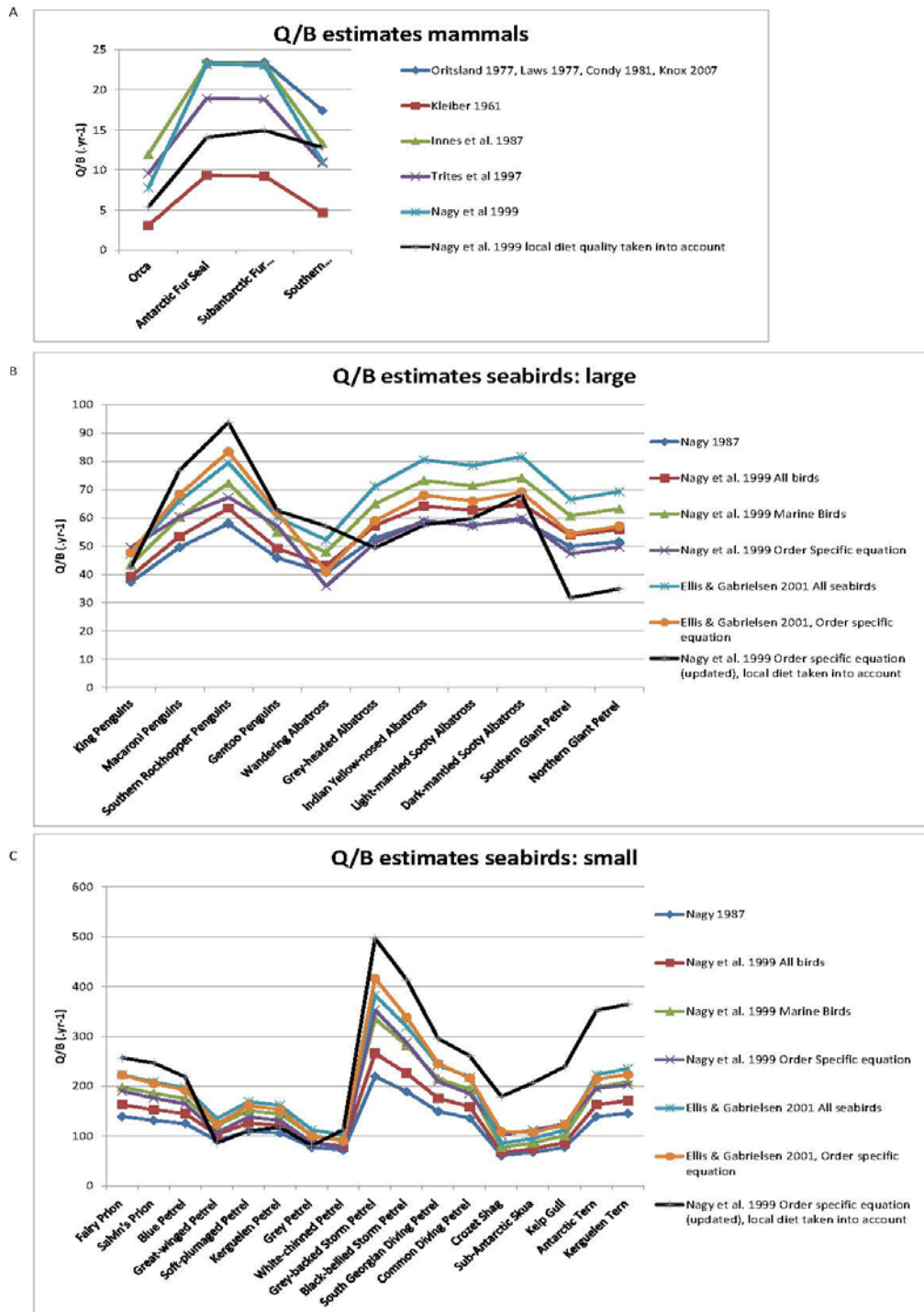


Figure 7.1 Illustration of the variation in the consumption to biomass rate estimates (yr^{-1}) as calculated for selected A) mammals, B) large seabirds and C) small seabirds found at the Prince Edward Islands.

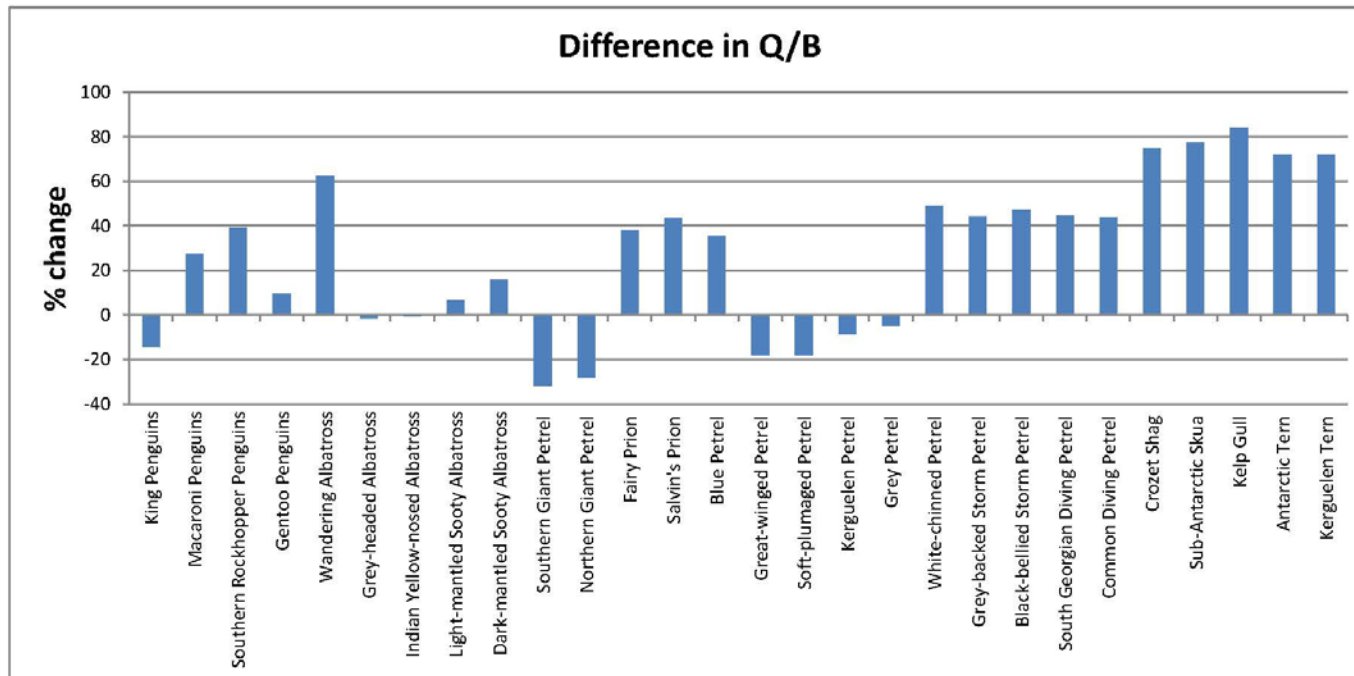


Figure 7.2. Graph showing the percentage difference between consumption to biomass rate estimates (Q/B , yr^{-1}) calculated using Nagy et al.'s (1999) field metabolic rates with standard processing versus using local diet and energetic density of prey for all breeding bird species found at the Prince Edward Islands.

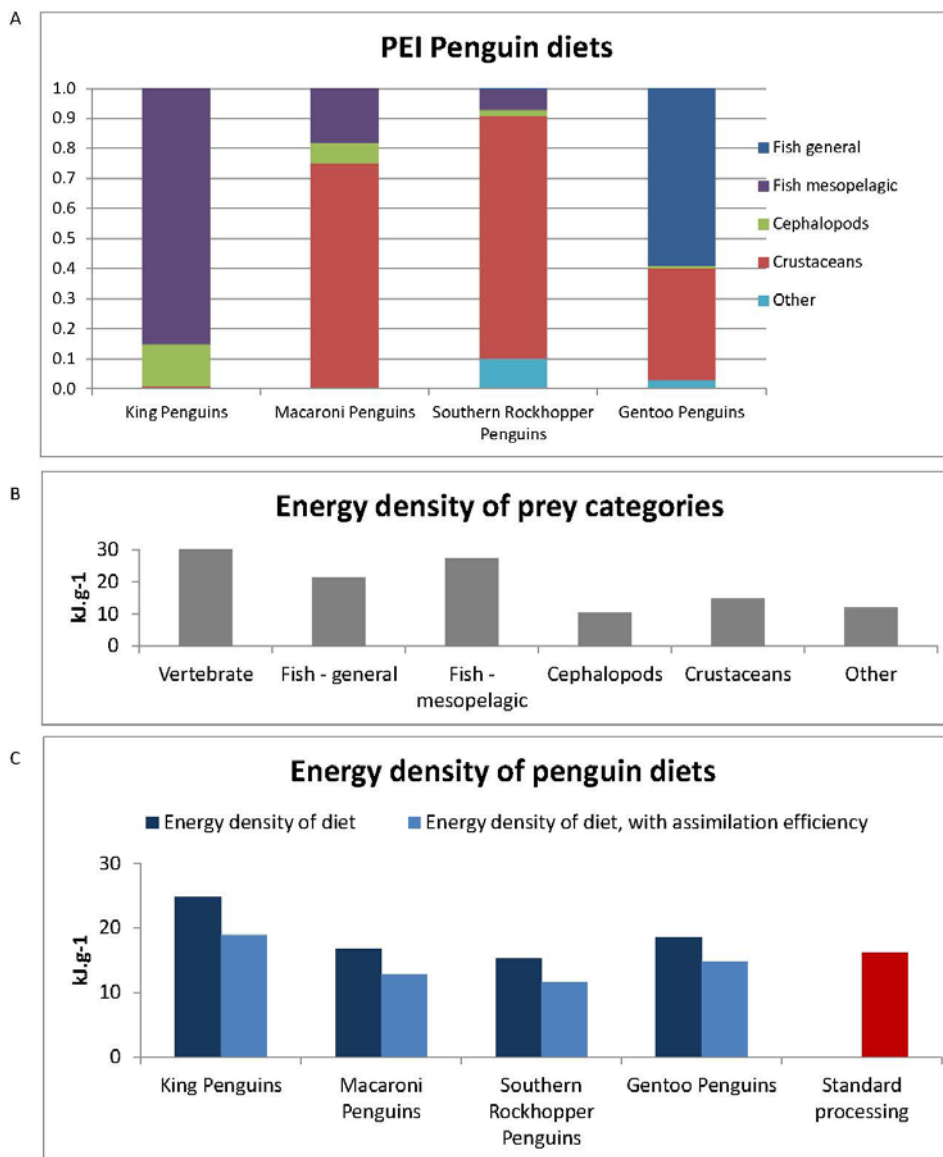


Figure 7.3. Illustration of the A) diets of the penguin species summarised into six prey categories ('fish general', 'fish – mesopelagic', 'cephalopods', 'crustaceans', 'vertebrates' and 'other'), energetic density of the B) prey categories and C) penguin diets with and without assimilation efficiencies as compared to standard processing (shown in red).

Chapter 8 Population dynamics at the Prince Edward Islands:

Hindcasting of three known events

8.1. Introduction

In the past, the communities at the Prince Edward Islands have experienced a number of changes which have been linked in some instances to known direct effects of human impacts. These include exploitation events at the islands such as the fur seal fishery (started in 1800s and terminated in the first half of the 19th century), which resulted in a depletion of the fur seal population from over 100 000 individuals to a few hundred. Another example is that of the Patagonian toothfish fishery (began in the 1990s and is ongoing today, 2013). Initial illegal, unregulated and unreported (IUU) fishing in the region resulted in a collapse of the fishery stock within a few years of the resource being identified. In addition, introductions of alien invasive species have had marked effects on the islands. The introduction of the domesticated cat (*Felis catus*) had devastating effects on the small bird populations, resulting in the local extinction of one species before the cats were finally eradicated (Bester et al. 2000).

Other changes that have been well documented in the scientific literature are less well understood and the effects of fisheries, interactions between species and environmental changes have all been considered to play a role. In an attempt to untangle the multitude of potential drivers in such complex biological systems, it can be useful to use an ecological model to explore the effects of known drivers, and through such analysis, better understand the system. Simple exploration can provide insight into the performance of the model (and assessment or reconsideration of parameterization) and insights into ecosystem effects as illustrated by the model. Following on from this, investigations into indirect effects and exploration of potential drivers can be carried out through temporal simulations. Ecosystem effects of fisheries on top predators and interactions between the top predators have received attention in the Southern Ocean and have been assessed in terms of their implications for fisheries management, e.g., Mackerel icefish, *Champsocephalus gunnari*, at South Georgia (Reid et al. 2005) and Patagonian toothfish at Heard (Green et al. 1998) and Macquarie (Goldsworthy et al. 2001) Islands. Concerns regarding such interactions (for instance the increasing fur seal populations and their

potential effect on seabirds) have been raised for the PEIs (Hofmeyr and Bester 1993; Guinard et al. 1998). These interactions can be explored through an ecosystem model, which includes consumption by competing fauna. Results from such work can inform management strategies and assist, for example, in setting fisheries quotas for the region.

South Africa is a member of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) and as such is committed to promote an ecosystem approach to fisheries (EAF) (Constable et al. 2000), yet no ecosystem model has been used for the management of the PEIs to date although the fishery is ongoing. The aim of this work was to create temporal simulations of the Prince Edward Island marine ecosystem to hindcast the ecosystem dynamics directly resulting from three examples of known human impacts: 1) the exploitation of the fur seals, 2) the Patagonian toothfish fishery and 3) the effects of the cat predation on the small flying bird population, and to assess the ecosystem effect in terms of changes of biomass for all functional groups for each scenario.

8.2. Method

Dynamic temporal model (Ecosim)

The dynamic simulation capability of the model (Ecosim) is described in Walters et al. (1997) and is based on the initial parameters that are defined in the mass balanced model (Ecopath). The basics of the temporal simulation consist of biomass dynamics expressed through a series of coupled differential equations. The equations are derived from the Ecopath production equation for the system:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M2_i + M3_i + E_i)B_i$$

Where dB_i/dt represents the growth rate during the time interval dt of group (i) in terms of its biomass, B_i , g_i is the net growth efficiency (production/consumption ratio), Q_{ji} is the consumption of predator j on prey i, $M2_i$ the non-predation ('other') mortality rate, $M3_i$ fishing mortality rate, E_i is the emigration rate, I_i is the immigration rate. The first summation estimates the total consumption by group (i), and the second the predation by all predators on the same

group (i). The consumption rates Q_{ij} , are calculated based on the ‘foraging arena’ concept where B_i ’s are divided into vulnerable and invulnerable components and it is the transfer rate (v_{ij}) between these two components that determines if control is top-down (Lotka-Volterra), bottom-up (i.e. donor driven) or of an intermediate type (Christensen et al. 2008). Unless otherwise stated, the vulnerability settings were left as default values (2.0). The set of differential equations is solved in Ecosim using a Runge-Kutta 4th order routine (Walters et al. 1997; Walters et al. 2000, Christensen et al. 2008).

The temporal simulation allows for time series data to be imported into the system and the model may be fitted to this data. The process of improving model fit can be done through an automated routine, which minimizes the sums of squared residuals (SS) by adjusting the vulnerability settings (of particular groups as defined by the user) or through identifying forcing functions that may contribute to creating a better SS for a particular model.

Three scenarios were created to explore how well the model is able to replicate the observed time series data available from the fur seal exploitation (on both the Antarctic and Subantarctic fur seals), the Patagonian toothfish fishery (on the Patagonian toothfish with some associated fish bycatch also included) and the impact of the introduction of the feral cats on the small flying birds (the *Prion* and *Petrel* group) at the PEIs.

8.2.1. Fur seal exploitation

The history of the fur seal industry was summarised by Hänel and Chown (1999). The earliest recorded sealing on the PEIs was in 1803 and by 1860 sealing was no longer economically viable. In 1909 an attempt to revive the industry was made without success and finally all sealing was stopped in the 1930s. In order to create a simulation of this exploitation, a fur seal fishery was created targeting both the Subantarctic and the Antarctic fur seals. Hunting commenced in the early 1800s, ceased by 1860 and recommenced for a short period in the first part of the 1900s. Data were created to drive the two fur seal populations through exploitation (Appendix 6.A). The Ecopath model from the 1960s time period (see Chapter 5) was used as the base from which to create a model to represent the ecosystem in the first decade of the 1800s. The only amendment made to this model was an adjustment of the fur seal biomass estimates to reflect the

most recent biomass estimates that are available from the islands. The estimates are from 2004 for the *Subantarctic Fur Seals* (Hofmeyr et al. 2006) and from 2008 for the *Antarctic Fur Seals* (Bester et al. 2009). Following this adjustment, the new 1800s Ecopath model needed to have additional adjustments to attain mass balance. The Ecotrophic Efficiencies (EEs) that were generated from the initial balancing attempt presented the *Patagonian Toothfish*, *Myctophid Fish*, *Large Cephalopods* and *Small Cephalopods* all to be over consumed with $EEs \geq 1$ (values of 1.02, 1.04, 1.00 and 1.00 respectively). In order to balance the model adjustments were made to each of these groups. The *Patagonian Toothfish* biomass was adjusted with an increase of 2% (from 0.0900 to 0.0918 t.km²), an increase (of 18%) in *Myctophid Fish* (from 3.375 to 4.000 t.km²) with a decrease of 12.5% in *Small Pelagic Fish* from 1.125 to 1.000 t.km², and small adjustments of less than 2% to both the cephalopod groups (increase in *Large Cephalopods* from 0.065 to 0.066 t.km², and an increase in *Small Cephalopods* from 0.045 to 0.046 t.km²). With these adjustments the model balanced. Data to drive the fur seal exploitation was then imported into the model along with reference biomass estimates from survey data to compare the model outputs with time series from the islands. Following the output of the Ecosim run (FS S1), the automated fitting to time series capability of the EwE software was employed to refine the fit of the model to the data. The vulnerability settings for both the *Subantarctic Fur Seals* and *Antarctic Fur Seals* were selected to be adjusted in the search to reduce the sum of squares residuals (SS) to gain a better fit.

8.2.1. Patagonian toothfish fishery

The fishery was initiated in the 1990s and is ongoing today. The legal fishery began in October 1996, though IUU fishing is known to have been in operation by 1995 and perhaps earlier (CCAMLR report 2009 Appendix Q). Estimates from a simple age-structured production model (ASPM) showed that the spawning biomass was depleted to, at most, a few percent of its pre-exploitation level during the early phase of this fishery (Brandao et al. 2002). Up to 7 vessels have been licensed to fish at the islands during any one year, however, since 2001 this has been reduced to only two operators (CCAMLR report 2009 Appendix Q). Annual fisheries catches, including IUU fishing, were estimated to be over 20 000 t in the first year of fishing, which rapidly declined to less than 1000 t by 2001 and declined to approximately 323 t by 2006

(Brandao and Butterworth 2009). In order to simulate this fishery, the 1980s Ecopath PEI EEZ model was used as a starting point (see Chapter 5). A time series file with the estimated catch data from 1997 to 2006 for the Patagonian toothfish fishery from Brandao and Butterworth (2009) was used to drive the model, along with catch data derived from the CCAMLR report series accounting for bycatch of other groups (*Sharks and Rays*, *Large Demersal Fish*, *Large Notheniid Demersal Fish* and *Large Pelagic Fish*, data provided in Appendix 7.A.). Two scenarios were run for the fishery. For the initial run (FPT S1), a dataset where no depredation due to cetaceans is considered was used (Brandao and Butterworth 2009, Appendix 1, $z = 0$). A relative abundance index for toothfish provided by the standardized commercial catch-per-unit-effort (CPUE) series for the PEIs EEZ for the longline fishery (Brandao and Butterworth 2009) was used as reference data to compare the output of the model. The time series data (of catch for all groups and the CPUE data for the toothfish) were imported into EwE and the model was run. In order to improve the model performance, the automated fitting to time series procedure was followed by conducting a vulnerability search for the *Patagonian Toothfish* functional group. Loss of toothfish to toothed cetaceans during landing procedures have suggested very high levels of depredation (up to two fish taken for each fish landed). Therefore, the procedure was repeated with data which included depredation to cetaceans according to the estimates from Brandao and Butterworth (2009) with $z=1$ (depredation starting in the year 2000, and increasing to a maximum of 1 fish per landed fish by 2002 and remaining at this level to 2006) and run as the second scenario (FPT S2). A vulnerability search was completed for the *Patagonian Toothfish* group.

8.2.1. Cat predation on small flying birds

The house mouse (*Mus musculus*), which apparently reached Marion island from shipwrecks and sealers' boats in the 19th century (Siegfried 1978; Skinner et al. 1978; de Villiers and Cooper 2008), became a pest at the meteorological station and in 1949 five domestic cats (*Felis catus*) were taken to Marion to keep the mouse infestation at the base under control (Skinner et al. 1978). The cats soon became feral (Anderson and Condry 1974) and by 1974-1975 an estimated cat population of 2137 was found on Marion Island (Van Aarde 1979; Van Aarde 1980; Bester et al. 2000, est 2139). Crude estimates of 3.7 to 10.6 cats per km² (Skinner et al. 1978) were made

with an estimated intrinsic rate of growth of 23.3% per year (Van Aarde 1978) and a total energy requirement of 9.97×10^8 kJ (Van Aarde 1977) or 10.2×10^8 kJ (van Aarde 1980). It was estimated that between 90 and 95% of the dietary requirements of the cats was satisfied by predation on small petrels. With the main energy content of bodies of petrels equal to 25.4 kJ.g^{-1} (dry weight) a minimum of 35 t (dry weight) of birds would have been required. The impact of the predation resulted in the Common Diving petrel *Pelecanoides urinatrix*, previously reported to breed on Marion Island, made locally extinct and other species (including the Great-winged petrel *Pterodroma macroptera* (Cooper and Fourie 1991) and the burrowing petrels (Cooper et al. 1995)) were heavily impacted. A control program using a viral disease, hunting, trapping and ultimately poisoning resulted in more than 3000 cats being killed and none being sighted since 1991 (Bester et al. 2000).

An Ecopath model that reflects the island system for the 1940s was generated from the 1960s Ecopath model (See chapter 5). No amendments were made to the functional groups of the model, though a fishery was added and named ‘Cats on birds’ to introduce the cat population to the model without having to include all biological aspects of this species as an additional functional group. Based on the historical data available, a time series was created to simulate the cat population on Marion Island. An exponential regression line between known data points from Bester et al. (2000) was used to generate a cat population estimate from 1949 to 1992 (Appendix 8.A.). Between 410 430 (van Aarde 1977) and 455 000 birds (Van Aarde 1980; Bester 2000) were estimated to have been consumed each year, which equates to between 192 and 213 birds per cat. Using the rate estimate of 201 birds per cat per year, the biomass of small *Prions and Petrels* (t) to be taken by cats was set based on the cat population and an average wet weight estimate of 0.324 kg per bird (used by Van Aarde 1977; Van Aarde 1980). These data were then imported into the 1940s Ecopath model and run in Ecosim with the cat predation treated as a ‘fishery’ removing biomass of the *Prion and Petrel* functional group. This simulation (CAT S1) resulted in extinction of the *Prion and Petrel* functional group and reductions in the predation by the cats were explored to find a predation rate from which the group would ultimately recover (partial recovery CAT S2; full recovery CAT S3).

8.3. Results

8.3.1. Fur seal exploitation

Results from the automated fitting to time series procedure for the fur seal populations improved the sum of squared (SS) residuals from 10.84 at the start of the procedure to 3.87 for the fourth iteration. A figure illustrating the hunting mortality, the model output and the survey data for both species of fur seal in terms of biomass (t.km^{-2}) is provided in Figure 8.1. A and B. The model captures the recent population growth, but does not manage to correctly simulate the rate of recovery and lags in its simulation of the current population biomass estimates.

The ecosystem effect of the fur seal hunting, as reflected in the changes in biomass (t.km^{-2}) for all functional groups for the FS S1 scenario, is illustrated in Figure 8.2. Functional groups which were affected by a change of $\pm 3\%$ compared to their starting biomass at any time during the 211 year simulation totaled 20 (See Table 8.1).

As expected, both fur seal populations experienced the greatest changes, being brought close to extinction (-99.9% of biomass as compared to the initial 1800 biomass) and showing recovery in the final years of the simulation. The *Orcas*, *Southern Elephant Seals*, *King Penguins* and *Gentoo Penguins* all showed positive responses to the seal culling of between 4 and 14%, and with the recovery of the fur seal populations, these all subsequently declined. The *Wandering Albatross* showed an initial positive response followed by a decline but the overall effect was negligible in terms of total biomass. For all other albatross groups, increases in relative biomass were between 1 and 6% but all declined in the latter part of the 211 year simulation. *Giant Petrels* showed an immediate increase in biomass following the start of the seal hunting with a high of 12% increase from the initial starting value followed by a decline. *Sharks and Rays* showed an initial positive response (maximum increase from initial starting value of 6 %) followed by a decline to initial biomass estimates. This pattern was repeated for almost all fish groups (*Large Demersal Fish*, *Large Nototheniid Demersal Fish*, *Small Continental Slope Demersal Fish*, *Small Inshore Demersal Fish*, *Large Pelagic Fish*, *Patagonian Toothfish* and *Myctophids*) with initial positive responses of between 2% and 12% followed by declines, returning to starting biomass values. In contrast, the remaining fish group, the *Small Pelagics*,

showed the opposite pattern but of negligible magnitude (0%). The *Large cephalopods* group initially responded with a peak of 5 % but soon returned to within a percent of original biomass estimates. Responses of all other groups were less than $\pm 3\%$.

8.3.2. Patagonian toothfish fishery

Mortality estimates (from catch data) used to drive the model, excluding (FPT S1) and including (FPT S2) cetacean depredation, are shown along with the catch-per-unit-effort data used as an index of the population biomass in Figure 8.3.A. The simulation of the Patagonian toothfish fishery provided promising results, where the model was able to effectively simulate the fishery and provide a relatively good fit to the CPUE data (Figure 8.3.B) for both simulations.

Following the automated fitting to time series for the Patagonian toothfish data, the sum of squared residuals (SS) value of 1.27 was improved to 0.57 and the vulnerability of the *Patagonian Toothfish* group was adjusted from the default value of 2.000 to 1.493 to provide the best result. Repeating the exercise with the inclusion of the cetacean depredation produced SS of 288.40, which was reduced to 0.81 by the 6th iteration and a vulnerability setting of 1.132.

The ecosystem response to this driver, as seen in the changes in biomass in all functional groups is provided in Figure 8.4. Changes in biomass for all groups for both scenarios (FPT S1 and FPT S2) following the application of the Patagonian toothfish fishery as a driver were similar, differing only in the magnitude of change within a functional group of a few percent of the starting biomass depending on the scenario (with or without cetacean depredation) (Table 8.2). The figure shows the results from the first described scenario where no cetacean depredation is used in the driver. The *Patagonian Toothfish* group was brought to within -92 and -93% of its initial standing stock. Seventeen functional groups experienced a change in biomass greater or less than 3% as compared to their starting biomass due to the Patagonian toothfish fishery (Table 8.2). Most groups responded positively, including the *Southern Elephant Seals* (increases of between 10 and 14%), *Macaroni Penguins*, *Gentoo Penguins* (7 to 8%) and the *Southern Rockhopper Penguins*, but to a lesser extent (1-2%). The *Light-mantled Sooty Albatross* showed a decline, while all other albatross groups increased, with the *Wandering Albatross* having the greatest positive response (of 11-13% as compared to its initial starting biomass). Positive

responses were shown by *Sharks and Rays* (between 29 and 37%), *Large Demersal Fish* (14 to 17%) and *Large Pelagic Fish* (52 to 60%). *Small Continental Slope Demersal Fish* showed an increase (13 to 15%), but the trend turned towards a decline by the end of the simulation. *Small Inshore Demersal Fish* initially increased, then declined, but the magnitude of the change was less than 5%. Increases were found for *Large Cephalopods* (27 to 32%), *Benthos*, *Large Zooplankton Crustaceans* and *All Other Zooplankton*. The *Benthic Decapod* had a varied response through the simulation. Fish groups that were adversely affected included, along with the already mentioned toothfish, the *Large Demersal Nototheniid Fish*, the *Small Pelagic Fish*, and the *Myctophid Fish*, the latter two showing a slight recovery towards the end of the simulation. The *Orcas* (-5 to 7%) and both *Antarctic* and *Subantarctic Fur Seals* were adversely affected (between 5 and 7%), and the *King Penguins* and *Prions and Petrels* both had initial increases followed by declines, but of insignificant magnitude.

8.3.3. Cat predation of small flying birds

Following the initial simulation (CAT S1), the cat predation results in extinction of the *Prion and Petrel* group by 1975 (Figure 8.5). Only when the predation rate on the *Prions and Petrels* was reduced to 1/7th of its original estimate (30 birds per cat per year) (CAT S2) did the model show a recovery of this functional group following the cat predation (Figure 8.5). Further exploration of the model showed only at a rate of 1/10th of the original estimate (21 birds per cat per year) (CAT S3) would the *Prion and Petrel* population recover to its initial starting biomass estimate (equivalent to the 2000s estimate).

Ecosystem effects of this scenario on the biomass of all other groups are shown in Figures 8.6 (CAT S1) and 8.7 (CAT S3). The initial simulation which results in the *Prion and Petrel* extinction has, as would be expected, a larger impact on all the functional groups (as measured by the change in each functional group compared to its starting biomass) and the impact is in most cases sustained. Magnitudes of changes that exceed $\pm 3\%$ of the original starting biomass total 16 (Table 8.1) and include sustained positive responses for the *Orcas* (3%), *Southern Elephant Seals* (9%) and *King Penguins* (5%). The *Macaroni Penguins* and *Rockhopper Penguins* both showed positive responses. The *Gentoo Penguins* had an initial positive response followed by a decline, but not of any appreciable magnitude. The *Giant Petrels* showed a decline

(-8%), while all the albatross species showed positive gains between 6 and 11%. Almost all of the fish groups (*Sharks and Rays*, *Large Demersal Fish*, *Large Nototheniid Demersal Fish*, *Small Continental Slope Demersal Fish*, *Small Inshore Demersal Fish*, *Large Pelagic Fish*, *Patagonian Toothfish* and *Myctophid Fish*) show increases of up to 6% of initial biomass followed by declines of various severity, but none greater than -1%. The *Small Pelagic Fish* group shows the opposite pattern with an initial decline followed by a recovery, but the magnitude seems inconsequential (within 0.2 of a percent). For the cephalopod groups, the *Large Cephalopods* initially increase by approximately 8% as compared to their starting biomass, but subsequently decline to an intermediary level between their initial and peak biomass. The *Small Cephalopods* respond with an initial increase of as much as 10% and remain at this elevated level. The responses of all other functional groups were less than $\pm 3\%$.

The pattern of the response for all groups is similar to that for the scenario where the predation rate is reduced to one seventh of the original estimate (CAT S2), but responses are slower to initialise and the magnitude of the response is reduced (no figure provided), though 14 groups still reach the criteria of a positive or negative response equal to or exceeding $\pm 3\%$, including the *Prions and Petrels* which come to -91% of their starting biomass estimate (Table 8.1). A positive response was observed for the *Southern Elephant Seals* (7%), *King penguins* (4%) and all albatross species (between 4% and 7%). The large pelagic fish groups (*Sharks and Rays*, *Large Pelagic Fish*, *Patagonian Toothfish*) and both cephalopod groups also showed positive responses (of between 3 and 8%). The *Giant Petrels* had the greatest negative response (-7%), following the declining *Prion and Petrel* numbers. In the final simulation (CAT S3), the *Prions and Petrels* were reduced to half of their original population and the ecosystem effects were limited, with only 7 groups affected positively or negatively by the change and none more than $\pm 3\%$ of their starting biomass.

8.4. Discussion

8.4.1. Fur seal simulation

While the hindcasting of the fur seal industry is able to capture some of the qualities of the recovery of the fur seal population, their rate of increase over the final 50 years of the 211 year

simulation is not accurate. The discrepancy between the survey data and the model predictions may be due to the failure to create an accurate reflection of the culling patterns, an underestimation of the production term for the fur seals, or possibly, the higher rate of population growth observed is due to migration to the islands from neighboring subantarctic islands. Further exploration of the driver and the response by the fur seal population should be explored to improve the model performance and consultation with mammal experts would be beneficial.

In terms of the ecosystem response, this simulation does generate some patterns in other functional groups that have been observed in the time series data available for the islands. The decline of the *Southern Elephant Seals* at the PEIs has been well documented, and the results of the simulation suggest that the recovery of the fur seals may impact the *Southern Elephant Seals*, though the magnitude of this effect in the simulation is limited (the initial increase was only 4% and the subsequent decline does not exceed this amount). It is also interesting to note the simulation shows a similar pattern for the *King Penguins*, which respond in a positive manner to the seal hunting (up to 8% increase) and follow with declines over the last 50 years of the simulation. A first glance at the *Southern Rockhopper Penguin* data shows a pattern that is clearly opposite to observations from the islands. The population at the PEIs has been in decline over the past 30 years, yet the simulation suggests that this group should respond in a positive way to the recovery of the fur seal population. The magnitude of these changes, however, is small and possibly inconsequential when other drivers in the system are considered. Other responses that are worth mentioning include what would be a positive response by the *Gentoo Penguins* to this driver (of 9%), and also a decline in the *Patagonian Toothfish* following the recovery of the fur seal population (but of only 5% in magnitude).

8.4.2. Patagonian toothfish fishery simulation

The low vulnerability settings found during the vulnerability search following the fitting to time series procedure for the *Patagonian Toothfish* fishery simulation suggest that the Patagonian toothfish stock was close to its carrying capacity prior to the exploitation in the mid 1990s. Anecdotal evidence from over-wintering researchers suggests that this may indeed be the case. However, it is unlikely that the earlier illegal fishing activity in the 1970s and 1980s in other

areas of the sub-Antarctic (Goldsworthy et al. 2001) would not have affected the stocks in the vicinity of the PEIs.

In the proposed management procedure for the toothfish for the PEIs, Brandao and Butterworth (2009) put forward four different Operating Models (OMs) which reflect ‘Optimistic’, ‘Intermediate’, ‘Less Pessimistic’ and ‘Pessimistic’ status for the resource. From these models it is possible to compare the estimates for the pre-exploitation spawning biomass (K^{sp}) for each scenario with that estimated from the ecosystem model developed here. The ‘Optimistic’ scenario has a K^{sp} of 138 499t, ‘Intermediate’ is 88 205t, ‘Less Pessimistic’ is 45 703t and ‘Pessimistic’ is 29 723t. The K^{sp} that allows for the best fit of the model in this study is 32 326t without the cetacean depredation and up to 34 481t with cetacean depredation. This sets the estimates generated here between the ‘Less Pessimistic’ and ‘Pessimistic’ estimates of Brandao and Butterworth’s (2009) (See Figure 8.8) OMs and lends confidence that the model is at least generating results that are in line with other assessments.

In terms of the ecosystem response of all functional groups, many responses shown are contrary to patterns observed at the islands. The results of the simulation suggest increases in the *Southern Elephant Seals*, the *Macaroni Penguins* and the *Southern Rockhopper Penguins*, and decreases in the fur seal populations and the *King Penguins*. Survey data from the islands for all these groups show opposite trends. The simulation, however, does show the magnitude of all these responses to be relatively minor and probably insignificant and other drivers in the system apparently overshadow the patterns observed here. In the case of the fur seals, for instance, the recovery from exploitation appears to be the over-riding driver responsible for the observed population patterns. Once the effect of this driver is no longer a consideration, other drivers may begin to play a role.

8.4.3. Cat predation on small flying birds

The initial simulation of the effect of the predation impact of the cat population on the *Prion* and *Petrel* population (CAT S1) suggests that the estimates of 290 birds per cat per year would be in excess of what would be sustainable for the PEIs, unless the *Prion* and *Petrel* population was up to 10 times greater than present day estimates. It must be stressed that the population estimates

for this group are not considered precise, but it seems unlikely that the population estimates would be out by such a large margin. The literature suggests that up to 95% of the cat diet would have been based on birds (Van Aarde 1980), but it seems more likely that mice would have made a portion of the diet, with the small bird populations contributing during the relevant breeding seasons. Seasonality of bird consumption was found by Van Aarde (1980), where the winter breeding Great-winged petrels were only taken from June to August, White-chinned petrel chicks in December, and Salvins prions not found in cat diets between March and May, but found throughout the rest of the year with a peak in August and September. Some birds were also found year round (including Soft-plumaged and Kerguelen terns) (Van Aarde 1980). This would affect the consumption rate of the bird populations, perhaps reducing it to a level that would be more sustainable. The breeding success of the Great-winged and Blue petrel was found to improve following the cat eradication (Cooper et al. 1995) and this is reflected in the results of the second and third simulation runs (CAT S2 and CAT S3) where the predation impact was reduced to 1/7th and 1/10th of the original suggested consumption rate respectively.

In terms of ecosystem effects, the pattern observed is in general an increase in most groups as a response to the declining *Prion and Petrel* group. In the simulations where the *Prion and Petrel* group are not driven to extinction (CAT S2 and CAT S3), a decline in most populations is observed. The only exception is the *Giant Petrels*, which track the *Prions and Petrels* biomass trends, but lag in their response time. These responses are of appreciable magnitude for the first simulation (CAT S1) (as high as 10%), but are much reduced by the third simulation (maximum of 4%).

8.5. Conclusions

The first criterion set for using ecosystem models for fisheries management is whether they can replicate historic trends in ecosystems (Christensen and Walters 2011) and, with the exploration of the temporally dynamic version of the PEI model, it was possible to hindcast past known events and to examine the ecosystem effects of the drivers. The findings presented demonstrate that the model in its current form is able to capture and replicate, to some degree, the patterns observed in the field data, particularly in the case of the fur seal populations and the Patagonian toothfish fishery for those groups that are directly affected by the driver. The drivers assessed

here do not, however, result in ecosystem effects that are found in the survey data from the islands and the conclusion must be that additional drivers need to be investigated in the search for model outcomes that reflect the observed trends. Further development of the temporal simulations where such drivers are combined and the ecosystem effects are assessed against the time series data that exist for all groups should be explored.

Table 8.1. Estimates of the maximum and minimum % difference as compared to the starting biomass (t.km⁻²) for each functional group in the PEI marine ecosystem model for each hindcasting scenario run.

Group	FS S1		FPT S1		FPT S2		CAT C1		CAT S2		CAT S3	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
Orcas	10.0	-0.1	0.0	-5.4	0.0	-7.1	3.4	-0.2	2.5	-0.2	1.0	-0.1
Southern Elephant Seals	4.1	0.0	13.5	-0.1	9.8	-0.3	8.7	0.0	6.7	-0.1	2.9	-0.1
Antarctic Fur Seals	0.0	-99.9	0.1	-4.7	0.1	-4.1	2.4	0.0	2.0	0.0	1.0	0.0
Sub-Antarctic Fur Seals	0.0	-99.9	0.0	-6.8	0.0	-5.9	2.2	0.0	1.9	0.0	0.9	0.0
King Penguins	13.8	0.0	1.4	-0.9	1.0	-0.8	4.7	0.0	3.8	0.0	1.7	-0.1
Macaroni Penguins	0.7	-0.8	3.8	0.0	3.3	0.0	1.8	0.0	1.4	0.0	0.6	0.0
Southern Rockhopper Penguins	0.1	-2.0	1.4	0.0	1.2	0.0	1.2	-0.1	1.0	-0.1	0.5	-0.1
Gentoo Penguins	8.6	0.0	7.9	0.0	6.9	0.0	0.8	-1.1	0.6	-0.9	0.3	-0.5
Wandering Albatross	1.1	-1.4	13.3	0.0	11.3	0.0	10.7	0.0	7.1	-0.1	2.7	-0.1
Grey-headed Albatross	5.3	0.0	2.8	0.0	2.3	0.0	6.9	0.0	4.8	-0.1	1.9	-0.1
Indian Yellow-nosed Albatross	5.9	0.0	1.8	0.0	1.5	0.0	5.5	0.0	3.6	0.0	1.3	0.0
Light-mantled Sooty Albatross	4.0	0.0	0.2	-0.4	0.1	-0.4	7.9	0.0	5.2	0.0	1.9	-0.1
Dark-mantled Sooty Albatross	2.7	0.0	2.1	0.0	1.8	0.0	8.3	0.0	5.4	0.0	2.0	-0.1
Giant Petrels	11.9	-0.3	3.0	0.0	2.5	0.0	0.0	-7.8	0.2	-7.3	0.2	-4.4
Prions and Petrels	2.4	-2.9	1.3	0.0	1.1	0.0	0.6	-100.0	1.7	-90.9	1.8	-49.2
Sharks and Rays	5.5	0.0	36.6	0.0	29.2	-0.2	5.8	0.0	4.6	-0.5	2.5	-1.5
Large Demersal Fish	6.3	0.0	16.6	0.0	14.3	0.0	3.2	-0.5	2.4	-0.9	1.3	-1.0
Large Nototheniid Demersal Fish	12.3	0.0	0.3	-2.3	0.2	-2.0	1.3	-1.4	0.9	-1.4	0.5	-0.8
Small Continental Slope Demersal Fish	1.7	0.0	15.0	0.0	13.6	0.0	0.7	-1.1	0.3	-1.0	0.2	-0.6
Small Inshore Demersal Fish	5.0	0.0	1.3	0.0	1.1	0.0	0.5	-1.1	0.3	-1.0	0.2	-0.6
Large Pelagic Fish	8.0	0.0	59.5	0.0	52.1	0.0	4.4	0.0	3.2	-0.9	1.8	-1.1
Patagonian Toothfish	4.6	0.0	0.0	-92.9	0.0	-91.9	6.4	0.0	5.5	-0.1	2.8	-0.4
Small pelagic Fish	0.0	-0.4	0.0	-1.4	0.0	-1.3	0.0	-0.2	0.0	-0.1	0.0	-0.1
Myctophid Fish	5.4	0.0	0.0	-4.3	0.0	-3.9	0.9	0.0	0.7	0.0	0.4	-0.1
Large Cephalopods	5.1	0.0	32.4	0.0	27.3	0.0	8.1	0.0	5.0	-0.1	2.8	-0.5
Small Cephalopods	0.0	-2.7	4.2	0.0	3.5	0.0	9.6	0.0	8.1	-0.1	4.1	-0.1
Benthos	0.0	-0.3	1.3	0.0	1.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Benthic Decapod	0.0	-1.1	0.2	-0.1	0.1	-0.1	0.2	0.0	0.2	0.0	0.1	0.0
Large Zooplankton Crustaceans	0.0	-2.3	1.5	-0.1	1.3	-0.1	0.0	-0.2	0.0	-0.2	0.0	-0.1
Small Zooplankton Crustaceans	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
All Other Zooplankton	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Open Ocean Large Phytoplankton	0.1	0.0	0.0	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0
Open Ocean Small Phytoplankton	0.1	0.0	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Island Associated Blooms	0.1	0.0	0.0	-0.6	0.0	-0.6	0.0	0.0	0.0	0.0	0.0	0.0
Macrophytes	0.0	-0.1	1.2	0.0	1.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0
Macrophyte Detritus	0.2	0.0	1.0	0.0	0.9	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Detritus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

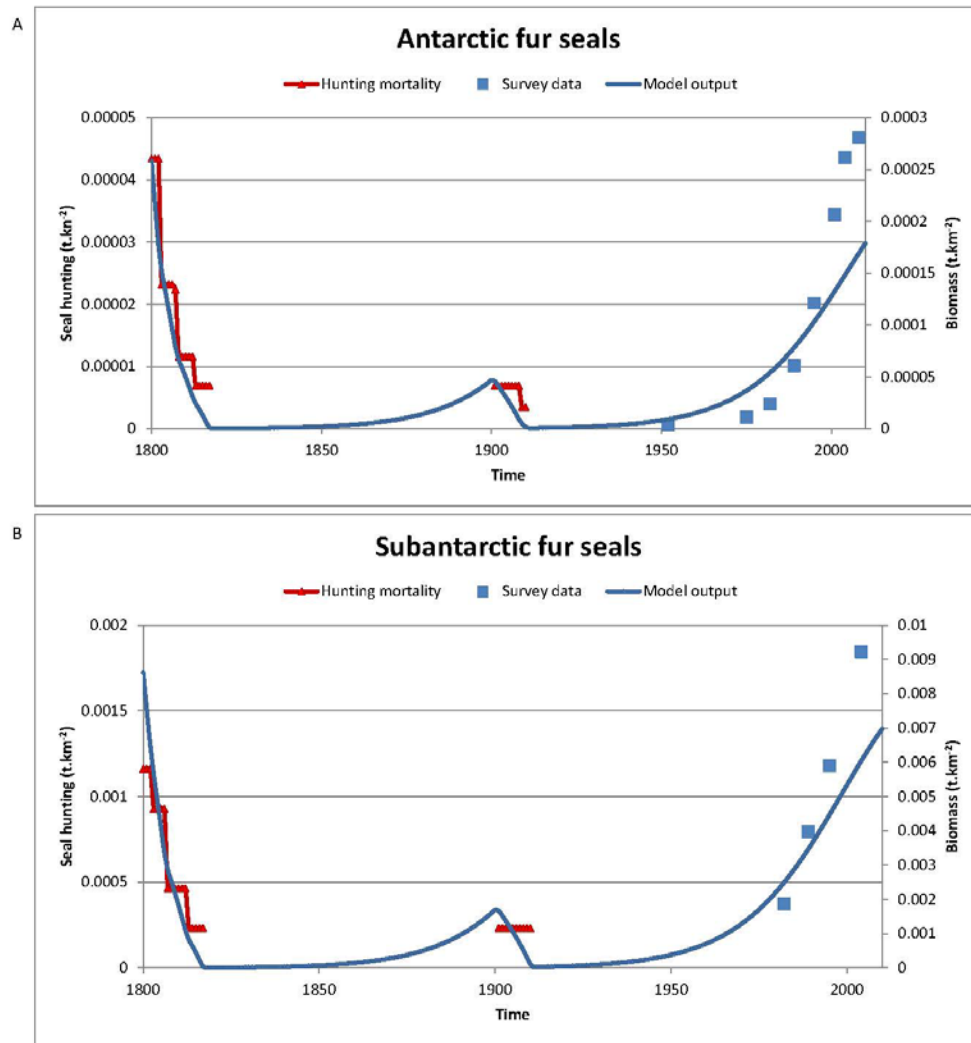
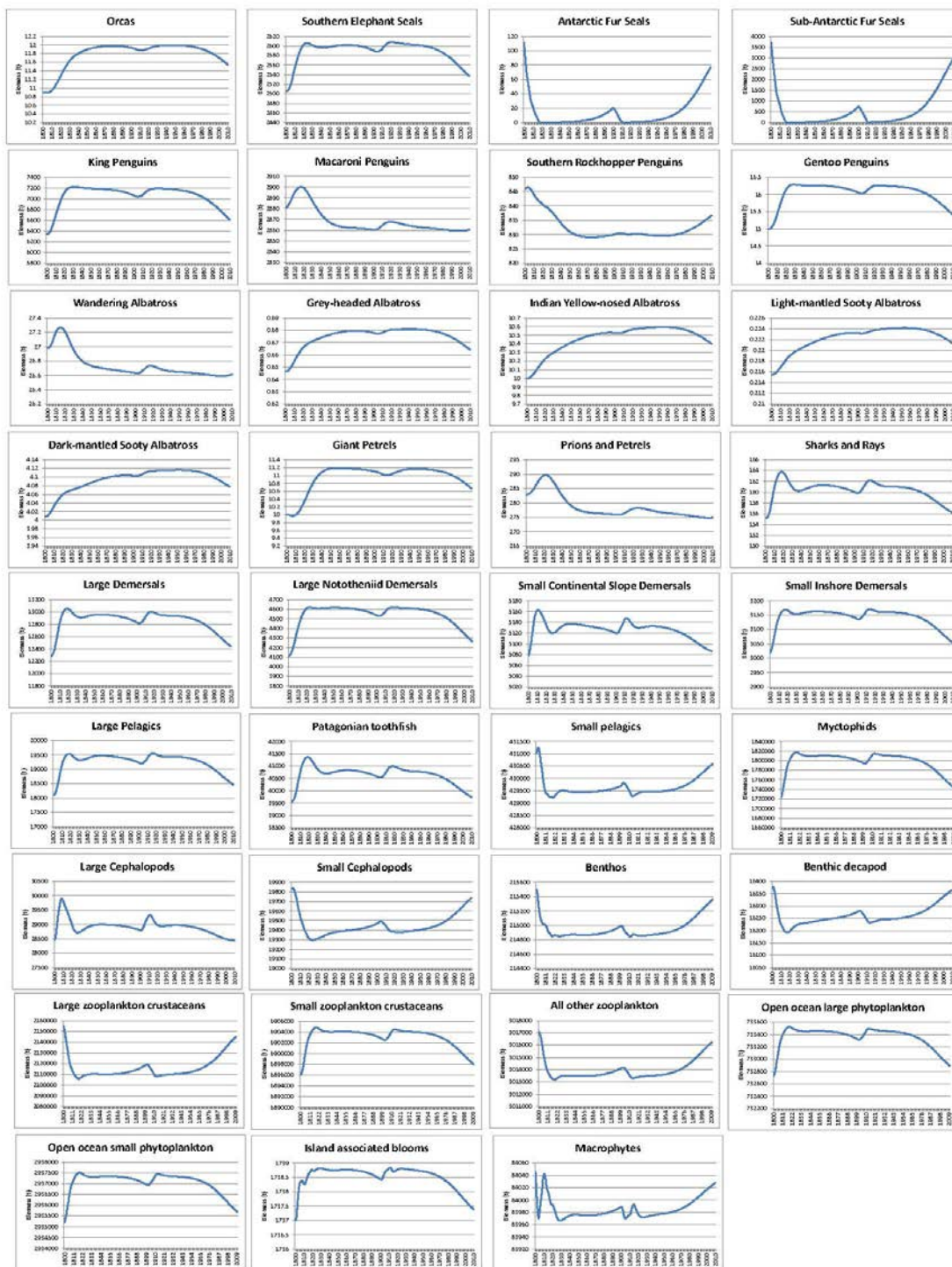


Figure 8.1. Reconstruction of fur seal exploitation driven by hunting with model results compared to time series survey biomass data for the PEI EEZ from 1800 to 2010 for Antarctic Fur Seals A) and Subantarctic Fur Seals B).

Biomass (t.km^{-2})



Time (years, 1800 - 2010)

Figure 8.2. Trends in biomass estimates (t.km^{-2}) from 1800 to 2010 for all functional groups of the Prince Edward Islands marine ecosystem following the system being driven by a reconstruction of the fur seal industry.

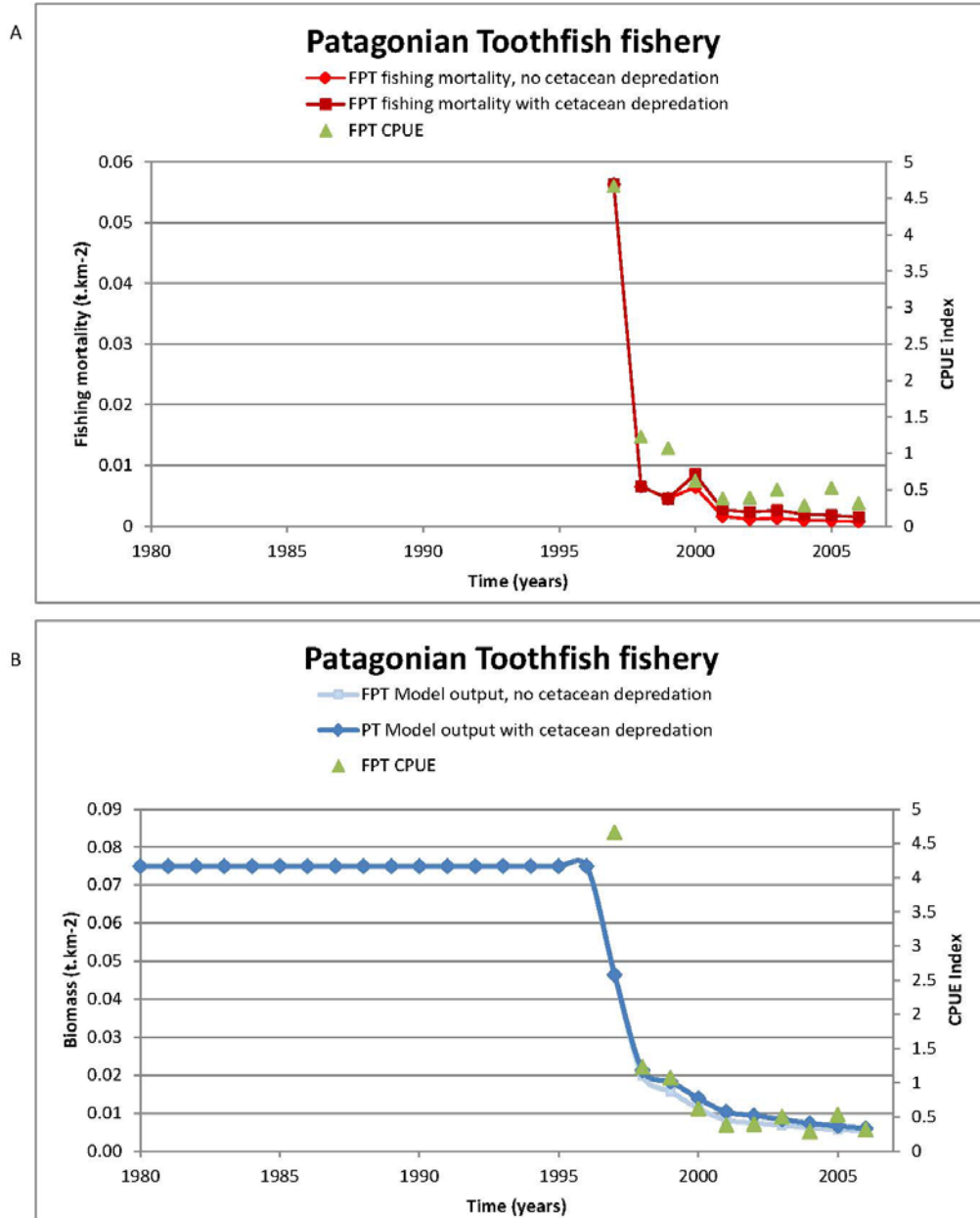
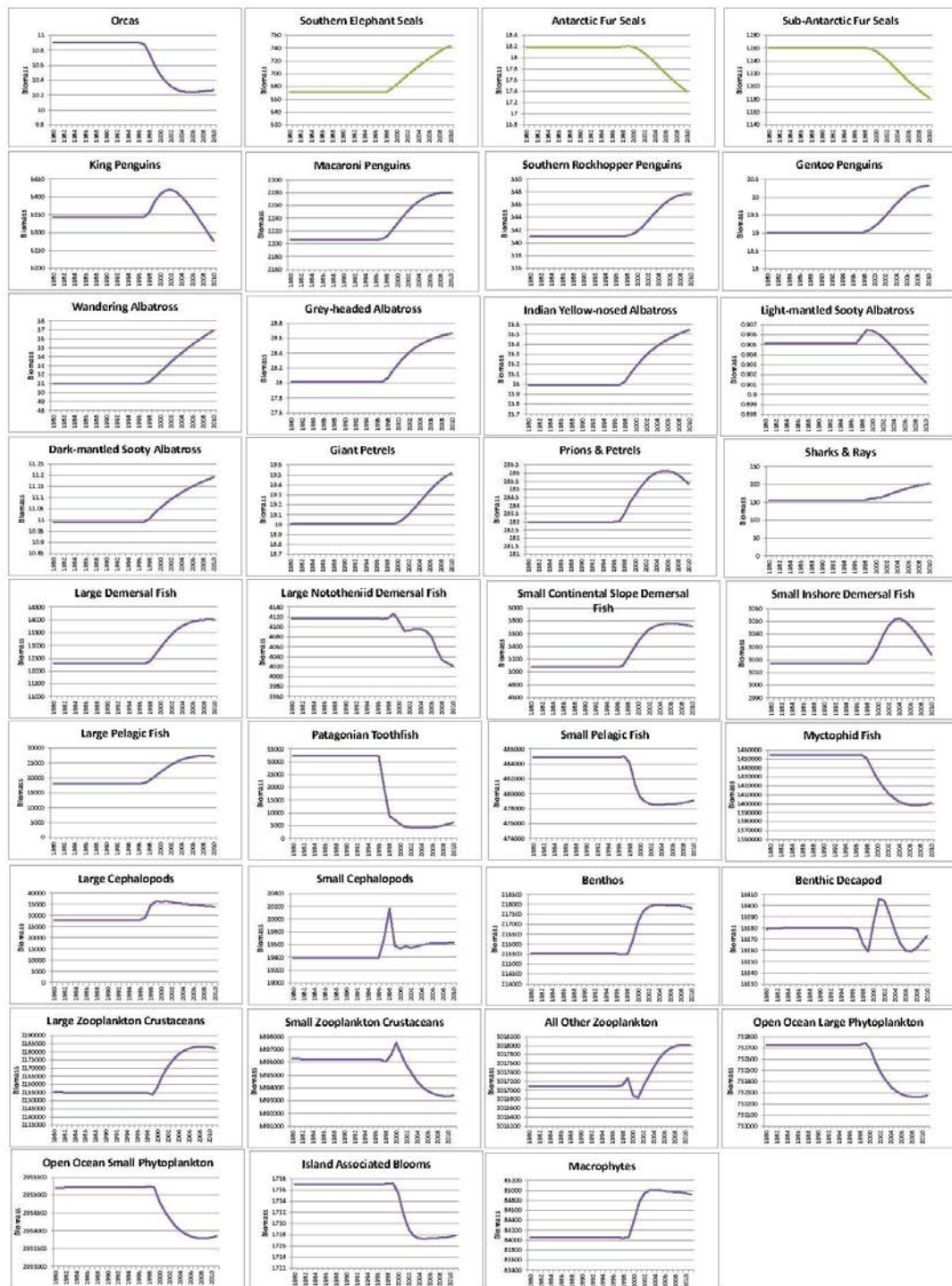


Figure 8.3. Reconstruction of the Patagonian toothfish fishery from 1980 to 2006 presented with fishing mortality (as catch data, $t.km^{-2}$) used to drive the model (A) and model output shown in (B), with and without cetacean depredation as compared to time series relative abundance data (from catch-per-unit-effort (CPUE)) data provided by Brandao and Butterworth (2009) for the PEI EEZ.

Biomass (t.km⁻²)



Time (years, 1980 - 2010)

Figure 8.4. Trends in biomass estimates (t.km⁻²) from 1980 to 2006 for all functional groups of the Prince Edward Islands marine ecosystem following the system being driven by a reconstruction of the Patagonian toothfish fishery.

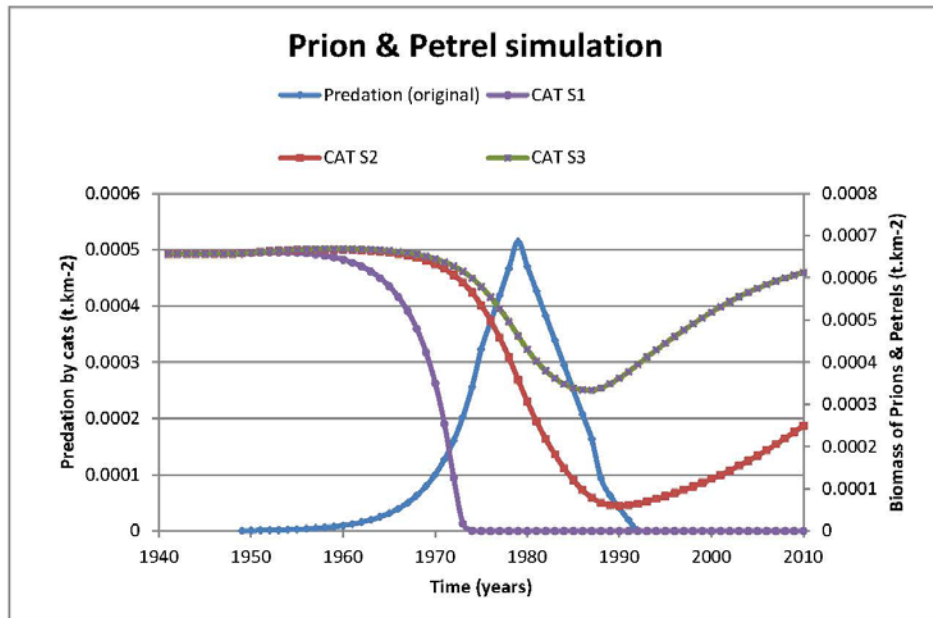
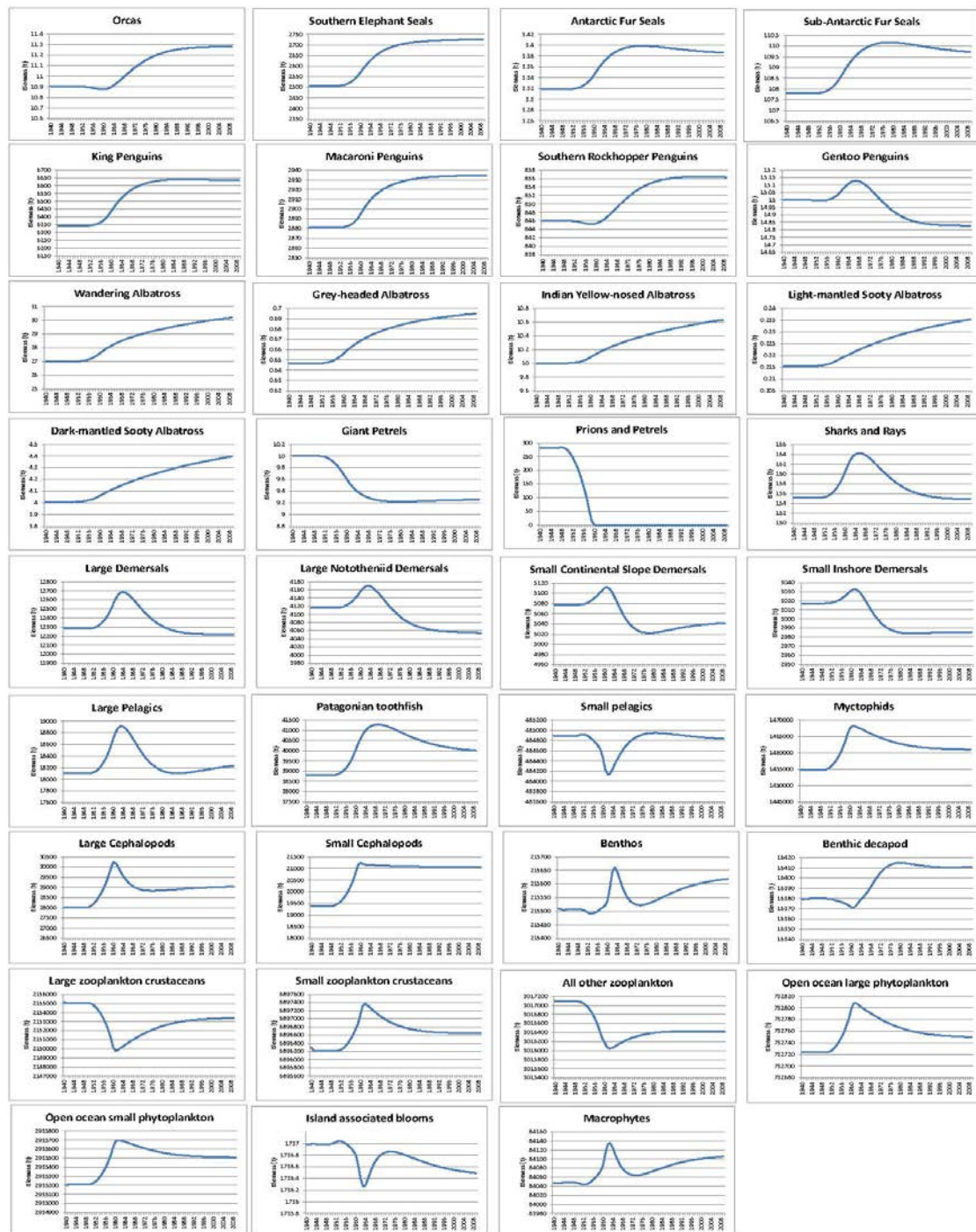


Figure 8.5. Reconstruction of the cat predation on small flying birds (*Prions and Petrels*) from 1940 to 1990 with predation estimates (derived from cat population and consumption estimates from Bester et al. 2000) driving the model (with original estimates (CAT S1), 1/7th original estimates (CAT S2) and 1/10th original estimates (CAT S3)).

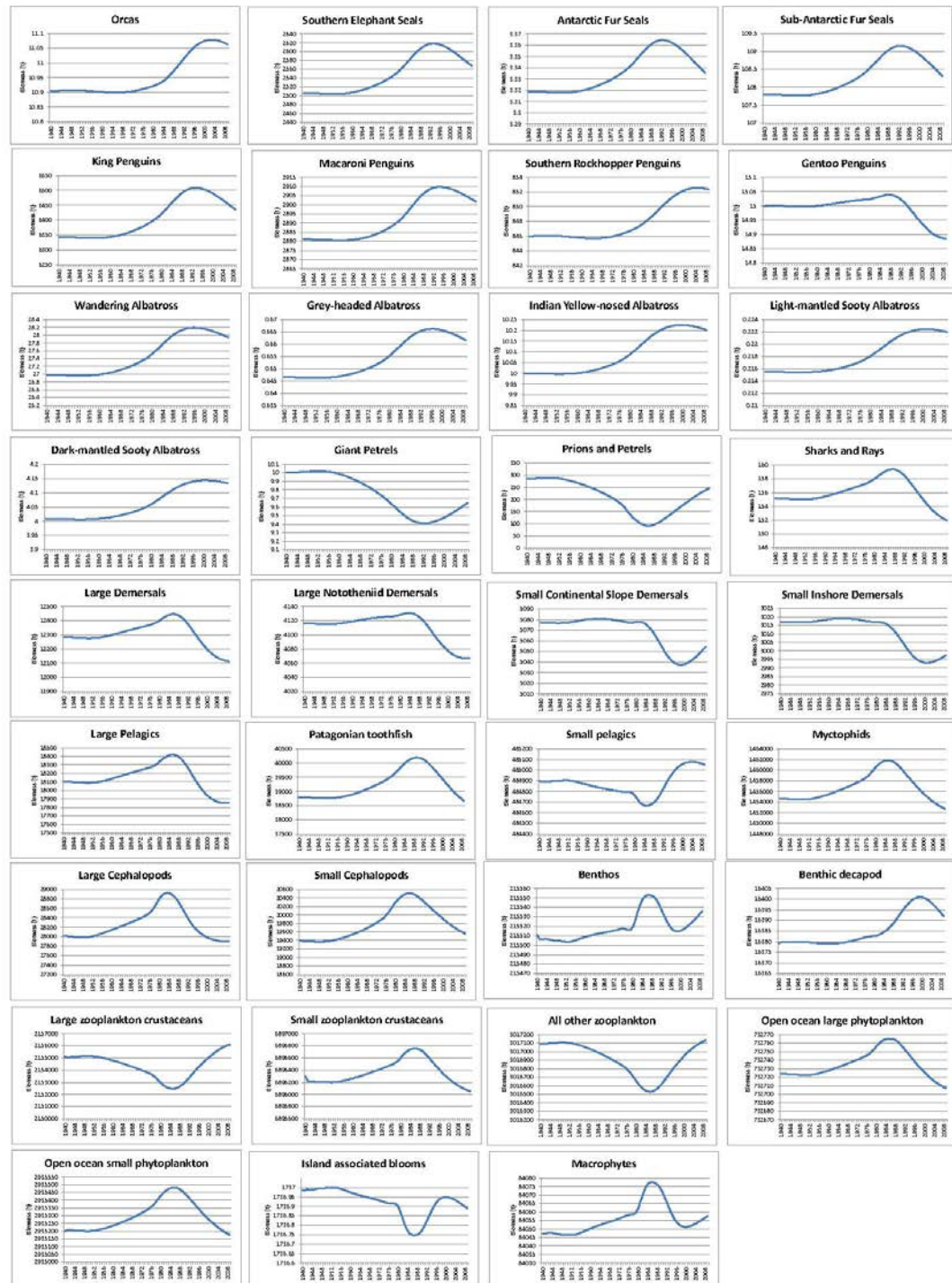
Biomass (t.km^{-2})



Time (years, 1940 - 2010)

Figure 8.6. Trends in biomass estimates (t.km^{-2}) for all functional groups of the Prince Edward Islands marine ecosystem following the system being driven by a reconstruction of the cat predation on the small flying birds (*Prions and Petrels*) from 1940 to 1990 based on original consumption estimates (CAT S1).

Biomass (t.km^{-2})



Time (years, 1940 - 2010)

Figure 8.7. Trends in biomass estimates (t.km^{-2}) for all functional groups of the Prince Edward Islands marine ecosystem following the system being driven by a reconstruction of the cat predation on the small flying birds (*Prions and Petrels*) from 1940 to 1990 based on estimates $1/10^{\text{th}}$ of original predation estimates (CAT S3).

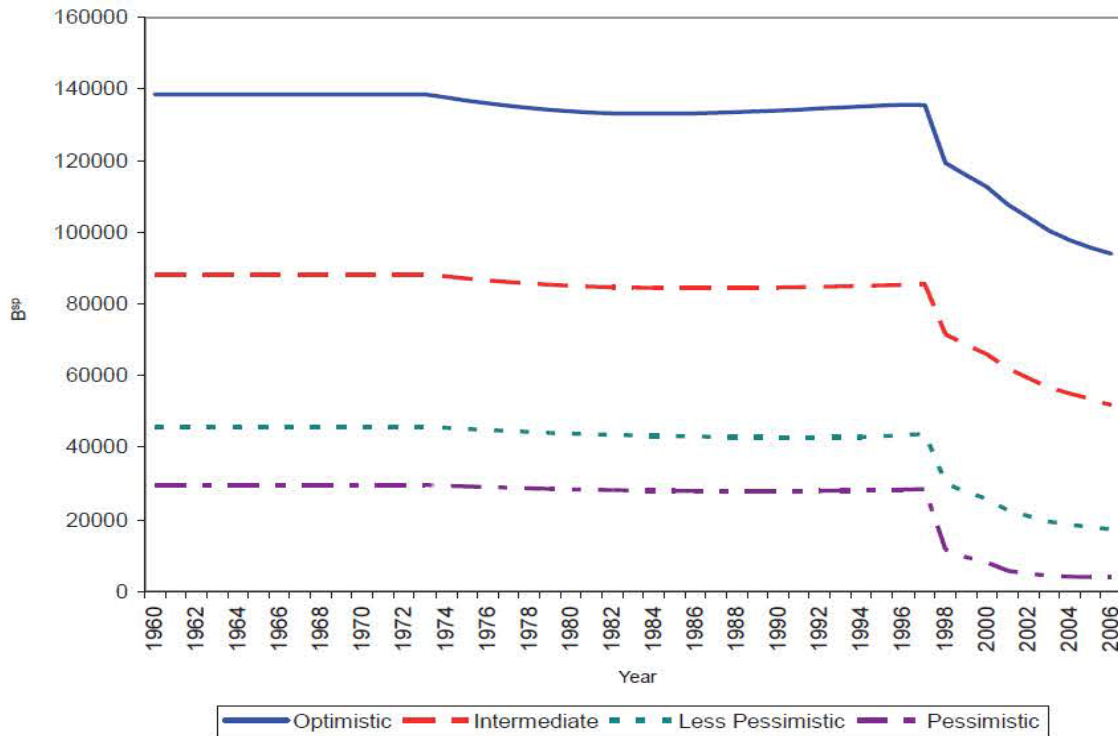


Figure 8.8. Spawning biomass estimates taken from Brandao and Butterworth's (2009) Figure A.1. for the Patagonian toothfish at the Prince Edward Islands. Original caption from figure: Spawning biomass estimates (note that recruitment can vary prior to the onset of harvesting). Estimates are given for the Optimistic, Intermediate, Less Pessimistic and Pessimistic scenarios (details of the conditioning of these scenarios to the data are provided in the text; see also the caption to Table A.4). All results shown assume a cetacean depredation factor $z=1$, i.e. recent losses to cetacean depredation are equal to the landed longline catch.

Chapter 9 Population dynamics at the Prince Edward Islands: Forecasting of climate change scenarios through forcing of primary producers

9.1. Introduction

Climate change and its potential impacts present a challenge for biologists by providing an additional dimension that needs to be considered when interpreting ecosystem dynamics. Along with identifying natural patterns in ecosystems, the effects of climate change are superimposed on systems and these effects need to be teased apart. Investigating how organisms, ecological processes and whole ecosystems respond to a changing climate is a challenge and Subantarctic islands have been identified as having much to offer in furthering our understanding in this regard (Hänel and Chown 1998; Smith 2002). With the threat of climate change becoming more widely accepted, the subantarctic and Antarctic ecosystems have been identified as critical areas for global change research (Smith 2002). These ecosystems, in general, have impoverished biota and occur in harsh environments with relatively simple ecosystems that are sensitive to perturbations and therefore make ideal systems to study (Smith 2002). Ecosystems at higher latitudes are expected to show effects of global climate change relatively early and the Prince Edward Island (PEI) ecosystem therefore lends itself to investigations into exploring climate change scenarios. Long term changes in the populations of a number of the top predators in the subantarctic have been connected with climate warming (Weimerskirch et al. 2003).

Interpretation of long term changes in populations will be confounded because of the variety of levels of interaction that may be considered. Understanding biological patterns and how they change across measurement scales is a fundamental conceptual problem in ecology (Levin 1992 in Francis et al. 1998), which holds true for climate variability and its analyses, which act across all temporal and spatial scales and result in difficulties in creating ecosystem models that can accurately predict responses to climate change (Francis et al. 1998; Trites et al. 2007).

Observations of climate change at the PEIs have been made since the early 1990s (Smith and Steenkamp 1990; Chown and Smith 1993) with a warming and drying of the islands recorded from observations dating back to 1949 (Smith 1991; Smith 1992). Annual mean surface air

temperature at Marion island has increased by 1.2°C between 1969 and 1999 (Smith 2002) and sea-surface temperatures rose by 1.4°C at Marion from 4.5°C in 1949 to 5.9°C in 1998 (Melice et al. 2003). One of the potential effects of climate change is the change in position of the frontal systems. This theoretically could have at least two possible consequences. In the first instance, the position of the Sub-Antarctic Front (SAF) with respect to the islands is thought to determine the type of production that occurs at the islands and a southward shift in the SAF (already documented in Hunt et al. 2001) may have important implications for the PEI ecosystem, potentially affecting the productivity (Pakhomov and Froneman 1999a). A southward shift would increase the ‘flow through’ mode, bringing allochthonous production to the islands and benefiting the offshore feeders, but reducing the water retention mode, and potentially adversely affecting the benthic community and the inshore foragers (Pakhomov and Chown 2003) by reducing the occurrence of the island-associated blooms. The warming at the islands and the decline in rainfall (Smith 2002) would also contribute to a reduction in the river run off and potentially reduce the occurrence of the island associated blooms, which are thought to be linked to the water column stability that such run-off generates. An investigation into such a phenomenon and its effect on the PEI system would be beneficial for understanding future potential changes at the islands.

With this in mind, satellite remote sensing data, centered on the island area (Latitude 46.5 – 47.1S; Longitude 37.4 – 38.4E), were extracted on a monthly basis, initially using the Giovanni tool (NASA) for SeaWiFS data (<http://disc.sci.gsfc.nasa.gov/giovanni>), and finally reprocessed for this study by F. Mélin (of the Joint Research Centre, EC) for all available marine data (SeaWiFS, MODIS-Aqua, MODIS-terra) (See Figure 9.1). The figure provides the results of *chl-a* estimates derived from the satellite data. There is evidence of a reduction in the magnitude of the seasonal bloom between 2003 and 2009, though it remains to be known whether this reduction would persist into the future. Preliminary investigations (through collaborations with Sokolov and Rintoul, pers. comm.) into whether the patterns observed in the timing and magnitude of the bloom were linked with the position of the middle branch of the SAF as identified by Sokolov and Rintoul (2009), showed no relationship. Despite being unable to relate the occurrence and magnitude of the blooms to the position of the SAF, the data from the remote sensing does indicate a premise on which to hypothesize that the reduction in magnitude of the

spring bloom may be a realized phenomenon and exploration of such a hypothesis could provide useful insights into the system.

In terms of the open ocean productivity in the region, there are a number of scenarios which may be considered. Increased productivity associated with frontal features is well documented and many top predators (e.g. seals, penguins and albatross species) visit the frontal features to feed. The migration south of such features due to global climate change may have an effect on these populations. A southward shift of the Antarctic Polar Front (APF) due to warming may take this highly productive front out of foraging range of these species, effectively reducing the open ocean productivity associated with this feature. Relatively minor shifts in frontal features can have lasting impacts as many of the centrally placed foragers that are island based during their breeding cycle are restricted in the distance they can travel from shore when their offspring are young. Extension of trip duration to reach productive zones can increase the energetic costs of foraging and increase time away from the young, which can both negatively affect breeding success. The scenario of reduced reproductive success for the King penguins due to the southward migration of the APF (Kooyman 2002) was realized, as illustrated by Guinet et al. (1997) where the population at Crozet was unable to forage at the APF as it became out of range when it moved further south with the season. This particularly affected breeding birds with newly hatched chicks that were limited in the amount of time that they could spend at sea (Guinet et al. 1997).

On the other hand, elevated productivity associated with eddies generated both upstream and downstream of the islands has been observed and could provide additional foraging areas for the top predators (Ansorge and Lutjeharms 2002; Ansorge and Lutjeharms 2003; Ansorge et al. 2004). An increase or decline in the rate at which such features are generated in the vicinity of the islands, the longevity and path that such eddies travel, and their proximity to the islands, would all potentially play a role in affecting the productivity in the region. Evidence that this particular region of the Southern Ocean is experiencing a decline in open water productivity has been shown by Vantrepotte and Melin (2011) who have identified it as a region which has experienced a significant declining trend over the decade between 1997 and 2007.

Finally, visual evidence from satellite imagery of the islands (Google Earth 2013) shows an extension of the kelp beds in the vicinity of the islands that exceeds the distribution of the kelp forests when compared to illustrated maps from the 1980s (Attword et al. 1991, See Figure 4.2). A change, whether positive or negative on the open ocean productivity would have an effect on the ecosystem.

Considering these various points raised here, the aim of this work was to produce forecasting scenarios of the marine ecosystem behaviour under the potential effects of climate change by driving the system through changes (both positive and negative) on the primary producers to investigate ecosystem effects of such drivers.

9.2. Method

Dynamic temporal model (Ecosim)

The model is described in the previous chapter, Chapter 8. Please refer to section 8.2.

Forcing functions

Two simple forcing functions (F1 and F2) were defined to drive the PEI ecosystem model that represents the 2000s time period. Both were defined as linear functions. F1 increased from zero to 1 over a 100 year period, while F2 decreased from 1 to zero over a 100 year period. The Ecopath model representing the 2000s time period was used as the starting point for the simulations. The simulations therefore began in 2000 and ended in 2099. These two functions were applied to act on each of the four primary producers (see Christensen et al. 2008, pg 45) for individual simulation runs which resulted in 8 different scenarios (S1-S8, see Table 9.1). Model outputs of biomass changes for each functional group were created and percent changes for each functional group as compared to their starting biomass for each scenario were summarised.

9.3. Results

Plots showing the changes in biomass (t) for each functional group for each of the 8 climate change scenarios (S1-S8) are presented in Figures 9.2 to 9.9. The response of each functional

group in terms of its minimum and maximum change in the biomass for each group (as compared to its starting biomass) resulting from the forcing function are provided in Table 9.2.

Scenario 1: Increasing *Island Associated Blooms*

Using the F1 function to drive the system with a gradual increase in *Island Associated Blooms* (PIA), resulted in this production increasing by three fold by the end of the 100 year simulation. This increase had a limited effect on the ecosystem as a whole. The only other producer affected was the *Macrophytes* which declined by 3%. All other deleterious effects were less than 3%. The greatest effect overall was on the *Benthos* group which increased by 18 % from its starting biomass. Other groups that were affected more than 3% from their starting biomass were the *Gentoo Penguins* (4%), *Sharks and Rays* (8%); *Large Demersal Fish* (4%); *Small Continental Slope Demersal Fish* (6%), *Small Inshore Demersal Fish* (6%). Almost all patterns were linear or unidirectional, except the *Dark-mantled Sooty Albatross*, which showed a sigmoidal pattern in changes of biomass estimates through time, the magnitude of which, however, was inconsequential.

Scenario 2: Decreasing *Island Associated Blooms*

The F2 function was used to drive the system with a decline in the *Island Associated Blooms* (PIA), resulting in effectively no biomass of this producer by 2060. A similar set of functional groups were adversely affected by this driver as were positively affected by F1 on the same producer. The *Benthos* functional group decreased the most (-9%), followed by the *Sharks and Rays* (-4.3%), the two small demersal fish groups (-3%) (*Small Continental Slope Demersal Fish* and *Small Inshore Demersal Fish*) and the *Gentoo Penguins* (-2%).

Scenario 3: Increasing *Open Ocean Large Phytoplankton*

Using the F1 function which generates a gradual increase in *Open Ocean Large Phytoplankton* (POL), by the end of the 100 year simulation this group had doubled. Overall, this created large, generally linear responses for almost all groups (31 out of the possible 34 living groups). Those that were negatively affected were the other primary producer groups: the small fraction of the open ocean production was reduced by 10% as compared to its starting biomass, the PIAs by

16% and the *Macrophytes* by 19%. Positive responses were of a high magnitude with maximum values reached by the end of the simulation. The *Benthos* group showed the greatest response to this input with an increase (as compared to its starting biomass) of 90%. Many groups associated with the benthic system showed strong positive responses, including the *Sharks and Rays* (69%), the *Gentoo Penguins* (56%), *Benthic Decapod* (49%) and the demersal fish groups (*Large Demersal Fish* (47%), *Large Nototheniid Fish* (22%), *Small Continental Slope Demersal Fish* (46%) and *Small Inshore Demersal Fish* (54%)). All the remaining large top predators also benefited in terms of increasing biomass from this production, with biomasses increasing between 20 and 45% (*Orcas* (44%), *Southern Elephant Seals* (37%), *Antarctic Fur Seals* and *Subantarctic Fur Seals* (27%), *King Penguins* (22%), *Macaroni Penguins* (36%), *Rockhoppers* (38%) and *Giant Petrels* (33%)). All albatross groups showed positive responses (*Grey-headed Albatross* (29%), *Wandering Albatross* (25%), *Indian Yellow-nosed* (19%), *Light-mantled Sooty* (15%), *Dark-mantled Sooty* (16%)) as did the smaller *Prions and Petrels* (19%). The pelagic fish (*Large Pelagic Fish* (40%), *Patagonian Toothfish* (23%), *Small Pelagics* (31%) and *Myctophid Fish* (24%)) all had positive responses as did all nekton and plankton groups (*Large Cephalopods* (32%), *Large Zooplankton Crustaceans* (39%), *Small Zooplankton Crustaceans* (5%), *All Other Zooplankton* (22%), *Small Cephalopods* (13%)).

Scenario 4: Decreasing *Open Ocean Large Phytoplankton*

Using the F2 function generated a gradual decrease in *Open Ocean Large Phytoplankton* (POL) and by the end of the 100 year simulation the POL group had decreased to zero. This had limited positive effects on the other primary producers with *Open Ocean Small Phytoplankton* (POS) increasing by 6%, PIAs 18% and the *Macrophytes* by 15%. Negative effects were seen throughout the system. Those groups that were affected most by the increasing POL were conversely affected by the greatest magnitude in this simulation, with *Gentoo Penguins* (-25%), *Orcas* (-24%), *Large Demersal Fish* (-23%) and *Small Inshore Demersal Fish* (-23%) all showing negative responses. Most functional groups (17) registered negative responses of between 10 and 20% by the end of the simulation (Table 9.2). Those least affected (>-10%) were the two Sooty albatross species, the *Prions and Petrels*, *Large Nototheniid Fish*, the *Patagonian Toothfish*, *Small Cephalopods* and the *Small Zooplankton Crustaceans*.

Scenario 5: Increasing *Open Ocean Small Phytoplankton*

Using the F1 function which generates a gradual increase in *Open Ocean Small Phytoplankton* (POS), by the end of the 100 year simulation the group had doubled (increased by 105%). The other producers were all negatively affected with *Macrophytes* declining by 47%, PIAs 12% and POL by 2%. This simulation generated the largest response of all the 8 scenarios, with responses positive for all consumers and biomass estimates showing doubling or tripling of starting values for almost all groups. The group which showed the least response was the *Benthic Decapod* which increased by 23%.

Scenario 6: Decreasing *Open Ocean Small Phytoplankton*

The F2 function was used to generate a gradual decrease in *Open Ocean Small Phytoplankton* (POS) and by 2080 this group was reduced to close to zero. The responses seen through the community were non linear and with both positive and negative effects. Of the other producer groups, the *Macrophytes* were affected dramatically, showing an increase to over three times the original starting value. *Open Ocean Large Phytoplankton* biomass increased by a small amount (6%), while PIAs showed a minor decline (-21%) and then remained constant. The *Gentoo Penguins* initially declined, but ultimately doubled in biomass. Groups that showed a positive response included the *Benthic Decapod*, which also doubled in biomass through the simulation, reaching a plateau after 60 years and remaining at this level. Two of the demersal fish groups, the *Large Nototheniid Demersal Fish* (130%) and the *Small Inshore Demersal Fish* (54%), also showed positive trends. Other demersal fish groups showed mixed responses with declining biomass estimates initially followed by positive trends, resulting in biomass estimates similar to starting values (*Large Demersal Fish* 9%, *Small Continental Slope Demersal Fish* 4%). The *Benthos* group also showed an overall minor increase (11%).

All remaining groups were adversely affected by this change, with some being run down to extinction (*Macaroni Penguins*, *Large Pelagic Fish*, *Small Pelagic Fish*, *Large Cephalopods*, *Large Zooplankton Crustaceans*) or near extinction i.e. = or > -90% (*Southern Elephant Seals*, *Southern Rockhopper Penguins*, *Wandering Albatross*, *Grey-headed Albatross*, *Giant Petrels*, *Prions and Petrels*, *Patagonian Toothfish*, *Small Cephalopods*, *Small Zooplankton Crustaceans*).

All the remaining groups had declines of greater than 50% (*Orcas* -87%, *Antarctic Fur Seals* (-77%), *Subantarctic Fur Seals* (-74%), *King Penguins* (-71%), remaining 3 albatross (between -76 and -82%), *Sharks and Rays* (-72%), *Myctophid Fish* (-66%) and *All other Zooplankton* (-53%).

Scenario 7: Increasing *Macrophytes*

F1 was used to drive an increase in the *Macrophyte* (PMA) producers over a 100 year period. At the end of the simulation, the biomass of this group had increased to almost 3 times its starting biomass. In all but three cases, following an initial stabilizing period, the response was unidirectional, 20 of those increasing and the remaining 13 declining. For the three groups that had a mixed response (the *Macaroni Penguins*, *Dark-mantled Sooty Albatross* and *Patagonian Toothfish*), the magnitude was negligible. Those groups that showed the greatest positive response included the *Gentoo penguins*, *Large Notheniid Fish* and the *Benthic Decapod*, all of which experienced approximate doubling of their initial starting biomass estimates. All the demersal fish groups experienced positive gains (between 40 and 50% for the *Large Demersal Fish*, *Small Continental Slope Demersal Fish* and the *Small Inshore Demersal Fish*). *Sharks and Rays* also benefitted (increase of 16%) as well as the *Benthos* group (5%). The pelagic predators showed mixed responses with positive gains found for the *Orcas* (14%), *Southern Elephant Seals* (8%) and *Southern Rockhopper Penguins* (10%), while negative responses were observed for both fur seal groups (- 6 to - 7%), *King Penguins* (-4%) and *Giant Petrels* (-3%). The small pelagic fish also had mixed responses with the *Small Pelagics* experiencing a positive response (17%), while the *Myctophid Fish* declined by a small percentage (-3%).

Scenario 8: Decreasing *Macrophytes*

The F2 function was used to drive the system with a decline in the macrophytes, resulting in zero macrophyte biomass by 2067. Positive responses equal or greater than 3% from starting biomass estimates were limited to four groups (*Antarctic Fur Seals*, *Subantarctic Fur Seals*, *King Penguins* and *Giant Petrels*) with the greatest change only 5% (Table 9.3). Two groups showed mixed responses, depending on the time of the simulation (*Macaroni Penguins* and the *Prions and Petrels*), but both responses were inconsequential in terms of the magnitude of the changes.

Negative responses were greater in number and magnitude. The *Benthic Decapod* was affected the most at -68%. Of the top predators, the *Gentoo Penguins* showed the greatest response, (-53%) followed by the *Orcas* (-9%), *Southern Rockhopper Penguins* (-7%) and the *Southern Elephant Seals* (-5%). Of the fish groups, the demersals had the greatest negative impact (*Large Nototheniid Demersal Fish* -45%, *Small Inshore Demersal Fish* -29%, *Large Demersal Fish* -24%, *Small Continental Slope Demersal Fish* -23%). The *Sharks and Rays*, *Small Pelagic Fish*, and *Small Cephalopods* all had negative responses of approximately -10%.

9.4. Discussion

The simulation results represent a simplistic exploration of a variety of possible scenarios that may be experienced in the future at the Prince Edward Islands. It is unlikely that any one of these scenarios would function in isolation, and it is also unlikely that the changes will be driven in a linear fashion. None-the-less, the exercise offers the opportunity to examine the ecosystem response of such theoretical changes and to attempt to extract emerging properties.

In the scenarios that were driven using the forcing function to increase productivity, a doubling (in the case of the POS) or a tripling (for the remaining three producers) in the biomass of the primary producers was reached by the end of the 100 year simulations. As might be expected, some of the responses to the increased productivity were positive, particularly in the scenarios of the two open ocean phytoplankton groups where all consumers across the board showed positive responses. The increasing productivity of the PIAs also showed a positive effect, but it was limited to those groups associated with the benthic community, with the *Benthic Decapod* experiencing the greatest change (doubling), and the demersal fish community showing positive gains. Interestingly, in scenario 7 (S7), where the productivity of the *Macrophytes* was increased, a mixed response resulted. The benthic community responded in a positive manner as did a number of the top predators (e.g., *Orcas*, *Southern Elephant Seals*, *Gentoo Penguins*), while other pelagic predators showed declines (both fur seal groups and the *King Penguins*). Such patterns are interesting to observe as groups such as the fur seals, with their predominantly myctophid diet, would seem to be independent of changes in the macrophyte biomass, yet are predicted to be affected, even if only in a minor way, by such changes. The explanation for such responses can be seen through the indirect effects of the simulation. A decline in the

phytoplankton production (both large and small fractions) results from the increase in the *Macrophyte* group, which has a knock on effect on the crustacean zooplankton groups (both large and small) that both decline, which impacts the myctophids negatively. Therefore those groups that have myctophids as their primary diet are adversely affected, (e.g., fur seals and *King Penguins*) while those that have a benthic fish component to their diet, (e.g., *Orcas*, *Southern Elephant Seals*, *Gentoo Penguins*) are not.

Scenarios where declines in production were simulated also produced some unexpected results. While in some instances, for example the decline in production for the PIAs (S2) or the POL (S4), the results were as expected and decreases followed the decline in production, in the two remaining scenarios (S6 and S8) the results were mixed. Declining productivity of the POS group resulted in initial declines in the benthic associated community, but these were followed by recovery towards the end of the 100 year simulation. Those groups that may be considered truly pelagic were all severely negatively affected. Likewise, for the decline in the *Macrophyte* production (S8), the responses were mixed, with the fur seals responding positively along with the *King Penguins*, and yet other pelagic predator groups showed declines (*Orcas*, *Southern Elephant Seals*, *Southern Rockhopper Penguins*). The positive responses were linked to the increasing myctophid biomass, which tracked the elevated phytoplankton and zooplankton trends, while the declines were less straightforward to interpret. For the *Southern Elephant Seals* for instance, some prey groups increased (*Myctophid Fish*, *Large Cephalopods*, *Large Pelagics* and *Patagonian Toothfish*), while others declined (*Large Nototheniid Fish*, *Small Pelagic Fish* and *Small cephalopods*). For *Southern Rockhopper Penguins*, which have a high zooplankton contribution to the diet (75% crustacean zooplankton), the decline in population does not track the prey trends (which increase through the simulation) and competition between groups must therefore be responsible for the observed decline.

The key to understanding the differences in the responses to the declining productivity for each producer when assessed separately, as has been done in this study, can be found in the response of the remaining producers in each scenario. For both the PIAs and the PMA, the changes in the productivity result in no change in the biomass estimates of any of the other producers. In the case of the POL, an increase or decrease of this production results in an opposite response in the

Macrophyte group with a change of approximately $\pm 20\%$ from the starting biomass. The most dramatic effect on another producer, however, occurs when the POS is forced. An increase in this production results in a decrease of approximately 50% of the *Macrophyte* group, but a far greater response is seen when the POS is reduced. In this situation, the *Macrophytes* increase linearly until reaching a plateau at three times their original biomass and are the reason that the responses of the groups to this apparent declining productivity are mixed. Such a response to a simulation is not intuitive, and the results demonstrate why it is useful to construct such a model and consider seemingly trivial simulations.

Theoretical scenarios are all very well, but how do they relate to the data for the islands and the patterns summarised in earlier chapters? It might be a reasonable assumption to suppose that blooms at the islands have reduced in intensity (this study, Figure 9.1). Supporting evidence has recently been published with stable isotope signatures for the benthic community showing such a trend (Allen et al. 2013). The scenario for exploring this (S2) shows a limited effect. Two points of explanation can be considered. The first is an issue of scale when considering the benthic subsystem. This ecosystem model has been built at the scale of the EEZ and the core of the benthic system is on the shelf, an area that accounts for only 1% of the total model area (see Table 6.1). Secondly, this benthic subsystem has not been considered in an appropriate manner in the model – a shortcoming that should be addressed in future development of the model. Production that gets channeled through the all encompassing *Benthos* group is effectively lost (or at least the signal is dampened) because some possibly important components (filter feeders, versus deposit feeders for example) were not explicitly considered. Dividing the benthos group into a number of functional groups may benefit the model and may also do a better job of tracking the fate of the islands associated blooms by channeling this production through the appropriate consumer groups.

Regarding the open ocean productivity, there is evidence that productivity in general in the vicinity of the islands is declining (Vantrepotte and Melin 2011), along with anecdotal evidence that macrophytes may be increasing (see introduction, section 9.1). Scenario 6 (decreasing of POS) demonstrates that a decline in POS could result in the increasing macrophyte distribution and therefore these two effects are occurring simultaneously in S6. While the blooms appear to

have little effect at the scale of the EEZ, the declining POS and increasing macrophytes should be evident in the time series data available for the islands.

Declining POS predicts a decline in most top predators except for the *Gentoo Penguin* because of their association with the benthic community. In general, the demersal fish populations are not deleteriously affected, and some populations show some recovery towards the end of the simulation (e.g., the *King Penguins*) or at least stabilize without going extinct (e.g., all albatross species excepting the *Wandering albatross*). In general, the patterns observed here can be linked in many cases to the observed trends, in the absence of other well known direct drivers. For example, the declining of the *Southern Elephant Seals*, *Rockhopper Penguins*, *Macaroni Penguins*, have been observed at the islands. The Gentoo penguins have had a mixed history with declines followed by apparent recent recovery. A decline followed by a recovery is predicted by the simulation and it may be considered to be contributing to the observed pattern. In the case of the fur seals, clearly the projected declining trend, which results from this scenario is not the dominant driver for this group; other drivers (the historic exploitation) are not included here, and they alter the observed dynamics. The results of this simulation are also in contrast to observed changes in seabird populations at the islands, where the albatross species have been increasing and yet are predicted to show declines in this scenario.

9.5. Conclusions

Running simulations to forecast possible future climate change dynamics by applying simple theoretical forcing functions may be considered trivial, but an assessment of the resulting dynamics provides insight into the ecosystem that is not otherwise apparent, as the most powerful effects of climate change may be indirect (Allen et al. 2013). Modelling scenarios of climate change, even when limited to changes in the biomass of algal groups, is challenging but can be informative (e.g., Watson et al. 2013). Development of the temporally dynamic version of this model, where past known drivers and future potential climate change scenarios are developed together, would enable further discussion on the fate of the populations at the islands and guide management advice. The work presented here is put forward as an example of how the model can be used, and it is hoped that it generates interest in this modelling platform that will encourage future collaboration with both researchers and the management body of the PEIs.

Table 9.1. Matrix of climate change scenarios (S) from 1 through 8 with Forcing functions (F) 1 and 2 acting on each of the 4 primary producers at the Prince Edward Islands.

	Island Associated Blooms	Open Ocean Large Phytoplankton	Open Ocean Small Phytoplankton	Marcrophytes
F1	S1	S3	S5	S7
F2	S2	S4	S6	S8

Table 9.2. Estimates of the maximum and minimum % difference as compared to the starting biomass (t.km⁻²) for each functional group in the PEI marine ecosystem model for each forecasting scenario run (S1-S8).

	S1 (F1 on PIA)		S2 (F2 on PIA)		S3 (F1 on POL)		S4 (F2 on POL)		S5 (F1 on POS)		S6 (F2 on POS)		S7 (F1 on PMA)		S8 (F2 on PMA)	
	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min	Max	Min
Orcas	1	0	0	-1	44	0	0	-24	269	0	0	-87	14	0	0	-9
Southern Elephant Seals	1	0	0	0	37	0	0	-19	259	0	0	-98	8	0	0	-5
Antarctic Fur Seals	0	-1	1	0	27	0	0	-14	195	0	0	-77	0	-6	4	0
Sub-Antarctic Fur Seals	0	-1	1	0	27	0	0	-13	189	0	0	-74	0	-7	5	0
King Penguins	0	-1	0	0	22	0	0	-10	175	0	0	-71	0	-4	3	0
Macaroni Penguins	0	0	0	0	36	0	0	-17	227	0	0	-100	0	0	0	0
Southern Rockhopper Penguins	0	0	0	0	38	0	0	-18	196	0	0	-99	10	0	0	-7
Gentoo Penguins	4	0	0	-2	56	0	0	-25	148	0	117	-24	85	0	0	-53
Wandering Albatross	0	0	0	0	25	0	0	-13	226	0	0	-98	0	0	1	0
Grey-headed Albatross	1	0	0	0	29	0	0	-15	221	0	0	-91	2	0	0	-1
Indian Yellow-nosed Albatross	0	0	0	0	19	0	0	-11	159	0	0	-79	0	0	0	0
Light-mantled Sooty Albatross	0	0	0	0	15	0	0	-8	151	0	0	-76	0	0	0	0
Dark-mantled Sooty Albatross	0	0	0	0	16	0	0	-9	159	0	0	-82	0	0	0	0
Giant Petrels	0	0	0	0	33	0	0	-17	250	-1	1	-96	0	-3	3	0
Prions and Petrels	0	0	0	0	19	0	0	-9	196	0	0	-99	0	0	1	0
Sharks and Rays	7	0	0	-4	69	0	0	-36	235	0	0	-72	16	0	0	-9
Large Demersal Fish	4	0	0	-2	47	0	0	-23	177	0	9	-44	43	0	0	-24
Large Nototheniid Demersal Fish	2	0	0	-1	22	0	0	-8	90	0	130	-7	85	0	0	-45
Small Continental Slope Demersal Fish	6	0	0	-3	46	0	0	-22	149	0	4	-30	41	0	0	-23
Small Inshore Demersal Fish	6	0	0	-3	54	0	0	-23	110	0	54	-10	49	0	0	-29
Large Pelagic Fish	0	0	0	0	40	0	0	-19	239	0	0	-100	0	0	1	0
Patagonian Toothfish	0	-1	0	0	23	0	0	-9	206	0	0	-90	0	0	1	0
Small pelagic Fish	2	0	0	-1	31	0	0	-14	205	0	0	-100	17	0	0	-10
Myctophid Fish	0	0	0	0	24	0	0	-11	166	0	0	-66	0	-3	2	0
Large Cephalopods	0	0	0	0	32	0	0	-15	211	0	0	-100	0	-1	1	0
Small Cephalopods	0	0	0	0	13	0	0	-5	173	0	0	-96	1	0	0	-1
Benthos	18	0	0	-9	90	0	0	-45	98	0	11	-10	5	0	0	-2
Benthic Decapod	0	-2	2	0	49	0	0	-14	23	-3	120	-1	109	0	0	-68
Large Zooplankton Crustaceans	0	0	0	0	39	0	0	-19	170	0	0	-100	0	0	0	0
Small Zooplankton Crustaceans	0	0	0	0	6	0	0	-2	160	0	0	-98	0	0	0	0
All Other Zooplankton	0	0	0	0	22	0	0	-11	93	0	0	-53	0	0	0	0
Open Ocean Large Phytoplankton	0	0	0	0	195	0	0	-100	0	-2	6	0	0	0	0	0
Open Ocean Small Phytoplankton	0	0	0	0	0	-10	6	0	105	0	0	-100	0	0	0	0
Island Associated Blooms	187	0	0	-100	0	-16	18	0	0	-12	1	-21	0	0	0	-1
Macrophytes	0	-3	2	0	0	-19	15	0	0	-47	233	0	178	0	0	-100
Macrophyte Detritus	0	-5	3	0	0	-27	27	0	0	-51	175	0	161	0	0	-100
Detritus	0	0	0	0	68	0	0	-35	77	0	0	-55	0	0	0	0

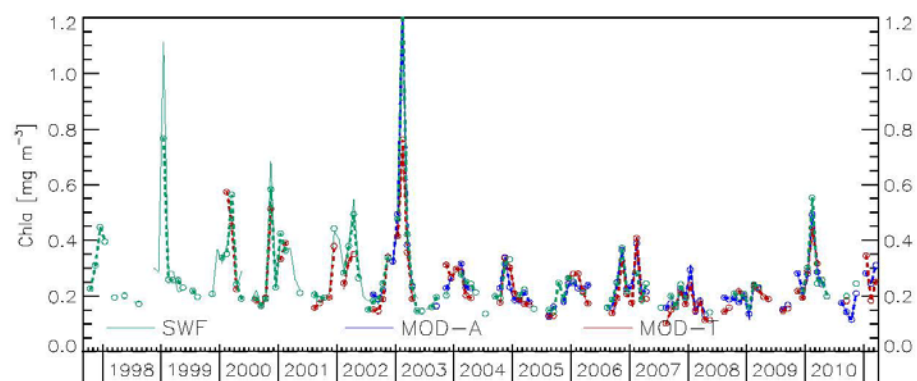
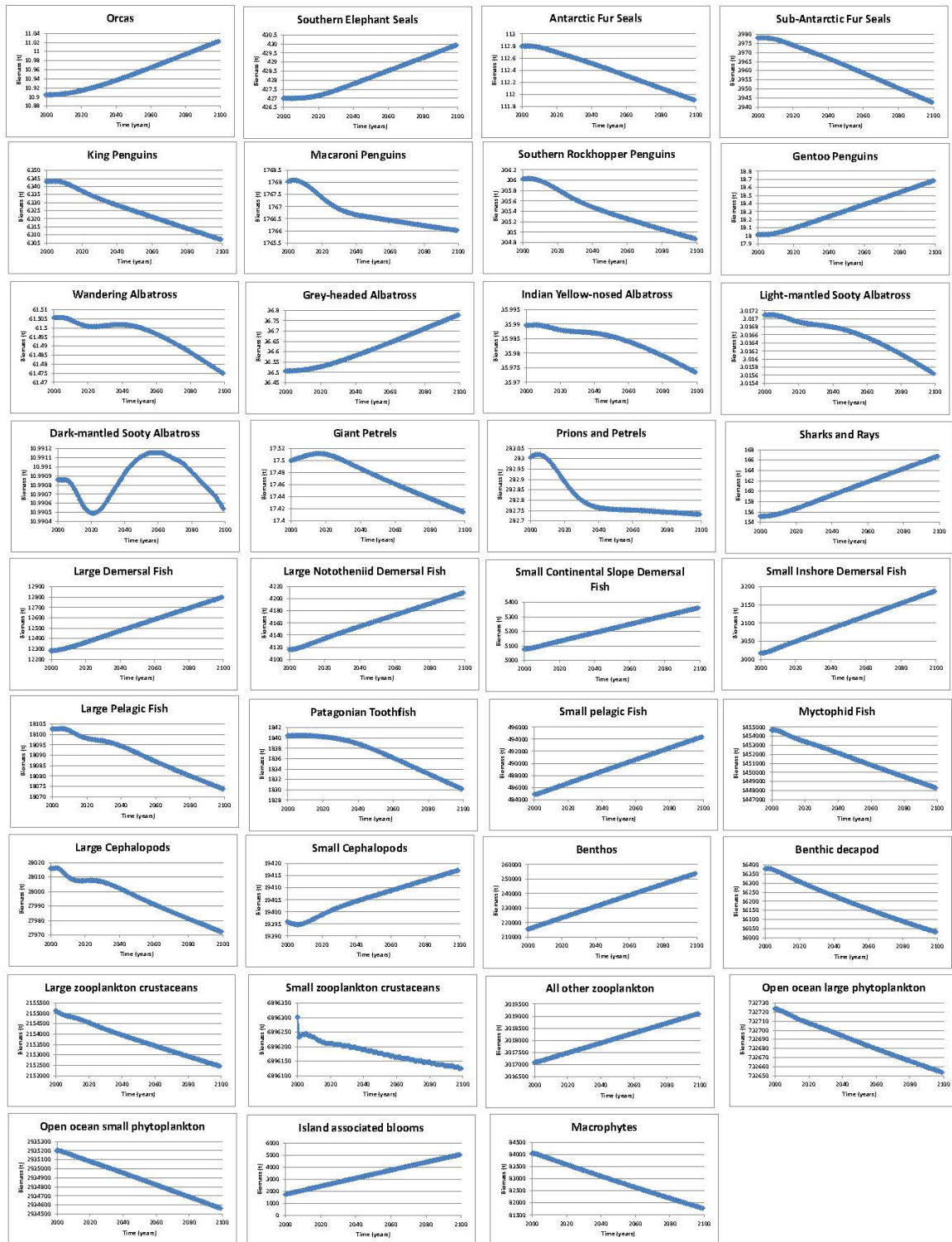


Figure 9.1. Plot of satellite derived *chlorophyll-a* values from 3 sensors (SeaWiFS, MODIS-Aqua, MODIS-Terra) from 1997 to 2010 centered on the Prince Edward Islands (see text).

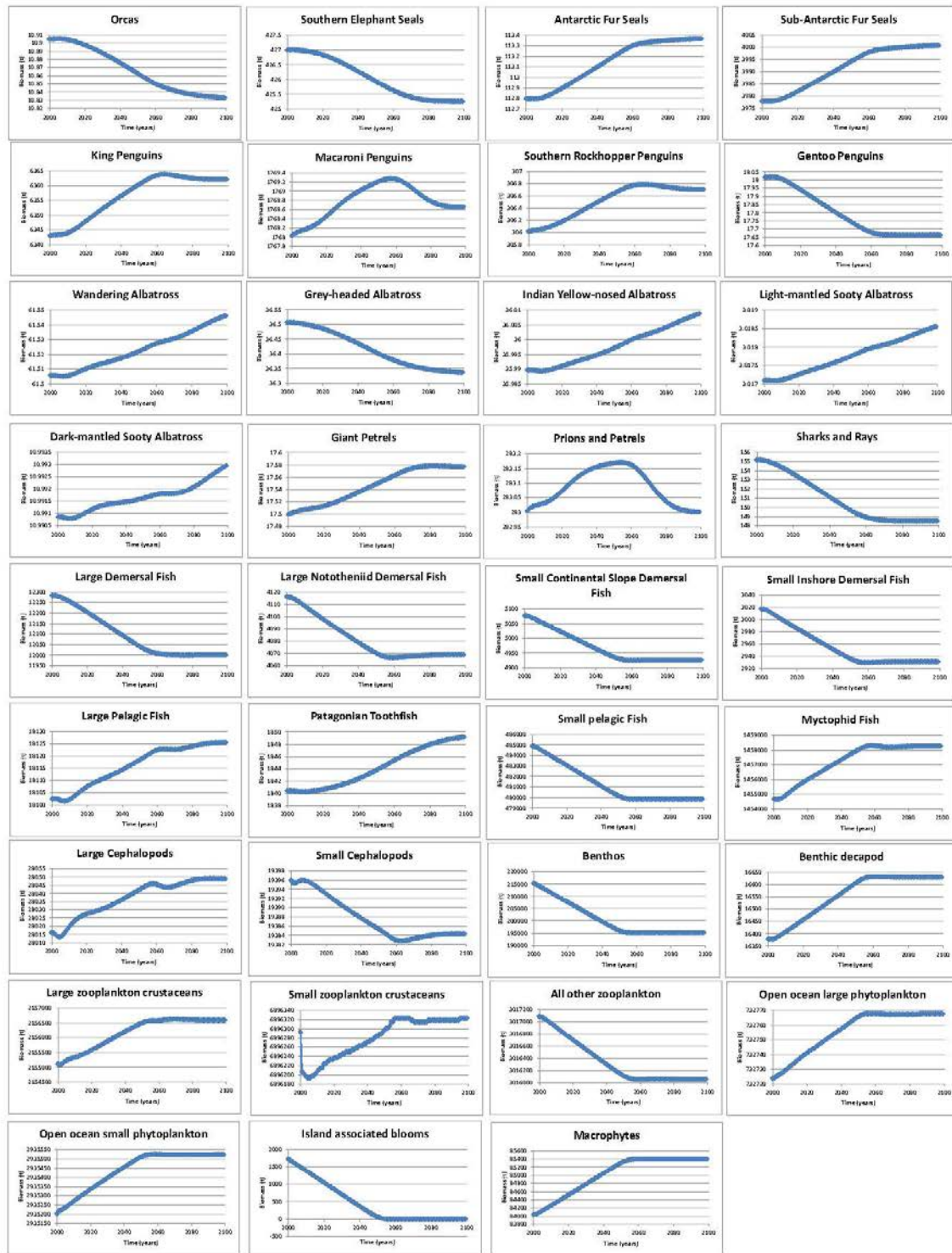
Biomass (t.km^{-2})



Time (years, 2000 - 2099)

Figure 9.2. Trends in biomass estimates (t.km^{-2}) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a positive effect on the PIA production term.

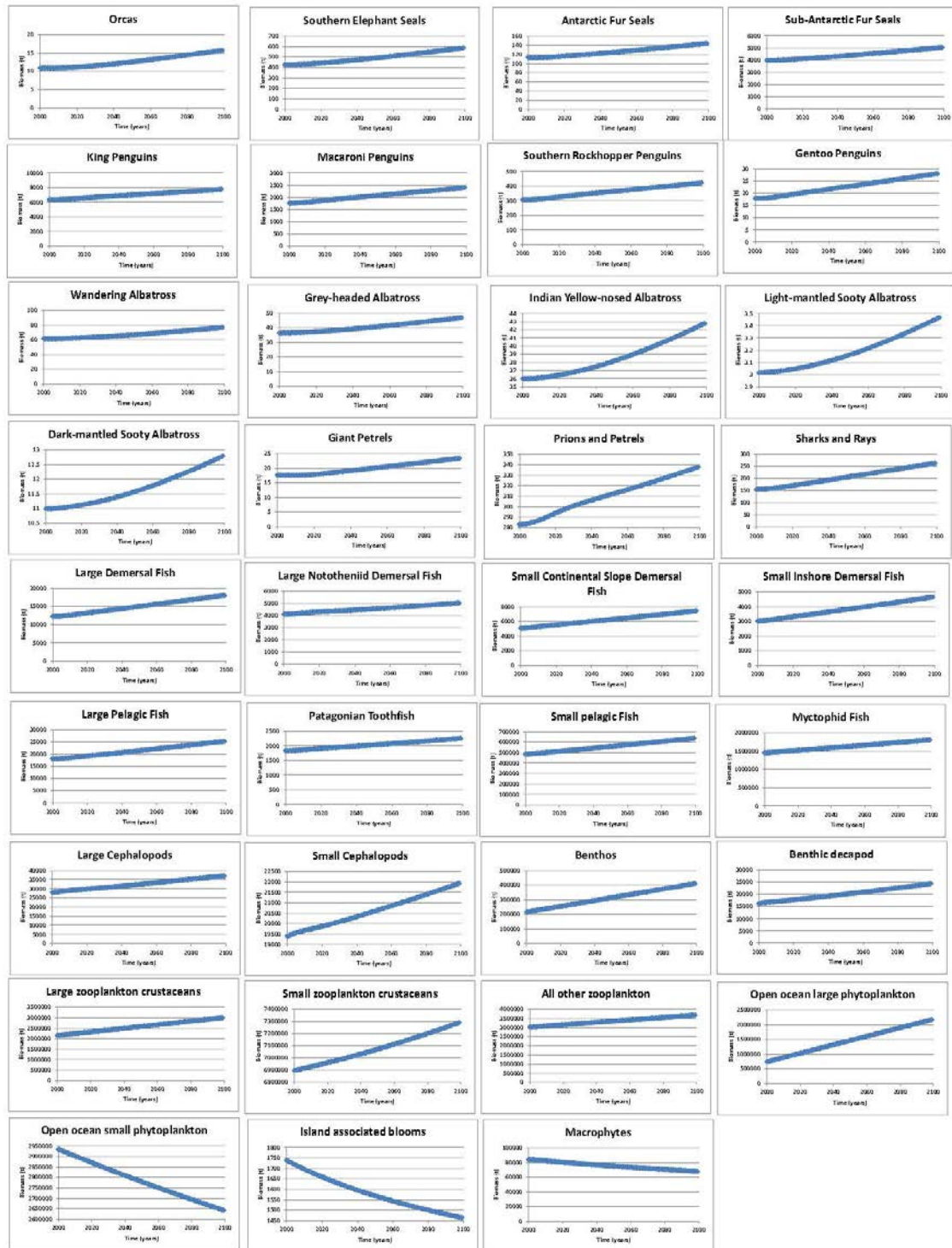
Biomass (t.km^{-2})



Time (years, 2000 - 2099)

Figure 9.3. Trends in biomass estimates (t.km^{-2}) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a negative effect on the PIA production term.

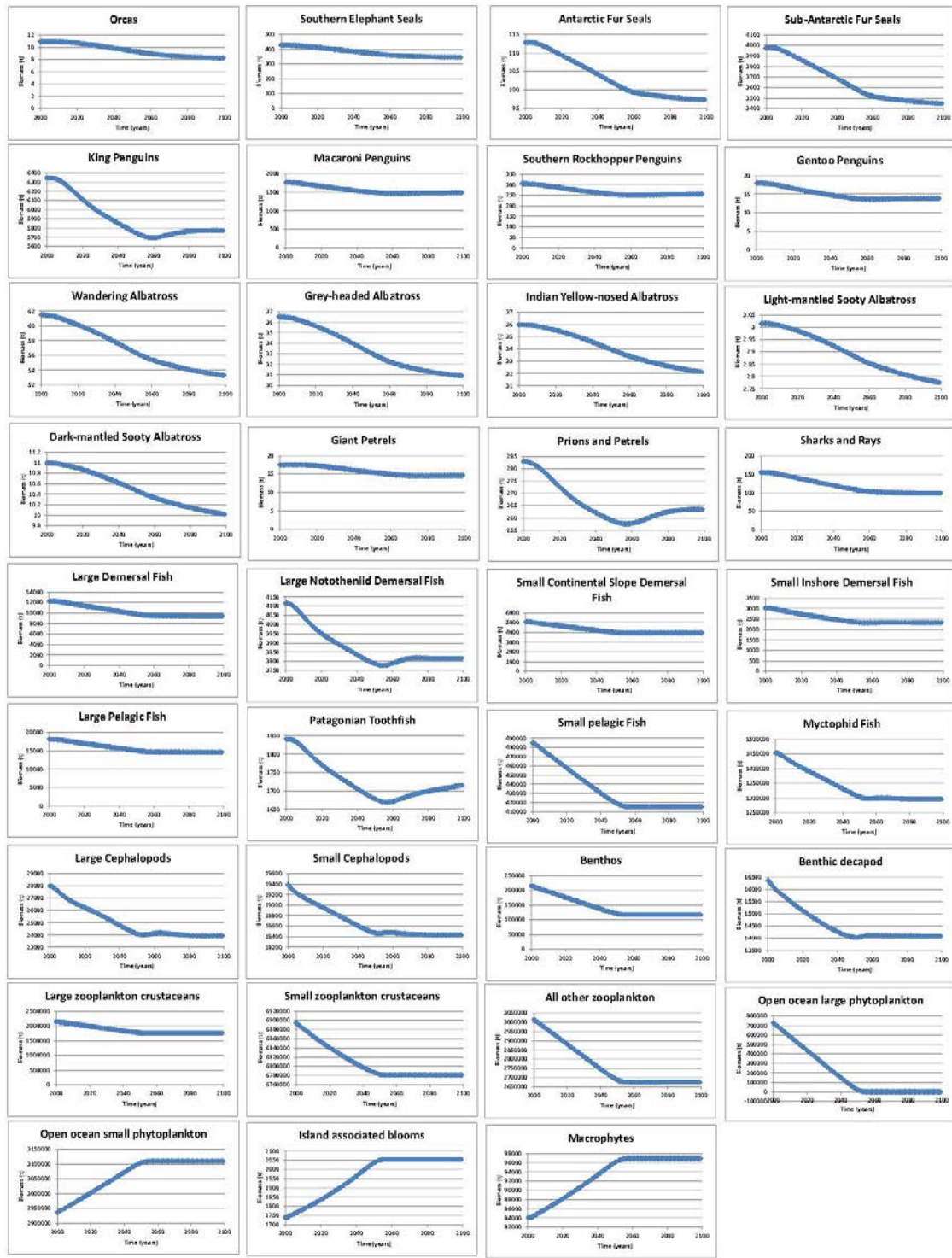
Biomass (t.km^{-2})



Time (years, 2000 - 2099)

Figure 9.4. Trends in biomass estimates (t.km^{-2}) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a positive effect on the POL production term.

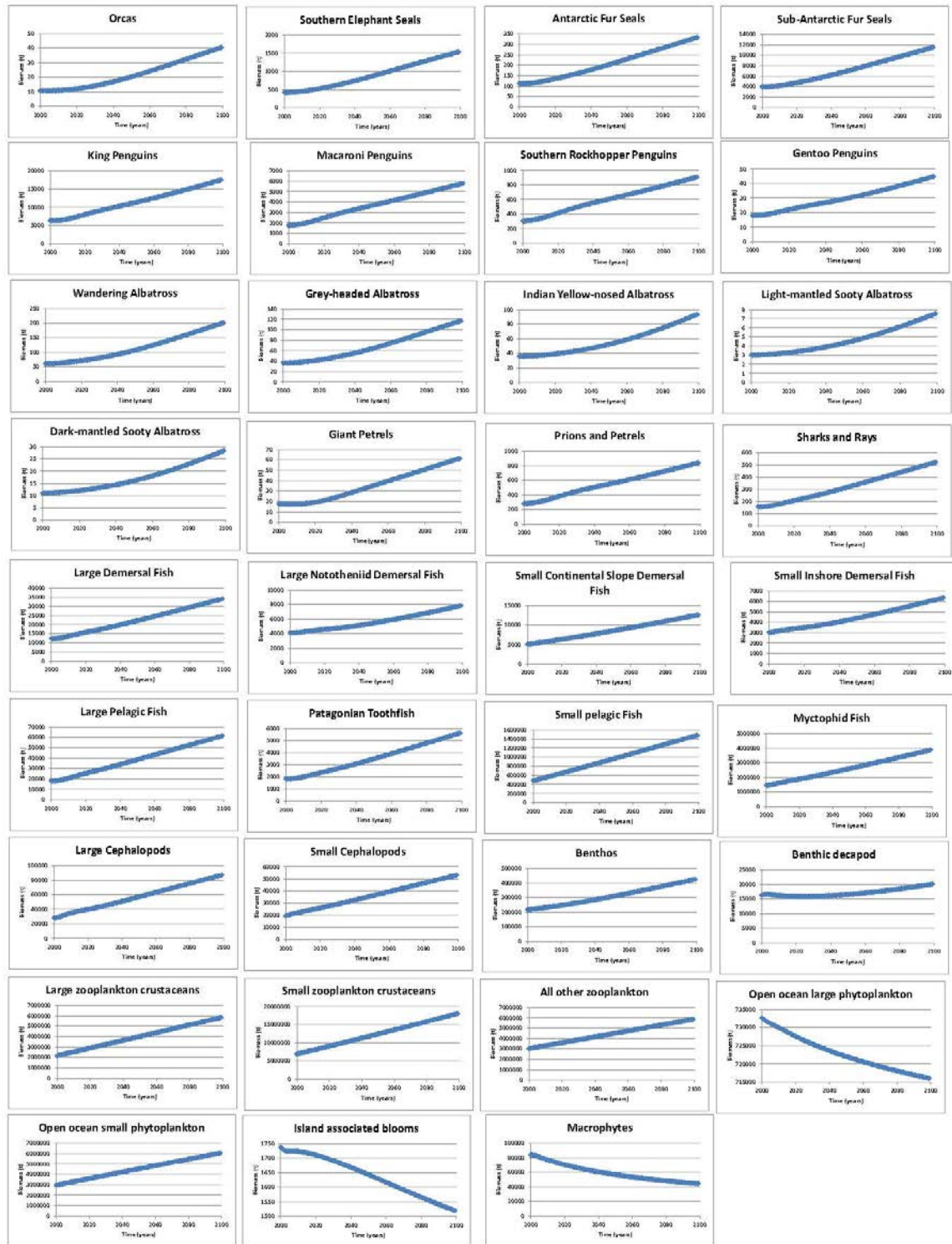
Biomass (t.km^{-2})



Time (years, 2000 - 2099)

Figure 9.5. Trends in biomass estimates (t.km^{-2}) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a negative effect on the POL production term.

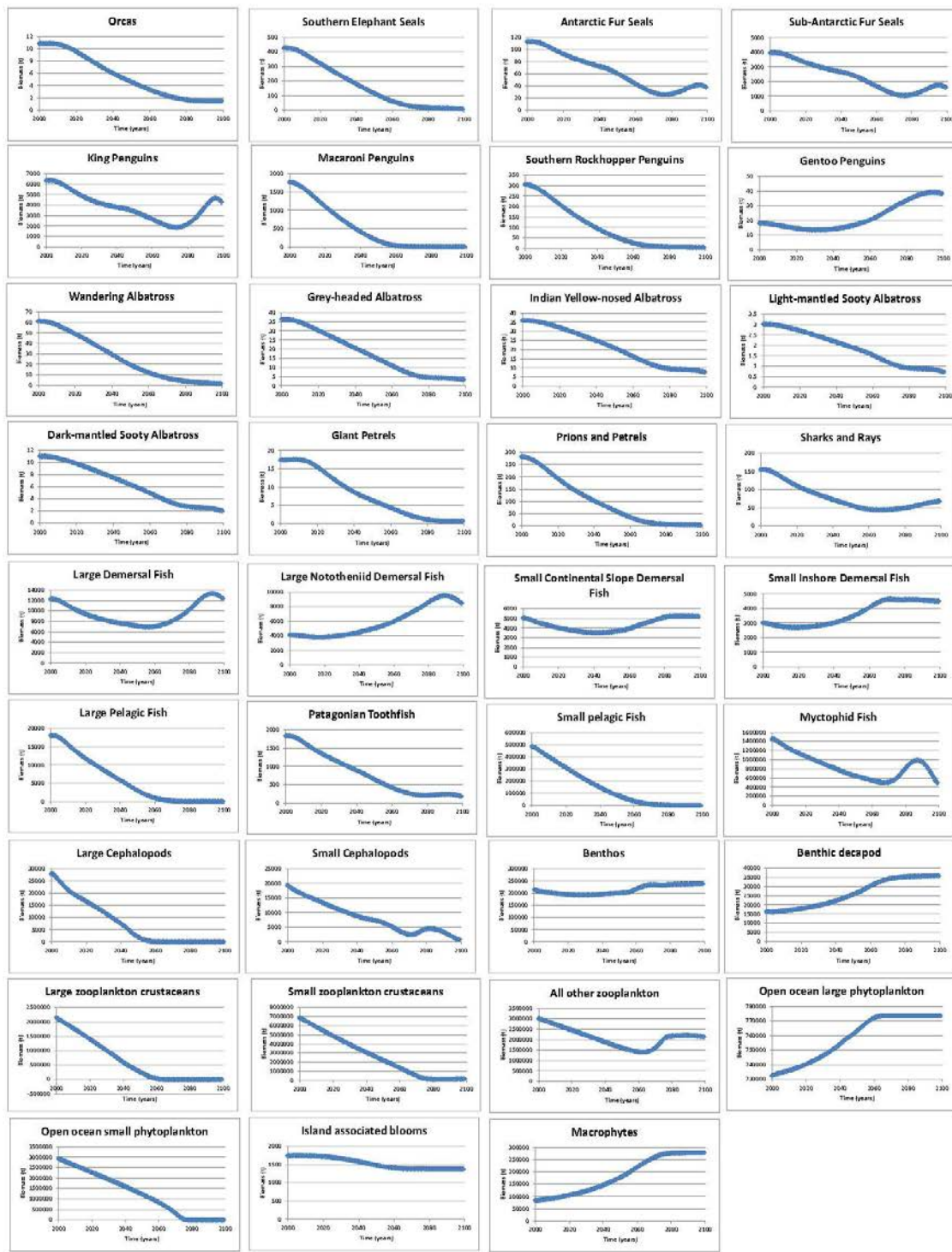
Biomass (t.km^{-2})



Time (years, 2000 - 2099)

Figure 9.6. Trends in biomass estimates (t.km^{-2}) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a positive effect on the POS production term.

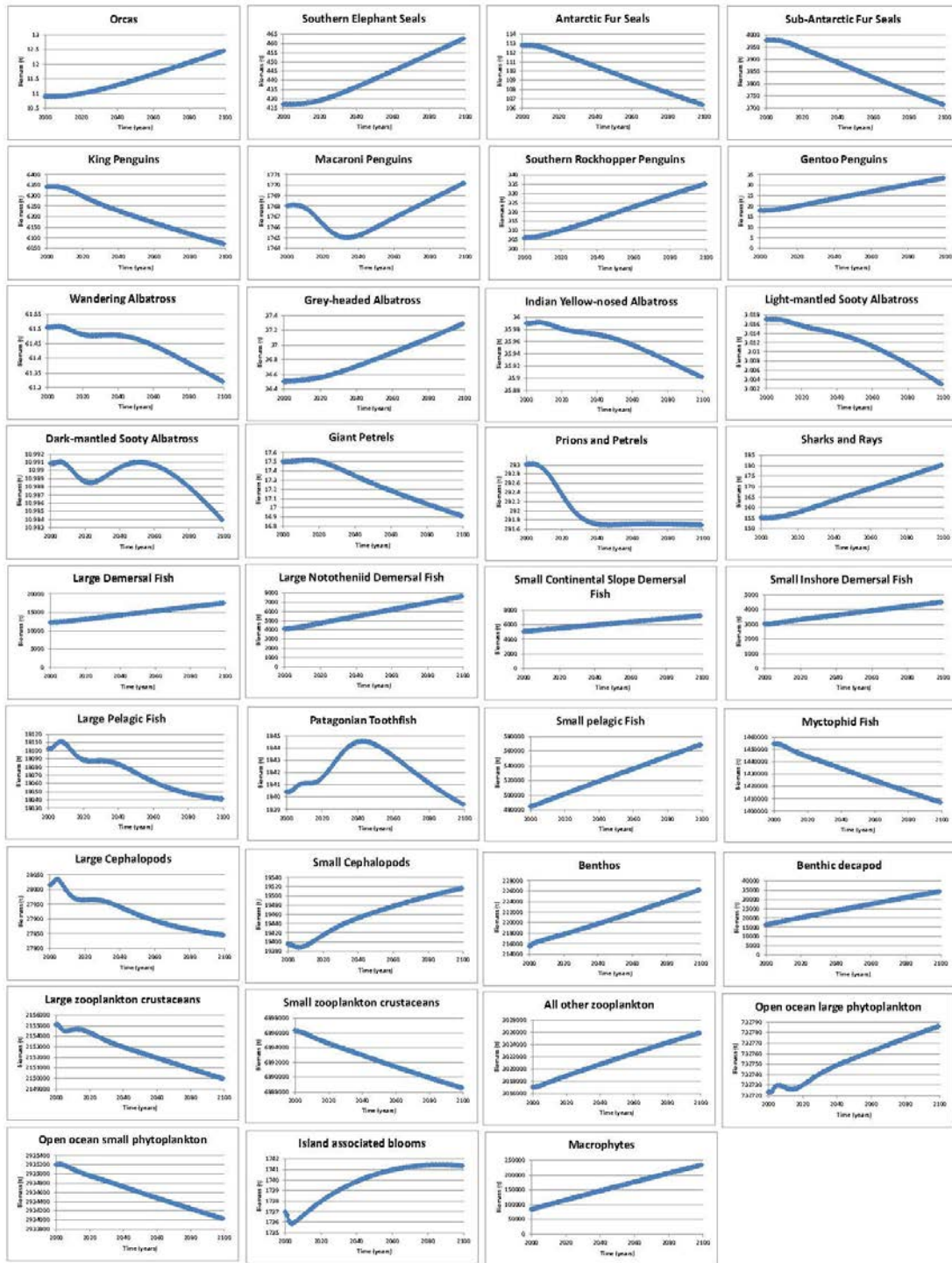
Biomass ($t.km^{-2}$)



Time (years, 2000 - 2099)

Figure 9.7. Trends in biomass estimates ($t.km^{-2}$) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a negative effect on the POS production term.

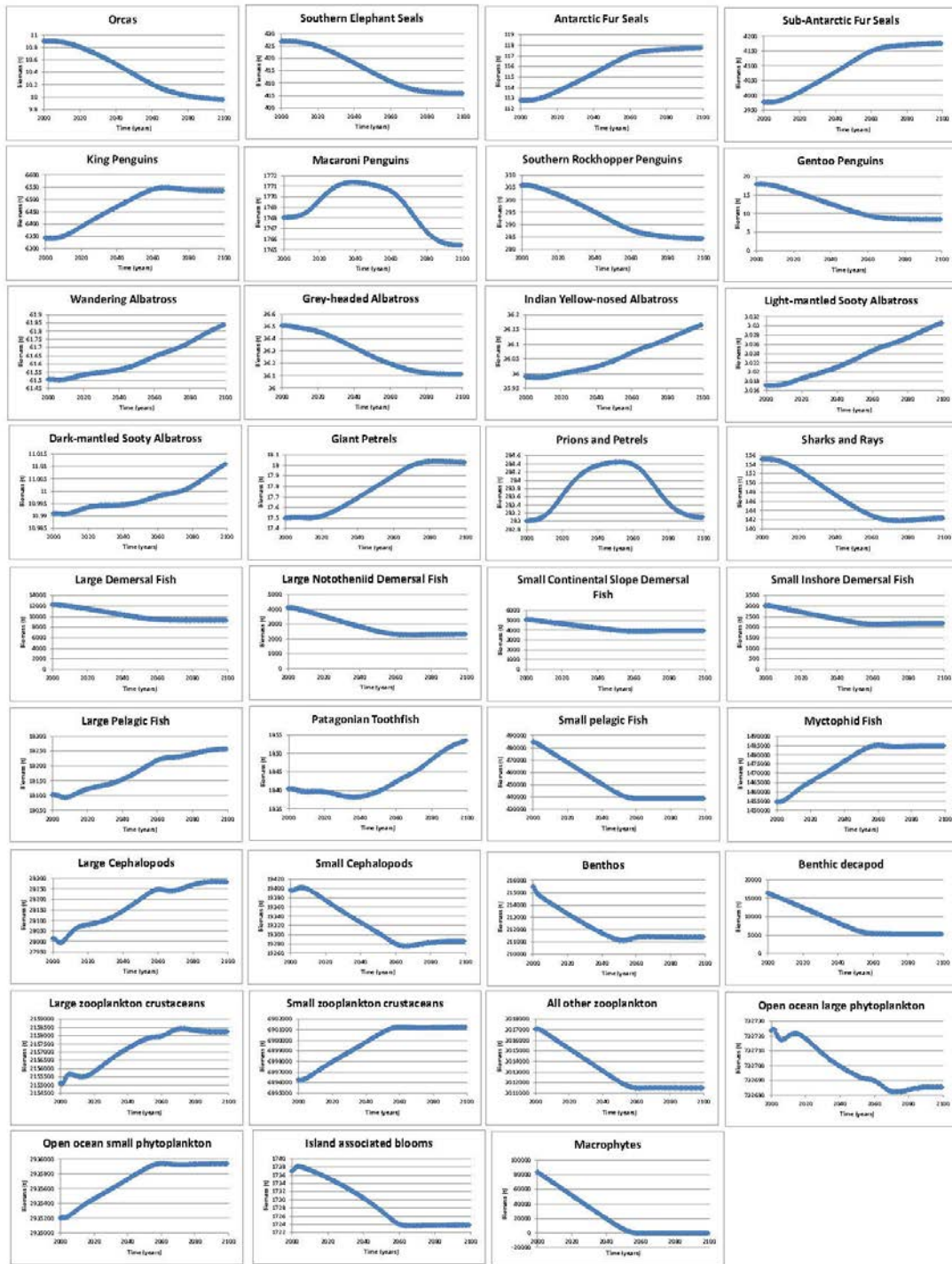
Biomass ($t.km^{-2}$)



Time (years, 2000 - 2099)

Figure 9.8. Trends in biomass estimates ($t.km^{-2}$) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a positive effect on the PMA production term.

Biomass (t.km⁻²)



Time (years, 2000 - 2099)

Figure 9.9. Trends in biomass estimates (t.km⁻²) from 2000-2099 for all functional groups of the PEI marine ecosystem following a linear forcing function created to produce a negative effect on the PMA production term.

Chapter 10 Conclusion

This work was intended to generate an ecosystem model for the Prince Edward Islands (PEIs) that could be used to inform an ecosystem approach to marine resource management. In the process a number of objectives were addressed and are highlighted here. The generation of the model identified data gaps, research priorities, and shortcomings of current research and recommendations for future research.

Findings

A transparent data collation process has brought together a variety of datasets for the Prince Edward Islands and formed the basis to construct a network mass balanced ecosystem model (using Ecopath). The food web of the marine component of the PEI ecosystem has been described in terms of biomass (Chapter 2) and consumption (Chapter 3). The model investigated the sources of productivity and their relative importance to the system at various spatial scales (Chapter 4), described the ecosystem across a range of time periods (1960s, 1980s, 2000s) (Chapter 5), and helped to assess the appropriate ecosystem boundary size (Chapter 6). Using the dynamic temporal simulation approach (Ecosim), the model was shown to be able to successfully hindcast three past ecosystem disturbance events (Chapter 8), and some potential effects of climate change were demonstrated (Chapter 9). The inclusion of energetic density of prey led to model improvements (Chapter 7) and suggested that this additional step is worth incorporating in consumption estimates for the parameterization of ecosystem models.

There appears to be a carrying capacity of land based top predators at the islands of approximately 10 500t ($\pm 1\ 000$ t) for the time periods assessed (1960, 1980s and 2000s). When this estimate was adjusted for the time each species spends at the islands, a progressive decline in biomass (t) was observed. In terms of consumption for the land based top predators, the dominant prey species shifted from a balance between crustaceans and myctophids to one dominated by myctophids, reflecting the changes in the community structure, and total consumption was estimated to be between 500 000t and 600 000t per year.

Generating static models of the ecosystem allowed some generalisations about the system to be drawn. The PEI ecosystem, in comparison to other subantarctic systems, is smaller in size in terms of its total biomass and most similar to the neighbouring Kerguelen Islands. For the shelf region of the archipelago, the autochthonous production (production generated by the islands) dominated, however, at all larger scales, the open water productivity (allochthonous production) was more important as has been suggested in past studies. The system is highly complex with the zooplankton and small pelagic fish supporting a diverse predatory fish population, and, along with other nekton groups (the cephalopods), the large avian and mammalian populations already mentioned. An investigation into the ecosystem boundary size was conducted, with all constituents able to satisfy their energetic requirements if considered at the scale of the EEZ.

Ecosystem indicators

One of the objectives of building an ecosystem model was for it to aid in developing ecosystem indicators that can be used for an ecosystem based approach to marine resource management. These include fisheries and conservation measures to provide new methods for setting management objectives and procedures. The challenge is to develop indicators that are informative in a managerial framework (both short and long term), and that are tractable and meaningful to all stakeholders (scientific community, industry and the public sector). In this context, the search for indicators that can be used for an ecosystem approach to fisheries (EAF) in particular has been ongoing since the 1990s. A number of efforts have been made towards making progress in this field. These include the SCOR/IOC Working Group (#119, Cury and Christensen 2005), which was set up to develop Quantitative Ecosystem Indicators for Fisheries Management and ran from 2001-2005. A suite of publications in the ICES Journal of Marine Science (2005; Volume 62) summarized these findings which included suggestions for management (Fulton et al. 2005; Garcia and Cochrane 2005; Jennings and Dulvy 2005; Link 2005; Shin et al. 2005; Walters et al. 2005), suites of indicators and the testing of such indicators (e.g. Cury et al. 2005; Fulton et al. 2005), which were done using a number of different models (including Atlantis, EwE and size-based models). Following this, the IndiSeas Working Group was established (Shin and Shannon 2010), a Eur-Oceans European Network of Excellence (NoE) initiative to develop synthetic indicators for cross system comparisons. The initiative ran from

2005 to 2010 and culminated in the suite of papers published in the ICES Journal of Marine Science (2010; Volume 67) and the launch of the website (www.indiseas.org). The final results of the working group are summarized in a selection of management papers (Jouffre et al. 2010; Shin et al. 2010a; Shin and Shannon 2010; Shin et al. 2010b), with demonstrations on how to use indicators to compare states and trends between ecosystems (Blanchard et al. 2010; Coll et al. 2010; Shannon et al. 2010; Bundy et al. 2010) and a paper relating ecosystem indicators to fishing and environmental drivers (Link et al. 2010).

In November 2010, IndiSeas spawned IndiSeas II, an initiative to continue the work of IndiSeas but to refine the fisheries related suite of indicators and to incorporate environmental, biodiversity and socio-economic elements into the indicators selected. I was fortunate to be invited to join IndiSeas II (following discussions with C. Piroddi, M. Coll and L. Shannon) and to add the PEI ecosystem to the set of ecosystems used for developing an expanded set of indicators. Participation in this working group allowed me the opportunity to be at the cutting edge of current developments (Shin et al. 2012). In order to add the PEI system to the initiative, I had to generate the ecosystem indicators. This involved producing the already established IndiSeas I fisheries indicators, and the initial IndiSeas II indicators, which included environmental, biodiversity and socio-economic indicators for the system (TGs 1, 2 and 3) to be tested. This process highlighted a number of shortcomings in the PEI model. IndiSeas I indicators (Shin et al. 2010) were intended to generate fisheries indicators and the majority of the eight indicators required fish survey data. As survey data is only available for one year at the PEIs, no time series data could be generated from this dataset and the summary set of indicators has many entries of 'no data' because of this shortfall (see <http://www.indiseas.org/ecosystems/prince-edward-islands>). This has severely hampered use of this system in the IndiSeas II initiative. The PEI system is rich in survey data for avian and mammalian groups, but is lacking in fish survey data. This has highlighted an area for future research to include the collection of survey data for the fish populations if this system is to be assessed using an EAF. In a more positive light, the validation of model-generated indicators tested against survey-based indicators currently under development through IndiSeas II for ecological indicators (TG2 - L. Shannon, M. Coll and collaborators), which includes both fishery

and biodiversity indicators, means that in the future indicators generated by models, like this one, will be able to be used in the context of EAF.

Future research and development

Data

With respect to the highlighting of data gaps, the above example illustrates one that needs to be addressed in future research programs for the PEIs. The lack of survey data for the fish fauna was identified through the data gathering process for the ecosystem model. Along with continuing to collect survey data of the top predators in the system, a routine sampling program should be considered, not only for the large pelagic and demersal fish (the Nototheniids in particular) but also for the nekton groups (including the myctophids and cephalopods), which are key groups in the ecosystem, and for which routine survey data are completely lacking. In addition, a qualitative assessment of groups' importance identified the orcas, Southern elephant seals, Giant petrels, Gentoo and King penguins. A notable omission from such a list is the decapod shrimp, which has been identified as a key species in the island system. The large scale of the model (encompassing the EEZ) and the lack of resolution of the benthic subsystem are two possible reasons for this species not being identified as playing an important role. Reassessment of the scale of the model and the construction of a benthic sub-model (or better resolution of the benthos group into a number of functional groups) should be considered in future developments of the model.

Regarding the groups for which there are time series data, particularly the avian and mammalian groups, it would be valuable to have the researchers directly involved in the data collection to assess and validate the data preparation process. Upscaling from pup numbers or breeding populations to biomass estimates involves a series of steps and assumptions and best practices should be ensured. Improvements in parameterisations for diets and production rates for all groups would also be beneficial.

Model construction

Along with consulting experts for the data included in the model, an exercise such as the ‘Prebal’ recommended by Link (2010) should be conducted to highlight areas where issues of model structure and data quality can be assessed, providing a way to evaluate initial conditions of the model. Additionally, rigorous sensitivity testing of the model would also help to prioritise where future research efforts should be focussed. Funding of the Ecoranger capability to be incorporated into the EwE Version 6 would be of great benefit in this endeavour.

Collaboration efforts between those working on other subantarctic and Antarctic ecosystems could also improve model construction. Independent groups have worked in parallel on similar tasks and issues that are common to all the Antarctic research groups and initiatives such as ICED (Integrating Climate and Ecosystem Dynamics <http://www.iced.ac.uk/>), which is an international multidisciplinary programme that addresses the need to develop integrated circumpolar analyses of Southern Ocean climate and ecosystem dynamics, have an important role to play.

Model dynamics

In terms of the temporal model simulations, the model in its current form is capable of hindcasting simulations for past known drivers, with those groups that are directly affected following observed patterns found in the relevant survey data. The hindcasting exercise illustrated the knock on effects of a top down driven system with the ecosystem effects demonstrated.

Exploring forecasting of the potential future effects of climate change through simulations illustrated the changes in the system when driven from the bottom up. These were shown to be extensive, affecting almost all functional groups. A reduction in productivity for the phytoplankton groups (open ocean as well as island associated blooms) and associated increase in the macrophytes seems to be a plausible scenario considering the current literature and findings at the PEIs. However, not all groups follow the trends that are found in such scenarios and it becomes clear that no one driver is responsible for the overall patterns observed at the islands. Declines in the majority of the land based top predators would ensue from such a

scenario, but not all groups follow such a trend. Independent drivers such as the historic sealing on the fur seal populations need to be incorporated into the interpretation of such a system to help reach a scenario which can be considered appropriate. Combining known past drivers with future potential drivers to identify the appropriate suite of them at the right scale could be a fruitful way forward and should be the focus of future work with temporal simulations for this system.

Ultimately, the intention of creating an ecosystem model is not only to hindcast past events and explore forecasting scenarios (though the success or failure of such provides a measure of credibility), but also to provide a platform which allows us to test and assess the dynamics of a system as we understand it. An ecosystem model allows for ‘what-if’ scenarios to be explored and can help refine and redefine our understanding of the system. Counter-intuitive results can be informative as they result in further examining of the system, often opening up new avenues to be explored.

In addition to the exploration of alternative simulations with a combination of drivers, it would be valuable to consider incorporating the energetic density of the prey into the dynamic version of the Ecosim software. Prey switching occurs through the temporal simulation and such behaviour would result in the average energetic density of prey items changing, but in its current configuration, this was not accounted for. The development of a plug-in for the EwE program would enable the issue of prey quality to be incorporated into the dynamic version of the package and potentially make a meaningful step towards addressing the issue of prey quality in ecosystem models (Plaganyi and Butterworth 2004) for both the static and dynamic forms.

Spatial resolution

The creation of a spatially resolved ecosystem model for the PEIs would open the door for spatially resolved marine planning to complement existing management platforms such as the one developed by Lombard et al. (2007). The effectiveness of the newly ratified PEI MPA (April 2013) could be explored through spatially resolved dynamic simulations. In addition, spatially resolved datasets, including satellite derived primary production and regions identified as being important from satellite tracked avian and mammalian fauna could be used to further improve the

model, particularly for conservation efforts. Combining such information would aid in identifying Ecologically or Biologically Significant Areas (EBSAs), also termed IBAs (Important Bird Areas) (Croxall et al. 2012) or Areas of Ecological Significance (AES) (Hindell et al. 2011), which have become increasingly important in conservation efforts with the recognition that not only do the breeding sites need to be conserved, but marine regions of elevated productivity need also be included when considering protected areas. The development of a spatially resolved model would also allow recent developments in the EwE, software such as the capability of driving the model with spatially resolved primary production data (Steenbeek et al. 2013), to be used to enhance (improve) model performance.

Finally, in parallel with the further development of this model within the EwE framework, different modelling approaches should also be considered as suggested for best practices in ecological modelling (FAO 2008). The explicit presentation of the data preparation allows for full transparency and easy analysis and improvement of the existing database, which will hopefully ease the development of additional models to be used to address ecological issues at the islands. Interest in developing an ECOTRAN model (Steele and Ruzicka 2011) based on the output of this Ecopath model was initiated by Anne Treasure (Oceanography Department, University of Cape Town) and is currently under development. It is hoped that such collaboration efforts can be expanded and the development and use of ecosystem modelling for the PEIs becomes a standard tool in addition to existing options currently in use for the management for both fisheries and conservation efforts at the Prince Edward Islands.

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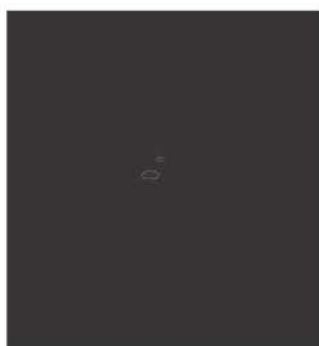
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Appendix 1.A. Remotely sensed satellite data of chlorophyll-a centered on the Prince Edward Islands.

Data retrieved at 1 km resolution over a six by six degree area centered over the islands (44°S to 50°S, and 35°E to 41°E) from SeaWiFS (1998 to 2004) and a two by two degree area (45.8°S to 47.8°S and 36.8°E to 38.8° E) from MODIS-Aqua (2005-2008). The following pages include one page per year with an image for each month. Absence of images means no data available for that month.



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March



April



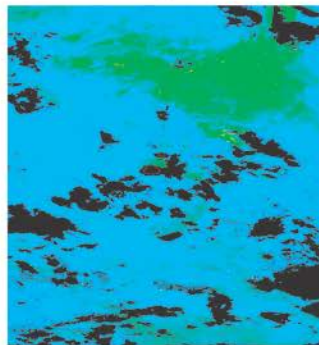
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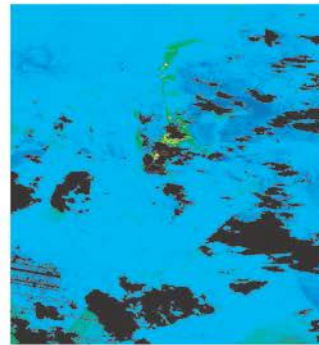
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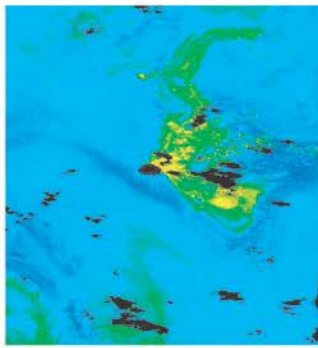
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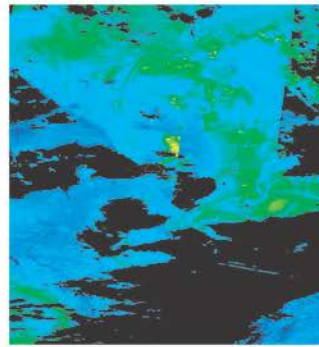
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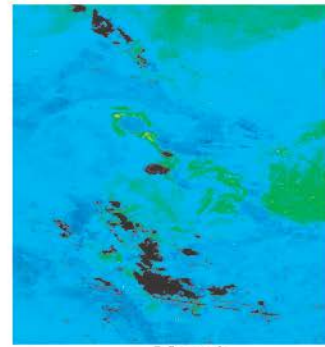
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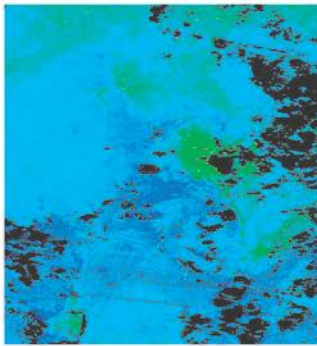
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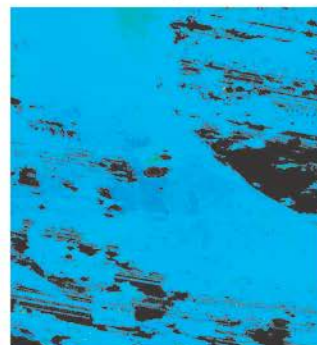
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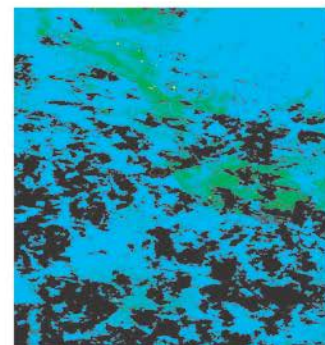
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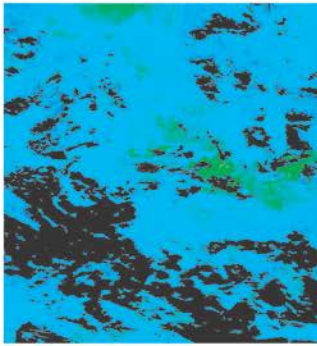
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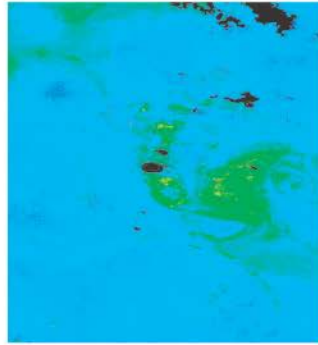
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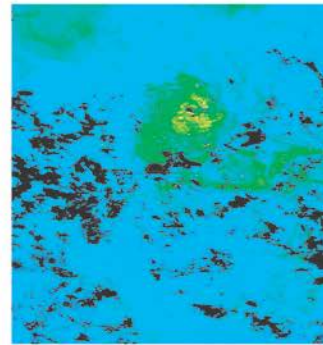
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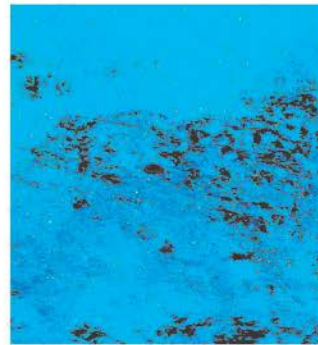
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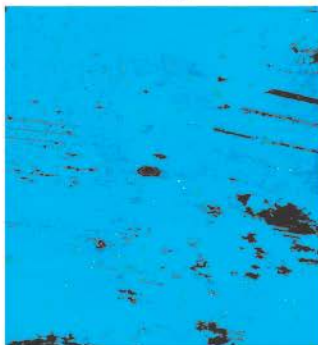
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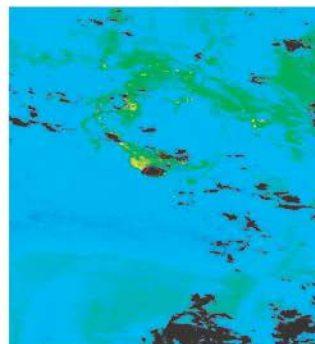
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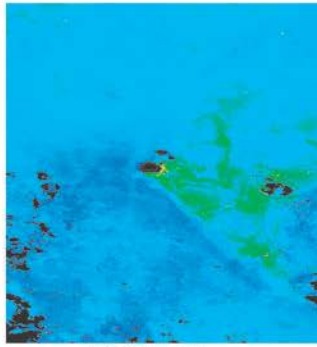
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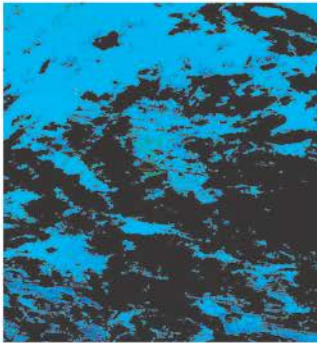
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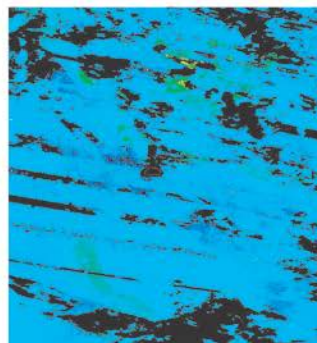
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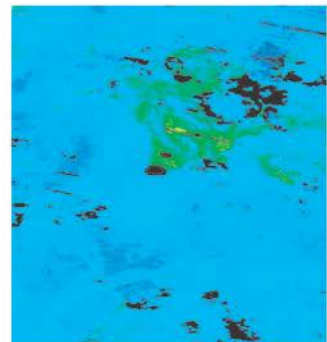
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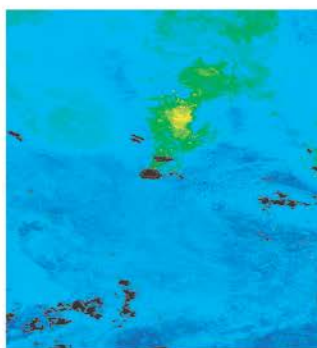


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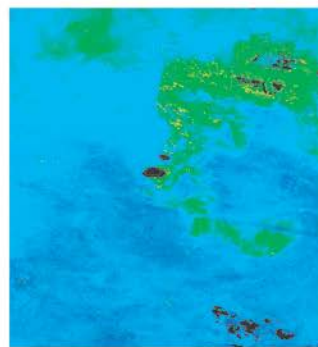
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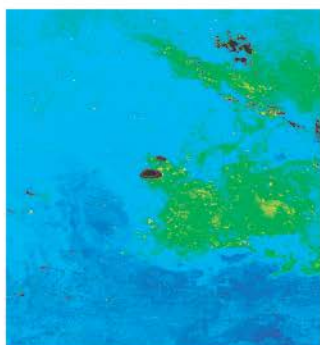
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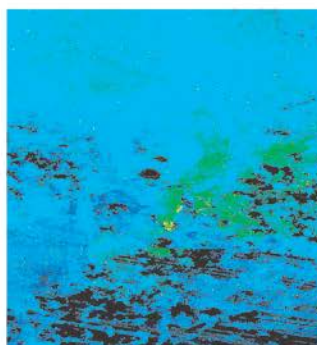
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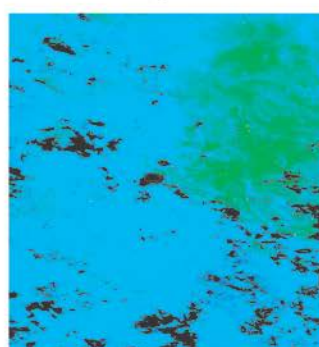
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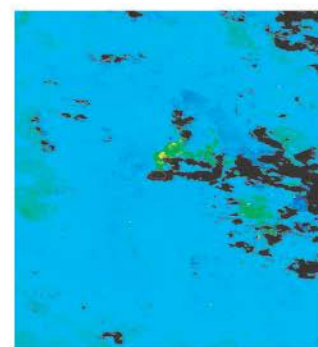
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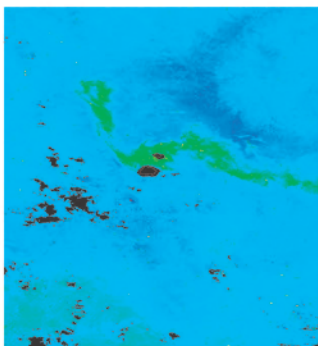


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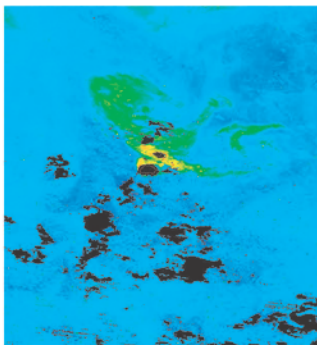


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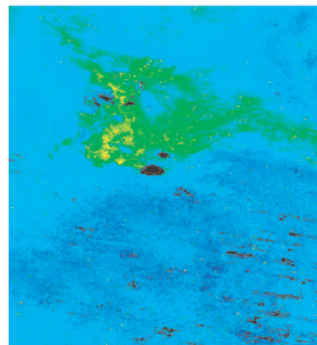
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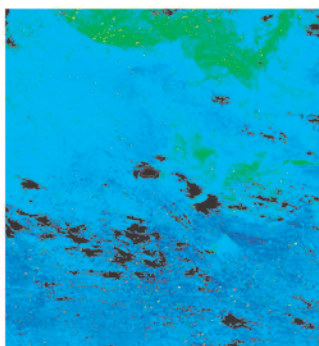
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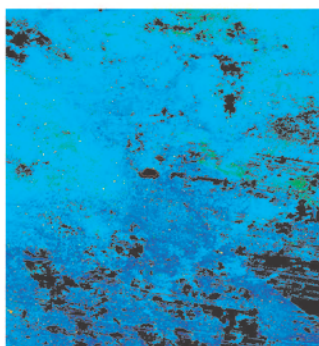
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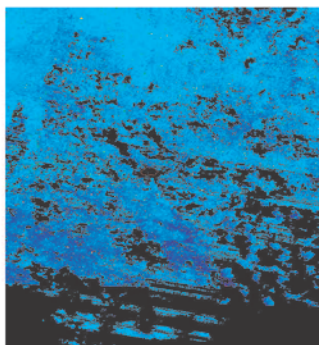
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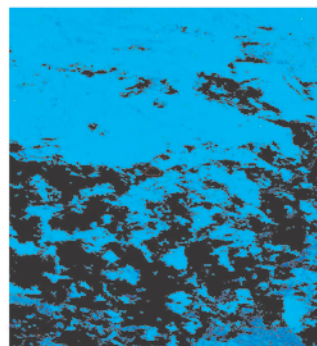
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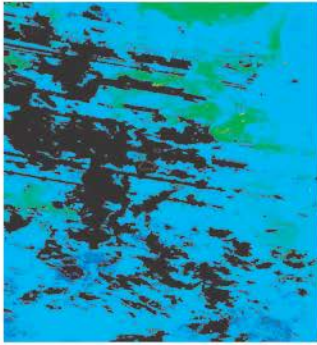
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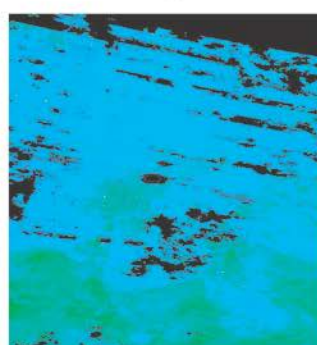
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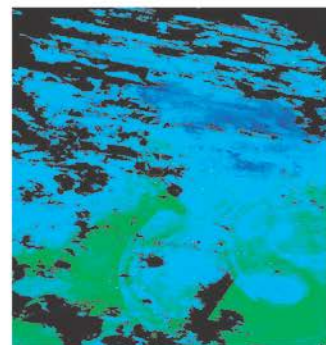
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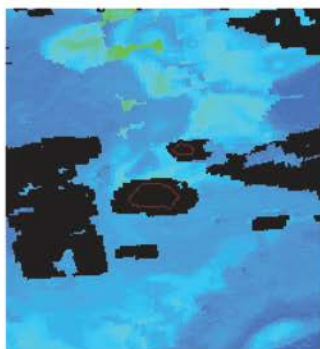


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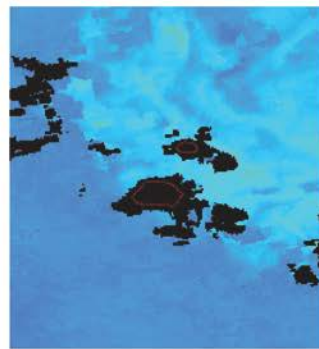
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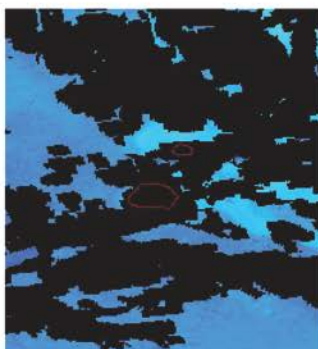
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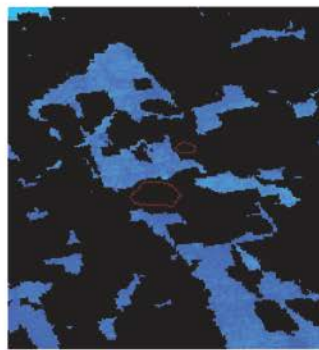
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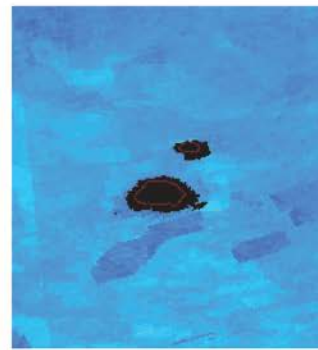
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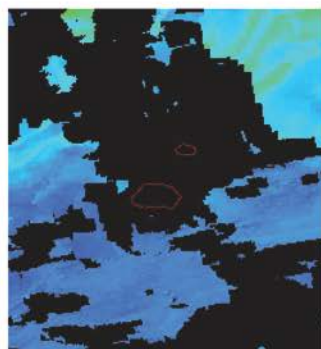
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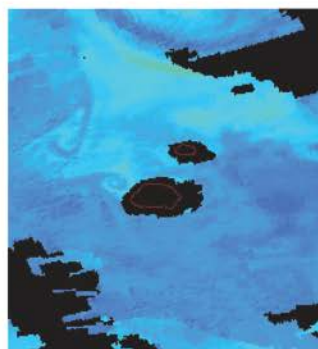
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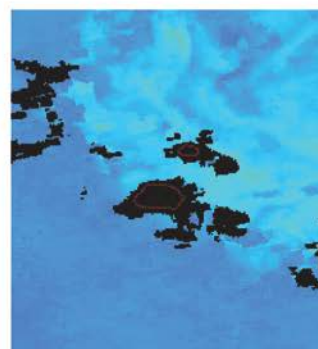
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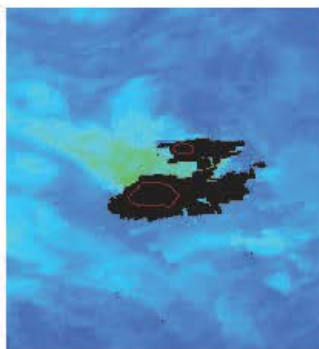
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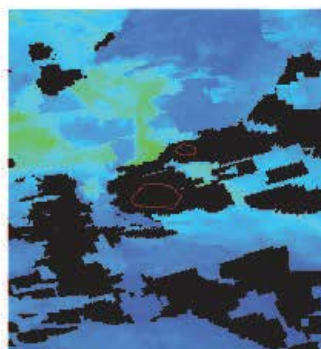
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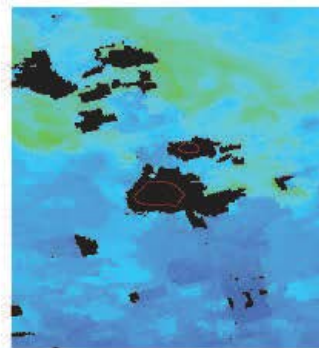
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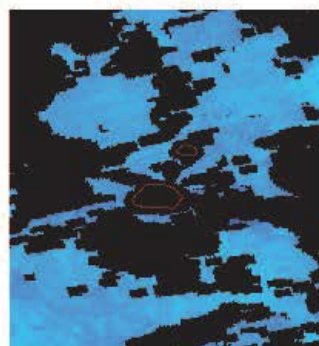
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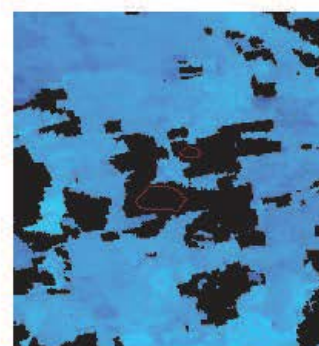
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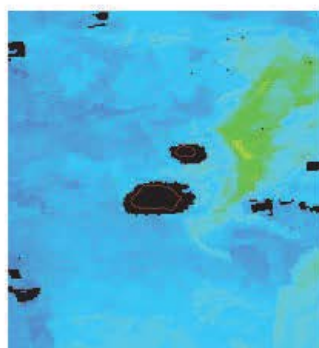
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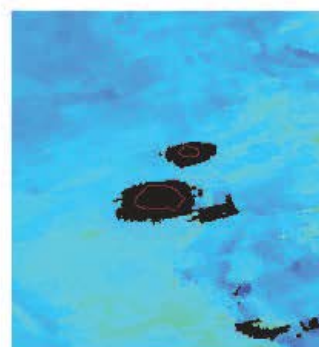
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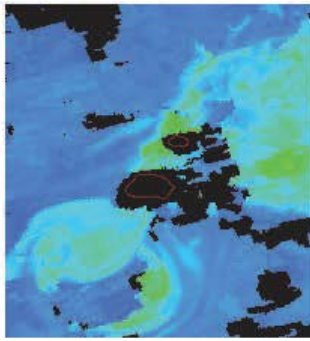
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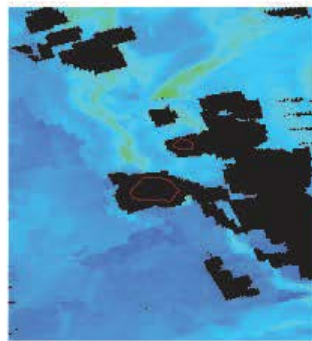
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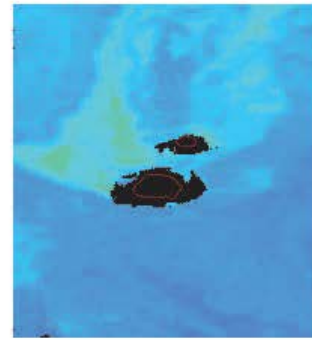
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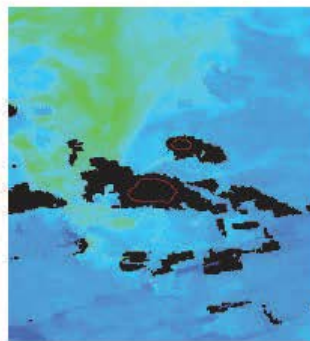
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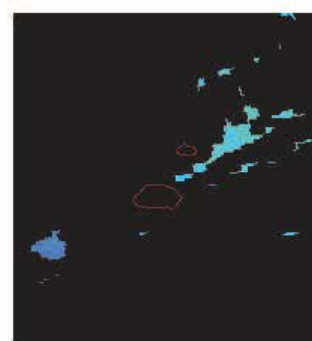
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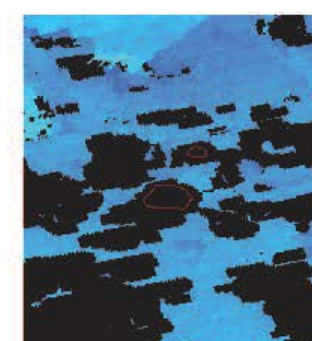
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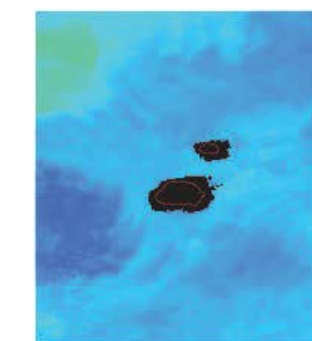
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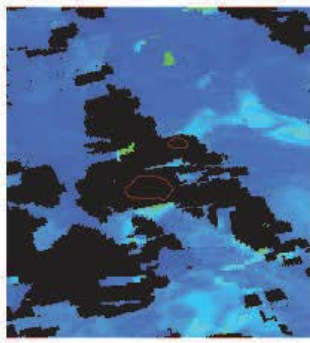
October



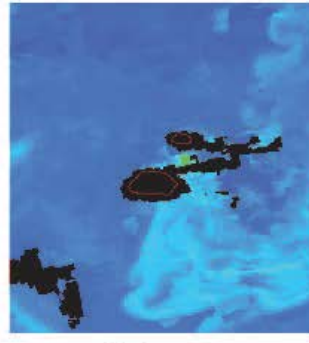
November



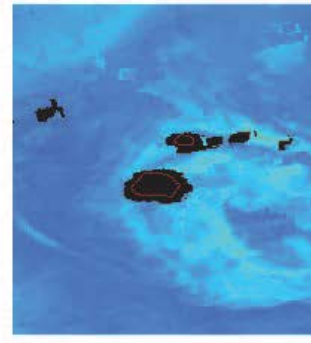
December 2007



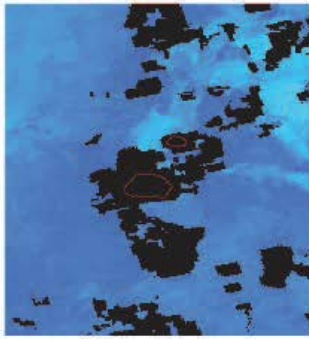
January



February



March



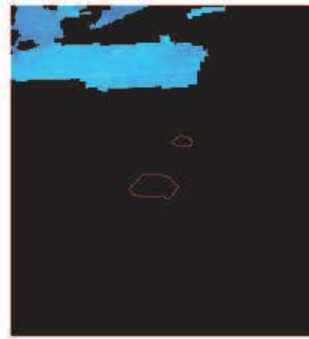
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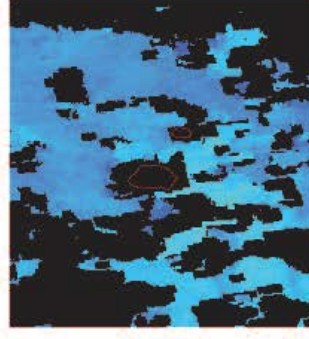
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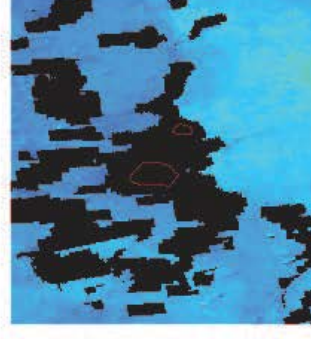
June



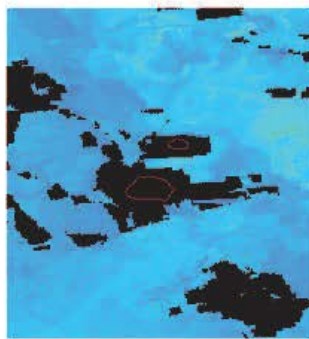
July



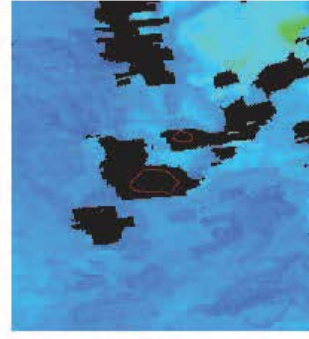
August



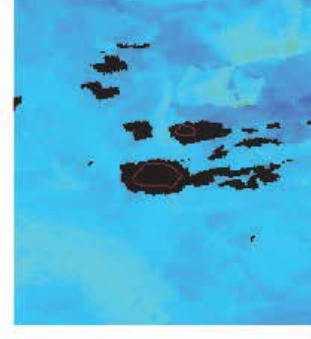
September



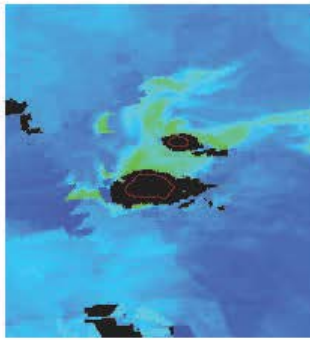
October



November



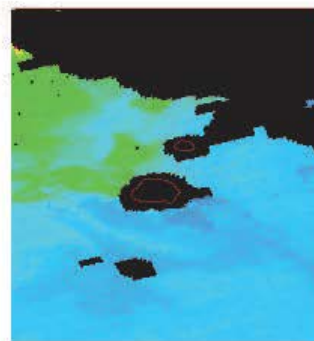
December 2008



January



February



March

April

May

June

July

August

September

October

November

December 2010

Appendix 2.A. Summary of bird population data and biomass estimates

Colour coding:

Data extracted from graph in Ryan et al. 2009

Grey: Data extrapolated between two known points using a linear regression.

Green: Assumption that the population between Marion Prince Edward is the same as for the 2001/02 season.

Estimate assumed equivalent to nearest (in time) known value

Data adjusted from Crawford et al. 2009

Species	YEAR	Marion Pairs	PE pairs	Total pairs	Numbers	bird wt	biomass (kg)	biomass (t)	Biomass in 200nm model (t km ²)	Reference
King Penguin	1952				752410	12				Conroy & White 1973 (Br Antarctic Surv Bull #32 p 31-40) xref Rand 1954 and Winter bottom 1971 and van Zinderen Bakker 1971 Van Zinderen Bakker 1971 in Williams et al. 1975 Williams et al. 1979 Cooper and Brown 1990 x-ref Williams et al. 1979 Ryan and Bester 2008 adapted from Cooper & Brown 1990, Crawford 2003 a, b, c Crawford et al. 2009
	1965-6	215230	5000	220230	72000000	12	24000000	24000	0.06692	
	1975	215230	5000	220230	440480	12	5285520	5286	0.01472	
	1980s				440480	12	5285520	5286	0.01472	
	2001/2 2008	218000	3000	221000	442000	12	5304000	5304	0.01477	
Macaroni Penguin	1965/66				1080000	4.6	4968000	4968	0.011526297	Van Zinderen Bakker 1971 in Williams et al. 1975 Williams et al. 1979 & Watkins 1987 Fitzpatrick records & Watkins 1987 Brown 1989, Cooper & Brown 1990 x ref Watkins 1987 and Williams et al. 1979 Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2009
	1977			450000	900000	4.6	4140000	4140	0.009605248	
	1983			405000	810000	4.6	3728000	3728	0.008644723	
	719897	405084	17000	422084	844168	4.6	3883172.8	3883	0.009009381	
	1994/95	434000	18000	452000	900000	4.6	4140000	4140	0.009605248	
	1995/96	395000	15000	410000	820000	4.6	3772000	3772	0.008751448	
	1996/97	395000	14000	409000	818000	4.6	3762800	3763	0.00873010	
	1997/8	405000	13000	418000	836000	4.6	3845600	3846	0.00922208	
	1998/9	361000	12000	373000	746000	4.6	3431600	3432	0.007961683	
	1999/2000	388000	11000	399000	798000	4.6	3670800	3671	0.008516653	
	2000/01	407000	10000	417000	834000	4.6	3836400	3836	0.008900863	
	2001/02	363000	9000	372000	744000	4.6	3422400	3422	0.007940338	
	2002/03	356000	11250	367250	734500	4.6	3378700	3379	0.007839949	
	2008/09	280000	12000	302000	604000	4.6	2778400	2778	0.006446188	
Southern Rockhopper	1965/66				1000000	2.7				Van Zinderen Bakker 1971 in Williams et al. 1975 Van Zinderen Bakker 1971 est, using survival rate of 84%, adult breeding at 4 yrs (From Guinard et al. 1988 for nothorn rhs) gives 270K breeding birds Crawford et al. In Crawford et al. recent - referenced as Williams et al. 1975, and underestimate because of late census (Jan-March); in my notes Watkins 1987 Williams et al. 1975 Williams et al. 1975, 1979 and Siegfried et al. 1978 (Crawford et al. is accredited to Watkins 1987) Cooper & Brown 1990 x-ref Fitzpatrick data and Williams et al. 1979 Brown 1989 Woehler and Croxall 1987 (Marine Ornithology) Crawford & Cooper 2003. Conserving Seabirds at the Prince Edward Islands & Crawford et al. 2003 Seabirds at Marion Crawford et al. 2009
	1965/66	235000	35000	270000	540000	2.7	1458000	1458	0.003382718	
	1973/74	212300								
	1974/75	212300	35000	247300	494600	2.7	1335420	1335	0.003099319	
	1974-77	83280	35000	128280	256580	2.7	692766	693	0.001607282	
	1987	137652	35000	172652	345304	2.7	932321	932	0.002163085	
	719897	157000	35000	192000	385200	2.7	1040040	1040	0.002413005	
	1984	173077	38000	211077	422154	2.7	1138916	1140	0.002644486	
	1986/87	150000	42000	192000	384000	2.7	1036800	1037	0.002405488	
	2001/2002	67000	45000	112000	224000	2.7	604800	605	0.001403201	
Gentoo Penguin	2008/2009	45221	37980	83201	166402	2.7	449295	449	0.001042391	
	1965/66				2500	6	15000	15	3.48016E-05	Van Zinderen bakker 1971 in Williams et al. 1975 Williams et al. 1975 Williams et al. 1979 Cooper & Brown 1990 Woehler and Croxall 1987 (Marine Ornithology) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2003d (Table 2) Crawford et al. 2009
	1974	801	158	960	1820	6	11520	12	2.67276E-05	
	1977	1300	200	1500	3000	6	18000	18	4.17619E-05	
	71984	888	655	1543	3086	6	18516	19	4.29591E-05	
	1984/85	1352	761	2113	4226	6	25355	25	5.88258E-05	
	1985/86	1355	763	2118	4235	6	25411	25	5.89564E-05	
	1986/87	1119	630	1749	3489	6	20985	21	4.8888E-05	
	1987/88	958	538	1494	2988	6	17928	18	4.15958E-05	
	1988/89	990	557	1547	3094	6	18566	19	4.30752E-05	
	1989/90	846	476	1322	2644	6	15888	16	3.88097E-05	
	2000/01	801	451	1252	2504	6	15022	15	3.48517E-05	
	2001/02	844	475	1319	2638	6	15828	16	3.87227E-05	
	2002/03	806	454	1260	2519	6	15115	15	3.50893E-05	
	2008/09	1100	619	1719	3438	6	20629	21	4.78613E-05	
Wandering albatross	1952	700	693	1393	2786	9	25072	25	0.00005817	Rand 1954 in Williams et al. 1975; Note: probably an underestimate - could be pairs and not total pop (not clear) Van Zinderen Bakker 1971 in Williams et al. 1975 Williams et al. 1975 Williams et al. 1979 & Watkins 1987 Watkins 1987 Watkins 1987 Watkins 1987 ? Published 1988 Cooper & Brown 1990 x-ref Watkins 1987 and Unpubl Fitzpatrick data Crawford & Cooper 2003. CCAMLR Science vol 13 2006 Ryan et al. 2009
	1965/66				3000	9	27000	27	0.00006264	
	1974	1557	847	2404	4808	9	43272	43	0.00010040	
	1977	1652	868	2618	5636	9	50724	51	0.00011768	
	1982		1100	2164	4328	9	38852	39	0.00008037	
	1983		1400	2272	4544	9	40886	41	0.00008488	
	1984		1300	2461	4922	9	44298	44	0.00010278	
	1985			2081	4162	9	37458	37	0.00008891	
	719887			2400	4800	9	43200	43	0.00010023	
	1980s	1533	1277	2810	5620	9	50580	51	0.000117351	
	1994/95	1794	1494	3288	6577	9	59191	59	0.000137331	
	1995/96	1765	1470	3235	6471	9	58235	58	0.000135111	
	1996/97	1741	1450	3191	6383	9	57443	57	0.000133273	
	1997/8	1910	1591	3501	7002	9	63019	63	0.00014821	
	1998/9	1780	1488	3268	6452	9	58070	58	0.000134728	
	1999/2000	1611	1342	2953	5906	9	53154	53	0.000123322	
	2000/01	1860	1549	3409	6819	9	61369	61	0.000142383	
	2001/02	1869	1850	3719	7438	9	66942	67	0.000155313	
	2002/03	1593	1577	3170	6340	9	57057	57	0.000132377	
	72006			2707	5414	9	48726	48	0.00011305	
	2008	2010	1840	3650	7300	9	65700	66	0.00015243	

Colour coding:

Data extracted from graph in Ryan et al. 2009

Grey: Data extrapolated between two known points using a linear regression.

Green: Assumption that the population between Marion Prince Edward is the same as for the 2001/02 season.

Estimate assumed equivalent to nearest (in time) known value

Data adjusted from Crawford et al. 2009

Species	YEAR	Marion Pairs	PE pairs	Total pairs	Numbers	bird wt	biomass (kg)	biomass (t)	Biomass in 200nm model (t km ⁻²)	Reference
Yellow-nosed Albatross	1965/66	0	2000	2000	4000	2.6	10400	10	0.00002	Van Zinderen Bakker 1971 in Williams et al. 1975
	1977	0	5000	5000	10000	2.6	26000	26	0.00006	Williams et al. 1979
	1980	0	7000	7000	14000	2.6	36400	36	0.00008	Cooper & Brown 1990 xref Berruti et al. 1981
	2001/02	0	7500	7500	15000	2.6	39000	39	0.00009	
	2006	0	6000	6000	12000	2.6	31200	31	0.00007	CCAMLR Science vol 13 2006
	2008	0	7000	7000	14000	2.6	36400	36	0.00008	Ryan et al. 2009
Grey-headed Albatross	1952	41	16	57	115	3.7	424	0	0.00000098	Rand 1954 in Williams et al. 1975
	1965/66			150	300	3.7	1110	1.1	0.00000258	Van Zinderen Bakker 1971 in Williams et al. 1975
	1974	2203	878	3081	6162	3.7	22799.4	23	0.00005290	Williams et al. 1975
	1977	3370	870	4240	8480	3.7	31376	31	0.00007280	Williams et al. 1979
										Cooper & Brown 1990 xref Fitzpatrick unpublished & Berruti et al. 1981
	1980	5037	1500	6537	13074	3.7	48374	48	0.00011223	
	1994/95	8217	1851	8068	16137	3.7	59706	60	0.000138525	
	1995/96	5219	1554	6773	13546	3.7	50122	50	0.000116288	
	1996/97	8600	1965	8565	17131	3.7	63384	63	0.000147059	
	1997/98	7641	2275	9916	19833	3.7	73382	73	0.000170254	
	1998/99	7728	2301	10029	20059	3.7	74217	74	0.000172192	
	1999/2000	5573	1660	7233	14465	3.7	53521	54	0.000124175	
	2000/01	8757	2012	8769	17538	3.7	64892	65	0.000150557	
	2001/02	8229	3000	9229	18458	3.7	68294.6	68	0.000158451	
	2002/03	5005	2410	7415	14831	3.7	54875	55	0.000127315	
	2006			7717	15434	3.7	57105.8	57	0.000132492	CCAMLR Science vol 13 2006
	2008		2000	9500	19000	3.7	70300	70	0.000163104	Ryan et al. 2009
Light-mantled Sooty Albatross	1965/66			50	100	2.8	280	0	6.4983E-07	Van Zinderen Bakker 1971 in Williams et al. 1975
	1974/75	92		92	184	2.8	515	1	1.19532E-06	Williams et al. 1975
	1977	176	40	216	432	2.8	1210	1	2.6064E-06	Williams et al. 1979
										Cooper & Brown 1990 xref Fitzpatrick unpubl & Williams et al. 1979
	1980s	201	40	241	482	2.8	1350	1	3.13122E-06	
	1997/98	334	85	429	858	2.8	2402	2	5.57383E-06	
	2001/02	179	150	329	658	2.8	1842	2	4.27457E-06	
	2002/03	127	106	233	467	2.8	1307	1	3.03279E-06	
	2006			241	482	2.8	1350	1	3.13122E-06	CCAMLR Science vol 13 2006
	2008	534		800	1600	2.8	4480	4	1.03941E-05	Ryan et al. 2009
Dark-mantled Sooty Albatross	1965/66			1000	2000	2.5	5000	5	1.16005E-05	Van Zinderen Bakker 1971 in Williams et al. 1975
	1974/75	1126	240	1366	2732	2.5	6830	7	1.58463E-05	Williams et al. 1975
	1977	2030	700	2730	5460	2.5	13650	14	3.16695E-05	Williams et al. 1979
										Cooper & Brown 1990 xref Fitzpatrick unpubl data and Williams et al. 1979
	1980s	2055	700	2755	5510	2.5	13775	14	3.19595E-05	
	1996/97	1701	700	2401	4802	2.5	12005	12	2.78529E-05	
	1997/98	1541	700	2241	4482	2.5	11205	11	2.59968E-05	
	1998/99	1775	700	2475	4950	2.5	12375	12	2.87113E-05	
	1999/2000	1012	700	1712	3424	2.5	8560	9	1.98601E-05	
	2000/01	1269	700	1969	3938	2.5	9845	10	2.28415E-05	
	2001/02	564	1000	1564	3128	2.5	7820	8	1.81432E-05	
	2002/03	721	1278	1999	3999	2.5	9997	10	2.31938E-05	
	2006		1300	2755	5510	2.5	13775	14	3.19595E-05	CCAMLR Science vol 13 2006
	2008		1500	2900	5800	2.5	14500	15	3.36416E-05	Ryan et al. 2009
Southern Giant Petrel	1977	1337	410	1747	3494	4.5	15723	16	3.64791E-05	Williams et al. 1979
										Cooper & Brown 1990 (more recent Marion data, Williams PE data)
	1980s	2891	410	3301	6602	4.5	29709	30	6.89281E-05	
	1994/95	2947	500	3447	6894	4.5	31023	31	7.19767E-05	
	1996/97	1198	650	1848	3696	4.5	16632	17	3.8588E-05	
	1997/98	2173	700	2873	5746	4.5	25857	26	5.9991E-05	
	1998/99	1381	750	2131	4262	4.5	19179	19	4.44974E-05	
	1999/2000	1468	800	2268	4536	4.5	20412	20	4.7358E-05	
	2000/01	1473	900	2373	4746	4.5	21357	21	4.95505E-05	
	2001/02	1430	1000	2430	4860	4.5	21870	22	5.07408E-05	
	2002/03	1759	1000	2759	5518	4.5	24831	25	5.76106E-05	
Northern Giant Petrel	2006			1790	3580	4.5	16110	16	3.73769E-05	CCAMLR Science vol 13 2006
	2008			2800	5600	4.5	25200	25	5.84667E-05	Ryan et al. 2009
	1977	210	100	310	620	4	2480	2	5.75387E-06	Williams et al. 1979
	1980s	314	180	494	988	4	3952	4	8.16807E-06	Cooper & Brown 1990 xref Fitzpatrick unpublished
	1994/95	411	195	606	1212	4	4848	5	1.12479E-05	
	1996/97	387	210	597	1194	4	4776	5	1.10808E-05	
	1997/98	453	230	683	1366	4	5464	5	1.26771E-05	
	1998/99	364	240	604	1208	4	4832	5	1.12108E-05	
	1999/2000	275	260	535	1070	4	4280	4	9.93006E-06	
	2000/01	341	280	621	1242	4	4968	5	1.15263E-05	
Sub-Antarctic Skua	2001/02	295	300	595	1190	4	4760	5	1.10437E-05	
	2002/03	196	199	395	791	4	3163	3	7.33752E-06	
	2006			540	1080	4	4320	4	1.00229E-05	CCAMLR Science vol 13 2006
	2008			750	1500	4	6000	6	1.39206E-05	Ryan et al. 2009

Appendix 2.B. Summary of Southern Elephant seal population and biomass estimates

Year	# females	# estimate pups	Population estimate	# males if 1:11	#males if 1:16	# sub-adults if 1:11	# sub-adults if 1:16	Biomass (t)			Average of 3	Std dev of 3 est	Marion and PE combined	Reference
								Average seal unit wt 353kg (+/- 137.6t) Condy 1981	Sex ratio 1:11 and Ryan & Bester 2008 weights	Sex Ratio 1:16 and Ryan & Bester 2008 weights				
Alt 1952	4000	4200	13230	364	250	8866	8980	4670	4942	4558	4723	197	6263	Rand 1962
1952	3662	3845	12112	333	229	8117	8221	4276	4524	4173	4324	181	5734	Rand 1962 referenced in Skinner et al. 1978, with assumption that the 3662 number is FEMALES (calculations are in line with other estimates)
1975	1115	1171	3688	101	70	2471	2503	1302	1378	1271	1317	55	1746	Condy 1977 referenced in Skinner et al. 1978, with assumption that the 1115 number is FEMALES (calculations are in line with other estimates)
Alt 1977	1062	1115	3512	97	66	2354	2384	1240	1312	1210	1254	52	1663	Condy 1978
1977	1313	1379	4538	115	82	3110	3143	1602	1631	1520	1584	58	2101	Condy 1981
1986	640	674	2123	58	40	1425	1443	749	791	730	757	31	1004	
1987	599	631	1988	54	37	1334	1351	702	741	683	709	29	940	
1988	605	637	2007	55	38	1347	1364	708	748	690	716	30	949	
1989	547	576	1814	50	34	1217	1232	640	676	624	647	27	858	
1990	477	502	1581	43	30	1061	1075	558	590	544	564	23	748	
1991	467	492	1550	42	29	1041	1054	547	578	533	553	23	733	
1992	449	473	1490	41	28	1000	1013	526	555	512	531	22	704	Pistorius et al. 1999, Ant Sci
1993	454	478	1506	41	28	1011	1024	532	561	518	537	22	712	
1994	402	423	1332	37	25	893	905	470	497	458	475	20	630	
1995	428	451	1421	39	27	954	966	501	529	488	506	21	671	
1996	407	428	1348	37	25	904	916	476	503	464	481	20	638	
1997	400	421	1326	36	25	890	901	468	495	456	473	20	627	
1999	413	434	1330	38	26	879	891	469	506	466	481	22	637	Ryan and Bester 2008, PEI book

Blue text: Numbers of males given in paper (115) is close to 1:11 (but not exact); resulting average mass from these estimates 1602kg which is close to Condys 1981 1420kg, but not exact.

Appendix 3.A. Diets of the top predators at the Prince Edward Islands

A summary of the diet for each of the land based top predators is described in this appendix.

1. King penguins

King penguins are offshore consumers (Croxall and Lishman 1987) which forage by diving, feeding primarily on mesopelagic fish (myctophids) and squid with a small crustacean component (Adams and Klages 1987, Adams and Brown 1989, Cherel and Ridoux 1992). At the PEIs the diet has been found to vary seasonally with fish contributing 30% (by mass) in winter, and up to 80-100% in summer (Adams and Klages 1987, Adams and Brown 1989) as was found for Kings at the Crozet islands (Cherel et al. 1996). The composition of Myctophid species varies with season as has been found at Crozet (Cherel et al. 1996). Data from Crozet suggests that crustaceans (e.g. *Themisto gaudichaudii* and *Euphausia vallentini*) when found in diets of King penguins, are the remains of prey of myctophids (Kozlov and Tarverdiyeva 1989) and so are largely consumed secondarily (Cherel and Ridoux 1992). The size limitation of prey is between 3 and 20cm and they probably eat a large number of prey in a small number of food patches because myctophids usually occur in dense monospecific shoals which was indicated by the high proportion of only one or two food items (Cherel and Ridoux 1992). King penguins may starve for 5-6 weeks at the beginning of their breeding cycle and are thought to forage in neritic waters over shelf areas during chick rearing and travel further afield when not constrained (Cherel et al. 1993).

Summaries for diet for the year shows the diet to consist predominantly of myctophid fish (86% wet mass; species composition dominated by *Krefftichthys anderssoni*, *Protomyctophum tenisoni*, *Electona carlsbergi*) and cephalopods (14% wet mass, dominated by *Kondakovia longimana*) with crustaceans forming a very small contribution (<1%) (Adams and Klages 1987, Ryan and Bester 2008). The contribution of cephalopods is higher than that found for Macquarie (Hindell 1988), Heard (Klages et al 1990) or earlier studies from Crozet (Possession Island) (Cherel and Ridoux 1992). At the Crozet islands, the King penguin diet is also dominated by fish at 99% of the diet with myctophids comprising approximately 86% (*E. carlsbergi* 73% and *K. anderssoni* 13%) (Putz and Bost 1994). At Kerguelen findings also show the diet dominated by

fish (95.3% of prey by number, although the eel-cod *Muraenolepis marmoratus* is more abundant (56.5%) than the myctophid, *Krefftichtys anderssoni* 32.9%) (Bost et al. 2002). The King Penguin diet for this study has been set to 85% mesopelagic fish, 14% cephalopods, 1% crustacean zooplankton group.

Macaroni Penguins

Macaronis feed mainly on crustaceans (Euphausiids: mainly *T. macrura* but also *E. vallentini*), small pelagic fish (dominated by myctophids) and cephalopods (Williams and Laycock 1981, Brown 1989, Brown et al. 1990, Cooper et al. 1990, Crawford et al. 2003c). There is seasonality in the diets, with the largely euphausiid diet (>90%) for chicks being replaced by a completely fish and cephalopod diet at the end of the chick rearing season (Brown 1989). Of the myctophid fish in the diet, *Krefftichtys anderssoni*, *Protomytophum tensioni* and *P. normani* dominate. As found for some of the albatross species, the most important of the cephalopod species was *Kondadovia longimana* (Cooper et al. 1990).

The final diet composition for the Macaronis for this study was predominantly crustaceans (75%), followed by small pelagic fish (18%) (dominated by myctophids), and cephalopods (7%). These estimates were based on reconstituted mass by Cooper et al. (1990), and higher contributions of cephalopods found by Brown (1989) (Crustaceans 62%, Fish 25%, Cephalopods 13%), differing only marginally from the summary in Ryan and Bester (2008) (Crustacea 79%, Squid 3% and Fish 18%) based on data from (Brown et al. 1990; Crawford et al. 2003c).

Southern Rockhopper Penguins

The diet of Southern Rockhoppers largely consists of crustacean zooplankton at 81% (Brown and Klages 1987, Brown et al. 1990, Cooper et al. 1990). Over half of this component of the diet is composed of large crustacean zooplankton (50%), with species included being the dominant euphausiid, *Euphausia vallentini*, as well as *Thysanoessa macrura*, *T. gregaria*, *T. vicina*, and the amphipods, *Themisto gaudichaudii* and *Primno macropa*. The benthic decapod *Nauticaris marionis* also contributes to the diet (approximately 5%). The remainder of the crustacean diet is made up of small crustaceans (primarily copepods, 26%). After the crustaceans, mesopelagic fish are the next most important group (6.9% of the diet), dominated by the myctophids

(*Kreffthichthys andersoni*, *Protomychophum tenisoni*, *P. normani*, *P. bilini*, *Electrona carlsbergi*, *E. subaspera*) with the small pelagic fish, *Paranotothenia magellinica*, also found (Cooper et al. 1990). The ‘fish general’ group made a small contribution (0.1%). Cephalopods contribute approximately 2% with the most important contributor being the cephalopod *Kondadovia longimana* (Cooper et al. 1990) and the remainder of the diet was classified as ‘Other’.

The diet of the Southern Rockhoppers has been shown to be variable with seasonal and annual variations recorded. Like the Macaronis, during chick rearing the predominantly crustacean diet changes with small fish and cephalopods more common towards the end of the chick rearing season (Williams and Laycock 1981). Differences between years were found for both the Macaroni and Rockhopper penguins’ diets for both long and short term considerations. For the 1983-84 breeding season diets were dominated by the benthic decapod (*Nauticaris marionis*), while in 1984-85 pelagic euphausiids (*Euphausia vallentini* and *Thysanoessa vicina*) dominated (Brown et al. 1990). Longer term investigations into the diet composition in the early 1980s as compared to data from 1994-2002 have shown an increase in zooplankton and corresponding reduction in fish in the diet, with the exception of the 1999/2000 season (where fish were a large proportion of the diet) Crawford et al. (2003). Prey switching from a benthic prey source (the benthic decapod) to a pelagic one (pelagic crustaceans) is thought to be due to changes in the food availability (as expected) and has been put forward as being a reflection of the different hydrodynamic events in the region (Brown et al. 1990). In the longer term, a switch to a diet consisting of a higher contribution of crustaceans would result in a difference in diet quality (decrease in quality) and such observations should be taken into consideration when investigating the decline in these populations.

Gentoo Penguins

Fish constitute the greatest portion of the Gentoo diet at the PEIs, followed by crustaceans and a small contribution of cephalopods (La Cock et al. 1984, Adams and Wilson 1987, Adams and Klages 1989). Fish in the diet includes the notothenid *Lepidonotothen squamifrons* (recorded as *Notothenia squamifrons*, a synonym Adams and Wilson 1987, Adams and Klages 1989), and the small inshore demersal *Harpagifer georgianus* (La Cock et al. 1984). Of the crustaceans the

pelagic component consisting of both euphausiids (*Euphausia vallentini* (Adams and Wilson 1987, Adams and Klages 1989) and small crustacean zooplankton is important, with the benthic decapod, *Nauticaris marionis* the next greatest contributor (La Cock et al. 1984, Adams and Wilson 1987). Other zooplankton forms and small cephalopods while present in the diet are not important components. Diets have been found to vary seasonally, with differences in contributions of the main diets, as well as variations in the species composition (La Cock et al. 1984, Adams and Klages 1989). As stated previously, Gentoo penguins are known to stay within a range of 40km of the shore (Adams and Wilson 1987) and are not deep divers (dives over 40m are unusual) (Adams and Brown 1983). They are inshore feeders at the PE islands (Williams 1980, Lacock et al. 1984) as well as at Crozet (Cherel et al. 1993). Their limited foraging range is evident in the species composition of their diet, which consists of inshore fish species. Diets of Gentoo penguins vary between Subantarctic systems, with populations in South Georgia, the South Shetlands and parts of the Antarctic Peninsula feeding extensively on Antarctic krill during their breeding season, while at the PE islands, Heard and the South Orkneys, fish dominates in the diet (Lacock et al. 1984). Williams (1981) postulated that Gentoos breed during mid-winter at the northernmost localities (e.g. the PEIs) to reduce competition for food from other penguin species and to ensure a crustacean diet for their chicks in the first few weeks of life (Lacock et al. 1984).

The final diet matrix of the Gentoo Penguins for this study was based on the summary in Ryan and Bester (2008) with additional information from La Cock et al. (1984), Adams and Wilson (1987) and Adams and Klages (1989). ‘Fish general’ constituted the bulk of the diet (59%), comprising 19% large notothenid demersals (Adams and Wilson 1987, Adams and Klages 1989), and 20% of each of the small continental slope demersals along with the small inshore demersals (e.g. *Harpagifer georgianus* (La Cock et al. 1984)). Cephalopods contributed just 1%, while the crustacean zooplankton formed the bulk of the remaining diet (37%). *Nauticaris marionis* was a large component of the crustacean diet (15%) (La Cock et al. 1984, Adams and Wilson 1987), with large crustacean (predominantly *Euphausia vallentini* (Adams and Wilson 1987, Adams and Klages 1989)) and small crustacean zooplankton combined contributing another 22%. Finally ‘All other’ contributed the remaining 3%.

Albatross

Satellite tracking has been used to track albatross in the Southern Ocean, which travel great distances to feed (Cherel and Weimerskirch 1995, Weimerskirch et al. 1995). In general, the albatross's two main prey components are fish and cephalopods. Fish comprise between 10% and 60% of the diets of the 5 species recorded at the islands, while cephalopods make up between 35% to 80% of the diets. Detailed descriptions of the diets of each of the five species breeding at the islands are found below.

Wandering Albatross

Based on Adams et al. (1986), cephalopods accounted for 80% of the diet (divided equally between large and small fractions), small pelagic fish contributed 10%, with crustaceans forming the next largest contribution (5% large crustacean zooplankton and 3.7% small crustacean zooplankton). The remaining contributors were other zooplankton (1%), and 0.1% contributions of the most abundant penguin species (Kings, Macaroni and Rockhopper) which are consumed as carrion. This estimate has a higher contribution of squid and lower contribution of fish compared to the data summarized in Ryan and Bester (2008) (Crustacea <1%, Squid 59%, Fish 35%, other 5%) which is more in line with Cooper et al. (1992) where the contribution of fish to the diet is considered important. Twenty-three taxa of the Cephalopods have been observed in the diets of Wandering albatross, with *Kondakovia longimana* being the most important (Cooper et al. 1992).

Grey-headed Albatross

Fish and cephalopods are the two main prey items of the Grey-headed albatross at the PEIs and the diets were based on Hunter and Klages (1989) and Ryan and Bester (2008) which were very similar. Final assignments of the diets were fish 58.6%, Cephalopods 35%, Crustaceans 3%, with other zooplankton 1%, benthos 2%, and penguins 0.4% making up the remainder of the diet. Cephalopods that dominated in terms of species as estimated from regurgitated squid beaks were *Kondakovia longimana* and *Moroteuthis nipovitchi*. Diet for the Grey-headed albatross is similar to that at the Crozet Islands but contrasted with that of birds at South Georgia which had a higher proportion of cephalopods and crustaceans (Hunter and Klages 1989).

Indian Yellow-nosed Albatross

The diet composition was based on the summary by Ryan and Bester (2008), with small pelagic fish dominating (58%), followed by cephalopods (38%) and crustacean zooplankton (3%) and other zooplankton (1%).

Light-mantled Sooty Albatross

Pelagic fish dominated the diet (50%), followed by squid (46%) the remainder comprising zooplankton (3% crustacean, 1% other). Slight deviations from the summary of Ryan and Bester (2008; crustacea 4%, cephalopods 34%, fish 46%, other 16%) with studies by Cooper and Klages (1995) and Berruti and Harcus (1978) taken into account. Although bird remains have been recorded in the Sooty albatross diets (Cooper and Klages 1995), this component has not been included in the diet description.

Dark-mantled Sooty Albatross

The diet summary in Ryan and Bester (2008) is based on Berruti and Harcus (1978) where cephalopods were found to dominate (42%), followed by fish (33%). Crustaceans form less than 1 % of the diet, with ‘other’ forming the remainder of the diet (25%). For the matrix used in this model, data from Cooper and Klages (1995) was included and cephalopod and fish estimates (all small pelagic/myctophids) were increased by 13% (to 55%) and 8% (to 41%) respectively, and total zooplankton contribution extended to 4% (3% crustacean, 1 % other). The most important species of cephalopod was *Kondakovia longimana*. Cephalopod families Onychoteuthidae, Crachiidae and Histioteuthidae were all important. Although bird remains have been recorded in the Sooty albatross diets (Cooper and Klages 1995), this component has not been included in the diet description

Giant petrels

Giant petrels are both predators (see Ryan et al. 2008) and scavengers (de Bruyn and Cooper 2005; de Bruyn et al. 2007) with a large contribution of their diet coming from penguins (between 67 and 80%). Along with the high contribution of vertebrate prey to their diet

(including seals, birds, eggs and carrion), smaller amounts of fish, cephalopods and zooplankton are also eaten (Rand 1962; Williams et al. 1975; Hunter 1985; Hunter and Brooke 1992).

Southern Giant Petrels dominate in terms of numbers so the diet was calculated using weighted contributions of the two species based on their biomass contribution to the group (5:1). A combined diet was set to vertebrates 91.1% (seals 3.5%, penguins 79%, prions and petrels 8.6%), small pelagic fish 3.5%, cephalopods 5.35% and crustaceans 0.05%.

Prions and petrels

Of the 14 species included in this group (see species list), the Salvin's Prion, Blue Petrel, Great-winged Petrel and White-chinned Petrel dominate the small flying seabirds in both population numbers and also in biomass (together constituting 89% and 85.7% of the totals respectively). The diet for this group was broadly based on Salvin's Prion and the Blue Petrel because they are the two species with the highest abundance and biomass. Both of these species have diets dominated by crustacea (59% and 66% respectively), followed by fish (21% and 22%) and squid (9% and 16%) with the remainder considered as 'other' (4%) (Steele and Klages 1986; Fugler et al. 1987; Gartshore et al. 1988; Ryan and Bester 2008), and the final diet matrix for this group (combined), had crustacean zooplankton making the highest contribution to the diet set at 60%, followed by mesopelagic fish 22%, cephalopods 14% with the remainder considered 'other'.

Elephant seals

Elephant seals may be considered deep diving opportunistic generalist feeders (Field et al. 2007) and their foraging range is extensive, with trips to the Antarctic continental shelf having been recorded (Jonker and Bester 1998). Studies of elephant seals suggest a high contribution of cephalopod species (75%) to elephant seal diets, with fish and a small proportion of benthic invertebrates thought to make up the remainder of the diet (Laws 1977; Green and Burton 1993; Pauly et al. 1998; Field et al. 2007). Studies from Subantarctic islands with large shelf areas (e.g. Heard and Kerguelen) were found to have higher contributions of fish to the diet, while those sampled at Macquarie Island (with a small shelf area) had more squid in the diet (Eder et al. 2010). This system, with its small shelf area, would be more similar to the Macquarie situation.

The diet of elephant seals at PEIs is virtually unknown with only the squid *Kondakovia longiamana* found in one stomach (M.N. Bester unpublished data). The diet composition used in this study of cephalopods 55% and fish 45% was based on a summary by Ryan and Bester (2008) whose estimates are based on adjacent sub-Antarctic islands (Green and Burton 1993). The contribution of different groups of fish to the diet was set at 25% mesopelagic fish and 20% general fish, a decision that was based on additional information from Field et al. (2007), where Myctophids dominated the fish diet, although fish from demersal and benthic habitats were also found. Within this framework, the diet contribution for each fish prey group was set in proportion to the biomass available during that specific time period.

Antarctic fur seals

Diet of Antarctic fur seals at Marion were dominated by myctophid fish (96%), supplemented by cephalopods (4%) with other contributions being less than 1% (Makhado 2002). At Marion, predation of King penguins, Macaroni penguins and less commonly Rockhopper penguins has been observed (Hofmeyr and Bester 1993, unpublished data) but hardly ever contained in scats (possible explanation regarding position of colonies) (Makhado et al. 2008). The only crustacean found was *Nauticaris marionis*, which was only found in 1999 in studies between 1989 and 2001 (Klages and Bester 1998, Makhado 2002, Makhado et al. 2008). The Myctophid species that dominated were *Electrona carlsbergi*, *E. subaspera*, *Gymnoscopelus fraseri*, *G. piabilis*, *Krefftichthys andersoni*, *Electrona antarctica* and *Protomyctophum choriodon* and diets varied seasonally with different species of myctophids being taken in summer and winter (Klages and Bester 1998, Makhado 2002, Ryan and Bester 2008). Also present (as with many of the other diets listed) was the small pelagic *Paranotothenia magellanica*. A similar diet was found at the Kerguelen Islands where myctophid fish dominated in terms of reconstituted mass accounting for between 54 and 82% of biomass (Cherel et al. 1997; Lea et al. 2002). Also important for biomass (but not number because of large size), the Channichthyid *Champscephalus gunnari* (Cherel et al. 1997) which is a species of fish not found at Marion, and the Southern driftfish *Ichthyopsis australis* and mackerel icefish (Lea et al. 2002). Crustaceans formed a minor component of the diet with the hyperiid amphipod *Themisto gaudichaudii* being the most abundant crustacean prey item (Cherel et al. 1997). Myctophids also dominated the diet of this species at Macquarie Island

(Goldsworthy et al. 1997) and Heard Island (Green et al. 1997) in contrast to krill-dominated diets that were found for South Georgia (Doidge and Croxall 1985, Reid and Arnould 1996) and Bouvet (Kirkman et al. 2000). It has been noted that at localities where the shelf is wide (e.g. Heard Island, Iles Kerguelen) benthic fish such as Nototheniids and skates are more important in the diet than at localities with a narrow shelf area (e.g. Macquarie Island, Marion Island) where myctophids dominate the diet (Klages and Bester 1998 Makhado 2002, Makhado et al. 2008). Because of the species of fish found in the Antarctic fur seal diet, it is thought that they feed further offshore (Goldsworthy et al. 1997; Klages and Bester 1998; Makhado et al. 2008). The diet matrix used in this consumption model for this species was vertebrate prey 0.5%, general fish 0.6%, mesopelagic fish 94.8%, cephalopods 4.0% and crustaceans 0.1%.

Sub-Antarctic Fur seals

As described for the Antarctic fur seals, the Sub-Antarctic fur seals' diet is also dominated by myctophid fish at 99%, with a small cephalopod contribution (1%) (Makhado 2002; de Bruyn et al. 2009). The dominant myctophid species were *Electrona carlsbergi*, *E. subaspera*, *Gymnoscopelus fraseri*, *G. piabilis*, *Krefftichthys andersoni*, *Electrona antarctica* and *Protomyctophum choriodon* (Klages and Bester 1998, Makhado 2002, Ryan and Bester 2008) and the diets vary seasonally with different species of myctophids being taken in summer and winter (Klages and Bester 1998, Makhado 2002). This dominance of myctophid fish is in contrast to Antarctic systems described for instance by Laws (1977) where the diet comprised 50% squid, 45% fish, 5% krill, or diets summarised in Pauly et al. (1998) (cross referencing Rand 1956; Condry 1981; Bester 1987) where contributions of cephalopods (small 30%, large 15%) and fish (small pelagics 10%, miscellaneous fishes 25%) dominated, with large zooplankton 15% and higher vertebrates 5% making up the remainder. The diet matrix used for this species in the consumption model was 98.2% mesopelagic fish, 1% cephalopods, 0.6% general fish and 0.2% crustaceans.

Appendix 3.B. Table of energetic content of prey (summary from the literature)

Prey Categories		wet weight kJ.g-1	References	dry weight kJ.g-1	References
Vertebrates	Penguin cation	7.96	Burger 1981 in Hunter 1985		
	Fur seal	10.47	DW Doidge pers comm in Hunter 1985		
	Average	9.22			
Fishes	Myctophid <i>Protomyctophum</i> spp	7.54	Tiemey unpublished in Goldsworthy et al. 2001		
	Myctophid <i>Protomyctophum andriashevi</i>			39.3	Tiemey et al. 2002
	Myctophid <i>Protomyctophum bolini</i>			28	Tiemey et al. 2002
	Myctophid <i>Protomyctophum parallelum</i>			28.3	Tiemey et al. 2002
	Myctophid <i>Protomyctophum tenisoni</i>			20.5	Tiemey et al. 2002
	Myctophid <i>Krefflichthys anderssoni</i>	8.36	Tiemey unpublished in Goldsworthy et al. 2001	27.5	Tiemey et al. 2002
	Myctophid <i>Krefflichthys anderssoni</i>	8.10	Cherel & Ridoux 1992	26.4	Cherel & Ridoux 1992
	Myctophid <i>Electrona anartartica</i>	8.77	Tiemey unpublished in Goldsworthy et al. 2001	30.8	Tiemey et al. 2002
	Myctophid <i>Electrona anartartica</i>	9.4	van de Putte et al. 2006	29.4	van de Putte et al. 2006
	Myctophid <i>Electrona carlsbergi</i>	5.37	Tiemey unpublished in Goldsworthy et al. 2001	21.7	Tiemey et al. 2002
	Myctophid <i>Electrona carlsbergi</i>	7.00	Cherel and Ridoux 1992; used by Guinet et al. 1996 and Kirkman et al. 2000 & Halsey et al. 2008	23.5	Cherel and Ridoux 1992
	Myctophid <i>Electrona subaspera</i>	7.42	Tiemey unpublished in Goldsworthy et al. 2001	26.6	Tiemey et al. 2002
	Myctophid <i>Gymnoscopelus spp/ braueri</i>	9.05		39.0	Tiemey et al. 2002
	Myctophid <i>Gymnoscopelus braueri</i>	8.9	van de Putte et al. 2006	29.4	van de Putte et al. 2006
	Myctophid <i>Gymnoscopelus fraseri</i>			29.3	Tiemey et al. 2002
	Myctophid <i>Gymnoscopelus microlampus</i>			22.6	Tiemey et al. 2002
	Myctophid <i>Lampanyctus intracarius</i>			23.66	Bulman et al. 2002
	mesopelagic <i>Bathylagus</i> spp			19.88	Bulman et al. 2002
	Average	7.99		27.4	
	large pelagic <i>Paradiplosinus gracilis</i>	4.6	Cherel & Ridoux 1992	21.8	Cherel & Ridoux 1992
	large demersal <i>Halargyreus johnsonii</i>			20.1	Bulman et al. 2002
	large pelagic <i>Idiacanthus atlanticus</i>			21.94	Bulman et al. 2002
	large demersal <i>Antimora rostrata</i>	1.26	Tiemey unpublished in Goldsworthy et al. 2001	21.8	
	large demersal <i>Lepidonotothen squamifrons</i>	5	Tiemey unpublished in Goldsworthy et al. 2001		
	general fish	3.97	Croxall et al. 1984 in Guinet et al. 1996	21	Schneider and Hunt 1982 in Abrams 1985
	general fish	3.97	Clark & Prince 1980 in Adams et al. 1993		
	general fish	3.98	Croxall and Prince 1982 in Hunter 1985		
		3.97	Doige and Croxall 1985 in Kirkman et al. 2000		
	Average	3.82		21.3	
Cephalopods	<i>Todarodes</i> spp	4.01			
	<i>Moroteuthis</i> spp	1.84			
	<i>Gonatus</i> spp	3.78	Clarke et al. 1985 in Goldsworthy et al. 2001		
	<i>Histeoteuthis</i> sp	2.65		22.46	Bulman et al. 2002
	<i>Mastigoteuthis</i> spp	1.82			
	General	3.25			
		3.57	Brown 1987 Croxall et al. 1984 in Adams et al. 1993 Croxall et al. 1984 used in Ridoux 1989, Woehler and Green 1991, Guinet 1996; same value in Doige and Croxall 1985 in Kirkman et al. 2000		
		3.47	Croxall and Prince 1982 in Hunter 1985		
	Average	3.10			
Crustaceans	General	4.68	Brown 1987		
	General	4.51	Mauchline 1980 in Abrams 1985		
	General	4.35	Croxall et al. 1984 in Adams et al. 1993, Ridoux 1989, Woehler & Green 1991, Guinet et al. 1996		
	<i>Euphausia</i> spp.	4.35	Croxall and Prince 1982 in Hunter 1985		
	<i>Euphausia superba</i>	4.35	Doige and Croxall 1985 in Kirkman et al. 2000		
	Average	4.45			

Dry weight to wet weight conversion of *3.33 used

Appendix 4.A. Species list for the Life Support System model

#	Functional Group	Species list	Species name	no. of spp.
1	Seals	Southern Elephant Seal Antarctic Fur Seal Subantarctic Fur Seal	<i>Mirounga leonina</i> <i>Arctocephalus gazella</i> <i>Arctocephalus tropicalis</i>	3
2	Penguins	King Penguin Macaroni Penguin Southern Rockhopper Penguin Gentoo Penguin	<i>Aptenodytes patagonicus</i> <i>Eudyptes chrysolophus</i> <i>Eudyptes chrysocome filholi</i> <i>Pygoscelis papua</i>	4
3	Albatross	Wandering Albatross Grey-headed Albatross Yellow-nosed Albatross Light-mantled Sooty Albatross Dark-mantled Sooty Albatross	<i>Diomedea exulans</i> <i>Thalassarche chrysostoma</i> <i>Thalassarche carteri</i> <i>Phoebastria palpebrata</i> <i>Phoebastria fusca</i>	5
4	Giant Petrels	Southern Giant Petrel Northern Giant Petrel	<i>Macronectes giganteus</i> <i>Macronectes halli</i>	2
5	Prions and Petrels	Fairy Prion Salvin's Prion Blue Petrel Great-winged Petrel Soft-plumaged Petrel Kerguelen Petrel Grey Petrel White-chinned Petrel Grey-backed Storm Petrel Black-bellied Storm Petrel South Georgian Diving Petrel Common Diving Petrel	<i>Pachyptila turtur</i> <i>Pachyptila salvini</i> <i>Halobaena caerulea</i> <i>Pterodroma macroptera</i> <i>Pterodroma mollis</i> <i>Lugensa brevirostris</i> <i>Procellaria cinerea</i> <i>Procellaria aequinoctialis</i> <i>Garrodia nereis</i> <i>Fregetta tropica</i> <i>Pelecanoides georgicus</i> <i>Pelecanoides urinatrix</i>	12
6	Large Demersal Fish	Blue antmora Southern seadevil Unicorn icefish Grenadier or rattail Slender codling Abyssal halosaur Moid cod Grey rockcod Ridge scaled rattail Bigeye grenadier Finless flounder Black rockcod Marbled rockcod Longnose tapirfish	<i>Antimora rostrata</i> <i>Ceratias tentaculatus</i> <i>Channichthys rhinoceros</i> <i>Coryphaenoides</i> sp. <i>Halargyreus johnsonii</i> <i>Halosaurus macrochir</i> <i>Lepidion</i> sp. <i>Lepidionotothen squamifrons</i> <i>Macrourus carinatus</i> <i>Macrourus holotrachys</i> <i>Neoschiropsetta milfordi</i> <i>Notothenia coriiceps</i> <i>Notothenia rossii</i> <i>Polyacanthopus challengerii</i>	15
7	Small Demersal Fish	Slickhead Messmate Triangular rockcod Lobe-lip notothen Austral cod South Georgia spiny plunderfish Painted notie Snailfish Antarctic armless flounder Marbled moray cod Patagonian moray cod Cod & Haddock Southern flounder Antarctic horsefish	<i>Alepocephalus</i> sp. <i>Echiodon cryomargarites</i> <i>Gobionotothen acuta</i> <i>Gobionotothen marionensis</i> <i>Guttigadus kongi</i> <i>Harpagifer georgianus</i> <i>Lepidionotothen larseni</i> <i>Liparidae</i> gen. sp. <i>Mancopsetta maculata maculata</i> <i>Muraenolepis marmorata</i> <i>Muraenolepis orangiensis</i> <i>Physiculus</i> sp. <i>Pseudomancopsetta andriashevi</i> <i>Zanclus cornutus spinifer</i>	13
8	Large Pelagic Fish	Short snouted lancetfish Daggertooth Skate Patagonian toothfish Southern lanternshark Black dragonfish Porbeagle Barracudinas Southern barracudina Barracudinas Slender escolar Southern driftfish Skate/ray Bighorn skate Smallscale waryfish Greenland shark Barracudinas	<i>Alepisaurus brevirostris</i> <i>Anotopterus pharao</i> <i>Bathyrhina</i> sp. (tuff) <i>Dissostichus eleginoides</i> <i>Etmopterus granulosus</i> <i>Idiacanthus atlanticus</i> <i>Lamna nasus</i> <i>Macroparalepis</i> sp. <i>Magnisudis prionosa</i> <i>Notolepis</i> sp. <i>Paradiplosinus gracilis</i> <i>Pseudoclichthys australis</i> <i>Raja</i> sp. <i>Rajella bairdii</i> <i>Scopelogadus hamiltoni</i> <i>Somniosus microcephalus</i> <i>Stemonosudis</i> sp.	17

Appendix 5.A. Data preparation for the ecosystem model of the Prince Edward Islands

A comprehensive review of each functional group for the ecosystem model is covered in this appendix. Where appropriate, species included in a group are listed (a summary table is also provided) and for each functional group a review on how the basic parameters are calculated is given. These include descriptions of Biomass estimates (B , t or $t.km^2$), Production to Biomass ratios (P/B yr^{-1}), Consumption to Biomass ratios (Q/B , yr^{-1}), Unassimilated Consumption (UC, fractional), and a summary of the diets used in the model.

With respect to the Q/B estimates, a full summary of the energy content of the components of the diets (summarised into 5 broad groups) are provided in Chapter 3 and are used in these estimates. Briefly, the five categories were (with energetic value of 1g of dry weight given in parenthesis) 1. Top predators (30.7 $kJ.g^{-1}$), Fish – general (21.3 $kJ.g^{-1}$), 3. Fish – mesopelagic (27.4 $kJ.g^{-1}$), 4. Cephalopods (10.3 $kJ.g^{-1}$), 5. Crustacea (14.8 $kJ.g^{-1}$), 6. Other (15.88 $kJ.g^{-1}$). Unless otherwise stated, water content was assumed to be 70% (Nagy et al. 1999), therefore dry weight to wet weight conversion was assumed to be 3.33. Digestive efficiency for each group was incorporated into the calculation and the information is provided in the summary for each functional group, along with a description of the diet (full diet matrix provided in Table 5.2).

Regarding the unassimilated consumption (UC), the value is discussed in terms of assimilation efficiency (how much of what is consumed is absorbed), but the value provided is given as how much is not absorbed. If no reference is made to this parameter in the text for a particular group, the default value for UC of 0.2 was used.

Functional groups

Wherever mentioned specifically, the functional groups are italicised and capitalised to identify the term as the specific functional group and not a general reference to a generic grouping. Also, each functional group has been assigned a 3 letter code for easy reference.

Mammals

The biomass estimates for each of the mammal groups are made from estimates from the Prince Edward Islands. Extrapolations from population sizes were made using data from the site where possible, and from the literature where these were not available. The assimilation efficiency for all mammal groups was set to 0.90 (i.e. 0.1 is not assimilated) which was based on digestive efficiencies recorded in the literature for fur seals (93% Mecenero et al. 2006; Miller 1978) and juvenile Steller sea lions 92-96% (Rosen and Trites 2000). These figures are similar to those found for harp seals which ranged between 93.5 and 96.6% (Lawson et al. 1997). It is noted that digestive efficiency may vary with age (Rosen and Trites 2000) but this is not considered for the purposes of this model.

1. Orcas (MOR)

Species: *Orcinus orca*

Biomass: A review of orca populations based on opportunistic observations from 1973 to 1996 shows the average pod size is 3.56 individuals and the maximum size is 28 individuals.

Populations peak October to December, decrease in January, and have a small increase in late April to early May after which killer whale sightings during most years decreased to almost nothing (Van Zinderen Bakker Sr et al. 1971; Skinner et al. 1978; Keith et al. 2001; Pistorius et al. 2002; Tosh et al. 2008). Using Trites and Pauly's (1998) weight estimates (for male and female, and female weights for sub-adults) which represent the 'average' mass of individuals within a population, average group sizes and sex ratios from Keith et al. (2001), and having the orcas in the vicinity year round the total biomass estimate is 9.473t. Alternatively, if the sub-adults' weights are considered to be half of females, biomass estimates for the islands are 7.421t (with a pod of 3.6 whales). Alternatively, if 18 whales are in the area for 4 months of the year, the biomass estimate would be 12.244t. Finally a biomass estimate that has the orcas in the vicinity of the islands for 3 months, using the maximum number of 28 individuals for this whole period with Trites and Pauly's (1998) weight estimates, in combination with the least amount of time at islands, equates to 14.441t (range for all above considerations: 7.421t – 14.441t). The resultant number is one tenth of the value for the Kerguelen model: 114t (Pruvost et al. 2005).

Biomass: 10.895 t

P/B: 0.06 (yr⁻¹)

Using the annual survival estimate of Evans and Stirling (2001) to estimate mortality, the P/B ratio was estimated to be 0.06 yr⁻¹. This compares favourably to the Kerguelen model (Pruvost et al. 2005) which has a value of 0.05 yr⁻¹ (taken from the 'Newfoundland' model of Heymans and Pitcher (2002).

Q/B: 5.39 (yr⁻¹)

Calculated using Nagy et al. (1999), with diets informed from Pauly et al. (1998) and local data (see diet composition below), combined with an average weight estimate (of 2280.5kg) from Trites and Pauly (1998) (assuming a 1:1 ratio of males to females in the total population). Assumptions used in this calculation are given on page 1 of the appendix (dry weight to wet weight conversion x 3.33) and an average energetic content of prey of 24.57 kJ.g⁻¹ was used which resulted in a Q/B of 5.39 yr⁻¹. This value is lower than 9.56 yr⁻¹ calculated using Innes et al.'s (1987) ingestion equation for growing mammals ($I = 0.123M^{0.8}$) and average weight from Trites and Pauly (1998). Using this equation as adapted by Trites et al. (1997) for growing animals results in 7.77 yr⁻¹. In comparison, the Q/B ratio for hunting marine mammals used in the Kerguelen model was estimated at 8.3 yr⁻¹, from a consumption of 0.33t.km⁻² (Pruvost et al. 2005, adapted from Table 1 of Guinet et al. (1996) where consumption was estimated at 188 240 t). Q/B from the Falklands model for toothed whales, dolphins and porpoises is 5.488 yr⁻¹ (Cheung and Pitcher 2005), which is closer to the value used here, and also similar to 4.8 yr⁻¹ which was used for killer whales (Laws 1977; Lockyer 1981) in Bredesen's Antarctic model (Bredesen 2003).

Diet Composition: Diet composition was set to *Cephalopods* 10%, *Small Pelagic Fish* 10%, all other fish groups 40% and higher vertebrates 40%, which is based on information for Orcas in general and is not site specific (Pauly et al. 1998). Within this framework, the contribution of the diet of each functional group was set in proportion to that functional group's contribution to the biomass within the broad groups (e.g., seal, penguin, etc), allowing for the decreased or increased biomass of the prey for each time period to be taken into account. Data from Southern

Ocean islands have recorded Orcas feeding on Southern elephant Seals (pups and females), and penguins (Guinet 1992; Keith et al. 2001; Pistorius et al. 2002; Ryan and Bester 2008) and Patagonian Toothfish (off longlines during hauling) (Ryan and Bester 2008). In an Antarctic Peninsula model, a higher contribution of mammals (46%) (consisting of 6% of *Arctocephalus gazella*, 8 % *Mirounga leonina*, *Lobodon carcinophagus*, *Hydrurga leptonyx*, *Leptonychotes weddelli* and *Ommatophoca rossii*) and birds (18 % total consisting of 10 % penguins, and 8% other) was set with demersal and pelagic fish groups each with 16% spread evenly across generic size classes and one additional species specific class in each (4% for small, medium and large categories, an additional 4% assigned to each of *N. rossii* (*Large Nototheniid Demersal*) *Electrona Antarctica* (*Small Pelagic Fish*)) and the remaining 4% assigned to cephalopods (Cornejo-Donoso and Antezana 2008).

2. Southern Elephant Seals (MES)

Species: *Mirounga leonina*

Biomass: Biomass estimates for Southern elephant Seals on Marion Island were calculated from published values in (Rand 1962; Condry 1977; Skinner et al. 1978; Condry 1979; Condry 1981; Pistorius et al. 1999b; Pistorius and Bester 2002; Pistorius et al. 2004; Ryan and Bester 2008). Conversions from female numbers to pups were made using the conversion of 1.05 (Pistorius et al. 1999), and extrapolations to full populations were made using a conversion of 3.15 (Pistorius et al. 1999). Two estimates of male numbers were made using male to female ratios of 1:11 (Rand 1962, Condry 1977) and 1:16 (Skinner and van Aarde 1983). Subadult numbers were then calculated by subtraction. Total population biomass estimates were calculated using these population structure estimates along with Ryan and Bester's (2008) average weights for each population class, as well as a third estimate using Condry's (1981) average 'seal unit mass' (of $353 \pm 137.61\text{kg}$). The average values from these three estimates were used for each year in the study, and the standard deviations around the means were used as a measure for data quality in the pedigree routine. In order to account for elephant seals on PE Island, the population estimate was increased by 32.6% (this value is the average taken from ratio of M:PE in 1970s of 34.6 (Condry 1978a) and most recent survey 30.6 (Ryan and Bester 2008)). Elephant seals do not

remain at the islands year round and adjustment was made to account for the time spent in the area which has been set at 8 months (67% of the year) (Condy 1979).

B 1960s: 2506 t

B 1980s: 672 t

B 2000s: 427 t

P/B: 0.074 yr⁻¹

The mortality for Southern elephant Seals at Marion averaged over 13 years is 0.074 yr⁻¹ (Pistorius et al. 1999) and this value was used as the P/B estimate. It is close to the 0.08 yr⁻¹ used in Erfan and Pitcher (2005).

Q/B: 12.78 yr⁻¹

The Field Metabolic Rate (FMR) for this group was based on Nagy et al.'s (1999) equation: 4.82 (body mass in g)^{0.734} kJ.d⁻¹. Using this equation with diet composition weighted for calorific content, and assuming that digestive efficiency is 90%, Q/B was 12.78 yr⁻¹ using Condry's (1981) weight estimates or 12.27 yr⁻¹ using Trites and Pauly (1998) average mass estimates. If we use Nagy's (1999) energy conversion (with calorific content of a gram of diet equivalent to 16.8 kJ for a carnivore), we get 11.03 yr⁻¹. Using Innes et al. (1987) ingestion (I) in biomass for growing mammals $I = 0.123(\text{mass in kg})^{0.8}$ we get a Q/B of 13.89 yr⁻¹ (using Condry 1981 average weight) or 13.32 yr⁻¹ (using Trites and Pauly 1998 average weight). Results for maintenance are much lower (6.83 yr⁻¹ and 6.52 yr⁻¹ respectively). These calculations are an advancement from earlier estimates where food consumption was considered to be a percentage of body weight. Estimates for Southern elephant Seals were assumed to consume 6% of body weight daily (Knox 2007b). Elephant seals were assumed to feed 290 days a year resulting in a Q/B of between 17.4 yr⁻¹ and 20.1 yr⁻¹ (Laws 1977 and Condry 1981), which are much higher than estimates used here.

Diet Composition: The diet composition was set to cephalopods 55% and fish 45% based on a summary by Ryan and Bester (2008) whose estimates are based on adjacent sub-Antarctic islands (Green and Burton 1993). Additional information from Field et al. (2007) was used where

the fish diet was found to be dominated by Myctophids, although fish from demersal and benthic habitats were also found. Studies from Subantarctic islands with large shelf areas (e.g. Heard and Kerguelen) were found to have higher contributions of fish to the diet, while those sampled at Macquarie Island (with a small shelf area) had more cephalopods in the diet (Green and Burton 1993; Eder et al. 2010). This system, with its small shelf area, would be more similar to the Macquarie situation, therefore the diet was set 20% all the fish excluding the *Small Pelagic Fish* and *Myctophid Fish* groups which were assigned the remaining 25%. Within this framework, the diet contribution for each individual functional group was set in proportion to the biomass available during that specific time period.

Adjustments: For the 1960s time period, the model did not balance, and consumption by elephant seals on both the large pelagics and the Patagonian Toothfish were over-consumed (EE = 1.07 and 1.65 respectively). An adjustment of an increase in the contribution of large cephalopods by 5%, combined with a reduction by 1% for large pelagics, and 4% for Patagonian toothfish was able to resolve model balancing procedure. For all other time periods the contributions were left in proportion to their biomass contributions. Another solution would have been to increase the biomass of the fish groups, as biomass data for these groups is uncertain.

3. Antarctic Fur Seals (MAF)

Species: *Arctocephalus gazella*

Biomass: Antarctic Fur Seal estimates of pups were taken from Appendix in Hofmeyr et al. (2006) (for Marion) and numbers from Tables 1 and 2 in Bester et al. (2003). Using the conversion of Kerley (1983a) of 1:4.8 for pup to population estimates; and using the 'seal unit mass' of 46.92 kg for Antarctic Fur Seals (Condy 1981) biomass estimates were made. Estimates for the 1960s model were taken from the average of the 1951/52 (Rand 1956) and the 1974/75 (Condy 1978b) estimates, estimates for the 1980s model were taken from the average of the 1981/2 and 1987/88/89 estimates (Kerley 1983a; Wilkinson and Bester 1990a; Bester et al. 2003), and the final estimate for the 2000 model is from the 2003/04 estimate (Hofmeyr et al. 2006). As Antarctic Fur Seals are at the islands only for 4 months of breeding their time at the islands was adjusted to just 6 months of the year.

B 1960: 3.3 t

B 1980: 18.2 t

B 2000: 112.8 t

P/B: 0.10 yr⁻¹

This value was estimated as the mean of the Falklands model (Cheung et al. 2005) for the seals and sea lion group (0.136 yr⁻¹) and Prince William Sound model (Frost 1999; Okey and Pauly 1999) for Pinnipeds (0.06 yr⁻¹).

Q/B: 14.06 yr⁻¹

Calculating the consumption rate using the equation of Nagy et al. (1999) and taking into account the calorific content of the diet, a value of 14.06 yr⁻¹ was estimated using Condry's (1981) 'average' seal weights. Using Trites and Pauly's 1998 estimates the value was 16.34 yr⁻¹. This compares well with the Falklands model, with seals and sea lion estimated at 14.23 yr⁻¹ (Cheung and Pitcher 2005). These values contrast to those calculated using the standard processing with the same equation for mammals (Nagy et al. 1999) where the diet is assumed to have an average energetic content of 16.8 kJ.g⁻¹ (having taken digestive efficiency into account), which results in a value of 23.18yr⁻¹. This higher estimate is in line with the estimate for pinnipeds from the Prince William Sound model at 25.55 yr⁻¹ (Frost 1999, Okey and Pauly 1999) and is similar to consumption estimates of 23.45 yr⁻¹, which is calculated based on 7% of body mass for fur seals scaled for feeding occurring for 335 days of the year (allowing for fasting for the remaining days) (Condry 1981 referencing Oritsland 1977, Laws 1977, Condry 1981, Knox 2007b). Both these estimates are considerably higher than the value used here.

Diet Composition: Diet of Antarctic Fur Seals at Marion data dominated by myctophid fish (96%), supplemented by cephalopods (4%) with other contributions being less than 1% (Makhado 2002). At Marion, predation of king penguins, macaroni penguins and less commonly rockhopper penguins has been observed (Hofmeyr and Bester 1993, unpublished data) but hardly ever contained in scats (possible explanation regarding position of colonies) (Makhado et al.

2008). The only crustacean found was *Nauticariss marionis* (and only in 1999, the only occurrence between 1989 and 2001 (Klages and Bester 1998; Makhado 2002; Makhado et al. 2008). The diet matrix was therefore set with *Myctophid Fish* comprising 90% of the diet, *Small Pelagic Fish* forming 4.8% and cephalopods 4%. Penguin contributions to the diet were included (0.2% King, 0.2% Macaroni, 0.1% Rockhopper) and 0.1 % assigned to each of the *Large Demersal Fish*, *Large Nototheniid Demersal Fish*, *Small Continental Slope Demersal Fish*, *Small Inshore Demersal Fish*, *Large Pelagic Fish*, *Patagonian Toothfish*, and finally the *Benthic Decapod*, *Nauticariss marionis*.

4. Sub-Antarctic Fur Seals (MSF)

Species: *Arctocephalus tropicalis*

Biomass: Sub-Antarctic Fur Seal estimates of pups were taken from Hofmeyr et al. 2006 (for Marion) and numbers from Tables 1 and 2 in Bester et al. 2003; using the conversion of Kerley (1983) of 1:4.8 for pup to population estimate; and using the 'seal unit mass' of 33.67kg for for Sub-Antarctic Fur Seals (Condy 1981), the biomass was calculated. For each time period an average of the closest estimates to the midpoint of the decade was used. For the 1960s estimates the average between the 1951/52 (Rand 1962) and the 1974/75 (Condy 1978) estimate were used. For the 1980s model the average between 1981/82 (Kerley 1983) and 1988/89 (Wilkinson and Bester 1990a) was used (Bester et al. 2003). All biomass estimates were adjusted for the amount of time spent at the islands, which was based on the breeding cycle and has been estimated as being 10 months of the year.

B 1960s: 107.8t

B 1980s: 1 260.7t

B 2000s: 3 978.0t

P/B: 0.10 (yr⁻¹)

This value was estimated as the mean of the Falklands model (Cheung and Pitcher 2005) for the seals and sea lion group (0.136 yr^{-1}) and Prince William Sound model (Frost 1999, Okey and Pauly 1999) for Pinnipeds (0.06 yr^{-1}).

Q/B: $14.97 \text{ (yr}^{-1}\text{)}$

Calculating the consumption rate using the equation of Nagy et al. (1999) and taking into account the calorific content of the diet, a value of 14.97 yr^{-1} was estimated using Condy's (1981) 'average' seal weights, which is similar to the Q/B value if weight estimates from Trites and Pauly (1998) are used (15.82 yr^{-1}). This compares well with the Falklands model (Cheung and Pitcher 2005), with seals and sea lion estimated at 14.23 yr^{-1} . These values contrast to those calculated using the standard processing with the same equation for mammals (Nagy et al. 1999) where the diet is assumed to have an average energetic content of 16.8 kJ.g^{-1} (having taken digestive efficiency into account), which results in a value of 23.03 yr^{-1} , which as noted for the Antarctic Fur seals is closer to the estimates returned when the consumption is calculated using the % body mass. From the literature annual consumption for fur seals has been estimated at 7% body mass for 335 days of the year (to allow for fasting). This equates to $23.45 \times$ mean body mass (Laws 1977) (Condy 1981 referencing Oritsland 1977, Laws 1977, Knox 2007b) which is similar to the Q/B estimated for pinnipeds 25.55 yr^{-1} by Frost (1999) in Okey and Pauly's (1999) version 2 of the Prince William Sound Model.

Diet Composition: The diet of this species is dominated by myctophid fish (99%) with a small contribution of cephalopods (1%) (Makhado 2002; de Bruyn et al. 2009). Myctophid species are primarily *Electrona carlsbergi*, *E. subaspera*, *Gymnoscopelus fraseri*, *G. piabilis*, *Krefftichthys andersoni*, *Electrona antarctica* and *Protomyctophum choriodon* (Klages and Bester 1998, Makhado 2002, Ryan and Bester 2008). Diets vary seasonally with different species of Myctophids being taken in summer vs winter (Klages and Bester 1998, Makhado 2002). The diet of this group was set to *Myctophid Fish* 95%, *Small Pelagic Fish* 3.2%, cephalopods 1%, and each of the fish groups (*Large Demersal*, *Large Notothenid Demersal*, *Small Continental Slope Demersal*, *Small Inshore Demersal*, *Large Pelagics* and *Patagonian Toothfish*) all contributing 0.1% (total 0.6%) along with the decapod *N. marionis* (0.1%) and *Large Crustacean Zooplankton* (0.1%). This is in contrast to Antarctic systems described for instance by Laws

(1977) where the diet comprised 50% squid, 45% fish, 5 krill, or diets by Pauly et al. (1998) (citing Rand 1956; Condry 1981; Bester 1987) where large zooplankton 15%, small squid 30%, large squid 15%, *Small Pelagics* 10%, miscellaneous fishes 25%, higher vertebrates 5% were recorded to make up the diet.

Avian fauna

The Sub-Antarctic Skua, Crozet shag, Kelp Gull, and Lesser Sheathbill have been omitted from the model. All other breeding birds found at the islands are included in the model. Biomass estimates for all bird groups were made using extrapolations from breeding population estimates from published the literature. Complete datasets for both islands were not available as surveys on Prince Edward (PE) island were not conducted annually. In instances where similar trends were observed for both islands, the proportional relationship established in years where data were available was used to make estimates for PE when data were not available. Alternatively, in instances where data showed dissimilar trends, linear regressions between known data points for the PE island populations were used. For production to biomass rates, survival rates from the literature were used to generate mortality estimates using the relationship $\text{survival} = e^{-Z}$, based on the assumption that total mortality, under the condition assumed for the construction of mass-balance models, is equal to production over biomass (Christensen et al. 2008). For consumption estimates the field metabolic rates of Nagy et al. (1999) for specific bird orders were used. Calorific content of the diet for each group was determined from a review of literature. Values for each group were 11 kJ.g^{-1} for cephalopods, 15 kJ.g^{-1} for crustaceans, 27 kJ.g^{-1} for fish (assumed to be predominantly myctophid in origin) and 16 kJ.g^{-1} for other diet types (Abrams 1985). Values were taken from (Croxall 1984; Abrams 1985; Hunter 1985; Brown 1987; Chérel and Ridoux 1992; Adams et al. 1993; Kirkman et al. 2000; Tierney et al. 2002) and values therein (including Croxall et al. 1984 and Clark and Prince 1980 in Adams et al. 1993; Croxall and Prince 1982 and Burger 1981 in Hunter 1985; Doige and Croxall 1985 and Guinet et al. 1996 both in Kirkman et al. 2000. Species specific diets for each group were used in the calculation, and digestive efficiency estimates, unless specified where data exists for particular species, were set to 80% (Clark and Prince 1981 in Abrams 1985) (Unassimilated Consumption (UC) therefore set to the default value of 0.20).

5. King Penguins (PKI)

Species: *Aptenodytes patagonicus*

Biomass: It is thought that the earliest estimates of King Penguin numbers at the islands are inaccurate (an estimate of 2 million birds by Williams et al. 1975) (Crawford et al. 2003a), and there is a consensus in the literature that the population has not changed significantly over the past four decades. Therefore only one estimate has been calculated. The number of breeding pairs on Marion and Prince Edward (PE) island combined 221 00 (218 000 on Marion, and 3 000 on PE) (Crawford and Cooper 2003) (Crawford and Cooper 2003). This number is a midpoint between the upper estimate of van Heezik (1995) (380 000 pairs) and Crawford et al. (2003d) (165 000 pairs). This amounts to a total of 442 000 birds, using an average mass of 12kg (Ryan and Bester 2008) and gives a total of 5 304 t (close to the estimates given in Ryan and Bester (2008) of 440 000 on Marion and 6 000 PE, giving a total biomass of 5 352 t). Because approximately 20% of the birds do not breed in any one year, this estimate has been increased by 20% and the final estimate is 6 364.8 t. King penguin breeding cycle takes more than 1 year to complete (Duplessis et al. 1994) and so they are resident at the islands year round (Brown et al. 1990) therefore no adjustment to the biomass has been made to account for the time they spend outside of the area even though it is well known that they have extensive foraging ranges.

Biomass: 6 343 t

P/B: 0.125 (yr⁻¹)

Annual survival has been reported as between 82-93% (Schreiber and Burger 2001). Using a conversion from survival (s) to mortality (z) of $s=e^{-z}$ the estimate would range between 0.08 and 0.20. A value of 0.125 yr⁻¹ was used which fits between the higher estimates used in the Kerguelen model of 0.06 yr⁻¹ (Pruvost et al. 2005) from Orstrand and Irons (1999) in the Prince William Sound model (Okey and Pauly 1999) and the 0.05 yr⁻¹ used in the Falklands model (Cheung and Pitcher 2005) (taken from Heymans and Pitcher 2002), and the 0.2 yr⁻¹ used in the Antarctic Peninsula model (Cheung and Pitcher.2005)

Q/B: 42.46 (yr⁻¹)

Using Nagy et al.'s (1999) field metabolic rate equation for penguins (Order: Sphenisciformes equation $C = 4.53M^{0.795} \text{ kJ.d}^{-1}$) with the average bird weight of 12kg (Ryan and Bester 2008), taking into account diet preferences (see diet section) and energy content, digestion efficiency of 76%, water content of diet assumed to be 70%, the consumption to biomass ratio was calculated as 42.46 yr^{-1} . This compares well with calculations that result from Ellis and Gabrielson's (2001) equations where $Q/B = 40.87 \text{ yr}^{-1}$. For the King Penguins at the Iles Crozet, Bost et al. (1997) calculated the average per day ingested was 2.4kg. A calculation of consumption for the year would be 67.3 yr^{-1} using (Abrams 1985) weight estimate of 13kg ($2.4\text{kg} \times 365 = 876\text{kg/biomass}$) or 73 yr^{-1} if weight is 12 kg as in Ryan and Bester (2008). If the birds only feed 2 out of 3 days the estimate would be 36 yr^{-1} ($2.4 \times 200 = 480/13$). No accounting for diet quality was made in this estimate. Estimates of Q/B made from feeding studies result in high consumption rates for these birds. Putz and Bost (1994) examined the feeding behaviour of free ranging king penguins from October to November in 1991. Using the average daily intake of food (2.32 kg.d^{-1}) from an average of 132 food ingestion events per day over a period of 125 days would give a Q/B ratio of 65.138 yr^{-1} ($2.32 \times 365/13$) (Abrams average weight 13kg). For the Kerguelen model a Q/B value of 67.9 yr^{-1} (from total prey B of 1.99 t.km^{-2}) was calculated (Pruvost et al. 2005), but this was considered too high, as was the estimate of 38 yr^{-1} (based on 1985 data) from (Cherel et al. 2005). The value of 12 yr^{-1} from the Weddell Sea model (Jarre-Teichmann et al. 1997) was used for the Kerguelen model (Pruvost et al. 2005) which was considered to be in line with other similar systems (e.g. 18 year^{-1} for the Southern Plateau, New Zealand; (Bradford-Grieve et al. 2003)). This is in contrast to the Falklands model which has a value of 80yr^{-1} for Q/B for all penguins (Cheung and Pitcher 2005).

Unassimilated Consumption: 0.24

Assimilation efficiency for King Penguins was estimated to be 81% on a cephalopod diet (Adams 1984, Brown 1989). Estimates for King Penguins fed on fish (75.5%) and squid (73%) (Adams 1984, and Adams unpublished, both in Adams 1993) suggest the value should be lower and has been set to 0.76 (or UC or 0.24), which is in line with the other penguin species in this model.

Diet Composition: The King Penguin diet for this model has been set to 79% *Myctophid Fish*, 6% *Small Pelagic Fish*, 7% of each of *Small Cephalopods* and *Large cephalopods*, and 0.5% of each of the two crustacean zooplankton groups. These estimates were based on data from the PEIs which shows the diet to consist predominantly of Myctophid fish (86% wet mass; species composition dominated by *Krefftichthys anderssoni*, *Protomyctophum tenisoni*, *Electona carlsbergi*) and cephalopods (14% wet mass, dominated by *Kondakovia longimana*) with crustaceans forming a very small contribution (<1%) (Adams and Klages 1987; Ryan and Bester 2008). At the Crozet islands, the King Penguin diet is also dominated by fish at 99% of the diet with Myctophids comprising approximately 86% (*E. carlsbergi* 73% and *K. anderssoni* 13%) (Putz and Bost 1994). At Kerguelen findings also show the diet dominated by fish (95.3% of prey by number, with the eel-cod *Muraenolepis marmoratus* is more abundant (56.5%) than the myctophid, *Krefftichthys anderssoni* 32.9%) (Bost et al. 2002).

6. Macaroni Penguins (PMA)

Species: *Eudyptes chrysolophus*

Biomass: Biomass estimates were calculated making extrapolations from data of breeding pairs. For the 1960s data, data collected in the 1965/66 breeding season were used (Van Zinderen Bakker Sr et al. 1971; Williams et al. 1975). The 1980s estimates are an average of the census from 1983 (Fitspatrick Institute records) and from data representing the late 1980s (Williams et al. 1979; Watkins 1987; Brown 1989; Cooper and Brown 1990). Estimates for the 2000s model were made from the 2002/03 and 2008/09 census (Crawford et al. 2009). Most of the estimates are made only for Marion island although data for Prince Edward (PE) island exists for the late 1980s estimate and the 2001/02 estimates. A linear decline in population at PE was assumed between these two censuses to have an approximate population estimate for all time periods. Data shows that the population decline on PE is greater (50% decline) (Ryan et al. 2003a) than the one on Marion (10-15% decline) (Crawford et al. 2003b). Biomass calculations were made using the weight estimate published in Ryan and Bester (2008) of 4.6kg. These biomass estimates were then adjusted to account for the duration of the year the Macaroni Penguins are at the islands which was estimated as 58% (Cooper and Brown 1990). Although this adjustment has been made, it may well result in a severe underestimate of the population as the proportion of

non-breeders to breeders in a Northern Rockhopper population at Amsterdam Island was shown to be 3.7 times breeders (Guinard et al. 1998) and no accounting for non breeders has been considered in this estimate.

Biomass: 1960s: 2 881t

Biomass: 1980s: 2 207t

Biomass: 2000s: 1 786t

P/B: 0.185 (yr⁻¹)

Annual survival is between 77 and 86% (Schreiber and Burger 2001) which equates to a mortality of between 0.15 and 0.26. A value of 0.185 yr⁻¹ was used which is higher than those used in the Kerguelen model (Pruvost et al. 2005) with a value of 0.06 yr⁻¹ from Orstrand and Irons (1999) in the Prince William Sound model (Okey and Pauly 1999) and lower than the 0.2 yr⁻¹ used in the Antarctic Peninsula model (Cheung and Pitcher.2005)

Q/B: 76.75 (yr⁻¹)

Using the field metabolic equation of Nagy et al. (1999), for penguins (Order: Sphenisciformes equation $C = 4.53M^{0.795} \text{ kJ.d}^{-1}$) with the energy content of the preferred diet taken into account, along with digestive efficiency, water content assumed 70%, and Ryan and Bester (2008) mass estimates (4.6kg) a consumption estimate of = 76.75 yr⁻¹ was calculated. In comparison, using Ellis and Gabrielsen's (2001) equation Q/B is higher at 87.89 yr⁻¹. The higher Q/B in comparison to the King Penguins is a reflection of the lower average energetic content of the diet (24.88 kJ.g⁻¹ for King penguins versus 16.75kJ.g⁻¹ for Macaroni penguins) reflecting the higher contribution of zooplankton in Macaroni diets as opposed to the predominantly myctophid diet for King penguins. An estimate made by Brown (1989) based on energy requirements and food consumption of Eudyptes penguins at the PEIs found the total estimated food consumption over the breeding season (about 200 days) for both Macaroni and Rockhopper Penguins to be 165 800 tonnes. As 75% of the population at that time was Macaroni penguins (3883t Macaronis: 1040t Rockhoppers Brown 1989), the Q/B estimate for the year would have been 58.7 yr⁻¹ ((125

000t/200days*365days) /3883t). This estimate is higher than that used for the Kerguelen model estimates for Macaroni penguins with a Q/B 46 yr⁻¹ (Cherel et al. 2005; Pruvost et al. 2005).

Unassimilated Consumption: 0.24

A value of 76% efficiency was used for Macaroni Penguins, as was used by Brown (1989). This estimate was supported by a summary of assimilation efficiencies for other penguins (African penguins (previously ‘Jackass’ penguin), 74% on a diet of fish (Cooper 1977), King penguins 81% on a cephalopod diet (Adams 1984), fed on fish (75.5%) and squid (73%) (Adams 1984, and Adams unpublished, both in Adams 1993).

Diet Composition: Diet is dominated by crustaceans (75%), followed by small pelagic fish (18%) (dominated by Myctophids), and cephalopods (7%). These estimates were based on reconstituted mass by Cooper et al. (1990), and higher contributions of cephalopods found by Brown (1989) (Crustaceans 62%, Fish 25%, Cephalopods 13%). In Ryan and Bester (2008) the summary of Macaroni penguin diets (Crustacea 79%, Squid 3% and Fish 18%) based on data from (Brown et al. 1990; Crawford et al. 2003b). There is seasonality in the diets, with the largely euphausiid diet (>90%) for chicks being replaced by a completely fish and cephalopod diet at the end of chick rearing season (Brown 1989). Of the myctophid fish in the diet, *K. anderssoni*, *Protomyctophum tenisoni*, *P. normani* dominate. The most important of the cephalopod species is for the PEIs is Marion and PE *Kondadovia longimana* (Cooper et al. 1990).

7. Southern Rockhopper Penguin (PSR)

Species: *Eudyptes chrysocome filholi*

Biomass: A value of 2.7kg was used as the average bird weight for Rockhopper penguins (Ryan and Bester 2008). Biomass estimates were made from population estimates of breeding birds. An estimate of 270 000 breeding birds was made (Crawford, unpublished) from the van Zinderen Bakker (1971) total population estimates of 1 million birds in 1951/52 using a survival rate of 84%, and the breeding age assumed to start at 4.7 years based on Northern Rockhoppers (Guinard et al. 1998). As Crawford et al. 2003c point out, the early estimates vary widely, but the estimates between 1965/66 and 1987/88 have a mean of about 169 000 pairs (SD 66 000)(n=4),

not dissimilar from 1994/95 = 173 000; and 1996/97 = 150 000. Mean from 1965/66 to 1996/97 = 167 000 pairs (SD 52 000) (n=6). The variation may also be linked to the timing of the census taken in the 1970s (Williams et al. 1975; Siegfried 1978; Williams et al. 1979) where in some instances this would have occurred after many of the birds would have left the islands (Crawford, unpublished). Estimates for the 1980s were made from Cooper and Brown (1990, with cross referencing to the Fitzpatrick Institute records, Williams et al. 1979, and Cooper unpublished data), and for 2000 model from the average of the 2002/03 (Crawford and Cooper 2003) and 2008/09 estimates (Crawford et al. 2009). These estimates do not capture the peak of the Rockhopper population which occurred in the mid 1990s at over 150 000 pairs on Marion (Woehler and Croxall 1997; Crawford and Cooper 2003), which now has approximately 45 000 pairs (Crawford et al 2009). On PE census in 1987 (Cooper and Brown 1990) was 35 000, and in 2001/2 was 45 000, so overall decrease for both islands is approximately half the population. Adjustments to the biomass estimates to account for the amount of time these penguins spend in the vicinity of the islands was set at 58% of the year (Cooper and Brown 1990). As with the Macaroni estimates this may in fact result in a large underestimate of the biomass at the islands, as the ratio of breeding to non breeding birds may be as high as 3.7 which was found for a population of Northern Rockhoppers (Guinard et al. 1998).

Biomass: 1960s: 846t

Biomass: 1980s: 541t

Biomass: 2000s: 306t

P/B: 0.16 (yr⁻¹)

The value is close to the value derived from the survival for Northern Rockhopper penguins on Amsterdam Island which was 84% (Guinard et al. 1998) and equates to a mortality estimate of 0.17 yr⁻¹ ($z = -\ln(\text{survival})$). This estimate is higher than the 0.06 yr⁻¹ used in the Kerguelen model (Pruvost et al. 2005) (taken from Orstrand and Irons (1999) in the Prince William Sound model (Okey and Pauly 1999)) and lower than the 0.2 yr⁻¹ used in the Antarctic Peninsula model (Cheung and Pitcher.2005).

Q/B: 93.70 (yr⁻¹)

Using the Field Metabolic Equation of Nagy et al. (1999), for penguins (Order: Sphenisciformes equation $C = 4.53M^{0.795} \text{ kJ.d}^{-1}$) using the mass estimates summarised in Ryan and Bester (2008), with the energy content of preferred diet taken into account along with digestive efficiency, water content assumed 70%, and Ryan and Bester (2008) mass estimates (2.7kg), a consumption to biomass estimate of $= 93.70 \text{ yr}^{-1}$ was calculated. This is higher than the estimate of 60 yr^{-1} for the Rockhopper population at Kerguelen, even though this number was considered too high to be accurate and an estimate of 12 yr^{-1} was used for diving seabirds (Pruvost et al. 2005). Calculation of the Q/B estimates for this species at Marion can also be done using the energy requirement for food as specified by Brown (1989). With the total estimated food consumption over breeding season (about 200 days) for both Macaroni and Rockhopper penguins being 165 800 tonnes, and the Rockhopper population forming 26.75% of the population at that time, the Q/B ratio can be estimated as $(44268\text{t}/200 \times 365/1040\text{t (historic biomass from 1980s)}) = 77.68 \text{ yr}^{-1}$. This estimate is high as the birds consumption is during their breeding season only, and not an accurate measure for the entire year. However, as the estimate that is relevant for this study need only cover the time period for which the birds are at the islands (i.e. their breeding season) the estimate may be considered appropriate. The adjustment for the time period spent at the islands is taken into consideration in the Biomass term.

Unassimilated Consumption: 0.24

A value of 76% efficiency was used for Macaroni Penguins, as was used by Brown (1989). This estimate was supported by a summary of assimilation efficiencies for other penguins (African penguins (previously 'Jackass' penguin), 74% on a diet of fish (Cooper 1977), King penguins 81% on a cephalopod diet (Adams 1984), fed on fish (75.5%) and squid (73%) (Adams 1984, and Adams unpublished, both in Adams 1993).

Diet Composition: Diet composition was based on data in Brown and Klages (1987) and Brown et al. (1990) (summarized in Ryan and Bester 2008), with crustacean zooplankton forming the bulk of the diet (81%). This component was dominated by *Large Crustacean Zooplankton* (50%), followed by *Small Crustacean Zooplankton* (26%) and included a contribution of the

Benthic Decapod (Nauticaris marionis) (5%) and *Other Zooplankton* (10%). Fish (7%) (dominated by *Myctophid Fish* but including some *Small Inshore Demersal Fish* species) were the next most important group, followed by *Small Cephalopods* (2%). A higher contribution of fish and cephalopods was recorded by Cooper et al (1990) when working with reconstituted mass (crustaceans 84%, fish 11%, Cephalopods 5%). Crustacean zooplankton species included the dominant euphausiid, *Euphausia vallentini*, as well as *Thysanoessa macrura*, *T. gregaria*, *T. vicina*, and the amphipods, *Themisto gaudichaudii* and *Primno macropa*. The fish species were dominated by the Myctophids, *Krefftichthy andersoni*, *Protomychophum tenisoni*, *P. normani*, *P. bilini*, *Electrona carlsbergi*, *E. subaspera*, *Champscephalus gunnari*, as well as the small pelagic *Paranotothenia magellonica*. The most important of the cephalopod species is for the PEIs is Marion and PE *Kondadovia longimana* (Cooper et al. 1990).

8. Gentoo Penguins (PGE)

Species: *Pygoscelis papua*

Biomass: Population estimates for Gentoo Penguins are made from extrapolations from breeding pair numbers. Estimates for the 1960s are based on van Zinderen Bakker's 1965/66 estimates (in Williams et al. 1975). The 1980s estimates are from Cooper and Brown (1990), and the 2000s estimates are from the average of the estimates from the 2002/03 and 2008/09 season (Crawford et al. 2003a; Crawford et al. 2009). Because the breeding season for the Gentoo penguin is approximately 1 year, and these birds do not forage more than 40km from the coast, they are assumed to be resident at the islands year round and no adjustment for time spent away from the islands was made for this species.

Biomass: 1960s: 15t

Biomass: 1980s: 19t

Biomass: 2000s: 18t

P/B: 0.20 (yr⁻¹)

The value is taken from the Cheung and Pitcher (2005) model for the Adelie penguin with an assumed longevity of 5 years. This value was supported by the annual survival of Gentoo Penguins which is 80% (Schreiber and Burger 2001). Calculation of a mortality estimate (using $z = -\ln(\text{survival})$) results in a mortality estimate of approximately 0.22 yr^{-1} .

Q/B: $62.50 \text{ (yr}^{-1}\text{)}$

Using the field metabolic equation of Nagy et al. (1999) for penguins (Order: Sphenisciformes eq $C = 4.53M^{0.795} \text{ kJ.d}^{-1}$) using the mass estimates summarised in Ryan and Bester (2008) with the energy content of preferred diet taken into account, along with digestive efficiency, water content assumed 70%, and Ryan and Bester (2008) mass estimates (6.0 kg) a consumption estimate of 62.50 yr^{-1} was calculated. This is higher, but not dissimilar to the estimate of 55 yr^{-1} (assumed typing error '5' should have been '55' using Nagy 1987 equation) in Pruvost et al. (2005), cross referencing Cherel et al. 2005.

Unassimilated Consumption: 0.20

The Gentoo penguin assimilation efficiency was set to 80% (Clark and Prince 1981 in Abrams 1985).

Diet Composition: The diet of the Gentoo Penguins was based on the summary in Ryan and Bester (2008) with additional information from (Lacock et al. 1984; Adams and Wilson 1987; Adams and Klages 1989). Fish constituted the bulk of the diet (59%). This comprised 19% *Large Notothenid Demersal Fish* (recorded as *Notothenia squamifrons*, a synonym for *Lepidonotothen squamifrons*; Adams and Wilson 1987, Adams and Klages 1989), and 20% of each of the *Small Continental Slope Demersal Fish* along with the *Small Inshore Demersal Fish* (e.g. *Harpagifer georgianus* (La Cock et al. 1984)). *Small Cephalopods* contributed just 1%, while the crustacean zooplankton formed the bulk of the remaining diet (37%). *Nauticaris marionis*, the *Benthic Decapod* was a large component of the crustacean diet (15%) (La Cock et al. 1984, Adams and Wilson 1987), with *Large Crustacean Zooplankton* (predominantly *Euphausia vallentini* (Adams and Wilson 1987, Adams and Klages 1989)) and *Small Crustacean Zooplankton* combined contributing another 22%. Finally *Other Zooplankton* contributed the remaining 3%. Diets have been found to vary seasonally (La Cock et al. 1984), with differences in contributions of the

main diets, as well as variations in the species composition (Adams and Klages 1989). Gentoo Penguins are known to stay within a range of 40km of the shore (Adams and Wilson 1987) and are not deep divers (dives over 40m are unusual) (Adams and Brown 1983).

9. Wandering Albatross (AWA)

Species: *Diomedea exulans*

Biomass: Estimates were made from extrapolations of estimates of breeding populations. Estimates for the 1960s model were made using data from van Zinderen Bakker (1971) published in Williams et al. (1975). Data for the 1980s model are from population estimates published in Cooper and Brown (1990), and estimates for the 2000s model were made from averages of the 2002/03 season (Crawford and Cooper 2003), and the 2008/09 season (Ryan et al. 2009). No adjustments were made to account for non breeding birds, nor were adjustments made to account for time spent away from the islands as the Wandering albatross take a full year to breed. Many however, breed only every second year, although in years when breeding failure occurs early, they may attempt to breed in two consecutive years (pers comm. G. Jones).

Biomass: 1960s: 27.0 t

Biomass: 1980s: 51.0 t

Biomass: 2000s: 61.5 t

P/B: 0.04 (yr⁻¹)

Annual survival for Wandering Albatross was estimated to be 96% (Schreiber and Burger 2001) [Longevity = 35 years for Wandering albatross (1/35 = 0.03)]. This value is close to mortality estimates of 4.3% (Nelson 1979), and or a mortality value of 0.04 from survival = e^{-Z} (where Z = mortality).

Q/B: 57.10 (yr⁻¹)

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to C=17.9M^{0.6} kJ.d⁻¹ (was C=18.4M^{0.599} kJ.d⁻¹) using the mass

estimates summarised in Ryan and Bester (2008), taking into account local diet preferences summarized in Ryan and Bester (2008), and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be 80% (Clark and Prince 1981 in Abrams 1985), the Q/B estimate was calculated to be 57.10 yr⁻¹. Using this same equation without the local diet information the estimate is lower at 35.84 yr⁻¹. Using the more recent equation of Ellis and Gabrielsen (2001), the value is higher than this estimate at 66.62 yr⁻¹. Using the data provided in Adams et al. (1986), a value of 40 yr⁻¹ can be calculated based on the energy expenditure of free ranging wandering albatrosses *Diomedea exulans*, where the annual food requirements of the population of wandering albatrosses (2 200 to 2 600 breeding pairs) at the PEIs was estimated to be 1.69x10⁶ kg (if 4 800 birds at 8.6 kg each = 41280kg; Q/B= 1 690 000/ 41280 = 40 yr⁻¹).

Diet Composition: Based on Adams et al. (1986) cephalopods accounted for 80% of the diet (divided equally between large and small fractions), *Small Pelagic Fish* and *Myctophid Fish* together contributed 10%, with crustaceans forming the next largest contribution (5% *Large Crustacean Zooplankton* and 3.7% *Small Crustacean Zooplankton*). The remaining contributors were *Other Zooplankton* (1%), and 0.1% contributions of the most abundant penguin species (Kings, Macaroni and Rockhopper) which are consumed as carrion. This estimate has a higher contribution of squid and lower contribution of fish compared to the data summarized in Ryan and Bester (2008) (Crustacea <1%, Squid 59%, Fish 35% other 5%) which is more in line with Cooper et al. (1992) where the contribution of fish to the diet is considered important. Twenty-three taxa of the Cephalopods have been observed in the diets of Wandering Albatross, with *Kondakovia longimana* being the most important (Cooper et al. 1992).

10. Grey-headed Albatross (AGH)

Species: *Thalassarche chrysostoma*

Biomass: The average mass of this species was considered to be 3.7 kg (Ryan and Bester 2008). Biomass estimates were made from extrapolations of estimates of breeding populations. Estimates for the 1960s model were made using data from van Zinderen Bakker (1971) published in Williams et al. (1975). Data for the 1980s model are from population estimates published in Cooper and Brown (1990), and estimates for the 2000s model were made from

averages of the 2002/03 season (Crawford and Cooper 2003), and the 2008/09 season (Ryan et al. 2009). No adjustments were made to account for non breeding birds. Biomass estimates were adjusted to account for time spent away from the islands, which for Grey-headed albatross was considered to be 5 months (i.e. present for 7 months of the year) (Cooper and Brown 1990).

B 1960s: 0.64 t

B 1980s: 28.0 t

B 2000s: 36.5 t

P/B: 0.05 (yr⁻¹)

Based on an annual survival of 95% (Schreiber and Burger 2001), the mortality estimated (from $Z = -\ln(\text{survival})$) was 5% and the P/B ratio was set to 0.05 yr⁻¹. For comparison, Nelson (1979) has an estimate of mortality for Grey-headed albatross of 7%.

Q/B: 49.39 (yr⁻¹)

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to $C = 17.9M^{0.6} \text{ kJ.d}^{-1}$ (was $C = 18.4M^{0.599} \text{ kJ.d}^{-1}$) using the mass estimates summarised in Ryan and Bester (2008), taking into account local diet preferences and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be 80% (Clark and Prince 1981 in Abrams 1985), the Q/B estimate was calculated to be 46.92 yr⁻¹ (For the Kerguelen model (Pruvost et al. 2005), estimate the $Q/B = 62 \text{ yr}^{-1}$ (Cherel et al. 2005)).

Diet Composition: Fish and cephalopods are the two main prey items of the Grey-headed Albatross at the PEIs and the diets were based on Hunter and Klages (1989) and Ryan and Bester (2008) which were very similar. Final assignments of the diets were fish 58.6%, cephalopods 35%, crustaceans 3%, with *Other Zooplankton* 1%, *Benthos* 2%, and penguins 0.4% making up the remainder of the diet. Cephalopods that dominated in terms of species as estimated from regurgitated squid beaks were *Kondakovia longimana* and *Moroteuthis nipovitchi*.

11. Indian Yellow-nosed Albatross (AYN)

Species: *Thalassarche carteri*

Biomass: The average mass of this species was considered to be 2.6 kg (Ryan and Bester 2008). Biomass estimates were made from extrapolations of estimates of breeding populations. Estimates for the 1960s model were made using data from van Zinderen Bakker (1971) published in Williams et al. (1975). Data for the 1980s model are from population estimates published in Cooper and Brown (1990), and estimates for the 2000s model were made from averages of the 2002/03 season (Crawford and Cooper 2003), and the 2008/09 season (Ryan et al. 2009). No adjustments were made to account for non breeding birds and no adjustment was made to account for time spent away from the islands for this species.

B 1960s: 10 t

B 1980s: 36 t

B 2000s: 36 t

P/B: $0.027(\text{yr}^{-1})$

No values for Yellow-nosed albatross were found for the islands. This species is closest in size to the Light-Mantled Sooty albatross and so a value of 0.027 yr^{-1} was assumed.

Q/B: $57.48 (\text{yr}^{-1})$

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to $C=17.9M^{0.6} \text{ kJ.d}^{-1}$ (was $C=18.4M^{0.599} \text{ kJ.d}^{-1}$) using the mass estimates summarised in Ryan and Bester (2008), taking into account local diet preferences and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be 80% (Clark and Prince 1981 in Abrams 1985), the Q/B estimate was calculated to be 57.48 yr^{-1} . This value is similar when using the Nagy et al. (1999) equation without local diet preferences (58.97 yr^{-1}), and lower than that when using Ellis and Gabrielsen's (2001) equation with local diet preferences (67.57 yr^{-1}).

Diet Composition: The diet composition was based on the summary by Ryan and Bester (2008). With *Small Pelagic Fish* dominating (58%), followed by cephalopods (38%) and zooplankton (4%).

12. Light-mantled Sooty Albatross (ALM)

Species: *Phoebastria palpebrata*

Biomass: The average mass of this species was considered to be 2.8 kg (Ryan and Bester 2008). Biomass estimates were made from extrapolations of estimates of breeding populations. Estimates for the 1960s model were made using data from van Zinderen Bakker (1971) published in Williams et al. (1975). Data for the 1980s model are from population estimates published in Cooper and Brown (1990), and estimates for the 2000s model were made from averages of the 2002/03 season (Crawford and Cooper 2003), and the 2008/09 season (Ryan et al. 2009). No adjustments were made to account for non breeding birds, but an adjustment was made to account for time spent away from the islands which was assumed to be 4 months of the year (Cooper and Brown 1990).

B 1960s: 0.2 t

B 1980s: 0.9 t

B 2000s: 3.0 t

P/B: 0.027 (yr⁻¹)

Annual survival estimated to be 97.3% (Schreiber and Burger 2001). The mortality estimate ($Z = -\ln(\text{survival})$) therefore, 2.7%.

Q/B: 59.82 (yr⁻¹)

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to $C = 17.9M^{0.6} \text{ kJ.d}^{-1}$ (was $C = 18.4M^{0.599} \text{ kJ.d}^{-1}$) using the mass estimates summarised in Ryan and Bester (2008), taking into account local diet preferences and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be

80% (Clark and Prince 1981 in Abrams 1985), the Q/B estimate was calculated to be 57.04yr^{-1} . This value is similar to the Q/B estimate without diet preferences (57.24yr^{-1}) and lower than that estimated using Ellis and Gabrielsen's (2001) equation with local diet preferences (67.03yr^{-1}). These estimates are all lower than that in the Kerguelen model (81yr^{-1}) (Cherel et al. 2005; Pruvost et al. 2005).

Diet Composition: Pelagic fish dominated the diet (50%), followed by squid (46%) the remainder comprising of zooplankton. Slight deviations from the summary of Ryan and Bester (2008; crustacea 4%, cephalopods 34%, fish 46%, other 16%) with studies by Cooper and Klages (1995) and Berruti and Marcus (1978) taken into account. Although bird remains have been recorded in the Sooty albatross diets (Cooper and Klages 1995), this component has not been included in the diet description.

13. Dark-mantled Sooty Albatross (ADM)

Species: *Phoebastria fusca*

Biomass: The average mass of this species was considered to be 2.5 kg (Ryan and Bester 2008). Biomass estimates were made from extrapolations of estimates of breeding populations. Estimates for the 1960s model were made using data from van Zinderen Bakker (1971) published in Williams et al. (1975). Data for the 1980s model are from population estimates published in Cooper and Brown (1990), and estimates for the 2000s model were made from averages of the 2002/03 season (Crawford and Cooper 2003), and the 2008/09 season (Ryan et al. 2009). No adjustments were made to account for non breeding birds but an adjustment was made to account for the birds spending time away from the islands which was estimated to be 2.5 months (Cooper and Brown 1990).

Biomass: 1960s: 4 t

Biomass: 1980s: 11 t

Biomass: 2000s: 11 t

P/B: $0.027\text{ (yr}^{-1}\text{)}$

In the absence of a value for Dark-mantled Sooty Albatross the estimate for Light-mantled Sooty Albatross of 0.027 yr^{-1} was used (Schreiber and Burger 2001).

Q/B: $68.11 \text{ (yr}^{-1}\text{)}$

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to $C=17.9M^{0.6} \text{ kJ.d}^{-1}$ (was $C=18.4M^{0.599} \text{ kJ.d}^{-1}$), using the mass estimates summarised in Ryan and Bester (2008), taking into account local diet preferences and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be 80% (Clark and Prince 1981 in Abrams 1985), the Q/B estimate was calculated to be 68.11 yr^{-1} . This is higher than the estimate without local diet preferences (59.91 yr^{-1}) and lower than that estimated using Ellis and Gabrielsen's (2001) equation with local diet preferences (80.09 yr^{-1}).

Diet Composition: The diet summary in Ryan and Bester (2008) is based on Berruti and Harcus (1978) where cephalopods were found to dominate (42%), followed by fish (33%). Crustaceans form less than 1 % of the diet, with 'other' forming the remainder of the diet (25%). For the matrix used in this model, data from Cooper and Klages (1995) was included and cephalopod and fish estimates (all small pelagic/*Myctophids*) were increased by 13% (to 55%) and 8% (to 41%) respectively, and total zooplankton contribution extended to 4%. The most important species of cephalopod was *Kondakovia longimana*. Cephalopod families Onychoteuthidae, Crachiidae and Histioteuthidae were all important. Although bird remains have been recorded in the Sooty albatross diets (Cooper and Klages 1995), this component has not been included in the diet description.

14. Giant Petrels (BGP)

Species: *Macronectes giganteus* and *Macronectes halli*

Biomass: Both the Northern and Southern Giant Petrels are included in this group. The average mass of the Northern Giant Petrel is 4.0kg, while the Southern Giant Petrel is slightly larger at 4.5kg (Ryan and Bester 2008). Biomass estimates were made from extrapolations of estimates of breeding populations for each of the three models. No data for Giant Petrels was available for the 1960s model, so the data from 1977 was used (Williams et al. 1979). Data for the 1980s estimate

was taken from Cooper and Brown (1990) and finally data from Crawford et al. (2003d), Crawford and Cooper (2003) and Ryan et al. (2009).

Biomass: 1960s: 10 t

Biomass: 1980s: 19 t

Biomass: 2000s: 17.5 t

P/B: 0.07 (yr⁻¹)

No value was available for Northern Giant Petrels, and so the value of 93% survival for Southern Giant Petrels (Schreiber and Burger 2001). was used for the composite group (range between 90-96%, resulting in mortality estimates of between 0.04 and 0.1 yr⁻¹)

Q/B: 32.24 (yr⁻¹)

Using the field metabolic rate equation of Nagy et al. (1999) for Procellariiformes, adjusted in Ellis and Gabrielsen (2001) to $C=17.9M^{0.6} \text{ kJ.d}^{-1}$ (was $C=18.4M^{0.599} \text{ kJ.d}^{-1}$), using the mass estimates summarised in Ryan and Bester (2008), taking into account local diet preferences and energy content of prey, with water content assumed 70%, and digestive efficiency assumed to be 80% (Clark and Prince 1981 in Abrams 1985), Q/B calculations for both the Southern and Northern Giant Petrels were 31.67yr⁻¹ and 34.94 yr⁻¹ respectively. The value of 32.24.yr⁻¹ was calculated from the weighted contribution of these two species (of approximately 5:1, Southern Giant Petrel: Northern Giant Petrel as a general approximation over all three time periods).

Diet Composition: Giant petrels are both predators (see Ryan et al. 2008) and scavengers (de Bruyn and Cooper 2005; de Bruyn et al. 2007) with a large contribution of their diet coming from penguins (between 67 and 80%). The diet composition was of the group was based on Hunter and Brooke (1992). Southern Giant Petrels dominate in terms of numbers so the diet was calculated using weighted contributions of the two species based on their biomass contribution to the group. A combined diet was set to seals 3.5%, penguins 79%, *Prions and Petrels* 8.6%, *Small Pelagics* and *Myctophids* 3.5%, cephalopods 5.35% and crustaceans 0.05%. For each of the three time periods, the contribution to the diet of each functional group within these broad categories

was determined according to that particular groups relative contribution to the biomass of that group (ie. weighted). For each time period, this matrix had to be adjusted to balance the model. The contribution of *Prions and Petrels* to the diet had to be reduced by 1% in the 1960s model, and by 5% in the 1980s and 2000s models to allow the model to balance. In each case diet was reassigned to the penguin contribution. The most logical explanation for this issue is related to the probable underestimate of the Prions and Petrels as the census are considered underestimates (Ryan and Bester 2008). This finding is also supported by simulations of this model which suggest a higher prion and petrel population exists.

15. Prions and Petrels (BPP)

Species: This group includes the Fairy Prion (*Pachyptila turtur*), Salvin's Prion (*Pachyptila salvini*), Blue Petrel (*Halobaena caerulea*), Great-winged Petrel (*Pterodroma macroptera*), Soft-plumaged Petrel (*Pterodroma mollis*), Kerguelen Petrel (*Lugensa brevirostris*), Grey Petrel (*Procellaria cinerea*), White-chinned Petrel (*Procellaria aequinoctialis*), Grey-backed Storm Petrel (*Garrodia nereis*), Black-bellied Storm Petrel (*Fregetta tropica*), South Georgian Diving Petrel (*Pelecanoides georgicus*), Common Diving Petrel (*Pelecanoides urinatrix*), Antarctic tern (*Sterna paradisaea*), Kerguelen tern (*Sterna virgata*)

There are no accurate estimates for the small seabird populations from the 1980s. Cooper and Brown (1990) summarized the bird populations and found that the estimates for many of the species were limited to 1000s, 10 of 1000s, or 100s of 1000s. With time these estimates have been refined (in the PEI EMP of 1996 and 2005). The most recent collation of data from Ryan and Bester (2008) has been used here. Using average weights for all species from Ryan and Bester (2008) with these population estimates, the combined biomasses for all small seabirds is approximately 283 tons. The Salvin's Prion, Blue Petrel, Great-winged Petrel and White-chinned Petrel dominate the small flying seabird biomass as together they constitute 85.7% of the total (Salvin's prion, 105 000 pairs, Blue Petrel 63 000 pairs, Great-winged Petrel 23000 pairs, White-chinned Petrel 36 300 pairs). The Soft-plumaged Petrel, Kerguelen Petrel and the Grey Petrel contribute 3.3%, 5.0% and 4.3% to the total small seabird biomass. Finally, the Fairy prion, Grey-backed petrel, Black-bellied storm petrel, South Georgian Diving Petrel, Common Diving Petrel and the two terns, all contribute a total of 5.381t to the seabird biomass, which is less than

2% of the small seabird biomass. The biomass estimates for each group were adjusted to account for the time spent away from the islands (Fugler et al. 1987; Cooper and Brown 1990) and scaled up by a factor of 2 (considered conservative) to represent the whole population and not just breeding birds.

Biomass: 283 t

P/B: 0.16 (yr⁻¹)

As no other estimates were available, a survival rate of 85% was assumed, resulting in a mortality estimate of 0.16 yr⁻¹. This was close to the survival estimate for Salvin's Prion of 84% (Schreiber and Burger 2001) which result in a mortality estimate of 0.17 yr⁻¹. This value is lower than the P/B for surface seabirds in Kerguelen model = 0.3 yr⁻¹ (Pruvost et al. 2005).

Q/B: 191.70 (yr⁻¹)

Using the bird order specific field metabolic rate equations from Nagy et al. (1999) with a summary of the diets of these small birds at the PEIs (Ryan and Bester 2008), accounting for energy in diet, and water content (assumed to be 70%, Nagy et al. 1999), and a digestive efficiency of 0.76. The Q/B estimate of 191.70 yr⁻¹ was calculated from weighted contributions (according to the biomass contributions) of each species included in this group.

Diet Composition: The diet for this group was broadly based on Salvin's Prion and the Blue Petrel because they are the two highest in numbers and biomass. Their diets comprise of crustacea (59% and 66% respectively), cephalopod (9% and 16%), fish (21% and 22%) and 'other' (4%) (Gartshore et al. 1988; Bester et al. 2009). Final numbers for the diet matrix had *Small Crustacean Zooplankton* making the highest contribution to the diet (40%), followed by *Large Crustacean Zooplankton* and *Myctophid Fish* which both comprised 20%. The contribution of *Small Cephalopods* was 12%, followed by *Other Zooplankton* 4%, with *Large Cephalopods* and *Small Pelagics* both contributing 2%.

Unassimilated Consumption: An assimilation efficiency of 76% was used for this group, as was used in previous studies by Brown (1989) which was based on a study of White-chinned petrels fed on crustaceans, squid, fish (Jackson 1986).

Fish

Biomass estimates for the area are almost completely lacking with only one fisheries independent survey having been conducted in April 2001 by the *MV Iris* (Pakhomov et al. 2006). In determining the functional groups for this model, divisions were based on perceived importance of groups as current fisheries targets (e.g. Patagonian toothfish) (Brandao et al. 2002; Brandao and Butterworth 2009) or potential future fisheries targets (Large Nototheniid Demersals, Myctophid fish). The division between large and small groups was made based on maximum fish length (L_{inf}) for any species as listed in fishbase (www.fishbase.org), with the division between large and small being made at 50cm. The fisheries independent survey carried out on the *MV Iris* in the early 2000s provided data on species composition and some relative abundance estimates which are used where appropriate. All biomass estimates are provided in $t.km^{-2}$. Models from neighboring subantarctic islands were used where possible and trawl data from the Kerguelen islands was used. Estimates for both P/B and Q/B were largely taken from data for the Kerguelen model (Pruvost et al. 2005) (see description below). Diet data were taken from information from fishbase (www.fishbase.org) except where region specific data was available.

Calculations for P/B and Q/B for fish species:

P/B values were calculated using 1. Froese and et al. 2000 $M = 10^{(0.566-0.718.\log_{10}L_{inf}+0.021T)}$, where L_{max} is 95% L_{inf} given the assumption no growth parameters are available; or 2. Pauly (1980) $\log_{10}M=0.0066-0.279.\log_{10}L_{inf} + 0.65431.\log_{10}K + 0.4631\log_{10}T$, where L_{inf} is in cm of Total Length, K in yr^{-1} and T in $^{\circ}C$.

Q/B values calculated using 1. Palomares and Pauly (1998), $\log_{10} Q/B = 7.964 - 0.204.\log_{10}W_{inf}-1.96T+0.083.A + 0.532h+0.398d$ where W_{inf} (asymptotic weight in grams) is the weight converted from $W=aL^b$, T is mean environmental temperature ($=1000/(^{\circ}C+273)$), A

is the aspect ratio of the caudal fin indicative of metabolic activity and expressed as the ratio of the square of the height of the caudal fin and its surface area, 'h' and 'd' are dummy variables indicating herbivores (h=0, d=1), omnivores (h=0.5, d=0.5) and carnivores (h=0, d=0). In cases where no length-weight relationships were available, the estimates of W_{inf} were obtained using values of a=1 and b=3. In cases where L_{max} and L_{inf} are available only as standard length and no conversion relationships are given SL:TL ratios were measured from morphologically correct drawings provided in the 'www.fishbase.org' gallery for the species].

16. Sharks and Rays (FSR)

Species: Only 5 shark species have been recorded in the Southern Ocean where their biology is virtually unknown (Cherel and Duhamel 2004). The three most common species are: *Etmopterus granulosus* (lanternsharks), which are small (average size $L=0.3m$), the *Lamna nasus* (porbeagle) which is intermediate in size (average length =1.9m), and the *Somniosus microcephalus* (Greenland Shark/sleeper sharks) which may be considered large (average size 3.9m) (Cherel and Duhamel 2004). For this model, also included in this group is *Bathyrāja tuff*, *Rajella barnardi* and a 'other *Raja* sp'.

Biomass: Catch rates for just one species from this group *Bathyrāja tuff* (Pakhomov et al. 2006) (in this paper as taaf) show very low occurrence of = 0.02 ind.h⁻¹ out of 45.45 ind.h⁻¹ for deep demersals in one of three assemblages considered. The resulting estimate would be very low (at 0.843t) for the system. A biomass estimate for two species of *Bathyrāja* at the Kerguelen islands found 28 431 t, or 12% of the Patagonian toothfish biomass estimate (Duhamel and Hauteceur 2009). Based on this, the estimate was set to 0.12*0.003 (the most recent toothfish survey from the PEIs) = 0.00036 t.km⁻². This is in contrast to the estimate of 0.001 t.km⁻² made in the Kerguelen model (Pruvost et al. 2005).

Biomass: 0.00036 t.km⁻²

P/B: 0.14 (yr⁻¹)

This number is the same as that used for *Bathyrāja irrassa* in the Kerguelen model (Pruvost et al. 2005). An estimate for *Bathyrāja eatonii* returns a similar result (0.16 yr⁻¹). Calculations were

made using the empirical equation of Palomares and Pauly 1989, 1998. ($M = K^{0.65} * L_{inf}^{0.279} * T^{0.463}$).

Q/B: 3.7 (yr⁻¹)

Taken from the value for basking sharks from the Falklands model (Cheung and Pitcher 2005).

Diet Composition: Very little data was available for this group. Diets from fishbase (www.fishbase.org) were used in conjunction with diet data on cephalopods from a neighbouring system (Cherel and Duhamel 2004). *Benthos* contributed 20%, cephalopods 45%, *Small Pelagics* and *Myctophids* contribution 50% and the remainder was distributed evenly between all other fish groups (5% each).

17. Large Demersal Fish (FLD)

Species: This group includes a single flounder species *Neoachirosetta milfordi*, Unicorn/crocodile icefish *Channichthys rhinoceratus*, 3 Grenadier (rattails) *Macrourus holotrachys*, *M. carinatus*, *Coryphaenoides* sp, 3 Morid cods *Antimora rostrata*, *Halargyreus johnsonii*, *Lepidion* sp, a *Halosaur* *Halosauropsis macrochir* and Deep-sea spiny eel *Polyancanthonotus challengerii*, the Sea devil *Ceratius tentaculatus* and the Slickhead *Alepocephalus* sp.

Biomass: Using data from the fisheries independent survey for all assemblages (Pakhomov et al. 2006) the Patagonian Toothfish catch rate was 38.88 ind.hr⁻¹ compared to rate for *Large Demersal Fish* (as categorized for this model) which was approximately 55.45 ind.hr⁻¹. Keeping in mind that the trawls were not targeting Patagonian Toothfish, the Toothfish were probably under represented. A recent trawl survey at Kerguelen showed the Large Demersal fish group to consist of approximately 50% of the Patagonian Toothfish biomass and this estimate was used in combination with the local PT data. *The Large Nototheniid Demersal Fish* were considered to be 12% of the *Patagonian Toothfish* population, which leaves a remaining 38% to be classified as *Large Demersal Fish*. Using this approach with the pre crash Patagonian Toothfish data from the 1980s model (0.075t. t.km⁻²), the approximate value would be 0.0285 t.km⁻². This estimate is less

than that for the Kerguelen model (0.5 t.km^{-2}) (Pruvost et al. 2005) and Falklands model (0.4 t.km^{-2}) (Cheung and Pitcher 2005)].

Biomass: 0.0285 t.km^{-2}

P/B: $0.19 \text{ (yr}^{-1}\text{)}$

This value is based on Kerguelen model for large benthic fishes 0.19 yr^{-1} (Pruvost et al. 2005). The Grenadier/rattail *Macrourus carinatus* has a P/B ratio of 0.18 yr^{-1} . These estimates are lower than those found for Grenadier at the Falklands Islands (3 species, $P/B = 0.431 \text{ yr}^{-1}$ Cheung and Pitcher 2005).

Q/B: $1.98 \text{ (yr}^{-1}\text{)}$

Based on Kerguelen model for large pelagic fishes (Pruvost et al. 2005) a value of 1.98 yr^{-1} was used. Grenadier from the Falklands were found to have a higher Q/B (4.243 yr^{-1}).

Diet Composition: The diet of juvenile *M. carinatus* for the area was dominated by myctophids (82%), followed by pelagic crustaceans (14%) and benthic crustaceans (3%) (Pakhomov et al. 2006). In contrast, the diet of *A. antipodanus* was dominated by squid (85%), pyrosomes (12%) and pelagic crustaceans (3%) (Pakhomov et al. 2006). The diet of *Halargyreus johnsonii* comprises mostly of crustaceans and squid; *Channichthys rhinoceratus* mainly on fishes and occasionally algae, and *Polyacanthonotus challengerii* on benthic invertebrates; *Halosaurus macrochir* predominantly on benthos (www.fishbase.org). This information was used in conjunction with the diet data for large nototheniid demersals group (see below) and the diet matrix was defined as *Myctophids* 22%, *Small Pelagics* 4%, *Large Cephalopods* 19%, *Benthos* 16%, *Large Crustacean Zooplankton* 15%, *Small Crustaceans Zooplankton* 7%, *Other Zooplankton* 4% and *Macrophytes* 13%.

18. Large Nototheniid Demersal Fish (FLN)

Species: This group includes 3 species of large Nototheniids: the Grey Rockcod *Lepidonotothen squamifrons*, the Black Rockcod *Notothenia coriiceps* and the Marbled Rockcod *N. rossii*. *Notothenia rossii* and *N. squamifrons* were noted back in the 1980s to be exploited in

neighboring areas (Duhamel et al. 1983) and selected as potential fishery species for the PEI area by Pakhomov and Bushula (Pakhomov and Bushula 2003).

Biomass: No quantitative assessment exists for this group. Data from Pakhomov et al. (2006) showed *Lepidonotothen squamifrons* was caught at 4.53 and 1.45 ind.hr⁻¹, compared with 35.55 and 1.93 ind.hr⁻¹ for *Dissostichus eleginoides* in community assemblages A and B respectively (which represent different trawl depths) (Pakhomov et al. 2006). The relative contribution of *L. squamifrons* was therefore between 12 and 75 % of the toothfish biomass for these assemblages. The data for Assemblage A is similar to that found for the Kerguelen population (Duhamel and Hauteceur 2009) where *L. squamifrons* and *N. rossi* had a biomass of approximately 10% of the Patagonian toothfish estimate. Using the lower estimate (12% of the Patagonian Toothfish data) with the intermediate estimate of the Patagonian Toothfish data (pre-crash) (0.075t.km⁻²) we get an estimate of 0.00955 t.km⁻² or 4119t.

Biomass: 0.00955 t.km⁻²

P/B: 0.21 (yr⁻¹)

Using the empirical equation of (Palomares and Pauly 1989; Palomares and Pauly 1998) ($M = K^{0.65} * L_{inf}^{-0.279} * T^{0.463}$) for *L. squamifrons* and data from fishbase ($K=0.1$, $T = 3.5C$, and $L_{inf} = 55cm$) a P/B of 0.13 yr⁻¹ was calculated. This returns the same value for *L. squamifrons* as that calculated for the Kerguelen model (Pruvost et al. 2005). *N. rossii* = 0.19, *N. coriiceps* = 0.30 were also calculated for this model. Using the assumption that these three occur in the similar proportions to each other, then the average is P/B=0.21 yr⁻¹. This is similar to the value of 0.370 yr⁻¹ used for the large demersal fish group in the Falklands model (Cheung and Pitcher 2005).

Q/B: 3.4 (yr⁻¹)

The average Q/B ratios of the estimates from the Kerguelen model for *N. rossii* (1.5 yr⁻¹), *N. Coriiceps* (6.2 yr⁻¹) and *L. squamifrons* (2.5 yr⁻¹) were used to determine Q/B for this group (Pruvost et al. 2005). This is similar to the value of 3.8 yr⁻¹ used for the large demersal fish group in the Falklands model (Cheung and Pitcher 2005).

Diet Composition: The diet matrix for this group was constructed using the diet data for *Lepionotothen squamifrons* (grey rockcod) (De Witt et al. 1990; Perissinotto and McQuaid 1992b; Bushula et al. 2005; Pakhomov et al. 2006) and *Notothenia coriiceps* (Blankley 1982). For *L. squamifrons*, Perissinotto and McQuaid (1992b) found the diet dominated by euphausiids and copepods (pelagic zooplankton), while later studies found the diet contained a higher proportion of myctophid fish (53%), followed by salps and polychaetes (20.1% and 16.2% respectively) and crustaceans (7.5%) with a small cephalopod contribution (Pakhomov and Bushula 2003; Pakhomov et al. 2006). In contrast the diet of *Notothenia coriiceps* was found to be dominated by macrophytes (56.6%), molluscs (27.5%), fish (7.5%) and crustaceans (6.5%) with other invertebrates making up the remainder (1.2%)(Blankley 1982). A study of *N. rossi* at Kerguelen also found it to have a predominantly pelagic diet (Duhamel 1982). Based on the above the diet was set to 27% *Myctophids*, 4% *Small Pelagic Fish*, 0.5% *Small Inshore Demersals*, 25.5% zooplankton, 1% cephalopods, 14% *Benthos* and 28% *Macrophytes*.

19. Small Continental Slope Demersal Fish (FSD)

Species: This group includes 10 species: Those that are considered benthopelagic include the nototheniid, Painted Notie *Lepidonotothen larseni*, and 2 eel cods *Muraenolepis orangiensis* and *M. marmoratus*. The Seadevil *Echiodon cryomargarites*, Morid cod *Guttigadus kongi* along with the cod/haddock *Physiculus* spp, are considered bathydemersal, while the remainder in this group: *Zanclus cornutus* (Spiny horsefish), 2 small flounder *Pseudomancopsetta adriashevi* and *Mancopsetta maculata*, a member of the Snailfish group *Liparidae* spp, are demersal.

Biomass: *Lepidonotothen larseni* occurs at a density of 0.2 ind.m⁻² and the mass varies in wet weight from 0.2 to 8 g. If we consider an average fish to weigh 5g, biomass 1g.m⁻² (equivalent to t.km²), using bathymetry data (GEBCO_08 Grid version 20100927; <http://www.gebco.net>) from the vicinity of the islands, an estimate of the shelf area extending from the islands between the depths of 300 m to 1500m is 1695.11 km² (see Table 2.2, Figure 2.3). If we presume that this one species is 1/3rd of the total for this group, 1693.11km² x 3 t/km² = 5079.33 t, or 0.01178 t.km⁻².

Biomass: 0.01044 t.km⁻²

P/B: 0.502 (yr⁻¹)

This value was taken from the Kerguelen model where the P/B for both the small benthic fish group and the 'other benthic fish' was = 0.502 .yr⁻¹ (Pruvost et al. 2005). This value is intermediary between the value used for the 'small demersal fish' from Falklands the model = 0.897 (Cheung and Pitcher 2005) and the species specific value calculated for *Zanclus cornutus* (Spiny horsefish) in the Kerguelen model (P/B = 0.3) (Pruvost et al. 2005) (Based on L_{max} 40, (Heemstra and Duhamel 1990), L_{inf} = 41.7 W_{inf} = 275, A = 1.32 carnivore).

Q/B: 7.33 (yr⁻¹)

The value is taken from the 'other benthic fishes' group from the Kerguelen model (less than 50cm max length) (Pruvost et al. 2005), and again is between the values given for the 'small demersal' group from Falklands model (Q/B of 8.9 yr⁻¹) (Cheung and Pitcher 2005) and the species specific value provided for *Zanclus cornutus* (Spiny horsefish) from Kerguelen model = 2.5 yr⁻¹ (Pruvost et al. 2005).

Diet Composition:

The matrix is based on the diet for *Lepidonotothen larseni* (Bushula et al. 2005) and *Echiodon cryomargarites* (Pakhomov et al. 2006) which both have predominantly pelagic prey (*L. larseni*, copepods 46% and arrow worms 40%; *E. cryomargarites*, mesopelagic hyperiids 68%, gonostomatiid fishes 28%) but as the group includes other species (e.g. the spiny horsefish and flounder) which will have a higher benthic and macrophyte component to their diet (www.fishbase.org), this has been added. This group has benthopelagic species and demersal species in it, therefore the diet reflects both groups: *Macrophytes* 10%; *Benthos* 20%; crustacea 45% (split between large 10% and small 30% and the *Benthic Decapod* (*Nauticaris marionis*) 5%) and *Other Zooplankton* 25%.

20. Small Inshore Demersal Fish (FID)

Species: This group includes 2 Nototheniids *Gobionotothen marionensis* and *G. acuta* as well as the Spiny Plunderfish, *Harpagifer georgianus* (which has been recorded up to depths of 90m).

Biomass: *Gobionotothen marionensis* is endemic to Marion Island (Duhamel et al. 1983) and has a range in mass from 0.2 to 20 g wet weight, and where it is found, occurs at 0.2 ind.m^{-2} . If the average weight for *G. marionensis* were estimated at 10 grams (half way of range) then $= 0.2 \text{ ind} \cdot 10 \text{ g} = 2 \text{ g.m}^{-2}$ (equivalent to ton per km^{-2}). To scale for area in which they would be found: again, using an approximation of the area of the continental slope from 0-1000m (area estimate from a digital map of the bathymetry of the islands - GEBCO) is approximately 1576.02 km^2 (see Table 2.2, Figure 2.3). A value of 1500 km^2 was used which resulted in 3000t. For the 200nm model $= 0.007 \text{ t.km}^{-2}$.

Biomass: 0.007 t.km^{-2}

P/B: $0.32 \text{ (yr}^{-1}\text{)}$

This value is based on species data *G. acuta* taken from the Kerguelen model (Pruvost et al. 2005) and is similar to the value provided in the Falklands model (0.502 yr^{-1}) by Cheung and Pitcher (2005).

Q/B: $6.0 \text{ (yr}^{-1}\text{)}$

This value is based on species data *G. acuta* taken from the Kerguelen model (Pruvost et al. 2005).

Diet Composition: The diet composition for this group was dominated by the *Small Crustacean Zooplankton* (35%), followed by the *Benthic Decapod* (27%), *Benthos* (25%), *Large Crustacean Zooplankton* (10%), and a small *Macrophyte* contribution (3%). This configuration was determined from the diets of *G. marionensis* (diet 54% *Nauticaris marionis*, 30% benthic polychaetes) (Bushula et al. 2005) and *Harpagifer georgianus* (diet amphipods 75% and isopods 18.5%, Blankley 1981; amphipods and isopods 82.5%, polychaetes 10.4% and algae 2.4%, Blankley 1982).

21. Large Pelagic Fish (FLP)

Species: This group consists of 10 species. The Lancetfish, *Alepisaurus brevirostris*; the Barbeled dragonfish *Idiacanthus atlanticus*; the Pearleye *Scopelosaurus hamiltoni*; four genus of

the Barracudinas *Magnisudis prionosa*, *Stemnosudis* spp, *Notolepis* sp, and *Macroparalepis* sp; the Southern driftfish *Pseudoicichthys australis*; Daggertooth *Anotopterus pharao*; and the Snake mackerel *Paradiplospinus gracilis*.

Biomass: The biomass estimate for this group was made following the relative abundance of large pelagic fish in comparison to the estimates made for the Patagonian toothfish and was set to 0.042 t. km^{-2} , less than half of the estimate for the Kerguelen stock (0.0940 t.km^{-2} - model generated, Pruvost et al. 2005). This number should be revised in future when data becomes available.

Biomass: 0.042 t.km^{-2}

P/B: $0.22 \text{ (yr}^{-1}\text{)}$

This estimate was taken from the Kerguelen model for the large pelagics (excluding the Patagonian Toothfish, as done for this model) (Pruvost et al. 2005).

Q/B: $2.56 \text{ (yr}^{-1}\text{)}$

This estimate was taken from the Kerguelen model for the large pelagics (excluding the PT, as done for this model) (Pruvost et al. 2005).

Diet Composition: *Anotopterus pharao* feeds predominantly on mesopelagic fishes (www.fishbase.org). Diet composition was set using this information combined with that of the local Patagonian Toothfish diet data resulted in 50% *Myctophids*, 15% *Small Pelagics*, 10% large cephalopods, 5% small cephalopods and 20% large crustaceans.

22. Patagonian Toothfish (FPT)

Species: This group consists solely of the Patagonian Toothfish, *Dissostichus eleginoides*. The juveniles of this species are semi-pelagic and then become demersal (depth between 150-400m initially, adults migrate to deeper waters greater than 100m) (Dewitt et al. 1990). **Biomass:** A biomass estimate of 1168 tonnes with coefficient of variance of 213% was estimated from the survey voyage of the Iris using swept area for the Patagonian Toothfish (Brandao et al. 2002).

This amounts to a biomass of $1168/434101.4 = 0.00271$ for the Economic Exclusion Zone of the PEI. Considering the coefficient of variance of 213% the upper limit of this estimate may be considered to be 0.005772. This biomass estimate is presumed to be a small percent of the original biomass that would have been in the system prior to the fishery crash of the mid 1990s. If the current estimate is 5% of original biomass, estimated biomass for the 1960s and 1980s model are between 0.054198 and 0.115441. In balancing the model, these ranges were taken into account and the values chosen within this range to satisfy the systems requirements. The highest value was used for the 1960s model (0.09 – required to ‘feed’ the high elephant seal population), an intermediate value of 0.075 was used for the 1980s model (the amount required to get a good fit of the toothfish fishery data in the temporal simulation, see Chapter 4) and a value of 0.00429 in 2000 (close to the upper range of the survey data of that time period). In the Kerguelen model, an estimate for the adults of this species was set at 0.129 t.km^{-2} (Pruvost et al. 2005). A more recent estimate of current biomass at Kerguelen is higher at 0.288 t.km^{-2} (124000t), which is approximately half of the estimated fish biomass for the system in total (245000t, 0.57 t.km^{-2}) (Duhamel and Hautecoeur 2009).

Biomass 1960s: 0.090 t.km^{-2}

Biomass 1980s: 0.075 t.km^{-2}

Biomass 2000s: 0.0043 t.km^{-2}

P/B 1960s: $0.08 \text{ (yr}^{-1}\text{)}$

P/B 1980s: $0.08 \text{ (yr}^{-1}\text{)}$

P/B 2000s: $0.13 \text{ (yr}^{-1}\text{)}$

Population parameters are published in Brandao and Butterworth (2009) (which reference Agnew et al. 2006). The natural mortality $M \text{ (yr}^{-1}\text{)}$ is 0.13; $L_{\text{inf}} \text{ (cm)} = 152$; $K \text{ (yr}^{-1}\text{)} = 0.067$; age at maturity is estimated at 13 years, and the stock-recruitment steepness (h) = 0.75. In the absence of fishing total mortality, $M = K^{0.65} * L_{\text{inf}}^{-0.279} * T(\text{in } ^\circ\text{C})^{0.463}$ (Palomares and Pauly 1998) which equates to $M = (0.067)^{0.65} * (152)^{-0.279} * (4)^{0.463}$? Natural $M =$

0.08 from this calculation; does not match above (0.13). Needs to include fishing mortality in this term: fishing mortality is approx 500t per year. 2000s model: Fishing mortality = Catch/Biomass catch (approximately 100t)/ biomass (1850t) (average of estimates = 0.054). So, natural mortality plus fishing mortality = $0.08 + 0.054 = 0.134$ (similar to the data in Brandao and Butterworth 2009). This figure is less than 0.265 in Bredesen (2003) (from Kock et al. 1985) and the 0.2 in the Kerguelen model (Pruvost et al. 2005). Based on this information the value is set to 0.08 for the 1960 and 1980 models and 0.13 for the 2000s model.

Q/B: $1.6 \text{ (yr}^{-1}\text{)}$

The value used here is from Bredesen's (2003) value, which is based on Kock et al. (1992) and is similar to the Kerguelen model value for Patagonian toothfish adults of 0.105 yr^{-1} (Pruvost et al. 2005).

Diet Composition: Pakhomov and Bushula (2003) and Pakhomov et al. (2006) describe the diet of the Patagonian toothfish where cephalopods dominated at 61% (comprising of *Kondokovia longimana* 12%, *Moroteuthis sp* 47.5%, *Histioteuthis macrohista* 1.2%, and Teuthida (digested) 0.4%) and fish comprised 33.3% (*Myctophids* 18.7%, Gonostoma (Bristlemouths) 1.1% and *Stomias* (Barbled dragonfish) 8.7% (both *Small Pelagics*); *Echiodon* 0.6% (small continental slope demersal), *Anotoptorus* (Daggertooth) 2.8% (large pelagic), Macrouridae 0.7% (large pelagic) and general digested fish 0.7% with crustaceans contributing the least at 0.1%. In comparison to fish sampled from Macquarie islands (Goldsworthy et al 2002 MFR) fish dominated the diets (58%), with cephalopods the second largest component (32%), followed by crustaceans (10%). Based on this information, the diet matrix for this group was therefore set to 0.6% *Small demersal Fish*; 3.5% *Large Pelagic Fish*; 9.8% *Small Pelagic Fish*; 20.1% *Myctophids*; 41% *Large Cephalopods*; 20% *Small Cephalopods*; 5% large crustacean zooplankton.

23. Small pelagics (FSP)

Species: This group consists of 18 species: four Bristlemouth species, *Vinciguerrria attenuata*, *Dyplophos rebainsi*, *Photichthys argenteus*, and a Cyclothone sp; six Barbeled Dragonfish species, *Stomias boa boa*, *Borostomias antarcticus*, *Trigonalampa miriceps*, *Chanciloidus*

sloani, *Malacosteus niger*, *Astronesthes boulengeri*; the Pearleye *Benthabella macropinna*, the flying fish *Cheilopogon pinnatibarbatus altipennis*; the Nototheniid *Paranotothenia magellanica* (previously known as *Notothenia macrocephalata*); Deep-sea smelt *Bathylagus tenuis*; two species of snaketooth *Dysalotus alcocki* and *Chiasmodon niger*, the Bigscale or Ridgehead *Promitra crassiceps*, and the Tubeshoulder *Platytracidae* sp.

Biomass: This biomass estimate was used for the Kerguelen model for small pelagic fish and surveys of this group at these islands showed that 70% of the small pelagic group were Myctophids (by weight caught) (Pruvost et al. 2005). The division between these two small pelagic functional groups was therefore based on this information, though the proportioning between these two groups was set at 75% *Myctophids* and 25% *Small Pelagics* (3.375 t.km⁻² *Myctophids*, 1.125 t.km⁻² *Small Pelagics*). See the section on Myctophid biomass for more information.

Biomass: 1.125 t.km⁻²

P/B: 0.9 (yr⁻¹)

The average value from three models of similar ecosystems were used (Mesopelagic fish = 1 yr⁻¹ (Bradford-Grieve et al. 2003, Southern Plateau, NZ); Myctophids 1.2 yr⁻¹ (Falklands, Cheung and Pitcher 2005); Small pelagic fish = 0.5 yr⁻¹ (Kerguelen, Pruvost et al. 2005). Data from the Kerguelen model were obtained from empirical equations Froese and Binohlan (2000) and Palomares and Pauly (1998) and parameters taken from www.fishbase.org. Summarized: *Electrona antarctica* L_{max} = 10.3 cm, P/B = 0.21 yr⁻¹, Q/B = 5.8 yr⁻¹; *Electrona carlsbergi* L_{max} = 8.9 cm, P/B = 0.59 yr⁻¹, Q/B = 6.9 yr⁻¹; *Gymnoscopelus braueri* L_{max} = 13.2 cm, P/B = 0.6 yr⁻¹, Q/B = 5.5 yr⁻¹.

Q/B: 10.5 (yr⁻¹)

The average value from three models from similar ecosystems were used [Mesopelagic fish = 16 (Bradford-Grieve et al. 2003, Southern Plateau, NZ); Myctophids = 9.4 (Falklands model, Cheung and Pitcher 2005); Small pelagic fish = 6.1 yr⁻¹ (Kerguelen model, Pruvost et al. 2005)].

Diet Composition: Data from Blankley (1982) on *P. magellanica* shows a high contribution of alga to the diet, with crustaceans (including a small contribution of *Nauticaris marionis*), other invertebrates including molluscs and fish were also found. Both *Vinciguerria attenuata* and *Poromitra crassiceps* feed on small crustaceans, *Borostomias antarcticus* on crustaceans and mid-water fishes, *Chiasmodon niger* on pelagic fish, and *Chauliodus sloani* on midwater fishes (mainly myctophids) and crustaceans; (www.fishbase.org). Based on this data, the diet of this group was set to 75.9% crustacean zooplankton (divided between the two size groups with *Large Crustacean Zooplankton* comprising 24.2% and *Small Crustacean Zooplankton* 51.7%), 5% *Myctophid Fish*, 7% to each of the *Benthos* and *Other Zooplankton* group, 2.5 % assigned to *Macrophytes* with a very small contribution of the benthic decapod, *Nauticaris marionis* (0.01%).

24. Myctophids (FMY)

Species: This group includes 17 species of Myctophid species. These are *Protomyctophum bolini*, *P. normani*, *P. choriodon*, *P. tenisoni*, *Gymnoscopelus nicholsi*, *G. braueri*, *B. bolini*, *G. hintonoides*, *G. opisthopterus*, *G. piabilis*, *G. fraseri*, *Krefflichthys anderssoni*, *Electrona subaspera*, *E. carlsbergi*, *Lampanctus intricatus*, *Nannobranchium archirus* and a species of the genus *Diaphus*.

Biomass: The estimate for mesopelagic fish in the Southern Ocean of 4.5 t.km^{-2} was used to determine the biomass for this group (Gjosaeter and Kawaguchi 1980) and later revised globally by Lam and Pauly (2005) with the estimate remaining the same for this area. This biomass estimate was used for the Kerguelen model for small pelagic fish and surveys of this group at these islands showed that 70% of the small pelagic group were Myctophids (by weight caught) (Pruvost et al. 2005). The division between these two small pelagic functional groups was therefore based on this information, though the proportioning between these two groups was wet at 75% *Myctophid Fish* and 25% *Small Pelagic Fish* (3.375 t.km^{-2} *Myctophids*, 1.125 t.km^{-2} *Small Pelagics*). Estimates for Myctophid fish in the Southern Ocean are generally in this range (Filin et al. 1991; Kozlov et al. 1991) though these estimates exceed those made by Pakhomov et al. (1996) based on 5 voyages of the South African National Antarctic Program between 1985 and 1995 where dry weight estimates ranged from 0.01 to $1.1 \text{ g dry wt.m}^{-2}$ with an average of

0.138g dry wt.m⁻². With a dry to wet weight conversion of 5, the average biomass would be 0.69 t.km⁻², approximately 6.5 times lower than that used in this model, however, the sampling gear used in this study was not considered appropriate. An adjustment to this important estimate should be considered in the future.

Biomass: 3.375 t.km⁻²

P/B: 0.5 (yr⁻¹)

The value is the average of 3 Myctophid fish species (*Electrona antarctica* 0.21, *Electrona carlsbergi* 0.59 *Gymnoscopelus braueri* 0.60) calculated for the Kerguelen system (Pruvost et al. 2005). A maximum age for both *E. antarctica* and *E. carlsbergi* was thought to be 4-5 years (Sabourenkov 1991) which equates to a P/B of 0.2 yr⁻¹, and mortality estimates (Z) for *Gymnoscopelus nicholsi* were calculated to be 0.45, 0.67 and 0.70 yr⁻¹ for the South Georgia, South Shetlands and South Atlantic populations respectively of this myctophid (Linkowski 1985).

Q/B: 6.1 (yr⁻¹)

The estimate is from the Kerguelen model which was obtained from empirical equations for 3 myctophid species (Pruvost et al. 2005). This is lower than the estimate of 11 yr⁻¹ calculated using stomach fullness indices (Pakhomov et al. 1996).

Diet Composition: Based on a summary of South African National Antarctic Program surveys between 1985 and 1995 in the Southern Ocean, the Myctophid Fish diet is based on a mixed assemblage of mesozooplankton as they feed on the most abundant species of copepods, euphausiids, hyperiids and pteropods (Pakhomov et al. 1996). A summary by Sabourenkov (1991) suggests a diet of mainly copepods. Local data on the myctophid *Krefflichthys anderssoni* showed a diet dominated by copepods in number, with approximately 33% euphausiid contribution by mass and small contributions of chaetognaths, larval amphipods and benthic crustaceans Perissinotto and McQuaid (1992). Based on this information, the diet matrix was set to 35% each for the *Large* and *Small Crustacean Zooplankton* groups and the remainder (30%) to *Other Zooplankton*.

25. Large Cephalopods (CLA)

Species: Not considered at the species level, this group includes all cephalopods greater than 10cm in mantle length.

Biomass: Quantitative data on the cephalopods in the vicinity of the islands is lacking. Biomass estimates for this functional group were derived from information from other Sub-Antarctic systems. The Kerguelen model has a biomass estimate of 0.355 t.km^{-2} (Pruvost et al. 2005) and the Falklands model 0.35 t.km^{-2} (for large cephalopods) (Cheung and Pitcher 2005). Because the PEI system is in general less productive than both the Kerguelen and Falklands systems, the estimate for this model has been approximated at $1/3^{\text{rd}}$ of these systems and then partitioned between the small and large groups (approximately 0.1183, divided between large and small 0.0650 and 0.0450). These estimates were adequate to supply the system needs and were a best approximation as no data exists. Revision of this parameter should be considered in the future.

Biomass: 0.065 t.km^{-2}

P/B: $2.7 \text{ (yr}^{-1}\text{)}$

This estimate was made using the principle that P/Q for this group should be 0.25 yr^{-1} . Based on this, using the Q/B value of 10.95 yr^{-1} , an estimate of 2.73 yr^{-1} was calculated. This is similar to the estimate used in the Falklands model of 2.34 yr^{-1} (Cheung and Pitcher 2005), which is intermediary between the Southern Plateau model (value of 8 yr^{-1} , Bradford Grieve et al. 2003) and the Kerguelen model (0.6 yr^{-1} , Pruvost et al. 2005 based on Jarre et al. 1991 for the Weddell Sea).

Q/B: $10.95 \text{ (yr}^{-1}\text{)}$

Boyle and Rodhouse (2005, pg 233), estimate feeding rates for cephalopods to be between 1 - 12% of mean body mass per day. As the larger cephalopods may be considered mesopelagic, a feeding rate of 3% has been assumed, resulting in an estimate of 10.95 yr^{-1} . This value is intermediary between the Kerguelen model value (2 yr^{-1} , for large cephalopods, Pruvost et al. 2005) and the Southern Plateau model of 22 yr^{-1} (Bradford-Grieve et al. 2003)

Diet Composition: Cephalopods in the Antarctic Polar Frontal zone consume predominantly crustaceans and mesopelagic fish (Rodhouse et al. 1996; Boyle and Rodhouse 2005). A study from the Kerguelen islands (Cherel and Duhamel 2003) showed the cephalopod *Moroteuthis ingens* to be predominantly piscivorous (87% fish by mass), followed by squid (12%) and then crustaceans (<1%). For this model, diet of the large cephalopod group have been set to 40 % *Myctophid Fish*, 12 % *Small Pelagic Fish*, 10% *Small Cephalopods*, 24% *Large Crustacean Zooplankton*, 10% *Small Crustacean Zooplankton*, and the final 4 % *Other Zooplankton*.

26. Small cephalopods (CSM)

Species: Not considered at the species level, this group includes all cephalopods less than 10cm in mantle length.

Biomass: As for the description of the large cephalopods, there is no quantitative data for small cephalopod species, only descriptions of species from diet analysis of top predators at the islands. Biomass estimates for this functional group were therefore made using data from other sub-Antarctic systems as described for the large cephalopod group. The Kerguelen model has a biomass estimate of 0.355 yr^{-1} (Pruvost et al. 2005) and the Falklands model 0.35 yr^{-1} (for large cephalopods) (Cheung and Pitcher 2005). Both estimates are above the estimates for this model. The PEI system is in general less productive system than both the Kerguelen and Falklands systems. The estimate for this model has been made as $1/3^{\text{rd}}$ of these systems and then partitioned between the small and large groups (approximately 0.1183, divided between large 0.0650 and small 0.0450). These estimates were adequate to supply the system needs and were a best approximation as no data exists.

Biomass: 0.0450 t.km^{-2}

P/B: $4.5 \text{ (yr}^{-1}\text{)}$

This estimate was made using the principle that P/Q for this group should be 0.25 yr^{-1} . Based on this, using the Q/B value of 18.25 yr^{-1} (see below), an estimate of 4.5 yr^{-1} was used. This is similar to the estimate used in the Falklands model has 2.34 yr^{-1} , which is intermediary between

the Southern Plateau model (value of 8 yr^{-1} , Bradford Grieve et al. 2003) and the Kerguelen model (0.6 yr^{-1} , Pruvost et al. 2005, based on Jarre et al. 1991 for the Weddell Sea).

Q/B: $18.25 \text{ (yr}^{-1}\text{)}$

Boyle and Rodhouse (2005), estimate feeding rates for cephalopods to be between 1 -12% of body mass per day. With a feeding rate estimate of 5% of body mass per day, the consumption rate may be estimated to be 18.25 yr^{-1} . This is similar to the value of 22 yr^{-1} provided in the Southern Plateau model of Bradford Grieve et al. (2003).

Diet Composition: The diet for this group was set as 10% *Large Crustacean Zooplankton*, 60% *Small Crustacean Zooplankton* and finally 30% *Other Zooplankton*. The prey of this group is considered to be mostly composed of euphausiids, hyperiid amphipods, mysids and decapods (Boyle and Rodhouse 2005).

27. Benthos (BBE)

Species: The benthic subsystem at the PEIs has been considered in this model in only two functional groups. The macrozoobenthos consists of over 200 species and is dominated by polychaetes, crustaceans, echinoderms, molluscs, sponges and bryozoa (Beckley and Branch 1992).

Biomass estimates have been quantified and found to increase with increasing depth (0.12 kg.m^{-2} at 5m, 0.34 kg.m^{-2} at 10m, 0.46 kg.m^{-2} at 15m) (Beckley and Branch 1992). Using an estimate of the shelf area from bathymetry data (Table 2.2, Figure 2.3; source GEBCO_08 Grid version 20100927; <http://www.gebco.net>), the area around the islands which falls in the 0 – 500m is 887.37 km^2 . Using the biomass value at 15m depth (0.46 kg.m^{-2}), an estimate for the model area (EEZ) would be approximately ($408 \text{ 190 t} / 431014 \text{ km}^2 = 0.947045 \text{ t. km}^{-2}$). Data from (Perissinotto and McQuaid 1990) however provide an estimate of approximately 6.4 g.m^{-2} in the area where it occurs (Bryozoa 4.5 g.m^{-2} , Asteroidea 1.0 g.m^{-2} ; Echinus sp 0.5 g.m^{-2} , Ophiuroidea 0.2 g.m^{-2} , bivalves 0.1 g.m^{-2} , polychaetes 0.1 g.m^{-2}). This lower estimate results in a value of $0.013176 \text{ t.km}^{-2}$. For this study a biomass value of 0.5 t.km^{-2} has been used as the average between these two estimates.

Biomass: 0.5 t.km⁻²

P/B: 2.5 (yr⁻¹)

This estimate has been taken from as the midpoint between values for the three groups in the Kerguelen model (Deep benthic omnivores = 3.0 yr⁻¹, Shallow benthic omnivores = 2.1 yr⁻¹, Shallow benthic omnivores = 2.0 yr⁻¹; Pruvost et al. 2005)

Q/B: 10 (yr⁻¹)

This estimate has been taken from the Kerguelen model for all three groups of Benthos (Deep benthic omnivores, Shallow benthic omnivores and Shallow benthic omnivores) (Pruvost et al. 2005).

Unassimilated Consumption: 0.2

A value of 0.4 was considered following the Prince William Sound Model (Okey and Pauly 1999), but an assimilation efficiency of the predominant benthic macro-invertebrate (the limpet *Nacella delessertii*) of between 0.14 (in small limpets) and 0.06 (in adults) was found (Blankley and Branch 1985) and so the value was left at its default setting of 0.2.

Diet Composition: The diet of this broad group has been set with the bulk of the material coming from *Detritus* (60%) as well as *Macrophyte Detritus* (1.9%). Zooplankton components include the *Benthic Decapod* (0.1%), *Large Crustacean Zooplankton* (5%), *Small Crustacean Zooplankton* (8%) and *Other Zooplankton* (8%). All phytoplankton groups are consumed (*Large Open Ocean*, *Small Open Ocean*, *Island-associated Blooms* each 5%), as well as feeding on *Macrophytes* directly (2%).

28. Benthic decapod (BBD)

Species: *Nauticaris marionis*

Biomass: Estimates of biomass for the model were based on data from Branch et al. (1993) where abundance estimates of *Nauticaris marionis* are 20 ind.m⁻³. If swarms are considered 3.5m deep (or alternatively using an depth integrated estimate of 70 ind.m⁻²), with a wet weight

biomass estimate of an individual equal to 226 mg (average length of *N. marionis* between 25-30mm, if use 27mm, wet weight is estimated at 266mg), the estimate of biomass = $70 \text{ ind.m}^{-2} \times 0.266\text{g} = 18.62 \text{ g.m}^{-2}$. Assuming the decapod is found in the area between 0 and 500m (= 887.37 km^2 ; Table 2.2, Figure 2.3; GEBCO_08 Grid version 20100927; <http://www.gebco.net>), a total of 16 522 t of decapods may be found at the islands. If this is scaled for the EEZ, the estimate is 0.0383 t.km^{-2} . Estimates from Perissinotto and McQuaid (1990) are approximately 1.4 g.m^{-2} , and if calculated in the same way (found in the same area) the result would be $0.00288 \text{ t.km}^{-2}$. This estimate does not take into consideration the depth of the swarms, and so the former estimate has been used for this model.

Biomass: 0.038 t.km^{-2}

P/B: $1.45 \text{ (yr}^{-1}\text{)}$

This value is taken from the value for shrimp from the 'Newfoundland' model (Heymans and Pitcher 2002).

Q/B: $4.42 \text{ (yr}^{-1}\text{)}$

This estimate is taken from estimates of the benthic crustaceans from the Falklands model of 4.42 yr^{-1} , which is based on estimates for shrimp from the 'Newfoundland' model (Heymans and Pitcher 2002) and is similar to the estimates for Euphausiids used in the Kerguelen model of (3.8 yr^{-1}) (Pruvost et al. 2005).

Diet Composition: Studies on the diet of this important group have indicated a very high detritus contribution (up to 100%) (Vumazonke et al. 2003). Differential feeding between males and females was observed with gastropods and amphipods being the most numerous in male stomachs, and bivalves and isopods most common benthic prey in female diet. The benthic component constituted about 10% of prey volume, and pelagic prey less than 2%. A high degree of cannibalism has been observed in large females and this has been incorporated into the diet matrix. Based on this information, 74% of the diet was attributed to detritus (split equally between the macrophyte detritus and general detrital group), *Benthos* contributed 10%, benthic

decapod 1% (canibalism), *Small Crustacean Zooplankton* 5%, and 5% for each of the large and small fractions of *Open Ocean Phytoplankton*.

29. Large zooplankton crustaceans (ZLC)

Species: This group comprises mostly of the Euphausiids and amphipods and is not species specific.

Biomass: In a review by McQuaid and Froneman (2008) zooplankton biomass was estimated to range between 0.01 and 150 mg dry weight.m⁻³, and an intermediary range of 17 and 45 mg dry weight.m⁻³ was summarised by Pakhomov and Froneman (1999b). Using a dry weight to wet weight conversion of x 5 (Cushing 1958) [(Alternate conversions x 4 (Atkinson et al. 2001) x 4.26 (Whitehouse et al. 1999)], with a depth integration to 200m, divided by 1000 (mg to g), the range in g.m⁻² was equivalent to the above estimates quoted in mg dry wt.m⁻³. An intermediate value of 28g.m⁻² was used and divided between the three zooplankton groups with 5 g.m⁻² for large crustaceans, 16g.m⁻² for small crustaceans and 7g.m⁻² for *Other Zooplankton*.

Biomass: 5.0 t.km⁻²

P/B: 5.0 (yr⁻¹)

Q/B: 14.0 (yr⁻¹)

Diet Composition: Highest diet component has been set to the *Small Crustacean Zooplankton* at 40%, with *Other Zooplankton* contributing 20%. The small open ocean phytoplankton contribution was set at 30% and the large open ocean contribution set at 10%.

30. Small zooplankton crustaceans (ZSC)

Species: This group is dominated by copepods, which dominates the zooplankton biomass in the vicinity of the islands (Perissinotto and Boden 1989; Hunt et al. 2001; Bernard and Froneman 2002; Bernard and Froneman 2003) and individual species are not considered.

Biomass: 16.0 t.km⁻²

P/B: 10.0 (yr⁻¹)

Kerguelen model has for omnivorous zooplankton P/B 10 yr⁻¹ (Pruvost et al. 2005), lower than the estimate for the NZ model for mesozooplankton has P/B 20 yr⁻¹ (Bradford Grieve et al. 2003).

Q/B: 43.0 (yr⁻¹)

This value was made using estimates from data for omnivorous zooplankton (43 yr⁻¹) from the Kerguelen model (Pruvost et al. 2005) and is not dissimilar to the estimate for mesozooplankton (57 yr⁻¹) from the Southern Plateau model (Bradford Grieve et al. 2003).

Diet Composition: Small Crustacean Zooplankton 10%, Other Zooplankton 20%, Small Open Ocean Phytoplankton 60% and Detritus 10%.

31. Other zooplankton (ZOT)

Species: All remaining zooplankton are included in this group: medusae, salps, ctenophores, siphonophores, tuincates, chaetognaths, polychaets, pteropods.

Biomass: 7.0 t.km⁻²

P/B: 24.0 (yr⁻¹)

This value was taken from the Kerguelen model for herbivorous zooplankton (Pruvost et al. 2005).

Q/B: 96.0 (yr⁻¹)

Diet Composition: Small Open Ocean Phytoplankton 70% and Detritus 30%.

32. Open ocean nano- and picophytoplankton (POS)

Species: All phytoplankton < 20µm

Sub-Antarctic Open ocean productivity: 0.22 mg chl $a \cdot m^{-3}$. To convert the *Chl-a* estimates to biomass: /1000 convert to g (from mg), use a *Chl-a*:Carbon ratio of 32.25 (based on the relationship from Hewes et al. (1990): $C = 80 \text{ chl } a^{0.6}$, using the value of 0.22 mg *Chl-a* $\cdot m^{-3}$); a conversion factor of x 10 for Carbon to wet weight (Dalsgaard and Pauly 1997); and a euphotic depth of 120m (Read et al. 2000), resulting in an estimate of 8.51 t.km⁻² (or a total of 3667929 t for the EEZ). This was divided into microphytoplankton component (>20 µm) of 1.70 (~20%) and nano and picophytoplankton component of 6.81 (~80%) based on the relative contributions of these size fractions to the open ocean phytoplankton assemblages. [Chl-a measurements in the vicinity of the islands under non-bloom conditions between 0.05 and 0.45 mg.m⁻³. Value of 0.22 (El-Sayed et al. 1979b); 0.2 (Boden 1988), value of 0.22 (Gurney et al. 2002) average for 1998; average annual value of 0.22 for remote sensing satellite data 1998 to 2004 at 6x6 degree scale (SeaWiFs), combined with 2005 to 2008 data at 2x2 degree scale (MODIS)].

Biomass: 6.81 (t.km⁻²)

Open ocean production was estimated at 240 mg C.m⁻².d⁻¹ (Boden 1988) and 94-442 mg C.m⁻².d⁻¹ (Balarin 2000). Conversion from mg C to mg wet wt x 10; for year x 365 = lower est: 343.1 g wt wt.m⁻².yr⁻¹/(lower est of biomass=2.7 g.m⁻² Perissinotto et al. 2000; lower estimate of integrated chl $a = 7 \dots \times 43.9 \times 9 = 2.7 \text{ g.m}^{-2}$) = 127.03; or higher estimate 1613.3/11.8 (Perissinotto et al. 2000; higher estimate integrated chl $a = 30$, biomass = 11.8) = 136.7; used 150, same as the Kerguelen estimate (Pruvost et al. 2005).

P/B: 150.0 (yr⁻¹)

33. Open ocean microphytoplankton (POL)

Species: All phytoplankton > 20µm

Biomass: $1.70 \text{ (t.km}^{-2}\text{)}$ (see above #32)

P/B: $150.0 \text{ (yr}^{-1}\text{)}$ (see above #32)

34. Island associated blooms (PIA)

Species: Predominantly *Chaetoceros radiacans*, *Rhizoselena curvata*, *Dictyocha speculum* or *Fragilariopsis*.

When island-associated blooms occur chl-a concentrations exceed 1.5 mg.m^{-3} (measurements of up to 2.8 mg.m^{-3} have been made) (Boden 1988; Duncombe Rae 1989b) and species composition is dominated by microphytoplankton diatoms species. Quantifying the blooms: Remotely sensed ocean colour satellite chlorophyll-a data from a small subarea centred on the islands (46.5 to 47.1S and 37.5 to 38.3E) from 1998 to 2008 was processed. Monthly averages peaked during the summer months and values of up to $1.4 \text{ mg chl.a.m}^{-3}$ showed clear seasonal blooms in the vicinity of the islands. The annual average productivity for the sub-area was $0.27 \text{ mg chl.a. m}^{-3}$. Therefore an average annual increase of $0.05 \text{ mg chl.a.m}^{-3}$ (over and above the open ocean value of 0.22) was attributed to the elevated production associated with the islands. A euphotic depth of 25m for the blooms was assumed (Knox 2007a). To convert the *Chl-a* estimates to biomass: $0.05 \text{ mg chl.a. m}^{-3} / 1000$ to convert to g (from mg), x 32.25 for *Chl-a*:Carbon ratio (based on the relationship from Hewes et al. 1990: $C = 80 \text{ chl a}^{0.6}$, using the value of $0.22 \text{ mg Chl-a.m}^{-3}$, same as for the open ocean conversion); x 10 for Carbon to wet weight (Dalsgaard and Pauly 1997); and a euphotic depth of 25 (Knox 2007a), resulting in an estimate of Calculations: $0.05 / 1000 \times 32.25 \text{ (Chla:C)} \times 10 \text{ (C:wet wt)} \times 25 \text{ (Euphotic depth)} = \text{Biomass estimate of } 0.403 \text{ t.km}^{-2} \text{ in the area which it occurs (the smallest model area, circle radius of 20nm), equating to an estimate of approximately } 1737.47 \text{ t total or } 0.00403 \text{ t.km}^{-2} \text{ for the largest model size.}$

Biomass: $0.00403 \text{ t.km}^{-2}$

Island-associated production ranged from 84 to 3000 $\text{mg C.m}^{-2}.\text{d}^{-1}$ (El-Sayed et al 1979; Allanson et al 1985; Van Ballegooyen et al. 1989; Perissinotto and Duncombe Rae 1990; Balarin 2000); Production (lower estimate) 84×10 (for Carbon to wet weight Dalsgaard and Pauly (1997) = $840 \text{ g wet wt.m}^{-2}.\text{d}^{-1}$ $840 \times 365 = 306\,600 \text{ mg wet wt.yr}^{-1}$ (or $306 \text{ g.m}^{-2}.\text{yr}^{-1} = 306 \text{ t.km}^{-2}$).

Production (highest) $3000 \times 10 = 30\,000 \text{ g wet wt g wet wt.m}^{-2}.\text{d}^{-1} \times 365/1000 = 10950 \text{ wet wt.yr}^{-1}$. P/B then $306/8.69 = 35\text{yr}^{-1}$ (lowest) or $10950/8.9 = 1230.01 \text{ yr}^{-1}$. A production value of $476 \text{ mg C m}^{-2}.\text{d}^{-1}$ results in a P/B of $200.\text{yr}^{-1}$ which was used in the model.

P/B: $200 (\text{yr}^{-1})$

35. Macrophyte production (PMA)

Species: *Macrosystis laevis* and *Durvillea antarctica* are the two macrophytes that dominate the system.

Biomass: Quantitative estimates of the macrophytes were made from both photographs and from diving surveys in the 1980s and an estimate of $63\,500\text{t}$ for *M. laevis* (Attwood et al. 1991) and $3\,300\text{t}$ for *D. antarctica* (Haxen and Grindley 1985) were made. Average holdfast density of *M. laevis* $0.875 \text{ plants.m}^{-2}$; average wet mass per plant of $13.21 \text{ kg} = 0.875 \times 13.21 = 11.55\text{kg.m}^{-2} = 11\,550 \text{ g.m}^{-2}$ which is equal to $11\,550 \text{ tons per km}^2$. With 5.5km of macrophyte beds suggests a standing stock of *M. laevis* around Marion of $6.35 \times 10^7 \text{ kg wet mass} (11\,550\text{t} \times 5.5\text{km}^2)$;

Estimates of the understory algae (chiefly rhodophytes) decrease with increasing depth: 1.57kg.m^{-2} at 5m , 0.75kg.m^{-2} at 10m^{-2} and 0.49kg.m^{-2} at 15m . An extrapolation of these estimates to include macrophyte beds around PE based on the ratio of the perimeter of Marion to Prince Edward resulting in a total biomass of $88\,549\text{t}$ for the system (If the understory is included: consider it to exist as the same area as *M. laevis* divided equally between these zones, then 1.83km^2 for each, therefore 2.873t at 5m , 1.373t at 10m , and $0.897 = 5.147 \text{ t}$ at Marion, plus 30% for PE = 6.85 t . Total = $84\,455\text{t}$ *M. laevis*, and 6.85t understory = 84461.85t . For 200nm model = 0.195 t.km^{-2}).

Biomass: 0.195 t.km^{-2}

P/B: 5.22 yr^{-1}

Production and standing stock of *Macrocystis laevis*. net production is $7.7 \text{ gC.m}^{-2}.\text{d}^{-1}$ in April, net production is $11.5 \text{ gC.m}^{-2}.\text{d}^{-1}$ in August and mean biomass of kelp is 0.67 kgC.m^{-2} within kelp beds (Attwood et al 1991). Therefore the range of P/B is $7.7 / 670 = 0.0114925$ per day *

365 = 4.19 per year (April) and $11.5/670 = 0.0171641 * 365 = 6.2648965$ (August). Result. 4.19 (April) and 6.26 (August) average is 5.22 yr^{-1} which compares favourably with the Kerguelen model data of 4.00 yr^{-1} (Pruvost et al. 2005)).

36. Macrophyte detritus (DMA)

Detritus estimated from empirical equation (Pauly et al. 1993): $\log_{10}D = -2.41 + 0.954\log_{10}(PP) + 0.863 \log_{10}(E)$, where D is detritus biomass (gC.m^{-2}), PP is primary productivity ($\text{gC.m}^{-2}.\text{yr}^{-1}$) and E is euphotic depth (m). Productivity for *Macrocystitis laevis* (Attwood et al 1991) average (April and August) = $9.6\text{gC.m}^{-2}.\text{d}^{-1}$ (so for the year $9.6 \times 365 = 3504 \text{ gC.m}^{-2}.\text{yr}^{-1}$), and euphotic depth set to 20m. Production of *Durvillaea antarctica* year round $7.1 \text{ gC.m}^{-2}.\text{d}^{-1}$ (Haxen and Grindley 1985) (so for year $7.1 \times 365 = 2591 \text{ gC.m}^{-2}.\text{yr}^{-1}$), and euphotic depth set to 10m. The calculations were done for each species separately, and conversion of C to wet weight was set at 17.25. The total amount for *M. laevis* was scaled for the area the macrophyte occupies (5.5km for Marion) with the total being 11 788.4 t. *Durvillaea antarctica* was assumed to occur in 5% of the area of *M. laevis* (i.e. 0.28km^2) (based the biomass proportion of the two species as spatial data not available) = 247.4 t. Combined these two contribute 12035.8t of detritus to the system per year. This figure was increased by $1/3^{\text{rd}}$ to account for Prince Edward island with the final number = 16007.61t. Scaled for the 200nm model this results in $= 0.037139 \text{ t.km}^{-2}$.

Biomass: 0.037 t.km^{-2}

37. Detritus (DGD)

Biomass: 29 t.km^{-2}

Estimates made empirical equation from Pauly et al. (1993): $\log_{10}D = -2.4 + 0.954\log_{10}PP + 0.863 \log_{10} E$ where D is detritus biomass (gC.m^{-2}), PP is primary productivity ($\text{gC.m}^{-2}.\text{yr}^{-1}$) and E is euphotic depth (m). Large range in PP for Island area: from Pakhomov and Froneman (1999). Productivity range $47 - 3000 \text{ mg C m}^{-2}.\text{d}^{-1}$. Use $47 \text{ mgC.m}^{-2}.\text{d}^{-1} = 47 \times 365$ (from day to year) = $17.155 \text{ gC.yr}^{-1}$ and assume euphotic depth 100m. Conversion to wet weight (done using Bundy et al. (2000) conversion 1 to 9)) = 28.66 as compared to 100 in Kerguelen model (Pruvost et al. 2005).

Appendix 5.B. Mixed trophic impact (MTI) values for the 1980s model of the Prince Edward Islands

Appendix 5.B.

Impacting / Impacted	CODE	MOR	MES	MAF	MSF	PKI	PMA	PSR	PGE	AWA	AGH	AYN	ALM	ADM	BGP	BPP	FSR	FLD	FLN	FSD
1 Orcas	MOR	0.0915	0.245	0.265	0.258	0.479	0.596	0.665	0.461	-1.181	-1.177	-1.186	-1.181	-1.183	-0.636	0.568	-0.356	-0.226	-0.338	-0.023
2 Southern Elephant Seals	MES	-0.111	-0.0378	-0.0385	-0.0422	-0.0541	-0.0623	-0.0794	-0.0477	0.203	0.122	0.129	0.104	0.126	0.078	-0.0677	-0.868	-0.668	-0.117	0.242
3 Antarctic Fur Seals	MAF	0.000029	0.000836	0.000627	0.000615	-0.000574	-0.00295	-0.00626	0.000679	0.000269	0.000012	0.000023	-0.000015	0.000054	-0.000869	0.000871	-0.000702	-0.00133	-0.00131	-0.000311
4 Sub-Antarctic Fur Seals	MSF	0.0332	-0.00249	-0.013	-0.0141	-0.00497	0.0123	0.0169	-0.0054	-0.0316	-0.0405	-0.0413	-0.0408	-0.0386	-0.0106	0.00786	-0.00289	-0.0537	-0.0484	-0.011
5 King Penguins	PKI	0.114	-0.291	-0.313	-0.313	-0.316	-0.186	-0.123	-0.145	-0.231	-0.191	-0.204	-0.18	-0.191	0.211	-0.228	0.192	0.18	0.13	0.0386
6 Macaroni Penguins	PMA	0.0547	-0.0971	-0.065	-0.0634	-0.0726	-0.0806	-0.0642	-0.0563	-0.0906	-0.062	-0.0617	-0.0523	-0.0617	0.0784	-0.0797	0.0688	0.066	0.0638	0.0152
7 Southern Rockhopper Penguins	PSR	0.0135	-0.0184	-0.0158	-0.0165	-0.0174	-0.02	-0.0222	-0.0476	-0.0148	-0.014	-0.0147	-0.0161	-0.0162	0.0195	-0.0205	0.018	0.0162	0.0345	0.00833
8 Gentoo Penguins	PGE	-0.0221	-0.0162	-0.00622	-0.00606	-0.00986	-0.0134	-0.0108	-0.203	0.0233	0.0249	0.0247	0.0245	0.0243	0.0139	-0.0125	-0.0331	0.0189	-0.479	-0.263
9 Wandering Albatross	AWA	-0.00296	-0.000411	0.00563	0.00601	-0.00259	-0.0169	-0.0751	0.00656	-0.00518	0.00131	0.000774	0.000695	-0.000603	-0.00594	0.00482	-0.00739	-0.00355	-0.00583	-0.00119
10 Grey-headed Albatross	AGH	-0.00114	0.0026	0.00406	0.0042	-0.00327	-0.00685	-0.0349	0.00424	0.000095	0.000512	0.000665	0.000163	0.000089	-0.00369	0.00348	-0.0023	-0.00164	-0.00252	-0.000051
11 Indian Yellow-nosed Albatross	AYN	0.000746	-0.00201	0.000231	0.000362	-0.000014	0.000662	0.00119	0.000913	-0.00445	-0.0027	-0.0028	-0.0033	-0.00364	-0.000825	0.000099	0.000427	0.00113	0.000163	0.000716
12 Light-mantled Sooty Albatross	ALM	0.000014	-0.000061	0.000004	0.000006	-0.000008	0.000018	0.000033	0.000023	-0.000141	-0.000097	-0.000102	-0.000148	-0.000015	-0.000022	-0.000013	0.000051	0.000047	0.000004	0.000017
13 Dark-mantled Sooty Albatross	ADM	0.000118	-0.00106	0.000096	0.000146	-0.000105	0.000163	0.000393	0.000264	-0.0021	-0.00117	-0.00125	-0.00175	-0.00187	-0.000266	-0.000192	0.000431	0.000595	0.000062	0.000222
14 Giant Petrels	BGP	-0.0833	-0.38	-0.408	-0.403	-0.484	-0.588	-0.569	-0.484	0.181	0.177	0.186	0.186	0.186	-0.374	-0.581	0.48	0.324	0.38	-0.0026
15 Prions and Petrels	BPP	0.000168	-0.0327	-0.0176	-0.0169	-0.0228	-0.0157	-0.0101	-0.0105	-0.034	-0.0199	-0.0216	-0.0315	-0.0328	0.015	-0.0235	0.0255	0.0218	0.0119	0.00421
16 Sharks and Rays	FSR	-0.0112	-0.00502	-0.00299	-0.00315	-0.00471	-0.00604	-0.00683	-0.0262	0.0161	0.0126	0.0129	0.0117	0.0127	0.00689	-0.00602	0.000829	-0.0785	-0.059	-0.018
17 Large Demersals	FLD	0.0623	0.0322	0.0146	0.0152	0.0258	0.0338	0.0403	0.0257	-0.0804	-0.0652	-0.0664	-0.056	-0.0612	-0.038	0.0355	-0.0212	-0.0454	-0.0324	0.00465
18 Large Nototheniid Demersals	FLN	0.0153	0.0104	0.00287	0.00277	0.00539	0.00912	0.0127	0.141	-0.0162	-0.0179	-0.0178	-0.0172	-0.0171	-0.00915	0.00828	0.022	-0.0119	-0.0937	-0.0414
19 Small Continental Slope	FSD	0.023	0.0158	0.00653	0.00639	0.0103	0.0122	0.0102	0.154	-0.0243	-0.025	-0.0248	-0.0249	-0.0249	-0.0131	0.0117	0.0178	-0.0186	-0.104	-0.056
20 Small Inshore Demersals	FID	0.0113	0.0082	0.0035	0.0034	0.0052	0.00616	-0.00268	0.128	-0.0116	-0.0122	-0.0121	-0.0123	-0.0121	-0.00658	0.00589	0.0288	-0.00994	-0.0783	-0.0516
21 Large Pelagics	FLP	0.0951	0.0449	0.0231	0.025	0.0381	0.0551	0.0671	0.0483	-0.131	-0.117	-0.116	-0.106	-0.113	-0.0585	0.0523	-0.0277	-0.0423	-0.0272	0.0123
22 Patagonian toothfish	FPT	0.0689	-0.0128	0.0259	0.03	0.0317	0.0314	0.0476	-0.0346	-0.171	-0.0788	-0.0871	-0.068	-0.0904	-0.047	0.0362	-0.127	-0.0491	0.00214	-0.394
23 Small pelagics	FSP	-0.0645	0.0352	-0.188	-0.218	-0.148	0.00593	-0.0031	-0.0915	0.0783	0.111	0.0458	0.0193	0.0492	-0.025	-0.0215	-0.218	-0.231	-0.255	-0.196
24 Myctophids	FMY	0.207	0.0263	0.573	0.612	0.496	-0.147	-0.209	-0.0846	-0.225	0.0211	0.0732	0.0238	-0.0433	0.0715	-0.0114	0.0526	0.0697	0.222	-0.013
25 Large Cephalopods	CLA	0.053	0.191	0.00475	-0.00989	0.0216	0.0483	0.0232	0.0329	0.155	-0.118	-0.0966	-0.234	-0.154	-0.0107	-0.00919	0.269	0.0677	0.0297	0.0175
26 Small Cephalopods	CLS	0.0492	0.208	-0.0139	-0.0201	0.0468	0.0121	-0.0217	-0.00653	0.349	0.181	0.202	0.367	0.374	0.00723	0.103	-0.174	-0.143	-0.0253	-0.0223
27 Benthos	BBE	0.00686	0.0102	-0.0106	-0.0125	-0.00565	0.000003	-0.0128	0.0293	-0.0102	0.0112	-0.0117	-0.0114	-0.00993	-0.0111	0.00327	0.182	0.0887	0.0373	0.135
28 Benthic decapod	BBD	0.00113	-0.000498	0.000512	0.000489	-0.000388	-0.000653	0.0402	0.135	-0.00108	-0.00146	-0.00105	-0.00121	-0.0012	0.00074	-0.000733	-0.000256	-0.00216	-0.083	-0.00806
29 Large zooplankton crustaceans	ZLC	0.112	0.0191	0.105	0.11	0.0976	0.3	0.335	0.0537	-0.0561	-0.0436	-0.0348	-0.0707	-0.075	0.0352	0.0931	0.0528	0.137	0.0484	-0.0156
30 Small zooplankton crustaceans	ZSC	0.0409	0.0434	-0.0205	-0.0272	-0.000406	0.198	0.12	0.0306	0.0661	0.0412	0.0299	0.0442	0.05	0.0203	0.229	-0.0273	-0.019	-0.102	0.000439
31 All other zooplankton	ZOT	0.0503	0.0456	0.106	0.111	0.102	-0.0373	0.0118	-0.00668	0.0219	0.0301	0.0485	0.063	0.0535	0.0128	0.0179	-0.0605	-0.0156	0.0969	0.0942
32 Open ocean large phytoplankton	POL	0.0116	0.0024	0.00996	0.0104	0.00946	0.03	0.0348	0.0136	-0.00617	-0.00388	-0.00412	-0.0077	-0.00806	0.003	0.00944	0.0144	0.0181	0.00255	0.00481
33 Open ocean small phytoplankton	POS	0.0936	0.0642	0.0924	0.094	0.0999	0.183	0.182	0.0379	0.0376	0.0332	0.0408	0.0488	0.0444	0.0311	0.178	-0.0338	0.0233	0.0191	0.0679
34 Island associated blooms	PIA	0.000343	0.000511	-0.000531	-0.000625	-0.000283	0	-0.000639	0.00146	-0.00051	0.000558	-0.000586	-0.000569	-0.000496	-0.000556	0.000163	0.0091	0.00443	0.00186	0.00677
35 Macrophytes	PMA	0.0119	0.0109	-0.00617	-0.00766	-0.00149	0.00865	0.00932	0.0581	-0.0141	-0.0106	-0.0144	-0.0142	-0.0133	-0.0105	0.00727	-0.00123	0.109	0.225	0.0748
36 Macrophyte Detritus	DMA	0.000549	0.00001	-0.000012	-0.000056	-0.000251	-0.000242	0.0146	0.0503	-0.000595	-0.000328	-0.000612	-0.000664	-0.000634	0.000062	-0.000209	0.00336	0.000886	-0.03	-0.00041
37 Detritus	DGE	0.0237	0.024	0.0234	0.0234	0.0269	0.00838	0.0227	0.0684	0.00667	0.0193	0.0101	0.0161	0.0147	-0.000548	0.0299	0.0882	0.0458	0.0106	0.107

Appendix 5.B.

Impacting / Impacted	CODE	FID	FLP	FPT	FSP	FMY	CLA	CLS	BBE	BBD	ZLC	ZSC	ZOT	POL	POS	PIA	PMA	DMA	DGE
1 Orcas	MOR	-0.259	0.145	-0.324	-0.0706	-0.108	-0.127	-0.0856	0.0702	-0.0231	0.0684	-0.0047	0.00192	-0.0684	-0.000461	-0.0702	0.0557	-0.0333	-0.000998
2 Southern Elephant Seals	MES	-0.0158	0.45	-0.749	-0.0781	0.00873	0.247	-0.015	0.0728	-0.00429	0.00963	0.000584	-0.00135	-0.0118	0.000192	-0.0728	0.0596	-0.0423	0.000051
3 Antarctic Fur Seals	MAF	0.000091	0.000411	-0.000798	0.000005	-0.000121	0.000655	0.000121	0.000001	0.000751	0.000132	-0.000014	0.000005	-0.000128	0	-0.000001	0.00003	-0.000298	-0.000001
4 Sub-Antarctic Fur Seals	MSF	-0.0269	0.00294	-0.0224	-0.00604	-0.0185	0.00583	0.000852	0.00646	0.00401	0.0118	-0.000963	0.000433	-0.0117	-0.000062	-0.00646	0.00542	-0.00549	-0.000149
5 King Penguins	PKI	0.107	-0.127	0.137	0.00942	-0.124	-0.249	-0.0296	-0.013	-0.0155	0.078	-0.00731	0.00378	-0.0748	-0.000438	0.013	-0.0101	0.014	-0.000804
6 Macaroni Penguins	PMA	0.0415	-0.0311	0.0498	-0.0207	0.0129	-0.091	-0.000493	0.0167	-0.000548	-0.0146	0.00186	-0.000814	0.0135	-0.00009	-0.0167	0.013	-0.0099	-0.000051
7 Southern Rockhopper Penguins	PSR	-0.107	-0.00962	0.0154	-0.0046	0.00253	0.00179	-0.00708	0.00712	-0.0955	-0.00484	0.000666	-0.000321	0.00453	-0.000026	-0.00712	0.00228	0.0335	0.000012
8 Gentoo Penguins	PGE	-0.297	-0.00763	0.0166	0.00596	0.00307	0.000967	0.00142	0.00301	0.0869	-0.0027	0.000163	-0.000033	0.0024	0.000004	-0.00301	0.00425	-0.0362	-0.00007
9 Wandering Albatross	AWA	0.00586	0.00397	-0.00557	0.00766	0.000422	-0.014	-0.00642	-0.00698	0.00754	-0.00109	-0.00004	0.000105	0.00129	-0.000009	0.00698	-0.00522	0.00124	0.000007
10 Grey-headed Albatross	AGH	0.00296	0.00188	-0.00279	-0.00172	0.00103	0.000204	-0.00283	0.00138	0.0037	0.000038	0.000025	-0.000043	-0.000089	0.000001	-0.00138	0.00127	-0.0023	0.000001
11 Indian Yellow-nosed Albatross	AYN	-0.000083	0.000288	-0.000095	-0.00115	-0.000142	-0.00395	-0.00527	0.00101	-0.000144	0.000401	-0.000007	-0.000012	-0.000421	0	-0.00101	0.000787	-0.000551	0
12 Light-mantled Sooty Albatross	ALM	-0.000002	0.000002	-0.000019	-0.000033	-0.000008	-0.000032	-0.000285	0.000029	-0.000004	0.000014	0	0	-0.000014	0	-0.000029	0.000023	-0.000016	0
13 Dark-mantled Sooty Albatross	ADM	-0.000056	0.000115	-0.000327	-0.000062	-0.000035	-0.0014	-0.00356	0.000047	-0.000055	0.000072	0.000002	-0.000002	-0.000071	-0.000002	-0.000047	0.000035	-0.000007	0
14 Giant Petrels	BGP	0.266	-0.21	0.437	0.0782	0.112	0.122	0.109	-0.0774	0.0124	-0.0731	0.00495	-0.00194	0.0731	0.000466	0.0774	-0.0622	0.0419	0.00103
15 Prions and Petrels	BPP	0.00779	-0.00763	0.00838	0.00126	-0.00411	-0.018	-0.0657	-0.00159	-0.00094	0.00111	-0.000135	0.000183	-0.00101	-0.000059	0.00159	-0.00126	0.00133	-0.000083
16 Sharks and Rays	FSR	-0.0334	0.0104	-0.0258	-0.00174	0.00115	0.0122	0.00005	0.00278	0.0105	-0.000286	0.00006	-0.00006	0.000168	0.00001	-0.00278	0.00287	-0.00583	-0.000004
17 Large Demersals	FLD	-0.0211	0.0282	-0.0527	0.00968	-0.00845	-0.0661	0.0214	-0.0176	0.0006	0.00244	-0.000422	0.000392	-0.00175	-0.000063	0.0176	-0.0149	0.0104	0.00001
18 Large Nototheniid Demersals	FLN	-0.194	0.00559	-0.0126	-0.00694	-0.00317	-0.00156	-0.000164	0.00349	0.0479	0.00316	-0.000147	-0.000018	-0.00323	0.000002	-0.00349	-0.0053	-0.0211	0.000001
19 Small Continental Slope	FSD	-0.0867	0.00447	-0.0112	-0.00283	-0.00169	-0.000696	-0.00232	-0.0117	-0.0643	0.0011	-0.000102	0.000029	-0.00058	0.00001	0.0117	-0.00575	0.0325	0.000147
20 Small Inshore Demersals	FID	-0.111	0.0049	-0.00924	-0.00136	-0.000907	0.000664	-0.0011	-0.00229	-0.207	0.000579	-0.000059	0.000061	-0.000241	-0.000015	0.00229	0.00159	0.0831	0.000042
21 Large Pelagics	FLP	-0.0192	0.0117	-0.0475	-0.0545	-0.00852	-0.0803	-0.00627	0.0492	-0.00279	0.015	-0.00033	-0.000511	-0.0162	0.000055	-0.0492	0.0387	-0.0286	-0.000079
22 Patagonian toothfish	FPT	0.00123	-0.719	-0.108	0.103	-0.000563	-0.249	-0.00938	-0.0844	0.0229	-0.0181	-0.000234	0.00144	0.0203	-0.000198	0.0844	-0.0677	0.0419	-0.000081
23 Small pelagics	FSP	-0.127	-0.0332	0.0265	-0.0945	-0.292	0.0404	0.0113	-0.799	-0.00639	-0.0236	-0.0133	0.0193	0.0503	-0.00321	0.799	-0.626	0.486	-0.00213
24 Myctophids	FMY	0.0229	0.212	0.0517	-0.147	-0.253	0.0012	-0.14	0.132	0.0503	-0.404	0.0393	-0.0228	0.385	0.00327	-0.132	0.0996	-0.0998	0.00546
25 Large Cephalopods	CLA	0.0348	-0.0656	0.0694	-0.38	-0.00142	-0.112	-0.357	0.337	0.00705	0.0722	0.00114	-0.0054	-0.0813	0.000518	-0.337	0.265	-0.206	-0.000002
26 Small Cephalopods	CLS	0.00146	-0.00743	0.0189	-0.0375	-0.0105	0.0575	-0.0591	0.035	0.0059	0.00647	-0.00192	0.00042	-0.00746	0.000496	-0.035	0.028	-0.0235	-0.000213
27 Benthos	BBE	0.119	0.00164	-0.0179	0.0519	-0.0237	-0.00761	0.00397	-0.112	-0.241	-0.0196	-0.000094	-0.00159	-0.0114	0.00108	-0.888	-0.17	-0.441	-0.00849
28 Benthic decapod	BBD	0.155	-0.000149	0.000552	-0.000252	0.000448	0.000509	-0.000557	-0.0203	-0.189	-0.000034	-0.000014	0.000042	-0.000205	-0.000017	0.0203	0.00394	-0.308	0.000011
29 Large zooplankton crustaceans	ZLC	-0.0642	0.173	0.0821	0.00314	0.164	0.116	-0.0977	-0.00632	-0.061	-0.228	-0.123	0.0431	-0.744	0.0158	0.00632	-0.00343	0.0279	-0.000736
30 Small zooplankton crustaceans	ZSC	0.167	0.0175	0.0366	0.22	-0.0126	0.0524	0.155	-0.078	-0.0097	0.0711	-0.419	-0.466	-0.0659	-0.0243	0.078	-0.169	0.051	0.198
31 All other zooplankton	ZOT	-0.122	0.0389	0.0159	-0.0439	0.138	0.0318	0.119	-0.201	-0.0943	-0.0565	-0.065	-0.316	0.0615	-0.324	0.201	0.0622	0.159	-0.485
32 Open ocean large phytoplankton	POL	0.00728	0.0174	0.00734	0.0029	0.0152	0.0112	-0.0096	0.0427	0.0224	0.0762	-0.0123	0.00424	-0.075	0.00164	-0.0427	-0.00864	-0.0347	-0.000497
33 Open ocean small phytoplankton	POS	0.00897	0.0896	0.0568	0.105	0.137	0.0881	0.147	-0.146	-0.0616	0.234	0.266	0.212	-0.22	-0.237	0.146	-0.0674	0.113	-0.221
34 Island associated blooms	PIA	0.00595	0.000082	-0.000897	0.0026	-0.00119	-0.000381	0.000198	0.0444	-0.0121	-0.000978	-0.000005	-0.000008	-0.000572	0.000054	-0.0444	-0.00849	-0.0221	-0.000424
35 Macrophytes	PMA	-0.043	0.0042	-0.0108	0.0453	-0.0173	-0.00722	0.00312	-0.0248	-0.00428	-0.000239	-0.000776	0.000986	0.00109	-0.000146	0.0248	-0.0387	0.0167	-0.000259
36 Macrophyte Detritus	DMA	0.0596	-0.000024	-0.000136	0.000893	-0.000285	0.000044	-0.000131	0.00934	0.296	-0.000384	-0.000007	-0.000015	-0.000293	0.000014	-0.00934	-0.00177	0	-0.000157
37 Detritus	DGE	0.109	0.0143	-0.00213	0.0399	0.026	0.0104	0.0534	0.457	0.126	-0.0216	0.0386	0.157	0.00494	-0.0991	-0.457	-0.0987	-0.326	0

Appendix 6.A. Data used to drive the fur seal simulations of the PEI ecosystem model.

Appendix 8.A. Data used to reconstruct the fur seal hunting that occurred at the PEIs from 1800 to the 1930s. Fur seal survey data used in this chapter is described in Chapter 2, part 1 and provided here for reference. Model output data is also provided.

Appendix 8.A

Year	Antarctic Fur Seals			Sub-Antarctic Fur Seals		
	Survey data	Hunting mortality	Model output	Survey data	Hunting mortality	Model output
	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²
1800		0.0000434	0.000258127		0.00116	0.008617
1801		0.0000434	0.000217659		0.00116	0.007538
1802		0.0000434	0.00017893		0.00116	0.006513
1803		0.0000232	0.000151731		0.000928	0.005644
1804		0.0000232	0.000133792		0.000928	0.004893
1805		0.0000232	0.000115762		0.000928	0.004142
1806		0.0000232	9.75E-05		0.000928	0.003384
1807		0.0000232	7.92E-05		0.000464	0.002859
1808		0.0000116	6.65E-05		0.000464	0.002533
1809		0.0000116	5.83E-05		0.000464	0.002195
1810		0.0000116	4.98E-05		0.000464	0.001844
1811		0.0000116	4.08E-05		0.000464	0.001478
1812		0.0000116	3.15E-05		0.000464	0.001094
1813		0.0000069	2.42E-05		0.000232	0.000817
1814		0.0000069	1.87E-05		0.000232	0.000632
1815		0.0000069	1.29E-05		0.000232	0.000437
1816		0.0000069	6.76E-06		0.000232	0.000232
1817		0.0000069	1.36E-06		0.000232	4.86E-05
1818			2.74E-07			9.91E-06
1819			2.93E-07			1.06E-05
1820			3.12E-07			1.13E-05
1821			3.33E-07			1.20E-05
1822			3.55E-07			1.28E-05
1823			3.79E-07			1.37E-05
1824			4.04E-07			1.46E-05
1825			4.31E-07			1.56E-05
1826			4.59E-07			1.66E-05
1827			4.90E-07			1.77E-05
1828			5.22E-07			1.89E-05
1829			5.57E-07			2.02E-05
1830			5.94E-07			2.15E-05
1831			6.33E-07			2.30E-05
1832			6.75E-07			2.45E-05
1833			7.20E-07			2.61E-05
1834			7.67E-07			2.78E-05
1835			8.18E-07			2.97E-05
1836			8.72E-07			3.17E-05
1837			9.30E-07			3.38E-05
1838			9.91E-07			3.60E-05
1839			1.06E-06			3.84E-05
1840			1.13E-06			4.10E-05
1841			1.20E-06			4.37E-05
1842			1.28E-06			4.66E-05
1843			1.37E-06			4.97E-05
1844			1.46E-06			5.30E-05
1845			1.55E-06			5.65E-05
1846			1.65E-06			6.02E-05
1847			1.76E-06			6.42E-05
1848			1.88E-06			6.85E-05
1849			2.00E-06			7.30E-05

Year	Antarctic Fur Seals			Sub-Antarctic Fur Seals		
	Survey data	Hunting mortality	Model output	Survey data	Hunting mortality	Model output
	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²
1850			2.14E-06			7.79E-05
1851			2.28E-06			8.30E-05
1852			2.43E-06			8.85E-05
1853			2.59E-06			9.44E-05
1854			2.76E-06			0.000101
1855			2.94E-06			0.000107
1856			3.13E-06			0.000114
1857			3.34E-06			0.000122
1858			3.56E-06			0.00013
1859			3.80E-06			0.000139
1860			4.04E-06			0.000148
1861			4.31E-06			0.000157
1862			4.59E-06			0.000168
1863			4.89E-06			0.000179
1864			5.21E-06			0.000191
1865			5.56E-06			0.000203
1866			5.92E-06			0.000216
1867			6.31E-06			0.000231
1868			6.72E-06			0.000246
1869			7.16E-06			0.000262
1870			7.62E-06			0.000279
1871			8.12E-06			0.000297
1872			8.64E-06			0.000316
1873			9.20E-06			0.000337
1874			9.80E-06			0.000358
1875			1.04E-05			0.000382
1876			1.11E-05			0.000406
1877			1.18E-05			0.000432
1878			1.26E-05			0.00046
1879			1.34E-05			0.00049
1880			1.42E-05			0.000521
1881			1.51E-05			0.000554
1882			1.61E-05			0.000589
1883			1.71E-05			0.000627
1884			1.82E-05			0.000666
1885			1.93E-05			0.000708
1886			2.06E-05			0.000752
1887			2.18E-05			0.000799
1888			2.32E-05			0.000849
1889			2.46E-05			0.000901
1890			2.62E-05			0.000957
1891			2.78E-05			0.001015
1892			2.95E-05			0.001077
1893			3.13E-05			0.001142
1894			3.31E-05			0.00121
1895			3.51E-05			0.001283
1896			3.72E-05			0.001358
1897			3.94E-05			0.001438
1898			4.17E-05			0.001522
1899			4.42E-05			0.00161

Appendix 8.A

Year	Antarctic Fur Seals			Sub-Antarctic Fur Seals		
	Survey data	Hunting mortality	Model output	Survey data	Hunting mortality	Model output
	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²
1900			4.67E-05			0.001702
1901		0.0000069	4.56E-05		0.000232	0.001671
1902		0.0000069	4.12E-05		0.000232	0.001529
1903		0.0000069	3.66E-05		0.000232	0.001381
1904		0.0000069	3.17E-05		0.000232	0.001225
1905		0.0000069	2.66E-05		0.000232	0.001061
1906		0.0000069	2.12E-05		0.000232	0.000889
1907		0.0000069	1.55E-05		0.000232	0.000707
1908		0.0000069	9.48E-06		0.000232	0.000516
1909		0.00000345	5.03E-06		0.000232	0.000315
1910		0.00000345	1.96E-06		0.000232	0.00011
1911			6.64E-07			3.18E-05
1912			7.08E-07			3.39E-05
1913			7.55E-07			3.61E-05
1914			8.05E-07			3.86E-05
1915			8.59E-07			4.11E-05
1916			9.16E-07			4.39E-05
1917			9.77E-07			4.68E-05
1918			1.04E-06			4.99E-05
1919			1.11E-06			5.32E-05
1920			1.18E-06			5.68E-05
1921			1.26E-06			6.05E-05
1922			1.35E-06			6.46E-05
1923			1.44E-06			6.88E-05
1924			1.53E-06			7.34E-05
1925			1.63E-06			7.83E-05
1926			1.74E-06			8.35E-05
1927			1.85E-06			8.90E-05
1928			1.98E-06			9.49E-05
1929			2.11E-06			0.000101
1930			2.25E-06			0.000108
1931			2.40E-06			0.000115
1932			2.55E-06			0.000123
1933			2.72E-06			0.000131
1934			2.90E-06			0.000139
1935			3.09E-06			0.000148
1936			3.30E-06			0.000158
1937			3.51E-06			0.000169
1938			3.74E-06			0.00018
1939			3.99E-06			0.000192
1940			4.25E-06			0.000204
1941			4.53E-06			0.000218
1942			4.83E-06			0.000232
1943			5.14E-06			0.000247
1944			5.48E-06			0.000263
1945			5.84E-06			0.00028
1946			6.22E-06			0.000298
1947			6.62E-06			0.000318
1948			7.05E-06			0.000338
1949			7.51E-06			0.00036
1950			8.00E-06			0.000384
1951						8.52E-06
1952	3.92E-06					9.07E-06
1953						9.66E-06
1954						1.03E-05
1955						1.09E-05
1956						1.16E-05
1957						1.24E-05
1958						1.32E-05
1959						1.40E-05
1960						1.49E-05
1961						1.59E-05
1962						1.69E-05
1963						1.79E-05
1964						1.91E-05
1965						2.03E-05
1966						2.15E-05
1967						2.29E-05
1968						2.43E-05
1969						2.58E-05
1970						2.73E-05
1971						2.90E-05
1972						3.08E-05
1973						3.26E-05
1974						3.46E-05
1975	1.12E-05					3.66E-05
1976						3.88E-05
1977						4.11E-05
1978						4.34E-05
1979						4.59E-05
1980						4.86E-05
1981						5.13E-05
1982	2.38E-05					5.42E-05
1983						5.72E-05
1984						6.03E-05
1985						6.36E-05
1986						6.70E-05
1987						7.05E-05
1988						7.42E-05
1989	6.09E-05					7.80E-05
1990						8.19E-05
1991						8.60E-05
1992						9.02E-05
1993						9.45E-05
1994						9.89E-05
1995	0.000121					0.000103
1996						0.000108
1997						0.000113
1998						0.000118
1999						0.000123
2000						0.000128
2001	0.000207					0.000133
2002						0.000138
2003						0.000143
2004	0.000262					0.000148
2005						0.000153
2006						0.000158
2007						0.000164
2008	0.000281					0.000169
2009						0.000174
2010						0.000179

Appendix 7.A. Data used to drive the Patagonian toothfish simulations of the PEI ecosystem model.

Appendix 8.B. Data used to reconstruct the Patagonian toothfish fishery at the PEIs from 1980 to 2006. Catch data and catch-per-unit-effort data is provided and was sourced from Brandao and Butterworth 2009. Model output data for results including and excluding cetacean depredation ($z=1$ as defined by Brandao and Butterworth 2009) are provided.

Appendix 8.B Patagonian Toothfish fishery

	Sharks & Rays bycatch mortality	Large Demersals bycatch mortality	Large Nototheinid Demersals bycatch mortality	Large Pelagics bycatch mortality	FPT fishing mortality, no cetacean depredation	FPT fishing mortality with cetacean depredation	FPT CPUE (Brandao & Butterworth 2009)	FPT Model output, no cetacean depredation	PT Model output with cetacean depredation
Year	FSR t.km ⁻²	FLD t.km ⁻²	FLN t.km ⁻²	FLP t.km ⁻²	FPT t.km ⁻²	FPT fishing t.km ⁻²	FPT CPUE t.km ⁻²	PTF S1 t.km ⁻²	PTF S2 t.km ⁻²
1980								0.075000	0.075000
1981								0.075000	0.075000
1982								0.075000	0.075000
1983								0.075000	0.075000
1984								0.075000	0.075000
1985								0.075000	0.075000
1986								0.075000	0.075000
1987								0.075000	0.074999
1988								0.075000	0.074999
1989								0.075000	0.074999
1990								0.074999	0.074999
1991								0.074999	0.074999
1992								0.074999	0.074999
1993								0.074999	0.074999
1994								0.075000	0.075000
1995								0.075000	0.075000
1996	0	0	0	0				0.075000	0.075000
1997	0	0	0	0	0.05631	0.05631	4.665	0.046241	0.046515
1998	2.32E-06	0	0	2.32E-06	0.00654	0.00654	1.229	0.019847	0.021221
1999	0	0	0	0	0.00457	0.00457	1.071	0.015693	0.018286
2000	0.0000162	0.00005723	0.00011446	0.0000255	0.00643	0.00857	0.623	0.011225	0.013891
2001	2.32E-06	0.000017	0.000034	4.64E-06	0.00163	0.00272	0.381	0.008196	0.010341
2002	0	0.0000054	0.0000108	0	0.00117	0.00235	0.393	0.007437	0.009384
2003	0	0	0	0	0.00132	0.00264	0.503	0.006755	0.008315
2004	0	0.00000077	0.00000155	0	0.00098	0.00197	0.286	0.006136	0.007327
2005	0	0	0	0.0001091	0.00091	0.00181	0.531	0.005670	0.006612
2006	0	0.00000927	0.00001853	2.32E-06	0.00075	0.00150	0.317	0.005291	0.006041
2007	0	0.00003558	0.00007115	0.0000116				0.005372	0.006388
2008	0	0.00000387	0.00000773	2.32E-06				0.005819	0.007539
2009								0.006300	0.008854
2010								0.006816	0.010343
2011									

Appendix 8.A. Data used to drive the cat predation on small flying seabird simulations of the PEI ecosystem model.

Appendix 8.C. Data used to reconstruct the effect of the cat predation on small flying birds (*Prions and Petrels*) between 1940 and 1990 are provided with predation estimates derived from cat population and consumption estimates taken from Bester et al. (2000).

Appendix 8.C Cat predation on small birds

Year	Predation exponential original	Predation exponential 1/7th	Predation exponential 1/10th	Model output original	Model output 1/7th	Model output 1/10th
	Predation (original)	Predation	Predation	CAT S1	CAT S2	CAT S3
	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²	t.km ⁻²
1941				6.57E-04	6.57E-04	6.57E-04
1942				6.57E-04	6.57E-04	6.57E-04
1943				6.57E-04	6.57E-04	6.57E-04
1944				6.57E-04	6.57E-04	6.57E-04
1945				6.57E-04	6.57E-04	6.57E-04
1946				6.57E-04	6.57E-04	6.57E-04
1947				6.57E-04	6.57E-04	6.57E-04
1948				6.57E-04	6.57E-04	6.57E-04
1949	7.55E-07	1.08E-07	7.55E-08	6.57E-04	6.58E-04	6.58E-04
1950	9.53E-07	1.36E-07	9.53E-08	6.59E-04	6.60E-04	6.60E-04
1951	1.20E-06	1.72E-07	1.20E-07	6.60E-04	6.61E-04	6.62E-04
1952	1.52E-06	2.17E-07	1.52E-07	6.60E-04	6.63E-04	6.63E-04
1953	1.92E-06	2.74E-07	1.92E-07	6.60E-04	6.64E-04	6.64E-04
1954	2.42E-06	3.46E-07	2.42E-07	6.60E-04	6.65E-04	6.66E-04
1955	3.06E-06	4.37E-07	3.06E-07	6.59E-04	6.66E-04	6.67E-04
1956	3.86E-06	5.51E-07	3.86E-07	6.58E-04	6.67E-04	6.67E-04
1957	4.87E-06	6.96E-07	4.87E-07	6.56E-04	6.67E-04	6.68E-04
1958	6.15E-06	8.78E-07	6.15E-07	6.53E-04	6.68E-04	6.68E-04
1959	7.76E-06	1.11E-06	7.76E-07	6.49E-04	6.68E-04	6.68E-04
1960	9.80E-06	1.40E-06	9.80E-07	6.43E-04	6.67E-04	6.68E-04
1961	1.24E-05	1.77E-06	1.24E-06	6.36E-04	6.67E-04	6.68E-04
1962	1.56E-05	2.23E-06	1.56E-06	6.27E-04	6.66E-04	6.68E-04
1963	1.97E-05	2.82E-06	1.97E-06	6.15E-04	6.65E-04	6.67E-04
1964	2.49E-05	3.55E-06	2.49E-06	6.00E-04	6.63E-04	6.66E-04
1965	3.14E-05	4.49E-06	3.14E-06	5.80E-04	6.60E-04	6.64E-04
1966	3.97E-05	5.66E-06	3.97E-06	5.54E-04	6.57E-04	6.62E-04
1967	5.01E-05	7.15E-06	5.01E-06	5.22E-04	6.53E-04	6.59E-04
1968	6.32E-05	9.03E-06	6.32E-06	4.79E-04	6.48E-04	6.56E-04
1969	7.98E-05	1.14E-05	7.98E-06	4.23E-04	6.41E-04	6.51E-04
1970	0.000100706	1.44E-05	1.01E-05	3.50E-04	6.32E-04	6.45E-04
1971	0.000127129	1.82E-05	1.27E-05	2.54E-04	6.21E-04	6.37E-04
1972	0.000160486	2.29E-05	1.60E-05	1.26E-04	6.07E-04	6.27E-04
1973	0.000202594	0.00028942	2.03E-05	1.75E-05	5.89E-04	6.15E-04
1974	0.000255751	3.65E-05	2.56E-05	9.55E-07	5.65E-04	5.99E-04
1975	0.000322855	4.61E-05	3.23E-05	5.22E-08	5.35E-04	5.78E-04
1976	0.000370877	5.30E-05	3.71E-05	2.85E-09	4.99E-04	5.54E-04
1977	0.000418681	5.98E-05	4.19E-05	1.56E-10	4.58E-04	5.27E-04
1978	0.000466484	6.66E-05	4.66E-05	8.50E-12	4.11E-04	4.96E-04
1979	0.000514208	7.35E-05	5.14E-05	4.65E-13	3.59E-04	4.62E-04
1980	0.000470312	6.72E-05	4.70E-05	2.54E-14	3.07E-04	4.30E-04
1981	0.000426415	6.09E-05	4.26E-05	1.39E-15	2.60E-04	4.03E-04
1982	0.000382519	5.46E-05	3.83E-05	7.60E-17	2.18E-04	3.80E-04
1983	0.000338622	4.84E-05	3.39E-05	4.16E-18	1.81E-04	3.62E-04
1984	0.000294726	4.21E-05	2.95E-05	2.28E-19	1.49E-04	3.48E-04
1985	0.000250829	3.58E-05	2.51E-05	1.51E-20	1.21E-04	3.39E-04
1986	0.000206933	2.96E-05	2.07E-05	1.00E-20	9.75E-05	3.34E-04
1987	0.000163122	2.33E-05	1.63E-05	1.00E-20	7.88E-05	3.34E-04
1988	9.39E-05	1.34E-05	9.39E-06	1.00E-20	6.72E-05	3.39E-04
1989	6.28E-05	8.98E-06	6.28E-06	1.00E-20	6.17E-05	3.49E-04
1990	4.12E-05	5.89E-06	4.12E-06	1.00E-20	5.97E-05	3.62E-04
1991	1.93E-05	2.76E-06	1.93E-06	1.00E-20	6.07E-05	3.77E-04
1992	1.21E-06	1.73E-07	1.21E-07	1.00E-20	6.48E-05	3.95E-04
1993	0	0	0	1.05E-20	7.04E-05	4.12E-04
1994				1.15E-20	7.64E-05	4.29E-04
1995				1.26E-20	8.30E-05	4.45E-04
1996				1.38E-20	9.00E-05	4.61E-04
1997				1.51E-20	9.75E-05	4.76E-04
1998				1.66E-20	1.06E-04	4.91E-04
1999				1.82E-20	1.14E-04	5.05E-04
2000				1.99E-20	1.23E-04	5.19E-04
2001				2.18E-20	1.33E-04	5.31E-04
2002				2.39E-20	1.44E-04	5.43E-04
2003				2.61E-20	1.55E-04	5.55E-04
2004				2.86E-20	1.67E-04	5.65E-04
2005				3.14E-20	1.79E-04	5.75E-04
2006				3.44E-20	1.92E-04	5.84E-04
2007				3.76E-20	2.06E-04	5.92E-04
2008				4.12E-20	2.20E-04	6.00E-04
2009				4.51E-20	2.35E-04	6.06E-04
2010				4.95E-20	2.50E-04	6.13E-04