Modelling the impact of the South African small pelagic fishery on African penguin dynamics

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Declaration

I hereby declare that this thesis has not been submitted to this or any other university for a degree, either in the same or different form.

I know the meaning of plagiarism and declare that all of the work in the thesis, save for that which is properly acknowledged, is my own. In that context, it is to be noted that the general linear models presented in Chapter 3 are an extension of an approach first proposed by Brandão and Butterworth (2007).

W Robinson

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Abstract

Under an ecosystem approach to fisheries, managers aim not only to achieve a good yield from targeted stocks, but also to preserve the functioning of the whole ecosystem. The population demographics of predators such as penguins that are dependent on forage fish for food can give an indication of the health of the ecosystem in which they live.

The rapid decline in the African penguin *Spheniscus demersus* population in the twenty-first century prompted the re-classification of the IUCN conservation status of the species as "endangered" in 2010. Reasons suggested for the decline include scarcity of quality accessible prey, predation, and oil spills. The South African fishery for small pelagics catches predominantly sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*, which are the two most important prey species of African penguins. This project aims to quantitatively assess the past and future impact of the fishery on penguin population dynamics and abundance trends.

The working group which provides scientific advice on the management of the sardine-anchovy fishery convened a task team to conduct a feasibility study to evaluate the power of an experiment to detect an effect on penguin demographics and foraging behaviour of fishing restrictions around penguin breeding colonies. The colonies considered include Dassen Island and Robben Island off the west coast of South Africa and St Croix Island and Bird Island in Algoa Bay. The extent of relationships between penguin demographic parameters at these colonies and extractions of forage fish was explored with general linear models, taking account of fish abundance through biomass estimates from surveys. Under the assumption that prey densities at neighbouring islands should vary in approximate synchrony, the differential effect of fishing was evaluated. Results indicate (perhaps surprisingly) that penguin reproduction is better when catches are larger. Furthermore, the CVs of the standard deviations of the residuals of the response variables were estimated.

These estimates are necessary to determine whether an island closure experiment will have the power to detect an effect of fishing within a reasonable period.

A model of the Robben Island penguin population dynamics was developed. Penguin adult annual mortality was related to the sardine 1+ biomass observed west of Cape Agulhas in the November hydroacoustic survey for small pelagic fish. Data from moult counts and re-sightings of tagged penguins were integrated in a rigorous and statistically defensible manner. Results suggest that the rapid growth of the colony during the 1990s was driven primarily by immigration. Furthermore, the sardine–penguin mortality relationship predicts that on average penguin survival decreases only when the sardine 1+ survey biomass west of Cape Agulhas is less than approximately one-quarter of the maximum level observed (1 343 thousand tonnes in 2003).

The population model was used to calculate ten-year projections of penguin numbers. Adult survival rates were based on future sardine abundances predicted under the sardine and anchovy operational management procedure (formula for setting total allowable catches) currently being tested and its associated base case operating model. Projections were compared to equivalent scenarios without fishing. Results indicate that the effect of fishing is likely to be rather small, especially when compared to uncertainties in the dynamics related to the variable spatial distribution of the sardine population.

The coupling of the penguin population model to the sardine operating model provides an objective assessment of the impact of fishing on Robben Island penguins. This is an example of how a fishery can be managed considering not only single-species goals but also ecosystem-related effects. Such quantitative consideration and fitting to data of a non-target predator is rarely found in fisheries management. This work advances implementation of an ecosystem approach to fisheries, which is important in the context of increasing pressure worldwide to account for the foraging needs of dependent predators.

Acknowledgements

I am indebted to the many scientists whose fieldwork and analyses contribute to the data series which are essential for this project. I acknowledge in particular the work of Rob Crawford and Newi Makhado (moult and nest counts), Richard Sherley (breeding success), Antje Steinfurth and Lorien Pichegru (foraging effort data), and SAFRING (tag data). Collecting seabird data is labour intensive, and none of the important data series would exist without the efforts of these and their teams. Of equal importance to this work are the time-series of small pelagic abundance (prepared by Janet Coetzee and Carryn de Moor) and fisheries catches (prepared by Jan van der Westhuizen and Carl van der Lingen).

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I thank my supervisors Éva and Doug for introducing me to the field of ecological modelling and providing expert guidance throughout. I thank all my MARAM colleagues for friendship, support, and advice readily given. In particular, their proofreading of this work was much appreciated.

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Abbreviations

A term is given in full where it first appears in each chapter, and is abbreviated thereafter.

ADMB	AD Model Builder (http://admb-project.org)
ADMB-RE	ADMB random-effects module
AIC	Akaike information criterion
CCAMLR	Commission for the Conservation of Antarctic Marine Living Resources
CEMP	CCAMLR Ecosystem Management Programme
cpue	catch per unit effort
$\boldsymbol{CV}$	coefficient of variation
DAFF	Department of Agriculture, Forestry and Fisheries (South African)
EAF	ecosystem approach to fisheries
FAO	Food and Agriculture Organization (of the United Nations)
GLM	general linear model
HCR	harvest control rule
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
LTL	low trophic level

MP	management procedure
MCM	Marine and Coastal Management (Department of Environmental Affairs and Tourism, South Africa)
MCMC	Markov-chain Monte Carlo
MPA	marine protected area
MRM	minimally realistic model
MSE	management strategy evaluation
MSY	maximum sustainable yield
OM	operating model
OMP	operational management procedure
SAFRING	South African Bird Ringing Unit
SWG–PEL	Small Pelagic Scientific Working Group (of DAFF)
TAB	total allowable bycatch
TAC	total allowable catch
VIF	variance-inflation factor
VPA	virtual population analysis

Chapter 1

Introduction

The world's oceans are constantly changing. Some changes are driven by natural environmental processes, while others are driven by human influences, including fishing. The challenge for fisheries scientists and decision makers (ultimately, usually politicians) is to manage the world's fisheries effectively in this dynamic environment in a sustainable manner. Unfortunately, the sustainability of many fisheries has been put in doubt for reasons such as bad governance, demand exceeding resource availability, poverty, and insufficient knowledge (Hilborn 2007a). In addition, fisheries and seabirds sometimes compete for the same resources (Karpouzi *et al.* 2006; Okes *et al.* 2009).

In South Africa, the small pelagic fishery exploits primarily sardine *Sardinops sagax*[1] and anchovy *Engraulis encrasicolus*[2]. Concern has been raised that excessive fishing pressure impacts the abundance of these fish to the detriment of other components of the ecosystem. In particular, the African penguin *Spheniscus demersus*, a top predator which preys on sardine and anchovy, has suffered recent declines in abundance at several important colonies. This thesis investigates the relationship between forage fish abundance and penguin demographics. The goal is that models developed in this work will enable scientific recommendations for the future management of the small pelagic fishery to include consideration of the foraging needs of penguins.

This chapter provides some historical background to ecosystem considerations in fisheries management, African penguins, the South African small pelagic fishery, and management of this fishery.

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[1] Or pilchard, previously known as *Sardinops ocellatus*.

[2] Previously known as *Engraulis capensis*.

In Section 1.1, studies leading to the development of an ecosystem approach to fisheries are reviewed, as well as the role of seabirds as indicator species. Section 1.2 reviews previous studies involving interactions between seabirds and fisheries. Section 1.3 describes the population trend of the African penguin. Various factors which may influence penguin survival and reproduction rates are discussed. Section 1.4 provides an overview of the South African sardine and anchovy fishery. A description of the operational management procedure approach to fisheries management is given in Section 1.5, followed by a review of the management of the small pelagic fishery in South Africa. Section 1.6 reviews previous approaches to the assessment interactions between penguins and the small pelagic fishery. Section 1.7 outlines the objectives and structure of the following chapters of this thesis.

1.1 The ecosystem approach to fisheries with a focus on impacts on seabirds

1.1.1 Concern over global fishing intensity

The concern that fishing is degrading marine ecosystems has led to numerous frequently cited articles published in high-profile journals, notably *Science* and *Nature*. Hilborn (2007b) lists several examples of these. Some assert that often these papers unfortunately present a heavily distorted or exaggerated view of reality (Hilborn 2007c). However, such publications have contributed to the general perception of readers that fisheries science and management have failed (Hilborn 2010a), despite numerous rebuttals (Banobi *et al.* 2011).

Worm *et al.* (2006) published the sensationalist projection that all wild fish stocks would have collapsed by 2048, based on extrapolation of a recent perceived trend. This result has been discredited by many critics (e.g. Branch 2008). In fact, the number of overfished stocks[3] is actually decreasing in several countries where fisheries are well managed (Hilborn 2007d). One reason for the discrepancy in views is the debate over whether reported catch data alone can reliably inform about abundance trends (Branch *et al.* 2011b; Daan *et al.* 2011; Carruthers *et al.* 2012; Pauly *et al.* 2013). However, there are indeed many regions where overexploitation of marine resources continues, especially in developing countries (Worm *et al.* 2009).

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[3] Often defined as stocks whose abundance is below 50% of B_{MSY}, the biomass at which maximum sustained yield is attained (Hilborn and Stokes 2010).

Severe depletion of a fish stock may have long-term consequences. In an analysis of 90 fish stocks, Hutchings (2000) found that amongst several families there was little sign of recovery from low biomass levels, even after 15 years. Although generally there seems to be no substantial decline in reproductive success rates at low biomass levels (Myers *et al.* 1995), recovery time-scales may be very long, especially if fishing effort remains high. This evidence raises doubts concerning the resilience of fish to heavy fishing pressure, and hence the resilience of marine ecosystems as a whole.

One effect that fishing may have on an ecosystem is that the relative abundances of species from different trophic levels may be altered. From an analysis of global fisheries landings and estimated trophic levels, Pauly *et al.* (1998) concluded that the mean trophic level of catches had been gradually declining since 1950. The hypothesis was that fisheries-induced changes in food webs had led to a shift in targeted stocks away from long-lived piscivorous bottom fish and towards low trophic level invertebrates and small pelagic fish. This seemed to be supported by the estimate of Myers and Worm (2003) that large predatory fish biomass had been reduced to only 10% of pre-fishing levels (sometimes taken to be the threshold defining "collapse"). However, this conclusion has been strongly rebutted (see e.g. Branch *et al.* 2010), and furthermore Essington *et al.* (2006) showed that, in most ecosystems, the change in mean trophic level could be attributed to the addition of low trophic level fisheries, while landings of high trophic level species had not decreased. Thus, lower mean trophic levels of catches are generally not an indication that species in the high trophic levels have been fished to economic extinction. Indeed, assessments of Pacific tunas indicated that the biomasses of most of these species were well above standard fisheries management targets (Sibert *et al.* 2006). Nevertheless, the rise in catches across trophic levels can increase the susceptibility of fisheries to collapse, regardless of changes in mean trophic level (Branch *et al.* 2010). Thus, the development and expansion of new fisheries has implications for management strategies which often do not take interactions between fisheries targeting different trophic levels into account.

Global fishing effort increased substantially in the decades following the Second World War, leading to rapidly increasing total landings (Pauly 2009). However, since landings reached a plateau in the 1980s, the capacity of the global fishing fleet has remained high, often supported by government subsidies (Pauly *et al.* 2002). Ecologists and fisheries scientists agree that exploitation rates generally need to be reduced, and that removing subsidies (without which continuing to exploit overfished stocks would often no longer be profitable) is an important goal (Hilborn 2007b). Meanwhile, scientific advice is not always respected, and politicians have been slow to reform policies which encourage overcapitalization of fleets and the "race to fish" (Worm and Myers 2004; Hilborn 2007b).

1.1.2 Ecosystem considerations in fisheries

A growing concern is that intensive fishing is degrading marine ecosystems to a degree which is not sustainable. Based on a meta-analysis of published data from many studies at both local and global scales, Worm *et al.* (2006) concluded that a decrease in marine biodiversity leads to poorer water quality and higher rates of resource collapse. Conversely, restoring biodiversity increased primary and secondary productivity. The implication is that implementing management decisions with the objective of maintaining marine ecosystem health is of benefit not only to the ecosystem in terms of reducing species collapse, but also has the advantage of sustaining good fishery yields at relatively low operating costs (Worm *et al.* 2009).

As a result of the growing concern about the sustainability of fishing practices, since the 1990s many scientists have attempted to move towards fisheries management strategies which consider not only target species but also the impact which fishing may have on other components of the ecosystem (Botsford *et al.* 1997; Sainsbury *et al.* 2000; Constable 2001). This has come to be known as the ecosystem approach to fisheries (EAF, see Garcia *et al.* 2003), or ecosystem-based fishery management (EBFM, see Pikitch *et al.* 2004).

Hilborn (2011) points out that single-stock management techniques may be insufficient for ecosystem preservation, even if they are perfectly implemented. Some reasons for this are that bycatch of charismatic or endangered species is not considered, habitat may be modified (e.g. by trawling), and depletion of forage fish to maximum sustainable yield (MSY) target levels may result in a loss of yield among predatory fish because of trophic connections. In general, management strategies which maximize the harvest of individual components of the ecosystem will not result in sound management of the ecosystem as a whole.

Plagányi and Butterworth (2005) list several situations in which important interactions are likely to occur between fisheries and marine mammals, most of which apply equally well to seabirds such as penguins. For example, interactions should be expected where fisheries and predators overlap spatially and target the same type and size of fish. This is especially the case if the predators have no easy access to suitable alternative food sources. This could be because the predators have developed a high degree of specialization in the prey they target, or because they have a foraging range that is restricted, for example, to the vicinity of a land-based breeding colony.

Key objectives of EAF/EBFM[4] include environmental conservation efforts such as the control of pollution and the protection of habitat (Larkin 1996), and species conservation through the maintenance of biodiversity, genetic variability, and trophic level balance (Gislason *et al.* 2000). For an example of the various biological and socio-economic considerations involved in the implementation of ecosystem-based management, see Witherell *et al.* (2000) for details of the various aspects considered in the management of Alaska groundfish fisheries.

1.1.3 Implementations of EAF/EBFM

Various international agreements have progressively developed EAF concepts and encouraged their implementation, including the Convention on the Law of the Sea (concluded in 1982), the 1992 UN Conference on Environment and Development, the 1995 FAO code of Conduct for Responsible Fisheries, the 2001 Reykjavík declaration on incorporating ecosystem considerations into fisheries management, and the 2002 World Summit of Sustainable Development held in Johannesburg, South Africa. At this last meeting, delegates (including South Africa) agreed to encourage the application of the ecosystem approach by 2010.

The rapid adoption of EAF as policy has somewhat outpaced the development of methods for its implementation. The Fisheries Department of the Food and Agriculture Organization (FAO) of the United Nations has compiled a set of guidelines for implementing EAF as an extension to existing fisheries management methods (FAO 2003). Guidelines are given on how to express operational objectives in terms of economic, social and ecological goals.

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[4] These terms are used synonymously in this work.

All fisheries are recognized to have substantial interactions either with other fisheries or with other ecosystem components, thus necessitating EAF considerations in pursuit of sound overall management. In turn, modelling is required to take these interactions into account. Butterworth and Plagányi (2004) discussed various issues relating to multispecies modelling. Questions considered included whether multispecies models should be used to inform decisions, whether uncertainty is reduced relative to single-species models, and whether whole ecosystem or minimally realistic models are more appropriate. Advancement of an ecosystem approach requires much data to be collected and time for analysis. Nevertheless, in some countries advances along these lines have been made.

In Australia, various scientific tools have been developed for the implementation of EBFM, including an extension to the management strategy evaluation (MSE) approach (see also Section 1.5) and a harvest strategy framework (Sainsbury *et al.* 2000; Smith *et al.* 2007). An ecological risk assessment framework for fisheries, incorporating a precautionary approach to uncertainty, has been developed with a hierarchical structure, which makes the best use of the available data (Hobday *et al.* 2011).

In the United States, a five-step process for "integrated ecosystem assessments" has been developed (Levin *et al.* 2009). First, since an attempt to understand any ecosystem in its entirety would be naive given available data and knowledge, specific objectives and ecosystem pressures deemed to be of primary importance are identified, in consultation with stakeholders. Second, appropriate ecosystem indicators are selected and validated in order to provide a method for assessing ecosystem trends. Third, the risk that these indicators reach or remain in an undesirable state is evaluated. Fourth, MSE is used to test which policies and decision rules meet the stated objectives. Finally, continued monitoring of ecosystem indicators is necessary to assess whether management strategies are delivering the desired results.

In South Africa, the Marine Living Resources Act No. 18 of 1998 provides a legal framework for progressing towards an EAF (Cochrane *et al.* 2004). Strategies geared towards the implementation of an ecosystem approach to South Africa's major fisheries are discussed by Shannon *et al.* (2006). An EAF task group was established in 2003, focusing on the sardine and anchovy fishery as an initial case study. This fishery was selected because it targets fish on which many predators depend for food.

Temporal and spatial management have often been proposed as management tools that can provide an insurance against inaccuracies in stock assessments or unknown impacts of a fishery on other species in the ecosystem. Spatial closures that permanently prohibit fishing, termed no-take reserves, can be used to manage fishing effort, complementing alternative controls such as quota management (Mangel 2000). Such measures are discussed further in Section 1.1.5.

1.1.4 The importance of forage fish

Forage fish, such as sardine and anchovy, are small pelagic species which feed on zooplankton and phytoplankton. In turn, many marine predators including larger fish, mammals, and seabirds primarily consume forage fish (Pikitch *et al.* 2012b). Many marine ecosystems, including the Benguela Upwelling System, have what is known as a "wasp-waist" structure of species richness (Cury *et al.* 2000). This structure is characterized by a large diversity of species both at the lowest trophic levels (primary producers) and at high trophic levels (predatory fish, birds, and mammals). In between, the "low trophic level" (LTL) is dominated by a very large biomass represented by only a few species of forage fish.

As a result of the position of forage fish in the food web, heavy fishing pressure on these fish has the potential to affect the ecosystem at all trophic levels. This can occur through both the top-down control of zooplankton and the bottom-up control of predators (Shannon *et al.* 2000). However, it is difficult to predict what system-wide effects, including possible regime shifts, different fishing management strategies may have on such complex systems (Cury and Shannon 2004; Bakun *et al.* 2009).

Recently, there has been a strong research focus on the ecosystem effects of fishing LTL species. This is because historically about twice as many LTL fisheries have collapsed[5] as fisheries targeting large predators (Pinsky *et al.* 2011). Note, however, that more variability in stock size is expected

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[5] In this study, an assessed stock was defined to be collapsed if the minimum annual biomass was below 20% of the biomass necessary to support MSY, and for landings data a stock was defined to be collapsed if landings remained below 10% of the average of the five highest landings recorded for more than two years.

in short-lived LTL species, and therefore instances of “collapse” of such stocks may be expected to occur naturally from time to time regardless of fishing pressure.

Smith *et al.* (2011) used various ecosystem models to explore the effects that fishing low trophic level species such as forage fish and krill may have on the ecosystem. Results indicated that at traditional MSY-related levels, fishing could result in large impacts on other components of the ecosystem, including marine mammals, seabirds, and predatory fish with high commercial value. Simulations suggested that halving exploitation rates would reduce most impacts on other ecological groups while still producing a yield of about 80% of MSY.

The Lenfest Forage Fish Task Force recently concluded a comprehensive analysis of forage fish, the role that these species play in marine food webs, and associated fisheries (Pikitch *et al.* 2012a). Key results from this study are in close agreement with those of Smith *et al.* (2011). In particular, simulations suggested that reducing fishing effort to half of traditional levels would reliably sustain both the forage fish and their dependent predators. The considerable economic value of forage fish has been highlighted, with about two-thirds of this attributed to fisheries on species which consume forage fish (Pikitch *et al.* 2012b).

1.1.5 Current trends in fisheries management

Simulations have shown how the pursuit of different management objectives can result in very different outcomes[6] (Pauly *et al.* 2003). Consensus among scientists is that widespread changes are required in the management of global fisheries to promote the future sustainability of both fishery yields and marine ecosystems at large. Cochrane (2000), however, argues that generally these goals are not being seriously pursued, often for political reasons. A more recent analysis reveals that although more countries are adopting international treaties on the conservation and optimal utilization of marine living resources, implementation of measures to control fishing pressure continues to lag (Ye *et al.* 2013).

Many scientists agree that a reduction in global fishing effort is necessary in order to rebuild depleted stocks (Worm *et al.* 2009). The trend is to move away from the traditional fisheries

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[6] For example, maximising profit resulted in reduced effort, while maximising sales resulted in heavy resource depletion.

objectives of maximizing yield and employment, which usually result in heavily depleted stocks and low catch rates (Hilborn 2007a). Instead, management strategies that target lower levels of stock depletion are now favoured for the benefits of better ecosystem preservation as well as more profitable fishing.

The two primary functions of fisheries management are specifying catch limits and allocating quotas to fishers (Hilborn *et al.* 2003; Hilborn 2008). Of the many contrasting fisheries governance structures which exist, those which incorporate more restrictive access and set appropriate incentives for fishers and managers have been more successful in terms of societally desirable outcomes (Hilborn *et al.* 2004a, 2005). Lessons learned from successful fisheries may be applied to facilitate the reform of unsustainable fisheries (Hilborn 2007b). In particular, governance systems should be instituted and incentives devised which reduce fleet capacity and stop the “race to fish” through providing dedicated access rights. After all, accurate assessment and detailed analysis of stocks is pointless if fishing effort cannot be regulated (Hilborn 1992). Co-management between fishers and managers has been advocated as a promising tenet of fisheries governance (Gutiérrez *et al.* 2011).

Hilborn (2010b) performed simulations which suggest that it is possible to achieve a sustainable yield of at least 80% of MSY across a wide range of stock sizes, independent of the life-history parameters of the stock. He argues that other fisheries objectives are generally more important than obtaining the absolute MSY, as long as the yield remains “pretty good”, that is, close to MSY. Thus, little yield is lost through maintaining a stock size above MSY level on account of economic or ecosystem considerations; however, if a stock is below this level, opposition to recovery plans can be expected if these result in heavy reductions in catches and profits in the short to medium term (Ye *et al.* 2013). Branch *et al.* (2011a) advocate that the role of scientists is to advise managers on rebuilding or maintaining fish stocks, targeting biomass levels which will allow fisheries to be profitable as well as ecologically responsible.

Selective fishing is employed as a management tool, often with ecosystem considerations in mind. However, Zhou *et al.* (2010) suggest that a more balanced exploitation of marine resources would reduce the disturbance of ecosystem functioning. Heavily targeting a particular species, stock, size or sex of fish, or restricting harvesting seasonally or spatially, could cause unwanted ecological effects by removing a particular component of the ecosystem.

One form of spatial selection is effected through the establishment of marine protected areas (MPAs). Some ecologists advocate for huge sections of the ocean to be designated no-fishing zones (Pauly *et al.* 2003; Pauly 2009). The hope is that no-take marine reserves protect habitat and biodiversity, buffer against uncertainty in stock assessments, and ultimately increase fisheries yields (Attwood *et al.* 1997). However, Agardy *et al.* (2011) review several reasons for which MPAs may not produce the benefits desired. For example, MPAs are unlikely to be of much benefit to fisheries of highly mobile species (Edwards *et al.* 2008), or to ecosystems when there is little bycatch or habitat impact (Hilborn *et al.* 2004b). Also, large no-take reserves located near traditional fishing communities may necessitate longer fishing trips, increasing both cost and risk.

Hilborn (2013) notes that because demand for fish for human consumption is unlikely to decrease, aquaculture and fishing effort in areas remaining open to fishing will tend to increase as MPAs become more widespread. Alternatively, if reduced fishery yields are to be compensated for by additional agricultural produce, more forests will have to be cleared, resulting in accelerated biodiversity loss.

An important area where spatial management has been advocated is as a mitigation measure against localized depletion of forage fish (Pikitch *et al.* 2012a). If fishing activity should cause such local reductions in fish abundance to occur in key foraging areas, dependent predators would be severely affected. An example of this type of intervention which aims to ensure adequate provision for Antarctic predators has been discussed in Section 1.2.1. The efficacy of both spatial management measures and reductions in total catches is investigated in this thesis in the context of interactions between the South African small pelagic fishery and African penguins.

1.1.6 Ecosystem modelling

Various different modelling approaches for implementing an EAF have been developed. Plagányi (2007) gives a wide overview and critical assessment. Three main classes of EAF models are whole ecosystem models such as Ecopath with Ecosim (Christensen and Walters 2004; Plagányi and

Butterworth 2004) and the biogeochemical model Atlantis (Fulton *et al.* 2005), minimally realistic models (MRMs) which only include a small number of species thought most likely to interact with the target species of interest (Punt and Butterworth 1995, for example), and dynamic system models such as the individual-based model OSMOSE (Shin and Cury 2001). Related to MRMs are models of intermediate complexity for ecosystem assessments which incorporate a reduced set of ecosystem components deemed to be important for the problem at hand (Plagányi *et al.* 2012).

A particular challenge in ecosystem modelling, which is inherently characterized by complexity and associated uncertainty, is to take the effects of climate change into account (Rose *et al.* 2010; Plagányi *et al.* 2011a,b). Such modelling requires additional flexibility to allow for changing baselines, and adaptive management responses provide robustness to nonlinear effects.

The main consideration when selecting the modelling approach used in the analysis presented in Chapter 4 was the need for a rigorous approach, because this work could potentially have large socio-economic consequences on the South African small pelagic fishery. Few ecosystem models are fitted to data, but here an approach was needed that enabled both fitting to various types of predator data and the ability to statistically assess the quality of these fits. Also, many ecosystem modelling approaches are constrained by a generic framework. However, to adequately address the key management questions in this case, it was helpful to develop a specially tailored modelling approach. The resulting model is simultaneously rigorous and pragmatic, and it accounts for a range of uncertainties.

1.1.7 Seabirds as ecological indicators

Marine animals, including seabirds, may provide ecologists with information about changes occurring in the ecosystem in which they forage. For this to be effective, the animal studied must show a response to such changes, which may be more difficult or more costly to observe directly. Pitfalls may be encountered: several are discussed by Durant *et al.* (2009) including statistical bias, time lags, and handling effects.

Piatt *et al.* (2007) list several advantages which seabirds have over other marine species as ecological indicators. Seabirds are highly visible, they congregate in large land-based colonies, and biologists are readily able to collect data for various demographic and life-history parameters. Penguins, being flightless, are particularly easily studied. As central-place but wide-ranging foragers, penguin foraging patterns provide a reflection of oceanographic conditions around breeding colonies (Boersma *et al.* 2009). In the South African context, the African penguin is considered a good indicator species of ecosystem impacts of the sardine and anchovy fishery. Reasons for this include the importance of these species in the penguin diet, the restricted foraging range of penguins during the breeding season, and the availability of extensive penguin research and data.

Wilson (1992) reviews a range of seabird parameters which may be measured: adult mortality, population size, nesting attempts, chick growth, stomach contents, foraging effort, and a proposed measure of seabird catch per unit effort (cpue). Many of these are confounded as indicators of prey availability by other environmental variables or seabird effort compensation, making inferences difficult unless foraging effort can be measured directly. Nevertheless, one might expect, for example, decreased adult survival when prey biomass drops below some threshold and increased chick fledging rates when food is more plentiful (Cairns 1992). Besides sensitivity to changes in prey availability, seabirds may also be used to track geographical and temporal patterns of ecosystem pollution caused, for example, by oil spills and mercury contamination (Furness and Camphuysen 1997).

Seabird diet and breeding success have been shown to predict future sardine catches and catch rates in the Gulf of California (Velarde *et al.* 2004). However, in the Benguela system, an early study (Adams *et al.* 1992) cast doubt on the utility of seabirds for informing on the abundance of their commercially important prey species. In particular, the proportion of anchovy in the African penguin diet was not a good predictor of anchovy recruitment as monitored by hydroacoustic surveys. Other seabird parameters were thought to reflect fluctuating prey abundance poorly due to the ability of seabirds to switch between different prey species and adjust foraging effort in this system.

Trophodynamic indicators for measuring the strength of interactions between ecosystem components and structural changes have been assessed in the context of the northern and southern Benguela ecosystems by Cury *et al.* (2005) and Australia by Fulton *et al.* (2005) using computer simulations. Cury *et al.* show that the trophic impact on seabirds by horse mackerel during the 1990s was negative in the northern Benguela, but the impact by sardine in the southern Benguela was positive. Fulton *et al.* found that reproductive success of seabirds was responsive only in the case of a closed population.

Underhill and Crawford (2005) proposed an index derived from abundance data of ten seabird species as an indication of ecosystem health in the Benguela. Three variations of the index were developed, one weighting each species equally and two involving different methods of weighting the species according to IUCN conservation status.

1.2 Review of approaches to modelling and mitigating seabird–fishery interactions worldwide

Apex predators such as seabirds are positioned at the top of complex ecosystem-wide food webs. Typically, forage fish have highly variable recruitment, leading to fluctuating abundances. While aggregating behaviour tends to limit changes in shoal density, the spatial range of a fish stock may vary substantially with total biomass. Seabirds have evolved various mechanisms to adapt to such changes. However, throughout the southern hemisphere, penguin populations have declined in recent decades, pressurized by both climate warming and human activity (Boersma 2008). Of concern to ecologists is whether vulnerable penguin species and other seabirds will continue to exist as conditions become more challenging.

Seabirds are affected by fisheries through both incidental mortality (bycatch) and competition when fishing substantially reduces the abundance of prey available. On the other hand, fisheries discards provide a regular food source for some species (Wagner and Boersma 2011). These mechanisms may affect the survival rates of adult birds as well as reproductive success. The work of the CCAMLR Ecosystem Monitoring Programme is reviewed in Section 1.2.1, and other studies are mentioned in Section 1.2.2.

1.2.1 CCAMLR Ecosystem Monitoring Programme

Antarctic fisheries have been managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) since 1984. The goal of the Commission is to enable the sustainable exploitation of target species while maintaining the ecological relationships of the ecosystem. This refers particularly to the potential impact which a decrease in the abundance of prey may have on predators such as marine mammals and seabirds. Article II of the CAMLR Convention requires that any disturbance to the marine ecosystem as a result of fishing should be potentially reversible over two or three decades (CCAMLR 1980). The Commission also recognizes the possible need for spatial management so as not to prejudice land-breeding predators which have a restricted foraging range while breeding.

The CCAMLR Ecosystem Monitoring Programme (CEMP), one of the first international efforts at monitoring a large marine ecosystem, has been implemented since 1987 (Agnew 1997). Data are collected at various sites on both predator and prey population dynamics. The main prey species studied is Antarctic krill *Euphausia superba*. Predator monitoring includes four species of penguin: Adélie *Pygoscelis adeliae*, chinstrap *P. antarcticus*, gentoo *P. papua*, and macaroni *Eudyptes chrysolophus*. The predator parameters monitored relate to reproduction, growth, feeding behaviour and abundance, all of which could potentially respond to changes in both prey availability and environmental factors. A key prey parameter monitored is the krill cpue, which gives an indication of krill density and hence prey availability in areas surrounding the study sites.

CCAMLR has adopted a precautionary target for krill abundance, set at 75% of the pristine spawner biomass (SC-CAMLR 1994). This was not based directly on predator–prey models, which were judged to be too uncertain. Nonetheless, several pioneering models were developed. For example, following the joint meeting of CCAMLR's Working Group on Krill and the Working Group for the CEMP in 1992, Butterworth and Thomson (1995) developed a one-way interaction model in which changes in krill abundance have an effect on predator populations. Simulations suggested that resilience of predators was negatively affected by krill recruitment variability. This approach has been developed for modelling krill–fur seal interactions (Thomson *et al.* 2000) and krill–baleen whale interactions (Mori and Butterworth 2004). Plagányi and Butterworth (2012) and Watters *et al.* (2013) have developed a krill–predator–fishery interaction operating model for the Scotia Sea to facilitate the testing of candidate management strategies for the krill fishery. These initiatives have potential implications for the spatial allocations of future krill catches with the aim of reducing the impact of the krill fishery on predators.

1.2.2 Other seabird–fishery interaction studies

Cury *et al.* (2011) studied the response of various seabird populations from different parts of the world to fluctuating levels of forage fish abundance. Their analysis showed that seabird breeding success was reduced and became more variable when the available biomass of key prey species (forage fish) dropped below one-third of the maximum observed abundance. This study included analyses of gannets and penguins from the Benguela Current large marine ecosystem. Breeding success of these seabirds was compared with the combined spawner biomass of sardine and anchovy west of Cape Agulhas estimated from the annual November hydroacoustic survey for small pelagic fish.

Studying a declining population of kittiwakes off the east coast of Scotland, Frederiksen *et al.* (2004) emphasized the importance of monitoring both breeding success and adult survival. Both of these population parameters were negatively correlated with winter sea temperature. Warmer temperatures depress sandeel recruitment, affecting prey abundance for many North Sea seabirds. Both breeding success and adult survival were further impacted from 1991 to 1998 when a sandeel fishery was active.

Incidental mortality in fisheries may occur when birds are snagged in nets or when they ingest longline hooks, attracted by bait. Tuck *et al.* (2011) report on bycatch rates of several species of albatross in Atlantic tuna fisheries. Bycatch is considered to be a major factor contributing to the decline of albatross populations since 1960. Various measures of bycatch mitigation are available such as employing bird-scaring lines and setting lines at night.

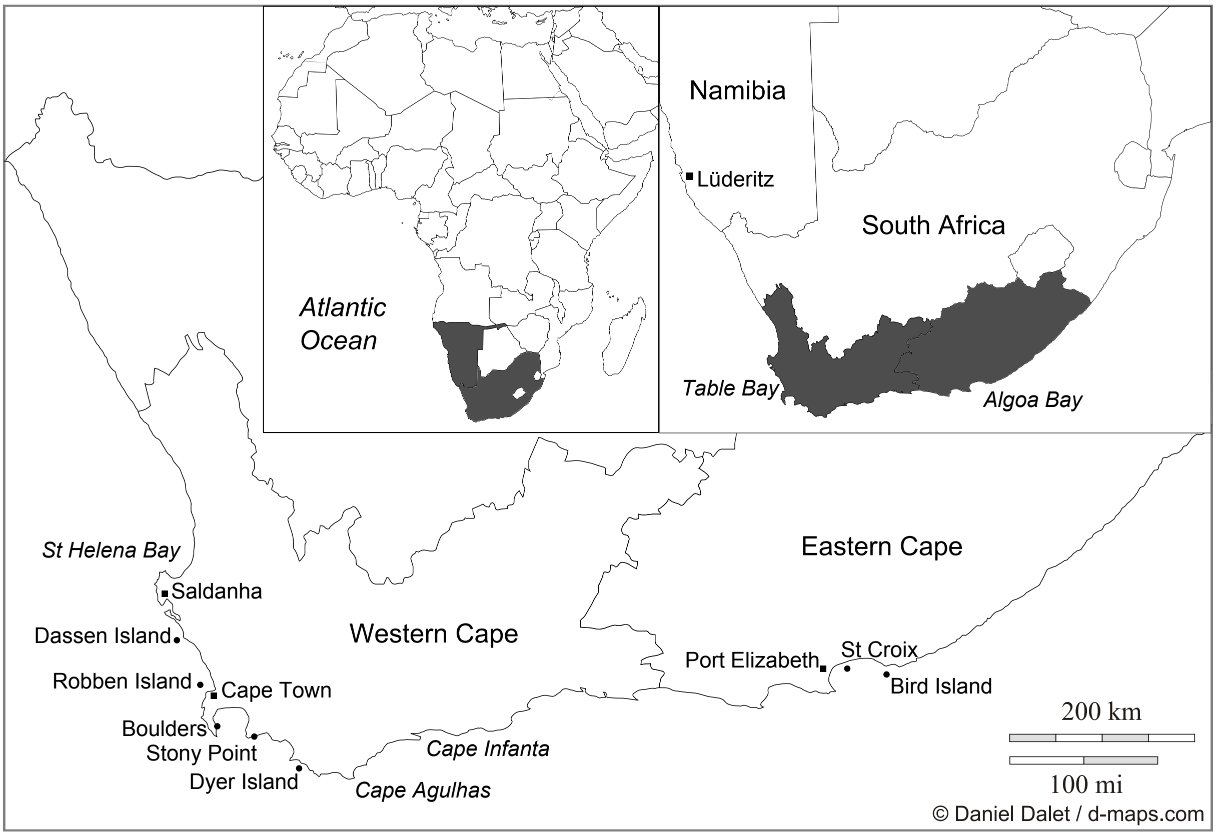

Figure 1.1: Map indicating the locations of the largest African penguin breeding colonies.

1.3 African penguins

The African penguin[7] is endemic to southern Africa and is the only species of penguin which breeds on the African continent. Breeding is restricted to several coastal islands and a few mainland colonies (Figure 1.1) ranging from Namibia in the northwest to Algoa Bay in the southeast (Shelton *et al.* 1984; Crawford *et al.* 2011a).

1.3.1 Population trends

There is considerable uncertainty about the size of the African penguin population during the earlier part of the twentieth century. Based on egg harvests, which took place until 1967, Crawford *et al.* (1995) suggest that the entire nesting population for the species in the early 1900s was about 575 000 adults, including 300 000 at Dassen Island. Later, an egg harvest modelling

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[7] Before 1995, the African penguin was known as the jackass penguin on account of its braying call. South American species from the genus *Spheniscus* have similar calls, so the new name is more distinctive.

exercise by Shannon and Crawford (1999) revised the estimated population at Dassen Island at that time upward to 1.45 million adults[8]. By applying recently observed nesting densities to the areas of Dassen Island where penguins were reported to breed in 1921–1931, Crawford *et al.* (2007) estimated that in the 1920s the colony could have contained about one million nesting pairs. The total penguin population supported by the Benguela ecosystem at that time was estimated to be in the range 1.5–3.0 million adults[9].

The size of the penguin breeding population at Robben Island since 1900 is much more certain. When European colonists arrived at the Cape in the 17th century, a thriving penguin colony was located at the island[10]. However, exploitation of penguins, including hunting and egg collecting, eventually extirpated the colony in the 19th century. The island was used regularly as a release site for rehabilitated penguins in the 1970s, but breeding was first observed there in 1983 (Shelton *et al.* 1984), marking the re-establishment of the Robben Island colony.

In the following years, the colony grew rapidly, driven primarily by immigration. Underhill *et al.* (2006) reported that the population of the new colony peaked in 2004 at 8 500[11] pairs. However, this was followed by a steep decline in the nest counts to less than 2 700 in 2008–2010 (Crawford *et al.* 2011a), and just 1 817 nests in 2011. Similar declines have been reported at all Western Cape colonies apart from Boulders and Stony Point. Furthermore, the number of breeding pairs at the Eastern Cape colonies has halved since 2001. Two other seabird species abundant in the Benguela have also declined severely in the last 50 years: Cape gannets *Morus capensis* and Cape cormorants *Phalacrocorax capensis* (Hamann *et al.* 2012).

The main factors causing the decline in African penguin abundance since the early twentieth century are thought to be egg harvesting (until 1967), guano collection (until 1990), and the collapses of the South African and Namibian sardine resources in the 1960s and 1970s respectively (Best *et al.* 1997). Factors thought to contribute to the ongoing decline in penguin numbers include scarcity of food, predation, and oil spills (Koenig 2007).

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[8] The associated 95% confidence interval was 0.51 to 3.13 million adults.

[9] This is still considerably fewer than a lighthouse keeper's anecdotal report of 9 million penguins at Dassen Island in 1906 (Shannon and Crawford 1999).

[10] A map of South Africa produced by French traveller and ornithologist François Le Vaillant in 1790 labels Robben Island as the "Island of the Penguins".

[11] This figure has since been revised downward to 7 798 pairs (see Table 2.1).

1.3.2 Prey abundance and distribution

African penguins prey on shoaling epipelagic fish, particularly sardine and anchovy (Crawford *et al.* 2006a). If these are not available, they will eat other fish. For example, after the collapse of the Namibian sardine resource, diet samples taken from 1978 to 1982 indicated that pelagic gobies *Sufflogobius bibarbatus* had become the most important prey of penguins at colonies north of Lüderitz (Crawford *et al.* 1985), while south of Lüderitz, recent observations indicate that cephalopods are the main diet component (Kemper *et al.* 2001). From a linear modelling exercise, Crawford *et al.* (2008c) reported results indicating strong positive correlations between prey abundance and both penguin numbers and participation in breeding.

Penguins compete for prey with other predators such as Cape fur seals *Arctocephalus pusillus pusillus* (Crawford *et al.* 1992b), which are known to prey on sardine and anchovy (David 1987; Punt *et al.* 1995). The Cape fur seal population increased substantially from about 100 000 at the start of the 20th century to an estimated 1.7 million adults in 1993 (Butterworth *et al.* 1995).

Competition for sardine and anchovy also comes from the commercial fishing sector (Crawford *et al.* 1992b). Heavy fishing, particularly in areas close to penguin colonies, is argued to reduce the density of forage fish available to penguins (Crawford *et al.* 2001). Crawford (2004, 2007) emphasizes the importance of taking the foraging needs of seabirds into account in fisheries management.

Of particular concern are the shifting distributions of forage fish which may result in a spatial mismatch between the main penguin breeding colonies and their preferred prey (Crawford *et al.* 1990; Crawford 1998). The foraging range of penguins during the breeding season is particularly limited, as foraging trips typically last less than one day (Petersen *et al.* 2006; Pichegru *et al.* 2009).

1.3.3 Predation

Although attacks on African penguins by a variety of predators have been observed or inferred, few quantitative data are available which would allow predator impacts to be evaluated in a modelling framework. Nevertheless, predatory threats that could have some influence on penguin population dynamics are discussed below. These include both marine predators which threaten foraging penguins and predators which threaten penguins at their colonies, mainly affecting reproductive success.

Seals

In the last two decades, Cape fur seals have been observed killing penguins and other seabirds at Dyer Island (Marks *et al.* 1997), Lambert's Bay (Crawford *et al.* 2001) and Malgas Island (Makhado *et al.* 2006). A small number of young male seals seem to be responsible for most seabird killings. Kirkman (2009) gives a thorough review of seal–seabird interactions in southern Africa. Theories accounting for the recent perceived increase in seal predation on seabirds include decreased availability of regular prey (e.g. sardine), localized increases of seals near major seabird colonies, an increased awareness as a result of the rising emphasis on conservation of seabirds, and young seals having the opportunity to observe and learn from a few proficient seabird hunters. In response to the last point, a culling programme to remove offending seals was introduced in 1993, as the level of seabird predation by seals at some colonies was suspected to be unsustainable (David *et al.* 2003). Indeed, penguins have not bred at Lambert's Bay since 2005 (Crawford *et al.* 2011a).

Sharks and whales

The impact of large marine predators on penguin populations is particularly difficult to assess. There is certainly evidence that sharks are a threat to penguins (Randall *et al.* 1988). Killer whales *Orcinus orca* have been suggested as possible predators on African penguins (Randall and Randall 1990), although they are uncommon in South African coastal waters (Williams *et al.* 2009).

Threats to nests

During the breeding season, penguin eggs and chicks are threatened by feral cats *Felis catus* at some colonies (Underhill *et al.* 2006), and kelp gulls *Larus dominicanus* prey on penguin eggs (Hockey and Hallinan 1981; Pichegru *et al.* 2012). Despite eradication attempts, the Robben

Island feral cat population increased substantially during the early 2000s (Braby and Underhill 2007), and kelp gulls have bred at Robben Island since 2000 (Calf *et al.* 2003). The impact of both these predators on penguin breeding success should be monitored, especially if their numbers increase substantially.

Mole snakes *Pseudaspis cana* are known to consume the eggs of penguins and other birds at Robben Island (Dyer 1996), but most eggs eaten are likely to have been scavenged from abandoned nests (Sherley 2010). However, at least one instance of a snake attacking an occupied nest has recently been observed (Underhill *et al.* 2010). It may be necessary in future to consider the impact of interactions between snakes and penguins.

1.3.4 Oil pollution

The threat of oil spills to seabirds has increased with the rapid growth of international shipping during the twentieth century, especially since oil replaced coal as the primary fuel. Every ship carrying fuel oil has the potential to cause an ecological disaster. The South African coastline is notorious for shipwrecks. Furthermore, several of the largest colonies of African penguins are located in close proximity to major ports in Saldanha Bay, Table Bay and Algoa Bay. In response to oil spills, the South African National Foundation for the Conservation of Coastal Birds (SANCCOB) was established in 1968, becoming a world-renowned seabird rehabilitation institution. Oiling is considered to be an ongoing potential threat to the African penguin (Crawford *et al.* 2001).

Shannon and Crawford (1999) used a modelling exercise to investigate the potential long-term impact of both catastrophic and chronic oiling events on an African penguin colony. Results indicated that the reduction in colony size caused by a serious oil spill would still be evident after half a century. However, regular searches for oiled birds combined with effective rehabilitation would go some way towards offsetting this impact.

The breeding success rate of penguins de-oiled after the *Apollo Sea* spill in 1994 was found to be lower than that of penguins which had not been oiled (Wolfaardt *et al.* 2008c). Contributing factors were a higher mortality of chicks aged 40 days and older and a slower chick growth rate, especially when feeding conditions were less favourable. Mate fidelity, which has a positive association with breeding success, was also found to be lower for de-oiled penguins.

Following the major oil spill resulting from the wreck of the *Treasure* in 2000, Wolfaardt *et al.* (2008b) studied the survival rates of Dassen Island penguins. They found that among non-breeding penguins, survival rates of de-oiled birds were similar to those of birds which had been evacuated to escape oiling. However, once birds resumed breeding, de-oiled penguins had lower survival rates than those which had been evacuated. Barham *et al.* (2008a) reported on the survival and breeding success of penguins hand-reared as chicks following the *Treasure* spill, lauding the effort as a worthwhile conservation success.

1.3.5 Other influences on penguin dynamics

Disturbance to African penguins at breeding colonies has been found to have a negative impact on breeding success (Hockey and Hallinan 1981), though other evidence suggests that penguins are tolerant to the presence of humans (Heezik and Seddon 1990).

Seals are known to compete with penguins for space on some islands which have limited areas available for colonies (Crawford *et al.* 1995). Some islands previously covered by guano (suitable for burrowing) provided good habitat for nesting penguins, but were inaccessible to seals. Harvesting the guano has eliminated much ideal nesting space for penguins, but expanded potential breeding areas for seals, introducing additional competition with penguins. However, space availability for penguins is not a concern at the Robben Island colony.

Outbreaks of disease, such as avian cholera *Pasteurella multocida*, have been known to cause widespread fatalities of seabirds around the Western Cape coast, including some penguins (Crawford *et al.* 1992a). Recently, the trematodes *Cardiocephaloides physalis* and *Renicola sloanei* have been identified in several penguins admitted to the Penguins Eastern Cape Marine Rehabilitation Centre. These parasites appear to have had little effect on adult penguins, but certainly contributed to the death of several of the chicks examined (Horne *et al.* 2011). It is unknown how widespread infections of these parasites are, but they are likely to exacerbate the condition of birds which may be weakened by other factors.

1.4 The South African fishery for small pelagics

Species of sardine and anchovy coexist in a number of regions worldwide (Schwartzlose *et al.* 1999). The long-term fluctuations in the abundance of both fish is a common characteristic of these ecosystems. Peaks in abundance of sardine and anchovy often occur out of phase (Kawasaki 1992), resulting in a regime dominated by one or other of the species (Lluch-Belda *et al.* 1989). With changes in abundance, the range of these fish tends to change in terms of both extent and location (MacCall 1990; Schwartzlose *et al.* 1999). The primary reasons for these fluctuations are thought to be environmental variations and fishing, although often the specific mechanisms involved are poorly understood (Fréon *et al.* 2005; Checkley *et al.* 2009).

The management of the South African small pelagic fishery falls under the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF). The Fisheries Branch of DAFF was established in 2010 following a restructuring of the previous fisheries management authority, Marine and Coastal Management (MCM) which had fallen under the Department of Environmental Affairs and Tourism. Scientific advice in relation to management is provided by the Small Pelagic Scientific Working Group (SWG–PEL), which includes non-governmental scientists among its members, and representatives of both industry and NGOs as observers.

The South African purse-seine fishery developed in the 1940s, initially targeting sardine (van der Lingen *et al.* 2006). Following a series of large catches from 1958 to 1965, sardine was replaced by anchovy as the dominant forage fish in the southern Benguela (Figure 1.2). The Namibian sardine fishery persisted for another decade before it collapsed (Crawford 2007). At the time that sardine catches were decreasing, the minimum legal net mesh size was reduced from 1.5 inches to half an inch, facilitating fishing for anchovy recruits (Cochrane *et al.* 1997). These are primarily processed into fishoil and fishmeal, and the balance are used for human consumption.

Anchovy dominated South African pelagic landings from 1966 until 1995, by which time the sardine biomass was recovering and sardine catches were increasing steadily. Anchovy and sardine reached record abundance peaks in 2001 and 2002 respectively (de Moor and Butterworth 2009). Since 2007, anchovy has again dominated landings following several years of poor sardine recruitment (Coetzee *et al.* 2008b).

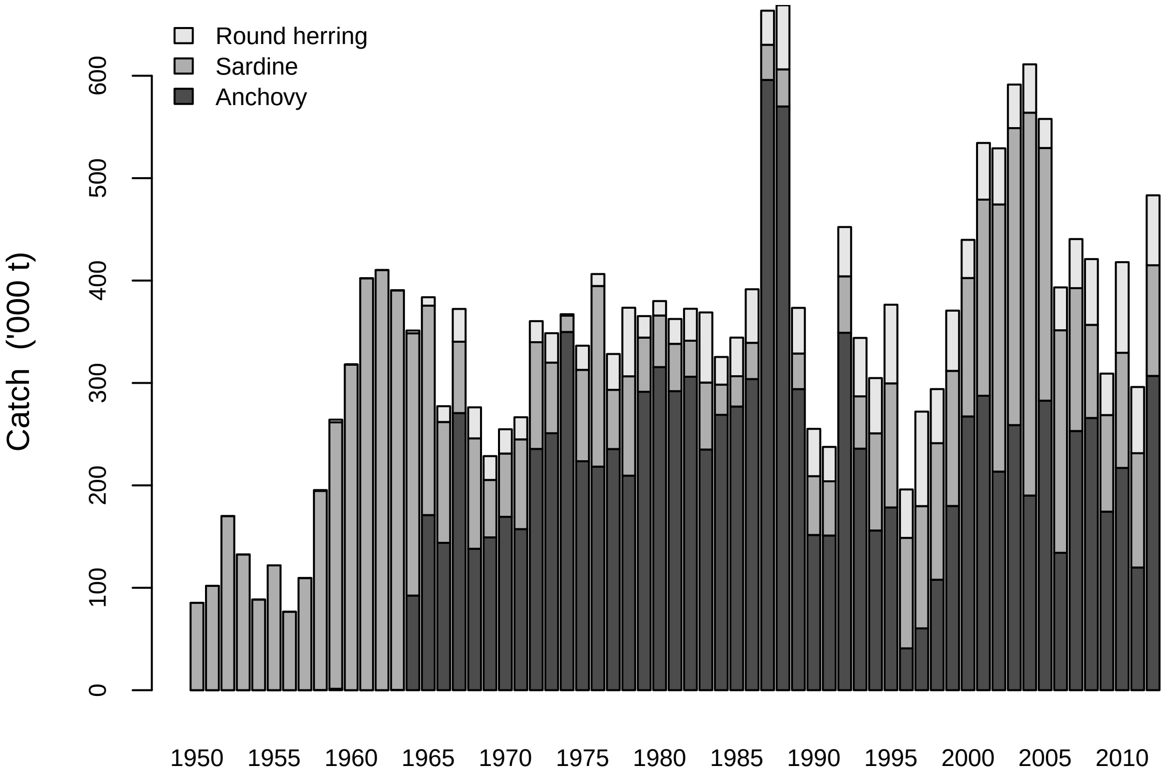

Figure 1.2: Annual catches landed by the South African small pelagic fishery from 1950 to 2012 (Fairweather *et al.* 2006, with recent data provided by J. Coetzee, DAFF). The sardine catch includes both directed and bycatch components.

Detailed knowledge of the magnitude and variation of sardine and anchovy abundance has been greatly enhanced since the inception of hydroacoustic surveys in 1984 (Hampton 1992). These have continued annually since then. Two surveys are conducted each year: a recruitment survey every May–June, and a 1+ biomass[12] survey in November. The early surveys indicated that anchovy spawning biomass was much greater than had been thought previously[13], sardine was recovering, and round herring was considerably underexploited (Hampton 1992).

Most sardine and anchovy are caught from January to September, after which time the shoals tend to disperse offshore. Juvenile anchovy is targeted as it moves south along the west coast from inshore nursery areas towards spawning grounds on the Agulhas Bank during the winter months (Hutchings 1992). Some juvenile sardine are taken as bycatch in this anchovy recruit

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[12] Biomass of fish aged one year and older (de Moor *et al.* 2011), assumed to be the spawning stock for anchovy. Sardine reproduce at age 2.

[13] Virtual population analysis (VPA) assessments had been based on the assumptions that fishing selectivity was constant across age classes and that cpue was proportional to abundance, both of which were subsequently shown to be incorrect.

fishery, though the industry tries to limit this as sardine are more valuable when caught as adults for canning (De Oliveira and Butterworth 2004). The mixed shoaling of sardine and anchovy necessitates that they be managed jointly, as landings of the two species cannot be maximized simultaneously. Controlling the level of sardine bycatch has enabled the fishery to better utilize the sardine resource in the last two decades.

The small pelagic fishery also takes substantial quantities of round herring *Etrumeus whiteheadi* during the first half of the year. Furthermore, small amounts of horse mackerel *Trachurus trachurus capensis*, chub mackerel *Scomber colias* and lanternfish *Lampanyctodes hectoris* are landed. The median total annual catch since 1950 is about 360 000 tonnes. The fishery is currently South Africa's second most valuable in monetary terms (de Moor *et al.* 2011), and is the largest in terms of landed mass (De Oliveira and Butterworth 2004). Besides exploitation by the fishery, South African pelagic fish stocks are an important food source for marine predators such as seals (David 1987) and seabirds (Crawford *et al.* 1991).

1.4.1 Recent prey distribution shift

From its inception, the South African small pelagic fishery developed on the west coast of the country. Sardine were abundant there for most of the year, and adult anchovy were caught during the summer months. The industry developed substantial processing infrastructure around St Helena Bay (Coetzee *et al.* 2008b). However, in recent years, surveys have shown that a far greater proportion of both sardine and anchovy is now spawning to the east of Cape Agulhas (Coetzee *et al.* 2008b).

The hydroacoustic biomass survey in 1996 showed an abrupt eastward shift of anchovy spawners, which coincided with a cooling of the eastern Agulhas Bank (Roy *et al.* 2007). This shift has subsequently persisted. Until 1998, most adult sardine measured in the November hydroacoustic surveys were found to the west of Cape Agulhas. Between 1997 and 2005, the distribution of sardine catches shifted steadily south and east by a distance of about 400 km (Crawford *et al.* 2008a). This coincided with the steady increase in the proportion of sardine east of Cape Agulhas estimated in the November hydroacoustic surveys from 1999 until 2004.

Coetzee *et al.* (2008b) questioned whether the actions of the pelagic fishery contributed to the shift in distribution of sardine through the depletion of a possible western component (sub stock) of the population by heavy fishing pressure. During the peak period of sardine abundance from 2000 to 2004, directed catch quotas increased from 126 000 tonnes to 457 000 tonnes (Fairweather *et al.* 2006). Over this period, about 80% of commercial catches took place to the west of Cape Agulhas, a consequence of the historical placement of the fishing fleet and processing factories in the west. However, by 2004, the proportion of survey-estimated biomass west of Cape Agulhas had declined to just 11% of the total (Coetzee *et al.* 2008b). This was further reduced to 7% in 2005. Up to the present time (2013), the sardine resource has been managed as a single stock without regulation of where catches may be taken. However, a spatial aspect to sardine assessment and management is now being considered (de Moor and Butterworth 2013a).

The overall sardine abundance as indicated by the surveys decreased rapidly following the peak of 4.2 million tonnes in 2002, dropping to 0.26 million tonnes in 2007, the lowest observed biomass since 1989. From 2004 to 2007 the proportion of adult sardine found to the west of Cape Agulhas was very low—less than 25% of the total each year (Shabangu *et al.* 2012). From 2008 there were signs of recovery of sardine in the west, though this trend was reversed in 2011.

Besides having implications for the fishing industry, the altered pelagic fish distribution may have had a strong effect on predatory seabird population dynamics, notably African penguins, Cape gannets, Cape cormorants, and swift terns *Sterna bergii* (Crawford *et al.* 2008a). The shift of sardine away from the west coast coincided with declines in the number of African penguin breeding pairs at the northernmost South African colonies at Lambert's Bay and Saldanha Bay (Underhill *et al.* 2006). At the same time, on the south coast, numbers increased at Stony Point and stabilized at Dyer Island after several years of decline.

1.5 The management procedure approach and its implementation for the South African sardine-anchovy fishery

During the 1980s and 1990s, the Scientific Committee of the International Whaling Commission (IWC) was tasked with the development of a Revised Management Procedure for the management of commercial and aboriginal subsistence whaling using a simulation testing approach to check for robustness in a situation of uncertainties about whale population abundance and dynamics (Kirkwood 1992; Punt and Donovan 2007). The management procedure (MP) approach, based on the methods developed in the IWC, has since been adopted for the management of a number of fisheries worldwide (Cochrane *et al.* 1998). In the South African anchovy fishery, a simulation-tested MP was first implemented in 1991 (Butterworth and Bergh 1993), and in 1994 a joint MP was implemented to set catch limits for both sardine and anchovy (De Oliveira and Butterworth 2004). By 1998, operational management procedures (OMPs), that is MPs which have been implemented in practice (Plagányi *et al.* 2007), were also being used in South Africa for managing the fisheries for Cape hake (*Merluccius capensis* and *M. paradoxus*) and West Coast rock lobster *Jasus lalandii* (Geromont *et al.* 1999).

1.5.1 Description of the MP approach

The MP approach (Butterworth 2008), alternatively called MSE[14] (Smith *et al.* 1999), consists of two primary components. First, an operating model (OM) is constructed to represent the underlying population dynamics of the resource and the impact of harvesting. Second, an MP is formulated to assess the resource if required and compute a scientific recommendation for management, such as a total allowable catch (TAC) or effort control. The MP includes a management decision rule and a specification of the data required for the associated calculations. The performance of the MP is evaluated, considering both harvesting and resource dynamics. Butterworth and Punt (1999) give various practical suggestions for the implementation of MPs and the selection of statistics for assessing MP performance.

The performance of an MP over a period of 10–20 years (for short-lived resources) must be tested using simulated resource-monitoring data generated by the OM. Furthermore, tests should be conducted to check that this MP performs reasonably well with alternative plausible OMs. This accounts for uncertainty in the underlying population dynamics of the resource. The testing process should determine to which uncertainties management strategies are robust, and which uncertainties are likely to result in unsatisfactory performance of a particular management strategy (Punt 2008). Furthermore, robustness to possible variation of biological parameters in

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[14] Rademeyer *et al.* (2007) provide a useful glossary of terms related to management procedures.

light of climate and environmental uncertainty can be evaluated (Punt *et al.* 2013). Butterworth *et al.* (1996) suggest guidelines for ranking OMs reflecting alternative hypotheses by plausibility.

For each time-step (typically one year), management measures chosen by the decision rule are fed back into the OM to update the population dynamics. This feedback control enables some degree of self-correction in the face of the various uncertainties which are always present. Note that during this calculation process the MP has no knowledge of the value of any OM variables, apart from the simulated artificial data, to reflect the situation that applies in reality. These should be of the same type as data which are to be collected in practice, such as survey abundances. Most importantly, the simulated data should have the same error structures and magnitudes as real data.

MPs are evaluated via appropriate performance measures drawn from the simulation results. Typical performance statistics drawn from the OM could include the average annual catch, the variability of the annual catch taken over the simulation period, the risk that the resource drops below a specified threshold at least once over this period, and the long-term growth of the resource. Performance statistics may also be drawn from the MP itself, such as the average TAC allocated. As the OM should account for variability in the population dynamics (e.g. recruitment variability) and errors in the simulated “observed” data, Monte Carlo simulation trials should be repeated many times and the results summarized with appropriate statistics of the distributions of the measures of performance (Punt 1992).

The suitability of several alternative candidate MPs should be considered by comparing them relative to specified management objectives. The favoured MP is chosen by considering trade-offs between different performance statistics. Rademeyer *et al.* (2007) give some suggestions concerning the choice of performance statistics and MP selection. The simulation-testing process, including its focus on robustness in the face of uncertainties, goes some way towards satisfying the requirements of the precautionary approach to fisheries management prescribed by the FAO (Punt 2006).

An important aspect to MP development is the involvement of all stakeholders. As Hilborn (1992) says, “Fisheries management is primarily a problem in managing people, not fish.” Butterworth

(2007) concludes by stating, “Industry, conservationists, scientists, and managers need to agree the rules before a fisheries management game is played.” This promotes transparency and confidence in the decision-making process, allowing all parties to consider the trade-offs between conflicting objectives. Hilborn *et al.* (2001) provide a reminder that the precautionary approach of the FAO requires that not only risk to fish stocks be considered, but also risk to fishing communities in terms of sustainable employment, income, and food. The MP decision rules should be chosen by (ideally) consensus among stakeholders, and implemented for a period of three to five years before review and possible revision if scientific understanding of the resource or fishery has changed substantially. Cochrane (2000) highlights the importance of defining clear objectives and establishing a management strategy designed to achieve these specified objectives, preferably within a legal framework.

The MP approach is not without its critics. Rochet and Rice (2009) question whether MSE is nothing more than “ignorance disguised as mathematics”, and Kraak *et al.* (2010) bemoan the mechanical nature of MP implementation. However, Butterworth *et al.* (2010) counter that annual “tinkering” tends to result in advice which follows noise rather than signal. Also, MPs certainly allow for intervention in the case of “exceptional circumstances” arising, such as when evidence suggests that the resource has moved outside the range considered during simulation testing (Rademeyer *et al.* 2008).

In summary, while the MP approach is not without its difficulties (e.g. lengthly development time, difficulty with reference case selection, little flexibility after implementation—see Butterworth 2007), it does have several key advantages over other fisheries management methods. It includes specific structures for taking scientific uncertainty into account, it has the ability to incorporate feedback derived from updated trend information to improve robustness during implementation, and it provides a framework for considering trade-offs between conflicting performance statistics (Butterworth *et al.* 2010). Hilborn (2007e), for one, expects the MP approach to become more widespread in fisheries management with time. This will be facilitated by the development of more powerful computer hardware and software, and the development of a common framework for MP testing could streamline implementation (Schnute *et al.* 2007).

1.5.2 Management of the South African small pelagic fishery

Until 1971, the only controls on commercial pelagic catches related to vessel size and processing capacity (Butterworth and Bergh 1993). A global TAC was then introduced for the pelagic fishery. The TAC was revised annually, based on cpue data and assessment using virtual population analysis (VPA), and averaged about 400 000 tonnes. An important development in 1975 was the introduction of individual quotas for processing companies. This led to a steady reduction of total fleet capacity as companies were no longer in competition for a greater proportion of the overall TAC (Cochrane *et al.* 1997).

After annual hydroacoustic surveys were introduced in 1984, species-specific TACs have been set, based primarily on the survey results. Butterworth and Bergh (1993) describe the evolution of management strategies for anchovy during the first decade of surveys. Moving away from what had been effectively a constant catch strategy, a constant escapement strategy was implemented in 1987. Although this strategy is predicted to result in a greater average catch, TACs tend to be highly variable which is undesirable for industry stability. As it happened, the scientific recommendation for TAC dropped from 600 000 tonnes in 1987 and 1988 to 0 tonnes[15] (closure of the fishery) in 1990. To address the issue of TAC variability, a new strategy was adopted in 1991 whereby the TAC was set as a constant proportion of the estimated escapement in the absence of fishing.

For sardine, a VPA assessment using commercial catch-at-age data was used to set TACs over 1984–1986 (De Oliveira *et al.* 1998). By 1987, confidence in the hydroacoustic biomass survey had increased. Accordingly, the TAC calculation was adjusted to incorporate a constant proportion of the November biomass survey each year from 1987 to 1989. For the 1990–1993 TACs, the harvesting strategy adopted was to maintain fishing mortality at the same level as the average over the period 1987–1989, during which sardine abundance was increasing. Such an $F_{\text{status-quo}}$ strategy attempts to maintain fishing mortality at the same level as it was in the past, even though the value of this level may not be well determined (Butterworth *et al.* 1992). However, as the relative abundances of sardine and anchovy were fluctuating, concern was raised

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[15] Decision makers chose rather to set the TAC at 150 000 tonnes for socio-economic reasons.

that sardine bycatch was not being managed effectively, and that the sardine resource was not being optimally exploited.

The next step was the development, with industry input, of a joint MP for sardine and anchovy, first implemented in 1994 (Cochrane *et al.* 1998). This was necessary because interaction between the two fisheries (joint shoaling of juveniles) precluded optimal management of each separately. The total sardine catch was split into a directed sardine component (assumed to be adult fish) and a bycatch component caught with round herring and anchovy (assumed to be recruits). Simulations indicated a strong sensitivity of average annual directed sardine catches to the proportion of the anchovy TAC allocated as a juvenile sardine total allowable bycatch (TAB).

Management favoured setting conservative sardine TABs to maximize the more valuable directed sardine catches and to promote growth of the resource. However, this was met by resistance from the industry as they foresaw unwelcome disruption to the anchovy fishery. Prevailing stock conditions resulted in much higher sardine bycatch proportions with anchovy from 1994 than had been observed previously (Geromont *et al.* 1999). Consequently, the MP recommendations were adjusted by managers for socio-economic reasons both in 1994 and 1996, as concerns for short-term income and job security outweighed predicted reductions in long-term yield.

In the 1999 MP revision, TAB allocations were adjusted to more realistic levels by including estimates of species mix from both surveys and commercial catches. Furthermore, trade-off curves were produced which showed explicitly how increasing the average anchovy TAC would decrease the average directed sardine TAC, and *vice versa* (Geromont *et al.* 1999). This is because setting a higher anchovy TAC requires increasing the sardine TAB and thus reducing the directed sardine TAC. Several refinements to the procedure were incorporated in the 2002 revision (known as OMP-02), which enhanced utilization of both resources (De Oliveira and Butterworth 2004).

The record survey abundance estimates in 2001 and 2002 necessitated further adjustments to the OMP. New assessments including the recent survey data resulted in revised stock–recruitment relationships[16] (de Moor and Butterworth 2009). Also, for the first time, the assessments followed

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[16] For sardine, maximum deterministic recruitment increased while variability decreased. For anchovy, there was little change to the stock–recruitment curve, but variability about the curve increased substantially.

the Bayesian approach which takes account of the full range of uncertainties relating to both model selection and parameter values (Punt and Hilborn 1997). These advancements were incorporated in the simulation testing of the next version of the OMP, which allowed the industry to take advantage of the resource boom (Plagányi *et al.* 2007; de Moor *et al.* 2011).

This last point warrants further attention. The MP approach stems from IWC research into managing cetaceans, which are long-lived, slow growing, and generally assumed to have a constant intrinsic growth rate. In contrast, small pelagic fish are short-lived with highly variable recruitment. One may well question whether the MP approach is suitable for managing such a volatile resource, prone to wild swings in abundance. In particular, one might ask whether an MP designed to minimize catch variability might pose excessive risk of resource depletion in the case of recruitment failure, and whether the lengthly MP development process might be unsuitable for a resource which tends to fluctuate very rapidly. However, de Moor *et al.* (2011) report that OMP-04 was sufficiently flexible to achieve high utilization without putting the sardine resource at risk after subsequent poor recruitment. Exceptional circumstances were never invoked and all subsequent OMP-based recommendations were accepted.

The next revision of the MP, known as OMP-08, was adopted in 2008 (de Moor and Butterworth 2008). Changes from OMP-04 relate to rules for exceptional circumstances, various thresholds and constraints, and the key OMP control parameters. The control parameters were adjusted as a consequence of the updated assessment, which incorporated both revised and new data. The median directed catches projected for 2008–2027 were 152 000 tonnes of sardine and 400 000 tonnes of anchovy.

Although the fishery has an average escapement that is already similar to the level being advocated by Smith *et al.* (2011), additional management measures are now being developed which are designed to ensure that sufficient fish are available to provide for the foraging needs of predator species (Crawford 2004; Plagányi *et al.* 2007). This is in line with the DAFF policy to implement EAF management, and evaluating the penguin–pelagic fishery interaction is seen as the flagship project in this regard. The African penguin is particularly vulnerable to localized prey depletion because of ties to island colonies where breeding and moulting take place (Durant *et al.* 2010). In future, the aim is to include an evaluation of the risk to penguins due to different TAC allocations in the MP simulation testing. Initial implementation of such methods was included in the testing of OMP-08.

The most recent major revision of the South African small pelagic OMP was scheduled for adoption in 2012. However, several important new features were being developed, in particular the consideration of spatial management of the sardine resource, evaluating the consequences of different fishing efforts on the west and south coasts. These required extensive testing that prevented the adoption of the new OMP in time for calculating recommended initial TACs and TABs for 2013. Instead, an updated version of OMP-08 was adopted for use in December 2012. At the time that the analyses presented in Chapter 5 were conducted, this was the latest available small pelagic OMP, known as "Interim OMP-13" (de Moor and Butterworth 2012c).

1.6 Past approaches to assessing African penguin–small pelagic fishery interactions

Crawford *et al.* (1999) constructed an age-structured population model for Robben Island penguins, running for the years 1988–1995. Correlation analysis was used to investigate relationships between population parameters and prey abundance. A significant positive relationship was found between the model-estimated proportion of adults breeding each year and sardine spawner biomass. Observed breeding success (chicks fledged per breeding pair) from 1989 to 1995 was significantly related to anchovy spawner biomass. Model results showed that the rapid growth of the Robben Island colony during the 1990s could not be explained without including immigration. Estimated numbers of penguins in immature plumage immigrating to Robben Island, peaking at 1 463 birds[17] in 1991, were significantly related to anchovy spawner biomass.

Crawford *et al.* (2006a) looked for correlations between penguin breeding success at Robben Island and pelagic survey results, this time for a time-series extending from 1989 to 2004. Significant correlations were found with the estimated biomass of sardine, anchovy, and the two species combined, where these were obtained both from the recruit survey and from the spawner biomass survey. The best fit was with the combined sardine and anchovy spawner biomass. The authors

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[17] Assumed values for adult and juvenile annual survival were 0.82 and 0.50 respectively in this analysis.

also estimated values of breeding success required to maintain a population in equilibrium for various fixed values of first-year and adult survival.

Crawford *et al.* (2011a) showed that Western Cape penguin nest counts for 1990–2010 were significantly correlated with the combined spawner biomass of sardine and anchovy from the survey of the previous year. However, while a nest count may be an indicator of fish abundance, such observations do not inform on whether the change in fish abundance is being driven primarily by fishing or whether climate change is in fact the main driver (Durant *et al.* 2009). In South Africa, several seabirds have shown concurrent population declines. An eastward shift of breeding sites of some seabird species which prey on commercially exploited fish matches the recent shift in distribution of these fish. However, other seabirds which eat different prey have also shifted their breeding eastward, implying that climate is likely to have had some influence (Crawford *et al.* 2008b).

1.7 Thesis objectives and outline

As part of the development of the latest iteration of the South African sardine and anchovy MP (OMP-13), this work aims to advance EAF by investigating the impact of fishing on the African penguin, a key predator in the southern Benguela ecosystem. The potential impact of fishing in the vicinity of breeding colonies is assessed, in particular on reproductive success. An attempt is made to link penguin dynamics to small pelagic fish abundance so that the impact of prey depletion by the fishery can be considered in choosing an OMP.

Chapter 2 describes all data used as inputs in the models which follow. For the time-series of penguin moult counts, a new method is described for extrapolating (roughly) fortnightly counts to estimates for each annual moult season. As these counts constitute one of the key sets of inputs to the population models, an improved, consistent and reliable basis for their calculation is desirable.

Chapter 3 describes various general linear models relating penguin population demographics and foraging behaviour to fisheries data. These models explore the effects which fishing in the vicinity of the penguin colonies at Dassen Island, Robben Island, St Croix Island, and Bird Island may have on penguin survival, breeding participation, reproductive success, foraging path length, and foraging trip duration.

Chapter 4 fully describes a model of penguin population dynamics at the Robben Island colony. Using this model, penguin adult annual survival is found to depend on the abundance of sardine as estimated by the November hydroacoustic survey.

In Chapter 5, this model is used to project the penguin population forward for a period of ten years under various future fish abundance scenarios. These are generated by the operating model for sardine that underpins testing of OMPs for small pelagic fish currently under development. The results assist advice on the selection of the OMP in a manner which takes appropriate account of the impact of fishing on the dynamics of the Robben Island penguin colony.

Finally, in Chapter 6 the results and conclusions of the thesis are summarized and suggestions are made for extensions to this work.

Chapter 2

Data

This chapter describes those data which are used as inputs to the general linear models (GLMs) reported on in Chapter 3 and the penguin–fish interaction model described in Chapter 4. Data are required both for fish targeted by the commercial small pelagic fishery and for the African penguin, a valued species from a conservation perspective. In the case of each data series used in the analyses of the following chapters, the aim is to describe its derivation in a rigorous manner.

Teams of seabird biologists have been collecting African penguin data for several decades. Parameters studied include population size, survival, and indices of reproductive success which include chick condition and growth rate, foraging trip distance and duration, and diet composition (e.g. Bouwhuis *et al.* 2007; Pichegru *et al.* 2010; Crawford *et al.* 2011a; Waller 2011). Collection of seabird data is laborious. In general, repeated visits to remote island colonies are required, and handling of aggressive adult birds is often necessary. Collection of some types of data (e.g. foraging tracks) requires expensive equipment.

The following sections describe the sources of the raw data and, where applicable, the subsequent analyses which produce the final data series used as inputs to the models. Counts of nests and moulting penguins enable estimation of colony population size (Section 2.1). Re-sighting records of tagged penguins enable the estimation of survival rates (Section 2.2). In Section 2.3, information regarding the numbers of penguins which died as a direct result of two major oil spills is provided. Section 2.4 covers the time-series of sardine biomass estimated from hydroacoustic surveys. Finally, penguin and fish data used in the GLM models are described in Section 2.5.

2.1 Moult and breeder counts

Best *et al.* (1997) review the various strategies which have been attempted for obtaining total penguin abundances at colonies, such as making total counts of nests or adults and estimates from aerial photography. Estimates of numbers have also been obtained by extrapolation of penguin density in a sample to the area of the whole colony (Randall *et al.* 1986). All of these methods will give a negatively biased population estimate if penguins are absent from the colony at the time of the count. For this reason, counts are ideally made at the height of the egg-laying phase of the breeding season, because during incubation, at least one parent must be present at its nest. However, the African penguin has an extended breeding season lasting from January to October. The time of the peak of the breeding season may vary amongst colonies and from year to year, and not all pairs necessarily lay at the same time. Indeed, the proportion of mature penguins which breed varies from year to year (Crawford and Dyer 1995).

Despite these drawbacks, nest counts are the most readily implemented method of tracking penguin population trends. Since 1987, counts have been made at most penguin colonies in South Africa in most years (Underhill *et al.* 2006). If possible, several counts are made at a colony during the breeding season, and the maximum of these is recorded. Of all the colonies, Robben Island is the best monitored—a complete time-series[1] exists (Table 2.1). The close proximity of the island to Cape Town and the convenient harbour make the colony easily accessible, which facilitates regular fieldwork (Crawford *et al.* 1995).

Because nest counts tally the breeding portion of the population only, an alternative method of abundance estimation was proposed by Randall *et al.* (1986) based on an annual count of moulting penguins. The premise is that every penguin must moult annually. It was believed that African penguins always returned to their breeding colonies to moult, until recent observations provided some evidence to the contrary (Wolfaardt *et al.* 2009a). The conspicuous feather-shedding phase of the moult process has been reported to have a mean duration of 12.7 days (Randall 1983). Thus, an estimate for the population of a colony which is only slightly negatively biased should be obtainable from summing counts of moulting birds at fortnightly intervals throughout the

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[1] Although each count represents a complete census of the colony (not a sample), observation error is inevitable, and perhaps substantial. However, such errors have not been reliably estimated.

year. These counts would include both young adults which had not yet commenced breeding, as well as older mature birds which might abstain from breeding in some years. This makes the moult count more robust than the nest count to variations in seasonal conditions.

One requirement for deriving the moult-based abundance series is that colonies must be visited regularly, especially around the peak of the moult season. This can give rise to problems, as about 20 visits per year are necessary, which makes the method impractical for many colonies on account of limited resources. Thus, in the Western Cape, annual series of moult counts have been recorded only for Robben Island (since 1988), Boulders (since 1992), and Dassen Island (since 1994) (Crawford *et al.* 2000b; Wolfaardt *et al.* 2009a). Another problem is that not all moulting birds may be visible—some may moult in burrows, and birds moulting inland are usually not counted. As a result, the moult count at Dassen Island (where many birds moult inland) is known not to represent the whole population (Wolfaardt *et al.* 2009a).

In a study at Robben Island, Crawford and Boonstra (1994) found that the maximum nest count was usually obtained in May, which was identified as the peak of the breeding season. Also, moult counts and nest counts were found to be highly correlated, and on average the number of moulting adults was 3.2 times greater than the maximum nest count. Furthermore, the tallies of a few counts of moulting birds made around the peak of the moult season at the beginning of December gave a good index for the total number of moulters. Thus, reasonable abundance indices could in principle be obtained from the moult count approach without the need for observations to be made throughout the whole year. However, atypical conditions could cause a shift in the timing of the seasonal peaks, resulting in high variance about the true numbers. Interannual variability in moult phenology is thought to be influenced by factors such as the success or failure of the previous breeding season, food availability, and major oil spills (Crawford *et al.* 2006b).

A high degree of synchrony in the timing of the feather-shedding phase has been observed in the African penguin moult season, especially at Robben Island (Underhill and Crawford 1999; Wolfaardt *et al.* 2009a). As most penguins in the Western Cape moult between September and January, the annual moult season is defined to run over the split year beginning on 1 July and lasting until 30 June the following year. Underhill and Crawford (1999) used linear interpolation to estimate the number of penguins moulting on each day between the days when actual counts were made. They then summed the resulting numbers and divided by 12.7 (the mean duration of the feather-shedding phase—see Randall 1983) to obtain an aggregate count of moulters for the whole year. This method should give good results if intervals between counts are reasonably short, but the estimation becomes rather coarse if there are large gaps between counts, especially over the peak period (November and December).

The juvenile moult season is often characterized by two peak periods. The first peak occurs in late spring, coincident with the peak period of the adult moult at Robben Island, and the second peak occurs late in the summer (Underhill and Crawford 1999). Kemper and Roux (2005) and Wolfaardt *et al.* (2009a) suggest that the first peak may comprise birds which delay moulting into their adult plumage until their second summer when they moult with the majority of the colony ("skippers"), while birds which fledge early in the year may moult during late summer or autumn, soon after they reach 12 months of age ("squeezers").

2.1.1 Double Gaussian method for interpolating moult counts

Because of the difficulties mentioned above associated with the linear interpolation method for obtaining annual moult count estimates, an alternative method for calculating such estimates was developed. This method makes the assumption that the sum of two Gaussian functions can provide a good representation of the number of birds moulting each day. The expected number of birds moulting on each day d is thus:

$$\hat{M}_d = \frac{N_1}{\sqrt{2\pi\sigma_1^2}} \exp\left[-\frac{(d-\mu_1)^2}{2\sigma_1^2}\right] + \frac{N_2}{\sqrt{2\pi\sigma_2^2}} \exp\left[-\frac{(d-\mu_2)^2}{2\sigma_2^2}\right] \tag{2.1}$$

where:

$N_1 + N_2$ is the total number of moulting birds which would be counted if counts were made daily (if the moult season was "infinitely" long),

μ_1 and μ_2 are the days on which the two peaks of the moult season occur, and

σ_1 and σ_2 characterize the degree of synchrony within each moulting period.

The sum of two Gaussian curves was chosen because the juvenile penguin moult season is known to have two peaks, and the additional flexibility is useful as it can take account of asymmetric shapes of the overall distribution.

Values for the six parameters in equation (2.1) are obtained by minimizing the negative log-likelihood for the Poisson process of sighting moulting birds given the data:

$$-\ln L = \sum_{i=1}^{n} \left(\hat{M}_i - M_i^{\text{obs}} \ln \hat{M}_i \right) \tag{2.2}$$

where i indexes each moult count with a total of n such observations made during the season. This method seems likely to be more robust than the linear interpolation method, both in the case of noisy data and when the intervals between consecutive counts are several weeks or even months.

If σ_1 and/or σ_2 are large, the Gaussian functions have wide tails, resulting in values of $\hat{M}_d \gg 0$ for days outside of the split year in question. This has been taken into account by subtracting the tails T_1 and T_2 of each of the Gaussian functions:

$$T_1 = N_1 \left[\operatorname{erfc}\left(\frac{\mu_1 - d_1}{\sqrt{2}\sigma_1} \right) + \operatorname{erfc}\left(\frac{d_{L+1} - \mu_1}{\sqrt{2}\sigma_1} \right) \right] \tag{2.3}$$

$$T_2 = N_2 \left[\operatorname{erfc}\left(\frac{\mu_2 - d_1}{\sqrt{2}\sigma_2} \right) + \operatorname{erfc}\left(\frac{d_{L+1} - \mu_2}{\sqrt{2}\sigma_2} \right) \right] \tag{2.4}$$

where the subscripts 1 and L indicate the first and last days of the moult year (1 July and 30 June respectively) and the complementary error function is defined as:

$$\operatorname{erfc}(x) = \frac{1}{\sqrt{\pi}} \int_x^{\infty} \mathrm{e}^{-t^2}\, \mathrm{d}t \tag{2.5}$$

The total number of birds moulting in one year is then calculated as:

$$M = \frac{N_1 + N_2 - T_1 - T_2}{12.7} \tag{2.6}$$

By using the optimization program AD Model Builder (Fournier *et al.* 2012) to fit the double Gaussian curves to the annual moult counts, the Hessian-based coefficient of variation s is readily obtainable for each estimate under the assumption that model errors are Poisson distributed. However, the actual errors are greater than this assumption suggests, and hence account needs to be taken of overdispersion in calculating reliable coefficients of variation. After grouping observations so that each $\hat{M}_i > 5$, the overdispersion for each annual estimate is calculated as:

$$D = \sqrt{\frac{1}{n^* - p} \sum_{i=1}^{n^*} \left(M_i^{\text{obs}} - \hat{M}_i \right)^2 \Big/ \hat{M}_i} \tag{2.7}$$

where n^* is the number of observations in that year (after grouping) and p is the number of parameters estimated. Coefficients of variation (CVs) are then calculated as:

$$CV = s\tilde{D} \tag{2.8}$$

where $\tilde{D}$ is the median of all overdispersion parameters calculated for each series.

An alternative to the maximum likelihood approach is to use the Markov-chain Monte Carlo (MCMC) method to obtain a Bayes posterior distribution for M. This was attempted for a few years and gave very similar results to the Hessian-based estimates of CV.

2.1.2 Results

Double Gaussian functions were fitted to all the available adult and juvenile moult count data for Robben Island. The numbers of adult and juvenile moulters were estimated and the corresponding CVs were calculated for each year (Table 2.2). The only notable differences between the estimates calculated following the double Gaussian method and those published by Wolfaardt *et al.* (2009a) obtained by linear interpolation are for the seasons 1996/1997 and 2001/2002 (Table 2.3). The underlying reasons for these discrepancies are discussed below.

According to Underhill and Crawford (1999), “The abnormal pattern in 1996/97 was a result of errors in the November and December counts, which were undertaken by an inexperienced observer.” Consequently, three data points were excluded when fitting the double Gaussian

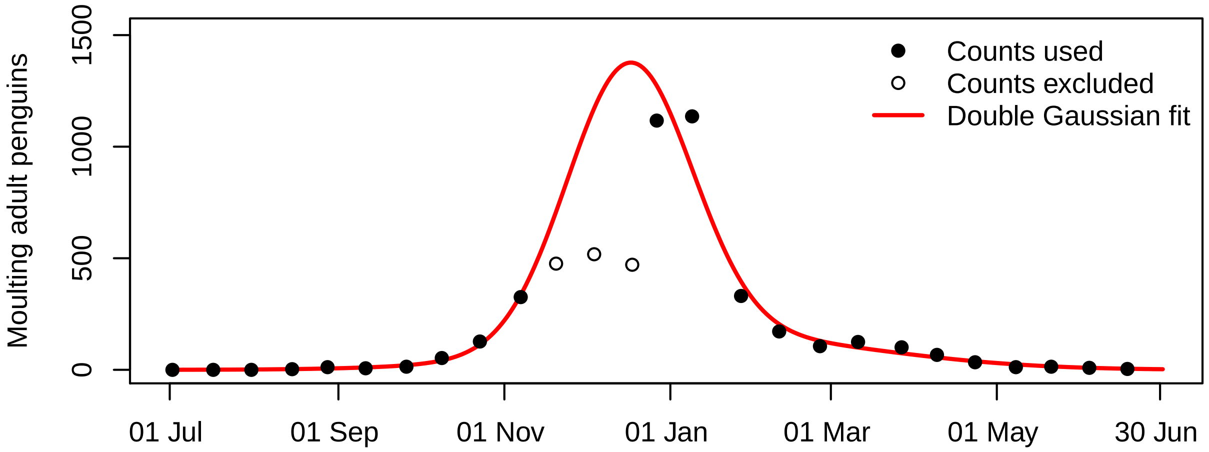

Figure 2.1: Counts of moulting adult penguins taken at Robben Island in the 1996/1997 season. Open circles indicate the three counts excluded from the aggregating procedure.

function for this season (Figure 2.1). The result is a 30% larger estimate for adult moulters and a 7% larger estimate for juvenile moulters for 1996/1997.

The 2001/2002 estimate for Robben Island is unreliable because only nine counts were taken during that year, with none before November. A decrease in moulters in the year following the *Treasure* oil spill would perhaps be expected, as was the case in 1995/1996 following the sinking of the *Apollo Sea*. Compared to the results of Wolfaardt *et al.* (2009a), the double Gaussian estimates given here are 25% and 31% lower for the adults and juveniles respectively.

2.1.3 Discussion

Results from deriving aggregate moult count estimates via the method of fitting a double Gaussian are in most cases similar to the results from linearly interpolating the count data. However, particularly in seasons where there are large gaps between some counts, the double Gaussian approach seems preferable. The linear interpolation method tends to provide an overestimate when there is a large gap between consecutive counts during the spring or autumn (Figure 2.2a), and it tends to provide an underestimate when there is a large gap between consecutive counts around the peak of the moult season (Figure 2.2b). Accordingly, the estimates associated with the double Gaussian approach are used in the modelling presented below.

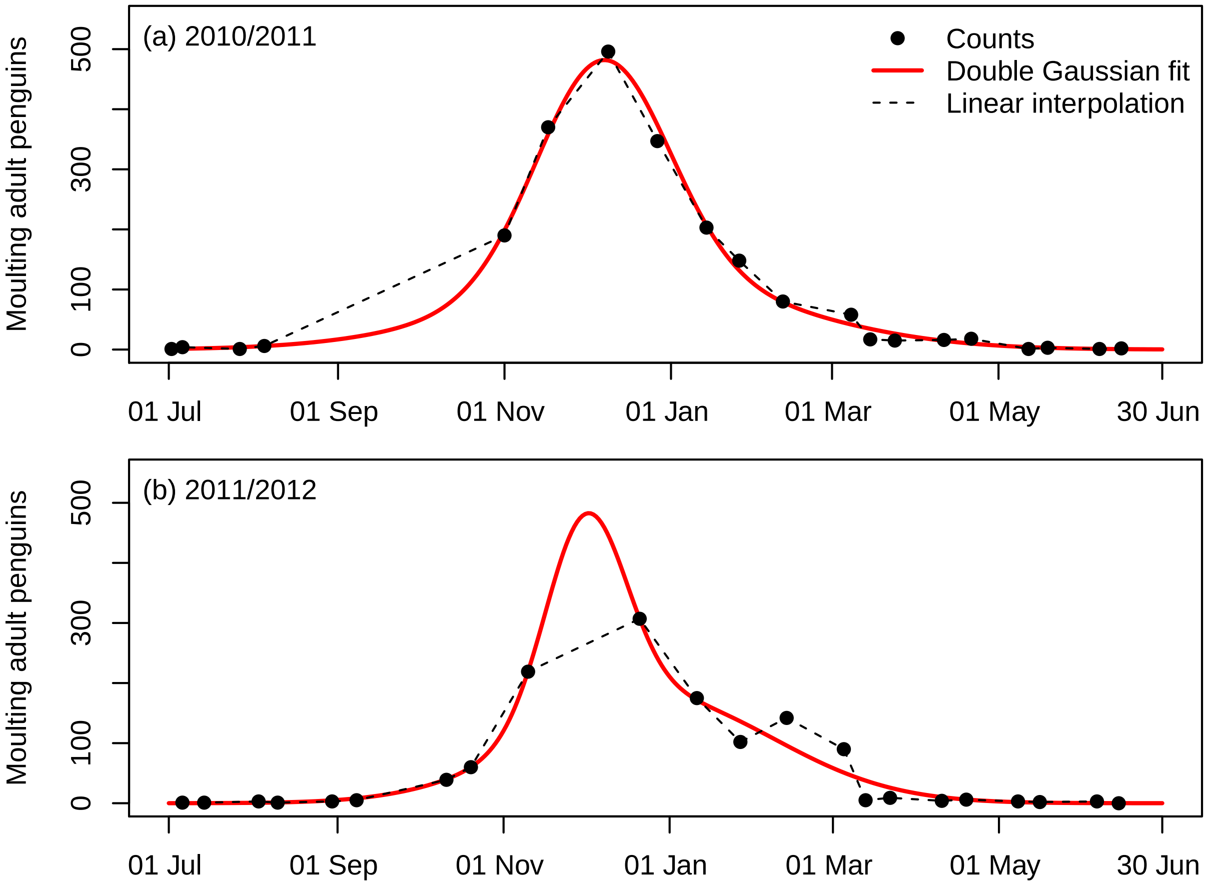

Figure 2.2: Counts of moulting adult penguins taken at Robben Island in (a) the 2010/2011 season and (b) the 2011/2012 season. Solid and dashed curves indicate the Gaussian fit and the linear interpolation respectively.

The motivation for use of the double Gaussian was bimodality in the juvenile count distributions, and the corresponding estimates of μ_1 and μ_2 are broadly consistent with a first peak in early summer and a second peak in late summer (Table 2.4). The fits to the adult counts do not show a similar pattern (Table 2.5), and the justification of the use of two Gaussian curves there is more to provide greater overall shape flexibility. A more refined approach might involve fitting through the use of a Hermite polynomial series expansion, but this does not seem justified here as the double Gaussian approach achieves a sufficiently good fit to the data to provide estimates of adequate accuracy for population modelling purposes.

The estimates of overdispersion always exceed 1, but are also very variable and sometimes very large. The last category generally arises from instances where counts are relatively high at either end of the 12 month period considered, which are times when the double Gaussian predicts very low values. Although these differences are not large in the context of the overall count estimate M, they can influence the estimates of overdispersion D considerably. For this reason, CVs have been presented based on the median of the D estimates for each season. This is of course a somewhat coarse approach, but seems useful to provide some broad indication of the precision of the estimates obtained.

A concern is that, in recent years, numbers of adult moulters at Dassen Island and at Robben Island have been lower than expected based on the nest counts. While one possibility is that a higher proportion of birds is moulting inland in areas not checked by the counters, it appears that the main reason for this discrepancy is that substantial numbers of Robben Island breeders are not returning to the colony to moult. A rapidly increasing number of penguins have been observed moulting at the Stony Point colony at Betty's Bay, amounting to about 5 000 adults in the 2009/2010 moult season (Crawford *et al.* 2011a). Several of these birds are known to have bred previously at Robben Island or Dassen Island (UCT Animal Demography Unit, unpublished data).

The first penguin nest was recorded at Stony Point in 1982. Between 1982 and 2004, the count of active nests at the colony reached a peak of 123 nests in 2003. Since then, substantial increases (in percentage terms) from the previous year were recorded in 2005 (98 to 186 nests), 2009 (310 to 487 nests) and 2011 (466 to 948 nests). A year-on-year increase of the order of 50–100% indicates that the colony is attracting large numbers of possibly permanent immigrants. The most recent increase is substantial compared to the breeding population at Robben Island (Table 2.1). If this trend continues, it would have problematic implications for the future application of the modelling process that follows.

2.2 Re-sightings of banded birds

Capture–mark–recapture analysis is a common method for tracking changes in avian life history parameters. In particular, the ability to track marked individuals through time enables researchers to obtain estimates for annual survival rates. This is possible even though the marked birds may not be seen every year and, indeed, their time of death is usually unknown (Lebreton *et al.* 1992).

The calculations for these survival estimates are independent of abundance data (e.g. moult counts and nest counts), allowing for the estimation of immigration in an integrated population model.

African penguins have been tagged with individually identifiable flipper bands since 1947. Prior to 1972, penguins had to be caught in order to read the bands, but in that year stainless steel bands were introduced which could be read with the aid of binoculars (Cooper and Morant 1981; Randall *et al.* 1987). Re-sightings of banded African penguins have been recorded throughout their range, including at Robben Island since 1989 (Whittington *et al.* 2005b). A few hundred adult penguins in addition to some juvenile birds have been fitted with bands annually. Re-sighting efforts were greatly increased following the *Apollo Sea* oil spill in 1994. During the massive relocation and cleaning operation following the *Treasure* oil spill in 2000, many thousands of penguins were banded. As a result of this large tagging cohort, most of the re-sightings recorded for Robben Island come from that group.

There has been much recent debate about the possibility that flipper bands may be harmful to penguins (Petersen *et al.* 2005; Le Maho *et al.* 2011). Studies on various species, especially in the Antarctic, have shown that bands can damage tissue and that swimming efficiency is affected, leading to impaired survival and breeding success. Factors thought to influence the effects include the material, size and colour of bands, prey availability, and the species involved. Saraux *et al.* (2011) call into question the conclusions of studies considering population trajectories based on banding data when the banding itself may severely alter life-history traits.

However, studies on African penguins have indicated that breeding success, at least, is not negatively affected by flipper bands (Barham *et al.* 2008b; Hampton *et al.* 2010). Also, after a 15 year study of Magellanic penguins *Spheniscus magellanicus* (a close relative of the African penguin), Boersma and Rebstock (2010) found that double stainless-steel flipper bands had no apparent effect on the survival rates of male penguins. Survival rates of females were reduced by about 8%, but reproductive success was not affected. There is an interest in the development of alternative techniques for long-term monitoring of individual African penguins, such as subcutaneously implanted radio frequency transponders (Jackson and Wilson 2002) and automated photo-recognition (Sherley *et al.* 2010).

The database of African penguin re-sighting records is administered by the South African Bird Ringing Unit. The number of records it contains is approaching a quarter of a million. There are some 76 367 records for birds seen at least once at Robben Island for the years 1970–2010. Of the 25 248 individuals banded, 15 603 were re-sighted at least once. The records indicate that 16 807 were banded as adults, 6 790 were banded as chicks, and the age group when banded for the remaining 1 651 penguins is unknown. The database includes 734 recoveries of bands from dead penguins, which is less than 1% of the total records.

Results of an analysis of a subset of these data published by Crawford *et al.* (2011a) indicate that adult penguin survival rates decreased at both Robben Island and Dassen Island between 2002 and 2006. For Robben Island, the annual survival rate was estimated to have decreased from 0.77 to 0.55, recapture probabilities ranged from 0.17 to 0.48, and the percentage of transients (birds sighted only once at banding and so considered unlikely to be residents of the colony) was estimated to be 27%.

The subset of records used in this analysis includes only the birds banded as adults, and excludes dead recoveries. Since the model presented in this work is for the Robben Island colony, an effort has been made to exclude the capture histories of penguins which were occasional visitors to the island. Hence, capture histories were rejected if more than half of the sighting locations for an individual were not at Robben Island.

A further consideration is that in an ideal capture–mark–recapture experiment, the duration of the capture season should be negligible compared to the interval for which survival rates are to be calculated (a year, in this case). However, penguin re-sightings are made throughout the year, meaning that the length of time between sightings of a bird recorded in consecutive years could in fact be anything from less than a month to as much as 23 months. In order to minimize any possible bias which this might cause, a decision was made to include only records of sightings made during the months April–September, restricting the inter-sighting period to between 6 and 18 months. Nearly 80% of all sightings at Robben Island have taken place during this autumn–winter period.

The set of records consequently selected for use in this analysis comprises 12 207 capture histories for the period 1989–2010.

2.3 Major oil spills

The proportion of the African penguin population which has been affected by oil spills is considered to be among the highest of all seabird species globally (Wolfaardt *et al.* 2009b). The vast majority of oiled Robben Island penguins were contaminated as a result of the wrecks of the bulk ore carriers *Apollo Sea* on 20 June 1994 and *Treasure* on 23 June 2000 (Wolfaardt *et al.* 2008a). Because such large numbers of penguins were affected by these two incidents during the relatively short existence of the Robben Island colony in recent times, special account is taken in the population model which follows (Chapter 4) of the deaths of both adults and chicks as a direct result of these oil spills (Sections 2.3.1–2.3.2). Note that the numbers of adults $2N_y^{\text{oil}}$ given below are halved for the model since only the female component of the population is considered. Sensitivity of the model results to the numbers of oil-related deaths given in Table 2.6 is checked in Section 5.5.

2.3.1 *Apollo Sea*

Shortly after sailing from Saldanha Bay in June 1994, the *Apollo Sea* sank near Dassen Island. Fuel oil washed ashore at both Dassen Island and Robben Island, and approximately 10 000 penguins were oiled. Underhill *et al.* (1999) suggest that nearly all the penguins affected reached land alive, as during searches along the coastline very few dead penguins were found despite the prevailing onshore wind. This is consistent with observations following other spills (Wolfaardt *et al.* 2009b). Of the penguins rescued, about 2 400 came from Robben Island, half of which were successfully released, resulting in the loss of about 1 200 adult birds (Crawford *et al.* 1999).

The number of chicks which died as a result of the spill is more difficult to estimate. Wolfaardt *et al.* (2009b) give two methods of estimation. In the first method, an observed loss of 23 chicks from a sample of 38 nests is extrapolated over the whole Robben Island colony which had

2 155 active nests at the time of the oil spill. The result is a projected loss of 1 680 chicks. The second estimate is based on the number of adults which were removed from the island, which could have represented up to 1 500 nests. Multiplying by 0.47, which is the mean number of chicks fledged per nest at Robben Island during 1989–1995, gives a loss of 705 chicks due to oiling for the season. Note that the first estimate does not account for chicks which would not have fledged due to other factors, while the second estimate does not account for losses due to the disturbance to penguins which were not oiled.

As a rough estimate for the proportion of chicks lost as a result of the oil spill, the average of the two estimates given above, divided by the estimated total number of chicks which would have been present at the time of the spill, is used. The observed mean clutch size in 1994 was 1.92 eggs per nest (Crawford *et al.* 1999). Thus, the estimated proportion of chicks lost due to the oil spill is:

$$p_{1994}^{\text{oil}} = \frac{(1\,680 + 705)/2}{2\,155 \times 1.92} = 0.29 \tag{2.9}$$

2.3.2 *Treasure*

The bulk ore carrier *Treasure* sank between Robben Island and Dassen Island, and on 24 June 2000 spilt oil washed ashore on Robben Island, contaminating any penguin attempting to leave the island or to return after foraging. Crawford *et al.* (2000a) relate that of the 19 000 oiled penguins collected for cleaning, 14 825 were caught at Robben Island. By 18 July, about 1 659 of the oiled adult and juvenile penguins which had been captured had died. A total of 19 506 penguins which had not been oiled were captured, with 7 161 of these being removed from Robben Island, to safeguard them from oiling. Of these, 241 penguins died during or after transportation to Cape Recife (800 km to the east), where they were released to swim back so as to arrive after the oil had dispersed. Of the adult penguins collected from Robben Island, 70% of rehabilitated birds and 40% of relocated birds had been re-sighted at the colony by the end of 2004, and another 7% had been re-sighted elsewhere (Barham *et al.* 2006).

During a search of about 250 nests at the Robben Island colony, only four oiled penguins were found dead, which can be extrapolated to surmise the death of 90 adult penguins in the entire colony. As the number of penguins collected at Robben Island was several thousand more than the estimated population of the colony (18 000), a sizeable proportion of these penguins must have been from other colonies. A rough estimate for the total number of adults collected from the island plus the few thousand penguins which remained is 26 500. The number of adults[2] from the Robben Island colony which died due to oiling is thus estimated to be:

$$2N_y^{\text{oil}} = \left(1\,659 \times \frac{14\,825}{19\,000} + 241 \times \frac{7\,161}{19\,506} + 90\right) \times \frac{18\,000}{26\,500} \simeq 1\,000 \tag{2.10}$$

The number of chicks which died at Robben Island after the *Treasure* spill is estimated to be about 3 000 (Crawford *et al.* 2000a). Furthermore, 367 of the 3 350 chicks which were collected for captive rearing also died, and 2 643 of these chicks came from Robben Island. There were an estimated 6 000 chicks at the Robben Island colony at the time of the spill. The proportion of chicks lost at the time of the spill is thus estimated to be:

$$\left(3\,000 + 367 \times \frac{2\,643}{3\,350}\right) \Big/ 6\,000 = 0.55 \tag{2.11}$$

However, breeding attempts were likely successfully completed both before and after the spill, reducing the overall impact of the spill. Thus the proportion assumed for p_{2000}^{oil} in this analysis is reduced somewhat to $p_{2000}^{\text{oil}} = 0.4$.

2.4 Pelagic biomass

Hydroacoustic surveys have played a major role in the assessment of South African pelagic fish resources since 1984. The annual May survey estimates the strength of the recruitment to the sardine and the anchovy population each year, while the annual November survey estimates the biomass of their 1+ populations. The early surveys established that during the 1980s anchovy was more abundant and widespread than had been previously thought, and that the sardine resource was recovering strongly following earlier heavy depletion (Hampton 1992). Additional data from subsequent years suggested relationships amongst trends in the biomass data and

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[2] The factor of 2 appears on the left-hand side of equation (2.10) because N_y refers only to the female component of the population in the model which follows in Chapter 4.

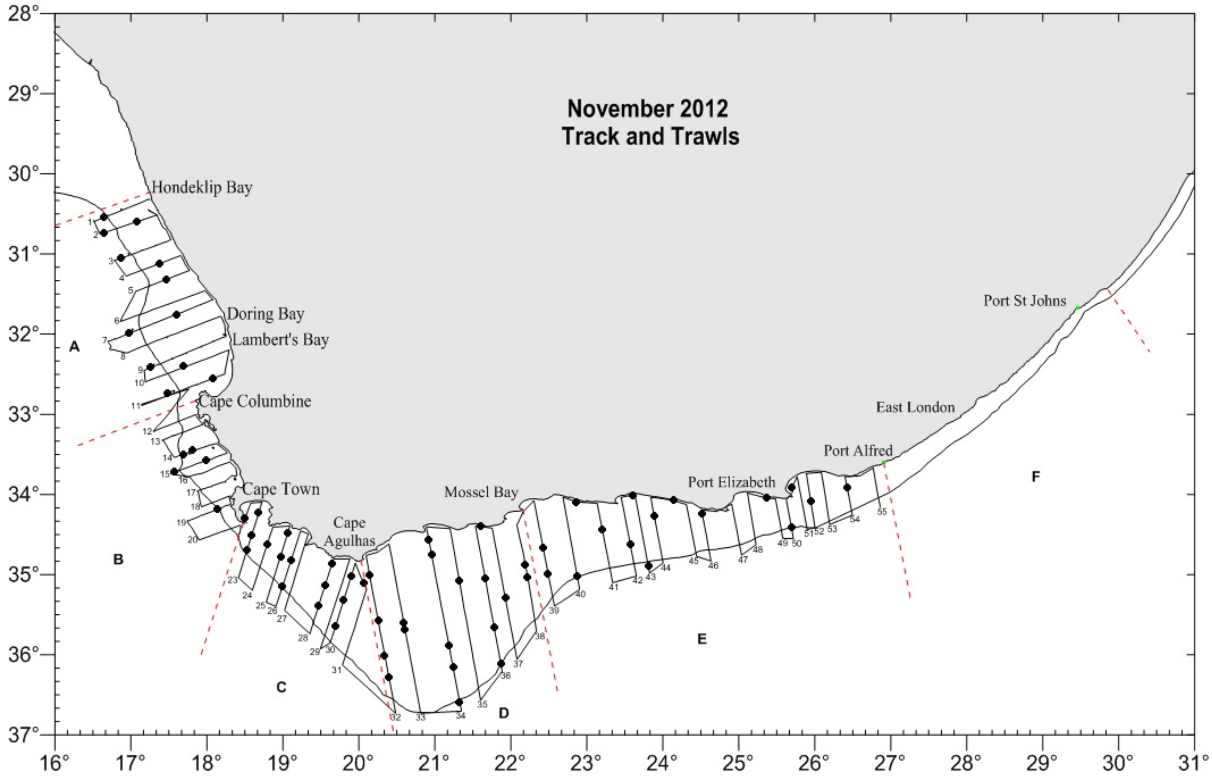

Figure 2.3: Cruise track of the November 2012 pelagic biomass survey (from Shabangu *et al.* 2012). Black circles indicate the positions of the mid-water trawls.

spatial distributions (Barange *et al.* 1999). After the upgrading of survey equipment in 1997, earlier data were revised to correct for echosounder receiver saturation at high signal levels and attenuation effects in dense sardine shoals (Coetzee *et al.* 2008a). With the incorporation of these revisions, comparable data series for sardine and anchovy now extend unbroken from 1984 to 2012 (de Moor *et al.* 2008; Coetzee 2012; Shabangu *et al.* 2012).

The surveys are divided into strata (Figure 2.3). This allows for comparisons of abundance in a specific region over time. Of interest for the penguin–fishery model (Chapter 4) is the biomass series of sardine spawners west of Cape Agulhas (Moseley *et al.* 2011). In recent years, the divisions between the survey strata have remained fixed. The area west of Cape Agulhas corresponds to strata A–C.

Table 2.7 lists the annual 1+ biomass of sardine observed in the standard November survey area, the area west of Cape Agulhas (strata A–C), and the proportion observed west of Cape Agulhas. Note that, in absolute terms, it is possible that the survey estimates may be biased. For example, there may be an error in the hydroacoustic target strength used, or the survey may not cover the entire range of the resource. However, such possible bias is not of importance here as the model needs only a relative index of abundance.

2.5 Data series for GLM analyses

Data series used as inputs in the general linear models of Chapter 3 are described in this section. The GLMs considered relate fish abundance to penguin population parameters for the Western Cape colonies at Robben Island and Dassen Island, and to foraging behaviour at these as well as at the Algoa Bay colonies at St Croix Island and Bird Island. Some of these series are derived from data described in the previous sections.

2.5.1 Fledging success

At Robben Island, two long-term studies have monitored breeding success. In each study, nest sites at a study plot were checked roughly every two weeks during the main breeding season. Records were kept of eggs laid, chicks hatched, and chicks successfully attaining adult plumage. Crawford *et al.* (2006a) report on observations made from 1989 to 2004 when between 42 and 172 nests were successfully monitored each year. Sherley (2010) reports the results of a separate study for the years 2001–2009 during which between 119 and 344 nests were monitored annually. Two key objectives of this last study were comparing the breeding success of penguins oiled in the *Treasure* spill with that of birds which had never been oiled (Barham *et al.* 2007), and comparing breeding success in different nest types (Sherley *et al.* 2012). About 70% of the nests studied involved penguins which had not been oiled. Two further data points have been provided by R. Sherley (pers. comm.) for 2010–2011.

The data for the final five years of the Crawford study (2000–2004) have not been retained for the GLM analyses. Breeding was severely disrupted in 2000 by the *Treasure* oil spill, resulting in a very low success rate that year. The results for 2001–2004 in the Crawford study were somewhat higher than those reported in the Sherley study, the reason for which could possibly be a data processing error (Sherley 2010).

At Dassen Island, a study of breeding success took place following the *Apollo Sea* oil spill of 1994 (Wolfaardt *et al.* 2008c). The focus of the study was to determine whether reproductive success among pairs where one or both birds had been oiled was different to the success rate of pairs which had not been oiled. About 250 nests per year were monitored. The number of nests which involved oiled penguins was about 10% higher than the number of nests which involved only birds which had not been oiled. Only burrow nests were monitored. For most of the study period, nests were checked every five days. This study yielded average breeding success rates for the five years from 1995 to 1999. Further observations have been made since 2008, yielding four more data points (Visagie *et al.* 2012).

Thus, three fledging success data series are available as inputs to the GLM analyses (Table 2.8). The first Robben Island series records chicks fledged per pair per year. The second Robben Island series records chicks fledged per breeding attempt, treating double clutches as separate nests. An additional reason for the incomparability of these two series is that the first series includes failures occurring during incubation, while the second series only takes failures subsequent to hatching into account. The series used here differs slightly to that listed by Sherley (2012) as those last results include only breeding attempts first monitored during incubation. The series excludes birds known to have been oiled in the *Treasure* spill of 2000, which are known to have a lower breeding success rate (Sherley 2010).

The Dassen Island series is also expressed in terms of chicks per pair per year. Note that the data reported by Wolfaardt *et al.* (2008c) have been multiplied by 1.27 to account for pairs laying a second clutch in the same season.

2.5.2 Breeders per adult moulter

All penguins moult annually, but adults may abstain from breeding in certain years at their discretion. Thus, dividing the annual nest count at a colony by the number of adult penguins observed moulting at the colony in the corresponding year should give an indication of the proportion of birds which attempt to breed each season (Crawford *et al.* 1999). In practice, there are several difficulties with this index (for a discussion, see Wolfaardt *et al.* 2009a). Nevertheless, the series for Robben Island and Dassen Island have been calculated for use as inputs in the

GLMs (Table 2.9). The series are terminated in 2007 because since then the moult counts have been deemed incomparable to those of earlier years (too low given the nest counts and the fact that all penguins must moult annually). Possible reasons for this are that a larger proportion of birds has been moulting inland (and hence not included in the moult count) or at a different location entirely (e.g. Stony Point). This last reason could be linked to an eastward shift in the distribution of small pelagic fish (Coetzee *et al.* 2008b).

2.5.3 Active and potential nests

Since 1999, nests counted at Dassen Island and Robben Island have been split into two categories. These have been labelled “currently active” and “potential”, which when combined form the series of “total active” nests (Wolfaardt *et al.* 2009a). Nests counted as “currently active” contain fresh eggs, chicks, or a defending non-moulting adult. “Potential” (or “recently used”) nests include signs of fresh guano, nesting material, recent burrowing activity, or many penguin footprints in the vicinity. An increase in the proportion of nests classified as “potential” is thought to indicate a decrease in the number of birds participating in breeding (Crawford *et al.* 2011a).

Wolfaardt *et al.* (2009a, see their Table 3) lists the numbers of nests classified in the various categories for Dassen Island and Robben Island from 1999 to 2006. These series are extended (Table 2.10) by including data from Crawford *et al.* (2011a). Note that Crawford *et al.* (2011a) refer to the total nest counts as the “occupied” nests, even though these include “potential” nests, which in fact are not occupied at the time of counting.

2.5.4 Survival

A capture–mark–recapture analysis was performed on penguin banding data from birds seen at both Dassen Island and Robben Island between 2001 and 2008 (Crawford *et al.* 2011a). This analysis produced estimates of annual survival for the years 2002–2007 (Table 2.11). The year indicates the starting year of the relevant survival interval. A reliable survival estimate for the first year of the study period (2001–2002) could not be calculated. This is because the proportion of birds seen at a location for the first time which are visitors as opposed to residents is not known and cannot be estimated for the first year of the study. Also, the survival rate for the final year of any survival analysis is not reliably estimated. However, the 2007–2008 survival estimates reported in Altwegg *et al.* (2009) have been retained for inclusion in the GLM analyses below so that the time-series are of reasonable length.

2.5.5 Foraging trip parameters

Studies investigating the foraging behaviour of African penguins using GPS data loggers have been conducted since 2003. The methodology of the studies conducted on penguins nesting at Robben Island and Dassen Island is described by Steinfurth and Robinson (2012), and the results from these studies are summarized by Robinson (2012). The methodology for the Algoa Bay studies is described by Pichegru *et al.* (2012) who also include results for the years 2008–2010. The values of mean foraging path length and trip duration are used as GLM inputs (Table 2.12). This table includes revised results for 2011–2012 for Dassen Island and Robben Island provided by A. Steinfurth (pers. comm.) and also results for 2011–2012 for St Croix Island and Bird Island provided by L. Pichegru (pers. comm.).

Although a third foraging behaviour time-series exists, namely the mean maximum distance travelled from the nest, this was not considered in the analyses which follow. From the perspective of the foraging bird, energy expenditure depends only on distance swum (path length) and time spent in the water (trip duration). From the perspective of a hungry chick, trip duration is most important (assuming the parent does not return before foraging successfully). Furthermore, Pichegru *et al.* (2013) show that maximum distance is highly correlated with path length, with $r^2 > 0.5$ in the case of each island considered here. Mean maximum distance may be important in other considerations such as when regulating the extent of areas closed to fishing.

2.5.6 Sardine and anchovy catches

Catches of sardine and anchovy which were estimated to have been taken from around the major South African penguin colonies were calculated and reported by van der Westhuizen (2010). The time-series of catch estimates taken within 15 nautical miles of Robben Island and Dassen Island were preferred for the GLM analyses over catches within either 5 or 10 nautical miles of the island in question (Table 2.13). The reason is that this first area is a better approximation of the penguin foraging range during the breeding season (Petersen *et al.* 2006). The values were calculated by estimating the proportion of each pelagic fishing block (PFB) which lies within a 15 nautical mile radius of the colony in question (van der Westhuizen 2010).

When these time-series were updated with 2010 and 2011 data, an alternate method was used to estimate catches in all years (van der Lingen and van der Westhuizen 2012). Three time-series were generated, quantifying sardine and anchovy catches taken within, nominally, 10, 20, and 30 nautical miles of Robben Island, Dassen Island, St Croix Island, and Bird Island. The "10 nautical mile" series comprises catches recorded for the PFB in which the island in question is situated. The "20 nautical mile" series includes catches recorded in this PFB plus all immediately surrounding PFBs. The "30 nautical mile" series includes catches recorded in the PFBs which contribute to the 20 nautical mile series plus all PFBs immediately surrounding those.

Following discussions by penguin biologists in the DAFF Pelagic Scientific Working Group, the 20 and 30 nautical mile time-series were deemed appropriate for use in GLM analyses (Table 2.14). The 20 nautical mile time-series for sardine and anchovy caught around Robben Island and Dassen Island are very highly correlated with the "old" 15 nautical mile time-series (Table 2.13), with $r^2 = 0.99$ in each case. Thus, results of GLM analyses using these time-series are effectively comparable to results obtained using the old catch time-series.

2.5.7 Sardine and anchovy biomass

In Section 2.4, the hydroacoustic survey providing the sardine biomass series (Table 2.7) used in Chapter 4 is briefly described. The survey also yields an estimate of anchovy abundance. GLM analyses reported on in Chapter 3 include both November 1+ biomass and May recruitment biomass[3]. Analyses involving Western Cape penguin colonies use sardine, anchovy, and the sum of sardine and anchovy biomass estimated by the survey each season. From the November survey, the portion of 1+ biomass observed west of Cape Agulhas (strata A–C) is used for each of the three series. Analyses involving Eastern Cape penguin colonies use only sardine biomass, as

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[3] Both 1+ biomass and recruitment biomass estimates in the assessment model follow survey trends reasonably well, but it should be noted that it is estimated that on average the recruitment survey biomass estimates correspond to only 39% of the true biomass, as the coverage of the recruitment survey is limited (de Moor and Butterworth 2012a).

almost no anchovy is caught in Algoa Bay. From the November survey, the portion of November 1+ biomass observed from Cape Agulhas to Port Alfred (strata D–E) is used. All analyses involving the recruit biomass use the estimates from the standard recruit survey region (west of Cape Infanta). Therefore six series are used for Western Cape analyses (Table 2.15). The additional November 1+ biomass series used for Eastern Cape analyses is obtained from Table 2.7 by subtraction.

It is to be expected that catches in the vicinity of penguin colonies should be related to survey biomass estimates. Indeed, some correlation between these data is evident for catches near Robben Island, especially for sardine (Figure 2.4). Less correlation is evident in the corresponding plots for catches around Dassen Island (Figure 2.5) and the Algoa Bay islands (Figure 2.6).

Table 2.1: Total penguin nest counts at Robben Island since the island was recolonized in 1983. The maximum nest count for each year is indicated. Subsets of this series were published by Crawford *et al.* (1995) for the years 1983–1994 and Underhill *et al.* (2006) for the years 1987–2005. Note, however, that this table includes subsequent revisions for 2000–2004. These revisions, as well as counts for 2006–2008 were supplied by R. Crawford (pers. comm.). Nest counts for the most recent years (2009–2011) were reported by Crawford *et al.* (2011b).

Year	Number of breeding pairs
1983	9
1984	24
1985	103
1986	227
1987	476
1988	849
1989	829
1990	1 278
1991	1 879
1992	2 027
1993	2 176
1994	2 799
1995	2 279
1996	3 097
1997	3 336
1998	3 467
1999	4 399
2000	5 407
2001	6 427
2002	7 099
2003	5 968
2004	7 798
2005	7 152
2006	3 697
2007	5 935
2008	2 234
2009	2 415
2010	2 628
2011	1 817

Table 2.2: Numbers of penguins moulting at Robben Island as estimated using the double Gaussian approach described in Section 2.1. The column for the number of adults is labelled $2N_y^{\mathrm{obs}}$ because these estimates must be halved before being input to the population model to represent the female component only.

	Counts	Adults		Juveniles		Proportion
Season	n_y	$2N_y^{\mathrm{obs}}$	$CV(\%)$	J_y^{obs}	$CV(\%)$	J_y^{prop}
1988/1989	18	3 466	7.9	800	10.7	0.188
1989/1990	25	3 397	7.4	851	10.7	0.200
1990/1991	24	4 724	6.1	915	10.1	0.162
1991/1992	26	4 939	6.0	1 603	7.5	0.245
1992/1993	26	6 544	5.3	1 631	7.6	0.199
1993/1994	24	7 915	4.8	1 574	7.6	0.166
1994/1995	25	7 932	4.8	1 368	8.3	0.147
1995/1996	25	6 674	5.4	1 406	8.3	0.174
1996/1997	23	7 300	8.0	2 292	9.5	0.239
1997/1998	25	8 556	4.4	2 381	6.0	0.218
1998/1999	20	9 125	4.3	2 738	5.9	0.231
1999/2000	21	11 694	4.0	2 811	5.8	0.194
2000/2001	15	12 883	3.8	2 417	8.5	0.158
2001/2002	9	12 361	8.6	2 712	8.5	0.180
2002/2003	16	14 521	3.9	3 430	6.4	0.191
2003/2004	14	16 975	3.6	3 326	5.8	0.164
2004/2005	15	12 442	4.0	2 508	5.5	0.168
2005/2006	20	7 660	4.9	2 614	6.0	0.254
2006/2007	17	6 453	6.0	1 889	8.9	0.226
2007/2008	19	5 157	6.4	1 393	10.7	0.213
2008/2009	26	3 745	7.2	1 799	7.2	0.325
2009/2010	26	4 209	19.1	1 730	8.1	0.291
2010/2011	20	3 000	9.9	1 199	13.9	0.286
2011/2012	22	2 496	40.8	636	16.1	0.203

Table 2.3: Numbers of penguins moulting at Robben Island as estimated by the linear interpolation approach published by Wolfaardt *et al.* (2009a) and by the double Gaussian approach described in Section 2.1.1.

	Adults			Juveniles		
Season	Linear interpolation	Double Gaussian	Difference (%)	Linear interpolation	Double Gaussian	Difference (%)
1988/1989	3 459	3 466	0.2	842	800	−4.9
1989/1990	3 392	3 397	0.1	866	851	−1.7
1990/1991	4 730	4 724	−0.1	911	915	0.4
1991/1992	4 915	4 939	0.5	1 598	1 603	0.3
1992/1993	6 538	6 544	0.1	1 597	1 631	2.1
1993/1994	8 002	7 915	−1.1	1 585	1 574	−0.7
1994/1995	7 948	7 932	−0.2	1 373	1 368	−0.3
1995/1996	6 563	6 674	1.7	1 403	1 406	0.2
1996/1997	5 608	7 300	30.2	2 138	2 292	7.2
1997/1998	8 696	8 556	−1.6	2 351	2 381	1.3
1998/1999	9 397	9 125	−2.9	2 834	2 738	−3.4
1999/2000	11 765	11 694	−0.6	2 803	2 811	0.3
2000/2001	13 362	12 883	−3.6	2 565	2 417	−5.8
2001/2002	16 439	12 361	−24.8	3 921	2 712	−30.8
2002/2003	14 737	14 521	−1.5	3 330	3 430	3.0
2003/2004	17 424	16 975	−2.6	3 440	3 326	−3.3
2004/2005	12 871	12 442	−3.3	2 617	2 508	−4.2
2005/2006	7 769	7 660	−1.4	2 654	2 614	−1.5

Table 2.4: Estimates of the parameters in equation (2.1) which best fit the counts of moulting juvenile penguins at Robben Island.

Season	N_1	μ_1	σ_1	N_2	μ_2	σ_2
1988/1989	6 654	1 Dec	11.4	3 516	23 Feb	42.1
1989/1990	2 986	3 Dec	6.0	7 859	16 Jan	62.7
1990/1991	5 322	4 Dec	14.9	6 419	17 Feb	64.6
1991/1992	10 597	10 Dec	14.1	9 846	6 Jan	68.6
1992/1993	8 746	7 Dec	7.6	11 986	24 Dec	59.0
1993/1994	12 337	3 Dec	13.4	7 690	28 Jan	58.9
1994/1995	6 721	27 Dec	14.0	10 681	16 Jan	57.6
1995/1996	8 924	28 Nov	31.5	8 934	2 Mar	32.0
1996/1997	23 105	19 Dec	22.9	6 013	24 Mar	31.7
1997/1998	17 602	24 Nov	25.3	12 716	20 Jan	63.5
1998/1999	18 893	28 Nov	26.2	15 954	21 Jan	60.2
1999/2000	24 837	30 Nov	20.8	10 857	3 Mar	26.9
2000/2001	22 681	15 Nov	27.6	8 017	16 Mar	33.8
2001/2002	21 819	26 Nov	12.3	12 701	26 Feb	49.5
2002/2003	24 436	4 Dec	12.9	19 999	11 Jan	89.4
2003/2004	29 857	25 Nov	26.8	12 386	1 Mar	17.8
2004/2005	20 654	2 Dec	17.5	11 256	5 Jan	64.5
2005/2006	25 724	29 Nov	19.6	7 644	14 Jan	77.8
2006/2007	16 736	19 Nov	18.9	8 033	22 Nov	83.8
2007/2008	6 331	5 Dec	13.6	11 547	20 Dec	75.4
2008/2009	7 275	30 Nov	17.7	15 586	14 Jan	52.7
2009/2010	8 475	1 Dec	12.4	13 536	6 Jan	60.8
2010/2011	12 289	4 Nov	36.2	2 941	7 Mar	30.4
2011/2012	6 268	5 Dec	30.3	1 805	16 Mar	33.0

Table 2.5: Estimates of the parameters in equation (2.1) which best fit the counts of moulting adult penguins at Robben Island.

Season	N_1	μ_1	σ_1	N_2	μ_2	σ_2
1988/1989	39 248	13 Dec	19.3	4 828	19 Jan	66.2
1989/1990	33 982	13 Dec	16.3	9 164	7 Jan	54.7
1990/1991	48 582	12 Dec	19.1	11 425	11 Jan	56.0
1991/1992	46 954	12 Dec	20.4	15 806	11 Jan	57.8
1992/1993	71 918	10 Dec	17.0	11 210	4 Jan	56.8
1993/1994	91 001	12 Dec	21.9	9 547	16 Jan	58.2
1994/1995	32 724	12 Nov	13.6	68 015	23 Dec	41.0
1995/1996	64 385	7 Dec	19.5	20 401	11 Jan	56.9
1996/1997	72 095	17 Dec	22.9	20 668	20 Jan	57.3
1997/1998	83 273	5 Dec	22.4	25 436	8 Jan	58.1
1998/1999	98 177	14 Dec	25.6	17 742	14 Jan	57.1
1999/2000	117 280	6 Dec	18.6	31 249	12 Jan	51.3
2000/2001	113 540	22 Nov	17.1	50 074	22 Dec	42.1
2001/2002	101 810	27 Nov	19.6	55 507	6 Jan	65.8
2002/2003	169 441	4 Dec	26.2	14 992	19 Mar	34.5
2003/2004	111 400	30 Nov	18.2	104 350	11 Dec	54.9
2004/2005	116 200	30 Nov	20.2	41 817	1 Jan	48.2
2005/2006	80 941	1 Dec	28.9	16 646	29 Dec	77.1
2006/2007	66 480	29 Nov	31.1	15 793	15 Dec	77.1
2007/2008	52 628	4 Dec	22.5	13 021	2 Jan	72.3
2008/2009	39 798	11 Dec	28.7	7 821	6 Jan	67.9
2009/2010	10 484	11 Dec	7.7	42 988	16 Dec	49.7
2010/2011	22 367	7 Dec	24.1	15 759	19 Dec	55.9
2011/2012	12 269	1 Dec	14.7	19 424	26 Dec	44.2

Table 2.6: Model inputs related to oiling.

Quantity	Description	Value
N^{oil}_{1994}	Number of adult females which died as a result of the *Apollo Sea* oil spill	600
N^{oil}_{2000}	Number of adult females which died as a result of the *Treasure* oil spill	500
p^{oil}_{1994}	Proportion of chicks which died due to the *Apollo Sea* oil spill	0.29
p^{oil}_{2000}	Proportion of chicks which died due to the *Treasure* oil spill	0.40
m_{1994}	Time of year of the *Apollo Sea* oil spill (months)	5.7
m_{2000}	Time of year of the *Treasure* oil spill (months)	5.8

Table 2.7: Survey estimates of sardine 1+ biomass for the standard assessment survey area (strata A–E), the biomass west of Cape Agulhas (strata A–C), the proportion of the assessment total in strata A–C, and the average inter-transect sampling CV for the assessment total. The complete time-series of total biomass is taken from Shabangu *et al.* (2012), along with the associated CVs. The proportions west of Cape Agulhas were provided by J. Coetzee (pers. comm.).

Year	Total (t)	Strata A–C (t)	Proportion	CV
1984	48 378	48 009	0.992	0.972
1985	45 013	25 457	0.566	0.449
1986	299 797	238 230	0.795	0.696
1987	111 285	94 165	0.846	0.402
1988	134 362	128 043	0.953	0.715
1989	256 655	198 328	0.773	0.225
1990	289 876	248 855	0.858	0.276
1991	597 858	517 180	0.865	0.308
1992	494 157	247 756	0.501	0.488
1993	560 019	480 822	0.859	0.316
1994	518 354	389 730	0.752	0.280
1995	844 727	348 832	0.413	0.515
1996	529 456	257 763	0.487	0.359
1997	1 224 632	964 835	0.788	0.244
1998	1 607 328	1 082 547	0.674	0.251
1999	1 635 410	708 029	0.433	0.212
2000	2 292 380	726 230	0.317	0.500
2001	2 309 600	669 617	0.290	0.142
2002	4 206 250	1 184 713	0.282	0.227
2003	3 564 171	1 343 118	0.377	0.197
2004	2 615 715	292 522	0.112	0.334
2005	1 048 991	75 604	0.072	0.300
2006	712 553	177 885	0.250	0.346
2007	256 727	57 666	0.225	0.345
2008	384 080	211 871	0.552	0.422
2009	502 254	262 853	0.523	0.271
2010	508 392	309 465	0.609	0.235
2011	1 037 060	182 825	0.176	0.235
2012	345 054	186 109	0.539	0.344

Table 2.8: Time-series of fledging success at Robben Island and Dassen Island. Different methodologies were used in each of the three studies, so the time-series are not directly comparable (see Section 2.5.1).

Year	Island	Series	Fledging success
			Chicks fledged per pair per year
1989	Robben	Robben1	0.415
1990	Robben	Robben1	0.319
1991	Robben	Robben1	0.592
1992	Robben	Robben1	0.590
1993	Robben	Robben1	0.535
1994	Robben	Robben1	0.446
1995	Robben	Robben1	0.383
1996	Robben	Robben1	0.654
1997	Robben	Robben1	0.968
1998	Robben	Robben1	0.748
1999	Robben	Robben1	0.600
			Chicks fledged per pair per breeding attempt
2001	Robben	Robben2	0.756
2002	Robben	Robben2	0.516
2003	Robben	Robben2	0.449
2004	Robben	Robben2	0.487
2005	Robben	Robben2	0.811
2006	Robben	Robben2	0.627
2007	Robben	Robben2	1.142
2008	Robben	Robben2	1.031
2009	Robben	Robben2	0.937
2010	Robben	Robben2	0.900
2011	Robben	Robben2	1.096
			Chicks fledged per pair per year
1995	Dassen	Dassen	0.825
1996	Dassen	Dassen	1.022
1997	Dassen	Dassen	1.180
1998	Dassen	Dassen	1.343
1999	Dassen	Dassen	1.376
2008	Dassen	Dassen	1.010
2009	Dassen	Dassen	1.060
2010	Dassen	Dassen	0.909
2011	Dassen	Dassen	1.136

Table 2.9: Time-series of breeders per adult moulter at Robben Island and Dassen Island.

	Breeders per adult moulter	
Year	Robben	Dassen
1989	0.478	
1990	0.753	
1991	0.796	
1992	0.821	
1993	0.665	
1994	0.707	
1995	0.575	
1996	0.928	1.536
1997	0.914	1.336
1998	0.810	1.348
1999	0.926	1.408
2000	0.925	1.354
2001	0.998	1.636
2002	1.149	1.760
2003	0.825	1.604
2004	0.919	2.993
2005	1.150	2.610
2006	0.965	2.335
2007	1.839	3.050

Table 2.10: Time-series of active nests as a proportion of the total number of occupied nests at Robben Island and Dassen Island. Occupied nests include both active and potential nests. See Figure 5 of Crawford *et al.* (2011a).

	Ratio of active to total nests	
Year	Robben	Dassen
1999		0.95
2000	0.96	0.92
2001	0.95	0.85
2002	0.94	0.80
2003	0.97	0.66
2004	0.88	0.54
2005	0.79	0.49
2006	0.86	0.40
2007	0.82	0.43
2008	0.99	0.61
2009	0.83	0.48
2010	0.77	0.40
2011	0.66	0.43

Table 2.11: Time-series of adult survival at Robben Island and Dassen Island estimated through a capture–mark–recapture analysis (see Section 2.5.4).

	Adult survival	
Year	Robben	Dassen
2002	0.765	0.697
2003	0.752	0.682
2004	0.644	0.561
2005	0.620	0.535
2006	0.548	0.462
2007	0.385	0.307

Table 2.12: Time-series of (a) mean foraging path length (in kilometres) and (b) mean average trip duration (in hours) at Robben Island, Dassen Island, St Croix Island and Bird Island.

(a) Foraging path length mean and standard deviation (km).

	Dassen		Robben		St Croix		Bird	
Year	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
2003	33.6	2.7	31.2	9.3				
2004	21.2	8.3						
2007							57.8	17.0
2008	57.1	24.9	42.7	10.4	69.3	28.6	36.5	10.0
2009					50.2	17.0	40.0	12.4
2010	61.1	25.7	49.2	18.3	69.2	26.0	52.1	24.2
2011	76.1	41.7	54.4	35.1	67.8	15.9	56.1	31.4
2012	50.7	26.5	33.5	9.7	89.9	12.4	61.5	15.5

(b) Foraging Trip duration mean and standard deviation (h).

	Dassen		Robben		St Croix		Bird	
Year	Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
2003	9.6	1.8	11.0	1.8				
2004	12.5	4.5						
2007							20.3	5.1
2008	22.6	11.6	13.8	2.5	22.5	7.2	15.3	4.1
2009					17.1	4.0	18.4	5.8
2010	13.8	6.5	18.0	9.1	27.1	9.7	20.5	6.9
2011	17.7	9.6	16.5	10.4	20.1	4.9	21.7	9.6
2012	12.7	7.2	11.0	3.1	23.8	4.1	19.3	3.8

Table 2.13: Time-series of annual catches (in tonnes) of sardine and anchovy taken within 15 nautical miles of Robben Island and Dassen Island.

	Robben Island			Dassen Island		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1987	1 577	34 686	36 263	5 706	51 526	57 232
1988	2 953	44 734	47 687	10 026	33 909	43 935
1989	2 395	30 736	33 131	4 090	24 990	29 080
1990	5 262	5 130	10 392	9 961	8 686	18 647
1991	2 880	15 993	18 873	4 657	10 433	15 090
1992	4 166	32 012	36 178	6 677	42 180	48 857
1993	3 526	7 767	11 293	9 205	14 977	24 182
1994	4 861	21 589	26 450	5 674	29 424	35 098
1995	2 777	9 498	12 275	10 616	20 223	30 839
1996	5 981	4 243	10 224	23 849	7 530	31 379
1997	9 523	7 945	17 468	7 041	3 463	10 504
1998	9 678	3 252	12 930	19 455	2 927	22 382
1999	9 275	17 000	26 275	25 922	36 286	62 208
2000	2 264	12 908	15 172	6 441	30 003	36 444
2001	4 029	12 023	16 052	6 465	51 926	58 391
2002	19 829	17 397	37 226	21 152	36 436	57 588
2003	24 511	30 581	55 092	16 583	31 338	47 921
2004	2 388	17 925	20 313	2 543	25 800	28 343
2005	385	11 046	11 431	1 679	56 067	57 746
2006	2 455	21 442	23 897	3 685	40 325	44 010
2007	1 977	35 374	37 351	3 912	39 741	43 653
2008	808	48 139	48 947	1 977	13 338	15 315
2009	1 409	33 100	34 509	330	3 359	3 689

Table 2.14: Time-series (in tonnes) of annual small pelagic catches (sardine and anchovy) taken in the vicinity of Western Cape and Eastern Cape penguin colonies. Table 2.14a and Table 2.14b include catches taken within 20 nautical miles of the island in question, while Table 2.14c and Table 2.14d include catches taken within 30 nautical miles of that island.

(a) Sardine and anchovy catches taken within 20 nautical miles of Robben Island and Dassen Island.

	Robben Island			Dassen Island		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1987	1 733	37 283	39 016	7 280	55 122	62 401
1988	3 222	47 413	50 635	11 539	37 539	49 077
1989	2 653	32 766	35 419	5 038	30 498	35 536
1990	6 784	6 224	13 008	12 548	10 028	22 575
1991	3 092	17 309	20 400	5 285	11 977	17 262
1992	4 465	35 917	40 382	7 886	46 421	54 307
1993	3 757	8 960	12 718	11 818	16 144	27 961
1994	5 594	26 707	32 301	7 638	35 678	43 316
1995	3 087	9 911	12 998	13 536	24 930	38 467
1996	6 147	4 665	10 812	28 978	8 353	37 331
1997	10 168	8 351	18 519	9 730	3 672	13 402
1998	9 301	3 595	12 896	25 706	3 635	29 341
1999	9 588	18 767	28 355	33 526	41 325	74 851
2000	2 112	14 096	16 208	8 916	35 551	44 467
2001	3 982	13 282	17 263	8 518	57 509	66 027
2002	21 328	18 975	40 303	27 062	39 423	66 485
2003	25 545	35 309	60 853	21 528	36 957	58 486
2004	2 336	20 957	23 293	2 911	30 179	33 091
2005	486	12 943	13 430	1 862	61 371	63 233
2006	2 760	23 764	26 523	4 004	43 067	47 071
2007	2 036	40 881	42 917	5 278	45 981	51 260
2008	802	53 327	54 129	3 324	21 071	24 395
2009	1 315	34 991	36 306	420	5 256	5 676
2010	2 487	20 145	22 632	5 337	22 264	27 601
2011	1 143	2 558	3 701	5 355	14 888	20 243
2012	845	20 318	21 162	1 511	40 590	42 101

Table 2.14: Time-series of small pelagic catches taken within the vicinity of penguin colonies (continued).

(b) Sardine and anchovy catches taken within 20 nautical miles of St Croix Island and Bird Island.

	St Croix Island			Bird Island		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1987	0	0	0	0	0	0
1988	0	0	0	0	0	0
1989	12	0	12	0	0	0
1990	163	0	163	40	0	40
1991	471	0	471	16	0	16
1992	231	0	231	58	0	58
1993	143	0	143	0	0	0
1994	355	0	355	31	0	31
1995	509	0	509	0	0	0
1996	614	0	614	0	0	0
1997	36	0	36	0	0	0
1998	2 660	0	2 660	0	0	0
1999	1 482	0	1 482	0	0	0
2000	668	0	668	0	0	0
2001	1 100	0	1 100	20	0	20
2002	4 105	0	4 105	12	0	12
2003	14 818	0	14 818	0	0	0
2004	3 976	0	3 976	90	0	90
2005	1 071	0	1 071	125	0	125
2006	9 485	0	9 485	5 570	0	5 570
2007	2 606	0	2 606	5 854	0	5 854
2008	491	0	491	3 600	2	3 602
2009	320	0	320	3 214	1	3 215
2010	1 736	0	1 736	2 028	0	2 028
2011	678	0	678	68	0	68
2012	3 906	0	3 906	0	0	0

Table 2.14: Time-series of small pelagic catches taken within the vicinity of penguin colonies (continued).

(c) Sardine and anchovy catches taken within 30 nautical miles of Robben Island and Dassen Island.

	Robben Island			Dassen Island		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1987	3 702	66 013	69 715	14 422	86 864	101 286
1988	7 524	70 147	77 672	18 313	95 111	113 425
1989	4 961	53 854	58 815	10 620	66 531	77 152
1990	10 960	10 671	21 631	17 610	21 891	39 501
1991	7 098	24 133	31 232	9 409	23 440	32 849
1992	8 619	64 193	72 812	12 602	69 627	82 228
1993	10 385	18 919	29 303	17 881	20 260	38 142
1994	9 778	41 629	51 407	15 499	49 627	65 126
1995	8 126	22 973	31 099	21 854	35 136	56 990
1996	20 291	8 806	29 096	42 300	15 911	58 211
1997	23 327	12 393	35 720	27 355	7 072	34 427
1998	31 819	4 546	36 365	48 784	6 575	55 360
1999	34 134	37 722	71 855	55 403	59 061	114 465
2000	13 687	31 168	44 855	26 860	50 397	77 257
2001	18 082	34 875	52 958	19 972	76 641	96 613
2002	53 139	34 561	87 700	52 559	56 635	109 195
2003	59 125	66 775	125 900	47 771	59 216	106 987
2004	13 944	41 472	55 416	7 107	44 065	51 172
2005	1 742	49 668	51 410	2 241	74 423	76 664
2006	6 035	49 640	55 675	6 033	62 184	68 218
2007	6 403	83 681	90 083	10 618	72 429	83 047
2008	3 468	91 143	94 610	8 284	60 033	68 317
2009	5 380	54 009	59 390	1 608	34 281	35 888
2010	9 879	48 946	58 825	13 290	34 357	47 647
2011	5 939	17 291	23 229	10 640	23 924	34 564
2012	4 753	79 331	84 085	2 606	63 357	65 963

Table 2.14: Time-series of small pelagic catches taken within the vicinity of penguin colonies (continued).

(d) Sardine and anchovy catches taken within 30 nautical miles of St Croix Island and Bird Island.

	St Croix Island			Bird Island		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1987	0	0	0	0	0	0
1988	0	0	0	0	0	0
1989	12	0	12	12	0	12
1990	220	0	220	144	0	144
1991	500	0	500	211	0	211
1992	778	0	778	351	0	351
1993	244	0	244	60	0	60
1994	1 271	0	1 271	194	0	194
1995	1 548	0	1 548	281	0	281
1996	1 596	0	1 596	326	0	326
1997	209	0	209	8	0	8
1998	3 272	0	3 272	694	0	694
1999	2 796	0	2 796	825	0	825
2000	875	0	875	196	0	196
2001	2 333	0	2 333	20	0	20
2002	5 706	0	5 706	74	0	74
2003	15 754	0	15 754	483	0	483
2004	7 666	0	7 666	936	0	936
2005	7 029	0	7 029	2 851	0	2 851
2006	21 855	0	21 855	15 895	0	15 895
2007	7 353	0	7 353	8 339	0	8 339
2008	3 471	2	3 473	5 529	2	5 531
2009	3 366	1	3 367	5 346	1	5 347
2010	3 974	0	3 974	3 235	0	3 235
2011	1 982	0	1 982	350	0	350
2012	4 230	0	4 230	154	0	154

Table 2.15: Time-series of pelagic hydroacoustic survey estimates of sardine and anchovy biomass. The May series comprises the total recruit biomass west of Cape Infanta. The November series comprises the aggregate 1+ biomass west of Cape Agulhas. All data up to 2006 were published by de Moor *et al.* (2008). Recent updates to the spawner biomass time-series are taken from Shabangu *et al.* (2012). Coetzee (2012) lists the up-to-date recruit biomass time-series.

	May recruit biomass (t)			November spawner biomass (t)		
Year	Sardine	Anchovy	Total	Sardine	Anchovy	Total
1984				48 009	1 461 636	1 509 645
1985	38 265	368 623	406 888	25 457	1 014 215	1 039 672
1986	50 073	621 089	671 162	238 230	1 978 652	2 216 883
1987	98 643	721 578	820 220	94 165	1 866 430	1 960 595
1988	5 223	563 107	568 329	128 043	1 289 624	1 417 668
1989	66 081	173 349	239 430	198 328	517 293	715 622
1990	31 208	170 083	201 291	248 855	342 812	591 667
1991	26 665	528 177	554 842	517 180	1 254 359	1 771 539
1992	74 822	458 455	533 278	247 756	1 036 580	1 284 337
1993	114 956	481 108	596 064	480 822	439 121	919 942
1994	72 462	145 336	217 797	389 730	309 981	699 711
1995	205 149	392 016	597 164	348 832	468 678	817 510
1996	73 612	74 842	148 453	257 763	29 748	287 511
1997	396 718	404 620	801 338	964 835	377 663	1 342 498
1998	134 907	453 210	588 116	1 082 547	206 586	1 289 132
1999	235 720	826 090	1 061 810	708 029	741 961	1 449 990
2000	299 473	2 553 502	2 852 975	726 230	1 960 122	2 686 351
2001	573 427	1 998 427	2 571 854	669 617	2 301 999	2 971 617
2002	616 331	1 560 101	2 176 432	1 184 713	2 018 570	3 203 283
2003	600 667	1 434 900	2 035 567	1 343 118	1 181 111	2 524 229
2004	40 419	1 071 419	1 111 838	292 522	736 973	1 029 495
2005	11 236	560 518	571 754	75 604	670 730	746 334
2006	50 394	275 797	326 191	177 885	1 027 009	1 204 894
2007	34 575	1 534 523	1 569 099	57 666	889 676	947 342
2008	24 461	1 491 847	1 516 308	211 871	1 421 593	1 633 464
2009	63 468	1 317 059	1 380 527	262 853	2 098 253	2 361 106
2010	499 986	1 687 118	2 187 104	309 466	354 149	663 615
2011	53 681	281 260	334 941	182 825	173 390	356 215
2012	86 089	990 378	1 076 467	186 109	1 022 471	1 208 580

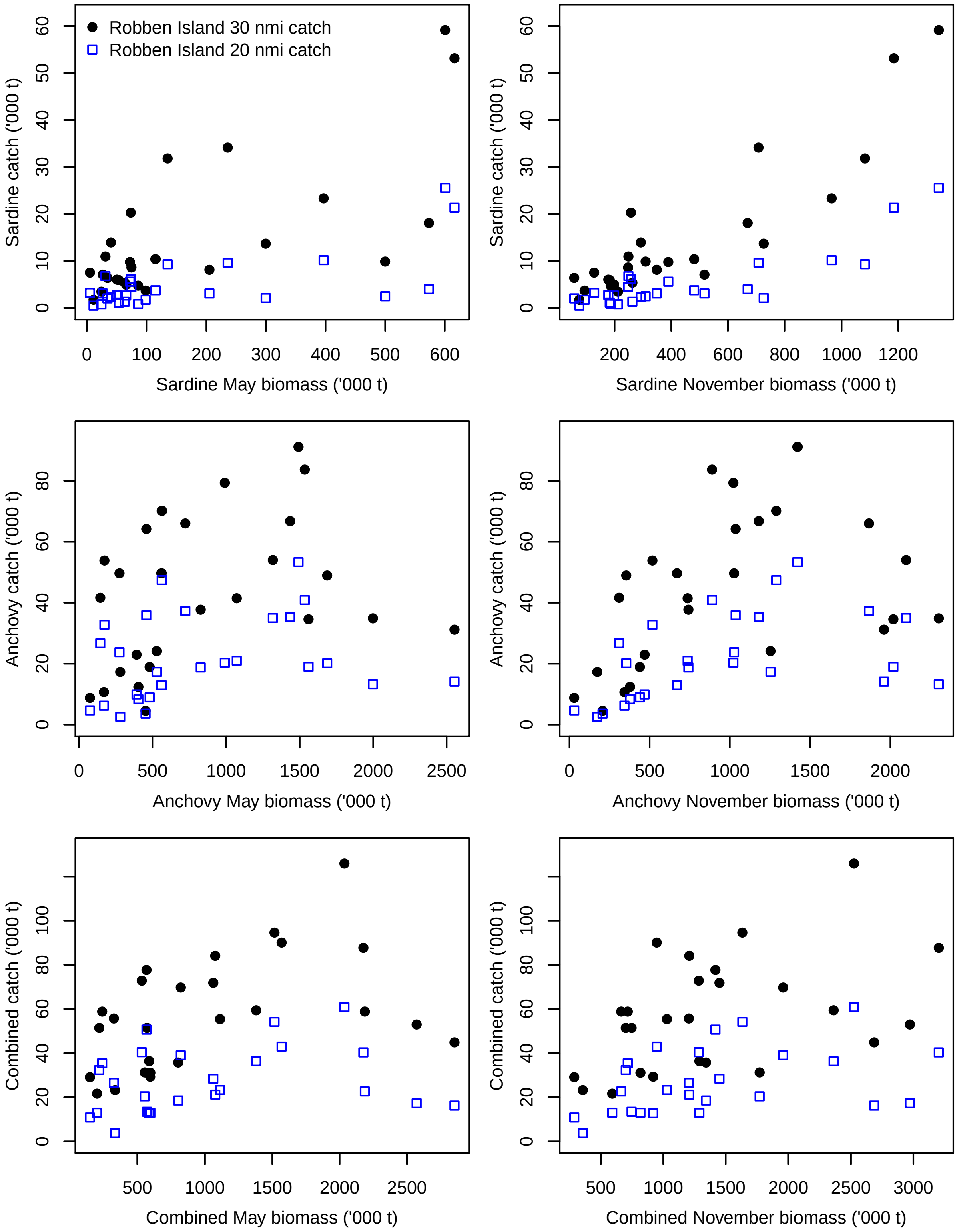

Figure 2.4: Sardine, anchovy, and their combined survey biomasses for May (west of Cape Infanta) and November (west of Cape Agulhas) plotted against the corresponding catches taken within either 20 or 30 nautical miles of Robben Island.

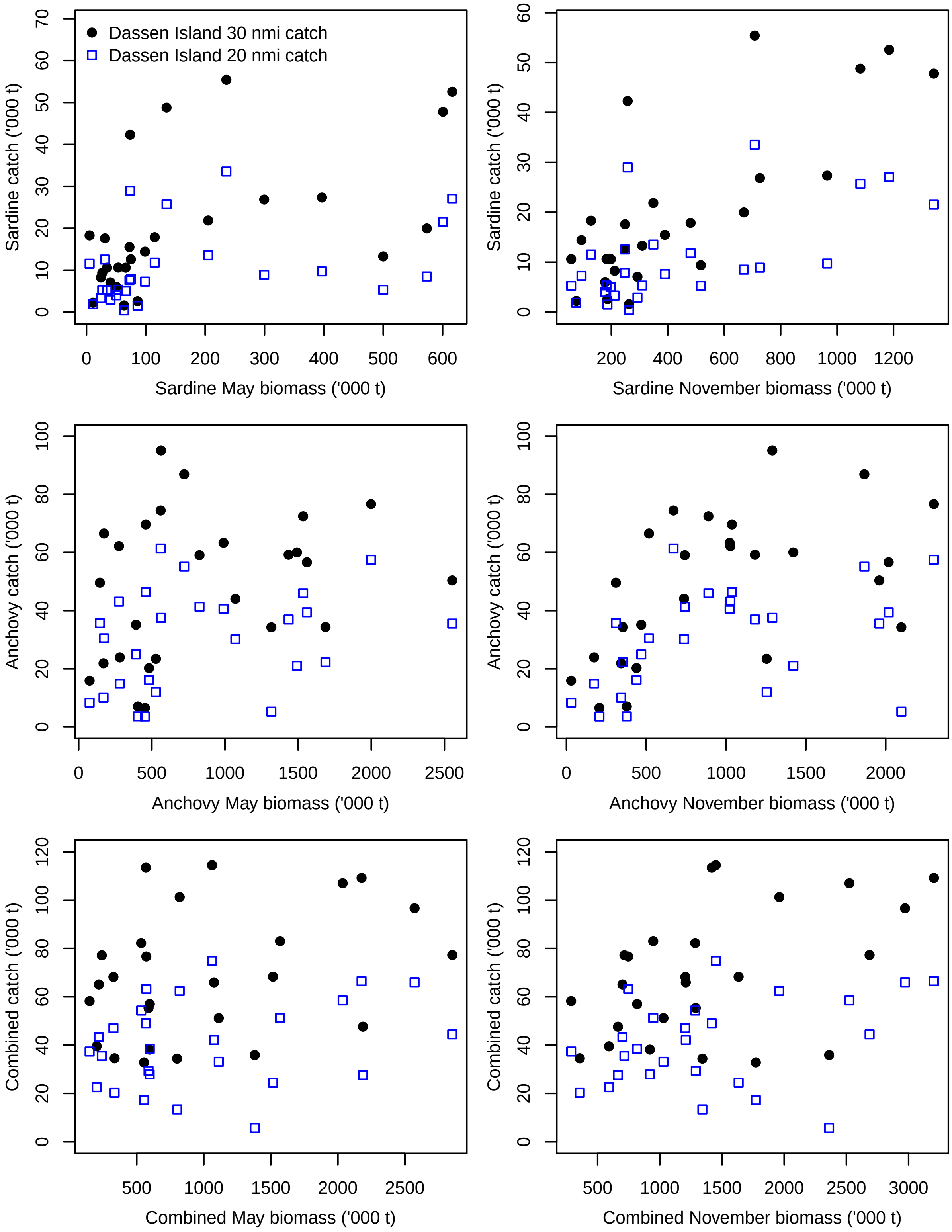

Figure 2.5: Sardine, anchovy, and their combined survey biomasses for May (west of Cape Infanta) and November (west of Cape Agulhas) plotted against the corresponding catches taken within either 20 or 30 nautical miles of Dassen Island.

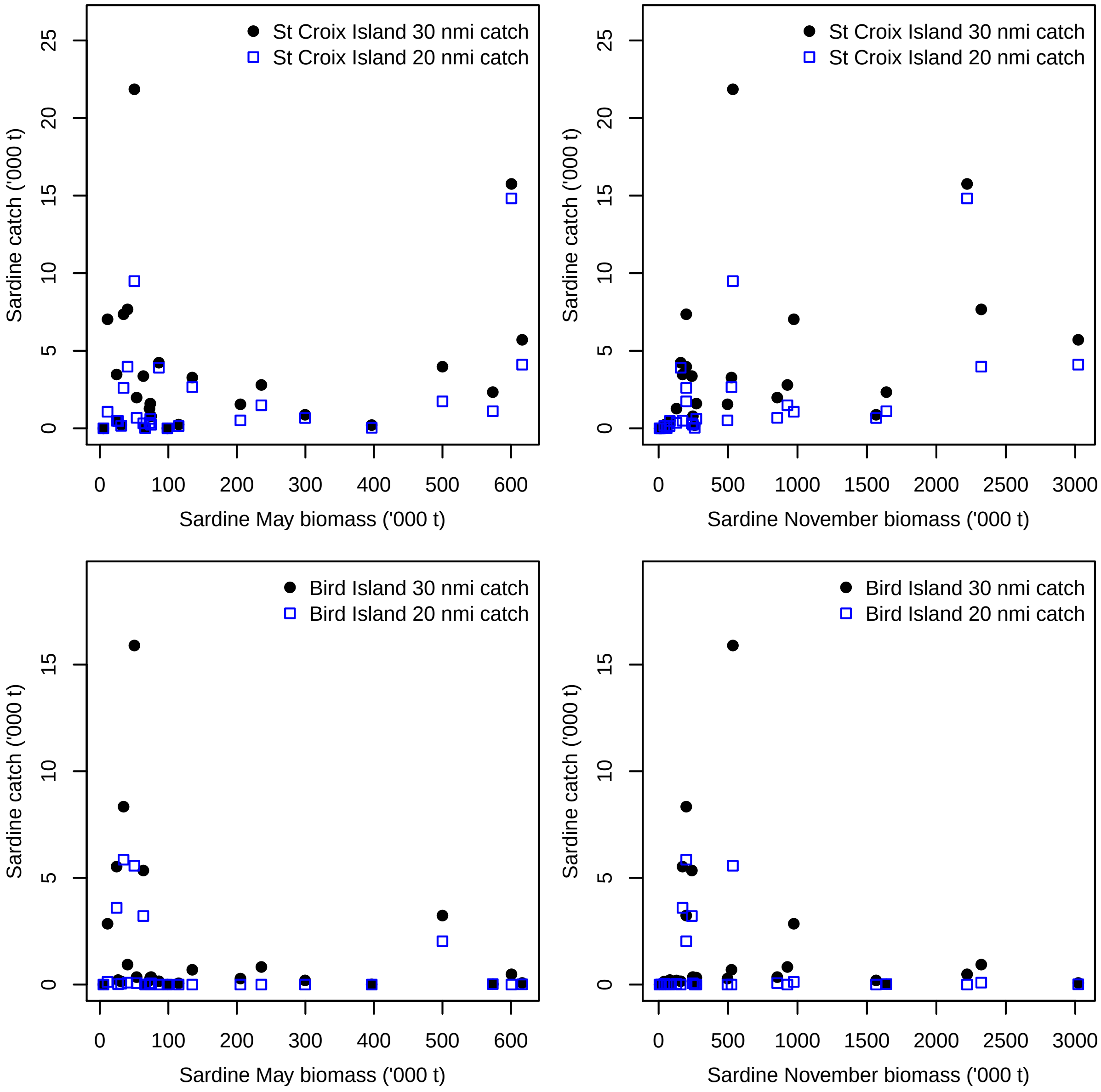

Figure 2.6: Sardine survey biomasses for May (west of Cape Infanta) and November (east of Cape Agulhas) plotted against the corresponding catches taken within either 20 or 30 nautical miles of St Croix Island (top row) and Bird Island (bottom row).

Chapter 3

GLMs relating penguin demographics and foraging behaviour to forage fish abundances

In recent years, the importance of local food availability for penguins has been highlighted (e.g. Durant *et al.* 2010; Pichegru *et al.* 2012; Sherley *et al.* 2013). Analysis by means of general linear models (GLMs) provides a useful and rigorous method of identifying and exploring relationships between data sets and testing alternative hypotheses. This work contributes towards estimation of the possible impact of pelagic fishing in the vicinities of penguin colonies on the foraging behaviour and hence the population dynamics of penguins breeding at those colonies (Section 3.1). A wide set of data series has been used; these are described in Section 2.5.

Two separate sets of analyses are presented below, divided into Part A (Section 3.2) and Part B (Section 3.3). The reason for this division is historical. While the model framework in each case is the same, different analyses were conducted at different times, and each set of results is of interest in its own right. The two sets of analyses were conducted in 2010 and 2013 respectively and presented to a task team (see Section 3.1), each in response to a specific question of interest at the time. Part A analyses include estimates of the change in penguin population growth rate which could be expected as a result of suspending fishing near the colonies. Part B analyses measure the precision of estimates for the residual variance about predictions for the response variables.

The details of the model equations and assumptions for the analyses presented in Part A are described in Section 3.2.1. These analyses include GLMs for which fledging success, active nest proportions, breeders per moulter, and adult survival are the response variables. At the beginning of 2013, new GLM analyses were conducted with updated data sets (Part B). In addition, several further GLMs were run involving new data sets. Specifically, foraging behaviour time-series had by then become of sufficient length to allow reliable estimation of the parameters of GLMs, both for Dassen Island and Robben Island in the Western Cape and for St Croix Island and Bird Island in the Eastern Cape.

3.1 Fishery closures experiment

Marine and Coastal Management (MCM) convened an Island Closure Task Team in 2010. This was prompted by concern about the conservation status of the African penguin, as time-series of abundance indices suggested that the population of the species had been decreasing rapidly over the previous few years (e.g. Altwegg *et al.* 2009). The role of the task team was to provide the Pelagic and Ecosystem Approach to Fisheries Scientific Working Groups (SWG–PEL and SWG–EAF) of MCM[1] with advice relating to the merits of closing areas around certain penguin breeding colonies to purse-seine fishing (DAFF 2011).

An island closure feasibility study was approved. The aim of this study was to evaluate the power of a long-term experiment to detect the effects of fishery closures around penguin colonies on penguin demographic parameters and foraging behaviour. In this regard, the principle contribution of the work presented in this chapter is the provision of estimates of the variances of response variable residuals which are needed for such power analyses. Data have been collected both in the Western Cape (e.g. Steinfurth and Robinson 2012; Sherley *et al.* 2013) and the Eastern Cape (Pichegru *et al.* 2012).

A key feature of the experiment as conceived is that both the Western Cape and the Eastern Cape have a pair of islands in relatively close proximity, each of which hosts an important penguin breeding colony. Dassen Island and Robben Island off the Western Cape coast are 50 km apart, the same distance that separates St Croix Island and Bird Island in Algoa Bay (Figure 1.1). If

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[1] MCM later became the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries.

fishing pressure in the vicinity of a penguin colony impacts demographic parameters negatively, then differences in demographics at the two islands making up a pair should be related to catches taken around the islands. A necessary assumption is that the biomasses of forage fish available to penguins in the vicinity of each island in a pair would be in similar proportions at any time, were it not for extractions made by the fishery.

As the presence of noise degrades the ability to detect signals, it is desirable to increase the contrast in those signals whenever possible. Thus, for the best chance of detecting any fishing effects, one island of a pair should be closed to fishing while fishing should take place freely around the other island. Such closures should follow an alternating schedule so that the otherwise confounded effects of differences between the islands and the impact of fishing can be separated. Currently, a closed area is bounded by a circle of radius 20 km centred at the island concerned. This area was agreed after considering the typical foraging range of breeding penguin as well as practical matters.

In December 2010, various aspects related to the impact of pelagic fishing near penguin breeding colonies were considered at the International Fisheries Stock Assessment Workshop held at the University of Cape Town. The international review panel at the workshop made several recommendations in this regard (Parma *et al.* 2010). They noted that while changing which islands were open or closed to fishing would not affect the estimation of the magnitude of the residual variance, an alternation scheme involving opening closed islands and *vice versa* would allow data collected during the feasibility study to be used in a long term experiment (if conducted). A three-year period before switching the status of an island between open and closed was recommended.

3.2 Part A—GLM analyses conducted in 2010

The response and explanatory variables used in these analyses are described in Section 3.2.1, where the model equations used for these analyses are listed. The results follow (Section 3.2.2). These results do not take account of data from the years 2010–2012 as those were not available for inclusion at the time that this first set of the analyses reported here was carried out. Additionally, the fledging success at Dassen Island in 2008 was not known. Based on these results, Section 3.2.3

describes analyses which estimate expected changes in penguin population growth rate as a result of terminating fishing in the vicinity of the colonies. Discussion follows in Section 3.2.4.

3.2.1 Response and explanatory variables

Penguin response data considered comprise fledging success P (Table 2.8), the ratio of breeders to adult moulters Q (Table 2.9), the ratio of currently active nests to the total nest count R (Table 2.10), and annual adult survival rates S estimated by a capture–mark–recapture analysis of tag data (Table 2.11). Because the proportion of nests and the survival rates fall in the range $[0, 1]$, these two data sets are transformed using a logistic transformation in models (3.3)–(3.4) and (3.7)–(3.8) below.

These response variables were chosen because they represent measures of two key demographic parameters that have a bearing on population abundance trends: reproductive success and adult survival. The first three responses considered are all related to reproductive success. Both the ratio of breeders to adult moulters and the proportion of nests which are active are measures of breeding participation (penguins do not necessarily attempt breeding every year). Fledging success measures the performance of pairs that decide to breed in terms of the average number of chicks that are successfully nurtured until they attain juvenile plumage.

The independent variables considered are the catches C of sardine and anchovy within 15 nautical miles of Robben Island and of Dassen Island (Table 2.13) and biomass estimates B of sardine and anchovy from the hydroacoustic surveys (Table 2.15). The pelagic catches provide a measure of potential impact on the penguins at the breeding colony concerned. The biomass survey estimates give an indication of the abundance of the prey populations over a wider area. These biomass estimates do not cover the complete distributional extent of these populations, but rather the western part of this distribution within which the colonies analysed (Robben Island and Dassen Island) are to be found (Moseley *et al.* 2011). Specifically, for the May recruit survey the area west of Cape Infanta is used, and for the November 1+ biomass survey the area west of Cape Agulhas is used.

If reliable prey abundance estimates at a more local spatial scale were available, measures such as local harvest rates or local escapement could be calculated. Such measures might explain the impact of fishing on penguins better than catches alone. Going to the extreme of attempting to calculate biomass estimates from the annual surveys that match the spatial scale of the series of catches taken near the islands certainly does not seem feasible, as the coverage intensity of these surveys is too low to give estimates of reasonable precision[2] at such a scale. The possibility of obtaining refined local biomass estimates is being investigated further through the initiation of additional hydroacoustic surveys at regular intervals throughout the year within limited areas around the Robben Island and Dassen Island colonies (Merkle *et al.* 2012).

The following factors influencing the penguin response variables are taken into account:

(a) a year effect, relating (either directly or indirectly) to feeding conditions common to both islands,

(b) an island effect, accounting for colony-specific differences in response, and

(c) a fishing effect.

Two sets of GLMs[3] are considered. The first set of equations, which is denoted GLM A, relates the penguin response variables to pelagic catches:

$$\ln(P_{y,i,s}) = \alpha_y + \gamma_s + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i,s} \tag{3.1}$$

$$\ln(Q_{y,i}) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.2}$$

$$\ln\left(\frac{R_{y,i}}{1-R_{y,i}}\right) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.3}$$

$$\ln\left(\frac{S_{y,i}}{1-S_{y,i}}\right) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.4}$$

Here, the parameter subscripts denote year y, island i, data series s, and pelagic species p (sardine, anchovy, or the two combined). The equations involve the following parameters:

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[2] Such estimates would be based on only about 4 survey transects each, compared to about 30 transects covering strata A–C (Figure 2.3), increasing the CVs of abundance estimates from roughly 40% to 100%.

[3] To be specific, these models can be classified as ordinary least squares regressions with log-transformed dependent variables.

α_y are estimable parameters relating to a year effect[4] (indirectly accounting for annual changes in common feeding conditions),

β_i are estimable parameters relating to an island effect,

γ_s are parameters allowing for an estimable bias between the three fledging success data series (two for Robben Island and one for Dassen Island, so that this parameter subsumes any island effect),

λ_i are estimable parameters relating commercial fishery catches to the penguin response variables,

$C_{y,i,p}$ are the annual commercial catches taken in the vicinity of the islands,

$\overline{C}_{i,p}$ are the average catches taken around each island, calculated over the years for which there are penguin data available for the model concerned, and

$\varepsilon_{y,i,s}$ and $\varepsilon_{y,i}$ are error terms, assumed to be normally distributed with a mean of zero and variances estimated within the models.

Clearly these equations are approximations intended to apply over the range of the data to hand. Over a wider range there must be nonlinear behaviour as eventually for very large catches demographic parameters must react negatively.

The reason for scaling the catches near islands by their averages $\overline{C}_{i,p}$ is so that the estimates for λ_i are of a similar magnitude.

In the second set of models considered (GLM B), the year effect α_y is replaced by the parameter μ multiplied by the annual pelagic biomass estimate $B_{y_q,p,q}$ where q refers to either the November 1+ survey or the May recruit survey. This attempts to take annual feeding conditions into account directly. If this relationship with biomass accounts for much of the year effect α_y in equations (3.1)–(3.4), the alternative models can potentially yield more precise estimates of the

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[4] The year parameters could alternatively have been treated as random effects. This was tried in a few cases, and the results obtained were very similar.

key λ_i parameters since these models involve fewer estimable parameters:

$$\ln(P_{y,i,s}) = \gamma_s + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i,s} \tag{3.5}$$

$$\ln(Q_{y,i}) = \beta_i + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.6}$$

$$\ln\left(\frac{R_{y,i}}{1-R_{y,i}}\right) = \beta_i + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.7}$$

$$\ln\left(\frac{S_{y,i}}{1-S_{y,i}}\right) = \beta_i + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.8}$$

Because penguins gain condition over the summer months before the breeding season, $y_q = y - 1$ when q denotes the November 1+ survey while $y_q = y$ when q denotes the May recruit survey.

The parameters of particular interest are μ and λ_i, which respectively relate pelagic fish abundance and commercial fishery catches to the penguin response variables.

Ideally, the predictor variables in such models should be close to orthogonal, as a high level of collinearity can result in unstable parameter estimates with high variances. In the models considered here, clearly a correlation is expected between pelagic biomass and catches, at least when areas around islands are not closed to fishing. A review of the correlation coefficients r between the biomass and catch time-series used in each model considered revealed that the average correlation is $r \approx 0.3$, which is reasonably small. (Compare the plots of survey biomass versus catches for the full time-series in Figures 2.4–2.6.) Severe distortion of parameter estimation tends to occur only when $|r| > 0.7$ (Dormann *et al.* 2013), and this threshold is breached in only a very few cases. In these cases, the variance-inflation factor[5] (VIF) was calculated. Results never exceeded 10, which is often used as a threshold for indicating severe collinearity, although even higher VIFs are often acceptable (O'Brien 2007).

Ridge regression[6] is often suggested as a remedy for serious collinearity of predictor variables, as it results in parameter estimates with reduced variance. However, this introduces a bias, and thus the variance estimates for the parameters become less reliable. As estimation of parameter

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[5] The square root of the VIF is the factor by which the standard error of the parameter in question is increased because of collinearity between predictor variables.

[6] This method penalizes the least-squares likelihood function by adding a scalar multiple of the sum of the squares of the parameter estimates. As the scalar selected is increased, the absolute values of the parameters decrease, as do their variances.

variance is integral to the analyses performed here, attempting ridge regression does not seem appropriate in this case.

3.2.2 Results

The values of the estimated parameters λ_i and μ are given in Table 3.1, along with standard errors and significance levels. Note that no estimates are given for model (3.4) since there proved to be insufficient data for reliable estimation in this case.

Table 3.2 summarizes the number of occurrences of λ_i and μ parameter estimates with positive and negative signs. Positive values of λ_i indicate that more fishing has a beneficial effect on the applicable response variable. Positive values of μ indicate that a higher fish abundance benefits the applicable response variable.

From these tables, it is evident that overall the clear majority of estimates for both μ and λ_i are positive. The same comment applies to estimates of λ_i that are significant at the 15% level, although there is a more even split between the few estimates of λ_i that are significant at the 5% level. The implication of these results is that penguins tend to respond positively both to higher levels of fish abundance and to more intensive fishing.

3.2.3 Analysis

The estimates of the GLM λ_i parameters may be used to calculate estimates for the change in the penguin population growth rate to be expected from stopping fishing in the vicinity of the islands.

Assuming reproductive maturity occurs at age 4, a basic density-independent model for the penguin population N in year y is:

$$N_{y+1} = N_y S + H_{y-3} S^3 N_{y-3} \tag{3.9}$$

where S is the adult annual survival rate and H is a measure related to egg production and fledging success. In the situation where the population growth rate η is the same for each year

($N_{y+1} = \eta N_y$), η is accordingly related to S and H as follows:

$$\eta^4 = \eta^3 S + HS^3 \tag{3.10}$$

Differentiating implicitly and solving for $\Delta\eta$ (a change in the growth rate) gives (to first order):

$$\Delta\eta = \frac{\eta^3 + 3S^2H}{4\eta^3 - 3\eta^2 S}\Delta S + \frac{S^3}{4\eta^3 - 3\eta^2 S}\Delta H \tag{3.11}$$

The growth rates η_{Robben} and η_{Dassen} were estimated from logarithmic regressions of moult time-series (from Crawford *et al.* 2011a, assumed to represent reasonable indices of abundance) for Robben Island from 2004 to 2007 and for Dassen Island from 2003 to 2007. These years correspond to the periods of recent major declines at the two colonies. These are the periods of interest because they span the time of the declines and hence are relevant to management efforts to stem and reverse these trends. The average survival rates from Table 2.11 for the years corresponding to these periods (2004–2006 at Robben Island and 2003–2006 at Dassen Island) were used as the adult survival rates S_{Robben} and S_{Dassen}. Values for H_{Robben} and H_{Dassen} were then calculated using equation (3.10). The results are as follows:

	η	S	H
Robben	0.712	0.604	0.178
Dassen	0.760	0.560	0.501

The parameters λ_i correspond to the effect on the dependent variable in question of increasing the catch around the island concerned from zero to its average value. Thus if such catches are suspended, the estimated change ΔH is given by $\mathrm{e}^{-\lambda_i} - 1$ for the fledging success and breeders per adult moulter GLMs. The active/total nests ratio does not translate readily into such a relationship, but the λ_i parameters of adult survival models of equations (3.4) and (3.8) relate similarly to ΔS after allowing through differentiation for the effect of the logistic transformation.

Table 3.3 shows estimates with approximate 95% confidence intervals of the change in penguin population growth occasioned by suspending fishing around colonies, as estimated from these various models. These results are shown graphically in Figure 3.1, in which the same vertical scale is used throughout to aid making comparisons between the results from the different models. These plots are expanded in Figure 3.2 so that the growth rates predicted for different islands by models involving different pelagic biomass series can be compared more easily. Note that the upper six plots in each figure correspond to results based on GLM analyses of reproduction-related data, while the final two plots relate to model (3.8) which considers survival.

In nearly all cases, the 95% confidence intervals span the horizontal axis. The exceptions are the anchovy catch effect at Dassen Island for the fledging success GLM when the year effect is not related to anchovy biomass (which predicts that suspending fishing would have a negative effect on penguin population growth), and the anchovy catch effect at Robben Island for the adult survival GLMs when the year effect is related to either anchovy 1+ biomass or recruitment (which predict that suspending fishing would have a positive effect on penguin population growth).

3.2.4 Discussion

In terms of the λ_i parameters which estimate the effect of fishing near to islands on penguin demographic parameters, there are five cases (three positive and two negative) where the estimate is significant at the 5% level (Table 3.1). However, interpretation of such “significance” must be tempered by the multiplicity of the tests conducted and the lack of complete independence given use of partially common data. Similar problems would apply if performing non-parametric tests on the tallies of positive and negative estimates shown in Table 3.2. Nevertheless, the broad trends shown there are of interest and probably also not without meaning. The following trends are of note:

(a) When biomass is used rather than estimating a year factor separately for each year, relationships of reproduction and survival rates to pelagic biomass are nearly all positive.

(b) Estimates of the impact of additional fishing on penguin parameters related to reproduction are preponderantly positive rather than negative.

(c) Estimates of this impact on penguin survival rates are near equally split between positive and negative.

Figure 3.2 provides probably the most easily interpretable summary of the estimated impacts on penguin growth rates of suspending pelagic fishing close to west coast colonies. For data series related to reproductive success, the point estimates for changes in growth rate are in the main a few percent and negative, with the strongest effects related to the fledging success data for Dassen Island. The one notable positive effect is for Dassen Island for the breeders to adult moulters ratio when only sardine abundance is used to reflect the common interannual variability for the islands.

Virtually the same comments could be made concerning the results for survival rate when the November spawner biomass surveys provide the co-variate to reflect that common interannual variability. If the recruit survey results are used instead, all but one of the point estimates reflect positive impacts from suspending fishing, but the associated variances are much higher than for the other seven plots shown.

In summary, obtaining clear results from these analyses is frustrated by the short time series available, which precludes precise estimation of the effects of interest. Likely the most that could be said with some confidence is that the results of the analyses do not support the hypothesis that suspending fishing around Robben Island or Dassen Island would enhance penguin reproductive success there. While further analyses of this type could be pursued (e.g. assuming different functional forms or error distributions for the models investigated), that would seem unlikely to yield results dissimilar to those above.

3.3 Part B—GLMs including updated data

At the end of 2012, the Island Closure Task Team met to update data sets and analyses conducted previously. This section describes the results of re-running GLMs with updated data as well as running GLMs involving new data sets. Results from these 2013 analyses are compared to those obtained in 2010.

3.3.1 Response and explanatory variables

The data set for fledging success was extended from 2009 to 2011. Also, the time-series of the proportion of active nests in the total nest counts was updated with data collected from 2010 to 2012. No further analyses have been conducted for the GLMs for breeders per adult moulter, however. The reason for this is the continued doubt about the comparability of the moult counts since 2007 to earlier years, especially at Dassen Island (see Section 2.5.2).

A new GLM involving penguin adult survival has been run. This GLM includes the same survival estimates for Dassen Island for the years 2002–2007 which were used previously (obtained directly from analysis of tag data), but the corresponding Robben Island time-series has been replaced by survival estimates for the years 1988–2011 from the integrated penguin–fish model described in Chapter 4.

Furthermore, GLMs incorporating penguin foraging data have now also been run. The response variables chosen are the mean foraging path length U and the mean foraging trip duration V. The meanings of the other symbols in the equations below are the same as those described in Section 3.2.1. The equations are as follows:

$$-\ln(U_{y,i}) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.12}$$

$$-\ln(U_{y,i}) = \beta_i + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.13}$$

$$-\ln(V_{y,i}) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.14}$$

$$-\ln(V_{y,i}) = \beta_i + \mu B_{y_q,p,q} + \lambda_i \frac{C_{y,i,p}}{\overline{C}_{i,p}} + \varepsilon_{y,i} \tag{3.15}$$

Here, the negative signs appear on the left-hand side of the equations because smaller values of the response variables U and V indicate better feeding conditions than larger values. Hence, the signs of λ and μ retain their previous meanings.

In addition to Dassen Island and Robben Island, foraging time-series are also available for St Croix Island and Bird Island in Algoa Bay (Table 2.12). However, as almost no anchovy are caught in Algoa Bay, only GLMs with sardine catches and abundance estimates are considered for the Eastern Cape penguin colonies. When B refers to the sardine 1+ biomass, estimates for strata D–E are used (Cape Agulhas to Port Alfred, obtained by subtraction from the data given in Table 2.7).

3.3.2 Results

GLM results using updated and new data sets were obtained for each of the response variables (fledging success, active nest proportion, foraging path length and trip duration for both Western Cape and Eastern Cape island pairs, and adult survival). For each response variable, GLMs considering six different pelagic catch time-series were run—sardine, anchovy, and the combination of two, each within either 20 nautical miles or 30 nautical miles of the island concerned. For each response variable, three GLM variants were run for each of these six cases:

(a) GLM A, in which the year effect is estimated directly,

(b) GLM B, in which the year effect is accounted for by the November survey 1+ biomass from the previous year, and

(c) GLM B, in which the year effect is accounted for by the May survey recruit biomass from the current year.

This gives a total of 18 GLMs for each response variable, except for Eastern Cape foraging parameters where only sardine is considered for the explanatory variables (hence six GLMs for each). Full results are provided in the interest of completeness (Tables 3.4–3.9). In addition, results from the 2010 analyses are listed where applicable for comparison, because examining whether an additional three years of data have effected a reduction in the width of the confidence intervals of the parameter estimates is of interest. Figures 3.3–3.8 show the λ_i estimates and standard errors graphically.

Table 3.10 gives counts of positive and negative estimates for μ and λ_i for the various models related to reproduction. Of note is the preponderance of significantly positive λ_i estimates for fledging success (in GLM A), active nest proportion (in GLM A and B), and foraging trip duration (for Dassen Island in GLM B). Overall, about 80% of the λ_i estimates are positive, indicating that feeding conditions are more favourable when small pelagic catches are higher (having taken into account the overall abundance of fish either directly or indirectly). This result is even stronger when considering statistically significant results based on a two-sided t-test.

3.3.3 Analysis

The main aim of the feasibility study for the island closure experiment is to determine the precision of estimates for the residual variance about predictions for the response variables. The precision of these estimates is important because the power of the experiment cannot be reliably determined if these variances cannot be estimated precisely. If the residual variance is high then the power of the experiment to detect a significant effect will be low. Additional data points increase the degrees of freedom which increases the power. Of interest is the expected number of years for which the experiment would be required to run before there is a reasonable chance of detecting a meaningful effect at a pre-specified probability level.

For a model with n data points, the negative log-likelihood of a parameter vector $\bar{p}$ and residual variance σ^2 is:

$$\begin{aligned} -\ln L(\bar{p},\sigma) &= \sum_{i=1}^{n}\left[\ln\sigma + \frac{1}{2\sigma^2}\big(y_i - \hat{y}_i(\bar{p})\big)^2\right] \\ &= n\ln\sigma + \frac{1}{2\sigma^2}X \end{aligned} \tag{3.16}$$

where $\hat{y}$ is the vector of responses predicted by the maximum likelihood estimates of the parameters and

$$X = \sum_{i=1}^{n}(y_i - \hat{y}_i)^2 \tag{3.17}$$

is the sum of the squares of the residuals. The likelihood profile for σ is thus

$$f(\sigma) = n\ln\sigma + \frac{1}{2\sigma^2}X \tag{3.18}$$

which has a minimum at $\hat{\sigma} = \sqrt{X/n}$, the standard deviation of the residuals. The lower and upper bounds of the 95% confidence interval $[\sigma_{-95}, \sigma_{+95}]$ for $\hat{\sigma}$ are the corresponding values of σ such that $f(\sigma) = 1.92 + f(\hat{\sigma})$. The coefficient of variation (CV) is then calculated approximately by dividing the length of the confidence interval by 3.84 and by the maximum likelihood estimate $\hat{\sigma}$:

$$CV = \frac{\sigma_{+95} - \sigma_{-95}}{3.84\hat{\sigma}} \tag{3.19}$$

The *CV*s give a rough indication of the precision of the variance estimate for each model (Tables 3.11–3.15 and Figures 3.9–3.13).

3.3.4 Discussion

Comparing 2010 results with 2013 results using the 20 nautical mile catch series, the width of the confidence intervals has decreased in most cases. This reflects the benefit to precision provided by additional data. The proportion of estimates significant at the 5% level has increased, as might be expected given time-series which are now longer. However, since many different models have been run, Bonferroni corrections should be applied to enforce more conservative thresholds for statistical significance.

Qualitatively, the results are similar to those obtained in 2010. Only about 20% of the λ_i parameter estimates are negative, so once again the great majority are positive (Table 3.10). This suggests that penguins enjoy better feeding conditions when fishing pressure is higher, having taken into account the overall abundance of fish through a year effect.

The longer time-series now available allow for more reliable parameter estimation. Note, however, that the benefit is greater if data points for additional years are obtained for both islands in a pair. This is the case for the survival GLMs in particular, where a long time-series for Robben Island was used, but only a short time-series was available for Dassen Island.

The *CV*s of the standard deviation of the residuals are estimated to be 13% for fledging success GLMs, 14% for adult survival GLMs, 15% for active nest ratio GLMs, and 24% for foraging behaviour GLMs. As might have been expected, the models with the shortest time-series result in the largest *CV*s. In the 2013 analyses, the *CV*s for fledging success GLMs (two years of additional data) and active nest ratio GLMs (three years of additional data) were each reduced by 2% from the 2010 *CV*s. These results provide a basis for deciding whether the current feasibility study has progressed sufficiently to have met its objectives.

The power of an experiment in relation to each of the response variables available is now able to be calculated across the range of plausible values for the *CV*s of the associated residual variance. If even at the current high ends of these ranges sufficient power would be achieved by an experiment to determine the impact of fishing within a reasonable period, then the feasibility study could be ended and the experiment immediately begun. In contrast, if even at the lower end of these ranges sufficient power would not be achieved within a reasonable period, the experiment as conceived would not seem justified. Finally, if neither of these results eventuates, the feasibility study should be continued further to estimate these CVs with greater precision before a decision on whether or not to continue into the full experiment is made.

In GLM B, survey biomasses over a very wide area are used as an indication of feeding conditions common to both islands in a pair. These are the best currently available data suitable for this purpose. However, this assumption might be questioned, particularly for St Croix Island and Bird Island where fish shoaling may be affected by the geography of the bay. This could influence both the foraging strategy of penguins and the fishing strategy of skippers. The island effect incorporated into the models does, however, take this into account indirectly. Further small-scale hydroacoustic surveys may provide better data for local pelagic fish abundance around the islands in the future once a long time-series has been developed.

This analysis considers annual pelagic catches around islands. Another option would be to consider only catches taken during the penguin breeding season, as at other times of the year penguins are not bound to returning to their nests every day or two. Outside of the breeding season, a local depletion of forage fish should not adversely affect penguins as they would be able to forage elsewhere. In principle, such an analysis could be performed, but results are unlikely to differ much. This is because annual catches are well correlated with breeding season catches as most small pelagic fish are caught during the winter months.

A concern with the 30 nautical mile catch series is that several pelagic fishing blocks (PFBs) contribute to the catch series for both islands in a pair. Among the 20 PFBs around Dassen Island and the 14 PBFs around Robben Island, eight of these blocks are common to both series. In Algoa Bay, 10 blocks contribute to the St Croix Island 30 nautical mile series and 20 blocks contribute to the Bird Island 30 nautical mile series. Of these, six are common to both. On the other hand, only one PFB is common to more than one 20 nautical mile series (Robben and Dassen). This could potentially lead to a situation where the 30 nautical mile catch for two adjacent islands may be the same (if it is all taken in the PFBs common to both islands), although one island may be nominally closed to fishing and the other open. The closed area (which has a 20 km radius) lies within the 20 nautical mile catch series PFBs.

In a previous analysis of Eastern Cape penguin foraging tracks, Pichegru *et al.* (2010) purportedly showed that closing the area around St Croix Island to fishing in 2009 provided large benefits to penguins breeding there compared to 2008 when the island was open to fishing. The analyses took account of the foraging performance of penguins at Bird Island (open to fishing in both years) as a "control". The firmness of the conclusion was surprising: indications are that the power to detect the impact of fishing is relatively weak (Brandão and Butterworth 2007), and the time-series was extremely short (two years). The main flaw in the methodology used by Pichegru *et al.* was that they took only observation error variance into account and failed to allow for process error (sometimes called "additional") variance which reflects factors such as the annually varying relative availability of fish at the two islands in a pair considered. In other words, they failed to account for the fact that differences might reflect real differences in prey availability rather than effects of fishing. The analyses reported here take account of such additional variance.

Another problem with the Pichegru *et al.* (2010) analysis is that in the two years concerned, the small pelagic catches taken within 20 nautical miles of St Croix Island were similar: 491 tonnes in 2008 and 320 tonnes in 2009. These amounts are typically an order of magnitude less than had been taken annually during the previous decade (Table 2.14b). Linking an effect on penguins to the actions of the fishery when relatively little fishing had taken place in both the "open" and "closed" years is questionable.

Furthermore, diet samples collected from Algoa Bay penguins in 2008–2010 revealed that anchovy constituted 97% by mass of the small pelagic fish consumed by penguins (Pichegru *et al.* 2012). In contrast, anchovy contributed less than 0.1% to the small pelagic catch over this period. Penguins and fishermen thus seemingly target different species in Algoa Bay.

In a subsequent analysis, Pichegru *et al.* (2013) again purportedly found that foraging effort of St Croix penguins increased significantly with the size of sardine catches. However, the entire data set of GPS tracks was used, treating each as independent, rather than averaging the data for each year or using appropriate mixed-effects models to account for the lack of independence. This approach amounts to pseudoreplication (Hurlbert 1984), and is problematic as process error associated with a year effect is not taken into account. The inclusion of year-dependence would likely substantially affect the significance of the results obtained.

Having noted these issues, the results presented here (using a five-year time-series) do nonetheless suggest that fishing may increase the foraging effort of penguins at St Croix Island (resulting in greater energy expenditure by foraging penguins). The estimates for $\lambda_{\text{St Croix}}$ are negative in 11 out of 12 cases, but none of the results are statistically significant (Table 3.8 and Figure 3.7).

The fact remains though that, perhaps surprisingly, 80% of the λ coefficients are positive rather than negative, suggesting that fishing assists rather than inhibits the reproductive success of penguins. The explanation which first comes to mind is that fishery catches are naturally higher when a high abundance of fish is present in dense shoals—precisely the feeding environment which favours penguins. However, assuming that fish are similarly abundant around neighbouring islands, this is accounted for in the GLMs by a year effect. The λ coefficients then reflect any differential effect of fishing.

One possible mechanism underlying the apparent benefit of fishing to penguins is that the shoaling behaviour of small pelagic fish is a predator defence mechanism: although larger shoals are more readily located, surface to volume effects mean that in a larger shoal an individual fish is less likely to be eaten (Clark 1976). Because fishing tends to break up large shoals, this may be to the benefit of predators such as penguins.

While some seabirds, especially gulls, benefit directly from fishing activity by consuming fishery discards (Wagner and Boersma 2011), this behaviour has not been reported for African penguins. Another hypothesis, which also seems unlikely, is that fishing vessels deter penguin predators such as sharks, facilitating foraging for penguins in areas where fishing is more intense.

Table 3.1: Estimates of λ_i in GLM A (a) and values of λ_i and μ in GLM B with spawner biomass (b) and recruit biomass (c). For each estimate, the standard error and t-probability (statistical significance based on a two-sided t-test) are given.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Fledging success	λ_{Dassen}	0.254	0.250	0.417	0.436	0.145	0.095	0.361	0.181	0.184
	λ_{Robben}	0.221	0.277	0.509	1.142	0.586	0.191	0.335	0.505	0.575
Breeders per adult moulter	λ_{Dassen}	−0.160	0.115	0.198	0.076	0.154	0.633	−0.011	0.223	0.962
	λ_{Robben}	−0.006	0.074	0.938	−0.051	0.152	0.745	0.002	0.147	0.992
Ratio of active to potential nests	λ_{Dassen}	1.662	0.961	0.127	−0.437	0.518	0.427	0.301	0.499	0.566
	λ_{Robben}	1.006	0.559	0.115	1.698	0.491	0.011	1.300	0.452	0.024

(b) GLM B with q denoting November 1+ biomass.

		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Fledging success	μ	−0.083	0.202	0.686	−0.245	0.124	0.061	−0.184	0.095	0.068
	λ_{Dassen}	0.145	0.213	0.505	−0.020	0.122	0.870	0.075	0.174	0.670
	λ_{Robben}	−0.074	0.078	0.359	0.110	0.119	0.364	0.066	0.151	0.667
Breeders per adult moulter	μ	0.025	0.147	0.868	0.022	0.089	0.811	0.015	0.075	0.843
	λ_{Dassen}	−0.254	0.113	0.033	0.259	0.161	0.120	0.143	0.251	0.573
	λ_{Robben}	0.015	0.072	0.834	0.065	0.123	0.598	0.073	0.150	0.630
Ratio of active to potential nests	μ	0.268	0.556	0.636	0.164	0.414	0.698	0.189	0.269	0.492
	λ_{Dassen}	0.680	0.310	0.044	0.346	0.780	0.664	0.998	0.719	0.184
	λ_{Robben}	0.230	0.237	0.346	0.661	0.742	0.387	0.924	0.700	0.205
Adult survival	μ	0.441	0.262	0.137	0.740	0.197	0.007	0.500	0.129	0.006
	λ_{Dassen}	0.366	0.184	0.087	0.268	0.700	0.713	0.889	0.750	0.274
	λ_{Robben}	0.287	0.156	0.108	−0.792	0.438	0.113	−0.305	0.389	0.459

Table 3.1: continued.

(c) GLM B with q denoting May recruit biomass.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Fledging success	μ	0.246	0.516	0.639	0.132	0.167	0.439	0.068	0.137	0.627
	λ_{Dassen}	0.117	0.198	0.561	0.012	0.130	0.927	0.073	0.189	0.704
	λ_{Robben}	−0.127	0.102	0.230	0.066	0.128	0.610	−0.036	0.163	0.827
Breeders per adult moulter	μ	−0.226	0.296	0.451	0.070	0.078	0.377	0.046	0.069	0.513
	λ_{Dassen}	−0.229	0.111	0.050	0.234	0.155	0.144	0.122	0.243	0.621
	λ_{Robben}	0.054	0.080	0.505	0.061	0.115	0.602	0.065	0.138	0.643
Ratio of active to potential nests	μ	1.180	1.190	0.336	0.862	0.349	0.025	0.707	0.241	0.010
	λ_{Dassen}	0.564	0.328	0.105	0.552	0.672	0.424	1.014	0.582	0.101
	λ_{Robben}	0.101	0.276	0.719	0.675	0.634	0.302	0.881	0.567	0.139
Adult survival	μ	3.390	2.810	0.267	0.380	0.440	0.417	0.385	0.328	0.279
	λ_{Dassen}	−0.530	0.833	0.545	−0.270	1.170	0.821	0.560	1.230	0.664
	λ_{Robben}	−0.420	0.683	0.558	−0.867	0.784	0.305	−0.110	0.696	0.879

Table 3.2: Tallies of positive and negative estimated μ and λ_i parameters listed in Table 3.1 for (a) GLMs involving reproduction, (b) GLMs involving adult survival, and (c) all sets of GLMs combined.

(a) Reproduction GLMs.

	Sardine	Anchovy	Combined	Overall
All μ	4 : 2	5 : 1	5 : 1	14 : 4
All λ_i	12 : 6	15 : 3	16 : 2	43 : 11
λ_i significant at 15%	4 : 2	4 : 0	3 : 0	11 : 2
λ_i significant at 5%	1 : 2	1 : 0	1 : 0	3 : 2

(b) Survival GLMs.

	Sardine	Anchovy	Combined	Overall
All μ	2 : 0	2 : 0	2 : 0	6 : 0
All λ_i	2 : 2	1 : 3	2 : 2	5 : 7
λ_i significant at 15%	2 : 0	0 : 1	0 : 0	2 : 1
λ_i significant at 5%	0 : 0	0 : 0	0 : 0	0 : 0

(c) All GLMs.

	Sardine	Anchovy	Combined	Overall
All μ	6 : 2	7 : 1	7 : 1	20 : 4
All λ_i	14 : 8	16 : 6	18 : 4	48 : 18
λ_i significant at 15%	6 : 2	4 : 1	3 : 0	13 : 3
λ_i significant at 5%	1 : 2	1 : 0	1 : 0	3 : 2

Table 3.3: Point estimates and approximate 95% confidence intervals for the changes in penguin population growth (in % per year) attributable to stopping fishing, as estimated by various GLMs. All values are expressed as percentages. See Section 3.2.3 for the reason that the ratio of active to total nests is not included in this table.

(a) GLM A: estimating the year effect directly.

		Sardine			Anchovy			Sardine and Anchovy		
		$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%
Fledging success	Dassen	−5.0	−14.7	4.7	−7.9	−13.8	−2.0	−6.8	−14.0	0.5
	Robben	−6.6	−26.4	13.2	−22.7	−59.0	13.7	−9.5	−42.0	23.0
Breeders per adult moulter	Dassen	3.9	−0.9	8.6	−1.6	−7.9	4.6	0.2	−8.5	9.0
	Robben	0.2	−5.7	6.1	1.7	−9.8	13.3	−0.1	−11.3	11.1

(b) GLM B with q denoting November spawner biomass.

		Sardine			Anchovy			Sardine and Anchovy		
		$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%
Fledging success	Dassen	−3.0	−11.4	5.4	0.5	−4.6	5.5	−1.6	−8.6	5.4
	Robben	2.5	−3.6	8.7	−3.5	−12.7	5.7	−2.1	−13.6	9.4
Breeders per adult moulter	Dassen	3.9	−0.9	8.6	−1.6	−7.9	4.6	0.2	−8.5	9.0
	Robben	0.2	−5.7	6.1	1.7	−9.8	13.3	−0.1	−11.3	11.1
Adult survival	Dassen	−8.7	−18.1	0.7	−6.7	−34.9	21.4	−16.8	−46.3	12.7
	Robben	−6.3	−13.5	0.8	30.5	13.0	48.1	9.0	−6.9	25.0

(c) GLM B with q denoting May recruit biomass.

		Sardine			Anchovy			Sardine and Anchovy		
		$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%	$\Delta\eta$	−95%	+95%
Fledging success	Dassen	−2.5	−10.3	5.4	−0.3	−5.6	−5.1	−1.6	−9.1	6.0
	Robben	4.5	−3.4	12.5	−2.1	−12.0	7.7	1.2	−11.1	13.6
Breeders per adult moulter	Dassen	5.7	1.1	10.3	−4.7	−10.9	1.6	−2.6	−12.0	6.9
	Robben	−1.8	−8.0	4.5	−2.0	−10.9	6.9	−2.1	−12.7	8.5
Adult survival	Dassen	19.9	−11.7	51.6	8.8	−29.7	47.4	−12.2	−51.8	27.3
	Robben	13.2	−11.3	37.7	34.9	7.9	61.8	2.9	−21.9	27.8

Table 3.4: Fledging success GLM parameter estimates with the standard error and t-probability (statistical significance based on a two-sided t-test) given for each estimate.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	λ_{Dassen}	0.254	0.250	0.417	0.436	0.145	0.095	0.361	0.181	0.184
	λ_{Robben}	0.221	0.277	0.509	1.142	0.586	0.191	0.335	0.505	0.575
Catches within 20 nmi of the colony	λ_{Dassen}	0.190	0.124	0.186	0.161	0.082	0.108	0.226	0.109	0.092
	λ_{Robben}	0.234	0.176	0.242	0.015	0.094	0.879	0.019	0.115	0.879
Catches within 30 nmi of the colony	λ_{Dassen}	0.400	0.333	0.283	0.400	0.148	0.043	0.473	0.215	0.079
	λ_{Robben}	0.287	0.292	0.371	0.293	0.170	0.145	0.272	0.227	0.284

(b) GLM B with q denoting November 1+ biomass in strata A–C.

2010 analysis	μ	−0.083	0.202	0.686	−0.245	0.124	0.061	−0.184	0.095	0.068
	λ_{Dassen}	0.145	0.213	0.505	−0.020	0.122	0.870	0.075	0.174	0.670
	λ_{Robben}	−0.074	0.078	0.359	0.110	0.119	0.364	0.066	0.151	0.667
Catches within 20 nmi of the colony	μ	−0.089	0.182	0.628	−0.199	0.091	0.039	−0.169	0.078	0.040
	λ_{Dassen}	0.124	0.128	0.343	−0.011	0.128	0.935	0.079	0.149	0.601
	λ_{Robben}	−0.092	0.066	0.175	0.032	0.100	0.749	−0.025	0.119	0.836
Catches within 30 nmi of the colony	μ	−0.151	0.211	0.480	−0.200	0.092	0.039	−0.178	0.082	0.039
	λ_{Dassen}	0.192	0.158	0.235	0.015	0.157	0.925	0.159	0.221	0.478
	λ_{Robben}	−0.054	0.084	0.529	0.046	0.122	0.713	0.011	0.162	0.947

Table 3.4: Fledging success GLM parameter estimates (continued).

(c) GLM B with q denoting May recruit biomass.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	μ	0.246	0.516	0.639	0.132	0.167	0.439	0.068	0.137	0.627
	λ_{Dassen}	0.117	0.198	0.561	0.012	0.130	0.927	0.073	0.189	0.704
	λ_{Robben}	−0.127	0.102	0.230	0.066	0.128	0.610	−0.036	0.163	0.827
Catches within 20 nmi of the colony	μ	0.147	0.356	0.682	0.002	0.125	0.990	−0.001	0.099	0.988
	λ_{Dassen}	0.096	0.114	0.408	−0.012	0.142	0.934	0.070	0.163	0.671
	λ_{Robben}	−0.128	0.074	0.096	−0.008	0.110	0.944	−0.106	0.128	0.415
Catches within 30 nmi of the colony	μ	0.003	0.374	0.994	0.009	0.133	0.945	0.003	0.102	0.978
	λ_{Dassen}	0.133	0.136	0.339	−0.043	0.184	0.817	0.131	0.240	0.590
	λ_{Robben}	−0.093	0.087	0.292	0.003	0.135	0.982	−0.144	0.172	0.410

Table 3.5: Active and potential nests GLM parameter estimates, standard errors and statistical significance.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	λ_{Dassen}	1.662	0.961	0.127	−0.437	0.518	0.427	0.301	0.499	0.566
	λ_{Robben}	1.006	0.559	0.115	1.698	0.491	0.011	1.300	0.452	0.024
Catches within 20 nmi of the colony	λ_{Dassen}	1.164	0.886	0.218	0.034	0.381	0.930	0.450	0.419	0.309
	λ_{Robben}	0.702	0.481	0.175	1.328	0.303	0.001	1.264	0.314	0.002
Catches within 30 nmi of the colony	λ_{Dassen}	0.774	1.071	0.486	0.445	0.848	0.611	1.000	0.868	0.276
	λ_{Robben}	0.593	0.737	0.440	1.464	0.611	0.038	1.843	0.718	0.028

(b) GLM B with q denoting November 1+ biomass in strata A–C.

2010 analysis	μ	0.268	0.556	0.636	0.164	0.414	0.698	0.189	0.269	0.492
	λ_{Dassen}	0.680	0.310	0.044	0.346	0.780	0.664	0.998	0.719	0.184
	λ_{Robben}	0.230	0.237	0.346	0.661	0.742	0.387	0.924	0.700	0.205
Catches within 20 nmi of the colony	μ	0.458	0.551	0.415	0.192	0.302	0.531	0.161	0.210	0.452
	λ_{Dassen}	0.581	0.270	0.043	0.719	0.678	0.300	1.296	0.585	0.037
	λ_{Robben}	0.221	0.192	0.263	1.009	0.545	0.077	1.143	0.492	0.030
Catches within 30 nmi of the colony	μ	0.297	0.580	0.614	0.267	0.321	0.414	0.130	0.216	0.553
	λ_{Dassen}	0.749	0.324	0.031	0.928	1.081	0.400	1.987	0.782	0.019
	λ_{Robben}	0.340	0.263	0.209	0.742	0.784	0.354	1.342	0.715	0.074

Table 3.5: Active and potential nests GLM parameter estimates (continued).

(c) GLM B with q denoting May recruit biomass.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	μ	1.180	1.189	0.336	0.862	0.349	0.025	0.707	0.241	0.010
	λ_{Dassen}	0.564	0.328	0.105	0.552	0.672	0.424	1.014	0.582	0.101
	λ_{Robben}	0.101	0.276	0.719	0.675	0.634	0.302	0.881	0.567	0.139
Catches within 20 nmi of the colony	μ	0.380	1.059	0.723	0.797	0.291	0.012	0.568	0.209	0.013
	λ_{Dassen}	0.637	0.277	0.032	0.697	0.591	0.250	1.201	0.508	0.027
	λ_{Robben}	0.242	0.215	0.272	0.862	0.477	0.084	1.025	0.424	0.024
Catches within 30 nmi of the colony	μ	−0.216	1.162	0.854	0.845	0.309	0.012	0.508	0.226	0.035
	λ_{Dassen}	0.872	0.347	0.020	0.706	0.951	0.466	1.685	0.709	0.027
	λ_{Robben}	0.441	0.299	0.154	0.627	0.685	0.370	1.155	0.643	0.086

Table 3.6: Robben Island and Dassen Island foraging path length GLM parameter estimates, standard errors and statistical significance.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Catches within 20 nmi of the colony	λ_{Dassen}	0.160	0.187	0.480	−0.281	0.194	0.285	0.067	0.176	0.742
	λ_{Robben}	0.048	0.135	0.755	−0.182	0.086	0.167	−0.090	0.109	0.496
Catches within 30 nmi of the colony	λ_{Dassen}	0.266	0.133	0.185	0.151	0.674	0.843	0.480	0.536	0.465
	λ_{Robben}	0.142	0.111	0.331	0.110	0.532	0.855	0.268	0.470	0.627

(b) GLM B with q denoting November 1+ biomass in strata A–C.

Catches within 20 nmi of the colony	μ	0.826	0.227	0.011	0.046	0.162	0.786	0.102	0.124	0.442
	λ_{Dassen}	−0.116	0.115	0.350	0.719	0.468	0.175	0.440	0.448	0.364
	λ_{Robben}	−0.125	0.095	0.234	0.162	0.230	0.506	0.112	0.277	0.701
Catches within 30 nmi of the colony	μ	0.841	0.227	0.010	0.105	0.161	0.540	0.111	0.121	0.397
	λ_{Dassen}	−0.117	0.115	0.348	0.465	0.547	0.428	0.284	0.453	0.554
	λ_{Robben}	−0.157	0.110	0.202	0.334	0.435	0.471	0.287	0.409	0.509

(c) GLM B with q denoting May recruit biomass.

Catches within 20 nmi of the colony	μ	−0.403	0.829	0.644	0.048	0.253	0.855	−0.036	0.221	0.874
	λ_{Dassen}	0.170	0.230	0.488	0.708	0.478	0.189	0.618	0.461	0.229
	λ_{Robben}	0.140	0.164	0.426	0.177	0.219	0.449	0.230	0.304	0.477
Catches within 30 nmi of the colony	μ	−0.498	0.866	0.586	0.016	0.322	0.961	−0.063	0.235	0.797
	λ_{Dassen}	0.198	0.239	0.438	0.445	0.608	0.492	0.494	0.504	0.365
	λ_{Robben}	0.176	0.197	0.405	0.327	0.508	0.544	0.483	0.462	0.336

Table 3.7: Robben Island and Dassen Island foraging trip duration GLM parameter estimates, standard errors and statistical significance.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Catches within 20 nmi of the colony	λ_{Dassen}	0.635	0.781	0.502	−0.663	0.348	0.197	0.441	0.444	0.426
	λ_{Robben}	0.383	0.564	0.568	−0.448	0.154	0.100	0.233	0.275	0.485
Catches within 30 nmi of the colony	λ_{Dassen}	0.121	0.912	0.906	0.399	1.319	0.791	1.143	1.509	0.528
	λ_{Robben}	0.004	0.762	0.996	0.605	1.042	0.620	1.016	1.325	0.523

(b) GLM B with q denoting November 1+ biomass in strata A–C.

Catches within 20 nmi of the colony	μ	0.259	0.227	0.298	0.023	0.104	0.834	0.010	0.071	0.888
	λ_{Dassen}	0.092	0.115	0.452	0.620	0.300	0.084	0.602	0.257	0.058
	λ_{Robben}	0.003	0.095	0.978	0.114	0.147	0.467	0.155	0.159	0.367
Catches within 30 nmi of the colony	μ	0.272	0.230	0.282	0.064	0.116	0.600	0.035	0.082	0.686
	λ_{Dassen}	0.088	0.117	0.480	0.187	0.393	0.651	0.338	0.308	0.314
	λ_{Robben}	−0.007	0.112	0.954	0.299	0.312	0.375	0.309	0.278	0.308

(c) GLM B with q denoting May recruit biomass.

Catches within 20 nmi of the colony	μ	−0.063	0.520	0.908	−0.035	0.161	0.834	−0.063	0.118	0.613
	λ_{Dassen}	0.170	0.144	0.281	0.635	0.305	0.082	0.664	0.246	0.036
	λ_{Robben}	0.078	0.103	0.476	0.137	0.140	0.365	0.206	0.162	0.250
Catches within 30 nmi of the colony	μ	−0.080	0.552	0.890	−0.057	0.228	0.812	−0.070	0.150	0.656
	λ_{Dassen}	0.175	0.152	0.294	0.221	0.431	0.627	0.453	0.321	0.208
	λ_{Robben}	0.089	0.125	0.504	0.344	0.360	0.377	0.419	0.295	0.205

Table 3.8: Algoa Bay foraging path length and trip duration GLM parameter estimates, standard errors and statistical significance.

(a) GLM A with sardine catch, estimating the year effect directly.

		Foraging path length			Foraging trip duration		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
Catches within 20 nmi of the colony	$\lambda_{\text{St Croix}}$	−0.091	0.124	0.540	−0.162	0.131	0.340
	λ_{Bird}	0.206	0.188	0.388	0.244	0.198	0.343
Catches within 30 nmi of the colony	$\lambda_{\text{St Croix}}$	−0.224	0.435	0.659	−0.507	0.447	0.375
	λ_{Bird}	0.094	0.164	0.624	0.041	0.168	0.831

(b) GLM B with sardine catch, with q denoting sardine November 1+ biomass in strata D–E.

Catches within 20 nmi of the colony	μ	−0.454	0.269	0.143	0.045	0.252	0.864
	$\lambda_{\text{St Croix}}$	−0.042	0.108	0.714	−0.106	0.101	0.337
	λ_{Bird}	0.059	0.084	0.510	0.045	0.078	0.591
Catches within 30 nmi of the colony	μ	−0.526	0.220	0.054	−0.046	0.207	0.830
	$\lambda_{\text{St Croix}}$	0.045	0.360	0.905	−0.333	0.338	0.362
	λ_{Bird}	0.067	0.092	0.493	0.047	0.086	0.602

(c) GLM B with sardine catch, with q denoting sardine May recruit biomass.

Catches within 20 nmi of the colony	μ	−0.016	0.366	0.967	−0.347	0.244	0.205
	$\lambda_{\text{St Croix}}$	−0.162	0.099	0.153	−0.081	0.066	0.270
	λ_{Bird}	0.081	0.101	0.456	0.030	0.068	0.673
Catches within 30 nmi of the colony	μ	−0.022	0.435	0.961	−0.320	0.263	0.269
	$\lambda_{\text{St Croix}}$	−0.282	0.483	0.581	−0.263	0.292	0.403
	λ_{Bird}	0.104	0.128	0.448	0.039	0.077	0.633

Table 3.9: Adult survival GLM parameter estimates, standard errors and statistical significance.

(a) GLM A: estimating the year effect directly.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	λ_{Dassen}	−0.000	0.003	0.931	−0.001	0.002	0.725	−0.002	0.003	0.490
	λ_{Robben}	−0.000	0.002	0.888	−0.002	0.002	0.239	−0.002	0.001	0.341
Catches within 20 nmi of the colony	λ_{Dassen}	0.531	0.918	0.604	−1.786	1.669	0.363	1.063	1.902	0.615
	λ_{Robben}	−0.063	0.479	0.904	0.678	0.833	0.475	−0.391	0.696	0.614
Catches within 30 nmi of the colony	λ_{Dassen}	−0.217	1.168	0.865	−1.640	2.556	0.567	1.850	2.399	0.497
	λ_{Robben}	−0.566	0.765	0.513	0.581	1.044	0.616	0.078	1.259	0.954

(b) GLM B with q denoting November 1+ biomass in strata A–C.

2010 analysis	μ	0.441	0.262	0.137	0.740	0.197	0.007	0.500	0.129	0.006
	λ_{Dassen}	0.366	0.184	0.087	0.269	0.700	0.713	0.889	0.750	0.274
	λ_{Robben}	0.287	0.156	0.108	−0.792	0.438	0.113	−0.305	0.389	0.459
Catches within 20 nmi of the colony	μ	0.521	0.373	0.175	−0.160	0.239	0.510	0.058	0.183	0.754
	λ_{Dassen}	0.334	0.308	0.289	−1.012	1.407	0.479	0.961	1.482	0.523
	λ_{Robben}	0.029	0.148	0.844	0.025	0.259	0.922	0.004	0.304	0.990
Catches within 30 nmi of the colony	μ	0.453	0.412	0.282	−0.214	0.237	0.374	−0.072	0.204	0.727
	λ_{Dassen}	0.324	0.304	0.297	−2.033	1.872	0.288	1.257	1.290	0.339
	λ_{Robben}	0.071	0.185	0.706	0.166	0.297	0.580	0.357	0.402	0.383

Table 3.9: Adult survival GLM parameter estimates (continued).

(c) GLM B with q denoting May recruit biomass.

		Sardine catch			Anchovy catch			Sardine and anchovy catch		
		Estimate	s.e.	t pr.	Estimate	s.e.	t pr.	Estimate	s.e.	t pr.
2010 analysis	μ	3.387	2.811	0.267	0.380	0.440	0.417	0.385	0.328	0.279
	λ_{Dassen}	−0.530	0.833	0.545	−0.274	1.167	0.821	0.560	1.232	0.663
	λ_{Robben}	−0.420	0.683	0.558	−0.867	0.784	0.305	−0.110	0.696	0.878
Catches within 20 nmi of the colony	μ	−0.926	0.977	0.352	0.147	0.226	0.523	0.112	0.185	0.553
	λ_{Dassen}	0.686	0.411	0.108	−0.663	1.386	0.637	0.856	1.488	0.570
	λ_{Robben}	0.234	0.182	0.212	−0.085	0.243	0.730	−0.002	0.287	0.995
Catches within 30 nmi of the colony	μ	−1.509	1.009	0.147	0.134	0.229	0.565	0.021	0.207	0.922
	λ_{Dassen}	0.830	0.397	0.047	−1.642	1.859	0.386	1.068	1.303	0.420
	λ_{Robben}	0.416	0.214	0.064	−0.010	0.285	0.973	0.262	0.379	0.496

Table 3.10: Tallies of positive and negative estimated μ and λ_i parameters listed in Tables 3.4–3.8. The tallies concern GLMs involving (a) fledging success, (b) active and potential nests, (c) foraging behaviour, and (d) all three sets combined. The GLMs include small pelagic fish catches taken within either 20 nautical miles or 30 nautical miles of the island in question (i.e. results from analyses conducted in 2010 are not included in these tallies).

(a) Fledging success GLMs (Robben Island and Dassen Island).

	Sardine	Anchovy	Combined	Overall
All μ	2 : 2	2 : 2	1 : 3	5 : 7
All λ_i	8 : 4	8 : 4	9 : 3	25 : 11
λ_i significant at 15%	0 : 1	3 : 0	2 : 0	5 : 1
λ_i significant at 5%	0 : 0	1 : 0	0 : 0	1 : 0

(b) Active and potential nests GLMs (Robben Island and Dassen Island).

	Sardine	Anchovy	Combined	Overall
All μ	3 : 1	4 : 0	4 : 0	11 : 1
All λ_i	12 : 0	12 : 0	12 : 0	36 : 0
λ_i significant at 15%	4 : 0	4 : 0	10 : 0	18 : 0
λ_i significant at 5%	4 : 0	2 : 0	8 : 0	14 : 0

(c) Foraging GLMs (all cases).

	Robben and Dassen				St Croix and Bird
	Sardine	Anchovy	Combined	Overall	Sardine
All μ	4 : 4	6 : 2	4 : 4	14 : 10	1 : 7
All λ_i	19 : 5	20 : 4	23 : 1	62 : 10	13 : 11
λ_i significant at 15%	0 : 0	2 : 1	2 : 0	4 : 1	0 : 0
λ_i significant at 5%	0 : 0	0 : 0	1 : 0	1 : 0	0 : 0

(d) All Western Cape GLMs.

	Sardine	Anchovy	Combined	Overall
All μ	9 : 7	12 : 4	9 : 7	30 : 18
All λ_i	39 : 9	40 : 8	44 : 4	123 : 21
λ_i significant at 15%	4 : 1	9 : 1	14 : 0	27 : 2
λ_i significant at 5%	4 : 0	3 : 0	9 : 0	16 : 0

Table 3.11: Standard deviation of fledging success GLM residuals with confidence intervals.

(a) 2010 analysis.

Model		n	X	σ	95% CI		CV
GLM A	sardine	26	0.077	0.054	0.042	0.073	15%
	anchovy	26	0.016	0.025	0.020	0.034	15%
	combined	26	0.039	0.039	0.030	0.052	15%
GLM B	sardine	26	1.907	0.271	0.211	0.365	15%
q – November	anchovy	26	1.739	0.259	0.202	0.349	15%
	combined	26	1.779	0.262	0.204	0.353	15%
GLM B	sardine	26	1.901	0.270	0.211	0.365	15%
q – May	anchovy	26	2.018	0.279	0.217	0.376	15%
	combined	26	2.085	0.283	0.221	0.382	15%

(b) 2013 analysis, catches within 20 nautical miles.

GLM A	sardine	31	0.081	0.051	0.041	0.067	13%
	anchovy	31	0.076	0.049	0.039	0.065	13%
	combined	31	0.072	0.048	0.038	0.063	13%
GLM B	sardine	31	2.002	0.254	0.202	0.333	13%
q – November	anchovy	31	1.990	0.253	0.201	0.332	13%
	combined	31	1.923	0.249	0.198	0.327	13%
GLM B	sardine	31	2.008	0.255	0.202	0.334	13%
q – May	anchovy	31	2.369	0.276	0.220	0.363	13%
	combined	31	2.284	0.271	0.216	0.356	13%

(c) 2013 analysis, catches within 30 nautical miles.

GLM A	sardine	31	0.105	0.058	0.046	0.076	13%
	anchovy	31	0.052	0.041	0.033	0.054	13%
	combined	31	0.065	0.046	0.036	0.060	13%
GLM B	sardine	31	2.075	0.259	0.206	0.339	13%
q – November	anchovy	31	1.987	0.253	0.201	0.332	13%
	combined	31	1.909	0.248	0.197	0.325	13%
GLM B	sardine	31	2.118	0.261	0.208	0.343	13%
q – May	anchovy	31	2.364	0.276	0.219	0.362	13%
	combined	31	2.270	0.271	0.215	0.355	13%

Table 3.12: Standard deviation of nest GLM residuals with confidence intervals.

(a) 2010 analysis.

Model		n	X	σ	95% CI		CV
GLM A	sardine	21	2.491	0.344	0.262	0.482	17%
	anchovy	21	1.135	0.232	0.177	0.325	17%
	combined	21	1.458	0.264	0.200	0.369	17%
GLM B	sardine	21	14.296	0.825	0.627	1.155	17%
q – November	anchovy	21	20.754	0.994	0.755	1.391	17%
	combined	21	16.966	0.899	0.683	1.258	17%
GLM B	sardine	21	13.664	0.807	0.613	1.129	17%
q – May	anchovy	21	15.162	0.850	0.646	1.189	17%
	combined	21	11.383	0.736	0.559	1.030	17%

(b) 2013 analysis, catches within 20 nautical miles.

GLM A	sardine	27	4.272	0.398	0.311	0.533	15%
	anchovy	27	1.704	0.251	0.197	0.337	15%
	combined	27	1.932	0.268	0.209	0.358	15%
GLM B	sardine	27	20.556	0.873	0.683	1.169	15%
q – November	anchovy	27	25.389	0.970	0.759	1.299	15%
	combined	27	19.601	0.852	0.667	1.142	15%
GLM B	sardine	27	21.078	0.884	0.692	1.184	15%
q – May	anchovy	27	19.282	0.845	0.661	1.132	15%
	combined	27	15.081	0.747	0.585	1.001	15%

(c) 2013 analysis, catches within 30 nautical miles.

GLM A	sardine	27	4.871	0.425	0.332	0.569	15%
	anchovy	27	3.234	0.346	0.271	0.464	15%
	combined	27	3.086	0.338	0.265	0.453	15%
GLM B	sardine	27	20.062	0.862	0.675	1.155	15%
q – November	anchovy	27	28.537	1.028	0.805	1.378	15%
	combined	27	19.888	0.858	0.672	1.150	15%
GLM B	sardine	27	20.269	0.866	0.678	1.161	15%
q – May	anchovy	27	21.977	0.902	0.706	1.209	15%
	combined	27	16.431	0.780	0.611	1.045	15%

Table 3.13: Standard deviation of foraging path length GLM residuals with confidence intervals.

(a) Dassen Island and Robben Island, catches within 20 nautical miles.

Model		n	X	σ	95% CI		CV
GLM A	sardine	11	0.006	0.024	0.016	0.039	24%
	anchovy	11	0.010	0.030	0.021	0.049	24%
	combined	11	0.017	0.040	0.028	0.065	24%
GLM B	sardine	11	0.365	0.182	0.126	0.296	24%
q – November	anchovy	11	0.850	0.278	0.193	0.451	24%
	combined	11	0.839	0.276	0.191	0.449	24%
GLM B	sardine	11	1.125	0.320	0.222	0.519	24%
q – May	anchovy	11	0.856	0.279	0.193	0.453	24%
	combined	11	0.930	0.291	0.201	0.472	24%

(b) Dassen Island and Robben Island, catches within 30 nautical miles.

GLM A	sardine	11	0.003	0.016	0.011	0.026	24%
	anchovy	11	0.032	0.054	0.037	0.088	24%
	combined	11	0.017	0.039	0.027	0.063	24%
GLM B	sardine	11	0.354	0.179	0.124	0.291	24%
q – November	anchovy	11	1.025	0.305	0.211	0.496	24%
	combined	11	0.869	0.281	0.195	0.457	24%
GLM B	sardine	11	1.106	0.317	0.220	0.515	24%
q – May	anchovy	11	1.096	0.316	0.219	0.513	24%
	combined	11	0.978	0.298	0.207	0.484	24%

(c) St Croix Island and Bird Island, catches within 20 nautical miles.

GLM A		11	0.041	0.061	0.042	0.099	24%
GLM B	q – November	11	0.172	0.125	0.087	0.203	24%
GLM B	q – May	11	0.254	0.152	0.105	0.247	24%

(d) Foraging path length, catches within 30 nautical miles.

GLM A		11	0.048	0.066	0.046	0.107	24%
GLM B	q – November	11	0.173	0.125	0.087	0.204	24%
GLM B	q – May	11	0.338	0.175	0.121	0.285	24%

Table 3.14: Standard deviation of foraging trip duration GLM residuals with confidence intervals.

(a) Dassen Island and Robben Island, catches within 20 nautical miles.

Model		n	X	σ	95% CI		CV
GLM A	sardine	11	0.109	0.100	0.069	0.162	24%
	anchovy	11	0.032	0.054	0.037	0.088	24%
	combined	11	0.111	0.100	0.070	0.163	24%
GLM B q – November	sardine	11	0.364	0.182	0.126	0.296	24%
	anchovy	11	0.349	0.178	0.123	0.289	24%
	combined	11	0.276	0.159	0.110	0.257	24%
GLM B q – May	sardine	11	0.442	0.200	0.139	0.326	24%
	anchovy	11	0.349	0.178	0.123	0.289	24%
	combined	11	0.265	0.155	0.108	0.252	24%

(b) Dassen Island and Robben Island, catches within 30 nautical miles.

GLM A	sardine	11	0.133	0.110	0.076	0.179	24%
	anchovy	11	0.123	0.106	0.073	0.172	24%
	combined	11	0.133	0.110	0.076	0.178	24%
GLM B q – November	sardine	11	0.366	0.182	0.126	0.296	24%
	anchovy	11	0.528	0.219	0.152	0.356	24%
	combined	11	0.401	0.191	0.132	0.310	24%
GLM B q – May	sardine	11	0.450	0.202	0.140	0.328	24%
	anchovy	11	0.549	0.223	0.155	0.363	24%
	combined	11	0.398	0.190	0.132	0.309	24%

(c) St Croix Island and Bird Island, catches within 20 nautical miles.

GLM A		11	0.046	0.064	0.045	0.105	24%
GLM B	q – November	11	0.151	0.117	0.081	0.190	24%
GLM B	q – May	11	0.113	0.101	0.070	0.165	24%

(d) Foraging trip duration, catches within 30 nautical miles.

GLM A		11	0.051	0.068	0.047	0.110	24%
GLM B	q – November	11	0.153	0.118	0.082	0.191	24%
GLM B	q – May	11	0.123	0.106	0.073	0.172	24%

Table 3.15: Standard deviation of adult survival GLM residuals with confidence intervals.

(a) 2010 analysis.

Model		n	X	σ	95% CI		CV
GLM B	sardine	26	1.907	0.271	0.211	0.365	15%
q – November	anchovy	26	1.739	0.259	0.202	0.349	15%
	combined	26	1.779	0.262	0.204	0.353	15%
GLM B	sardine	26	1.901	0.270	0.211	0.365	15%
q – May	anchovy	26	2.018	0.279	0.217	0.376	15%
	combined	26	2.085	0.283	0.221	0.382	15%

(b) 2013 analysis, catches within 20 nautical miles.

GLM A	sardine	31	0.081	0.051	0.041	0.067	13%
	anchovy	31	0.076	0.049	0.039	0.065	13%
	combined	31	0.072	0.048	0.038	0.063	13%
GLM B	sardine	31	2.002	0.254	0.202	0.333	13%
q – November	anchovy	31	1.990	0.253	0.201	0.332	13%
	combined	31	1.923	0.249	0.198	0.327	13%
GLM B	sardine	31	2.008	0.255	0.202	0.334	13%
q – May	anchovy	31	2.369	0.276	0.220	0.363	13%
	combined	31	2.284	0.271	0.216	0.356	13%

(c) 2013 analysis, catches within 30 nautical miles.

GLM A	sardine	31	0.105	0.058	0.046	0.076	13%
	anchovy	31	0.052	0.041	0.033	0.054	13%
	combined	31	0.065	0.046	0.036	0.060	13%
GLM B	sardine	31	2.075	0.259	0.206	0.339	13%
q – November	anchovy	31	1.987	0.253	0.201	0.332	13%
	combined	31	1.909	0.248	0.197	0.325	13%
GLM B	sardine	31	2.118	0.261	0.208	0.343	13%
q – May	anchovy	31	2.364	0.276	0.219	0.362	13%
	combined	31	2.270	0.271	0.215	0.355	13%

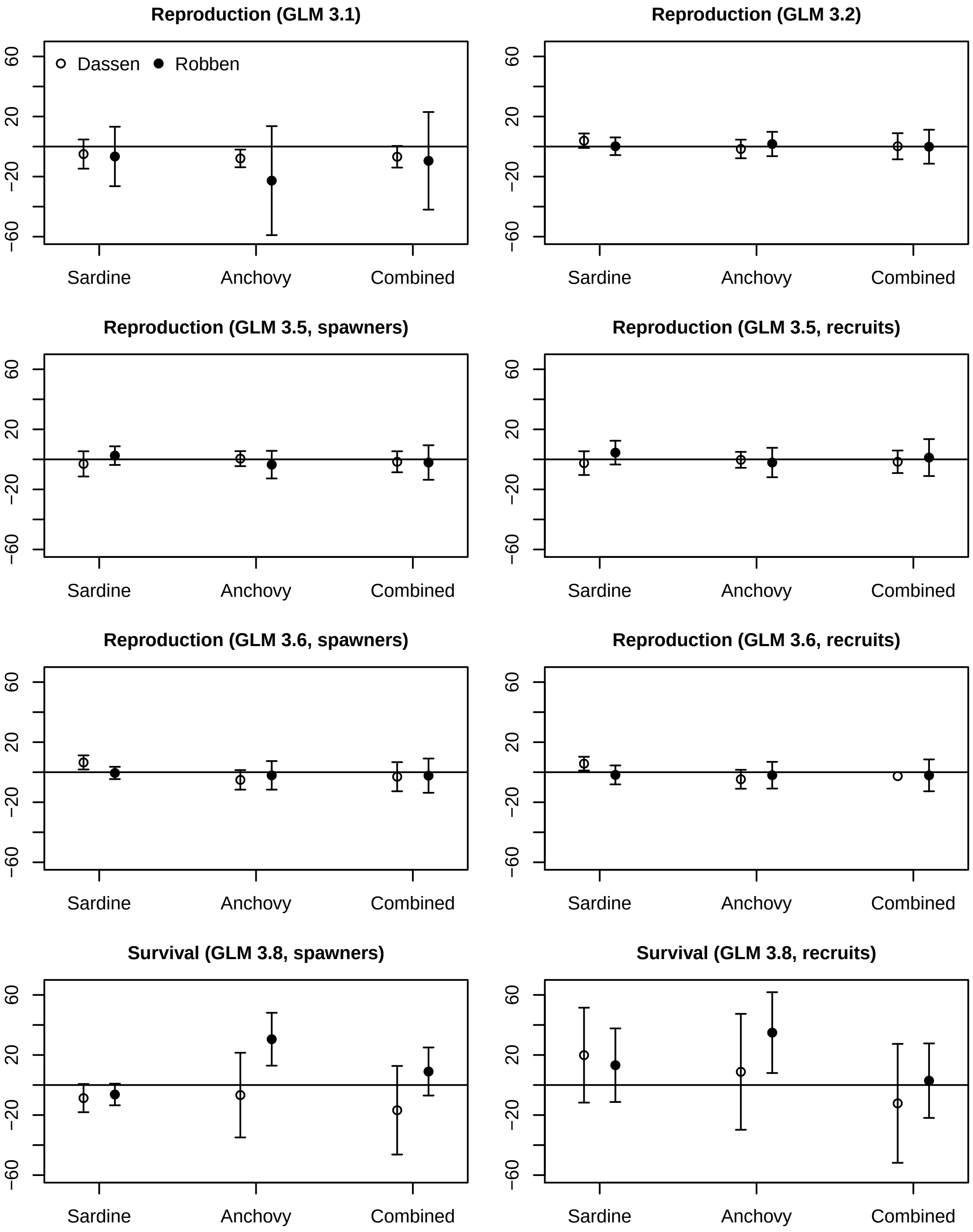

Figure 3.1: Plots of growth rate (in % per year) change projected for suspending fishing, with 95% confidence intervals, corresponding to the horizontal blocks in Table 3.1. The GLM number above each frame refers to the corresponding equation in Section 3.2.1. In each case, growth rates are given for Dassen Island and then Robben Island for the GLMs relating to catches of sardine, anchovy, and both species combined.

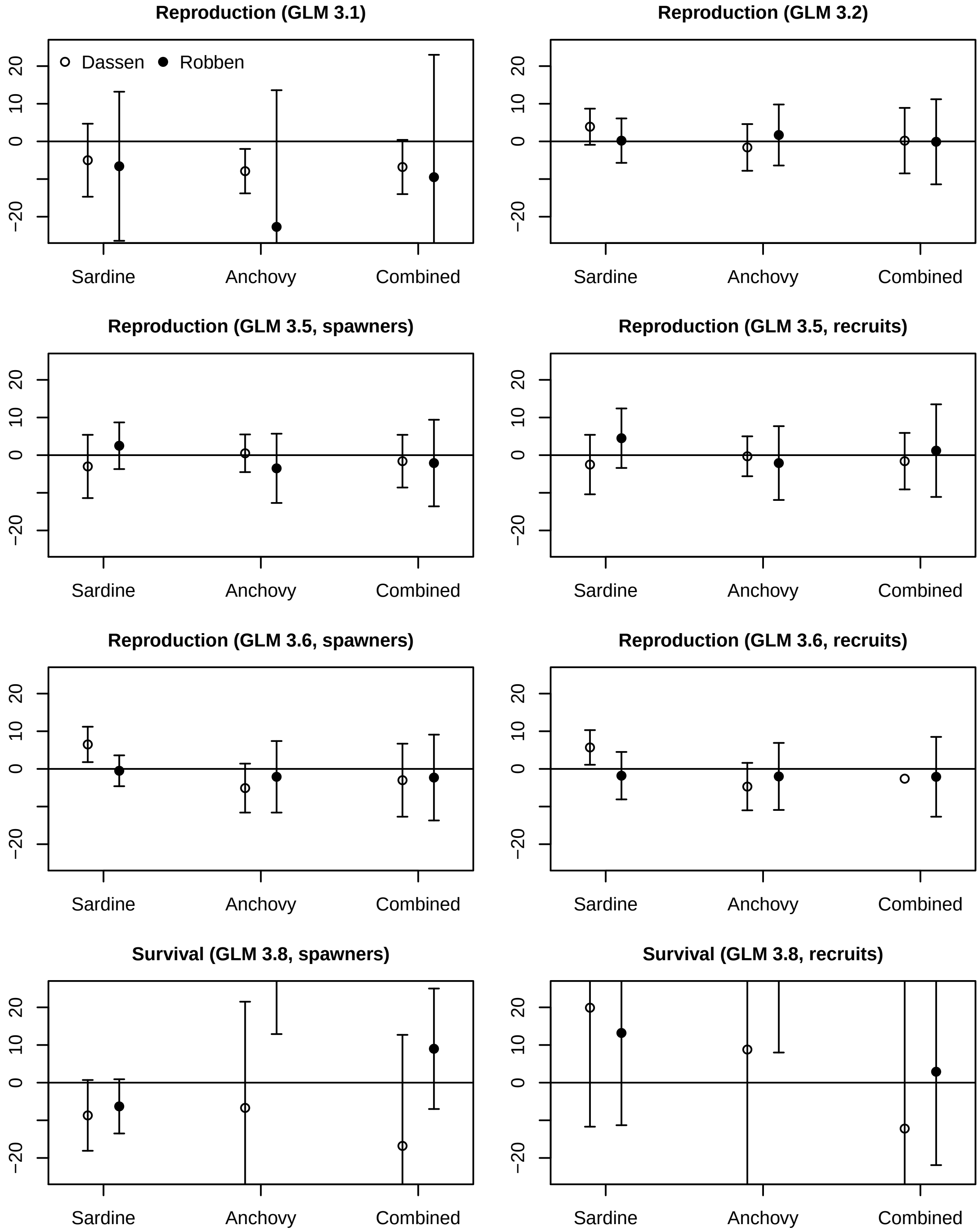

Figure 3.2: The growth rates and 95% confidence intervals from Figure 3.1 redrawn on a larger vertical scale.

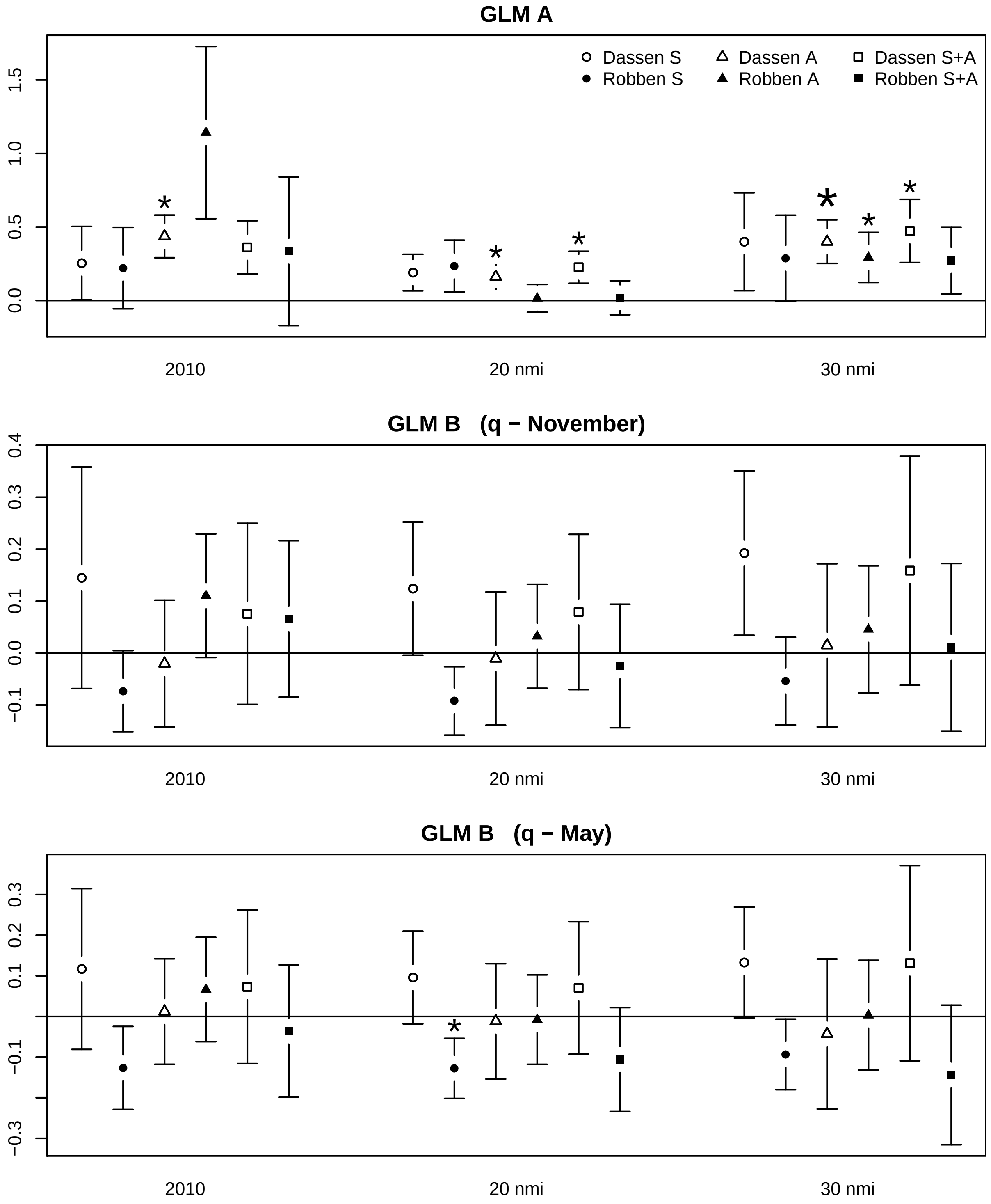

Figure 3.3: Fledging success GLM estimates and bars indicating plus and minus one standard error of the parameters λ_{Dassen} (light shapes) and λ_{Robben} (dark shapes). Circles, triangles and squares denote sardine, anchovy, and the combination respectively. Large stars indicate significance at 5% and small stars indicate significance at 15%.

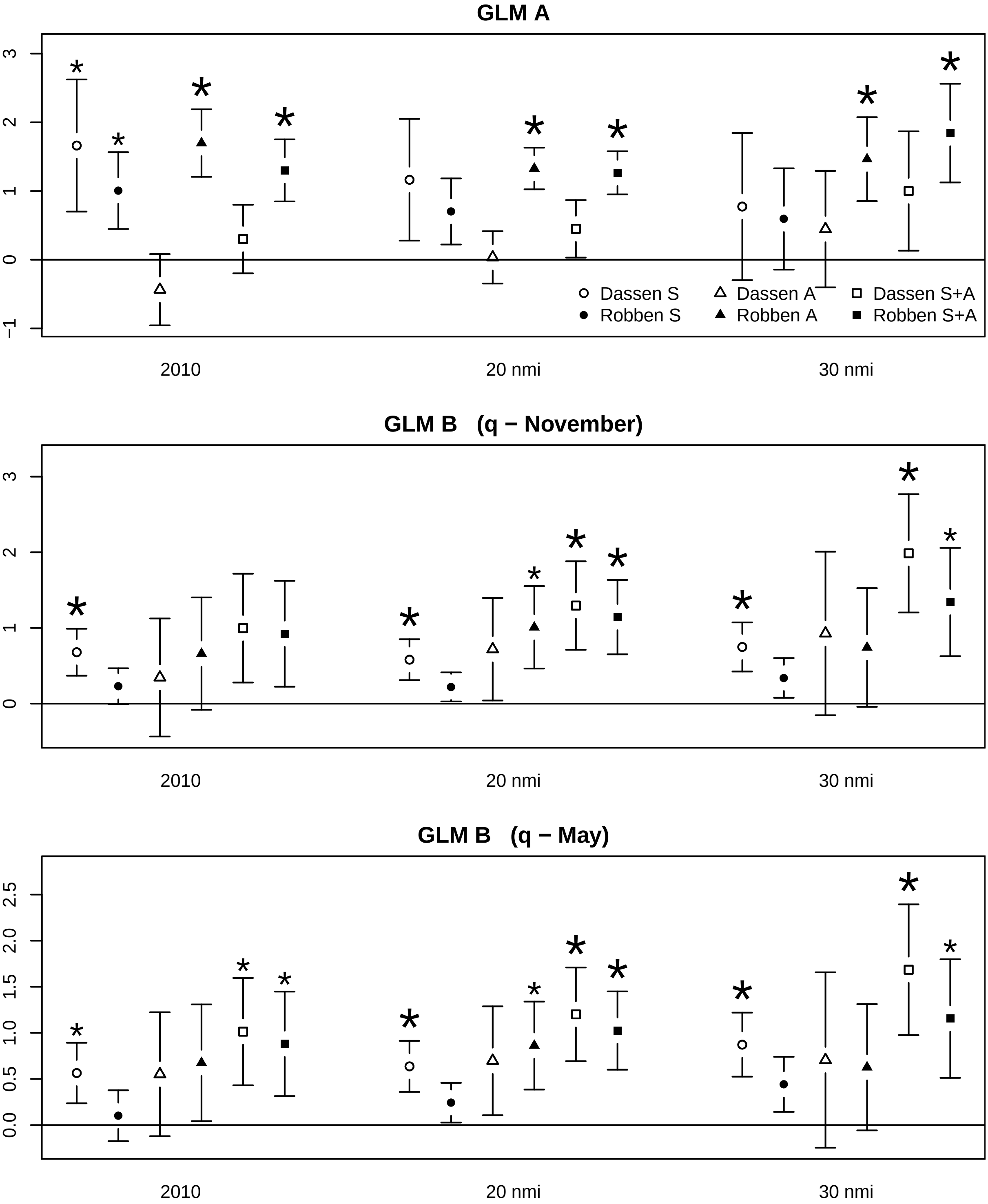

Figure 3.4: Active and potential nests GLM estimates and one standard error bars for the λ_i parameters.

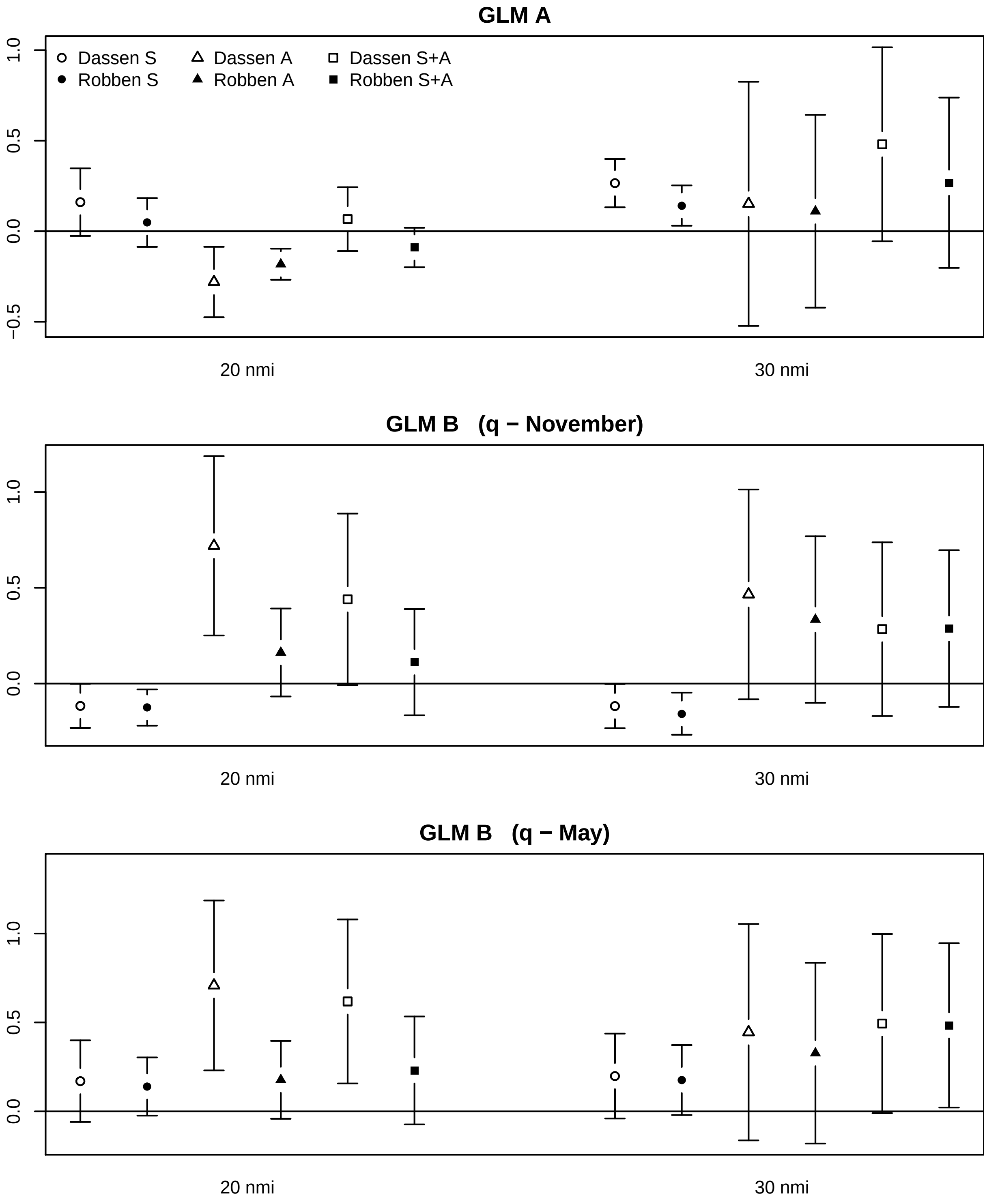

Figure 3.5: Western Cape foraging path length GLM estimates and one standard error bars for the λ_i parameters.

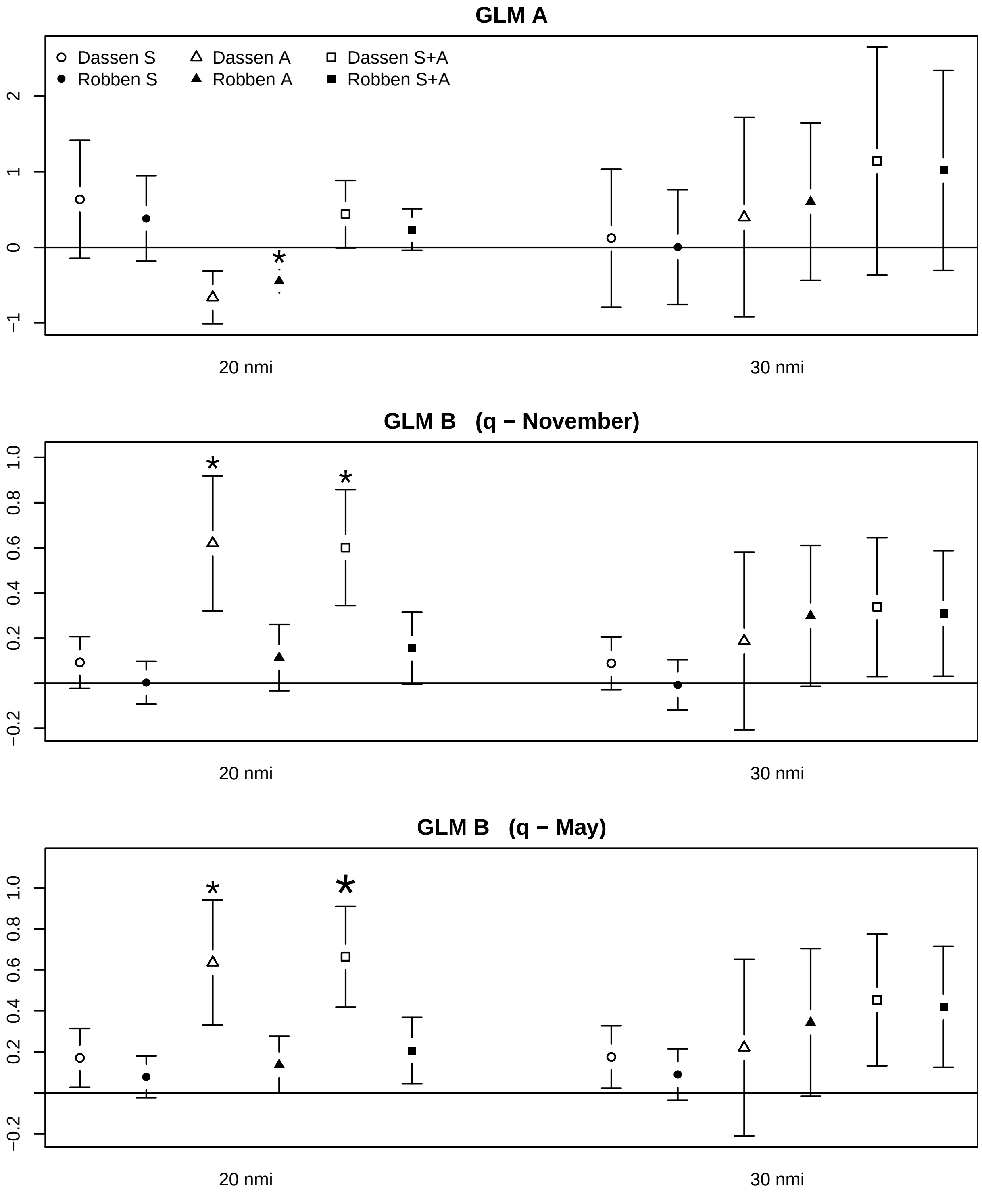

Figure 3.6: Western Cape foraging trip duration GLM estimates and one standard error bars for the λ_i parameters.

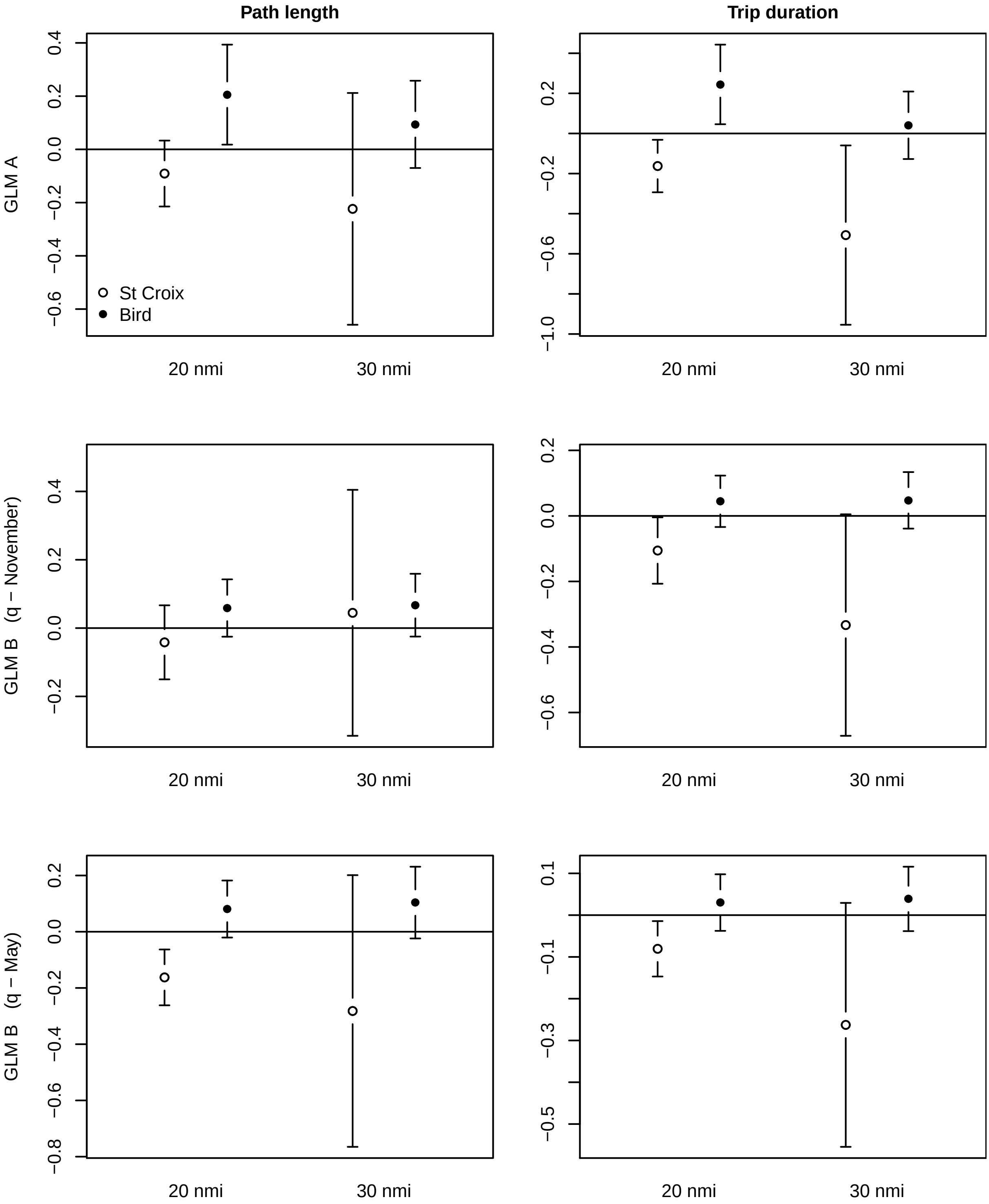

Figure 3.7: Eastern Cape foraging behaviour GLM estimates and one standard error bars for the parameters $\lambda_{\text{St Croix}}$ (light circles) and λ_{Bird} (dark circles). Results consider only sardine catches and biomass/recruitment estimates.

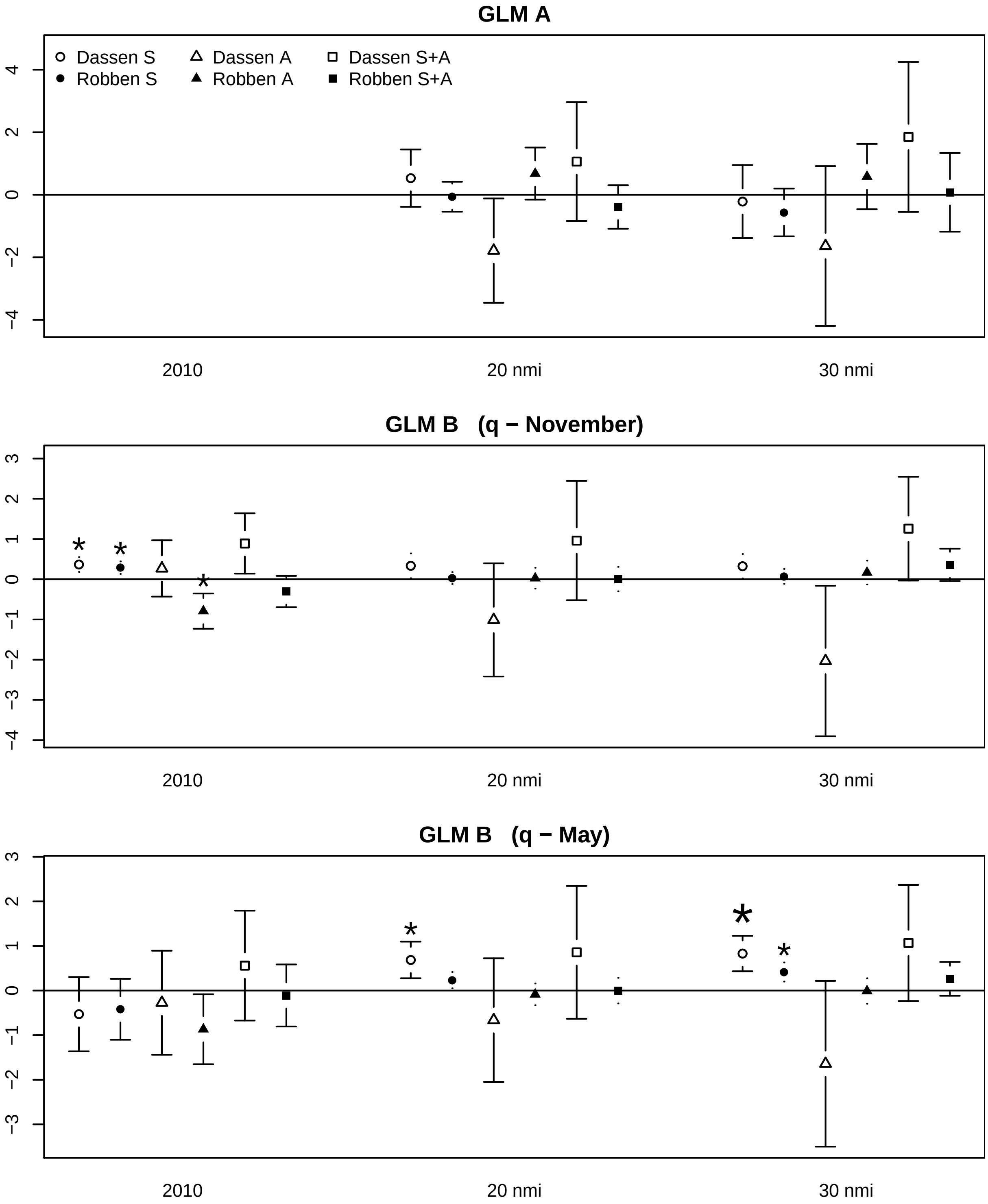

Figure 3.8: Adult survival GLM estimates and one standard error bars for the λ_i parameters.

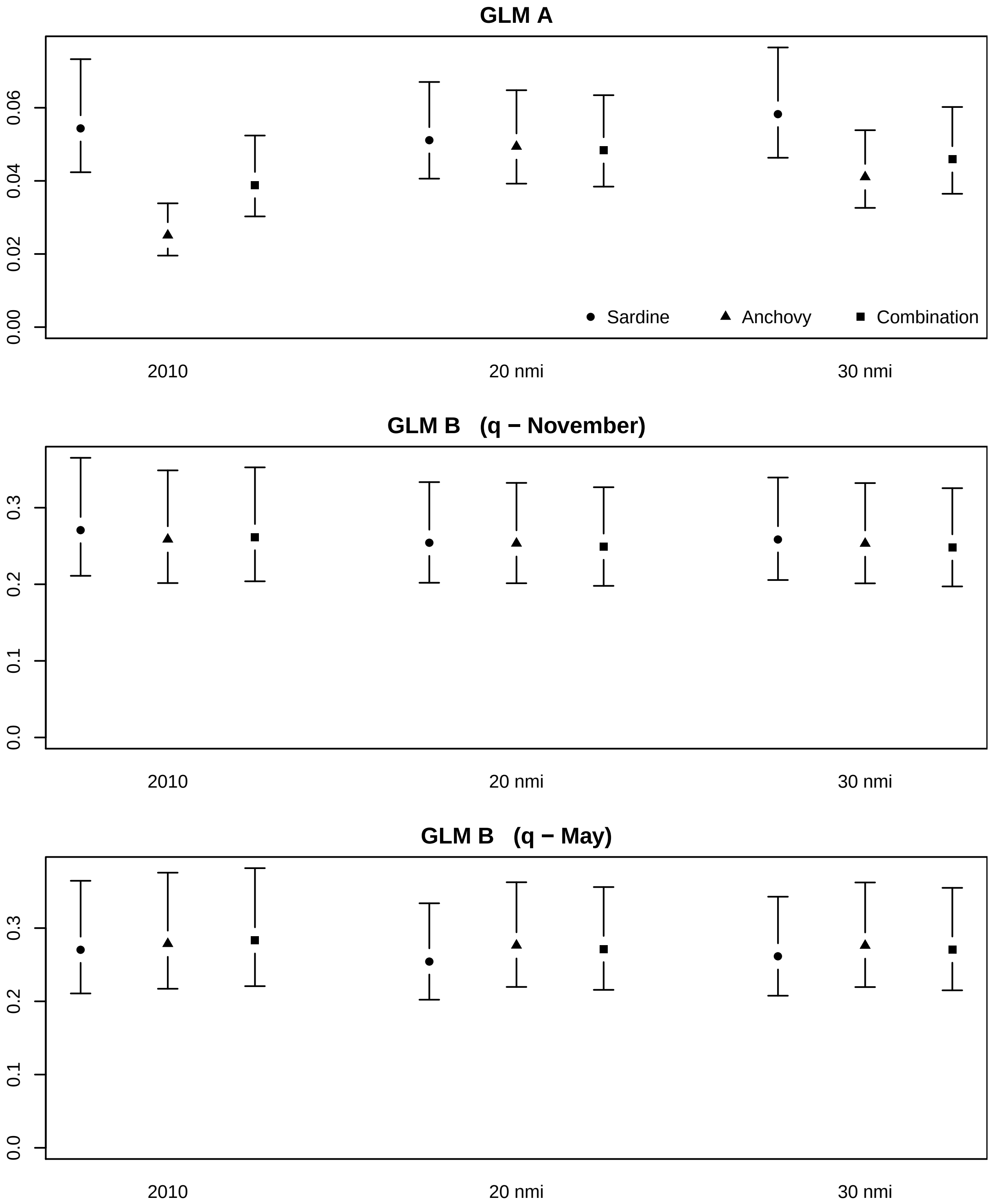

Figure 3.9: Dassen Island and Robben Island fledging success GLM standard deviation of the residuals and 95% confidence intervals.

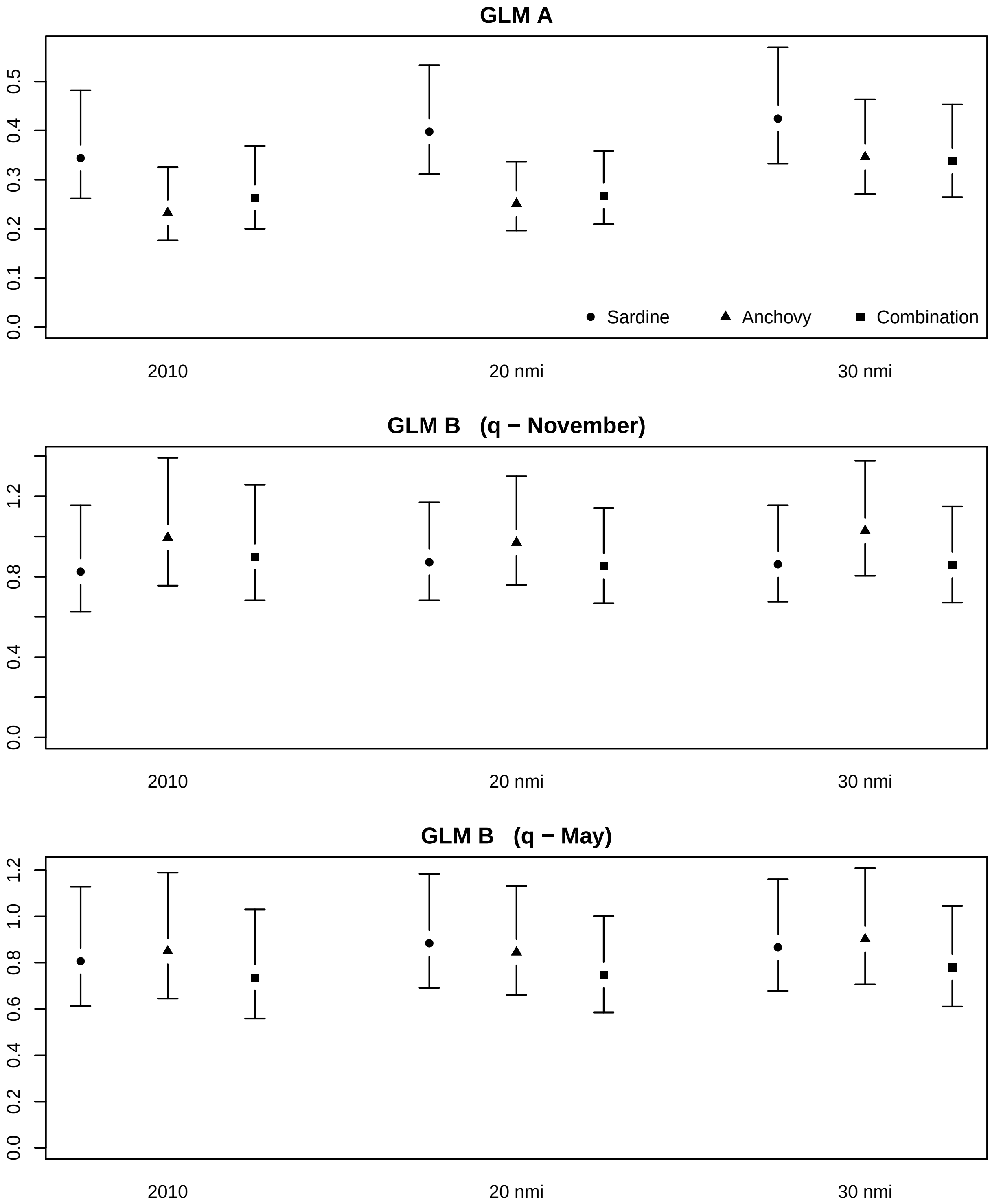

Figure 3.10: Dassen Island and Robben Island active nest proportion GLM standard deviation of the residuals and 95% confidence intervals.

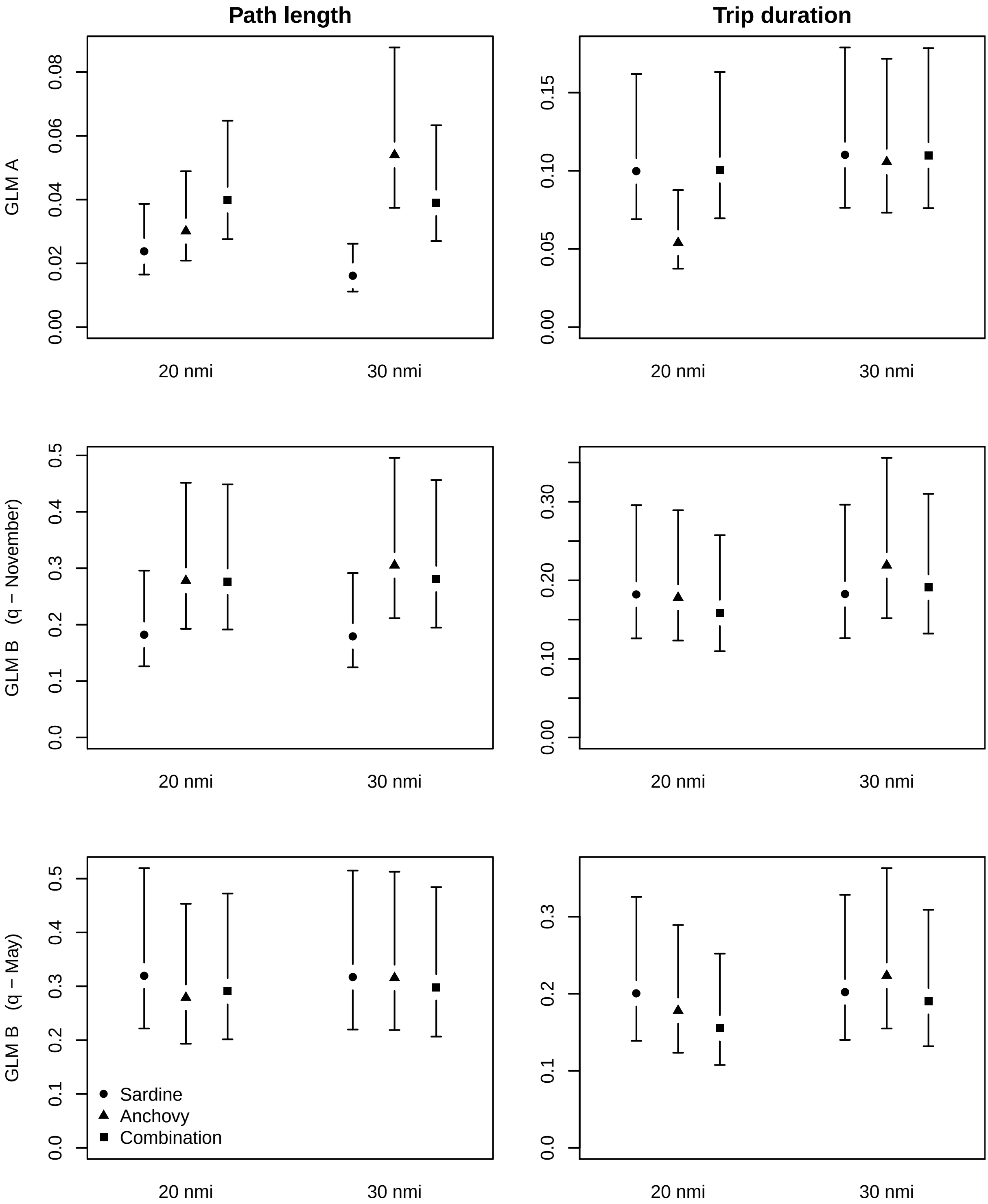

Figure 3.11: Dassen Island and Robben Island foraging behaviour GLM standard deviation of the residuals and 95% confidence intervals.

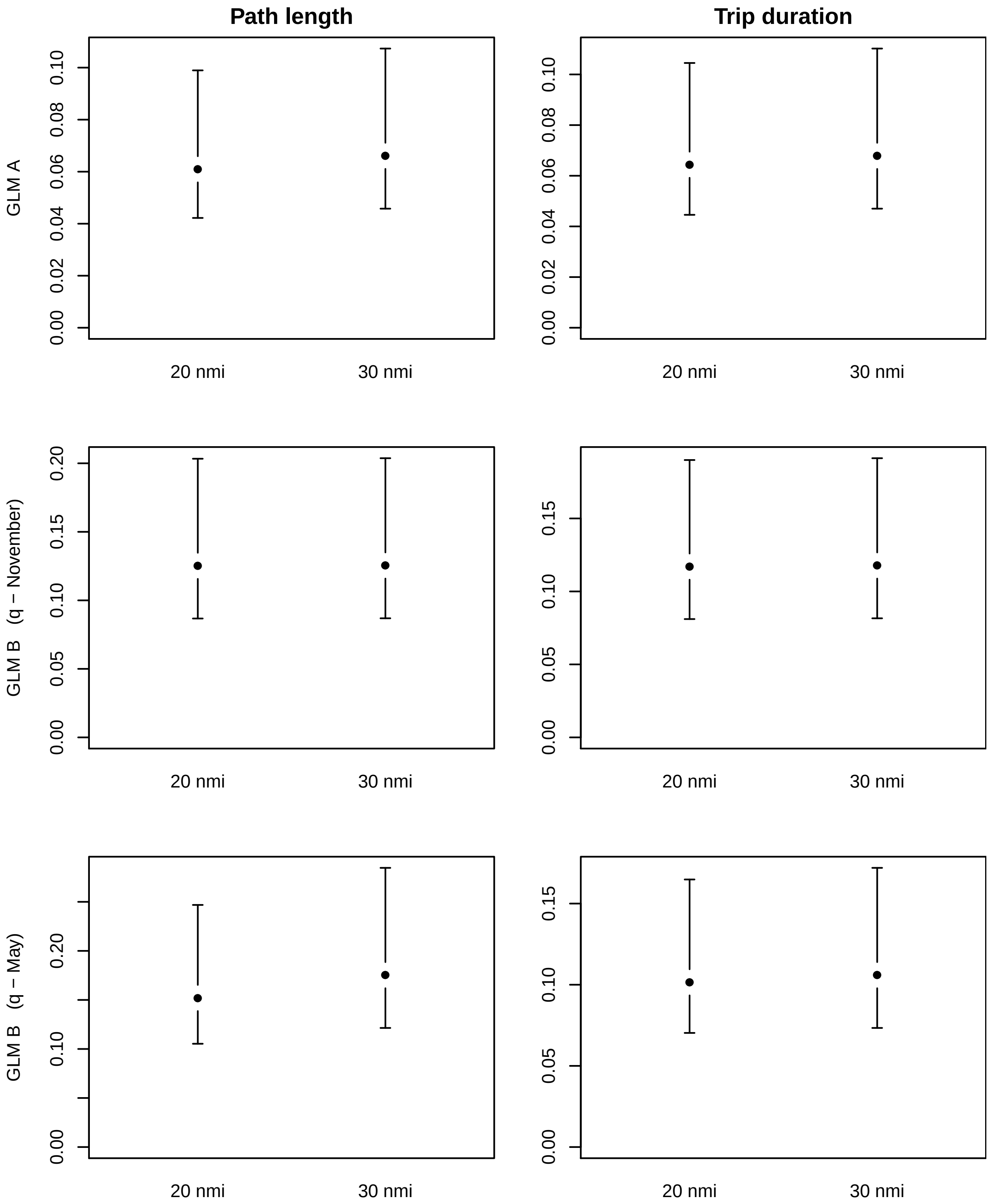

Figure 3.12: St Croix Island and Bird Island foraging behaviour GLM standard deviation of the residuals and 95% confidence intervals. Results involve only sardine catches and biomass/recruitment estimates.

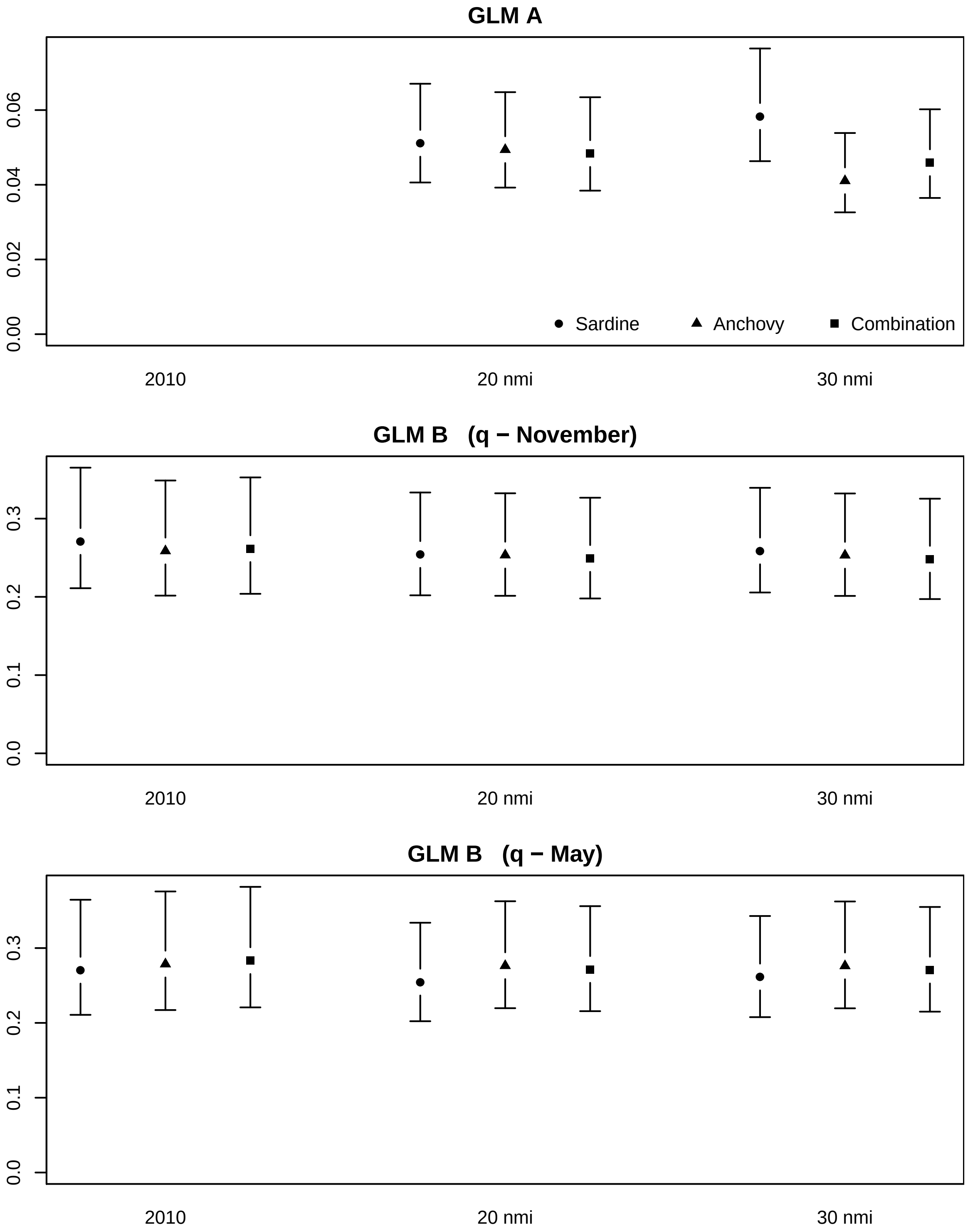

Figure 3.13: Dassen Island and Robben Island adult survival GLM standard deviation of the residuals and 95% confidence intervals.

Chapter 4

Penguin–fish interaction model

This chapter describes a population model for the Robben Island penguin colony. The primary purpose of the model is to provide insight into penguin population dynamics so that projections of abundance can be effected under different levels of fishing. A key feature of the model is the relationship between penguin adult survival and sardine abundance. This was found to explain penguin dynamics much better than a number of other possible relationships between penguin demographics and the abundance of small pelagic fish. This enables the evaluation of the influence that future sardine biomass levels may have on the penguin population trend. Expected sardine biomass, in turn, is affected by fishery catches. This enables the evaluation of the performance of the small pelagic operational management procedure in terms of the effect of fishing on penguin abundance through depletion of forage fish (see Chapter 5).

Rather than attempting to construct a model for the total abundance of African penguins, or perhaps of the Western Cape population, the Robben Island subpopulation has been chosen for two main reasons: the length of the moult time-series and the availability of tag-recapture data. The time-series of moult counts for this colony is complete from 1988. Although Dassen Island hosted a larger penguin colony until very recently, moult counts are not available for that colony for years earlier than 1995. Also, the comparability of Dassen Island moult counts from 2008 onwards to the rest of the time-series is questionable (see Section 2.5.2). Furthermore, a large proportion of African penguin tag-recapture records relate to Robben Island birds.

As the Robben Island colony is clearly not a closed population, immigration must be considered. As the tag-recapture data are independent of the moult count time-series, the inclusion of these data in the model allows for the distinction to be made between immigration and increased adult survival.

The key components of the model are the penguin population dynamics (Section 4.1), the population model including the relationship between penguin annual adult mortality and sardine biomass (Section 4.2), and parameter estimation effected through fitting to moult counts and tag-recapture data (Section 4.3). Results are presented in Section 4.3.4 and key points are discussed in Section 4.4.

4.1 Basic dynamics

The model considers the number of female penguins $N_{y,a}$ of age a at the start (1 January) of year y at Robben Island. The initial population size (at the start of year $y_0 = 1988$) is N_0 and its age structure is taken to correspond to steady change:

$$N_{1988,a} = \begin{cases} N_0\, \mathrm{e}^{-a\lambda} & \text{for } 1 \le a < A \\ \dfrac{N_0\, \mathrm{e}^{-a\lambda}}{1 - \mathrm{e}^{-\lambda}} & \text{for } a = A \end{cases} \tag{4.1}$$

where A is the plus-group age, taken here to be $A = 5$. Both N_0 and λ are parameters whose values are estimated.

The following equations describe the population trajectory:

$$N_{y+1,a} = \begin{cases} \dfrac{1}{2} H_y \exp\left(-M_y^{4/12}\right)\left(1 - p_y^{\mathrm{oil}}\right) \sum\limits_{a=a^*}^{A} N_{y,a} & \text{if } a = 1 \\ N^*_{y,a-1} \exp\left(-M_y\right) & \text{if } a = 2 \\ N^*_{y,a-1} \exp\left(-M_y\right) + I_y & \text{if } a = 3 \\ N^*_{y,a-1} \exp\left(-M_y\right) & \text{if } 4 \le a < A \\ \left(N^*_{y,a-1} + N^*_{y,a}\right) \exp\left(-M_y\right) & \text{if } a = A \end{cases} \tag{4.2}$$

where:

H_y is the annual reproductive success (number of chicks per mature female reaching 1 January of the year following birth, where 50% of these chicks are assumed to be female),

M_y is the adult (post 1 January of the first year of life) annual mortality rate in year y, taken to the power $4/12$ in the equation for $a = 1$ since the peak of the breeding season is assumed to be on 1 May (see Figure 4.1),

p_y^{oil} is the proportion of chicks estimated to have died as a result of a major oil spill in year y,

a^* is the age at which the penguins first attempt to breed (taken here to be $a^* = 4$),

I_y is the number of penguins (all assumed to be of age 3) immigrating to Robben Island in year y (investigations allowing more flexible variation over time suggested that it is appropriate, given estimation variance consideration (see Section 4.2.4 following), to estimate this as four constant levels for the periods 1989–1990, 1991–1993, 1994–1996, and 1997–1999),

$N_{y,a}^*$ is the number of penguins in year y of age a which survive the major oil spills:

$$N_{y,a}^* = N_{y,a} S_y^{\mathrm{oil}} \tag{4.3}$$

where:

$$S_y^{\mathrm{oil}} = 1 - \frac{N_y^{\mathrm{oil}}}{\exp\left(-M_y^{m_j/12}\right) \sum\limits_{a=1}^{A} N_{y,a}} \tag{4.4}$$

N_y^{oil} is the number of juvenile and adult penguins estimated to have died as a result of oiling in year y, and

m_y is the month in which the oil spill occurred in year y.

Table 2.6 lists model inputs related to the major oil spills. Parameter values which are fixed on input to the model are given in Table 4.1. Sensitivity of projected penguin abundances to variations of these values is explored in Section 5.5.

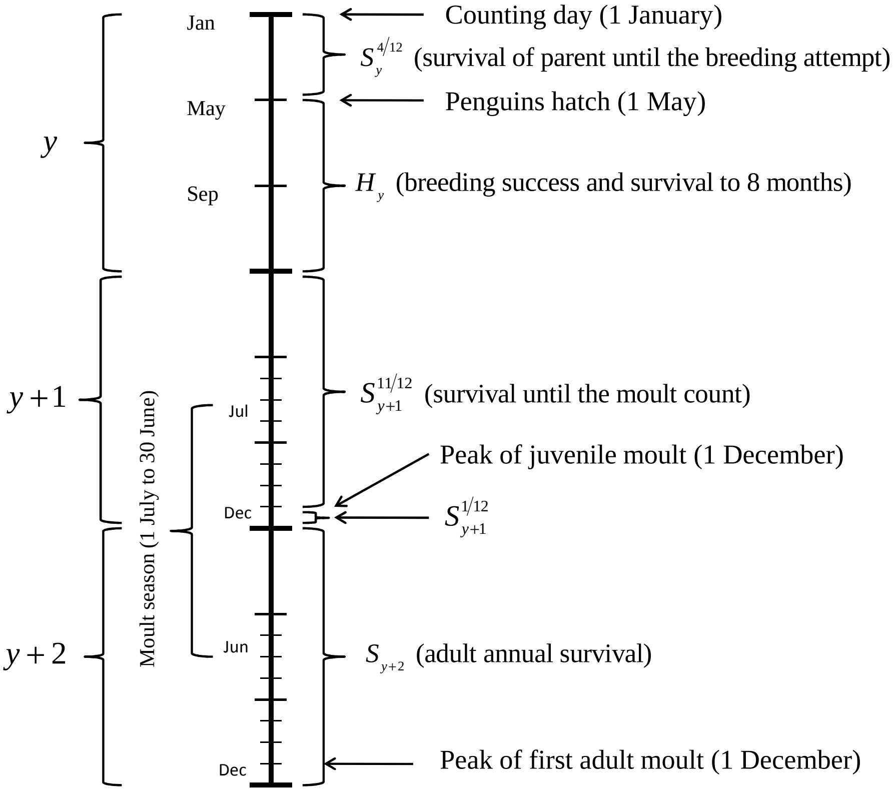

Figure 4.1: A time-line of the first years of the life of a penguin. As the peak of the breeding season is in autumn, hatching is assumed to take place on 1 April. Most juvenile penguins moult into adult plumage at the end of the following year. The first adult moult usually takes place around the beginning of the following December, in the third year of a penguin's life. As most penguins moult during the spring and summer months, for the purpose of integrating the moult counts the annual moult season is taken to run from 1 July until 30 June the following year.

4.1.1 Annual adult mortality

Adult mortality is assumed to be age-independent. Note that the mortality rate M_y does not include loss of penguins as a result of the major oil spills, while the total survival rate S_y, defined as:

$$S_y = \exp\left(-M_y\right) S_y^{\text{oil}} \tag{4.5}$$

includes both natural mortality and oil-induced mortality.

4.1.2 Age at first breeding

In a study at Robben Island over the period 1995–1999, Whittington *et al.* (2005a) recorded the ages at which penguins which had been banded as chicks were first observed breeding. Their results indicated that 32% were breeding by age 3, 57% by age 4, and 89% by age 5. It is possible that the first breeding attempt of some penguins may have been missed, so that the true percentages may be higher than those recorded. These figures are similar to those obtained from an earlier Robben Island study (Crawford *et al.* 1999), at other African penguin colonies (Randall 1983), and in studies of related penguin species.

The choice here for the age at which penguins enter the breeding population in the model ($a^* = 4$) reflects the median of the observed ages. Sensitivity to this choice is checked in Section 5.5. Note that this is the age at which the penguins become *potential* breeders in the model, and no explicit assumptions are made about the proportion of pairs which actually attempt breeding each season. While it has been suggested that this proportion may be related to pelagic biomass (Crawford *et al.* 1999), it seems unlikely that the inclusion of such a relationship would be of much value in this model. The reason is that the annual reproductive success H_y provides a measure of the composite effect of the proportion which breed, fledging success, and juvenile survival. These factors are difficult to separate because data on juvenile survival are difficult to obtain.

4.2 Population model

Both the annual adult survival rate S_y and the annual reproductive success H_y are assumed to depend on some function of prey biomass (the deterministic effect), but to be influenced also by some noise (random effects). For reproductive success, the estimates are drawn from a beta distribution which ensures that biologically plausible bounds are respected. For adult survival, the alternative approach below was developed and has been found to work satisfactorily.

Adult survival depends on the normalized annual biomass levels $B_{S,y}$ determined from surveys, where the time series I_S is some function of the sardine and anchovy November 1+ biomass and

May recruit biomass survey results for particular spatial regions:

$$B_{S,y} = I_{S,y} / \max\{I_S\} \tag{4.6}$$

In the same way, reproductive success depends on a similar index of biomass level $B_{H,y}$:

$$B_{H,y} = I_{H,y} / \max\{I_H\} \tag{4.7}$$

In the base case model implemented here, I_S is taken to be the sardine 1+ biomass west of Cape Agulhas estimated in the November survey (Figure 4.2). The series I_H is taken to be the anchovy recruit biomass west of Cape Infanta estimated in the May survey (Figure 4.3). These choices seem biologically reasonable for the following reasons (Moseley *et al.* 2011):

(a) before and after moulting (summer), penguins are thought to fatten on sardine, gaining condition in preparation for breeding, and

(b) during the breeding season (winter), the fish caught for provisioning chicks are predominately anchovy.

Furthermore, a correlation analysis of various pelagic survey time-series with penguin abundance estimates showed that the sardine 1+ biomass survey best reflected the rapid decrease in penguin numbers since 2003. Anchovy biomass remained high during this period. The selection of November survey strata to those west of Cape Agulhas is appropriate considering the foraging range of non-breeding penguins which spend several weeks at a time at sea. Although breeding penguins have a limited foraging range as they must return to their nests every day or two, the choice of the anchovy recruit biomass series west of Cape Infanta is appropriate for the reason that most of the fish covered by the survey are thought to migrate past Robben Island from West Coast spawning grounds during autumn and winter (Hutchings 1992).

4.2.1 Adult mortality

Annual adult penguin natural mortality M_y is assumed to depend on prey abundance $B_{S,y}$, modelled as follows:

$$M_y = M_{\min} + f_S\left(B_{S,y}\right) \mathrm{e}^{X_y} \tag{4.8}$$

Note that M_y does not include any mortality due to the major oil spills (see equations (4.2)–(4.5)). The $M_{\min}$ term is included to impose a biologically plausible lower bound on the mortality rate, set here to be $M_{\min} = 0.04$. (Sensitivity to this value of $M_{\min}$ is checked in Section 5.5.) The random effects[1] X_y are distributed as $N\left(0, \sigma_y^2\right)$ with:

$$\sigma_y = \sqrt{\exp\left[\tilde{\sigma}/f_S\left(B_{S,y}\right)\right]^2 - 1} \tag{4.9}$$

Thus there is a lognormal random effect, but since the σ_y depend on the biomass $B_{S,y}$, the M_y distributions will all have exactly the same standard deviation. This is considered appropriate because then the data related to each year receive roughly equal weighting in the model fitting process, and further, when projecting, high resource biomass does not necessarily lead to low penguin mortality.

The negative log-prior added to the negative log-likelihood for each year to reflect assumptions made above for the X_y random effects is:

$$P_X = \sum_y \left[\ln \sigma_y + \frac{1}{2}\left(\frac{X_y}{\sigma_y}\right)^2\right] \tag{4.10}$$

An additional penalty term ("prior") is added to aid estimation stability. The term chosen follows, and ensures that the annual mortality rates are evenly distributed about the curve relating mortality and biomass (i.e. the sum of the residuals is forced to zero):

$$P_{\text{B–M}} = 10^5 \left\{\sum_y \left[M_y - \left(M_{\min} + f_S\left(B_{S,y}\right)\right)\right]\right\}^2 \tag{4.11}$$

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[1] Under this formulation, the random effects are median-unbiased.

4.2.2 Biomass–mortality relationship

A variety of different functional forms have been implemented for the assumed relationship between pelagic biomass and penguin adult annual survival. A reason for the difficulty in choosing an appropriate function for this relationship is that the survival values are estimated within the model, and thus tend to depend on the relationship itself.

The first candidate function, which has an inverse power form, was defined as:

$$f_S\left(B_{S,y}\right) = M^*_{\text{min}} + \left(\alpha + \frac{B_{S,y}}{\beta}\right)^{-n} \tag{4.12}$$

The motivation for including the M^*_{min} term is that, when calculating M_y in equation (4.8), it is not possible for the term additional to M_{min} to go to zero when biomass is high. This would be problematic as then σ_y in equation (4.9) would become infinite, rendering the associated data point redundant because of its infinite variance. The lower bound on achieved M_y remains M_{min}, but the lower bound on the median of its distribution is $M_{\text{min}} + M^*_{\text{min}}$. For the base case model, the constant value used was $M^*_{\text{min}} = 0.02$.

Instead of α and β, equation (4.12) can be reparameterized in terms of the values of $f_S\left(B_{S,y}\right)$ at $B_S = 0.1$ and $B_S = 1$ in order to introduce estimable parameters that are more orthogonal (i.e. these new parameters have low correlation), which assists with statistically stable estimation. If $U = f_S\left(B_S = 1\right)$ and $V = f_S\left(B_S = 0.1\right) - f_S\left(B_S = 1\right)$, then

$$\begin{aligned}\beta &= \frac{0.9}{\left(U - M^*_{\text{min}}\right)^{-1/n} - \left(U + V - M^*_{\text{min}}\right)^{-1/n}}\\ \alpha &= \left(U - M^*_{\text{min}}\right)^{-1/n} - \frac{1}{\beta}\end{aligned} \tag{4.13}$$

The estimable parameters are then U, V, and n, where sensibly $V \geq 0$.

A concern arising from analyses with this functional form is that the likelihood could always be increased by raising the value of the power parameter n, leading to difficulty in choosing an appropriate prior for n. This indicates that this functional form is perhaps not the most appropriate. An alternative function then considered is defined by connected straight lines between the points:

$$\begin{aligned} f_S\left(1.0\right) &= \alpha \\ f_S\left(B^*\right) &= \alpha \\ f_S\left(0.0\right) &= \alpha + \beta \end{aligned} \tag{4.14}$$

Here, the relationship is flat above a critical biomass level B^*. Examining the scatterplot of mortality estimates suggested a preference for the relationship to flatten as the biomass tends towards zero. This suggested that the logistic function might be more suitable:

$$f_S\left(B_{S,y}\right) = \alpha + \left(\beta - \alpha\right) \frac{1}{1 + \exp\left[\left(B_{S,y} - \gamma\right)/\delta\right]} \tag{4.15}$$

This four-parameter function was found to perform better than the other forms. However, the data prefer a very steep gradient in increasing mortality as prey biomass drops below a critical value (i.e. an estimate for δ very close to zero, whose biological realism seems questionable as one would not expect step functions to provide the most realistic models for biological relationships). For this reason, a prior for the δ parameter was added, which itself has a logistic form to exclude very high gradients:

$$\text{prior}(\delta) = \frac{1}{1 + \exp\left[-\left(\delta - d^*\right)/\sigma_\delta\right]} \tag{4.16}$$

The effect of this prior is for a more gradual increase in penguin mortality as sardine biomass decreases. Values of the parameters of this logistic were chosen to be $d^* = 0.02$ and $\sigma_\delta = 0.005$, which give seemingly realistic results.

4.2.3 Reproductive success

The parameters $\bar{H}^*_y = f_H\left(B_{H,y}\right)$ are estimated on the interval $[0, 1]$. These are transformed predicted annual reproductive success rates $\bar{H}_y$ which fall in the interval $[0, H_{\max}]$:

$$\bar{H}_y = H_{\max} \bar{H}^*_y \tag{4.17}$$

The relationship between $\bar{H}_y^*$ and the fish biomass index $B_{H,y}$ is assumed to be constant in expectation for the base case (allowing for estimable fluctuations), given that analyses[2] did not provide any indication of dependence:

$$\bar{H}_y^* = f_H\left(B_{H,y}\right) = \eta \tag{4.18}$$

but alternative functional forms may readily be considered.

The parameters H_y^* are estimated for each year on the interval $[0, 1]$ and then transformed to the range $[0, H_{\max}]$ to obtain the annual reproductive success rates H_y as follows:

$$H_y = H_{\max} H_y^* \tag{4.19}$$

The H_y^* parameters are assumed to be beta-distributed about their predicted values $\bar{H}_y^*$. Setting $\kappa_{H,y} = \bar{H}_y^*\left(1 - \bar{H}_y^*\right)/\sigma_H^2 - 1$, the parameters of this beta distribution $\alpha_{H,y}$ and $\beta_{H,y}$ are:

$$\begin{aligned} \alpha_{H,y} &= \bar{H}_y^* \kappa_{H,y} \\ \beta_{H,y} &= \kappa_{H,y}\left(1 - \bar{H}_y^*\right) \end{aligned} \tag{4.20}$$

In order to obtain beta distributions which have a single mode and which vanish at the ends of the interval, the estimation procedure ensures that both $\alpha_{H,y}$ and $\beta_{H,y}$ are greater than 1.

The negative log-prior added to the negative log-likelihood, which reflects the assumption that H_y^* is beta-distributed, is:

$$P_H = \sum_y \left[\ln \frac{\Gamma\left(\alpha_{H,y} + \beta_{H,y}\right)}{\Gamma\left(\alpha_{H,y}\right)\Gamma\left(\beta_{H,y}\right)} - \left(\alpha_{H,y} - 1\right)\ln H_y^* - \left(\beta_{H,y} - 1\right)\ln\left(1 - H_y^*\right)\right] \tag{4.21}$$

An additional penalty term ensures that the annual reproductive success rates are evenly distributed about the assumed relationship, that is the sum of the residuals is forced to zero

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[2] For example, when allowing for a linear relationship between anchovy recruit biomass and penguin reproductive success, the estimate for the slope parameter came out very close to zero.

(this was found to aid estimation stability):

$$P_{\text{B–H}} = 10^5 \left[\sum_y \left(H_y - \bar{H}_y \right) \right]^2 \tag{4.22}$$

4.2.4 Immigration

The inclusion of tag-recapture information (see Section 4.3.2 following) allows, in principle, for the estimation of immigration in the model. All immigrants are assumed to be pre-breeders in adult plumage as reflected by equation (4.2). Initially, a separate estimate was made for the number of birds immigrating to Robben Island each year, but there was not support for the addition of so many parameters. Therefore, years were grouped together and an appropriately parsimonious model was selected using the Akaike information criterion (AIC). There was no support for immigration from the year 2000 onwards.

4.3 Model fitting

4.3.1 Fitting to moult counts

The population model is fitted to annual moult count data for both adult and juvenile birds. Assuming an equal sex ratio, the numbers of adult moulters in Table 2.2 are halved to correspond to females only. The counts are taken into account through the following negative log-likelihood functions:

$$\begin{aligned} -\ln L_{\text{M}} &= \sum_y \left[\ln \sigma_{\text{M},y} + \frac{1}{2\sigma^2_{\text{M},y}} \left(\ln N_y^{\text{obs}} - \ln N_y^{\text{model}} \right)^2 \right] \\ -\ln L_{\text{J}} &= \sum_y \left[\ln \sigma_{\text{J}} + \frac{1}{2\sigma^2_{\text{J}}} \left(\ln J_y^{\text{prop}} - \ln J_y^{\text{model}} \right)^2 \right] \end{aligned} \tag{4.23}$$

$\sigma_{\text{M},y}$ and σ_J are respectively the standard errors of the logarithms of the adult moult counts and juvenile proportions of these counts about their true values (i.e. these reflect observation errors). The terms in the likelihood for the adult moult counts are weighted according to the coefficients of variation of the observations with:

$$\sigma_{M,y} = \sqrt{CV\left(N_y^{\text{obs}}\right)^2 + 0.05^2 + \sigma_{\text{add}}^2} \tag{4.24}$$

where the additional variance term σ_{add}^2 is an estimable parameter, with the true additional variance forced to be at least 0.05^2. The value of the variance of the proportion of juveniles σ_{J} is fixed at $\sigma_{\text{J}} = 0.1$.

N_y^{model} is the number of female birds in adult plumage (aged 2 and over) counted in year y, which is calculated as:

$$N_y^{\text{model}} = q_{\text{M}} \sum_{a=2}^{A} N_{y,a} S_y^{11/12} \tag{4.25}$$

The proportion of these birds susceptible to observation is assumed here to be $q_{\text{M}} = 0.9$. The survival rate S_y is taken to the power of $11/12$ since the peak of the counting season is at the beginning of December (see Figure 4.1).

J_y is the proportion of juvenile birds in the model at the time of the moult count, calculated as:

$$J_y = p_{\text{J}} N_{y,1} \Big/ \sum_{a=1}^{A} N_{y,a} \tag{4.26}$$

Note that $S_y^{11/12}$ factors in the numerator and denominator cancel. It has been suggested that some moulting juveniles are counted as adults, as distinguishing the different forms can be difficult during the last few days of the moult. The factor p_{J} allows for this possibility, but is assumed here to be $p_{\text{J}} = 1$.

N_y^{obs} is the number of female adult moulters observed in year y (taken to be one half of the total adult moult count).

J_y^{prop} is the observed proportion of moulters in immature plumage counted in year y.

4.3.2 Fitting to tag data

In addition to the moult counts, tag data for the period 1989–2010 have been incorporated into the analysis (see Section 2.2). This addition provides an independent estimate of annual survival rates and allows for the estimation of immigration. Based on the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965), the multinomial likelihood of the encounter histories is calculated through the estimation of re-sighting probabilities and survival rates for each year. Results (point estimates and their standard errors) from this implementation of the standard CJS model were checked against results produced by program MARK (White and Burnham 1999), and were found to be in agreement.

The standard CJS model was found to produce a poor fit of expected numbers of penguins re-sighted to the observed data (Figure 4.4), especially in certain years (notably 1990–1992 and 2001–2003). A variation on the standard CJS model was therefore included in this analysis to address this, namely the estimation of a transient factor (Pradel *et al.* 1997) relating to tags which are never re-sighted after deployment. For example, tags improperly attached could fall off, or animals might move to an area which is inaccessible or infrequently visited by tag spotters. In some cases, an improperly attached tag could contribute to a premature fatality. These short-term effects are modelled as additional mortality (which may in fact incorporate emigration) in the year that a penguin is banded. Note that this "transient" rate does not depend on prey abundance in any way.

Initially, a single estimated transient rate was applied to all years, except for the years of the two major oil spills, 1994 and 2000. However, a clear lack of fit to the tag-resighting data for some tag cohorts indicated that the assumption of this constant transient rate is inappropriate in this case. This was addressed by estimating a separate transient rate for each year. This improves the fit, but it is questionable whether the addition of so many parameters is statistically justifiable. Using AIC as the basis for model selection, various options of pooling of estimates for different years were explored. Table 4.2 denotes to which years the estimated parameters apply in the base case model. This scheme improves the fit to the observed tag-recapture data considerably (Figure 4.5).

The log-likelihood function for the multinomial distribution, ignoring the constant multinomial coefficient, is:

$$\ln L_{\text{T–R}} = \frac{1}{\hat{c}} \sum_{j=1}^{m} n_j \ln \hat{p}_j \tag{4.27}$$

where:

$\hat{p}_j$ is the estimated probability of the jth encounter history occurring,

n_j is the number of times which that history has been observed,

m is the number of unique encounter histories, and

$\hat{c}$ is a scalar included to account for overdispersion.

For details of the calculation of $\hat{p}_j$ for each observed encounter history, refer to Lebreton *et al.* (1992) and Maunder *et al.* (2009). The value used for $\hat{c}$ is obtained from analysing the data using MARK (see Table 4.1).

4.3.3 Objective function minimized

The overall negative log-posterior is obtained by summing penalties (negative log-priors) (4.10), (4.11), (4.21), and (4.22), and subtracting the log-likelihoods (4.23) and (4.27):

$$-\ln P_{\mathrm{post}} = P_X + P_{\mathrm{B\text{–}M}} + P_H + P_{\mathrm{B\text{–}H}} - \ln L_{\mathrm{M}} - \ln L_{\mathrm{J}} - \ln L_{\mathrm{T\text{–}R}} \tag{4.28}$$

4.3.4 Parameter estimation

The model described above was implemented in AD Model Builder (Fournier *et al.* 2012). Parameters listed in Table 4.1 were fixed on input.

A difficulty arises regarding the estimation of the parameter $\tilde{\sigma}$, which quantifies the degree of spread of survival estimates about the assumed relationship with pelagic fish abundance. When treating $\tilde{\sigma}$ as any other parameter in the (penalized) maximum likelihood (i.e. posterior mode) estimation, the program converges to a solution with $\tilde{\sigma}$ tending towards zero. This is because the negative log prior term P_X in equation (4.10) is minimized when both the X_y parameters and σ_y (and hence $\tilde{\sigma}$ from equation (4.9)) tend to zero.

This “difficulty” is not, however, a real one. It arises from an incorrect statistical treatment of the X_y parameters in a frequentist context in circumstances where these residuals relate entirely to estimable model quantities rather than differences between model estimates and data. The appropriate approach is to treat the X_y parameters as random effects in a mixed effects model, and then integrate them out of the likelihood, so that $\tilde{\sigma}$ is the only remaining estimable parameter from this term. In a full Bayesian context, integration over all X_y parameters is effected, so in theory no problem should occur.

However, the Markov-chain Monte Carlo (MCMC) method for generating a Bayesian posterior distribution fails in this case. The reason for this is because the constraint in equation (4.11) is very tight, and hence the region within which the negative log-likelihood is near its minimum is very small. Jumps away from the starting value give such large changes in the negative log-likelihood that these jumps are always rejected in the MCMC algorithm. An attempt to attain the relative likelihood of different values of $\tilde{\sigma}$ using the Deviance Information Criterion (DIC) also failed for the same reason.

Instead, therefore, ADMB-RE was used. With this program, random effects are integrated out using the Laplace approximation (Skaug and Fournier 2006). Once a maximum likelihood estimate was obtained of $\tilde{\sigma} = 0.088$ (with an associated Hessian-based standard error of 0.013), MCMC was used to integrate over the other parameters to obtain posterior distributions.

Strictly, the integration of the random effects should occur at each step of the MCMC process to obtain "step-specific" $\tilde{\sigma}$ estimates. This was attempted, but it proved beyond the capabilities of the software to obtain convergence. This does mean, however, that the results obtained are conditional on the ADMB-RE maximum likelihood estimate for $\tilde{\sigma}$, and make no allowance for the variance about this estimate.

Parameters estimated within the model are listed in Table 4.2 and Bayesian 90% probability intervals are given in Table 4.3. Fits to the data and residual patterns are plotted in Figures 4.6–4.9. Further plots show time-series of estimated adult annual survival (Figure 4.10) and female moult counts (Figure 4.11), with 95% probability intervals. Figure 4.12 shows estimated immigration, and Figure 4.13 shows estimated "transient" rates associated with the tag-recapture data.

4.4 Results and discussion

This work is novel in that it integrates data from different sources in a rigorous manner. Specifically, the model includes abundance estimates from adult and juvenile moult counts as well as survival estimates from tag-recapture data.

There are two potential difficulties with the tag-recapture data which should be investigated further. First, penguin mortality may increase with age. As the number of penguins tagged each year varies considerably, with more than half having been tagged in a single year (2000, Figure 4.5), age-dependent mortality could confound estimates of the relative re-sighting probabilities in different years. Secondly, some penguins may be "trap-happy" while others are "trap-shy", that is different individuals may be more or less likely to be re-sighted. These two issues both violate tag-recapture model assumptions.

A worrying aspect of the fit to the tag-recapture data is the systematic trend of more observed than expected re-sightings from 2002 to 2010 (Figure 4.6). It is possible to force expected re-sightings to match observed data exactly (Figure 4.7), resulting in higher re-sighting probabilities over this period. Although the fit to the moult data remains acceptable, the tag-recapture likelihood suffers considerably (Table 4.4). This suggests that it is the re-sighting histories of the birds which are not compatible with some assumptions of the recapture model being used; consideration of either or both of the age dependent mortality and heterogeneous re-sighting probability factors mentioned in the previous paragraph might possibly improve the fit of the model to the re-sighting numbers. Sensitivity of projections to forcing the model to fit to the annual re-sighting numbers in this way is checked in Chapter 5.

The model fits to both the adult moult counts (Figure 4.8a) and the proportion of juveniles in the moult count (Figure 4.8c) are reasonable, perhaps with the exception of the juvenile proportions in 2008–2010. The higher than expected proportions in those years could reflect the unexpected absence of moulting adults (perhaps partially accounted for by the large number of moulters at Stony Point) rather than an excess of juveniles. Plots of the residuals in Figure 4.8 (b), (d), and (f) show nothing to suggest any obvious trend, supporting the assumption of randomness that underlies the model fitting procedure.

The posterior distribution percentiles (see Table 4.3) for the parameter β of the relationship between sardine biomass and penguin mortality show that this increase in mortality at low biomass is substantial and well determined. The shape of this relationship (Figure 4.9a) suggests that penguins gain very little additional benefit as the sardine biomass index increases above $B_S = 0.25$ which corresponds to some 335 000 tonnes (west of Cape Agulhas). However, penguin mortality increases rapidly as sardine biomass drops lower, up to roughly $M = 0.6$. The model applied prefers the relationship to flatten as the biomass index approaches zero.

There is some model mis-specification evident given the series of negative residuals for the years 1988–1996 in the penguin mortality versus sardine biomass relationship, reflecting mortalities over these years which are lower than the model suggests (Figure 4.9b and d). This artifact could be removed by increasing the weight of the associated term in the likelihood function. However, this would have the effect of transferring the mis-specification to the fit to some other time-series. Alternatively, much of the trend in the residuals would be removed by the inclusion of an autocorrelation factor[3]. It seems unreasonable to expect a model with a relatively simple structure such as this to give a perfect representation of all the data. Furthermore, the limited number of degrees of freedom precludes the possibility of reliably linking this effect to, for example, some further environmental signal.

The Bayesian 90% probability intervals for adult survival (Figure 4.10) and adult moulters (Figure 4.11) are fairly narrow, reflecting relatively precise estimation. In contrast, the probability intervals for the estimated number of penguins immigrating to Robben Island are rather wide (Figure 4.12).

The estimates for transient-related apparent mortality rates are rather large in the years 1990–1992 and 2001–2003 (Figure 4.13). This may suggest that penguins were emigrating from Robben Island in those years, or that a large proportion of the birds tagged were visitors rather than residents. Alternatively, poor quality of either the tagging or the tags in these years might be the cause.

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[3] Projections including such autocorrelation modelled as an AR(1) process were explored; posterior medians hardly changed, though 80% probability envelopes for the projections expanded slightly.

With the inclusion of immigration in the model, the upper bound imposed on adult survival is not hit (Figure 4.9e). A noticeable aspect of the results is the large number of penguins estimated to immigrate to Robben Island from 1989 to 1993. This warrants further investigation. The model predicts that the Robben Island population would scarcely have been self-sustaining without immigration (Figure 4.14), showing only a moderate increase in abundance during the years of high sardine biomass (1997–2003). Here, the dark curve represents the model-fitted trajectory of adult female moulters, and the dashed curve below is a trajectory corresponding to the same demographic parameter estimates (birth and death rates) but with immigrating birds removed. This graph shows that virtually all increases in the size of the Robben Island colony during the 1990s are attributable to immigrants.

This observation has implications for future expectations of penguin abundance at Robben Island. Since penguins have apparently stopped immigrating to the colony in large numbers, it may be overly optimistic to assume that numbers at the colony will increase rapidly in the future, even if sardine biomass in the region increases substantially. This matter is explored in the following chapter.

Table 4.1: Parameter values fixed on input to the penguin–fish model.

Parameter	Description	Value
A	Plus group age	5
p_{J}	Detectability of juveniles relative to adults in the moult count	1.0
a^*	Age of first breeding attempt	4
σ_{J}	Standard errors of the logarithms of the juvenile proportions	0.1
σ_H	Standard deviation of reproductive success	0.1
$H_{\max}$	Maximum allowed reproductive success	1.8
q_{M}	Proportion of moulters susceptible to observation	0.9
$M_{\min}$	Minimum allowed mortality rate	0.04
d^*	Parameter of logistic prior on δ in the biomass–mortality relationship	0.02
σ_δ	Parameter of logistic prior on δ in the biomass–mortality relationship	0.005
$\hat{c}$	Overdispersion factor for the tag-recapture likelihood	5.57

Table 4.2: Parameters estimated within the model. Where the parameter is estimated as the log of an abundance, the corresponding abundance value follows in parenthesis.

Parameter	Description	Prior	Posterior mode	
$\ln N_0$	Log of initial population size	$U[1, 10]$	6.794	(892)
λ	Initial population profile parameter	$U[0, 3]$	0.205	
σ_{add}	Additional variance in moult counts	$U[0, 1]$	0.000	
$\tilde{\sigma}$	Parameter related to variability about the assumed biomass–mortality relationship	$U[0.001, 0.5]$	0.088	
η	Reproductive success relationship	$U[0, 1]$	0.512	
X_y	Adult mortality random effects	$U[-4.5, 4.5]$		
H_y	Reproductive success	$U[0.001, 0.999]$		
p_y	Tag re-sighting probabilities	$U[0, 1]$		
α	Parameters of the biomass–mortality relationship (equation (4.15))	$U[0, 1]$	0.087	
β			0.589	
γ			0.173	
δ			0.041	
$\ln I_{1989-1990}$	Log of the number of three-year-old penguins immigrating to Robben Island in the years indicated	$U[-4, 10]$	6.691	(805)
$\ln I_{1991-1993}$			6.034	(417)
$\ln I_{1994-1996}$			−3.999	(0)
$\ln I_{1997-1999}$			5.670	(290)
	Transient-related apparent mortality rates			
t_1	1989, 1993, 1995–1999, 2004–2009	$U[0, 5]$	0.109	
t_2	1990		1.259	
t_3	1991		0.633	
t_4	1992		1.956	
t_5	1994		0.000	
t_6	2000		0.000	
t_7	2001–2003		0.684	

Table 4.3: Bayesian posterior medians of model estimated parameters with 90% probability intervals. Where the parameter is estimated as the log of an abundance, the corresponding abundance value follows in parenthesis.

Parameter	5th percentile		50th percentile		95th percentile	
$\ln N_0$	6.467	(644)	6.775	(876)	7.105	(1218)
λ	0.175		0.208		0.251	
η	0.488		0.517		0.548	
α	0.059		0.076		0.098	
β	0.512		0.688		0.952	
γ	0.079		0.140		0.185	
δ	0.025		0.050		0.085	
$\ln I_{1989\text{–}1990}$	5.870	(354)	6.527	(683)	6.936	(1029)
$\ln I_{1991\text{–}1993}$	−2.473	(0)	3.603	(37)	6.187	(486)
$\ln I_{1994\text{–}1996}$	−3.578	(0)	0.225	(1)	4.446	(85)
$\ln I_{1997\text{–}1999}$	−3.424	(0)	1.805	(6)	5.574	(264)
t_1	0.068		0.144		0.229	
t_2	0.882		1.436		2.155	
t_3	0.458		0.738		1.059	
t_4	1.609		2.070		2.610	
t_5	0.000		0.001		0.002	
t_6	0.000		0.000		0.000	
t_7	0.503		0.695		0.908	

Table 4.4: Values of negative log likelihoods and negative log priors contributing to the total negative log posterior for both the base case model and a version in which expected numbers of re-sighted penguins each year are forced to fit observed numbers exactly.

Component	Symbol	Base case	Forced tag fit	Difference
Adult moult count	$-\ln L_{\mathrm{M}}$	−51.21	−43.80	7.41
Proportion of juveniles	$-\ln L_{\mathrm{J}}$	−50.78	−46.95	3.83
Tag-recapture	$-\ln L_{\mathrm{T\text{–}R}}$	6 102.05	6 138.77	36.72
Survival	P_X	−7.26	−6.85	0.41
Reproductive success	P_H	−23.43	−22.21	1.22
Total		5 969.39	6 018.97	49.58

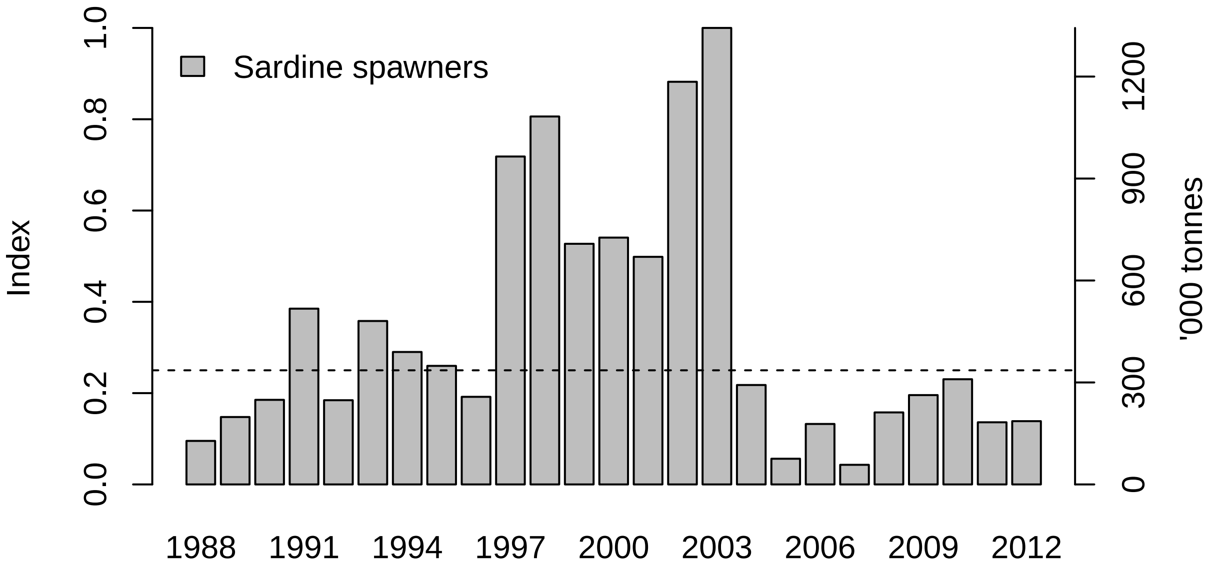


Figure 4.2: The index for the sardine spawner biomass west of Cape Agulhas (strata A–C) estimated from the November hydroacoustic survey is expressed relative to the maximum (observed in 2003) on the left axis. The right axis indicates the corresponding biomass in thousands of tonnes. The biomass index value of 0.25 is indicated by the dashed horizontal line..

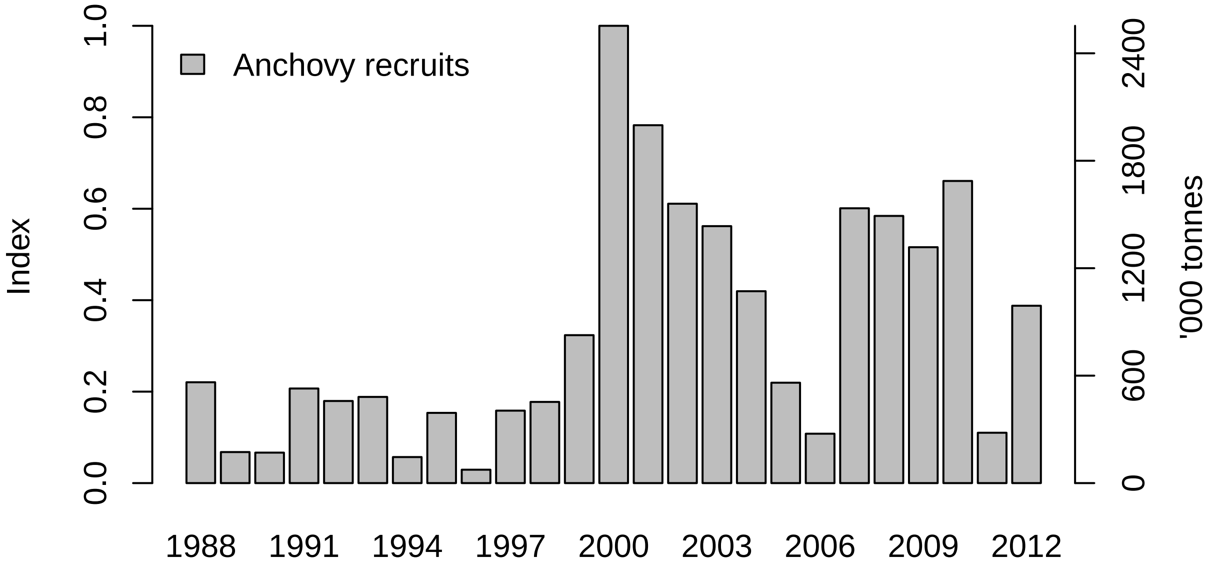
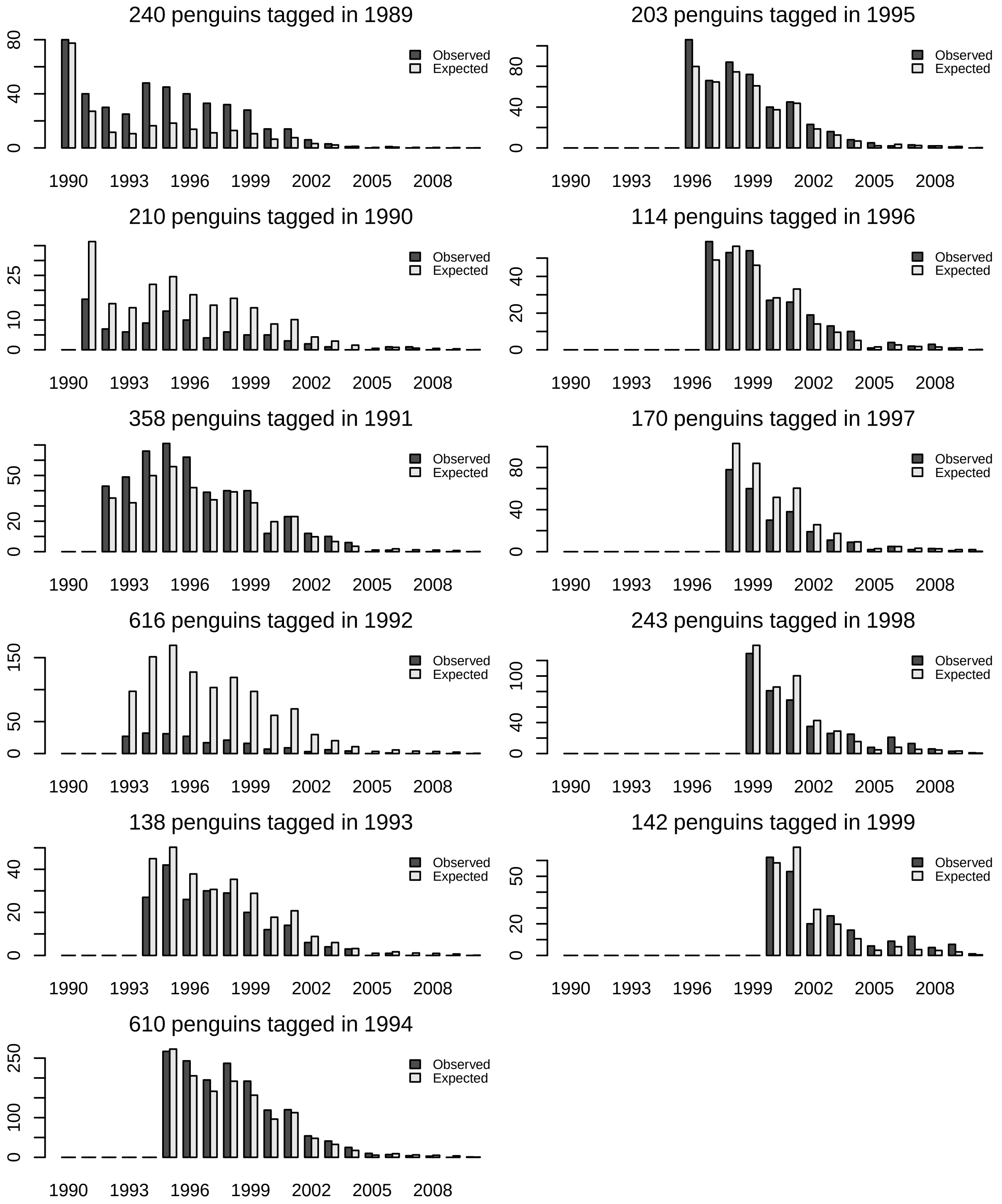


Figure 4.3: The index of the anchovy recruit biomass west of Cape Infanta estimated from the May hydroacoustic survey is expressed relative to the maximum (observed in 2000) on the left axis. The right axis shows the corresponding biomass in thousands of tonnes.



240 penguins tagged in 1989

203 penguins tagged in 1995

210 penguins tagged in 1990

114 penguins tagged in 1996

358 penguins tagged in 1991

170 penguins tagged in 1997

616 penguins tagged in 1992

243 penguins tagged in 1998

138 penguins tagged in 1993

142 penguins tagged in 1999

610 penguins tagged in 1994

Figure 4.4: (a) Fits to tagging data for birds tagged in the years 1989–1999 making no allowance for "transient" birds.

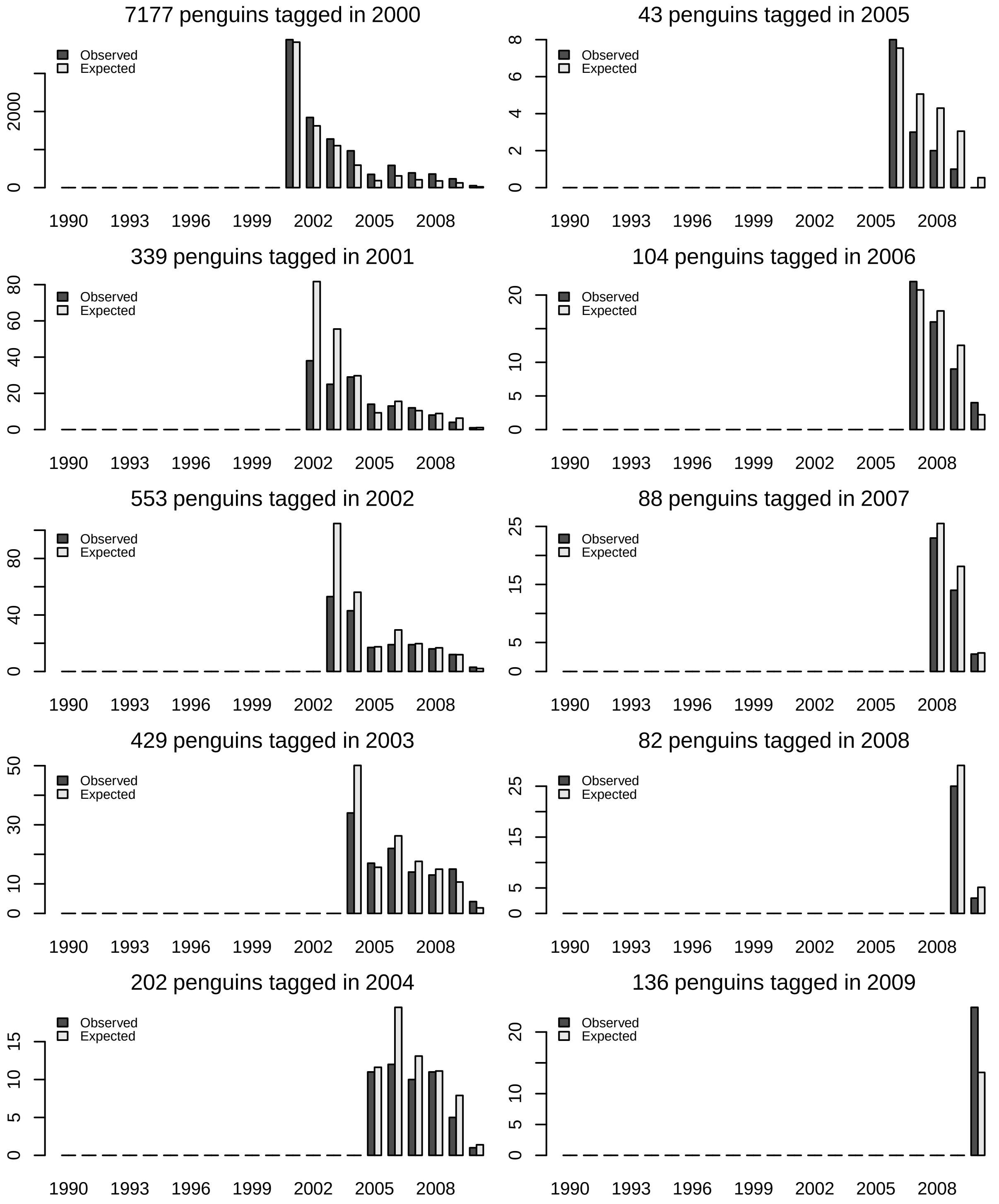


Figure 4.4: (b) Fits to tagging data for birds tagged in the years 2000–2009 making no allowance for "transient" birds.

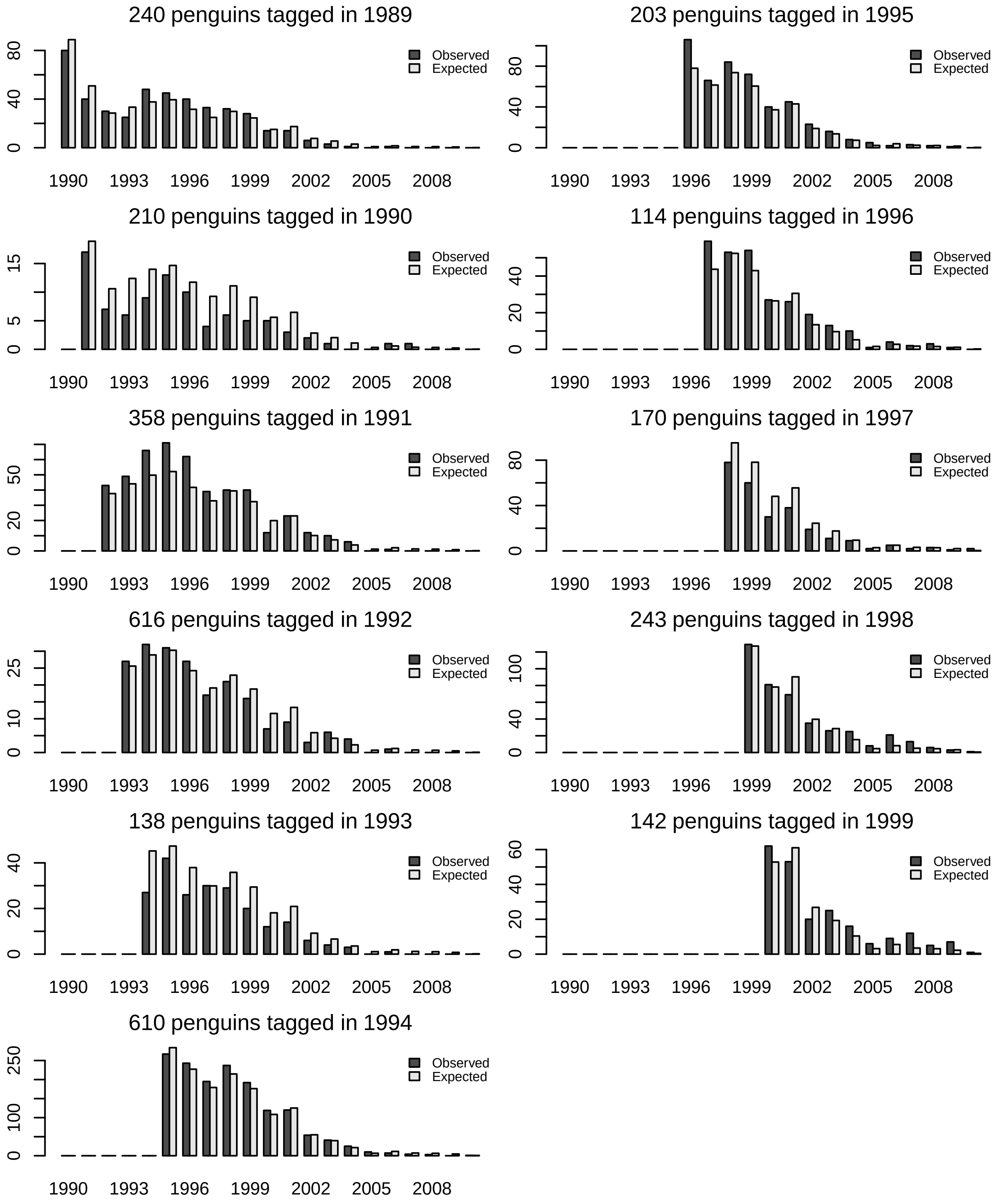
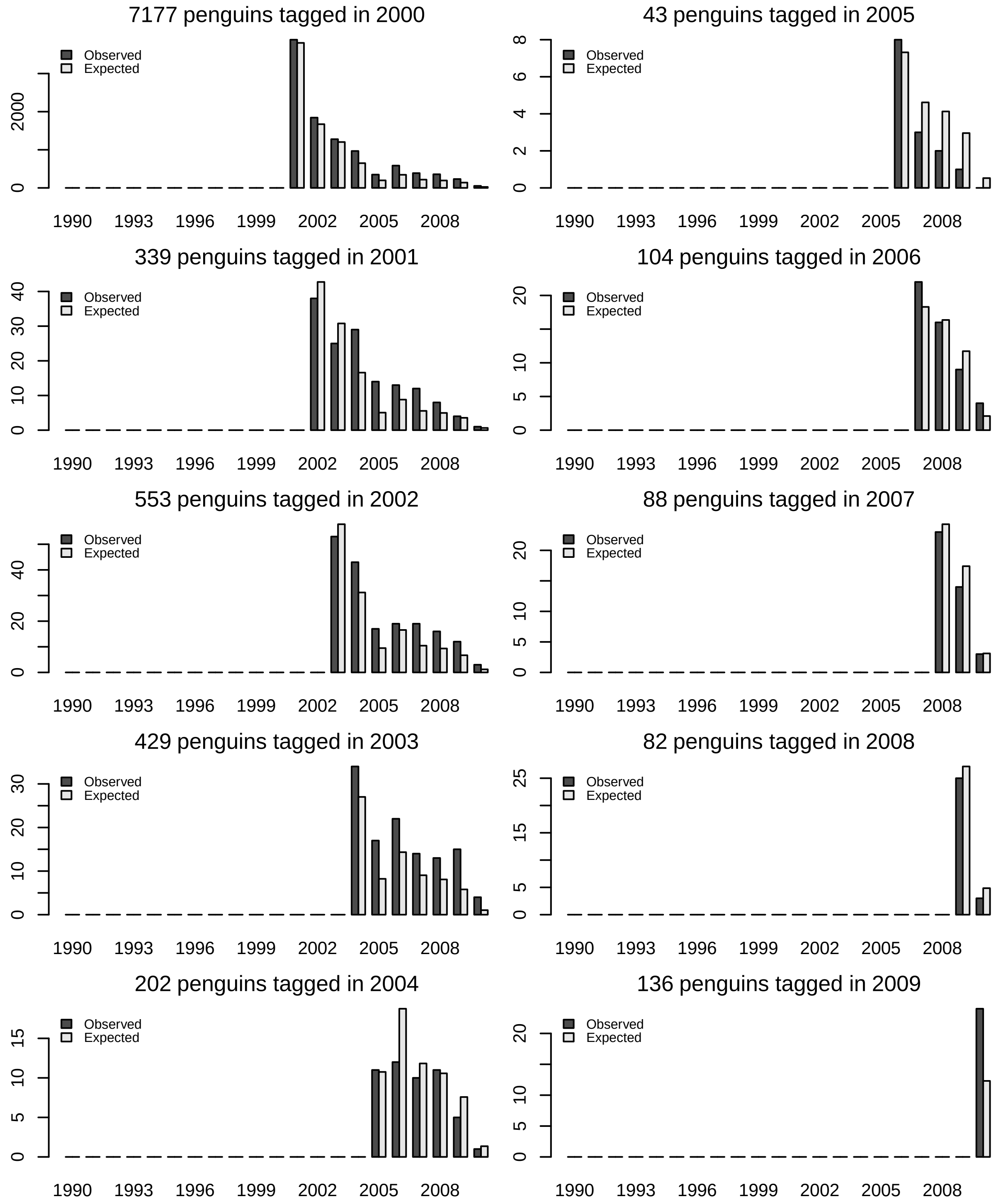


Figure 4.5: (a) Fits to tagging data for birds tagged in the years 1989–1999, with estimated "transient" rates.



7177 penguins tagged in 2000

43 penguins tagged in 2005

339 penguins tagged in 2001

104 penguins tagged in 2006

553 penguins tagged in 2002

88 penguins tagged in 2007

429 penguins tagged in 2003

82 penguins tagged in 2008

202 penguins tagged in 2004

136 penguins tagged in 2009

Figure 4.5: (b) Fits to tagging data for birds tagged in the years 2000–2009, with estimated "transient" rates.

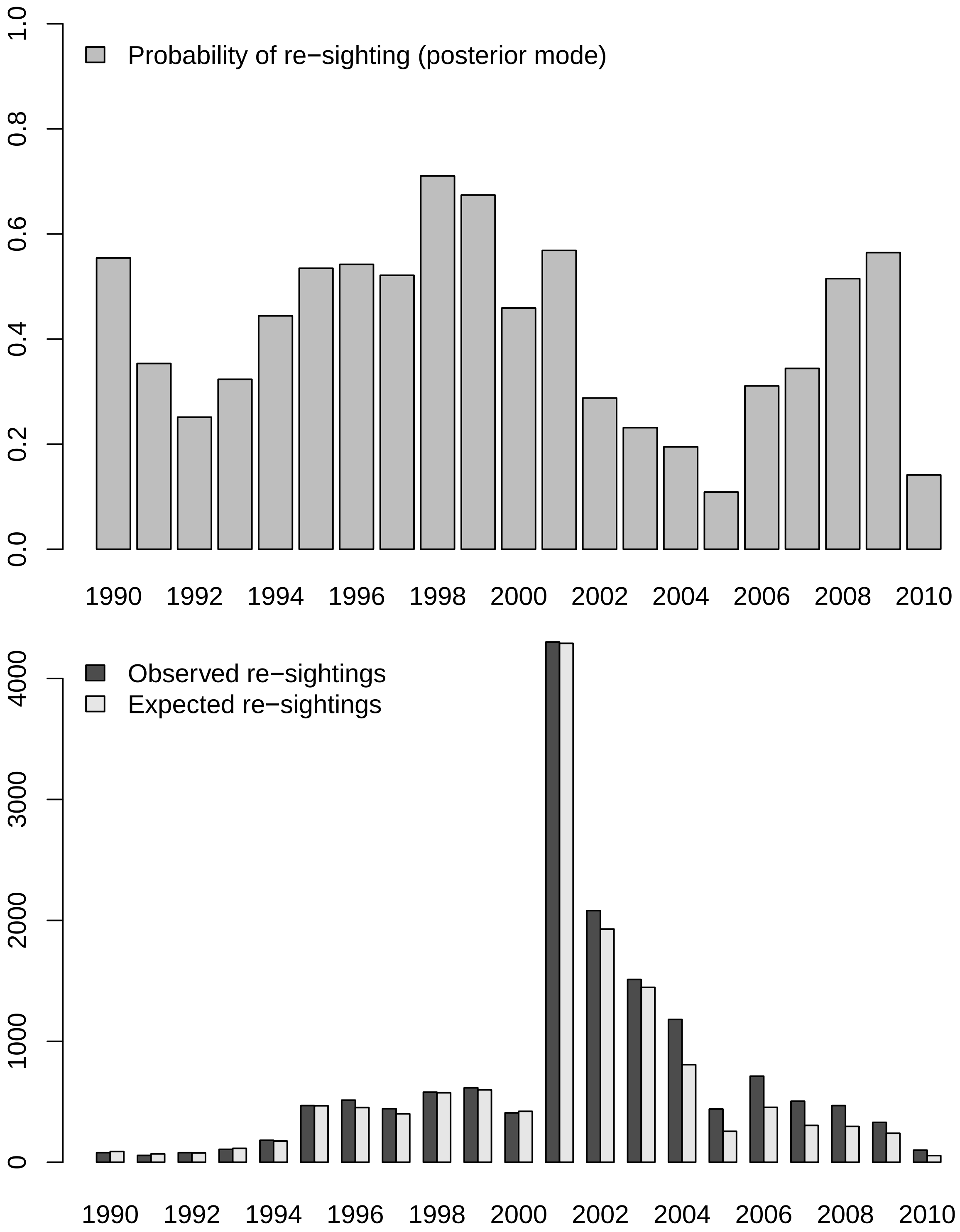


Figure 4.6: Results of fitting the penguin–sardine interaction model to the Robben Island tag-recapture data. Top: annual probability of re-sighting banded birds. Bottom: comparison of observed and expected numbers of banded penguins re-sighted each year for the joint posterior mode.

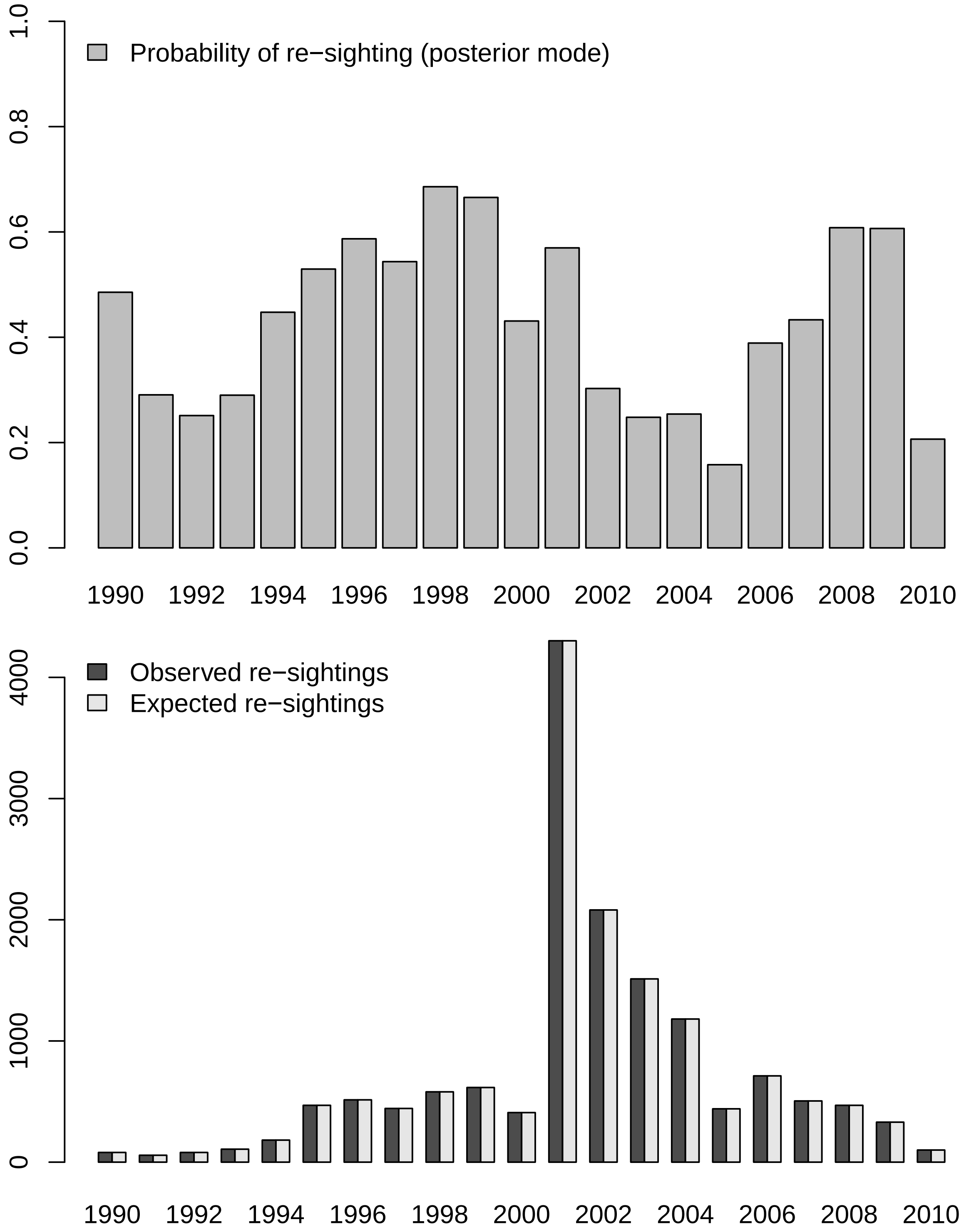


Figure 4.7: Expected number of penguins re-sighted each year forced to match the observed data. Top: annual probability of re-sighting banded birds. Bottom: comparison of observed and expected numbers of banded penguins re-sighted each year for the joint posterior mode.

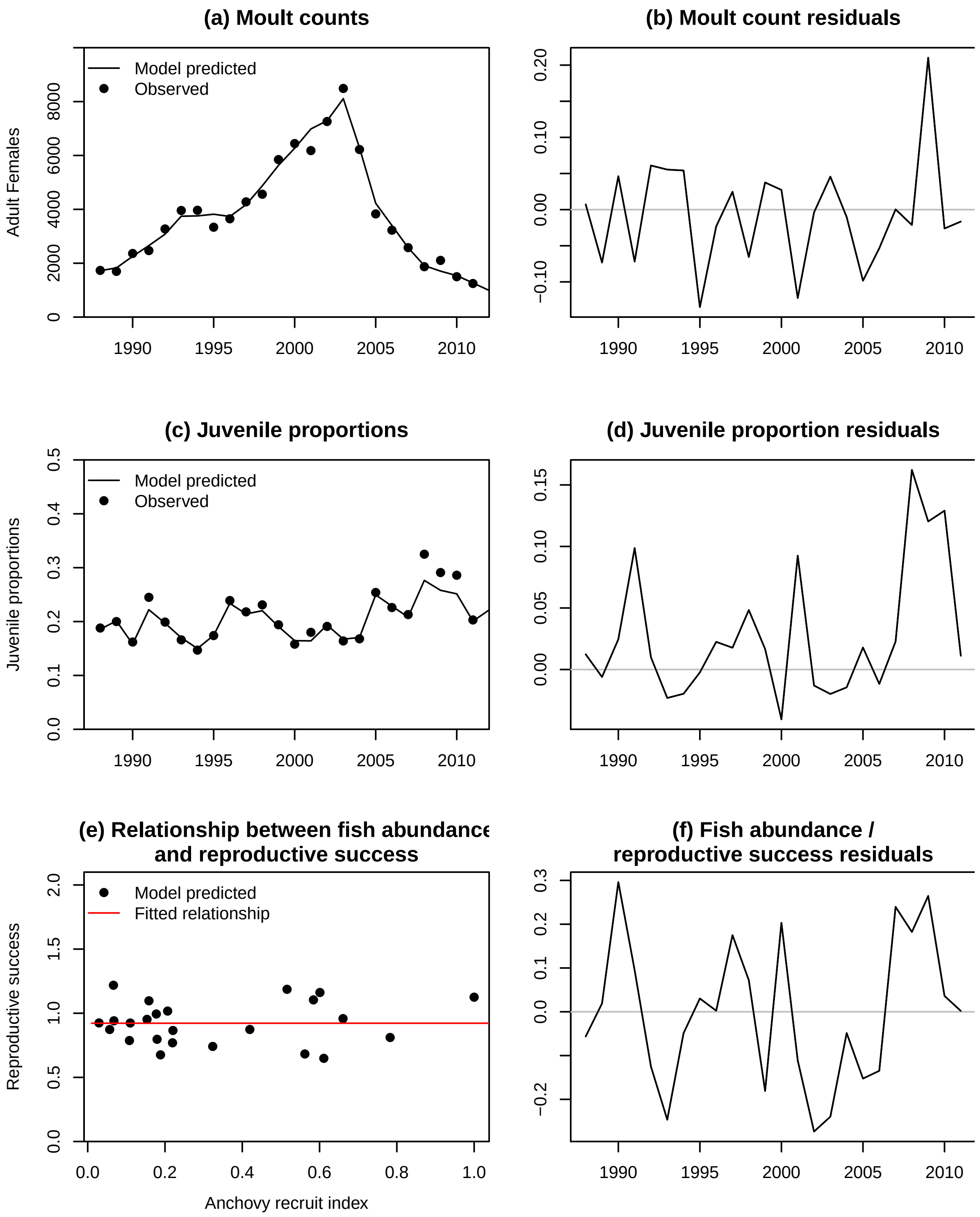


Figure 4.8: Fits to data/relationships and associated residuals at the joint posterior mode for the base case Robben Island penguin–sardine interaction model. The residuals in (b) and (d) are the differences between the logarithms of the observations and the model predicted values. The residuals in (f) are the differences between the estimated reproductive success rates and the assumed relationship.

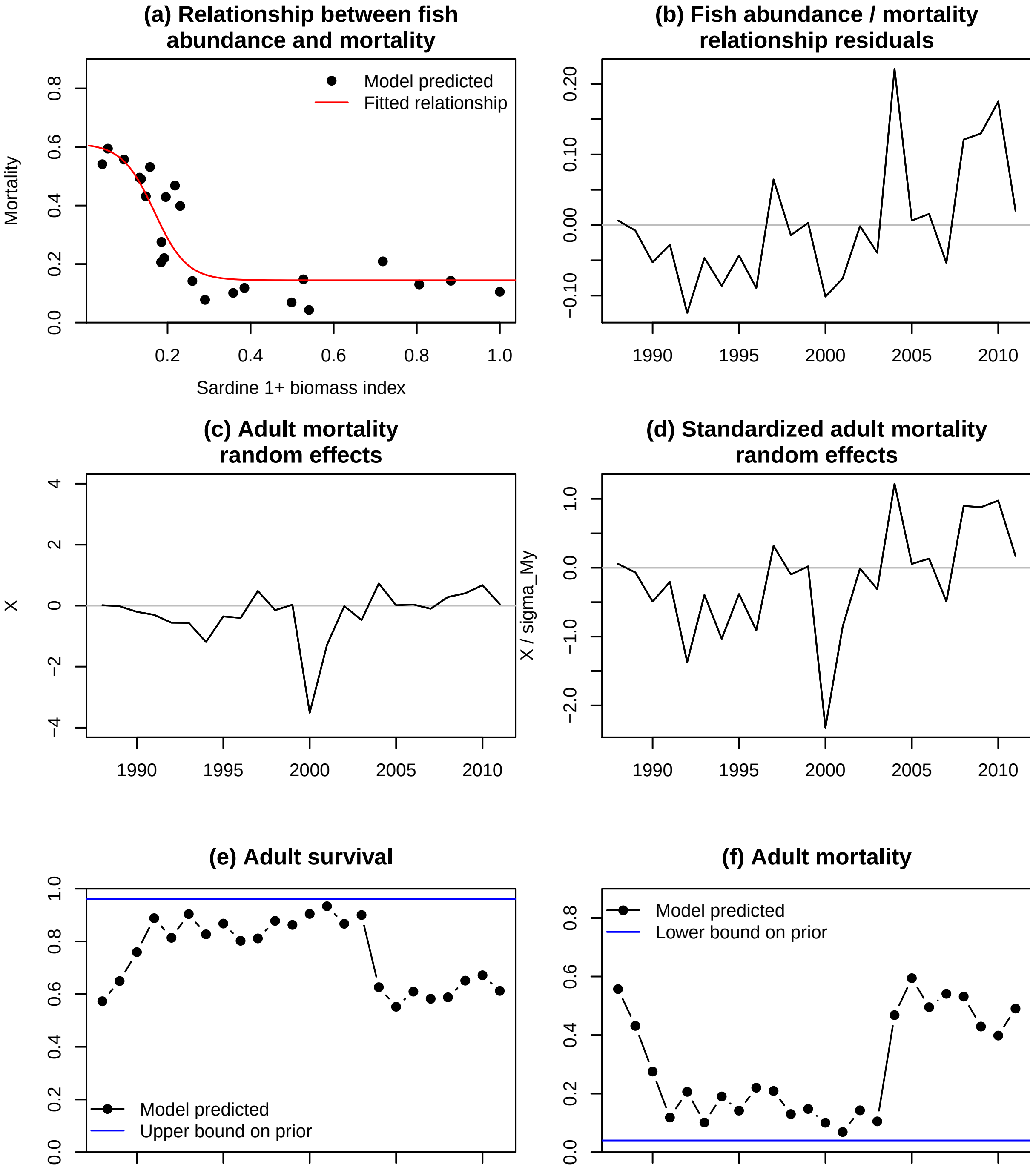


Figure 4.9: Further fits to data/relationships and associated residuals for the joint posterior mode for the base case Robben Island penguin–sardine interaction model: (a) Estimated sardine–mortality relationship, (b) differences between the estimated annual mortality rates and those predicted by the relationship with fish abundance, (c) random effects X_y, (d) random effects standardized by dividing by σ_y, (e) time-series of estimates for the adult survival rates, and (f) corresponding mortality rates.

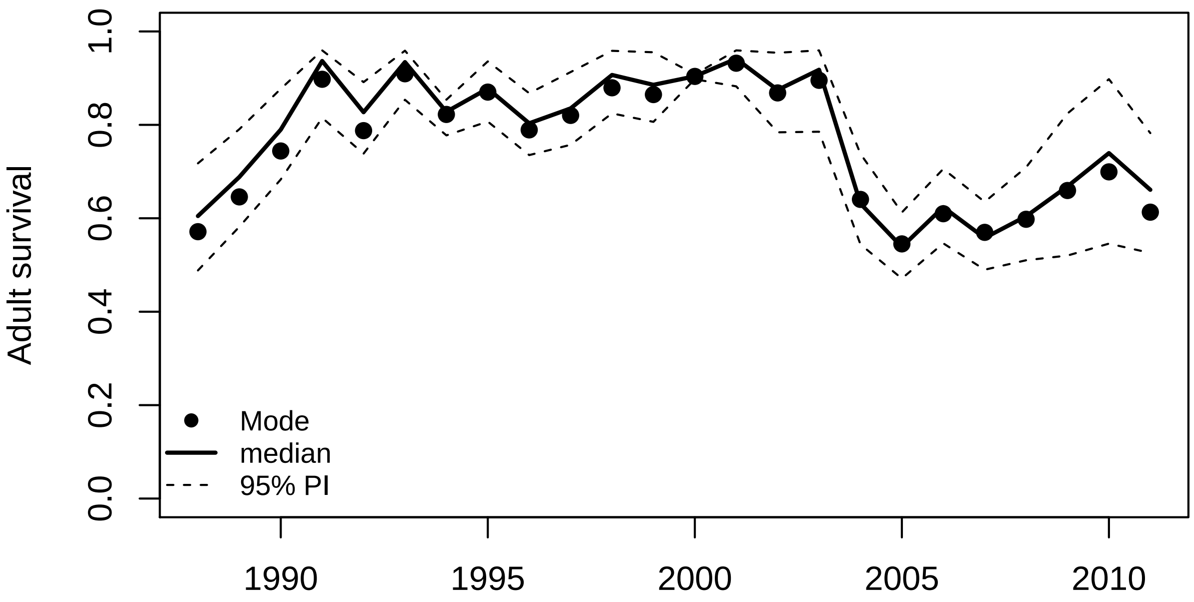


Figure 4.10: Time-series of estimated adult penguin annual survival rates for Robben Island at the joint posterior mode (black circles). The median and 95% probability interval of the Bayesian posterior distribution are indicated with lines.

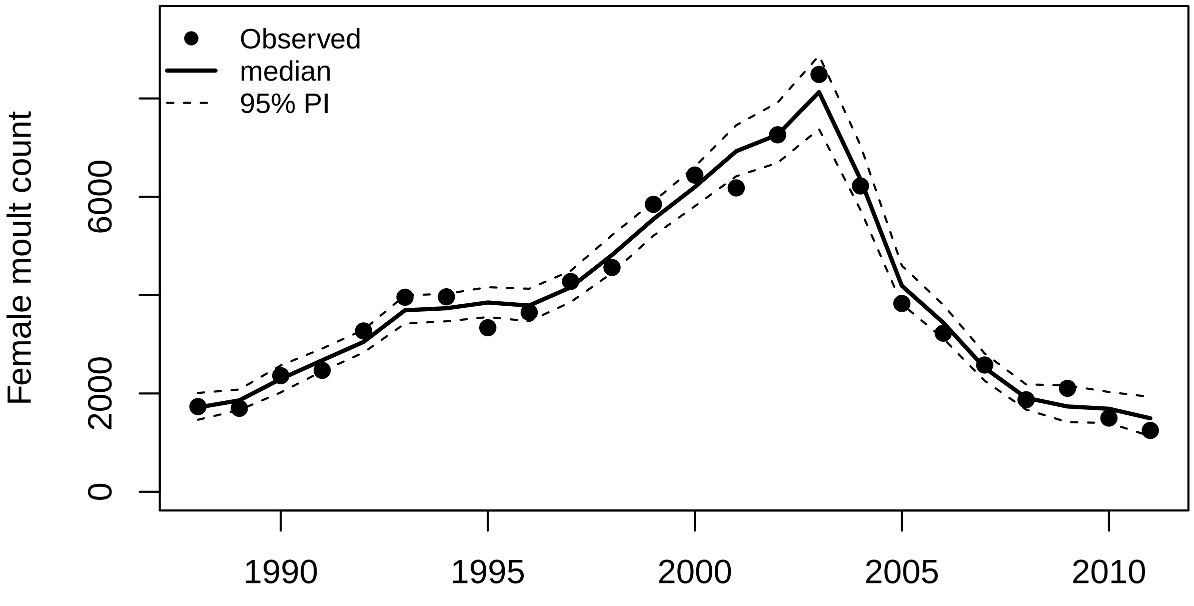


Figure 4.11: Time-series of female moulting penguins at Robben Island from observations (black circles). The median and 95% probability interval of the Bayesian posterior distribution of the model-predicted moult counts are indicated with lines.

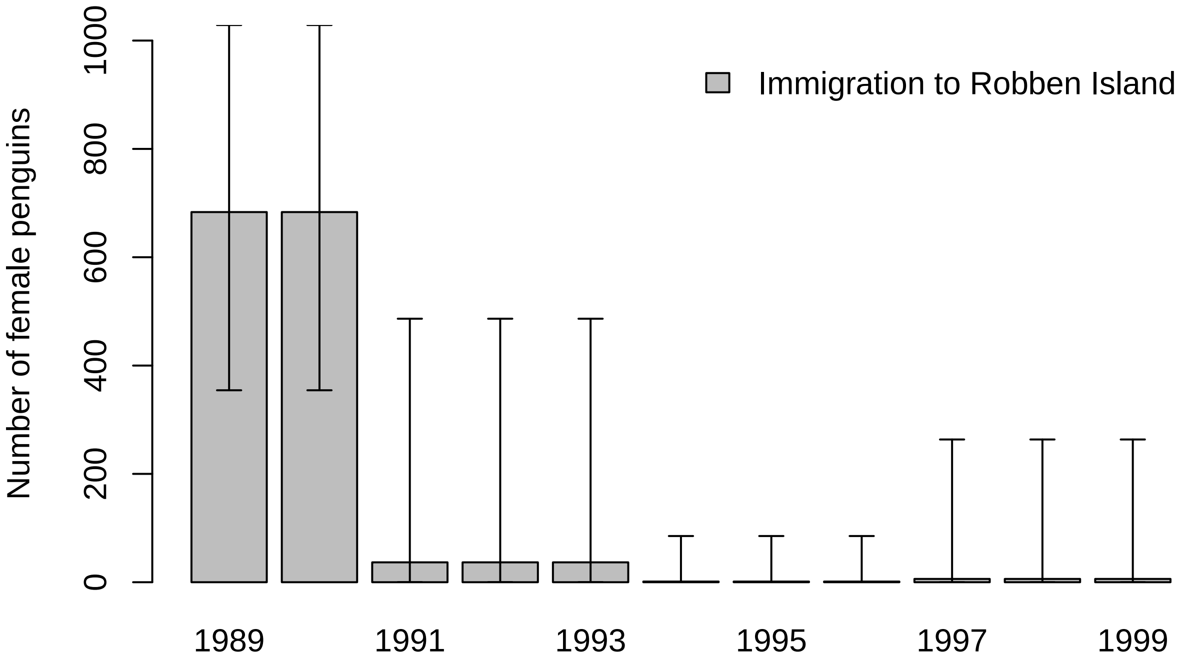


Figure 4.12: Median number of three-year-old female penguins estimated to immigrate to Robben Island each year, with associated 90% probability intervals.

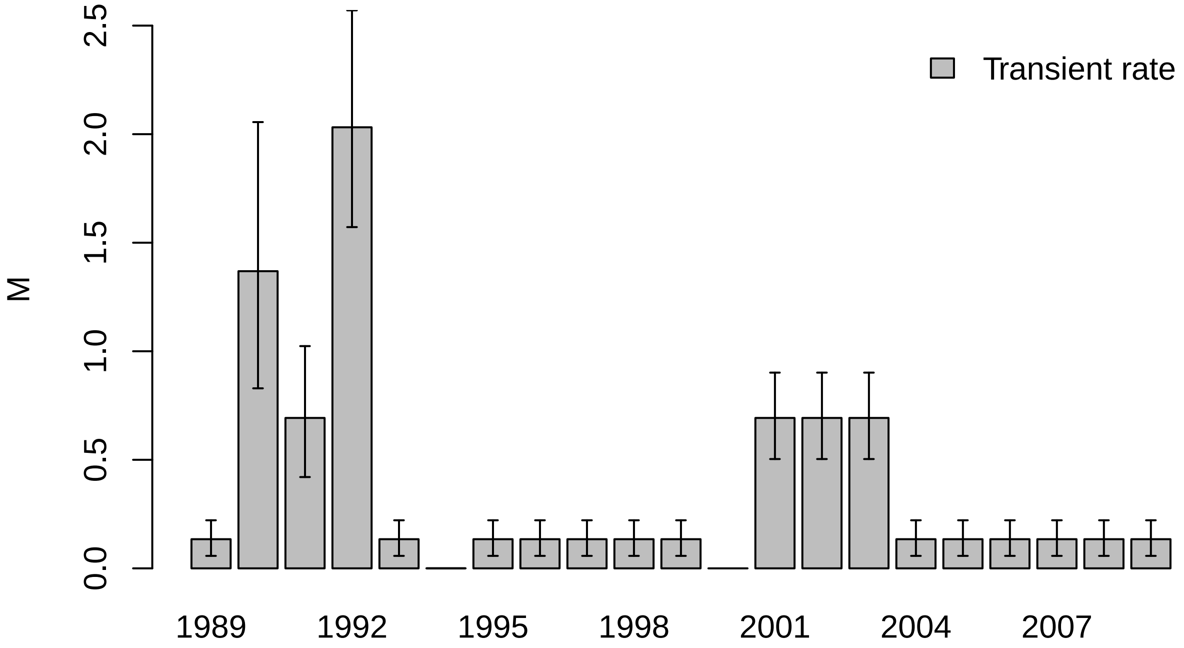


Figure 4.13: Median transient-related apparent mortality rates, with associated 90% probability intervals.

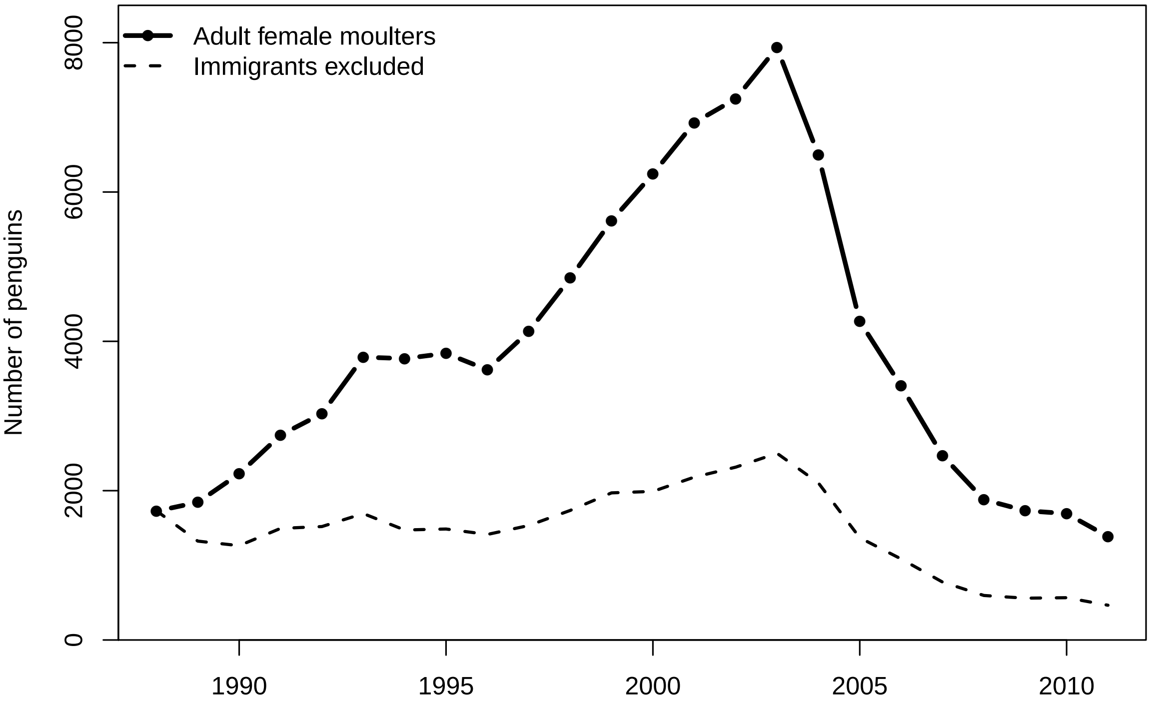


Figure 4.14: The fitted adult female penguin trajectory (dark line) is compared to results for the same demographic parameter estimates but with no immigration (thin dashed line).

Chapter 5

Penguin population projections

The results of the penguin–sardine model presented in Chapter 4 provide several interesting insights regarding recent penguin population dynamics at Robben Island. However, the main purpose for the development of the model is to provide information on possible future trends in penguin abundance, and how these may be affected by fishing pressure. In order to accomplish this, the amount of sardine likely to be available to penguins in the future must be considered. Plausible sardine abundance trajectories are provided by the latest available operational management procedure (OMP) for small pelagics (Section 5.1). Furthermore, assumptions must be made concerning the spatial distribution of sardine biomass in the future (Section 5.2). Projected penguin numbers are calculated using the assumed relationship between penguin mortality and sardine abundance (Section 5.3). Results of the penguin population projections are presented in Section 5.4. Sensitivity of these results to various model assumptions is explored in Section 5.5. The chapter concludes with a discussion of the results (Section 5.6).

5.1 Linkage with the small pelagic OMP

A key aspect to the penguin–sardine model is the assumed relationship between adult penguin annual mortality and sardine abundance (Section 4.2.2). In the base case model, this mortality is taken to depend on the sardine 1+ biomass west of Cape Agulhas estimated in the November survey (Section 4.2). Future sardine abundance is dependent on future fishing mortality. Distributions of plausible future sardine abundances under different fishery management options[1] are

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[1] That is, harvest control rules (Rademeyer *et al.* 2007).

generated with the operating models that underpin the testing of OMPs for sardine and anchovy (de Moor and Butterworth 2012b).

A brief history of the management of the South African sardine and anchovy resources is described in Section 1.5.2. The management procedure adopted in December 2012, known as Interim OMP-13 (de Moor and Butterworth 2012c), has been used to supply a distribution of plausible projected sardine survey abundances (Figure 5.1).

The directed sardine total allowable catch (TAC) specified for each year y is calculated as a function of B_{y-1}, the sardine 1+ biomass estimated in the November survey of the previous year, as follows (both TAC_y and B_{y-1} are expressed in thousands of tonnes):

$$\text{TAC}_y = \begin{cases} 0 & \text{if } 0 \leq B_{y-1} \leq 75 \\ 90\left(\dfrac{\frac{B_{y-1}}{300} - 0.25}{1 - 0.25}\right)^2 & \text{if } 75 < B_{y-1} \leq 300 \\ 90 & \text{if } 300 < B_{y-1} \leq 1\,000 \\ 0.09B_{y-1} & \text{if } 1\,000 < B_{y-1} \leq 5\,555 \\ 500 & \text{if } B_{y-1} \geq 5\,555 \end{cases} \tag{5.1}$$

This TAC value (indicated graphically by the solid curve in Figure 5.2) is modified by a constraint on the maximum amount by which it may decrease annually, in the interest of industry stability. This constraint, applied only when $B_{y-1} > 300$, specifies that if $\text{TAC}_{y-1} < 255$ then TAC_y should not be less than 80% of TAC_{y-1}, otherwise TAC_y should not be less than 204. The addition of linear smoothing in the range $300 < B_{y-1} < 700$ ensures continuity as B_{y-1} approaches 300 from above. The application of this constraint, and associated linear smoothing, is illustrated by the dashed lines in Figure 5.2 for two cases, $\text{TAC}_{y-1} = 180$ and $\text{TAC}_{y-1} \geq 255$. Furthermore, if $B_{y-1} < 300$ then only half of the TAC specified by equation (5.1) is awarded initially. An additional allocation is made in June, dependent on the result of the May recruitment survey.

Note that it is assumed that the link between projected sardine biomass and penguin abundance is unidirectional. Under this assumption, a change in penguin abundance does not substantially affect sardine mortality as a result of increased or decreased predation. The distribution of projected sardine abundances for any particular management option can thus be calculated independently of the penguin population dynamics.

The assumption that a change in penguin abundance does not substantially affect sardine production is justified as reasonable for the following reasons. African penguins consume approximately 1.2 tonnes of prey per pair per year, comprising mostly sardine and anchovy (Crawford *et al.* 1991). As about 19 000 pairs currently breed along the South African coast (Crawford *et al.* 2012), the total consumption of forage fish by penguins amounts to roughly 23 000 tonnes per year. The contribution of sardine to the total prey consumption is difficult to estimate as all recent diet studies have taken place only during the breeding season when anchovy forms the principle component of the penguin diet (Crawford *et al.* 2011a). Nevertheless, this amount is negligible compared to the total sardine annual production which, for example, is estimated to have been approximately 1.3 million tonnes in 2011 (de Moor and Butterworth 2012a).

The reason for calculating projected penguin numbers is to evaluate which potential OMPs for sardine and anchovy satisfy the objective of an ecosystem approach to fisheries (EAF) of not having an excessively negative impact on penguins. In theory, a range of candidate OMPs could be tested, and only those which satisfy this EAF criterion would be considered for implementation as the adopted OMP.

5.2 Future sardine biomass spatial distribution

In addition to the total annual abundance of sardine over the projection period, the proportion of sardine located to the west of Cape Agulhas is required for the calculation of future adult penguin annual mortality. As described above, plausible future sardine biomass trajectories are obtained from the operating model of sardine biomass, assuming future catches are generated using Interim OMP-13. The sardine resource is currently managed as a single stock[2]. As such, the operating model used when developing the OMP provides a single overall sardine abundance for

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[2] An alternative OMP to take account of the possibility that there are two sardine populations (a west coast stock and a south coast stock) is under development (de Moor and Butterworth 2013a,b).

each year with no spatial disaggregation. This means that an assumption is required concerning the proportion of sardine biomass located to the west of Cape Agulhas in future years.

As discussed in Section 1.4.1, the proportion of sardine observed to the west of Cape Agulhas has been rather variable over the history of the small pelagic hydroacoustic surveys (Figure 5.3). The mean proportion to the west from 1984 to 1998 was 74%. This dropped to a mean of just 26% over the years 1999–2007, but has since increased to 48% for 2008–2012.

In the simulations which follow (Section 5.4), two alternatives regarding the future spatial distribution of sardine biomass are considered. Historic proportions of sardine biomass observed west of Cape Agulhas in the November hydroacoustic surveys are split into two sets: 1984–1998 and 1999–2012. This essentially provides two scenarios for penguin population projections. In the more optimistic scenario, sardine is assumed to return to a spatial distribution similar to that observed prior to 1999, resulting in a higher proportion of sardine being available to the penguins on average. In the alternative scenario, the sardine distribution is assumed to remain similar to that observed thus far in the twenty-first century.

For each year of each of the simulated projections, a value is chosen at random from the relevant set of historically observed proportions. This value is then multiplied by the total sardine abundance for that year. The first scenario (1984–1998 proportions) clearly results in a higher biomass of sardine available to Robben Island penguins than the second scenario (1999–2012 proportions) on average (Figure 5.1). The biomass index of $B = 1$ corresponds to the maximum sardine 1+ biomass previously observed to the west of Cape Agulhas (1 343 thousand tonnes in 2003). The horizontal axis has been truncated at $B = 2$ so that the different shapes of the distributions for smaller values of B are more readily apparent.

5.3 Projected penguin numbers

A distribution of ten-year penguin population trajectories is calculated from 1 000 plausible future sardine abundance trajectories for a particular fishery management option, given an assumption regarding the proportion of sardine to the west of Cape Agulhas in the future. From an ecological perspective, the most conservative fishery management decision is when fishing is suspended entirely. Distributions of projected sardine biomass indices indicate that on average more fish would be available to Robben Island penguins under a "no catch" scenario compared to under Interim OMP-13 (Figure 5.4).

The calculations for the projected penguin population dynamics are analogous to equation (4.2). For each projection k, the following equations give the number of penguins in year $y+1$ in each age class a:

$$N_{k,y+1,a} = \begin{cases} \frac{1}{2} H \exp\left(-M_{k,y}^{4/12}\right) \sum\limits_{a=a^*}^{A} N_{k,y,a} & \text{if } a = 1 \\ N_{k,y,a-1} \exp\left(-M_{k,y}\right) & \text{if } 2 \leq a < A \\ \left(N_{k,y,a-1} + N_{k,y,a}\right) \exp\left(-M_{k,y}\right) & \text{if } a = A \end{cases} \tag{5.2}$$

Note that major oil spills are not explicitly taken into account in the future, and no immigration term is included in the projection equations. For simplicity, the reproductive success factor H is calculated as the mean of the estimated H_y values over the years of the model fit ($H = 0.92$, see Figure 4.8e). The adult penguin mortality rate is calculated as follows:

$$M_{k,y} = M_{\min} + f_S\left(B_{S,k,y}\right) \mathrm{e}^{\sigma_{k,y} X_{k,y}} \tag{5.3}$$

Here, f_S is the sardine–mortality relationship in equation (4.15) with parameter values as given in Table 4.2. $B_{S,k,y}$ is the index of sardine abundance available to penguins. Natural variation about the annual mortality rate predicted by the sardine–mortality relationship (the curve in Figure 5.5) is accounted for by the exponential factor in equation (5.3) (compare equations (4.8)–(4.10)). Here, $X_{k,y}$ is a random number drawn from the standard normal distribution, and the standard deviation $\sigma_{k,y}$ of the random effect is calculated for each projection k and year y as:

$$\sigma_{k,y} = \sqrt{\exp\left[\tilde{\sigma}/f_S\left(B_{S,k,y}\right)\right]^2 - 1} \tag{5.4}$$

Strictly, uncertainty about the value of $\tilde{\sigma}$ should be taken into account when projecting into the future. However, results obtained using selected fixed values for $\tilde{\sigma}$ are nonetheless informative.

Table 4.1 provides the values of the fixed parameters a^*, A, and $M_{\min}$.

5.4 Results

Ten-year penguin abundance trajectories have been calculated for two different assumptions concerning the spatial distribution of future sardine biomass (Figure 5.6). In each case, 1 000 plausible sardine observed 1+ biomass trajectories have been generated using the underlying operating model for sardine and anchovy, assuming either Interim OMP-13 or no future fishing. The median penguin population trajectories (in terms of adult females) and 80% probability intervals are indicated in each diagram. A dashed line indicates the median penguin abundance trajectory for the corresponding sardine 1+ biomass projections without fishing.

In the first column of Figure 5.6, future proportions of sardine west of Cape Agulhas are drawn at random from the set of 1984–1998 proportions. In the second column, future proportions are drawn from the 1999–2012 set.

A different value of $\tilde{\sigma}$ is used in each row. In the middle row, the maximum likelihood estimate of $\tilde{\sigma} = 0.088$ (see Table 4.2) is used in equation (5.4). For the top row, the value used is $\tilde{\sigma} = 0.063$, which is two standard errors below the maximum likelihood value (see Section 4.3.4). This was chosen to reflect the minimum plausible value for $\tilde{\sigma}$ that is "consistent" with the data, which gives more optimistic results in terms of projected penguin numbers. For the bottom row, the value used is $\tilde{\sigma} = 0.114$, which is two standard errors above the maximum likelihood estimate. This reflects an upper bound on plausible values for $\tilde{\sigma}$. This value gives more pessimistic results.

A key statistic of interest is the median ten-year projection of the number of observable adult penguins, which is comparable with the historic adult moult count time-series (Table 2.2) to which the model is fitted. The ratio of this statistic to the most recent adult penguin moult count as predicted by the model gives the proportional change in penguin numbers over the projection period. This ratio can be compared for different fishery management options and also for alternative sardine spatial distribution assumptions. Sensitivity of this ratio to different model assumptions can also be readily investigated (see Section 5.5).

For each median trajectory in Figure 5.6, the ratio of penguin numbers in 2022 to those in 2012 is calculated (Table 5.1). This ratio gives the median increase in penguin numbers over the ten-year projection period. The ratio of median projected penguin abundance in 2022 with fishing to that without fishing is also tabulated.

5.5 Sensitivity tests

The base case penguin–sardine model includes several assumptions and constants for which realistic values have been chosen. The sensitivity of the results to these choices needs to be checked. The following variations to the base case model are considered:

(a) Relative detectability of juvenile moulters p_{J}

(b) Age of first breeding a^*

(c) Standard error of the logarithms of the juvenile proportions σ_{J}

(d) Maximum breeding success rate $H_{\max}$

(e) Proportion of moulters susceptible to observation q_{M}

(f) Overdispersion factor for the tag-recapture likelihood $\hat{c}$

(g) Numbers of oiling-related deaths

(h) Minimum adult mortality rate $M_{\min}$

Importance of the effect of these variations is judged on the median ten-year projections of penguin abundance using future sardine biomass levels generated assuming Interim OMP-13 (Table 5.2).

5.6 Discussion

5.6.1 Base case results of linkage with the pelagic OMP

In all cases, the impact of fishing on penguin numbers through the reduction of total sardine biomass by the fishery is rather small, especially when compared to other factors influencing the dynamics (Figure 5.6). The predictions considered the most likely should be based on the best estimate of $\tilde{\sigma}$. For that value ($\tilde{\sigma} = 0.088$), the median projection for penguins assuming future spatial distributions of sardine similar to 1984–1998 is virtually flat (Table 5.1 and Figure 5.6c). Even in the absence of fishing, only a small increase in penguin abundance is predicted. This result may seem surprising, as the penguin population grew rapidly in the early- to mid-1990s (before the sardine boom) at sardine biomass levels which were similar to those now projected. However, as discussed in Section 4.4, the main reason for the growth in the Robben Island penguin population over that period in the 1990s was immigration, not any substantial excess of the reproduction rate over the death rate (see Figure 4.14).

One explanation for the relatively small projected effect of fishing on penguins is that the design of OMP-13 is relatively conservative (by global standards) with regard to the sardine resource (de Moor and Butterworth 2012c). Under simulation testing, the average sardine biomass at the end of the 20-year projection period is 75% of the carrying capacity, and 45% higher than the 2011 biomass.

Figure 5.5 indicates that penguin mortality increases only when the sardine biomass index drops below about $B = 0.25$. For the distributions of sardine biomass trajectories in Figure 5.4, the proportion of indices in each set that is below this critical value is given in Table 5.3. When assuming a future spatial distribution of sardine similar to 1999–2012, 52% of the projected distribution that is generated assuming Interim OMP-13 is below the index $B = 0.25$, resulting in a drop in adult survival rate. Hence, the natural death rate frequently exceeds the reproduction rate, and consequently the penguin population declines (Figure 5.6d).

In contrast, when assuming that the future spatial distribution of sardine is similar to that of the 1984–1998 period, only 13% of the projected sardine distribution lies below the critical value. In this case, the sardine biomass is at a level where the average penguin adult survival rate is as high as possible most of the time, and population abundance is stable in median terms (Figure 5.6c). Furthermore, sardine abundance higher than this would provide negligible additional benefit to penguins, as average survival does not increase with increasing biomass above approximately $B = 0.25$.

The differences between the proportions of indices in Table 5.3 which are below $B = 0.25$ with and without fishing (12% for 1999–2012 proportions and 7% for 1984–1998 proportions) are rather small compared to the differences between the proportions resulting from alternative assumptions regarding spatial distribution (39% with fishing and 34% without fishing). This is clearly evident in Figure 5.4. This explains why in Figure 5.6 the effect of fishing is rather small compared to the effect of different spatial distribution assumptions.

If $\tilde{\sigma}$ is smaller, the variation about the relationship between sardine biomass and penguin adult mortality (Figure 5.5) is less. This results in fewer instances when adult annual mortality reaches high values. Consequently, there is a greater likelihood of penguin population increase for $\tilde{\sigma} = 0.063$ (Figure 5.6a), if the future proportion of sardine biomass west of Cape Agulhas returns to the 1984–1998 average. In contrast, larger values of $\tilde{\sigma}$ allow more variation around the predicted sardine biomass–penguin mortality relationship. This results in more frequent high values of adult annual mortality and subsequent population decline, even when the proportion of sardine biomass west of Cape Agulhas is favourable (Figure 5.6e). Indeed, this last result, which applies even in the absence of fishing, suggests that the associated higher value of $\tilde{\sigma} = 0.114$ is probably outside the plausible range.

Fishing stress and consequent reduced ecosystem biomass may result in environmental anomalies having a more severe effect than would be the case in a pristine ecosystem (Watermeyer *et al.* 2008). The recent low sardine recruitment in several consecutive years combined with a possible increased adult sardine mortality (not accounted for by the fishery) have resulted in a marked decline in the resource (Coetzee *et al.* 2008b). It may be that the disproportionately high fishing pressure on the west coast led to the current relatively low sardine biomass proportion west of Cape Agulhas (Coetzee *et al.* 2008b), exacerbating the situation for Western Cape penguins.

5.6.2 Sensitivity tests

Of the variations considered on the base case penguin model where likelihood values are comparable, the following resulted in a higher likelihood (i.e. a lower negative log-likelihood, see Table 5.2):

(a) minimum allowed age at first breeding reduced from $a^* = 4$ to $a^* = 3$ ($\Delta(-\ln L) = 5.95$ compared to the base case),

(b) proportion of moulters susceptible to observation reduced from $q_{\mathrm{M}} = 0.9$ to $q_{\mathrm{M}} = 0.8$ ($\Delta(-\ln L) = 3.45$),

(c) oiling related deaths down 50% from the values given in Table 2.6 ($\Delta(-\ln L) = 15.59$), and

(d) minimum allowed adult annual mortality reduced from $M_{\min} = 0.04$ to $M_{\min} = 0.03$ ($\Delta(-\ln L) = 5.71$).

Each of these variations works to give the model more flexibility by allowing a faster rate of increase of the population, either through more reproduction or higher survival. The values assumed for these fixed parameters in the base case model (Table 4.1) are nevertheless seemingly more realistic, for the following reasons:

(a) As discussed in Section 4.1.2, penguins younger than four years have been observed breeding relatively seldom, while a substantial proportion do not breed before age five (Whittington *et al.* 2005a). Thus the choice of $a^* = 4$, reflecting the median age of first breeding, seems sensible.

(b) There is some uncertainty concerning the proportion of the Robben Island penguin population that is reflected in the moult count, which includes only birds moulting along the coast (Wolfaardt *et al.* 2009a). Also, this proportion may vary from year to year. However, given that researchers maintain that the Robben Island moult count captures the bulk of the population (R. Crawford, pers. comm.), a value of $q_{\mathrm{M}} = 0.8$ seems somewhat low.

(c) The numbers of penguins affected by the two major oil spills are well documented (Section 2.3). It is unlikely that the values used are inaccurate by as much as 50%.

(d) An annual adult mortality rate of $M = 0.03$ corresponds to an annual survival rate of $S = 0.97$, which would seem remarkably high for a small penguin.

Of primary importance in the context of this work is the change in penguin abundance over the ten-year projection relative to the base case, which coincidentally is almost flat. Of the variations giving a higher likelihood mentioned above, the only one for which the ten-year projection is substantially different to the base case is $M_{\text{min}} = 0.03$, which results in an 11% increase in penguin abundance. Correspondingly, $M_{\text{min}} = 0.05$ results in a 10% decrease in penguin abundance.

Larger values of the overdispersion coefficient $\hat{c}$ for the tag-recapture data result in an increased projected penguin abundance, while smaller values result in a decreased projected abundance. Doubling the value of the standard error of the logarithms of the proportions of juveniles in the population to $\sigma_{\text{J}} = 0.2$ results in an 8% decrease in projected penguin abundance.

The only really large difference in the projected change in penguin abundance of the variations tested is for the relative detectability of juveniles in the moult count $p_{\text{J}} = 0.8$, which results in a substantial increase of 48%. While the base case choice of $p_{\text{J}} = 0.9$ was chosen on the basis of seeming reasonability rather than being estimated from data, the negative log-likelihood value for this variation indicates that lower values of p_{J} are considerably less likely.

Table 5.1: Ratios of projected adult female penguins in 2022 to those in 2012 with and without fishing, as well as the ratio of these two ratios, for alternative assumptions regarding future spatial distributions of the sardine biomass and for a range of values of $\tilde{\sigma}$.

	1984–1998 sardine distribution			1999–2012 sardine distribution		
	With fishing	No fishing	Ratio	With fishing	No fishing	Ratio
$\tilde{\sigma} = 0.063$	1.61	1.85	0.87	0.37	0.57	0.65
$\tilde{\sigma} = 0.088$	1.00	1.15	0.87	0.30	0.42	0.71
$\tilde{\sigma} = 0.114$	0.59	0.63	0.94	0.23	0.32	0.74

Table 5.2: Sensitivity to various model assumptions of ten-year adult female penguin projections. Proportions similar to 1984–1998 were assumed for the sardine biomass to the west of Cape Agulhas in the future, and $\tilde{\sigma} = 0.088$.

Variation	Base case	2012	2022	Ratio	$\Delta(-\ln L)$
Base case		1024	1021	1.00	
$p_J = 0.8$	1.0	1056	1560	1.48	−27.91
$a^* = 3$	4	1017	1005	0.99	5.95
$a^* = 5$	4	1120	1112	0.99	−10.95
$\sigma_J = 0.2$	0.1	1000	924	0.92	−10.52
$H_{\max} = 1.5$	1.8	1022	1007	0.99	−3.63
$q_M = 0.8$	0.9	1028	1032	1.00	3.45
$q_M = 1.0$	0.9	1021	1012	0.99	−3.54
$\hat{c} = 4$	5.57	1029	968	0.94	−2 399.13
$\hat{c} = 7$	5.57	1022	1069	1.05	1 244.10
Oiling-related deaths up 50%		1013	1020	1.01	−21.47
Oiling-related deaths down 50%		1039	1029	0.99	15.59
$M_{\min} = 0.03$	0.04	1029	1146	1.11	5.71
$M_{\min} = 0.05$	0.04	1018	917	0.90	−6.04

Table 5.3: Proportions of indices of projected sardine biomass west of Cape Agulhas below $B = 0.25$ for alternative assumptions regarding future spatial distributions of the sardine biomass, with and without fishing (see Figure 5.4).

	With fishing	No fishing	Difference
1999–2012 proportions	0.52	0.40	0.12
1984–1998 proportions	0.13	0.06	0.07
Difference	0.39	0.34	

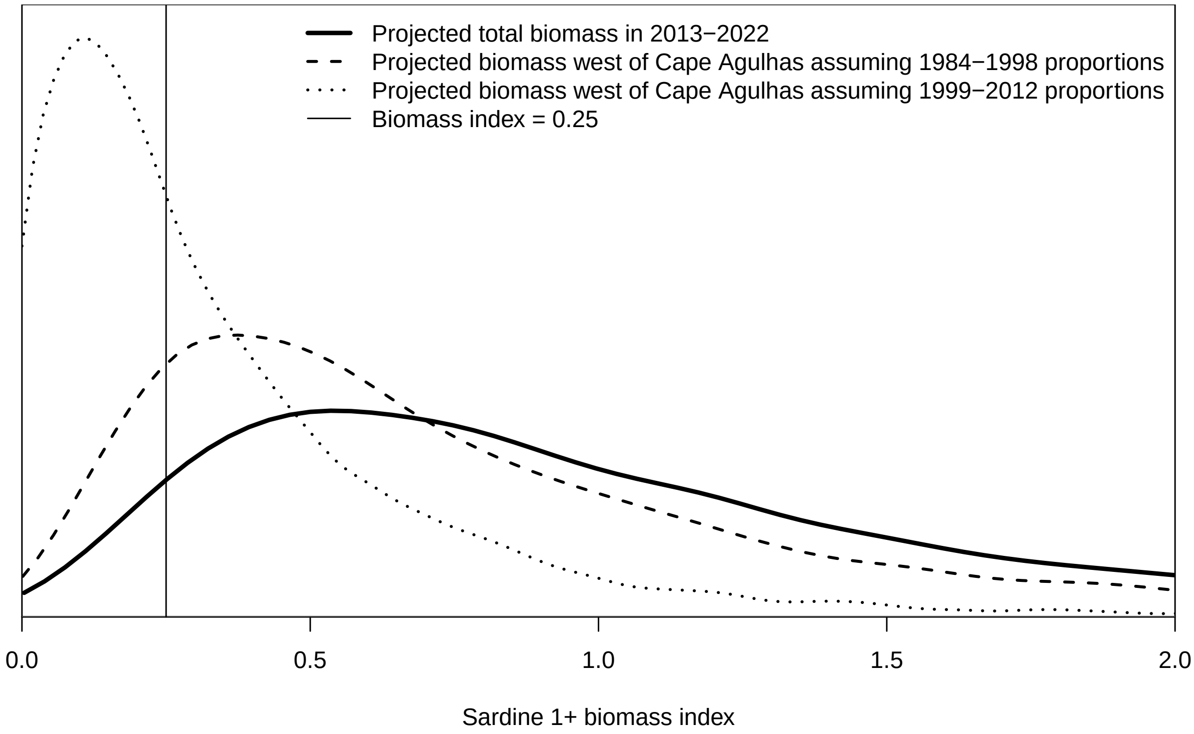

Figure 5.1: Distributions of ten-year projections of total sardine observed 1+ biomass indices assuming Interim OMP-13 (solid line), the amount to the west of Cape Agulhas assuming 1984–1998 proportions (dashed line), and the amount to the west of Cape Agulhas assuming 1999–2012 proportions (dotted line).

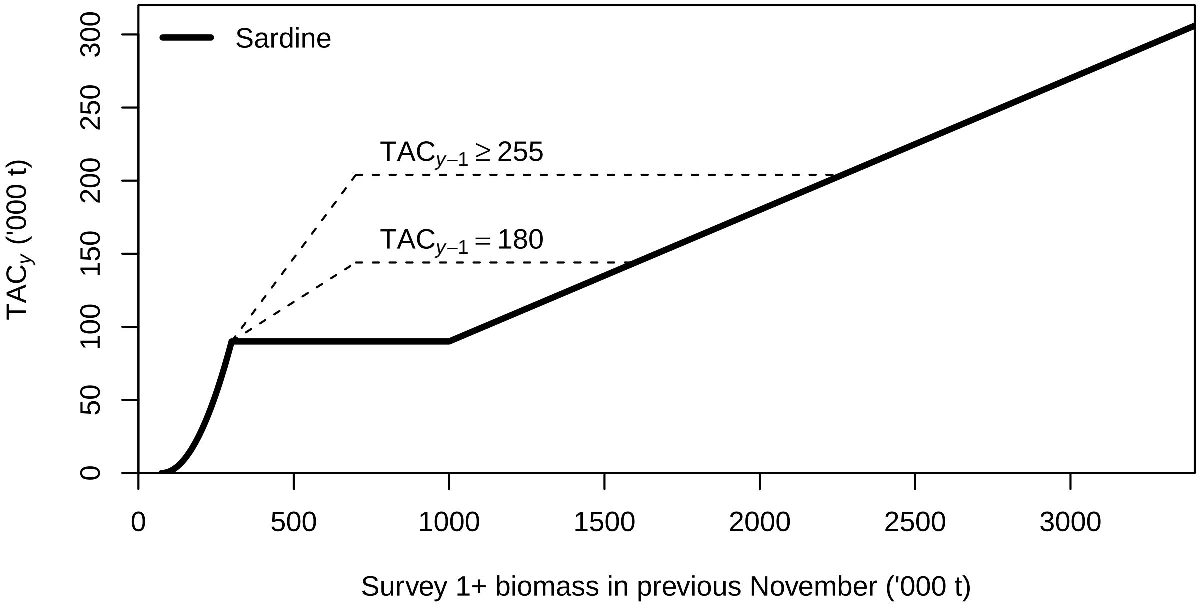

Figure 5.2: Harvest control rule and constraints under Interim OMP-13 for the directed sardine TAC as a function of the sardine 1+ biomass estimated in the November survey of the previous year. The TAC is constrained by a maximum of 500 000 tonnes. The dashed lines reflect the constraint on the permitted decrease from TAC$_{y-1}$.

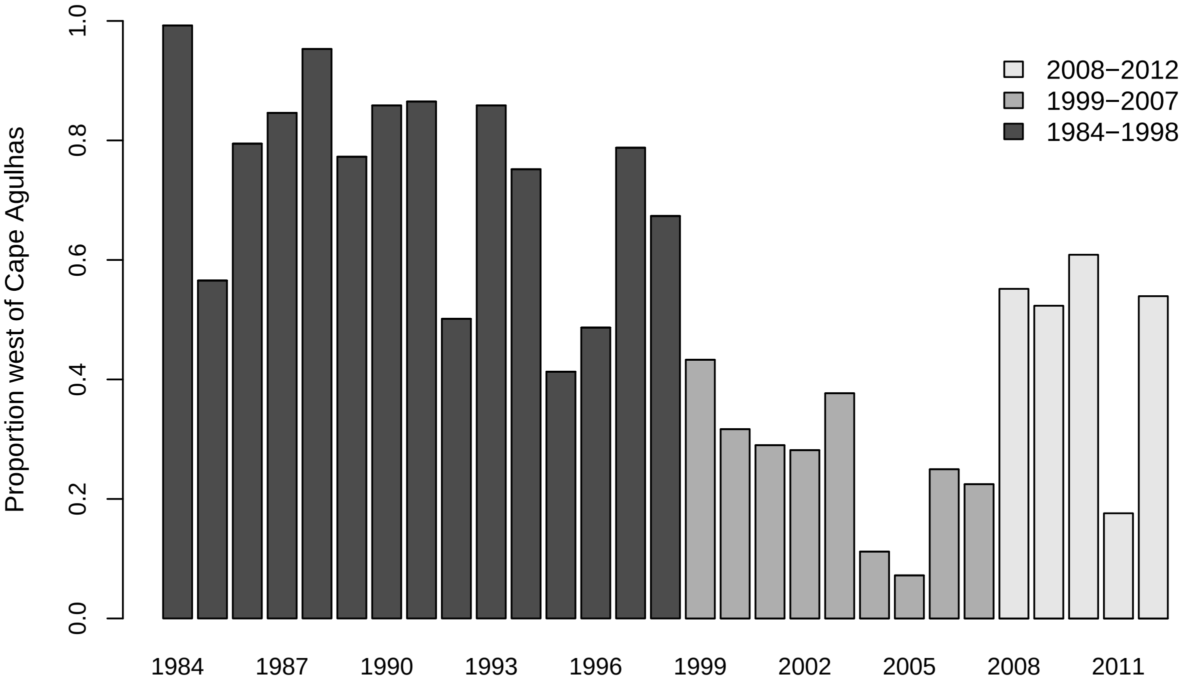

Figure 5.3: The proportion of 1+ sardine biomass observed to the west of Cape Agulhas in the annual November survey (see Table 2.7).

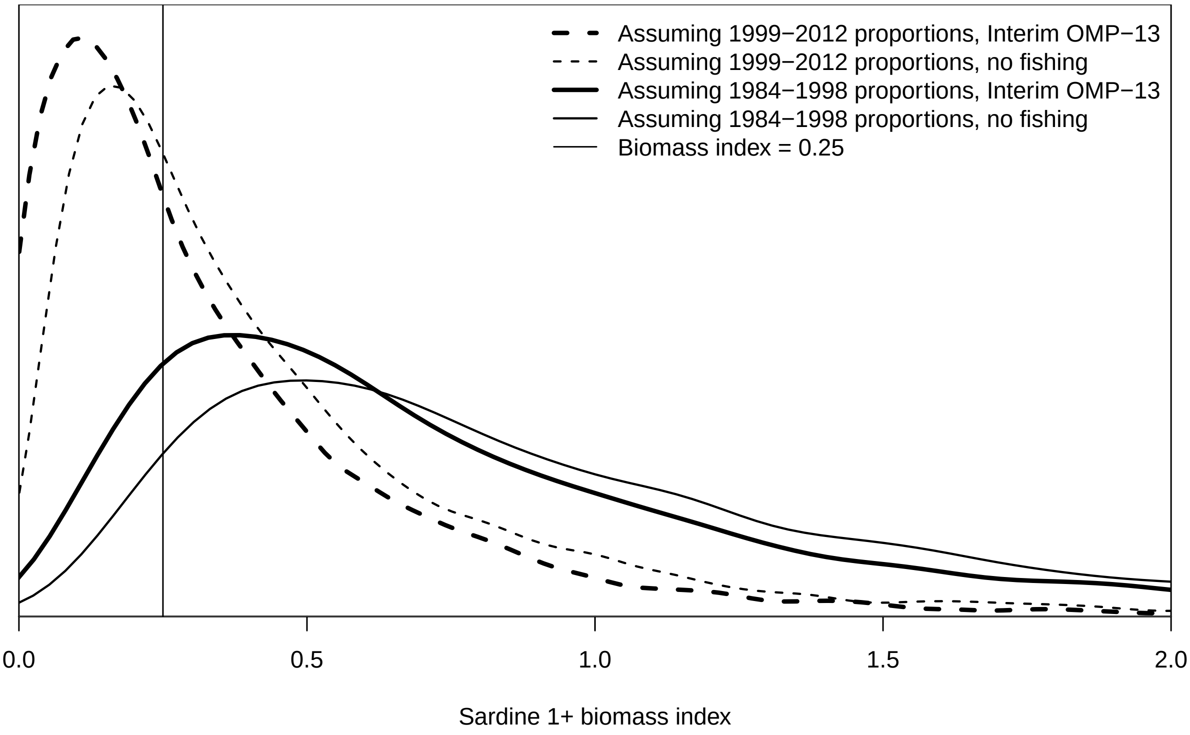

Figure 5.4: Distributions of ten-year projections of sardine observed 1+ biomass indices west of Cape Agulhas assuming 1984–1998 proportions (solid lines) and assuming 1999–2012 proportions (dashed lines). The thick lines are for projections assuming Interim OMP-13 and the thin lines are for projections assuming no future fishing.

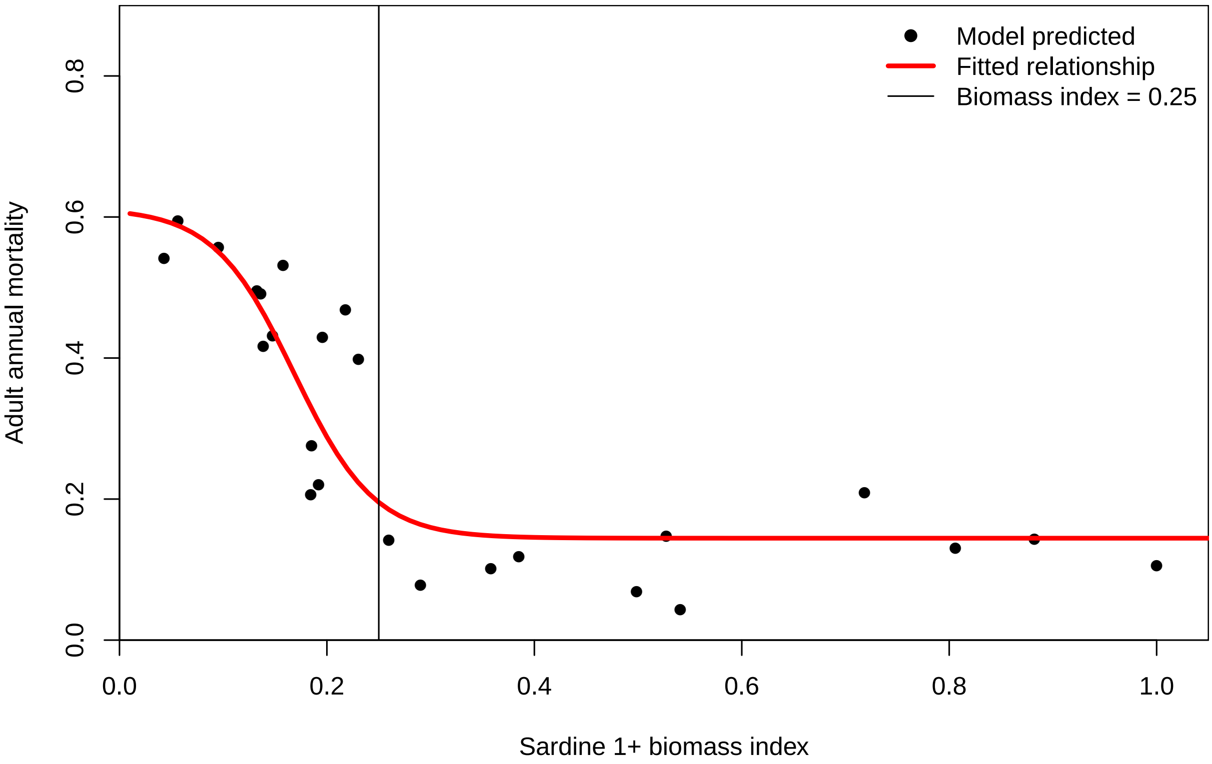

Figure 5.5: The fitted relationship between the sardine 1+ biomass index and penguin adult mortality. One-quarter of the maximum observed biomass is indicated.

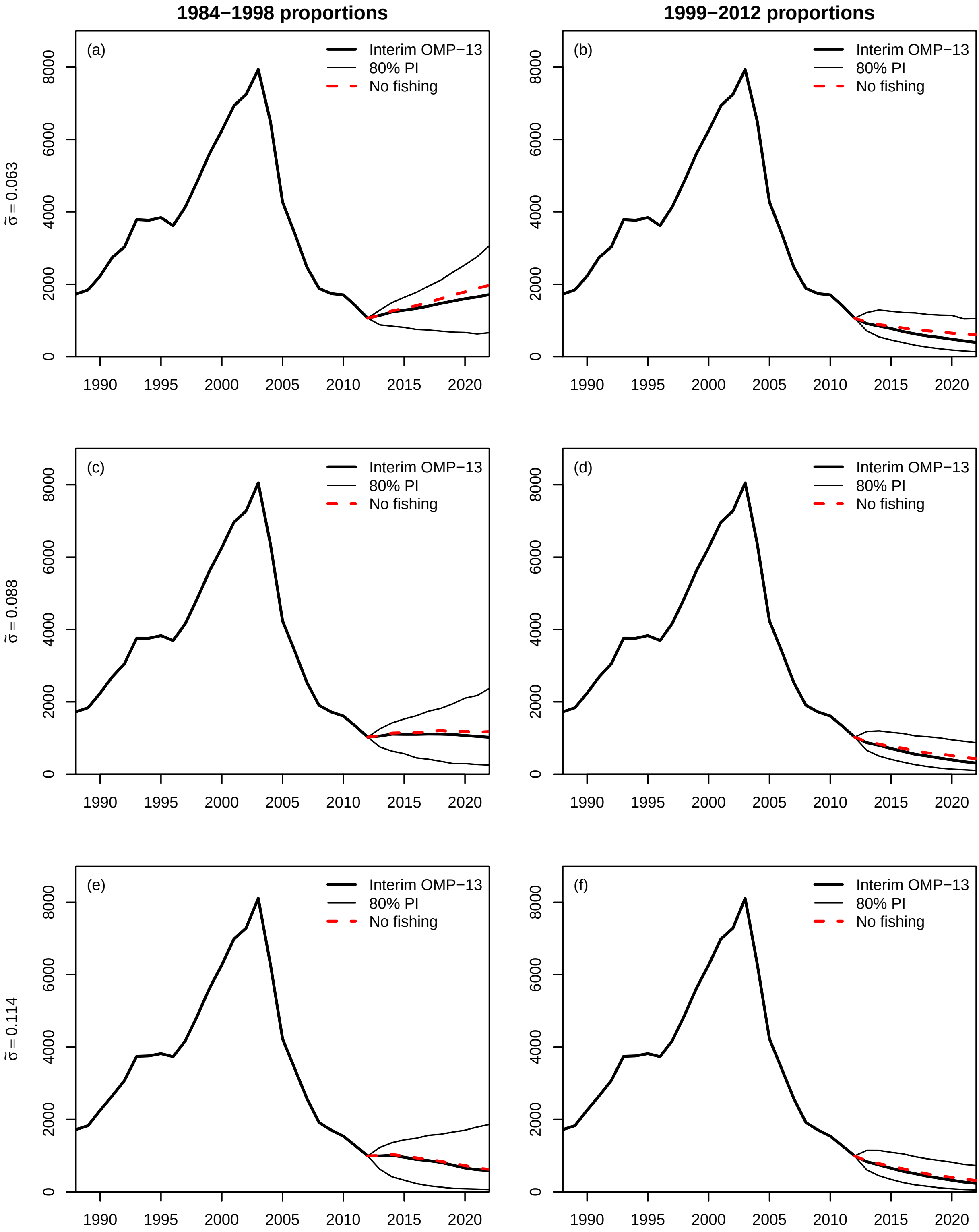

Figure 5.6: Comparison of median projected penguin numbers with and without fishing for alternative future sardine distributions and for a range of plausible values of $\tilde{\sigma}$. The 80% probability intervals are indicated for the projections under Interim OMP-13.

Chapter 6

Conclusions

In this final chapter, the main results of this project are summarized and discussed in Section 6.1. Directions in which this research might be extended and refined in the future are suggested in Section 6.2. The thesis concludes with some brief final remarks (Section 6.3).

6.1 Thesis summary

6.1.1 Moult count aggregation

A new method was developed for calculating aggregate numbers of moulting penguins over an annual cycle from counts taken at approximately two-week intervals (Section 2.1.1). This method, which involves fitting Gaussian functions, seems more robust than the linear interpolation scheme used previously, especially when no counts are available at key times of the moult cycle. An additional benefit of the new method is that an estimated coefficient of variation (CV) is available for each year, which while coarse gives an indication of the relative reliability of each annual moult count estimate.

6.1.2 GLMs for penguin demographics and foraging behaviour

General linear models (GLMs) were used to explore the extent of relationships between demographic parameters and foraging behaviour of penguins and forage fish abundance at four island breeding colonies (Chapter 3). The response variables were penguin fledging success, breeder to moulter ratio, active to total nests ratio, annual adult survival rates, and foraging performance.

The explanatory variables were the annual sardine and anchovy catches taken in the vicinity of each penguin colony and the pelagic fish biomass estimates from hydroacoustic surveys. May recruit biomass and November 1+ biomass of sardine, anchovy, and the two species combined were all considered.

GLM parameters were estimated for a very large number of combinations of response and explanatory variables. In the majority of cases, results indicate (somewhat surprisingly) that penguins enjoy better feeding conditions when fishing pressure is higher, after taking the overall abundance of fish into account. A possible explanation for this result is that fishing vessels tend to break up large shoals of pelagic fish, and predators are more likely to encounter prey if there are many small shoals rather than few large shoals (Clark 1976).

The indices used for overall fish abundance were 1+ biomass and recruit biomass survey estimates aggregated over several strata. These indices may be somewhat coarse as a measure of the amount of prey available to penguins each year, but long time-series of localized prey abundances (which may vary from month to month) are currently not available.

This work contributes to the feasibility study being conducted by the Island Closure Task Team of the DAFF Small Pelagic Scientific Working Group. The aim is to determine whether a long-term experiment would have sufficient power to detect the effects of fishery closures around penguin colonies on penguin demographics and foraging behaviour. To this end, the CVs of the standard deviations of the residuals of the response variables were estimated. These estimates are to be used in a power analysis to determine whether or not the experiment is likely to determine the impact of fishing within a reasonable period. If this proves not to be possible, the feasibility study could be continued to estimate these CVs with greater precision.

6.1.3 Penguin–fishery interaction model

A model was developed to capture the population dynamics of the Robben Island penguin colony (Chapter 4). Penguin adult survival was related to the sardine abundance observed in the November hydroacoustic survey for small pelagic fish. The 1+ sardine biomass observed to the west of Cape Agulhas was used as this provided the best relationship, and one which was better than any relationship involving anchovy. The model was fitted to adult and immature penguin annual moult counts as well as to tag data. The model allows for immigration to the Robben Island colony up to the year 2000.

Satisfactory fits to the data were obtained, producing acceptable time-series of residuals. There was some indication of a systematic trend in the differences between observed and expected numbers of re-sightings of tagged penguins, which reflects an element of incompatibility between the tag data and the moult counts.

A particular difficulty encountered in the model fitting process was the estimation of the $\tilde{\sigma}$ parameter, which determines how tightly adult survival values are distributed around the assumed relationship with sardine biomass. When using the standard ADMB program, better likelihood values were always obtained for lower values of $\tilde{\sigma}$, resulting in an unrealistically low estimate for this parameter. This procedure is however known to be statistically flawed, and the difficulty was overcome by using the ADMB-RE program, which treats adult survival and reproductive success as random effects.

The sardine biomass–penguin mortality relationship (Figure 5.5) predicts that average adult penguin mortality increases only when sardine biomass drops below a certain threshold. This threshold is estimated to be at an index of about $B = 0.25$ (one-quarter of the maximum observed biomass), which corresponds to a November survey estimate of about 336 000 tonnes west of Cape Agulhas. The relationship probably indicates that sardine is a more important prey species for penguins than anchovy, at least at certain times of the year. While diet studies indicate that anchovy accounts for the majority of consumption during the breeding season when adult penguins catch it for provisioning chicks (Crawford *et al.* 2011a), sardine may be the preferred prey of adults during spring and summer when they must gain condition in preparation for moulting and breeding. Indeed, Sherley *et al.* (2013) found that the length of time taken for chicks to fledge at Robben Island was related to the sardine biomass in the preceding November. A possible reason for the preference for sardine over anchovy is that each sardine caught is likely to be larger and more nutritious than an anchovy, thus providing a better energy return for the foraging effort exerted.

Conventionally, poor feeding conditions for seabirds are thought to primarily affect reproduction (e.g. Einoder 2009; Cury *et al.* 2011). The breeding season is usually the period when food requirements are greatest as additional foraging is necessary for provisioning chicks (Pichegru *et al.* 2009). If food within penguin foraging range of the breeding colony is scarce, adults can abstain from breeding or abort a breeding attempt, preserving themselves in anticipation of better conditions in a subsequent season.

However, no relationship was found between estimated penguin reproductive success at Robben Island and forage fish abundance. Adult survival changes appear to have had a much larger impact on the population trend than variations in breeding success. In fact, the available data indicate that breeding success may have increased on average during the past decade when the Robben Island population was in decline (Table 2.8). Furthermore, anchovy abundance has generally remained high during this period, which should have provided an adequate food source for provisioning chicks.

In a meta-analysis of seabird populations from various worldwide locations, Cury *et al.* (2011) found that breeding success was reduced when prey abundance dropped below approximately one-third of the maximum observed level. In this study, prey abundance was instead correlated with penguin adult survival. Nevertheless, a consistent pattern is that in both studies seabirds exhibit a negative response only once prey abundance drops below a relatively low level. Additional prey availability above this threshold provides little, if any, additional benefit to the birds.

While the result that prey availability has a larger effect on adult survival than on breeding success is surprising, it is not unprecedented. Sandvik *et al.* (2005) found through a tag-recapture analysis that prey abundance affected adult survival in some seabird species in the western Barents Sea. They note that a decrease in adult survival is likely to have a dramatic effect on the population of a longer-lived species, as seems to have been the case for the African penguin.

The analyses suggest that the rapid growth of the Robben Island colony during the 1990s can be attributed almost entirely to immigration (Figure 4.14). Thus without immigration, the population would have grown very little even in the years of high sardine abundance. This is seemingly because there is minimal additional benefit to penguin adult survival when sardine biomass increases above about a quarter of the maximum level that has been observed. This last result suggests that Robben Island offers a marginal breeding location for penguins, even under optimal feeding conditions. As it appears that the colony was barely self-sustaining even during periods when sardine biomass was high, it may be unreasonable to expect any substantial growth in penguin numbers at the island if the conditions of the last two decades persist, unless additional birds again immigrate from elsewhere.

There are several reasons which could explain why the Robben Island penguin population increased little apart from as a result of immigration. Most immigrants were likely to be pre-breeders, and first-time breeders are expected to have a relatively low success rate, improving in subsequent years as partners gain experience (Crawford *et al.* 2000a; Wolfaardt *et al.* 2008c). The two major oil spills off the west coast caused great disruption to the population and the subsequent reproductive performance of penguins which had been oiled was negatively affected (Wolfaardt *et al.* 2008c; Sherley 2010). Finally, most penguins at the colony nest under vegetation, as much of the soil is too sandy for constructing stable burrows. Evidence that breeding success at surface nests is lower than that for artificial nest boxes or nests in buildings suggests that vegetation does not provide optimal nesting habitat for penguins (Sherley 2010). Surface nests may be more susceptible to predators such as feral cats and kelp gulls (Underhill *et al.* 2006), especially if guarding adults vacate their nests for some reason (e.g. to alleviate heat stress). At Dassen Island, Frost *et al.* (1976) found that diurnal temperature variation was lower for both air and eggs in burrow nests than in surface nests. Air in burrows was substantially cooler during the day, and eggs in burrows were kept warmer, both of which are advantageous.

6.1.4 Penguin population projections

A method was developed for calculating projections of the Robben Island penguin population using adult survival rates based on future sardine abundances predicted under the operational management procedure (OMP) for sardine and anchovy and its associated base case operating model (Chapter 5). Scenarios considered included plausible future fish abundance series both with and without fishing. Projected penguin populations were calculated for different assumptions concerning the proportion of sardine located to the west of Cape Agulhas in the future.

Sensitivity of the projected penguin numbers to various model assumptions and the values of parameters fixed on input was investigated. Results were found to be most sensitive to the value chosen for $\tilde{\sigma}$ (which specifies the degree of variability around the assumed sardine biomass–penguin mortality relationship) and p_{J} (which specifies the relative detectability of juveniles in the moult count compared to adults).

Analysis of the distributions of plausible future sardine biomass trajectories predicted by the OMP shows that fishing is likely to have a relatively small impact on future penguin abundance when compared to the effect of different sardine spatial distributions. This is because the proportion of total sardine allowed by the OMP to be captured annually is relatively small, whereas natural mortality is relatively high for this short-lived species of forage fish.

A question which arises is to what extent the results obtained for Robben Island may be representative of population projections for other African penguin colonies. Noting the importance of alternative assumptions regarding the spatial distribution of sardine, it seems reasonable to expect that trends at other west coast penguin colonies (Dassen Island and Saldanha Bay) will be broadly similar to those at Robben Island. Similar trends should not be expected at south coast colonies (Stony Point and Dyer Island) or Algoa Bay colonies (Bird Island and St Croix Island). Such “regionally coherent trends” have been observed at South Africa’s penguin colonies over the past decade (Underhill *et al.* 2006; Crawford *et al.* 2011a).

This project provides a framework for making an objective assessment of the impact of fishing from an EAF perspective by evaluating its effect on the population trend of a dependent predator. Under this framework, the impact of fishing on a predator caused by any management procedure suggested for a fishery can be evaluated. The goal is to prevent not only overfishing in the conventional single-stock assessment context, but also “ecosystem overfishing” (Powers and Monk 2010), using penguin performance in this case as an ecological indicator of the state of the ecosystem. Avoiding such ecosystem overfishing should help to preserve both the functioning of the ecosystem as well as the productivity of the target stock.

6.2 Future research

6.2.1 Moult count aggregation

The method presented in Section 2.1.1 for deriving an estimate for the aggregate number of penguins moulting each year could be refined and made more robust. Wolfaardt *et al.* (2009a) showed that at Robben Island there is good consistency between years in the timing of the peak of the moult season and the degree of synchrony of the moult. Such prior information could be incorporated to inform on the expected shape of the fitted function, giving a more reliable result when intervals between counts are wide or the data are noisy. As the data may not warrant fitting the sum of two Gaussian curves (with six estimable parameters) in all years, a statistical selection criterion such as AIC could be used to choose the curve fitted.

6.2.2 GLMs for penguin demographics and foraging behaviour

The possible continuation of the GLM work relating penguin demographics and foraging behaviour depends on the decisions of the Island Closure Task Team and the outcome of the power analysis relating to the island closure experiment (Section 3.1).

Continuation of the small-scale acoustic surveys in the vicinity of the penguin breeding colonies at regular intervals during the breeding season could provide important additional time-series to be used as explanatory variables in the GLMs. These would potentially provide a more precise reflection of local forage fish abundance than the large-scale survey aggregates currently used.

Pichegru *et al.* (2013) note that it may perhaps be unreasonable for one to expect to detect differences between the penguin responses to food availability at Robben Island and Dassen Island resulting from small closed areas around those colonies. The reason is that the steady southward migration of fish along the west coast towards the Agulhas Bank is likely to swamp any changes in fish density caused by small-scale fishing restrictions. Furthermore, since very little fishing takes place around Bird Island even when the area is open to fishing, less contrast in penguin responses is likely to be evident in Algoa Bay, so that reliable detection of relationships for that region would likely prove more difficult.

6.2.3 Penguin–fishery interaction model

The annual nest count is an additional data series which could be incorporated into the model fit. This would provide another index of abundance in addition to the moult count time-series. However, including the nest data is not as straightforward as using the moult data. While all penguins must moult annually, they can refrain from breeding in certain years so that the further information provided by these data may be limited. This would perhaps occur if they were unable to obtain sufficient condition during the summer preceding the breeding season (Crawford *et al.* 2011a).

Another data series which could be incorporated into the model is breeding success. This could potentially be related to some forage fish abundance index. However, the advantage of this is doubtful because there is little information on the survival rate of penguins between fledging and attaining adult plumage. Limited tag data exist concerning penguins banded as chicks which might possibly be of use for the estimation of a year-dependent juvenile survival rate.

Studies on penguin breeding at both Robben Island and Dassen Island following the major oil spills of 1994 and 2000 have shown that penguins which were oiled have a lower breeding success rate than penguins which had not been oiled (Barham *et al.* 2007; Wolfaardt *et al.* 2008c; Sherley 2010). A factor accounting for this decreased productivity could be included in the model.

Tag records show that a few African penguins have lived beyond 25 years of age (Whittington and Dyer 2000), but this is very unusual. By far the majority of records in the penguin tag data set correspond to penguins which were banded at the time of the *Treasure* oil spill in 2000. A contributing factor towards the larger model estimates of annual mortality in recent years could be the advanced age of this dominant cohort of tagged birds. To investigate this, the implementation of an age-dependent mortality rate in the model could be attempted, but this would be a complex task and might be facilitated by first awaiting a longer time-series of data.

Besides the spatial distribution of the sardine biomass affecting the amount of prey available to penguins, the vertical distribution of forage fish in the water column could also be important. There is a limit to the depth to which penguins can dive when foraging. If the fish are located at a greater depth than this for substantial periods in some years, and hence are unavailable to foraging penguins, this could confound any relationship between pelagic fish abundance and penguin survival or breeding success. This hypothesis could be tested in the future if more data on the depth distribution of small pelagic fish become available.

An important process in the development of any model is the simulation testing of the estimation method. It is important to ascertain whether the estimator is capable of reliably providing the values of quantities which may be of interest. However, given that fitting the model to data proved less than straightforward, in particular as regards the $\tilde{\sigma}$ parameter, simulation testing could prove a major exercise.

The model uses a lognormal error distribution for the sardine biomass–penguin mortality relationship. Alternatives to this implementation could be investigated, in particular to examine whether the skewness implicit in the lognormal shape is having an undue impact on the results.

The work presented here would not have been possible without several time-series of penguin data, some spanning more than twenty years. If this analysis is to be extended, consistent future monitoring of penguin demographics at Robben Island is essential so that the time-series can be continued unbroken. Furthermore, given the recent indications of substantial movement of penguins in the Western Cape (e.g. the migration, or at least moulting, of a substantial number of Robben Island penguins to Stony Point), monitoring at other colonies should not be neglected so that the effects of emigration and survival can be disentangled.

This penguin population modelling work could in principle be extended to other penguin colonies. However, in practice the data available for other colonies are somewhat sparse. Extension to other Western Cape colonies in principle eliminates difficulties regarding migration between Robben Island and Dassen Island, Boulders, Stony Point, and Dyer Island. However, conditions are likely to be different for penguins at each colony resulting in different reproductive success and adult survival rates. Robben Island has the longest and most complete data series. The next best is the Dassen Island moult series, but this is difficult to use as an index of abundance because penguins moulting inland, which make up a substantial proportion of the colony, are not counted.

6.3 Concluding remarks

As the African penguin is a top predator, the status of the population should give an indication of the health of the marine ecosystem which it inhabits (Boersma 2008). The recent downward trend in penguin abundance, in particular at Robben Island, is certainly worrying, and reasons for this decline should continue to be investigated. However, the results of this thesis suggest that the reason most commonly suggested for the decrease in penguin abundance—heavy fishing pressure—is unlikely to be the primary cause, unless the mechanisms for this negative interaction have not been reflected appropriately in the analyses conducted here.

To be more specific, the analyses presented in this thesis show that levels of pelagic fishing permitted by the OMP tested are unlikely to have a substantial effect on penguin abundance at Robben Island. In particular, this effect is small when compared to the effect of changes in the spatial distribution of sardine.

The penguin population model described in Chapter 4 reflects the application of rigorous quantitative methods in which data from a variety of sources are integrated in a statistically defensible manner. Similar techniques are typically used in a rigorous single-species fisheries assessment. Here, however, they have been applied to a non-target predator which is dependent for food on fish stocks under harvest. This is important in the context of advancing the ecosystem approach to fisheries (EAF). It is unusual for approaches as quantitative as this to be implemented to address an EAF issue. Nevertheless, some modelling work has been conducted relating to the dependence of predators on Antarctic krill (Thomson *et al.* 2000; Plagányi and Butterworth 2012; Watters *et al.* 2013), as well as predator-prey interactions affecting Steller sea lions *Eumetopias jubatus* in the Bering Sea (Kinzey and Punt 2009). Although still very rare, there is at least one example of a whole-of-ecosystem model being fit to similar data to that used in stock assessments (e.g. Gaichas *et al.* 2011). However, this requires very large data sets and computation resources.

In a broader context, there is increasing pressure worldwide to account for the foraging needs of dependent predators in setting catch limits for target species. In particular, much recent work has focused on suggested modifications to default harvest level specifications for low trophic level species such as sardine and anchovy to safeguard food requirements of dependent predators (Cury *et al.* 2011; Smith *et al.* 2011; Tyrrell *et al.* 2011; Pikitch *et al.* 2012a; Essington and Plagányi 2013). More generally, ecosystem models of varying quality (and rarely conditioned on data) are commonly being applied, typically in a strategic rather than tactical context, to provide guidance as to recommended caps on harvest levels to protect ecosystem biodiversity. Perhaps the main guidance emanating from this work is to caution that marine ecosystem interactions are not necessarily straightforward, so that the temptation to jump to conclusions before conducting careful and desirably quantitative analyses should be avoided.

References

Adams NJ, Seddon PJ, and Van Heezik YM. 1992. *Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment?* South African Journal of Marine Science, 12: 959–974.

Agardy T, di Sciara GN, and Christie P. 2011. *Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning.* Marine Policy, 35: 226–232.

Agnew DJ. 1997. *Review—The CCAMLR Ecosystem Monitoring Programme.* Antarctic Science, 9: 235–242.

Altwegg R, Barham BJ, Barham PJ, Crawford RJM, Dyer BM, Geldenhuys D, Leshoro TM, Makhado AB, Parsons N, Pichegru L, Sherley RB, Underhill LG, Upfold L, Visagie J, and Waller LJ. 2009. *Report on monitoring of African Penguins at colonies around which purse-seine fishing was disallowed or permitted in 2008, with early information for 2009.* Unpublished scientific document, Marine and Coastal Management, South Africa. Report No. MCM/2009/SWG–PEL/16.

Attwood CG, Harris JM, and Williams AJ. 1997. *International experience of marine protected areas and their relevance to South Africa.* South African Journal of Marine Science, 18: 311–332.

Bakun A, Babcock EA, and Santora C. 2009. *Regulating a complex adaptive system via its wasp-waist: grappling with ecosystem-based management of the New England herring fishery.* ICES Journal of Marine Science, 66: 1768–1775.

Banobi JA, Branch TA, and Hilborn R. 2011. *Do rebuttals affect future science?* Ecosphere, 2: art37.

Barange M, Hampton I, and Roel BA. 1999. *Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys.* South African Journal of Marine Science, 21: 367–391.

Barham PJ, Crawford RJM, Underhill LG, Wolfaardt AC, Barham BJ, Dyer BM, Leshoro TM, Meÿer MA, Navarro RA, Oschadleus D, Upfold L, Whittington PA, and Williams AJ. 2006. *Return to Robben Island of African Penguins that were rehabilitated, relocated or reared in captivity following the* Treasure *oil spill of 2000.* Ostrich, 77: 202–209.

Barham PJ, Underhill LG, Crawford RJM, Altwegg R, Leshoro TM, Bolton DA, Dyer BM, and Upfold L. 2008a. *The efficacy of hand-rearing penguin chicks: evidence* *from African Penguins (*Spheniscus demersus*) orphaned in the* Treasure *oil spill in 2000.* Bird Conservation International, 18: 1–9.

Barham PJ, Underhill LG, Crawford RJM, and Leshoro TM. 2007. *Differences in breeding success between African Penguins (*Spheniscus demersus*) that were and were not oiled in the MV* Treasure *oil-spill in 2000.* Emu, 107: 7.

Barham PJ, Underhill LG, Crawford RJM, Leshoro TM, and Bolton DA. 2008b. *Impact of flipper-banding on breeding success of African penguins* Spheniscus demersus *at Robben Island: comparisons among silicone rubber bands, stainless-steel bands and no bands.* African Journal of Marine Science, 30: 595–602.

Best PB, Crawford RJM, and Van Der Elst RP. 1997. *Top predators in southern Africa's marine ecosystems.* Transactions of the Royal Society of South Africa, 52: 177–225.

Boersma PD. 2008. *Penguins as marine sentinels.* BioScience, 58: 597–607.

Boersma PD and Rebstock GA. 2010. *Effects of double bands on Magellanic Penguins.* Journal of Field Ornithology, 81: 195–205.

Boersma PD, Rebstock GA, Frere E, and Moore SE. 2009. *Following the fish: penguins and productivity in the South Atlantic.* Ecological Monographs, 79: 59–76.

Botsford LW, Castilla JC, and Peterson CH. 1997. *The management of fisheries and marine ecosystems.* Science, 277: 509–515.

Bouwhuis S, Visser GH, and Underhill LG. 2007. *Energy budget of African Penguin* Spheniscus demersus *chicks.* In: SP Kirkman (editor), *Final Report of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME*, chapter 15, 125–127. Cape Town: Avian Demography Unit.

Braby J and Underhill LG. 2007. *Was poor breeding productivity of African Black Oystercatchers on Robben Island in 2004/05 caused by Feral Cats, Kelp Gulls, Mole Snakes or the Sumatra tsunami?* Wader Study Group Bulletin, 113: 66–70.

Branch TA. 2008. *Not all fisheries will be collapsed in 2048.* Marine Policy, 32: 38–39.

Branch TA, Austin JD, Acevedo-Whitehouse K, Gordon IJ, Gompper ME, Katzner TE, and Pettorelli N. 2011a. *Fisheries conservation and management: finding consensus in the midst of competing paradigms.* Animal Conservation, 1–3.

Branch TA, Jensen OP, Ricard D, Ye Y, and Hilborn R. 2011b. *Contrasting global trends in marine fishery status obtained from catches and from stock assessments.* Conservation Biology, 25: 777–786.

Branch TA, Watson R, Fulton EA, Jennings S, McGilliard CR, Pablico GT, Ricard D, and Tracey SR. 2010. *The trophic fingerprint of marine fisheries.* Nature, 468: 431–435.

Brandão A and Butterworth DS. 2007. *An initial analysis of the power of monitoring certain indices to determine the effect of fishing on penguin reproductive success from an* *experiment where pelagic fishing is prohibited in the neighbourhood of Robben Island, but continues around Dassen Island.* Unpublished scientific document, Marine and Coastal Management, South Africa. Report No. EAFWG/OCT2007/STG/04.

Butterworth DS. 2007. *Why a management procedure approach? Some positives and negatives.* ICES Journal of Marine Science, 64: 613–617.

Butterworth DS. 2008. *Some lessons from implementing management procedures.* In: K Tsukamoto, T Kawamura, T Takeuchi, TD Beard Jr, and MJ Kaiser (editors), *Fisheries for Global Welfare and Environment, 5th World Fisheries Congress*, 381–397.

Butterworth DS, Bentley N, De Oliveira JAA, Donovan GP, Kell LT, Parma AM, Punt AE, Sainsbury KJ, Smith ADM, and Stokes TK. 2010. *Purported flaws in management strategy evaluation: basic problems or misinterpretations?* ICES Journal of Marine Science, 67: 567–574.

Butterworth DS and Bergh MO. 1993. *The development of a management procedure for the South African anchovy resource.* In: SJ Smith, JJ Hunt, and D Rivard (editors), *Risk Evaluation and Biological Reference Points for Fisheries Management*, 83–99. Canadian National Research Council.

Butterworth DS and Plagányi ÉE. 2004. *A brief introduction to some approaches to multi-species/ecosystem modelling in the context of their possible application in the management of South African fisheries.* African Journal of Marine Science, 26: 53–61.

Butterworth DS and Punt AE. 1999. *Experiences in the evaluation and implementation of management procedures.* ICES Journal of Marine Science, 56: 985–998.

Butterworth DS, Punt AE, Bergh MO, and Borchers DL. 1992. *Assessment and management of South African marine resources during the period of the Benguela Ecology Programme: key lessons and future directions.* South African Journal of Marine Science, 12: 989–1004.

Butterworth DS, Punt AE, Oosthuizen WH, and Wickens PA. 1995. *The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal Arctocephalus pusillus pusillus.* South African Journal of Marine Science, 16: 161–183.

Butterworth DS, Punt AE, and Smith ADM. 1996. *On plausible hypotheses and their weighting, with implications for selection between variants of the Revised Management Procedure.* Report of the International Whaling Commission, 46: 637–640.

Butterworth DS and Thomson RB. 1995. *Possible effects of different levels of krill fishing on predators—some initial modelling attempts.* CCAMLR Science, 2: 79–97.

Cairns DK. 1992. *Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models.* The Condor, 94: 811–824.

Calf KM, Cooper J, and Underhill LG. 2003. *First breeding records of kelp gulls* Larus dominicanus vetula *at Robben Island, Western Cape, South Africa.* African Journal of Marine Science, 25: 391–393.

Carruthers TR, Walters CJ, and McAllister MK. 2012. *Evaluating methods that classify fisheries stock status using only fisheries catch data.* Fisheries Research, 119-120: 66–79.

CCAMLR. 1980. *CAMLR Convention.* http://www.ccamlr.org/en/organisation/camlr-convention-text.

Checkley DM Jr, Alheit J, Oozeki Y, and Roy C. 2009. *Climate Change and Small Pelagic Fish.* Cambridge: Cambridge University Press.

Christensen V and Walters CJ. 2004. *Ecopath with Ecosim: methods, capabilities and limitations.* Ecological Modelling, 172: 109–139.

Clark CW. 1976. *Mathematical bioeconomics.* New York: John Wiley & Sons.

Cochrane KL. 2000. *Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away?* Fish and Fisheries, 1: 3–21.

Cochrane KL, Augustyn CJ, Cockcroft AC, David JHM, Griffiths MH, Groeneveld JC, Lipinski MR, Smale MJ, Smith CD, and Tarr RJQ. 2004. *An ecosystem approach to fisheries in the southern Benguela context.* African Journal of Marine Science, 26: 9–35.

Cochrane KL, Butterworth DS, De Oliveira JAA, and Roel BA. 1998. *Management procedures in a fishery based on highly variable stocks and with conflicting objectives: experiences in the South African pelagic fishery.* Reviews in Fish Biology and Fisheries, 8: 177–214.

Cochrane KL, Butterworth DS, and Payne AIL. 1997. *South Africa's offshore living marine resources: the scientific basis for management of the fisheries.* Transactions of the Royal Society of South Africa, 52: 149–176.

Coetzee JC. 2012. *Final TAC recommendation of the Small Pelagic Scientific Working Group for the sustainable management of small pelagic resources for the season 2012.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/JUL/SWG–PEL/37.

Coetzee JC, Merkle D, de Moor CL, Twatwa NM, Barange M, and Butterworth DS. 2008a. *Refined estimates of South African pelagic fish biomass from hydro-acoustic surveys: quantifying the effects of target strength, signal attenuation and receiver saturation.* African Journal of Marine Science, 30: 205–217.

Coetzee JC, van der Lingen CD, Hutchings L, and Fairweather TP. 2008b. *Has the fishery contributed to a major shift in the distribution of South African sardine?* ICES Journal of Marine Science, 65: 1676–1688.

Constable AJ. 2001. *The ecosystem approach to managing fisheries: achieving conservation objectives for predators of fished species.* CCAMLR Science, 8: 37–64.

Cooper J and Morant PD. 1981. *The design of stainless steel flipper bands for penguins.* Ostrich, 52: 119–123.

Cormack RM. 1964. *Estimates of survival from the sighting of marked animals.* Biometrika, 51: 429–438.

Crawford RJM. 1998. *Responses of African penguins to regime changes of sardine and anchovy in the Benguela system.* South African Journal of Marine Science, 19: 355–364.

Crawford RJM. 2004. *Accounting for food requirements of seabirds in fisheries management—the case of the South African purse-seine fishery.* African Journal of Marine Science, 26: 197–203.

Crawford RJM. 2007. *Food, fishing and seabirds in the Benguela upwelling system.* Journal of Ornithology, 148: S253–S260.

Crawford RJM, Allwright DM, and Heÿl CW. 1992a. *High mortality of Cape Cormorants (*Phalacrocorax capensis*) off western South Africa in 1991 caused by* Pasteurella multocida. Colonial Waterbirds, 15: 236–238.

Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB, Pichegru L, Ryan PG, Underhill LG, Upfold L, Visagie J, Waller LJ, and Whittington PA. 2011a. *Collapse of South Africa's penguins in the early 21st century.* African Journal of Marine Science, 33: 139–156.

Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, and Upfold L. 2006a. *The influence of food availability on breeding success of African penguins* Spheniscus demersus *at Robben Island, South Africa.* Biological Conservation, 132: 119–125.

Crawford RJM and Boonstra H. 1994. *Counts of moulting and breeding jackass penguins* Spheniscus demersus*: a comparison at Robben Island, 1988–1993.* Marine Ornithology, 22: 213–219.

Crawford RJM, Cruickshank RA, Shelton PA, and Kruger I. 1985. *Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system.* South African Journal of Marine Science, 3: 215–228.

Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux JP, Underhill LG, Ward VL, Williams AJ, and Wolfaardt AC. 2001. *African penguins as predators and prey—coping (or not) with change.* South African Journal of Marine Science, 23: 435–447.

Crawford RJM, Davis SA, Harding RT, Jackson LF, Leshoro TM, Meÿer MA, Randall RM, Underhill LG, Upfold L, van Dalsen AP, van der Merwe E, Whittington PA, Williams AJ, and Wolfaardt AC. 2000a. *Initial impact of the* Treasure *oil spill on seabirds off western South Africa.* South African Journal of Marine Science, 22: 157–176.

Crawford RJM and Dyer BM. 1995. *Responses by four seabird species to a fluctuating availability of Cape Anchovy* Engraulis capensis *off South Africa.* Ibis, 137: 329–339.

Crawford RJM, Dyer BM, Fox R, Geldenhuys D, Leshoro TM, Makhado AB, McGeorge C, Pichegru L, Upfold L, Visagie J, and Waller LJ. 2012. *Numbers of African Penguins breeding in South Africa, 2000–2012.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/04.

Crawford RJM, Hemming M, Kemper J, Klages NTW, and Randall RM. 2006b. *Molt of the African penguin,* Spheniscus demersus*, in relation to its breeding season and food availability.* Acta Zoologica Sinica, 52: 444–447.

Crawford RJM, Ryan PG, and Williams AJ. 1991. *Seabird consumption and production in the Benguela and western Agulhas ecosystems.* South African Journal of Marine Science, 11: 357–375.

Crawford RJM, Sabarros PS, Fairweather TP, Underhill LG, and Wolfaardt AC. 2008a. *Implications for seabirds off South Africa of a long-term change in the distribution of sardine.* African Journal of Marine Science, 30: 177–184.

Crawford RJM, Shannon LJ, and Whittington PA. 1999. *Population dynamics of the African penguin* Spheniscus demersus *at Robben Island, South Africa.* Marine Ornithology, 27: 139–147.

Crawford RJM, Shannon LJ, Whittington PA, and Murison G. 2000b. *Factors influencing growth of the African penguin colony at Boulders, South Africa, 1985–1999.* South African Journal of Marine Science, 22: 111–119.

Crawford RJM, Tree AJ, Whittington PA, Visagie J, Upfold L, Roxburg KJ, Martin AP, and Dyer BM. 2008b. *Recent distributional changes of seabirds in South Africa: is climate having an impact?* African Journal of Marine Science, 30: 189–193.

Crawford RJM, Underhill LG, Coetzee JC, Fairweather TP, Shannon LJ, and Wolfaardt AC. 2008c. *Influences of the abundance and distribution of prey on African penguins* Spheniscus demersus *off western South Africa.* African Journal of Marine Science, 30: 167–175.

Crawford RJM, Underhill LG, Raubenheimer CM, Dyer BM, and Martin J. 1992b. *Top predators in the Benguela ecosystem—implications of their trophic position.* South African Journal of Marine Science, 12: 675–687.

Crawford RJM, Underhill LG, Upfold L, and Dyer BM. 2007. *An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (Spheniscus demersus).* ICES Journal of Marine Science, 64: 570–576.

Crawford RJM, Waller LJ, Upfold L, Pichegru L, Makhado AB, Geldenhuys D, and Dyer BM. 2011b. *Numbers of African Penguins breeding in South Africa in 2011.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2011/SWG–PEL/Island Closure Task Team/01.

Crawford RJM, Williams AJ, Hofmeyr JH, Klages NTW, Randall RM, Cooper J, Dyer BM, and Chesselet YJ. 1995. *Trends of African penguin* Spheniscus demersus *populations in the 20th century.* South African Journal of Marine Science, 16: 101–118.

Crawford RJM, Williams AJ, Randall RM, Randall BM, Berruti A, and Ross GJ. 1990. *Recent population trends of jackass penguins* Spheniscus demersus *off Southern Africa.* Biological Conservation, 52: 229–243.

Cury PM, Bakun A, Crawford RJM, Jarre AC, Quiñones RA, Shannon LJ, and Verheye HMS. 2000. *Small pelagics in upwelling systems: patterns of interaction and structural changes in wasp-waist ecosystems.* ICES Journal of Marine Science, 57: 603–618.

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux JP, Shannon LJ, and Sydeman WJ. 2011. *Global seabird response to forage fish depletion—one-third for the birds.* Science, 334: 1703–6.

Cury PM and Shannon LJ. 2004. *Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela.* Progress In Oceanography, 60: 223–243.

Cury PM, Shannon LJ, Roux JP, Daskalov G, Jarre AC, Moloney CL, and Pauly D. 2005. *Trophodynamic indicators for an ecosystem approach to fisheries.* ICES Journal of Marine Science, 62: 430–442.

Daan N, Gislason H, Pope JG, and Rice JC. 2011. *Apocalypse in world fisheries? The reports of their death are greatly exaggerated.* ICES Journal of Marine Science, 68: 1375–1378.

DAFF. 2011. *Draft terms of reference: Task team to investigate the merits of additional closures to purse-seine fishing of all or part of areas around African penguin breeding colonies.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2011/SWG–PEL/28.

David JHM. 1987. *Diet of the South African fur seal (1974–1985) and an assessment of competition with fisheries in southern Africa.* South African Journal of Marine Science, 5: 693–713.

David JHM, Cury PM, Crawford RJM, Randall RM, Underhill LG, and Meÿer MA. 2003. *Assessing conservation priorities in the Benguela ecosystem, South Africa: analysing predation by seals on threatened seabirds.* Biological Conservation, 114: 289–292.

de Moor CL and Butterworth DS. 2008. *OMP-08.* Unpublished scientific document, Marine and Coastal Management, South Africa. Report No. MCM/2008/SWG–PEL/23.

de Moor CL and Butterworth DS. 2009. *The 2004 re-assessment of the South African sardine and anchovy populations to take account of revisions to earlier data and recent record abundances.* African Journal of Marine Science, 31: 333–348.

de Moor CL and Butterworth DS. 2012a. *Assessment of the South African sardine resource using data from 1984–2011, with some results for a single stock hypothesis.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/SEP/SWG–PEL/48.

de Moor CL and Butterworth DS. 2012b. *The simulation testing framework used during the development of OMP-13.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/58.

de Moor CL and Butterworth DS. 2012c. *Interim OMP-13.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/DEC/SWG–PEL/64.

de Moor CL and Butterworth DS. 2013a. *Assessment of the South African sardine resource using data from 1984–2011: further results for a two stock hypothesis.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2013/FEB/SWG–PEL/01rev.

de Moor CL and Butterworth DS. 2013b. *Timeline for remaining OMP-13 development.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2013/MAY/SWG–PEL/08.

de Moor CL, Butterworth DS, and Coetzee JC. 2008. *Revised estimates of abundance of South African sardine and anchovy from acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine.* African Journal of Marine Science, 30: 219–232.

de Moor CL, Butterworth DS, and De Oliveira JAA. 2011. *Is the management procedure approach equipped to handle short-lived pelagic species with their boom and bust dynamics? The case of the South African fishery for sardine and anchovy.* ICES Journal of Marine Science, 68: 2075–2085.

De Oliveira JAA and Butterworth DS. 2004. *Developing and refining a joint management procedure for the multispecies South African pelagic fishery.* ICES Journal of Marine Science, 61: 1432–1442.

De Oliveira JAA, Butterworth DS, Roel BA, Cochrane KL, and Brown JP. 1998. *The application of a management procedure to regulate the directed and bycatch fishery of South African sardine* Sardinops sagax. South African Journal of Marine Science, 19: 449–469.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, and Lautenbach S. 2013. *Collinearity: a review of methods to deal with it and a simulation study evaluating their performance.* Ecography, 36: 027–046.

Durant JM, Crawford RJM, Wolfaardt AC, Agenbag K, Visagie J, Upfold L, and Stenseth NC. 2010. *Influence of feeding conditions on breeding of African penguins—importance of adequate local food supplies.* Marine Ecology Progress Series, 420: 263–271.

Durant JM, Hjermann DO, Frederiksen M, Charrassin JB, Le Maho Y, Sabarros PS, Crawford RJM, and Stenseth NC. 2009. *Pros and cons of using seabirds as ecological indicators.* Climate Research, 39: 115–129.

Dyer BM. 1996. *Predation by snakes on seabirds at three South African islands.* South African Journal of Marine Science, 17: 309–313.

Edwards CTT, Rademeyer RA, Butterworth DS, and Plagányi ÉE. 2008. *Investigating the consequences of Marine Protected Areas for the South African deep-water hake (*Merluccius paradoxus*) resource.* ICES Journal of Marine Science, 66: 72–81.

Einoder L. 2009. *A review of the use of seabirds as indicators in fisheries and ecosystem management.* Fisheries Research, 95: 6–13.

Essington TE, Beaudreau AH, and Wiedenmann J. 2006. *Fishing through marine food webs.* Proceedings of the National Academy of Sciences of the United States of America, 103: 3171–5.

Essington TE and Plagányi ÉE. 2013. *Pitfalls and guidelines for "recycling" models for ecosystem-based fisheries management: evaluating model suitability for forage fish fisheries.* ICES Journal of Marine Science, DOI: 10.1093/icesjms/fst047.

Fairweather TP, van der Lingen CD, Booth A, Drapeau L, and van der Westhuizen JJ. 2006. *Indicators of sustainable fishing for South African sardine* Sardinops sagax *and anchovy* Engraulis encrasicolus. African Journal of Marine Science, 28: 661–680.

FAO. 2003. *The ecosystem approach to fisheries.* FAO Technical Guidelines for Responsible Fisheries. Rome: FAO.

Fournier DA, Skaug HJ, Ancheta J, Ianelli JN, Magnusson A, Maunder MN, Nielsen A, and Sibert J. 2012. *AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models.* Optimization Methods and Software, 27: 233–249.

Frederiksen M, Wanless S, Harris MP, Rothery P, and Wilson LJ. 2004. *The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes.* Journal of Applied Ecology, 41: 1129–1139.

Fréon P, Cury PM, Shannon LJ, and Roy C. 2005. *Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review.* Bulletin of Marine Science, 76: 385–462.

Frost PGH, Siegfried WR, and Burger AE. 1976. *Behavioural adaptations of the Jackass penguin,* Spheniscus demersus *to a hot, arid environment.* Journal of Zoology, 179: 165–187.

Fulton EA, Smith ADM, and Punt AE. 2005. *Which ecological indicators can robustly detect effects of fishing?* ICES Journal of Marine Science, 62: 540–551.

Furness RW and Camphuysen CJ. 1997. *Seabirds as monitors of the marine environment.* ICES Journal of Marine Science, 54: 726–737.

Gaichas SK, Aydin KY, and Francis RC. 2011. *What drives dynamics in the Gulf of Alaska? Integrating hypotheses of species, fishing, and climate relationships using ecosystem modeling.* Canadian Journal of Fisheries and Aquatic Sciences, 68: 1553–1578.

Garcia SM, Zerbi A, Aliaume C, Do Chi T, and Lassere G. 2003. *The ecosystem approach to fisheries.* FAO Fisheries and Aquaculture Technical Papers. Rome: FAO.

Geromont HF, De Oliveira JAA, Johnston SJ, and Cunningham CL. 1999. *Development and application of management procedures for fisheries in southern Africa.* ICES Journal of Marine Science, 56: 952–966.

Gislason H, Sinclair M, Sainsbury KJ, and O'Boyle R. 2000. *Symposium overview: incorporating ecosystem objectives within fisheries management.* ICES Journal of Marine Science, 57: 468–475.

Gutiérrez NL, Hilborn R, and Defeo O. 2011. *Leadership, social capital and incentives promote successful fisheries.* Nature, 470: 386–9.

Hamann MH, Grémillet D, Ryan PG, Bonadonna F, van der Lingen CD, and Pichegru L. 2012. *A hard-knock life: the foraging ecology of Cape cormorants amidst shifting prey resources and industrial fishing pressure.* African Journal of Marine Science, 34: 233–240.

Hampton I. 1992. *The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf.* South African Journal of Marine Science, 12: 1031–1050.

Hampton S, Ryan PG, and Underhill LG. 2010. *The effect of flipper banding on the breeding success of African Penguins* Spheniscus demersus *at Boulders Beach, South Africa.* Ostrich, 80: 77–80.

Heezik Y and Seddon PJ. 1990. *Effect of human disturbance on beach groups of jackass penguins.* South African Journal of Wildlife Research, 20: 88–93.

Hilborn R. 1992. *Current and future trends in fisheries stock assessment and management.* South African Journal of Marine Science, 12: 975–988.

Hilborn R. 2007a. *Defining success in fisheries and conflicts in objectives.* Marine Policy, 31: 153–158.

Hilborn R. 2007b. *Moving to sustainability by learning from successful fisheries.* Ambio, 36: 296–303.

Hilborn R. 2007c. *Reinterpreting the state of fisheries and their management.* Ecosystems, 10: 1362–1369.

Hilborn R. 2007d. *Biodiversity loss in the ocean: how bad is it?* Science, 316: 1281–2.

Hilborn R. 2007e. *The state of the art in stock assessment: where we are and where we are going.* Scientia Marina, 67: 15–20.

Hilborn R. 2008. *Knowledge on how to achieve sustainable fisheries.* In: K Tsukamoto, T Kawamura, T Takeuchi, TD Beard Jr, and MJ Kaiser (editors), *Fisheries for Global Welfare and Environment, 5th World Fisheries Congress*, 45–56.

Hilborn R. 2010a. *Apocalypse forestalled: why all the world's fisheries aren't collapsing.* The Science Chronicles, 1–9.

Hilborn R. 2010b. *Pretty Good Yield and exploited fishes.* Marine Policy, 34: 193–196.

Hilborn R. 2011. *Future directions in ecosystem based fisheries management: A personal perspective.* Fisheries Research, 108: 235–239.

Hilborn R. 2013. *Environmental cost of conservation victories.* Proceedings of the National Academy of Sciences of the United States of America, 110: 9187.

Hilborn R, Branch TA, Ernst B, Magnusson A, Minte-Vera CV, Scheuerell MD, and Valero JL. 2003. *State of the world's fisheries.* Annual Review of Environment and Resources, 28: 359–399.

Hilborn R, Maguire JJ, Parma AM, and Rosenberg AA. 2001. *The Precautionary Approach and risk management: can they increase the probability of successes in fishery management?* Canadian Journal of Fisheries and Aquatic Sciences, 58: 99–107.

Hilborn R, Orensanz JM, and Parma AM. 2005. *Institutions, incentives and the future of fisheries.* Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 360: 47–57.

Hilborn R, Punt AE, and Orensanz JM. 2004a. *Beyond band-aids in fisheries management: fixing world fisheries.* Bulletin of Marine Science, 74: 493–507.

Hilborn R and Stokes K. 2010. *Defining overfished stocks: have we lost the plot?* Fisheries, 35: 113–120.

Hilborn R, Stokes K, Maguire JJ, Smith ADM, Botsford LW, Mangel M, Orensanz JM, Parma AM, Rice JC, Bell J, Cochrane KL, Garcia SM, Hall SJ, Kirkwood GP, Sainsbury KJ, Stefansson G, and Walters CJ. 2004b. *When can marine reserves improve fisheries management?* Ocean & Coastal Management, 47: 197–205.

Hobday A, Smith ADM, Stobutzki I, Bulman CM, Daley R, Dambacher J, Deng R, Dowdney J, Fuller M, Furlani D, Griffiths S, Johnson D, Kenyon R, Knuckey I, Ling S, Pitcher R, Sainsbury KJ, Sporcic M, Smith T, Turnbull C, Walker TI, Wayte S, Webb H, Williams A, Wise B, and Zhou S. 2011. *Ecological risk assessment for the effects of fishing.* Fisheries Research, 108: 372–384.

Hockey PAR and Hallinan J. 1981. *Effect of human disturbance on the breeding behaviour of jackass penguins* Spheniscus demersus. South African Journal of Wildlife Research, 11: 59–62.

Horne EC, Bray RA, and Bousfield B. 2011. *The presence of the trematodes* Cardiocephaloides physalis *and* Renicola sloanei *in the African Penguin* Spheniscus demersus *on the east coast of South Africa.* Ostrich, 82: 157–160.

Hurlbert SH. 1984. *Pseudoreplication and the design of ecological field experiments.* Ecological Monographs, 54: 187–211.

Hutchings JA. 2000. *Collapse and recovery of marine fishes.* Nature, 406: 882–5.

Hutchings L. 1992. *Fish harvesting in a variable, productive environment—searching for rules or searching for exceptions?* South African Journal of Marine Science, 12: 297–318.

Jackson S and Wilson RP. 2002. *The potential costs of flipper-bands to penguins.* Functional Ecology, 16: 141–148.

Jolly GM. 1965. *Explicit estimates from capture-recapture data with both death and immigration—stochastic model.* Biometrika, 52: 225–247.

Karpouzi VS, Watson R, and Pauly D. 2006. *Modelling and mapping resource overlap between seabirds and fisheries on a global scale.* Unpublished scientific document, ICES CM 2006/L:01.

Kawasaki T. 1992. *Mechanisms governing fluctuations in pelagic fish populations.* South African Journal of Marine Science, 12: 873–879.

Kemper J and Roux JP. 2005. *Of squeezers and skippers: factors determining the age at moult of immature African Penguins* Spheniscus demersus *in Namibia.* Ibis, 147: 346–352.

Kemper J, Roux JP, Bartlett PA, Chesselet YJ, James JAC, Jones R, Wepener S, and Molloy FJ. 2001. *Recent population trends of African penguins* Spheniscus demersus *in Namibia.* South African Journal of Marine Science, 23: 429–434.

Kinzey D and Punt AE. 2009. *Multispecies and single-species models of fish population dynamics: comparing parameter estimates.* Natural Resource Modeling, 22: 67–104.

Kirkman SP. 2009. *Evaluating seal–seabird interactions in southern Africa: a critical review.* African Journal of Marine Science, 31: 1–18.

Kirkwood GP. 1992. *Background to the development of revised management procedures.* Report of the International Whaling Commission, 42: 236–243.

Koenig R. 2007. *African penguin populations reported in a puzzling decline.* Science, 315: 1205.

Kraak SBM, Kelly CJ, Codling EA, and Rogan E. 2010. *On scientists discomfort in fisheries advisory science: the example of simulation-based fisheries management-strategy evaluations.* Fish and Fisheries, 11: 119–132.

Larkin PA. 1996. *Concepts and issues in marine ecosystem management.* Reviews in Fish Biology and Fisheries, 6: 139–164.

Le Maho Y, Saraux C, Durant JM, Viblanc VA, Gauthier-Clerc M, Yoccoz NG, Stenseth NC, and Le Bohec C. 2011. *An ethical issue in biodiversity science: the monitoring of penguins with flipper bands.* Comptes Rendus Biologies, 334: 378–84.

Lebreton JD, Burnham KP, Clobert J, and Anderson DR. 1992. *Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies.* Ecological Monographs, 62: 67–118.

Levin PS, Fogarty MJ, Murawski SA, and Fluharty D. 2009. *Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean.* PLoS Biology, 7: 23–28.

Lluch-Belda D, Crawford RJM, Kawasaki T, MacCall AD, Parrish RH, Schwartzlose RA, and Smith PE. 1989. *World-wide fluctuations of sardine and anchovy stocks: the regime problem.* South African Journal of Marine Science, 8: 195–205.

MacCall AD. 1990. *Dynamic geography of marine fish populations.* Seattle: University of Washington Press.

Makhado AB, Crawford RJM, and Underhill LG. 2006. *Impact of predation by Cape fur seals* Arctocephalus pusillus pusillus *on Cape gannets* Morus capensis *at Malgas Island, Western Cape, South Africa.* African Journal of Marine Science, 28: 681–687.

Mangel M. 2000. *Trade-offs between fish habitat and fishing mortality and the role of reserves.* Bulletin of Marine Science, 66: 663–674.

Marks MA, Brooke RK, and Gildenhuyst AM. 1997. *Cape fur seal* Arctocephalus pusillus *predation on cape cormorants* Phalacrocorax capensis *and other birds at Dyer Island, South Africa.* Marine Ornithology, 25: 9–12.

Maunder MN, Skaug HJ, Fournier DA, and Hoyle SD. 2009. *Comparison of fixed effect, random effect, and hierarchical Bayes estimators for mark recapture data using AD Model Builder.* In: DL Thomson, EG Cooch, and MJ Conroy (editors), *Modeling Demographic Processes in Marked Populations*, 917–946. New York: Springer.

Merkle D, Coetzee JC, Mushanganyisi K, and Rademan J. 2012. *Small scale hydro-acoustic surveys 2012.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/09.

Mori M and Butterworth DS. 2004. *Consideration of multispecies interactions in the Antarctic: a preliminary model of the minke whale–blue whale–krill interaction.* African Journal of Marine Science, 26: 245–259.

Moseley C, Wanless RM, Altwegg R, Crawford RJM, and Badenhorst A. 2011. *Hypotheses for relating anchovy and sardine abundance with African Penguin population processes.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2011/SWG–PEL/03.

Myers RA, Barrowman NJ, Hutchings JA, and Rosenberg AA. 1995. *Population dynamics of exploited fish stocks at low population levels.* Science, 269: 1106–8.

Myers RA and Worm B. 2003. *Rapid worldwide depletion of predatory fish communities.* Nature, 423: 280–283.

O'Brien RM. 2007. *A caution regarding rules of thumb for Variance Inflation Factors.* Quality & Quantity, 41: 673–690.

Okes NC, Hockey PAR, Pichegru L, van der Lingen CD, Crawford RJM, and Grémillet D. 2009. *Competition for shifting resources in the southern Benguela upwelling: Seabirds versus purse-seine fisheries.* Biological Conservation, 142: 2361–2368.

Parma AM, Punt AE, and Stefansson G. 2010. *International review panel report for the 2010 International Fisheries Stock Assessment Workshop.* Unpublished scientific document, University of Cape Town. Report No. MARAM IWS/DEC10/REP/1.

Pauly D. 2009. *Beyond duplicity and ignorance in global fisheries.* Scientia Marina, 73: 215–224.

Pauly D, Alder J, Bennett E, Christensen V, Tyedmers P, and Watson R. 2003. *The future for fisheries.* Science, 302: 1359–61.

Pauly D, Christensen V, Dalsgaard J, Froese R, and Torres, Francisco J. 1998. *Fishing down marine food webs.* Science, 279: 860–863.

Pauly D, Christensen V, Guénette S, Pitcher TJ, Sumaila UR, Walters CJ, Watson R, and Zeller D. 2002. *Towards sustainability in world fisheries.* Nature, 418: 689–95.

Pauly D, Hilborn R, and Branch TA. 2013. *Fisheries: does catch reflect abundance?* Nature, 494: 303–306.

Petersen SL, Branch GM, Ainley DG, Boersma PD, Cooper J, and Woehler EJ. 2005. *Is flipper banding of penguins a problem?* Marine Ornithology, 33: 75–79.

Petersen SL, Ryan PG, and Grémillet D. 2006. *Is food availability limiting African Penguins* Spheniscus demersus *at Boulders? A comparison of foraging effort at mainland and island colonies.* Ibis, 148: 14–26.

Piatt JF, Harding AMA, Shultz M, Speckman SG, van Pelt TI, Drew GS, and Kettle AB. 2007. *Seabirds as indicators of marine food supplies: Cairns revisited.* Marine Ecology Progress Series, 352: 221–234.

Pichegru L, Grémillet D, Crawford RJM, and Ryan PG. 2010. *Marine no-take zone rapidly benefits endangered penguin.* Biology letters, 6: 498–501.

Pichegru L, Ludynia K, Makhado AB, McInnes A, Moseley C, Robinson K, Sherley RB, Waller LJ, and Crawford RJM. 2013. *Insufficient precautionary management of South Africa's purse-seine fishery for conservation of the African Penguin.* Unpublished scientific document, Department of Agriculture, Foresty and Fisheries, South Africa. Report No. Fisheries/2013/SWG–PEL/ICTT/04.

Pichegru L, Ryan PG, Le Bohec C, van der Lingen CD, Navarro RA, Petersen SL, Lewis S, van der Westhuizen JJ, and Grémillet D. 2009. *Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas.* Marine Ecology Progress Series, 391: 199–208.

Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D, and Wanless RM. 2012. *Industrial fishing, no-take zones and endangered penguins.* Biological Conservation, 156: 117–125.

Pikitch EK, Boersma PD, Boyd IL, Conover DO, Cury PM, Essington TE, Heppell SS, Houde ED, Mangel M, Pauly D, Plagányi ÉE, Sainsbury KJ, and Steneck RS. 2012a. *Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs.* Washington, DC: Lenfest Ocean Program.

Pikitch EK, Rountos KJ, Essington TE, Santora C, Pauly D, Watson R, Sumaila UR, Boersma PD, Boyd IL, Conover DO, Cury PM, Heppell SS, Houde ED, Mangel M, Plagányi ÉE, Sainsbury KJ, Steneck RS, Geers TM, Gownaris N, and Munch SB. 2012b. *The global contribution of forage fish to marine fisheries and ecosystems.* Fish and Fisheries, DOI: 10.1111/faf.12004.

Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P, Fluharty D, Heneman B, Houde ED, Link JS, Livingston PA, Mangel M, McAllister MK, Pope J, and Sainsbury KJ. 2004. *Ecosystem-based fishery management.* Science, 305: 346–7.

Pinsky ML, Jensen OP, Ricard D, and Palumbi SR. 2011. *Unexpected patterns of fisheries collapse in the world's oceans.* Proceedings of the National Academy of Sciences of the United States of America, 108: 8317–22.

Plagányi ÉE. 2007. *Models for an ecosystem approach to fisheries.* FAO Fisheries Technical Paper. Rome: FAO.

Plagányi EE, Bell JD, Bustamante RH, Dambacher JM, Dennis DM, Dichmont CM, Dutra LXC, Fulton EA, Hobday AJ, Ingrid van Putten E, Smith F, Smith

ADM, and Zhou S. 2011a. *Modelling climate-change effects on Australian and Pacific aquatic ecosystems: a review of analytical tools and management implications.* Marine and Freshwater Research, 62: 1132.

Plagányi ÉE and Butterworth DS. 2004. *A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management.* African Journal of Marine Science, 26: 261–287.

Plagányi ÉE and Butterworth DS. 2005. *Indirect fishery interactions.* In: JE Reynolds III, WF Perrin, RR Reeves, S Montgomery, and TJ Ragen (editors), *Marine Mammal Research: Conservation Beyond Crisis.* Baltimore: Johns Hopkins University Press.

Plagányi ÉE and Butterworth DS. 2012. *The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey.* Ecological Applications, 22: 748–761.

Plagányi ÉE, Punt AE, Hillary R, Morello EB, Thébaud O, Hutton T, Pillans RD, Thorson JT, Fulton EA, Smith ADM, Smith F, Bayliss P, Haywood M, Lyne V, and Rothlisberg PC. 2012. *Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity.* Fish and Fisheries, DOI: 10.1111/j.1467–2979.2012.00488.x.

Plagányi ÉE, Rademeyer RA, Butterworth DS, Cunningham CL, and Johnston SJ. 2007. *Making management procedures operational—innovations implemented in South Africa.* ICES Journal of Marine Science, 64: 626–632.

Plagányi ÉE, Weeks SJ, Skewes TD, Gibbs MT, Poloczanska ES, Norman-López A, Blamey LK, Soares M, and Robinson WML. 2011b. *Assessing the adequacy of current fisheries management under changing climate: a southern synopsis.* ICES Journal of Marine Science, 68: 1305–1317.

Powers JE and Monk MH. 2010. *Current and future use of indicators for ecosystem based fisheries management.* Marine Policy, 34: 723–727.

Pradel R, Hines JE, Lebreton JD, and Nichols JD. 1997. *Capture–recapture survival models taking account of transients.* Biometrics, 53: 60–72.

Punt AE. 1992. *Selecting management methodologies for marine resources, with an illustration for southern African hake.* South African Journal of Marine Science, 12: 943–958.

Punt AE. 2006. *The FAO Precautionary Approach after almost 10 years: have we progressed towards implementing simulation-tested feedback-control management systems for fisheries management?* Natural Resource Modeling, 19: 441–464.

Punt AE. 2008. *Refocusing stock assessment in support of policy evaluation.* In: K Tsukamoto, T Kawamura, T Takeuchi, TD Beard Jr, and MJ Kaiser (editors), *Fisheries for Global Welfare and Environment, 5th World Fisheries Congress*, 139–152.

Punt AE, A'mar T, Bond NA, Butterworth DS, de Moor CL, De Oliveira JAA, Haltuch MA, Hollowed AB, and Szuwalski C. 2013. *Fisheries management under climate and environmental uncertainty: control rules and performance simulation.* ICES Journal of Marine Science, DOI: 10.1093/icesjms/fst057.

Punt AE and Butterworth DS. 1995. *The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus.* South African Journal of Marine Science, 16: 255–285.

Punt AE, David JHM, and Leslie RW. 1995. *The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 2. Feeding and diet of the Cape fur seal Arctocephalus pusillus pusillus.* South African Journal of Marine Science, 16: 85–99.

Punt AE and Donovan GP. 2007. *Developing management procedures that are robust to uncertainty: lessons from the International Whaling Commission.* ICES Journal of Marine Science, 64: 603–612.

Punt AE and Hilborn R. 1997. *Fisheries stock assessment and decision analysis: the Bayesian approach.* Reviews in Fish Biology and Fisheries, 7: 35–63.

Rademeyer RA, Butterworth DS, and Plagányi ÉE. 2008. *A history of recent bases for management and the development of a species-combined Operational Management Procedure for the South African hake resource.* African Journal of Marine Science, 30: 291–310.

Rademeyer RA, Plagányi ÉE, and Butterworth DS. 2007. *Tips and tricks in designing management procedures.* ICES Journal of Marine Science, 64: 618–625.

Randall BM, Randall RM, and Compagno LJV. 1988. *Injuries to jackass penguins (Spheniscus demersus): evidence for shark involvement.* Journal of Zoology, 214: 589–599.

Randall RM. 1983. *Biology of the Jackass Penguin* Spheniscus demersus *(L.) at St Croix Island, South Africa.* PhD thesis, University of Port Elizabeth.

Randall RM and Randall BM. 1990. *Cetaceans as predators of jackass penguins* Spheniscus demersus*: deductions based on behaviour.* Marine Ornithology, 18: 9–12.

Randall RM, Randall BM, Cooper J, and Frost PGH. 1986. *A new census method for penguins tested on jackass penguins* Spheniscus demersus. Ostrich, 57: 211–215.

Randall RM, Randall BM, Cooper J, La Cock GD, and Ross GJ. 1987. *Jackass Penguin* Spheniscus demersus *movements, inter-island visits, and settlement.* Journal of Field Ornithology, 58: 445–455.

Robinson K. 2012. *Dassen and Robben Island breeding African Penguin foraging data requested for ICTT power analysis.* Unpublished scientific document, Department of Agriculture, Foresty and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/01b rev 1.

Rochet MJ and Rice JC. 2009. *Simulation-based management strategy evaluation: ignorance disguised as mathematics?* ICES Journal of Marine Science, 66: 754–762.

Rose KA, Allen JI, Artioli Y, Barange M, Blackford J, Carlotti F, Cropp R, Daewel U, Edwards K, Flynn K, Hill SL, HilleRisLambers R, Huse G, Mackinson S, Megrey B, Moll A, Rivkin R, Salihoglu B, Schrum C, Shannon LJ, Shin YJ, Smith SL, Smith C, Solidoro C, St John M, and Zhou M. 2010. *End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps.* Marine and Coastal Fisheries, 2: 115–130.

Roy C, van der Lingen CD, Coetzee JC, and Lutjeharms JRE. 2007. *Abrupt environmental shift associated with changes in the distribution of Cape anchovy* Engraulis encrasicolus *spawners in the southern Benguela.* African Journal of Marine Science, 29: 309–319.

Sainsbury KJ, Punt AE, and Smith ADM. 2000. *Design of operational management strategies for achieving fishery ecosystem objectives.* ICES Journal of Marine Science, 57: 731–741.

Sandvik H, Erikstad KE, Barrett RT, and Yoccoz NG. 2005. *The effect of climate on adult survival in five species of North Atlantic seabirds.* Journal of Animal Ecology, 74: 817–831.

Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, Park YH, Yoccoz NG, Stenseth NC, and Le Maho Y. 2011. *Reliability of flipper-banded penguins as indicators of climate change.* Nature, 469: 203–6.

SC-CAMLR. 1994. *Report of the thirteenth meeting of the Scientific Committee.* Hobart, Australia: CCAMLR.

Schnute JT, Maunder MN, and Ianelli JN. 2007. *Designing tools to evaluate fishery management strategies: can the scientific community deliver?* ICES Journal of Marine Science, 64: 1077–1084.

Schwartzlose RA, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, Lluch-Belda D, Lluch-Cota SE, MacCall AD, Matsuura Y, Nevárez-Martínez MO, Parrish RH, Roy C, Serra R, Shust KV, Ward MN, and Zuzunaga JZ. 1999. *Worldwide large-scale fluctuations of sardine and anchovy populations.* South African Journal of Marine Science, 21: 289–347.

Seber GAF. 1965. *A note on the multiple-recapture census.* Biometrika, 52: 249–259.

Shabangu F, Coetzee JC, Merkle D, Mushanganyisi K, and Phillips M. 2012. *Results of the 2012 spawner biomass survey.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/DEC/SWG–PEL/66.

Shannon LJ and Crawford RJM. 1999. *Management of the African penguin* Spheniscus demersus*—insights from modelling.* Marine Ornithology, 27: 119–128.

Shannon LJ, Cury PM, and Jarre AC. 2000. *Modelling effects of fishing in the Southern Benguela ecosystem.* ICES Journal of Marine Science, 57: 720–722.

Shannon LJ, Cury PM, Nel DC, van der Lingen CD, Leslie RW, Brouwer S, Cockcroft AC, and Hutchings L. 2006. *How can science contribute to an ecosystem approach to pelagic, demersal and rock lobster fisheries in South Africa?* African Journal of Marine Science, 28: 115–157.

Shelton PA, Crawford RJM, Cooper J, and Brooke RK. 1984. *Distribution, population size and conservation of the jackass penguin* Spheniscus demersus. South African Journal of Marine Science, 2: 217–257.

Sherley RB. 2010. *Factors Influencing the Demography of Endangered Seabirds at Robben Island, South Africa: Implications and Approaches for Management and Conservation.* PhD thesis, University of Bristol, UK.

Sherley RB. 2012. *Update on the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island.* Unpublished scientific document, Department of Agriculture, Foresty and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/06.

Sherley RB, Barham BJ, Barham PJ, Leshoro TM, and Underhill LG. 2012. *Artificial nests enhance the breeding productivity of African Penguins (*Spheniscus demersus*) on Robben Island, South Africa.* Emu, 112: 97–106.

Sherley RB, Burghardt T, Barham PJ, Campbell N, and Cuthill IC. 2010. *Spotting the difference: towards fully-automated population monitoring of African penguins* Spheniscus demersus. Endangered Species Research, 11: 101–111.

Sherley RB, Underhill LG, Barham BJ, Barham PJ, Coetzee JC, Crawford RJM, Dyer BM, Leshoro TM, and Upfold L. 2013. *Influence of local and regional prey availability on breeding performance of African penguins* Spheniscus demersus. Marine Ecology Progress Series, 473: 291–301.

Shin YJ and Cury PM. 2001. *Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model.* Aquatic Living Resources, 14: 65–80.

Sibert J, Hampton J, Kleiber P, and Maunder MN. 2006. *Biomass, size, and trophic status of top predators in the Pacific Ocean.* Science, 314: 1773–6.

Skaug HJ and Fournier DA. 2006. *Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models.* Computational Statistics & Data Analysis, 51: 699–709.

Smith ADM, Brown CJ, Bulman CM, Fulton EA, Johnson P, Kaplan IC, Lozano-Montes H, Mackinson S, Marzloff M, Shannon LJ, Shin YJ, and Tam J. 2011. *Impacts of fishing low-trophic level species on marine ecosystems.* Science, 333: 1147–50.

Smith ADM, Fulton EJ, Hobday A, Smith DC, and Shoulder P. 2007. *Scientific tools to support the practical implementation of ecosystem-based fisheries management.* ICES Journal of Marine Science, 64: 633–639.

Smith ADM, Sainsbury KJ, and Stevens RA. 1999. *Implementing effective fisheries-management systems—management strategy evaluation and the Australian partnership approach.* ICES Journal of Marine Science, 56: 967–979.

Steinfurth A and Robinson K. 2012. *Foraging strategies and energetic requirements of African Penguins in the Western Cape: an approach to fisheries and ecosystem management.* Unpublished scientific document, Deparment of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/01a.

Thomson RB, Butterworth DS, Boyd IL, and Croxall JP. 2000. *Modeling the consequences of Antarctic krill harvesting on Antarctic fur seals.* Ecological Applications, 10: 1806–1819.

Tuck GN, Phillips RA, Small C, Thomson RB, Klaer NL, Taylor F, Wanless RM, and Arrizabalaga H. 2011. *An assessment of seabird–fishery interactions in the Atlantic Ocean.* ICES Journal of Marine Science, 68: 1628–1637.

Tyrrell M, Link JS, and Moustahfid H. 2011. *The importance of including predation in fish population models: Implications for biological reference points.* Fisheries Research, 108: 1–8.

Underhill LG, Bartlett PA, Baumann L, Crawford RJM, Dyer BM, Gildenhuyst AM, Nel DC, Oatley TB, Thornton M, Upfold L, Williams AJ, Whittington PA, and Wolfaardt AC. 1999. *Mortality and survival of African Penguins* Spheniscus demersus *involved in the* Apollo Sea *oil spill: an evaluation of rehabilitation efforts.* Ibis, 141: 29–37.

Underhill LG and Crawford RJM. 1999. *Season of moult of African penguins at Robben Island, South Africa, and its variation, 1988–1998.* South African Journal of Marine Science, 21: 437–441.

Underhill LG and Crawford RJM. 2005. *Indexing the health of the environment for breeding seabirds in the Benguela ecosystem.* ICES Journal of Marine Science, 62: 360–365.

Underhill LG, Crawford RJM, Wolfaardt AC, Whittington PA, Dyer BM, Leshoro TM, Ruthenberg M, and Upfold L. 2006. *Regionally coherent trends in colonies of African penguins* Spheniscus demersus *in the Western Cape, South Africa, 1987–2005.* African Journal of Marine Science, 28: 697–704.

Underhill LG, Sherley RB, Dyer BM, and Crawford RJM. 2010. *Interactions between snakes and seabirds on Robben, Schaapen and Meeuw Islands, Western Cape province, South Africa.* Ostrich, 80: 115–118.

van der Lingen CD, Fréon P, Fairweather TP, and van der Westhuizen JJ. 2006. *Density-dependent changes in reproductive parameters and condition of southern Benguela sardine* Sardinops sagax. African Journal of Marine Science, 28: 625–636.

van der Lingen CD and van der Westhuizen JJ. 2012. *Catches of sardine and anchovy around four penguin-breeding colonies, 2009–2012.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/10.

van der Westhuizen JJ. 2010. *Estimating anchovy and sardine catches in the region of the penguin colonies.* Unpublished scientific document, Marine and Coastal Management, South Africa. Report No. MCM/2010/SWG–PEL/ICTT/04.

Velarde E, Ezcurra E, Cisneros-Mata MA, and Lavín MF. 2004. *Seabird ecology, El Niño anomalies, and prediction of sardine fisheries in the Gulf of California.* Ecological Applications, 14: 607–615.

Visagie J, Upfold L, Makhado AB, and Crawford RJM. 2012. *Breeding success of African Penguins at Dassen Island, 1995–2011.* Unpublished scientific document, Department of Agriculture, Forestry and Fisheries, South Africa. Report No. Fisheries/2012/NOV/SWG–PEL/ICTT/12.

Wagner EL and Boersma PD. 2011. *Effects of fisheries on seabird community ecology.* Reviews in Fisheries Science, 19: 157–167.

Waller LJ. 2011. *The African Penguin* Spheniscus demersus*: Conservation and Management Issues.* PhD thesis, University of Cape Town.

Watermeyer KE, Shannon LJ, and Griffiths CL. 2008. *Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing.* African Journal of Marine Science, 30: 351–382.

Watters GM, Hill SL, Hinke JT, Matthews J, and Reid K. 2013. *Decision-making for ecosystem-based management: evaluating options for a krill fishery with an ecosystem dynamics model.* Ecological Applications, 23: 710–725.

White GC and Burnham KP. 1999. *Program MARK: survival estimation from populations of marked animals.* Bird Study, 46: 120–139.

Whittington PA and Dyer BM. 2000. *Maximum longevities of African penguins* Spheniscus demersus *based on banding records.* Marine Ornithology, 28: 81–82.

Whittington PA, Klages NTW, Crawford RJM, Wolfaardt AC, and Kemper J. 2005a. *Age at first breeding of the African Penguin.* Ostrich, 76: 14–20.

Whittington PA, Randall RM, Crawford RJM, Wolfaardt AC, Klages NTW, Randall BM, Bartlett PA, Chesselet YJ, and Jones R. 2005b. *Patterns of immigration to and emigration from breeding colonies by African penguins.* African Journal of Marine Science, 27: 205–213.

Williams AJ, Petersen SL, Goren M, and Watkins BP. 2009. *Sightings of killer whales* Orcinus orca *from longline vessels in South African waters, and consideration of the regional conservation status.* African Journal of Marine Science, 31: 81–86.

Wilson RP. 1992. *Environmental monitoring with seabirds: do we need additional technology?* South African Journal of Marine Science, 12: 919–926.

Witherell D, Pautzke C, and Fluharty D. 2000. *An ecosystem-based approach for Alaska groundfish fisheries.* ICES Journal of Marine Science, 57: 771–777.

Wolfaardt AC, Underhill LG, Altwegg R, and Visagie J. 2008a. *Restoration of oiled African penguins* Spheniscus demersus *a decade after the* Apollo Sea *spill.* African Journal of Marine Science, 30: 421–436.

Wolfaardt AC, Underhill LG, Altwegg R, Visagie J, and Williams AJ. 2008b. *Impact of the* Treasure *oil spill on African penguins* Spheniscus demersus *at Dassen Island: case study of a rescue operation.* African Journal of Marine Science, 30: 405–419.

Wolfaardt AC, Underhill LG, and Crawford RJM. 2009a. *Comparison of moult phenology of African penguins* Spheniscus demersus *at Robben and Dassen islands.* African Journal of Marine Science, 31: 19–29.

Wolfaardt AC, Underhill LG, Nel DC, Williams AJ, and Visagie J. 2008c. *Breeding success of African penguins* Spheniscus demersus *at Dassen Island, especially after oiling following the* Apollo Sea *spill.* African Journal of Marine Science, 30: 565–580.

Wolfaardt AC, Williams AJ, Underhill LG, Crawford RJM, and Whittington PA. 2009b. *Review of the rescue, rehabilitation and restoration of oiled seabirds in South Africa, especially African penguins* Spheniscus demersus *and Cape gannets* Morus capensis*, 1983–2005.* African Journal of Marine Science, 31: 31–54.

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, and Watson R. 2006. *Impacts of biodiversity loss on ocean ecosystem services.* Science, 314: 787–90.

Worm B, Hilborn R, Baum JK, Branch TA, Collie JS, Costello C, Fogarty MJ, Fulton EA, Hutchings JA, Jennings S, Jensen OP, Lotze HK, Mace PM, McClanahan TR, Minto C, Palumbi SR, Parma AM, Ricard D, Rosenberg AA, Watson R, and Zeller D. 2009. *Rebuilding global fisheries.* Science, 325: 578–85.

Worm B and Myers RA. 2004. *Managing fisheries in a changing climate.* Nature, 429: 15.

Ye Y, Cochrane KL, Bianchi G, Willmann R, Majkowski J, Tandstad M, and Carocci F. 2013. *Rebuilding global fisheries: the World Summit Goal, costs and benefits.* Fish and Fisheries, 14: 174–185.

Zhou S, Smith ADM, Punt AE, Richardson AJ, Gibbs MT, Fulton EA, Pascoe S, Bulman CM, Bayliss P, and Sainsbury KJ. 2010. *Ecosystem-based fisheries management requires a change to the selective fishing philosophy.* Proceedings of the National Academy of Sciences of the United States of America, 107: 9485–9.