Limiting factors in colonial seabirds, with emphasis on predation, disease, parasites and diet, and implications for monitoring studies

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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ABSTRACT

Marine habitats have undergone dramatic changes, particularly over the last few decades. Human-related causes, such as habitat alteration, overexploitation, pollution, climate change and introduction of alien species have affected marine ecosystems worldwide, with severe impacts on many species, including several seabirds. Seabirds, and particularly (but not exclusively) those species that act as top-predators, are excellent monitors of the health of marine ecosystems. However, in order to make use of them as bioindicators, we have to understand how potential limiting factors influence their ecology. In turn, this information is also useful for the conservation of their populations.

In this thesis I study a diversity of limiting factors of potential importance for the breeding ecology of two threatened seabirds, the southern rockhopper penguin and the black-browed albatross, at a mixed seabird colony on the Falkland Islands. An analysis of nesting habitat quality (Chapter 2) indicated that this did not explain variation in rockhopper penguin breeding success, which was most likely influenced by predation. An analysis of spatial and temporal variability of nesting success of black-browed albatrosses has shown that disease (Chapter 3), possibly coupled with parasites (Chapter 4) was the main cause for chick mortality differences between areas and years, whilst the consequences of a diet (Chapter 5) with a strong fisheries-related component for breeding success and chick development are still to be determined conclusively.

This multi factor approach together with a relatively long-term set of data are important to produce more robust conclusions (with atypical years put into context), and to tentatively assign changes in breeding parameters to individual factors. My results help to provide a more complete insight of the potential factors threatening two species of conservation importance at this colony and in the context of the Falklands.

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STATEMENT OF CONTRIBUTION TO CO-AUTHORED PAPERS

All chapters in this thesis were written by RFS Matias with additional editing by P. Catry and S. Bearhop.

Chapter 2

In preparation for submission to Oikos. **Matias, R.**, S. Bearhop & P. Catry. **Variation in breeding success of penguins and albatrosses over very short spatial scales, with implications for seabird monitoring.**

Original concept by PC. Developed in the field by RM with additional field work from PC. SB improved writing and statistical analyses.

Chapter 3

In preparation for submission to the Condor: **Matias, R.**, K. M. Bowgen, J. P. Granadeiro, A. W. Sainsbury, S. Bearhop & P. Catry. **An epidemiological study of black-browed albatross *Thalassarche melanophris* chick mortality in the Falkland Islands.**

Initial concept by PC, developed by RM and KMB. PC and RM carried out fieldwork. JPG contributed with the spatial analysis. SB improved the manuscript. AWS provided veterinarian expertise and together with KMB was responsible for post-mortem analyses.

Chapter 4

In preparation for submission to Journal of Zoology: **Matias, R.**, S. Bearhop & P. Catry. **Costs of coloniality: are growth and survival of black-browed albatross chicks affected by ticks?**

Original concept developed by RM and PC. Fieldwork performed by RM. Statistical analyses by RM. PC and SB gave important input on statistical methods and improved writing.

Chapter 5

In preparation for submission to the Ibis. **Matias, R.**, S. Bearhop, O Anderson & P. Catry. **Fish and ships: seabirds subsidizing natural diet with fisheries waste?**

Field study initiated by PC. Fieldwork done by PC, RM and OA. Manuscript drafted by RM, improved by PC and SB.

CHAPTER 1: GENERAL INTRODUCTION

1.1 FACTORS OF POPULATION LIMITATION IN BIRDS AND OTHER ANIMALS

All animal populations have growth constrained by a number of factors, both intrinsic, such as fertility, productivity, individual longevity and age of senescence, and extrinsic, including habitat quality, interspecific competition and predation, incidence of diseases, abundance, quality and accessibility of resources (including food), weather conditions and climate, incidence of contaminants in the food chain among many others (e.g. Newton 1998, Stephens et al 2007). These factors rarely act in isolation, but rather in a jigsaw style, where each piece explains part of the broader pattern, the result of their interaction (Newton 1998).

Birds have been a focus of numerous studies of population limitation (Newton 1998 and references therein). As a group they are often long-lived, exceptionally mobile and routinely cover thousands of kilometres within one annual cycle. They can breed colonially (allowing large samples to be obtained in short periods of time) with nests as discrete units, and can be easily marked for permanent individual recognition. For these reasons birds present the opportunity to address a number of key questions relating to the manner in which populations and variation in demographic rates might be influenced by extrinsic factors and, despite their study being also subject to a number of difficulties, they are preferred organisms in many ecological studies (Konishi et al. 1989, Newton 1998).

1.1.1. The importance of habitat quality

Both feeding and breeding habitat quality are key drivers of population dynamics in birds (and other animals) (Newton 1998).

Habitat quality can be measured in different terms: resources abundance and general stability (including food resources and availability of nesting sites), as well as in terms of intraspecific (density-dependent) competition and predation probability. All these measures can affect individual fitness. For example, presence of adequate food allows individuals to build up reserves that will enable them to be in sufficient condition to breed (e.g. Stephens et al. 2007). Intraspecific competition and predation intensity are also interconnected with how rewarding feeding is for the individual, with consequences at the intake of resources (and fitness) and on the survival probability, for example (e.g. Lewis et al. 2001, Stephens et al 2007, Wakefield et al. 2013). The stability or predictability of a habitat during the whole of the breeding cycle, the availability of shelter from weather and from predators, parasite burden levels and distance from feeding habitat are other aspects (breeding) habitat quality can be measured against (Martin 1993, Cairns 1992b, Stephens et al 2007), and all are important for successful breeding. In turn, all factors that influence individual fitness might reflect on population dynamics. It has been shown that a decrease in habitat quality can be responsible for population declines or even extinctions in many species, and on the other hand that careful habitat management or restoration has created conditions for population increases or recoveries (Tilman et al. 1994, Bender et al. 1998, Bried et al. 2009). Different habitats can thus be hierarchically classified in those allowing individual survival only, those allowing breeding and finally those leading to population growth (Newton 1998).

1.1.2 Disease and parasites as limiting factors

As outlined above, wild animal populations are kept in a dynamic balance by a number of extrinsic influencing factors and, among these, disease and parasites are two important and interconnected ones (e.g. Grenfell & Gulland 1995, Newton 1998). Parasites (with consequent disease) have been shown to influence population cycles in several species (in particular several Galliiformes; Newton 1998, Hudson et al. 2002); they are recognized as well as demographic modulating factors (Boulinier & Danchin 1996) and as driving factors of evolution (Renaud et al. 1996). Most studies on parasite-host relationship in birds have focussed on ectoparasites, and particularly on ticks, which have been linked with transmission of diseases, reduction in nestling growth rates, blood loss and anaemia and nest abandonment or re-location of nesting place (Brown et al. 1995, Boulinier & Danchin 1996, Merino & Potti 1996, Gauthier-Clerc et al. 1998, Proctor & Owens 2000, Friend & Franson 2001, Gilardi et al. 2001, Norcross & Bolen 2002, Labuda & Nuttall 2004, Muzaffar & Jones 2004). However, it is worth noting that disease from introduced blood parasites has been one of the main causes for strong population declines and species extinction among Hawaiian endemic passerines (Warner 1968). Among birds, seabirds are especially prone to be affected by parasites, due to their colonial habits, philopatry, re-use of the same nest sites across multiple breeding seasons and long offspring developmental periods (Schreiber & Burger 2002). Despite the proven negative effects of a range of parasites and disease upon seabirds, there remains little evidence of parasites and disease being responsible (as a primary factor) for the population declines of any of the seabird species that have experienced recent demographic changes and are classified with an unfavourable conservation status. The case of the albatrosses declines at Amsterdam Island due to disease (particularly the yellow-nosed albatrosses *Thalassarche chlororhynchos*) is one of the few documented (Weimerskirch 2004). However, in this instance their major importance in driving seabird population dynamics might be that of potentiating the effects of other factors, such as low food availability (Newton 1998).

1.1.3 Food quality and availability as driving factors of breeding success

Breeding is a fundamental activity for any species to persist, yet it is not free of costs for the individuals and for their life history (see e.g. Wernham & Bryant 1998, Davis et al. 2005). All activities related to the breeding process require energy to be expended, which must be balanced by adequate food intake (both regarding quality and quantity). In the case of most birds, both males and females need to attain a minimum condition in order to attempt breeding. Females have the specific task of producing eggs, needing to accumulate both energy and a range of specific nutrients during the period preceding the breeding season. Either sex (most commonly males) may defend a breeding territory (often comprising only a nest), incubate the eggs (with some exceptions) and forage to replenish their own lost food reserves and to feed their offspring (which includes avoiding predation and inter and intra specific competition). In many instances one sex (usually males) also engage in display and build complicated nests in order to attract a partner. In a large proportion of species, breeding is preceded by a migration period from the non-breeding feeding areas. Additionally, from the point of view of the offspring, quality food needs to be ingested in adequate quantity (e.g. Ricklefs et al. 1987). Lack of enough or adequate food represents lower growth rates, lower body condition and reduced fledging probability or post-fledging survival (Stephens et al. 2007, Grémillet et al. 2008), and these are not independent from the consequences for adults outlined above. In fact, chick condition might be related to parental effort in previous breeding seasons, and costs of reproduction (for e.g. future breeding output) have been shown experimentally on a few occasions using supplementary food during the chick rearing period (see Wernham & Bryant 1998, Davis et al. 2005). Diet is thus determinant for breeding success, allowing parents to be in the right condition to carry over the task, ensuring the successful fledging of their offspring and avoiding jeopardizing future breeding attempts.

The accessibility of food and predictability of food sources are also important to consider. During the breeding season, food resources need to be close enough to be reached by the adults in a time that allows them to provision their offspring at an appropriate frequency. Accessibility and predictability are intimately connected with environmental variables, which in turn reflect foraging strategies (Stephens 2007). In seabirds, for example, both accessibility and predictability of foraging resources are closely coupled with oceanographic conditions and their annual variability (together with weather and stochastic factors; e.g. Adams et al. 2004). Perhaps the most well known example of how a change in accessibility of food, mediated by oceanographic factors influences directly breeding success is the catastrophic breeding success of seabirds nesting along the Humbolt current on years of strong El Niño Southern Oscillation events (e.g. Schreiber & Burger 2001).

1.2 COLONIAL SEABIRDS AS STUDY MODELS

Despite the fact that colonial seabirds include diverse taxa, such as albatrosses and petrels (Procellariiformes), penguins (Sphenisciformes), auks, gulls and skuas (Charadriiformes), gannets, pelicans and cormorants (Pelecaniformes), and others, they have functional similarities and converging ecological requirements, as they are subject to very specific conditions and selection pressures (Schreiber & Burger 2001).

Colonial seabirds are central place foragers with separate feeding and breeding habitats, as they all feed at sea (with a few exceptions, such as some skuas and gulls), but must come to land in order to breed. Most species nest in isolated locations, be it on inaccessible cliffs, on remote islands, or both. This is probably a response to predation, mainly mammalian but also from other birds (Schreiber & Burger 2001).

The fact that they gather in colonies for breeding allows large sets of data to be collected in a relatively short period of time. Their notorious philopatry (with a few exceptions) enables researchers to follow the same individuals among multiple breeding seasons, sometimes for many years.

Seabirds are also believed to be good indicators of the state of the oceans, including the presence of contaminants, variations in prey stocks (which might reflect overfishing from commercial fisheries), and others (Cairns 1992a, Bost et al. 2008, Mallory et al. 2010), although this approach does have limitations (e.g. Durant et al. 2009). Their demographic and breeding parameters are thus expected to reflect environmental conditions, with population trends, length of foraging trips, growth rates of chicks and adult body mass variation being among the most frequently used indicators (e.g. Schreiber & Burger 2001). This information is then in a position to be used to inform the management of marine resources or for conservation measures to be implemented (e.g. Cairns 1992a, Monaghan 1996, Karpouzi et al. 2007, Velarde et al. 2013).

1.2.1 Fisheries and global seabird declines

Large scale changes in fisheries policies worldwide, particularly since the 1950’s, have been implicated in changes in the population dynamics of many seabird species (FAO 2011, Croxall et al. 2012). An increased demand for fish has led to an intensification of the fishing effort and to overexploitation of the stocks of many species. Associated with these fisheries is the production of enormous quantities both of offal, from processing fish onboard, and of discarded unwanted or over-quota fish. Reductions in the availability of natural prey and the increased availability of scavenging opportunities have had a severe impact upon the populations of many seabirds, some decreasing markedly (such as several seabirds in North Atlantic, as kittiwakes *Rissa tridactyla* and terns *Sterna* spp.; e.g. Jennings et al. 2009), others increasing sharply (such as fulmars *Fulmarus glacialis* and several gull species; e.g. Furness et al. 1992, Oro et al. 2005, Duhem et al. 2008). An additional problem was clearly illustrated by a study on breeding great skuas *Stercorarius skua* on the Shetland Islands: the populations of this predator benefitted from the discards produced and consequently increased; however, on years of low discards availability, the artificially increased population would predate disproportionately on other seabird species (Votier et al. 2004a); similar situations have been reported for gulls (e.g. Stenhouse & Montevecchi 1999). Other impacts of fisheries are not as obvious. For example, the Cape gannet *Morus capensis*, a seabird depending on lipid-rich pelagic fish, frequently forages on discards. The available discards are mostly of demersal fish, of a much lower nutritional value than “natural” food (they can be called “junk-food”), and the chicks of birds utilising these resources have poorer development (Grémillet et al. 2008, Mullers et al. 2009).

Further to the above, seabirds also suffer direct mortality during associations with fishing vessels via drowning after being caught on fishing apparatus, accidentally captured as by-catch or purposefully captured in order to use the birds as bait, as food for the ship crew, or for being sold as gastronomic delicacies (e.g. Zino 1971, Gilman 2001, Favero et al. 2011 and references therein, Croxall et al. 2012). This is considered the single most important cause of population decline for several seabirds, particularly albatrosses, shearwaters and other petrels (Croxall et al. 2012); as a consequence, many albatrosses, including the black-browed, and petrels, are now classified as Endangered (IUCN 2010). In areas such as the Falkland Islands, mitigation measures have been implemented to minimize seabird deaths on fishing operations, with already visible success (Sullivan et al. 2006, Falkland Islands Government 2012).

1.2.2 Study species: the black-browed albatross

The black-browed albatross *Thalassarche melanophris* is a long-lived pelagic and highly philopatric seabird, with protracted maturity, breeding colonially on islands at sub-Antarctic latitudes where it is one of the most important top-predators. Most of its breeding population is concentrated on the South Atlantic, and especially on the Falkland Islands, where approximately 67% of the global population nest at 12 breeding sites; other important colonies are located on Chilean islands, South Georgia and in smaller numbers in South Indian Ocean, with an estimated global population of 602,000 breeding pairs (Gales 1998, Huin 2002, ACAP 2010).

Black-browed albatrosses live at sea from May to August and breed during the Austral summer, re-occupying their nests in mid-September. Nests are weather-resistant chimney-shaped structures, built on rocky cliffs, or sometimes on rocky patches surrounded by tussock grass on hill sides, being re-occupied annually, usually by the same pair. The mean age of first breeding is around 10 years after fledging. In common with other albatrosses it lays single egg clutches, starting in the second week of October and the first chicks hatch in mid-December, after an incubation period of ca. 68 days. The chick is permanently attended by one of the parents during the early development stages, on average the first 20 days of life (the brooding period), both for protection against predators and for thermoregulation. The chick is fed by both parents until March when the adults migrate to offshore waters, leaving juveniles alone until they fledge from the beginning of April onwards (after an average period of 116 days after hatching). At the end of the brooding period the chick is particularly vulnerable to predation (which becomes rare at later stages), but other causes of death are disease and parasites, heavy storms, and malnutrition (Waugh et al. 1999, Tickell 2000, Reid et al. 2004, Catry et al. 2010).

Adult black-browed albatrosses feed at the ocean surface on squid, fish and crustaceans (with a variable percentage originating from fishing vessels) and the chick is fed the same diet by both parents (Prince 1980, Thompson 1992, Thompson & Riddy 1995). Foraging trips are longer during the incubation period, and the distance covered is probably optimized in relation to the abundance of food (Cairns 1992b, Stephens et al. 2007).

The black-browed albatross has been classified with very unfavourable conservation status for many years, and, despite observed increases in some colonies, is still considered as Endangered (IUCN 2010, Catry et al. 2011b). The reasons behind this were steep and prolonged population declines observed at several breeding colonies (decrease of 80,000 breeding pairs from 1988 to 2010), together with heavy mortality of adults recorded at fishing operations (trawlers, longliners and jiggers), and these two observations are thought to be connected (Gales 1998, ACAP 2010). However, it is unclear whether there may be additional factors that may underpin these declines (in addition to those associated with commercial fisheries and it is very possible that habitat quality, food quality, and parasites and disease (as outlined above) may play a role.

1.2.3 Study species: the Southern rockhopper penguin

The Southern rockhopper penguin *Eudyptes chrysocome* is one of the smallest penguins and nests colonially on islands on sub-Antarctic waters, usually associated with good tussock grass cover. In common with albatrosses they share the longevity, the delayed maturity (though less marked), the philopatry and pelagic habits. This species breeds on a number of archipelagos on the Atlantic, Indian and Pacific oceans, with a total population estimated at over 1.23 million pairs (BirdLife International 2013a, but see Baylis et al. 2013). The most important breeding sites for this species in the Atlantic are located on the Falkland Islands (319,163 breeding pairs in 55 breeding colonies) and on Argentinean and Chilean islands off Patagonia (e.g. 173,793 breeding pairs at Isla de los Estados; Baylis et al. 2013, BirdLife International 2013a).

Nests are placed among tussock grass or on exposed rocky ground, and are re-occupied every year. Males arrive first to the breeding colony (early October, on the Falkland Islands) guarding the nest site permanently until the arrival of the female, sometimes up to a few weeks later. Like all "crested penguins" (genus *Eudyptes*) rockhoppers lay annual clutches of two eggs, in a period running from the end of October until mid-November, and are incubated for 32-34 days until hatching around the beginning of December. Both eggs are of different sizes, the first one usually smaller and known as "A" egg and the second as the "B" egg. Generally, one of the eggs is lost during the incubation period and only one chick fledges, despite the two eggs laid (despite exceptions being relatively frequent on the Falklands; Poisbleau et al. 2008). After a guarding period of around 24 days the chicks are left alone and start gathering in crèches; by February, when about 65-75 days old all fledge (see Strange 1982, Williams 1995, Poisbleau et al. 2008).

The populations of this species declined steeply during the last century at most colonies and, despite being currently considered to be stable or increasing (on the Falklands), it is classified as Vulnerable (Baylis et al. 2013, BirdLife International 2013a). For example, on the Falkland Islands a loss of up to 87% (or 1.4 million pairs) has been estimated to have occurred since 1932 (Pütz et al. 2003, BirdLife International 2013a); similar decreases have been recorded elsewhere (BirdLife International 2013a). The Falkland populations were at their minimum around 2005, and increased since then (Baylis et al. 2013). In the past, causes for population decline have included egg collection, killing of adults for bait and oil extraction and habitat change through the introduction of domestic grazing animals. More recently, reported factors included disease, the taking of adults for zoological collections, changes in marine communities via commercial fisheries or/and climate change (affecting food webs and food availability) as well as competition and predation from fur seals (BirdLife International 2013a). The marked rockhopper population decline coincided with extensive habitat deterioration, mostly due to overgrazing by cattle and burning, leading to the loss of 80% of all original tussock cover on the Falklands (Clark & Dingwall 1985, Birdlife International 2010). This led to hypothesizing habitat loss/changes as a potential cause for population decline on several breeding areas (Birdlife International 2010), a factor which probably requires further study. The causes for the recent population decline (from 2000 to 2005) are not clear, but might include stochastic factors, such as storms, harmful algal blooms, starvation before moulting and other marine based factors (Birdlife International 2010).

1.3 IMPORTANCE OF LONGITUDINAL DATA SETS AND LONG TERM STUDIES

Changes in growth trend at the population level are difficult to measure correctly on most wild animal species. The factors influencing variation in demographic rates are subject to temporal variation, both within a year and across years, which include stochastic factors. The impact of this variation over individuals and populations will vary according to a given species longevity; thus longer lived individuals of long lived species are potentially exposed to more temporal stochastic variation than the individuals of species with a shorter generation overturn. Given fitness is a lifelong process, longer lived species (compared to short lived ones) will need more years of data in order to identify factors that are important in explaining variation in fitness, which eventually reflect at the population level. Despite the importance of short-term ecological studies to provide a snapshot of a given problem, this image tends to be an incomplete one, and ideally they should be complemented with longer series of data. Frequently short-term studies are inconclusive regarding the assumptions they offered to analyse, or those conclusions are only applicable for similar circumstances, and it is often not possible to extrapolate them for a broader time period.

Rare or infrequent events, or environmental perturbations (that can potentially have profound effects on populations and life histories), such as unpredictable variations in prey populations, El Niño events, weather-related catastrophes, are unlikely to be picked up using shorter series of data. However, they need to be studied, given the potentially great importance they can have in driving population trajectories (e.g. Tiller et al. 2013). Long-term studies are also key in behavioural and other demographic studies such as mate fidelity, the effect of age on behaviour and breeding performance (Nisbet 1989). In short, any factor that is subject to temporal variation (diet, breeding success/failure or incidence of disease) should be studied using data series that cover as many years as possible.

The required length of such studies (and time-scale used) increases with the longevity of the study species. Seabirds (especially the Procellariiformes) are particularly long-lived, and therefore long-term ecological studies are fundamental to produce results that are meaningful.

1.4.1 STUDY AREA: FALKLAND ISLANDS, THE PATAGONIAN SHELF AND THE MALVINAS CURRENT

In the SW Atlantic, the Patagonian Shelf extends adjoins the coasts of Uruguay, Argentina and the Falkland/Malvinas Islands. The sea is relatively shallow, with the ocean floor at around 200 m of depth and the waters around the Falklands are dominated by the northerly flowing Malvinas Current, which brings cold water to the surface in a series of upwellings and eddies as it hits the continental slope. The whole Patagonian Shelf area is notoriously productive, however the upwelling areas are particularly so, due to the higher concentration of nutrients and oxygen. These conditions favour high rates of primary production, which is the basis of a rich ecosystem that hold high concentrations of crustaceans, fish and cephalopods, and consequently of their predators: marine mammals and seabirds (e.g. Croxall & Wood 2002, Arkhipkin 2012, Miloslavich et al. 2011).

1.4.2 STUDY AREA: NEW ISLAND

Most of the field work included in this Thesis was carried out at New Island (51° 42' S, 61° 17' W), which is the westernmost island of the Falklands archipelago and is classified as an Important Bird Area (BirdLife International 2013b). It holds important breeding populations of black-browed albatross (29,000 pairs), Southern rockhopper penguin (13,950 pairs), king cormorant *Phalacrocorax atriceps* (more than 3,000 pairs), thin-billed prion *Pachyptyla belcheri* (estimated at 2 million pairs), gentoo penguin *Pygoscelis papua* (more than 6,500 pairs), Falklands skua *Stercorarius antarcticus antarcticus* (333 pairs, decreasing), as well as numbers of Magellanic penguin *Spheniscus magellanicus*, Southern giant petrel *Macronectes giganteus*, striated caracara *Phalcoboenus australis*, Falklands steamer-duck *Tachyeres brachypterus* and South American tern *Sterna hirundinacea*, among others (BirdLife International 2013b, Catry et al. 2003, 2011a, personal observations).

1.5 FRAMEWORK OF THE CURRENT STUDY

The studies included in this thesis were developed within a long-term study of black-browed albatross ecology taking place on New Island (Falkland Islands) since 2003, coordinated by Dr. Paulo Catry, and therefore include data that would be impossible to obtain within the time frame of this PhD. Demographic data started to be gathered at this colony during the 1980’s by Ian J. Strange (Strange 2008). This long-term study focuses on a range of demographic parameters, including annual breeding parameters, annual survival rates, diet and foraging ecology, disease and parasites, mass regulation, among others (see e.g. Catry et al. 2010, 2011b, 2013, Granadeiro et al. 2011).

1.6 OBJECTIVES AND STRUCTURE OF THIS THESIS

The current thesis consists of 4 chapters, besides the General Introduction and the Final Discussion. They are focused on how different limiting factors explain the population changes of two endangered seabirds, the black-browed albatross and the rockhopper penguin (this species is only treated on Chapter 2), and how they are interdependent.

Chapter 2 focuses on explaining spatial variation in breeding success of seabirds through the study of factors such as habitat quality and predation. I studied two sympatric colonial seabirds, the black-browed albatross and the rockhopper penguin *Eudyptes chrysocome* (for this species with data collected on two field seasons previous to the present PhD, coinciding with its lowest population numbers on the Falklands; Baylis et al. 2013) and compare the results obtained from two different, yet simultaneously available, study models. The study of two sympatric species, by providing two different (yet, complementary) views on the same subject to be obtained, allows for more robust and broader conclusions to be produced (with a higher degree of generalization), given that they are subject to similar circumstances regarding a number of factors (such as same breeding habitat, predation and influence of broad oceanographic factors on food availability patterns).

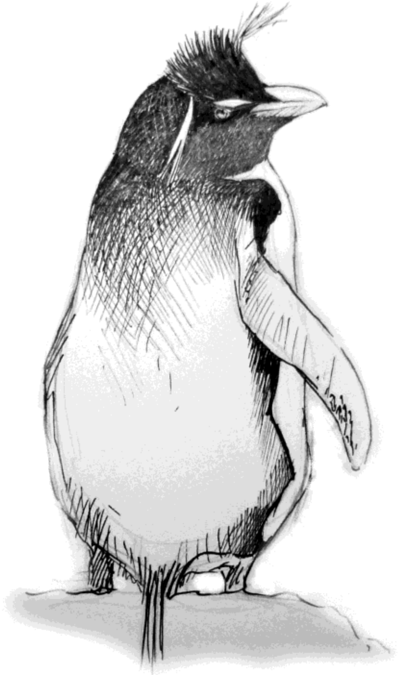
Chapter 3 describes irregular black-browed albatross nestling mortality in relation to disease, with emphasis on spatial analysis. Since 2003, abnormal mortality has been observed within several study sub-colonies and the necessity of documenting this phenomenon and to investigate possible causes prompted this study.

Chapter 4 complements chapter 3 in that it explores the importance of parasites, in this case the tick *Ixodes uriae*, for successful breeding of black-browed albatrosses. As preliminary post-mortem analyses of chicks suspected to have died from the above-mentioned disease were negative, I explored also the possible contribution of ticks for the asymmetrical mortality phenomenon.

Chapter 5 presents the results of a 7-year study of black-browed albatross diet, based on regurgitations from recently fed chicks. The main objective of this chapter, besides characterizing the diet of this species during the mid-chick rearing period, is to examine the potential relationship of albatross foraging ecology with commercial fisheries, speculating from diet composition and its variation across years.

Finally, chapter 6 discusses all the information gathered under the light of current knowledge of seabird and albatross ecology. Thus, the importance of the studied population limiting factors is analysed in a general context, and their interactions with others (including commercial fisheries and other man-originated factors) is analysed.

CHAPTER 2. VARIATION IN BREEDING SUCCESS OF PENGUINS AND ALBATROSSES OVER VERY SHORT SPATIAL SCALES, WITH IMPLICATIONS FOR SEABIRD MONITORING



Abstract

Seabirds are important biomonitors of the health of marine ecosystems and thus it is vital that we must be sure of the accuracy and appropriateness of any measured parameter we use. Monitoring of breeding parameters is often based on samples from one or two study plots taken to be representative of a larger population. However, if there is substantial variation in breeding success over spatial scales similar to such study plots, representativeness may be compromised. Here I present evidence for marked differences in breeding success of both rockhopper penguins *Eudyptes chrysocome* and black-browed albatrosses *Thalassarche melanophris* that can be found among sub-colonies separated by tens or, at most, few hundreds of metres. Such variation does not appear to be linked to any obvious potential habitat-related explanatory variables such as the physical protection afforded by the nests or nesting substrate. Furthermore, I found no differences in chick condition between sub-colonies of contrasting breeding success, which suggests that the observed pattern is not a consequence of differences in adult quality among sub-colonies. In the case of albatrosses, the differences in nesting success among colonies were not consistent across different years. My results suggest that differences in breeding parameters among rockhopper penguin sub-colonies were mostly due to variation in predation pressure (largely driven by the activities of a few highly efficient specialised individual Falkland skuas *Stercorarius antarcticus*) together with edge effects and density of nests. In contrast, variation among black-browed albatross sub-colonies was likely due to disease outbreaks. Irrespective of the exact underlying causes, these within sub-colony correlations and among sub-colony differences highlight that individual nests may not be the most appropriate sampling units from the point of view of monitoring breeding

success. This in turn has implications for ecological and evolutionary studies of colonial seabirds as well as for the use of seabird populations as monitors of the marine environment. Monitoring of seabird breeding populations should therefore be undertaken by sampling as many plots over the widest range of the study colony as feasible. Additionally I suggest multiple potential concurrent factors for breeding success to be examined whenever possible, including spatial variation in predation.

Introduction

There are growing concerns that seas and oceans are being overexploited as stocks of several fish species are known to have decreased considerably in the last decades (Reynolds et al. 2005, FAO 2011). Such changes in fish populations are difficult to measure and often only become apparent when the effects of the contributing factors, such as overfishing, are already catastrophic. As such the marine mammals and seabirds that depend primarily upon fish resources are often advocated as monitors (Cairns 1987, 1992a, Goldsworthy et al. 2001). Seabirds in particular are convenient biomonitors due to their colonial habits, making the measurement of potential indicators such as population size, breeding and fledging success, individual body mass and others a relatively easy task (e.g. Schreiber & Burger 2001).

However, in order to use seabird population parameters as effective indicators it is vital that the limitations of current monitoring methods are understood. For example, some monitoring methods may rely upon assumptions that are in fact not met and they are often based on the intensive study of one (sometimes a few) specific colonies on an island, or of a plot(s) within a large colony (e.g. St. Clair & St. Clair 1996, Mougin 1999, Zino et al. 2008, Pistorius 2009, Hipfner et al. 2010). Such plots are often assumed to be representative of the population as a whole, on the grounds that habitat features are broadly similar to other nesting sites on the same island or archipelago. Further, these sites are assumed to contain a representative range of adult age-classes, given that many (but not all) species are highly faithful to their nest sites from one year to the next (i.e. there is little age-segregation at colony sites). Finally, it is generally assumed that birds nesting in close proximity do not have significant spatial segregation in foraging ranges, despite the fact that evidence points to marked differences in this measure both within and among colonies (e.g. Cherel & Weimerskirch 1995, Pütz et al. 2002). Violation of any of these assumptions (e.g. differences in breeding performance between sub-colonies or parts of a large colony) would severely limit a study's applicability, yet they are rarely investigated. Moreover, problems associated with these assumptions are not restricted to monitoring studies, for example in studies of the impact of a range of phenomena often rely on a second study plot, selected on the basis that it is superficially similar to the first one, to be used as a "control" (e.g. Gillett et al. 1975, Giese 1996, Hull & Wilson 1996, Tremblay & Cherel 2003). If there were significant spatial heterogeneity in breeding parameters then the results of such work would be very difficult to interpret.

A number of studies have shown that there can be quite dramatic spatial variation in breeding success within a seabird colony. Some of this variation is linked to edge effects which are well known and widely reported and taken into consideration when selecting monitoring plots (e.g. Coulson 1968, Tenaza 1971, Emslie *et al.* 1995, Jackson et al. 2005, Liljesthröm et al. 2008, Forster & Phillips 2009) and I will not consider these in detail here. Other sources of spatial variation in success can result from nest site quality and characteristics (e.g. Potts et al. 1980) and the protection it affords in relation to weather (e.g. Potts et al. 1980) and variation in the activities of predators (e.g. Stokes & Boersma 1998). Although some features of the habitat can be easily measured and perceived by an observer, other may not be so obvious and therefore nest site "quality" can be very difficult to quantify. These, in turn, may lead to variation in the effects of predator activity, disturbance (by both conspecifics and heterospecifics) and environmental factors such as moisture and temperature. With respect to predators it is also important to recognise that predators are themselves not all equal. Even within a species there are often different degrees of specialisation and predation efficiency (Votier et al. 2004b) and when this is combined with the territorial nature of many predators, it means that their impact will likely be spatially heterogeneous. Such variability has the potential to generate spatial variation in breeding success at relatively small scales within seabird colonies. Likewise the effects of disease and parasites may also produce spatially heterogeneous patterns and again the potential importance of these is not always fully acknowledged (e.g. Johnstone et al. 1975, Weimerskirch 2004).

Rockhopper penguins *Eudyptes chrysocome* and black-browed albatrosses *Thalassarche melanophris* are two colonial seabirds nesting in sub-Antarctic islands with contrasting ecology and foraging ranges (e.g. Williams 1995, Tickell 2000, Pütz et al. 2002, Boersma et al. 2002, Huin 2002); their diets show limited overlap (e.g. Clausen & Pütz 2002, Thompson 1992). Rockhoppers and albatrosses breed in similar habitats, constructing their nests in coastal rocky areas, including cliffs, and among tussock covered areas, sometimes in mixed colonies. Both species are among the most important top-predators of the SW Atlantic, due to their numbers and body mass, and together they constitute potential biomonitors of sub-Antarctic marine environments (particularly of the Patagonian Shelf waters). For example, rockhopper penguins have been used as indicators of marine food supplies as inferred from local productivity (Clausen & Pütz 2002), and other studies have contributed to understand long-term changes in marine ecosystems under the light of climate change (Dehnhard et al. 2013). In turn, studies on black-browed albatrosses have been used for learning about their prey (e.g. when tracking and diet sampling techniques were used together; Cherel & Weimerskirch 1995), or to better understand seabird-fisheries interactions (e.g. Thompson 1992).

In this chapter I investigate the existence of spatial variation on the breeding success of two long-lived seabirds, the rockhopper penguin *Eudyptes chrysocome* and the black-browed albatross *Thalassarche melanophris*. I relate it to factors such as habitat, nest quality, colony size and predation pressure and conclude by showing that I am unable to predict such variation with habitat-related or colony-related factors only. These results underpin the great difficulties existent when trying to choose a limited number of representative study plots.

Methods

Study area

This study was conducted at the New Island South rookery (51º43’S, 61º17’W), New Island, Falkland Islands. Fieldwork was carried out at a mixed seabird colony where rockhopper penguins (ca 5,000 pairs) nest together with black-browed albatrosses (more than 1,500 pairs) and king cormorants *Phalacrocorax atriceps* (ca 3,000 pairs). The whole seabird colony is surrounded by dense tussock grass *Paradiochloa flabellata* cover, among which a substantial proportion of the colony nests, with the rest of the birds breeding in large clearings or on bare rock areas and in areas adjacent to the coastal cliffs. Breeding biology of southern rockhopper penguins (hereafter rockhopper penguins or rockhoppers) was studied in the breeding seasons of 2004/05 and 2005/06, and black-browed albatross breeding was studied from 2003/04 to 2010/11, from late September to early March, during the Austral summer.

Study species: rockhopper penguins and black-browed albatrosses

Rockhoppers arrive at the breeding colonies during early October (Strange 1982). Clutches of two eggs are laid from late October until mid-November, hatching after 32-34 days (beginning of December). The chicks are guarded for around 24 days (the guarding period; Williams 1995) and then left alone in the colony towards the end of December, gathering in small groups or crèches; from this period onwards it is no longer possible to match chicks to their original nests without using individual markings. The chicks start fledging by early February, when they are 65-75 days old (Williams 1995). For a detailed account on the biology of this species see Strange (1982), Williams (1995) and Poisbleau et al. (2008).

Male black-browed albatrosses guard their nests from mid-September onwards, with the laying of their single-egg clutch occurring from beginning of October; this is followed by a 68 day incubation period in shifts by both adults. The brooding period lasts 11-33 days (Catry et al. 2010). The chick usually stays in the nest until fledging (around 116 days old). A detailed account of the biology of this albatross can be found in Tickell (2000).

Rockhopper and albatross nests do not distribute homogeneously throughout the study area but rather in discrete aggregations (referred to as sub-colonies from here on).

At the study site, rockhoppers nest in two main habitats. The first is more open, exposed and rocky, comprising rocks of different sizes creating a heterogeneous surface. The second breeding habitat is found side-by-side with the first, comprising areas covered in tussock grass of variable density (penguins build their nests at the bases of these plants). Some of the sub-colonies have a mix of these two habitat types, with some of the nests located among tussock and others in the more open rocky areas. Albatrosses also nest under the same two habitats, but the nests located in tussock are mostly free of its direct influence as adults actively remove most of the adjacent cover.

Some of the rockhoppers and albatrosses nest in mixed sub-colonies with king cormorants, although most pairs breed in pure (single-species) sub-colonies.

On New Island, the main predators of rockhoppers (chicks and eggs) are Falkland skuas *Stercorarius antarcticus antarcticus.* Other, apparently less important, rockhopper predators are striated caracaras *Phalcoboenus australis*, southern giant petrels *Macronectes giganteus* and feral cats *Felis catus* (see Strange 1982, Matias & Catry 2008). Albatross chicks suffer predation from Falkland skuas and striated caracaras (personal obs.).

Breeding parameters

1. *Rockhopper penguins*. In 2004/05 I studied 11 sub-colonies within the study area; the furthest distance between the two sub-colonies was ca 430 m and the minimum was around 20 m. Right before laying took place (while nests were being constructed), an average number of 26 nests were selected (range: 8 – 42) in each sub-colony, in a total of 308 nests. A map of each study plot was made, which allowed us to follow each of the selected nests throughout the breeding season without using nest tags, hence minimizing disturbance. Individual penguins were not marked. The contents of each nest were checked daily from the edge of each sub-colony using a 3 m long pole; one individual at a time was gently stimulated to stand up for brief seconds allowing the nest contents to be checked. The number of chicks or eggs on each nest was recorded from 29 October to 10 January (when the last chick of the studied nests entered the crèche period). In order to reduce disturbance, nest checking and movements were made slowly and in a crouched position when necessary; this procedure does not affect the breeding success of rockhoppers (Hull & Wilson 1996).

2. *Black-browed albatrosses*. From the breeding season of 2003/04 onwards (until 2009/10) nests were marked on the day of laying at 3 different sub-colonies (A, B and C) using permanent numbered tags. The total number of nests studied annually was of 170-207, with 45-53, 38-48 and 87-114 on sub-colonies A, B and C, respectively. The 3 sub-colonies are separated by ca. 80 m from each other (approximately defining a triangle). All breeding birds are individually marked with alphanumerical Darvic rings. Parental attendance and nest contents were then checked daily until the end of brooding and weekly until the end of the study period on each season (early March).

For each nest of both species the following parameters were obtained: laying date, hatching date, hatching success (number of eggs hatched per nest), breeding success (number of chicks fledged per nest) and the number of days until breeding failed. For rockhopper penguins, breeding success was considered as the number of live chicks per nest until the crèche period started. From the crèche period onwards chick mortality is usually very low (Strange 1982) and the same applies to albatrosses after early March.

Sub-colony size

For rockhoppers I assessed the size of the sub-colonies by counting occupied nests at the beginning of the laying period in rocky areas, and by measuring the density of nests and total area of each sub-colony in tussock areas. Black-browed albatross sub-colony size was determined by counting all nests with an egg at the end of the laying period each year. A very small number of nests that failed earlier than this are thus not taken into account in this study.

Nesting habitat

For rockhoppers variables that would describe nesting habitat characteristics were chosen and quantified, for both each nest and each sub-colony (micro and macro-habitat description, respectively). Accordingly, at each sub-colony, each nest was characterized in detail for 10 variables while egg laying was still taking place (descriptions of each variable can be found in Table 1). In addition, for each rockhopper sub-colony two variables were characterized: "*slope*" and "*exposure*" (Table 1).

The selection of variables in Table 1 was based on preliminary observations, with all hypothesised to be related to variation in breeding success. Thus "*ground*" and "*nest lining*" might affect hatching probability; for example, eggs placed on dirt substrate have been seen to be buried in mud after rain and those on a rocky substrate might have the probability of egg cracking increased. Likewise the amount of vegetation placed around and inside the nest cup can minimize the risk of eggs rolling from the nest. Other variables ("*main habitat*", "*edge*", "*top*" and "*lateral protection*") potentially influence the probability of predation of individual nests. Distance to nearest neighbours (and resulting index "*density*"), along with presence of albatrosses and cormorants in the adjacent surroundings of the nest might be related to the probability of intraspecific and interspecific conflicts, respectively (or of enhanced protection from predators). Finally, "*slope*" and "*exposure*" were measured for each sub-colony and are potentially related to the irreversible rolling of eggs out of the nest cup (the steeper the slope less likely will be that a displaced egg will be recovered back into the nest cup) and to the accessibility to aerial predators (the aspect of some sub-colonies has them facing prevailing winds making them more attractive for predators; personal observation), respectively.

No study of the influence of (micro-) habitat on albatross nesting was made. In fact, most albatross nests were very similar in terms of protection from aerial predators (benefiting from almost no protection by external elements). Furthermore the number of available sub-colonies was much lower than for rockhoppers, precluding analysis of habitat influence at this level.

Skua predation pressure during incubation and chick rearing of rockhoppers

In 2004/05, from 12 November to 1 December (during incubation), daily counts of skuas attending each rockhopper sub-colony were made during a 7 minute focal observation period recording the following: the individuals that were flying over the colony (apparently actively hunting) and individuals landed on the edge of each sampling area. From this an index of the potential predation pressure at each sub-colony was generated (hereafter “predation pressure”), by summing the number of birds landed and flying over. Artificial and natural individual marks allowed recognition of most individual skuas within the study area.

In order to assess the reliability of the above predation index and the consistency of the differences in predation pressure over different rockhopper sub-colonies, a simple experiment was carried out in 2005/06, during the late incubation period. Twenty rejected rockhopper penguin eggs (that had rolled out from unknown nest cups during the early laying period) were placed in two rockhopper sub-colonies that had markedly different breeding success in the previous season. One egg was placed on each of the 2 sub-colonies, one at a time, alternating between the 2 sub-colonies; the first (sub-colony 3), was located at the top of a sloped area (favouring predation by hovering skuas), the second (sub-colony 4) was at the bottom of a 15 m deep bowl-shaped depression (where slow or motionless flight by skuas was difficult or impossible). A new egg was placed (at the second sub-colony) only after the first had been predated (at the first), or until one hour had passed with the egg still untouched by predators (at which point it was removed). Each egg was placed on different failed rockhopper nests at each trial within each sub-colony. Only one pair of eggs was used on any given day (one egg per sub-colony). No skuas were seen to observe the experiment being set up or were patrolling when eggs were placed. Time till predation was then recorded (time between the moment the egg had been placed until predation occurred); predation time for eggs not consumed after 1 hour was considered as 3600 seconds.

Condition of chicks and assessment of mortality at the nest

Rockhopper chicks were captured and weighed during the final stage of the crèching period, just before departure to the sea. In 2004/05 80 chicks were weighed, from 4 different sub-colonies (20 from each), with two of these sub-colonies located on open rocky areas and the other two on thick tussock. Each chick was captured randomly and its down marked with yellow paint to avoid double sampling. All chicks were weighed on one single date and before they started being fed by adults on that day.

Black-browed albatross chicks were weighed when 58 and 60 days old. For the analyses the mean of those 2 measurements was used, representative of mass at 59 days of age. No chicks were weighed on 2004/05.

In many seabirds, pre-fledging body mass of the chicks is directly related to the survival during the first year of life and with the provisioning ability of adults (e.g. Cairns 1987, Morrison et al. 2009, but see Gray *et al.* 2003 and Piatt et al. 2007). Hence, mass measurements can be used as indicators of parental quality. In instances where a chick was found dead in the nest cup during daily visits, possible causes of death were tentatively determined by visual observation.

Data analysis

Rockhopper penguins

Generalized linear mixed models (GLzMMs) were used to identify possible habitat-related predictors of rockhopper breeding success amongst all variables characterized (Table 1). GLzMMs were fitted with *lmer* function in the *lme4* R package (Bates & Maechler 2009, R Core Team 2012). Nests with one and two “fledged” chicks (live chicks per nest until the crèche period started) were grouped into one single category, so that variable “*number of chicks fledged*” comprised a two-level response variable (success or fail: variable “*success 01*”) in a GLzMM with a binomial distribution. This simplification of data has little effect over real data, as among rockhoppers very few pairs manage to successfully rear two chicks (Poisbleau et al. 2008). Additionally, from the initial 308 rockhopper nests, 35 were excluded: 13 that had been abandoned before laying, four that were extreme outliers relatively to the laying date, five contained an abnormal number of eggs (possibly resulting from two females laying in the same nest or from eggs rolling from other nests with subsequent adoption); finally another 13 nests were excluded where data for some variables was missing. This included the whole of sub-colony 11 (8 nests) where data on skua presence was missing. For some analyses the scores for the variables "*top protection*" and "*lateral protection*" (Table 1), were summed to produce a "*total protection*" variable (to reduce the number of explanatory variables). The resulting scores of "*total protection*" were then grouped in 4 categories: 0 (no protection, when total score equaled to 0), 1 (low protection; total score between 1 and 5), 2 (medium protection; total score between 6 and 10) and 3 (high protection; total score between 11 and 15). The continuous variables "slope" and "sub-colony size" were recoded into multilevel factors (to avoid pseudo-replication): thus 3 levels were used for "slope" (slope angles of 0º-5º, 10º-25º and 30º-45º) and 3 levels for "sub-colony size" (less than 200 nests, 200-380 nests and 450-800 nests). Finally, the index "*skuas*" (mean number of skuas recorded landed on the edge of each sub-colony) was also transformed into a 3-level factor, with low (0-0.15), medium (0.38-0.88) and high (2.35-2.72) presence of skuas landed on the edge of each sub-colony.

All potentially explanatory variables habitat related and the presence of skuas (predictor "*skuas*"), as above (Table 1), were used to produce a global model with binomial errors and logit link-function, where sub-colony identity was used as a random factor (since the observations from individual nests within one sub-colony may not be independent). All independent variables in the model were checked for multicollinearity (which was absent). My initial global model included the following 10 predictor variables: "*main habitat*", "*edge*", "*total* *protection*”, “*density*”, “*albatross*”, “*cormorant*”, “*slope*”, “*exposure*”, “*subcolony size*” and “*skuas*”. At this stage no interactions were included due to model complexity. Two variables were removed from the model (“*ground*” and “*nest lining*”), due to an excess of predictors, these being the ones with an apparently lower biological meaning.

For the first stage of analysis an information theoretic approach was used in the first instance to produce a candidate model set using the functions *dredge* and *model.avg* (model averaging) of *MuMIn* R package (Barton 2013). Subsets of all possible models were generated and ranked according to lowest AIC (Akaike information criterion) values. A simplified global GLzMM was then produced by including only predictors with relatively high importance (from this initial analysis). At this second stage any biologically plausible interactions between the remaining predictors were included, and it was then subject to a second model selection process and model averaging to produce final averaged parameters (and relative importance and standard error estimates for each predictor; Grueber et al. 2011, Nakagawa & Freckleton 2011). The best candidate models used for producing the average model were the top 2ΔAIC models (Burnham & Anderson 2002). Note that whilst these models aim at describing variation in a binary variable at individual nests, the representativeness of my samples of nests is not being tested.

Kruskal-Wallis tests were used to compare numbers of skuas between sub-colonies, as ANOVA assumptions were not fulfilled (Quinn & Keough 2002). A Mann-Whitney U-test was used to compare periods of time in the predation experiment. Masses of rockhopper chicks were compared with ANOVAs followed by Tukey post-hoc tests. Data were analyzed with IBM SPSS Statistics 19.0 and with R 2.15.2 (R Core Team 2012).

Black-browed albatrosses

In order to interpret variation in patterns of breeding success across years and among sub-colonies, GLzMMs with a binomial distribution were used. In these models “breeding success” was a response variable, and year and sub-colony (and their interaction) were predictors. Individual nest was used as a random factor (due to the lack of independency of repeated measures across years), in which I included data only from the same unique combination/pair of breeding birds (same breeding pair for a given nest). The best candidate models were then ranked by AIC, and the top 2ΔAIC models were subjected to model averaging, as described for rockhoppers.

A similar method was used for the mass of 59 day-old chicks as a response variable. GLzMMs were developed, with a Gaussian error distribution, where sub-colony and year (and their interaction) were the predictors, with individual nest as a random factor (as above). The best candidate models were ranked by AIC, and model averaging was used (from top 2ΔAIC models) to produce averaged parameters, as above.

Results

1. Rockhopper penguins

All breeding parameters differed significantly ($p < 0.05$) among sub-colonies (for example, breeding success: Kruskall-Wallis $\chi^2 = 41.38$, df = 10, $p < 0.001$; Table 2). Only 17 pairs (6.1 %) managed to rear 2 chicks up to the start of the crèching period. Below, I further investigate the factors that could have been responsible for the differences on the breeding parameters between rockhopper sub-colonies.

From my first exploratory analysis (the initial global GLzMM) I retained only three predictors identified from my candidate model set, which comprised the variables: "*skuas*", "*edge*" and "*density*", with relative importances of 1, 0.88 and 0.75, respectively. All other variables were non-significant and had relative importance of 0.19 or lower. Three candidate models were within the top 2ΔAIC (Table 3) and model averaging was then used to produce averaged parameters (Table 4). No interactions between parameters were significant.

1.1. Influence of habitat characteristics on breeding success

The analysis suggests that, except for predictors "*edge*" and "*density*", most habitat characteristics were relatively unimportant for rockhopper breeding success ("*breeding success01*") and differences in breeding success among sub-colonies must be caused by other factors.

The position of the nest relatively to the edge of the sub-colony (predictor "*edge*") was the only statistically significant microhabitat characteristic in the final averaged model, with the outermost nests (parameter "Edge 3") suffering the highest failure rates (Table 3). The predictor “*density*”, a proxy for nest density, was included in the top 2ΔAIC candidate models (Table 3), however this variable was not statistically significant (Table 4).

The analysis also indicates the physical protection of the individual nests (“total protection”) had no influence apparent on breeding success; the mean physical protection of nests within each sub-colony was also not related to their respective mean breeding success (Fig. 1). Furthermore, nesting success was not influenced by breeding macro-habitat (rocky and tussock). It is also worth noting that the date when first eggs were laid (predictor “*laydate*”) did not predict whether nests were successful or not (successful and failed nests had similar mean laying date: ANOVA $F_{1, 262} = 2.384$, $p = 0.124$).

1.2. Influence of other breeding species in mixed sub-colonies

Analyses at the nest level did not detect any effect of the proximity of breeding king cormorants or black-browed albatrosses (predictors “*albatross*” and “*cormorant*”; both excluded from the top 2ΔAIC candidate models; Table 3). The size of my sample (with only 3 mixed-colonies) precludes any statistical analysis to be made at the sub-colony level, but the results seem to indicate that differences in breeding success among these sub-colonies are not related to the presence of other breeding species (see Fig. 1). This is perhaps surprising as the breeding failure in rockhopper nests could be directly related to direct interactions with king cormorants (8 nests on 4 sub-colonies) and black-browed albatrosses (3 nests on 3 sub-colonies) due to fights for breeding space (personal observations).

1.3. Sub-colony size

Sub-colony size was not correlated with any of the rockhopper breeding parameters (for example, breeding success r = -0.336, n = 11, p = 0.31). Given its very low relative importance in the initial global model this variable was not selected for inclusion in the final analysis.

1.4. Influence of aerial predators

The number of skuas recorded was significantly different between rockhopper sub-colonies, both when considering the number of flying-over (hunting) individuals (Kruskall-Wallis $\chi^2 = 30.4$, df = 9, $p < 0.001$) and the number of skuas landed on the edge of the sub-colonies (Kruskall-Wallis $\chi^2 = 76.871$, df = 9, $p < 0.001$). Numbers of skuas landed and flying over each sub-colony were highly correlated (r = -0.728, n = 10, p = 0.017).

Even though samples are small, results suggested a relationship between rockhopper breeding success and the number of skuas that frequented a sub-colony, either in hunting flight (r = -0.55, n = 10, p = 0.10) or landed at the edge (Fig. 2). This is further suggested by a significant correlation between predictor "*skuas*" and the percentage of all nests in each sub-colony plot that failed on the outermost layer (r = 0.689, n = 10, p = 0.028).

This relationship is strongly supported by the modeling of the influence of landed skuas on the edge of the sub-colonies (predictor "*skuas*", a proxy for predator activity) upon rockhopper breeding success (Tables 3 and 4).

Predation experiment

The time one egg took to be attacked by skuas (in 2005/06) was shorter on sub-colony 3 (mean predation time = 357 s; SD = 509.2, n = 10) than on sub-colony 4 (mean predation time = 2818 s; SD = 1254.5, n = 10), being significantly different between the two experimental sub-colonies (Mann-Whitney, *U* = 4.0, p < 0.001).

1.5. Condition of the chicks

The pre-fledging mass of rockhopper chicks (by the end of the crèche period) was not significantly different between sub-colonies (Fig. 3). Breeding success was statistically different between those 4 sub-colonies where chicks were weighed (Pearson χ^2 = 14.54, df = 3, p = 0.002).

2. Black browed albatrosses

2.1. Breeding parameters

Breeding success differed significantly between sub-colonies and across some years throughout the study period (Table 5). Only one candidate model (the global model) was considered appropriate to explain breeding success, as the remainder were beyond the interval of 2ΔAIC from the top model considered (with clearly higher AIC; Tables 6 and 7). The best supported model indicated that not only sub-colonies differed in breeding success, but their ranking in terms of success significantly changed in different years (as indicated by the interaction between year and sub-colony; Table 7).

2.2. Condition of the chicks

Mass of black-browed albatross chicks at 59 days of life (Fig. 4) was best explained by both predictors “*year*” and “*sub-colony*” and by interactions of both (the global model), which illustrate the change in rank of mean chick mass between sub-colonies across years (Table 8).

Figures

Figure 1

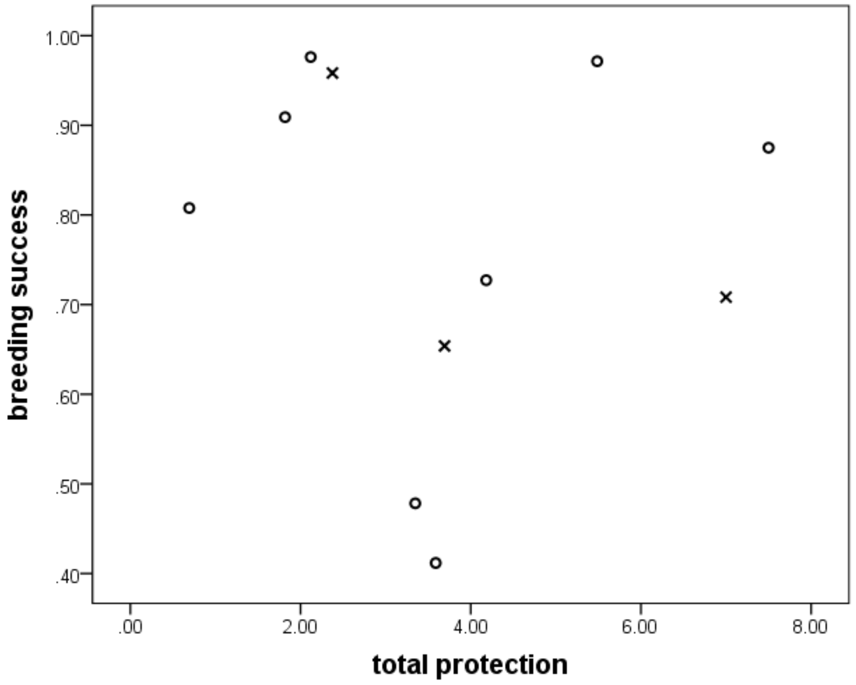


Figure 1. **Breeding success of each rockhopper sub-colony in relation to protection (composite index "Total protection").** Pure rockhopper sub-colonies are represented by a cross, being the remainder mixed with albatrosses and/or king cormorants (r = -0.07, n = 11, p = 0.85).

Figure 2

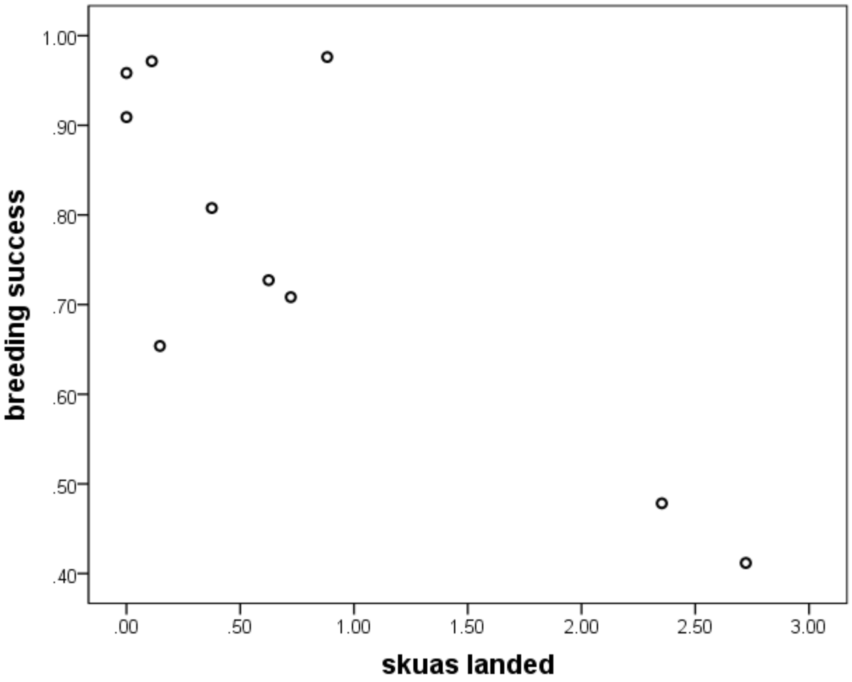


Figure 2. **Breeding success on rockhopper sub-colonies in relation to the presence of skuas landed on their edges (r = -0.82, n = 10, p= 0.004).**

Figure 3

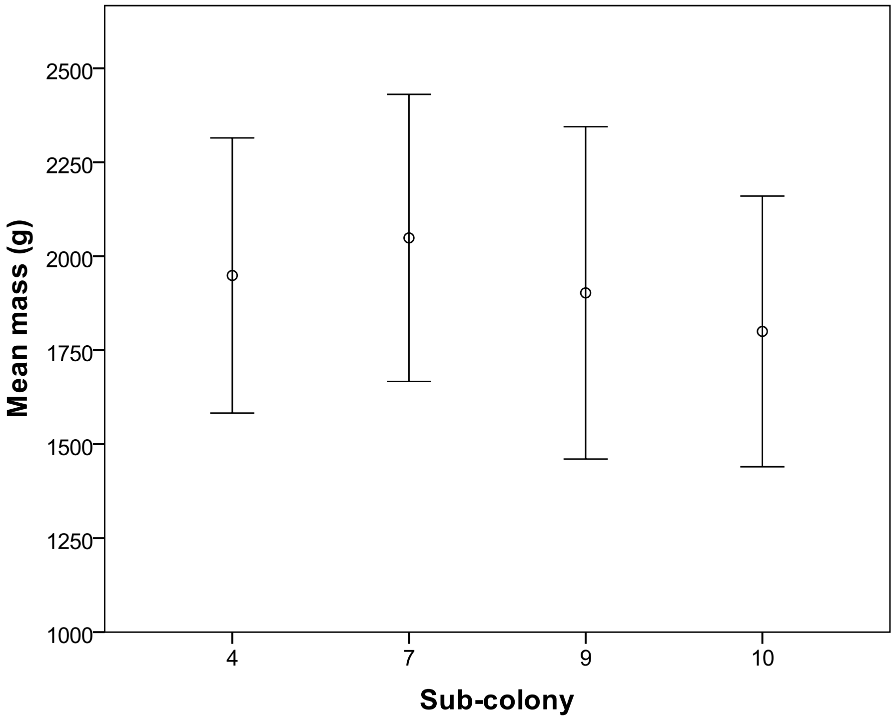


Figure 3. **Mass of rockhopper chicks from four sub-colonies.** Total mean mass was 1925.0 ± 391.9 g (N = 80). Differences between sub-colonies were non-significant (ANOVA, $F_{3,76} = 1.41$, $p = 0.25$). Central dot represents the mean and error bars are ± 1SD.

Figure 4

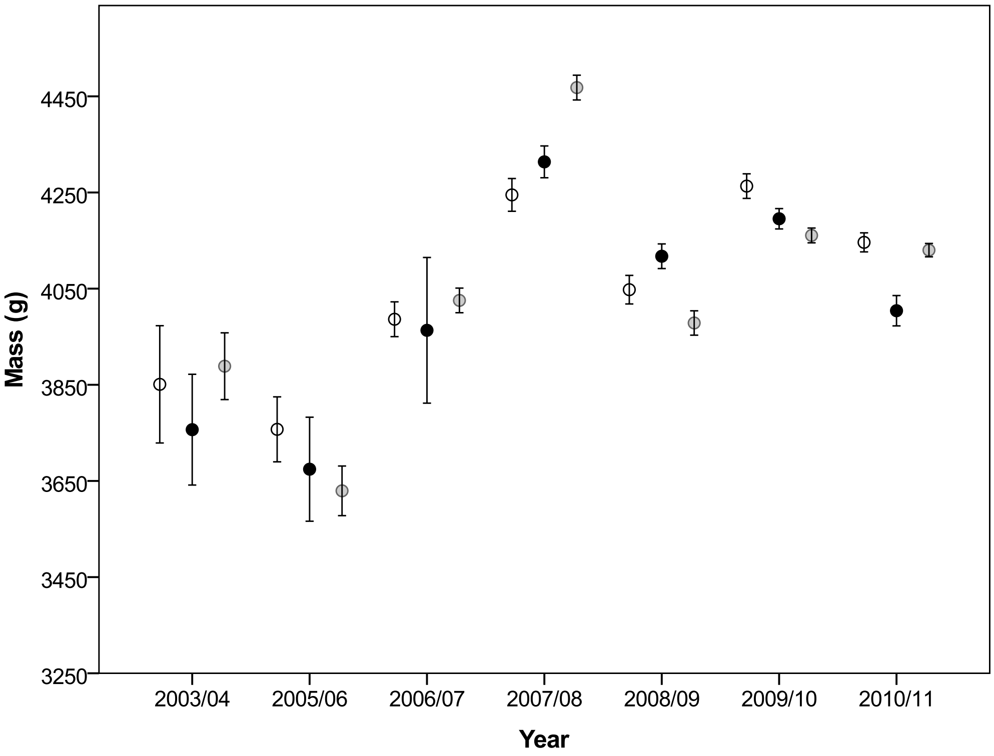


Figure 4. Mean mass (g) of black-browed albatross chicks when 59 days-old from three sub-colonies over 7 breeding seasons (2004/05 not represented). Error bars represent ± 1SE. Sub-colonies A, B and C are represented by empty, black and grey circles, respectively.

Tables

Table 1. Variables studied for each rockhopper penguin nest (1-9) and sub-colony (10-12).

	Variable	Description
1	Ground	The type of ground underlying each nest cup (substrate), classified as (1) dirt/peat, (2) rock, (3) mixed (dirt/peat and rock) and (4) tussock;
2	Nest lining	The presence and amount of vegetable material lining up the nest cup was classified according to the following scale: 0: none, 1: traces, 2: few, 3: some, 4: abundant;
3	Main habitat	The placement of the nest regarding two main macro-habitats: tussock covered areas *versus* open areas with bare soil and/or rocks;
4	Edge	The position of each nest in relation to the edge of the sub-colony was described as: 1. outer nest, 2. nest on the second outermost layer, 3. inner nest;
5	Lateral protection	Each nest was considered to be centered in a square. For each of the sides I classified the height of the lateral obstacle (rock, tussock stool, etc.) that offered protection from 0 to 2, being “0” without protection, “1” when half of the bird height was hidden when it adopted a normal stance over the nest, and “2” when the obstacle had a similar or higher height to that of the bird on the nest. The values obtained for each side of the square were summed resulting in a number between 0 and 8 for each nest;
6	Top protection	A 3 point scale was used to score obstacles above the nest (against aerial predators): it was scored 4 points if it covered half of the top nest area (seen from above) or 8 if it covered the whole of the nest area. When there was no protection above, this parameter was given 0 points;
7	Density of nests	The distances of each sampled nest to its two nearest rockhopper nests were estimated according to the length of an adult penguin (about 0.5 m long) and these two values were summed (distance to nearest neighbour 1 + distance to nearest neighbour 2); I used the inverse value of this sum which represents a nest density index to which I call “density”;
8 9	Albatross Cormorant	For each rockhopper nest I counted the number of black-browed albatross (variable “Albatross”) and king cormorant (variable “Cormorant”) nests that were active or that had an adult at the time of this classification in a radius of 2 rockhopper penguins (about 1 m); if within one sub-colony nesting of rockhoppers was mixed with either albatrosses or cormorants, sub-colonies were classified as mixed (1) or pure (0);
10	Slope	For each sub-colony, the approximate average angle (degrees) of the slope where the nests were installed (by estimation);
11	Exposure	The direction which each sub-colony was facing to;

12	Skuas	Daily counts of skuas landed on the edge of each rockhopper sub-colony were made from 12 November to 1 December 2004; to the index represented by the mean daily number of skuas landed around each sub-colony I gave the name “skuas”, which was transformed in a 3-level factor representing low, medium and high presence (please see text for further details).

Table 2. Summary of mean breeding parameters for each rockhopper sub-colony, together with main breeding habitat (R: rocky, T: tussock, M: mixed), total number of nests on each sub-colony ("*sub-colony size*") and the number of nests sampled on each ("N"); see also the Methods section for the definition of each parameter.

Sub-colony	**Habitat**	**Sub-colony size**	**N**	**Hatching success**	**Breeding success**	**Success 01**
1	R	311	22	0.91	0.73	0.73
2	R	449	24	1.13	0.83	0.79
3	R	310	23	0.74	0.48	0.48
4	R	278	22	0.96	0.91	0.82
5	R	248	23	1.35	0.96	0.87
6	M	131	42	1.48	0.98	0.83
7	R	195	34	0.82	0.38	0.35
8	M	105	34	1.41	0.97	0.82
9	T	369	24	1.33	0.71	0.71
10	M	893	26	1.15	0.65	0.65
11	R	8	7	1.15	0.86	0.86
Mean ± SD				1.15 ± 0.70	0.77 ± 0.55	0.71 ± 0.46

Table 3. Top 2ΔAIC candidate models (GLzMM), ranked by AIC, predicting the effect of habitat characteristics and predators upon rockhopper penguin breeding success (n = 273 nests).

Rank	**Model**	**Intercept**	**df**	**logLik**	**AIC**	**ΔAIC**	**Weight**
1	Skuas + Edge + Density	-0.01942	7	-147.88	309.76	0.00	0.56
2	Skuas	1.32780	4	-151.81	311.61	1.85	0.22
3	Skuas + Edge	0.76812	6	-149.83	311.67	1.91	0.22

Table 4. GLzMM averaged parameters, for the effect of habitat characteristics and predators upon rockhopper penguin breeding success; sub-colony identity was used a random factor.

Parameter	**Estimate**	**SE**	**z value**	**P**
Intercept	0.45025	0.74193	0.607	0.5439
Skuas 2	0.03076	0.34614	0.089	0.9292
Skuas 3	-1.68733	0.36615	4.608	**<0.001**
Edge 2	0.89510	0.46818	1.912	0.0559
Edge 3	0.83107	0.38834	2.140	**0.0324**
Density	0.23513	0.14707	1.599	0.1099

Table 5. Black browed albatross breeding success on 3 sub-colonies; in brackets the number of study nests (nests with egg).

Sub-colony	2003/04	2004/05	2005/06	2006/07	2007/08	2008/09	2009/10
A	0.51 (45)	0.45 (53)	0.35 (49)	0.59 (51)	0.68 (53)	0.50 (50)	0.66 (50)
B	0.42 (38)	0.29 (48)	0.22 (45)	0.71 (45)	0.73 (45)	0.74 (43)	0.81 (43)
C	0.30 (87)	0.56 (94)	0.33 (92)	0.76 (96)	0.77 (105)	0.29 (114)	0.72 (112)
Mean ± SD	0.38 ± 0.49	0.47 ± 0.50	0.31 ± 0.46	0.70 ± 0.46	0.74 ± 0.44	0.44 ± 0.50	0.72 ± 0.45
Pearson χ^2	5.969	9.513	2.047	4.748	1.561	27.411	2.790
P	0.051	0.009	0.359	0.093	0.458	<0.001	0.248

Table 6. Five best candidate models (GLzMM) ranked by AIC, predicting the effect of year and sub-colony on black-browed albatross breeding success. Individual breeding pair (nesting in the same nest throughout the whole period) was used a random factor.

Rank	**Model**	**Intercept**	**df**	**logLik**	**AIC**	**ΔAIC**	**weight**
1	Year+Subcolony+Year*Subcolony	0.558900	25	-733.004	1516.0	0.0	1
2	Year	0.007624	9	-764.249	1546.5	30.49	0
3	Year+Subcolony	-0.154900	11	-762.653	1547.3	31.30	0
4	Subcolony	0.196000	4	-826.702	1661.4	145.39	0
5	(Null)	0.404900	2	-829.142	1662.3	146.27	0

Table 7. Parameters of the best GLzMM predicting the effects of year and sub-colony (and their interaction) over black-browed albatross breeding success. Statistical significance is marked in bold.

Parameter	**Estimate**	**SE**	**z value**	**P**
Intercept	0.55890	0.38868	1.438	0.150
subcolony2	-0.05233	0.62342	-0.084	0.933
subcolony3	-1.15053	0.50418	-2.282	**0.023**
year2004	-0.82270	0.49776	-1.653	0.098
year2005	-0.98071	0.49828	-1.968	**0.049**
year2006	-0.11700	0.49145	-0.238	0.812
year2007	0.53897	0.51441	1.048	0.295
year2008	-0.63419	0.49421	-1.283	0.199
year2009	0.33042	0.54522	0.606	0.545
year2010	-1.26381	0.54129	-2.335	**0.020**
subcolony2:year2004	-0.51238	0.81774	-0.627	0.531
subcolony3:year2004	1.86306	0.65672	2.837	**0.005**
subcolony2:year2005	-0.74315	0.80657	-0.921	0.357
Subcolony3:year2005	0.97773	0.64561	1.514	0.130
Subcolony2:year2006	0.62941	0.77597	0.811	0.417
Subcolony3:year2006	2.14336	0.65085	3.293	**0.001**
subcolony2:year2007	0.15390	0.79612	0.193	0.847
subcolony3:year2007	1.42505	0.65468	2.177	**0.030**
subcolony2:year2008	1.13862	0.77931	1.461	0.144
subcolony3:year2008	0.30244	0.62572	0.483	0.629
subcolony2:year2009	0.65359	0.84632	0.772	0.440
subcolony3:year2009	1.47442	0.67515	2.184	**0.029**
subcolony2:year2010	1.57986	0.81498	1.939	0.053
subcolony3:year2010	2.86399	0.67230	4.260	**< 0.001**

Table 8. Five best candidate models (GLzMM) predicting albatross chick mass, ranked by AIC. Sub-colony, year and their interaction were used as predictors of chick mass at 59 days of age; individual nest (and unique associated breeding pair) was used a random factor. The year of 2004 was removed from the analysis as only one sub-colony was then sampled.

Rank	**Model**	**Intercept**	**df**	**logLik**	**AIC**	**ΔAIC**	**Weight**
1	Sub-colony + Year + Subcolony*Year	3801	23	-4486.349	9018.7	0.0	1
2	Sub-colony + Year	3827	11	-4561.880	9145.8	127.06	0
3	Year	3837	9	-4571.583	9161.2	142.47	0
4	Sub-colony	4044	5	-4655.129	9320.3	301.56	0
5	(Null)	4107	3	-4666.520	9339.0	320.34	0

Discussion

This study shows that marked differences can occur in the breeding success of both rockhopper penguins and black-browed albatrosses nesting in sub-colonies separated by tens or, at most, few hundreds of meters. It is a well-known fact that in colonial birds different sub-colonies of a given population may differ in breeding parameters (e.g. Harris et al. 1997, Neve et al. 2006). However, in this study, such variation could not be predicted by variables that previous research on penguins and albatrosses found to be significant explanatory factors, such as nesting habitat (e.g. St. Clair & St. Clair 1996) or physical protection afforded by rocks or vegetation to the nests (e.g. Stokes & Boersma 1998). My analysis indicated that most variation in rockhopper breeding success could be explained by the intensity of the presence of skuas landed on the edge of each sub-colony (used as a proxy for predation activity), whilst edge effects and nest density may be further indications of predation. The importance of predation in defining spatial heterogeneity in rockhopper breeding parameters is discussed below as well as the potential factors underlying spatial and temporal patterns of black-browed albatrosses breeding success. These observations have implications for seabird monitoring studies, especially regarding plot selection and independency of data points.

Many of the factors studied for both species did not explain the observed variability (the case of habitat-related physical factors). Main breeding habitat was not a significant predictor of rockhopper breeding success and, similarly, physical characteristics and protection associated with individual nest-sites seem not to have been important. The results are at least partly at odds with those of St. Clair & St. Clair (1996) who, relying on data from only 3 rockhopper sub-colonies in the same rookery of this study, concluded that nests in tussock enjoyed enhanced breeding success (perhaps from being better protected from predatory skuas). The quoted study might have suffered from not sampling enough truly independent nest locations.

Similarly, for albatrosses, the habitat around the nest is also unlikely to have been important in relation to spatial variation in breeding success. This conclusion is based on two observations. First, albatross nests do not benefit from cover provided by habitat features and albatross colonies with different success are structurally very uniform. Second, changes in the rank order of nesting success between sub-colonies happened from year to year (Table 5) despite the fact that the habitat where they were situated remained virtually unchanged, and the number of adults that changed their nesting place was minimal (personal data, unpublished).

The size of a (sub) colony has also been demonstrated to affect breeding parameters of several seabirds (Tenaza 1971, Barbosa et al. 1987, Liljesthröm et al. 2008). However, for rockhoppers, I failed to find a relation between this variable and breeding success; my sample might have lacked enough very small and large sub-colonies for such an effect to be detected. For black-browed albatrosses, the number of sub-colonies available and their range of sizes were insufficient to analyze the influence of this factor. Besides size, sub-colony shape can also be important for breeding success (e.g. Tenaza 1971, Jackson et al. 2005) acting via edge effects. The influence of edge effects was significant for rockhopper breeding success, particularly for the outermost nests of each-subcolony (Tables 3 and 4); however this is not surprising as this is one of the factors most frequently linked with spatial patterns in breeding success for other colonial species, and are associated with differences in individual quality of breeders (Coulson 1968), and with the action of predators, which prefer more exposed nests in the periphery (e.g. Emslie et al. 1995, Liljesthröm et al. 2008). Although I was unable to determine causes for breeding failure for most nests, it is plausible that both edge effects and predation are related in this study. This is consistent with the significant correlation found between landed predators and percentage of nests that failed on the outermost part of each sub-colony plot.

The data strongly suggest that the breeding output of several rockhopper colonies was related to the presence of potential predators (skuas), when these were in higher numbers (Fig. 2, Tables 3 and 4). For the purpose of monitoring studies, this is a factor where spatial occurrence would be very difficult to predict, as it depends on specific characteristics of the local predators (species involved, their age and experience, individual efficiency, etc.). At the study site non-systematic observations suggest that some individuals might be more efficient hunters (for example, most predation losses recorded on sub-colony 7 were apparently caused by a single very efficient and aggressive skua), but this aspect would require further research. The potentially severe influence of individual predators on the breeding success of other colonial seabirds has been shown by other studies (e.g. Guillemette & Brousseau 2001). At the population level, it has been shown for the great skua *Stercorarius skua* that a small percentage of individuals are specialized in eating seabirds, whilst most eat primarily fish despite eating seabirds opportunistically (Votier et al. 2004b).

Other studies have shown how different efficiency or preferences of individual predators can strongly bias the results of predator-prey interaction studies on a broad range of animals, from insects (Wotton et al. 1993) to all kinds of vertebrates (Pettorelli et al. 2011 and references therein). These individual differences reflect factors such as social status, age, or breeding condition (Pettorelli et al. 2011). Predator territoriality was an explanation for spatial differences in predation pressure over rockhopper penguin sub-colonies on Staten Island (Liljesthröm et al. 2008) and similar observations have been reported by Emslie *et al.* (1995) for the chinstrap penguin *Pygoscelis antarctica*.

The experiment indicated that numbers of skuas were linked to rates of egg predation. The experiment performed further suggests that predation pressure can indeed differ between (sub) colonies. This may be mediated by topography (see also Votier et al. 2008) but at broader topographical scales than the ones measured for this study. Skuas had clearly different efficiency at finding and taking eggs on the two experimental sub-colonies, being much faster on sub-colony 3. Such topography effects might explain the differences in breeding success verified between these two colonies in 2004/05.

Different predation pressures over various sections of one large colony have been reported previously (e.g. South Polar skuas *Stercorarius maccormicki* and Adélie penguins *Pygoscelis adeliae*; Müller-Schwarze & Müller-Schwarze 1973) and have been attributed (besides to predator territoriality and topography; Votier et al. 2008) to density of nests and sub-colony size (Emslie *et al.* 1995, Oro 1996) and to sub-colony shape (Tenaza 1971). In addition, regarding the predation experiment, it is tempting to speculate that dominant wind direction better favoured predation on sub-colony 3 by hovering or “hanging” on the wind than on sub-colony 4, where local currents did not allow an easy aerial prospection. Thus, I suggest that what could be termed as “asymmetrical predation” in a large colony (mediated by edge effects and density of nests) is one potentially important factor explaining success differences between the studied rockhopper sub-colonies. However, unlike previous studies, such asymmetries could not be easily associated with habitat or colony specific characteristics.

Black-browed albatross chick mortality was markedly variable not only across years, but most importantly among sub-colonies. What seem to have been outbreaks of an apparently undescribed disease (Bowgen 2007) might have been the main cause for differences on breeding success between sub-colonies (on some years), due to the fact that it did not spread throughout the study area, affecting more severely one different sub-colony on each year; a spatial analysis indicated disease to be the most likely cause of death among young chicks (own unpublished data; see Chapter 3 of this thesis for details). Similar unpredictable spatial asymmetries in breeding success were described for the yellow-nosed albatross *Thalassarche chlororhynchos* due to outbreaks of avian cholera (Weimerskirch 2004). Other possible causes for asymmetries on specific years are stochastic weather events together with sub-colony location (i.e. in some years storms caused black-browed albatross chicks to fall from the nest and being subsequently predated on more exposed sub-colonies; see e.g. Potts et al. 1980 for a development of this aspect applied to the shag *Phalacrocorax aristotelis*) and direct predation. All these factors deserve further research.

The results of the albatross study also tend to refute the idea that there are marked differences in parental quality among sub-colonies as although mean chicks mass differed from year to year, differences in the rank order between sub-colonies across years were inconsistent, despite the breeding pairs on each sub-colony being approximately the same each year. Similarly, there were no differences in chick mass among rockhopper colonies with contrasting nesting success.

Conclusions

This work shows spatial variation in breeding output within penguin and albatross colonies could not be predicted by habitat-related variables. To further complicate matters, the patterns of such spatial variation were not constant over time. Of course it does not follow from this that spatial variation in rockhopper penguin and black-browed albatross breeding success is impossible to predict, but rather that many of the variables measured in this study may not have managed to capture the most appropriate habitat-related characteristics. For rockhoppers, however, I show how spatial variation within breeding colonies may be well explained by variation in skua predation together with edge effects and density of nests, the last two variables perhaps also themselves related to predation pressure. Most studies and monitoring programs do not generally involve a direct effort to understand spatial variation in breeding success and so are likely to be even less able to predict and understand such variation than in this study. Hence, the choice of main study and control plots probably is, generally, an uninformed one. If patterns such as the ones reported here are common in seabird colonies (which is not unlikely), many studies may suffer from problems of representativeness.

These findings have important implications for researchers at the time of selecting colonies or study plots. Small sub-colonies or plots should not be assumed to be representative of larger colonies simply on the basis of apparent uniformity of the physical or biological environment.

If differences in the breeding parameters can be caused by factors such as the action of individual predators, it means that individual nests are not statistically independent sampling units from the point of view of monitoring of breeding success. This conclusion has wide reaching implications not only for seabird monitoring, but also in general for behavioural and ecological studies of colonial seabirds.

Therefore, in order to minimize the problems detailed above, I would suggest the monitoring of any seabird population should be done by sampling nests from as many sub-colonies or patches as it is feasible. This information should be complemented by the measurement of other variables besides breeding output, such as, for example, the causes of nest failure, chick-growth and begging behaviour (e.g. Hull et al. 2004, Quillfeldt & Masello 2004), parental time budgets and provisioning rates (e.g. Huin et al. 2000, Litzow & Piatt 2003, Pinaud et al. 2005) and diet (e.g. Croxall et al. 1999, Clausen & Pütz 2002).

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CHAPTER 3. AN EPIDEMIOLOGICAL STUDY OF BLACK-BROWED ALBATROSS *THALASSARCHE MELANOPHRIS* CHICK MORTALITY IN THE FALKLAND ISLANDS

Abstract

Despite diseases and parasites being potentially important limiting factors influencing animal demographic rates, our understanding of these processes is still limited in some taxa. Species both philopatric and colonial, such as seabirds, are among the groups likely to be most susceptible. I investigated patterns of mortality affecting the nestlings of an endangered seabird, the Black-browed Albatross *Thalassarche melanophris* during the brooding stage at two colonies on the Falkland Islands. The consistency of the clinical signs exhibited by many of the chicks that died, within and across years, suggested an infectious disease was involved. This suspected infectious disease likely caused the failure of between 4% (in the best year) and 33% (the worst) of the nesting attempts at one of the study colonies. A post-mortem analysis performed on a sample of ten nestlings in 2006/07, identified several significant infectious agents; parasites (nematodes and ticks) were probable secondary disease agents which potentially contributed to the ill-health of the chicks. In 2008/09, ticks had a prevalence of 100% in the studied sub-colonies. A spatial analysis of mortality clearly indicated a clustered pattern within sub-colonies. Furthermore, the prevalence of mortality varied between sub-colonies separated by ca. 80 m. The epidemiological analysis provides clear evidence that an infectious disease is associated with epidemics in Black-browed Albatross colonies in the Falkland Islands. Given the levels of mortality among nestlings recorded in some places and years, research to understand the precise aetiology of this disease and to monitor its prevalence in future years is desirable.

Introduction

Disease and parasites are known to be important extrinsic factors influencing animal demographic rates (Lack 1954, Scott 1988, Cairns 1992b, Grenfell and Gulland 1995, Hudson et al. 2002, Møller 2005). Among others, their reported effects have included population fluctuations and marked population declines that on extreme cases have resulted in the extinction of populations or whole species (van Riper et al. 1986, Cooper 1989, Cully et al. 1997, Hochachka and Dhondt 2000).

Both philopatry and coloniality are behavioural traits that have been shown to increase the transmission and incidence of disease and parasites (Hoogland 1979, Brown and Brown 1986, Møller 1987, Danchin 1992). Among the groups with populations most susceptible to be influenced by disease and parasites are gregarious and herd-forming mammals, several colonial waterbirds (such as herons), colonial passerines and particularly seabirds (Hoogland 1979, Brown and Brown 1986, Cairns 1992b, Dulberger et al. 2010). Despite the recognized importance of disease and parasites at influencing demographic rates (for the above mentioned groups and others), studies on population dynamics have focused mostly on other factors that comprise, among others, the abundance and availability of food, the number and quality of nest-sites and the impact of predators (e.g. Lack 1954, Scott 1988, Cairns 1992b).

Seabirds, particularly those that are top-predators (such as albatrosses and penguins), are important components of marine ecosystems and are health indicators of their prey populations and of the whole food chain (e.g. Cairns

1987, Monaghan 1996). Some life history traits common to many seabird species, such as colonial nesting habits and extreme philopatry (not infrequently returning to the same exact nest), makes them potentially very vulnerable to disease threats. These habits allow pathogens to potentially spread quickly during the breeding season and also to persist in an area for long periods. Knowing the potential of diseases and parasites to affect population dynamics and given the importance of seabirds as components of marine ecosystems it is surprising that their effects have only occasionally been systematically studied (e.g. Morgan et al. 1985, Weimerskirch 2004, Nunn et al. 2006a, b, Thoisy et al. 2009). Therefore, it is vital to gain more information on the dynamics of disease and parasites in this group of birds. Moreover, the exposure of seabirds (typically nesting on remote and isolated areas) to new pathogens might be increasing in the short term due to growing human trade and travel adding urgency for research to be carried out on these subjects (e.g. Pearce and Wilson 2003).

Albatrosses (family Diomedeidae) are typical seabirds. All albatross species are currently listed as near threatened or threatened to some degree after dramatic population declines were documented in several populations (IUCN 2010). For most species, the main causes underlying these declines are thought to be fisheries-related (Sullivan et al. 2006, Huin and Reid 2007, Snell et al. 2012 and references therein). However, other factors may also be important, diseases being potentially one of them (e.g. Weimerskirch 2004). Although various diseases have been described for albatrosses their significance in terms of influence over breeding parameters and demographic rates has only rarely been investigated. Cases of disease or disease causing agents described for these seabirds have included bacteria (Work et al. 1998, Weimerskirch 2004), fungi (Tham et al. 1974), viruses (Young and VanderWerf 2008), blood parasites (Peirce and Prince 1980), biotoxins (Thomas et al. 2007), chemical toxins (Sileo et al. 1990), pollution (Auman et al. 1997), trauma (Sileo et al. 1990) and ectoparasites (Bergström et al. 1999a, Haemig et al. 1999, Gilardi et al. 2001). As shown by Weimerskirch (2004), infectious diseases can be an important cause of mortality in albatrosses, impacting their demography and may present the potential for extinguishing small isolated populations. The semi-precocial nature of albatross nestlings (reducing physical contact between individuals), makes them perhaps less vulnerable to contagious diseases during their early life period (compared to penguins or other creching birds, for example), yet it might still render them susceptible to ectoparasite infestation, as their permanent nests offer long-term shelter to several kinds of parasites (R. Matias pers. obs.).

The Black-browed Albatross *Thalassarche melanophris* is currently classified as endangered (IUCN 2010). The Falkland Islands contain most of the world Black-browed Albatross breeding population (ca. 65%), concentrated in 12 colonies (Huin and Reid 2007, Strange 2008). During a long term study on Black-browed Albatross demography and ecology taking place on New Island, West Falklands (Catry et al. 2011b), nestling mortality episodes have been noted annually during the brooding period since the research began in 2003/04. Brief references made a few decades before by Tickell and Pinder (1975) to “virus-like infections” occurring from “time to time” in Black-browed Albatross colonies in the Falklands, may or may not refer to the same disease, but are suggestive.

The causes for this mortality remain to be explained. Therefore, the objectives of this paper are to describe the epidemiological and pathological parameters of the disease and, by using this information, to draw conclusions about its aetiology and to understand whether other factors might have been involved that may help explain variations in mortality patterns. In order to study this phenomenon, among other methods, I made a spatial analysis to the nest mortality and performed detailed post-mortem analyses on a sample of 10 nestlings.

Methods

Study area and study species

Fieldwork was conducted mainly at the Settlement rookery (51º43’S, 61º17’W), New Island, during the Austral summers of 2003/04 through 2009/10 (with a gap on the brooding stage in 2007/08). Black-browed Albatrosses nest colonially both on coastal cliffs and on clearings amongst tussock grass *Paradiochloa flabellata*. Somewhere between 10,000 and 13,000 pairs breed on New Island, of which more than 1,500 nest in the rookery of the present study (Huin and Reid 2007, Strange 2008). Complementary work was done at Steeple Jason (51º19’S, 61º13’W) during the Austral summer of 2011/12; this is where the largest colony in the world of this albatross is found, with nearly 200,000 breeding pairs. Black-browed Albatrosses are long-lived and extremely philopatric birds, with pairs nesting in the same area of a given sub-colony year after year (usually re-occupying the same nest). The percentage of divorces (*sensu* Catry et al. 1997) is typically very low (own unpublished data). They lay clutches of one egg per year (in the beginning of October) with the hatching period occurring during the last three weeks of December. The chick is guarded by one parent (brooding period) for 11-33 days (Catry et al. 2010), and stays in the nest until fledging (when around 116 days old; see Tickell 2000 for more details of the breeding biology of this species).

Breeding success

On New Island, I studied three Black-browed Albatross sub-colonies (A, B and C) where all nests are individually marked (170-207 nests altogether annually: 45-53 in sub-colony A, 38-48 in B and 87-114 in C). Each sub-colony is located ca 80 m from the other two (roughly defining a triangle). The status of the nest contents was verified on a daily basis for all nests from the date of laying, through the hatching period and until the end of the brooding period (January), and then weekly until the end of February. A chick that was alive by the end of February was considered fledged, as mortality (all factors combined, including predation) after this period is typically very low (own unpublished data). Albatross chicks were weighed to the nearest gram when 58 and 60 days old (for the analyses a mean value between the two last measurements was used, representative of mass at 59 days old) in order to produce an indicator of annual food availability (e.g. Cairns 1992b, Gaston and Hipfner 2006, Lyons and Roby 2011).

On Steeple Jason, linear transects were established crossing breeding colonies, scattered all over the island, and contents of all nests (empty or with a live or dead chick) within ca 1.5 m from the transect were sequentially noted down on the 25 December and 2 January.

Mortality in the nest

After the brooding period ends and the chick is left alone for the first time, causes of mortality are difficult or impossible to determine as predation or scavenging by Falkland skuas *Stercorarius antarcticus* or striated caracaras *Phalcoboenus australis* might follow quickly. Thus the study of chick mortality was restricted broadly to the brooding period, when predation is extremely rare. Whenever a chick was found dead in the nest possible causes were investigated. I did not consider the cases where there was no chick to examine if there was no further indication of the cause of death. This is likely to cause an underestimation of the number of chicks that died due to an infectious disease, but enables me to exclude all healthy chicks that eventually died from other causes. Also, on all years, notes were taken of live chicks showing signs of ill-health (according to my personal experience; see Results for details). Clinical signs shown by chicks were not systematically recorded after the end of the brooding period. On two cases (one in 2004/05, another in 2009/10), chicks that disappeared from the nest were considered to have died from infectious disease because they showed unequivocal signs of ill-health on the previous visit.

Monitoring of tick numbers

In 2008/09, from 25 December onwards, after nestling mortality started, the total number of ticks was counted on every chick of the study colonies (New Island) when 5 days old.

Spatial analysis within sub-colonies (epidemiologic approach)

Disease is usually non-randomly distributed within a population, and in order to analyze its spatial structure (which may provide important clues about its aetiology) mapping and cluster analyses are two of the most powerful tools available (Hungerford 1991, Carpenter 2001). All nests of the three sub-colonies studied in New Island were mapped by measuring the distance between the center of each nest and several neighbors (to the nearest 5 cm). I only carried out spatial analyses in years where, within a sub-colony, at least 20% of the chicks apparently died from disease, to avoid testing samples with few cases and little statistical power. I tested the null hypothesis that each mortality event was spatially independent and the existence of spatial clustering within sub-colonies was investigated using Moran's *I* (Moran 1950), the *K*-function and its derived *L*-function (e.g. Carpenter 2001 and references therein). The statistical significance of Moran's *I* and *K*-function was assessed by a Monte Carlo test using 1000 simulations, at 0.05 *P*-value. Analyses were carried out using the splancs library (Rowlingson et al. 2000) within R statistical package.

Testing for the existence of space-time clustering (see e.g. Carpenter 2001) violated several assumptions of the available methods (for example, the continuous availability of nestlings to be potentially infected) and therefore was not attempted.

To test whether dead chicks occurred in clusters in transects carried out in Steeple Jason, the Wald-Wolfowitz Runs Test for Randomness was used.

Further to the above, in 2008/09 on sub-colony C, several parameters associated with spatial structure for the nests monitored for ticks were characterized. These variables were the "distance to the nearest neighbour", the "distance to the nearest neighbour that died affected by disease" and the "average distance to the four nearest neighbours" (indicating nest density). Distances were measured from the centre of each nest monitored for parasites to the centre of the others.

Complementary data: pathological studies

Ten chicks found in the nest less than 24 hours after death in 2006/07 (on New Island) were collected, frozen and analysed using a standard necropsy examination protocol. All organs (brain, lungs, heart, liver, gall bladder, spleen and intestines) were examined for modifications in colour, shape, consistency and size. The alimentary tract was opened and contents noted; a wet preparation slide from the intestinal contents was made and observed under a light microscope.

Swabs for bacteriology were taken from sterile incisions made to the heart, liver, spleen, lungs and intestines (proventriculus, gizzard, small and large intestine) with any additional lesions (for example, adhesions and unexplained fluid in the coelomic cavity also examined). In addition, mycology was carried out on the lung. These samples were aseptically inoculated onto Colombia blood agar base (CM331, Oxoid Ltd., Basingstoke, UK), with 5% horse blood and were incubated aerobically, anaerobically and in a CO_2 atmosphere (GENbox, bioMérieux, Basingstoke, UK) at 37ºC and observed at one, two and five days for bacterial and fungal isolates. Additional media (e.g. Sabouraud's agar (CM0041, Oxoid Ltd.) with gentamicin, CCDA (CM0739, Oxoid Ltd.)) was used to isolate other micro-organisms.

Cytological slides (two per chick), made on heart blood smears, were fixed in absolute methanol for three minutes before air drying, and then one slide per pair stained with RapiDiff® (Cytocolor Inc., Hinckley, Ohio 44233, USA), washed and air dried and examined microscopically under 40x and 400x magnifications.

Samples of approximately 10 × 10 × 10 mm of the heart, liver, spleen, lungs, kidneys and intestines (small and large) were taken for virology; subsamples were put into two pools per bird and examined as described by Gough et al. (1988). Each pool was inoculated into chicken embryo fibroblasts, chicken embryo liver cells and ten day old embryonated chicken embryos. A second passage was then performed and a VERO cell culture was used for flaviviruses detection.

Ecto and endoparasites were counted, stored in 70% ethanol and sent to the Natural History Museum (London) for identification.

Statistical analyses

Generalized linear models (GzLMs) were used to analyse the influence of year and sub-colony on chick mortality in the nest, using a binary logistic response variable (presence or absence of live chick in the nest). Differences between years and sub-colonies in the age at which chicks were found dead in the nest were analysed using 2-WAY ANOVA.

Results

Mortality of nestlings

Black-browed Albatross chick mortality was highly variable (Table 1). This variability was mainly explained by significant differences among years (generalized linear model, GzLM, with a binary logistic response variable: Wald $\chi^2 = 17.370$, df = 5, $P = 0.004$), but not by sub-colonies (GzLM, Wald $\chi^2 = 3.620$, df = 2, $P = 0.164$, NS). There was, however, a strong interaction between year and sub-colony (GzLM, Wald $\chi^2 = 47.238$, df = 10, $P < 0.001$), indicating the importance of annual variation between sub-colonies.

The age of the chicks found dead in the nest (Table 2) was significantly different between sub-colonies (2-WAY ANOVA $F = 10.697$, df = 2 and 132, $P < 0.001$) as well as between years (2-WAY ANOVA $F = 4.417$, df = 5 and 132, $P = 0.001$), with a significant interaction between sub-colony and year (2-WAY ANOVA $F = 2.001$, df = 9 and 132, $P = 0.044$); the mean age of death (all years and sub-colonies combined) was 10.1 days ± 5.3 SD.

On most years, a large proportion of the chicks that were found dead in the nest (many still guarded by one adult) showed consistent clinical signs in the days prior to death suggesting a common aetiology. They differed from apparently healthy chicks by showing swollen gape flanges, serous conjunctival discharge, swollen and purplish colored inter-phalangeal joints and a lower carriage of the neck (with apparent difficulty in lifting the head up); most of them were also visibly leaner than other chicks of the same age. Although I do not have equivalent (fully quantified) data for some of the remaining years, in 2008/09 for example, 90% (*n* = 69) of the chicks exhibited these clinical signs prior to death. Only on a few occasions were chicks found dead in the nest showing evidence from what appeared to be differing causes of mortality, such as infestation by red mites (undetermined species) or obvious malformations; these cases are not considered further here. The above clinical signs (usually followed by death) occurred mostly during the first two weeks of life (see Table 2 for ages of death). However, a small number of chicks (seven from sub-colony C in 2008/09) that exhibited the described clinical signs for a few days survived at least to pre-fledging age (representing 21% of the chicks that survived on sub-colony C). Although not systematically recorded, I only rarely saw chicks with these clinical signs after the period of brood-guarding.

The transects carried out on Steeple Jason on 25 December 2011 revealed that 13% of all chicks seen were dead (*n* = 2,818 nests with chicks, alive or dead) and, on 2 January 2012, 12% of the chicks were dead (*n* = 1,736 nests with chicks); these numbers must be considerable underestimates of chick mortality, as many dead chicks would have disappeared within a few days of dying. On 2 January, only 56% of all nests (*n* = 2,725) contained a live chick. Where clinical signs of disease were observed in chicks they were similar to those described for New Island.

Effects on breeding success

Nestlings showing the above clinical signs were found dead in every year, with the levels of mortality depressing the overall breeding success by ca. 4% (of the nesting attempts) in the best years and by ca. 33% in the worst. I did not find a relationship between the apparent annual availability of food (indicated by the mass of the chicks when 59 days old) and the levels of annual prevalence of mortality during brooding (r_s = 0.029, P = 0.96, n = 6, NS).

Prevalence of ticks

In 2008/09 all chicks (n = 49) in the study colonies were infested by ticks when 5 days old (mean number of ticks = 99.7, SD = 70.0, range = 4 - 273). The chicks that survived had a much lower number of ticks when 5 days old (Fig. 1). Also, there was a tendency for the age at death to be negatively correlated with the total number of ticks when 5 days old (r = -0.401, P = 0.072, n = 21 chicks).

Fine scale spatial analysis

Nestling mortality acquired apparent epidemic characteristics within some sub-colonies in several years: infectious disease (as described above) was the suspected and apparent cause of death of more than 20% of all hatched chicks in five cases distributed across four breeding seasons (Table 1). The calculated Moran's I indicated clear spatial clustering of mortality in 2008/09 within sub-colony A (Moran's I = 0.3688, P = 0.001) and in sub-colony C (Moran's I = 0.1713, P = 0.001; Fig. 2), while near-significant clustering was found in 2006/07 in sub-colony B (Moran's I = 0.1016, P = 0.066). No clustered pattern was found in the two other situations, both on sub-colony B, namely in 2004/05 (Moran's I = -0.057, P = 0.594) and in 2005/06 (Moran's I = -0.0805, P = 0.605), which may be due to smaller sample sizes.

The above five cases were further analyzed with the K-function and L-function, and spatial clustering was again found to be significant in 2008/09 within sub-colonies A and C (Fig. 3), and in 2006/07 within sub-colony B. No clustering was detected in the remaining two cases.

Results from the Wald-Wolfowitz Runs Test for Randomness indicated that nestling mortality in Steeple Jason was clearly not spatially random in December or in January ($P < 0.0001$ on both occasions), indicating that mortality events were clustered. This was extremely obvious to observers walking through the colonies, with patches with many dead chicks and empty nests alternating with areas where most nests contained live chicks.

Interaction between ticks and spatial structure of the colony

When the relationship between survivorship and number of ticks infesting 5 days old chicks (Fig. 1) is re-analysed for sub-colony C, after including spatial parameters in the model, the number of ticks remains as a significant predictor (Table 4). There was no correlation between the number of ticks per nest and any of the variables associated with the distribution of occupied nests surrounding them (for example, number of ticks and the average distance to the four nearest neighbours: $r = -0.261$, $P = 0.171$, $n = 29$).

Complementary data: pathological findings

All 10 sampled chicks in 2006/07, five females and five males, aged between two and 22 days, were visibly emaciated. Relationships between organ weights (taken as a percentage of the individuals body weight) and tick counts proved non-significant, as did organ weights and sex.

Nematodes, identified as *Anisakis diomediae* larvae (E. Harris), had a prevalence of 70%, being found in 7 chicks (detected in the proventiculus of seven birds and in the oesophagus of two) and numbered between 2 and 15 (mean intensity of parasitisation = 9). In three chicks the nematodes were associated with ulcers in the proventriculus, and in one of these chicks the ulcer was perforated, nematodes were found in the coelom and there were adhesions between the spleen, intestine, liver and coelomic wall.

At least 12 different species of bacteria were isolated (Table 3). In three chicks pure isolates of bacteria (*Enterococcus faecalis* and *Clostridium perfringens*) were grown from multiple organs. No fungi were isolated from any organs. No parasites were detected in the heart blood smears. Due to autolysis all cell structure was absent except for the nuclei. No viruses were isolated from two sets of passages (see Bowgen 2007 for detailed post-mortem findings and further details).

Ticks *Ixodes uriae* (A. Baker) were identified on nine birds (range 1 – 184 ticks; mean number of ticks on the chicks that were infested = 59).

Figures

Figure 1

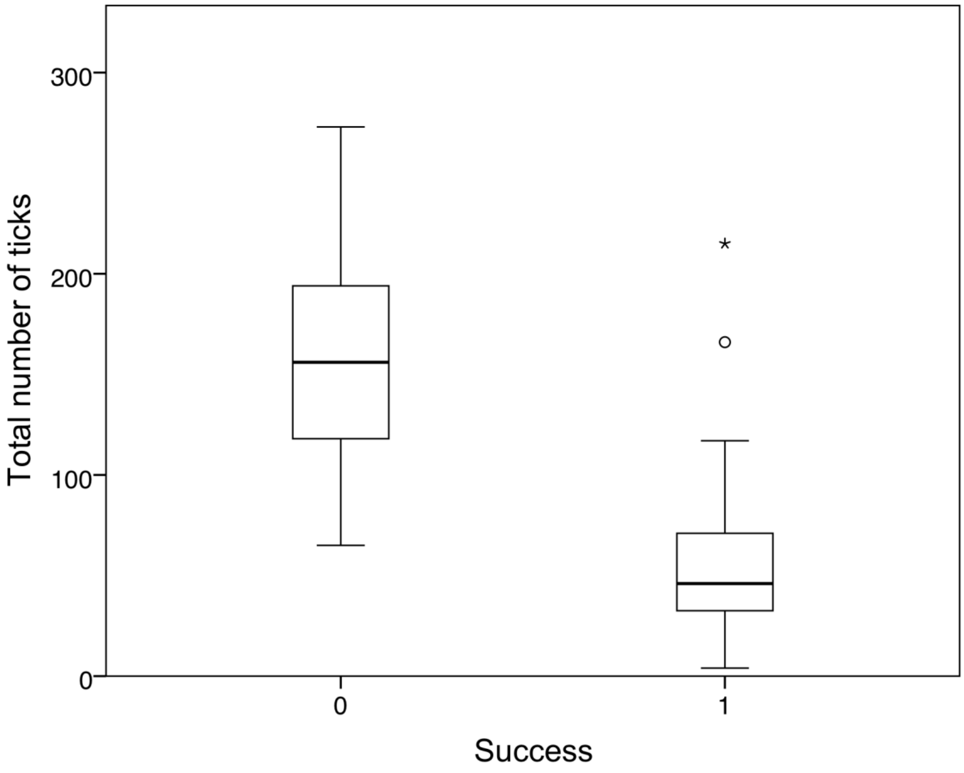

Figure 1. **Number of ticks on 5 days old Black-browed Albatross nestlings (2008/09) in relation to survival.** "Survival" represents whether a chick survived to the end of February (thus discriminating those that died before 60-days old and those that survived). The relationship between survivorship and number of ticks at 5 days old was significant and inverse (logistic regression, effect of variable "total number of ticks when 5 days old": β = -0.031 ± 0.008, *n* = 49, Wald = 13.964, P <0.001).

Figure 2

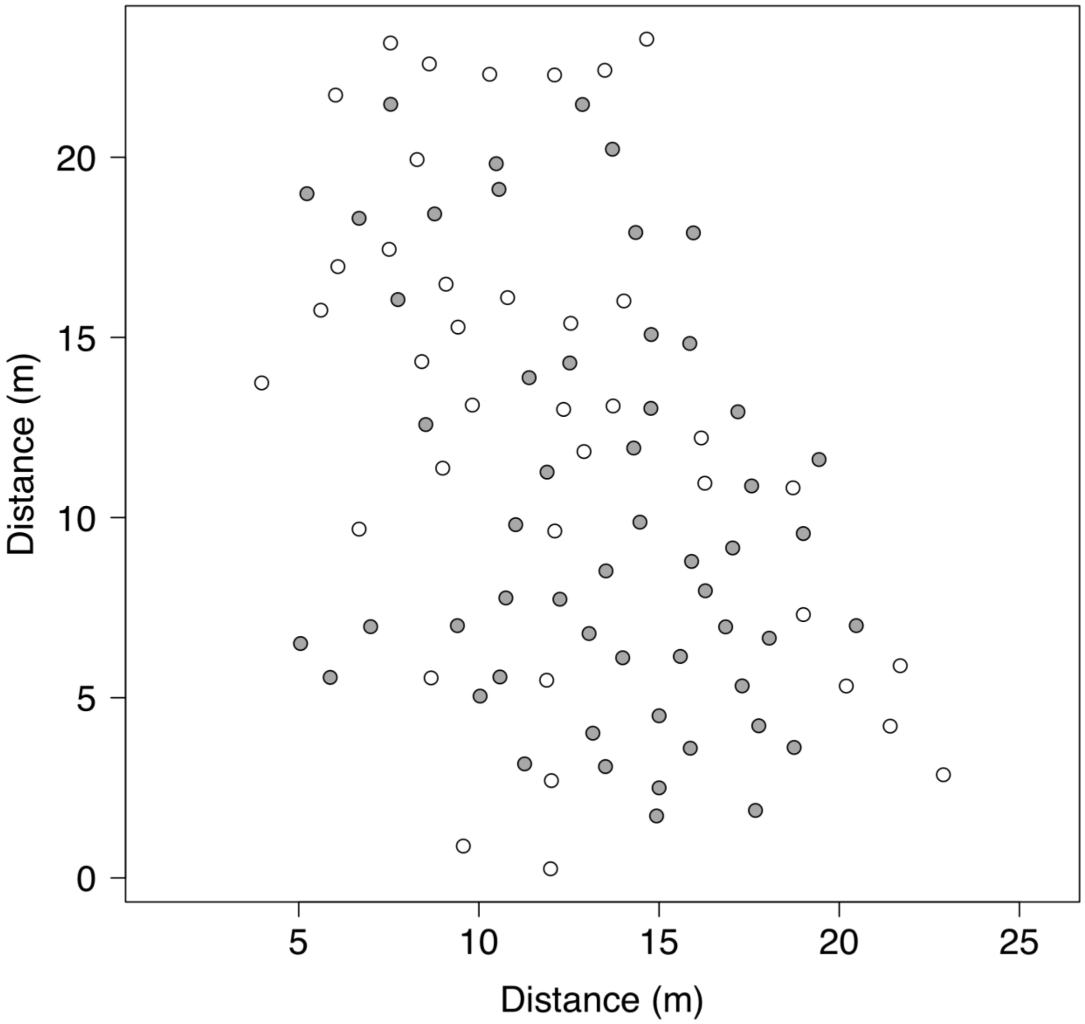

Figure 2. **Spatial distribution of Black-browed Albatross active nests in 2008/09 on sub-colony C.** Each circle represents one individual nest with the ones filled in grey being where chicks died apparently from disease.

Figure 3

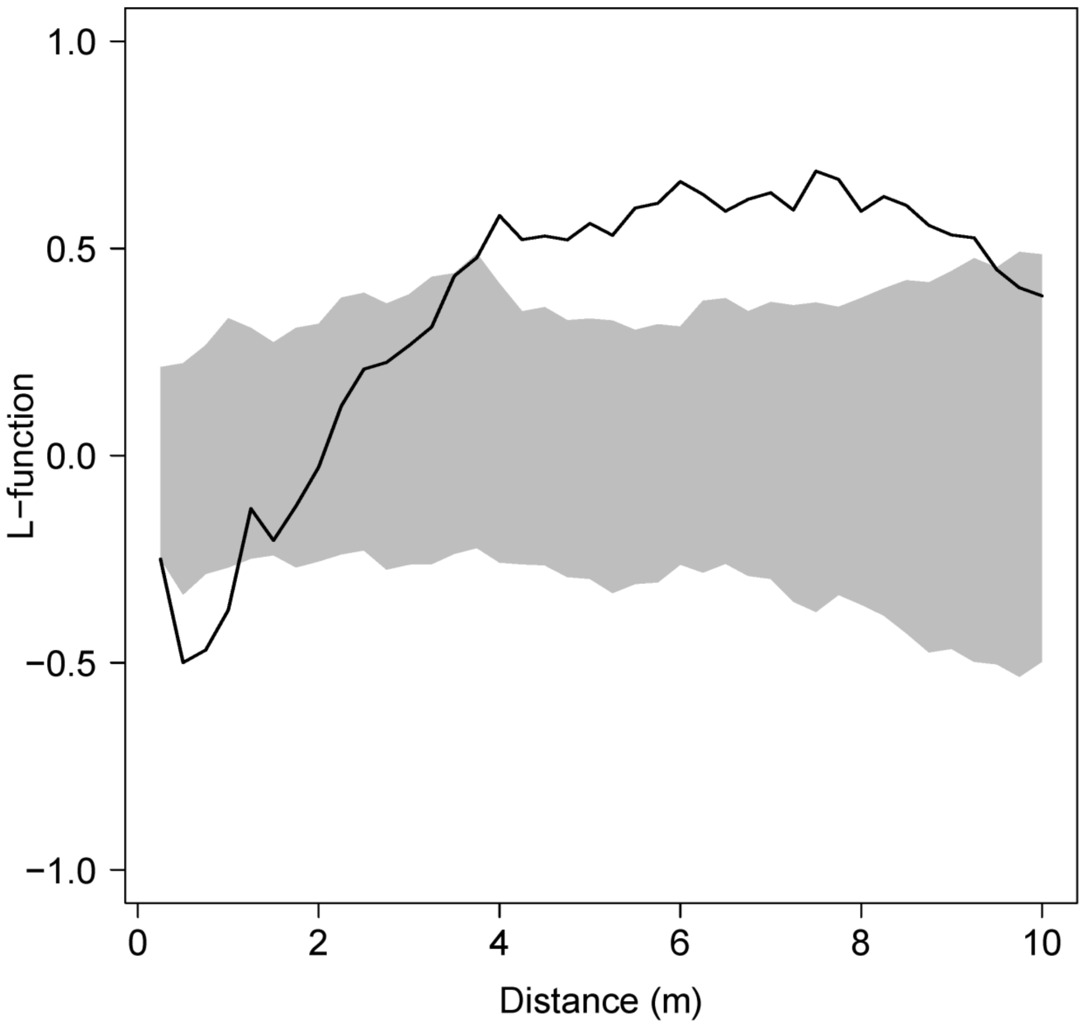

Figure 3. **Distribution of the *L*-function for nests where the chick died during brooding (2008/09, sub-colony C).** Where the continuous line passes above the shaded interval it indicates clustered distribution whereas below indicates regular distribution). Note that the regular distribution at very short distances reflects the natural spacing of albatross nests resulting from behavioral interactions between neighbors.

Tables

Table 1. Percentage of chicks that were found dead in the nest during the brooding period on New Island. In brackets the total number of chicks that hatched.

Sub-colony	Breeding season					
	2003/04	2004/05	2005/06	2006/07	2008/09	2009/10
A	5.3 (38)	6.3 (48)	2.4 (41)	4.8 (42)	20.6 (34)	4.7 (43)
B	19.4 (36)	45.2 (42)	27.3 (33)	20.0 (40)	10.3 (39)	0.0 (36)
C	5.3 (75)	7.7 (78)	6.8 (74)	11.4 (88)	59.2 (98)	6.6 (91)
Total	8.7 (149)	16.7 (168)	10.1 (148)	11.8 (170)	40.4 (171)	4.7 (170)

Table 2. Age (± SD) of the chicks found dead in the nest during brooding. In brackets the range of ages (in days), followed by sample size.

	Breeding season					
Sub-colony	**2003/04**	**2004/05**	**2005/06**	**2006/07**	**2008/09**	**2009/10**
A	13.5 ± 4.5 (9-18; 2)	12.7 ± 3.8 (10-17; 3)	27 (- ; 1)	19.0 ± 1.4 (18-20; 2)	13.9 ± 4.5 (8-21; 7)	10.5 ± 3.5 (8-13; 2)
B	9.6 ± 1.8 (4-16; 7)	9.9 ± 5.1 (0-21; 18)	11.0 ± 4.8 (4-18; 9)	9.9 ± 6.6 (4-22; 8)	13.0 ± 7.1 (5-22; 4)	- (- ; 0)
C	8.5 ± 1.6 (6-13; 4)	15.3 ± 4.0 (11-23; 6)	13.8 ± 5.5 (6-19; 5)	11.2 ± 5.3 (2-18; 10)	8.1 ± 3.6 (2-19; 58)	3.0 ± 1.6 (1-5; 4)
Total	9.9 ± 4.5	11.4 ± 5.1	13.0 ± 6.2	11.5 ± 6.0	8.9 ± 4.4	5.5 ± 4.4

Table 3. Bacteria detected in ten Black-browed Albatross chicks. Abbreviations: S: spleen, Li: liver, H: heart, Ln: lungs, I: intestine, CF: coelomic fluid, PF: peritoneal fluid.

Species	**Number of chicks**	**Organs in which bacterium was detected in at least one chick**
Bacillus spp.	1	S, Li
Clostridium perfringens	7	S, Li, H, Ln, I, CF
Clostridium sporogenes	1	S, H, I, CF
Clostridium histolyticum	1	S, Li, H, Ln
Clostridium sordellii	1	S, Li, H, Ln
Citrobacter farmer	1	S, Li, H, I
Edwardsiella hoshinae	1	S, Li, H, CF, PF
Edwardsiella tarda	1	H
Enterococcus faecalis	8	S, Li, H, Ln, I, CF
Escherichia coli Type 1	1	S, Li, H, I, CF
Serratia odorifera	1	S, Li, H, Ln
Staphylococcus saprophyticus	3	S, Li, H, Ln, I

Table 4. Modelling of the relationship between the binary response variable "chick survival" and the number of ticks infesting 5 day old albatross nestlings (variable "ticks") and three spatial parameters measured for each sampled nest through logistic regression (*n* = 29 chicks/nests). Non-significant predictors were sequentially removed with no qualitatively different models produced (only the variable "ticks" is retained as statistically significant).

	β	**Wald**	**P**
Ticks	-0.030	6.830	**0.009**
Nearest neighbour	1.494	0.253	0.615
Nearest neighbour that died	-1.055	0.252	0.616
Average distance between four nearest neighbours	-0.601	0.041	0.839

Discussion

High levels of mortality were found in Black-browed Albatross nestlings across several years, between 2003 and 2010, at the New Island South rookery and on 2011/12 at Steeple Jason, Falkland Islands. This mortality affected sub-colonies to different extents in different years and, at least locally, had a significant impact on overall breeding success. A significantly clustered spatial pattern was recorded in several cases and clinical signs were consistent across birds, which suggested that a common aetiological agent was involved and that this aetiological agent was infectious. In 2006/07, post-mortem analyses identified four parasites (*Clostridium perfringens*, *Enterococcus faecalis*, *Anisakis diomediae*, *Ixodes uriae*) that may have contributed to the death of chicks, although other agents cannot be discounted. All of these findings have potentially important implications for our understanding of the factors influencing demographic rates in Black-browed and other albatross species, all of which have been reported to be undergoing important population declines.

Non-systematic observations in 2009/10 at Steeple Jason, also indicated many cases of chicks with similar clinical signs of ill-health and mortality to the ones described for New Island (P. Catry pers. obs.) and other researchers have also noticed it elsewhere in the archipelago in other years. These observations, together with the possibly related reports from Tickell and Pinder (1975), suggest this type of mortality is much more widespread in the Falklands than has been thought previously.

I do not know exactly what caused the described mortality. The clustered spatial mortality patterns are strongly suggestive of and are consistent with the activity of an infectious disease (e.g. Carpenter 2001). Also interesting is the difference in the prevalence of mortality among chicks between years, and that the areas most affected could change from one year to another.

Although I found significant evidence that the number of ticks attached to the chicks was related to their age at death and probability of dying, this is clearly not proof of cause in itself. My results (Fig. 1) show a large overlap in the number of ticks infesting chicks that died and those that survived, which suggests the relationship between chick survival and number of ticks, albeit significant, is not strong. The results also suggest there was no relationship between the number of ticks and the spatial patterns of mortality observed. As most chicks that died had ticks attached, some in considerable numbers, the possibility exists that ticks were the mechanical vectors for an infectious agent. It is widely recognised that ticks may transmit infectious agents such as viruses and other pathogenic agents, while the way this happens is still largely unknown (Labuda and Nuttall 2004, Thomas et al. 2007). There were no viruses found in the tissues of my sample of dead chicks from 2006/07, but this might have been due to tissue autolysis, which can reduce the probability of detection. It is also possible that ticks were able to attach in larger numbers to chicks that were already weak due to a disease unrelated to these parasites (and thus would be a consequence of the disease) and future research and more evidence should be able to shed light over this aspect.

Bergström et al. (1999a) tried to find a relationship between Black-browed Albatross chick mortality on Bird Island (South Georgia) and the prevalence of *Ixodes uriae* but their results were inconclusive. The description made by Johnstone et al. (1975) of white-capped albatross *Thalassarche cauta* nestlings suffering from tick infestation bears remarkable similarities with the situation observed on New Island (the number and attachment locations of the ticks, the clinical signs of the chicks, and even in the spatial patterns of mortality described) but again no definite conclusions on the causes of mortality could be made. A number of chicks that died aged 1, 2 or even 4 days (Table 2), suggest that in these cases at least, death is unrelated to direct tick activity, such as toxin inoculation or through blood loss. In fact, most of the blood meal of a tick is taken during the last day of attachment (Labuda and Nuttall 2004, Anderson and Magnarelli 2008) of a minimum period of around 6 days; on other host species, inoculated pathogens are known to start to disperse to remote areas of the host only by the end of the attachment period (e.g. Shih et al. 1992) and if the same holds true for albatrosses, death by pathogen inoculation would be unexpected for the younger chicks.

The different ages at death between years and sub-colonies might eventually be the result of different tick activity levels. The number of ticks in one given host may influence the volume of toxins that are inoculated into the host, the probability of infection occurring, or the volume of blood lost (e.g. Gauthier-Clerc 1998, Randolph 1998, Nunn et al. 2006b). Hence, the higher the tick load the stronger the effect over the chick which in turn may die faster (as suggested by Fig. 1); this is put in evidence by the negative correlation found between age at death and tick load.

The clinical signs observed in the chicks do not seem to match any of those seen in common diseases of free-living birds (see e.g. Friend and Franson 2001, Thomas et al. 2007).

Some of the clinical signs shown by the nestlings in the days prior to their death could eventually be indicative of malnutrition or of insufficient food (e.g. the emaciated state of some chicks when found dead). However, the clustered patterns of mortality described here do not fit within malnutrition as a primary cause of death, as in a case of lack of food resources I would expect mortality to be evenly distributed throughout the breeding colonies. There were no signs of mass mortality either among chicks from other neighboring colonies on New Island when several study colonies were more severely affected. Furthermore, the differences in prevalence of mortality among brooded chicks between sub-colonies are not explained by this possibility either, as there is no evidence that adults from neighboring sub-colonies have different foraging areas and therefore would have different resources available. The results also indicate that the effects of an unknown disease agent are not being exacerbated by hypothetical food shortages, since the mass of the chicks at 59 days of age (a general indicator of food availability) and the prevalence of mortality during brooding were not correlated. Additionally, as a result from Black-browed Albatrosses being long lived and philopatric birds, breeders that might be considered of lower quality (younger birds, or pairs that consistently fail breeding) are not spatially segregated from the remainder and are found on all sub-colonies (own personal observations); therefore the quality of the adults cannot be an explanation for the patterns of mortality recorded. Some of the chicks that clearly exhibited the general described clinical signs survived and reacquired a normal condition. This suggests that immunity was developed to the infectious agent present and could indicate why older chicks are not observed exhibiting the described clinical signs. To the best of my knowledge, no mass mortality events have been witnessed at older ages on the Falklands.

Although the pathological studies were done over a small sample of chicks and for only one breeding season (2006/07), they can still give an indication of the potential disease agents that commonly affect albatross chicks at New Island colonies and are thus helpful as complementary data. The extrapolation for other years and areas should be done only with care.

Several significant infectious agents were detected in the ten albatrosses examined post-mortem. Nematodes (*Anisakis* spp.) have been associated with disease in several species of free-living birds (Riley 1972, Harrigan 1992, Rokicki et al. 2011) and were considered a significant factor in an outbreak of mortality in Dalmatian pelicans *Pelecanus crispus* (Pyrovetsi and Papazahariadou 1995). Therefore, the finding of *Anisakis diomediae* in seven of the chicks examined and in association with pathological lesions in three of these chicks suggests that disease in albatrosses in the Falkland Islands due to this nematode warrants further study. However, given the clustered spatial patterns of mortality recorded on several years, and given the nature of their life cycle (Anderson 2000), nematodes are unlikely to be the primary cause of disease in the recorded mass mortality episodes (see also Atkinson et al. 2008).

There are a number of bacterial diseases that can be spread as aerosols from the excreta of infected birds (Friend and Franson 2001, Thomas et al. 2007).

Spatial asymmetries in breeding success and nestling mortality patterns similar to the ones here have also been described in yellow-nosed albatross *Thalassarche chlororhynchos* colonies due to outbreaks of avian cholera, a disease caused by the bacterium *Pasteurella multocida* (Weimerskirch 2004, Thomas et al. 2007). The fact that none of those bacteria had been reported before for this albatross species (see Barbosa and Palacios 2009) might indicate a need for further research and information in this area. The bacterium *Clostridium perfringens* causes necrotizing enteritis in other bird species (e.g. Friend and Franson 2001), through the production of toxins in the intestine which lead to toxaemia, and is thought to be linked to changes in diet associated with seasonal changes and migration (Friend and Franson 2001). *C. perfringens* was detected in multiple organs in one chick in culture with *Clostridium sporogenes*, and therefore associated with its death. Although the clinical and pathological signs shown by the live chicks were not typical of necrotising enteritis seen in other species, the disease may present differently in albatrosses.

Enterococcus faecalis was grown in pure culture from multiple organs in two chicks and bacteraemia/septicaemia may have been the ultimate cause of their demise. Like *Clostridium* spp., *Enterococcus faecalis* (normally a commensal organism) is an opportunistic pathogen (e.g. Coles 2007), needing another infectious agent or other stressor (to induce a change in intestinal microflora) and the primary cause of disease in those cases was not apparent. If a bacterial disease was responsible for the death of these chicks, I would expect the aetiological agent to be present in most of the 10 chicks, but freezing prior to post-mortem examination may have affected the growth of bacteria.

All of the significant infectious agents detected in the sample of ten chicks examined post-mortem cause disease secondary to other stressors. The cause of the common stressor in these birds is not apparent. Given these findings are interesting but not yet satisfactory, it would be valuable, in further investigations, to examine fresh carcasses of recently dead albatross chicks and improve the samples and range of diagnostic tests that can be performed, for example by carrying out histopathology, and through this to generate a better understanding of the pathogenesis of the disease or diseases in these colonies.

It is not possible to discard completely the potential influence of humans on the origin of this phenomenon. For example, some authors suggest (through the recent detection of specific seroreactors) that the infectious bursal disease virus might have been introduced in penguins in Antarctica (e.g. Gardner et al. 1997, Pearce and Wilson 2003, but see Barbosa and Palacios 2009), indicating that this possibility needs to be evaluated. Humans have been working on New Island since the 19th century and nowadays the site is regularly visited by tourists originating from small cruise-ships and by researchers. The sub-colonies studied here are not, however, accessible to tourists and the disease is widespread in albatross colonies or sub-colonies of the Falklands that are not subject to regular visits by humans. Hence, even if humans were originally responsible for the introduction of the disease in the archipelago, the role people can potentially play as vectors is questionable. Nevertheless, care should be taken by anyone paying visits to little visited colonies to follow biosecurity protocols, should the disease be still absent from those.

Conclusions

The spatial and temporal patterns shown by the mortality of many albatross nestlings within and between sub-colonies on the Falkland Islands, plus the consistent clinical signs, strongly suggest the existence of one main infectious disease. Several of the aetiological agents detected in 2006/07, including bacteria, nematodes and ticks, can all potentially contribute to the death of Black-browed Albatross chicks. It cannot be ruled out that other agents are involved. However, the aetiology and means of contagion of this disease remain unknown and further investigations would benefit from examinations of freshly dead chicks in the field.

This proposed disease is a potentially important factor for nest mortality and had a substantial impact over the breeding success of Black-browed Albatrosses, being yet another identified threat for this species. As almost all albatross species are currently threatened, and since the prevalence and impact of diseases affecting these birds can be modulated by climate change and by the human-related spread of pathogens, I believe that more research and monitoring is clearly needed on this and related issues.

Acknowledgments

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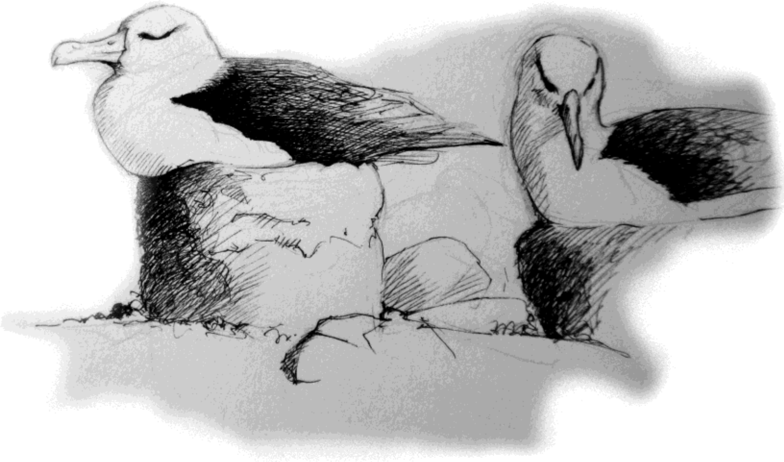
CHAPTER 4. COSTS OF COLONIALITY: ARE GROWTH AND SURVIVAL OF BLACK-BROWED ALBATROSS CHICKS AFFECTED BY TICKS?



Abstract

Parasites and disease are two important extrinsic influencing factors with proven impacts on host-species ecology and demography. Among the ectoparasites infesting birds, the tick *Ixodes uriae* has the widest worldwide distribution, being an obligate parasite of colonial seabirds. Negative consequences of being infested by this parasite have been mentioned for several hosts, but other studies have been inconclusive possibly due to very low tick loads (in connection with seasonal and annual variation), preventing the detection of a measurable effect. Unexplained death episodes among black-browed albatross *Thalassarche melanophris* chicks in some colonies on the Falklands, where this parasite has a high prevalence, raised the possibility that it could be inducing either death or morbidity. I studied the interaction between *Ixodes uriae* and the black-browed albatross, a typical host species in the Southern hemisphere, during two consecutive years at a colony on the Falkland Islands. I assessed the effects of ticks on the condition and survival of albatross chicks by determining the tick load on 5-day-old chicks in 2008/09 across 3 different plots. I also conducted an experiment at a single plot in 2009/10 where half of the chicks were fully disinfested, weighed and measured daily for the first 14 days of their lives. Despite very high annual prevalences (more than 98%), the tick load was significantly different between the two years, as was the mass of chicks at 59 days. Tick infestation was heavy in 2008/09, which coincided with high chick mortality. Although no effects upon survival were observed in 2009/10, my experimental disinfestation suggests that tick infestation might have been associated with reductions in mass gain and growth of late hatching chicks. Even without fully disentangling the effects of tick load from other

factors, results suggest that the impacts of *Ixodes uriae* can be severe, especially under heavier infestation conditions.

Introduction

Parasites and diseases are two inter-related factors with wide implications for animal evolution and demographic rates (Grenfell & Gulland 1995, Renaud et al. 1996). Parasites may influence or even control the population dynamics and demography of their hosts, particularly when hosts are gregarious or colonial (e.g. Grenfell & Gulland 1995, Boulinier & Danchin 1996, Hudson et al. 2002, Brown & Brown 2004, Rosà & Pugliese 2007, Reed et al. 2008). Therefore, in order to better understand the ecology of any host-species, the study of parasite-host interaction is vital (Marcogliese 2004).

Seabirds are particularly vulnerable to ectoparasite infestation (especially from ticks) largely because of their breeding ecology. First, most species are colonial, sometimes gathering in thousands of breeding pairs in a limited area. Second, many species are extremely faithful to the breeding site from year to year producing perennial colonies. Third, most seabirds are altricial and have long developmental periods. These traits make them predictable and reliable hosts for ectoparasites and there are a number of species (ticks, fleas, mites, among others) that specialize on them (e.g. Muzaffar & Jones 2004, ICES 2009 and references therein). Recent population declines affecting many seabird species have been largely attributed to anthropogenic factors, such as overfishing of food resources, pollution, introduction of non-native species and direct death caused by fishing gear (Croxall et al. 2012). However, disease and parasites can potentially play a role on seabird population dynamics and there is a dearth of studies in this area (e.g. Boulinier & Danchin 1996, Reed et al. 2008).

Many ectoparasites, such as mites, blow fly larvae, fleas and other biting arthropods are known to be potentially deleterious for their hosts (Howe 1992, Merino & Potti 1996, Proctor & Owens 2000, Friend & Franson 2001, Gilardi et al. 2001, Muzaffar & Jones 2004). In particular two major groups of ticks, the Argasidae, or soft ticks, and the Ixodidae, or hard ticks, have been shown to have negative impacts on wild birds (e.g. Brown et al. 1995, Boulinier & Danchin 1996, Gauthier-Clerc et al. 1998, Norcross & Bolen 2002); they can cause infections and are vectors for viruses and other pathogenic agents such as protozoans, which can be inoculated together with toxins present in saliva (Labuda & Nuttall 2004). *Ixodes uriae* is probably the most widespread tick species of all, being an obligate parasite on seabird colonies, with a circumpolar distribution across both hemispheres at high latitudes (e.g. Muzaffar & Jones 2004). While most reported effects of this parasite have been negative, such as reduced breeding success (Mangin et al. 2003), anaemia due to blood loss (Wanless et al. 1997, Gauthier-Clerc et al. 1998) and the transmission of the spirochete *Borrelia burgdorferi* s.l. which causes the Lyme disease (Olsén et al. 1993), a few studies have proved less conclusive (e.g. Haemig et al. 1998, Bergström et al. 1999a). Since the effects of parasites are known to vary both spatially and temporally, according to a range of environmental factors (Merino & Potti 1996, Oorebeek & Kleindorfer 2008), this might be one of the reasons underlying differences among studies.

The black-browed albatross *Thalassarche melanophris* breeds colonially with a circumpolar distribution in the southern hemisphere and therefore is a good model for studying the effects of the interaction with the tick *Ixodes uriae*. Episodes of unexplained mortality have been recorded regularly in black-browed albatross chicks during the early brooding period on several breeding colonies of the Falkland Islands (Tickell & Pinder 1975, personal observations). The high number of chicks infested by ticks at some colonies where mortality is high suggests that this parasite might be related to this problem.

Here I aim to determine (1) the influence of the presence of ticks on albatross breeding success and chick survival, and (2) the influence of the number of ticks (tick load) over the condition, growth and rate of weight gain of the chick across two years and several sub-colonies.

Methods

Study area and study species

This research was carried out at the Settlement rookery (51º43’S, 61º17’W), New Island, Falkland Islands, during the Austral summers of 2008/09 and 2009/10. A total of ca 10-13,000 black-browed albatross pairs breed on New Island, of which more than 1,500 nest in the colony where my study took place (Strange 2008, Huin & Reid 2007). Black-browed albatrosses lay a single egg and the chicks start hatching during the second week of December (after an incubation period of approximately 68 days), remaining in the nest until fledging (after ca 116 days, being brooded and provisioned by both parents; see Tickell 2000 for more details). I studied 3 sub-colonies in 2008/09 and a single sub-colony in 2009/10. Individual nests were visited at regular intervals (from pre-egg laying until early March) in order to determine nest contents status and chick survival.

Ixodes uriae has a three-host life cycle that takes 3-4 years to complete and comprises egg, larva, nymph and adult stages (Eveleigh & Threlfall 1974, but see Frenot et al. 2001). Each intermediate stage of the life cycle requires a 4 to 12-day feeding period (during which the tick has its mouthparts cemented to the host’s skin). It then moults into the next stage, remaining in and around the nests of the host in a dormancy state until the following nesting season (Eveleigh & Threlfall 1974, Finney et al. 1999 and references therein). *Ixodes uriae* infesting albatrosses feed mostly on the young nestlings during the brooding period (around the first 20 days of life; Catry et al. 2010), with adults or older chicks never showing comparable tick loads (pers. obs.).

Relationships between tick load, chick condition and survival

1) Assessment of tick load

The number of individual ticks infesting each host (or tick load) can be used as a proxy of infection, as the number of parasites is proportional to the probability of transmitting pathogens (e.g. Nunn et al. 2006b, see also Randolph 1998). Higher numbers of ticks can represent a decrease in fitness due to blood loss, among other causes. In 2008/09 I assessed the tick load by counting the number of ticks infesting each of 49 five-day-old chicks on three sub-colonies (A, B and C with 13, 8 and 28 chicks respectively). No discrimination was made between nymphs and adult females, but tick larvae were not considered.

In 2009/10 I focused on sub-colony C where a removal experiment was used to assess the effect of tick load on the survival and development of the chick. I counted all ticks on 91 chicks from hatching day (day 1 of life) until day 14 of life; all ticks were removed from 47 nestlings during the counting process; the distribution of control and disinfested chicks was as spatially and temporarily (with respect to hatching date) homogeneous as possible. Ticks were carefully removed (and destroyed) individually, grasping their mouthparts with fine tweezers and pulling them gently. Repeatability (*r*, Lessells & Boag 1987) of daily re-infestation was also calculated for disinfested chicks.

2) Condition, growth and rate of weight gain of chicks

In 2008/09, chick condition was assessed by weighing each to the nearest gram on days 6, 15, 59 and 61 of life, and in 2009/10 on a daily basis from hatching until day 14 of life (on sub-colony C only). In 2009/10 chicks from all three sub-colonies were weighed on days 59 and 61; for the analyses I used the averaged mass between days 59 and 61, representative of mass at day 60 of life. Although 14-day-old chicks were not weighed in the second year, I estimated this value by adding the mean increment of mass measured between 12 and 13-day-old chicks to the mass of 13-day-old chicks. In 2009/10 the bill length of the chicks from sub-colony C was also measured daily on the first 14 days of life using dial callipers. Daily mass and bill measurements were used to calculate weight gain and bill growth rates, respectively, through individual linear regressions. The individual fate of each chick was recorded in early March on both years. Mass at day 60 was considered also as an indicator of inter-annual food abundance as the mass of seabird chicks is frequently used as an indicator of food availability and diverse studies have shown this relationship (e.g. Lyons & Roby 2011 and references therein).

Statistical analyses

Generalized linear models (GzLMs) were used to model the influence of sub-colony and hatch date on tick load in 2008/09 and elsewhere, assuming a negative binomial distribution with a log-link function for the response variable.

For the removal experiment analyses, chicks in treatment groups that had 5 or less or in control groups that had up to a maximum of 5 ticks attached were excluded (total n excluded = 16). General linear mixed models (GLMMs) were used to assess the individual contributions of tick removal, hatch date and age to rates of mass gain and bill growth. The best fit model was chosen using the Akaike information criterion (AIC) backward selection. I included “individual chick” as a random factor in the model and the “observation number” (a number between 1 and 14) as a repeated measure. Values are presented as mean ± SD. Analyses were made using IBM SPSS Statistics 19.

Results

Tick load and prevalence on nestlings

In 2008/09 all chicks had some tick infestation at 5 days old (prevalence = 100%) and the total number of ticks per chick ranged from 4 to 273 (mean = 99.7 ± 70.0, median = 75, n = 49). A GzLM indicated that the clear differences in tick load between sub-colonies were significant (Wald $\chi^2 = 13.153$, df = 2, p = 0.001) and that hatch date had no influence on the observed variation (Wald $\chi^2 = 0.120$, df = 1, p = 0.729) (Fig. 1). There were no relationships between date of count and tick load, even when sub-colony was taken into account.

In 2009/10, the tick load of 5-day-old chicks was lower than in the previous year (mean = 12.0 ± 18.7, median = 3, range = 0-86, n = 28, prevalence = 93%); see Fig. 2. However all control chicks were infested by ticks by day 14 of life (prevalence = 100%; mean daily number of ticks per chick = 20.7 ± 25.6, range = 1 - 245, n = 44), with tick load increasing gradually during this period (Fig. 3). In 2009/10, the dates of tick counting (and thus also albatross hatch date) and the number of ticks per control chick (when 5 days old) were correlated (r = 0.453, p = 0.015, n = 28), indicating that the total number of active ticks in the colony increased with time. This same pattern was found between the tick loads of 14-day-old control chicks and date (Fig. 4).

The number of ticks on chicks at the same nest (assessed when each chick was aged 5 days old) was not correlated between years (r = -0.170, p = 0.716, n = 7, n.s.).

Effects on development and condition

In 2008/09 the number of ticks infesting 5-day-old chicks was not correlated with the mass of the nestling irrespective of age (at 5, 14 and 59-days-old) and there were no significance mass differences among sub-colonies with respect to chick age.

In 2009/10 the number of ticks at 5 days old was not correlated with chick mass (controls only) at 5 or 13 days (for example, with mass at 13 days old: $r = -0.022$, $p = 0.913$, $n = 28$, n.s.), but was highly and negatively correlated with mass at 59 days ($r = -0.544$, $p = 0.003$, $n = 28$). The bill length of the chicks at 13 days (controls only) was not correlated with their tick load when 5 days old ($r = 0.170$, $p = 0.386$, $n = 28$, n.s.).

The estimated mass of the chicks at 14 days in 2009/10 and the corresponding mass measured in 2008/09 (783.6 ± 199.6 g and 786.9 ± 130.4 g, respectively) were very similar (t-test for unequal variances, $t = -0.017$, $df = 81.145$, $p = 0.986$, n.s.). However, their variances were significantly different (Levene's test, $F = 5.646$, $p = 0.020$); the highest masses were reached by individual chicks in 2008/09 (Fig. 5).

The mass of the chicks at 59 days old was lower in 2008/09 (mean = 4042.3 ± 344.8 g, $n = 81$) than in 2009/10 (mean = 4189.6 ± 362.3 g, $n = 146$) and this difference was statistically significant (ANOVA $F_{1,225} = 8.917$, $p = 0.003$).

Experimental disinfestation

Chicks that were disinfested (treatments) and controls had similar masses at 59 days old (ANOVA $F_{1,80} = 0.453$, $p = 0.503$, n.s.).

Despite the similarity of mean mass between both groups, their growth rates were distinct during their first 14 days of life. Control chicks hatching earlier had higher growth rates than the ones hatching later (both rates of mass gain and bill growth are supported by significant correlations, Fig. 6); no correlation was found between hatch date and mass in 2008/09, for 5 day old chicks ($r = -0.199$, $p = 0.301$, $n = 29$, n.s.). There was a clear effect of treatment interacting with hatch date upon mass gain, as well as bill growth (Table 1, Fig. 6).

The disinfested chicks ($n = 47$) had new ticks attached each day and the number of ticks attached to one chick in 24 hours ranged from 0 to 107 (mean = 6.2 ± 4.6); the number of ticks removed was highly repeatable within each nest ($r = 0.55$, SE = 0.06, $p<0.001$; ANOVA $F_{40, 420} = 15.0$, $p<0.001$). On average 66.6 ticks (±106.0) were removed from each chick (range = 0-619) for the 14-day experimental period, and this total number was not significantly different from the total number of ticks the control chicks had when 13 days old (ANOVA $F_{1,89} = 0.717$, $p = 0.399$, n.s.).

Effects over breeding success and chick survival

In 2008/09 fledging success was low (52%, $n = 172$ hatched chicks) and significantly different between the 3 study sub-colonies (Pearson $\chi^2 = 34.257$, $p < 0.001$, df = 2), with 73.5%, 82.1% and 33.3% of chicks fledged in sub-colonies A ($n = 34$ hatched chicks), B ($n = 39$) and C ($n = 99$), respectively. The tick loads of the chicks that died (mean = 154 ± 58.9, n = 21, range = 65-273) and of the chicks that survived (mean = 59 ± 46.4, n = 28, range = 4-215) during the study period were significantly different (ANOVA $F_{1,47} = 39.619$, $p < 0.001$). In 2009/10 fledging success in sub-colony C was very high (89%, 91 hatched chicks) and no relationship was found between number of ticks and survival.

Figures

Figure 1

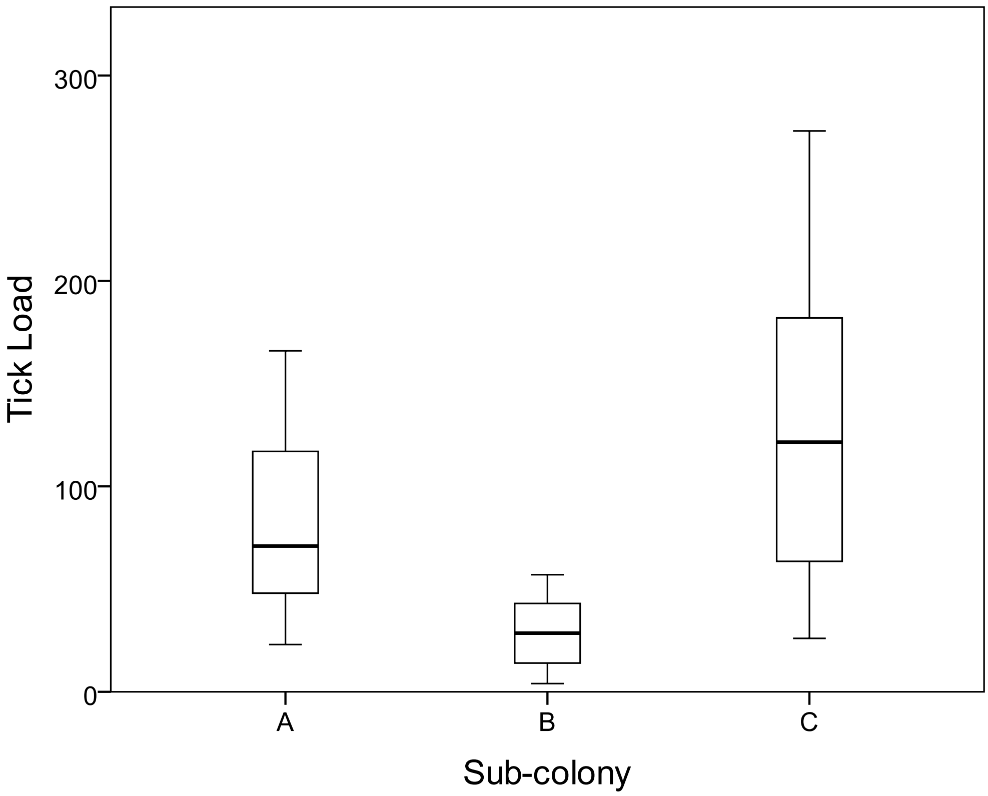


Figure 1. **Box-plots representing the number of ticks on 5 day-old black-browed albatross nestlings on 3 sub-colonies in 2008/09 (boxes represent percentiles 25 to 75, the horizontal line is the median and whiskers extend to 1.5 times the interquartile dispersion)**. Mean number of ticks (±SD) was 86.2 ± 48.4, 29.0 ± 18.4 and 126.2 ± 72.6, for sub-colonies A (n = 13), B (n = 8) and C (n = 28), respectively.

Figure 2

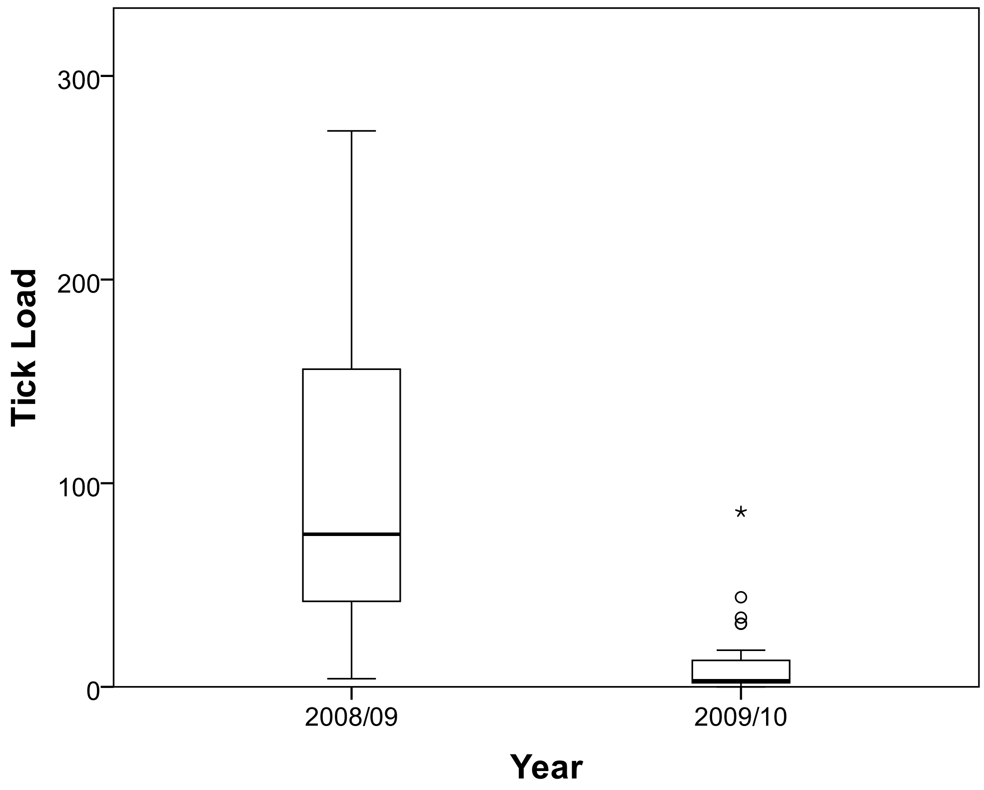


Figure 2. **Number of ticks per chick (when 5 days old) on two consecutive years/breeding seasons (all chicks included for 2008/09)**; this difference is statistically highly significant, both for all nests and for only sub-colony C nests (GzLM for the influence of year on tick loads of sub-colony C, Wald $\chi^2 = 74.14$, df = 1, $p < 0.001$). Interpretation of box-plots is as on Fig. 1; dots and stars represent outliers and extreme outliers, respectively (more than 1.5 and 3 times the interquartile dispersion).

Figure 3

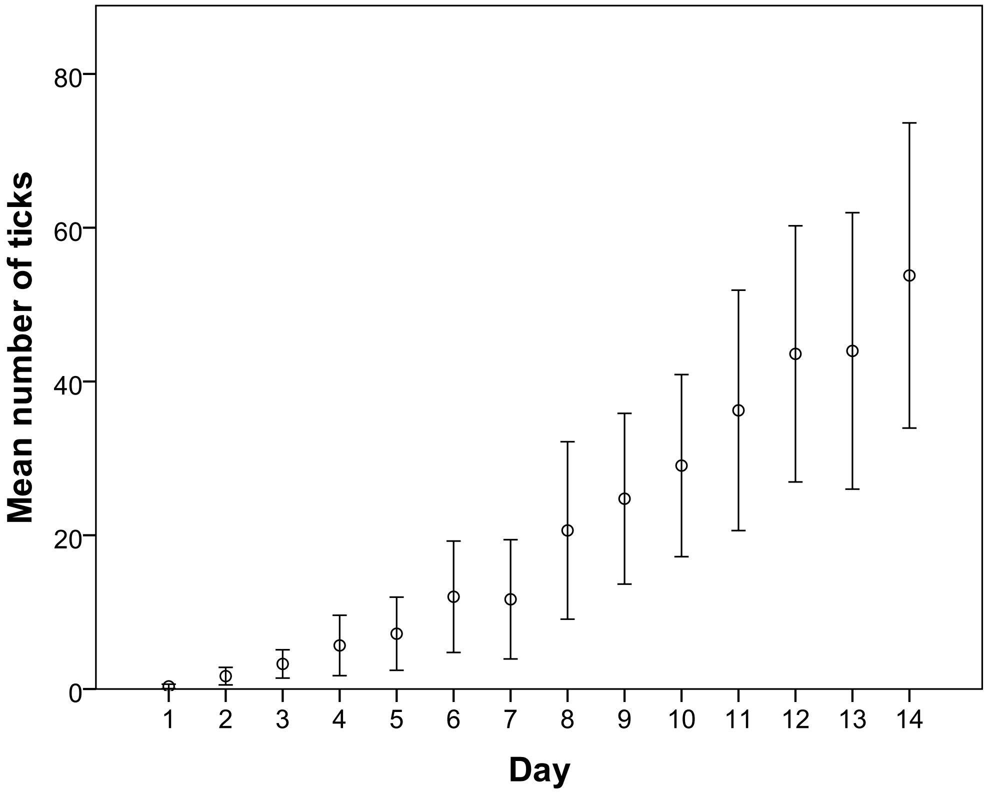


Figure 3. **Mean number of ticks per control chick (n = 44) during their first 14 days of life.** Error bars represent 95% CI.

Figure 4

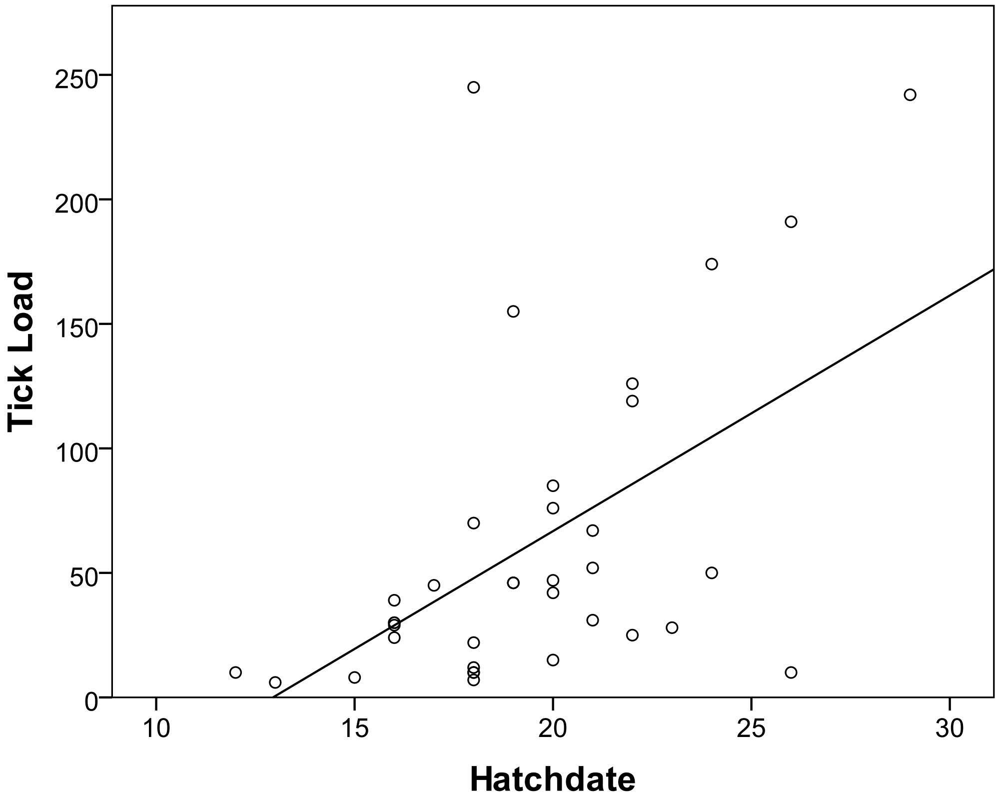


Figure 4. **Increase of tick load (on 14-day-old control chicks) with calendar date in 2009/10.** There was a tendency for chicks that hatched later to have a higher tick load (GzLM, Wald χ^2 = 35.01, df = 14, p = 0.001).

Figure 5

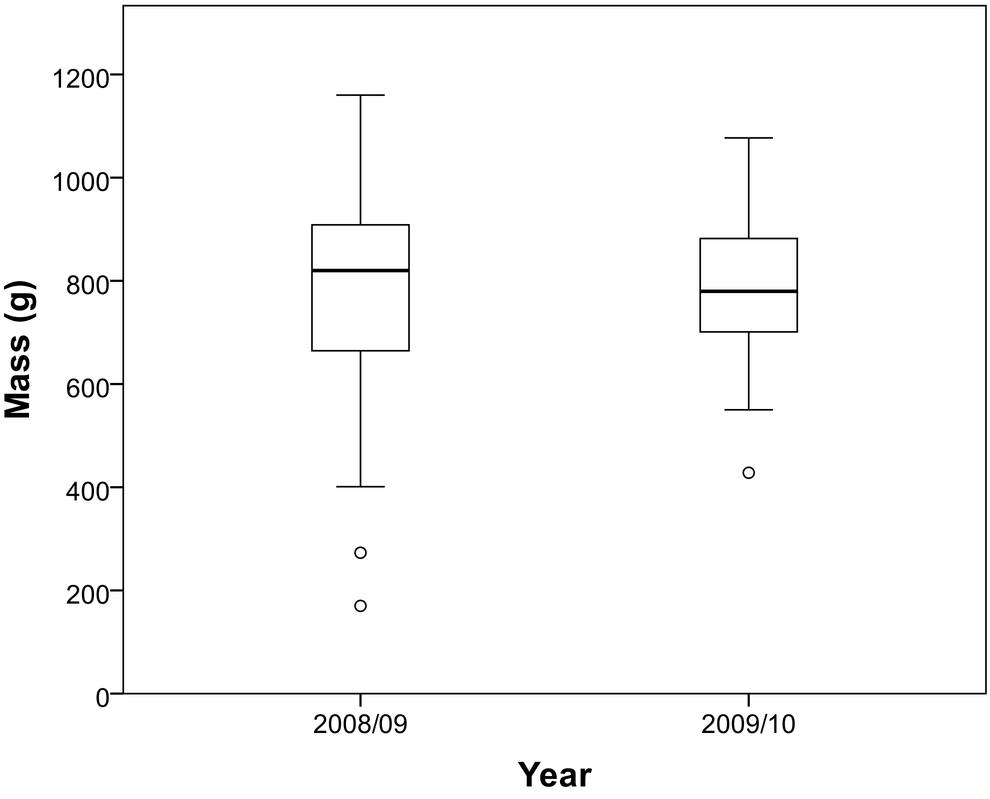


Figure 5. **Mass of individual chicks in 2008/09 and in 2009/10 (estimated) when 14 days old.** Interpretation of box-plots is as on Figs. 1 and 2.

Figure 6

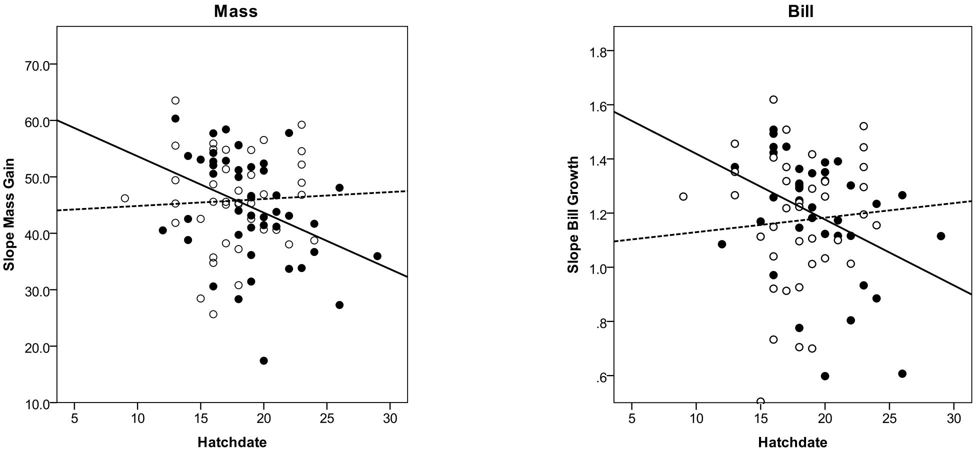


Fig. 6. **Effect of treatment over chick development.** The plots illustrate the relationships between mass gain (on the left) or bill growth (on the right) and hatch date. Control (n = 36) and treatments chicks (n = 38) are represented by black (●) and hollow circles (○), respectively. Fitted lines are continuous for controls and dashed for treatments.

Tables

Table 1. Influence of treatment (disinfestation) over the mass and bill length of the chicks during 14 days, modelled through a GLMM (see Methods).

	Mass		**Bill**	
	F	**p**	**F**	**p**
Corrected model	136.823	**< 0.001**	204.137	**< 0.001**
Treatment	4.329	**0.038**	9.366	**0.002**
Age of the chick	24.146	**< 0.001**	32.214	**< 0.001**
Hatchday	3.956	**0.047**	1.081	0.299
Treatment*Age of the chick	1.430	0.139	1.926	**0.024**
Treatment*Hatchday	4.603	**0.032**	10.327	**0.001**
Age of the chick*Hatchday	1.660	0.065	1.047	0.404
Treatment*Age of the chick*Hatchday	1.429	0.140	1.949	**0.022**

Discussion

Tick infestation levels were very high among albatross chicks at all study sub-colonies in both years, however tick loads varied considerably. The results from this study suggest the relationship between the tick load and the development, the condition or the survival of an albatross chick is not simple. Although the effect of ticks is often detrimental, its magnitude is variable, as other interacting factors seem to be involved. In some circumstances, these parasites are shown to be associated with either enhanced mortality or deficient growth.

Differences of tick load between areas and seasons

There were clear differences in the tick load between sub-colonies (Fig. 1), but the reasons behind this are unclear. The gradual individual tick load increase, during the first two weeks of life of each nestling, is consistent with migration of ticks (life-cycle related), probably from within or near the nest, which is supported by the similarity in the total number of ticks removed during 14 days and the tick load of control chicks at day 14 in 2009/10. The very variable tick load among chicks of the same age probably reflects variable numbers of ticks inhabiting a given nest (see Bergström et al. 1999b). At larger scales such variation might create differences in mean tick load between sub-colonies. In 2009/10, chicks hatching earlier had lower tick loads than chicks of the same age hatching later (Fig. 4), suggesting the early period is less favourable for tick feeding but possibly an advantage for early laying parents.

The age of the albatross nests in the study colonies is quite variable, with some new nests built each year but also many nests surviving and being re-utilised for over 10 years. Thus, the age of the nest could explain the number of ticks it contains (in a similar way that the age of a colony has an influence over the number of parasites; see e.g. Danchin 1992), and therefore the tick load affecting the chick. This is not supported by the data, which indicate one same nest can have very different tick loads on consecutive years, which is shown by a lack of correlation between tick loads affecting chicks in the same nest in successive years.

I do not know what might cause differences of tick load between years. The lower tick load in 2009/10 (Fig. 2) might have been linked to colder and wetter weather conditions in that year than in 2008/09, as deep fluid mud between the nests provided a very unfavourable environment for tick dispersal (following suggestions by Frenot et al. 2001 to explain differences in tick activity between seasons). The influence of the weather conditions over the annual mean tick load warrants further study.

Tick load, chick development and survival

Despite the significant correlation found in 2008/09 between tick load and probability of death, this relationship was not found in 2009/10. Two potentially important explanatory factors to consider are tick load and food availability. Ticks may deprive chicks of important nutrients for normal growth (in addition to the direct blood loss; see Gauthier-Clerc et al. 1998), if in sufficient number and especially if the food delivered to the chick is not optimal (see Lehmann 1993). Tick load was much higher in 2008/09 than on the following season (Fig. 2), reaching levels comparable to those recorded for king penguins (Gauthier-Clerc et al. 1998). This factor is likely to explain the observed relationship, at least partially, as the effects of ticks are potentially more marked when in higher numbers (e.g. Mangin et al. 2003), with an increased probability of developing anaemia (e.g. Gauthier-Clerc et al. 1998). If tick load is proportional to the probability of becoming infected by pathogenic agents (e.g. Nunn et al. 2006b), it could have been the main cause of higher mortality levels in heavily infested chicks. Also, there could have been combinations of the above factors with infectious diseases transmitted by the parasites, which might all have contributed for increased mortality.

The very similar mean mass of the chicks when 14 days old on both years could suggest the availability of food was similar between them. Yet, the different variances, with heaviest individual chicks found during the first year (Fig. 5) suggest that food availability might have been actually higher in 2008/09; higher food availability is further indicated by the significantly shorter distances the adults travelled from the colony to find food during the early brooding period compared to the following year (Granadeiro et al. 2011). It is possible that the increased variance was the result of tick activity, chicks being differentially and disproportionately affected according to their tick load and individual quality. However, the mass of the chicks at 59 days (higher in the second year) might represent different conditions from when the chicks were being parasitized (for example, more food might have been available later in the season in 2009/10) and, therefore, differences recorded between years need to be interpreted cautiously.

Nevertheless, a combination of tick load and food availability might explain also differences in chick mass both between years and between individuals. Thus, despite 2008/09 being a year of higher food availability for albatrosses (at least during brooding), the mass of the chicks later in the season (when 59 days-old) was lower. This might have resulted from higher tick feeding activity; the higher tick load might have also induced the allocation of more food resources to the immune system that would otherwise be used for chick growth (Olsen et al. 2010). The significant negative correlation between tick load (of 5 day-old chicks) and mass of the chicks at 59 days found in 2009/10 (but not in 2008/09), when chicks are well advanced in their development, might suggest ticks may have a long term effect on fitness over and above the more immediate impact on condition (as shown by Brown et al. 1995 for adult cliff swallows *Hirundo pyrrhonota*). Higher food availability in 2008/09 could in turn explain why there was no correlation between mass at 59 days and tick load despite the much higher number of parasites, as it could have diluted the effects of ticks by providing enough food for the chick and the parasites or by reducing the effect of a potential pathogen transmitted by the ticks (allowing enough allocation of resources for both growth and the immune system). Although chicks that died in 2008/09 tended to be the lighter ones, this has had no effect on the correlation, as the 59 days mass had a very similar distribution to 2009/10, both years with comparable variances.

The fact that the few previous studies that have been carried out on albatross species are inconsistent with respect to higher mortality in infested chicks is likely due to multiple factors: very low tick loads and small samples, sampling across a single year (e.g. Haemig et al. 1998 in grey-headed albatrosses *Thalassarche chrysostoma*) or to other unknown factors. The work by Bergström et al. (1999a) on black-browed albatrosses proved inconclusive, obtaining an apparent relationship between mortality and tick load at the colony level but no effect at the nest level. However, in this case, nest monitoring was done on a weekly basis (with no evaluation of the condition of the chicks) and other factors contributing to mortality might have not been taken into account, such as differential activity of predators among sub-colonies.

Although overall there seems to have been no general difference between controls and treatments, there might have been a positive effect of experimental disinfestation over the late hatched chicks (Fig. 6). This suggests that even at lower infestation levels ticks can have a marked effect (aside from mortality), and supports findings from other studies of ticks and seabirds. For example *Ixodes uriae* infestation has been linked to poor nestling growth rates in kittiwakes *Rissa tridactyla* (e.g. McCoy et al. 2002) and Cassin's auklets *Ptychoramphus aleuticus* (Morbey 1996). Other studies have also shown how the effects of ectoparasites on their hosts can be negligible during years of low infestation, although more severe effects are noted in years of high parasite activity (e.g. Howe 1992, Merino & Potti 1996, Mangin et al. 2003). The number of active ticks increased over time in 2009/10 (Figs. 3 and 6) which might have been disadvantageous for later hatched chicks. In fact, the effects of ticks over late hatched controls seem to have been disproportionate; this might have been caused by poorer quality of those chicks, but it is difficult to disentangle from the effect of a larger number of parasites. This factor might add to lower quality to potentially reduce the probability of subsequent survival compared to early hatched chicks. It would be relevant to repeat the disinfestation experiment made in 2009/10 in a year of higher tick abundance in order to further understand the consequences of tick infestation and the processes involved.

Even though I have no systematic data on parasite loads over chicks after my disinfestation experiment was over, it is very possible that the experimental chicks became reinfested. Even if this was the case, there was still a detectable impact of the experimental desinfestation upon chick growth. Reinfestation might have been a possible contributing cause for the similar masses of experimental and control chicks when 59 days old. Note that at 59 days old (and at later stages) chicks were apparently free of parasites (personal observations) which is probably explained by tick life history details (see Methods); given ticks feed only once per year, this is then a consequence of most ticks feeding more or less synchronously during the first weeks of life of the nestling.

My results also suggest parental grooming was ineffective at controlling the tick load of chicks, as the total number of ticks removed over 14 days was approximately the same as the tick load shown by control chicks when 13 days old. In face of the heavy tick infestation levels recorded, the ineffectiveness of parental grooming and the potential effects of ticks over chicks, experimental nest-treatment should perhaps be equated (see Norcross & Bolen 2002).

Conclusions

I have shown that the tick *Ixodes uriae*, under specific circumstances, may have a severe impact over black-browed albatross chicks. Chicks with large tick loads can show depressed growth and increased mortality. Further research is needed to understand the causes of spatial and temporal variations in tick abundance in albatross colonies, as well as the mechanisms by which ticks affect the birds.

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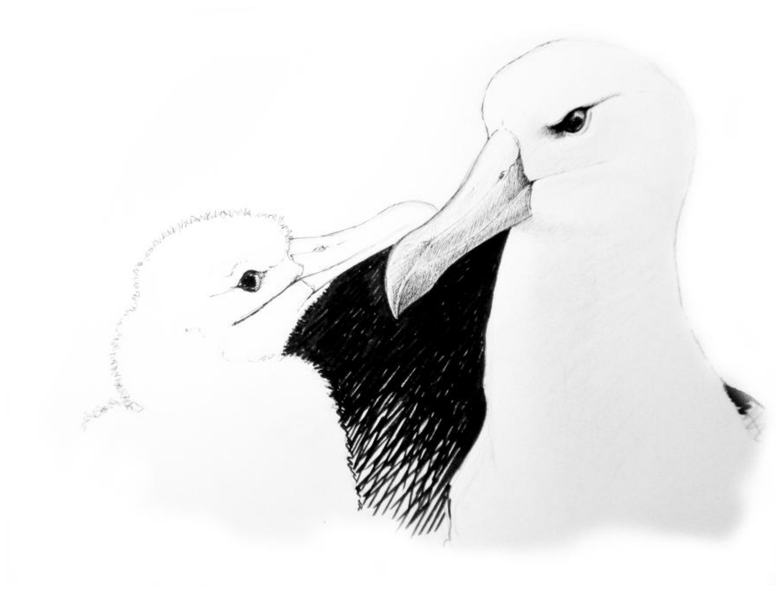
CHAPTER 5. FISH AND SHIPS: SEABIRDS SUBSIDIZING NATURAL DIET WITH FISHERIES WASTE?



Abstract

Commercial fisheries are impacting severely the marine environment, affecting directly and indirectly a multitude of organisms, including seabirds worldwide. As such, most albatross species are undergoing population declines thought to be linked with fishery activities and thus with their foraging behaviour and feeding decisions. The diet of the black-browed albatross *Thalassarche melanophris* was studied from 2003 to 2010 at one breeding colony on New Island, West Falkland Islands during the chick rearing period. I analyzed 202 food samples from chicks during the mid rearing stages obtained through induced regurgitation. Diet comprised fish, crustaceans (mainly lobster krill *Munida gregaria*) and to a lesser extent by cephalopods, with mean occurrences of 86.7%, 71.3% and 24.8%, respectively. Apart from Fuegian sprat *Sprattus fuegensis*, all identified fish were frequent commercial and by-catch species; the most frequent were hoki *Macruronus magellanicus*, rock cod *Patagonotothen ramsayi*, grenadier *Coelorhynchus fasciatus* and southern blue whiting *Micromesistius australis*. Sprat was very frequent in 2009/10, but it is possible that on other years its importance might have been underestimated due to the methodology used. Cephalopods were represented mainly by squid, with the most frequent being the Patagonian squid *Doryteuthis gahi*, followed by *Onykia ingens* and *Illex argentinus*. I estimated that in 2008/09 and 2009/10, 46.2% and 45% of all samples, respectively, contained some items strongly suggestive of foraging at fishing vessels, and 10.3% and 17.5%, respectively, were composed exclusively of items I considered originating from fisheries. Across-years patterns of occurrence of southern blue whiting, rock cod and *Doryteuthis gahi* in albatross diet and on fisheries catches seemed to be

connected, both illustrating probable discard consumption (for fish) and competition for a seasonally abundant resource (squid). The evidence I present on this study, albeit mostly circumstantial, indicates that black-browed albatross from New Island obtain food from fisheries. At least during the chick rearing period, the percentage of food with such origin is considerable, with the caveat that the importance of more easily digested natural prey might have been underestimated.

Introduction

The abundance, density, quality and accessibility of the food resources are important factors limiting animal populations (e.g. Kitaysky et al. 2000, Schreiber & Burger 2001, Benoit-Bird et al. 2013). The predictability with which those resources are found is crucial for population dynamics driving patterns of breeding. For example, failing to find adequate food resources before and/or during the breeding season can result in breeding failure, and even mortality in extreme cases (e.g. Schreiber & Burger 2001, Suryan et al. 2002, Kitaysky et al. 2006).

For many seabirds, the availability of food resources has been altered by anthropogenic factors, notably fisheries-related (e.g. Votier et al. 2004a, Grémillet et al. 2008 and references therein). Commercial fishery operations are extremely attractive to seabirds due to the large amount of discarded fish and offal produced, and they represent a potentially easily accessible and predictable source of food (Thompson & Riddy 1995, Witt & Godley 2007). In many areas, such as the SW Atlantic, most species being targeted or discarded are demersal fish or squid (Thompson 1992, Thompson & Riddy 1995, Laptikhovsky et al. 2006, FAO 2011), and it is assumed that these resources would be otherwise mostly unavailable for surface feeders, such as albatrosses (e.g. Reid et al. 1996, Arata & Xavier 2003, but see Cherel et al. 2000). Fisheries are also considered the main direct cause of population declines in several albatross species (and other seabirds) which die mostly either through colliding or becoming entangled with cables or nets and by being caught on hooks (causing death by drowning) (Favero et al. 2011 and references therein).

Albatrosses are adapted to forage in the open ocean and to explore patchy marine resources (Grünbaum & Veit 2003, Weimerskirch 2007). Their foraging behaviour and decisions at sea can be studied indirectly through the analysis of diet and this method can also be used to understand the role of fisheries as a source of food. The results of such studies, important for seabird population management, have been used for understanding population dynamics of other seabirds (e.g. Wanless et al. 2005), their relationship with fisheries (e.g. Votier et al. 2004a) and potentially can be used to suggest management actions of fisheries (e.g. Velarde et al. 2013). It is also important to note that we have no understanding of how fisheries-induced changes in marine communities and natural prey availability have altered albatross diet prior to the advent of industrial fishing (as there are no pre-industrial fishing data). The potential impacts of these changes are likely to be substantial and to affect various aspects of albatross ecology, and therefore need to be evaluated; for example, studies on other seabirds indicate that some food obtained at fishing vessels (instead of “naturally” obtained) is of lower quality, with potentially negative impact on chick development (junk-food hypothesis; Grémillet et al. 2008). In times of change in fishery policies and climate instability it is thus vital to monitor seabird diet as part of environmental management (Barrett et al. 2007).

The black-browed albatross *Thalassarche melanophris* is one of the species most affected by fisheries-related mortality, but the number of casualties has decreased significantly on recent years (especially on longline vessels) due to mitigation measures in areas such as the Falkland Islands waters in the South Atlantic (e.g. Falkland Islands Government 2012), where around 67% of their total breeding population concentrates (ACAP 2010). This species is currently classified as endangered (IUCN 2010), despite the recent population increases recorded at several colonies (e.g. ACAP 2010, Catry et al. 2011b).

The Falkland Islands are located just over the edge of the Patagonian Shelf, the continental platform extending from the southeastern part of South America; both shelf and shelf break constitute very productive areas, where high chlorophyll concentration, stimulated by strong cold nutrient-rich upwelling currents, sustains important fish, cephalopod and crustacean communities, in turn feeding very large seabird (including the black-browed albatross) and marine mammal populations (e.g. Arkhipkin 2012, Miloslavich et al. 2011). Such high productivity has attracted commercial fisheries to the Patagonian Shelf area where their activity has increased dramatically since the 1950's, with ever larger catches of fish and squid taking place which already resulted in marked changes over the stocks of several species (FAO 2011).

Detailed information on black-browed albatross diet is fundamental to understand both variation in chick growth and of breeding success between years, and the potential interactions between this seabird and commercial fisheries, factors that might have implications for its population dynamics and conservation. Despite this, there has been only one previous albatross diet study being made on the Falkland Islands (partly published both in Thompson 1992 and Tickell 2000), and few from nearby waters (Arata & Xavier 2003, González-Zevallos & Yorio 2011). These studies, and others from breeding sites on the Kerguelen islands (Cherel et al. 2000) and South Georgia (Xavier et al. 2003), indicate the diet of this albatross relies in a large measure on fish and squid, with crustaceans having a lower importance, underpinning the clear potential for competition with commercial fisheries, The lack of any recent specific and detailed knowledge on black-browed albatross diet at its most important breeding area highlights why this work is important for the ecology and conservation of this species.

Making use of induced chick regurgitations, I studied the diet of black-browed albatrosses during the chick-rearing period at a large colony on the Falkland Islands. The aims of this study, focusing on diet composition and its inter-annual variation, are to investigate the potential interactions with commercial fisheries and their consequences for the breeding parameters of this endangered marine top-predator.

Methods

Black-browed albatross diet was studied at New Island (51° 42’ S, 61° 17’ W), Falkland Islands, during six Austral summers: 2003/04 and 2006/07 through 2010/2011, during the mid chick rearing period, with all samples collected from ca. 21 January (when most chicks are about 40 days old) until late February. During this period of the reproductive cycle breeding albatrosses are known to forage mostly within Falkland waters (Huin 2002).

Fisheries and commercially targeted species

Commercial fisheries fleet operating in the southern Patagonian Shelf area (both Argentinean and Falklands EEZs) comprises mostly bottom trawlers (including surimi vessels), but also jiggers (which operate only from February onwards for squid) and longliners (e.g. Laptikhovsky et al. 2006, Gorini et al. 2008, Granadeiro et al. 2010). Targeted fin fish species include: Patagonian toothfish *Dissostichus eleginoides* (longlines), hakes *Merluccius* spp., red cod *Salilota australis*, hoki *Macruronus magellanicus*, southern blue whiting *Micromesistius australis* and (since 2007) rock cod *Patagonotothen ramsayi*. Squid species targeted include Argentinean short-finned squid *Illex argentines* and Patagonian squid *Doryteuthis gahi* (formerly *Loligo gahi*), these being the most important fisheries of the region. The most abundant by-catch species are grenadier *Coelorhynchus fasciatus* (and other Macrouridae), red fish *Sebastes oculatus*, blue antimora *Antimora rostrata* and frogmouth *Cottoperca gobio*, as well as the squid *Onykia ingens* (formerly *Moroteuthis ingens*), among other species. All species are captured in annually highly variable numbers. Likewise a variable amount of discards is produced during fishing activity and these include all undersized commercial fish, unwanted by-catch species, all fish heads and offal resulting from processing commercial species onboard (see details in Laptikhovsky et al. 2006).

Diet composition: sampling and prey identification

Diet samples were collected from recently fed black-browed albatross chicks at randomly selected nests. Immediately after being fed, each chick was carefully removed from the nest, held head down and stimulated to regurgitate into a plastic bag inside a bucket. At the end of the process each chick was immediately returned to its nest. No chick that was still being fed was sampled, and each individual was sampled only once. Other studies have shown that low frequency induced regurgitation does not seem to have a deleterious effect on chick growth and survival (see Phillips 2006).

Each food sample was frozen, helping to separate the oil fraction from the solid fraction, which contains undigested and identifiable parts of prey. The frozen samples were then individually weighed to the nearest gram, placed into sieves (1 mm mesh) and then washed carefully under slowly running water. The resulting solid fraction was then weighed and its components were sorted into the following categories: fish, squid (and other cephalopods), lobster krill (and other crustaceans) and other items (includes salps, internal parasites, vegetable matter, etc).

Fish bones were assembled where possible (in order to determine minimum number of individuals) and gathered in groups. Otoliths, some fish bones and cephalopod beaks were preserved in ethanol; otoliths were identified at the

Falkland Islands Fisheries Department, using a reference collection with assistance from specialists (P. Brickle). Cephalopod beaks were identified making use of published references (e.g. Xavier & Cherel 2009). Both otoliths (total length: TL) and cephalopod beaks (lower rostral length: LRL) were measured using a binocular microscope equipped with an ocular scale. Larger otoliths and beaks were measured with dial calipers (to the nearest 0.1 mm). The original size of prey was estimated from different allometric formulae (see Table 1). In addition to formulae presented in Table 1, an alternative total length formula was found for hoki (Schiavini et al. 1997) that yielded consistently higher values (an excess of 78.3 mm, SD = 0.6, n = 30) than the one used (from Arata & Xavier 2003); my choice was motivated by a conservative approach in estimating fish length. No adequate formulae were found for blue antimora, and therefore no size estimations are presented for this species. In order to estimate fish lengths from otolith length, otoliths that were eroded lengthwise were not used. Otoliths were paired whenever possible (left and right, according to size, fine details and erosion state) and only one from each pair (the one that appeared to be less eroded), plus unpaired ones, were used for reconstructing length classes and rates of occurrence. The total lengths of Fuegian sprats *Sprattus fuegensis* were measured directly from fresh individuals or estimated from nearly complete skeletons in samples. The available formulae for *Doryteuthis gahi* (e.g. Pineda et al. 1996, Xavier & Cherel 2009) relating beak length and mantle lengths (ML) seemed to slightly overestimate the mantle sizes of the whole individuals recovered from for my samples. I therefore calculated a regression of LRL against ML from a sample (N = 22 whole fresh individuals) obtained from 4 diet samples distributed through the whole sampling period of 2009/10, which seems to better represent the sizes of squid in my samples (Table 1)

Cases where squid presence was identified via beaks that were considered to be old (and no other squid tissue present) and where otoliths were clearly eroded, were not used for calculating frequencies of occurrence as they probably represented meal(s) prior to the one being sampled.

Lobster krill (*Munida* spp.) was identified to species/morph level whenever possible (according to Tapella & Lovrich 2006). In 2008/09 and 2009/10 carapace length were measured (dial calipers) on all whole individuals and, in cases where disassembled parts were found, a sample was measured in order to estimate the average size of the individuals consumed.

Both numeric frequency and frequency of occurrence are presented for fish and cephalopods (as percent); I define numeric frequency as the number of otolith/cephalopod beak pairs plus single (unpaired) otoliths/beaks of one given species (approximately equivalent to the number of individuals in a sample), divided by the total number of otoliths/beaks retrieved from food samples in a given year; frequency of occurrence is here defined as the number of samples a species was found in divided by the total number of samples obtained in a given year. In general, when I mention frequency elsewhere I am referring to frequency of occurrence. Some comparisons are made with the results from another study, made in 1987 in New Island (Thompson 1992). Measurements are presented as mean ± SD.

I did not attempt to reconstruct original prey mass as the uncertainty and potential error using this method is large and thus is prone to unquantifiable bias. It proved impossible to determine the percentage of mass ingested for one given prey (for example, it is not possible to discriminate between the consumption of whole fish from that of gutted fish heads from the study of otoliths) and in samples with a higher degree of digestion it was impossible to determine all the original prey in the meal. Finally it is important to note that the method used fails to detect items that have no hard parts.

Characteristics of diet samples and evidence of potential links with fisheries

Several approaches were used in order to investigate possible links between albatross diet and fisheries, based on the results from the diet analysis.

First, I classified each sample as containing prey associated with scavenging at fishing vessels if it met one of the following criteria: 1) presence of fresh otoliths of either rock cod or grenadier, 2) fresh otoliths of either red cod or southern blue whiting corresponding to fish of total length comprised within the limits of commercially captured individuals, 3) presence of blue antimora, 4) presence of isolated large fish heads, 5) presence of fresh fish tail articulated vertebrae (“fish tails”) with no otoliths associated. Occurrences of fish of this size and species were considered unlikely to be encountered during natural foraging behaviour and I assumed they indicate discard consumption (for other arguments see Discussion). This allows us to attempt to infer the minimum percentage of samples associated with fisheries. These criteria are relatively conservative compared to other studies (e.g. Arata & Xavier 2003 considered all hoki as originating from fisheries). It was only possible to perform this analysis for 2008/09 and 2009/10, as for other years the data were not sufficiently detailed.

Secondly, I compared frequencies of occurrence of prey found in albatross diet with published numbers of both total annual and monthly (January and February only) commercial catches within Falklands waters (see Falkland Islands Government 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012). Only annual totals are available for rock cod catches. I expect some degree of correspondence between the most frequent prey in albatross diet and the fish captured in larger quantities in case albatrosses obtain their food from fishing vessels. Bonferroni correction was applied when multiple tests were used with the alpha-level decreased accordingly (e.g. Rice 1989).

Thirdly, I compared the sizes of fish and squid captured within Falklands waters (as reported in Falkland Islands Government 2005, 2008, 2009, 2010, 2011, 2012) with those consumed by albatrosses (as estimated from otoliths). Published fisheries data on sizes of captured fish and squid were only available in graphical format (histograms), and the analyses I could perform from those were thus limited. Unlike commercially targeted species, there were no available published data regarding sizes captured for grenadier, blue antimora or Fuegian sprat (as by-catch) for the whole study period or for rock cod for 2004. Some level of overlap between albatross prey sizes and the sizes of commercially captured fish would be expected if albatrosses feed on discarded fish.

Albatross breeding success and chick mass

Albatross nests were marked annually with permanent numbered tags on the day of laying at 3 different sub-colonies, since the breeding season of 2003/04 onwards. Numbers of nests studied varied between 170-207 annually during this period. Breeding success was determined as the percentage of all nests (where egg laying occurred) that contained a live chick by the first week of March (mortality is typically low from then until mid-April, when fledging starts). Chicks were all weighed when 58 and 60 days old, and the average of these two measurements gave an index of body condition at 59 days old.

Implications of diet for chick development

The junk-food hypothesis (e.g. Grémillet et al. 2008, see also Wanless et al. 2005) predicts that chick development might be affected negatively by the lower quality of food obtained in association with fisheries. The benthopelagic grenadier in particular (but also other species originating from fisheries waste) has a much lower caloric content than epipelagic prey, such as Fuegian sprat (ca. 4.74 kJg^{-1} and 7.15 kJg^{-1} wet mass respectively; Eder & Lewis 2005, Ciancio et al. 2007). Given the variation in profitability of different prey types, I expect mean chick mass to reflect the annual frequencies of occurrence of these species in diet, with higher mass on years when epipelagic prey are more frequent and lower mass when grenadier is found in more individual meals. For testing this hypothesis I compared frequencies of occurrence of fisheries related species (grenadier, rock cod, hoki) and of sprat with annual mean chick mass at 59 days.

Results

General diet

A total of 202 diet samples were obtained from chicks, with the number ranging from 12 to 40 for each of 6 breeding seasons (Table 2). Three broad categories of prey were found in the samples (fish, squid, and lobster krill *Munida gregaria*), all of which were found with variable frequencies of occurrence across years (Table 2); the importance of other prey types (such as salps, Salpidae) was negligible.

Fish

On average this was the most frequent prey class (86.7%, all years considered), consistently present in more than 80% of all samples annually (Table 2); the proportion found on all years combined was not significantly different from that found in 1987 (details in Table 2). The higher percent frequencies of occurrence in 2003/04 and 2008/09, together with higher numbers of otoliths per sample (Tables 2 and 3) suggest that fish consumption was highest on those 2 years. I identified 9 species, with 4 other potential taxa detected which I was not able to determine to species level (Table 3). Depending on the year, the most abundant species were hoki (2003/04, 2006/07) and rock cod (2007/08, 2008/09, 2010/11; Table 3). The grenadier was also numerous on some years (2003/04, 2008/09 and 2009/10), and the southern blue whiting was important until 2006/07, but nearly absent afterwards (Table 3). Sprat was notably abundant in 2009/10, when high frequencies of occurrence were recorded (Table 3).

a) Hoki

There were hoki found every year with variable frequency of occurrence, but were especially numerous and frequent in 2003/04 (Table 2); differences in occurrence between years were significant (Fisher's exact test, $p < 0.001$). Total length of individuals varied from 23.9 to 71.8 cm (mean = 46.7 ± 11.6, n = 84), although on most years sizes were under 60 cm (Fig. 1); most (between percentiles 25 and 75) were fish between 37.1 and 54.3 cm. Mean fish length was progressively shorter since the first sampling season but size differences were non-significant across years (Kruskall-Wallis test). Corresponding estimated pre-anal lengths (approximately 0.45*total length) had a range between 10.8 - 32.3 cm, with a mean of 21.0 cm.

b) Rock cod

Rock cod was present on albatross diet on all years, and was the single most frequent species of fish (Table 2). Differences between frequencies of occurrence across years were significant (Fisher's exact test, $p = 0.009$). Total length of individuals consumed varied from 9.1 to 28.1 cm (mean = 20.5 ± 3.8 cm, n = 131; Fig 1); 50% of the observations (between percentiles 25 and 75) corresponded to fish between 17.2 and 23.5 cm. Mean total length varied significantly between years (Kruskall-Wallis $\chi^2 = 13.6$, df = 4, $p = 0.009$), with larger fish consumed in 2006/07.

c) Southern blue whiting

This gadid was found in albatross diet mainly in 2003/04 (when very frequent) and in 2006/07, with only a small presence on other years (Table 2); differences between years were significant (Fisher's exact test, $p < 0.001$). The reconstructed sizes (total length) of ingested fish indicated individuals of 9.2 to 60.8 cm being consumed (mean = 29.1 ± 12.9 cm, n = 33), with most fish (between percentiles 25 and 75) having lengths between 19.4 and 38.9 cm (Fig. 1). There were no significant differences in mean total length between years (Kruskall-Wallis test).

d) Grenadier

The frequency of occurrence of this species was variable between years (Table 2), differing significantly between years (Fisher's exact test, $p < 0.001$). It was more numerous and frequent in 2003/04 and in 2009/10 (Table 2). Pre-anal length of individuals reconstructed from otoliths varied from 2.6 to 10.4 cm (mean = 6.0 ± 1.3 cm, n = 90 otoliths; 50% of the observations (between percentiles 25 and 75) corresponded to fish with pre-anal lengths between 5.2 and 6.7 cm (the equivalent total length should be roughly in the order of the 15 to 20 cm) (Fig. 1). There were no significant differences in mean pre-anal length between years (Kruskall-Wallis test).

e) Other fish

Other species (Table 3) were much less frequent; due to small sample sizes their reconstructed total lengths are merely indicative (Table 4). Fuegian sprat was detected in 2008/09 in only one sample with 2 nearly complete skeletons, but no otoliths were found. Several samples (2 in 2009/10 and 3 in 2010/11) contained large quantities of delicate fish larvae that appeared relatively fresh, suggesting a close origin; I was unable to identify them specifically.

Squid and other cephalopods

Cephalopods were the third most frequent prey type, with an annual average frequency of occurrence of 24.8% (only fresh evidences considered; Table 2); this proportion was similar to that observed in 1987 (details in Table 2). Annual numbers were extremely variable, with the highest frequencies of occurrence on 2009/10 (Table 2). Most prey in this group were the squid *Doryteuthis gahi* and *Onykia ingens*, although abundances and frequencies varied annually (Table 5). *Doryteuthis gahi* varied in ML from 3.0 to 12.6 cm (mean = 5.6 ± 2.1 cm, n = 63 beaks; Fig. 2). *Illex argentinus* was rare, found in only 1 sample each in 2006/07 (1 individual), 2008/09 (2), 2009/10 (2) and 2010/11 (1); reconstructed ML (in mm) were 233 (2 individuals; 2008/09), 206 and 181 (both from 2009/10); on other years only upper beaks were found. Octopoda were infrequent, found in small numbers and were represented by at least 2 different species that were not possible to determine, but the most frequent was probably a *Benthoctopus* species.

Lobster krill and other crustaceans

Crustaceans were the second most frequent prey type, after fish, found in 75.7% of all samples (all years combined; Table 2); this proportion was significantly different from that found in 1987 (details in Table 2). Identified crustaceans consisted mostly of lobster krill *Munida gregaria*, which was the single most frequent prey species overall, present on average in 67.8% of all samples (Tables 2 and 6). The species/morph *M. subrugosa* was not detected, but I cannot exclude its presence in the most digested samples. In 2008/09, *M. gregaria* mean carapace length (CL) was of 20.2 ± 2.6 mm (range = 9 - 26 mm; n = 59), with a large percentage concentrated between 18 and 23 mm, whilst in

2009/10 mean CL was of 18.1 ± 4.0 mm (range = 7 - 22 mm; n = 21) (Fig. 3). The mean number of individuals (per sample that contained measurable remains of the species) was of 5.1 ± 4.0 (range 1-18; n = 33), and of 3.4 ± 3.5 (range 1-16; n = 18), in 2008/09 and 2009/10, respectively.

Other crustaceans were rare, except for the amphipod *Themisto gaudichaudii*, very abundant on some samples (Table 6). On several relatively undigested food samples, this amphipod was recorded still inside fish stomachs in very large numbers. Other crustaceans detected included goose barnacles (*Lepas* sp.), and two fish ectoparasites: one isopod (*Aega* sp.) and a Caligid copepod (possibly *Caligus* sp.).

Other items

Salps (Tunicata, Salpidae) were found in 4.5% of all samples, on 3 different years. Parts of kelp leaves were found regularly on samples. A large percentage of the chicks were infested with nematodes. Small pebbles were found on most samples in 2008/09. No fishing hooks or plastic were found.

Characteristics of diet samples and possible relation to fisheries

In 2008/09 and 2009/10, 71.8% and 62.5% of all samples, respectively, contained items strongly suggestive of foraging at fishing vessels, according to the criteria defined in the methodology; a large percentage of these (82% and 64% respectively) contained also prey indicating natural feeding, such as fresh squid, fish larvae or *Munida gregaria*. The percentage of all samples where I detected exclusively prey assumed to have originated in fisheries was however much lower, 12.8% and 22.5%, respectively. Blue antimora (deep waters fish) was rare (found in 1 and 3 samples, in 2008/09 and 2009/10 respectively; Table 3), and was present always associated with numbers of benthic species as the grenadier and rock cod.

I found an individual significant correlation ($p < 0.05$) between the frequency of occurrence of southern blue whiting on albatross diet and commercial catches for February (Fig. 4, Table 7). Correlations between the frequencies of occurrence of red cod and January catches, of *Illex argentinus* and February and total annual catches, and of *Doryteuthis gahi* and total annual catches were no longer statistically significant after the application of a Bonferroni correction (Table 7). For these analyses I removed the year of 2007/08, given the small number of samples analysed. Despite the lack of statistical correlation between rock cod frequencies of occurrence and catches, the tendency of sharp increase was very similar between both (Fig. 4).

Comparing sizes of albatross prey with those from commercial catches

There was a complete overlap between the sizes of rock cod (2007-2011) consumed and those captured by commercial fisheries; also their modal sizes were similar between albatross diet and fisheries (Falkland Islands Government 2005, 2008, 2009, 2010, 2011, 2012; Table 8, Fig. 1). Overlap was incomplete in some years for hoki and southern blue whiting. For hoki, despite a good correspondence between modal sizes, in 2003/04 and 2010/11, 12.5% and 28.6% (respectively) of all individuals consumed were below the lower sizes captured (15 and 14 cm PAL, respectively; Falkland Islands Government 2005, 2012). For the southern blue whiting, in 2004, 47% of the fish consumed were smaller than 25 cm TL, the minimum size captured by fisheries in the same year

(Falkland Islands Government 2005); nevertheless, I found that much larger fish (up to over 60 cm TL; Fig. 1) were also consumed by albatross (perhaps partially). Overlap was nearly non-existent for hake: those consumed were clearly smaller than those caught by fisheries (below lower limit of range), except for 2009/10, when the only individual recovered had a total length similar to the mode of catches (Tables 4 and 8). For red cod, despite the overlap in sizes, the distribution of size classes consumed was different from fisheries sizes; red cods taken by albatrosses were all relatively small fish (Table 4), all smaller than 30 cm TL and in 2004 the single individual recovered was even below the minimum size captured by fisheries (20 cm; Falkland Islands Government 2005); individuals from fisheries have TL up to 90 cm (e.g. Falkland Islands Government 2005).

Breeding success and chick mass

Breeding success was clearly variable across years (Fig. 5); differences were statistically significant (Pearson $\chi^2 = 637.391$, $p < 0.001$, df = 7), and so were for chick mass (ANOVA $F_{7,3921} = 86.636$, $p < 0.001$).

Diet and chick development

I found no correlation between chick mass and the frequencies of occurrence both of any of the prey associated with fisheries and the epipelagic sprat (Pearson r, all n.s.). In addition, mean size of the main detected prey (rock cod, grenadier, hoki, southern blue whiting and *Doryteuthis gahi*) were not correlated with mean chick mass or with breeding success across years.

Figures

Figure 1

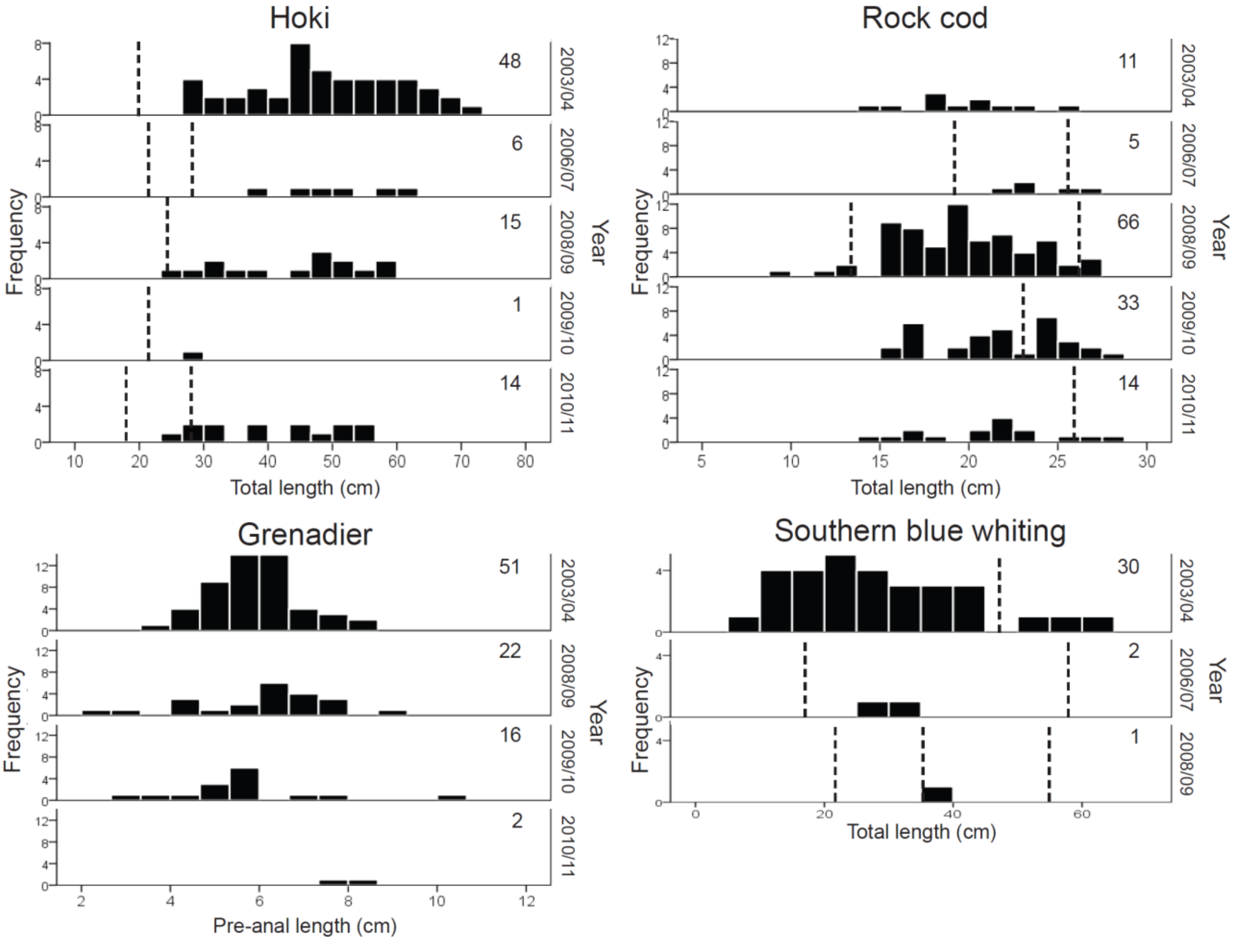


Figure 1. **Distribution of total length frequencies for hoki, rock cod and southern blue whiting, and pre-anal length for grenadier recovered from black-browed albatross regurgitations, as reconstructed from otolith length.** Sample sizes (total number of otoliths used) are indicated inside individual year cells (2007/08 is not included as otoliths were not measured). Dashed lines represent the modal lengths of commercially captured fish (from Falkland Islands Government 2005, 2008, 2010, 2011, 2012); multimodal distributions are represented by several lines.

Figure 2

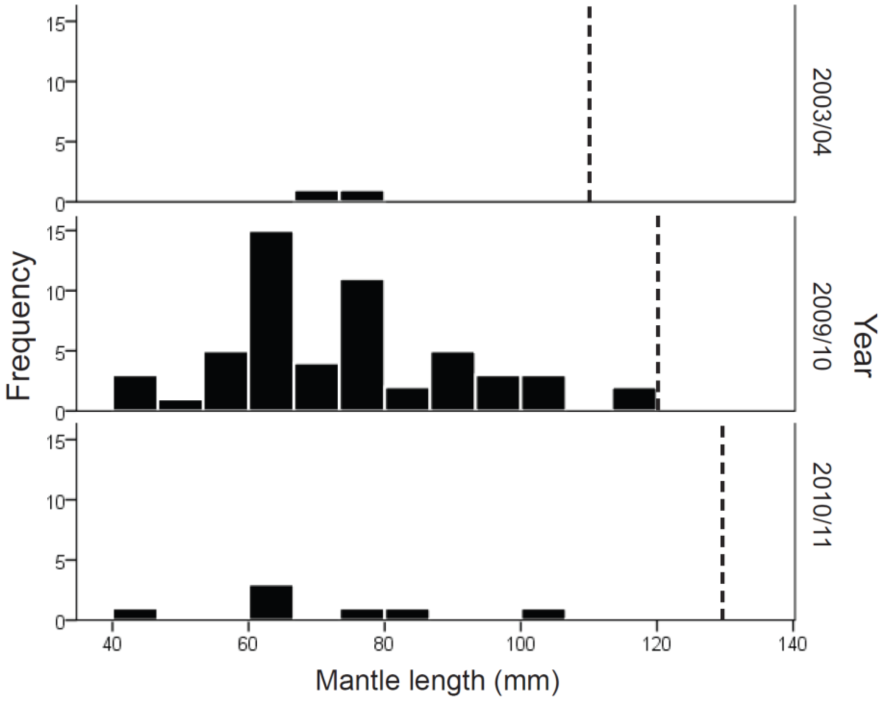


Figure 2. **Distribution of mantle length (ML, in mm) frequencies for Patagonian squid *Doryteuthis gahi* recovered from albatross regurgitations, as reconstructed from LRL.** There were no significant differences in mean mantle length between years (Kruskall-Wallis test). Dashed lines represent the modal lengths of commercially captured Patagonian squid (from Falkland Islands Government 2005, 2011, 2012).

Figure 3

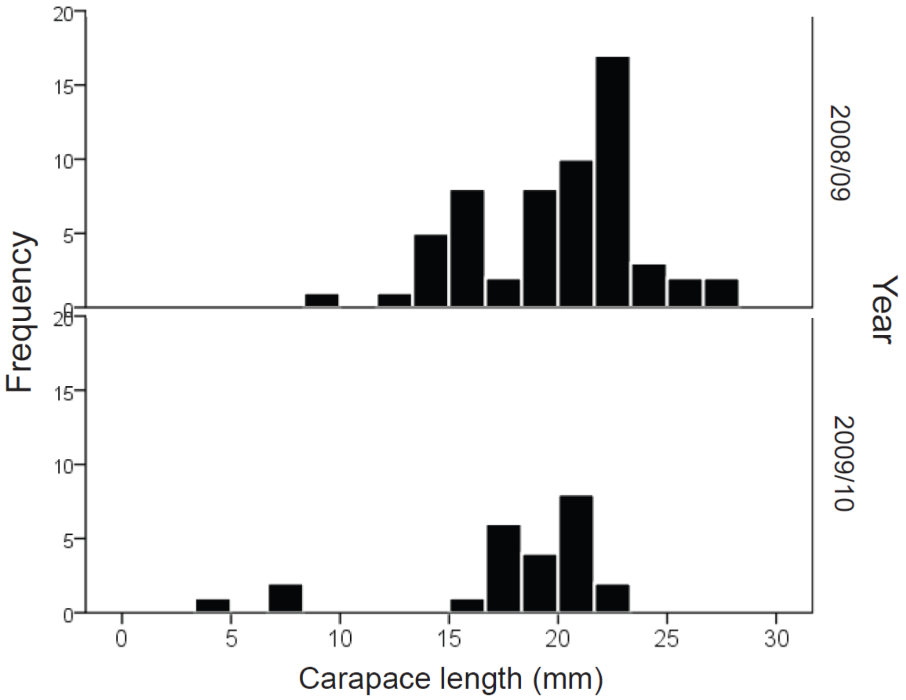
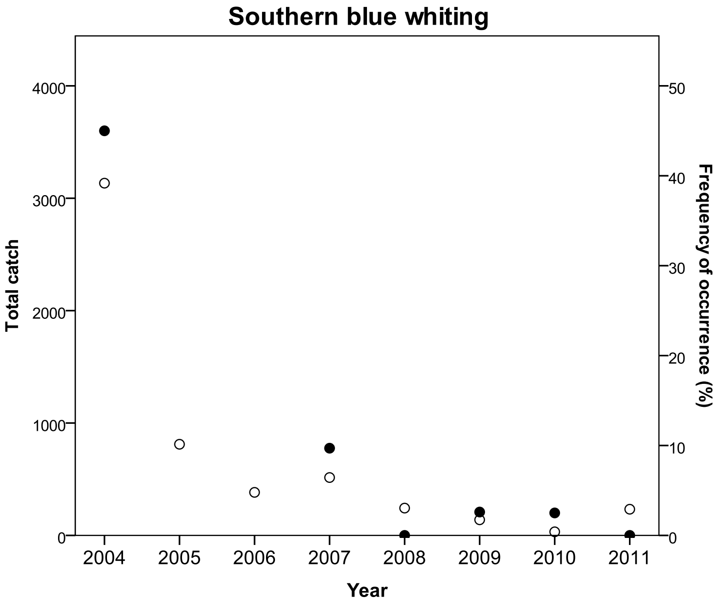


Figure 3. **Distribution of carapace length (CL, in mm) frequencies for *Munida gregaria* recovered from black-browed albatross regurgitations in 2008/09 and 2009/10.**

Figure 4



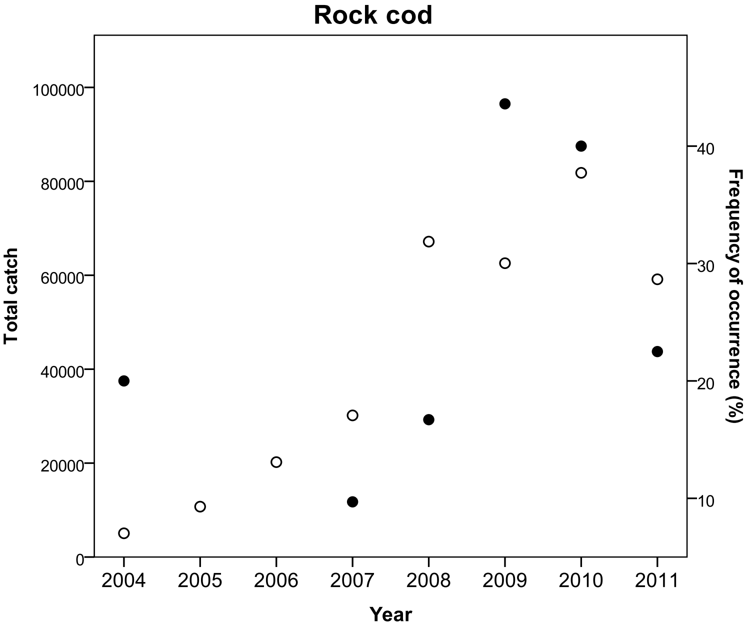


Figure 4. **Patterns of reported commercial catches (declared by-catch included) from Falkland Islands waters during the period 2004-2011 and frequency of occurrence in albatross diet for southern blue whiting (February catches only) and rock cod (total annual catches).** Catches (in metric tonnes) and frequencies of occurrence (%) are represented by open and black dots, respectively.

Figure 5

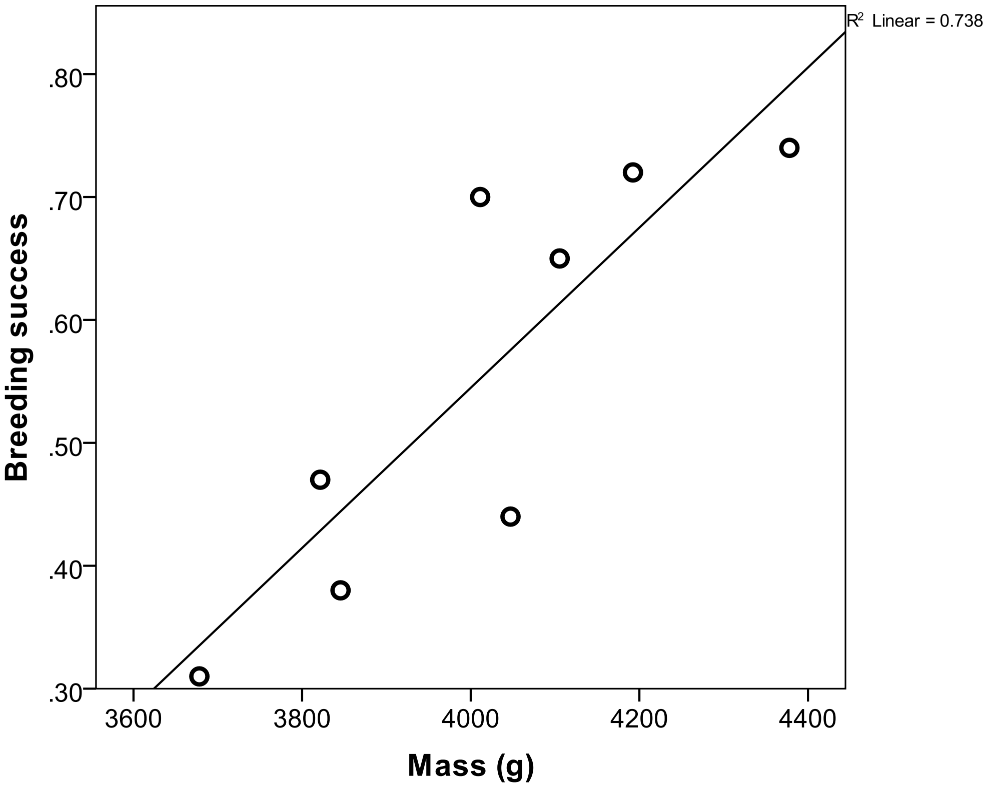


Figure 5. **Correlation between mean annual chick mass at 59 days of age and mean annual breeding success for 2003/04 and from 2006/07 to 20010/11.** Breeding success and mean chick mass were highly correlated (r = 0.859, p = 0.006, n = 8).

Tables

Table 1. Allometric formulae used for estimating total length and mass from otolith length. Abbreviations: TL = total length (mm), PAL = pre-anal length, OL = otolith length (mm), ML = mantle length (mm), LRL = lower rostral length (mm), CL = carapace length (mm), M = mass (g), WM = wet mass (g).

Species	**Relationship**	**Source**
Fish		
Patagonotothen ramsayi (rock cod)	$TL = (OL - 0.4141)/0.272$	Brown (2011)
Micromesistius australis (southern blue whiting)	$\ln TL = -0.259 + 1.47 \ln OL$	Thompson (1992)
Merluccius hubbsi (common hake)	$\ln TL = 0.72 + 1.04 \ln OL$	González-Zevallos et al. 2010
Macruronus magellanicus (hoki)	$TL:OL = 35:1$	Arata & Xavier 2003
Coelorhynchus fasciatus (grenadier)	$OL = 2.48*PAL^{0.71}$	Lombarte & Lleonart (1993)
Salilota australis (red cod)	$TL = -259.837 + 39.866*OL$	Schiavini et al. 1997
Cephalopods		
Gonatus antarcticus	$ML = -43.4 + 42.87*LRL$	Xavier & Cherel 2009
Doryteuthis gahi (Patagonian squid)	$ML = 24.128 + 118.805*\ln LRL$ ($r^2 = 0.639$, $n = 22$, rangeLRL: 1.2-2.0 mm)	This paper
Illex argentinus (Argentine shortfin squid)	$ML = -12.228 + 55.187*LRL$	Xavier & Cherel 2009

Table 2. Percent frequency of occurrence of three main prey types (fish, squid and crustaceans) on black-browed albatross diet at New Island over six breeding seasons (2003/04-2010/11) and in 1987 (from Thompson 1992). Note that most samples contained more than one type of food. For cephalopods only beaks considered to be new, bucal masses and presence of tissue considered. Fisher's exact test compares proportions of prey from the whole period 2003-2011 and those found in 1987 (Thompson 1992).

Breeding season	**N (samples analyzed)**	**Fish (%)**	**Cephalopods (%)**	**Crustaceans (%)**
2003/04	40	87.5	5.0	90.0
2006/07	31	80.0	32.3	87.1
2007/08	12	83.3	16.7	75.0
2008/09	39	87.2	15.4	97.4
2009/10	40	85.0	42.5	62.5
2010/11	40	100	32.5	45.0
Total (2003-11)	202	86.7	24.8	75.7
1986/87	32	87.5	21.9	40.6
	Fisher's exact test	n.s.	n.s.	p = 0.001

Table 3. Species of fish identified in black-browed albatross diet samples across six breeding seasons. Numbers presented are numeric frequency (N%) followed by frequency of occurrence (F%); see Methods. Species commercially targeted are marked with an asterisk (*); except for Fuegian sprat, all other species are commonly recorded as commercial fisheries by-catch (rock cod started being targeted in 2007). Otolith numbers for each year (N) are number of otoliths used (see Methods; total number of otoliths recovered not presented). a) Fuegian sprat was detected in 2008/09 through vertebrae only (see Table 4).

	2003/04		**2006/07**		**2007/08**		**2008/09**		**2009/10**		**2010/11**	
N (otoliths)	170		19		7		161		97		45	
% otoliths per sample	4.3		0.6		0.6		4.1		2.4		1.1	
Species	N%	F%	N%	F%	N%	F%	N%	F%	N%	F%	N%	F%
Family Clupeidae												
Sprattus fuegensis (Fuegian sprat)	0	0	0	0	0	0	a)	a)	19.6	20.0	2.2	2.5
Family Macrouridae												
Coelorhynchus fasciatus (grenadier)	34.7	55.0	0	0	11.1	8.3	18.0	33.3	24.7	22.5	4.4	2.5
Family Moridae												
Salilota australis (red cod)*	0.6	2.5	6.7	3.2	0	0	3.1	15.4	0	0	2.2	2.5
Antimora rostrata (blue antimora)	6.5	20.0	0	0	0	0	0.6	2.6	3.1	7.5	0	0
Family Merluccidae												
Merluccius hubbsi (common hake)*	1.2	7.5	0	0	0	0	1.2	5.1	0	0	0	0
Merluccius sp.*	0	0	0	0	0	0	0	0	2.1	2.5	2.2	2.5
Macruronus magellanicus (hoki)*	26.6	52.5	50.0	19.4	22.2	16.7	12.4	18.0	2.1	5.0	31.1	20.0
Merluccidae indet.	0	0	0	0	0	0	0.6	2.6	0	0	0	0
Family Gadidae												
Micromesistius australis (southern blue whiting)*	22.9	45.0	20.0	9.7	0	0	1.2	2.6	1.0	2.5	0	0
Family Psychrolutidae												
Psychrolutidae indet.	0.6	0.3	0	0	0	0	0	0	0	0	0	0
Family Nototheniidae												
Patagonotothen ramsayi (rock cod)*	7.6	20.0	23.3	9.7	33.3	16.7	53.4	43.6	42.3	40.0	53.3	22.5
Unidentified species	5.3	15.0	0	0	11.1	8.3	9.3	15.4	5.2	10.0	4.4	5.0

Table 4. Range of total lengths (cm) of fish species found in albatross diet (occasional or unrelated to fisheries), as reconstructed from otolith length or, for Fuegian sprat, measured directly. For fish taxa presented in Table 3 and not included here allometric formulae were not found or were inadequate. Sample sizes (total number of otoliths used, followed by total number of otoliths recovered, see Methods) are shown in brackets. Formula used for *Merluccius* sp. was the same as for *M. hubbsi*.

	2003/04	**2006/07**	**2008/09**	**2009/10**	**2010/11**
Fuegian sprat *Sprattus fuegensis*	-	-	14.6 (2)	8.9-18.1 (10)	15.4 (1)
Red cod *Salilota australis*	18.3 (1/1)	17.9 (1/2)	21.0 – 29.8 (4/9)	-	20.9 (1/1)
Common hake *Merluccius hubbsi*	23.4 (1/2)	-	18.9 – 36.0 (2/3)	-	-
Hakes *Merluccius* spp.	-	-	-	47.0 (1/2)	22.7 (1/1)

Table 5. Cephalopod species in black-browed albatross diet. Numbers presented are numeric frequency (N%) followed by frequency of occurrence (F%); see Methods. * = species commercially targeted.

	2003/04		**2006/07**		**2007/08**		**2008/09**		**2009/10**		**2010/11**	
Total number of beaks (Teuthida; Octopoda)	12 (10; 2)		54 (54; 0)		2 (1; 1)		52 (47; 5)		136 (131; 5)		31 (27; 4)	
N (lower beaks)	5 (4; 1)		-		-		25 (21; 4)		63 (59; 4)		16 (14; 2)	
Species	N%	F%	N%	F%	N%	F%	N%	F%	N%	F%	N%	F%
Teuthida (squid)	83.3	10.0	100	45.2	50.0	8.3	90.4	30.8	96.3	62.5	87.1	30.0
Family Gonatidae												
Gonatus antarcticus	0	0	5.6	3.2	0	0	0	0	0	0	6.9	5.0
Family Onychoteuthidae												
Onykia ingens	33.3	5.0	3.7	6.5	50.0	8.3	55.8	20.5	0.7	2.5	10.3	7.5
Family Ommastrephidae												
**Illex argentinus* (Argentinean short-finned squid)	0	0	20.4	12.9	0	0	5.8	2.6	2.9	2.5	3.5	2.5
Family Loliginidae												
**Doryteuthis gahi* (Patagonian squid)	33.3	2.5	64.8	29.0	0	0	0	0	91.2	57.5	48.3	17.5
Teuthida *indet*.	0	0	5.6	3.2	0	0	0	0	0.7	2.5	13.8	7.5
Octopoda (octopuses)	16.7	2.5	0	0	50.0	8.3	9.6	10.3	3.7	10.0	12.9	7.5
Family Octopodidae												
?*Benthoctopus* sp.?	0	0	0	0	0	0	3.9	5.1	0.7	2.5	6.9	5.0
Octopoda *indet*.	16.7	2.5	0	0	50.0	8.3	5.8	5.1	2.9	7.5	3.5	2.5
Cephalopoda *indet*.	16.7	2.5	0	0	0	0	0	0	0.7	2.5	6.9	5.0

Table 6. Crustaceans detected in black-browed albatross diet. Presented values are the percentage frequency of occurrence (percentage of samples that contained each prey item). In 2003/04, 2006/07 and 2007/08, only *Munida* sp. (lobster krill) was considered, as other crustaceans were residual. (*): items present in less than 5% (volume) of any given sample.

	2003-04	**2006-07**	**2007-08**	**2008-09**	**2009-10**	**2010-11**
<u>Copepoda</u>						
Caligidae *indet*.	-	-	-	0	0	10.0*
<u>Pedunculata</u>						
Lepas sp.	-	-	-	0	2.5	0
<u>Amphipoda</u>						
Themisto gaudichaudii	-	-	-	15.4	32.5	15.0
<u>Isopoda</u>						
Aega sp.	-	-	-	5.1*	0	7.5*
<u>Euphausiacea</u>						
Euphausiidae *indet.*	-	-	-	0	0	2.5*
<u>Decapoda</u>						
Munida gregaria	90.0	87.1	75.0	94.9	45.0	25.0
Campylonotus semistriatus	-	-	-	0	0	2.5*
All crustaceans	90.0	87.1	75.0	97.4	62.5	45.0

Table 7. Correlations (Pearson r) between catches of commercially targeted species (as in Falkland Islands Government 2005, 2008, 2009, 2010, 2011, 2012) and their annual frequency of occurrence in albatross diet. Comparisons are made with the months of January, February and whole year catches. Significance (alpha-level) was set to 0.002 (through the application of a Bonferroni correction, where alpha corrected = alpha/21). The significant correlation is shown in bold.

	Jan	**Feb**	**Whole year**
Red cod	r = 0.882, p = 0.048, n = 5	r = 0.495, p = 0.396, n = 5	r = 0.609, p = 0.275, n = 5
Common hake	r = 0.745, p = 0.148, n = 5	r = 0.353, p = 0.560, n = 5	r = -0.358, p = 0.554, n = 5
Hoki	r = 0.038, p = 0.951, n = 5	r = 0.766, p = 0.131, n = 5	r = 0.733, p = 0.159, n = 5
Southern blue whiting	r = -0.223, p = 0.718, n = 5	**r = 0.993, p = 0.001, n = 5**	r = 0.862, p = 0.060, n = 5
Rock cod	Data not available	Data not available	r = 0.839, p = 0.161, n = 5
Illex argentines	No captures	r = 0.951, p = 0.013, n = 5	r = 0.899, p = 0.038, n = 5
Doryteuthis gahi	No captures	r = 0.731, p = 0.160, n = 5	r = 0.972, p = 0.006, n = 5

Table 8. Range of sizes (total length for fish and dorsal mantle length for squid, in cm), followed by mode(s) in brackets, of species commercially captured within the Falkland Islands waters (Falkland Islands Government 2005, 2008, 2009, 2010, 2011, 2012). Legend: a) only pre-anal length available; b) only catches from trawlers; c) first fishing season only (Feb-Apr); nd: not detected in albatross diet and thus captured sizes not presented.

	2003-04	**2006-07**	**2007-08**	**2008-09**	**2009-10**	**2010-11**
Red cod	20-90 (37)	11-89 (13,25,57)	nd	15-88 (31-33)	nd	10-85 (23)
Common hake	36-90 (72)	nd	nd	30-90 (48)	30-80 (43)	33-90 (51,56)
Hoki (a)	15-41 (20)	12-43 (21,28)	15-38 (24)	11-43 (21)	14-46 (18,28)	14-46 (20,29)
Southern blue whiting (b)	25-66 (46)	10-67 (18,58)	nd	10-65 (22,35,55)	10-65 (28,55)	nd
Rock cod	-	5-40 (19,26)	10-39 (13,27)	8-41 (23)	8-42 (26)	7-38 (25)
Illex argentines	nd	9-36 (19,27)	nd	13-27 (19.5)	12.5-34.5 (15,25)	8-35.5 (12.5,25)
Doryteuthis gahi (c)	6-21 (11)	7-23 (12)	nd	nd	7-19.5 (13)	6.5-30 (12.5)

Discussion

Diet composition indicates black-browed albatrosses breeding on New Island behave as generalists, probably opportunistic, with important shifts regarding the species consumed across years; furthermore, the data suggests a high reliance of albatross diet on fisheries. During six breeding seasons fish was clearly the most frequent prey type detected in the diet fed to black-browed albatross chicks during the mid-late rearing period, and confirms this species as a mainly fish consumer. Cephalopod frequency of occurrence, mostly squid, was irregular and on most years low. Crustaceans were mainly represented by lobster krill, which was present on a large percentage of all samples.

The only previous work to study black-browed albatross diet on the Falklands (Thompson 1992) covered three different locations, each in a different year: Beauchêne Island in 1991 (early March), Steeple Jason in 1988 (January) and New Island in 1987 (chick rearing period). This study detected relatively small differences in diet, however there is no way of determining whether these resulted from an effect of location, year or stage of the breeding cycle.

In my study I remove location and breeding stage effects allowing us to focus on year. The results show that not only does the occurrence of different species vary across years in a single location, but the relative proportions of key prey types can also change dramatically. It is worth mentioning that the mean percent frequencies of occurrence for both fish and squid in this study are similar to the ones found in 1987 (Thompson 1992). However, the consumption of crustaceans in 1987 was much lower than in my study and comparable only with the poorer years of 2009/10 and 2010/11.

Black-browed albatross diet probably mostly reflects prey availability within its preferred foraging areas (shelves, shelf breaks and ocean fronts; e.g. Catry et al. 2013), and populations breeding elsewhere are likely to have different diet depending on what is locally available (as suggested by Xavier et al. 2003). Fish consumption is high on the Falklands compared with other areas, such as Diego Ramirez (Arata & Xavier 2003) or South Georgia (Xavier et al. 2003), and is only slightly lower to that reported for the Kerguelen Islands (Cherel et al. 2000). Cephalopods are present slightly more frequently than in Diego Ramirez (Arata & Xavier 2003), but were found more inconsistently and with lower frequency than in South Georgia (Xavier et al. 2003) or Kerguelen (Cherel et al. 2000). The occurrence of crustaceans is at least as frequent as in South Georgia; in Diego Ramirez, however, despite crustaceans in general having a relatively high frequency of occurrence, *Munida gregaria* is consumed with clearly lower frequencies (Arata & Xavier 2003); while on Kerguelen, crustaceans seem to have an only marginal importance, with *Themisto gaudichaudii* the most frequent species in samples (Cherel et al. 2000). Additionally, such differences probably reflect also foraging in different oceanographic environments. Compared to albatrosses breeding on the Falklands, that feed mostly over the continental shelf and slope (Huin 2002, Granadeiro 2011, Catry et al. 2013), birds from Diego Ramirez for example feed also away from these areas and much further south, down to the Antarctic Polar Front (Arata & Xavier 2003), whilst albatrosses from South Georgia may also forage on more oceanic areas, feeding mainly south of the Antarctic Polar Front (e.g. Croxall & Prince 1994, Xavier et al. 2003).

Interannual dietary shifts: what do they say of albatross feeding habits?

Interannual variation in diet composition (frequencies of occurrence) was mirrored closely by commercial catches only for some species, particularly the southern blue whiting, rock cod (Fig. 4) and the squid *Doryteuthis gahi* (despite the lack of statistical correlation for the latter two species), with marked shifts in diet coincident with changes in commercial landings of these species. Whereas the consumption of other species across years appears to be unrelated to respective volumes of catches.

From a sample of 169 otoliths, the southern blue whiting was the only fish species identified in the diets of black-browed albatrosses in 1987 (Thompson 1992). My study shows that this species was still important in 2004 (and 2007, when it represented about one fifth of all otoliths recovered), but outside these years it was minimal or absent in albatross diet abruptly (Table 3). This coincided with a marked decline in commercial catches of this species in Falklands waters, noticeable in 2005 and then sharply since 2008 (Falkland Islands Government 2006, 2009; Fig. 4), as the reduction of stocks no longer allowed profitable catches. Regional catches (including Argentinean waters) of this species increased sharply since it started being targeted in the 1970’s up to the 1990’s, and decreased steadily since then (in 2002 and 2009 catches were, respectively, 50% and 25% of those from the 1990’s; FAO 2011). This case clearly highlights the need for multi-year and long-term studies of diet, particularly when applied to species of conservation concern.

In contrast, rock cod was apparently absent from albatross diet at New Island in 1987 and elsewhere on the Falklands in 1988 and 1991 (Thompson 1992). During the first year of this study (2004), although this species was present, it was not one of the most abundant fish (Table 3). However, by 2009, the species had become by far the most abundant and frequent fish species in albatross diet, a pattern that persisted in all subsequent years. While rock cod were captured in large quantities as by-catch species (and commonly discarded) by different fishing fleets (Laptikhovsky et al. 2006), in 2007 it became targeted by the commercial fisheries (Winter et al. 2010) and annual catches increased markedly from this point compared with by-catch from previous years (an increase of 150% and more than 600% when compared with 2006 and 2004, respectively; Falkland Islands Government 2005, 2007, 2008; Fig. 4). Therefore the availability of rock cod to albatrosses has increased markedly and it seems very likely that increased occurrence in the diet is directly linked with discards and increasing fisheries targeting effort. However, rock cod stocks are also known to have increased in recent years (perhaps linked with southern blue whiting decrease; Falkland Islands Government 2012) and it is possible that this has somehow enhanced accessibility of this benthic fish for foraging albatrosses. It is also worth noting that red cod were generally rare dietary items throughout the study period, but were relatively frequent in 2008/09 (Table 2); this coincided with one of the highest catches of this species in the Falklands area (the catch for January 2009 alone was the highest for that month since 2001; Falkland Islands Government 2010).

Doryteuthis gahi represents one of the most important fisheries of the region; however, this fishery opens in late February, and my diet samples contained this species during January. For example, in 2010, the fishing season started on the 24th February (Falkland Islands Government 2011), after my sampling period had finished. This squid was recovered from albatross diet in highest numbers in January-February 2010, preceding what proved to be the highest commercial catches in 15 years around the Falklands (Falkland Islands Government 2011), yet it was completely undetected in 2008/09, when catches were within normal values (Falkland Islands Government 2010). The increased occurrence of this squid in diet matching higher catches in 2009/10 is likely a reflection of higher annual abundances in a broader area that encompassed both New Island albatross foraging areas and those where this squid is captured by fisheries, mostly to the south and east of the Falklands.

My data therefore suggest that at least some of the annual dietary shifts in albatross diet are linked to changes in fisheries. Given some of the obvious anomalies between albatross diet and fisheries data (e.g. squid occurrence), the information from diet as a predictor of fisheries abundances must be interpreted with care. More useful predictions could be made by studying foraging trips of diet sampled albatrosses with resource to available technologies, such as GPS tracking (e.g. Cherel & Weimerskirch 1995, Granadeiro et al. 2011).

Prey preferences of albatross: natural foraging or scavenging from ships?

Although albatrosses are apparently able of catching prey species that can potentially be obtained at fishing vessels under natural conditions (as shown by

Cherel et al. 1999 for New Zealand and by Cherel et al. 2000 for the Kerguelen), my data indicate that the presence and importance of most fish species in New Island albatross diet are related to fisheries. This is not merely a conclusion drawn from some correlational data (Table 7, Fig 4) as the overlap between the sizes of prey consumed and those from fisheries (or the high correspondence of modal sizes) for many species, such as rock cod, hoki and southern blue whiting (with large individuals of these species consumed) is considerable, reinforcing the idea that albatrosses are taking advantage of the opportunities that these fisheries present.

Benthopelagic or abyssal species, such as the grenadier or the blue antimora are likely to have been available only from scavenging at fishing vessels. The first is an abundant by-catch species (Cohen et al. 2010, Falkland Islands Government 2010) and, despite an irregular occurrence throughout the study period, it was very frequent in some years (for example, present in 55% of all samples in 2004; Table 3); as this fish is usually associated with deeper waters (known vertical distribution ranges at depths between 73-1086 m; Cohen et al. 2010) and thus is highly unlikely to be encountered by albatrosses foraging away from fishing vessels. Likewise I assume that all blue antimora in the diet must have originated from fisheries waste (a common discard species), as this fish is known to inhabit depths ranging between 350-3000 m (Cohen et al. 2010).

For red cod, a demersal species assumed to range at depths of 40-1000 m and mainly between 50-250 m (Cohen et al. 1990, Cassia & Hansen 2005), the size distribution of consumed fish was clearly biased towards smaller individuals

(Table 4) and the absence of larger fish is noteworthy. As above I believe this points to fishing activity and the pattern is consistent with the consumption of small discarded fish.

For hoki, another demersal fish, the available literature might suggest that on some periods of the year adults can be found in epipelagic waters; for example, hoki have been captured in nets in coastal shallow waters (0.5 m deep) in the Beagle Channel (Lloris et al. 2005), which suggests that even in deeper waters it might occur closer to the surface. For example juveniles of a deeper waters or even bathypelagic species, the Patagonian toothfish, occur much closer to the surface in depths around 50 m (Arkhipkin & Laptikhovsky 2010), and the same could be the case for hoki. Although it is very possible that this species might be occasionally available naturally, this cannot explain its regular and sustained presence in such important numbers in albatross diet unless a high relyiance upon fisheries is considered.

The occurrence of both small hoki and southern blue whiting (below lower limit of commercially captured fish) suggests natural foraging, but smaller fish could also indicate discarded individuals. With respect to the pelagic-demersal southern blue whiting, the fish lengths consumed by albatrosses reported by Thompson (1992) were also small (6-12 cm standard length, juveniles), and Cherel et al. (1999) have suggested that this species can be captured under natural conditions by albatrosses in New Zealand waters.

Of course, there are a range of additional species that are far more likely to have been captured naturally than in association with fishing vessels. This is the case of the Fuegian sprat, an epipelagic species not commercially targeted, which was detected in only three years and on two of them it was present simultaneously on the diet of other species breeding on New Island, namely the king cormorant *Phalacrocorax atriceps* (pers. obs.; Michalik et al. 2010). Another example is the squid *Doryteuthis gahi* which in 2010 was present in sustained high numbers throughout the season and in a fresh condition (also undamaged) in my samples, suggesting a “natural origin” located close to the colony. Likewise all lobster krill were probably obtained naturally, as this species constitutes abundant seasonal pelagic swarms (Diez et al. 2012), easily accessible to seabirds. Another smaller crustacean, *Themisto gaudichaudii*, was also recorded and is likely captured in one of two ways: surface seizing of individuals at swarms and from feeding on fish that fed on those swarms (Bocher et al. 2001). Ectoparasite crustacean species were probably ingested when whole fish were consumed; however it should be noted that Laysan albatrosses *Phoebastria immutabilis* have been recorded feeding from basking sunfish on very similar parasitic copepods to those I found (Abe et al. 2012).

The absence or near absence from diet of some important species commercially targeted in the region, such as hakes *Merluccius* spp. which occurred only irregularly (Table 3) or Patagonian toothfish (not detected in this study), is surprising as I would expect those species to be more frequent in a species relying on fishery by-catch and waste for food. The few hake that were recovered from diet were small and showed almost no overlap in sizes with those from Falklands fisheries (Tables 4 and 7). Hake occur over the Argentinean EEZ and appear in Falkland waters only as migratory fish in annually variable numbers (e.g. Lloris et al. 2005, Falkland Islands Government

2009); however this is well within the foraging ranges of black-browed albatrosses at New Island and the near absence of this species in the diet is not easily explained. The patterns for Patagonian toothfish are less puzzling. The areas where the largest toothfish catches are made within Falkland Islands waters in recent years lie to the south and southeast of this archipelago (e.g. Gorini et al. 2008, Falkland Islands Government 2009), where black-browed albatrosses from New Island are not known to forage (Granadeiro et al. 2011). Although substantial toothfish catches are also landed from Argentinean waters (Gorini et al. 2008), to the southwest of the Falklands that do overlap with albatross foraging areas. One reason for the lack of occurrence of this species in the diet of albatrosses may be the marked decrease of this fishery (Gorini et al. 2008) in recent years.

My attempt to estimate the minimum percentage of diet samples containing evidences from fisheries also suggests a relatively high dependency from fisheries, with visible evidences (according to my criteria) present in more than half of the samples I collected over two consecutive years (2008-09 and 2009-10). For some species, correlations between commercial catches and frequencies of occurrence (Table 7) are notoriously difficult to interpret, as they can either represent seabird attendance at fishing vessels or that both fishing vessels and albatrosses are targeting the same annually abundant prey. It seems likely that the occurrence of commercially targeted fish and their associated by-catch in the diets of albatrosses are likely a combination of both, where larger fish are captured at fishing vessels and smaller individuals are perhaps taken naturally. For squid, the correspondence in sizes might just indicate that fisheries and albatross are making use of the same cohorts.

Apparent conflicts with conclusions from other studies?

Recent data from GPS/GLS tracking studies of early brooding albatrosses from New Island, combined with data from the fishery Vessel Monitoring System operating within Falkland Islands waters, did not indicate any obvious relationship between foraging areas and fisheries (Granadeiro et al. 2011, Catry et al. 2013). Although this may seem at odds with my findings, the tracking studies focused on albatross behaviour earlier in the season, mostly December (hatching and early brooding period), and it may be that foraging behavior changes in January and February, when food demands from the chick are higher. In fact, the foraging range of post-guard black-browed albatrosses of the Falklands is probably more restricted than of incubating birds (Huin 2002), perhaps suggesting diet might differ, as different marine areas and thus resources are explored. Other seabird species are known to change diets across the season (e.g. Bearhop et al. 2001, Navarro et al. 2009), which might reflect prey availability.

My results also seem to indicate a greater importance of fisheries-related prey than that observed or predicted before for the region. It has been estimated that Falklands albatrosses fulfill up to 5.4% of their energetic needs during the breeding season from squid and finfish fisheries discards combined (Thompson 1992, Thompson & Riddy 1995), apparently considerably less than what is suggested by my results. However, the few diet study results presented by Thompson (1992) seem to agree with mine, in that most prey identified were related to fisheries, particularly fish. Both this and Thompson (1992) diet studies were indeed subject to similar sampling biases and are directly comparable, regardless of the potential prey that went under-detected and rendered my diet description incomplete.

There are several methodological reasons to consider incomplete both my diet description and that of Thompson (1992), contributing for the differences signaled between diet studies and estimates of discard consumption. First, diet sampling, through induced regurgitation, is subject to well known methodological limitations: there is a bias towards prey that contain hard parts, and prey items difficult to digest (such as squid beaks and otoliths) accumulate in the stomach making it difficult to isolate individual meals. In my study, salps and other soft bodied prey (such as fish larvae) might have been under-recorded or assumed absent due to lack of hard parts and consequent easiness of digestion. Fish with very small otoliths and soft skeleton, such as the pelagic and energy-rich Fuegian sprat, are also more likely to go undetected, either due to the sample filtering process or because smaller otoliths might be more difficult to regurgitate, remaining in the gut. This might lead to overestimate the relative importance of demersal and energy-poor fish. There was a concern that the absence of sprat on the 3 first years of this study could be a result of overlooking due to low otolith detectability. However, in the last two years, fresh whole fish or skeletons were also present in the samples in an obvious manner and I believe the pattern of occurrence of this epipelagic prey might correspond to a real change in abundance or availability (even if occasionally undetected before). Vertebrae from other species could not be used for identification purposes (as done by e.g. Cherel et al. 2000) due to the lack of complete and representative reference collections (see Alonso et al. 2013 and references therein for the importance of vertebrae in minimizing biases regarding relative importance of prey).

Although I present strong evidence of fishery bycatch and waste playing a role in the diets of black-browed albatross on the Falklands, the true importance of this resource cannot be quantified using my methodology. Moreover, this study focuses only the breeding season diet (restricted to the mid-chick-rearing period), the non-breeding season diet remaining basically unknown. It may be possible to address such knowledge gaps by using complementary techniques, such as stable isotope analysis (Inger & Bearhop 2008) and DNA identification (e.g. from faeces and other; e.g. Deagle et al. 2007 and references therein) in combination with bioenergetic approaches (e.g. Phillips et al. 1999, Votier et al. 2004b).

Accessibility of prey

Most demersal fish are unlikely to be available naturally to albatrosses as exposed above; in addition Notothenids, such as rock cod, have extremely low buoyancy (Fernández et al. 2012), making them unlikely to occur at the surface at any given time. It is frequently speculated that squid might be scavenged from the sea surface after mass mortality occurs following spawning (Croxall & Prince 1994 and references therein). This seems unlikely for *Doryteuthis gahi* in this study, as most individuals recovered were small and therefore probably immature.

It is also possible that cetaceans and other marine predators, such as seals, make live prey more accessible by conducting shoals to the surface (e.g.

Croxall & Prince 1994, Cherel et al. 2000) and thus driving them within the dive depths of albatrosses (at least down to 4.5 m in this albatross species; Prince et al. 1994) although data on the depths that the various albatross species can dive to are rare.

Many potential prey species also perform vertical migrations (of three different main types: ontogenic, diel and “frequent”) in the water column that might increase their accessibility (as mentioned by e.g. Croxall & Prince 1994). Ontogenic vertical migrations are performed by some species of fish and squid, age-segregating at different depths, with younger and smaller individuals occurring in epipelagic waters (e.g. Arkhipkin & Laptikhovsky 2010). This phenomenon could explain the occurrence of small red cod (and other species) in albatross diet at New Island. Other species, such as some squid species, have diel vertical migrations (e.g. Croxall & Prince 1994, Cherel & Weimerskirch 1995) and the recently described “frequent vertical migration” (Kaartvedt et al. 2012) might also contribute for increasing in the availability to albatrosses of some demersal fish.

Implications for chick development

The junk-food hypothesis (e.g. Grémillet et al. 2008) is difficult to test with my datasets, even superficially. Mean chick mass at 59 days did not correlate with the frequencies of occurrence of any particular species (fisheries related or not) present in diet, despite contrasting lipid and energetic contents of prey and their frequencies of occurrence. If the case is that albatrosses consume mostly fish heads from fisheries, prey caloric value should even be considerably lower. Despite strong shifts in diet composition, breeding success seems to be fairly high (Fig. 5), when compared with other breeding areas, such as South Georgia (Schreiber & Burger 2001, Xavier et al. 2003). The fact that a disease affecting young chicks caused breeding success to be lower on several years, including 2008/09 (own unpublished data), prevented meaningful comparisons between breeding success and the frequencies of occurrence of prey to be made.

Breeding success and chick mass were clearly linked (Fig. 5). However, despite what could be expected, diet was not a particularly good predictor of chick mass, perhaps because these measurements are taken at the population level, obscuring fine scale detail.

Conclusions

I found several lines of evidence pointing to a link between albatross diet and fisheries. These consistently support the view that, at least during the chick rearing period, a potentially important percentage of food, is obtained from foraging in the vicinity of fishing vessels. While I acknowledge that the evidence is largely correlative: interannual dietary shifts, coinciding with changes in species commercially targeted, a high correspondence with modal and ranges of sizes consumed for species, such as the benthic rock cod, and the presence of species known to inhabit abyssal depths, such as the blue antimora, the most likely explanation for the occurrence of species not known to be found naturally in depths beyond the known diving range of black-browed albatrosses (while being targeted by fisheries) is that they were obtained in the form of discards. However, methodological limitations that might lead to underestimate the importance of other prey, such as Fuegian sprat, prevent me from concluding about the true importance of fisheries for albatross diet on the Falklands.

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CHAPTER 6. GENERAL DISCUSSION

In this thesis, different approaches were used in order to characterize several potentially important factors influencing the breeding ecology of two threatened seabirds: the southern rockhopper penguin and the black-browed albatross. The roles of nesting habitat, predation, disease, parasites, and particularly diet as driving factors of seabird ecology were evaluated during several breeding seasons at a single mixed seabird colony on the Falkland Islands.

The most notable findings were:

1) that breeding success was variable between years and between sub-colonies (for both penguins and albatrosses);

2) that although variation in breeding parameters of rockhopper penguins throughout the breeding colony (and between sub-colonies) could not be explained by habitat related factors such as main breeding habitat or nest-site physical protection, it could be well explained by variation in predation ("asymmetrical predation" by specialized individual predators) together with edge effects and density of nests;

3) that variation in breeding success of black-browed albatrosses was caused mainly by an infectious disease (responsible for up to 33% of chick deaths in a given year), indicated by an epidemiological analysis (where spatial and temporal patterns of mortality were examined);

4) that the tick *Ixodes uriae* was possibly associated with reductions in mass gain and growth of late hatching chicks and that high parasite loads coincided with higher chick mortality, suggesting a severe effect of ticks (perhaps interacting with disease) especially under high infestation conditions;

5) that diet analysis confirms black-browed albatross breeding on New Island as a generalist and probably a variable forager or an opportunistic species, mainly fish eater, with my data suggesting a high reliance on fisheries.
6) and that potentially heavy reliance on fisheries by black-browed albatrosses does not seem to influence short term fitness of chicks, with the junk-food hypothesis not being confirmed by my data.

Despite the population declines undergone by black-browed albatrosses at several colonies throughout its range (Gales 1998), this species is at present increasing at New Island (West Falklands) (Catry et al. 2011b). The reasons identified for decreases elsewhere are all fisheries related. In particular entanglement in the fishing apparatus of various types of vessels is the major source of mortality (Gales 1998, ACAP 2010). While many of the albatrosses nesting at New Island clearly interact with vessels and are likely to be impacted in the same way and so it is uncertain as to why the species is increasing at this colony, or if this is a typical pattern among the other colonies within the Falklands. The various mitigation measures implemented in recent years within Falkland Island waters to reduce fisheries by-catch are suspected to be at least partially responsible for these dynamics (e.g. Sullivan et al. 2006, Catry et al. 2011b). However, additional factors were evaluated in the present work to produce a more complete picture of albatross population dynamics at New Island and in order to formulate better-informed decisions from a management point of view.

Nesting habitat and potential for habitat management

The first paper of this thesis (Chapter 2) focused on two different but sympatric nesting seabirds: the rockhopper penguin and the black-browed albatross. Here it has been shown how relatively close sub-colonies may differ markedly in breeding success and how these differences could not be explained (in this specific study) by one of the most likely candidate factors (the characteristics of the breeding microhabitat). Despite different predation levels at each sub-colony and at each of two very different habitats (open rocky areas and tussock grass *Paradiochloa flabellata* covered areas), neither physical protection of the individual nests or the different protection offered to whole sub-colonies could explain differences in reproductive success. Differences were observed spatially (at the sub-colony level), but none of the habitat variables I measured seemed to explain them. In the case of rockhoppers my data, together with non-systematic observations, indicated that individual aerial predators (mainly Falklands skuas) holding foraging territories on some sub-colonies might be responsible for many breeding failures in rocky areas. However, the nests located in tussock grass, despite being mostly free from aerial predation were subject to other factors, with the influence from the action of conspecifics being a probably important factor. Accordingly, mean breeding success of rockhopper penguins between sub-colonies in tussock grass or in open rocky areas did not differ.

Whatever was causing a decrease of the numbers of rockhopper penguin (at least until 2005, thus overlapping with my field work; Baylis et al. 2013) remains largely unknown, but is now thought to be related to oceanographic conditions, such as increases in sea surface temperature (SST) that might have resulted in changes in marine food-webs (e.g. Hilton et al. 2006, Dehnhard et al. 2013). Previously, the possible impact of introduced predators (feral cats *Felis catus*) on this species was evaluated on New Island, with only a minimal impact found (Matias & Catry 2008). Despite the recent increase of rockhopper penguin populations on the Falklands (Baylis et al. 2013), it remains important to try to understand the causes of previous declines, in order to mitigate any future problems.

In the case of the black-browed albatrosses, spatial variation of breeding success among sub-colonies could not explained by any of the variables investigated in Chapter 2 and therefore I investigated potential causes of variation in the mass mortality of nestlings among years. These aspects were further developed in Chapter 3 and 4.

The native bunch-grass, known as tussock grass, constitutes a prime habitat for the nesting of many seabird species on the Falklands (Woods 1970, Smith & Prince 1985). Since the Europeans started settling the Falklands, and especially after the 1860's, the area covered by this grass species has been markedly reduced (Clark & Dingwall 1985). New Island was no exception, and after the introduction of grazing cattle such as sheep, cows and horses, the native vegetation was markedly affected, the distribution of tussock grass shrunk progressively. Therefore, it could be argued that predation rates in rockhopper sub-colonies are enhanced due to increased exposure and accessibility to aerial predators created through anthropogenic habitat degradation and that the only reason nesting success is poor in tussock is because limited nesting habitat forces birds to breed at higher densities, which in turn increases conspecific disturbance and destruction of nests. Thus, even though the breeding success on these areas being on average similar to the more concealed sub-colonies, some habitat management could be conceivably desirable. However, livestock were largely eradicated from the island by the 1990’s and the native vegetation is starting to recover, including the tussock grass, which is slowly re-colonizing its former range. Habitat management is likely to be superfluous in the long term. Additionally, whilst tussock might be a beneficial habitat for many seabirds, including arguably the rockhopper penguin, more densely covered areas with this vegetation type are not an ideal breeding habitat for albatrosses. For example, taking off from dense vegetation is very difficult (personal obs.) and energetically costly, particularly in low winds, requiring the bird to climb up a tall vegetation clump or to walk slowly through the dense vegetation until a clearing is reached.

Influence of predation: a case for predator control?

Predation by Falkland skuas was the single most probable cause for breeding failure for rockhoppers on the rocky exposed areas (Chapter 2), with a few highly efficient individuals being responsible for the bulk of the predation events. In view of this, the possibility of culling certain individual skuas could be considered as a management action. For example, similar approaches have ben used to protect common tern *Sterna hirundo* colonies predated by large gulls *Larus* spp. (Guillemette & Brousseau 2001) with a resulting enhanced breeding success of the affected tern population.

The Falkland skua population at New Island is its largest breeding colony in the world (Catry et al. 2011a). However, it is now in decline and annual breeding success is very low (Catry et al. 2011a). Despite the direct impact of these specialized individuals, the effect does probably not last for many breeding seasons, as besides being limited to the longevity of such individuals, it is restricted to the period they are still efficient at this type of foraging (non-systematic observations suggest the overturn of the dominant individuals hunting at this rookery is relatively fast). Falkland skuas breeding in the vicinity of the seabird rookeries (and thus holding hunting territories in them) do include a high percentage of rockhopper penguin eggs in their diet (own unpublished data). However, these are most likely eggs knocked from nest cups, collected in large quantities during the laying and early incubation periods (own personal data) and thus the effect of the skuas here is not additive. Furthermore, New Island wide, most of the diet of Falkland skuas (most of which nest and forage away from the large rookeries) consists of thin-billed prions (own unpublished data), that nest throughout the island (Catry et al. 2003). Therefore, as the high predation levels inflicted by specialized individual skuas over rockhoppers are mostly spatially restricted within the rookery and, as a whole, probably within normal levels, and given the positive and negative population trends of rockhoppers and skuas, respectively, culling selectively efficient predators around the rockhopper colonies does not seem to be a priority or appropriate at the present.

Disease and parasites

Both disease and parasites have both direct and interactive effects on avian populations (e.g. Scott 1988). I treated them separately in this thesis in order to tentatively isolate the importance of each for the breeding success of black-browed albatrosses (which differed markedly between sub-colonies on New

Island). From my research, I concluded that an unknown disease is responsible for abnormal mortality levels among young albatross chicks, on different sub-colonies each year, and not every year with the same intensity. It is not clear how this disease and ticks are related, and what possible infecting mechanisms are involved. Ticks might be taking advantage from already weakened chicks or might act as vectors. More research in needed to understand the fine detail of this problem.

The potential importance of these two factors on black-browed albatross ecology across its breeding range seems to be currently underestimated, with most attention of researchers focused on the importance of albatross-fisheries interaction (which I cover in Chapter 5). However, work on yellow-nosed albatrosses *Thalassarche chlororhynchus* at Amsterdam Island indicates that disease can have a profound impact on albatross populations, and population declines that were thought to be mainly linked to fisheries related mortality were, on this case, shown to be disease-related. At Amsterdam Island avian cholera has been responsible for catastrophic breeding failures among yellow-nosed albatrosses, and was probably also the cause of high chick mortality among both the critically endangered Amsterdam albatross *Diomedea amsterdamensis* and sooty albatrosses *Phoebetria fusca* (Weimerskirch 2004).

The future recruitment from the cohorts most affected by disease or parasite induced mortality will be clearly reduced. However, this could only have a marked effect on demography (even at a local scale) if this situation is sustained consistently over many years. Under normal circumstances lower recruitment levels can be buffered at the population level by the longevity of breeding adults and may stay unnoticed for long periods also because of the delayed breeding maturity (with consequences of nestling mortality for recruitment only visible probably about 10 years later); an example illustrating how non-breeders might buffer breeding population numbers has been described for Guillemots *Uria aalge* (Votier et al. 2005). The relationship between disease and population dynamics of New Island black-browed albatrosses is unclear, but given the recently reported increase in population size(Catry et al. 2011b) it seems unlikely that the effects described in this thesis are having an important impact.

Diet as a reflection of foraging strategy and consequences for demography

Albatrosses from New Island include an apparently high percentage of food from fisheries in their diet. Both the absolute and relative importance of this source of food remain unknown, as my sampling approach (making use mostly of induced regurgitation) did not allow them to be determined, and it is possible that the percentage of small pelagic fish is underestimated in this study. Even if this is the case, the frequency of occurrence points to fisheries-related prey being a very important resource for New Island albatrosses.

I failed to find a direct link between diet and both breeding output and offspring condition. It is possible that no such relationship is detectable in albatross chicks due to metabolical specificities of the species (similar to most other Procellariiformes, for example the production of stomach oil; Schreiber & Burger 2001), compared to other seabirds where this aspect was studied (such as Cape gannets; Grémillet et al. 2008). It might also be that the relationship is only visible at a later stage, with post-fledging immatures being in worse condition than if fed a caloric-richer diet. Or alternatively that the proportion of undetected lipid-rich prey (small pelagic fishes and other natural prey) in diet is so large that it overweights any affects the nutritional-poorer discards might have. These aspects deserve further attention and additional detailed studies. To study this aspect properly and to isolate the potential effect of diet, the development and diet of individual chicks should be analysed, in order to avoid the dilution of effects at the population level. However, I hypothesise that regardless of the potentially negative effect of a lower caloric diet on chick development can have (Grémillet et al. 2008, Österblom et al. 2008), the constant availability of discards as a food source might act as a buffer on years of lower natural food abundance (potentially fisheries induced or climate change related), which might enable a more consistent breeding success and post-fledging survival. The present knowledge regarding the latter is non-existent, however this might partially explain the observed population increase (as per Catry et al. 2011b).

It is possible that the New Island colony represents a convenient departure and arrival location for birds feeding on fisheries, making it suitable from an energetics point of view for a central place forager. Most black-browed albatrosses observed by other authors foraging behind fishing vessels are adult-plumaged (e.g. Thompson 1992). However, black-browed albatrosses develop adult-like plumage at around the age of 5, which is 4 or 5 years prior to a first breeding attempt (personal obs. of marked birds, Prince et al. 1994, Bugoni & Furness 2009). Mitigation measures implemented within Falklands waters have effectively have reduced mortality in that area (e.g. Sullivan et al.

2006, Falkland Islands Government 2012). If some of the birds following ships are in fact immatures, then mitigation could have accounted for increased recruitment rates at colonies where birds have stronger ties with fisheries during the pre-breeding years. It should be noted that the recent GPS tracking studies of black-browed albatrosses at New Island (which indicated that interactions with fisheries do not seem to be frequent) have focused only on breeding adults (Granadeiro et al. 2011, Catry et al. 2013).

Albatrosses are mostly generalist predators, and generally very variable foragers, as illustrated in chapter 5. The shifts in preferred prey among the different years of the study period might reflect different species being targeted by commercial fisheries, as the species that change most in occurrence are often fisheries-related. As the stocks of each commercial species become progressively depleted (as it happened with the Southern blue whiting; FAO 2011), different species start to be commercially targeted (the rock cod being an example; Winter et al. 2010). If more restrictive fishing quotas are not implemented it is possible that the Patagonian Shelf fish community could be reduced to a point where most common fish species become too scarce for profitable commercial catches. Thus, a potential population growth based on this kind of resource, as I here speculate, might not be sustainable in the mid or even short-term, and eventually result in severe negative consequences for this marine seabird.

Spatial variation and scale-dependent interpretation of data

Chapters 2 to 4 highlight the need for the interpretation of ecological data in a context of spatial variation. The findings indicate that breeding parameters, predation, disease or parasites are distributed evenly throughout one same colony and there were clear differences between sub-colonies (as well as within sub-colonies). These examples highlight the importance of careful choice of multiple study plots in ecological and monitoring studies in order to produce representative results and to adequately document spatially restricted phenomena. The interpretation of data is also subject to the scale at which these studies are undertaken, and ideally studies at different scales should be used to complement each other (e.g. Levin 1992). This concept can be extended from spatial scale to temporal scale, and again the results in this thesis highlight the importance of longer time-series to set the study in a broader and more meaningful context.

The importance of long-term datasets

With the exception of the rockhopper penguin data (Chapter 2) and the study on albatross parasites (Chapter 4), the chapters had a minimum of 6 sampling field seasons. However 6-7 years is not yet a long-term series for an animal that may reach 50 years of age, but it does allow for more robust conclusions to be drawn in comparison to the 2-3 field seasons of data actually collected during a normal PhD thesis. The patterns of spatial and temporal variability in breeding success and associated chick mortality were only minimally adequately studied in this time scale. The same applies to the changes in diet described across the whole study period. These studies are still taking place at the same colony, and a more complete picture of the subjects included in this thesis will be hopefully produced in the future as more data will make clearer patterns emerge.

I was only able to study rockhopper penguin ecology for two seasons. All the arguments highlighted above stress why the conclusions from such a study should not be extrapolated and there is a real need for data to be collected over much longer periods. For example, the two field seasons studied in this work, 2004/05 and 2005/06, corresponded to the lowest numbers of breeding rockhoppers ever on the Falklands (Baylis et al. 2013), which may mean they are not representative of the general processes going on (although the factors studied in Chapter 2 are likely not to have been influenced by this).

Population changes and limiting factors

Within the time frame of this thesis, only a few of the multitude of possible factors limiting seabird populations were studied. Most were land-based factors, with diet being the only one that is directly related to the marine environment. Methodological limitations, have until very recently, prevented us undertaking in depth studies of seabirds while they are at sea. However, there have been substantial technological developments both in tracking technology (such as GPS tracking and very small digital video cameras; e.g. Sakamoto et al. 2009, Granadeiro et al. 2011) and indirect techniques (such as stable isotope analysis; Inger & Bearhop 2008), allowing for a more complete picture of the world of seabirds to be revealed.

Rockhopper penguins have only a minor role in this thesis, with only land-based limiting factors studied. Land-based predation of eggs and chicks was predicted to have a stronger effect on breeding parameters, but it seems unlikely that it could influence the demography of the species. The population decreases of this penguin are thought to be largely related to changes in marine foodwebs.

However it seems other causes, by causing additional periodic mortality of adults, might be also responsible by population declines; these mortality events are stochastic factors that are difficult to measure, driven by various phenomena such as high intensity weather events, harmful algal blooms and starvation before moulting (Birdlife International 2010). Regardless of the past declines, the populations of rockhopper penguins are now considered to be stable and increasing on the Falkland Islands, but the numbers are still only around 20% of those estimated in the 1930’s (Baylis et al. 2013).

The different approaches used to study limiting factors and threats affecting black-browed albatrosses in this thesis illustrated how a range of techniques and long time-series of data are needed in order to correctly interpret observed demographic changes and breeding parameters in seabird studies. Due to their complexity and interdependency, it is difficult to determine exactly what factors control the fine scale patterns of breeding parameters across years. However, the years experiencing the lowest breeding success were probably better explained by the influence of disease, possibly coupled with parasites. Had these factors not been studied, early albatross chick mortality (at least in the years it was more widespread) could have been easily have been linked to food availability and oceanographic factors. However the processes that underlie interannual variation in the occurrence of disease are not well understood and may well interact with other factors, such as diet. Therefore, the possibility remains that interactions may result in enhanced chick mortality, as my data do not allow for evaluating this hypothesis. More data will be needed in order to further understand the phenomena here studied.

Final considerations

Numerous other studies have highlighted the importance of each of the factors studied in this thesis in driving seabird population parameters, but perhaps not surprisingly there was no single factor that could explain breeding output patterns, even those observed for black-browed albatross throughout 7 consecutive years. Rather, my observations suggest there was an additive effect of all, with probable interactions. Throughout the study period, the most important factors causing differences in breeding success between colonies of both seabirds studied were predation, disease and parasites. Diet had possibly a cumulative effect on breeding output together with the previously mentioned factors, potentially exacerbating them, but was not a cause for spatial differences observed. The isolation of the effects and importance of each one of those factors in driving the population trajectories at New Island will be only possible through the continued study and monitoring of this seabird colony.

APPENDIX 1. PREDICTING THE DISTRIBUTION OF A THREATENED ALBATROSS: THE IMPORTANCE OF COMPETITION, FISHERIES AND ANNUAL VARIABILITY

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Predicting the distribution of a threatened albatross: The importance of competition, fisheries and annual variability

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ABSTRACT

The ability to predict the distribution of threatened marine predators is essential to inform spatially explicit seascape management. We tracked 99 individual black-browed albatrosses *Thalassarche melanophris* from two Falkland Islands' colonies in 2 years. We modeled the observed distribution of foraging activity taking environmental variables, fisheries activity (derived from vessel monitoring system data), accessibility to feeding grounds and intra-specific competition into account. The resulting models had sufficient generality to make reasonable predictions for different years and colonies, which allows temporal and spatial variation to be incorporated into the decision making process by managers for regions and seasons where available information is incomplete. We also illustrated that long-ranging birds from colonies separated by as little as 75 km can show important spatial segregation at sea, invalidating direct or uncorrected extrapolation from one colony to neighboring ones. Fisheries had limited influence on albatross distribution, despite the well known scavenging behavior of these birds. The models developed here have potentially wide application to the identification of sensitive geographical areas where special management practices (such as fisheries closures) could be implemented, and would predict how these areas are likely to move with annual and seasonal changes in environmental conditions.

1. Introduction

Past and predicted widespread changes in marine ecosystems demand intensive monitoring and improved management practices based on sound scientific data. Although many attributes of marine communities are poorly known, valuable insights may be derived from studies on species thought to convey information on particular components, such as, for example, spatial and temporal variations in the abundance of prey (Block et al., 2011). Seabirds are relatively easy to study and thus are increasingly being used for environmental assessment and monitoring (Boyd et al., 2006). Furthermore, many seabird species are globally threatened, hence their inclusion in frameworks for ecosystem-based management of fisheries, in marine zoning and in the design of marine protected areas (Hyrenbach et al., 2000).

In this context, the ability to predict the distribution of threatened marine predators such as albatrosses, petrels and other seabirds is essential to inform spatially explicit seascape management (Louzao et al., 2011). The identification of hotspots where predators are concentrated has recently been placed high on the applied research agenda (White et al., 2002; Terauds et al., 2006; Falabella et al., 2009; Louzao et al., 2011). Understanding the factors responsible for, and making accurate predictions of seabird distributions is a progressing field but comprehensive models of the spatial distribution of marine predators are still scarce (Tremblay et al., 2009; Wakefield et al., 2009a).

During reproduction, seabirds are central-place foragers. Their at-sea distribution can be assessed through ship-based surveys or through remote tracking. Both methods have their own advantages, with tracking often better at distinguishing birds in transit from birds foraging, birds from different colonies of origin, or age and sex classes, and hence allowing the establishment of links between areas of high resource abundance where energy-transfer is taking place and population vital rates (reproductive output and

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survival). Furthermore, remote tracking allows the coverage of the entire marine area that is relevant for the animal populations under study, something that ship-based surveys rarely achieve.

Research suggests that birds from neighboring colonies can have markedly different at-sea distributions, which may result from intra-specific competition (Huin, 2002; Ainley et al., 2004; Grémillet et al., 2004; Trathan et al., 2006). Furthermore, inter-annual variation in oceanographic conditions may also be important (Kappes et al., 2010). Such sources of variability need to be incorporated in models attempting to predict the spatial distribution of seabirds. Scavenging seabirds, including black-browed albatrosses *Thalassarche melanophris*, often gather in huge flocks behind fishing vessels, taking advantage of escaped fish, discards and offal (Sullivan et al., 2006; Pierre et al., 2010). Hence, it is plausible that fishing fleets will also influence the distribution of tracked seabirds (Bartumeus et al., 2010), although some studies suggest that the attraction effect may be only of local nature (Skov and Durinck, 2001). Whatever the relationship, fishing vessel distribution needs to be taken into account. Most studies so far have examined this issue at coarse spatial and temporal scales (Xavier et al., 2004; Phillips et al., 2006; Weimerskirch et al., 2010, but see Peterson et al., 2008; Votier et al., 2010; Granadeiro et al., 2011 for important exceptions) and more work is needed in this area.

Here we developed models to predict the distribution of black-browed albatrosses foraging over the southern Patagonian shelf, part of the Patagonian large marine ecosystem and one of the most productive areas in the world (Arkhipkin et al., 2012). This area is made up of a temperate ecosystem in the north and a sub-Antarctic system in the south which is partitioned by a boundary running from south-west to north-east through the Falkland Islands (Boltovskoy, 1999). The region hosts outstanding populations of foraging marine mammals and seabirds, but so far no official marine protected areas for biodiversity conservation have been created here (Falabella et al., 2009). Black-browed albatrosses represent a large part of the avian biomass of this ecosystem. They are known to gather behind fishing vessels in large numbers, suffering heavy incidental mortality (Sullivan et al., 2006; ACAP, 2009), and are categorized as Endangered by the World Conservation Union (IUCN, 2008). Our study aimed to develop robust models for predicting the distribution of albatrosses, taking into account factors such as accessibility (or travel costs), intra-specific competition, oceanography, fisheries and the corresponding inter-annual variation. We tested our models using independent data sets obtained from different colonies and seasons, which represent one of the most stringent tests available to assess the generality and usefulness of predicted distributions and the relevance of explanatory covariates.

2. Methods

2.1. Study sites and bird tracking

Black-browed albatrosses were tracked during the brooding stage (December and early January) from colonies on New Island (in 2008/2009 and 2009/2010) and on Steeple Jason (2009/2010). New Island (51°43′S, 61°18′W) holds ca. 12,000 black-browed albatross pairs, and Steeple Jason (51°01′S, 61°13′W) holds ca. 200,000 pairs (the largest colony for this species). Tracking was conducted through the deployment of GPS loggers (E&O Technologies, mass 25–30 g), attached to the mantle and scapular feathers, that recorded bird positions every 7 or every 14 min (depending on the size of the battery). Birds were also fitted with British Antarctic Survey geolocator-immersion loggers (Mk 7; 3.5 g) on a plastic or metal leg band, to record the timings of all changes of state (from wet to dry, and *vice versa*, with 3 s resolution). Estimated bird positions every 3 s were obtained through linear interpolation of GPS data and the location of all landings (on the sea) was inferred by combining the timings of locations with those provided by the logger data.

We tracked a total of 170 trips from 99 individual albatrosses (1–3 trips per individual) including 72 trips (39 birds) in 2008/2009, 65 trips (35 birds) in 2009/2010 on New Island and 33 trips (25 birds) from Steeple Jason.

2.2. General approach and options

We modeled the number of “dry–wet” transitions per 20×20 km cell of the study domain, which was defined as the area 45–60°S, 55–70°W. No foraging activity was recorded beyond this box. The immediate vicinity (<1500 m) of the study colonies, where birds often congregate to rest, was excluded as potential foraging area (see Granadeiro et al., 2011). The maximum foraging distance from the colony recorded during this study was 603 km. We reasoned that marine areas where birds do not land are of comparatively minor relevance for albatrosses, as they do not provide resources, and hence of lower priority for special management. Taking-off from the sea surface is an energetically expensive exercise for albatrosses (Weimerskirch et al., 2000), and we therefore assume that landing is generally associated with foraging and is rarely conducted without purpose. Landing can also be associated with resting, but the proportion of landings with this function must be low in our study birds, which on average landed on the sea 60 times per day (Granadeiro et al., 2011). Furthermore, landing spots, even if not providing food sources, are relevant because birds can still be affected by oil spills or other sources of pollution.

We followed Wakefield et al. (2011) in suggesting that habitat suitability is determined by local biotic and abiotic features, its accessibility and from the competitive influence exerted by individuals from other colonies. Hence, we encapsulated these three types of factors in a habitat suitability index given by

$$H_i(s) = Q(s)\frac{A_i(s)}{C_i(s)} \tag{1}$$

In other words, starting from the habitat quality of a cell s of the study grid $[H_i(s)]$, which is independent of the colonies where birds originate, we obtain the habitat suitability for colony i by deflating the quality $[Q(s)]$, based on intra-specific competition $[C_i(s)]$ and the inverse of the cost of traveling between i and s, which is given by the accessibility factor $[A_i(s)]$.

Dry–wet transitions typically present an aggregated spatial distribution, for a number of reasons: (i) they belong to the same bird; (ii) feeding of one bird may attract others; (iii) non-measurable environmental features such as the occurrence of food patches may also cause clustering (Grünbaum and Veit, 2003). For this reason we considered our dependent variable ($Z_i(s)$ – the number of landings detected per cell) to have a negative binomial distribution, where the mean is proportional to $H_i(s)$. We estimated the overdispersion parameter, together with the parameters that define $H_i(s)$, using Poisson-gamma generalized linear models (GLMs) with log-link function (see Supplementary material 1). For this purpose we adapted the PRIMM software developed by Christiansen and Morris (1997) from the S language to R – version 2.10.1 (R Development Core Team, 2009).

2.3. Environmental quality factor

We considered sea surface temperature (SST), chlorophyll-*a* concentration (Chl) and depth and their gradients as potential determinants of environmental quality. Mean values per cell (plus quadratic terms) and gradients (Supplementary material 1) were tested as predictors of habitat quality.

Sea surface temperature and chlorophyll-*a* concentration – Level 2 Modis Aqua and Terra data – were retrieved from http://oceancolor.gsfc.nasa.gov/. The SeaBatch software (http://seabatch.com/) was used to detect and remove outliers, and to bin data into monthly 20 × 20 km resolution products. SeaDAS (http://oceancolor.gsfc.nasa.gov/seadas/) was used to visualize data and to produce ASCII files for input to PRIMM. Etopo 1 min bathymetry data were retrieved from NOAA NGDC GEODAS (http://www.ngdc.noaa.gov/mgg/gdas/). Further data preprocessing, including the computation of gradients, was performed with purpose-built Fortran code. Ocean Data View (Schlitzer, 2010) was used for data visualization and preliminary analyses.

The models also incorporated the presence of fishing vessels, as revealed by the Vessel Monitoring System (VMS). Information on each of the fishing vessels operating inside Falkland Island waters was obtained through VMS that recorded the position of each vessel every 3 h (2008/2009) or every 1 h (2009/2010). This information constitutes a complete portrait of fishing activity in Falkland waters (as there are no vessels operating there without VMS), but not in Argentinean or international waters where data were unavailable. Nevertheless, we included the available fisheries data given that in different years and colonies between 53% and 87% of the black-browed albatross time at sea was spent in sectors with complete VMS data (Granadeiro et al., 2011). During the study period, the vessels operating in the area (15 vessels in the first year and 21 in the second) were freezer/factory bottom trawlers targeting finfish. The main target species was the Patagonian rock cod (*Patagonotothen ramsayi*). Fishery products include headed and gutted trunks, fillets and skate wings, with offal, heads and under-sized fish or unwanted species being discarded directly and not minced (see Granadeiro et al., 2011 for more details). Fishing effort of the Falklands fleet was estimated based on hourly positions of vessels moving at <6 knots (in 2008, values were interpolated to 1 h). This speed filter was supported by a bimodal distribution of vessel speeds, and probably excludes the majority of vessels in rapid transit between hauling stations.

2.4. Accessibility factor

Albatrosses are central-place foragers that fly using dynamic soaring. Hence, habitat accessibility is a function of distance from the colony (Matthiopoulos, 2003; Aarts et al., 2008), together with wind velocity and direction, which affect air speed and energy cost per unit time (Weimerskirch et al., 2000; Wakefield et al., 2009b). We assumed that accessibility may not vary linearly with distance (it may increase faster, per unit distance, at greater distances from the colony) because of the need to provide food for offspring at regular intervals. As expounded in Supplementary material 1, we constructed the accessibility factor Ai(s) by taking all these factors into account. From daily ASCAT and QuikSCAT passes (ftp://podaac.jpl.nasa.gov/), we separately computed averages of zonal (East–West) and meridional (North–South) wind components; with these, we obtained the monthly mean vector of sea-level wind.

2.5. Competition factor

Within our study domain, there are 12 islands with black-browed albatross colonies in the Falklands, two large populations in Chile at the Diego Ramirez and Ildefonso island groups, and 2 small colonies on islands in southern Tierra del Fuego (ACAP, 2009). These include several large colonies holding in excess of 10,000 breeding pairs.

In our model, we take possible intra-competition effects into account by considering that habitat suitability for birds of a given colony is affected by the habitat's proximity to other colonies, in particular those of large size (see Supplementary material 1). Estimates of colony sizes were obtained from Huin and Reid (2007), Strange (2008) and ACAP (2009).

2.6. Validation

We carried out several tests to confirm the validity and generality of the main findings obtained from the models.

2.6.1. Validation of parameter estimates

We fitted three GLMs: the first used data from New Island in 2008/2009; the second used 2009/2010 data from the same colony; the third used data from Steeple Jason in 2009/2010. For each GLM, predictors were selected with a backward stepwise approach. If our conceptualization of habitat suitability and use is not too far from the truth, and if the fitting algorithm does not lead to spurious results, then the *z*-scores for any given parameter should vary little over the three GLMs. Conversely, if we have failed to capture nonlinearities, missed important factors, fitted the model incorrectly or overfitted the data provided, then the three GLMs should provide widely different parameter estimates.

2.6.2. Validation of spatial predictions

We produced maps of the distribution of observed and expected dry–wet transitions, separately for New Island in 2008/2009 and 2009/2010, and Steeple Jason in 2009/2010. By "expected values" we refer to the posterior mean of $Z_i(s)$, according to the model fitted with data from New Island in 2008/2009 only. With this procedure, we tried to detect strengths and weaknesses in the model, i.e., areas where observations and expected values showed the greatest or least correspondence.

2.6.3. Validation of factors

We investigated the contribution of the factors considered to affect the habitat suitability index by using the Akaike Information Criterion with a correction for finite sample sizes (AICc). Starting from a complete model, we removed predictors (one at a time) and examined the resulting AICc. To compare the resulting models to the full and to the null models, we computed

$$\Delta_j = \frac{\mathrm{AICc}(j) - \mathrm{AICc}(\mathrm{complete})}{AICc(\mathrm{null}) - \mathrm{AICc}(\mathrm{complete})} \tag{2}$$

which may be interpreted as the loss of the explanatory power of a submodel, relative to the complete model (Burnham and Anderson, 2002). Values close to 0 indicate minimal loss, while values close to 1 indicate total loss.

2.6.4. Validation of predictor–response curves

For each predictor variable, we compared binned means (or frequencies) of dry–wet transitions with corresponding 95% credibility intervals provided by the model. Exactness, precision and sensitivity criteria were considered to determine if the GLM link function was appropriate and the correct functional form was chosen. See Supplementary material 2 for details.

2.7. Inter-annual variability

During preliminary analysis of New Island data, we observed marked differences in the spatial distribution of 2008/2009 and 2009/2010 landings. To evaluate which distribution is more typical, we constructed a map of the expected mean occurrence of dry–wet transitions made by New Island birds, during the month of December, using climatological (i.e., decadal mean) SST, chlorophyll, and wind conditions. The New Island 2009/2010 GLM was used in this exercise. QuikSCAT wind climatology (1999–2008) was provided by Risien and Chelton (2008, data available at http://cioss.coas.oregonstate.edu/scow/). Upon preliminary inspection of these products, we observe that blooms (i.e., concentrations above 10 mg/m^3) are not present in the climatological chlorophyll product; more importantly, climatological wind vectors are spatially smoother and have smaller magnitude than those of December 2008 and 2009. Long-term means smooth out extremes, as expected, but we suspect that in the case of winds the difference in magnitudes may originate from the additional harmonic filtering performed by Risien and Chelton (2008) and/or the data source itself (ASCAT vs. QuikSCAT; Bentamy et al., 2012). To mitigate this problem, we decrease the intercept for the climatological prediction model by 2.5 units. Such subjective procedure nearly eliminates the bias in the global mean impact of wind on expected dry–wet transitions, while keeping the spatial ratios intact. In other words, the correction has no impact on the determination of the regions more frequented by the birds.

3. Results

During early chick-rearing, black-browed albatrosses from the west Falklands foraged over the Patagonian Shelf, mostly to the west and southwest of the nesting colonies (Fig. 1). The distributions of landing events of albatrosses in 2009/2010 showed clear differences in relation to the colony of origin, in a pattern consis-

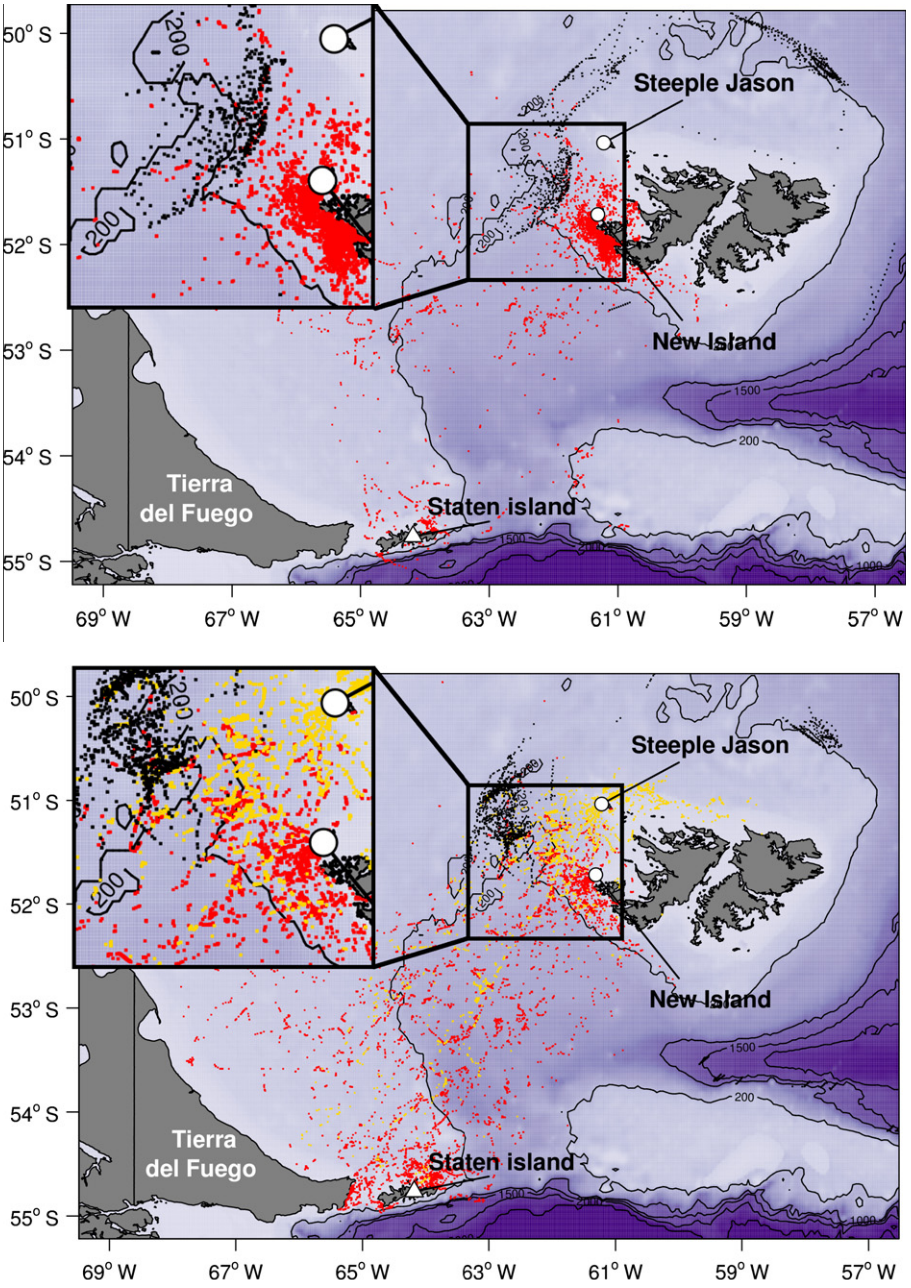

Fig. 1. Location of landings by GPS tracked birds from New Island (red dots – 39 individuals in first year and 35 in second) and Steeple Jason (yellow dots – 25 individuals, second year) in (a) December 2008–January 2009 and (b) December 2009–January 2010 (in 2009/2010 there is a complete and reciprocal overlap in the range of tracked dates from both colonies). Colony locations marked by white circles. Background shading indicates bathymetry. Black dots indicate (interpolated) hourly positions of fishing vessels obtained from VMS of the Falkland Island licensed fishing fleet, steaming at or below 6 knots.

Table 1
Posterior mean, standard error and upper and lower endpoint estimates of 95% credibility intervals for the predictors of the habitat suitability index in the model fitted to the New Island 2009/2010 data. Predictors are grouped into those that affect Environmental quality (Q), Accessibility (A) and Competition (C). The GLM overdispersion parameter is denoted as delta.

	Estimate	SE	EST/SE	Low point estimate	High point estimate
Intercept	−2.354	1.459	−1.614	−5.213	0.505
Q					
Log(bathymetry) (bat)	−1.586	0.167	−9.512	−1.913	−1.259
Log(bathymetry)^2 (bat2)	5.358	1.110	4.828	3.183	7.534
Gradient of Log(bathymetry) (batG)	0.522	0.128	4.088	0.272	0.772
Log(chlorophyll-*a* concentration) (chl)	0.472	0.077	6.128	0.321	0.623
Log(chlorophyll-*a* concentration)^2 (chl2)	1.347	0.226	5.964	0.904	1.789
Log(sea surface temperature) (sst)	0.138	0.811	0.170	−1.451	1.727
Gradient of Log(sea surface temperature)(sstG)	11.780	3.657	3.221	4.612	18.950
Log(density of fishing vessels) (vms)	0.015	0.007	2.176	0.002	0.029
A					
Log(overhead cost of flight) (ocost)	−5.810	0.823	−7.062	−7.422	−4.197
Log(distance to the colony) (dist)	−1.941	0.187	−10.390	−2.307	−1.575
C					
Log(scaled distance to closest colony) (dmin)	−1.564	0.179	−8.760	−1.914	−1.214
Log(size of closest colony) (dsize)	−0.115	0.011	−10.890	−0.136	−0.094
Overdispersion parameter (delta)	0.150	0.010	15.050	0.132	0.171
Log(overdispersion parameter) (log(delta))	−1.896	0.066	−28.530	−2.026	−1.766

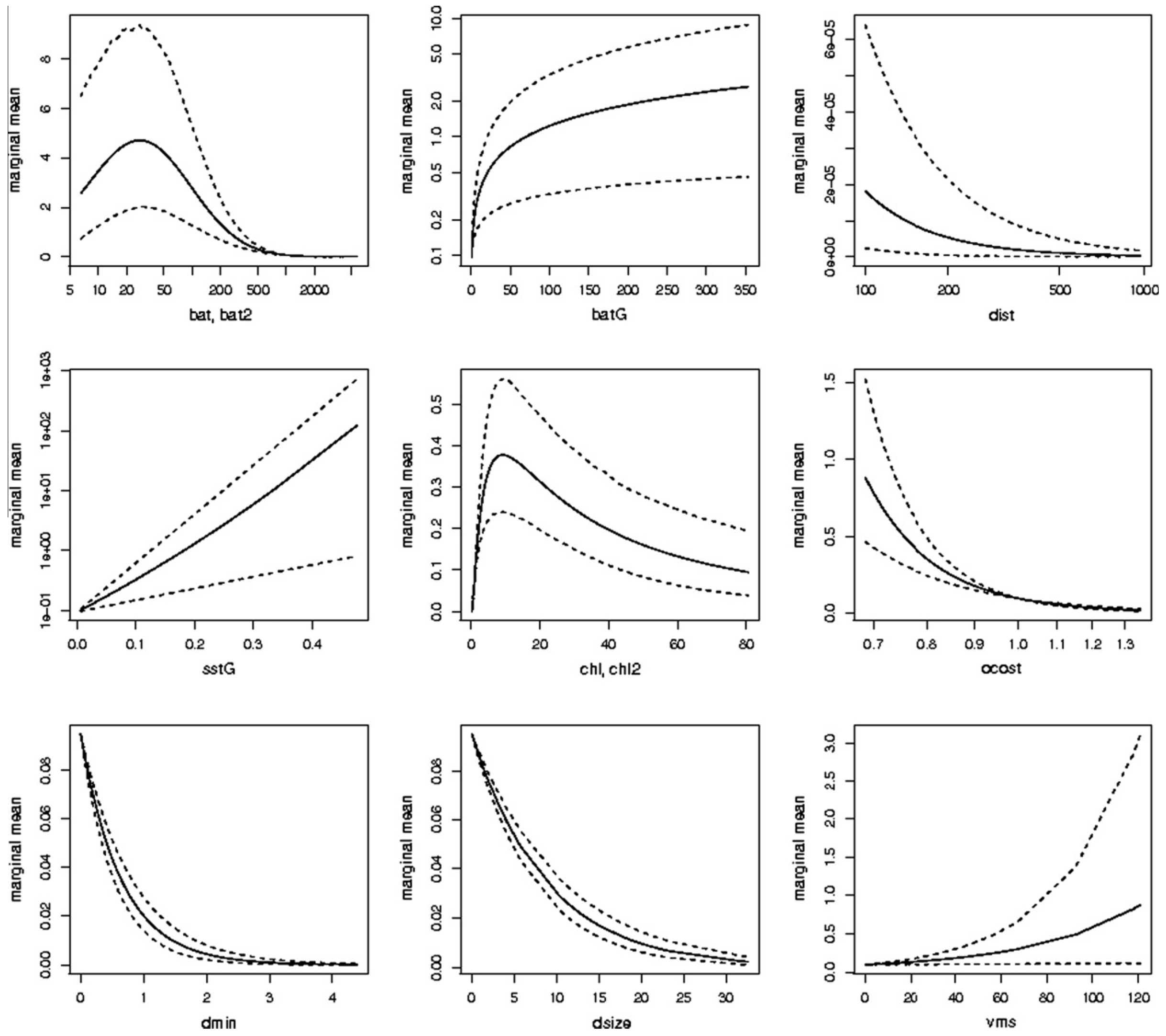

Fig. 2. Marginal effects of each predictor on the number of landings in each cell of the domain. All graphs relate to modeled distribution of birds from New Island in 2009/2010. Dashed lines indicate estimated 95% CIs.

tent with reciprocal avoidance of birds from adjacent sites (Fig. 1b). There were also clear inter-annual differences in the distribution of albatrosses from New Island: in the first year landings were tightly clustered near the colony, to the southwest and the south, while in the second year landings were more dispersed, and there was a much greater use of the distant area around Staten Island (east of Tierra del Fuego). There was a limited overlap between foraging activity and human fisheries (Fig. 1).

The coefficients of the habitat suitability model for New Island birds in 2009/2010 are presented in Table 1. Overall, this model and the ones fitted to New Island 2008/2009 and Steeple Jason data agreed in both sign and absolute value of coefficient *z*-scores (Fig. 1 of Supplementary material 2). Bathymetry, chlorophyll-*a* and distance from the colony displayed consistently strong associations with landings, while SST was more important to explain Steeple Jason landings than New Island's. Conversely, colony-related quantities were better predictors for New Island landings. Given that three GLMs fitted to distinct data sets produced similar results, we believe that the associations between landings and covariates are not spurious.

Ceteris paribus, the expected number of landings is higher in waters with 20–50 m depth, and close to zero outside the continental shelf (Fig. 2, top left panel). Oligotrophic regions with strong gradients in SST and bathymetry seem preferred. Distance between habitat and colony, together with additional costs of flight due to wind conditions, also affect expected habitat use (Fig. 2). While the impact of fishing vessels includes substantial uncertainty (Fig. 2, bottom right panel), the proximity of other colonies, particularly the larger ones, is clearly detrimental for habitat use.

We used the model derived for New Island in 2008/2009 to predict the distribution of landings by colony and year, and compared those with the observed distribution (Fig. 3). On average, the model derived for New Island in 2009/2010 differed from the observations by 3.8 landings per grid cell. This mean absolute difference (MAD) rises to 25.1, if zero-count cells are excluded. When used to predict the distribution of landings for a different colony or a different year (i.e., the coefficients are fixed and new predictor values are provided), this model did not lose precision: MAD = 3.3 for New Island 2008/2009 data, and MAD = 2.8 for Steeple Jason 2009/2010 data. If zero-count cells are excluded, the values become 25.2 and 18.2, respectively. These results are encouraging, since the number of landings per cell ranges from 0 to 1435. Fig. 3 presents a visual comparison of observed and predicted values. The most marked changes in the relative distribution for New Island birds from 1 year to another, including the greater concentration of landings around the nesting colony, and a reduction of activity near Staten Island and Tierra del Fuego in 2008/2009, are well captured by the model. The distribution of birds from Steeple Jason is also predicted reasonably well, although for all models there is a considerable area to the NE where predictions are not confirmed by observations. Note that the three distributions are quite different, which shows that the model has enough flexibility and responsiveness under different ranges of biotic and physical conditions.

All three components included in the habitat suitability index were important for the models' predictive capability, and for interpreting the distribution patterns of New Island birds. Of these, environmental quality was the most important, followed by competition and accessibility (Table 2). The similarity in results for New Island in 2008/2009 and 2009/2010 is striking. We interpret this as evidence that the predictors included in the model are key determinants of habitat use. The competition factor was relatively unimportant for Steeple Jason (Table 2), possibly because this is the largest colony in the Falkland Islands and therefore the impact of neighboring colonies is likely to be low, in comparison with the situation for birds from New Island. Another noteworthy aspect of the models was the minimal and marginally significant contribution of the fisheries predictor, which was responsible for no more than 2.3% of total explanatory power (Table 2). Fig. 4 provides visual support and further reinforces the conclusion extracted from Table 2 that each of the three main factors (environmental quality, accessibility and competition) are impor-

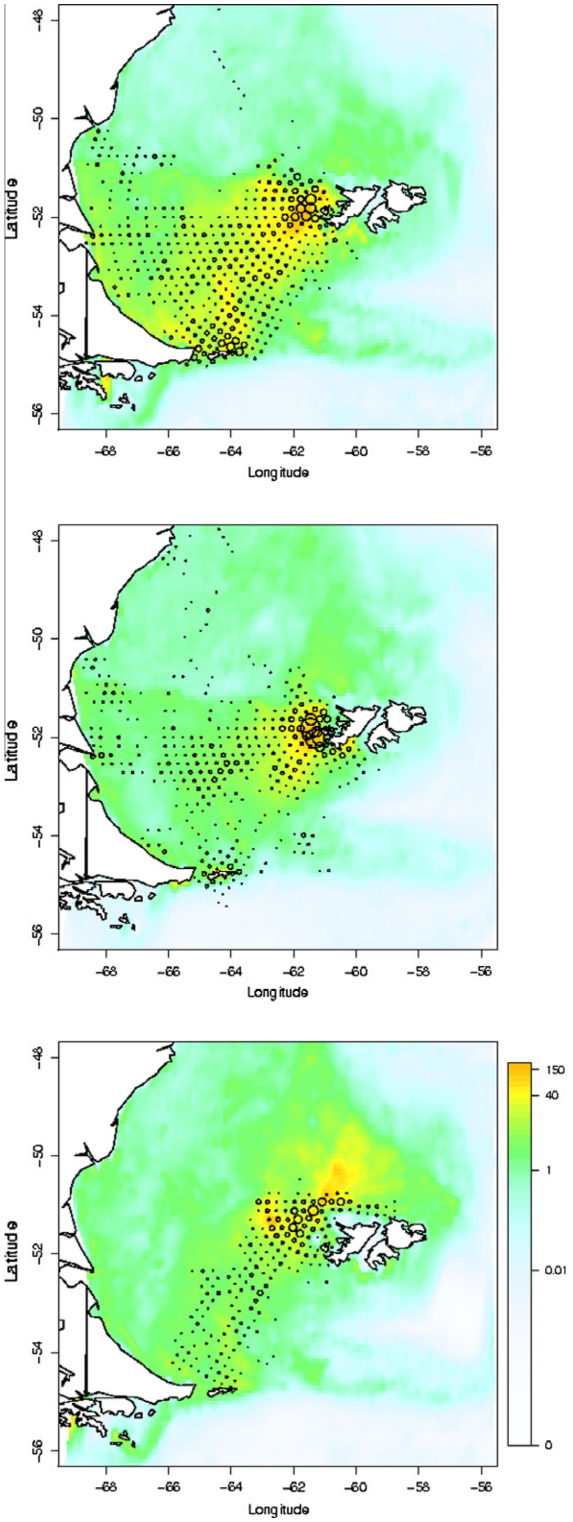

Fig. 3. Predicted number of landings (color log-scale) and observed values (black circles – circle area proportional to total number) for: (a) New Island 2009/2010; (b) New Island 2008/2009; (c) Steeple Jason 2009/2010. Predictions utilize a model whose coefficients were estimated from New Island 2009/2010 data only.

Table 2
Akaike Information Criterion for complete models predicting albatross at-sea distribution for each year, and submodels without predictors related to environmental quality (−Q), accessibility (−A), competition (−C) or fishing effort (−vms). The delta values (Δj) represent the position of each AICc relative to those of the null and complete models (see Eq. 2):

	New Island 2008/2009		New Island 2009/2010		Steeple Jason 2009/2010	
	AICc	Δj	AICc	Δj	AICc	Δj
Complete	124195.3	0.000	137067.2	0.000	54701.3	0.000
−Q	124592.0	0.373	137629.8	0.494	54986.0	0.324
−A	124383.1	0.177	137264.9	0.174	55214.5	0.583
−C	124402.2	0.195	137279.1	0.186	54713.2	0.013
−vms	124196.7	0.001	137075.4	0.007	54721.1	0.023
Null	125258.6	1.000	138205.4	1.000	55581.1	1.000

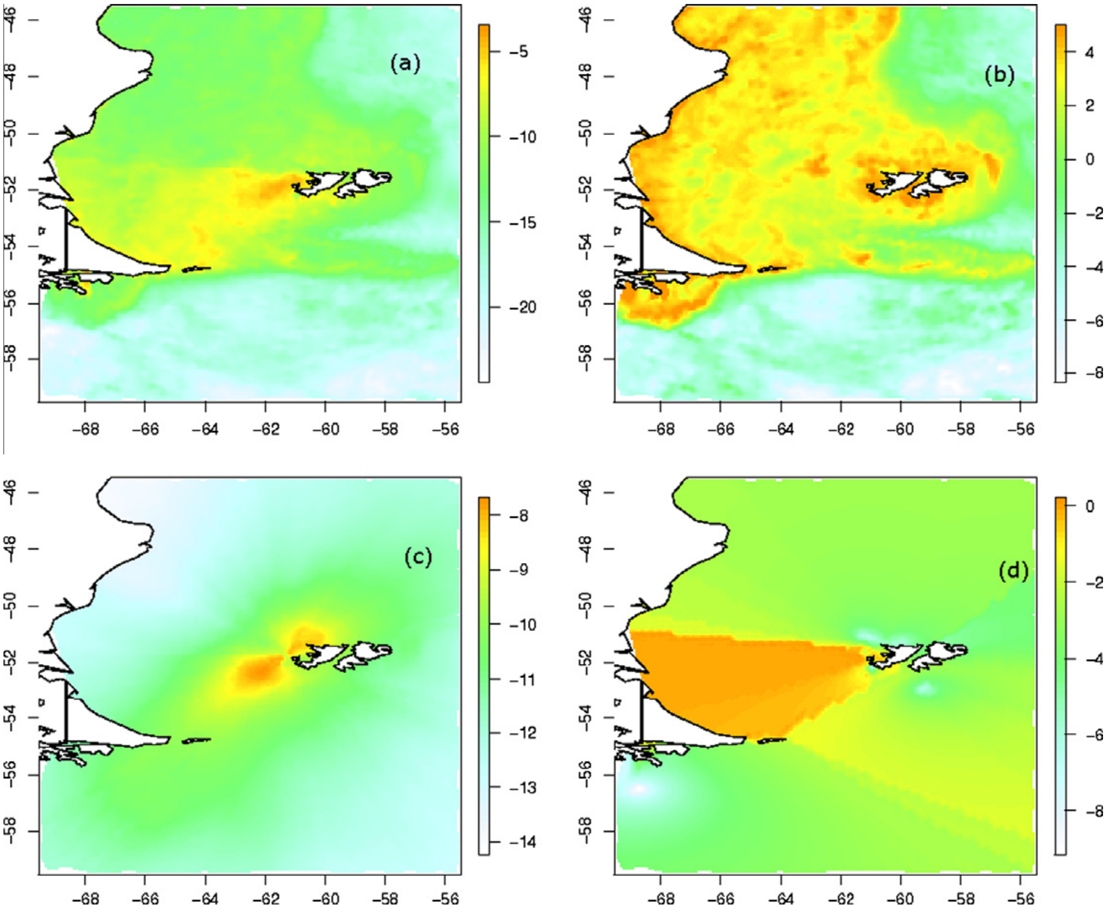

Fig. 4. Results from the model fitted with data from New Island in 2009/2010 data: habitat suitability log-index (a), log – environmental quality factor (b), log – accessibility factor (c), log – competition factor (d).

tant in defining the habitat suitability index, and hence in predicting the distribution of New Island birds (as depicted in Figs. 1 and 3).

With the exception of the zonal wind component, the 2000–2009 environmental climatology is more similar to the environmental conditions in 2008 than in 2009 (Table 3). It is therefore not surprising that, when this climatology is provided to a previously fitted GLM, the resulting posterior predictive mean field of landings (Fig. 5) resembles that of 2008/2009 (MAD = 3.1 landings per cell) more than that of 2009/2010 (MAD = 4.0; see also Fig. 3): habitat use near Staten Island is reduced, and most landings occur within 500 km west of the Falkland Islands.

Table 3
Mean of the absolute differences (MAD) between environmental conditions in December 2008 and 2009 and the 2000–2009 December climatology, for the study region.

	SST	Chl-*a*	u-wind	v-wind
2008 – Climatology	0.39	1.38	4.56	1.60
2009 – Climatology	0.47	3.54	2.45	3.48

4. Discussion

The present investigation incorporated several unusual or even unique features in the analysis of the distribution and habitat selection of pelagic predators under the central-place constraint. First, we used a large number of individuals providing few data each, rather than the more usual pattern of many data from fewer predators. Second, we focused our analyses on places where birds landed (calculated with fine-scale high quality data with minimal error) rather than using the entire route or trying to infer search

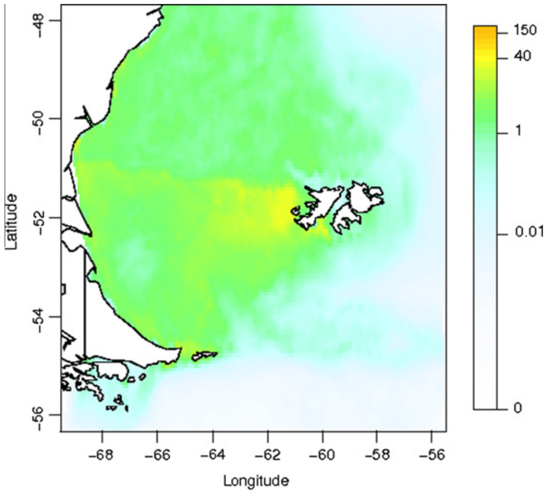

Fig. 5. Expected mean occurrence of landings of birds from New Island in December, when climatological (2000–2010) data are provided as input to the 2009/2010 model of the habitat suitability index.

and feeding areas from first-passage time analyses or other techniques likely to involve more uncertainty. Third, we used a modeling technique that is suitable for overdispersed data, i.e. data whose variability exceeds that predicted by a Poisson model. Fourth, we took accessibility and intra-specific competition into account. Fifth, we had high quality data on movements of fishing vessels in the area most used by the study birds. Sixth, by using data from more than 1 year and more than one colony, we were able to stringently test our models. Finally, we were able to assess how inter-annual variation is likely to influence any conclusions concerning the most important areas for the birds of the study colonies during early chick rearing.

4.1. Model strengths and weaknesses

We subjected the Poisson-gamma GLM to a suite of tests, in order to validate results. In all cases, we concluded the model fitted the data correctly and provided valuable insight into novel configurations of the predictors. The use of a Poisson-gamma GLM is a suitable alternative to the Generalized Additive Models (GAMs), also successfully used in these contexts (Aarts et al., 2008; Wakefield et al., 2011). GAMs are more flexible, but they lack a parametric formulation and so they are less useful for application with other datasets. Also, the larger flexibility of GAM can create response–predictor relationships which are potentially difficult to interpret, and are more susceptible to the influence of outliers. The GLM overdispersion parameter, highly relevant in all our models (Fig. 1 of Supplementary material 2, Table 1), enables a flexible relationship between mean and variance (Supplementary material 1). For our specific application, the overdispersion parameter allows the model to cope with residual spatial aggregation patterns, due to factors for which no information could be gathered, such as short-term meso-scale features and mutual attraction by feeding conspecifics. Together with other validation tests, the relative success of the New Island GLM (in 2009/2010) in predicting the distribution of albatrosses in another year and at another colony, as well as the results from the other tests, strongly support the validity and robustness of the modeling approach.

There were some mismatches between predictions and observations, particularly in an area immediately to the north of the Falkland Islands. A certain level of discrepancy is expected, as the available environmental information (depth, SST, chlorophyll) are no more than proxies for the actual cues used by black-browed albatross when foraging; the competition and accessibility components also required simplifications for reasons of parsimony and tractability. Still, we believe that this shortcoming does not compromise the usefulness of the models. It is important to note that the predicted area of usage north of the Falklands is indeed intensively used, at least in some years, by black-browed albatrosses from another colony (Huin, 2002).

We studied the foraging distribution of albatrosses at a particularly sensitive phase of their nesting cycle, the brooding stage. Most *Thalassarche* albatross chick mortality occurs at the end of this stage, and adult birds lose considerable body reserves during this period (Catry et al., 2006). Under presumably severe energetic and time constraints (the need to regularly attend and feed the offspring) accessibility of foraging areas is expected to have a major bearing on their relative use, and hence the general evaluation of habitat suitability (Matthiopoulos, 2003). Models that did not take accessibility into account lost considerable explanatory power, which suggests that both distance to colony and wind patterns are relevant in foraging decisions made by albatrosses and need be taken into consideration when trying to predict their behavior and distribution (see also Wakefield et al., 2009b).

4.2. Competition

The Cairns (1989) hinterland model proposes that foraging zones of adjacent seabird colonies should show virtually no overlap. This model has received considerable support from some studies (Wanless and Harris, 1993; Grémillet et al., 2004; Masello et al., 2010), but several others documented a broad range of overlaps in foraging areas (Ainley et al., 2004; Wakefield et al., 2011). The very fine-scale data presented here clearly indicate a mixed picture, with a large area of overlap in terms of maximum extent, but obvious avoidance by birds from New Island of the main foraging area used by albatrosses from Steeple Jason, and *vice versa*. This last observation justifies the inclusion of a competition factor when modeling habitat suitability (see also Wakefield et al., 2011). In fact, the removal of the competition factor from the models for New Island resulted in a major loss of predictive power (see Table 2). The importance of this factor is likely to be even greater when considering inshore waters around the Falkland Islands. Note for example that New Island birds only use a narrow sector of coastal waters, despite their apparently high environmental quality (Fig. 4b). Such areas are in fact used by foraging birds from neighboring colonies (Fig. 1 and Huin, 2002), and given that they are well within the foraging ranges of New Island albatrosses, it seems highly likely that they are not used simply as a result of intra-specific competition.

Theoretical models and empirical observations suggest that colonial birds from large colonies should, on average, travel further to find adequate feeding grounds (Furness and Birkhead, 1984; Lewis et al., 2001). However, there are several data sets apparently disproving this hypothesis (Ainley et al., 2004; Wakefield et al., 2011). Moreover, even though ca. 15 times as many black-browed albatrosses breed at Steeple Jason than at New Island, there was no indication that the former had a larger foraging domain (Fig. 1, see also Granadeiro et al., 2011), and hence there seems to be no strong reason to include the size of the colony of origin as a single predictor variable in habitat suitability models.

4.3. Habitat preferences

Black-browed albatrosses have long been known to show a strong, but not obligatory, association with shelf and shelf-break waters, although the underlying preference is likely to be modulated by other factors (Weimerskirch et al., 1988; Waugh et al., 1999; Huin, 2002; Wakefield et al., 2011). The present study provides an unusually fine picture of such a relationship and suggests, in the study domain, a selection of very shallow waters (around ca. 50 m, see Fig. 2) as well as an association with areas of steeper seafloor slope (Fig. 2). The distribution pattern of the study birds around Staten Island is interesting from this perspective. Despite the close proximity of different bathymetric habitats, tracked birds clearly concentrated in neritic waters and made little use of the immediately adjacent steep shelf break (Fig. 1). This is despite the disproportionate use of areas with a greater bathymetry gradient (see also Wakefield et al., 2011), and indicates that black-browed albatrosses prefer areas with steep seafloor even when foraging exclusively over the continental shelf. This may happen because in these areas there is a greater hydrodynamic activity, with enhanced productivity and prey concentration (Acha et al., 2004).

The zones intensively used by albatrosses immediately W and SW of West Falkland represent a productive shallow area, where there is enhanced mesoscale activity and eddies are often formed by the northward flow of the west Falkland current (Arkhipkin et al., 2010). This region is also a spring spawning area for pelagic fish including the Fuegian sprat *Sprattus fuegensis* and the southern blue whiting *Micromesistius australis* (Agnew, 2002), which are common prey for black-browed albatrosses (own unpubl. data), and also for demersal fish such as red cod *Salilota australis* (Arkhipkin et al., 2010). It is also an important feeding area for South American fur seals *Arctocephalus australis* (Thompson et al., 2003) and several seabirds, particularly penguins (Falabella et al., 2009; Masello et al., 2010).

Another area of obvious concentration of foraging effort includes the waters surrounding Staten Island, at the eastern tip of Tierra del Fuego (Fig. 1). In this area there is a highly energetic hydrographic front and important spawning grounds for the Fuegan spratt (Acha et al., 2004). The area around Staten Island, and immediately north of it, is also much used by southern giant petrels *Macronectes giganteus* and black-browed albatrosses from Chile (Falabella et al., 2009). Staten Island harbors very large colonies of penguins (which forage in its vicinity) and its waters are exploited by commercial fisheries (Schiavini et al., 1999), which also underscore the biological importance of the zone.

4.4. Fisheries

Several studies have documented significant overlap, at various scales, between fishing fleets and the foraging ranges of marine predators (Hyrenbach and Dotson, 2003; Phillips et al., 2006), but without suggesting a causal relationship. If the presence of fishing fleets influences the at-sea distribution of predators (particularly those that regularly scavenge behind vessels), efforts to identify areas of special conservation significance might be to a certain extent compromised. If the purpose of documenting areas where predators concentrate is to better regulate fishing activities through management decisions such as temporary closures or changes in discard management (e.g. Pierre et al., 2010), then there is a risk that the distribution of the species to be safeguarded might change as consequence of those very management practices, requiring further reassessment of the entire process.

A fine scale analysis of black-browed albatross and fishing vessel interactions using the present data set suggested that New Island and Steeple Jason birds showed limited reliance on fisheries during early chick rearing (Granadeiro et al., 2011). The present study further illustrates (Fig. 1) there is little geographical overlap between albatrosses and the fishing fleet and, more importantly, suggests that the presence of fishing vessels makes only a marginal contribution to the suitability of habitats used by foraging albatrosses at this time of year (Table 2). These studies and other research (Skov and Durinck, 2001; Peterson et al., 2008) indicate that although seabirds often aggregate in large numbers behind fishing vessels, this should not be automatically taken as implying that their broad at-sea distribution responds to the spatial pattern of fisheries in general.

4.5. Seascape management

Despite the remarkable predictive power of the models, in some areas there was a poor correspondence between expected and observed distributions (Fig. 3). It is beyond the scope of this paper to discuss in detail the many reasons why this could be so, but it is important to consider whether for a specific purpose such as the establishment of economically or operationally sensitive regulations for fisheries or other activities, the level of accuracy in our models is sufficient, particularly in the face of environmental variability and uncertainty. We would argue that despite the uncertainties, such models can already be of great applied value. For example, if we were to use the *observed* distributions of black-browed albatrosses from New Island to inform the management of the Southern Patagonian shelf, the modeling results presented here illustrate that the 2008/2009 data were likely to be typical of the average conditions in the last decade, leading to the conclusion that the importance of the Staten Island area was over-estimated by the 2009/2010 observations, and hence it should not rank as high as other priority sectors in the W–SW of West Falkland.

4.6. Conclusions

The present study suggests that conclusions regarding the marine distribution of central place foragers, such as albatrosses, may be problematic if spatial and temporal variation in their behavior are not taken into account. Results from one colony cannot be directly extrapolated to a neighboring one, and there may be important inter-annual variation. Models of the foraging distribution of albatrosses have a greater predictive power if accessibility and inter-colony competition are taken into account. Our results also show that at least in some situations, fisheries have a relatively weak influence on foraging decisions of albatrosses at large spatial scales, even in species known to scavenge extensively behind fishing vessels. Current predictive models for predators can provide important insights for the identification of resource hotspots and guide decision-makers, despite the incomplete nature of the information available.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2013.01.005.

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APPENDIX 2. LOW BREEDING SUCCESS AND SHARP POPULATION DECLINE AT THE LARGEST KNOWN FALKLAND SKUA COLONY

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SHORT NOTE

Low breeding success and sharp population decline at the largest known Falkland skua colony

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José Pedro Granadeiro · Rafael Matias

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Abstract The Falkland skua *Stercorarius antarctica antarctica* is a poorly known seabird. Demographic studies at the largest known colony of this taxon revealed a sharp population decline (47%) in just 5 years, between 2004 and 2009. The decline seems to be linked with a chronic low breeding success in the recent years and is consistent with a situation of virtually zero recruitment. The ultimate causes of the decline are, as of yet, unknown, but plausible explanations are examined and discussed. The reported population trends should be the cause of some concern, and more research and monitoring are desired.

Keywords New Island · Falkland Islands · Brown skua · Striated caracara · Phalcoboenus australis

The Falkland skua *Stercorarius antarctica antarctica*, a taxon nearly endemic to the Falkland Islands, is a little studied seabird, for which there are virtually no published ecological or demographic data (but see Lamey 1995; Woods and Woods 1997; Yorio 2005; Phillips et al. 2007). New Island (51°43′S, 61°18′W), on the west of the Falklands, holds the largest known colony of this subspecies (I. J. Stange, pers.com and own unpublished data), which is probably justified by the existence of a large concentration of skua bird prey, particularly thin-billed prions *Pachyptila belcheri* (Catry et al. 2003). Here, we show that this important colony is in rapid decline and that this is probably linked to a chronically low breeding success in recent years.

Skua breeding territories were censused between 12 and 20 December 2004 (in the incubation period), on the southern half of the island, and between 12 and 28 December 2009 on the whole island (with most of the southern part being visited before 20 December, similarly to 2004). Observers walked slowly covering the whole of the island ground and, using GPS, recorded the position of skua nests or of the centre of occupied territories (Phillips et al. 2004). Nesting sites and territories were easy to locate, due to the high territorial attendance of adult skuas during incubation, to the exceedingly tame nature of the birds (no birds flew away when approached), and to the open low vegetation that covers all nesting areas.

From 2003, we have regularly monitored skua-breeding success on New Island. Each season, a number of preselected territories were regularly visited from the pre-laying stage until the chicks were 40 days old (nearly fledged). Study territories included both pairs nesting close to penguin, cormorant and albatross colonies and pairs on prion colonies. Nest checks did not have any apparent negative effect on skua reproduction, which we would not have expected anyway, given the tame nature of the birds and the fact that no other studies of large skuas have reported such deleterious consequences on the birds.

In December 2004, there were 417 occupied territories in the south part of the island (Fig. 1). In 2009, the number

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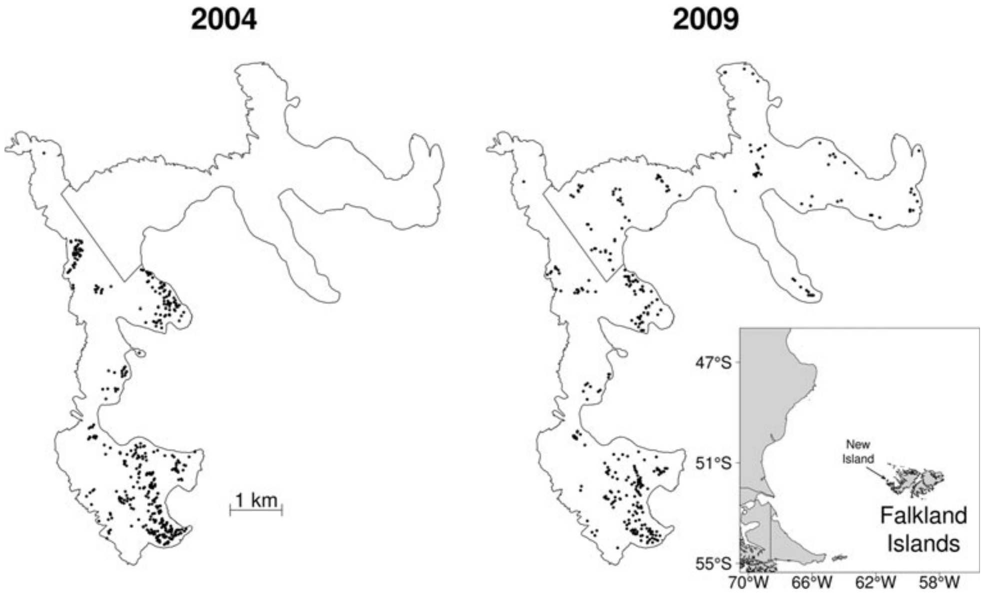

Fig. 1 Distribution of Falkland skua breeding territories on New Island in the breeding seasons of 2004–2005 and 2009–2010

Table 1 Breeding success (number of chicks per nesting pair) of Falkland skuas on New Island in the summer seasons from 2003–2004 to 2009–2010

Year	2003	2004	2005	2006	2007	2008	2009
Breeding success	0.05	0	0.35	0.53	0.80	0.23	0.44
N	42	26	34	17	10	26	43

of territories in the same area was 219. The distribution of the breeding population showed little change, but the density of territories decreased from 40.4 territories per km^2 in 2004 to 21.2 territories per km^2 in 2009. Overall, the number of Falkland Skua territories on New Island South suffered a reduction of 47.5% in the 5 years between the two surveys, which equates to a decline of 12.1% per year. The total number of occupied territories on the whole of New Island in December 2009 was 333 (Fig. 1). During the survey, nests with 1–2 eggs (the normal clutch for skuas) were recorded at 72% of those territories.

The mean nesting success between 2003/04 and 2009/10 was 0.34 ± 0.28 chicks per laying pair ($N = 7$ years; Table 1). This is a low value for Brown skuas *Stercorarius antarctica*, a species (which includes the Falkland skua subspecies) that, throughout its range, usually enjoys a high breeding success, often approaching or exceeding 1 chick per pair (e.g., Furness 1987, 1996; Mougeot et al. 1998; Phillips et al. 2004). Large skuas, and *S. antarctica* in particular, rarely start nesting before they are 6 years old (Furness 1987, 1996), which means that the recent population decline is unlikely to directly result from the low nesting success recorded in the recent years. It is plausible, however, that nesting success was also low during several years previous to 2003.

Usually, immature skuas gather at specific sites (called clubs) on the nesting islands, in the years before they start breeding (Klomp and Furness 1992). In large colonies, such clubs are often attended by hundreds of birds (Klomp and Furness 1992; Phillips et al. 2004). It is, therefore, most telling that we have never been able to locate any club site at New Island. Most sites where a few skuas gathered (all near bathing sites) had such small numbers of individuals that we were uncertain as to whether they were true clubs or simply places where off-duty breeders congregated after bathing. This paucity of pre-breeders may be the result of a very poor past breeding success. Although not strictly comparable, figures presented for nesting skuas on New Island in 1988 and 1990 (Lamey 1995) suggest that breeding success was within normal values for the species at that time. Therefore, low breeding success may only have started later in the 1990s.

Large skuas usually have a high annual adult survival rate, not below 0.89 (reviewed in Ratcliffe et al. 2002). Hence, a population decline of 12.1% per year is rather close to what we would have expected in a scenario of zero recruitment. It is possible that, besides the low breeding success, the decline in numbers also resulted from an increased adult mortality, or perhaps from high levels of breeding deferral (Catry et al. 1998). Of 56 New Island breeding birds marked with numbered darvic rings in 2008–2009, 91% returned the following nesting season, which suggest that adult survival may not be unduly low, but more data are needed to confirm this. Emigration is unlikely, as adult skuas are highly faithful to nesting colonies (Furness 1996). The lower number of territories recorded in December 2009 was not the result of an unusually high level of breeding deferral in that particular year, given that of the 51 adult birds recorded alive, only 11 (22%) apparently did not attempt to nest.

The consistently low breeding success and rapid population decline of skuas on New Island has not been paralleled by other seabird populations at the same site (own unpublished data). The main skua prey species on New Island (the thin-billed prion), for example, enjoyed a high breeding success between 1998 and 2006 (Catry et al. 2007), but there are no available data on its adult survival rates or population trends. A decline of unidentified food sources at sea seems an unlikely explanation for the patterns reported here. Skuas at New Island feed mostly on other birds and their eggs, and do not seem to fish much for themselves, which is confirmed by direct observations, pellet analyses and by GPS-tracking of breeders (own unpublished data). New Island hosts a population of feral cats, which could potentially prey on skuas, but cats have coexisted with skuas and other seabirds for over a century without noticeable impact at the population level and there are no confirmed instances of cat predation upon skuas (Matias and Catry 2008).

Interestingly, during the past two decades, another prion predator, the striated caracara *Phalcoboenus australis* has known a rapid population growth (15% per annum) and, at least in the recent years, a high breeding success, with ca 2.5 fledglings per successful nest (Catry et al. 2008). The New Island caracara population was estimated at ca 306 individuals at the beginning of the 2006–2007 nesting season (Catry et al. 2008). The caracaras feed mostly on other birds, are known to be able to take skua eggs and chicks, and often monopolize carrion or steal prey from skuas, which do not seem to be able to present resistance to such kleptoparasitism (own obs.). Could the skua decline largely result from the population increase of its main competitor and predator? We believe this hypothesis to be plausible, but more research is needed and this and other factors must be examined in more detail. Meanwhile, the magnitude of the reported decline at the most important colony of this restricted-range skua subspecies should be the cause of some concern.

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APPENDIX 3. ADOPTION OF A SOUTHERN ROCKHOPPER PENGUIN (*EUDYPTES CHRYSOCOME*) BY A BLACK-BROWED ALBATROSS (*THALASSARCHE MELANOPHRIS*)

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ADOPTION OF A SOUTHERN ROCKHOPPER PENGUIN (*EUDYPTES CHRYSOCOME*) CHICK BY A BLACK-BROWED ALBATROSS (*THALASSARCHE MELANOPHRIS*)

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Un pichón de Pingüino Penacho Amarillo (*Eudyptes chrysocome*) adoptado por un Albatros de Ceja Negra (*Thalassarche melanophris*).

Key words: Southern Rockhopper Penguin, Black-browed Albatross, adoption, parasitism, Falkland Islands.

INTRODUCTION

Although described in many species (Riedman 1982), adoption or kidnapping of offspring by birds is not a common phenomenon in altricial or semi-altricial species. However, its occurrence is more likely in colonially ground-nesting seabirds because of close proximity of neighbouring pairs and high mobility of the chicks (Graves & Whiten 1980, Pierroti & Murphy 1987).

All penguin chicks are semi-altricial. Although entirely dependent on their parents for thermoregulatory control and food, they possess downy feathers at hatch and have some locomotor ability (Williams 1995). Failed breeders of Emperor Penguin (*Aptenodytes forsteri*) are well known for their attempts to kidnap juveniles from other pairs (Jouventin *et al.* 1995, Angelier *et al.* 2006), while Little Penguins (*Eudyptula minor*) are able to perform true adoption of foreign chicks (Wienecke 1995). Southern Rockhopper Penguin (*Eudyptes chrysocome chrysocome*) chicks often try to beg towards adults other than their parents (Warham 1975), especially during the crèche period when both parents are absent from the colony during most of the day (pers. observ.). This behaviour is generally unsuccessful, parents being able to recognize calls of their own chicks before the end of the guard stage

(Warham 1975, Marchant & Higgins 1990, Williams 1995).

Quite differently from penguins, in most albatross species the single chick remains in the nest until it fledges, precluding adoptions to occur. However, cross-fostering experiments between Black-browed Albatross (*Thalassarche melanophris*) and Grey-headed Albatross (*Thalassarche chrysostoma*) have shown that breeders can accept a chick from a different species and rear it until fledging (Prince & Ricketts 1981).

In altricial or semi-precocial species, the only cases of an adult feeding a chick of a different species are usually considered as parasitism (cf. del Hoyo *et al.* 2005). In this paper, we report the temporary feeding of a Southern Rockhopper Penguin chick by a pair of breeding Black-browed Albatrosses.

OBSERVATIONS

The Settlement Rookery on New Island (51°43'S, 61°17'W), Falkland Islands, was visited daily during the Austral summer 2008–2009 to monitor breeding Black-browed Albatrosses and Southern Rockhopper Penguins. The monitored albatross nest 152 was occupied by two color-ringed adults, both marked in October 2008 (Paulo Catry pers. com.). The albatross chick hatched on 24 December 2008, at the end of the hatching period (9–26 December). On 27 December, a Southern Rockhopper Penguin chick of an unknown nest was observed inside the nest 152 together with the albatross chick. It was begging for food towards the male albatross but did not receive any food during our observations. At this date all the Southern Rockhopper Penguin chicks were between 15 and 25 days old (Poisbleau *et al.* 2008) and they had started to gather in crèches. Therefore, this particular chick was c. 20 days old and was in an apparent normal body condition, not especially fat or lean. On 28 December, both adult albatrosses were present at the nest at 09:30 h and soon after the male left and the female started its brooding shift, sitting over both chicks. The penguin chick then immediately started to beg, while the albatross chick did not show any reaction. We clearly observed the albatross feeding the penguin chick on several occasions within the first 30 min after the female's arrival (Fig. 1). On 29 December, only the albatross chick was present in the nest with the adult female. This chick eventually died on 7 January, weighing only 170 g (c. 20% of the normal weight for that age).

DISCUSSION

Although this "adoption" of a penguin chick by an albatross lasted for only two days, it is very interesting in several respects. The species involved are members of two orders (Sphenisciformes and Procellariiformes) and their morphologies are very different, although they are closely genetically related (Hackett *et al.* 2008). Several particular circumstances probably converged to allow the successful feeding of the penguin chick by the albatross. Both species share the same colony with nests heavily intermingled (Strange 1982). Both chicks hatched in December but the penguin chick was older, bigger, and more active than the albatross chick. Parents of both species need the stimulation provided by the pecking of the chick at their bills, and they enclose the chick's bill with their own for food transfer (Warham 1975, 1996). They feed on the same types of prey in the Falkland Islands (Huin 2003).

During the crèche period, Rockhopper Penguin chicks often beg without discernment towards any nearby adult (pers. observ.). Nevertheless, these begging attempts never result in food being given to the chick (Warham 1975). Therefore, while it was not really surprising that a Rockhopper Penguin chick

FIG. 1. A Southern Rockhopper Penguin chick fed by a Black-browed Albatross.

tried to beg towards an albatross, it was totally unexpected that the albatross allowed the penguin chick to enter its nest, to beg for food, and eventually to be fed. Usually, when a penguin is in such close proximity to an occupied albatross nest, the parent will attempt to peck at the penguin, sometimes causing it severe injury (pers. observ.).

Adoption has sometimes been attributed to reproductive errors (Riedman 1982) resulting from failure of parents to recognize their offspring (Pierroti 1991). It has been previously demonstrated that Black-browed Albatrosses either do not recognize their own chicks or ignore their identity when feeding the occupants of their nests (Tickell & Pinder 1972). In the event we report, the error is quite obvious. This pair of albatrosses was breeding in this colony for the first time (Paulo Catry pers. com.), and their lack of experience is also supported by the late hatching date. It seems that these inexperienced albatrosses were not able to recognize the penguin chick as foreign when it occupied their nest despite the strong differences in appearance between both chicks (color, size, calls, etc.). They hence responded to the chick's begging with a standardized feeding behavior. This event was also probably made easier because of the early age and the poor body condition of the albatross chick.

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