THE FORAGING ECOLOGY OF THE SHORT-TAILED SHEARWATER PUFFINUS TENUIROSTRIS

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ABSTRACT

The short-tailed shearwater *Puffinus tenuirostris* is one of the world's most abundant seabirds, with a population of around 23 million breeding birds. Despite this abundance we have a limited understanding of their role in the marine ecosystem. This is largely due to the many uncertainties surrounding the trophic interactions, resource requirements and foraging ecology of this wide ranging pelagic seabird. I studied the movement of adults during the short trip (ST) and long trip (LT) component of their dual foraging strategy to determine how they use their marine habitat. ST were primarily confined to neritic (continental shelf) waters 30 to100 km from their colony, and maximum depth gauges revealed that birds reached a depth of 21 ± 13 m (SD). Analysis of the time spent in area by 39 individuals performing ST revealed that 18 birds employed area restricted searches within circles of a diameter of 14 ± 3 km (SE). Prey returns from area restricted search flights were predominated by bony fish, whereas prey diversity increased for non-area restricted search flights, with more krill and cephalopods. Thus, direct flights were performed when birds were exploiting prey patches dominated by fish, in contrast to the more varied diet returned when birds covered greater distances. LT flights were highly variable ranging from 11 - 32 days duration, and reaching 912 – 6,952 km from the colony. Foraging trips of extended duration enabled birds to exploit temperate waters further away from the colony, as well as sub Antarctic and Antarctic waters. A wider range of search patterns were performed on LT, as birds either: (1) showed no signs of area restricted search; (2) concentrated area restricted search directly at small scales of within circles of 33 ± 11 km (SE) diameter; or, (3) adopted a hierarchical mode of foraging, where large scales of area restricted search are first performed, followed by nested searches at smaller scales. This variation in foraging behaviour indicates that a range of foraging tactics are employed by the short-tailed shearwater. LT to sub Antarctic and Antarctic waters commonly involved a period of commuting travel to regions with elevated chlorophyll *a* associated with ocean fronts, where search effort was increased.

How adults allocated time and energy during the entire chick-rearing period was investigated via the simultaneous assessment of adult attendance, adult mass change, the rate of energy delivery to chicks, and chick survival. Adults who reared chicks to good condition spent 80 % of the 90 day chick rearing period performing five - six LT of 13 ± 3 days (SE) duration. The remaining 20 % of time involved 14 ± 3 ST (SE) of one to three days duration. Comparison with chicks of moderate and poor condition revealed that, despite extensive variation in the day to day rate of provisioning, a small change in the proportion of time spent performing ST and LT over the entire chick rearing period can spell the difference between breeding success and failure. By allocating all of the food collected on ST to chicks birds depleted stored energy reserves, which were replenished on LT. Of the total energy required by chicks from hatching to adult abandonment 75 % was delivered from LT in the form of energy rich stomach oil, with the remainder being supplied in ST meals of raw prey. The advantages of the dual foraging strategy to both adult and chick was demonstrated by considering the daily food requirements of chicks and the likely energy flow from alternate feeding regimes. Under regimes of all ST or all LT, energy flow to chicks could not meet chick energy requirements. This highlights that LT of more than seven days duration are required to accumulate stomach oil. Oil boosts the energy value of meals beyond that achievable in continuous ST foraging. Under continuous ST the estimated rate of food consumption achieved by adults would not sustain both adult and chick requirements. Therefore the dual strategy enables short-tailed shearwaters to overcome many of the constraints of central-place foraging.

Comparisons between years and short-tailed shearwater colonies revealed extensive variation in the dietary composition of meals returned to chicks, as well as the rate of food delivery. A year of increased ST foraging resulted in an increase in feeding frequency, but not provisioning rate, as smaller meals were returned. In this same year ST meals also contained a high % mass of low energy neritic prey (Australian krill *Nyctiphanes australis* and cephalopods). These factors reduced the rate of energy flow to chicks compared to other years where fewer ST meals of increased mass contained mostly higher energy fish (jack mackerel *Trachurus declivis* and anchovy *Engraulis australis*). While the rate of chick growth at different ages varied between years, a similar peak mass was gained in all three years. These findings demonstrate considerable flexibility in the dual foraging strategy of the short-tailed shearwater, providing evidence that adults are able to maintain a suitable rate of energy flow to chicks in years of varied neritic foraging conditions. This is achieved by modifying the time spent performing ST, and the volume of oil returned from LT, likely in response to changing prey availability.

A review of the use of seabirds in fisheries management identified the most commonly used indicators (species and parameters) in environmental, ecological and fisheries management. For the short-tailed shearwater the most useful parameters for identifying the size of pelagic fish stocks in neritic waters include the size and dietary composition of meals returned on ST. The varied importance of pilchard *Sardinops sagax* and anchovy *Engraulis australis* in the diet between years suggest that their occurrence in the diet meals present a potential indicator of the availability of pre-recruits into the South Australian pilchard fishery. The occurrence of Australian Krill in ST meals may also provide a means of investigating the ecological role of upwelling events in neritic waters. The usefulness of provisioning parameters as indicators of prey availability are likely to be limited in this species, due to the extent of flexibility and plasticity in the short-tailed shearwaters provisioning strategy.

Documenting the extent of flexibility in the foraging strategy, and quantifying the value of the ST and LT component of the dual foraging strategy has provided an insight into the habitat utilisation and prey requirements of this species. This demonstrates that despite the various constraints incurred in sourcing and transporting prey over long distances, dual foraging presents the most optimal foraging strategy for the delivery of energy to adult and chick. The sheer abundance of this species is evidence that the separation of their foraging and breeding grounds over 3000 km is a beneficial strategy. An opportunistic diet, and flexibility in foraging suggests that the short-tailed shearwater is more resilient to changes in prey availability than other seabirds in their community. However, we have highlighted that breeding success is sensitive to small changes in the time spent foraging in near and distant waters. Sourcing prey over large spatial scales also exposes birds to feeding conditions over a broader area, increasing their exposure to the potential effects of current and future climate change. For these reasons the short-tailed shearwater presents a valuable indicator species for short and long-term monitoring programs of both neritic and oceanic ecosystems.

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CHAPTER 1
INTRODUCTION

As food is heterogeneously distributed across most landscapes, and its availability fluctuates in space and time, animals must constantly respond to their surroundings so they can locate areas of suitable food supply. This is because an animal's fitness is largely determined by its ability to locate food. So instead of randomly sampling the environment, a forager should modify their behaviour in a manner that maximises net energy gain (Stephens and Krebs 1986). This is a key assumption of optimal foraging theory, and can be achieved by increasing the time spent in areas of elevated food density (Stearns 1992), and/or selecting food items that maximize the rate of energy intake (Stephens and Krebs 1986). Studies of foraging ecology provide a means of investigating how this is achieved.

During breeding, many animals must source an increased quantity of food to meet the added energy demands of their offspring. Central place foragers are further constrained, because they must regularly return to a central place to provision offspring. The need to maintain a suitable rate of energy delivery to offspring limits the time that can be spent locating food, and the distance that can be travelled. The resultant feeding strategy involves alternating the allocation of food between periods of self-feeding and provisioning (feeding offspring) (Houston 1987). Foraging behaviour varies widely among species, and is influenced by their physiological, behavioural and life-history constraints. Foraging behaviour also varies among individuals within a species based on the past experience and quality of a parent, and between populations due to the distribution and availability of prey. Examining the foraging capabilities, dietary preferences, and time/energy budget of an animal provides an indication of how they exploit their environment, and how they allocate energy and time to maximise their fitness.

The study of foraging strategies is most interesting in birds due to the extent of adaptive radiation that has occurred in this group of animals. Birds inhabit almost every environment on earth, and exhibit a diverse range of anatomical, physiological and behavioural attributes that enable them to exploit these environments in different ways. This is evident in the wide range of foraging strategies that are employed by the members of a bird community. For example, seabirds vary widely in the spatial scale that they travel. Some species forage within close proximity of their colony, and deliver prey multiple times per day. While other species feed their chicks irregularly, and are capable of exploiting waters thousands of kilometres away. This is largely due to their varying abilities to transport food, and to store and utilise energy reserves (i.e. fat and protein) (e.g. Lill and Baldwin 1983, Frank and Becker 1992). Species that can carry single (single prey loaders) and multiple prey items (multiple prey loaders) in their bills can only deliver small meals to offspring. This means that they must return to feed their offspring multiple times per day, limiting their foraging range. During each foraging trip they generally self feed on smaller prey items, and then gather single or multiple larger prey items to return to their offspring (e.g. roseate terns *Sterna dougallii* Ramos *et al.* 1998). Multiple prey loaders may also undertake a number of short foraging trips to feed their young, then perform an extended foraging trip of a few hours for self-allocation. Prey-choice by these foragers is critical in order to maximise the energy gain and delivery to their offspring (Ydenberg *et al.* 1992).

Compared to single and multiple prey loaders, seabirds that regurgitate their stomach contents to feed their chicks are able to deliver larger, more concentrated meals of increased energy value. This reduces the rate that adults need to return to their chicks, enabling them to potentially exploit more distant foraging areas. The periods of allocation can also be extended, as birds may self-feed during the first part of a foraging trip, then gather prey for provisioning (e.g. rhinoceros auklets *Cerorhinca monocerata* Davoren and Burger 1999). Compared to single and multiple prey loaders, prey-choice may not be as important a factor in species that feed offspring by regurgitation (Ydenberg *et al.* 1992). In addition to regurgitating their prey, many Procellariiforms (albatrosses, shearwaters and petrels) partially digest the meal, and delaying gastric emptying to accumulate stomach oil. The production of oil enables adults to deliver a meal that is 5-10 times the energy value of raw prey (Obst and Nagy 1993). Meals can therefore be delivered less regularly. This enables adults to further increase the duration and distance of their foraging trips, which increases the habitats they can potentially exploit (Chaurand

and Weimerskirch 1994). Procellariiforms alternate between long duration trips (LT) and short duration trips (ST), in what has been termed a dual foraging strategy. The term dual strategy suggests that seabirds have two alternative strategies, but in reality they have two foraging tactics (short or long), which enable them to exploit two foraging regions (close neritic waters, or distant waters). The ability to employ LT, and thereby alternate foraging trips of different duration, provides a selective advantage over the performance of ST alone, as seabirds are able to escape the variable productivity that is common to many neritic environments.

The delivery of stomach oil is one of a number of factors that are central to the Procellariiforms dual foraging strategy. The energy storage capabilities of adults and chicks are also important. For example, the chick's ability to rapidly accumulate lipids, and their protracted growth period (Drent and Dann 1980, Ricklefs and Schew 1994) enables adults to feed them more irregularly than other seabirds. Also, adults build their energy reserves during LT so they can fuel the majority of their energy needs during ST foraging. This enables them to deliver all of the prey they collect on ST to their chicks, maximising energy flow (Chaurand and Weimerskirch 1994).

Increasing the distances travelled in search of food modifies the scale at which an animal interacts with its environment. This is an important element in the study of foraging ecology, because, in addition to being heterogeneously distributed food is also arranged in a hierarchical patch structure in most habitats. This means that high-density small-scale patches are nested within low-density large-scale patches (summarised by Fauchald *et al.* 2000). Where prey availability varies in this way, optimal foragers should respond by tracking food towards the small-scale end of the spectrum, so they search more thoroughly in an area of elevated food density (Kotliar and Weins 1990). This is based on the general assumption of optimal foraging theory, whereby animals should strive to elevate foraging efficiency by concentrating their search effort in areas of high food density (Stearns 1992). Increased search effort in accordance with the distribution of food has been identified in a wide range of animals from insects (e.g. Crist *et al.* 1992), to herbivorous mammals (e.g. Rettie and Meisser 2000), and predatory birds (e.g. Fritz et al. 2003), and enables the forager to concentrate their search in an area of interest (Fauchald and Tveraa 2003). Numerous studies have identified that the foraging behaviour employed by seabirds reflects the spatial structure of prey distribution and density (e.g. Fritz *et al.* 2003, Weimerskirch *et al.* 2007). Studies that track seabirds at sea provide a means of identifying habitat use, and how environmental stimuli are translated into search effort (e.g. Fauchald *et al.* 2000).

Studying the foraging ecology of marine predators by tracking their movement at sea, or assessing their diet and use of time and energy, provides an opportunity to increase our understanding of the marine environment. This is because seabirds forage exclusively at sea. Therefore, seabirds are dependent upon oceanographic conditions throughout their entire lives. As a consequence aspects of their foraging ecology often reflect seasonal and inter-annual changes in the productivity of the oceans, and are responsive to trophodynamic change (e.g. Furness and Nettleship 1990). Seabird foraging ecology can also be informative of changes in prey availability and their distribution and structure over a range of spatial and temporal scales (Diamond and Devlin 2003, Piatt *et al.* 2007). Monitoring seabird populations may provide information on changes in marine ecosystems that may be difficult to assess using conventional oceanographic methods (reviewed by Furness 1982). Like many other marine predators they can also locate prey efficiently, sample multiple trophic levels, and often feed on commercially and biologically important prey (e.g. Baillie and Jones 2003). Unlike pinnipeds, cetaceans and fish, seabirds can cover large areas rapidly, and also return to their breeding colony regularly. This means that they respond to their environment on a day-to-day basis, so can reflect the current state of feeding conditions, and respond rapidly to changes in prey availability and distribution. For these reasons seabirds and other marine predators are being increasingly incorporated into management practices in many marine systems (e.g. Kabuta and Laane 2003).

As almost 50% of world fish stocks are considered fully fished, and nearly 30% over fished (Pauly *et al.* 2002) alternate methods of fisheries and management are required. Given the additional pressures of global climate change more emphasis is being placed on an ecosystem based approach to marine and fisheries management. This approach involves identifying a suite of ecological-based indicators that serve as reference points to monitor ecosystem change. Top predators such as seabirds are proving to be integral in this process (Kabuta and Laane 2003). Despite the many advantages that seabirds present to monitor the marine environment there is much uncertainty surrounding their potential role as indicator species (Piatt *et al.* 2007). This is largely because each species responds differently to fluctuations in prey availability depending upon their physiological and behavioural constraints and limitations on aspects of their ecology, physiology, and life history. Understanding the importance that these constraints and limitations have on a species capacity to respond to changes in their marine environment is important for assessing their suitability as an indicator species. The role of a species as an indictor also requires information on their habitat utilisation, how they allocate food, their prey preferences, and the functional relationship between each seabird parameter and prey availability, as well as prey abundance.

The application of such an approach in the marine ecosystem of South Australia is currently being investigated. This region supports a diverse range of endemic and valuable species and communities, and provides critical habitat for a wide range of migratory and resident marine species. Productivity in this marine environment is evident as ~70 % of Australia's fisheries operations are located here, as well as the largest single species fishery in the country. The pilchard *Sardinops sagax* fishery has undergone rapid growth in South Australia since it commenced in 1991 (Ward *et al.* 2001). Due to its size, and the capacity for further expansion (Ward *et al.* 2001) fisheries managers initiated an ecosystem based management program in 2004 to supplement more traditional survey methods. One of the major aims of this initiative was to identify a suite of ecological performance indicators that could be incorporated into a multi-disciplinary management program.

Of the land breeding marine predators in Southern Australia the short-tailed shearwater *Puffinus tenuirostris* are the most abundant species (Copley 1993), with an estimated two million breeding birds (Robinson *et al.* 1996). Of the estimated 23 million breeding short-tailed shearwaters the majority live in Tasmania and Victoria, while around 9 % breed in South Australia (Skira 1991). This species migrates to the Northern Pacific Ocean during their non-breeding season to exploit the Northern Hemisphere summer, and returns to southern Australia in October to begin breeding. In this region they inhabit over 130 islands, where they dig underground burrows and rear a single chick. The foraging ecology of the short-tailed shearwater has been the topic of a number of colony-based studies (Hamer *et al.* 1997, Schultz and Klomp 2000, Weimerskirch and Cherel 1998). This work has revealed that, like the closely related sooty shearwater *Puffinus puffinus,* the short-tailed shearwater performs a relatively extreme version of the dual foraging strategy. Their absences from the colony during long foraging trips are among the longest performed by any Procellariiform, being exceeded only by a few of the much larger bodied albatross species (Baduini and Hyrenbach 2003). Despite past research, little is known about why this medium sized seabird performs such a strategy? Where and how breeding adults exploit their marine environment? and, How they are able to adequately provision their chicks given the extent of their absences from the colony? These knowledge gaps form the key topics of this thesis, and underlie the broad aims of: (i) identifying which traits facilitate the short-tailed shearwaters relatively extreme dual-foraging strategy; and, (ii) Assessing the application of this species as a bio-indicator of changes in prey availability in the marine environment.

More specifically, this thesis aims to:

- Conduct a literature review to identify the ecological parameters that are likely to be the most useful in using the short-tailed shearwater as an indicator of prey availability, and outline the key physiological, behavioural and life-history traits that must be considered when using seabirds as indicators;
- Assess habitat use and search effort of breeding short-tailed shearwaters, to provide the first direct indication of their use of neritic (continental shelf) and oceanic waters;
- Investigate the extent of inter-colony and inter-annual variation in foraging parameters and diet to identify the degree of flexibility in the dual foraging strategy;
- Quantify the costs and benefits of the short-tailed shearwaters dual foraging strategy to identify the fitness consequences of alternative feeding regimes to the adult and chick (growth, condition and survival); and,
- Identify the degree of sexual size dimorphism that exists in this species, to provide a sexing tool that can be easily applied in the field.

In **Chapter 2** I address the first aim, by providing a review of the use of seabirds as indicators in fisheries and marine management, to identify the most useful foraging, breeding and population parameters. I also outline the value of monitoring multiple seabird species in a single marine system, when they have varied ecological attributes and life-history traits. The use of different species and parameters are assessed by providing examples of their application as environmental, ecological and fisheries-based indicators of changes in prey availability. Integration of such information is warranted as ecosystem based management programs are at a very early stage in their development, and the value of seabirds and other top predators as ecological performance indicators is still being realised in many marine systems (Hamer *et al.* 1991).

In **Chapter 3** I aim to determine the importance of neritic and oceanic waters to adults during chick-rearing using satellite telemetry. The study of animal movements provides a means of identifying areas of increased search effort, and the occurrence and extent of any hierarchical foraging behaviour (Fauchald and Tveraa 2003). Hierarchical foraging involves an initial increase in search effort at a large scale, followed by intensification on search effort at smaller nested scales. These are important considerations in the study of habitat use by an animal to identify important foraging areas and the scale-specific response of an individual to its landscape. The foraging behaviour of animals also provides an indication of their prior knowledge, or memory, of the distribution of prey, and can be interpreted as an indication of the degree of predictability in prey distribution (Weimerskirch 2007). The relationship between search effort and a range of habitat variables will also be assessed.

Previous dietary studies have revealed that short-tailed shearwaters are generalist predators, who take a wide range of prey from numerous trophic levels (e.g. Skira 1986). Australian krill (*Nyctiphanes australis*) are among the most readily consumed prey type during the breeding season, and dominate the diet in terms of frequency of occurrence and numerical abundance. However, the actual contribution of each prey type to the energy value of a meal has not been assessed. Also, the provisioning strategy employed by adults has been documented in numerous studies (e.g. Hamer *et al.* 1997, Weimerskirch and Cherel 1998), and chick growth has been described (e.g. Saffer *et al.* 2000), but the extent of inter-annual and inter-colony variation in these parameters is unclear. These are the main topics addressed in **Chapter 4**, involving measures of the colony attendance of adults, prey returns to chicks, and their growth at numerous colonies over multiple years. The major aim of this work was to identify the relationships between diet, provisioning and chick growth. This was examined in order to determine the importance of short trip (ST) foraging on chick growth and the reproductive success in the species. Variability was expected because the study colonies are located across the eastern Great Australian Bight region of South-east Australia, where the primary and secondary productivity of neritic waters is highly variable (Ward *et al.* 2006). This variability is due to the influence of a coastal up-welling system that occurs during the Austral summer, the strength and duration of which fluctuates markedly (Ward *et al.* 2006).

The dual foraging strategy that is performed by the short-tailed shearwater exhibits some of the most protracted long trips (LT) of any Procellariiform. This enables adults to spend longer periods foraging at sea. The resultant pattern of time and energy allocation involves extended periods of self-allocation and provisioning, yet reproductive success can be maintained. The sheer abundance of this species is evidence that this strategy provides an efficient means of exploiting the marine environment. In **Chapter 5** I aim to quantify the adaptive significance of this strategy by estimating the costs and benefits of a range of measured and simulated foraging regimes, while considering the behavioural, physiological and life-history traits of this species. The hypothesis tested was that adults could provision their chick to fledging condition by exclusively conducting either ST or LT. This was examined by determining the age-specific growth and energy requirements of chicks, and the average energy delivery rates by parents after LT and ST. While the relationships between provisioning, chick growth and survival have been investigated in a range of Procellariiforms (e.g. Quillfeldt and Peter 2000), only a few studies have quantified the role of ST and LT energy delivery in reproductive success (Obst and Nagy 1993, Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 1997). Relationships between feeding parameters and chick condition and survival are analysed to assess how reproductive success is altered with different feeding strategies, and to assess whether the observed feeding strategy (a mix of ST and LT) maximises reproductive success.

The magnitude of sexual size dimorphism varies among seabird species, and also varies among different morphological features. Shearwaters commonly exhibit a degree of size dimorphism, with males being larger than males (male-biased sexual size dimorphism), but it is often only slight. In these instances sexing individuals requires applying a number of morphological traits to a sex model (e.g. Guicking *et al.* 2004). Male-biased sexual size dimorphism has been identified for the short-tailed shearwater (Bull *et al*. 2005), but its extent, and the skeletal traits which show the greatest degree of dimorphism has not yet been identified. This means that it is currently not possible to sex individuals in the field based on their body size. In **Chapter 6** I developed a sex discriminating function for this species to identify how the sexes differ in their provisioning effort and foraging strategy.

Chapter 7 discusses the findings of this thesis and focuses on three main topics. First, I examine the dual foraging strategy in the context of optimal foraging theory, and examine the importance of behavioural, physiological and life-history traits in shaping the short-tailed shearwater foraging strategy. Second, I discuss whether the short-tailed shearwaters performance of LT of relatively long duration (i.e. a relatively extreme strategy) has contributed to the success of the species. This is achieved by inferring the adaptive significance of this strategy from estimates of the costs and benefits of this pattern of time and energy allocation. Finally, I assess aspects of short-tailed shearwater breeding and feeding ecology as potential ecological performance indicators by combining my findings with existing knowledge. I conclude by suggesting further areas of research to assist in the application of seabirds to future ecosystem and fisheries management.

CHAPTER 2

A REVIEW OF THE USE OF SEABIRDS AS INDICATORS IN FISHERIES AND ENVIRONMENTAL MANAGEMENT

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I wrote the manuscript and acted as corresponding author.

I hereby certify that the statement of contribution is accurate

Signed

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ABSTRACT

This paper reviews the use of seabirds in fisheries management around the world, and provides a comprehensive overview of the many factors that should be considered in order to identify the most appropriate species and parameters. There are a growing number of examples where seabird monitoring programs are providing valuable information on the health of particular fish stocks, the health of the ecosystem, and on the effects of climatic change. Despite this, their suitability and usefulness as ecological performance indicators is still being developed in many marine systems. This is due largely to the many challenges involved in identifying the direct links between changes in prey composition and availability and measurable components of seabird ecology. A species' ability to respond and cope with changing environmental conditions differs due to the combined influence of their time/energy budget, dietary preferences, and specific life-history traits. These factors should be considered in order to identify the most suitable species to monitor, given their level of sensitivity or resilience to a given level of change. The most useful ranges of adult, chick, breeding or population parameters are outlined, and examples are provided of their application to fisheries management as environmental, ecological and fisheries-based indicators. The value of seabird data in investigating the mechanisms underlying the population dynamics of prey species is also discussed, and areas of future research suggested. By integrating information on this topic, this review will assist future studies in identifying the most appropriate species and suite of parameters that are most appropriate to monitor, in order to detect potential environmental and fisheries related impacts. This review also outlines many of the uncertainties that must be considered before they are applied as ecological performance indicators and management tools.

INTRODUCTION

Global fisheries landings have been declining since the late 1980s, and currently almost 50% of world fish stocks are considered fully fished, and nearly 30% over fished (Pauly *et al.* 2002, Garcia and Leiva-Moreno 2003, Myers and Worm 2003). This indicates that many present-day management approaches have not provided the necessary framework for protecting fish populations (Botsford *et al.* 1997, Livingston *et al.* 2005). For example, maximum sustainable yield is commonly used in single-species fisheries management, but its use has often led to stock depletions, due to the uncertainties associated with its measurement (see Garcia and Staples 2000, Pauly *et* *al.* 2002). In addition to the impact on the target species, the removal of top and mid-trophic level fishes by fisheries has flow on effects through marine food webs. Growing concern over the state of the marine environment, and the sustainability of some fisheries, has led to a shift in the focus of fisheries management, from a single-stock approach to management of the ecosystem (Piatt *et al.* 2007a). This style of management is based on an Ecologically Sustainable Development framework, which strives to integrate economic, social and ecological factors in order to ensure the longevity of fisheries, and maintenance of ecosystems. This process involves identifying a suite of indicators for each of these dimensions. Ecological-based indicators serve as reference points to monitor ecosystem status, and include: 1) environmental, quantifying the ecosystem effects associated with fisheries, climate change and environmental variability; 2) ecological, reflecting species composition, size distribution, and the structure and dynamics of the ecosystem (trophodynamics); and, 3) fisheries-based, quantifying the impact of fishing on different components of the ecosystem, and predicting the health status of fish stocks (summarised by Cury and Christensen 2005). There are a growing number of examples where these Ecological Performance Indicators have been integrated into a framework and applied to industry (e.g. Kabuta and Laane 2003). The selection of the most informative suite of physical and biological indicators is a complex and challenging process, due to the complexity and dynamics of marine food webs and trophic interactions (Cairns 1987), and our resultant uncertainty of the interrelationship between the physical and biological components of the environment (Freon *et al.* 2005). Also, selection of the most appropriate ecological indicators involves their evaluation relative to management objectives, and an assessment of the practicality, feasibility and accuracy associated with measuring them (Rice and Rochet 2005).

Top predators such as marine mammals and seabirds are proving to be integral in this management process, because they convey a range of information on the marine environment, and provide many advantages over conventional vessel-based survey methods (reviewed by Furness 1982, Diamond and Devlin 2003). For example, seabirds can cover a large area quickly, locate prey very efficiently, and often feed on commercially important fish (e.g. capelin *Mallotus villosus* Baillie and Jones 2003, lesser sandeel *Ammodytes marinus* Monaghan 1992, northern anchovy Anderson *et al.* 1982, Schaffner 1986, and sardines *Sardinops sagax* Bunce *et al.* 2002), and sample multiple trophic levels. They also return to their breeding colony regularly throughout the breeding season, are easily accessible, and can convey information over a range of spatial and temporal scales. Also, some seabird species sample pelagic prey as they arrive within foraging ranges, thus providing an indication of the succession or movement of forage fish (Velarde *et al.* 1994

Despite these advantages there is much uncertainty surrounding the role of seabirds as indicators of their environment (Frederiksen *et al.* 2007, Piatt *et al.* 2007a). This is largely because each species responds differently to fluctuations in the composition and availability of prey depending upon many aspects of their ecology, physiology, and life history traits. Our ability to accurately infer prey composition and availability from a measured response is also limited by the variability of a species' response to changing prey density, and requires an understanding of the functional relationship between each seabird parameter and food supply. This review provides an overview of the major factors that contribute to shaping the ways in which seabirds respond to changes in the composition and availability of their prey. The usefulness and application of adult, chick, breeding and population parameters are assessed, using examples from both sensitive and robust species. This is followed by an outline of the current application of seabirds in each type of fisheries management, and their likely role in future fisheries and ecosystem management. The major aim is to integrate information on this topic in a way that assists in the identification of indicator species in seabird communities, and to outline the range of limitations and uncertainties that must be considered before they are applied as management tools.

Differentiating between fisheries and environmental change

There are many examples of direct associations between seabirds and perturbations in ocean climate. For example, the large-scale cyclical effect of changes in ocean temperature associated with ENSO years is well known to strongly influence seabird populations around the Pacific Ocean (e.g. Ainley *et al.* 1988, Chavez *et al.* 2003). Various seabird parameters have also been shown to track monthly and annual variation in sea surface temperature (Guinet *et al.* 1998, Abraham and Sydeman 2004). Such environmental variability is an integral aspect of ecosystem processes: however, the added effects of climate change are likely to cause more dramatic changes to the physical state of ecosystems. Climate changes have been shown to cause regime shifts in ecosystem state, by physically forcing 'bottom-up' perturbations that influence producers and flow right through the food chain (Cury and Shannon 2004, Frederiksen *et al.* 2007), whereas a rapid change in the abundance of high trophic level species can force 'top-down' changes (Cury *et al.* 2000, Steele 1998). Differentiating between the influence of environmental and fisheries effects on these top-down changes is one of the major challenges in fisheries management. This is because physical processes and fisheries effects often confound each other, making it hard to accurately identify the effects of anthropogenic pressures, and to measure the effectiveness of management actions. For example, environmental variability and climate-forced changes may act to mask the effects that fisheries have on ecosystem processes: or depleted fish stocks may be more likely to collapse from environmental fluctuations or climate change (Steele 1998, Pauly *et al.* 2002). Monitoring seabird breeding numbers over decadal-scale periods is a valuable means of investigating changes in environmental conditions (Croxall 2006, Montevecchi 2007). These long-term monitoring studies are particularly valuable in unexploited marine systems in order to gauge the extent of natural variation in environmental conditions, and to assess the relationship with seabird breeding success. Where long-term monitoring studies coincide with fisheries closures they also provide a means of assessing the influence of anthropogenic and climatic effects (e.g. Scott *et al.* 2006). However, these applications are rarely feasible.

Ecosystem-based modeling is an alternative method that presents a means of differentiating between the effects of fisheries and climatic changes. This involves designing models that integrate the physical and biological factors associated with oceanographic processes, and inputting data based on current or predictive scales of change. This approach can be used in a diagnostic or predictive manner to quantify the dynamics of food webs (e.g. Yodzis 1998, Gribble 2003). Whilst these models are currently at an early stage of development they are rapidly being applied to marine communities and fisheries with varying but growing levels of success in their ability to advise management (summarised by Boyd *et al.* 2006). Given that future climate changes are likely to have a profound influence on the marine ecosystem, and influence commercially valuable fish stocks, ecosystem models and long term monitoring programs will be an important component of fisheries and environmental management.

Identifying the most appropriate indicator species

Of the many factors that should be considered when selecting the most informative seabird species for use in fisheries management, it is important that a species reflects conditions at the same spatial scale as the fishery operates (Montevecchi and Myers 1995). This is because pelagic seabirds that forage on an ocean-basin scale (1,000-10,000 km) are unlikely to accurately reflect feeding conditions at a local scale (10-100 km). Similarly, those that forage at a local scale, such as coastal seabirds, will not adequately reflect foraging conditions over shelf-slope or oceanic waters (Cairns *et al.* 1987). It is also important to consider the magnitude of change that is occurring in the marine system. Under small changes in food supply monitoring more sensitive species generally provides the most informative information (e.g. Furness and Tasker 2000). Moderate and widespread food shortage has been shown to result in breeding failure in sensitive species, whilst more resistant species may persist with breeding (e.g. Montevecchi 1993, Furness and Tasker 2000). However, under drastic levels of change it is expected that most species will show a similar response across a wide range of parameters (Croxall *et al.* 1988).

Seabird species coexist in marine communities by using their environment in different ways, based on their dietary preferences, foraging capabilities, and time/energy budgets. The degree of flexibility in each of these factors determines how changes in prey availability influence a species' behaviour or performance. Understanding the role of each of these elements is necessary to determine the relative sensitivity or robustness of a species to changes in their food supply, and in order to interpret accurately the ultimate cause(s) behind a measured response. For example, life-history theory suggests that longer-lived species should value their own survival over that of their offspring, meaning that they are likely to reduce reproductive effort under poor feeding conditions before prejudicing their own survival (Stearns 1992, Montevecchi 1993). This is evident in many of the Procellariiforms (albatrosses, shearwaters, petrels), which forgo breeding when their body condition deteriorates (e.g., blue petrels *Halobaena caerulea* Chastel *et al.* 1995). Another confounding life-history trait concerns clutch size, as many long-lived seabirds produce only one egg. This limits their ability to reduce reproductive output, compared to multiple egg-laying species. Longevity does, however, offer a range of advantages. These include the reduced food demand at the nest due to the combined role of slow postnatal development in chicks, and the lipid-storage capacity of chicks. These features mean that long-lived adults are better able to buffer breeding success through brief periods of reduced food availability compared to shorter-lived seabirds (Taylor and Konarzewski 1989, Ricklefs and Schew 1994). Body size is another factor that influences a seabird's ability to respond to reduced prey availability. For example, small body size limits the flexibility in time/energy budget due to the energy demands associated with rearing offspring (Furness and Ainley 1984, Furness and Camphuysen 1997). Smaller-bodied seabirds must feed their chicks more often, and commonly forage at their maximum rate during good foraging conditions, meaning that they are less able to alter their foraging parameters under reduced food availability (e.g., Monaghan 1992, Piatt *et al.* 2007a). In contrast, larger-bodied species often have greater flexibility in their time/energy budgets enabling them to buffer breeding success through periods of reduced prey availability, by reallocating rest time to foraging (e.g., Hamer *et al.* 2001, Piatt *et al.* 2007b). Therefore, changes in food supply are generally better reflected in the chick growth and breeding parameters of smaller-bodied species (e.g., Hamer *et al.* 2006), compared to the foraging parameters of larger-bodied species.

The behavioural and physiological capabilities of a seabird also influence how they respond to perturbations in food supply. Among these, dietary preferences are well known to influence the sensitivity or resilience of a species. Seabird species with a generalist diet, which consume a wide range of prey species, are able to prey-switch when a preferred prey is less available; however specialists, which depend upon a more restricted range of prey species, are less likely to prey-switch (Montevecchi *et al.* 1987, Furness and Nettleship 1991, Furness and Tasker 2000). As such, reductions in prey availability through stock depletion, or low-level fluctuations in oceanic conditions, are often more evident in the foraging behaviour and breeding success of a specialist (e.g. Furness and Ainley 1984, Montevecchi 1993), than in the diet of a generalist. Exceptions occur when a specialist has a degree of flexibility in their time/energy budget, as they can maintain their consumption despite declines in prey stocks (e.g. Barrett and Furness 1990, Bailey *et al.* 1991). Foraging capabilities also influence a species' sensitivity or resilience to changes in prey availability. Generally, surface feeders and shallow divers are more vulnerable to changes in their food supply as they cannot access prey at greater depths (e.g. Monaghan *et al.* 1992, Scott *et al.* 2006). In contrast, pursuit-divers are less constrained by foraging depth, as they can exploit prey through the water column (Daunt *et al.* 2006). As a consequence, surface feeders are considered more sensitive indicators of pelagic prey conditions, and show greater variation in their reproductive success (Montevecchi 1993, Monaghan *et al.* 1996). For example, the surface-feeding Arctic tern *Sterna paradisaea* and black-legged kittiwake *Rissa tridactyla* were more strongly affected by sandeel declines than the mid-water diving common guillemot *Uria aalge* (Enstipp *et al.* 2006). Wide-ranging seabirds are also more capable of overcoming the effects of localised prey depletion, compared to species with restricted ranges, as they are highly mobile and can exploit more distant prey aggregations if necessary (e.g. Weimerskirch 1998, Furness and Tasker 2000).

Identifying the most appropriate parameter

Temporal scale is one of the most important considerations when trying to identify the most informative parameter to indicate the direct or indirect effects of fisheries. Many parameters convey information about feeding conditions on a short-term scale of days to weeks (e.g. clutch size, adult and chick parameters), some reflect conditions over a period of months (e.g. chick growth and breeding parameters), while others reflect conditions over years to decades (e.g. population parameters). This means that short-term parameters are most useful when seeking information on prey assemblages or the age structure of a fish population (Montevecchi 1993), whereas mid to long-term parameters reflect seasonal and annual fluctuations, and are useful for gauging the effects of fisheries on the abundance of target species (Boyd and Murray 2001).

Adult parameters

The composition of a seabirds diet and rate of energy acquisition provides the clearest indication of prey availability on a day-to-day time span, while their body condition often reflects longer-term changes (Montevecchi 1993). Seabird’s with a generalist diet are more likely to reflect the prey assemblage, as they often sample the most abundant prey species from a range of trophic levels (Berruti and Colclough 1987, Martin 1989). In contrast, the relative abundance of different prey species is often poorly reflected in the diet of specialists, as they are more likely to over represent their more favored prey types, even if they are less abundant (Litzow *et al.* 2002, Suryan *et al.* 2002). This highlights the importance of understanding the prey preferences of a species, and suggests that the success of this approach depends, in part, on the absolute abundance of other prey species remaining constant

(Montevecchi and Myers 1995). Another of the limiting factors in the use of seabird's dietary composition is the uncertainty of the functional relationships between prey density and diet. This is due to the various constraints that often operate at each end of the prey-density spectrum, leading to a non-linear response at low and high prey densities (Piatt *et al.* 2007b). The nature of these relationships can be resolved by measuring prey abundance through vessel-based methods (Croxall *et al.* 1999, Piatt *et al.* 2007b). As a consequence, diet studies without additional data that reflect food abundance can be misleading (Montevecchi 1993).

Daily fluctuations in the availability of prey species can also be reflected in the energy acquisition rate of a seabird, which is considered one of the most promising avian indicators of prey availability (Cairns 1992, Montevecchi 1993). Colony-based methods give a rough estimate of daily food intake, by combining the mass of food returned with estimates of the food consumed for adult energy needs (Takahashi *et al.* 2003). More accurate methods involve the deployment activity- and dive-recording devices that provide an indication of the time spent flying, resting, foraging, and on the modes of foraging employed (Wilson and Wilson 1990, Takahashi *et al.* 2004). Prey ingestion can also be measured directly by stomach temperature loggers, which reveal the time of prey captures and prey mass (Wilson *et al.* 1992, Putz and Bost 1994). These activity recorders can be combined with energetic techniques to calculate activity-specific metabolic rates (Birt-Friesen *et al.* 1989, Enstipp *et al.* 2006), and rates of energy acquisition. When a seabird specialises on a commercially important species, these measures can provide a valuable indication of the direct effect of fisheries on fish stocks and on the seabird populations affected. However, when seabirds forage on species not targeted directly by commercial fishers, they may still provide information on the indirect effects of fisheries by reflecting the general state of foraging conditions. Studies of energy acquisition rate also provide insight into how a species responds to changing conditions, also are informative indicators of a seabird's performance (Jodice *et al.* 2006). For example, a study on common guillemots in the northern Atlantic found that parental foraging effort reflected prey abundance through a range of food conditions (poor, intermediate and good) (Cairns 1987).

Adult body condition is often measured in seabird studies, and there are many examples where condition deteriorates in food poor years (e.g. Chastel *et al.* 1995, Weimerskirch 1998). However, the direct relationships are unclear as concurrent measures of prey density and body condition have not as yet revealed any direct correlations (Reid *et al.* 2005, Piatt *et al.* 2007b). The most common measure of condition is an index of mass relative to structural body size (tarsus, bill or head length) (Chastel *et al.* 1995). The size of fat and protein stores is less often used, despite providing a more accurate indication of condition, due to the more complicated and intrusive methods involved (Groscolas *et al.* 1991).

Chick parameters

Provisioning rate is a measure of the amount of food collected (meal mass), and the time taken to collect it (trip duration), and is a valuable indicator of feeding conditions where trip duration is linearly related with prey density (Piatt *et al.* 2007b). The rate of provisioning most commonly declines with reduced prey availability as adults either take longer to locate and catch a suitable meal, or return to the colony with smaller meals (Monaghan 1992). In favourable years prey can be captured at a faster rate which is often reflected by shorter foraging trips and an elevated provisioning rate (Weimerskirch 1998). However, as outlined previously, the usefulness of this parameter relies on an understanding of the degree of flexibility in the time/energy budget of a species, and the foraging effort involved (Enstipp *et al.* 2006).

Chick growth is a valuable parameter as changes in the assemblage of prey species and reduced prey availability often corresponded with reduced growth rates (e.g. horned puffins *Fratercula corniculata* Harding *et al.* 2003). The impact of food shortages on chick growth has been shown to vary among body structures in a number of species (e.g. Harding *et al.* 2003). Thus, it is preferable to take a range of skeletal measurements and calculate an index of body size (Gray *et al.* 2003). There are various methods of assessing chick body condition, involving a comparison of the mass from known age chicks with derived mass from a fitted growth curve (Hamer and Hill 1997). More detailed assessments can be gained by studying the body composition of chicks to derive a lipid index from stored fat reserves (Taylor and Konarzewski 1989). Variation in the nutritional content of favoured prey has also been shown to influence chick growth and condition, with poorer quality prey resulting in reduced mass gain (Ricklefs *et al.* 1987, Golet *et al.* 2000, Diamond and Devlin 2003).

Chick growth is likely to be a better indicator of prey availability among species with inflexible time/energy budgets, and a less sensitive measure in species with a flexible time/energy budget, due to their ability elevate time spent foraging by reducing the time involved in other activities (Hamer *et al.* 1991). Fledgling mass is also an informative parameter as it presents a cumulative measure of the feeding conditions throughout the entire chick-rearing period, and may influence survival and recruitment (e.g. Harris 1984). Like growth, this parameter depends directly upon the availability of food and often varies among years (e.g. Ricklefs *et al.* 1985).

Breeding parameters

Breeding success can also reflect feeding conditions during the entire breeding season, and requires assessing the number of eggs that survive and fledge. There are many examples where seabird breeding success has been shown to decline under reduced prey availability (e.g. Croxall *et al.* 1988, Bost and LeMaho 1993), and in some instances this has also coincided with local fisheries failure (Montevecchi *et al.* 1988). Breeding success is often most sensitive in guillemots and terns due to the constraints associated with their specialist diet (Wanless *et al.* 2005). Reductions in the energy content of prey have also been shown to influence breeding success in some dietary specialists (e.g. Wanless *et al.* 2005). Breeding success of surface-feeding seabirds is also sensitive to changes in prey availability, as has been identified in gulls, kittiwakes and terns (Anderson and Gress 1984, Monaghan *et al.* 1992, Hamer *et al.* 1993, Rindorf *et al.* 2000). For example, the breeding success of Arctic terns in the Shetland Islands has been positively associated with estimates of post-larval sandeel abundance (Monaghan *et al.* 1989a). The application of this parameter as an indicator is limited in species where colony size is known to influence chick survival (Croxall and Rothery 1991), or where other factors such as human disturbance, weather, or predation are occurring (e.g. Hunt *et al.* 1986).

Laying and hatching dates have also been shown to correlate with seasonal fluctuations in food supply during the pre-laying period in a range of seabirds (e.g. Aebischer *et al.* 1990, Velarde *et al.* 1994). However, this parameter has limited application in highly synchronous seabird species. Pre-breeding foraging conditions have also been found to correlate with the number and size of eggs laid, and are considered to reflect variation in female mass or body condition before egg laying (e.g. Amundsen *et al.* 1996). The sensitivity of a species varies widely, as some respond only under marked changes in food supply (e.g. Hamer *et al.* 1991), while in others the number and size of eggs is not related to reduced prey availability (e.g. Monaghan *et al.* 1989b).

Population parameters

Because it is easier to count the number of nests rather than all individuals in a population, breeding numbers are the most common means of estimating population size. Accuracy is high with many ground-nesting species, but decreases with burrow and crevice-nesting species, due to difficulties in locating nests (Montevecchi *et al.* 1987, Furness 1990). The measurement of adult survival involves re-sighting individuals at the nest or colony over a number of years (Jones *et al.* 2003), followed by the use of demographic models based on capture-mark recapture methods (summarised by Breton *et al.* 2006). These methods are most robust and informative when they involve large sample sizes (Croxall and Rothery 1991). Also, identifying relationships between adult survival and changes in food supply requires knowledge of the study population and the magnitude of change, as other factors can confound the results (Bradley *et al.* 1989, Burger 1993, Lyver *et al.* 1999). For example, in a range of species, colony attendance is not considered a true indication of survival as adults abandon breeding attempts (e.g. Croxall and Rothery 1991, Cairns 1992), or move to other colonies when food is scarce (Danchin and Monnat 1992). Like adult survival, recruitment rates are also commonly estimated through demographic models (Danchin and Monnat 1992, Broekhuizen *et al.* 2003). Large sample sizes are again required due to elevated mortality rates in sub-adults (e.g. Becker and Wendeln 1997), and dispersion to other colonies (e.g. Bradley *et al.* 1989, Breton *et al.* 2006). Another important consideration in the use of adult survival and population numbers are the time delays between changes in the environment and changes in these parameters. This is most evident in longer-lived species with low reproductive rates and delayed maturity (MacCall 1984). As such, they indicate fluctuations over a temporal scale of years to decades, and are considered more useful as a means of assessing trends retrospectively (Montevecchi 1993, Furness and Camphuysen 1997). Under dramatic declines in food availability breeding numbers of most seabirds decline (e.g. Aebischer and Wanless 1992, Phillips *et al.* 1996). However, the response varies widely among species under moderate to low changes in food availability (Temple and Wiens 1989). In general, short-lived species which lay multiple clutches are more sensitive, and have been found to track measures of food availability more closely

(Schaffner 1986). In contrast, longer-lived seabirds experience reductions only under prolonged changes in food availability (Anderson and Gress 1984).

The current use of seabirds in fisheries management

The most popular use of seabirds in fisheries management is as an indicator of recruitment strength and the age structure of fish stocks. This is most informative where seabirds feed directly on a commercially exploited species (e.g. Anderson *et al.* 1982, Schaffner 1986, Monaghan *et al.* 1989a, Furness 1990, Montevecchi 1993). For example, a strong relationship was found between the percentage of herring in the diet of Arctic terns in the northwest Atlantic and the catch per unit effort of herring *Clupea harengus* in the local fishery two years later (Amey 1998). Where the age and size distributions of pelagic fish taken by seabirds correspond closely with fisheries, diet also provides practical information on the growth rate, recruitment, distribution and movement of different age classes of fish (e.g. Barrett 1991, Hatch and Sanger 1992, Bertram and Kaiser 1993). There are many other examples where measures of seabird dietary parameters reflect fisheries landings (e.g. Hislop and Harris 1985, Schaffner 1986, Montevecchi *et al.* 1987, Martin 1989). For example, the percentage of pilchard in the diet of cape gannets and commercial catches are significantly correlated over a number of years (Berruti and Colclough 1987, Montevecchi and Berruti 1991). In these instances there is enormous value in identifying seabird parameters that can be used as critical measures and a decision element in management frameworks.

Seabird dietary studies can also be useful in assessing the rate of by-catch in a fishery, by monitoring the diet of species that scavenge on discards. The amount of by-catch varies with fisheries equipment and methods, and has a large influence on the populations of non-target marine species. For example, in the North Sea, the total amount of by-catch was estimated as 22 % of the overall landings (Garthe *et al.* 1996). There are a wide range of examples where seabirds rely heavily on these discards. This is evident in the North Sea where fisheries waste is considered to have contributed to the rapid growth of some seabird populations (Dunnet *et al.* 1991). Where a population readily consumes discards, the foraging and breeding parameters of individuals often reflects changes in their availability (e.g. Oro *et al.* 1996). Seabird diet studies can more readily indicate changes in discard rates from year to year or from location to location (e.g. Votier *et al.* 2004). This approach provides a means of monitoring the amounts, species composition and sizes of fish discarded by fishers, and can potentially be applied to assess the effectiveness of management practices. This direct relationship between seabirds and fisheries operations is one example where reductions in fisheries catches, and improvements to fishing practices will have negative effects on seabirds.

Breeding success is another useful means of identifying the direct effects of fisheries activities on commercially important species, with a growing number of examples of its use. One of the earliest applications involves the breeding performance of the black-legged kittiwake in the sandeel fishery of the North Sea. When breeding success falls below a threshold level the fishery closes in that sector until kittiwake breeding success recovers in subsequent years (Lewis *et al.* 2001, Furness 2007). Indicators such as this, that incorporate parameters from several species, across multiple regions and trophic levels, are considered to provide a more robust indication of changes in prey availability and prey assemblages (e.g. de la Mare and Constable 2000, Fulton *et al.* 2005, Piatt *et al.* 2007a). For example, catch per unit effort in the sardine fishery of the Gulf of California was predicted with an accuracy of 73 % by a model based on the proportion of sardines in the diet of elegant terns *Sterna elagans*, the reproductive success of Heermann's gull *Larus heermanni,* and the SST anomaly in the area (Velarde *et al.* 2004).

The current use of seabirds in identifying fisheries effects on non-target species, and on the rest of the ecosystem, mainly involves their incorporation into multi-disciplinary ecosystem-based management or research programs. In one of the first examples of an Ecologically Sustainable Development management program the breeding numbers of two gull species constitute one of 13 important ecological performance indicators of ecosystem function in the North Sea (Kabuta and Laane 2003). In the Northwest Atlantic the diet and foraging effort of two seabird species have been incorporated into a similar multi-disciplinary management program (Davoren *et al.* 2007). An integrative multi-species research program exists in the South Atlantic Ocean, where the diet and breeding success of three seabird species are incorporated into an index of inter-annual changes in krill *Euphausia superba* abundance, being a measure of the productivity in this ecosystem (Croxall 2006). In addition to their management application, these ecosystem-based programs also aim to gain a better understanding of the interrelationship between the physical and biological components of the marine environment (Freon *et al.* 2005), and the major trophodynamic pathways in marine food webs (Cury *et al.* 2005). The existence of these multi-discipline programs provides an unparalleled opportunity to identify the role of seabirds in the marine environment, through simultaneous ecological research on a range of other species.

Another valuable application of seabird data to fisheries and ecosystem management is to combine dietary measures with estimates of the energy requirements of individuals, to calculate the total food consumed by a colony or population. The development of such energetics models provides an estimate of the mortality of a fish stock due to avian predation, and can be incorporated into multi-species analysis of fish populations. There are numerous examples where these methods have been applied to single species fisheries to assign an ecological allocation of the fish stock (e.g. Bailey 1986, Furness 1990, Bailey *et al.* 1991, Cairns 1992). This approach enables the development of more conservative catch allotments that take natural predators into account.

CONCLUSION

This review identifies the broad range of considerations that must be addressed when identifying the most appropriate seabird species and parameters to include in fisheries management programs, and stresses the wide range of factors involved in this process. In summary, the seabird species in a community that will be most sensitive to changes in prey availability are those that have one or more of: a restricted diet; a relatively small foraging range; an inflexible time/energy budget; and/or are surface feeders. In contrast, more resilient seabirds will be those with: a more generalist diet; a relatively large foraging range; increased flexibility in their time/energy budget; and greater dive capabilities. Both types of seabirds can provide an indication of low to moderate levels of change, due to the varied degree of constraints influencing their foraging and breeding parameters. The composition of the diet of species with a largely piscivorous diet is currently the most useful parameter in the assessment of the direct and short-term influences of fisheries activities, but measures of foraging trip duration and energy acquisition rates have gained popularity in recent times. Breeding performance presents the most useful indicator of longer-term trends in the direct and indirect influence of fisheries on prey availability and ecosystem status.

As has been highlighted in this review, the diverse range of species in a seabird community provides multiple and varied opportunities to detect and reflect changes in prey composition and availability and ecosystem dynamics. Given the current pressures on marine ecosystems, and the likely future increase through growing human needs and a changing climate, it is imperative that fisheries and environmental managers use all available data in order to move towards sustainability in world fisheries. Improved management will require the implementation of a suite of management actions, such as marine protected areas (Murawaski *et al.* 2000), and improved vessel-based operational standards (Ragonese *et al.* 2005), with Ecological Sustainable Development being another fundamental component (Piatt *et al.* 2007a). The role of seabirds in this process can be realised only through their widespread incorporation into existing and future fisheries management programs. Integration with fisheries research will also provide the concurrent measures of prey density and assemblage that are required in order to investigate many of the uncertainties that have been identified herein. This approach will provide the best opportunity to identify the most appropriate indicators, and their relationship with key physical and biological processes, and thus assess the value of seabirds in future ecological sustainable development frameworks.

CHAPTER 3

EXPLOITATION OF DISTANT ANTARCTIC WATERS AND CLOSE NERITIC WATERS BY SHORT-TAILED SHEARWATERS BREEDING IN SOUTH AUSTRALIA

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EXPLOITATION OF DISTANT ANTARCTIC WATERS AND CLOSE NERITIC WATERS BY SHORT-TAILED SHEARWATERS BREEDING IN SOUTH AUSTRALIA

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Collected all data, performed analysis on all samples, interpreted data, wrote manuscript and acted as corresponding author
I hereby certify that the statement of contribution is accurate
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Page, B.
Supervised development of work, contributed to planning of field work and analysis, and provided critical evaluation of drafts.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
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de Little, S. C.
Provided assistance with analysis
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Provided assistance with analysis and provided critical evaluation of a draft.
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ABSTRACT

Identifying the primary foraging grounds of abundant top predators is of importance in marine management to identify areas of high biological significance, and to assess the extent of competition with fisheries. We studied the search effort and habitat selection of the highly abundant short-tailed shearwater *Puffinus tenuirostris* to assess the search strategies employed by this wide-ranging seabird. During the chick-rearing period 52 individuals were tracked performing 39 short foraging trips (1 - 2 days), and 13 long trips (11 - 32 days). First-passage time analysis revealed that 46 % of birds performing short trips employed area-restricted searches, concentrating search effort at an average scale of 14 ± 5 kilometres. Foraging searches were more continuous for the other 54 %, who travelled faster to cover greater distances, with little evidence of area-restricted searches. The amount of prey returned indicated that continuous searchers consumed similar prey mass, but greater prey diversity than area-restricted search birds. On short trips there was no evidence for relationships between individuals' foraging locations and a range of environmental conditions. On long trips 23 % of birds travelled 500 - 1000 kilometres to neritic (continental shelf) habitats, showing weak evidence of preference for areas of higher chlorophyll *a* concentration, and foraged at a similar spatial scale to individuals on short trips. The other 76 % performed rapid outbound flights of 1000 - 3600 kilometres across oceanic habitats commuting to regions with higher chlorophyll *a*. The spatial scale of search effort in oceanic habitat varied widely with some performing broad-scale searches (260 - 560 kilometres) followed by finer-scale nested searches (16 - 170 kilometres). This study demonstrates that a range of search strategies are employed when exploiting prey across ocean basins. The trade-offs between different search strategies are discussed to identify the value of these contrasting behaviours to wide-ranging seabirds.

INTRODUCION

Food is heterogeneously distributed across most landscapes, meaning that its availability to foraging animals is often variable in space and time. This is especially true for seabirds that rely entirely on marine prey which is distributed in an exceptionally heterogeneous and dynamic environment (Hunt and Schneider 1987; Hunt 1990). The occurrence of seabirds often reflects the integration of the bio-physical processes that result in the production of prey resources (e.g., Cairns and Schneider 1990), with the highest densities typically occurring in regions of elevated productivity. The aggregations and behaviour of seabirds may therefore be particularly good bio-indicators by providing an insight into the location of predictable versus variable prey returns (e.g., Suryan *et al.* 2006). Using seabirds as a proxy of areas of biological importance is limited by our understanding of the search strategies that are employed, and how search effort is distributed relative to prey.

Pelagic seabirds are able to forage across larger spatial scales than coastal seabirds and other marine birds. Travelling further enables individuals to exploit broad-scale (> 300 km in diameter) physical features such as frontal systems, gyres, mesoscale eddies, and large scale upwellings. When foraging from their breeding colony pelagic seabirds can also exploit neritic waters closer to the colony, where finer-scale (< 50 km in diameter) physical features such as smaller scale eddies and local upwellings occur (Cairns and Schneider 1990; Catard and Weimerskirch 1999; Waugh *et al.* 1999). The advantages of being able to travel more widely when foraging are that prey aggregations associated with broad-scale features are relatively more stable compared to those associated with medium- and fine-scale features (Wu and Louks 1995; Fauchald *et al.* 2000). Therefore broad-scale features provide a degree of predictability in the location of profitable prey patches to pelagic seabirds

(Weimerskirch 2007). However, travelling further to forage has inherent disadvantages, as it increases absence from the colony, increases the areas to be searched, and elevates the cost associated with returning food to offspring.

The behavioural, physiological and life-history traits of many Procellariiform seabirds (albatrosses, shearwaters, petrels) enable them to exploit broad-scale oceanic features during their breeding season (Baduini and Hyrenbach 2003). The long-trip (LT) component of a dual foraging strategy enable some species to forage hundreds to thousands of kilometres from their breeding colonies for periods of 5-31 days (e.g., wandering albatross *Diomedea exulans* -Weimerskirch *et al.*1993, blue petrel *Halobaena caerulea* - Charaund and Weimerskirch 1994). Long trips are alternated with short trips (ST) of 1-3 days which are commonly confined to neritic (continental shelf) waters close to the colony (Baduini and Hyrenbach 2003). Due to their division of time between oceanic and neritic regions Procellariiforms exploit waters of varying productivity, where physical processes operate on a range of spatial and temporal scales.

Short-tailed shearwaters *Puffinus tenuirostris* are a medium-sized Procellariiform that breed along the coastline of South-eastern Australia, and travel to Antarctic waters during their breeding season (Klomp and Schultz 2000). During LT to the Southern Ocean they are assumed to target large-scale physical features associated with high productivity (Weimerskirch and Cherel 1998). In contrast, the physical processes that elevate productivity in neritic waters surrounding short-tailed shearwater colonies operate on a relatively short temporal scale, and are highly variable (Middleton and Bye 2007). Productivity in this region is influenced by a number of wind-driven upwellings, the strength and duration of which vary considerably within and between years (Ward *et al.* 2006). We studied the at-sea movement of short-tailed shearwaters *P. tenuirostris* in both neritic and oceanic habitats to compare the foraging strategies employed, and thereby assess the degree of predictability between these regions.

Tracking studies that incorporate either direct measures of food distribution (e.g. prey aggregations) or indirect measures (e.g. physical processes in the marine environment) provide an insight into how animals perceive spatial variance in their food, and how they modify their foraging effort accordingly (e.g., cetaceans - Jaquet and Whitehead 1996, seabirds - Fauchald *et al.* 2000, herbivorous mammals - Johnson *et al.* 2002, and pinnipeds - Bradshaw *et al.* 2004). One of the most common ways to measure effort is to quantify travel speeds and turning rates. Reducing travel speed and increasing turning rates in an area restricted search (ARS) enables animals to reduce the search area, and is a response to prey detection (Fauchald 1999). Thus, examining the occurrence and scale of ARS reflects the distribution of search effort across the landscape, and the scale at which a forager responds to its environment (Fauchald and Tveraa 2003).

Studies on a range of Procellariiforms have found that ARS is often performed after relatively direct commuting flights (Waugh *et al.* 1999; Catard *et al.* 2000; Pinaud and Weimerskirch 2005). This search strategy can be interpreted as birds having prior knowledge of the location of suitable foraging areas, or following individuals who do. An alternative foraging strategy involves more continuous searching behaviour, with little evidence of concentrated ARS (Weimerskirch *et al.* 2007). Continuous searches can be interpreted as an inability to find a suitable prey patch. However, for wide-ranging seabirds that exploit sparsely distributed prey this can present an optimal foraging strategy (e.g. wandering albatross *Diomedia exulans* Weimerskirch *et al.* 1997). We hypothesise that continuous searches will be employed by short-tailed shearwaters *P. tenuirostris* more readily in neritic compared to oceanic habitats, based on the expectation that prey distribution and availability is less predictable and more variable in neritic environments. Secondly, we expect that the scale of search effort in oceanic waters will be broader than in neritic waters as a response to the bio-physical features that influence prey distribution in each region. We also test the hypothesis that search effort during direct search strategies corresponds with the habitat features that shape prey structure better than during continuous search strategies. This is because direct searches presumably target larger more stable prey aggregations, whereas continuous searching is considered a more opportunistic mode of foraging (Weimerskirch 2007).

Individual birds are also expected to modify their movements based upon the size and shape of the prey patches that they encounter, instead of at some arbitrary scale. To consider this we provide a multi-scale based approach to habitat associations, expecting an increase in the strength of habitat associations derived at the scale of each individual compared to a median scale.

METHODS

Study site and chick capture

The study was conducted on Althorpe Island (35º 37' S, 136º 86' E) during the austral summers of 2005, 2006 and 2007. Each year numbered burrows containing hatched chicks were monitored to identify attendance patterns of parents ($n = 25$). This involved monitoring changes in the mass of chicks by weighing them each night using a spring balance (± 5 g). Chicks that increased in mass had received a feed, and no mass gain over 5 days indicated that both parents were on LT (Weimerskirch and Cherel 1998; Klomp and Schultz 2000). Burrows of those birds making LT were targeted by installing wooden trapdoors at the entrance. Arriving birds tripped a stick which closed the swinging trapdoor and triggered a flashing red LED light. Upon arrival from a LT birds were left in the burrow to feed their chick, and captured after 30-60 minutes, or until chick begging had ceased, thereby ensuring they had fed their chick.

Transmitter deployment

Satellite transmitters (KiwiSat 202, single AA Cell, Sirtrack Ltd, North Havelock, New Zealand) weighing 30 g and with a transmission interval of 60 s were glued to the back feathers of 52 individuals over the three year study (following Catard *et al.* 2000; Klomp and Schultz 2000) using Loctite 401 glue (Intek Adhesives Ltd, Northumberland, UK). Foraging trips of eight adults were tracked in 2005, 32 in 2006, and 13 in 2007. Midway through the 2006 season, two subcutaneous sutures were added to secure transmitters (Mauser and Jarvis 1991) because some transmitters fell off prematurely. No chick desertion flights were recorded, as all tracked individuals returned to their burrows.

Foraging success

We studied the 'foraging success' of adults performing ST, being the combined measure of adult mass loss and the mass of the meal returned from a single foraging trip (as in González-Solis *et al.* 2000). At the colony adults were weighed after they had fed their chicks, and before transmitter attachment. Upon their return from a tracked ST adults were reweighed after their stomachs were emptied by water offloading (Wilson 1984). Some adults avoided capture upon arrival, and began feeding their chicks, so were re-captured and re-weighted after they had completed feeding. Diet samples were collected from 20 of the 39 tracked ST, and were stored in plastic vials and frozen until analysis. After flushing, adults were re-fed 60 ml of a prepared mixture of blended pelagic sardine, and an additional 60 ml of Vitrate ® formula to reduce the chances of dehydration. Diet samples were not collected from LT, nor were mass changes recorded for LT.

The solid fraction of stomach samples was separated by gravity over a 0.25-mm sieve (Connan *et al.* 2005), and the wet weight of solids gained using an electronic balance (± 0.001 g). Species contribution was based on the reconstructed biomass of each prey component of meals using published material to identify cephalopod beaks (Lu and Ickeringill 2002), crustacean bodies (Ritz et al. 2003), and fish otoliths (Williams and McEldowney 1990). To estimate the length and mass of fish, otolith length was applied to species-specific regressions (Hindell 1988; Williams and McEldowney 1990; Cullen *et al.* 1992), and cephalopods from the upper or lower rostral length of beaks (Lu and Ickeringill 2002). Prey diversity was calculated as a percentage of the total number of meals that contained fish, squid, or crustaceans. The variability in prey types returned in ST meals between the birds that employed a direct ARS foraging strategy, and a continuous foraging strategy was assessed a using Kruskal-Wallis test.

Flight parameters

The movement of tracked birds was monitored by Argos satellites. All Argos locations were filtered by excluding locations of poorer quality than Class 0 (1 - 1.25 km accuracy, www.argos-system.org), and filtered based on a maximum travel speed of 60 km/h using the program 'TimeTrack' (version 1.0-9, M. D. Sumner, University of Tasmania, Hobart, following McConnell *et al.* 1992). Both ST and LT data were linearly interpolated in the R Statistical Package V2.6.2 (R Development Core Team, 2008) by adding a point every 15 minutes (time) between satellite-derived locations. Linear interpolation assumes straight-line travel at constant speed between locations (Guinet *et al.* 1997). Distances flown were calculated as the cumulative distance between interpolated points. Maximum distance from the colony was the straight-line distance from the colony to the most distant point (Guinet *et al.* 1997). Foraging parameters on ST were compared between years using ANOVAs, Kruskall-Wallace, or Mann-Whitney U tests, and parameters were transformed to homogenise variances where necessary.

First-passage time and area-restricted search

To test the hypothesis that a continuous search strategy will be more readily used in neritic compared to oceanic habitat, the search strategies employed by each individual was determined using First Passage Time (FPT) analysis. First-passage time, defined as the time required for an animal to cross a circle of a given radius, or how much time is spent in a given area, is particularly valuable for assessing hierarchical scales of movement (Fritz *et al.* 2003; Certain *et al.* 2007). This method has been applied to a range of Procellariiforms to identify the prevalence and scale of ARS (Fauchald and Tveraa 2003; Suryan *et al.* 2006; Pinaud and Weimerskirch 2005, 2007). A low FPT identifies areas where birds travelled rapidly, and high FPT signifies the slow travel speed and high sinuosity associated with ARS. Relative consistency in the travel speed along an entire track indicates that birds were performing a more continuous foraging strategy, with no obvious areas of ARS. To identify nested hierarchical searches where fine-scale searches were performed inside areas of broader-scale ARS, FPT was analysed within the most intensively searched area along (Fauchald 1999; Fauchald and Tveraa 2003).

The scale of ARS for each foraging trip was determined by examining the variance in log-transformed FPT for a wide range of spatial scales. First Passage Time was calculated at radii between 1 - 50 km at 2-km increments for each location along each ST, and at radii between 2 - 1000 km at 2-km increments for each LT. A peak in FPT variance signifies the spatial scale where ARS behaviour is most apparent for each foraging trip (following Fauchald and Tveraa 2003). The absence of a peak signifies that birds travelled at a relatively continuous speed along the entire track, providing little evidence of ARS behaviour. Where a peak occurs, the location of areas of ARS along each track was identified by plotting the FPT values for that corresponding scale as a function of time. This involved identifying a threshold FPT value above which an animal was assumed to be performing an ARS, and below which it was assumed to be travelling (i.e., faster movement) (following Pinaud and Weimerskirch 2007). Applying the threshold value to FPT data identified the: 1) number of ARS zones; 2) distance from the colony; and, 3) time in ARS as a percentage of the total foraging trip time (as in Pinaud and Weimerskirch 2007). ARS can be misinterpreted as periods when birds are not flying, but possibly resting on the sea surface, which many seabirds do at night. This presence of resting behaviour was assessed by inspecting the timing of FPT versus travelling behaviour for all foraging trips (Pinaud and Weimerskirch 2007). Where periods of ARS were identified to be occurring at night time location data were removed from the analysis.

Marine habitat characterisation

To investigate the correspondence between habitat features, prey aggregations, and seabird search effort, marine habitats exploited during ST were characterised by: depth, chlorophyll *a* (Chl *a*), sea surface temperature (SST), and the gradients of these three variables. For LT, sea surface height (SSH) and SSH gradient variables were also included. To examine whether changes in SST were an artefact of location, latitude was also included in long-trip analysis. Data for depth were obtained from GEBCO one-minute grid. Chl *a* concentration and SST data were downloaded from SeaWiFS MODIS satellites (www.reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs. shtml). For ST, 8-day averages of Chl *a* and SST were obtained at a resolution of 0.1 degree. For LT, monthly averages of both variables were obtained at 0.3 degrees. Monthly averages of SSH anomalies were obtained from AVISO Live Access Server V7 (http://las.aviso.oceanobs.com/las/servlets/dataset) at a resolution of 0.1 degree. All mapping was done in MapInfo Ver 8.0. Additional oceanic variables were identified by calculating gradients in SST, Chl *a*, SSH and Depth using the Vertical Mapper extension MapInfo Ver 8.0.

Habitat associations

Habitat associations for LT were assessed using two methods. Firstly, the correspondence between search effort and broad habitat features was analysed by assessing the proportion of a foraging trip that was spent in different habitats. This was achieved by plotting the % time spent in categorical classes of each habitat variable. Depth classes were defined as neritic (< 500 m), slope (500 - 1500 m), and oceanic waters (> 1500 m; Waugh and Weimerskirch 2003). SST classes were defined as: temperate (> 18 ºC), sub-tropical (14 - 18 ºC), subtropical front (12-14 ºC), subantarctic surface (11 - 12 ºC), Subantarctic Front (9 - 11 ^{o}C), Polar Frontal Zone (6 - 9 ºC), and Polar Front (< 6 ºC) following Park *et al.* (2002) and Pinaud and Weimerskirch (2005). Chl *a* was assigned a category A-E, following the gradient distribution variable of Pinaud and Weimerskirch (2005). This involved assigning five groups each representing 20% of the range between the highest and lowest Chl *a* values. ST were not analysed using this method as the habitat categories used were mainly applicable to larger scale movements in oceanic regions.

Secondly, a more detailed analysis of habitat associations was performed on LT to assess the correspondence between search effort and different habitat features at a range of spatial scales. This method of analysis was also applied to ST. Generalised linear mixed-effects models (GLMM) were used, with FPT as the response variable. GLMM also provided a means of identifying which habitat features were influencing search effort at the chosen spatial scale.

Habitat use was compared between different search strategies (ARS versus non-ARS), and between large and nested scales in hierarchical searches. ST and LT data were also modelled separately to allow comparisons between trip types. FPT and habitat variables were derived both at the scale of each individual, and at a median scale derived from the entire sample. Bird ID was included as a random factor in the models to account for intra-individual trends in FPT. At each spatial scale FPT was re-calculated to provide a measure of the total time taken to cross a circle of given radius. Habitat variables were also re-calculated to present averages at the appropriate scale for each model set, and were extracted from the area defined by the circles of FPT along each track. For ST, the habitat variables used as independent predictors were: depth, depth gradient, SST, SST gradient, Chl *a*, and Chl *a* gradient. The additional variables of SSH, SSH gradient, and latitude (LAT) were included in the long-trip analysis. Meaningful interactions between habitat variables were also added to the analysis, but kept to a minimum to reduce the number of models (Burnham and Anderson 2002). Where errors were non-Gaussian, we used Gamma error distributions in the GLMMs. FPT was log-transformed, and the independent predictors were transformed where appropriate. SST was highly correlated with latitude and was therefore removed from the analysis. We used the methods of Suryan et al. (2006) to sub-sample FPT data and thereby avoid temporal autocorrelation (Legendre *et al.* 2002).

The multi-scale approach employed involved presenting a number of candidate model sets, that were contrasted based on Akaike's information criterion corrected for small samples (AIC_c) and the Bayesian information criterion (BIC) (Burnham and Anderson 2002; Link & Barker 2006). AIC_c favours more complex models when tapering effects exist and samples are large, whereas BIC identifies the principal drivers of complex relationships within larger datasets (Link and Barker 2006). The strength of evidence for each model relative to the entire model set was assessed by calculating relative model weights ($wAIC_c$ and wBIC). Weightings vary from 0 (no support for a relationship between FPT and oceanic variables) to 1 (complete support) (Burnham and Anderson 2002).

RESULTS

Short trips

Two main types of foraging were observed during ST. The first foraging mode performed by 46 % of individuals (18/39) involved at least one distinct period of ARS (Fig. 3.1). The general pattern was characterised by direct flight to an area followed by an increased search effort (Fig. 3.2). Birds performed ARS at a scale of 14 ± 5 km, with 10/18 concentrating searches at a consistently fine spatial scale of 6 km, producing a narrow peak of high FPT variance (e.g., Bird 67826, Fig 3.1). The remaining 8/18 birds increased their search effort at a broader range of spatial scales resulting in a less distinct (i.e. flatter) peak (e.g., Bird 67141, Fig 3.1). The number of ARS zones performed during ST varied from 0 to 5. A second mode of foraging performed by 54 % of birds (21/39) involved a more continuous 'searching' strategy with no detectable periods of ARS. This was identified by the absence of a variance peak (e.g., Bird 67354, Fig 3.1 and 3.2), indicating that there was low variance in travel speed along their entire foraging path (i.e., relatively continuous movement).

Continuous searching flights were faster both in terms of average and maximum speed (Table 3.1). While the average distance travelled by continuous searchers was greater, this was not significant due to the extent of inter-individual variation within groups (Table 3.1).

Foraging success was comparable on both modes of ST foraging as the mass of meals returned, and the body-mass loss of foraging birds, did not differ (ARS meal mass = 39 ± 4 g (N = 10), non-ARS meal mass 36 ± 5 g (N = 10)): $F_{1,\,12} = 0.16$, p = 0.61, ARS mass loss = 47.6 ± 25.2 g/d, non-ARS mass loss = 39.9 ± 29.7 g/d: $F_{1,12} = 0.71$, p = 0.41). However, the composition of meals differed between foraging modes. We found 85 % of meals returned from ARS foragers contained a single prey type, and 14 % contained two prey types. In contrast, only 23 % of the meals of continuous searchers contained a single prey type. 61 % contained two prey types, and 15 % three prey types. There were also differences in the relative proportion of each major prey type (% mass) between search strategies. ARS meals contained a higher proportion of fish compared to continuous searchers ($\chi^2 = 4.2$, $P = 0.01$), whose meals contained more cephalopod and krill (Fig. 3.3).

Habitat associations were poor for both ARS and non-ARS birds when performing ST, indicating the extent of variability in the data and that none of the habitat variables were the major drivers of FPT at the scales studied.

Long trips

A hierarchical search pattern was performed by six of the 13 birds tracked. This involved an increase in search effort at a broad scale of 269 ± 84 km, then at a nested scale of 68 ± 28 km (Table 3.2). These birds commonly travelled the farthest from the colony compared to birds who directed ARS directly at small scales (Kruskal-Wallis: $\chi^2 = 5.4$, $p = 0.009$, $n = 9$), and non-ARS birds (Kruskal-Wallis: $\chi^2 = 4.5$, $p = 0.02$, $n = 10$). For example, bird 52463 reached a distance of 6,952 km by day 11, and covered a minimum distance of 15,220 km in the 32 - day trip (Fig. 3.4). Of the proportion of each trip recorded, 95 ± 4 % of the time was spent in oceanic habitat at the Polar Front (Fig. 3.5a and b), 18 % was spent in waters of medium Chl *a* (0.6 - 0.8 mg/m^3), and 17 % in high Chl *a* (>0.8 mg/m^3) (Fig 3.5c).

A second group of four birds engaged in ARS directly at a fine scale of 29 ± 6 km (Table 3.2). Three of these birds performed a LT to neritic waters (e.g., Bird 52478, Fig. 3.4), reaching a maximum distance of 912 to 990 km (Table 3.2). However, one individual foraged in oceanic waters, travelling 3012 km from the colony (Bird 52483, Table 3.2). Despite staying closer to their colony, a similar proportion of their LT was engaged in ARS (40 ± 7 %) compared to hierarchical foragers (37 ± 5 %) (Table 3.2). This was due to the faster maximum travel speed of hierarchical foragers enabling them to reach their foraging sites more quickly ($t = 6.27$, df = 7, $p = 0.03$, Table 3.2).

The remaining three birds had relatively low variance in FPT with the absence of a variance peak, indicating the absence of any distinct periods of ARS (Table 3.2). These non-ARS birds performed a more continuous search, and travelled faster (32 ± 2 km/h) than hierarchical foragers (23 ± 3 km/h) (*t* = -1.73, df = 6, p =0.03, Table 3.2). Despite this, non-ARS birds only covered half the distance of hierarchical foragers (Table 3.2). This indicates that non-ARS birds adopted a more convoluted and contorted flight path, representing a more continuous search strategy. Similar to hierarchical foragers, they spent most of their time in oceanic waters (98 %) (Fig 3.5a), but the habitat exploited differed as a wider range of SST zones were visited (Fig 3.5b), and they did not enter waters of high Chl *a* (Fig 3.5c).

There was weak evidence for a correlation between some habitat variables and the response variable, FPT (Table 3.3). For hierarchical foragers (i.e., broad-scale ARS with nested ARS zones) at the individual scale, two models containing latitude and Chl *a* had the highest BIC weights and the largest % deviance explained (LAT: *w*BIC = 0.057, %DE = 10.43; Chl *a*: wBIC = 0.049, %DE = 4.94) (Table 3.3). There was evidence for a negative correlation between latitude and FPT (Fig 3.6a) suggesting that birds concentrate their foraging effort at lower latitudes. A positive relationship with Chl *a* also indicates that these birds increased search effort within regions of elevated productivity (Fig 3.6b).

For hierarchical foragers at a single median scale (72 km, Table 3.2), model fits did not improve. LAT again had the highest BIC weights and % deviance explained (*w*BIC = 0.042 %DE = 3.67) (Table 3.3). There was also some evidence for a weak effect between Chl *a* gradient and FPT (*w*BIC = 0.039; %DE = 4.15) (Table 3.3). ARS birds that concentrated their search effort directly at a fine scale showed increased evidence of an effect, and improved goodness of fit (i.e., %DE) when examining habitat interactions at the median or population scale, compared to individual scale. Model fit was highest for models containing the single habitat variables LAT (*w*BIC = 0.104; %DE = 45.99) and Chl *a* (*w*BIC = 0.076; %DE = 21.22) (Table 3.3). A positive relationship between FPT and latitude reveals that most birds concentrated their search effort in more northerly waters (Fig 3.7a). Search effort again increased within regions of elevated productivity, with a weak positive relationship between FPT and Chl *a* (Fig 3.7b).

No habitat associations were apparent within the nested scale of search effort for hierarchical foragers. There was also no evidence of a relationship between habitat variables and FPT for non-ARS birds.

The duration of LT performed by tracked birds did not differ significantly from those of a control group. This suggests that tracked birds were not impacted by carrying a transmitter, and they were behaving normally.

DISCUSSION

Search strategies and prey predictability on short-trips

We provide evidence of comparable foraging success among short-tailed shearwaters *P. tenuirostris* performing varied search strategies. Specifically, during ST wider-ranging searches with no apparent ARS returned a comparable-sized meal to more direct and targeted foraging trips, indicating that a widespread searching tactic offers an effective foraging strategy for this species. While the contents of the stomach returned to the colony may only represent the final stages of a day long foraging bout, consideration of changes in adult body mass should account for prey that has already passed through the digestive tract of the adult. The foraging success achieved on continuous searches is evidence that the neritic waters exploited contained enough widely dispersed prey to provide adequate prey returns for chick-rearing short-tailed shearwaters *P. tenuirostris*.

The use of a continuous search strategy has also been identified in the wandering albatross *D. exulans*, where the dual deployment of satellite transmitters and stomach temperature loggers revealed that birds are able to maintain a comparable rate of foraging success from a continuous search strategy (Weimerskirch *et al.* 1993; Weimerskirch *et al.* 1997). While covering a larger area likely incurs greater energy costs it also increases the chances of encountering sparsely distributed prey, enabling albatross to maintain a suitable and predictable yield (Weimerskirch *et al*. 2005). For a short-tailed shearwater *P. tenuirostris* foraging with little certainty of prey distribution adopting a continuous search strategy provides advantages over direct searches. The major benefit being that a wide-scale search involving slower flight will increase the chances of locating new prey patches, where as the rapid travel involved in commuting behaviour may pass suitable foraging areas.

The return of a more variable range of prey on ST also implies that continuous searches are a more opportunistic mode of foraging as individuals consume whatever prey they can find. In contrast, the return of a single prey type suggests individuals are exploiting larger more stable prey aggregations (Weimerskirch 2007). We were unable to identify the foraging success achieved by birds on LT as they avoided re-capture upon their return to the colony. Further studies comparing the quantity of oil returned from different search strategies on LT would be of value to determine weather short-tailed shearwaters *P. tenuirostris* adopting a continuous search strategy are able to attain comparable foraging success to ARS foragers.

The higher frequency of birds employing continuous searching during ST compared to LT can be interpreted as supporting our hypothesis that neritic habitat has higher day-to-day variability in the location of foraging sites (prey patches) compared to oceanic waters. Continuous searching suggests that birds were unable to locate prey patches large enough to warrant a more concentrated bout of foraging. This assumption is based on the expectation that when an individual finds a profitable prey patch they will concentrate search effort, thereby attempting to reduce energy expenditure and maximize food intake rates (Stearns 1992).

Roughly half of ST foragers did travel directly to their primary foraging site, suggesting that they either had prior knowledge of the location of a suitable prey patch, or were following a bird who did. Past experience plays a large role in shaping foraging behaviour, as is evident when foragers show site fidelity by returning to an area of previous foraging success (e.g., seabirds Weimerskirch *et al.* 1993; Irons 1998; Hedd *et al.* 2001, pinnipeds Bradshaw *et al.* 2004). Short-tailed shearwaters *P. tenuirostris* embarking on ST should have prior knowledge of the location of profitable feeding areas, as neritic habitat is exploited when birds return from LT the previous day. This is evidenced by the return of fresh neritic prey in LT meals (Weimerskirch *et al.* 1993; Weimerskirch and Cherel 1998). However, the absence of ARS in many foragers suggests that birds were either: 1) unable to locate a profitable prey patch on the return from a LT the previous day, 2) unable to locate a previously exploited prey patch because it had dispersed, or had become exhausted, or 3) willingly employed this strategy at the outset of their trip to search for sparsely distributed prey.

Revisiting areas of past foraging success is a useful search strategy where there is a degree of stability in the location of profitable marine prey aggregations. In more variable areas, prey patches may move, disperse, or get depleted, changing foraging conditions from one foraging trip to the next. This means that seabirds, like many free-ranging predators, often have to make foraging decisions with little, if any knowledge of the current distribution and availability of their prey (Sims *et al.* 2008). Primary production in the study area fluctuates on a weekly basis through the summer due to the influence of a wind-driven upwelling system (Kampf *et al.* 2004; Ward *et al*. 2006; Middleton and Bye 2007), so pelagic fish abundance is likely to be highly variable (Dimmlich *et al.* 2004; Ward *et al.* 2006). However, the relative consistency in the direction of ARS areas on ST from the colony suggests that this feature has also created a broad region where short-tailed shearwaters *P. tenuirostris* direct their search effort. This suggests that despite its irregularity, local upwelling systems can provide a degree of predictability in the distribution of resources.

Search strategies and scale of foraging on long-trips

There was considerable variation between individuals in the scale of search effort during LT and in the movement patterns employed. The most common strategy was to employ direct and rapid outbound flight to cover 1000 - 3600 km before slowing to increase search effort. This commuting behaviour is common among wide-ranging seabirds (e.g, grey-headed albatross *Thalassarche chrysostoma* and black-browed albatross *T. melanophrys* Waugh *et al.* 1999, white-chinned petrels *Procellaria aequinoctialis* - Catard *et al.* 2000, wandering albatross *D. exulans*- Pinaud and Weimerskirch 2005), and suggests that birds have some prior knowledge about the location of productive areas (Waugh *et al.* 1999; Catard *et al.* 2000; Bradshaw *et al.* 2004). The inherent disadvantage of this strategy is that individuals likely bypass suitable foraging areas during the commuting phase. However, the benefit is that individuals can rapidly travel across areas they do not use for feeding, thereby maximise the time spent in distant foraging areas. The increased time spent in waters of elevated Chl *a*, and the correlation between FPT and Chl *a* indicates the value of these long-distance flights, which enable birds to maximise the time they spend in more productive habitat. Broad-scale oceanic features are commonly exploited by after a commuting phase to areas of higher Chl *a* (e.g., yellow nosed albatross *T. carteri* Pinaud and Weimerskirch 2005, short-tailed albatross *Phoebastria albatrus* Suryan *et al.* 2006). Therefore, wide-ranging seabirds are able to offset the costs incurred during their broad-scale movement by foraging in areas of anticipated higher productivity.

We have confirmed that the long-ranging flights identified in previous studies (Nicholls *et al.* 1998; Klomp and Schultz 2000) are regularly employed in the breeding season, with many individuals travelling in excess of 10,000 km and foraging in Antarctic waters. We also found that 23 % (3/13) of LT foragers remain in neritic waters during their entire LT. This provides further evidence that neritic regions contain areas of predictable prey returns that can meet the energy requirements of adults, as well as the energy demands of chick rearing. Neritic foraging on LT suggests that chick-rearing adults are not programmed to forage in the Southern Ocean, but instead make decisions about the broad-scale regions where they will concentrate their search. It remains unclear whether an individual mixes LT to neritic and oceanic waters, or if staying in neritic waters is a strategy used by some for an entire breeding season.

The comparably finer scale of search effort employed during LT over neritic waters, and consistency with ST in the same habitat supports our prediction that the scale of prey aggregations differs between neritic and oceanic waters. Finer scales of search effort have also been identified in other Procellariiforms when exploiting neritic waters around subantarctic islands (e.g., black-browed albatross *T.*

melanophrys 29 ± 11 km - Pinaud and Weimerskirch 2007). This foraging behaviour is considered to be a response to the smaller spatial scales of upwelling features that aggregate prey in shelf-edge and neritic habitats (Cairns and Schneider 1990; Waugh *et al.* 1999; Catard and Weimerskirch 1999).

Hierarchical foraging is commonly employed by wide ranging seabirds in oceanic habitat after a commuting phase (e.g., common murres *Uria aalge* - Fauchald *et al.* 2000, yellow-nosed albatross *T. carteri* - Pinaud and Weimerskirch 2005, short-tailed albatross *P. albatrus* - Suryan *et al.* 2006). Performing hierarchical searches enables birds to concentrate foraging effort at finer scales in areas where prey density is highest, thereby increasing foraging efficiency. A hierarchical response involves adopting ARS first at broad scales, and then at a range of smaller 'nested' scales (Fritz *et al.* 2003). This strategy is considered a response to the hierarchical patch structure of prey, where small, high-density patches are nested within large, lower-density patches (Kotliar and Weins 1990; Fauchald 1999). Interpreting the scale of physical features from the large scale hierarchical foraging of seabirds is confounded by role past experience. Studies on wandering albatross *D. exulans* have revealed that younger birds perform hierarchical patterns of ARS at a wide range of scales, whereas older birds tend to perform ARS directly at finer scales (Weimerskirch *et al.* 2007). This could be due to ontogenetic development in the foragers capacity (Field *et al.* 2005), or may reflect that individuals gain knowledge of where resources can be located predictably as they age (Greig *et al.* 1983).

Habitat associations and varying search strategies

Many have recognised the limitation of modelling movement at a single, arbitrarily defined scale (e.g., Bergman *et al.* 2000; Johnson *et al.* 2002; Marell *et al.* 2002;

Fauchald and Tveraa 2003). Suryan *et al.* (2006) extracted FPT and habitat features for short-tailed albatross *P. albatrus* at a range of consistent scales to identify a single optimum spatial scale at which to assess and quantify habitat associations. We modified this procedure further by extracting habitat features at the scale at which individuals foraged. However, habitat associations did not strengthen when considering search effort at the scale of each individual compared to a single median scale representative of the population. Poor performance of individual scale models are likely due to the extent of variation in the scale of initial searches performed (range 22 – 540km). Further attempt to assess habitat associations at individual scales would benefit by segregating hierarchical foragers from those who employ searches directly at small scales.

We only found relationships between foraging and habitat descriptors at broad scales during LT, suggesting that the structure of the marine environment has less influence over finer scales of search effort (i.e., nested ARS, small scale ARS, and ST foraging). The absence of a relationship at small scales supports our expectation of poorer habitat relationships at finer spatial scales (Hunt 1990; Wu and Louks 1995; Fauchald *et al.* 2000). Other seabird studies have also identified a greater mismatch between search effort and prey distribution at fine scales. For example, the search effort of common murres *Uria aalge* represents the spatial structure of their prey and corresponds with habitat features at broad (> 300 km) but not at medium or nested scales (~ 50 km) (Fauchald *et al.* 2000). Poor relationships between foraging and habitat descriptors at small scales may be influenced by the greater mismatch between physical features and prey aggregations that occurs at fine scales (Bradshaw *et al.* 2002).

The weak performance of models involving habitat associations of wide-ranging seabirds are no surprise as the distribution of prey, and resultant movement of birds is likely to be influenced by a wide range of unmeasurable factors additional to the habitat variables selected in this study. Many other factors can adversely affect the relationship between seabirds and their prey; e.g., exogenous factors (response lags, weather conditions, cycles in prey availability); and endogenous factors (individual variation in search patterns and search strategies) (Ryan and Cooper 1989). The limited temporal and spatial resolution of data available from remote sensing satellite equipment may also confound any relationships. We used 8-day averages of Chl *a* and SST, and monthly averages of SSH, where as seabirds are sampling their environment daily.

The poorer performance of habitat models for birds performing a continuous search strategy (non-ARS birds) during LT compared to ARS foragers suggests that the former respond differently to their oceanscape. Studies of other Procellariiforms also found that search effort during continuous searches is poorly correlated with oceanographic features (Weimerskirch *et al.* 1997). The absence of habitat associations on continuous searches is further evidence that individuals adopting this strategy are searching more opportunistically to sample a wider range of habitats than ARS foragers.

CONCLUSIONS

We have provided evidence to support the long held expectation that chick rearing short-tailed shearwaters *P. tenuirostris* commonly exploit distant foraging areas in the Southern Ocean (Weimerskirch and Cherel 1998). We have also highlighted the importance of neritic waters for foraging during both the short, and long-trip component of the dual foraging strategy. Neritic waters exploited correspond with a region where a coastal upwelling operates, and the search tactics employed infer a degree of predictability in the location of prey for wide-ranging seabirds. Foraging tactics involving continuous searches indicate that it is not necessary to direct search efforts towards highly productive patches; instead, an array of strategies reveals the degree of flexibility that exists in seabird foraging. This work demonstrates how tracking studies of top predators can provide a potentially valuable means of identifying the biological value and spatial predictability of physical processes. Such an approach has wide ranging applications to marine and fisheries management, especially at a time when the needs of top predators are being incorporated into ecosystem based management plans in many marine regions around the world.

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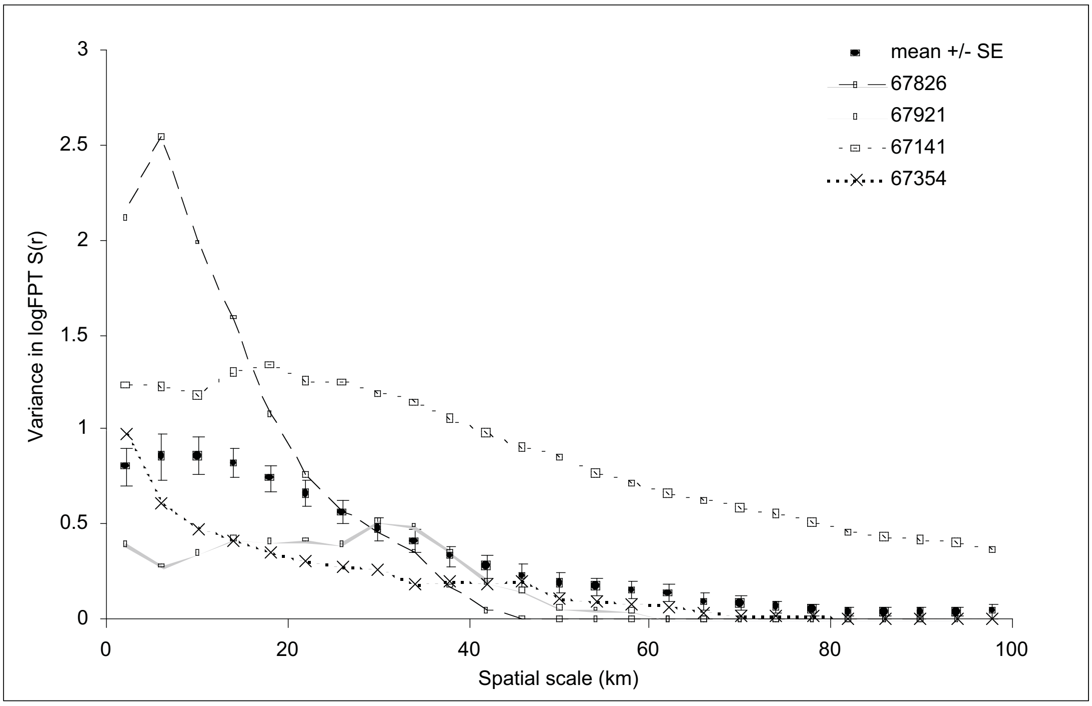

Fig. 3.1. First passage time analysis results, showing the variance in log FPT (i.e. identifies areas of more variable travel speeds) as a function of spatial scale (km). The mean and SE for all 19 individuals which showed a pattern of ARS is shown (black dots). Peaks in variance indicate an increase in search effort at that corresponding scale. Four examples of different types of trips are also shown. Bird 67354 shows no evidence of ARS.

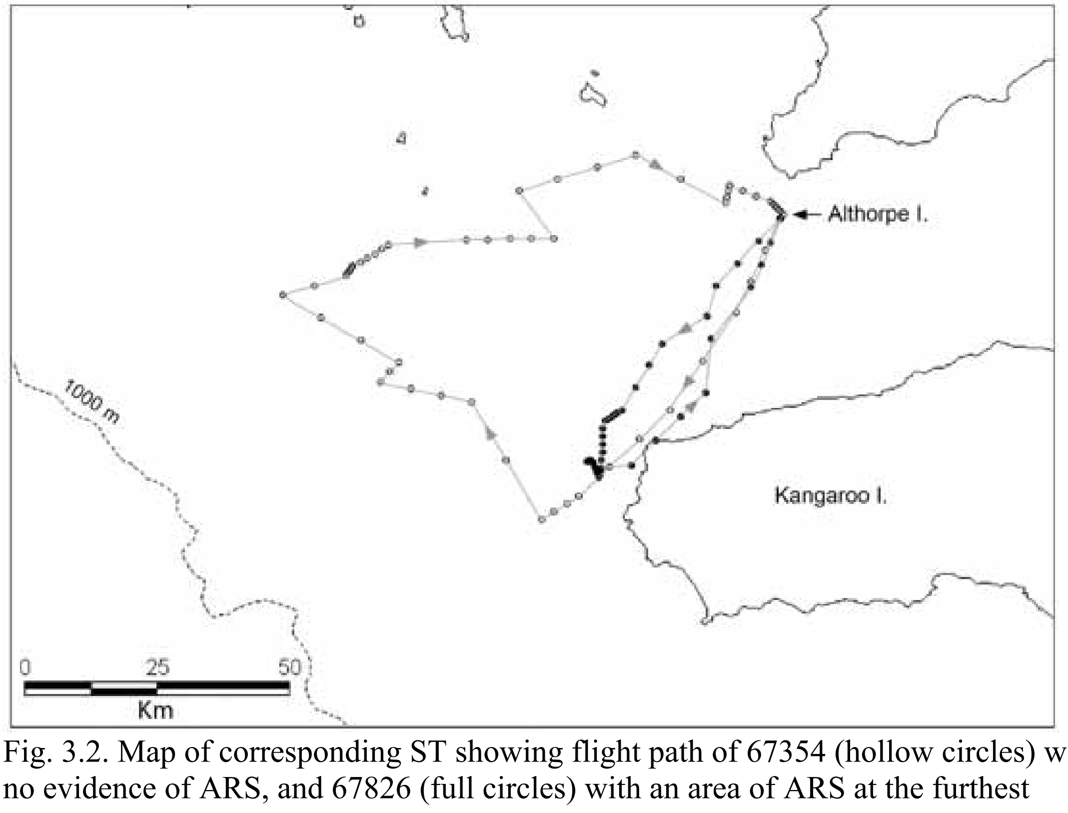

Fig. 3.2. Map of corresponding ST showing flight path of 67354 (hollow circles) with no evidence of ARS, and 67826 (full circles) with an area of ARS at the furthest extent of the foraging trip.

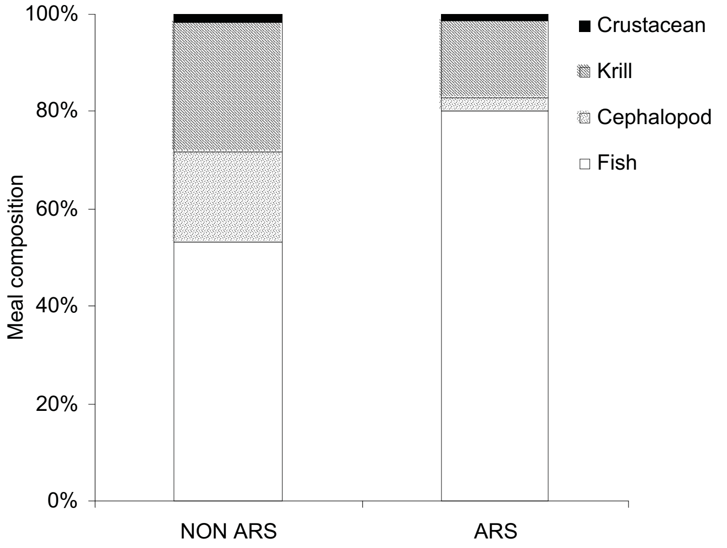

Fig. 3.3. Composition of ST meals returned from ARS and non ARS foraging trips.

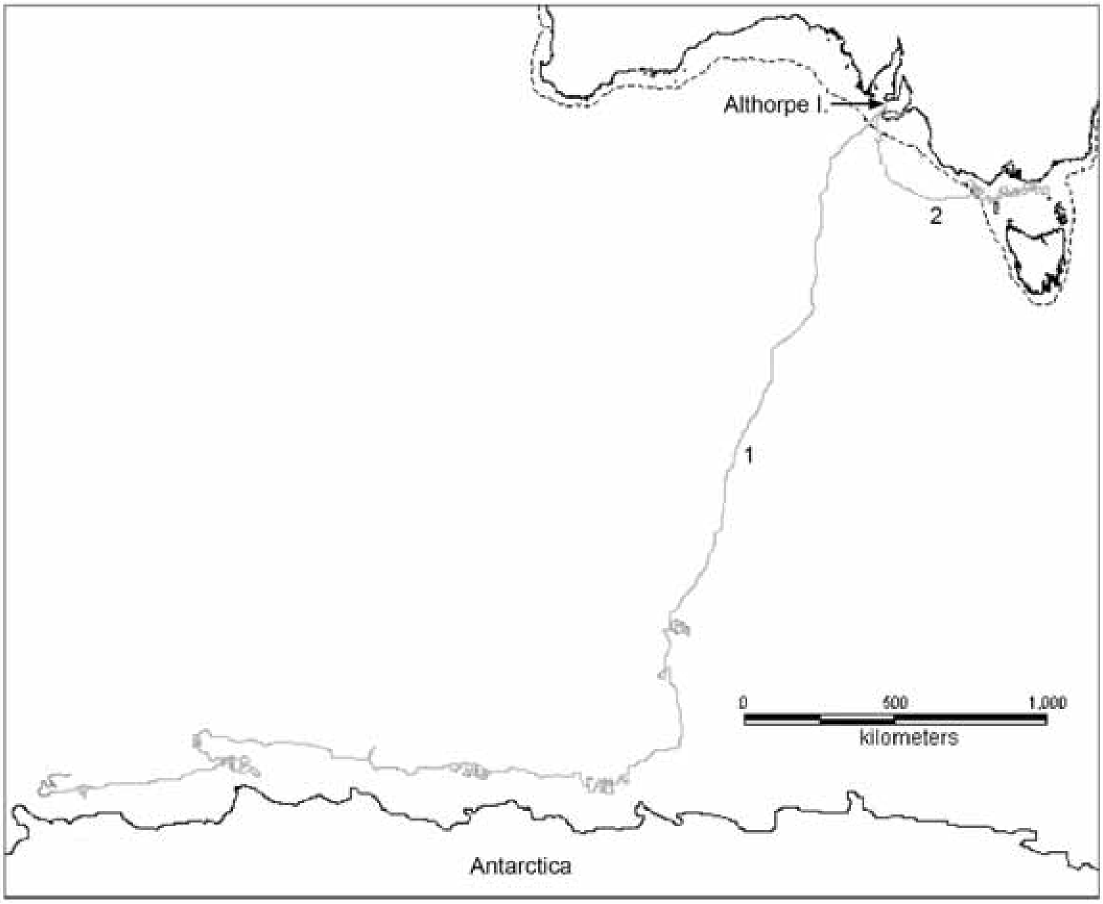

Fig. 3.4. Map showing the LT of: 1.) Bird 52463, and 2.) Bird 52478. Note that Bird 52463 travels into oceanic habitat, and concentrates foraging activity in Antarctic waters, while Bird 52478 focuses foraging activity in neritic waters to the east of Althorpe I. Dashed lines show the continental shelf (> 1000 m).

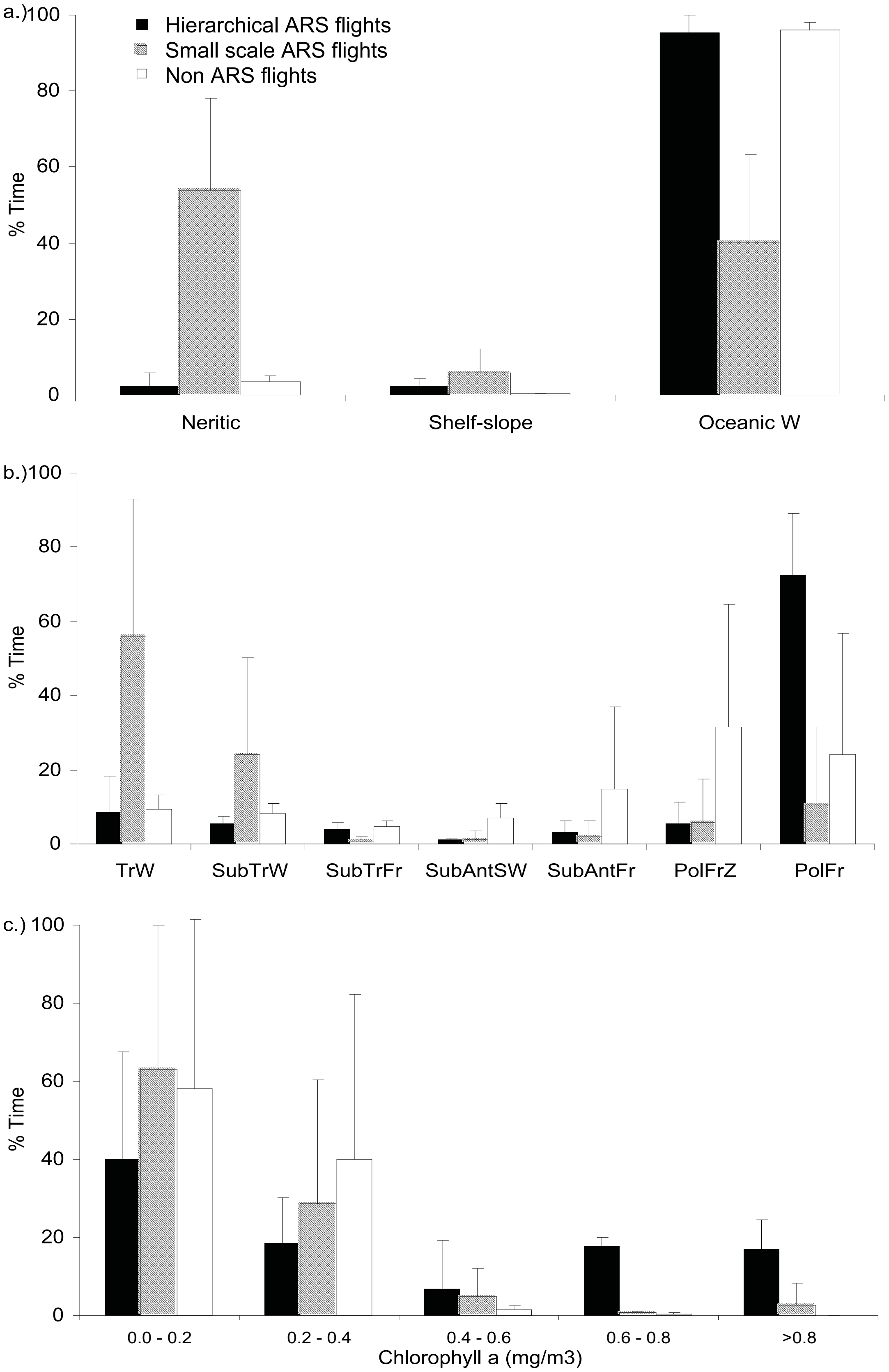

Fig. 3.5. Mean (SD) percent of time spent in each habitat type in relation to ARS spatial scales. Showing a.) Depth, b.) Sea surface temperature, and c.) Chlorophyll a concentration.

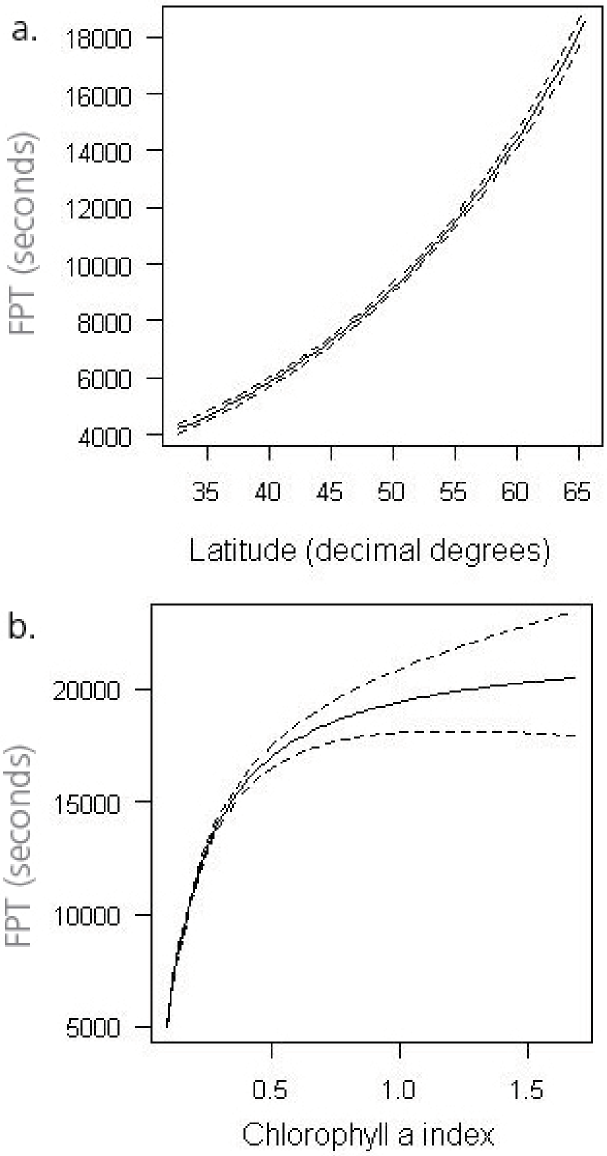

Fig. 3.6. Regression of GLMM models showing the residuals of the predicted relationship between FPT and oceanic variables for hierarchical LT foragers when analysed at the individual scale, showing: a.) positive relationship between FPT and LAT (Latitude); and b.) positive relationship between FPT and Chl *a* index.

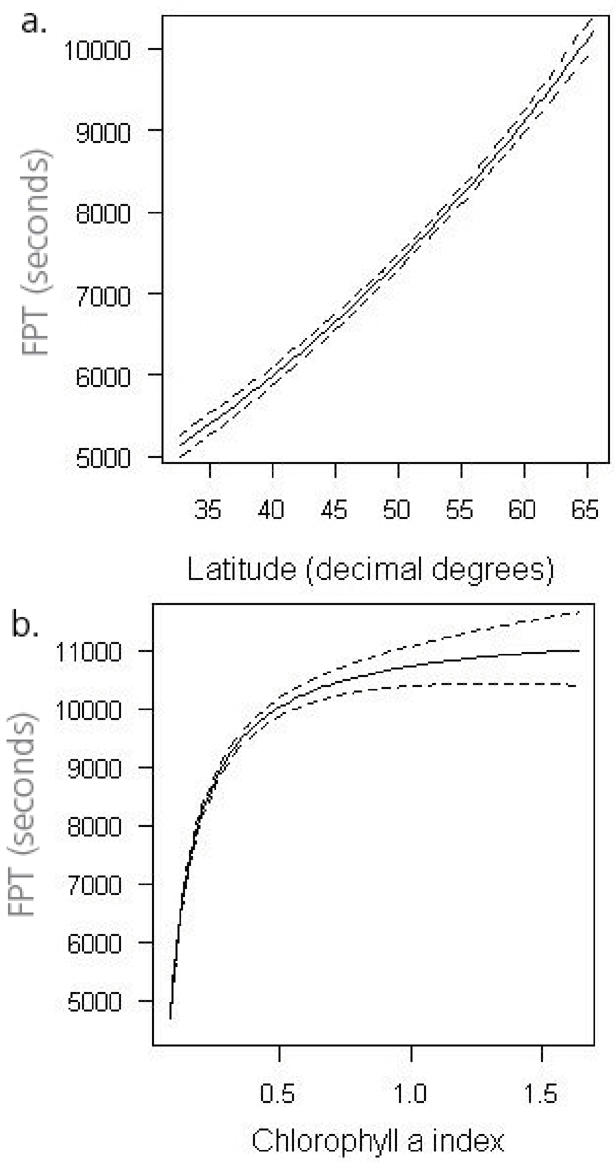

Fig. 3.7. Regression of GLMM models showing the residuals of the predicted relationship between FPT and oceanic variables for LT foragers who employed search effort directly at small scales (i.e. no nested scale of search effort detected), showing: a.) a positive relationship between FPT and LAT (Latitude); and b.) a positive relationship between FPT and Chl *a* index.

Table 3.1. Foraging parameters of ST showing comparison between ARS vs non ARS foraging parameters. †denotes Mann-Whitney U test, and ‡ denotes ANOVA.

	ARS		No ARS		ARS vs non ARS	
Parameter	Av	se	Av	se	U (†), F (‡)	P
N	19		20			
Trip duration (hrs)	17	2	21	2	†163.5	0.47
Av. speed (km/h)	13	1	15	1	‡0.1	**0.03**
Max speed (km/h)	51	3	66	3	‡4.2	**0.05**
Max. distance from colony (km)	64	7	97	20	†175.5	0.70
Total distance travelled (km)	200	19	266	45	†166	0.52
Av. bearing (degrees)	216	6	223	5	‡0.2	0.63
Meal mass (g)	36.3	5.2	39.5	4.6	†0.17	0.68

Table 3.2. LT flight parameters, and the spatial scale at which birds concentrated their search effort in terms of FPT analysis. Depth regions are: O=oceanic, N=neritic, and SS= shelf slope. NA denotes data that were not available.

Year	Bird ID	Days tracked	Trip duration (days)	Total distance tracked (km)	Distance from colony when signal lost	Min. total trip distance (km)	Max. distance from colony (km)	Max. speed	Av. speed	Large scale (km)	Nested ARS (km)	No. ARS zones	Distance to first ARS zone (km)	Prop. trip ARS (%)	Depth Region	Search Pattern
2005	52459	14	25	3060	4878	7938	4950	65.4	22	80	24	3	3540	32	O	hierarchical
2005	52460	7	28	4959	1790	6749	2667	68.3	33	None					O	non-ARS
2006	52463	24	32	9020	6200	15220	6952	68.2	16.2	500	138	3	3550	34	O	hierarchical
2006	52478	10	NA	2042	970	3012	990	46.2	18	24	None	9	540	42	N/SS	small scale
2006	52465	10	NA	1516	290	1806	927	47.8	9.6	22	None	8	640	30	N/SS	small scale
2006	52464	7	11	1270	710	1980	912	53.5	8	22	None	5	34	53	N/SS	small scale
2007	55958	17	25	8880	3800	12680	3988	68.3	24.4	540	170	9	940	45	O	hierarchical
2007	42962	7	NA	4480	2690	7170	2690	69.8	27.2	260	14	3	415	54	O	hierarchical
2007	52466	13	NA	3470	2800	6270	2831	62.1	12.8	172	48	1	2730	43	O	hierarchical
2007	55942	8	NA	6262	4600	10862	3110	64.6	35.6	64	16	6	2460	25	O	hierarchical
2007	52483	9	NA	5753	2000	7753	3045	55.2	23	48	None	7	2030	35	O	small scale
2007	55965	6	18	3690	2400	6090	2480	66.3	29.2	None					O	non-ARS
2007	55951	10	21	3050	1803	4853	1854	61.6	34.8	None					O	non-ARS
Hierarchical	Mean					10023	4087	66.4	23	269	68	4	2273	37		
	SE					1430	669	1.2	3	84	28	1	539	5		
Small scale	Mean					3638	1469	50.7	15	29		7	811	40		
	SE					1397	526	2.2	7	6		1	427	7		
Non-ARS	Mean					5897	2334	65	32							
	SE					556	246	2	2							
	Median									72						
Total	Mean	10.9	23	4419	2687											
	SE	1.4	1.9	697	486											

Table 3.3. Comparison of generalised linear mixed models of habitat associations of the short-tailed shearwater *P. tenuirostris* for models sets that contained models with some evidence of effects. Showing: a.) Hierarchical LT foragers using a multi-scale individual approach (n=7); b.) Hierarchical LT foragers using a median population scale (72km) (n=7); c.) Small scale LT foragers using a multi-scale individual approach, and excluding the individual LT that foraged in oceanic waters, i.e., neritic birds only (n=3); d.) Small scale LT foragers using a median population scale (72km). Explanatory variables are elevation = *LAT* latitude, *BATH* depth, *Chl a* chlorophyll a concentration, *Chl ag* chlorophyll a gradient, and *SSHg* sea surface height gradient. FPT was the response variable, and individuals were included as a random effects. wBIC and wAIC_c are the relative model weights, which denote the strength of evidence for each model relative to the entire model set.

Model	wBIC	_BIC	wAICc	_AICc	% dev
a.)					
Null model	0.694	0.000	0.225	0.000	0.00
lFPT ~ LAT + (Bird ID)	0.057	4.979	0.106	1.513	10.43
lFPT ~ Chla + (Bird ID)	0.049	5.309	0.089	1.843	4.94
lFPT ~ SSHg + (Bird ID)	0.047	5.396	0.086	1.930	3.50
b.)					
Null model	0.750	0.000	0.235	0.000	0.00
lFPT ~ Chlag + (Bird ID)	0.039	5.750	0.072	1.850	4.15
lFPT ~ LAT + (Bird ID)	0.042	5.770	0.092	1.884	3.67
lFPT ~ Chla + (Bird ID)	0.040	5.860	0.088	1.974	2.10
c.)					
Null model	0.615	0.000	0.192	0.000	0.00
lFPT ~ LAT + (Bird ID)	0.052	4.943	0.079	1.771	4.84
lFPT ~ BATH + (Bird ID)	0.051	4.977	0.077	1.806	4.34
lFPT ~ SSHg + (Bird ID)	0.050	4.995	0.077	1.823	4.09
d.)					
Null model	0.374	0.000	0.232	0.000	0.00
lFPT ~ LAT + (Bird ID)	0.104	2.565	0.112	1.455	45.99
lFPT ~ Chla + (Bird ID)	0.076	3.184	0.083	2.073	21.22

CHAPTER 4

INTER-YEAR VARIABILITY IN THE FORAGING REGIME, DIET AND CHICK GROWTH OF A WIDE RANGING SEABIRD

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INTER-YEAR VARIABILITY IN THE FORAGING REGIME, DIET AND CHICK GROWTH OF A WIDE RANGING SEABIRD

Einoder, L. D. (Candidate)
Collected all data, performed analysis on all samples, interpreted data, wrote manuscript and acted as corresponding author
I hereby certify that the statement of contribution is accurate
Signed
……………………………………………………………………………….Date…………………

Page, B.
Supervised development of work, contributed to planning of field work and analysis, and provided critical evaluation of drafts.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
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Goldsworthy, S. D.
Supervised development of work, and provided critical evaluation of a draft.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
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ABSTRACT

We examined the provisioning strategy and diet of the short-tailed shearwater *Puffinus tenuirostris* over three successive years to assess variability in energy delivery from the short-trip and long-trip component of their dual-foraging strategy. Inter-annual comparisons at a single colony revealed extensive variation in the number of successive short-trips, and in their duration. A year of increased short-trip foraging resulted in increased feeding frequency, but not provisioning rate, as smaller meals were returned. In this same year short-trip meals also contained a high % mass of low-energy prey (Australian krill *Nyctiphanes australis* and cephalopods). These factors reduced the rate of energy flow to chicks from short-trips compared to other years where fewer, but larger, short-trips meals contained mostly higher energy fish (jack mackerel *Trachurus declivis* and anchovy *Engraulis australis*). Prey composition of long-trip meals also differed between years, with the amount of high-energy oil being elevated in years of reduced short-trip foraging. Despite inter-annual and inter-colony variation in feeding and growth chicks attained a similar peak mass. These findings demonstrate considerable flexibility in the dual foraging strategy, and indicate that adults are able to maintain a suitable rate of energy flow to chicks in years of varied neritic foraging conditions. This is achieved by modifying the time spent performing short-trips, and the volume of oil returned from long-trips, likely in response to changing prey availability.

INTRODUCTION

The heterogenous distribution of resources in the marine environment has played a large role in the evolution of seabird foraging and reproductive strategies. This is evident in the dual-foraging strategy employed by many Procellariiforms (albatrosses, shearwaters and petrels), where adults rearing chicks can divide their time between foraging trips of short and long duration (Baduini and Hyrenbach 2003). Short trips (ST) are largely confined to neritic (continental shelf) and shelf-break waters surrounding breeding colonies, while long trips (LT) typically involve travel to more distant oceanic waters in search of prey (Weimerskirch and Cherel 1998). The major advantage being that individuals can make decisions about where to forage based on current conditions (Baduini and Hyrenbach 2003). Variable productivity, common of many neritic environments, can be avoided by exploiting more predictable resources associated with larger scale oceanic features (e.g. fronts, gyres, large-scale eddies and upwellings) (Pinaud and Weimerskirch 2005). This dual strategy provides a degree of flexibility to Procellariiforms, the extent of which is governed by their behaviour, physiology and life-history. Studying a seabirds foraging and breeding parameters across a range of feeding conditions provides a means of assessing the flexibility in their foraging regime, which is required to identify their ability to buffer chicks over variable feeding conditions (e.g., Weimerskirch 1998).

To test the extent of flexibility provided by the dual foraging strategy we selected a study species that employs a relatively extreme dual strategy, in a location of well known variability in neritic productivity. Breeding short-tailed shearwaters *Puffinus tenuirostris* divide their time between temperate neritic waters around their breeding colonies in south-eastern Australia and the distant oceanic waters of the Southern Ocean (Nicholls *et al.* 1998, Weimerskirch and Cherel 1998, Klomp and Schultz 2000). For colonies located in the eastern Great Australian Bight, ST are performed in neritic waters of higher primary and secondary productivity than in other parts of Australia (Ward *et al.* 2006). This is due to the influence of a coastal up welling system that operates during summer (Kampf *et al.* 2004, Ward *et al.* 2006).

The strength and duration of this feature fluctuates widely, and contributes to high variability in productivity in the region (Kampf *et al.* 2004, Ward *et al.* 2006). We hypothesise that the foraging regime performed by chick-rearing short-tailed shearwaters will vary spatially and temporally due to expected changes in neritic productivity around the study colonies.

Inter-annual and inter-colony variation in foraging parameters have been identified in a range of Procellariiforms (e.g., Weimerskirch *et al.* 1996, Quillfeldt and Peter 2000, Peck and Congdon 2005), and often provide an indication of variability in prey availability (Hamer *et al.* 1998, Peck and Congdon 2005). Despite a thorough documentation of the short-tailed shearwaters provisioning strategy (Hamer *et al.* 1997, Weimerskirch and Cherel 1998, Bradley *et al*. 2000, Schultz and Klomp 2000), and the pattern of chick growth (Oka *et al.* 1987, Saffer *et al.* 2000), no studies have identified the existence and extent of spatial or temporal variation in these parameters. Long term studies of this species have focused on breeding success and other population parameters, which provide an effective indication of long term demographic changes (Serventy and Curry 1984). However, nutritional and foraging parameters fluctuate on a much shorter time scale, and hence provide a more immediate indicator of changes in prey availability (Einoder 2009).

Changes in the rate of growth and peak mass of Procellariiform chicks are likely to reflect feeding conditions in both neritic and oceanic waters, due to the adults division of time between these two habitats. ST play a vital role in chick rearing as they act to boost energy flow to chicks by increasing feeding rates (Chaurand and Weimerskirch 1994, Weimerskirch 1998, Weimerskirch and Cherel 1998). LT are also of immense value as they enable adults to accumulate lipid-rich stomach oil, which is required to meet the energy demands of chicks (e.g. Obst and Nagy 1993).

Due to these roles the abundance and availability of prey in both LT and ST foraging areas is likely to influence trip duration and foraging success, which will influence the size and energy value of meals delivered to chicks. Under varied foraging regimes energy flow from ST and LT are expected to vary, however this has not been studied for any Procellariiform. We hypothesise that years of varied provisioning rates will have little influence on the peak mass attained by chicks. This is based on the expectation that adults are capable of overcoming moderate variability in foraging conditions in either neritic or oceanic waters due to the flexibility in their dual foraging strategy. We also expect that when relatively large meals of high energy value are returned from ST fewer successive ST will be performed. It is well known that ST come at a cost to adult body condition (Tveraa *et al.* 1998, Weimerskirch 1998), so the delivery of fewer meals of increased energy content will enable adults to meet the energy requirements of chicks more quickly.

Assessing relationships between provisioning and chick growth should also consider the composition of meals to gain a more accurate indication of energy delivery to chicks (Weimerskirch and Lys 2000). Dietary studies have revealed that short-tailed shearwaters are generalist predators, taking a wide range of prey from numerous trophic levels (Montague *et al.* 1986, Skira 1986, Weimerskirch and Cherel 1998). *Nyctiphanes australis* (Australian krill) are among the most readily consumed prey type during the breeding season, and dominate the diet in terms of frequency of occurrence and numerical abundance (Montague *et al.* 1986, Skira 1986, Weimerskirch and Cherel 1998). Due to the large discrepancy in size between *N. australis* and other components of the diet (fish and cephalopod), measures of frequency of occurrence and numerical abundance say little about the actual contribution of each prey type to the energy value of a meal. As such, past dietary studies are of little value when assessing how changes in the abundance and availability of certain prey are likely to influence this species.

METHODS

Diet sampling

Stomach samples were collected from adults during the pre-hatching (burrow preparation and incubation, Oct-Dec), and chick-rearing stage (Jan-Apr) on Althorpe I. (35°37'S, 136°86'E) (Fig 4.1). Stomach samples were collected using the water off-loading technique (Wilson 1984), stored in a vial and frozen. Birds were identified by a numbered leg band, to prevent sampling the same individual twice in a single breeding season. Most individuals were identified as returning from either a ST or LT by monitoring their time at sea. This was measured by assessing their visitation at numbered burrows on a nightly basis.

Identification of prey items

After defrosting diet samples in the lab, those containing oil were poured into a measuring cylinder to record the amount (± 1 ml), and mass (± 0.001 g). The remaining liquid and solid fraction was separated by gravity over a 0.25 mm sieve (Connan *et al.* 2005), and solids weighed using an electronic balance (± 0.001 g). Oil mass was added to the wet weight of the solid fraction. The sample was roughly divided into prey type (fish, cephalopods, crustacean) and a % of the whole sample mass was assigned to determine the approximate wet mass of each prey type (Cherel *et al.* 2002). Hard and soft parts were sorted under a dissection microscope for species identification. Counts of the number of right and left otoliths (fish), upper and lower beaks (squid), or pairs of eyes (crustaceans) were made for each taxon to provide estimates of the minimum number of individuals (Hull 1999). Reference collections and published material was used to identify cephalopods (Lu and Ickeringill 2002), crustaceans (Ritz *et al.* 2003) and bony fishes (Williams and McEldowney 1990). Otoliths that could not be identified, or were absent in samples containing other fish hard parts, were recorded as 'unidentified fish'.

Reconstructing diet composition

Numerical abundance, frequency of occurrence and percentage mass (% mass) were used to describe the diet (Duffy and Jackson 1986). Percentage mass differs from approximate wet mass (described above), as it involves a more accurate calculation of the contribution of each prey type, by reconstructing the diet based on prey remains. The degree of digestion of soft tissue and otoliths was scored using the digestion index of Robertson et al. (1994). In heavily digested samples % mass was reconstructed from the number and size of otoliths, beaks, and crustacean bodies. All otolith erosion categories were used to reconstruct the numerical abundance of fish prey, but the % mass of fish was only reconstructed for otolith erosion categories 1 and 2 of Robertson et al. (1994) (as in Hull 1999). Where more heavily digested otoliths were found, fish biomass was estimated using average values for the same species in other samples that were collected at the same time. In instances where otoliths were not present, the approximate wet mass (see above) of the fish component was considered the biomass of raw fish. Species-specific regressions were used to estimate the length and mass of prey (Hindell 1988, Williams and McEldowney 1990, Gales and Pemberton 1994). Cephalopod mass was estimated from the upper or lower rostral length of beaks using species-specific regressions (Lu and Ickeringill 2002, Rodhouse *et al.* 1996). Beaks were categorised according to their degree of erosion following Hull (1999) and % mass was only derived from erosion category 1 to avoid overestimation of cephalopods (Gauthier-Clerc *et al.* 2002). The wet mass of intact krill was gained directly by collecting and weighing 10 individuals per sample using an electronic balance (± 0.001 g). If krill were partially digested then the carapace length of 10 was measured using the graticule in a dissection microscope, and wet mass was calculated using regressions (O'Brien 1988). For other crustaceans (amphipod, copepod, and decapod zoea), wet mass was obtained by weighing 10 individuals (± 0.001 g).

Energy value of prey types

The energy content of raw prey items was measured by blending, drying, pulverising and combusting each sample in a bomb calorimeter, following Tierney *et al.* (2002). Examples of all major prey types were analysed. Raw whole fish of a number of species and ages were attained from vessel board surveys in the study area over the three-year period of this study. Where prey species could not be attained from independent sampling, prey items showing no signs of digestion were collected from stomach samples.

Feeding and growth parameters

Foraging trip duration and the growth rates of chicks were determined by regularly weighing 25 chicks. Each parent was marked using numbered leg-bands, and RFID micro-chips were also used so adults could be identified without capture using a 1 m aerial (ALIAS). The timing of adult visitation was determined when adults knocked down a stick at the burrow entrance which triggered a red light emitting diode. Foraging trips were classified as being either a ST (1 to 3 d) or a LT (> 7 d), as no 4 –

6 day trips were recorded. Meal sizes were determined by weighing chicks at 20:00 using a spring balance (1000 ± 5 g). The time of adult arrival and of chick re-weighing was noted in order to account for the mass lost since feeding through (Hamer *et al*. 1998). This species-specific correction factor is based on the rate of mass loss due to respiration and excretion for chicks of different ages. Measures of daily feeding frequency and meal mass (derived from chick mass changes) enabled the calculation of provisioning rate (g/d) for each individual chick during every 10-days of the entire growth period. Standard error is presented for every value unless specified otherwise.

Statistical analyses

Diet

The variability in prey species between derived groups (trip type, stage of season, year) was assessed using one-way Analysis of Similarity (ANOSIM) on % mass contribution of each prey species. Data were not transformed because biomass values already provide proportional representation that weights dominant taxa (Page et al. 2005). ANOSIM was performed with 1000 randomisations, based on a Bray-Curtis association matrix using the PRIMER package (Clarke and Warwick 2001). Only species/genera/families (depending upon the lowest level of classification attained) present in >2 % of samples were evaluated (Abookire and Piatt 2005). The prey taxa responsible for significant differences were identified using similarity percentages (SIMPER) (Clarke and Warwick 2001). Inter-seasonal variation in the diet was examined by splitting samples into four stages. Burrow preparation and incubation were pooled to represent pre-hatching (Oct to 17 Jan). Chick rearing was divided into three stages based on the age of each chick (as in Quillfeldt 2001): early (1 – 30 days old); mid (31 – 60 days old); and, late (61 – 90 days old). The oil component of LT meals was compared between years, and stages in season using one-way ANOVA. Due to significant differences in the species composition of ST and LT meals, % biomass was not pooled between trip types, and only ST meals were used for analysis due to larger sample sizes (Table 1). Significant inter-seasonal variation meant that inter-annual comparisons were only made from samples collected at the same stage of breeding. Also, inter-annual data was not pooled for seasonal analysis, because significant differences occurred between years.

Feeding parameters and chick growth

The size of stomach-flushed meals was compared between derived groups (trip type, stage of season, year) using one-way ANOVA. Daily mass change was determined by calculating the mass gain or loss for individual chicks over a 24 h period beginning at 20:00, and ending at 20:00 the next day (Peck *et al.* 2004). If chicks died, or were below average adult mass at the end of chick-rearing (~90 days old), they were excluded from feeding and growth analysis. Mean meal mass derived from stomach flushing underestimated mean chick mass changes for the same 10-day period by an average of 55 % for LT meals, and 60 % for ST meals. Due to this discrepancy provisioning rate was calculated using mean chick mass changes. Trip duration, provisioning rate and average daily mass change were compared using Kruskal-Wallis χ^2 and U-tests, because they were not normally distributed.

A series of growth curves were applied to mass data for each chick. In all instances the logistic model ($W=A/[1+e^{-k(t-t1)}]$) provided the best fit, by gaining the highest residual sum of squares (r^2). W is body mass (g) at age (t), k is slope which provides an index of growth rate (g/d), and A is the asymptote of each curve representing peak mass (g) (as in Lorentsen 1996, Hedd *et al.* 2002). One-way ANOVA and Kruskal-Wallis χ^2 was used to compare growth parameters between years. The relationship between prey composition of the diet and chick growth during each of the three chick rearing stages (defined previously) was examined using Pearson's correlation coefficient (χ^2), or Spearman's K.

RESULTS

Variation in the diet

Of the 460 stomach samples collected 342 (75 %) contained prey items and the remainder were empty. Of all samples *N. australis* occurred in 44 %, bony fish in 41 %, other crustaceans in 35 %, and cephalopods in 31 % (Table 4.2). Most samples contained more than one prey type. *N. australis* was the most numerically abundant prey, accounting for 77 % of the individual prey items consumed, and crustaceans from five other families (mainly Decapod zoea and *Hyperiidae sp*.) made up a further 22 %. Fish and cephalopods accounted for the remaining 1% numerical abundance (Table 4.2). *Nyctiphanes australis* accounted for 36 % mass, fish 35 % mass, and cephalopods 22 % mass (Table 4.2). Twelve pelagic fish species with distributions largely confined to continental shelf waters were recorded, as well as nine species from oceanic waters (seven *Myctophidae*, one *Paralepidae*, and one *Gonostomatidae*) (Table 4.2). Eight species of cephalopods were identified, with *Notodaris gouldi* accounting for 91 % of this prey type by number.

LT meals differed from ST meals by containing an oil component which averaged 30 to 60 % meal mass between years (Fig 4.2a). LT meals also differed by containing the remains of oceanic fishes, primarily *Myctophidae*, which constituted up to 20 % of the mass of some LT meals. The average % mass contribution of

Myctophidae in meals returned to chicks was low, ranging from 0 – 10 % between years (Fig 4.2b). The importance of each *Myctophidae* species was low, due to the diversity of species involved (n=9, Table 4.2). The remaining 40 – 70 % mass of the raw prey component of LT meals was comprised of neritic species (Fig 4.3b, and c), indicating that adults returning from LT foraged over neritic waters. The % mass of neritic prey types returned in LT and ST meals to Althorpe I. differed significantly ($P = 0.05$) in most years (Table 4.3). Differences were attributable to the return of an increased % mass of *N. australis* in ST meals in the 2005/06, compared to LT meals, which contained a larger proportion of cephalopods (Fig 4.2 b and c). Differences in the 2006/07 breeding season was again attributable to the increased importance of *N. australis* in ST meals, compared to the predominantly fish based LT meals (Fig 4.2b, c). This pattern was reversed in 2004/05 where LT meals contained more *N. australis* (Fig 4.2b, c).

Inter-seasonal comparisons of ST meal composition revealed an increase in the % biomass of fish and a decrease in the importance of *N. australis* through the breeding season in both 2005/06 and 2006/07 (Fig 4.3a and b). This transition in prey composition did not occur in 2004/05, as fish dominated the diet from early to late chick rearing (Fig 4.3a). ANOSIM showed that inter-seasonal differences in meal composition were significant between all stages of chick-rearing in 2005/06 (Table 4.3). ST meal composition did not differ significantly throughout the breeding season of 2004/05, due to the fairly consistent content of meals (Table 4.3). Despite variation in ST meals composition in 2006/07 (Fig 4.3a and b) this was not significant (Table 4.3). SIMPER analysis revealed that significant differences in 2005/06 were due to the relatively high amount of *N. australis* in early compared to late chick rearing, while the increase in cephalopod in late chick rearing also contributed highly (Fig

4.3). SIMPER also revealed that significant differences in early and mid chick-rearing in this year was attributable to the combined effects of a decrease in *N. australis*, and increase in cephalopod.

The composition of ST meals in 2004/05 could not be included in inter-annual comparisons due to a low sample size. ANOSIM showed that the diet in early-chick rearing was consistent between 2005/06 and 2006/07, characterized by the moderate importance of *N. australis*. Mid chick-rearing meal composition differed between years (Table 3), due to the increased importance of the fish *T. declivis* in 2004/05, in comparison to increased *N. australis* in 2005/06. Significant differences existed in the late chick-rearing stage also, with SIMPER analysis indicating that *T. declivis* was dominant in 2006/07, whereas cephalopods were of increased importance in 2005/06 (Fig 4.3c). Inter-colony comparisons revealed that *N. australis* was of reduced importance at the westerly located Evans I. (Fig 4.2b), however, this was not deemed significant using ANOSIM (Table 4.3).

LT meals were not included in the inter-annual analysis, but the raw prey component returned in 2005/06 also contained a larger proportion of cephalopods than in any other year (Fig 4.3b). *T. declivis* contributed to most inter-annual comparisons as it was the single most important fish species in ST meals, but its occurrence varied considerably from year to year (Fig 4.4). The fish component was most variable in 2004/05, when *Engraulis australis* was the second most important species, while *E. nitidus* was an important component of the diet in 2006/07 (Fig 4.4).

Variation in feeding parameters

LT and ST meals were smallest at early chick rearing (range average 17.7 g to 56.9 g) (Table 4.4), and largest during mid chick rearing (range average 74.7 g to 96.1 g) (Table 4.4). LT meals were larger than ST meals during all stages of chick rearing, in all years, and at Evans I. (Table 4.4). Size differences were most apparent in 2005/06 at Althorpe I. where LT meals were significantly larger during all stages of chick rearing.

LT meals delivered to chicks were fairly similar in mass between years and colonies, but ST meals were more variable in mass (Table 4.4). Variation was attributable to consistently smaller ST meals at Althorpe I. in 2005/06 compared to other years. This difference was significant in late chick rearing when ST meals averaged 23.5 g in 2005/06, but double to an average 55.1 g in 2004/05, and 57 g in 2006/07 (Table 4.4).

The consistently small size of ST meals in 2005/06 coincided with an increase in the number of successive ST that were performed between two LT by individual adults (Fig. 4.5). For example, in the early chick rearing stage of 2005/06 adults performed an average of 3.2 ± 0.2 successive ST, which was significantly more than the 2.3 ± 0.2 ST conducted in 2006/07 (Kruskal-Wallis: $\chi^2=12.22_2$, $P<0.05$). A significant increase in the number of successive ST also occurred during mid-chick rearing in 2005/06 compared to 2004/05 (Kruskal-Wallis: $\chi^2=16.83_1$, $P<0.05$, Fig 4.5). Inter-annual variation in feeding frequency was further influenced by the duration of ST. ST duration ranged from 1 to 3 days. Of all ST recorded in 2005/06, 91 % were a duration of 1d, compared to 82 % in 2006/07, and 55 % in 2004/05 (Fig 4.6). ST meal mass was not correlated with trip duration (Pearson $R^2=0.08$, $N=65$, $P=0.34$). These combined factors increased feeding frequency in 2005/06. Despite the return of smaller ST meals to the colony in this year, elevated feeding frequency enabled adults to maintain a provisioning rate comparable to that of the previous and following year (Table 4.5).

LT duration ranged from 7 to 32 d duration. The average duration of LT was consistent between years in both the early and mid chick rearing stages, but varied largely during late chick rearing. At this time LT averaged 21 ± 1 d in 2004/05, in comparison to 14 ± 1 d in 2006/07 (Fig 4.7). Oil content of LT meals was comparable between 2004/05 and 2005/06 on Althorpe I., but increased significantly in 2006/07 ($F_{1,3}$ =6.13, P <0.05, Fig 4.2a), accounting for an average 55.3 % meal mass. Oil volume was not correlated with LT duration (Pearson R^2=0.21, N=18, P=0.13), however, trip duration was only recorded for 15 of the birds from which oil was collected.

Inter-colony comparisons in 2004/05 revealed that ST meals returned at Evans I. were significantly smaller than those returned at Althorpe I. in the same year, but of similar size in 2005/06 (Table 4.4). LT meals were of more comparable size at both colonies (Table 4.4), but at Evans I. they contained a significantly higher proportion of oil (av 60.1 % meal mass) compared to Althorpe I. in the same year ($F_{1,28}$ =10.37, P <0.05) (Fig 4.2a). The significantly lower provisioning rate recorded at Evans I. in comparison to Althorpe I. (Table 4.5) is largely attributable to data collection being restricted to early chick rearing on Evans I.

Influence of feeding parameters and diet on chick growth

Despite inter-annual and inter-colony variation in a number of feeding parameters, the rate of chick growth and peak mass attained by chicks did not differ significantly between years or colonies (Table 5). Comparisons of the growth rate of chicks that survived to fledging during each chick-rearing stage revealed significant differences in average daily mass gain between years and colonies. Comparisons across all three years could not be made during early chick rearing at Althorpe I., due to an absence of data in 2004/05. Daily mass gain during early chick rearing was higher in 2005/06 compared to 2006/07, and approached significance (P=0.08, Table 4.5). Inter-annual differences were also apparent in the pattern of chick growth. In 2005/06 chicks grew fastest in early chick rearing, gaining an average of 25.0 ± 5.2 g/g (Table4.5). Whereas, in 2006/07, chicks grew fastest during the mid-chick rearing stage (Table 4.5). This different growth pattern contributed to a significant increase in 2006/07 compared to 2005/06 (Table 4.5).

The rate of chick growth during early chick rearing was significantly lower on Evans I. in 2004/05 compared to growth at Althorpe I. in the following two years (Table 4.5). This low growth rate is attributable to a significantly reduced provisioning rate in on Evans I.. Despite a slow growth rate in early chick rearing, peak mass of Evans I. chicks was comparable to Althorpe I. in the same year (Table 4.5), indicating that the rate of chick growth must have increased substantially during the mid and late chick rearing stages when data was not collected.

The daily mass change of individual chicks was positively correlated with the rate at which they were provisioned during the same early, mid, and late stage in 2004/05, and 2006/07, but not in 2005/06 (Table 4.6). Daily mass change of chicks was not correlated with the % mass of any single prey type in ST meals on Althorpe I. (Table 4.6). Despite the absence of any direct correlation, the reduced growth in the mid chick rearing stage of 2005/06 corresponded with the major dietary discrepancy between years, being the increased consumption of *N. australis* during this stage. Reduced growth rate in late 2005/06 (Table 4.6), also corresponded with an increase in the importance of cephalopods, which constituted 38 % biomass, compared to 9.8 % and 10 % in 2004/05 and 2006/07, respectively (Fig 4.3c). The implications of these dietary changes on growth are apparent when we consider that the energy value of *N. australis* and cephalopods is comparable to other crustaceans (*Hyperiid sp*., and Decapod zoea), but lower than the major pelagic bony fish species consumed (Table 4.7). The energy value of ST meals is also likely to be influenced by the pelagic fish species that are taken, as their energy content was also found to vary (Table 4.7). *E. australis* were more energy-dense than *T. declivis* (Table 4.7). As such, in 2004/05 and 2006/07 when *E. australis* and *Emmelichthys nitidus* (redbait) formed a larger part of the diet, the energy value of ST meals was likely to be higher than in 2005/06, when *T. declivis* accounted for 84 % of the identifiable fish component in the diet (Fig 4.4).

DISCUSSION

Inferring productivity from variation in the foraging parameters

We have documented extensive inter-annual and inter-colony variation in foraging parameters of the short-tailed shearwater. These findings support our expectation that adults from colonies within the eastern Great Australian Bight experience considerable variation in neritic productivity both within and between breeding seasons. Neritic productivity is largely influenced by a local wind-driven upwelling system (Kampf *et al.* 2004, Ward *et al.* 2006, Middleton and Bye 2007), which has been linked to measures of pelagic fish production and abundance in the region (Ward *et al.* 2006). Previous studies on short-tailed shearwaters in other parts of their breeding range found that chick rearing adults perform between one and three successive ST (Weimerskirch and Cherel 1998). Short-tailed shearwaters in the eastern Great Australian Bight performed an average of 3.4 ST in 2005/06, with a maximum of eight successive ST. This extent of ST foraging suggests that neritic waters surrounding breeding colonies in this region are able to sustain an elevated rate of ST foraging compared to other study areas. Or, conversely, increased foraging effort was required in neritic waters of the eastern Great Australian Bight to return an adequate supply of food to chicks.

Interpreting feeding conditions from seabird foraging behaviour is reliant upon our understanding of how seabirds respond to changes in the distribution and availability of their prey (Fauchald *et al*. 2000). Few studies provide evidence of a direct link between the provisioning of dual foraging Procellariiforms and near colony resource availability (Peck and Congdon 2005). More commonly, increased feeding frequency is interpreted as a response to increased food abundance (Quillfeldt and Peter 2000). In the absence of any direct measures of marine productivity or prey availability we cannot identify the direct links between feeding conditions and foraging parameters of the short-tailed shearwater. Instead, we interpret that the colony wide variation in feeding parameters and diet is a reflection of the dynamic nature of the prey community in the region (as in Montevecchi 1993, Litzow *et al.* 2002).

Several relationships that apply to wide-ranging seabirds are reasonably well founded. These include; that prey is captured at a faster rate when it is more available, reflected by reduced trip duration and an elevated provisioning rate (e.g. Weimerskirch 1998); and, when prey patches are more widely dispersed and harder to find trip duration often increases (e.g. Berrow and Croxall 1999, Hedd *et al.* 2002, Harding et al. 2003). If we assume these relationships apply to the short-tailed shearwater then the foraging conditions inferred from the range of parameters measured are contradictory. The predominance of single day ST in 2005/06 could be interpreted as an indication of increased neritic feeding conditions in this year, compared to the increased occurrence of two and three day ST in 2004/05 and

2006/07. Conversely, all other foraging parameters suggest poorer neritic feeding conditions in 2005/06.

For example, the return of smaller ST meals in 2005/06 does not support the notion of elevated neritic productivity. Smaller meals are often interpreted as the result of reduced availability as prey patches are less profitable, or harder to locate (Monaghan 1992). Also, the increased number of successive ST in 2005/06 indicates that adults had to forage more to deliver enough energy to chicks. This relationship is apparent when one considers the role of ST in the context of a dual foraging regime. They play a vital role in boosting energy flow to chicks, and provide the majority of the chick’s protein and nutrient requirements through the delivery of raw prey (Weimerskirch 1998). Therefore, adults should strive to deliver a suitable quantity of food of reasonable energy content to chicks when performing ST, and before the onset of a LT. The increased number of feeds delivered in the 2005/06 year of smaller ST meals suggests that adults respond to reduced foraging success by investing more time and energy into performing additional ST. The capacity of an adult to increase the time spent performing ST is considered to be reliant upon their body condition. This is because dual foragers fuel most, if not all, of their ST energy needs from energy reserves laid down during the previous LT (Tveraa *et al.* 1998, Weimerskirch 1998, Weimerskirch and Cherel 1998). The energy debt incurred during ST is apparent as adults loose mass with successive ST, until a threshold in body condition triggers the onset of a LT (Weimerskirch and Cherel 1998). As ST are detrimental to the adult, we can assume that adults attempt to maximise the rate of energy delivery to chicks. Based on this assumption, the delivery of fewer larger meals of increased energy content would meet the energy requirements of chicks more rapidly, meaning that adults could undertake a LT sooner. The correspondence between changes in the diet and altered foraging regime provides support for our hypothesis that larger ST meals of higher energy prey enable fewer ST meals to be delivered.

Investigating the relationship between time spent in ST, and foraging success in neritic waters may be more useful in studies of individual foraging behaviour, as parental quality is well known to influence foraging success and provisioning in seabirds (Chaurand and Weimerskirch 1994, Tveraa *et al.* 1998). Nevertheless, the colony-based variation in foraging strategy documented here provides an indication of the extent of flexibility in foraging achievable by this species when rearing chicks to fledging.

Variation diet composition

Seasonal dietary changes largely followed that identified by Montague *et al.* (1986), where *N. australis* and other crustaceans are important in the adult diet through to early chick rearing, being replaced by pelagic bony fish during chick rearing. This dietary shift is considered to be driven partly by the reduced availability of krill, but also by the recruitment of suitable sized fish into the population as summer progresses (Montague *et al.* 1986). *N. australis* (Australian krill) is a primary consumer that responds quickly to nutrient fluxes in the marine environment (Murphy *et al.* 1988), and often aggregates in areas of enhanced productivity associated with these upwellings (O’Brien 1988, Gill 2002). Much like other euphausiids and surface swimming crustaceans, fluctuations in the abundance and availability of *N. australis* is well known to be associated with primary productivity (e.g. Skira 1986, Abraham and Sydeman 2004). The prolonged importance of *N. australis* in the diet in 2005/06 suggests they were more available in that year. Availability may also be a reflection of abundance (i.e. neritic productivity), however, the nature of this relationship is unclear. The low importance of *N. australis* in the diet at Evans I. suggests this prey type is less abundant in the foraging areas exploited by breeding short-tailed shearwaters from this colony. This finding confers with a well known east to west gradient in neritic productivity across the region during the summer due to the influence of a coastal upwelling in the east, which diminishes as waters flow to the west (Ward *et al.* 2006, Middleton *et al.* 2007).

The relationship between upwelling intensity, neritic prey availability, and seabird foraging parameters warrants further investigation, as there are many examples where seabirds can provide an indication of prey availability (Einoder 2009). Future examination with more accurate measures of prey availability (e.g. Litzow *et al.* 2002), and vessel-based assessment of the prey assemblage (Montevecchi 1993) is required in order to accurately identify the prey preferences, and functional relationships between prey availability and their occurrence in the diet (Piatt *et al.* 2007).

The inter-annual and inter-colony variation in the size of LT meals, and in the volume of oil they contain provides an indication of the mechanisms by which LT foraging can play a varied role in energy delivery. For example, the reduced number of ST performed in 2006/07, and the increased quantity of oil delivered, would have boosted energy flow from LT meals. A similarly high oil content was retuned on Evans I. in 2004/05, which, given the small size of ST meals delivered, would have contributed to elevated energy returns from LT. The value of these LT meals is evident when we consider that chicks at Evans I. were able to attain a peak mass similar that of Althorpe I. chicks who received nearly double the rate of food delivery. The disproportionate role of LT meals in the allocation of energy to chicks confounds the interpretation of variable ST feeding conditions on chick growth in dual foraging seabirds.

Relationship between chick growth, diet and provisioning

Measures of chick growth provide a means of interpreting the fitness consequences of changes in feeding parameters and diet, with peak mass regarded as a particularly useful parameter reflecting growth conditions throughout the entirety of chick rearing (Montevecchi 1993). The comparable peak mass attained by chicks between years and colonies provides evidence that varied feeding strategies and growth patterns can be employed by the short-tailed shearwater. This supports our hypothesis that varied provisioning rates between years will have little influence on the peak mass attained by chicks. Specifically, we have demonstrated that the a similar rate of provisioning can be achieved by the delivery of a smaller number of larger meals of increased energy value, as with the delivery of a larger number of smaller meals of reduced energy value. Such flexibility enables adults to decide whether to forage in near or distant waters, based on current feeding conditions. This result suggests that peak mass may not be a very sensitive indicator of feeding conditions during the breeding season in this species. However, the extent of variation in foraging conditions during the study was not considered to represent anything more than natural variation.

A positive relationship between provisioning rate and chick growth has been identified previously in the short-tailed shearwater (Hamer *et al.* 1998), and is well known among Procellariiforms (e.g. Lorentsen 1996, Huin *et al.* 2000). Increased food delivery corresponded with elevated growth on Althorpe I. in 04/05 and 2006/07, but not in 2005/06. The absence of this expected relationship may be attributable to the wider ranging energy values of meals delivered in this year. The association between a decline in growth rate and lower energy prey has been documented among a broad range of seabirds (e.g. Golet *et al.* 2000, Lewis *et al.* 2001, Bertram *et al.* 2002, Hedd *et al.* 2002). These findings highlight the value of dietary information when interpreting the growth outcomes of varied provisioning.

The absence of a correlation between dietary variables and daily mass change suggests that no single prey type has a bearing on chick growth. This is no surprise given the generalist diet of the short-tailed shearwater. Our ability to identify such relationships was also confounded as the diet of study chicks was not measured directly. Instead, the composition of meals fed to chicks in neighbouring burrows was assumed to reflect that delivered to study chicks. Future studies investigating inter-relationships between diet and growth would benefit from assessing prey consumption of individual chicks (e.g. Roby 1991), and the inclusion of a range of morphometric measures (e.g. Shea and Ricklefs 1996).

An apparent negative association between the prolonged importance of low energy *N. australis* in the diet and reduced chick growth (in 2005/06) is of interest, as they are considered to be an important prey (Montague *et al.* 1986, Skira 1986). The presumed importance of this prey type has even led to suggestions that chick growth is governed by fluctuations in its abundance (Oka *et al.* 1987), as occurs for numerous krill specialists (Quillfeldt 2001). Findings presented here indicate no such link, as a comparable growth rate was attained in a year when *N. australis* was of low importance in the diet (2004/05).

CONCLUSION

This study indicates the extent of colony wide variation in the dual foraging strategy of the short-tailed shearwater under what are considered to be natural levels of environmental variability. While the direct role of elevated neritic productivity on chick growth was not ascertained, it was clear that increased foraging in near-colony waters did not boost energy returns to chicks. The common trend of shorter trip duration under good feeding conditions, apparent in many seabirds (Weimerskirch 1998, Berrow and Croxall 1999, Hedd *et al.* 2002, Harding *et al.* 2003), was not evident in the short-trip component of the short-tailed shearwaters dual foraging strategy. This suggests that trip duration may not be a good indicator of neritic prey availability in wide-ranging seabirds, unless it is accompanied by a consideration of diet. Also, the increased importance of *N. australis* in the diet may be reflective of elevated productivity in neritic waters, however it does not provide an indication of the profitability of ST foraging in terms of energy returns. This study has identified some of the complexities involved in the potential use of dual-foraging species as bio-indicators of neritic prey availability, largely due to the flexibility in their foraging strategy.

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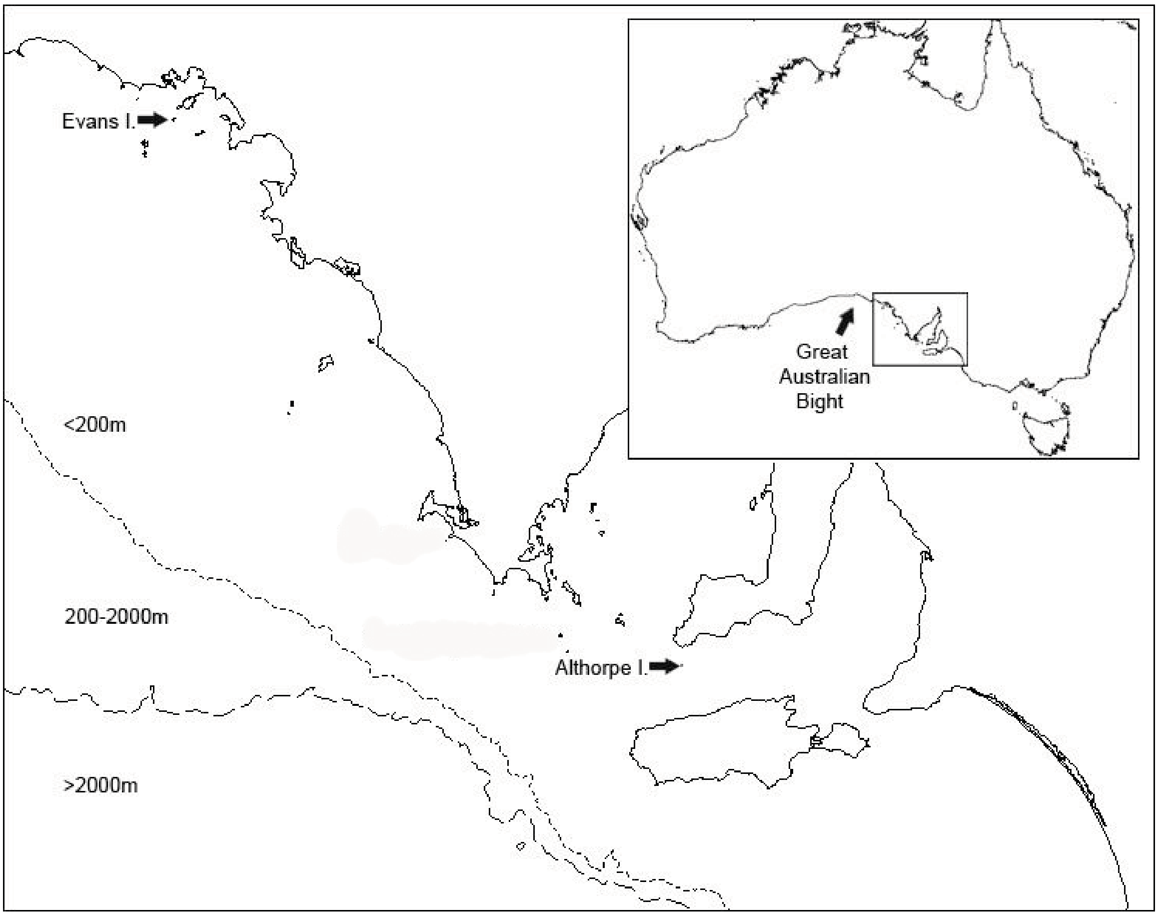

Fig 4.1. Map of the Eastern Great Australian Bight of South Australia, showing the study sites.

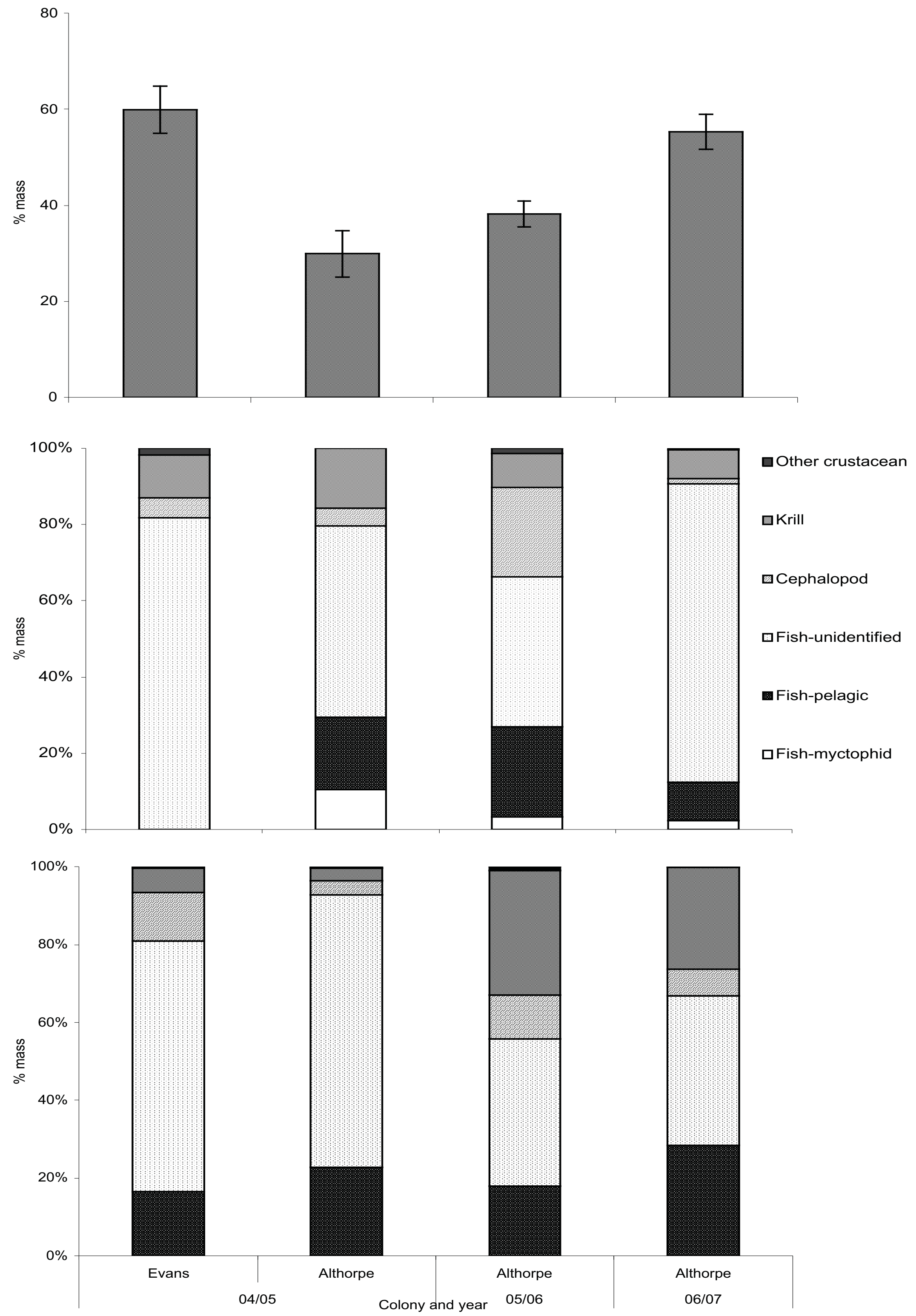

Fig 4.2. General composition (% biomass) of the short-tailed shearwater diet: a.) Proportion of oil in LT meals returned at Althorpe and Evans I. showing ± se (early, mid and late chick rearing combined); b.) Inter-colony inter-year comparisons of raw prey component of LT meals; c.) and ST meals.

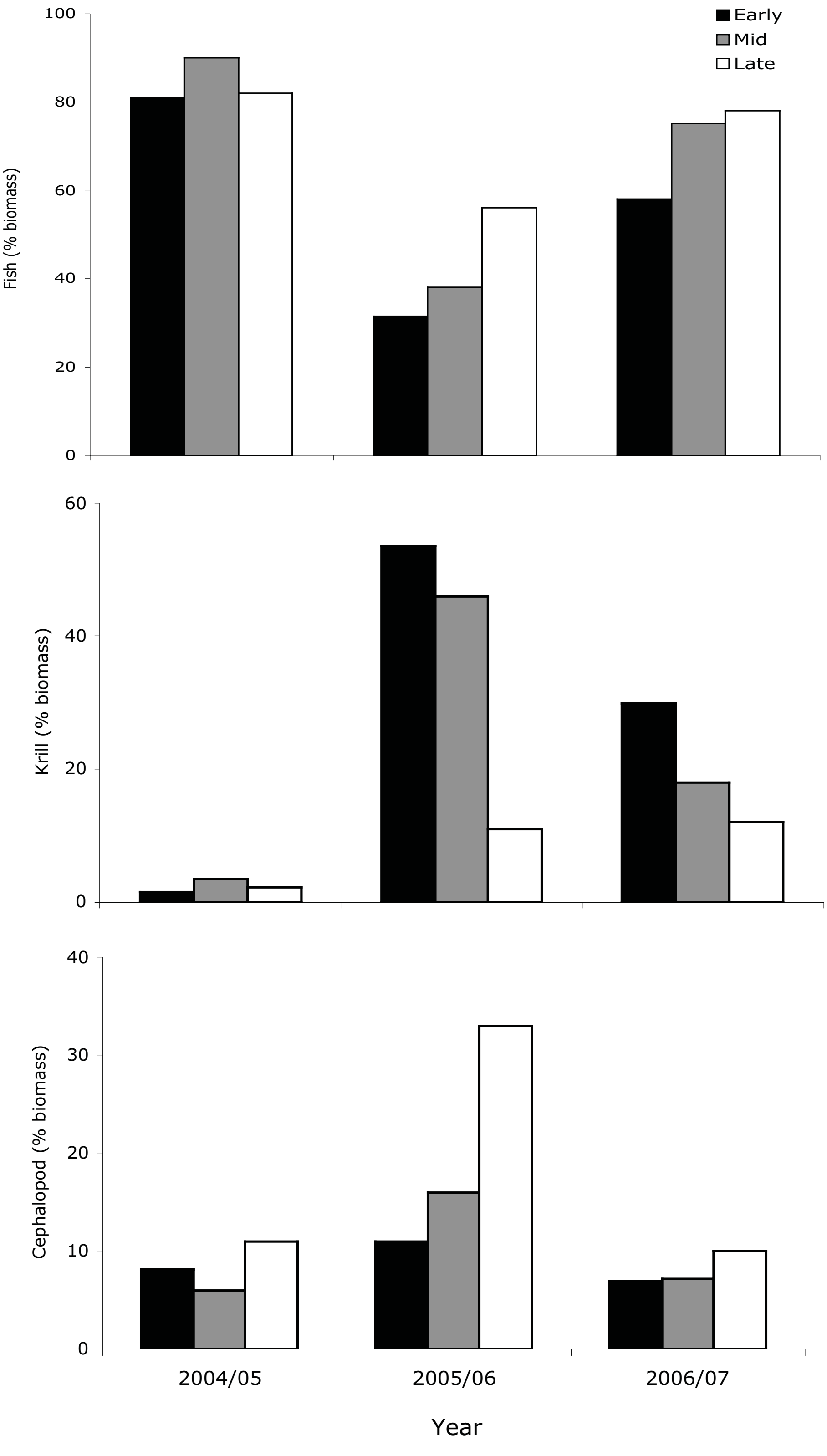

Fig 4.3. Intra and inter-annual variation in the proportion (% mass) of all major prey types in SA meals from Althorpe I, showing: a.) Fish; b.) Krill; and, c.) Cephalopod. Note, other crustaceans have not been included.

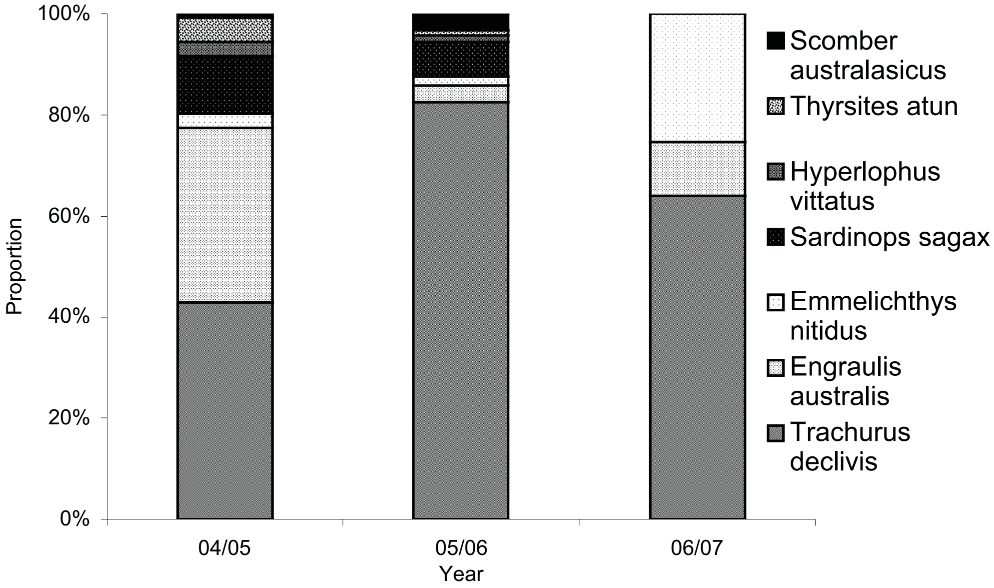

Fig 4.4. Inter annual comparison of the importance (% biomass) of each fish species in ST meals at Althorpe I.

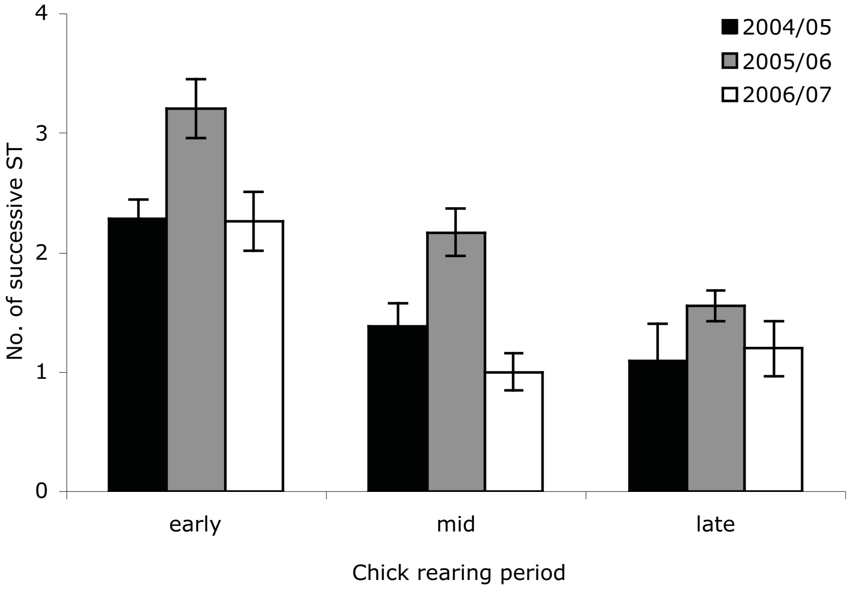

Fig 4.5. Inter-seasonal, and inter-annual variation in the number of successive ST performed by individual birds on Althorpe I. for burrows where chicks fledged.

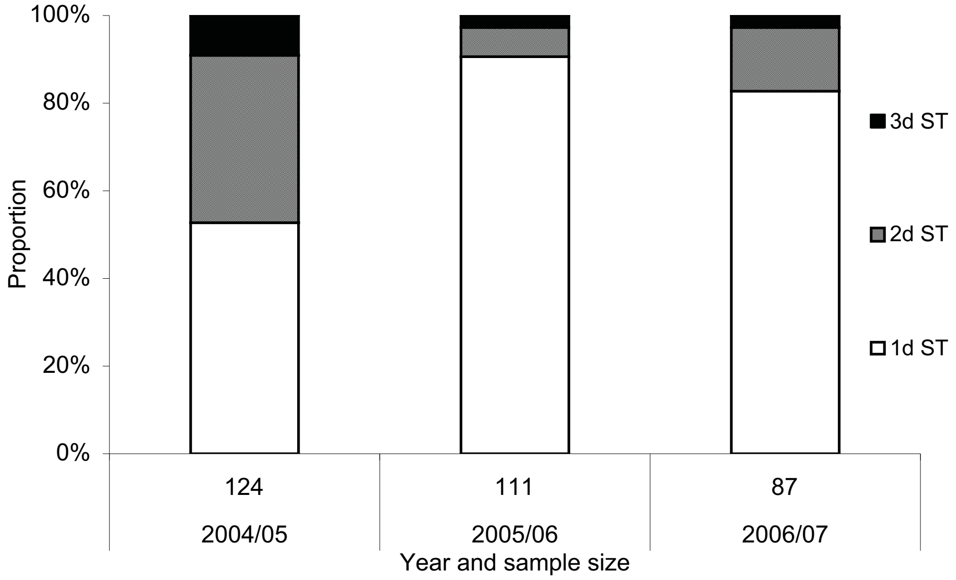

Fig 4.6. Inter-annual variation in the duration of ST at Althorpe I. during chick rearing.

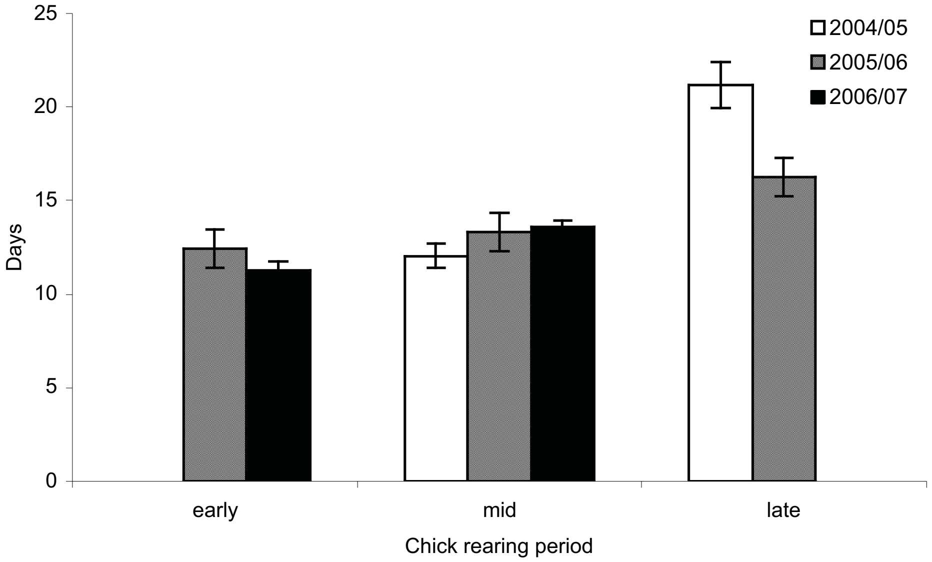

Fig 4.7. Inter-annual variation in the duration of LT at Althorpe I. during chick rearing.

Table 4.1: Digestion categories used in dietary analysis, for; fish tissue; fish otoliths; and, cephalopod beaks.

Category	1	2	3	4	5
Soft tissue	lightly digested, flesh coarsely textured, hard parts evident	moderately digested, fibrous with bones/flesh apparent	heavily digested, finely textured		
Otoliths	removed from the fish skull	no evidence of erosion	evidence of erosion but major features intact	clear signs of erosion, identification becoming difficult	features lost, very difficult to identify
Beaks	removed from buccal mass, flesh still attached	free in sample, with no evidence of erosion	free in sample, margins of wings/lateral walls showing some damage	free in sample, wing hoods/ateral walls completely lost	

Table 4.2. Sample sizes of stomach samples collected from Althorpe and Evans I. during the three year study, only showing the number of samples containing prey items.

		Stage in breeding season>	Early	Mid	Late	
Colony	Year	Trip type				Total
Evans I.	04/05	ST	12		15	27
		LT	10		10	20
Althorpe I.	04/05	ST		23	26	49
		LT		3	19	22
	05/06	ST	23	27	18	68
		LT	14	18	15	47
	06/07	ST	38		37	75
		LT	13		21	34
Total						342

Table 4.3. Species composition of all meals in all years from Althorpe and Evans I. showing the Frequency Of Occurrence (FOO), Numerical Abundance (NA), and Biomass of each species in the diet of short-tailed shearwaters.

	Family	**Species name**	**Common name**	**FOO**	**% FOO in all samples**	**Na**	**% Na in all samples**	**% of that prey type**	**Reconstructed biomass (g)**	**Proportionate biomass (%)**
Cephalopod		**total**		**106**	**31**	**385**	**0**	**100**		**26**
	Histioteuthidae	*Histioteuthidae macrohista*		**1**	0.4	2	<0.1	0.76	10.5	0.1
		Histioteuthis atlantica		**1**	0.2	1	<0.1	0.38	39.2	0.3
	Lepidoteuthidae	*Lepidoteuthis grimaldii*		**1**	0.2	3	<0.1	1.15	218.5	1.9
	Octopoteuthidae	*Octopoteuthis sp.*		**10**	2.8	28	<0.1	10.69	NA	
		uncertain		**1**	0.4	2	<0.1	0.76	NA	
	Ommastrephidae	*Nototodaris gouldi*	Arrow squid	**50**	14.5	239	0.15	91.22	2492.3	22.0
		Todarodes filippovae		**3**	0.8	9	<0.1	3.44	136.1	1.2
	Onychoteuthidae	*Ancistroteuthis sp.*		**1**	0.2	1	<0.1	0.38	1.1	<0.1
		uncertain		**1**	0.4	3	<0.1	1.15	NA	
	Sepiolidae	*Selpiolina nipponensis*		**1**	0.4	2	<0.1	0.76	NA	
	Uncertain			**1**	0.4	2	<0.1	0.76	NA	
	Unid. beaks (eroded)			**35**	10.4	93	<0.1	35.50	NA	
Krill	*Euphausidae*	*Nyctyphanes australis*	Australian krill	**159**	**47**	**122012**	**77**	**100**	4124	**36**
Crustaceans		**total**		**118**	**34.5**	**34533**	**21.88**	**100**		**3.0**
	Hyperid amphipod	NA		**63**	18.5	30781	2.40	43.6	227.5	2.0
	Copepoda	NA		**3**	0.8	17	0.01	0.3	NA	
	Decapoda (zoea)	NA		**34**	10.0	3694	3.06	55.6	118.2	1.0
	Gastropoda	NA		**6**	1.8	20	<0.1	0.3	NA	
	Caridea	NA		**12**	3.4	21	<0.1	0.3	NA	
Fish		**total with otoliths**		**141**	**41**	**866**	**1**	**100**		**35**
	Arripidae	*Arripis georgianus*	Tommy ruff	**2**	0.6	5	<0.1	0.1	NA	NA
	Carangidae	*Trachurus declivis*	Jack mackerel	**33**	9.8	405	0.26	0.1	2256.8	19.9
	Clupeidae	*Hyperlophus vittatus*	Sandy sprat	**1**	0.4	5	<0.1	0.9	NA	NA
		Sardinops sagax	Pilchard	**5**	1.6	8	<0.1	48.4	153.1	1.3
	Emmelichthyidae	*Emmelichthys nitidus*	Redbait	**16**	4.6	40	<0.1	25.2	98.9	0.9
	Engraulidae	*Engraulis australis*	Anchovy	**33**	9.6	247	0.16	0.5	894.0	7.9
	Gempylidae	*Thyrsites atun*	Barracouta	**6**	1.8	11	<0.1	0.1	46.5	0.4
	Gonostomatidae	*Photichthys argenteus*		**1**	0.2	2	<0.1	0.2	NA	NA
	Hemiramphidae	*Hyporhamphus melanochir*	Southern Garfish	**1**	0.2	3	<0.1	0.1	16.1	0.1
	Kyphosidae	*Scorpis lineolata*	Silver sweep	**1**	0.2	1	<0.1	0.5	NA	NA
	Mugilidae	*Aldrichetta forsteri*	Yellow-eyed mullet	**1**	0.2	1	<0.1	0.1	NA	NA
	Myctophidae	*Electrona carlsbergi*		**4**	1.2	21	<0.1	2.5	229.3	2.0
		Electrona paucirastra		**3**	0.8	3	<0.1	0.4	37.1	0.3
		Krefftichthys anderssoni		**2**	0.6	14	<0.1	1.6	100.8	0.9
		Electrona subaspera		**1**	0.4	2	<0.1	0.2	28.4	0.2
		Gymnoscopelus microlampus		**1**	0.2	22	<0.1	2.6	88.3	0.8
		Lampadera notialis		**1**	0.2	1	<0.1	0.1	NA	NA
		Lestidiops similis		**1**	0.2	1	<0.1	0.1	NA	NA
		Unid. Myctophid		**2**	0.6	4	<0.1	0.2	NA	
	Paralepididae	*Magnisudis prionosa*		**1**	0.2	1	<0.1	0.1	NA	NA
	Pomatomidae	*Pomatomus saltatrix*	Tailor	**1**	0.2	1	<0.1	0.2	NA	NA
	Scombridae	*Scomber australasicus*	Blue mackerel	**1**	0.4	2	<0.1	1.2	10.9	0.1
		Unknown species		**2**	0.6	4	<0.1	4.7	NA	NA
	Unid. Otoliths (eroded)			**22**	6.6	62	<0.1	7.3	NA	
	Unid. fish (no Otoliths)			**123**	36	NA	NA	NA	NA	
TOTAL				**342**		**157796**	**100**			**100**

Table 4.4. One-way Analysis of Similarity (ANOSIM) assessing the variation in the % biomass contribution of each prey species in the meals returned to the colony by adult short-tailed shearwaters. P indicates where significance exists for pair-wise comparisons, with significant differences highlighted in bold. See table 4.2 for sample sizes of each comparison.

	Comparison	04/05		05/06		06/07	
Factor		R	P	R	P	R	P
Trip type	ST vs LT	0.05	7.41	0.13	**<0.05**	0.08	**<0.05**
Stage of chick-rearing	early - mid			0.21	**<0.05**		
	early - late			0.16	**<0.05**	-0.05	5.92
	mid - late	0.11	0.13	0.36	**<0.05**		
	Comparison	early		mid		late	
Factor		R	P	R	P	R	P
Year	04/05 - 06/07					0.09	0.13
	04/05 - 05/06			0.38	**<0.05**	-0.03	6.11
	05/06 - 06/07	0.05	0.97			0.28	**<0.05**
Location	Alth - Evans (04/05)	-0.09	6.42			0.01	3.97

Table 4.5. Variation in the mass of meals (g) returned from ST and LT showing comparisons between trip types, years, and colonies. Data were not pooled as meal mass varies with chick age (Hamer et al. 1997). Kruskal-Wallis χ^2 approximations are shown for inter-annual comparisons, and Mann-Whitney U results are shown for trip type comparisons and inter-colony comparisons. P indicates where significance exists, with significant differences highlighted in bold.

	Colony	Year	Trip type	Early		Mid		Late	
Meal mass				Mean	SE	Mean	SE	Mean	SE
	Evans I.	04/05	ST	17.7	3.8			29.4	7.5
			LT	56.9	8.2			53.5	3.2
	Althorpe I.	04/05	ST			41.9	6.2	55.1	4.8
			LT			96.1	46.9	65.0	9.0
		05/06	ST	19.7	2.1	37.6	6.3	23.5	10.4
			LT	41.5	6.8	74.7	8.0	66.0	9.3
		06/07	ST	32.4	5.6			57.0	7.5
			LT	50.4	12.8			79.7	12.4
Comparison				*U*	*P*	*U*	*P*	*U*	*P*
ST vs LT	Evans I.	04/05		1.1	**<0.05**			1.0	**<0.05**
ST vs LT	Althorpe I.	04/05				10.0	0.19	29.5	0.35
ST vs LT		05/06		89.1	**<0.05**	99.5	**<0.05**	8.0	**<0.05**
ST vs LT		06/07		28.0	0.96			35.0	0.13
Inter-annual	Althorpe I.		ST	1.7	0.19	0.5	0.44	2.9	**<0.05**
Inter-annual			LT	0.6	0.43	0.6	0.86	0.6	0.80
Althorpe vs Evans I.		04/05	ST	19.3	0.38			1.1	0.21
Althorpe vs Evans I.		04/05	LT	26.1	0.11			11.0	0.34

Table 4.6. Inter-annual and inter-colony variation in growth (mass) and provisioning rate (g/d) of chicks. Mean logistic parameters are listed, which describe the growth of individual shearwater chicks from hatching to adult departure (1 – 90 days) (excluding mass recession, after adult abandonment and before fledging). The slope of the curve is a measure of growth rate, the asymptote a measure of peak mass, and r2 a measure of the goodness of fit of the model to the growth data. Mean daily mass change is also listed, as well as the mean provisioning rate (g/d) for each colony each year. Significant differences between years and colonies are determined using ANOVA and t-tests. Inter-annual comparisons were only performed at the same colony, and inter-colony comparisons were only performed within the same year.

Colony			Evans I.	Althorpe I.			Inter-annual			Inter-colony		
Year			04/05	04/05	05/06	06/07	*t*	*df*	*P*	*t*	*df*	*P*
Growth-curve parameters	Peak mass (g)	Mean	783.8	828.3	781.2	816.0	5.67	2	0.11	0.3	1	0.58
		SE	66.5	48.0	26.6	28.8						
	Growth rate (g/d)	Mean	7.2	10.9	8.7	10.2	1.79	2	0.18	7.2	1	0.12
		SE	1.1	0.9	1.1	0.8						
	r2	Mean	0.95	0.88	0.84	0.95						
		SE	0.01	0.01	0.02	0.01						
Growth-daily mass change	Early chick rearing	Mean	7.2		25.0	14.9	2.1	25	0.09	6.0	25	**<0.05**
		SE	3.9		5.1	3.6						
	Mid chick rearing	Mean		10.1	1.3	23.4	3.5	25	**<0.05**			
		SE		5.6	5.1	5.5						
	Late chick rearing	Mean		-4.5	-15	-1.1	1.6	24	0.19			
		SE		3.1	4.3	5.9						
Provisioning rate		Mean	28.7	44.8	53.4	47.0	7.0	2	0.33	16.4	1	**<0.05**
		SE	3.9	5.4	5.7	4.5						

Table 4.7. Relationship between chick growth as a measure of average daily mass change, and dietary composition at Althorpe I. showing the associations between growth and the importance of prey types in the diet for the same stage in the chick rearing (early, mid and late chick rearing). Data is pooled between years, due to low sample sizes. Note: dietary data for each growth stage is based on prey composition of meals returned to neighbouring burrows, thus not the actual diet of the study chicks.

Feeding parameters	*R*	*N*	*P*
Oil	0.28	11	0.41
Fish	-0.43	14	0.12
Krill	-0.41	14	0.15
Cephalopod	-0.41	14	0.15
Crustacean	0.32	14	0.26
Av. provisioning rate 04/05	0.60	32	**<0.05**
Av. provisioning rate 05/06	0.26	30	**0.08**
Av. provisioning rate 06/07	0.48	46	**<0.05**

Table 4.8. Mean (± sd) calorific content (kJ/g wet weight) of each of the major prey species, and major prey types in the diet. * A. Weibkin (unpubl. data). Source refers to the origin of the samples, being either caught directly in a net (i.e. raw), or retrieved from an undigested stomach sample returned to the colony by an adult short-tailed shearwater (i.e stomach).

Prey type	Species name	Common name	Age	N	source	kJ/g wet weight	Mean	SD
Pelagic fish	*Engraulis australis*	Anchovy	sub-adult	7	raw	5.47	4.56	0.68
			Juvenile	31	raw	5.12		
	Sardinops sagax	Pilchard	sub-adult	7	raw	4.08		
	Emmelichthys nitidus	Redbait	sub-adult	5	raw	*4.08		
	Trachurus declivis	Jack Mackerel	Juvenile	4	raw	4.04		
Cephalopod	*Sepioteuthis australis*	Southern Calamari	Juvenile	3	stomach	2.75	3.20	0.64
	Notodarus gouldi	Arrow Squid	Juvenile	2	stomach	3.65		
Crustacean	*Brachyura sp.*	megalopa		80	stomach	2.67	3.11	0.44
	Nyctiphanes australis	Australian Krill		800	stomach	3.11		
				400	stomach	3.54		

CHAPTER 5

THE LONG AND THE SHORT OF CHICK REARING: ADAPTIVE SIGNIFICANCE OF DUAL FORAGING IN THE SHORT-TAILED SHEARWATER

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THE LONG AND THE SHORT OF CHICK REARING: ADAPTIVE SIGNIFICANCE OF DUAL FORAGING IN THE SHORT-TAILED SHEARWATER

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Collected all data, performed analysis on all samples, interpreted data, wrote manuscript and acted as corresponding author.
I hereby certify that the statement of contribution is accurate
Signed
…………………………………………………………………………….Date…………………

Page, B.
Supervised development of work, contributed to planning of field work and analysis, and provided critical evaluation of drafts.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
Signed
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Goldsworthy, S. D.
Supervised development of work, and provided critical evaluation of a draft.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
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ABSTRACT

Procellariiforms (shearwaters, petrels and albatross) forage at much greater distances from their colony during the breeding season compared to other seabirds, by employing a dual foraging strategy. We studied the foraging and provisioning strategies of the short-tailed shearwater *Puffinus tenuirostris* to assess how chick growth and condition is influenced by varied foraging strategies. The relationships between foraging/provisioning parameters and chick growth and survival were analysed by grouping chicks based on their condition at the end of the 90 day chick rearing period. Chicks that died, and those that attained 'low' and 'moderate condition' experienced a significantly lower rate of growth, because they received significantly fewer and smaller meals from short-duration trips, compared to chicks that attained 'moderate' and 'high condition'. Adults that reared 'good condition' chicks spent 80 ± 6 % of the chick rearing period on 5.8 ± 0.8 long trips of 13.0 ± 0.2 (SE) day duration, and 20 ± 6 % on 13.5 ± 2.5 (SE) short trips of 1.1 ± 0.3 days duration. Most self-provisioning by adults occurred when they were performing long trips. Long trips also provided 74 ± 5 % of chick energy requirements in just 35 ± 3 % of the total food mass delivered. The energy value of these long trip meals was significantly higher because they contained stomach oil. Short trips provided significantly less energy because they only contained freshly caught prey, but they increased the energy flow to chicks. This was especially important during early chick rearing, as the number of short trip meals delivered during the early stage was directly correlated with condition at fledging. Short trip meals also increased the rate of protein delivery which is required for chick growth. The dual foraging strategy provides the optimal means of maximising the delivery of energy and nutrients to chicks, while maintaining adult energy requirements.

INTRODUCTION

An animal's fitness is determined by its ability to allocate time and energy between their own needs and those of offspring. The resultant pattern of allocation aims to maximize lifetime reproductive success, subject to the constraints imposed by life-history traits (Houston 1987, Stearns 1992). Reproductive success associated with a varied foraging strategy is important in the study of resource allocation, enabling a more accurate assessment of the adaptive significance of a foraging strategy.

Procellariiform seabirds (albatrosses, petrels and shearwaters) perform a dual foraging strategy when rearing chicks that involves adults alternating between short and long foraging trips. On long trips (LT) adults travel up to thousands of kilometres from their breeding colony to forage. In between these, adults undertake a number of short trips (ST) performed closer to the colony (Baduini and Hyrenbach 2003). Numerous species have been studied in recent decades to investigate how time and energy are allocated between adults and their offspring in this foraging strategy. Upon return from a ST adults regurgitate much of the food they consume to their chicks, and although maximising energy flow to offspring, adults typically lose mass and condition on ST (Weimerskirch and Cherel 1998, Weimerskirch *et al.* 2003). On LT adults self feed by exploiting more predictable distant foraging areas (Weimerskirch 2007). Birds travel further from the colony on LT to reach areas where elevated rates of prey intake can restore the condition lost on ST (e.g., blue petrel *Halobaena caerulea* and wandering albatross *Diomedea exulans,* Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 1997). LT also play an important role in chick provisioning, as adults synthesise high energy stomach oil from digested prey, to deliver to their chick when they return to the colony (Warham *et al.* 1976, Roby *et al.* 1989). This oil enables adults to concentrate the energy gained from distant foraging grounds into a small volume, enabling adults to elevate the rate of energy delivery to chicks (Obst and Nagy 1993, Weimerskirch *et al.* 1997).

Like most pelagic seabirds, Procellariiforms have a protracted provisioning period, which enables them to reduce the frequency at which food needs to be fed to chicks (Drent and Dann 1980), and parents can readily accumulate and deplete lipids (Ricklefs *et al*. 1980, Hamer and Hill 1993, Ricklefs and Schew 1994). These attributes allow parents to feed their chicks more irregularly than other seabirds. The ability to condense the energy value of prey, and transport large meals influences the foraging range of parents, by reducing the rate that food needs to be delivered to chicks. This can be explained by considering the three main food delivery mechanisms used by seabirds. Single and multiple-prey loaders deliver single or multiple prey items respectively, which are held in the bill. Only small meals can be delivered via this feeding method, requiring adults to feed their chick multiple times per day (e.g., roseate terns *Sterna dougallii* Ramos *et al.* 1998, tufted puffins *Fratercula cirrhata* and horned puffins *F. comiculata* Hatch and Sanger 1992). Regurgitation of stomach contents enables parents to deliver larger loads per visit to their chick, enabling parents to reduce their feeding rate, and thereby potentially exploit more extensive feeding areas (e.g., rhinoceros auklets *Cerorhinca monocerata* Kato *et al.* 2003, Cape gannets *Morus capensis* Ropert-Coudert *et al.* 2004). The production and accumulation of stomach oil enables parents to concentrate the energy value of the meal 5 - 10 times. This significantly extends the duration of foraging trips enabling parents to increase the range and area of foraging (Obst and Nagy 1993, Chaurand and Weimerskirch 1994). Stomach oil is a feature unique to the Procellariiforms, and largely facilitates the extended feeding strategies that occur in this seabird family. Given that LT are used by adults to restore their own depleted energy reserves, and enable the delivery of energy rich meals to chicks, it is not clear why Procellariiforms do not perform a feeding strategy of continuous LT. Studies that simultaneously compare the energy requirements of growing chicks with the rate of food delivery provide a useful means of assessing how varied feeding strategies influence chick condition and reproductive fitness.

Procellariiforms typically employ a dual foraging strategy when rearing chicks, but there is flexibility within and among populations of several species (Baduini and Hyrenbach 2003). The short-tailed shearwater *P. tenuirostris* is an obligate dual foraging species that undertakes some of the longest duration foraging trips of any Procellariiform (Hamer *et al.* 1997, Weimerskirch and Cherel 1998, Schultz and Klomp 2000). The dual foraging strategy enables this species to inhabit islands along the temperate coastline of Australia, but use prey from the distant and relatively productive waters of the Southern Ocean. The apparent success of the short-tailed shearwater strategy is supported by the fact that they are one of the most abundant pelagic seabirds in the world, with an estimated breeding population of 23 million birds (Skira 1991).

The relationships between provisioning, chick growth and survival have been investigated in a range of species (e.g., Lorentsen 1996, Quillfeldt and Peter 2000), but only a few studies have quantified the amount of energy delivered to the offspring on ST and LT (Obst and Nagy 1993, Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 1997). These studies indicate that the majority of energy delivered to offspring comes from LT, with ST providing a means to increase energy flow. However, none of these studies span the entire chick-rearing period. A consideration of chick growth and survival is also important in the study of resource allocation, as it enables a more accurate assessment of the fitness consequences of varying patterns of food delivery.

We explore the advantages and disadvantages of the short-tailed shearwaters dual foraging strategy by examining the growth and survival of chicks under a range of actual, and simulated, feeding regimes. We tested the hypotheses that parents could provision their chick so that it reached fledging condition by performing a feeding regime of either all ST, or all LT. To do this, we determined the age-specific growth and energy requirements of chicks, and the average energy delivery rates by parents after LT and ST. We assessed the: (1) influence of provisioning on the growth and survival of chicks; (2) energy requirements of chicks, to identify periods of fasting and energy surplus; (3) energy and nutrient value of ST and LT meals; (4) mass changes of adults on ST and LT; and, (5) energy and nutrient flows under simulated feeding regimes.

METHODS

Study sites

This study was undertaken during the 2005-06 austral summer on Althorpe Island (35°37'S, 136°86'E), South Australia. We identified 255 active burrows and marked them with numbered tags during the copulation period. The resident adults were captured and marked with a numbered leg band and a glass-encapsulated RFID transponder.

Growth and provisioning parameters

During the hatching period 35 burrows were inspected to identify the hatch date of chicks. Following hatching, the mass change of chicks was monitored over 90 consecutive nights until adult abandonment. This enabled the longitudinal assessment of feeding frequencies, the sizes of meals delivered, and the growth rate of chicks to be recorded. Meal mass was determined by weighing chicks with a spring balance (±1g) every 3 h between 20:00 - 05:00 h (Hamer *et al.* 1997). The exact feeding time was often unknown, so to account for mass loss through respiration and excretion meal mass was reconstructed using the NET versus SUM method (Phillips and Hamer 2000). Growth rate was calculated as the body mass changes (g/d) from 20:00 - 20:00 hrs (24 - hr period). Patterns of food delivery and growth were then averaged for each chick over consecutive 10 d periods. Absences of <3 d were defined as a ST, and >3 d a LT, following Weimerskirch and Cherel (1998). Standard error is presented for every value unless specified otherwise.

Growth and provisioning budget

A distinction was made between chicks in good, moderate and poor body condition at the time of adult abandonment (~90d after hatching). This involved calculating chick condition as the ratio of body mass (g) and tarsus length (mm) for each chick (Cezilly *et al.* 1995), then separating chicks into the upper, middle and lower 33 percentile. A fourth and fifth group was derived based on age of mortality. Chicks that died before 45 d were considered to have ‘died young’, and those that died after, ‘died old’. Breeding success of the study group was calculated as the proportion of chicks that were in good condition at adult abandonment, thereby having the largest chance of fledging successfully. Breeding success was assessed using the same method at 150 additional burrows, to assess the effects of handling on chicks, although this was expected to be negligible, following Saffer *et al*. (2000).

The growth parameters of chicks in ‘good condition’ were used to construct an energy budget to estimate the minimum food and energy requirements in different 10 day age classes. The total amount of food required (g/d) in different age classes was estimated by adding the: 1) estimates of daily mass gain 2) maintenance requirements of chicks, and 3) biosynthesis (tissue deposition) costs (as in Berruti *et al.* 1985). Body maintenance requirements were estimated by regressing reconstructed meal mass (see above) with the mass change of chicks over a 24 h period, following Granadeiro *et al.* (1999). We used an estimate of biosynthesis costs from Ricklefs *et al.* (1980), which is defined as being one third of the energy value of accumulated tissues. Food requirements were converted to energy requirements (kJ/d) based on the: 1) prey composition of ST and LT meals, 2) energy value of different prey (see below), and 3) relative contributions of meals from ST and LT. An assimilation efficiency of 89 % was assumed for the raw prey component (fish, cephalopod, krill, and other crustacean) (Ricklefs *et al.* 1980), and 90% for the oil component (Obst and Nagy 1993). The rates of fat and protein deposition in chicks were derived from estimates of the body composition of short-tailed shearwater chicks at different ages (Fitzherbert 1985). This enabled the assessment of daily fat and protein requirement based on the rate of mass gain.

The provisioning parameters of chicks in 'good condition' were used to construct the provisioning strategy that is required to fledge a chick. To estimate the rates of energy flow from ST and LT we combined the: 1) rate of meal delivery (g/d), 2) meal mass (g), and 3) energy value (kJ/g) of the prey (see below), following the methods of Obst and Nagy (1993). The protein content of ST and LT meals was estimated, based on the 1) rate of meal delivery (g/d), 2) meal mass (g), and 3) prey composition. Protein content was estimated to be 20 % for neritic fish (Bunce 2001), 15 % for myctophids (Clarke and Prince 1980), 19.4 % for cephalopod (Cherel and Ridoux 1992), 12.4 % for Australian krill *Nyctiphanes australis* (Green and Brothers 1989), and 0 % for stomach oil.

Species composition and energy value of meals

Species contribution of both ST and LT meals was based on the reconstructed biomass of meals collected from birds in nearby burrows (Chapter 4). The energy contents of prey were measured by drying, pulverising and combusting raw prey specimens in a bomb calorimeter, following the methods of Tierney *et al.* (2002). Combining the prey composition and the energy value of prey enabled the calculation of the energy delivered from ST and LT.

Adult mass changes

To record mass changes of adults after foraging trips, we monitored 30 breeding pairs at 30 additional burrows and weighed adults during successive ST, or at the start and end of a LT. An additional sample of burrows was used so not to impact on the feeding and growth of the chicks (see above). A wooden trapdoor was installed at the burrow entrance, and was monitored remotely via the use of a red light emitting diode, which flashed when the door was tripped. When an adult was trapped it was left undisturbed for 60 minutes, to give it time to feed its chick. Before weighing these adults any remaining food was first removed by stomach flushing (Wilson 1984). Adults were weighed with a spring balance (± 5 g), and returned to their burrows.

RESULTS

Chick survival and breeding success

Of the 35 chicks studied, 4 'died young' between the age of 11 - 20 d, and 6 'died old' between 50 - 60 d old. None of the adults studied died. The remaining 25 chicks survived to the end of the chick rearing period, and were grouped by their condition, with 8 deemed of ‘high’, 8 ‘moderate’ and 9 ‘low condition’. This resulted in a breeding success of 71 % which was not significantly different to the 72 % breeding success of control burrows (_^{2} = 2.95, *df=1, P* >0.5).

Growth rate of chicks relative to condition and survival

Chicks that attained ‘high condition’ grew fastest when 21 - 30 d old, when they gained 23.3 ± 2.1 g/d (Fig 5.1). Growth rate then declined through the remainder of the growth period until reaching peak mass at 51 - 60 d old, after which mass loss occurred (Table 5.1). A similar age-specific pattern occurred for all other condition groups, except for chicks who ‘died young’ (Fig 5.1). Growth rate was significantly elevated for ‘high’ and ‘moderate condition’ chicks during the peak period of mass gain (21 - 30 d), compared to chicks that attained ‘low condition’ or ‘died old’ ($F_{3,32}$=3.16, P <0.05; Fig 5.1). ‘High condition’ chicks retained consistently high growth rates for the remainder of the growth period, compared to all other condition groups, being significantly higher than ‘moderate’ chicks when 41 - 50 d old ($F_{1,\,15}$= 9.6, P < 0.005; Fig 5.1).

Chick condition at fledging was significantly correlated with growth rate when 1-20 d old (Table 5.2). This indicates the importance of the early chick rearing period over the mid and late chick rearing periods (Table 5.2).

Adult foraging parameters relative to chick condition

The majority of ST of all adults spanned a single daylight period (93 %), as adults departed at dawn and returned after nightfall. The remainder of ST spanned two days and one night, and rarely three days and two nights.

Adults that reared chicks to ‘high condition’ (n = 8) performed an average 80/20 division of time between LT and ST foraging. These adults made 14 ± 2.1 (SE) (9 - 18) ST represented 20 ± 5 % (SE) of the total time foraging during the 90 day chick rearing period, as some ST were two days duration, and some days were spent at the burrow. Adults spent the remaining 80 ± 6 % (SE) of their foraging time performing a total of 5.8 ± 0.8 LT (SE) (range = 4 - 6), the duration of which increased significantly with chick age ($F_{1,\,30}$=19.31, P<0.005). The proportion of foraging time spent performing ST by each adult decreased significantly with chick age (Pearsons R^2=-0.75, P<0.005, N=24, Fig 5.2). These patterns significantly reduced feeding frequency to 'high condition' chicks as they aged ($F_{3, 41}$=72.4, P<0.005).

Adults that reared chicks to 'moderate' and 'low condition' both performed an 84/16 foraging strategy. This involved an overall increase in the time spent on LT, and a decrease in ST foraging. Significant differences occurred in the proportion of time spent performing ST between 'high' and 'moderate' chicks when 1 - 20 d old ($F_{1,21}$=1.22, P<0.05, Fig 5.2). Adults of 'high' condition chicks also spent significantly more time in ST, compared to 'low' chicks when 21 - 40 d old ($F_{1,18}$=2.04, P<0.05, Fig 5.2).

Provisioning parameters relative to chick condition

Chick condition at fledging was positively correlated with the number of ST meals delivered by both parents when chicks were 21 - 40 d old and 41 - 60 d old (Table 5.2). The average provisioning rate to chicks 21 - 40 d old was also related to condition at fledging (Table 5.2).

Age specific patterns of provisioning also reveal increased variation in provisioning rate between condition groups at 21 - 30 and 31 - 40 d old (Fig 5.3). Chicks reared to 'high condition' were provisioned at a significantly higher rate than 'moderate condition' chicks at 31 - 40 d old ($F_{1,16} = 8.1$, $P < 0.005$; Fig 5.3). 'Moderate' condition chicks were provisioned at a significantly higher rate than those who 'died old' at 21 - 30 d ($F_{1,20}$ =3.88, P<0.05; Fig 5.3), and were significantly higher than 'low condition' chicks at 31 - 40 d old ($F_{1,10}$ =0.85, P<0.05; Fig 5.3).

Food requirements of growing chicks

For chicks that attained 'high condition' maintenance requirements accounted for 23 % of the food provisioned from 1 - 10 d, which increased to 92 % at peak mass (802 ± 120 g at 59 ± 5 d; Fig 5.4a and b). Estimates of chick food requirements roughly followed their actual provisioning rates (Fig 5.4b), and they were significantly positively correlated (Pearsons R^2=0.76, P<0.05, N=9). Provisioning rates exceeded estimates of total chick requirements at most stages of growth, except that they were fairly balanced at 45 - 50 d old, and negative at 11-20 d old, and again at 51 - 60 d old, which coincided with peak mass (Fig 5.4a and b).

Energy allocation via a dual foraging strategy

Chicks that attained ‘high condition’ received a combined 28 ± 3 ST and 12 ± 01 LT meals from both of their parents (Table 5.3). Based on the average mass of meals delivered, ST provided 65 ± 5 % of the mass, and LT 35 ± 3 % (Table 5.3). ST meals contained 52 % fish, 34 % cephalopods, 13 % krill, and 1 % other crustaceans (Table 5.4, Chapter 4). Using estimates of the energy value of these prey (Table 5.4), energy content of an average ST meal was 420 kJ (Table 5.3). LT meals contained raw prey (30% mass) of an equivalent energy value, but they also contained stomach oil (39 % mass), and heavily digested myctophid fish (31 % mass) (Table 5.4). The energy value of this oil (41 kJ/g) and myctophid (8 kJ/g) elevated the calorific density of LT meals to 22 kJ/g, compared to the 4 kJ/g for ST meals (Table 5.4). On average, LT meals contained an estimated 2895 kJ and contributed 75 ± 5 % of the total energy in 35 ± 3 % of the total mass delivered to chicks (Table 5.3).

Because LT were longer in duration than ST, the daily rate of energy delivered via LT was 193 kJ/d, and significantly less than 381 kJ/d for ST (Table 5.3). Because raw prey contain more protein than stomach oil, ST meals (Table 5.4) contained 17 % protein, compared to 10 % in LT meals (Table 5.3).

Adults were significantly lighter after ST (Paired t=8.5, P<0.005, N=56) (Fig 5.5), and the amount of mass lost increased with each successive ST (Fig 5.6). The average mass loss per day of ST was 22 ± 18 g. This represented 3.7 ± 2.8 % of the initial body mass. In contrast, when adults returned from a LT they had gained 57 ± 21 g (Fig 5.5), representing 7.5 ± 3.8 % of their initial body mass.

Energy delivery under alternative provisioning strategies

Based on the growth rates of chicks that attained ‘high condition’, peak energy demands of 877 kJ/d occurred at 41 - 50 d old (Table 1, Fig 5.8). If a feeding regime of continuous ST was employed, each parent could supply 440 kJ/d (Table 5.3). This total of 880 kJ/d exceeds the average daily requirements of chicks (577 kJ/d), even at the peak (Fig 5.8). In contrast, under a feeding regime of continuous LT each parent could deliver 192 kJ/d. In this scenario the energy flow provided by both parents (385 kJ/d) would not meet the energy requirements of chicks (577 kJ/d) (Table 5.1, Fig 5.8).

DISCUSSION

Foraging parameters and chick survival

Here we provide the first account of the attendance patterns of adults and provisioning rate of chicks for the entire 90 days of chick rearing, and have revealed that birds spend 80 % performing LT, and 20 % performing ST, representing an 80/20 division of time. Of the few other studies that have assessed time allocation in Procellariiforms, the closely related sooty shearwater *Puffinus griseus* performed an 84/16 strategy (Weimerskirch 1998) the blue petrel an 80/20 strategy (Chaurand and Weimerskirch 1994), and the Cory's Shearwater *Calonectris diomedea* an 80/20 strategy (Granadeiro *et al.* 1998). Also, male wandering albatross perform a 68/32 foraging strategy, while females perform a 48/52 foraging strategy during the middle period of chick rearing (Weimerskirch *et al.* 1997). We have presented a more informative measure of the dual foraging strategy by considering the condition and survival outcomes of chicks. Such an approach has revealed that the time spent performing ST and LT is highly variable between adults and between breeding pairs, and heavily influences reproductive success.

There has been much debate as to how Procellariiforms regulate food supply to their chicks (e.g. Baduini 2002, Granadeiro *et al.* 2000). Food delivery by adults of many species has been shown to be unresponsive to chick condition (e.g. Hamer and Hill 1994, Weimerskirch 1998, Mauck and Ricklefs 2005). This study has provided further evidence in support of this, as short-tailed shearwaters do not respond to short-term changes in the nutritional requirements of their chicks. For example, adults rearing chicks in low condition continue to provision them at a low rate, and the mass of chicks in the first 20 days is correlated to their fledging condition. Instead, provisioning rates are considered to reflect the foraging success of the adult, and are controlled by the adults own mass regulation (Ricklefs and Schew 1994, Weimerskirch 1998, Bradley *et al.* 2000).

Despite extensive variation in the day to day rate of provisioning, we have highlighted that a small change in the proportion of time spent performing ST over the entire chick rearing period can spell the difference between breeding success and failure. This is evident as a 20 % investment in ST by adults enabled them to rear chicks to high condition, but a decrease to 16 % resulted in moderate or poor condition chicks. The consequences of these varied feeding strategies are understandable when considering the elevated energy flow that is achieved from ST. Despite the increased energy value of LT meals, the delivery of a number of ST meals over a period of days provides a substantial boost in the delivery of protein, nutrients and water, which are essential for growth.

Constructing a comprehensive energy budget for seabird chicks provides a means of identifying how provisioning rates meet the energy requirements of chicks. Growth rates and maintenance requirements of chicks recorded in the current study were comparable to previous estimates for this species (Hamer *et al.* 1997). The 49,812 kJ estimate of the total energy requirements to fledge each chick was similar to an earlier estimate for this species (46,164 kJ Fitzherbert 1985), and are in line with the requirements of the larger bodied white-chinned petrel (67,000 kJ Berruti *et al.* 1985). We have identified that the amount of energy received by short-tailed shearwater chicks that attained 'good condition' exceeded their maintenance requirements up until peak mass, enabling the accumulation of lipid reserves. At the time of peak mass, chick requirements exceeded that delivered by their parents, so they meet their daily energy needs by catabolising previously stored lipids, resulting in mass loss (e.g. Hamer and Hill 1993, Ricklefs and Schew 1994). Lipid storage capabilities vary between species of Procellariiforms, and are among the most developed in short-tailed shearwaters (Hamer *et al.* 1997). For example, some chicks reached a peak body mass that was 30 % greater than the mass of their parents, because lipids comprised 30 - 45 % of their tissue (Fitzherbert 1985). Such levels of obesity among chicks are the result of overfeeding by parents, which acts to reduce the risk of excessive fasts that might arise from synchronised provisioning, or stochastic variation in foraging conditions (Ricklefs *et al.* 1980, Ricklefs and Schew 1994, Hamer and Hill 1997, Hamer *et al.* 1998, Phillips and Hamer 1999, Hamer *et al.* 2000).

Adult energy gains on LT

Adult mass gain documented in the current study provides evidence of the benefits of LT foraging. The extended period of foraging is required to recover an adults energy reserves, as has been identified previously (Weimerskirch and Cherel 1998). Restored energy reserves can then provide the energy for their return flight to the colony, subsequent ST, and return journey to sub-Antarctic foraging areas (see Chapter 3). By separating self-feeding and chick-provisioning, parents overcome some of the constraints of central place foraging, by reducing the amount of time spent foraging close to the colony, where prey availability may be relatively low. The relatively high energy value of prey that are consumed on LT are central to the relative efficiency of LT. In distant feeding areas shearwaters use myctophid fish, which comprise most of the stomach oil (Connan *et al.* 2005). Several Myctophidae species represent a rich source of energy for predators, and are known to feature predominantly in the diet of other seabirds in the Southern Ocean (e.g. Clarke and Prince 1980, Cherel and Ridoux 1992). Despite the increased distance travelled on LT, birds are able to elevate foraging efficiency by maximising the amount of time spent in areas where prey availability is relatively high (e.g. wandering albatross Weimerskirch *et al.* 1997, blue petrel Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 2003). This was demonstrated in Chapter 3, as birds performed commuting flights to maximise the time spent in waters of elevated chlorophyll *a* (Chapter 3). These factors enable short-tailed shearwaters to forage at an optimal rate in distant areas than could be achieved if they exclusively used regions closer to their colonies (as in Kacelnik *et al.* 1986). This is consistent with the time and energy budget common to many central place foragers, identified by Ydenberg *et al.* (1992).

The value of long trips to chicks

Long foraging trips enable adults to restore their energy reserves so they can deliver almost all of the prey they procure on ST to their chicks. The body condition of returning adults is thought to influence the number of ST that are subsequently performed before the next LT (Chaurand and Weimerskirch 1994, Weimerskirch 1998, Weimerskirch and Cherel 1998), however this has not yet been thoroughly documented. Based on the increased rate of mass loss when short-tailed shearwaters perform each successive ST, maximizing stored energy reserves would increase an adult's capacity to provision their chicks. Given the evident link between ST provisioning and chick condition, increasing the time spent in ST enables adults to maximize their reproductive success.

The extended absence incurred in a LT enables adults to accumulate stomach oil, which is a relatively efficient way of transporting energy (Obst and Nagy 1993). The accumulation of stomach oil occurs when prey intake exceeds the energy requirements of the adult, as if this dietary energy was required by the adult it would be assimilated, and stored in fat reserves. The delivery of oil is an attribute of many dual foraging Procellariiforms, with the proportion delivered by the short-tailed shearwaters (36 % of meal mass) in the middle of the recorded range (19 to 61 %: Clarke and Prince 1976, Prince 1980, Roby *et al.* 1989, Obst and Nagy 1993). Of the few studies that have quantified the importance of stomach oil in meeting the energy requirements of chicks, it represented 61 % of chick energy needs in the Wilson's storm-petrel *Oceanites oceanicu*s (Obst and Nagy 1993), and 34 % for wandering albatross chicks (Weimerskirch *et al.* 1997). The estimate of 74 % for short-tailed shearwaters in the current study is a conservative estimate, because we did not apply the 15 % adjustment of Obst and Nagy (1993) based on their estimates of oil retention. The relative importance of oil in meeting the energy requirements of chicks largely facilitates the foraging strategy in this species, as it enables adults to maintain a suitable energy flow to chicks while performing among the most extended absences of any Procellariiform (Baduini and Hyrenbach 2003).

Alternative feeding strategies and the benefits of dual foraging

The alternation between ST and LT provides an increased flow of energy to chicks than can be achieved by either continued ST or LT feeding. Estimates of energy flow from ST and LT of the sooty shearwater in comparison to the chicks energy requirements came to the same conclusion (Weimerskirch1998). The simulation of hypothetical feeding regimes reveals that the delivery of continuous ST feeds to short-tailed shearwater chicks could deliver suitable energy to chicks from single ST meals. This rate of energy flow could not be maintained due to the added energy requirements of the adult. Also, a feeding strategy of only ST provisioning was only just capable of satisfying chicks during their peak energy demands. It seems feasible that adults could extend the duration of ST to perform 3 - 5 d long trips, enabling them to gather food to meet their own requirements, as well as return a suitable sized meal to their chicks. But it is unlikely that a suitable amount of oil could be accumulated in this time to adequately boost the energy value of the meal. Therefore medium length foraging trips would further reduce the energy flow to chicks, and fall well short of peak energy demands. A regime of continuous ST would also increase the degree of inter-species competition in local waters around the colony (Berrow *et al.* 2000), which may deplete available resources and decrease the efficiency of ST foraging for themselves, as well as for other birds in the population (Weimerskirch 1998, Weimerskirch *et al.* 2005). In contrast, by extending some foraging trips beyond 7 d birds are not only capable of foraging much further a field, but they can accumulate oil, which substantially boosts the energy value of the subsequent feed. The time required to gather a suitable volume of oil may explain why no foraging trips of 4 - 7 d are performed by this species (Weimerskirch and Cherel 1998). Taylor *et al.* (1997) also identified the value of oil in the Antarctic prion *Pachyptila desolata*, and found that chicks could not be provisioned adequately without it, because oil supplied lipids and nutrients in a ratio that met the requirements of chicks. Another advantage of the delivery of oil is that it reduces the costs associated with digestion for the chicks. This enables chicks to assimilate more of the energy value from higher oil meals compared to meals of raw prey (Roby *et al.* 1989, Taylor *et al.* 1997).

Despite the 5 - fold increase in the calorific density of LT meals, energy flow achieved from long duration foraging trips was only 62 % of that achievable during ST. This highlights the importance of ST in meeting the energy requirements of chicks, and explains why chick condition and survival at fledging is heavily influenced by ST foraging. In addition, ST meals also provide an elevated rate of nutrient delivery, due to the increased protein content of raw prey. Considering that LT meals averaging 125 g contained an estimated 10.1 % protein, and were delivered an average of twice every 13 days (i.e. by each parent), protein could be delivered at a rate of 1.9 g/d. While this meets the estimate of chick needs (1.9 ± 0.2 g/d), they would likely experience shortages through variable LT durations. The increased regularity of energy and nutrient delivery provided by ST is especially important when chicks are young, as early growth was shown to largely determine the survival and condition of chicks at fledging. The supply of adequate nutrients is well known to be an important factor in optimizing the growth of seabird chicks (Prince 1980), as a wide range of nutrients are required for suitable growth (e.g. Roby 1991). Increased food delivery to chicks is also likely influenced by the limited capacity of small chicks to ingest and assimilate the entire meal delivered by the adults when they are still developing their digestive capabilities.

CONCLUSION

Dual foraging is an effective strategy that overcomes some of the constraints of central-place foraging and delivers energy to chicks at an increased rate than is achievable via a strategy of continuous ST or LT. Because adults dedicate extended periods towards LT foraging, which largely involves self-allocation, this strategy presents an extreme version of the time and energy allocation model which is common among central place foragers (Kacelnik 1988, Beauchamp *et al.* 1991, Ydenberg *et al.* 1992). The alternation between extended periods of self allocation (on LT), and provisioning (on successive ST) among Procellariiforms highlight the unique set of life history, behavioral and physiological traits that are shared by these seabirds. By quantifying the foraging parameters and food requirements of chicks, and considering alternative feeding regimes, we have detailed the adaptive significance of the foraging strategy employed by short-tailed shearwaters. We demonstrated how the energy storage capacities of chicks and the energy carrying capacity of adults has facilitated the dual foraging strategy. These attributes, together with the flight capabilities of adults have enabled this prolific species to inhabit islands along the temperate coastline of Australia, but use prey from the relatively productive waters of the Southern Ocean.

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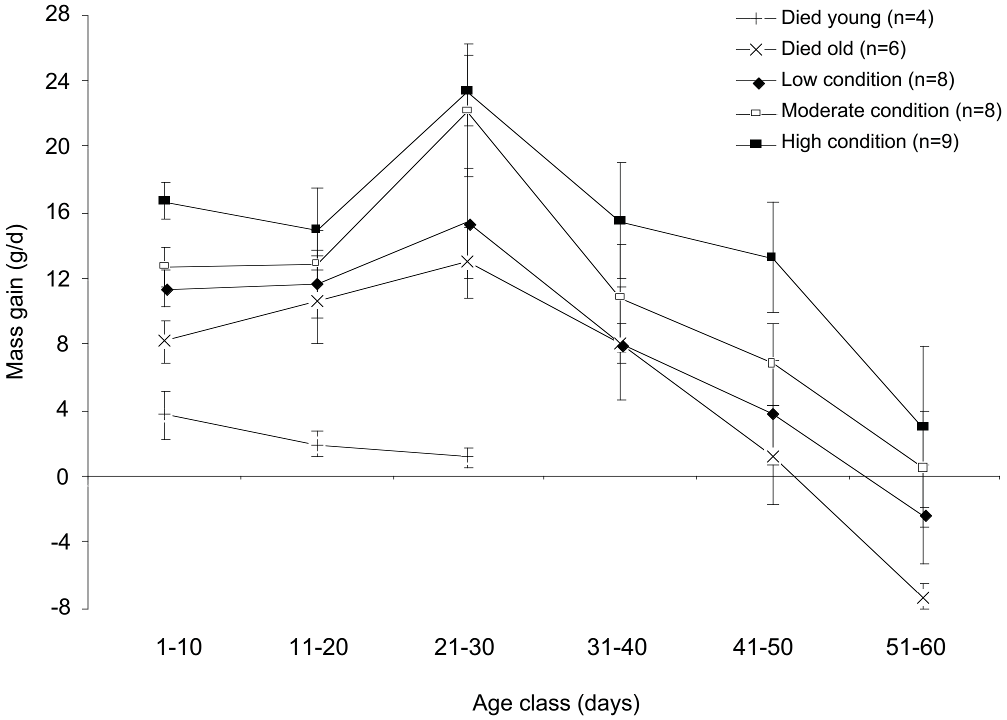

Fig 5.1: Age-specific patterns of growth during the period of mass gain (i.e. until peak mass) relative to chick condition and survival, showing average daily mass increases (g/d) for each 10 d period.

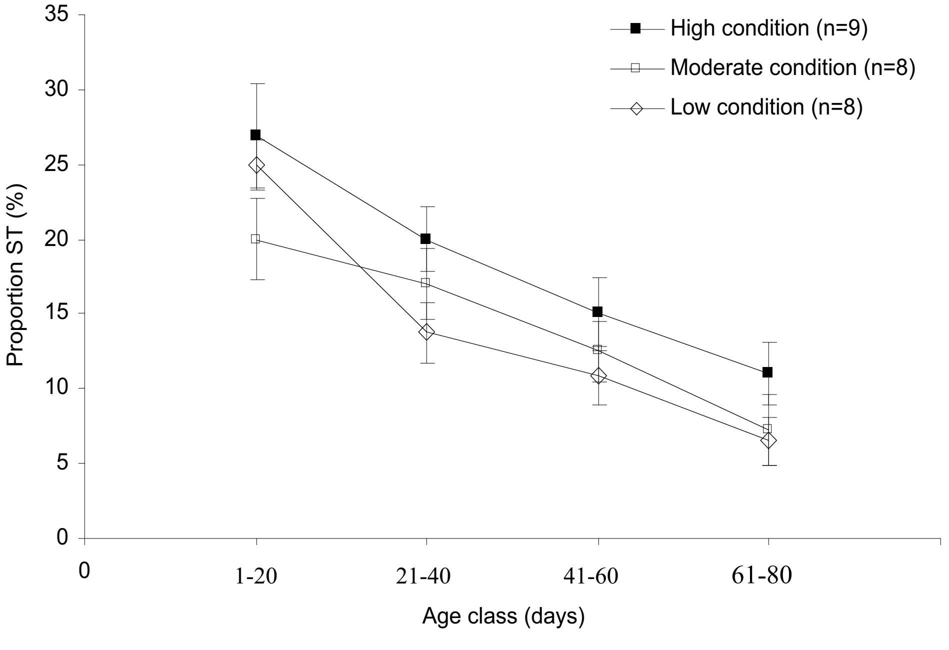

Fig 5.2. Age specific pattern of foraging activity relative to chick condition. Showing the average proportion of time spent performing ST by each parent of chicks in ‘high’, ‘moderate’ and ‘low condition’ at 90 days of age. Note, that the remainder of time in each age class is spent performing LT. ± represents se.

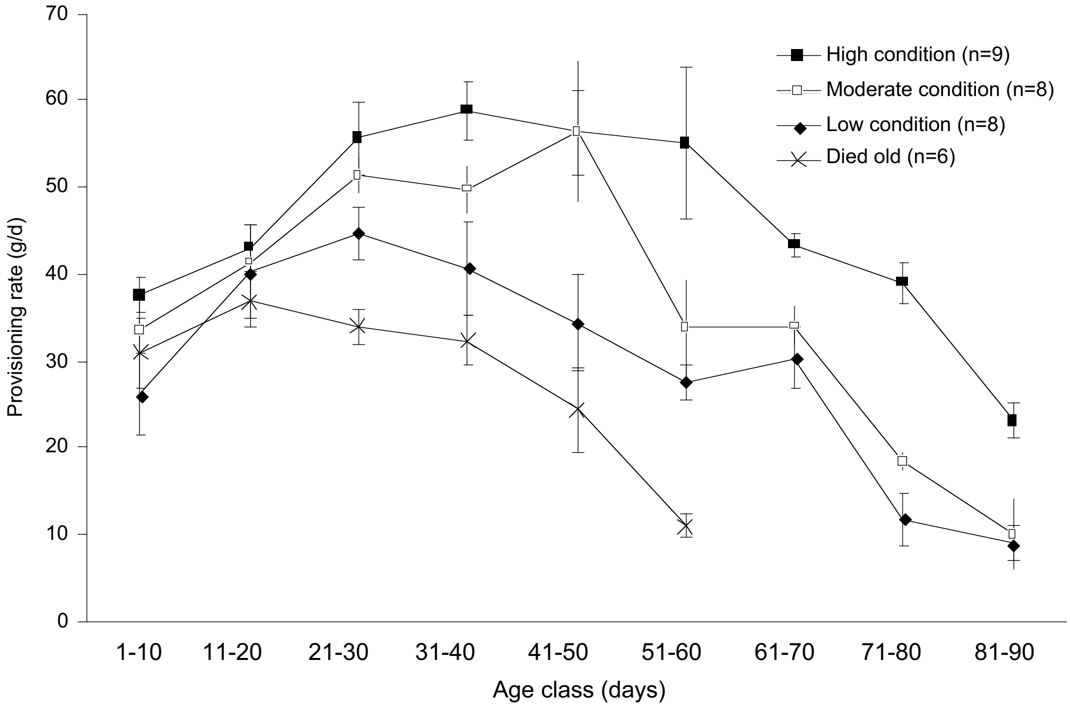

Fig 5.3: Age-specific patterns of provisioning rate (g/d) throughout chick rearing relative to chick condition and survival. Note the reduced provisioning rate to chicks that attained ‘low condition’, and to chicks that ‘died old’.

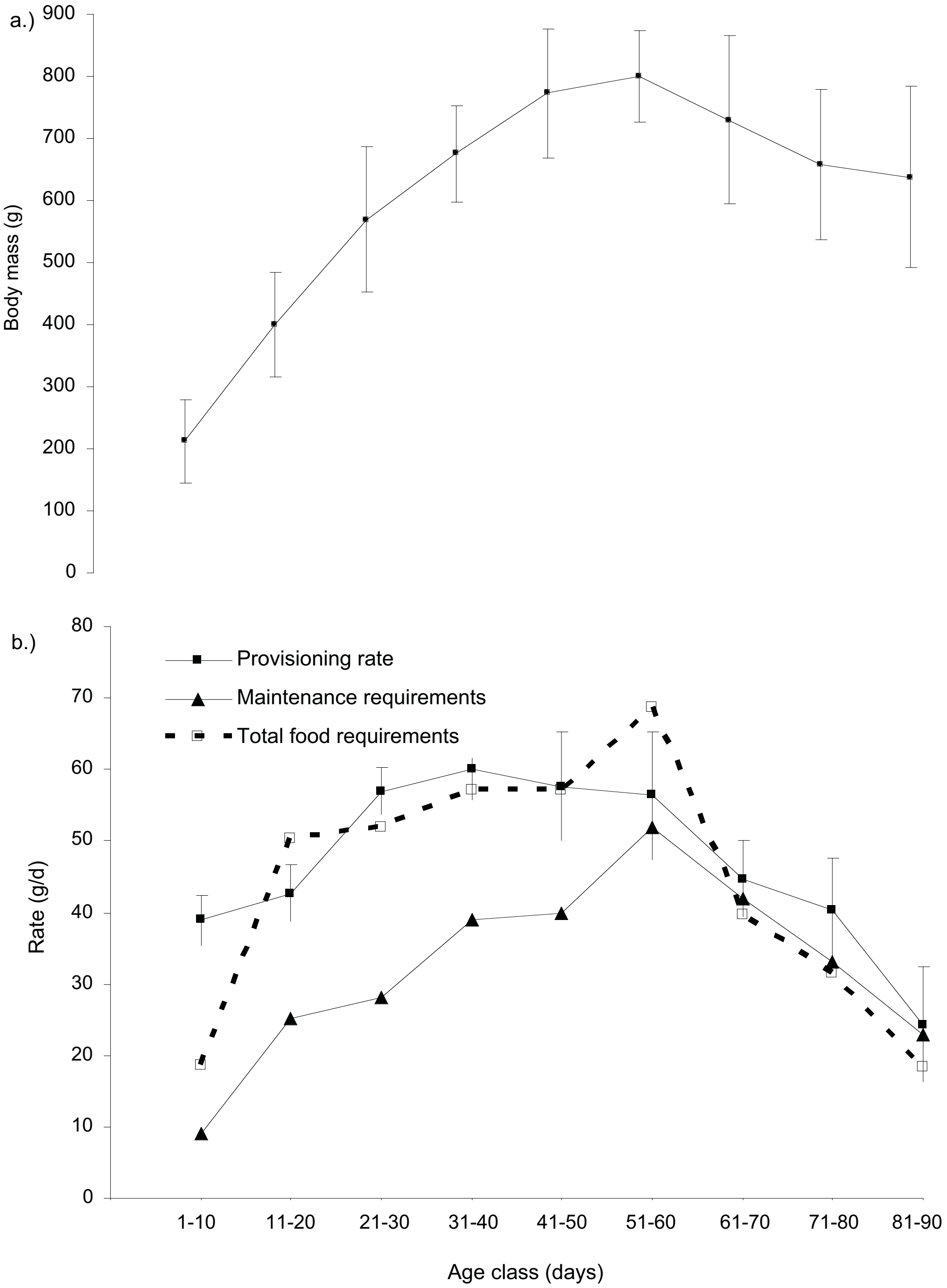

Fig 5.4. growth of growing chicks (n = 8) that attained 'high condition', showing the corresponding estimates of food requirements, maintenance requirements, and rate of food delivery, through the entire 90 day chick-rearing period. A) the average age-specific pattern of mass gain. B) provisioning rate, estimated maintenance requirements, and estimated total food requirements (growth + maintenance + biosynthesis costs). Note the elevated provisioning rate from age 30 - 60 d which largely mirrors total food requirements. Note the peak maintenance and food requirements at peak mass (51 – 60 d), followed by a drop in maintenance/food requirements, and a corresponding drop in provisioning rate between peak mass and adult abandonment.

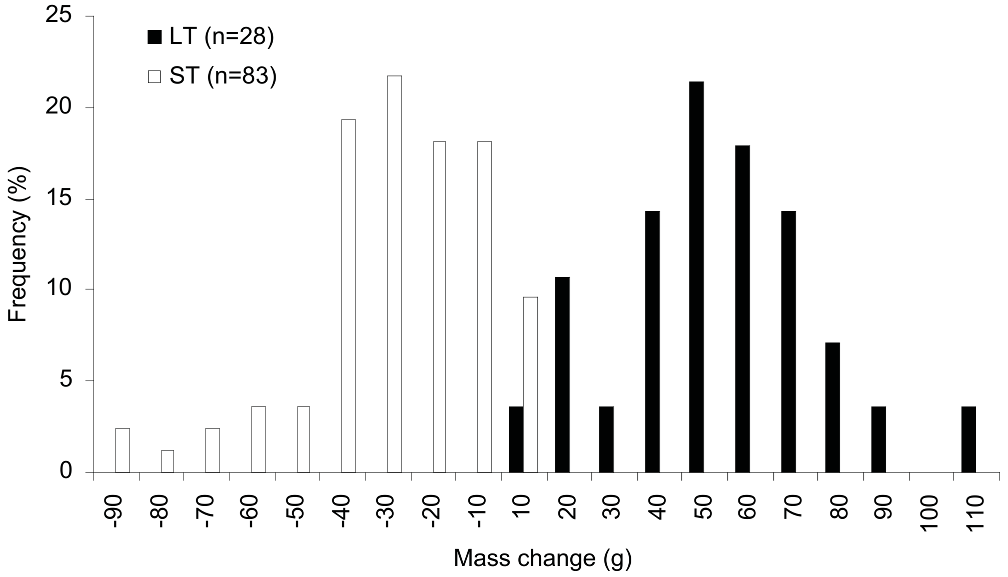

Fig 5.5. Frequency of different mass changes of chick rearing adults following single ST or LT. All ST shown were of a single days duration, and LT were of unknown duration. Sample size in legend shows the number of trips involved.

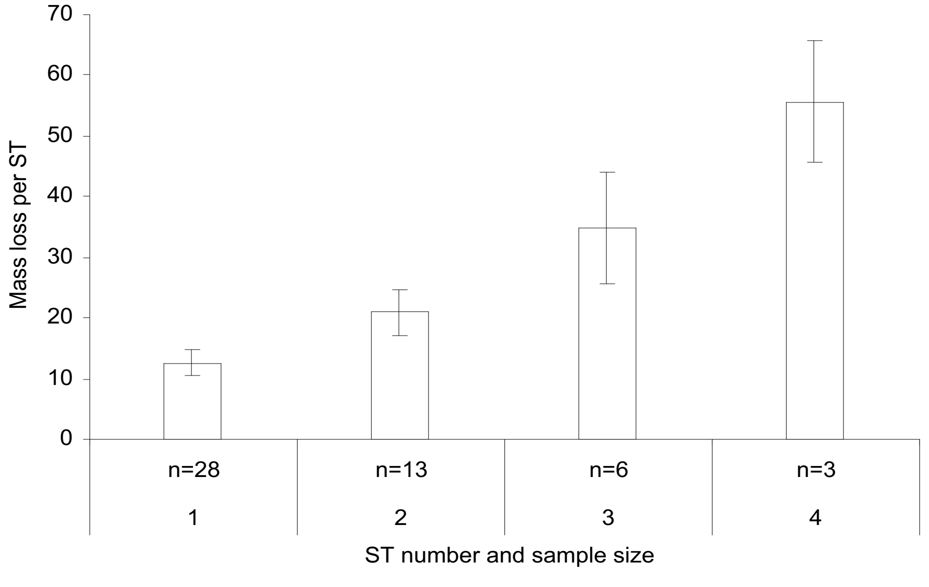

Fig 5.6. Mass loss of chick rearing adults per successive ST, showing the number of individual adults sampled in each group. Note: No individuals were sampled on all 4 successive trips.

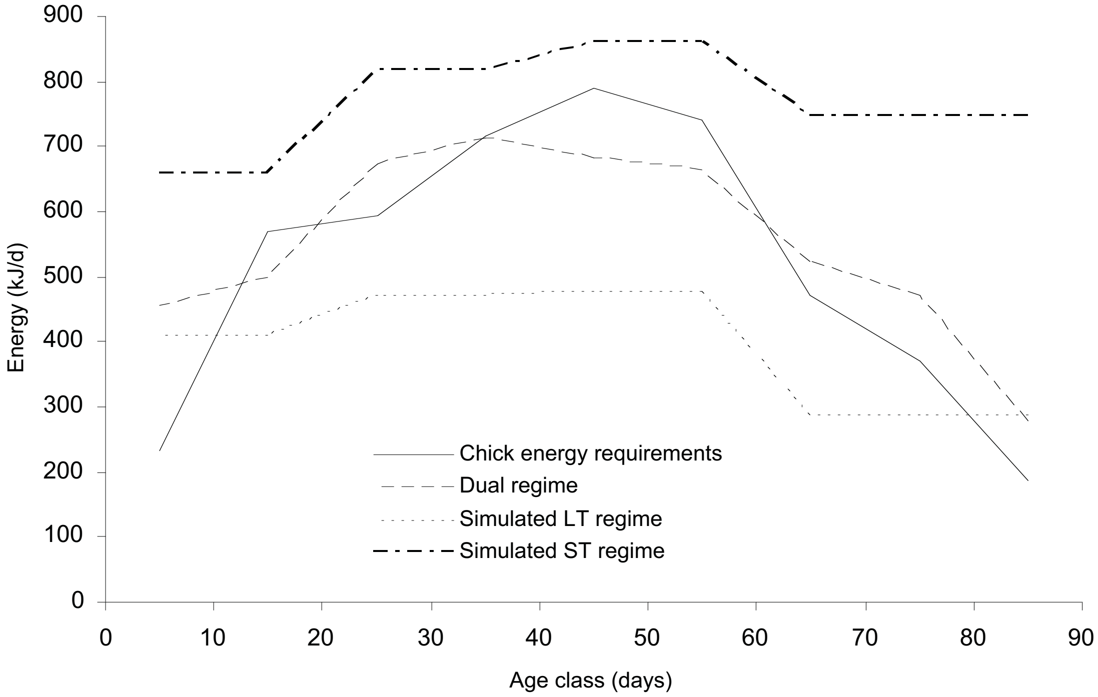

Fig 5.7: Estimated age-specific pattern of energy delivery by both parents through the 90 day chick rearing period, under: 1) the dual feeding regime of chicks that attained 'high condition'; 2) a simulated regime of continuous LT; and, 3) a simulated regime of continuous ST. Showing the actual energy requirements of chicks that attain 'high condition' at the end of the growth period. Age specific patterns of energy delivery are based on the average meal mass delivered in each 10 d age class, the rate of their delivery, and estimates of the energy value of these meals based on their species composition (Table 5.4).

Table 5.1. Age specific pattern of energy requirements of short-tailed shearwater chicks from hatching to adult abandonment. Total energy requirements include assimilation efficiency. Body maintenance requirements were estimated by regressing reconstructed meal mass with the mass change of chicks over a 24 h period, following Granadeiro *et al.* (1999). Biosynthesis costs were estimated as one third the energy value of accumulated tissues following Ricklefs *et al.* (1980). # denotes estimates of energy requirements (kJ/d), based on the energy value per gram of food, given the average species composition, and the % mass contribution of both ST and LT meals per age class (see Table 3).
based on: the prey composition of ST and LT meals; energy value of different prey (see Table 5.4); and relative contributions of meals from ST and LT. An assimilation efficiency of 89% was assumed for the raw prey component (fish, cephalopod, krill, and other crustacean) (Ricklefs *et al.* 1980), and 90% for the oil component (Obst and Nagy 1993). * denotes estimates of body composition from Fitzherbert (1985).

Growth						Maintenance			
Age class	Average mass (g)	*Fat deposition (g/d)	*Protein deposition (g/d)	Biomass (g/d)	Biosynthesis costs (kJ/d)	(g/d)	# (kJ/d)	Total estimated energy requirements (kJ/d)	#Total estimated rate of energy delivery (kJ/d)
1-10	212	1.9	2.0	111	37	9	84	257	454
11-20	399	5.2	2.6	252	83	25	234	631	500
21-30	569	5.3	2.4	250	83	28	261	659	673
31-40	675	6.2	1.5	266	88	39	363	795	712
41-50	773	6.2	1.4	264	87	40	440	877	681
51-60	802	4.4	1.4	159	11	52	572	824	666
61-70	730					42	473	525	524
71-80	660					33	372	412	472
81-90	637					20	225	214	278
Total (90 days)		291.5	112.4	13024	3877	2682	27975	49812	46520
Overall average (per day)		4.9	1.9	217	65	32	325	577	585
se		0.7	0.2	27	13	6	70	81	38

Table 5.2: Relationship between provisioning and growth parameters during different age classes and chick condition at fledging. Showing Pearson's correlation coefficient, R2 and P.

Development Stage (days)	1 - 20 d			21 - 40 d			41 - 60 d		
Pearson's Correlation	R^2	P	N	R^2	P	N	R^2	P	N
Average mass gain per 20 day period v fledging condition	0.70	<0.05	15	0.48	0.29	21	0.07	0.77	21
Number of ST v fledging condition	0.4	0.14	15	0.46	<0.05	19	0.42	<0.05	19
Provisioning rate v fledging condition	0.2	0.28	15	0.68	<0.05	19	0.12	0.62	19

Table 5.3. Provisioning model showing the average provisioning parameters to chicks reared in ‘high condition’. Energy density and protein content of meals delivered is also shown.

*Using published values of protein content in different prey types, and the average composition of meals delivered (Table 2).

see species composition and energy value of prey types from Table 2.

Parameter	ST Av	sd	LT Av	sd	Total	sd
Av. meals delivered (both parents)	28.3	3.2	12.1	0.6		
Av. meal size delivered (g)	105.1	21.3	129.8	26.9		
*Proportion of protein in Av. meal (%)	17.3		10.1			
# Energy density of meal (kJ/g)	4.0		22.3			
Energy value in Av. meal (kJ)	420.5		2895.5			
Av. duration of trip (days)	1.1	0.3	13.5	2.5		
E. flow (kJ/d from each trip)	381.0		192.9			
Estimated total food delivered (g)	2974	250	1558	124	4501	268
Estimated total protein delivered (g)	490	43	157	21		
Estimated total energy delivered (kJ)	11900	1336	34746	1986	46520	2053
% total protein delivered	76		24			
% total E. delivered	25	3	75	5		
% total food delivered	65	6	35	3		

Table 5.4. Species composition and energy values of average ST and LT meals. Energy value of crustacean from Wiebkin *et al. Unpublished*, and energy value of myctophid fish presents the average from multiple sources as mentioned in methods.

Prey type	% mass LT meals	% mass ST meals	Energy value (kJ/g-wet wt)
Oil	39.4	0.0	41.8
Myctophid fish	31.4	0.0	8.0
Neritic fish	13.7	52.3	4.7
Cephalopods	8.1	12.9	3.2
Krill	6.5	34.5	3.3
Other crustaceans	0.9	0.3	2.7
Energy value (kJ/g)	22.3	4.0	

CHAPTER 6

SEXUAL SIZE DIMORPHISM AND ASSORTATIVE MATING IN THE SHORT-TAILED SHEARWATER *PUFFINUS TENUIROSTRIS*

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STATEMENT OF AUTHORSHIP

SEXUAL SIZE DIMORPHISM AND ASSORTATIVE MATING IN THE SHORT-TAILED SHEARWATER *PUFFINUS TENUIROSTRIS*

Einoder et al. published paper

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Collected all data, performed analysis on all samples, interpreted data, wrote manuscript and acted as corresponding author
I hereby certify that the statement of contribution is accurate
Signed
…………………………………………………………………………….Date…………………

Page, B.
Supervised development of work, contributed to planning of field work and analysis, and provided critical evaluation of drafts.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
Signed
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Goldsworthy, S. D.
Supervised development of work, and provided critical evaluation of a draft.
I hereby certify that the statement of contribution is accurate and I give permission for the inclusion of the paper in the thesis
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ABSTRACT

Sexual size dimorphism (SSD) was assessed in the Short-tailed Shearwater *Puffinus tenuirostris*, and a sex-discriminating function produced, in order to improve methods for sexing live birds in field studies. Despite a degree of overlap in body size, males were significantly larger than females. A stepwise discriminant function analysis of five morphometric characters indicated that bill depth and head length were the most dimorphic characters, and the resultant sex model correctly discriminated 92.0 % of known males (n = 23/25), and 92.3 % of known females (n = 24/26). The model was validated by applying it to an additional group of birds whose sex was assumed, based on their pairing with known sex individuals. 93 % of assumed females were correctly classified (n=15), as were 96 % of males (n=15). Application of the sex model to another breeding colony decreased its performance to 70 - 82 % accuracy, due to the existence of significant geographic variation in body size in this species. For individuals where certainty was low (i.e. when small males are confused with large females), sexing could be improved by measuring the body size of their breeding partner. This was due to significant positive assortative mating with respect to bill depth and a body size index. This sex model provides a quick and easy means of sexing in instances where molecular methods and other techniques are not feasible.

INTRODUCTION

The magnitude of sexual size dimorphism (SSD) varies among seabird species, and among traits within each species. Male-biased SSD is most common among the world’s seabirds, however, female-biased SSD exists in the Fregatidae, Hydrobatinae and Sulidae (Serrano-Meneses and Székely 2006). In some species male-biased SSD is very pronounced, with females being only 80 % the size of males (e.g. northern giant petrel *Macronectes halli,* González-Solis 2004). In these cases birds can be sexed visually, as the larger body size and disproportionately broader bills of males are clearly recognisable (González-Solis 2004). However, in many other seabird species SSD is less pronounced, and size differences can only be identified by applying morphological traits to a sex model (e.g. Hamer and Furness 1991, Granadeiro 1993). The application of such a model first requires an investigation into the direction and extent of dimorphism that exists in a species, and the skeletal trait which shows the greatest degree of dimorphism must be identified. The general trend among the Procellariiforms (albatross, petrels and shearwaters) that breed at mid to higher latitudes of the Southern Hemisphere is that males are heavier and larger than females (Fairbairn and Shine 1993). This male-biased SSD has been identified for the short-tailed shearwater (Bull *et al*. 2005), with significant size differences suggesting that sex discrimination based on body size may be applicable.

Discriminant functions analysis (DFA) combines the discriminatory power of several morphometric variables into one formula that best discriminates between the sexes (Weidinger and van Franeker 1998). This method determines which morphometric traits are the most variable in terms of sex, and produces a model into which the measurements of birds of unknown sex can be entered, to assign a likelihood of being male or female. DFA has proven useful for identifying dimorphism in a range of Procellariiforms, such as the fulmarine petrels *Fulmarus* spp. (van Franker and Ter Braak 1993), cape petrel *Daption capense* (Weidinger and van Franeker 1998), Cory's shearwater *Calonectris diomedea* (Granadeiro 1993, Lo Valo 2001), pink-footed shearwater *Puffinus creatopus* (Guicking *et al.* 2004), and Balearic shearwater *P. mauretanicus* (Genovart *et al.* 2003).

This study aimed to: 1.) identify the degree of SSD in the Short-tailed Shearwater and determine in which traits it is expressed; 2.) develop a discriminant function based on the traits that show SSD; 3.) identify the extent of assortative mating with respect to body size; 4.) assess the degree of confidence in sex discrimination by the model; and 5.) determine the inter-colony applicability of the model. The overall aim was to provide an accurate means of determining sex in field studies where other means of establishing sex are either not present, or unavailable.

METHODS

Study area

This study was conducted at breeding colonies on Althorpe I. (35°37'S, 136°86'E) and Evans I. (32°22'S, 133°28'E) in South Australia. Althorpe Is. was visited on five occasions during the 2004 - 05 Austral summer breeding season (17 - 23 October 2004, 15 - 21 December 2004, 21 January - 11 February 2005, 18 - 25 March 2005, 4 - 8 April 2005), and Evans Is. on 4 occasions (28 October - 2 November 2004, 27 November - 12 December 2004, 24 January - 8 February 2005, 29 March - 1 April 2005) in conjunction with other research. All measurements were taken by the same researcher (LE) to avoid inter-sampler error.

Sexing and measurements

A group of breeding adults of known sex was used to develop the model. Females were positively identified by the presence of an egg *in utero* prior to laying, and the majority of males were sexed by observing copulation behaviour during the mating period. However, if a bird was present in the burrow with an egg-bearing female in the brief one to two day period prior to laying, then they were also considered to be males. Where a breeding partner joined one of these known sex individuals later on in the breeding season, they were assumed to be the opposite sex. This is based on the assumption that breeding pairs contain one male and one female, as there have been no documented cases of mating trios in this species. Adults were deemed to belong to a breeding pair if they were observed on multiple occasions at the base of the same numbered burrow, either incubating the egg, or provisioning food to the chick. These birds formed an additional group of assumed sex (Evans I. n=15, Althorpe I. n=20). Molecular sexing was not employed, as the accuracy of the above methods was deemed adequate for this study.

Each adult was leg-banded and body mass (BM) was determined with a spring balance (1000 ± 5 g). Four skeletal traits were measured to determine body size using digital vernier callipers (± 0.01 mm) (Fig. 6.1): head+bill length (HBL) from supra-occipital to front edge of bill; bill length (BL) from the edge of forehead feathers to the most distal part of the hook; bill depth (BD) from concave dorsal surface just in front of tubes to base of bill; and, tarsus length (TL) from distal end of tarsometatarsus to back of heel with leg bent (Reynolds *et al*. 2008).

Assessing SSD

Univariate analysis using SPSS (Ver. 13) was used to determine if overall external morphometrics varied with sex or colony. After checking all raw data for normality and homogeneity of variances, difference between group means were assessed using the appropriate tests. Means, and their associated ± standard deviation and significance level were calculated.

To measure the extent and direction of SSD in each trait average values were log10 transformed and SSD was calculated as log10 (male body size) – log10 (female body size) (Abouheif and Fairbairn 1997). Whilst ratios are commonly used to express SSD in animals most of them are considered to produce skewed data, and thus have undesirable statistical properties (Smith 1999). Thus, the difference between male and female size was expressed as a logarithm (following Smith 1999). Where males were larger than females the resulting Pearson's correlation coefficient value was positive; when females were larger, the value was a negative (as in Serrano-Meneses and Székely 2006). Student's t-test was also applied to each character for known breeding pairs to determine the extent of SSD occurring.

Developing a sex model and body size index

A cross-validated DFA was used to explore the nature of any SSD that occurred and produce a body size index, using SPSS (Ver. 13). No significant differences between group covariance matrices occurred in the data, and all the assumptions of DFA were met (Pearson and Hartley 1976, Klecka 1980). The Evans I. sample was used to develop the sex model, by entering each significant character into a stepwise DFA (see Bosch 1996, Weidinger and van Franeker 1998, Mawhinney and Diamond 1999 for a similar procedure). The Discriminant Function produced could then be used as a predictive tool to determine the sex of an individual based on the discriminant score gained. Whilst providing a sex model, the discriminant score was also used as an index of body size to further explore SSD. The value used to divide the frequency distribution of discriminant scores into sexes was the midpoint between the mean scores for males and females of known sex (Van Franeker and Ter Braack 1993, Weidinger and van Franeker 1998).

Performance of the sex model was validated by re-applying it to the original known sex group (jack-knife method)(e.g. Amat *et al.* 1985), and by applying it to the assumed sex group (described above). The classification success of the sex model can be inferred from the number of misallocations of known or assumed sex birds. Misallocations occurred when males were particularly small, or females particularly large. The inter-colony application of the model was assessed by applying it to a known and assumed sex group from Althorpe I. This required the re-calculation of the dividing point from the frequency distribution of discriminant scores of the new population (as recommended by Weidinger and van Franeker 1998).

Assessing assortative mating

Assortative mating in regard to body size parameters was tested by estimating the slope of the relationship between the log10 transformed male size and the log10 transformed female size using major axis (MA) regression (Sokal and Rohlf 1995).

MA minimises the sum of the squared distances of residuals. This type of regression, unlike least squares regression (Model I), does not assume that x and y were measured without error (McArdle 1988, Sokal and Rohlf 1995), and is performed when both variables are measured on the same scales and with the same units (Quinn and Keough 2002). MA regressions were performed with software for Model II major axis regression (Legendre 2001), available at the website <http://www.bio.umontreal.ca/Casgrain/en/labo/model-ii.html>. Parametric 95 % confidence intervals (lower CI – upper CI) were computed for the slope of the line by bootstrapping the variables, and a permutation test was used to determine the significance of the MA. The closer the slope to a 1:1 relationship between the sexes, the greater evidence of assortative mating for that character (as in Fairbairn and Preziosi 1994).

RESULTS

Sexual size dimorphism

For known sex groups from both Evans and Althorpe I. all five body size variables had equality of group covariance matrices, and all but BM were normally distributed. For the Evans I. population, inter-sexual differences were highly significant in BL, BD, and HBL (<0.0005), and significant for TL (<0.05) (Table 6.1). The positive SSD values gained for all of these characters reveal male-biased SSD, with the greatest degree of SSD occurring in BD (Table 6.1). On Althorpe I male-biased SSD appeared less marked, with the only significant size difference between the sexes occurring in BD, with males having the deeper bill. However, this result may be due to the smaller sample size studied at this colony because, while BL, HBL, and TL were not significantly different, they trended towards being larger in males, gaining positive SSD values (Table 6.1). Whilst BM is commonly dimorphic in seabirds (Serrano-Meneses and Székely 2006), it did not differ significantly between the sexes in this study (Table 6.1). This result is not surprising as BM varies widely across the population at any one time due to the body condition of individuals, and the potential errors gained when they have food in their stomachs. Also adults of this species, like many Procellariiforms, commonly undergo large mass changes through the breeding season (Meathrel *et al.* 1993).

Discriminant model

By running a stepwise DFA using all characters for birds of known sex from Evans I. (n = 26F, 25M), BD and HBL were identified as the largest contributors to the separation of the sexes. This was evident as they gained the largest canonical discriminant function coefficients (HBL=0.75, BD=0.73, BL=0.54, TL=0.25). The assumptions of DFA were met, because no significant differences between group covariance matrices, or deviations from multivariate normality were found (Box's M = 5.40, approximate $F = 0.84$, $P = 0.54$). The discriminant function (D) was:

$$D = -56.325 + 1.964*BD + 0.493*HBL$$

Jack-knifing produced a 92 % classification rate, and thus did not improve the performance of the model. This indicates that the classification success of the discriminant function was accurate, with an eigenvalue of 2.234 (Wilks' λ =0.309, $P < 0.0001$). The model correctly regrouped 92.3 % of females, and 92.0 % of males from the Evans I. known-sex group. Miss-classification of some individuals indicates that there is a degree of overlap in the discriminant scores between the sexes (Fig 6.2), due to a slight overlap in body size. When D is greater than 0 the individual is a male (mean score = 1.49), and when smaller, a female (mean score = -1.34) (Fig 6.2). In known breeding pairs where one individual was of known sex and the partner of assumed sex, males had a significantly larger body size index than their female partners in all cases ($t = -12.20$, $N = 52$, $P<0.001$) (Table 6.2). Within pairs, males also had a significantly larger BD, BL and HBL (paired t-test, $P<0.05$) (Table 6.2). BD, being the most dimorphic character, had an average difference of 0.68 ± 0.47 mm between partners (Table 6.2). However, in four cases, the female bore a slightly deeper bill than the male (0.01 - 0.2 mm).

The probabilities of group membership for each individual involved in the derivation of D were 46 % for females and 44 % for males, with a certainty of 0.99. By fitting these probabilities to the discriminant scores of each individual, critical scores for differing levels of probability were deduced from the non-linear regression produced (Fig 6.3). This provides an estimation of the reliability of allocating individuals to the correct sex using the model (Table 6.3) (as in Phillips and Furness 1997, Renner and Davis 1999). The model derived from the known sex group was then tested on the assumed sex group from Evans I. (n = 15), in order to assess its discriminatory power. This procedure confirmed the value of the model, as it correctly assigned 93 % of females, and 96 % of males.

Assortative mating of BD and body size

The BD of males and females in known breeding pairs were highly correlated (Fig 6.4.; R^2= 0.38, N = 48 pairs, P= <0.005), as was the body size index (Table 6.2.; R^2= 0.43, N= 52 pairs, P<0.005). The slope of the MA regression for BD reveals that mating is assortative based on this character, as it was close to 1:1 (BD: lower 95 % CI – upper 95 % CI: 0.53 - 1.14) (Table 6.2, Fig. 6.4). This indicates that deep-billed males were often paired with deep-billed females, and narrow-billed males paired with shallow-billed females. Whilst no association was found for BL, HBL or TL (Table 6.2), the body size index, which represents a combination of multiple characters, revealed that mating is also assortative based on body size.

Geographic variation in body size

Univariate analysis revealed significant differences in female BD, and HBL between colonies (Table 6.4), with Althorpe I. birds being larger than those on Evans I. (Table 6.1). For males, BD was the only significantly different character (Table 6.4), with Althorpe I. birds being larger (Table 6.1). However, the reverse occurred for BM, with Evans I. males and females being significantly heavier than their respective sex on Althorpe I. (Table 6.1 and 6.4). This result is most likely attributed to the time delay between each colony visit, and highlights the extensive seasonal variation in weight (e.g. Lill and Baldwin 1983, Weimerskirch and Cherel 1998). Because of inter-colony variation in body size, the performance of the discriminant model decreased when applied to Althorpe I., with a greater rate of misclassification. From the known sex group, 70 % of females were correctly classified (7/10), with the same success rate for males (7/10). The model was then applied to an additional 40 birds of assumed sex, with improved success, as 90 % of assumed females (18/20) and 75 % of assumed males (15/20) were sexed correctly.

DISCUSSION

The findings of male-biased SSD concur with previous studies for this species (Meathrel *et al.* 1993, Bull *et al.* 2005). The extent of SSD in the short-tailed shearwater is similar to that of other *Puffinus* species, as the sexing model has comparable discriminatory power (e.g. 92 % for Cory's shearwater LoValvo 2001, 90 % for Balearic shearwater Genovart *et al.* 2003, and 98.8 % for the pink-footed shearwater Guicking *et al.* 2004). BD was the most dimorphic trait, which is the case across the entire *Puffinus* genus (Bull *et al.* 2005). However, HBL had not been included in previous studies, and showed significant dimorphism contributing largely to the body size index.

The present discriminant model may be useful for field studies as it can be applied at any time during the breeding season, and sex can be derived instantly, and relatively easily. Despite the increased accuracy of molecular sexing, the need to perform lab-based analysis means that it is often impractical for seabird research in remote locations, or in instances where sex must be determined quickly. In addition it is much more expensive. Other more traditional methods, such as the presence of an egg, or cloacal examination (Serventy 1956, Warham *et al.* 1977), are of limited value as they are only apparent during certain stages of the breeding season. Whilst vocalisations are sexually dimorphic in some shearwater species, this method has only been validated in a few instances (e.g. Bretagnolle and Lequette 1990, Bretagnolle and Thibault 1995).

Assortative mating with respect to BD has been documented previously for the short-tailed shearwater (Meathrel and Bradley 2002). Whilst we provide further evidence of this size relationship, we also present a body size index, which reveals significant assortative mating. Assortative mating in bill dimensions also occurs in the common tern *Sterna hirundo* (Coulter 1986), Herring Gull *Larus argentatus* and lesser black-backed Gull *L fuscus* (Harris and Hope-Jones 1969). Brown noddys *Anous stolidus* mate assortatively based on body mass (Chardine and Morris 1989). The processes responsible for assortative mating between breeding partners are currently unclear. It has been suggested that assortative mating could occur through random mating alone (Coulter 1986, Chardine and Morris 1989), but this would only apply when the extent of SSD is large. More likely this relationship is the result of selective mate choice for body size or parental quality. There are many possible advantages that females attain from mating with large males, and vice versa (see review by Blanckenhorn 2005). For example, BD contributes to the snapping power of a bill, so males, and larger billed females should be able to handle larger prey, than should smaller birds (see Ashmole 1968, Koffijberg and Van Eerden 1995). Meathrel and Bradley (2002) found that BD correlated with breeding success in short-tailed shearwater's, suggesting that mate selection may be adaptive. Indeed the functional hypotheses proposed to explain assortative mating are similar to those proposed for SSD in seabirds, being; sexual selection, fecundity selection or differential niche-utilisation (see review by Bull *et al.* 2005, and Serrano-Meneses and Székely 2006). However, the adaptive significance of existing male-biased SSD in shearwaters is still unclear (Fairbairn and Shine 1993). Further research investigating the influence of body size on breeding success, foraging success and prey harvest (e.g. Barbraud *et al.* 1999, González-Solis 2004) are necessary in order to identify the processes responsible for SSD and assortative mating in this species.

The usefulness of a sexing model derived from a single colony across a species range depends on the degree of variation in the extent of SSD (Schreiber and Schreiber 1988, Evans *et al.* 1993, van Franeker and ter Braak 1993). Where seabirds are of comparable body size a reasonable accuracy may be obtained (e.g. Cory's shearwater Granadeiro 1993, cape petrel *Daption capense* Weidinger and van Franeker 1998, herring gull Coulson *et al.* 1980). However, significant spatial variation in body size will reduce the accuracy of a single-colony derived sexing model. In these instances the development of a broader generalised discriminant function based on combined data from geographically separate populations, can provide a more robust sexing tool (e.g. cape petrel *Daption capense* Weidinger and van Franeker 1998, fulmarine petrels van Franeker and Ter Braak 1993). Given the existence of significant inter-colony variation in Short-tailed Shearwater body size, when applying the current sex model it would be beneficial to compare the dimensions of an individual with the range reported herein. Also, when sexing a large number of birds, one can derive a new cut-point from the frequency distribution of the discriminant scores gained, as a crude means of modifying the current model (as in van Franeker and Ter Braak 1993, Weidinger and van Franeker 1998).

CONCLUSIONS

This study has provided a relatively efficient sexing model that requires two simple measurements in order to provide a body size index, as well as a likelihood of being either male or female. Whilst 60 - 70 % of birds could be sexed with a certainty of 95 %, within-pair comparisons of discriminant scores greatly improved sex determination of the remainder (due to significant assortative mating). Despite reduced success when applied to another colony, the degree of certainty provided by the current sex model is still comparable to that reported for many other seabird species. Thus, the current model represents a useful tool for gender determination in instances where molecular sexing and other methods are not available.

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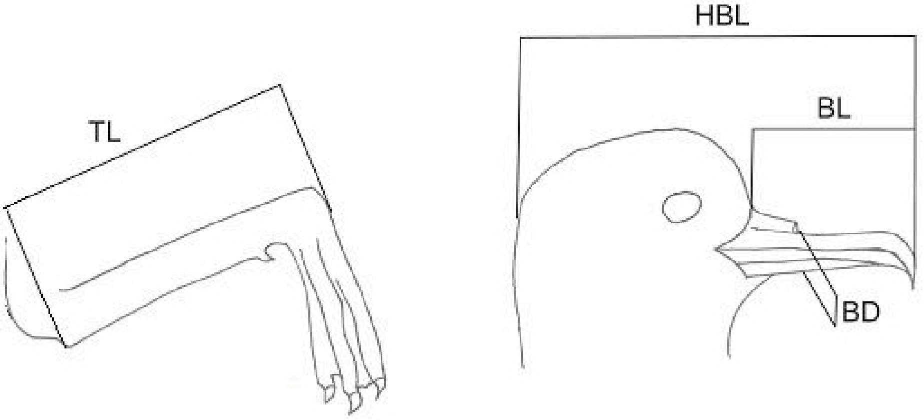

Fig. 6.1. Morphometric measurements: Head+bill length (HBL), bill length (BL), bill depth (BD), and tarsus length (TL).

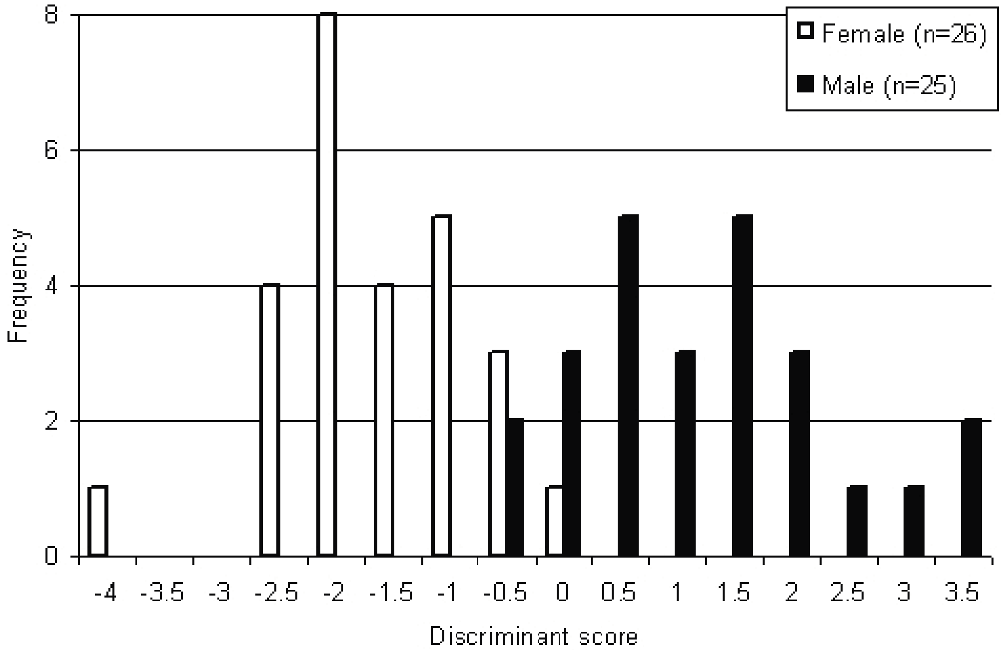

Fig. 6.2. Histogram of the canonical discriminant scores of breeding adults of known sex from Evans I. based on a DFA of four skeletal characters, with cut-point of 0. BD and HBL are the two characters that explain most of the spread across the x-axis and can be explained by the classification function (sex model) D= -56.325 + 1.964*BD + 0.493*HBL. Females are open columns, males solid columns.

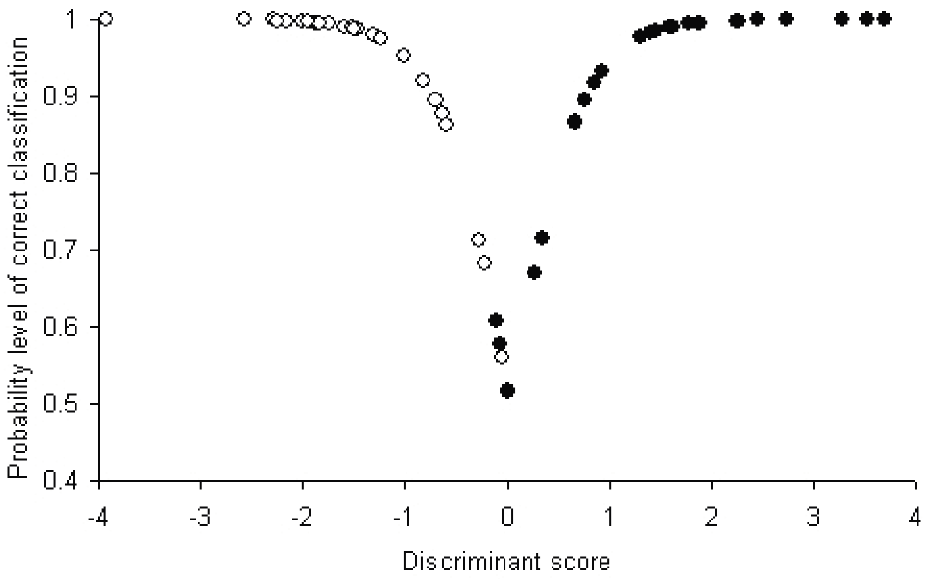

Fig. 6.3. Probability of correct classification as a function of discriminant scores, showing the posterior probability of belonging to the predicted group, based on the sex model. Open circles: probability of being female. Closed circles: probability of being male.

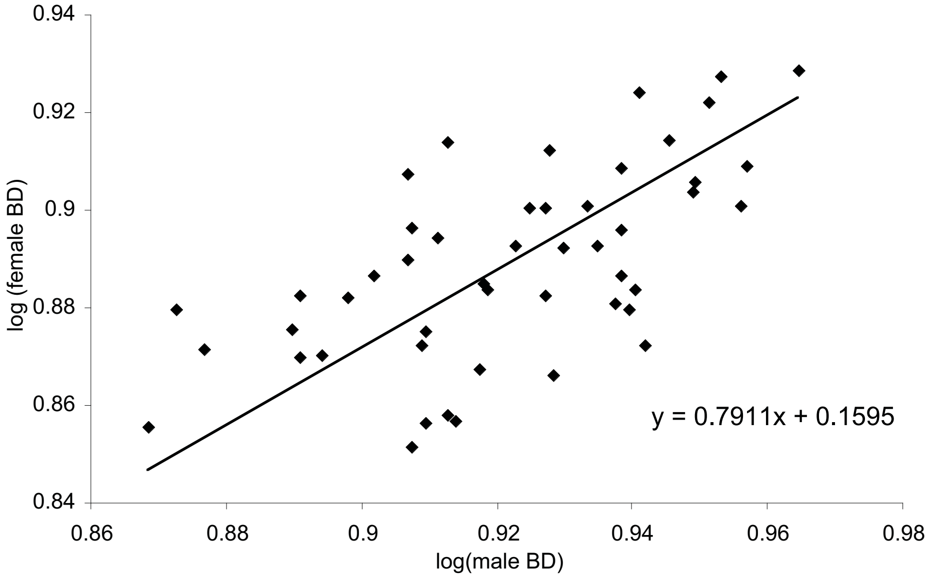

Fig. 6.4. Assortative mating by BD in short-tailed shearwaters. Major axis regression showing $\log_{10}$ female body size on $\log_{10}$ male body size. The slope of the regression is 0.79, with a lower and upper confidence interval 0.53 - 1.14.

Table 6.1: Variation in body size of males and female Short-tailed Shearwaters breeding at Evans and Althorpe I.s: mean, ± standard deviation, range, univariate ANOVA and U-test (*). The degree and direction of SSD is also represented by log transformed SSD values for each character, with a + value indicating that males are larger than females, and a – value, the reverse.

Colony	Group	Character	Sex	Mean	s.d	Range	F	P	SSD
Evans	Known sex	Body mass	F	729	18	580 - 885	2.53	*0.12	0.025
	n=26 F, 25 M		M	774	23	610 - 930			
		Bill Length	F	31.84	0.21	29.9 - 33.9	15.22	<0.05	0.015
			M	32.97	0.20	31.1 - 34.7			
		Bill Depth	F	7.43	0.06	6.7 - 8.0	58.53	<0.05	0.040
			M	8.14	0.07	7.3 - 8.9			
		Head-bill Length	F	81.75	0.26	78.8 - 83.7	63.03	<0.05	0.016
			M	84.85	0.29	81.8 - 87.7			
		Tar Length	F	59.40	0.26	56.5 - 61.4	4.65	<0.05	0.007
			M	60.28	0.32	57.3 - 63.4			
		BSIndex (d score)	F	-1.43	0.89	-3.9 - 0.01	109.00	<0.05	
			M	1.50	1.10	-0.1 - 3.6			
Althorpe	Known sex	Body mass	F	651	11	600 - 700	0.16	*0.69	-0.004
	n=10 F, 10 M		M	645	10	590 - 695			
		Bill Length	F	31.89	0.26	30.3 - 32.8	1.58	0.23	0.008
			M	32.50	0.41	30.9 - 35.1			
		Bill Depth	F	8.08	0.11	7.6 - 8.7	6.51	<0.05	0.018
			M	8.41	0.07	8.0 - 8.7			
		Head-bill Length	F	84.22	0.54	81.2 - 87.2	0.18	0.68	0.005
			M	84.54	0.53	81.8 - 87.7			
		Tar Length	F	59.92	0.33	57.9 - 61.1	0.69	0.42	0.003
			M	60.41	0.49	57.2 - 62.5			
		BSIndex (d score)	F	0.81	1.05	-1.2 - 2.2	5.60	<0.05	
			M	2.16	1.37	0.4 - 4.4			

Table 6.2: Assessing the magnitude of SSD, and the existence of assortative mating with respect to morphometric measurements and an index of body size within breeding pairs of known sex; also the slope and lower and upper confidence interval obtained by major axis (MA) regression of $\log_{10}$ (female size) against $\log_{10}$ (male size) for bill depth, and bill, tarsus and head-bill length within pairs. Sample sizes of some characters were smaller due to missing data.

	Cases correctly classified						
Character	Females	Males	Total	Jacknife	Eigenvalue	Wilks' lambda	P
Body mass						0.950	0.118
Tarsus Length	69.2% (18/26)	60.0% (15/25)	64.7%	64.7%	0.951	0.913	0.036
Bill Length	69.2% (18/26)	64.0% (16/25)	66.7%	66.7%	0.311	0.793	<0.05
Head-bill Length	92.3% (24/26)	88.0% (22/25)	90.2%	90.2%	1.286	0.457	<0.05
Bill Depth	88.5% (23/26)	92.0% (23/25)	90.2%	90.2%	1.194	0.456	<0.05
D=-56.325+(1.964*BD)+(0.493*HBL)	96.0% (25/26)	84.0% (22/24)	94.1%	92.2%	2.234	0.309	<0.05

Table 6.3: Critical discriminant scores for the probability of a bird being male or female.

P	female	male
0.999	-2.30	2.43
0.995	-1.80	1.83
0.990	-1.53	1.16
0.950	-0.96	1.08
0.90	-0.72	0.78
0.80	-0.49	0.52
0.70	-0.26	0.33
0.60	-0.12	0.20
0.50	0.00	0.00

TABLE 6.4: Inter-colony comparison of morphometric characters between adult of known sex, showing the extent of size difference between males from both colonies (n: Evans I. = 25, Althorpe I.= 10), as well as females (n: Evans I. = 26, Althorpe I. = 10)

Sex	Character	F	df	P	Colony where larger
Females	Body mass	7.11	34	<0.05	Evans
	Tarsus Length	3.82	34	0.06	Althorpe
	Bill Length	0.02	34	0.90	Althorpe
	Head-bill Length	21.42	34	<0.05	Althorpe
	Bill Depth	31.41	34	<0.05	Althorpe
Males	Body mass	12.71	32	<0.05	Evans
	Tarsus Length	0.52	32	0.48	Evans
	Bill Length	1.32	32	0.26	Evans
	Head-bill Length	0.18	32	0.67	Althorpe
	Bill Depth	4.69	32	<0.05	Althorpe

CHAPTER 7
DISCUSSION

A detailed account of the short-tailed shearwaters foraging strategy

This thesis has examined many of the behavioural, physiological and life-history traits of the short-tailed shearwater with the aim of identifying which traits facilitate their relatively extreme dual-foraging strategy. Ultimately the adult's ability to both synthesise and store energy, and accumulate a reasonable volume of oil are key to this feeding regime. The production of oil enables parents to maintain a suitable rate of energy flow to chicks after their extended absences on LT. While the energy stores of parents enable them to maximise energy flow to chicks during ST. This regime of food delivery exceeds chick energy demands, which facilitates the accumulation of excess lipid to provide an energy reserve during extended fasts, if and when they occur. Rearing a single chick per season which has a protracted growth period, and is housed in an underground burrow further reduces the energy demands at the nest. Many of these traits are common to all Procellariiforms (albatrosses, shearwaters and petrels), and also occur in other pelagic seabirds, but they are expressed at a relatively extreme level in this species. These combined traits enable parents to deliver food less regularly, providing more time for locating and acquiring prey, and travelling further afield to forage (Drent and Dann 1980). This is considered an advantage as locating prey in the marine environment is challenging, due to its heterogeneous distribution. In contrast, most inshore seabird's rear broods of two or more chicks that grow up to twice the rate of pelagic seabirds (Ricklefs 1990). While this has the advantage of reducing the time spent rearing chicks, the energy demands at the nest are increased. This means that inshore seabirds must return more regularly to deliver prey, limiting their ability to buffer chicks over variable feeding conditions.

The role of each of these traits in shaping the short-tailed shearwaters dual-foraging strategy can be demonstrated by considering numerous elements of their life-history, and by drawing on many of the findings of this thesis. Being long-lived, pelagic seabirds should accept fewer risks for the sake of a single breeding episode, so that they may enhance future reproductive success (Stearns 1992). It is therefore suggested that

Procellariiforms have evolved a fixed-level of parental investment independent of their chick's needs (e.g. Hamer and Hill 1993, Lorentsen 1996, Granadeiro *et al.* 1998). This seems to be the case in the short-tailed shearwater, as the condition of chicks does not influence the interval until the next meal, or the mass of the meal delivered (Weimerskirch and Cherel 1998, Bradley *et al.* 2000). However, recent studies on a range of Procellariiforms have show that parents in good body condition are able to respond to chick condition by modifying their provisioning rate, while parents in poor condition will not (e.g. Charaund and Weimerskirch 1994, Tveraa 1997, Tveraa *et al.* 1998, Baduini 2002). As there is no coordination in provisioning rate between parents who employ a relatively extensive dual-foraging strategy, the nutritional state of the chick at one feeding conveys little information to the parent about the chicks needs at the end of the succeeding foraging trip. In the absence of solicitation-response behavioural feedback (Ricklefs 1896) parents should err on the side of caution and return the maximum sized meal they can deliver. When parents maintain a regular pattern of food delivery this regime overfeeds chicks, leading to the deposition of substantial lipid reserves as was demonstrated in **Chapter 5**. The storage of lipid is a key component of the Procellariiform dual strategy as the growth period regularly incurs times of energy surplus and shortage (Ricklefs *et al.* 1980, Hamer and Hill 1993, Ricklefs and Schew 1994, Schultz and Klomp 2000). For example, **Chapter 5** identified that provisioning rate commonly exceeded energy requirements during most age classes, except at peak mass. This enabled the accumulation of lipid reserves, which peak at ~45 % of body mass at the end of the chick-rearing period (Fitzherbert 1985). Energy reserves are also an important buffer for the many short-tailed shearwater chicks who experience synchronous foraging by both parents, i.e. where both male and female depart on LT at the same time. These energy reserves reduce the chance of excessive loss of condition during lengthy fasts (Ricklefs *et al.* 1980, Ricklefs and Schew 1994, Phillips and Hamer 1999, Hamer *et al.* 2000, Schultz and Klomp 2000).

The energy storage capability of the parent is another attribute that is central to the dual-foraging strategy of the short-tailed shearwater. Adult body mass plays a central role in foraging decisions in many animals, linking foraging and allocation, and thus having implications on both reproductive fitness and survival (Kacelnik and Cuthill

1990). This is the case for all dual-foraging seabirds because adult body condition is largely considered to control the decision to self-feed or provision food to the chick (Lorensten 1996, Weimerskirch *et al.* 1997, Weimerskirch 1998, Weimerskirch and Cherel 1998). As shown in **Chapter 5**, parents perform LT to restore their own energy reserves, to fuel the return journey to the colony, and use stored energy to offset some of the energy demands of ST, when they don't self feed**.** The restoration of body condition on LT provides direct evidence that birds are able to forage optimally on these trips, by offsetting the costs incurred during their long distance movements (Optimal foraging theory: Kacelnik *et al.* 1986), as has been documented in a wide range of other dual-foraging Procellariiforms (Baduini and Hyrenbach 2003). The profitability of distant foraging areas is also apparent in the flight behaviour documented in **Chapter 3**. The prevalence of commuting behaviour on LT is widely considered to reflect the degree of predictability in the general location of prey in the Southern Ocean (Waugh *et al.* 1999, Catard *et al.* 2000, Hyrenbach *et al.* 2002, Pinaud and Weimerskirch 2005).

Studies on a range of other Procellariiforms have provided direct evidence as to how foraging efficiency is maintained on LT. The combined deployment of stomach temperature loggers and satellite transmitters has revealed that foraging success can be maintained on LT due to an increased rate of prey capture in distant foraging grounds (e.g. wandering albatross *Diomedea exulans* Weimerskirch *et al.* 1997, blue petrel *Halobaena caerulea* Chaurand and Weimerskirch 1994, Weimerskirch et al. 2003). Energy gains are also experienced due to the flight efficiencies of wide ranging seabirds. In contrast to the increased rate of take offs and landings on ST, birds can reduce energy expenditure on long distance travel by using wind patterns, and large looping flight patterns (e.g. wandering albatross Weimerskirch *et al.* 1997, Fritz *et al.* 2003, yellow-nosed albatross *D. carteri* Pinaud and Weimerskirch 2005, blue petrel Chaurand and Weimerskirch 1994, Weimerskirch *et al.* 2003). Increased energy returns can also be achieved on LT as birds commonly target prey aggregations associated with large scale oceanographic structures such as frontal zones, eddies and gyres (Waugh *et al*. 1999, Catard and Weimerskirch 1999). The bio-physical processes associated with these features are relatively more stable than in neritic and shelf-break regions, and therefore provide predictable areas of enhanced biological productivity (James *et al.* 2002, Tomczak 2004). Therefore, despite travelling long distances to reach these features, they provide the forager with a high certainty of maintaining foraging efficiency (Weimerskirch *et al.* 2005). While neritic and shelf-break waters of sub-Antarctic Islands are considered to provide a relatively predictable landscape for locating prey, they are more variable than large-scale oceanic features (e.g., Weimerskirch *et al.* 1997). This is likely to be the case for neritic and shelf break waters of south-eastern Australia, due to the influence of a number of up-wellings that occur, the strength and duration of which are known to vary throughout the summer/autumn months (Kampf *et al.* 2004, Ward *et al.* 2006). However, the finding that 23 % of LT are performed in neritic waters reveals that the abundance and availability of prey in this habitat must be sufficient to enable parents to restore their energy reserves. Given the energy incurred in the outbound flight of a LT to oceanic waters, and the challenges of locating prey over a larger spatial scale, neritic LT may represent an advantageous strategy for those individuals. Whether this is a strategy that some individuals adhere to through an entire breeding season, or is only performed by inexperienced or poor condition birds is yet to be determined.

Some central place foragers boost the profitability of distant foraging by selecting prey items of higher energy value (e.g. Antarctic fur seals *Arctocephalus gazelle* Staniland *et al.* 2007). The short-tailed shearwater experiences energy gains simply by their decision to forage further south in oceanic waters. This is due to the elevated energy content of pelagic prey harvested in the Southern Ocean, being up to 3 times more energy rich than their southeastern Australian counterparts (Clarke and Prince 1980, Cherel and Ridoux 1992, Bunce 2001, Tierney *et al.* 2002). Therefore, in line with central place foraging theory, the increased costs incurred by long distance movements can be offset by an increased rate of energy intake in distant waters.

The performance of a dual-foraging strategy enables the short-tailed shearwater to forage more optimally, by spatially and temporally separating the processes of foraging to self-feed and foraging to provision the chick. This is an advantage for central place foragers as it enables them to alter their foraging behaviour depending upon whether they are self-feeding or provisioning (Kacelnik 1988, Beauchamp *et al.* 1991). During self-feeding, foragers aim to maximise net energy gain (i.e. efficiency), but when foraging to provision chicks, they aim to maximise energy delivery to their offspring (Ydenberg *et* *al.* 1992). This disparity in foraging behaviour is apparent in the short-tailed shearwater as most, if not all of the self-feeding occurs on LT (Weimerskirch and Cherel 1998, Weimerskirch 1999). The optimal location for an individual to self-feed would be in habitat where prey are both plentiful and predictable, enabling them to maximise foraging efficiency. This was documented in **Chapter 3**, as most birds employed commuting flight to cooler waters of elevated chlorophyll a concentration in the Southern Ocean. Travelling to large-scale oceanic features where there is a higher probability of maintaining elevated foraging success would provide an advantage to parents. This is because rebuilding energy reserves would require the consumption of large quantity of prey. This process would occur most rapidly when exploiting larger scale prey aggregations, as an individual wouldn't have to travel as regularly, or perhaps as far, between prey patches. In a situation where prey are readily available, the deposition of suitable protein and fat reserves would take at least a number of days, due to the fixed rate that energy can be assimilated by seabirds (Ricklefs *et al.* 1980, Obst and Nagy 1993). Stomach oil would also accumulate most rapidly when foraging in a location of high daily energy intake. Little is known of the factors that govern the rate of oil accumulation in Procellariiforms. This work raises many questions, such as how rapidly does it accrue? do the birds forage until a set amount of oil is accumulated? is oil production mediated by the energy deficit of the adult?

Extended periods of self-feeding on LT are only achievable by short-tailed shearwaters because they are able to invest heavily in their offspring by returning an energy rich meal, and utilising stored energy reserves to maximise energy delivery in ST. Optimal foraging theory predicts that animals should only forage in distant patches if they can return with larger loads to offset the costs incurred by offspring during their absence (Orians and Pearson 1979, Stephens and Krebs 1986). Despite a reduced energy flow on LT, the return of oil enables parents to partially compensate their chicks for their absence. By producing stomach oil parents can concentrate dietary items into their most energy dense form, which has a smaller volume (Place *et al.* 1989). This provides considerable advantages as flying with a load increases the costs associated with travel (Croll *et al.* 1991, Niizuma *et al.* 2001).

The oil production capabilities of the short-tailed shearwater are within the middle of the recorded range in terms of the amount of oil delivered per LT meal (Clarke and Prince 1976, Prince 1980, Roby *et al.* 1989, Obst and Nagy 1993). But what sets this species apart is the overall role of oil in the energy budget. Due to the low number of ST meals delivered compared to other species, this oil accounts for ~75 % of the total energy delivered to chicks **(Chapter 4)**. Its value is likely to be higher in other years, given the inter-annual variation in the importance of LT and ST that was documented. And, this a conservative estimate, because we did not consider the volume of oil that may be retained (Obst and Nagy 1993). Of the few comparable estimates available, oil delivered by the Wilson's storm petrel *Oceanodroma leucorhoa* accounted for 61% of chick energy needs (Obst and Nagy 1993), and 34 % for wandering albatross chicks (Weimerskirch *et al.* 1997). Given the role of oil in the short-tailed shearwater, the time taken to accumulate a suitable volume may be one of the factors that dictates the duration of LT. This may be why the short-tailed shearwater does not perform any LT of less than 7 days duration.

By documenting the habitat use of the short-tailed shearwater, and quantifying the costs and benefits of the dual foraging strategy, this thesis has provided the first indication of the relative role of ST and neritic waters. This work has demonstrated that local feeding conditions are critical in successfully rearing chicks (**Chapter 5**). ST provide the increased energy flow that is required to sustain chicks while parents forage in distant waters. Therefore, ST can be viewed as facilitating the dual strategy, as distant foraging areas could not be accessed if local foraging areas could not provide adequate prey returns. Given the smaller spatial scales of movement and search effort on ST, and the limited time that parents have to acquire a suitable sized meal (i.e. usually 1 day), locating productive regions in this neritic habitat is critical. Whereas on LT birds can be more flexible in where they forage. Tracking results presented in **Chapter 3** reveal that adults are able to forage optimally in this habitat by either directing search effort towards a broad region, or performing a more widespread searching strategy. The comparable prey returns from these alternate strategies highlight the productivity in neritic waters, and provide a degree of evidence that the local up-welling features present a degree of predictability in the location of foraging areas.

Is the short-tailed shearwaters success attributable to their foraging strategy?

The abundance of the short-tailed shearwater over other Procellariiforms and inshore seabirds is largely attributable to their ability to spatially separate feeding and breeding sites over a latitudinal gradient of some 3000 km. These wide-ranging foraging capabilities provide many advantages over the more restricted foraging ranges of other seabirds in the communities at both their breeding and feeding sites. For example, compared to their counterparts in south-eastern Australia, the short-tailed shearwater is able of sourcing most of their energy requirements from distant oceanic waters. As shown in **Chapter 5** parents can meet the majority of their energy needs on LT, and also source 75 % of their chicks energy needs on LT. As 77 % of LT are performed in oceanic waters, this reveals that parents rely heavily oceanic habitats. This means that changes in the distribution and availability of prey in neritic waters near their colony are potentially less of a problem for this species, compared to inshore seabirds, who cannot escape such conditions. Short-tailed shearwaters can therefore make decisions about where to feed based on current feeding conditions, meaning that they are more capable of buffering their chicks through short-term fluctuations in foraging conditions around their colony. The extent of inter-individual variation in feeding parameters of successful parents documented in **Chapter 5**, and inter-colony and inter-annual variation documented in **Chapter 4** highlights the flexibility provided by the dual foraging strategy. This flexibility enables parents to vary energy flow from ST and LT, likely in response to changes in neritic and oceanic feeding conditions. Intra-colony and inter-annual variation in feeding parameters of Procellariiforms are commonly considered to reflect the spatial and temporal variability in prey availability (e.g. Weimerskirch *et al.* 1996, Granadeiro *et al.* 1998, Hamer *et al.* 1998, Quillfeldt and Peter 2000). While inter-annual variation in the proportion of oil returned was documented in **Chapter 4**, the relationship with ST feeding conditions and influence on chick condition warrants further research.

Another advantage of spending 70 % of their time on LT during chick rearing is the reduction in the extent of intra- and inter-specific competition that would be experienced in distant areas. This provides the added advantage of reducing the chances of depleting prey stocks in ST foraging areas (Ricklefs 1990), particularly given that they are likely to be relying on smaller scale and more variable prey aggregations in neritic habitat.

By spatially separating their breeding and feeding grounds the short-tailed shearwater also experiences a number of advantages over other seabirds in the Southern Ocean. In the sub-Antarctic there are limitations on the availability of suitable breeding sites. There are only a handful of islands, and burrow sites are limited at some of these sites as they already support diverse seabird and marine mammal communities. In many instances these islands are crowded with little opportunity for future expansion. By performing a 2500 - 4000 km flight to the more hospitable temperate environment along the south-eastern coastline of Australia the short-tailed shearwater is able to overcome these limitations. Space is not at such a premium as they are able to inhabit many hundreds of islands where inter-specific competition for breeding sites is less fierce. The larger bodied white-chinned petrel *Procellaria aequinoctialis* breeds on numerous subantarctic islands, and performs LT of 3 - 13 days duration, covering 1100 - 5900 km (Berrow *et al.* 2000, Catard *et al.* 2000). Also, the similarly sized Antarctic petrel *Thalassoica antarctica* performs foraging trips of 3 - 9 days from a total of 12 colonies, all confined to the Antarctic continent (Lorentsen *et al.* 1996, Mehlum *et al.* 2007). Limited breeding sites may explain why these species have a breeding population estimated at around one third to half the size of the short-tailed shearwater (white-chinned petrel ~7 million, Antarctic petrel 6-10 million (Mehlum *et al.* 2007), short-tailed shearwater 23 million (Skira 1991)).

Application of the short-tailed shearwater as an ecological performance indicator

As identified in **Chapter 2**, assessing the value of a seabird as an indicator requires a good understanding of the location and scale of their foraging efforts, and their sensitivity to changes in the marine system. We also must consider a wide range of factors in order to accurately interpret the reasoning behind an observed response. Given the current development of an ecosystem based management program in the eastern Great Australian Bight of South Australia, there is a need to identify useful ecological performance indicators. Here I integrate the knowledge gained in **Chapters 3, 4** and **5** with past information on the foraging and breeding ecology of the short-tailed shearwater to provide an assessment of their potential use in fisheries and ecosystem management programs.

This study has provided the first direct indication of the role of neritic waters to the short-tailed shearwater during their breeding season. In **Chapter 3** I confirmed the expectations of Weimerskirch and Cherel (1998), that the neritic zone is the primary site of ST foraging. The importance of neritic waters to this seabird is further exemplified in **Chapter 5**, as 65 % of the food mass delivered to each chick came from ST meals. The dietary results of **Chapter 3** also reveal the importance of this habitat as a foraging site on the return from LT, as birds returned neritic prey in LT meals to add to the oil component (as for Antarctic prions *Pachyptila desolata* Cherel *et al.* 2002). This region has also been identified as the site of LT foraging, as 23 % (3/13) of satellite tracked birds primarily foraged in neritic waters beyond their ST foraging zone.

The seabird community of the eastern Great Australian Bight of South Australia contains many specialist piscivorous seabirds (e.g. pied cormorant *Phalacrocorax varius*, little pied cormorant *P. malanoleucos*, Blaber and Wassenberg 2004, crested tern *Sterna bergii* Chiaradia *et al.* 2002, Blaber and Wassenberg 2004), and a number of species with a more generalist diet (e.g. little penguin *Eudyptula minor* Gales and Pemberton 1990, Cullen *et al*. 1992, Chiaradia *et al.* 2003). While monitoring the prey returns of seabirds with a more specialised diet (e.g. gannets, terns, puffins, cormorants) can reflect the abundance and age structure of a specific prey species (e.g. Hislop and Harris 1985, Schaffner 1986, Montevecchi and Myers 1995, Litzow *et al.* 2002), seabirds with a more generalist diet often sample the most abundant prey species from a range of trophic levels. This means that their diet more likely reflects the overall community structure in the marine environment (e.g. Berruti and Colclough 1987, Montevecchi 1993). This is evident from the mixed diet of the short-tailed shearwater, which included 12 pelagic fish species, 8 cephalopods, krill, and a range of other crustaceans. Assuming that birds are truly opportunistic the variable importance of commercial species such as sardines and anchovy between colonies, and between years is likely to reflect their availability/abundance in the ST foraging area. Monitoring the diet of generalists is likely to provide a more accurate indication of the availability of these species as they do not show the strong prey preferences of specialists. However, understanding the prey preferences of a species, and their response to changing prey density is required to accurately interpret dietary data (Piatt *et al.* 2007). This could be achieved by simultaneous studies of seabird diet and direct measures of the prey assemblage via vessel based surveys.

As identified in **Chapter 4**, fish is the major component of the short-tailed shearwaters diet, and sardine and anchovy were regularly returned in ST meals at numerous colonies. Monitoring the diet of the short-tailed shearwater over other seabirds in the eastern Great Australian Bight also provides the advantage of reflecting feeding conditions at a scale that is more representative of commercial fishing operations in this region. Satellite-tracking data in **Chapter 3** revealed that birds perform ST at a spatial scale of 10-100 km. This is comparable to the scale that the sardine fishery operates at (10-100 km), meaning that individual fishing vessels target and track fish aggregations within these areas. This avoids the limitations that are often incurred when studying seabirds with smaller spatial scales than the fishery (see Montevecchi and Myers 1995). Further advantages of monitoring the diet of the short-tailed shearwater over other seabirds in the community that forage over smaller scales, is that birds performing multi-day ST are also capable of foraging in neritic waters neighbouring the fishery. This means that they have the potential to integrate information about changes in prey availability over larger areas. This is of value as it can provide an indication on prey as they move into, or out of, the fishing zone.

As the sardine and anchovy consumed by short-tailed shearwaters are juvenile fish (pre-recruits) studies of their occurrence in the diet provide an opportunity to indicate the local abundance of the youngest age classes (0- and 1-group) of fish in the region. This is not achievable when monitoring the diet of crested terns and cormorants, as these species more commonly target larger fish. There are numerous examples where the diet of seabirds targeting pre-recruits have provided an index of the distribution and year-class abundance of fish recruiting into a fishery (e.g. Hatch and Sanger 1992). The strength of a relationship between the abundance of sardines and anchovy in the diet of the short-tailed shearwater and their occurrence in the fish community warrants further investigation via simultaneous studies of diet and direct measures of the prey assemblage.

An additional advantage of monitoring the diet of the short-tailed shearwater is that it provides a potential means of monitoring ecosystem function in neritic waters. This is apparent as **Chapter 4** identified a loose relationship between the abundance of Australian krill (*Nyctiphanes australis*) in the diet and levels of primary productivity in the area. The importance of this prey item in ST meals corresponded with inter-annual variation in the number of up welling events in the area, and the strength and duration of this process (Van Ruth *pers comm*.). The strength of this link warrants further research via more direct measures of local productivity, or by assessing the correlation between krill returns and direct measures of krill abundance, or primary productivity (e.g. Bost *et al.* 1994, Litzow *et al.* 2002). Relationships between remotely sensed indices of productivity (chlorophyll a concentration, sea surface temperature) and the abundance of krill also warrant investigation to validate these relationships.

N. australis is a primary consumer that responds quickly to nutrient fluxes in the marine environment (Murphy *et al.* 1988), and often aggregates in areas of enhanced productivity associated with up welling events (O'Brien 1988, Gill 2002). Much like other euphausiids and surface swimming crustaceans, fluctuations in the abundance and availability of *N. australis* is well known to be associated with primary productivity (e.g. Skira 1986, Cullen *et al.* 1992, Abraham and Sydeman 2004). Thus, the occurrence of *N. australis* in the diet presents a potentially valuable indicator of the spatial and temporal variation in primary productivity in the area. As such, the short-tailed shearwater represents an environmental proxy comparable to that of the Cassin's auklet *Ptychoramphus aleuticus* in the Californian Current system. The prey harvest of auklet is considered an indication of productivity levels in the marine environment, with the occurrence of euphausiids in the diet corresponding with productivity in the region (Abraham and Sydeman 2004).

In addition to diet sampling, provisioning parameters provide the potential to rapidly reflect the state of foraging conditions. A reduction in prey availability in neritic waters is commonly revealed by the return of smaller meals (e.g. Monaghan 1992), or increased trip duration as parents take longer to collect a suitable meal (e.g. Berrow and Croxall 1999, Hedd *et al.* 2002, Harding *et al.* 2003). The most valuable parameters of the ST feeding conditions experienced by short-tailed shearwaters would be ST duration, ST meal mass, and the number of successive ST performed, or proportion of time spent performing ST. Trip duration presents a more effective indicator in species with very flexible time-activity budgets, like the short-tailed shearwater (Hamer *et al.* 2006). However, combined measures of at-sea activity would be beneficial, to identify any changes in the time spent foraging versus resting (e.g. Enstipp *et al.* 2006). Foraging parameters are likely to provide a clearer indication of feeding conditions in seabirds that do not respond to the condition of their chicks. For example, the increased number of meals returned to a poor condition chick by species could be mis-interpreted as a response to increased prey availability. The primary role of adult body condition as the driver of foraging decisions the short-tailed shearwater (Weimerskirch and Cherel 1998) means that an increase in the number of meals delivered is likely a reflection of increased prey availability. Simultaneous measures of chick condition would provide a more robust measure of foraging parameters by identifying high quality parents. Targeting high quality parents would reduce the extent of inter-individual variation in foraging strategies that was identified in **Chapter 5**.

Where time or financial limitations apply to a monitoring program, short term single visits to a range of shearwater colonies would provide an effective means of measuring a range of foraging parameters. A more useful approach would be to visit each colony several times throughout a breeding season to gain repeat measures of dietary and foraging parameters. Repeat visits would also enable measures of chick growth and breeding success. There are many examples where long term monitoring of chick growth, chick condition and breeding success has provided a means of assessing a seabird's response to changes in climatic and oceanographic conditions (e.g. Bunce 2002). However, the relationship between chick growth and feeding conditions are still largely unresolved in the short-tailed shearwater. This was exemplified by the uncertainty surrounding the role of ST foraging conditions and chick growth in **Chapter 4**. The expected increase in chick growth and peak mass during a year of increased ST foraging (2005/06) did not occur. This was considered to be attributable to changes in energy flow from ST and LT. Flexibility in the dual-foraging strategy effectively confounds any evidence of environmental signals. For example, the reduced delivery of oil in the year of increased ST foraging suggests that elevated ST foraging may have been related to reduced foraging success in distant foraging grounds. This provides an indication of the mechanisms by which the time spent in ST and LT can be altered to modify the energy delivery from neritic and oceanic habitats. Therefore the dual foraging strategy seems to mask relationships between changes in the spatio-temporal variability in prey abundance and chick growth and breeding success. In contrast, there are numerous examples where chick growth and breeding success in seabirds with a less flexible strategy show a clear relationship with prey availability (e.g. horned puffins *Fratercula corniculata* Harding *et al.* 2003). Further investigations into the potential application of these parameters as an indicator of feeding conditions in this species would benefit from the additional measures of prey returns and meal mass from both ST and LT.

CONCLUSION

This thesis has provided an insight into the habitat utilization, trophic relationships, foraging strategies, and feeding regimes of the short-tailed shearwater. I have endeavored to provide a more quantitative measure of the role of this wide-ranging seabird in marine food webs, and to explore the adaptive significance of their foraging strategy. I have identified the major structural attributes and functional capabilities that have enabled this species to spatially partition breeding and foraging habitats in a way that maximizes reproductive fitness. This strategy involves minimizing the time spent on land, and extending the time at sea locating and feeding on prey. The resultant pattern of self-feeding and chick provisioning represents a relatively extreme example of energy transport that has enabled the short-tailed shearwater to become one of the most successful seabirds in the world. This thesis has also highlighted the complexities involved in identifying relationships between environmental and seabird parameters. An opportunistic diet, and flexibility in foraging suggests that the short-tailed shearwater is more resilient to changes in prey availability than other seabirds in their community. However, we have highlighted that breeding success is sensitive to small changes in the time spent foraging in near and distant waters. Sourcing prey over large spatial scales also exposes birds to feeding conditions over a broader area, increasing their exposure to the potential effects of current and future climate change. For these reasons I believe that the short-tailed shearwater presents a valuable indicator species for short and long-term monitoring programs of both neritic and oceanic ecosystems. Knowledge gained will be incorporated into trophodynamic models and food consumption estimates to provide a better understanding of food web dynamics of the marine environment of South Australia.

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