

**Modelling the foraging ecology of the flesh-footed
shearwater *Puffinus carneipes* in relation to fisheries
and oceanography**

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Statement of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.

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Abstract

Increasing numbers of animal and plant species are under threat, often through human activity. To improve management of these species, it is important to understand the spatio-temporal nature of these interactions. In this thesis the threats to flesh-footed shearwater breeding on Lord Howe Island were explored, and methods that can be adopted for lowering them were investigated.

A census of the population of flesh-footed shearwaters on Lord Howe Island indicated a continuing decline. Possible threats to the population that were identified as (i) offshore, in the form of fisheries by-catch and plastic pollution at sea, and (ii) onshore, with factors such as land clearance and road mortality on Lord Howe Island. Significant mortality was recorded on roads on Lord Howe Island.

Offshore threats were examined by quantifying the regions of interactions between flesh-footed shearwaters and vessels operating in the Eastern Tuna and Billfish Fishery using data from fisheries observers, Australian Fisheries Management Authority logbook data and remote sensing data of oceanographic variables. Recent changes in the regions of interaction between the shearwaters and the ETBF were modelled, and how this affected the by-catch rate was examined. The effect these changes had on the by-catch rate was used to recommend the potential of area closures as a method of conservation.

Using a novel statistical technique, the distribution of flesh-footed shearwaters and their interactions with the ETBF was further examined. Small scale oceanographic relationships between the shearwaters' attendance of vessels operating in the fishery were quantified using an arrivals and departures multi-component model. For this the same data as that used in the previous section was used. By comparing the arrivals and departures for shearwaters behind vessels, finer scale attendance was examined and compared with the hypothesis that shearwaters were more likely to attend a vessel when it was operating in conditions that were likely to be more productive.

Finally, the distribution of individual flesh-footed shearwaters during the breeding season was quantified using light based archival tags (GLS loggers). Discrete Choice Models were then used to examine if individuals returned to the same areas on successive trips. Flesh-footed shearwaters used experience to determine where they were foraging, returning to areas that they had visited during the previous two foraging trips, and returning to areas where they apparently were successful during those trips. This has rarely been demonstrated previously, especially for larger or oceanic animals.

Statement of publication and co-authorship

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Mark Hindell (University of Tasmania) *and Chris Wilcox* (Commonwealth Industrial and Scientific Research Association (CSIRO) Marine and Atmospheric Research) *assisted with guidance and supervision in all aspects of the PhD and producing publishable quality manuscripts*

Mark Bravington (Commonwealth Industrial and Scientific Research Association (CSIRO) Marine and Atmospheric Research) *assisted with development of ideas for one paper*

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Richard Phillips (British Antarctic Survey) *assisted with equipment for tracking shearwaters.*

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1. General Introduction

Conservation biology as a scientific discipline

Conservation biology is concerned with the long-term viability of systems and preserving biodiversity (Soulé 1985). Since the 1970's there has been increasing interest in the fields of biodiversity and conservation biology due to the influence of human activity on components of the natural environment (e.g. Soulé 1985; Costanza et al. 1997; Bowen 1999; Wood and Gross 2008). This increased interest has come from the recognition of the importance of ecosystems, as well as the apparently increasing rates of extinction of species (Soulé 1985). While there is growing importance placed on conserving biodiversity, there remain issues of which taxonomic levels conservation should be targeted, whether at conserving ecosystems, species, or identifiable genetic populations (Bowen 1999). The human activities are diverse, from land clearing of forests for agriculture to pollution of the atmosphere by industry.

There are a number of anthropogenic activities affecting the marine environment, including benthic habitat destruction, overfishing, introduced species, global warming, acidification, toxins and eutrophication due to runoff of nutrients. There is a general trend of transforming once complex ecosystems into much more simple ones, such as replacing coral reefs with muddy bottoms (Jackson 2001, 2008; Feely et al. 2004; Turner et al. 2008). In many areas, fish are being replaced by jellyfish as the dominant animals due to overfishing (Richardson et al. 2008). Off Canada, overfishing of cod has led to an increase in urchins (which adult cod naturally eat), which in turn eat the kelp the juvenile cod require for shelter (Myers and Worm 2005).

Threats to marine predators

Marine predators, especially those that spend time at the surface, being relatively conspicuous, are useful for monitoring ecosystem health. Aspects such as their growth rates or survival give useful measures of population health. This is especially true for seabirds (Cairns 1987). A greater proportion of seabird species are declining than for any

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other groups of birds (Birdlife International 2008; Gonzalez-Solis and Shaffer 2009). This indicates that many of these marine ecosystems are under stress. There are a range of threats to seabird populations, including ingestion of plastics, pollution, introduced predators on their colonies, habitat degradation (either at sea or on land) and fisheries mortality (Croxall 1998).

A number of species of seabirds ingest plastics (e.g. Laysan albatrosses *Phoebastria immutabilis* and flesh-footed shearwaters Aumann et al. 1998; Croxall 1998; Hutton et al. 2008). The plastics are ingested at sea being mistaken for food, and often much of it is transferred to the chicks on the colony. Mortality of chicks due to plastics has rarely been observed (Croxall 1998) but in some species there is a negative correlation between plastic load and body condition (Connors and Smith 1982, Ryan 1987, Spear et al. 1995, Auman et al. 1998).

Black-footed albatrosses *Phoebastria nigripes* from Hawai'i have been shown to have sufficiently high levels of organochlorines and DDT to be theoretically at risk of egg-shell thinning and for this to have deleterious effects on embryos (Ludwig et al. 1998). These chemicals are widely used in pesticides including in south and south-east Asia (Croxall 1998). Seabirds and seals can become entangled in plastic packaging (Laist 1987).

Introduced predators affect a number of seabird species. Many species breed on islands that have no native mammalian predators, and therefore have no evolved defences. Mammals have been introduced to islands deliberately (for agriculture or as a food source for ship wrecked sailors) or accidentally from ships. Pigs on Inaccessible Island have affected the productivity of Wandering albatrosses *Diomedea exulans* (Ryan et al. 1990). Mustelids need to be controlled around colonies of northern royal albatrosses *Diomedea sanfordi* (Robertson 1998). More commonly, cats *Felis catus*, rats *Rattus* sp. and mice *Mus musculus* have been implicated in seabird conservation. Cats prey on adult and chick seabirds such as petrels and shearwaters, while rats and mice predate chicks and eggs (McChesney and Tershy 1998; Cuthbert and Hilton 2004; Wanless et al. 2007; Le Corre

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2008; Rayner et al. 2008). Elimination of these predators from breeding colonies is likely to be beneficial, however it may be complicated by interactions between these predators, such as cats acting as mesopredators and controlling rats so that the removal of cats has in places increased the declines in seabird populations (Couchamp et al. 1999; Rayner et al. 2008). Problems such as these emphasise the need for greater understanding of all the threats to populations and how they interact with the ecology of the species being saved.

Habitat destruction can threaten seabirds either on their breeding colonies or at sea. Large introduced mammals such as cattle *Bos primigenius*, sheep *Ovis aries* and goats *Capra hircus* can damage breeding grounds through trampling (Croxall 1998; McChesney and Tershy 1998), while humans can destroy breeding grounds for agriculture and residential requirements (Priddel et al. 2006). Degradation of habitat at sea occurs through factors such as pollution and climate change (Croxall 1998). These cause foraging areas to decline in value either through a reduction of food at those areas or by causing the conditions that usually predominate in the foraging areas to move.

Fisheries

Fisheries waste

Fisheries affect seabirds either through overfishing, which can change what resources are available to seabirds, or through direct mortality of seabirds. Overfishing for sandeels *Ammodytes marinus* in the North Sea has affected the population and breeding success of seabirds such as the Arctic tern *Sterna paradisaea* and black-legged kittiwakes *Rissa tridactyla* (Monaghan 1992; Frederiksen et al. 2004). Fisheries offal can change the balance between seabird species (Oro and Martiez-Vilalta 1994; Furness 2003). Fisheries waste can also provide food to seabirds (Thompson and Riddy 1995; Oro et al. 1995), though this may not be of a high quality suited to successful breeding (Grémillet et al. 2008).

Fisheries by-catch

Fisheries by-catch has been implicated in the declines of a number of species of seabird (*e.g.* Croxall et al. 1990; Weimerskirch et al. 1997; Nel et al. 2002; Lewison and Crowder 2003). Mortality occurs in a number of fisheries, including long-lining (pelagic and demersal), gill-netting (high-seas and coastal) and trawling (pelagic and demersal) (Brothers 1991; DeGange et al. 1993; Sullivan et al. 2006a; Watkins et al. 2008). A number of methods have been developed for mitigation of seabird mortality in fisheries. These have included methodological approaches (such as fishing at night, or area closures) and technological (changing equipment). Many of the mitigation measures appropriate for one fishery have been adopted for others (with necessary adjustment for the fishery methods used) (Brothers et al. 1999; Sullivan et al 2006b).

Pelagic long-line fishing impacts

Pelagic long-line fishing is a common method for targeting a range of finfish and sharks (Tuck et al. 2003; Baker and Wise 2005), particularly large predatory fish such as tuna *Thunnus* spp. and swordfish *Xiphius gladius*. The technique is used widely both for coastal fisheries (which typically set hundreds of hooks), to high seas vessels setting thousands of hooks. Pelagic long-lines consist of a mainline (which acts as a type of backbone) set between a series of floats. This mainline may be up to 100 km long, with a series of baited hooks attached to the mainline at regular intervals by 10-40m branchlines (O'Toole and Molloy 2000). These baited hooks are floated at depths depending on the target species. For example lines targeting swordfish are frequently set with the hooks less than 50m below the surface, while lines targeting bigeye or bluefin tuna may be up to 300m depth. Lines are set by a vessel feeding the line out behind it to be left floating for some time (generally 4-6 hours; Tuck et al. 2003). The vessel then returns and retrieves the line, hooks and catch. The setting and retrieving usually takes approximately 24 hours. These lines may have up to 3,000 baited hooks set on them (Tuck et al. 2003).

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The major cause of seabird mortality in pelagic long-line fisheries is due to the seabirds (notably procellariiforms) taking baited hooks as the hooks are set behind the boat (Brothers et al. 1999). A variety of technological and methodological techniques have been developed to mitigate seabird by-catch in pelagic long-line fisheries (Brothers et al. 1999). Most distract seabirds from the baited hooks as they are set, or set the baited hooks so that seabirds are unaware of them. Bird lines, which are aerial streamer lines that flap erratically over the area that the bait are hitting the surface of the sea and initially sinking, or attaching lead weights to the branch line to make the baited hook sink more rapidly so that it is no longer within reach of the birds (Brothers et al. 1999). Methodological techniques include dying bait blue (so they are less visible from above) or setting hooks at night (when most species of seabirds are less active) (Brothers et al. 1999; Gilman et al. 2007a). Baits are vulnerable to seabirds in the initial period of line setting, when they are less than 5 m below the surface. Most of the mitigation methods have been designed with considerations of albatrosses, which generally dive to depths of less than 10 m (Brothers 1991; Prince et al. 1994; Brothers et al. 1999).

However, these standard techniques are not always effective. In pelagic long-line fisheries, more manoeuvrable, deep diving species such as the petrels of the genus *Procellaria* and shearwaters of the genus *Puffinus* are still caught in large numbers despite these mitigation methods (Huin 1994; Baker and Wise 2005; Barbraud et al. 2008; Thalmann et al. 2009).

Flesh-footed shearwaters

The flesh-footed shearwater *Puffinus carneipes* is a medium sized shearwater (550-800g) breeding in the southern hemisphere (on islands around New Zealand, Lord Howe Island, islands off southern Western Australia, and Illé St Paul in the southern Indian Ocean) and migrating to the northern hemisphere for the austral winter (Marchant and Higgins 1990).

The Eastern Tuna and Billfish Fishery is a pelagic long-line fishery operating in the Tasman Sea targeting a range of tuna and swordfish species. In this fishery, 12 million hooks were set in 2003 (Baker and Wise 2005), with most vessels setting between 1,000-

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1,200 hooks per day (Baker and Wise 2005). The fishery has a problem with seabird by-catch, with flesh-footed shearwater the most commonly caught species (Trebilco et al. 2010). Between 1998 and 2002 8,972-18,490 flesh-footed shearwaters were killed in this fishery, at rates that were considered unsustainable for the species (Baker and Wise 2005). The Lord Howe Island population declined between 1978 and 2002 (Priddel et al. 2006).

Several of the standard technological methods (including bird lines, attached weights, underwater setting devices) were trialled in this fishery at this time without success at lowering seabird by-catch rates (Baker pers. comm.). An alternative approach may be area closures (Thalmann et al. 2009). In this, some of an area that may be used by fisheries is closed so that there are no longer interactions between the vessels in the fishery, and the by-catch species. For example, over two years from 1999 over one million square miles of waters around the Hawaiian Islands were closed to a pelagic long-line fishery due to incidental mortality of sea turtles (Curtis and Hicks 2000; Gilman et al. 2007b). Closure of such large areas is extreme, and probably detrimental to the fisheries' continued viability. Alternatives may be communication within the fleet to identify real-time hot-spots (Gilman et al. 2006), which has been successfully adopted in several fisheries in the US. However to be effective, it required strong economic incentives, for interactions with the by-catch species to be rare events and for a large observer presence (Gilman et al. 2006). A second alternative may be to close more targeted areas, which are of particular importance to the birds. However, to have a more targeted area closure it is necessary to improve our understanding of the areas foraging requirements of the by-catch. By understanding these it may be possible to identify the areas the by-catch species will go and hence where interactions with fisheries are likely to occur. If interactions occur predominantly in these areas, this may allow area closures to be relatively focused. Knowledge of oceanographic features associated with foraging may allow information on how the areas may change with changing conditions. This may allow the use of dynamic area closures.

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Foraging

Marine predators do not forage randomly over the ocean but forage in areas that are likely to have increased productivity and so concentrations of their prey. These are often associated with up-welling areas where nutrient rich bottom water moves closer to the surface within the photic zone. Up-wellings occur due to the movement of currents in oceans due to wind or tides. When currents interact with barriers, such as land, underwater ridges, or other currents, they are re-directed, often to the surface. The resultant increased productivity then propagates up the food web until there are concentrations of prey for top predators. These concentrations may be relatively predictable in time and position, or they may be ephemeral. In the Tasman Sea, a western boundary current moves south along the east coast of Australia. Part way down, this splits with the Tasman Front passing near Lord Howe Island, where the flesh-footed shearwaters breed (Ridgeway and Dunn 2003). These currents drive strong oceanographic features such as up-wellings (Ridgeway and Dunn 2003), and so there are likely to be areas of increased productivity for the shearwaters. Areas of increased productivity are likely to have increased prey, and therefore increased foraging opportunities for the shearwaters. Hence they should have increased foraging efficiency by locating these areas (Charnov 1976). Therefore increasing understanding of these mechanisms has the potential to be useful for designing and using area closures. There are a number of alternatives for locating areas of prey concentrations. Several search methods, such as the use of correlated random walks, Levy flights or area restricted searches have been shown as increasing the efficiency of patches in an uneven environment (Viswanathan et al. 1996; Fauchald and Tveraa 2003; Trembley et al. 2007). An alternative is to use previous experience. For a central place forager, it is advantageous to return to a patch that has previously been used successfully. This has been demonstrated for a number of species, such as bumblebees and bluegill sunfish (Werner et al. 1981; Peat and Goulson 2005). This is reliant to some extent on the patches persisting so that they can be returned to. Areas of productivity (such as eddies) may be dynamic, but may re-occur in approximately similar areas. Thus, it is possible that the use of previous experience as well as efficient search methods would be beneficial to the

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searcher. If this occurs, it is likely that the shearwaters will return to approximately similar areas. This may decrease the area necessary to be covered by area closures.

Aims

Increasing numbers of species are under threat, often through human activity. In this thesis the threats to one species, the flesh-footed shearwater breeding on Lord Howe Island, will be considered. This species has been shown to have been declining since the 1970's. To understand the threats to this population and how to manage them requires increased information. Thus it is necessary initially to determine whether there are on-going issues with the population of flesh-footed shearwaters, and if so, what they are. Long-line fisheries by-catch has been a major issue for this species previously, while previous technological attempts to mitigate this have so far been ineffective. It was important therefore to examine spatial relations between the fishery and the foraging range of the species. To do this it is important to examine the areas of overlap between the fishery and the shearwaters, how this is changing over time and what effect this is having on the by-catch rate, and to determine how shearwaters choose to forage where they do. From this information consideration is given to how this may be useful toward conservation, focussing on the use of dynamic area closures as potential ways to lower the by-catch of this species. This thesis is organized into four research chapters and one chapter drawing them together in a final synthesis.

Population estimate and trend

In Chapter 2 the current population of flesh-footed shearwaters on Lord Howe Island was determined by conducting an island-wide census of the breeding colonies, and using estimates of the colony size and density of burrows in conjunction with data on occupancy and breeding success. Trends were determined by comparing the results of this census to two past censuses. Possible threats apart from fisheries, such as plastics and road mortality, were considered. Road mortality was estimated by calculating the density of carcasses by the road and their rotting rate.

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Overlap with the ETBF

In Chapter 3 areas of attendance of vessels operating in the Eastern Tuna and Billfish Fishery by flesh-footed shearwaters was quantified, using data from fisheries observers on board vessels, logbook data and remote sensing data of oceanographic co-variables. The areas of attendance were modelled, along with how these areas changed over the period 1998-2006. The changes in vessel attendance were compared to changes in by-catch rates in recent years. These changes in attendance with respect to area were used to consider whether area closures are a potential method of conservation through changes in the fisheries' locations affecting where interactions with the shearwaters occur.

Fine scale attendance of ETBF vessels by shearwaters

In Chapter 4 a novel statistical technique was used on the same data that was used in Chapter 3. Flesh-footed shearwater attendance of long-line vessels was examined by modelling their arrivals and departures between successive counts. Modelling these activities and their co-variables allowed examination of fine scale attendance through the changes in attendance with changes oceanographic conditions and activities of the vessels. From this model a hypothesis that shearwaters were more likely to attend the vessel when it is operating in good conditions was considered.

Individuals foraging distribution

Chapter 5 examines the at-sea distribution of individual flesh-footed shearwaters during the breeding season using light-based archival tags (GLS loggers). Discrete Choice Models were used to examine what cues were used by individuals to choose where they were going during a foraging trips, and comparing the use of habitat variables such as oceanography, and behaviour variables, such as experience. The use of previous experience to locate potential foraging areas is thought to increase foraging efficiency, either in comparison with, or in conjunction with other methods of searching. It has been observed in some animals, but rarely in larger, and especially oceanic, animals. Discrete Choice Models were used to make a quantitative examination of whether flesh-footed shearwaters use experience.

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Thesis structure

This thesis has been written as a series of separate manuscripts with a number of co-authors from the Antarctic Wildlife Research Unit, the British Antarctic Survey and CSIRO Marine and Atmospheric Research. All chapters, with the exception of this introductory and a final synthesis and summary chapter, consist of a series of manuscripts either in preparation, or an already submitted paper for publication. As a consequence of this layout, there is some overlap in ideas and text from each of these chapters. I was the senior author each paper and so responsible for data analysis and interpretation and preparation of the manuscripts, while the co-authors assisted with these. Co-authors are listed with the chapter title at the start of each chapter. A single bibliography is presented at the end of the thesis using Elsevier format (such as used in the journal *Biological Conservation*).

2. Status and trends of Flesh-footed shearwaters on Lord Howe Island.

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Chapter 2

ABSTRACT

The population of flesh-footed shearwaters breeding on Lord Howe Island have previously been shown to be declining between the 1970's and the early 2000's. This was shown to be predominantly due to the effect of breeding habitat clearance and fisheries mortality in the Australian Eastern Tuna and Billfish Fishery. Recent evidence suggests these influences have been reduced; therefore it was necessary to conduct a further census of the population to establish on-going trends. Results presented here suggest there is an 85% probability that flesh-footed shearwaters on Lord Howe continued to decline during 2003-2009, and a number of possible reasons for this are suggested. During the breeding season, road-based mortality of adults on Lord Howe Island is likely to result in reduced adult survival and there is evidence that breeding success is negatively impacted by marine debris. Interactions with fisheries on flesh-footed shearwater winter grounds and should be further investigated.

Keywords: Flesh-footed shearwater, Lord Howe Island, population trends, Bayesian analysis

INTRODUCTION

Globally, marine vertebrates face a number of significant threats (Croxall and Gales 1998; Clover 2004). For example, in a number of regions the structure of ecosystems has been altered by human-induced stresses such as overfishing, eutrophication or climate change, with fish being replaced by jellyfish as the dominant animals (Richardson et al. 2009). Seabird species are declining at a faster rate than any other groups of birds (Birdlife International 2008; Gonzalez-Solis and Shaffer 2009). The factors responsible for the declines are varied and include increased adult mortality caused by fisheries, effects of pollutants on fecundity and immunity, predation by introduced species, habitat destruction, and the effects of climate change (Birdlife International 2008). Many seabirds forage over a wide area and this brings them into contact with many impacted areas/habitats. Seabirds are relatively long-lived animals that exhibit delayed breeding and low fecundity, thus any additional adult mortality will have considerable demographic consequences. This life-history strategy presents challenges for researchers attempting to estimate population dynamics and manage multiple threats. While most studies focus on individual threats to populations, a number of recent studies have highlighted the need to consider multiple threats concurrently in order to improve our understanding of the overall status of a population, and how best to conserve it (Wilcox and Donlan 2007; Wanless et al. 2009). This can be most readily achieved with studies in locations where some level of accuracy on the full range of threats can be obtained.

Flesh-footed shearwaters *Puffinus carneipes* (Gould 1844) are one of the most common seabird by-catch (non-target mortality) species in long-line fisheries around Australia (Gales et al. 1998; Baker and Wise 2005). The only colony of flesh-footed shearwaters on Australia's east coast occurs on Lord Howe Island (Marchant and Higgins 1990), which contains 5-14% of the total Australian population (Ross et al. 1996) and 8% of the world's population (Brooke 2004). The Lord Howe Island population declined by 19% (with an annual decline of 0.9%) between 1978- 2002 (Priddel et al. 2006). During 1998-2002, an estimated 8,972-18,490 were killed in the Eastern Tuna and Billfish Fishery (ETBF) (Baker and Wise 2005), leading to the perception that by-catch was the principal factor driving the decline.

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In recent years, there has been a reduction in the observed by-catch rates, from 0.378 birds/1000 hooks between 1998 and 2002, to less than 0.07 birds/1000 hooks between 2002 and 2007 (Baker and Wise 2005; Lawrence et al. 2009). This decline in by-catch rate has been attributed to the fishery moving north as the principle target species changed from yellowfin tuna (*Thunnus albacares* Bonnaterre 1788) to albacore tuna (*T. alalunga* Bonnaterre 1788).

A number of other issues may have contributed to the decline in the Flesh-footed Shearwater population. First, the size of the breeding colonies on Lord Howe Island declined by 36% between 1978-2002 due to land conversion for agricultural and residential purposes (Priddel et al. 2006). Second, 79% of flesh-footed shearwater fledglings contained plastic in their proventriculus on Lord Howe Island (Hutton et al. 2008), almost twice that of wedge-tailed shearwaters (*P. pacificus* Gmelin 1789) breeding on the same island. However, it is unclear what the effect of the plastic was on the survival of the chicks. And finally, several roads pass through or adjacent to flesh-footed shearwater breeding colonies, and dead adults and fledglings are frequently found along the roadsides (DECC 2009).

The flesh-footed shearwater is listed by the Australian Environmental Protection, Biodiversity and Conservation (EPBC) Act as migratory under the JAMBA (Japan Australia Migratory Bird Agreement) and ROKAMBA (Republic of Korea Australia Migratory Bird Agreement) agreements (DEWHA 2009), and in New South Wales it is currently listed as Vulnerable (DECC 2009). The flesh-footed shearwater was recently identified as a strong candidate for inclusion under the international Agreement on the Conservation of Albatross and Petrels (ACAP; Cooper and Baker 2008).

Because only two censuses of the Lord Howe Island flesh-footed shearwater population have been undertaken, it is impossible to know if the observed declining trend between those two observations is on-going and hence, whether management action is required (Priddel et al. 2006; Tuck and Wilcox 2008). Tuck and Wilcox (2008) recently performed

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an Integrated Assessment Model on the status of flesh-footed shearwaters on Lord Howe Island. The identified a number of issues with the model, as there was only data on two threats to the shearwaters, while a number of others were identified. In light of the changing by-catch rates, the aim of this paper is to quantify the current status of the Lord Howe population and to increase the data available for a number of other threats identified.

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METHODS

Lord Howe Island is a small (1,455 ha) volcanic island located approximately 495 km east of Australia (Priddel et al. 2006). The island is crescent shaped with a coral reef on the western side. At each end of the island there are volcanic mountains, with the southern ones rising to 875 m. These are separated by an area of lowlands derived from coral-derived calcarinite (Priddel et al. 2006). Much of this lowland area has been developed for agriculture and settlement. For details of vegetation communities on the island see Pickard (1983).

Flesh-footed shearwaters are a medium sized shearwater, weighing between 550-750 g (Marchant and Higgins 1991). They breed on a number of islands in the southern hemisphere, around New Zealand, in southern Western Australia, on Lord Howe Island, and on Île Saint-Paul in the Indian Ocean, and migrate to the northern hemisphere for the Austral winter, concentrating in the Arabian Sea (Powell 2009) and Sea of Japan. On Lord Howe Island flesh-footed shearwater breed in lowland areas, predominantly in sandy soil under palm forests on the eastern side of the island. There are currently five discrete colonies on the eastern side (Ned's Beach, Steven's Point, Middle Beach, Clear Place and Little Muttonbird Ground), with a small number also breeding in a single colony on the western side (Hunter Bay) (Fig 1). Flesh-footed shearwaters are not known to breed on any of Lord Howe's offshore islands (Priddel et al. 2006).

Census of breeding colonies

The census method was similar to that used by Priddel et al. (2006). The area of each colony was measured by walking the perimeter with a hand held GPS (Magellan Professional Mobile Mapper 6).



Fig 2.1. Map of Lord Howe Island with location of flesh-footed shearwater breeding colonies and roads. Positions of stations used for estimating breeding success marked as circles.

The density of burrows within each colony was estimated using straight-line transects through each colony on the island (except Hunter Bay where it was possible to count all burrows). The transects used in this study were previously identified by Priddel et al. (2006). Transects were evenly separated and oriented perpendicular to the longest axis of the colony, passing from the colony edge to the centre of the colony. Transects were divided into 10 meter sections, all burrows within two meters of either side of the transect were counted. Apparent burrows were scored when they were judged to be large enough for a flesh-footed shearwater to enter (>10 cm long). Based on this survey design, data were divided into 40 m^2 sections for analysis. The data were treated as count data, with the total number of burrows per section as the response variable for statistical analysis. Fitted values for the number of burrows per transect section were then used to estimate

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standardized burrow density. Burrow counts were made between 29 October and 5 November 2008, after burrow cleaning had commenced but before egg-laying.

The number of burrows in each colony was estimated by calculating the mean (\pm s.d.) density of burrows in each colony from the transect counts, and multiplying that by the colony area (eqn. 1). The variance calculated during the estimate of burrow density was then used to estimate confidence limits.

$$B = \sum_1^i A_i B_i$$
$$\Pr\{B_i = b\} = \frac{\lambda^y e^{-\lambda}}{y!}$$

Equation 1.

Where A is the area of each colony i , B is the total number of burrows and λ is the density of each colony i .

A number of burrows within the Clear Place colony have been studied regularly since 2005, and were used to quantify burrow occupancy rates. This was used to give a measure of what proportion of burrows are occupied during a year, as not all burrows are occupied every year. From this, the number of eggs laid, and hence the number of breeding pairs, can be estimated. Burrows in this study colony were examined using a custom-made burrowscope (Hamilton 1998) in early January each year. As egg laying occurs in early December, it is likely that the estimate obtained here is a slight underestimate. Burrows in the study colony were again examined in early April to check for fledgling chicks. Breeding success (the number of eggs that produced chicks) was estimated from this colony for each year. A small number of burrows were found in April to contain chicks that had not been found to have eggs in January; this was adjusted for using methods outlined by Priddel et al. (2006).

Burrow productivity gives an estimate of how many chicks are produced on Lord Howe Island each year. This was measured by checking for the presence of chicks in a sample

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of burrows in all colonies between 6 April and 10 April 2009. It was assumed that because chicks fledged in late April or early May (Marchant and Higgins 1990), these chicks were likely to survive to fledging and the counts would therefore provide a reasonable estimate of burrow productivity. Three of the transects used in each colony for estimating burrow density were randomly chosen (three new transects were used at Ned's Beach due to considerations of road effects) and six equally spaced stations were created along each transect. The five closest burrows to these stations were examined using a burrowscope (Hamilton 1998) to check for the presence of a chick. Productivity was considered to come from a Bernoulli distribution (i.e. there are two possible outcomes in a burrow; a chick, or no chick), and this was used to estimate variance and confidence limits.

$$N = \sum_1^i B_i P_i$$

Equation 2.

$$\Pr\{P_i = y\} = \binom{1}{y} \theta^y (1 - \theta)^{1-y}$$

Where N is the total number of chicks produced, B_i is the number of burrows in colony i , θ is the probability of a burrow containing a chick, P is the number of chicks in a burrow and y is the mean productivity rate for each colony i .

The number of chicks produced was estimated as the product of the number of burrows in each colony, the area of the colony, and the productivity of that colony. For Hunter Bay and Little Muttonbird Ground, productivity was not measured and so the mean productivity of the other colonies was used.

An estimate of the total number of breeding pairs in each colony was calculated as the number of burrows multiplied by the occupancy rate (Priddel et al. 2006). Initially this was calculated with the results from the Clear Place study colony. However, this was only derived from one part of one colony, and so may not have been truly representative of the overall occupancy rate and breeding success. An alternative and more robust method used a Bayesian approach combining the occupancy rate for the study colony,

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and those from Priddel et al (2006). Using a Bayesian approach allows the combining of all previous information into the one framework for estimating the number of breeding pairs (McCarthy 2007). This allows the confidence that is held at each step in the process of making the estimate to be incorporated into the final estimate.

The mean population estimate is calculated by multiplying the occupancy rate by the colony area, as would have been done in a standard technique (the likelihood in Bayesian terms). However a Bayesian approach adopts a formal method to update this estimate with further information. This is done by multiplying the likelihood by a term (the prior), to give a posterior estimate. How much this posterior differs from the likelihood depends on the strength of the prior (which is dependent on the belief of the observer). Thus, if the observer has no particular prior belief, an uninformative prior can be used (which will essentially give a result similar to that found using standard statistical methods). In Bayesian modelling it is generally not possible to come to an analytical version of the sampling distribution; however this can be overcome using numerical methods (most commonly the Monte Carlo Markov Chain) (McCarthy 2007).

In this case, we had data on the productivity rate for all colonies in 2003 and 2009, and occupancy rates for all colonies in 2003, and for the Clear Place colony in 2007-2009. The occupancy rate for 2009 was then estimated using parameters for the occupancy and productivity rates for each colony and a year effect (incorporating an observer effect was not possible as there was no overlap within years of different observers). The estimated breeding population is then the number of burrows multiplied by the occupancy rate.

$$\begin{aligned} N &= B_i Occ_i \\ Occ_i &= \beta P_i \end{aligned} \text{ Equation 3.}$$

Where N is the total breeding population, B_i is the number of burrows in each colony i , Occ_i is the occupancy rate for each colony (and represents the breeding success in the equation) and P_i is the productivity in each colony i . β is a series of parameters potentially effecting each of these measures (year, observer).

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Estimating road-kill

The density of carcass was measured along three roads passing through or beside a colony (Ned's Beach Road at Ned's Beach, Skyline Drive and Muttonbird Drive by Steven's Colony) by walking 10 m transects at right angles from the road, counting all carcasses within 1 m of either side of the transect. Ten evenly spaced transects were made along Skyline and Muttonbird Drives, and 20 evenly spaced along Ned's Beach Road (all approximately 10 m apart).

Seven carcasses were marked on 1 January 2008 to determine how long carcasses would be detectable in the forest beside the road until they were re-checked in early April 2008. Using this rate of disappearance and assuming that road mortalities occurred at an approximately even rate throughout the summer, it is possible to estimate an approximate maximum for the number of carcasses required to end with the number located on the transects in April 2009 using Equation 4.

$$\begin{aligned} N &= N_0 e^{-\lambda t} \\ E(C_t) &= \sum_{t_0}^{t_2} X_\tau (1 - D_d)^{(t-\tau)} \\ X_\tau &= \binom{P}{X} p^X (1-p)^{(P-X)} \\ E(C_f) &= E(C_t) P_f \end{aligned} \quad \text{Equation 4.}$$

Where N is the total number of carcasses killed on the roads, λ is the rate of disappearance of corpses, t is the days from 0 to i , d is the daily probability of death, P is the total number of shearwaters available on the island to be run over, p is the probability of shearwaters dying, X is the rate of birds dying, $E(C_t)$ is the expected number of corpses, $E(C_f)$ is the expected corpses found and P_f is the probability that a corpse will be found.

Data analysis

A model-based approach, rather than a design-based estimate, was used to estimate the mean and variance in occupancy and productivity in this study. Data analysis was performed using R statistical software (version 2.9.0 R Foundation for Statistical Computing 2009). Bayesian analyses were performed using WinBUGS (version 1.4, Lunn et al. 2000).

RESULTS

Census

The total area of all colonies combined was estimated to be 24.73 ha (Table 2.1), with individual colony size ranging from 0.41 to 7.73 ha. The total area was lower than in 1978/9 (37.75 ha) but slightly higher than in 2002/3 (24.31 ha) (Priddel et al. 2006). Overall, burrow density in 2009 was 0.091 ± 0.016 burrows m^{-2} (Table 2.1). Burrow density was greatest in the three colonies that were relatively large and enclosed by palm forest (Ned's Beach, Middle Beach and Clear Place), and lowest in the small colonies (Little Muttonbird Ground and Hunter Bay) and at Steven's Point. Burrow density was lower in 2008/9 compared to 2002/3, but similar to 1978/9 (Fig. 2.2), and had declined the most at Steven's Point and at Little Muttonbird Ground (Fig. 2.2).

Table 2.1. Area and estimated flesh-footed shearwater burrow density (burrows m^{-2}) for each colony on Lord Howe Island, 2008-2009.

Colony	Area (ha)	Number of transects	Transect area (m^{-2})	No. of burrows	Mean burrow density (burrows m^{-2})	sd	95% confidence limits
Little Muttonbird Ground	0.41	2	560	16	0.029	0.007	0.017-0.043
Clear Place	7.73	4	2680	367	0.137	0.007	0.122-0.152
Middle Beach	5.88	4	2600	324	0.119	0.006	0.108-0.132
Ned's Beach	2.89	1	1240	149	0.121	0.010	0.103-0.139
Steven's Point	7.41	5	4000	204	0.051	0.004	0.044-0.059
Hunter Bay	0.41						

There were an estimated $25,066 \pm 783$ burrows on Lord Howe Island in 2008/9 (Table 2.2). Most burrows were at Clear Place (42%) and Middle Beach (28%). This represents a decline in burrow numbers of 2.9% per annum since 2002/3, following an annual decline of 0.9% between 1978-2002. Most of the decline was due to the estimates for Steven's

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Point and Clear Place, with marginally greater estimates of the number of burrows for Ned's Beach and Middle Beach compared to 2002/3 (Fig. 2.3).

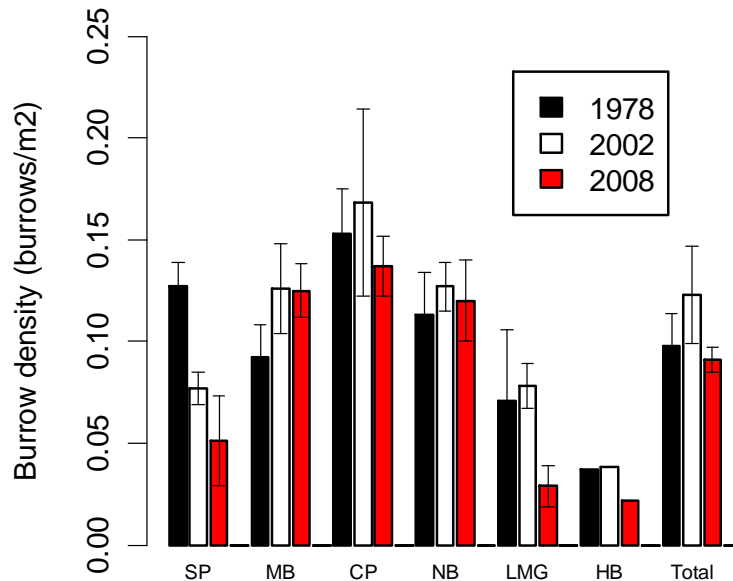


Fig 2.2. Burrow density (burrows m^{-2}) at each colony on Lord Howe Island in three years (error bars represent standard errors, as those are what was given in Priddel et al. 2006). (1978=1978/9; 2002=2002/3; 2008=2008/9; SP=Steven's Point; MB=Middle Beach; CP=Clear Place; NB=Ned's Beach; LMG=Little Muttonbird Ground; HB=Hunter Bay).

Burrow productivity

Burrow productivity was 0.359 ± 0.102 chicks burrow $^{-1}$ in 2009 (Table 2.3). Productivity was highest at Clear Place, and lowest at Ned's Beach (Table 2.3). It was slightly higher in 2008/9 than 2002/3, though not significantly. There was no consistent pattern between colonies among years, though it was almost three times higher at Steven's Point in 2008/9 than in 2002/3 (Fig 2.4).

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Table 2.2. Estimated number of burrows for each colony on Lord Howe Island, 2008-2009. Note all burrows counted at Hunter Bay.

Colony	burrows	sd	95% confidence limits
Little Muttonbird Ground	118	29	69-178
Clear Place	10588	568	9455-11720
Middle Beach	7001	369	6329-7750
Ned's Beach	3485	281	2970-4029
Steven's Point	3783	272	3269-4356
Hunter Bay	91		
Total	25066	783	23532-26600

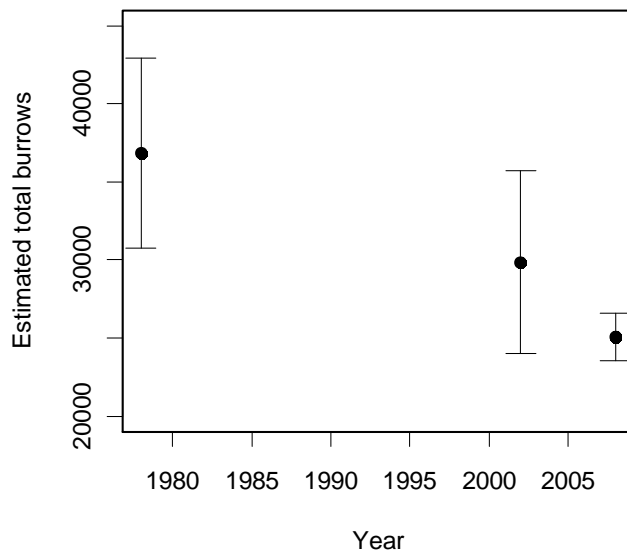


Fig 2.3. Estimated total number of burrows on Lord Howe Island in 1978/9, 2002/3 (Priddel et al. 2006) and 2008/9.

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Table 2.3. Estimated burrow productivity for each colony (fledglings burrow⁻¹) on Lord Howe Island, 2008-2009.

Colony	Burrows checked	occupied	mean	sd	95% confidence limits
Clear Place	90	39	0.435	0.052	0.333-0.540
Middle Beach	75	28	0.376	0.054	0.277-0.489
Ned's Beach	95	27	0.300	0.046	0.213-0.388
Steven's Point	85	30	0.358	0.052	0.262-0.465
Total			0.359	0.102	0.160-0.558

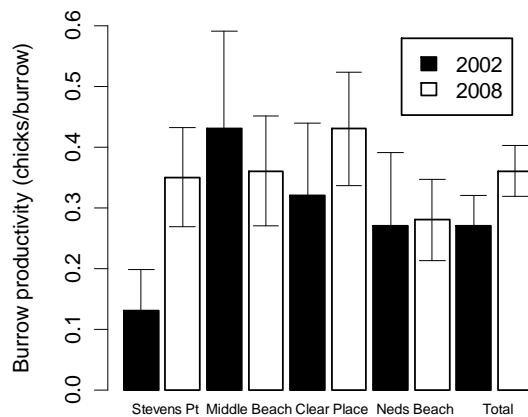


Fig 2.4. Burrow productivity (chicks burrow⁻¹) at each colony in 2002/3 and 2008/9 (error bars represent standard errors, as those are what was given in Priddel et al. 2006).

Number of chicks

An estimated 9,712 \pm 783 chicks were produced on Lord Howe Island in 2009 (Table 2.4). Most chicks were produced in Clear Place (47%) and Middle Beach (27%). This is an 8% increase in the estimated number of chicks produced compared with 2002/3, with most of the increase due to an apparent doubling in the number of chicks produced at Steven's

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Point (Priddel et al. 2006). On 27 January 2009 six adult flesh-footed shearwaters were located within a wedge-tailed shearwater colony at Signal Point on the west coast, south of Hunter Bay, where breeding had not previously been recorded. Breeding was not confirmed at this location, but there was some evidence to suggest a small number of nests present (<10) (pers. obs.). No other flesh-footed shearwaters were located in any of the other nearby wedge-tailed shearwater colonies.

Table 2.4. Estimated number of chicks from each colony on Lord Howe Island, 2008-2009.

Colony	chicks	sd	95% confidence limits
Little Muttonbird Ground	42	16	11-73
Clear Place	4607	609	3437-5833
Middle Beach	2631	402	1869-3448
Ned's Beach	1046	181	731-1447
Steven's Point	1354	218	946-1829
Hunter Bay	33	9	15-51
Total	9713	783	8177-11248

Breeding Success

Breeding success (eggs that produced chicks that were likely to fledge) was estimated in Clear Place for three years (2006/7, 2007/8 and 2008/9) (Table 2.5). Using the Bayesian model to combine these figures with those derived from Priddel et al. (2006), breeding success in 2009 was estimated at 0.55 (95% confidence limits 0.42-0.78).

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Table 2.5. Mean (\pm s.d.) breeding success (chicks egg⁻¹), occupancy (eggs burrow⁻¹) and productivity (fledglings burrow⁻¹) of burrows in the Clear Place study colony over three seasons.

	Breeding success	Occupancy	Productivity
2006/7	0.76 \pm 0.06	0.61 \pm 0.07	0.46 \pm 0.06
2007/8	0.71 \pm 0.04	0.70 \pm 0.05	0.49 \pm 0.05
2008/9	0.69 \pm 0.03	0.67 \pm 0.04	0.46 \pm 0.04

Using only the occupancy rate from Clear Place in 2009 to estimate numbers across all colonies, the population was estimated at 16,794 \pm 1,028 breeding pairs. In contrast, using the Bayesian method with occupancy rates from three years at the Clear Place study site and those provided in Priddel et al. (2006), the estimated number of pairs is 14,922 \pm 2,028 (95% confidence limits 10,840-18,911). This represents a population decline since 2002/3 of 2.7% per annum (CI: -7.6%-1.3%), with an 85% posterior probability that the population is declining.

Estimates of Road-kill

Ten carcasses were found along 40 10 m road-side transects on 6 April 2009, giving a density of 12.5 \pm 0.14 carcasses/1000 m². Most carcasses were located at the end of the transect closest to the road, with six (60%) found within 4 m of the road, and density declining with distance from the road (Fig 2.5). Between 6-10 April 2009 twelve transects a significant distance from roads in colonies were run totalling 4,116 m². Only two carcasses were located, giving a density of 0.49 \pm 0.37/1000 m². Thus the density of carcasses adjacent to roads was 25 times greater than that generally found in the colony.

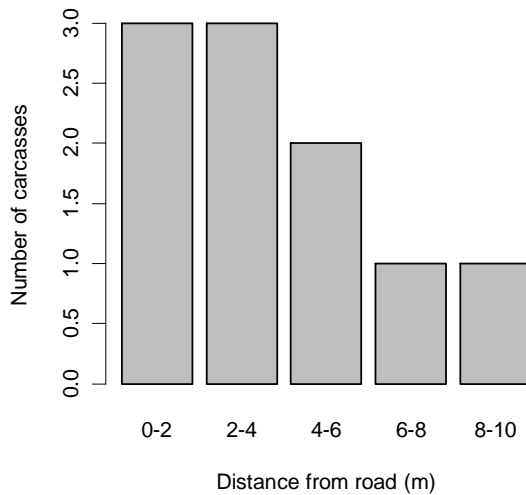


Fig 2.5. Number of flesh-footed shearwater carcasses along 10 m transects perpendicular to roads on Lord Howe Island (only those roads through colonies were observed).

Seven flesh-footed shearwater carcasses that were killed on Ned's Beach Road on the night of 31/12/2007 were marked. Four of these were still easily identifiable on 17/4/2008, indicating that the carcasses last for at least 3.5 months. Three had disappeared, presumably due to break down or being buried.

Assuming that all carcasses are detectable throughout a breeding season (this needs to be tested) and that all birds hit by cars die within 10 m of a road, using the density of carcasses within 10 m of the road edge for the length of the roads on Lord Howe Island, produces an estimate of 125 birds killed during the 2008/2009 breeding season. In comparison, using the background density recorded throughout the rest of the colony, multiplied by the colony size, there would be 121 carcasses by natural mortality. This suggests that the road mortality may be doubling natural mortality within the colony.

Alternatively, using the assumptions of Equation 4 (a constant rate of mortality and of carcass disappearance) to estimate road mortality, it is estimated 185 (C.I. 129-262) birds were killed on the roads.

DISCUSSION

Recently there has been an apparent reduction in the observed mortality of flesh-footed shearwaters on long-line fishing vessels in the ETBF off eastern Australia (Baker and Wise 2005; Lawrence et al. 2009). Flesh-footed shearwaters are considered Vulnerable in New South Wales, as the only breeding colony (Lord Howe Island) has been declining since 1978 (Priddel et al. 2006), and it is likely that the majority of flesh-footed shearwaters still taken in the ETBF each year originated on Lord Howe Island due to the proximity of the fishery to the island. Because fisheries mortality was considered one of the major causes of this decline, we conducted a census of the population on Lord Howe Island to estimate the most recent population trends.

The estimated number of burrows within all of the colonies on Lord Howe Island declined at an annual rate of 0.9% during 1978-2002 (Priddel et al. 2006). The rate increased to 2.9% during 2002-2008, giving an overall annual rate of decline in burrow numbers of 1.3% since 1978. Correspondingly, the number of breeding pairs was estimated to have declined by 2.7% per annum between 2002-2008. Overall there was a 14% decline in the estimated number of breeding pairs on Lord Howe Island between 2002-2008, though it was not significantly different from zero. Nevertheless, there is an 85% probability that the population had declined since 2002.

The decline in colony area between 1978-2002 (Priddel et al. 2006) seems to have halted in recent years. Much of this decline was due to land being converted to residential or agricultural uses, and management of the island has changed to reduce this (Priddel et al. 2006). Despite this, there was still a decline in the overall number of burrows. This was partly driven by the declining density of burrows in recent years, to a density similar to that in 1978. The declines in burrow density were most noticeable in the smaller colonies (Hunter Bay and Little Muttonbird Ground), and the colony most affected by urbanization (Steven's Point). This trend was also noted by Priddel et al. (2006).

Overall, parameters for the larger colonies (Clear Place, Middle Beach and Ned's Beach) have not changed greatly since 2002, with minimal changes observed at Clear Place and

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Ned's Beach since 1978 (Priddel et al. 2006). Middle Beach declined in area by 41% between 1978 and 2002, with an 18% decline in the estimated number of burrows since 1978. This pattern of declines at the edges of colonies has been noted for other species (e.g. Gochfeld 1980; Aebischer and Coulson 1990).

In this study a model-based approach using Bayesian statistical methods was adopted. This method was preferred over design-based inferences for two reasons. First, the modelling approach is better at accounting for sources of variation (Waugh et al. 2008). The use of Bayesian methods presents a way to formally incorporate data and variation from different sources into the estimate (McCarthy 2007). These methods were adapted in the current study due to the availability of previous estimates of breeding success from the Clear Place colony, which appeared to have consistently high success compared to previous observations more generally throughout the island (Dyer 2001; Priddel et al. 2006). This allowed for previous estimates to adjust the estimates of the population for 2009, and to better reflect the uncertainty about this estimate.

Fisheries interactions and population trends

Observed fisheries mortality in the ETBF was significant between 1998-2002 (Baker and Wise 2005), but has fallen drastically since 2002, therefore on-going declines are unlikely to be related to this. However, there may still be mortality in flesh-footed shearwater's wintering grounds. Flesh-footed shearwaters are known to migrate to the northern Pacific Ocean, with sightings and band records from the Sea of Japan (Shuntov 1972, Tuck and Wilcox 2008), east of Japan (Oka 1994; Ito 2002; Ogi 2008), and off western Canada (Wahl et al. 1989; Hay 1992). While banding records originate from Lord Howe Island, sightings may be of birds originating on Lord Howe, or alternatively, from colonies in New Zealand or off Western Australia. In the past, significant numbers of flesh-footed shearwaters have been taken as by-catch in a number of drift net fisheries in the north Pacific Ocean. In 1987, 116 flesh-footed shearwaters were killed in a salmon drift net fishery east of Japan (Degange and Day 1991), while in 1990 between 397-957 were killed in neon flying squid drift net fisheries in the North Pacific (Ogi 2008). While these high seas drift net fisheries have closed since the early 1990's, there continues to be a

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number of drift (gill) net fisheries operating in national waters, and these continue to pose a potential threat to shearwaters. Japan operates a large coastal long-line fishery in the waters to the east that potentially overlaps with the range of flesh-footed shearwaters (Tuck and Wilcox 2008).

Onshore development and population trends

The loss of breeding habitat on Lord Howe Island was implicated in the flesh-footed shearwater population decline during 1978-2002 (Priddel et al. 2006). The decline in colony area seems to have ceased, with a slight increase in colony area noted and one new colony detected in 2008. While the area of the colonies has not declined since 2002 and there has been little change in the three larger colonies, the number of burrows in the smaller and more fragmented colonies has declined. This would suggest that edge effects may be significant at those colonies. The areas with greatest burrow density are in sandy soil under palm forests; at the edges of the colonies there are often intrusions of kikuyu grass *Pennisetum clandestinum*, and other weeds from gardens or paddocks, and the shearwaters find this difficult to burrow into (Priddel et al. 2006). This suggests that if efforts are made to increase the area of breeding habitat, they would be best aimed at the edges of existing colonies, especially Ned's Beach, Middle Beach and Clear Place, or if possible, filling in gaps in colonies.

Marine debris

Fledgling flesh-footed shearwaters on Lord Howe Island contain significant quantities of plastics that likely negatively influence chick body condition and thus, breeding success (Hutton et al. 2008). Small numbers of adult flesh-footed shearwaters are killed each year as a result of perforations to the digestive tract by plastic debris (unpublished data). However, while there is substantial evidence that plastic load is negatively correlated with body condition in seabirds (e.g., birds who ingest large amounts of plastic have low fat reserves; Connors & Smith 1982, Ryan 1987, Spear et al. 1995, Auman et al. 1998), direct (statistical), quantitative evidence of the negative effects of plastics in any seabird species is lacking (Laist 1997, Robards et al. 1997).

Road mortality

Flesh-footed shearwater carcasses were much more common along the edge of roads, clearly demonstrating their vulnerability to traffic, with roads more than doubling natural mortality on land. Traffic has been highlighted as a problem on Lord Howe Island since the early 1970's (Recher and Clark 1974), and was recently identified as a significant threat to flesh-footed shearwaters (DECC 2009). We have assumed here that the carcasses recorded were from throughout the season, so that there was no loss of carcasses from earlier in the summer. In 2008, detectability of carcasses declined suggesting that the number of road mortalities may be much greater than that calculated assuming they remain visible for the complete season. To assess this more accurately, it would be necessary to mark a number of carcasses in order to follow their condition over time, and use a more detailed assessment of the carcasses counted in the survey.

Nevertheless, 125 carcasses killed on the road represents an annual adult mortality of approximately 0.2%. This mortality is up to 5 times that generated through by-catch in the ETBF long-line fishery (Tuck and Wilcox 2008). Long-lived seabirds, such as the flesh-footed shearwater, rely heavily on survivorship of breeding adults to maintain population numbers (Croxall and Rothery 1991). Using the life expectancy (LE) estimator formula $LE = -1/\ln(\Phi)$, where Φ = annual survival, we can observe the changes in life expectancy as a result of changes in the survival rate (Lack 1954). For example, an adult flesh-footed shearwater with $\Phi = 0.92$ will live to 28 years of age while an adult with $\Phi = 0.918$ would be expected to live only 22 years. Therefore, small changes in the adult mortality greatly influence the growth of a population by reducing both the lifespan and potential reproductive output of breeding adults.

CONCLUSION

Analysis of the flesh-footed shearwater population on Lord Howe Island showed an 85% chance that it was continuing to decline between 2002-2008. Four factors have been implicated in the decline; while habitat destruction and by-catch in the ETBF have

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previously been implicated they are currently no longer causing major issues. However we have demonstrated that there is significant mortality on the roads of Lord Howe Island, and that this may be sufficient to explain the continuing decline. There is evidence of plastics in the stomachs of birds, especially chicks, however it is unclear what effect this is having on the population and further investigation is warranted. Finally, flesh-footed shearwaters winter in areas that potentially could interact with fisheries. At present, flesh-footed shearwater by-catch in this region is poorly understood.

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3. Environmental determinants of the at-sea distribution of encounters between flesh-footed shearwaters *Puffinus carneipes* and fishing vessels

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ABSTRACT

Fisheries observer data were used to model the distribution of seabird encounters for identifying areas for fisheries closures. Data from the Eastern Tuna and Billfish Fishery (ETBF) in the Tasman Sea (off the east coast of Australia) were used and the focal bird species was the flesh-footed shearwater (the species most commonly killed in this fishery).

Encounters between flesh-footed shearwaters and long-line fishing vessels varied with season, distance from Lord Howe Island, and a number of environmental and oceanographic variables (in particular, chlorophyll-A levels, wind speed, sea height and bathymetry). Encounters were most common to the south-west of Lord Howe Island, in waters associated with the Tasman Front and the East Australia Current.

The resulting model was used to predict the overlaps between fisheries and flesh-footed shearwaters during three years (1997/1998, 2003/2004 and 2006/2007). During 2003/2004 the area predicted to have high interactions was also the area with high fishing effort. During that year, there were also high mortalities of shearwaters in the fishery (Trebilco et al. 2010). In 2006/2007 the main fishing effort was well to the north of areas with predictions of high interactions. Seabird by-catch was low during that year. The species of fish targeted by the majority of the fishery also changed between years. This result illustrates that the most likely reason for falling by-catch rates in this fishery were movements of the fishing effort to areas away from the birds, rather than changes in fishing technique.

These results emphasise the potential of area closures as a method of by-catch mitigation for species that are proving intractable for standard by-catch methods. The use of data collected from fisheries vessels to identify characteristic areas of interactions is also important. This would be improved with increasing data on the distribution of the shearwaters.

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Keywords: flesh-footed shearwater, long-line fishing, by-catch, Lord Howe Island, at-sea interactions

INTRODUCTION

Worldwide, many seabirds are killed in commercial fisheries operations, in some species, in sufficient numbers to adversely affect their conservation status (Bartle 1991; Brothers 1991; Nel et al. 2002; Sullivan et al. 2006a). Particular attention has concentrated on albatrosses (*e.g.* Bartle 1991; Brothers 1991; Nel et al. 2002; Sullivan et al. 2006a), however a number of species of shearwaters and petrels are also severely effected (Brothers et al. 1999; Baker and Wise 2005; Phillips et al. 2006). Flesh-footed shearwaters (*Puffinus carneipes* Gould 1844) are killed in significant numbers during long-line fishing in the Eastern Tuna and Billfish Fishery (ETBF) off the east coast of Australia (Baker and Wise 2005). The shearwaters killed in the fishery are thought to come primarily from the Lord Howe Island population, and a modelling study has suggested that the population cannot sustain the reported levels of mortality (Baker and Wise 2005). This population has been shown to be declining since the 1970's (Priddel et al. 2006).

A number of mitigation techniques have been used in fisheries to reduce this mortality, including night-setting, line-weighting, and bird-lines; however, so far none have been found to be effective with flesh-footed shearwaters in the ETBF (Lawrence et al. 2006). Most methods of mitigation aim to reduce the impact of interactions once by-catch species encounter fishing vessels (Brothers et al. 1999; Sullivan et al. 2006b), and these methods can be less effective against deep diving or night foraging seabirds such as flesh-footed shearwaters and white-chinned petrels (Brothers et al. 1999).

An alternative strategy may be to reduce mortalities by decreasing the number of seabirds that encounter fishing vessels in the first place, for example by preventing fishing in areas that have high numbers of seabirds. Seabird by-catch increases with abundance of seabirds around fishing vessels, so avoiding areas with high concentrations of frequently caught species of birds may provide a simple and effective measure (Lawrence et al 2006). However, to adopt this strategy, we need to improve our understanding of the at-sea distribution of seabirds such as flesh-footed shearwaters, and the underlying factors that determine it.

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Broadly speaking, there are two ways to quantify this; via telemetry (Shaffer et al. 2006), or using observations of seabirds at sea (Reid et al. 2002, Camphuysen et al. 2004). Data loggers and satellite tracking devices provide detailed information on (generally) small numbers of individuals. The weight of the devices also limits the size of birds that can be studied in this way, although with increasingly smaller devices the number of species that can be studied is steadily increasing. The alternative, data from at-sea observations has the advantage of being derived from larger numbers of birds. During fisheries operations, counts of attending seabirds are frequently made for fisheries management purposes but these data have rarely been used for looking at the distribution of the seabirds at sea, as the data are considered to be biased because some species of seabirds (*e.g.* albatross) are attracted to vessels, while others may avoid them (Hyrenbach 2001). Additionally, fisheries observers generally have a number of other activities relating to fisheries management, and so they do not have the time for using distance or area sampling techniques (Spear et al. 2004).

However, if the data for a single species are used for answering well-targeted questions, these issues are likely to be lessened. If a species is attracted to fishing vessels, counts of that species can appropriately be used for quantifying their relative distribution, and the likelihood of interaction with vessels. Seabirds, such as flesh-footed shearwaters, forage over the ocean in a targeted, rather than a random, manner (Pinaud and Weimerskirch 2005). The at-sea distribution will be restricted due to the constraints of central place foraging during the breeding season (Orians and Pearson 1979; Kacelnik 1984). They are likely to forage in areas where they will increase their chances of encountering food (Barraquand and Benhamou 2008), such as regions of mixing associated with fronts between currents, and up-wellings of nutrient rich bottom water in the vicinity of land and benthic features (Schneider 1982; Reid and Hindell 2000). However, these areas may not be easy to locate (either for fishers or the birds), and it may not be possible to measure the presence of prey directly. If we can identify environmental descriptors that are correlated with their distribution, it is possible to model the areas that are liable to have increased encounter rates between the seabird and fisheries. These could then be

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used to make forecasts of areas of high encounter rates, facilitating the use of avoidance as alternative method for reducing by-catch in some species of seabirds.

In this study we have used data collected from fishing vessels in the ETBF to examine the distribution of flesh-footed shearwaters in the Tasman Sea in relation to fishing vessels.

From these data we aimed to develop models to describe the environmental characteristics in the areas of the interactions, to predict areas where interactions between fisheries and shearwaters are most likely to occur, to identify areas likely to have increased seabird mortality, and discuss the management of fisheries in relation to seabird mortality and the potential use of area closures.

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METHODS

The flesh-footed shearwater is a medium sized procellariiform. These birds are trans-equatorial migrants, breeding off the North Island of New Zealand (25,000-50,000 breeding pairs), at Lord Howe Island (17,000 pairs), off the south coast of Western Australia (100,000-200,000 pairs) and on Ile St Paul in the southern Indian Ocean (600 pairs, Marchant and Higgins 1990; Ross et al. 1996; Priddel et al. 2006). They breed during the austral summer, with egg-laying occurring in late November, hatching in late January and chick departure in late April or early May. During the Austral winter, they migrate to the North Pacific and the north Indian Oceans (Marchant and Higgins 1990).

Lord Howe Island is a 1,455 ha volcanic island situated in the Tasman Sea at 31° 30'S 159° 05'E, 495 km east of Australia (Priddel et al. 2006). It is located on the western side of a significant bathymetric feature, the Lord Howe Rise. There are a number of other important oceanographic features in the Tasman Sea, in particular, the western boundary current running down the east coast of Australia (the East Australia Current, EAC), which transports warmer tropical waters into the Southern Ocean. The EAC consists of a series of anti-cyclonic eddies of approximately 250 km diameter moving south along the east coast of Australia (Stanton 1981). They are strongest during the Austral summer, moving south as far as Tasmania (Stramma et al. 1995). At approximately Coffs Harbour in New South Wales, the EAC splits, with most water flowing eastwards to the north island of New Zealand (Stramma et al. 1995). This flow is known as the Tasman Front, and it passes close to Lord Howe Island (to the south in summer and north in winter).

The ETBF operates off the east coast of Australia, from Cape York, to the Victorian/South Australian border, and includes waters around Norfolk Island and Tasmania. The main fishing technique used is long-lining, and the main target species are yellowfin tuna (*Thunnus albacares* Bonnaterre 1788), bigeye tuna (*T. obesus* Lowe 1839), albacore tuna (*T. alalunga* Bonnaterre 1788), broadbill swordfish (*Xiphias gladius* Linnaeus 1758) and Striped Marlin (*Tetrapturus audax* Philippi 1887). In March 2008 there were 72 active long-line licenses for this fishery with a total catch of 5,217 t (\$A 26.8 million) (AFMA 2008).

Data sources.

The Australian Fisheries Management Authority (AFMA) is required have observers on long-line vessels operating within Australian waters who record the number of seabirds observed within 500 m of the vessel for a 2-3 minute period during line setting. AFMA observers provide approximately 3% coverage of the total fishery (Lawrence et al. 2006). Vessels also record their fishing position and their daily catch, and these data are supplied to AFMA.

Data for environmental parameters were obtained from a number of sources using the SDODE software (Table 1) (Hobday et al. 2006). Bathymetric data (*Bathy*) was obtained from 2-minute Gridded Global Relief Data from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center, 2006 (<http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html>). Sea Surface temperature (*SST*) was a CSIRO 6 day composite, with accuracy to $0.036 \times 0.042^\circ$. Altimetry (*Altimetry*) was MSLA (Maps of Sea Level Anomaly), derived from the satellites TOPEX/POSEIDON and ERS-1. Altimetry anomaly (*AltAnom*) is a synTS CSIRO product (<http://www.marine.csiro.au/dods-data/bluelink/synTS/>) produced and maintained by M. Cahill. Current strength (*egv*, *ngv*) was weekly data with spatial accuracy of $0.179 \times 0.333^\circ$ (<http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/msla/index.html>). Wind speed (*Wind* (wind shear), *Uwind* (longitudinal component of wind speed), and *Vwind* (latitudinal component of wind speed)) was monthly data from using NCEP Reanalysis data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at <http://www.cdc.noaa.gov/>. Chlorophyll A data (*ChlA*) was obtained every 7.7 days at $0.0833 \times 0.0833^\circ$ from Seawifs (<http://seawifs.gsfc.nasa.gov/SEAWIFS>). Frontal density (*Front*) was obtained every 7.94 days with $0.25 \times 0.25^\circ$ accuracy from CSIRO (J. Hartog and A. Hobday unpublished). Distance (*Distance*) was calculated as the great circle distance of a sighting from Lord Howe Island. Time of year (*Breed*) was divided into parts of the breeding season of flesh-footed shearwaters (Table 3.1).

Data Analysis.

Up to 14 counts were made within single cruises, resulting in the potential for auto-correlation within a cruise. Therefore, auto-correlation was tested for using a correlogram of differences of shearwater counts during long-line setting at different time lags within a fishing trip (successively comparing each count in a fishing trip to the next one, the second one, the third one, etc), using methods from Cressie (1993).

Table 3.1. Variables tested in GLM model.

Variable Name	Categorical/Continuous	Values	Range
Breed	Categorical	Early Chick rearing, Egg, Late Chick rearing, Prospecting, Winter	
Distance	Continuous	Km from Lord Howe Island	69-2289
Altimetry	Continuous	Mean sea height (m).	-0.08-0.17
AltAnom	Continuous	Variation in sea height from mean (m).	-0.27-0.24
Bathy	Continuous	Depth (m).	-2- -5240
ChlA	Continuous	Ocean productivity (mg m^{-3}).	0.05-0.58
Front	Continuous	Concentration of oceanographic fronts	0-3.59
SST	Continuous	Degrees celcius	14.17-29.44
Uwind	Continuous	Longitudinal component of wind speed (m s^{-1}).	-7.89-6.16
Vwind	Continuous	Latitudinal component of wind speed (m s^{-1}).	-3.07-8.58
Wind	Continuous	Wind speed in m/s	4.24-9.46

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We modelled the counts of flesh-footed shearwaters with Generalized Linear Models (GLM), using the counts as the response variable, and environmental data as descriptors. Because the seabird data are counts we initially considered that a Poisson error distribution would be appropriate. However, the data were strongly over-dispersed (variance was considerably greater than the mean), so we used a zero-inflated model. A zero-inflated model takes the form of two probability functions, a binomial function modelling the excess zeros, and a function to describe the actual count component of the data. We explored a number of distributions to model the count component, including log-normal (e.g. Pennington 1996), Poisson (e.g. Lambert 1992) and negative binomial (e.g. Minami et al. 2007). Initial testing indicated a zero-inflated negative binomial (ZINB) model gave the best fit for our data. We used the *p scl* package (version 1.03) (Zeileis et al 2007) in the R statistical package (version 2.6.1 R Development Core Team 2007). Models resulting from these zero-inflated methods have two parts to them (and hence, two related models); one group of explanatory variables for the excess zeros in the data (the binomial model, modelling the chance of birds being observed), and a second group (which may include the same explanatory variables) for the counts in the data (and so, modelling the numbers present on those shots for which there is a chance that they are present). The zero-inflation part of the model can be considered equivalent to performing a binomial (presence/absence) test of the data.

Testing showed there was autocorrelation in the data, and so a bootstrap method was used to test the models. To deal with issues of model uncertainty, a two-step bootstrap model averaging approach was used (Buchholz et al. 2007). The first step in this process is designed to eliminate those variables that have negligible effect on the outcome (Buchholz et al. 2007). To do this, initially a single observation was randomly chosen from each cruise. A stepwise process was then used to identify the explanatory variables giving the best fit for the response variable (using the *step.zic* function from the *zic* package (version 1.0) of the R statistical program) (R Development Core Team 2007). This was then repeated 200 times, each time randomly selecting a single observation from each cruise. From these 200 models, only those explanatory variables that appeared in at least 20% of models were used.

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The second stage was a model averaging step, where the variables kept in the first step were used to run a further stepwise process 250 times (Buchholz et al. 2007). The models that occurred most frequently in these 250 (so that over 50% of models were used) were then used as the final model to predict the number of shearwaters. To predict a count of shearwaters from the final group of explanatory variables, the final model averaged the results for each of the models chosen in the second stage, weighting the average using the number of times the model occurred in the final grouping of models. Variance was calculated using methods from Buckland et al. (1997) and Buchholz et al. (2007).

We validated the final model in two steps. The first was by using the final model to predict the counts of a sub-sample of observations with observed counts that were not used in model development using the predict function in R. From these, the correlation between observed and predicted counts was compared. Secondly, the spatial and temporal distribution conjunction was examined by taking the mean squared differences of observed and predicted counts, and plotting how this varied for different seasons throughout the year. From this plot it is possible to identify patterns that may indicate if there are missing covariates.

To further investigate the final model, we applied it to three years of environmental data taken from fishing vessels in which observers were not present. Three years were used; 1997/8, 2003/4 and 2006/7. These years were chosen as years when the fishery generally targeted swordfish (1997/8), yellowfin (2003/4), and albacore (2006/7) (N.Dowling CSIRO Marine pers. comm.). AFMA logbook data for each year from July to June was taken for making predictions of encounter rates. Environmental data for each fishing vessel location was obtained using the SDODE interface (Hobday et al. 2006). The predict function in the R statistical program was then used to model the distribution of encounters between fishing vessels and flesh-footed shearwaters during the 12 month period. Effort data was plotted after being smoothed using the *interp* function with bilinear interpolation from the *akima* package (version 0.5.1) in R.

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RESULTS

A total of 2,148 counts were made of flesh-footed shearwaters on 864 cruises within the ETBF between 27 September 2001 to 8 July 2006, with a mean of 26.2 ± 85.6 flesh-footed shearwaters per count. The individual counts ranged from 0-825 birds, and 1,514 (70%) of all counts had no observed shearwaters.

Flesh-footed shearwaters sightings were most common during the Prospecting and Early Chick period (Table 3.2), and when vessels were targeting Broadbill Swordfish or Yellowfin Tuna (Table 3.3). They were seen in greater numbers closer to Lord Howe Island, and in waters of shallower depth.

Table 3.2. Mean and standard deviation of counts of observed flesh-footed shearwaters during different seasons of the year (Prospecting=Sep-Oct; Egg=Dec-Jan; Early Chick rearing=Feb; Late Chick rearing=Mar-Apr; Winter=May-Aug).

	Prospecting	Egg	Early Chick	Late Chick	Winter
n	340	211	181	381	1004
mean(\pm sd)	60.3 (\pm 201.8)	25.1 (\pm 76.4)	74.8 (\pm 139.2)	48.0 (\pm 94.1)	1.9 (\pm 18.0)

Table 3.3. Mean and Standard deviation of counts of observed flesh-footed shearwaters for different target species for fishing vessels (ALB=Albacore; BET=Bigeye Tuna; OTH=Other species; SBF=Southern Bluefin Tuna; SWO=Broadbill Swordfish; YFT=Yellowfin Tuna).

	ALB	BET	OTH	SBF	SWO	YFT
n	35	298	129	133	259	1263
mean(\pm sd)	0.9 (\pm 2.1)	10.2 (\pm 40.0)	10.2 (\pm 41.5)	0.2 (\pm 1.8)	63.7 (\pm 222.3)	30.6 (\pm 87.9)

Modelling shearwater counts.

For the first step of the 2-step bootstrap, five variables (*Distance*, *Breed*, *Wind*, *Altimetry* and *ChlA*) occurred in at least 20% of the count models, while six variables (*Distance*, *Breed*, *ChlA*, *Altimetry*, *AltAnom*, and *Bathy*) occurred in at least 20% of the zero-inflation models (Table 3.4). All of these variables occurred in at least one of the best models developed in the second step of the process, and so were used in the final model (Table 3.5). Coefficients for variables used in the final model only changed slightly between models (Table 3.5). *Time of year*, *Distance*, *ChlA* and *Sea Height* occurred in the zero inflated and the count model, *AltAnom* and *Bathy* occurred in the zero inflation model and *Wind* occurred in the Count model. Flesh-footed shearwaters were significantly more abundant around fishing boats in *Early Chick*, closer to Lord Howe Island, at lower wind speeds, with high *ChlA* concentrations, with decreasing sea depth, decreasing Sea Height and with increasing Sea Height Anomaly (Table 3.5).

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Table 3.4. Frequency of all variables in first step of bootstep modelling (Count refers to the variables in the negative binomial part of the model (i.e. the variables increasing the observed counts) and Zero inflation refers to the binomial part of the model (i.e. the variables affecting whether birds are present)).

Counts		
Distance	160	100.00
Breed	160	100.00
Wind	128	80.00
Altimetry	91	56.88
ChIA	56	35.00
Vwind	15	9.38
SST	18	11.25
Bathy	0	0.00
Front	8	5.00
AltAnom	14	8.75
Uwind	2	1.25
Zero inflation		
Distance	160	100.00
Breed	160	100.00
Wind	3	1.88
Altimetry	80	50.00
ChIA	134	83.75
Vwind	12	7.50
SST	6	3.75
Bathy	32	20.00
Front	26	16.25
AltAnom	47	29.38
Uwind	24	15.00

Model validation

When the final model was used to compare predicted shearwater counts for the data set with observer counts (Fig 3.1), there was a correlation coefficient of 0.58 (an adjusted R-squared value of 0.33). The predicted model showed a large proportion of the data being a zero, reflecting the pattern in the observed data (Fig. 3.1). The predicted counts were also similar to the observed counts at lower values, but at higher observed counts, the predicted counts tend to be underestimated (Fig. 3.1). In addition, there were less zero counts in the predicted data than in the observed data, making thus, the observed data over dispersed relative to the predicted data.

The season that showed the greatest difference between observed and predicted counts was the Prospecting period, while Winter had the least. Areas with the greatest mean deviation were around Lord Howe Island, and between Lord Howe Island and the mainland of Australia. Most of the larger counts (>200 flesh-footed shearwaters) were near mainland Australia between 30°S-33°S in 2001 and 2002.

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Table 3.5. Most frequently occurring models in second step of bootstrap averaging approach. Ten chosen models were the most common 142 of 250 models. N is number of times model occurred; Percent is percent of 142. Coefficients in Count model relate to counts (i.e. positive coefficient indicates increasing count); coefficients in Zero inflation model indicate proportion of zero counts (i.e. positive coefficient indicates increasing proportion of zero counts). Mean and standard deviation (sd) calculated using methods from Buckland et al. 1997 and Buchholz et al. 2007.

	Model	M15	M17	M11	M26	M3	M16	M22	M6	M12	M5	mean	sd
Count	Eggs	-0.97	-1.00	-0.97	-0.95	-0.89	-0.97	-0.91	-0.97	-0.98	-0.90	-0.96	0.31
	Late Chick	-0.59	-0.61	-0.57	-0.63	-0.56	-0.59	-0.58	-0.64	-0.60	-0.52	-0.59	0.25
	Prospecting	-0.53	-0.54	-0.53	-0.58	-0.45	-0.53	-0.46	-0.55	-0.51	-0.40	-0.52	0.29
	Winter	-2.07	-2.06	-2.04	-2.09	-1.83	-2.04	-1.84	-2.09	-2.06	-1.80	-2.01	0.36
	Distance	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Wind	-0.28	-0.27	-0.28	-0.27	-0.24	-0.27	-0.24	-0.27	-0.28	-0.23	-0.27	0.11
	Alt	-3.18	-3.21	-3.01	-3.13		-3.28		-2.97	-3.10		-2.50	1.83
	ChIA				0.97	1.06		1.08	0.99			0.29	0.56
	Intercept	8.45	8.31	8.42	8.20	7.80	8.37	7.73	8.03	8.50	7.96	8.25	0.89
Zero													
inflation	Eggs	0.98	0.94	1.11	1.02	1.04	1.04	1.10	0.98	0.93	1.02	1.01	0.45
	Late Chick	0.60	0.61	0.63	0.64	0.65	0.65	0.65	0.62	0.58	0.66	0.62	0.37
	Prospecting	1.84	1.90	2.00	1.87	1.87	1.83	2.03	1.93	1.72	1.88	1.88	0.39
	Winter	3.84	3.82	4.00	3.86	3.87	3.85	4.04	3.83	3.70	3.90	3.87	0.39
	Distance	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00
	ChIA	-2.67	-2.59	-2.40	-2.57	-2.72	-2.28	-2.41	-2.62	-2.50	-2.29	-2.55	1.30
	Alt			3.15			3.92	3.28			4.20	1.05	1.80
	AltAnom						-2.07			-1.11	-2.06	-0.32	0.68
	Bathy		-0.03						-0.03			-0.01	0.01
	Intercept	-4.15	-4.88	-4.43	-4.24	-4.18	-4.31	-4.47	-4.83	-4.05	-4.43	-4.38	0.72
N		40	22	14	11	11	10	10	8	8	8		
Percent		28.2	15.5	9.9	7.7	7.7	7	7	5.6	5.6	5.6		
AIC		3299	3305	3305	3301	3301	3303	3302	3296	3304	3309		

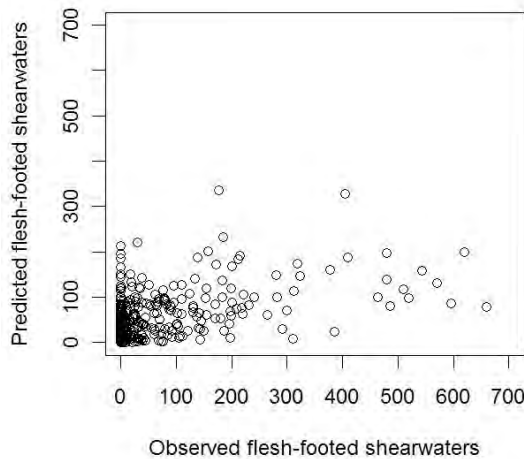


Fig 3.1. Observed and predicted counts of flesh-footed shearwaters

Table 3.6. Summary of effort and predictions of mean encounters (\pm s.d.) between flesh-footed shearwaters and long-line fishing boats in three years, with the percentage of shots made north of 25°S.

total	1997/8	2003/4	2006/7
Shearwaters	22.66 \pm 37.95	37.08 \pm 60.61	22.58 \pm 48.97
Latitude	-28.06 \pm 7.33	-27.44 \pm 5.91	-25.21 \pm 5.81
Longitude	152.38 \pm 3.51	154.68 \pm 4.62	154.03 \pm 3.52
> 25°S	26.12	22.11	38.94
Total shots	9,765	11,755	7,289

Predicting distribution from AFMA data

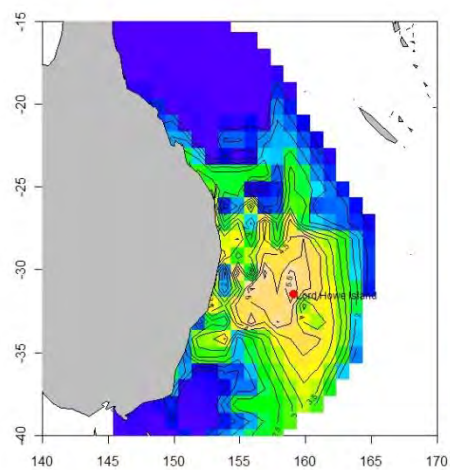
Environmental data were used to plot where flesh-footed shearwaters would be expected to encounter fishing vessels during these three years (1997/8, 2003/4 and 2006/7) (Fig. 3.2). For all three years, the model predicts that highest encounters with fishing vessels will occur around Lord Howe Island and to the south-west in the area around the Tasman Front, with other areas of concentration within the EAC (Figs 3.2a, c and e). In

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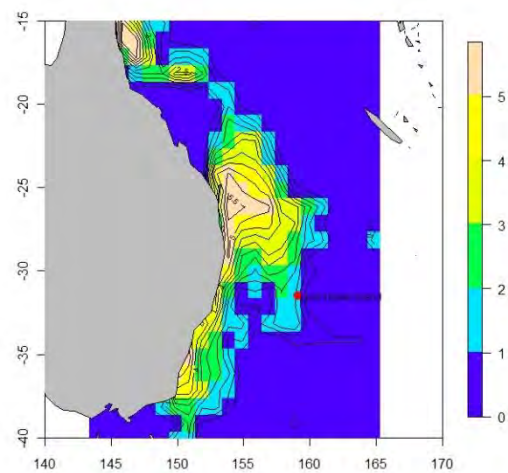
comparison, the distribution of fishing effort changed greatly between years. The greatest encounters between shearwaters and long-liners were expected in 2003/4 (Table 3.6). In 1997/1998 effort was concentrated close to the coast of Australia near the EAC and also to the north-west of Lord Howe Island in the area of 25°S 155°E off Mooloolaba (Fig 3.2b). In comparison, in 2003/2004 there was effort concentrated between Lord Howe Island and Australia, but also to areas to the east of Lord Howe Island (Fig 3.2d). In 2006/2007 effort was concentrated to the north of 30°S and west of 155°E (Fig 3.2f) with 39% of shots north of 25°S (Table 3.6), and relatively clear of areas of greatest encounters with flesh-footed shearwaters (Fig 3.2e).

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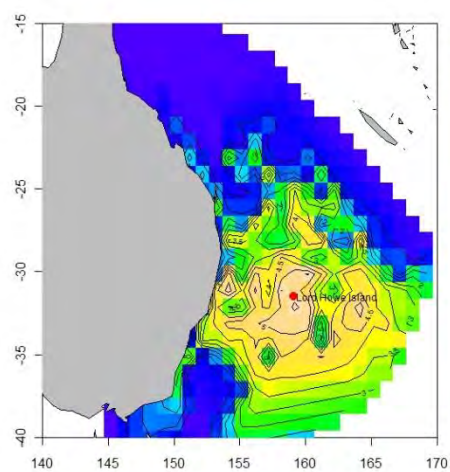
a.



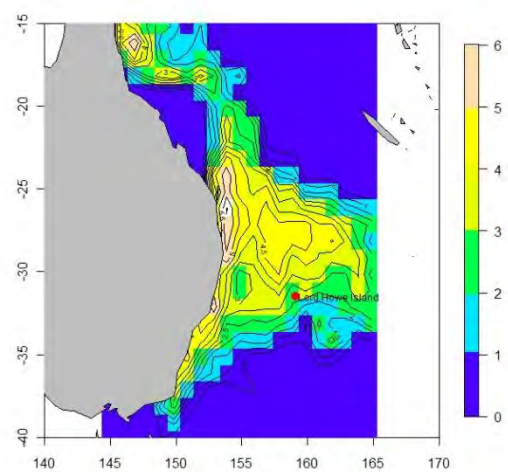
b.



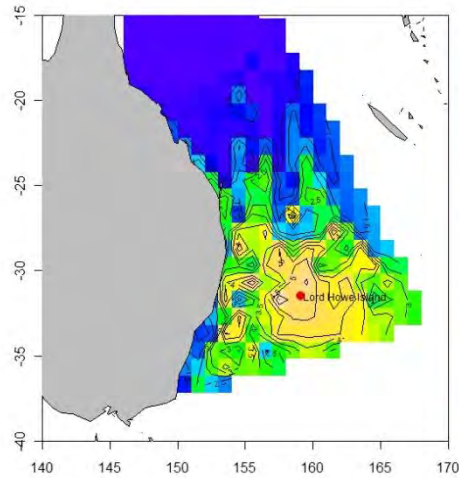
c.



d.



e.



f.

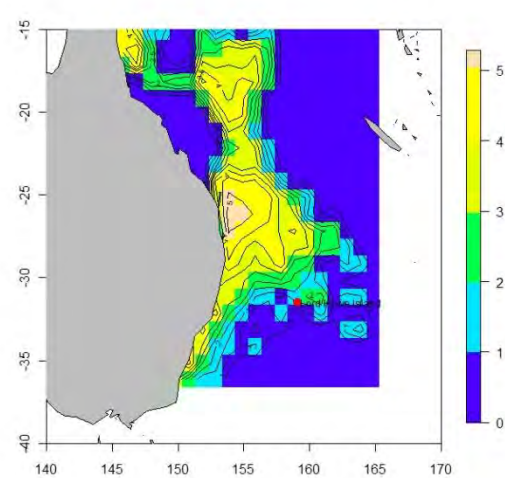


Fig 3.2. Predicted overlap between flesh-footed shearwaters and ETBF fishery, and distribution of fishing effort in the ETBF. (a) Predicted encounters of fishing vessels with flesh-footed shearwaters during 1997/1998. (b) Distribution of fishing effort in ETBF in 1997/8 (count for each one-degree block log transformed). (c) Predicted encounters of fishing vessels with flesh-footed shearwaters during 2003/2004. (d) Distribution of fishing effort in ETBF in 2003/4 (count for each one-degree block log transformed). (e) Predicted encounters of fishing vessels with flesh-footed shearwaters during 2006/2007. (f) Distribution of fishing effort in ETBF in 2006/7 (count for each one-degree block log transformed).

DISCUSSION

Efforts to mitigate seabird mortality in fisheries have largely focused on technological solutions that prevent the seabirds interacting with the hazardous features of the operation. However, a complementary approach may be to make the vessels themselves less available to the seabirds by having them fish in areas where seabirds are less likely to occur. These areas of higher overlap can then be highlighted, either to reduce fishing during high encounter periods or excluding fishing if that is needed. However, these areas of overlap are likely to also be important for fisheries. It is therefore important if using area closures to maximize the area closed for the foraging seabirds, but minimize the area for the fishery. Thus it is important to have as accurate a model of the distribution of the seabirds, hence the collection of environmental variables to characterize the important foraging areas.

While all predators should go to areas of relatively high food availability, these areas may not be the same for each species, as they will each perceive the environment differently, and may have different food requirements. For example, breeding seabirds such as flesh-footed shearwaters are central place foragers, since they are required to return to their nest for incubation and chick feeding at regular intervals, and so are restricted to within a certain range of their breeding site (Orlans and Pearson 1979; Kacelnik 1984). Fishing vessels operating in this fishery are also central place foragers. Fish such as tuna on the other hand have different constraints, not being required to return at regular intervals for nesting. Therefore, they may forage in areas of increased food other than those used by the shearwaters (Bestley et al. 2008).

Using models as explanatory tools

The distribution of flesh-footed shearwaters was best described by the time of year, and by the distance from Lord Howe Island. They were seen in greatest numbers in the chick-rearing, and in the prospecting periods, and least during incubation, and especially in winter. Numbers were also inversely proportional to the distance from Lord Howe Island,

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with no birds observed more than 1000 km away. These are broadly the expected results of the seasonal distribution of a migratory central-place forager.

In addition to the broader determinants of distribution, a number of environmental and oceanographic variables were also important in the models. Flesh-footed shearwaters were more commonly encountered by fishing vessels around the shelf edges or sea mounts, rather than the open ocean. This is similar to at sea observation of the distribution of the flesh-footed shearwaters in the Tasman Sea (Reid et al. 2002). They were also seen in greater numbers in water with higher chlorophyll A concentration (suggesting areas of higher productivity). Areas with lower sea height and sea height anomaly were also important. These features suggest meso-scale cold-core eddy features, and these and the fronts at their edges have been highlighted in previous studies of seabird distribution (*e.g.* Schneider 1982, Hunt and Schneider 1987, Skov and Durinck 2000). Wind strength was negatively correlated with the numbers of shearwaters observed. This may have indicated that the shearwaters were most active at lower wind speeds, or alternatively, that they were more difficult to observe at high wind speeds.

These ocean characteristics are known to influence the distribution of other seabirds. Grey-headed albatross' from Marion Island concentrated at the edge of both warm and cold eddies associated with the Agulhas Current (Nel et al. 2001). Yellow-nosed albatross' foraged in the Agulhas return current, concentrating in areas of increased chlorophyll-A concentrations and in areas of sea height anomalies that indicated productive cyclonic eddies (Pinaud and Weimerskirch 2005). Similar eddy structures are present in the Tasman Sea in the EAC and the TF. The fronts at the edge of eddies have been shown to be highly productive areas with increased prey (Pinaud and Weimerskirch 2005). While they are dynamic structures, and so are not going to remain in a place that shearwaters may return to each year, they are likely to be in approximately similar positions so that the shearwaters can move to a known region at least at larger scales. This will have the effect of reducing the area that may need to be visited to locate food.

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The data used in our study were collected by fisheries observers, and has a number of inherent problems, such as the attraction of fishing vessels to the birds (especially once the first bird has arrived), and the tendency of birds to remain with a vessel once they have located it. The quality of the data collected can be criticized due to it coming from “non-experts”. Nevertheless it has been suggested that if you take enough non-experts and add up their answers you will come up with the right answer by average.

Alternatively, to test the accuracy of the data, there may be a number of other methods. Multiple observers could be used (Spear et al. 2004), however there is usually difficulty in getting a single fisheries observer on a vessel, so opportunities for getting two on would be rare. Taking results from several vessels operating repeatedly may be used, however if they are close in time and space they are unlikely to be acting independently as far as seabirds are concerned and hence are unlikely to help in improving accuracy. Otherwise, using a modelling approach, such as adopted here, and judging if the result appears reasonable, while recognizing the limitations of the data is the most useful approach. Because of this, our data should be considered as encounters between the seabirds and fishing vessels rather than being of their “normal” distribution (though, these may be the same).

Using models as predictive tools

Models can be used for two purposes: explanatory, and predictive. Explanatory models look to highlight the variables most associated with the observed data. Predictive models take these relationships and attempt to use the variables to predict patterns of encounter. Data collected by fisheries observers were useful for improving our understanding of the distribution of flesh-footed shearwaters and in particular their encounters with long-line fisheries. This suggests the use of observer data from fishing vessels may be appropriate for predictive use, if the appropriate questions are being asked of it. In this case, the data were used to model where encounters occur, rather than making an overall estimate of the total distribution of the shearwaters. Data collected by fisheries observers is likely to be the main source for observations of seabirds at sea in many situations. Studies of the distribution of seabirds using at-sea observations generally exclude counts from around commercial fishing vessels (Camphuysen et al. 2004) as this is thought to bias the results,

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causing estimates of the distribution and abundance are likely to be overestimated (Hyrenbach 2001). However, several studies have shown that many seabirds derive a great deal of food from around fishing vessels (e.g. Thompson and Riddy 1995; Oro et al. 1995). While the fisheries collected data may be biased in relation to at-sea observation data, the underlying distribution of the seabirds is the same for both methods. Thus both methods could be used for understanding this underlying distribution, though it may be necessary to model them separately.

The model was used to predict areas with the greatest number of encounters with fisheries in three years. By-catch of flesh-footed shearwaters is positively correlated with the numbers present around long-liners (Lawrence et al. 2006). The years were chosen to represent typical variation in fishing effort between years. While, on the scale of the model, the major area of predicted interaction remained similar, the area that was actually used by the fishery did vary considerably. Thus in 2003/2004 when the fishery was targeting yellowfin more seriously, there was a great deal of effort into the areas that the encounters were predicted to be greatest. Seabird by-catch rates were high in that period (Trebilco et al. 2010). In 2006/2007 when the fishery was largely targeting albacore, most effort was well to the north of that where encounters with the shearwaters was greatest, and by-catch rates were relatively low (Trebilco et al. 2010). In 1997/1998 most effort was concentrated within the EAC close to the east coast of Australia, and east of Mooloolaba. There was relatively little effort to the south-west of Lord Howe Island in the area of highest predicted encounters. This may suggest that mortality would have been low for that year, though no data exists on seabird by-catch.

Broadly, the model predicted that the shearwaters will be foraging in similar areas from year to year, with differences due to spatio-temporal differences in conditions. The area with the highest predicted chance of encounters between fisheries and the shearwaters to the south-west of Lord Howe Island was the area with the greatest observed mortality over the period 1998-2004 (Baker and Wise 2005; Lawrence et al. 2006). The three years of fishing data had major shifts in the areas being used, depending on which species were being targeted. In recent years, fishing effort in the ETBF has changed to be targeting

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Albacore Tuna to the north of Lord Howe Island (Fig 3.2f; Baker pers. comm.). There has been a dramatic decrease in the mortality of flesh-footed shearwaters over this time (Baker pers. comm.). This observation validates the aims adopted in this study of highlighting areas of increased overlap between seabirds and fisheries.

The use of area closure appears to be a viable means to reduce the mortality of seabirds that do not prove amenable to more standard methods of mitigation. This can be seen as analogous to the method of using Marine Protected Areas for the protection of vulnerable fish species (Pauly et al. 2002; Hilborn et al. 2004). However, where generally in fisheries MPA's are used to close specific areas, this has been argued to be of limited use in the case of highly mobile species (Hilborn et al. 2004). Area closures were recently adopted to protect sea turtles in Hawaii in the longline fishery for Broadbill Swordfish (Curtis and Hicks 2000). However this involved closing a very large area from fishing. Having greater knowledge of the requirements of more mobile species (such as their relationships with oceanographic features) may make it possible to develop temporary area closures. Fishers may be willing to voluntarily forgo fishing in areas that are likely to have high by-catch if these areas can regularly be identified, and are not the only areas they have available, especially if this avoids situations of having their fishery closed down.

This study shows that a model with relatively simple inputs can greatly assist in our understanding of the distribution of seabirds, and their potential foraging areas and, importantly, where threats such as fisheries interactions are most likely to occur. This model was developed with the aim of identifying areas where most interactions occurred, and hence where mortalities would be likely to be highest, with the view of using it as a dynamic, rather than static, approach to short-term area closures. These areas would be identified from the use of a model such as this one, in particular using the explanatory variables within the model that are variable over shorter periods (the oceanographic and environmental variables). Further improvement could be made by identifying the rates of change of the explanatory variables. Thus the variables on seasonal timing and position never change, the oceanographic variables such as ocean colour and sea height potentially

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would change over periods of days and weeks, while environmental variables such as wind speed and direction would change over periods of hours or days. The more rapidly variables change, the less useful they are for making forward predictions, due to their being out of date more rapidly.

CONCLUSIONS

Data collected by fisheries observers were used to model areas of interactions between seabirds and fisheries in the ETBF. The model developed highlighted areas to the southwest of Lord Howe Island as having increased interactions. In one of three years when the fishery concentrated in this area there were high observed seabird mortalities, while in another year when it concentrated in other areas, there were low observed mortalities. This work shows the potential of area closures for the reduction of seabird mortality for species that prove intractable to standard seabird mitigation techniques.

ACKNOWLEDGMENTS

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4. Extracting information from incidental observation data: using an arrivals-departures multi-component model to quantify small scale habitat use in a marine predator, the flesh-footed shearwater.

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ABSTRACT

Collecting data for distribution or foraging information is often difficult, especially for marine species. Obtaining designed survey data is especially rare. There is however, a greater amount of incidental observations. These incidental data have difficulties with biases induced due to their collection methods; for example vessel attraction effects and autocorrelation. Statistical models that represent the processes underlying the observations can provide a mechanism to accommodate these complexities, allowing these other sources of data to be made available. An arrivals/departures multi-component model has been used to examine attendance by a marine predator (the flesh-footed shearwater) at long-line fishing vessels operating in waters of the Tasman Sea. Flesh-footed shearwaters were predominantly attending fishing vessels while they were operating in areas that were likely to have increased productivity, as demonstrated by oceanographic conditions suggesting eddies and the edges of bathymetric features. Attendance was also affected by energetic issues, as shown by their leaving vessels if they moved over greater distances between operations, or moved further from Lord Howe Island, the putative breeding area of the birds being observed. The results suggested that shearwaters were more likely to attend fishing vessels in areas the shearwaters were already likely to be feeding in, rather than the vessels acting as attractants to the areas. This suggests vessel attendance is likely to be a local effect, and so potentially, having vessels avoid these areas could be used by management to reduce vessel attendance by shearwaters, and hence reduce by-catch in this fishery. The statistical technique used here allow a better reflection of the counts than more conventional GLMs, providing better insights on the behaviour of flesh-footed shearwaters at smaller scales than was previously possible.

Keywords: Flesh-footed shearwater, Lord Howe Island, maximum likelihood, fishing, long-line, by-catch

INTRODUCTION

Predicting the distributions of species is a difficult task due to the twin challenges of complex environmental interactions and the paucity of data. This is particularly true for pelagic species, as they live far out to sea and thus are rarely observed. However, understanding their distributions and the factors driving them is essential for understanding their ecology, and is an essential component of predicting the impacts of threats such as climate change, habitat distribution, and over-harvest by fisheries. Many species of seabirds, especially of the family Procellariiformes, are susceptible to the effects of fisheries, climate change and habitat destruction (Croxall and Gales 1998). Fisheries in particular, have been linked to population declines in a number of species. Quantifying the foraging distribution of seabirds in order to identify areas that they are likely to interact with fisheries is an important component of managing these issues by identifying areas of threats (Chapter 3; Pichegru et al. 2009). Further to this, adding information from environmental drivers of these distributions will further define them at smaller and more targeted scales. With this it may be possible to predict how future encounters may change with changes in fisheries or climate.

There are a number of techniques that quantify the at-sea distribution of seabirds. Advances in telemetry are increasing our ability to understand where individual birds go (Prince et al. 1992; Shaffer et al. 2006). However, examining this has inherent biases; generally only breeding birds are studied, and only a small number of individuals are tracked. Alternatively, there are a great deal of data collected by observations from ships. Ship-board observations have the advantage of having data from a great number of birds, which is often accompanied by data on characteristics of the observation platform and the local environment. This can include information on oceanographic variables as well as fisheries related data such as target and non-target catch data.

There is also a range of methods that have been developed for analysing transect counts at sea (Tasker et al. 1984, Spear et al. 2004). These methods use standardized designs such as transect counts to minimise the effect of the observation platform. Hence they are typically only applicable on scientific cruises or non-fisheries related shipping, as

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operations of fisheries vessels do not follow standardized protocols, and often involve activities that attract birds making local densities higher than they otherwise would be. Concerns about fisheries impacts upon seabirds have led to the collection of a great deal of data from fishing boats, but these are rarely used for analyzing distribution as they do not fit into the criteria of the standardized methods (Melvin et al 2006, Otley et al. 2007, Chapter 3). Where fishery-based data have been used, analyses have concentrated on broad questions of distribution and the area that the birds are observed in, without looking at finer scale details or the oceanographic characteristics of these areas. Developing methods that can account for these problems with fishery-based data should allow description of seabirds' attendance behaviour around fishing vessels. The use of information on the conditions that lead to seabirds attending vessels may allow examination of these finer scales.

There are two major problems with using data from fisheries observations. The first is that the counts are correlated since birds may follow a boat for multiple days and hence the successive counts are not independent measures of local density. The second problem is that fisheries involve activities that may attract (*e.g.* due to disposal of fish wastes from fish processing) or repel birds (*e.g.* due to the presence of larger birds). Thus while the numbers of birds attending a vessel is likely to be proportional to the local density, it is not equivalent to it. This has been dealt with by previously either using boot-strapping (Chapter 3), or attempting to limit counts to those birds that have newly joined the vessel (Tasker et al. 1984, Spear et al. 2004). Boot-strapping utilises only some of the data and so there is a loss of information and statistical power (Chapter 3). Limiting counts to only newly joining birds is subjective, as the birds rarely have individual marks that unambiguously distinguish them.

Given some reasonable assumptions about the underlying process, it is possible to develop a statistical model that can accommodate these two issues. If we assume that bird counts are correlated in a constant fashion, we can model the underlying correlation. If we further assume that the attractiveness of the fishing vessel is either constant, or is predictable from co-variates, then we can use the vessel as a measure of relative density.

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This would then mean that changes in the background density of birds due to habitat quality are reflected in changes in the abundance of birds around the vessel. Thus, it seems possible that more birds will attend a vessel while it is fishing in “good” habitat but that they will leave when the vessel moves to “bad” habitat. From information on the change in habitat between counts it may be possible to examine small scale aspects of the distribution, rather than the larger scale used in previous studies. This allows information about oceanographic and energetic effects to be analysed. These questions cannot be answered using standard methods of analysing count data from fishing vessels.

Here a new approach to fisheries observed data has been developed using a multi-component model, which models the birds attending a vessel by explicitly modelling the arrivals and departures of individual birds between observations. This model was tested using simulated data, and then applied to data on attendance by flesh-footed shearwaters *Puffinus carneipes* around long-line fishing vessels in the Eastern Tuna and Billfish Fishery (ETBF) off the east coast of Australia. Based on analysis of data from the ETBF, the environmental and operational factors driving the spatial distribution of the shearwaters were determined. Finally this information was used to identify areas where encounters are predicted to be high, which is important information for management as flesh-footed shearwaters have been shown to be threatened by mortality in this fishery (Baker and Wise 2005).

METHODS

Data sources

The Australian Fisheries Management Authority (AFMA) requires observers on long-line vessels operating in Australian waters. The observers provide approximately 3% coverage of the total fishery (Lawrence et al. 2006). In addition to collecting data on fisheries catch and by-catch (including seabirds), observers record the number of seabirds observed within 500 m of the vessel for a 2-3 minute period during line setting. Vessels also record their fishing position and their daily catch, and this data is supplied to AFMA. This data was described in more detail in Chapter 3.

In order to collect extra data for models in this paper, observers were asked to follow a single shearwater for a period of a minute, and record whether it remained attending the vessel, or if it departed. Departing was defined as either the bird landing on the water to rest, or flying away to the sides or behind the vessel. Thus departure is a Bernoulli process, with a single bird having some probability of leaving in a one minute period (or staying as there are only two possible outcomes). Observers were also asked to record a number of other variables, including environmental conditions and the numbers of seabirds present at the start and finish of the counts.

Environmental parameters were obtained from a number of sources using the SDODE software (Table 4.1) (Hobday et al. 2006). Bathymetric data (*Bathy*) were obtained from 2-minute Gridded Global Relief Data from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center, 2006 (<http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html>). Sea Surface temperature (*SST*) was a CSIRO 6 day composite, with accuracy to $0.036 \times 0.042^\circ$. Sea Surface Height (*Altimetry*) was MSLA, derived from the satellites TOPEX/POSEIDON and ERS-1. Wind speed (*Wind*) was monthly data from using NCEP Reanalysis data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at <http://www.cdc.noaa.gov/>. Chlorophyll A data (*ChlA*) was obtained every 7.7 days at $0.0833 \times 0.0833^\circ$ from Seawifs (<http://seawifs.gsfc.nasa.gov/SEAWIFS>). Frontal

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density (*Front*) was obtained every 7.94 days with $0.25 \times 0.25^\circ$ accuracy from CSIRO (J. Hartog and A. Hobday unpublished). Distance (*Distance*) was calculated as the great circle distance of a sighting from Lord Howe Island. Time of year (*Breed*) was divided into parts of the breeding season of flesh-footed shearwaters. Changes in variables were calculated as the value for the previous count subtracted from the current count. The number of fish caught in the previous shot was calculated from fisheries logbook records.

Table 4.1. Co-variates used in fitting of environmental effects on arrivals and departures of flesh-footed shearwaters behind longline fishing vessels in the ETBF.

Variable Name	Description	Range
Distance	Km from Lord Howe Island	69-2289
Altimetry	Mean sea height (m).	-0.07-0.16
Bathy	Depth (m).	-2- -5236
ChlA	Ocean productivity (mg m^{-3}).	0.05-0.55
Front	Concentration of oceanographic fronts	0-3.59
SST	$^\circ\text{C}$	14.54-29.32
Wind	Wind speed (m s^{-1})	4.35-9.46
Fish	Number of fish caught on previous shot	0-185
DistToPrev	Distance to previous shot (km)	0-1111
Latitude	Latitude ($^\circ\text{S}$)	38.87-14.60
ChangeInBathy	Change in bathymetry since last shot (m)	-3365-3255
ChangeInSST	Change in SST since last shot ($^\circ\text{C}$)	-8.21-11.99
ChangeInAltimetry	Change in Sea Height since last shot	-0.17-0.14
ChangeInChlA	Change in Ocean productivity since last shot	-0.37-0.30

Model development

Changes in seabird abundance at a given vessel between successive observations were modelled as a mechanism for comparing the relative quality of different environmental conditions. It was assumed that the vessel, subject to covariates, has a constant attractiveness to birds, so that changes in the density of seabirds between fishing operations are due to changes in habitat quality between the sites. We modelled the changes in these counts using a multi-component model. Our approach considered three levels of uncertainty: process uncertainty, parameter uncertainty and measurement uncertainty.

In order to model the process, it was assumed that birds depart from the vessel after a count, and then subsequently new birds arrive prior to the next count. While this is somewhat artificial, it enables the intervening number of birds to be treated as a hidden variable that has a finite number of states, ranging from the number on the first count to zero. This is an essential feature, as it allows the integration of the likelihood over this hidden state, and thus we can estimate the likelihood of the observations given a set of parameters (Fig. 4.1).

Departures, D , were modelled for a given observation as an integer between the number observed on the first count, C_i , and zero, using a binomial distribution to describe the process.

$$\Pr\{D = d_i\} = \binom{C_i}{d_i} p_\delta^{d_i} (1 - p_\delta)^{C_i - d_i} \quad . \quad \text{Equation 1}$$

$$\text{logit}[p_\delta^{d_i}] = \beta X$$

where i is the observation number, d is the probability of departure, p is the leaving rate per minute, β is the coefficients of the departures variables, and X are the environmental

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variables that effect departure. The difference between this random variable and the first count, $C_i - D_i$, is a hidden variable that is not observed.

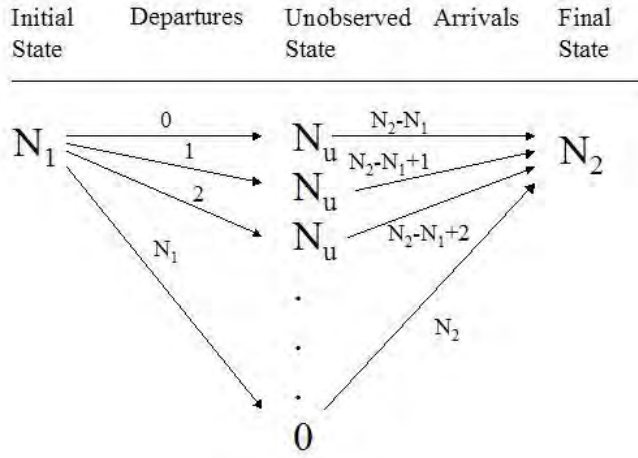


Fig 4.1. Simplified diagram of process involved between successive counts, where N_2 is the current count, N_1 is the observed number of birds during a previous count, and N_u is the number present at some unobserved time in between.

Arrivals of new birds at the vessel join this, yielding the count at the second observation. We model these arrivals as a Poisson process, yielding integers bounded by zero and infinity

$$\Pr\{A = a\} = \frac{e^{-\varphi} \varphi^a}{a!} \quad \text{Equation 2}$$

$$\ln(\varphi) = \alpha Y$$

where A is the number of arrivals, Y are the environmental variables that effect arrivals, a is the probability of arrivals, α is the coefficients on the arrivals variables, and φ is the arrival rate.

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Thus, the likelihood of an observation is the sum of the probabilities of each possible hidden state of departures (Equation 1) and arrivals (Equation 2)

$$L(C_2 | C_1, \alpha, \beta, X, Y) = \sum_{d=0}^{C_1} \text{Bin}(d, C_1, p) \text{Pois}(C_2 - d, \phi)$$
$$\ln(\phi) = \alpha Y$$
$$\ln(p/(1-p)) = \beta X$$

Equation 3

across all the possible hidden states for a pair of observations C_1 and C_2 .

The model was implemented using a maximum likelihood approach in the R statistical program (R Development Core Team 2009) using the `optim` function with a derivative-based unconstrained nonlinear numerical optimizer (BFGS; Broyden, Fletcher, Goldfarb and Shanno). The model is solved by integrating over all possible values of the hidden variable.

When this model was applied to data collected from observers, there was a modest fit, with large deviations for low and high counts, indicating the data were over-dispersed. We modified the approach to incorporate over-dispersion by shifting from a Poisson distribution for arrivals to a negative binomial distribution. The negative binomial is an appropriate modification, as it can be derived from a Poisson distribution with a rate that varies as a gamma distribution and can be parameterized by a mean and variance (Bolker 2008). Similarly, the distribution for departures was altered to a beta-binomial distribution, which is a binomial distribution with a probability that varies according to a beta distribution allowing for more flexibility in the relationship between the mean and variance (Bolker 2008). The beta distribution has two shape parameters, and these were derived with the delta method (Bolker 2008) (Equation 4).

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$$L(C_2 | C_1, \alpha, \beta, X, Y, k) = \sum_{d=0}^{C_1} \frac{\Gamma(C_1 - 1)}{\Gamma(p + 1)\Gamma(C_1 - p - 1)} \frac{\Gamma(s_1 + p)\Gamma(C_1 + s_2 - p)}{\Gamma(s_1 + s_2 + C_1)} \frac{\Gamma(s_1 + s_2)}{\Gamma(s_1)\Gamma(s_2)}$$

$$\binom{(C_2 - d) + k - 1}{k} \phi^{(C_2 - d)} (1 - \phi)^k$$

$$\ln(\phi) = \alpha Y$$

$$\ln(p / (1 - p)) = \beta \mathbf{X}$$

$$s_1 = p(1 - p) / (\text{var}(p) - 1)$$

$$s_2 = (1 - p)^2 p / (\text{var}(p) - 1)$$

Equation 4

where k is the dispersion parameter of the negative binomial distribution, and s_1 and s_2 are the shape parameters for the beta-binomial distribution and Γ is the gamma function. The shape parameters in the beta-binomial, and the size parameter in the negative binomial were estimated from the model.

Estimating departures rate

This model is ill-determined, as the data can be fit equally well by a fixed ratio of departure and arrival rates. There is some information on the magnitudes of the rates in the variance in the counts, as higher variance in the counts indicates that the rates are higher. It is also possible to improve the determination of the model if ancillary data can be supplied to constrain either the departure or the arrival rate. Due to the difficulty of measuring arrival rate, we chose to collect ancillary data on the departure rate, which we modelled as a binomial process

$$\Pr\{D = d_j\} = \binom{O_j}{d_j} \frac{p_\delta^{d_j}}{t} \left(1 - \frac{p_\delta}{t}\right)^{C_i - d_j}, \quad \text{Equation 5}$$

$$\text{logit}\left[p_\delta^{d_j}\right] = \beta X$$

where j is the number of observation on a trip, t is the number of observation periods in a 24 hour period between counts C_1 and C_2 above.

Model validation

The ability of this model to recover known parameters was tested by simulating data and then fitting the model to that data to see if the parameters could be accurately estimated. Initially, 1,000 first counts were simulated using a Poisson distribution. For each of these first counts, a second count was generated by having the birds of the initial count randomly leave following a binomial distribution, and other birds arriving following a Poisson distribution. The second count was therefore the first count minus the departures, plus the arrivals. These arrivals and departures were each effected by normally distributed co-variables multiplied by co-efficient values. These data were then run through the model that had been developed to test whether it would successfully retrieve the parameters in the data.

To test the effect of model complexity on fit, the model was run using from one to five generated explanatory variables. In order to test the performance of the model for a range of values, the coefficient for one of the random covariates was varied by one sequentially between -5 and 5 , and the value of the parameter used to generate the model, and the estimate derived from the maximum likelihood were recorded. The correlation between these was then calculated and evaluated for each of one to five generated variables. While the parameter for a single generated variable was varied, all other variables were held constant, and the estimates of these parameters, and the residuals of the estimates were recorded.

The ability of the model to recover true parameters for each of the components, arrivals or departures, and for both together was tested.

To test the effectiveness of the model in comparison to other methods, it was tested against a Generalised Linear Model (GLM) using a Poisson distribution with a log link function. To do this, data were simulated in the same way to that used to test the model. Counts at the two successive time steps were generated for 1,000 observations, using a single normal random explanatory variable and parameter to generate count 2. This was done for a range of parameter values, varying sequentially from -5 to 5 by one. A two

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component model was fit to the data using maximum likelihood. A standard Poisson GLM was then fit to the data, using the independent variable (the simulated co-variate) to describe the dependent variable (the final count). The fitted co-variate from this GLM was then recorded for each of simulated data sets. The parameters identified from each of the two component models and the Poisson GLMs were then plotted against the “true” parameter, to identify which model performed better in terms of recovering the underlying process.

Estimating departure of individuals

Individual departure data took the form of a binomial distribution. To test which variables were most affecting departures, it was analysed with a Generalised Linear Model (GLM) using a logistic link function using the R statistical program version 2.9.0 (R Development Core Team 2009). To test which variables were significant, we used a stepwise addition of variables using the step function in R. Variables were standardized by subtracting the mean and then dividing by the standard deviation (Sokal and Rohlf 1969).

Model fitting

In order to identify which variables were having the greatest effect on the number of shearwaters present, a forward stepwise process was used. Variables were added or subtracted using comparisons of the AICc (Burnham and Anderson 1998). Standardized residuals were then used to diagnose whether the distributions of the random variables accommodated the variation observed in the process. This process was carried out for the models developed from Equation 3 and Equation 4.

RESULTS

Observations of flesh-footed shearwaters collected by AFMA fisheries observers were used in the study; it was described in greater detail in Chapter 3. All data occurred off the east coast of Australia, with sightings of flesh-footed shearwaters recorded between 15-40°S (Fig 4.2). For analysis in this paper, 1,233 observations that were preceded by other counts were used.

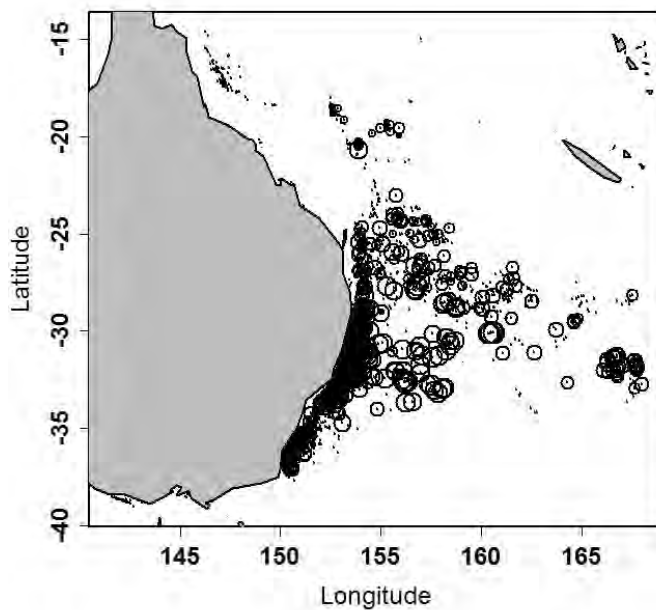


Fig 4.2. Locations of all observer counts of flesh-footed shearwaters by AFMA observers in the ETBF. Observations are represented by a point; counts by circles (circles proportional to the log of the number of shearwaters counted).

Model validation

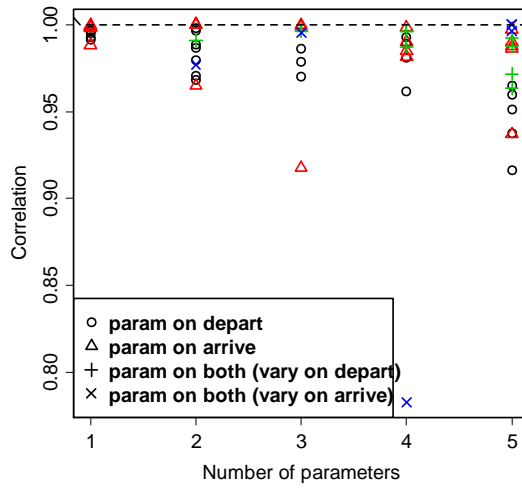
The model was successful at retrieving the parameters from simulated data (Fig. 4.3). Correlations were greater than 0.96 for up to 4 parameters, showing that the model could retrieve the patterns in the simulated data (Fig 4.3a). In one simulation with four parameters, there was a relatively poor correlation (0.78) when one level of one parameter value was retrieved inaccurately (Fig 4.3a). This was a case with the varied parameter describing the arrivals, while variables describing the arrivals were held

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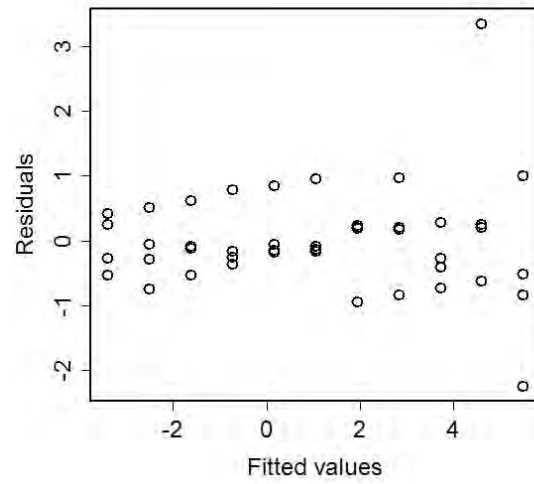
constant. The poor retrieval of this value may suggest that the likelihood surface was fairly flat, or that there were more than one minima in the surface or alternatively, because there is randomness in the data being modelled, some fraction of the estimated values will be poor. There was some deterioration in performance for 5 parameters, though all correlations were greater than 0.93 (Fig 4.3a). Mostly residuals remained close to the Fitted values, though they appeared to become greater at larger values (Fig 4.3b). In some cases where there were only parameters on one side of the model, the estimate of the constant probability of the other side of the model became less accurate with increasing numbers of parameters (Fig 4.3c). It was most inaccurate when the departures were held at constant probability (and hence the parameters were describing the arrivals) (Fig 4.3d). The coefficients that were held constant were retrieved accurately for up to four parameters (Fig 4.3e). For five parameters there was a tendency to overestimate the parameter on the departures (Fig 4.3f).

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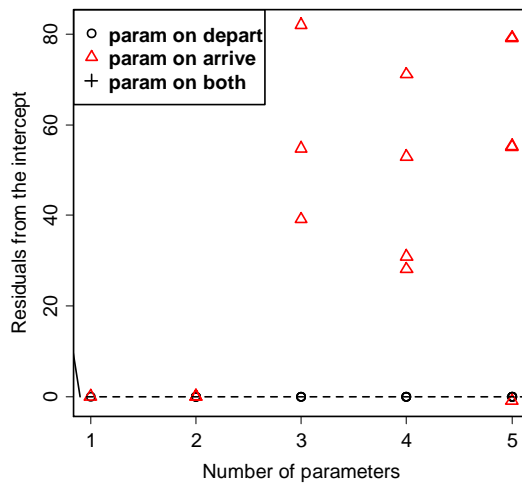
a.



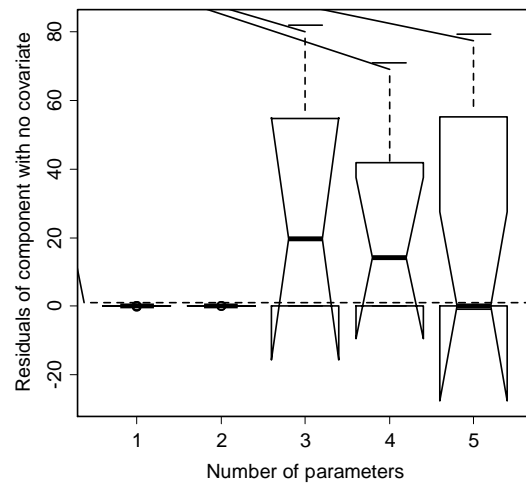
b.



c.



d.



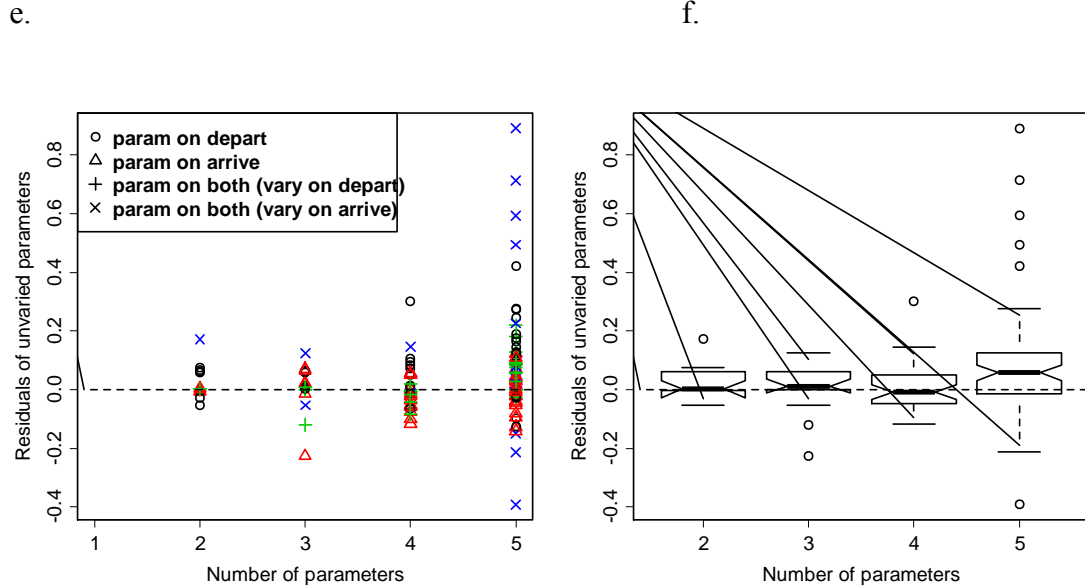


Fig 4.3. Results from simulation trial of model with up to five added parameters. (a). Correlation between the parameter that was varied, and the estimate of the parameter from the model. Horizontal line at 1 indicates level if there was perfect correlation. Var on arrive = parameters on arrivals; var on depart = parameters on departures; var on both = parameters on both parts of model. (b). Residuals for fitted values from simulation trials. (c). Residual values of the mean intercepts for different models with increasing numbers of parameters. Var on arrive = parameters on arrivals; var on depart = parameters on departures; var on both = parameters on both parts of model. (d). Mean and range of residual values of mean intercepts for models with increasing numbers of parameters. (e). Residuals of the estimated mean value of parameters held constant while correlation was examined for one parameter. Var on arrive = parameters on arrivals; var on depart = parameters on departures; var on both = parameters on both parts of model. (f). Mean and range of residuals of estimated mean values of parameters held constant while the correlation was examined for one parameter.

The performance of the model and a GLM was compared using simulated data. The correlation of parameters derived using the model showed a strong correlation with the simulated parameters (0.99); that between the parameters estimated from the GLM and the simulated parameters of -0.97, hence it retrieved the parameters poorly (Fig 4.4).

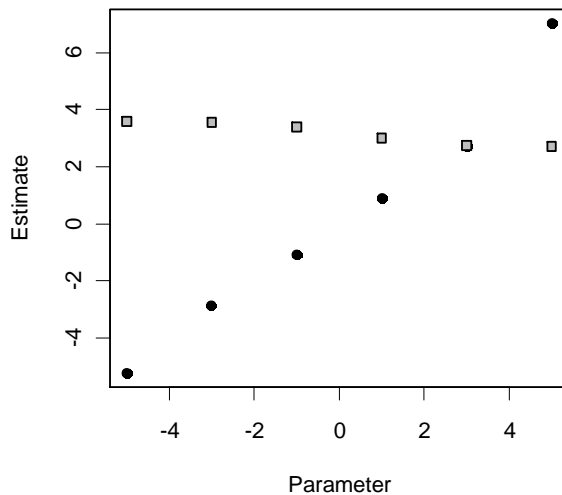


Fig 4.4. Comparison of retrieval of simulated parameters using the model (circles) and a Generalised Linear Model with a Poisson distribution and a log link (squares).

Departure rates

Observers made 270 one minute dedicated observations of flesh-footed shearwaters behind long-line fishing boats between 17 February 2008 and 8 July 2009. During these observations, 20 birds left during the observation period, giving a rate of 0.074 departures.m⁻¹ (s.d. = 4.30), giving a probability of leaving during one minute of 0.071. Flesh-footed shearwaters were more likely to stay behind the vessel with increasing numbers of shearwaters behind the vessel, with increasing distance from Lord Howe Island, with decreasing numbers of petrels behind the vessel and with increasing latitude. Latitude had the strongest effect on the number of shearwaters staying, while the number of petrels had the least influence (Table 4.2).

Model fitting

Initially, the data were modelled using Equation 3 (with binomial departures and Poisson arrivals). The best model using this structure was with departures affected by sea surface height and bathymetric gradient, and arrivals were affected by the wind strength (Table

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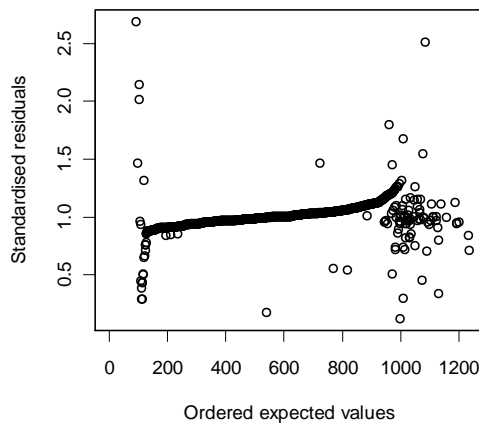
4.3a). The residuals of this model departed by up to 5.5 times the standard deviation, indicating over dispersion in the data relative to the model. Therefore we changed the model to have a more complex variance structure, by using negative binomial and beta binomial distributions for the arrival and departure components, respectively.

Table 4.2. Best model of departure data for individual shearwaters behind fishing vessels during one-minute observations.

Coefficients	Estimate	Std. Error	z value	p
Intercept	3.36	0.55	6.14	<0.00
Shearwater	2.17	0.96	2.25	0.02
Latitude	-3.46	1.62	-2.14	0.03
Petrel	-1.35	0.47	-2.85	<0.00
Distance	2.67	1.36	1.96	0.05

The model developed from Equation 5 (with negative binomial and beta binomial distributions) showed residuals that departed by up to 2.6 times the standard deviation, indicating that this model represented the data more satisfactorily than the simpler model (Fig 4.5a). The standardised residuals of this model were also much lower than those in the GLM used for this data in Chapter 3 (Fig 4.5b).

a.



b.

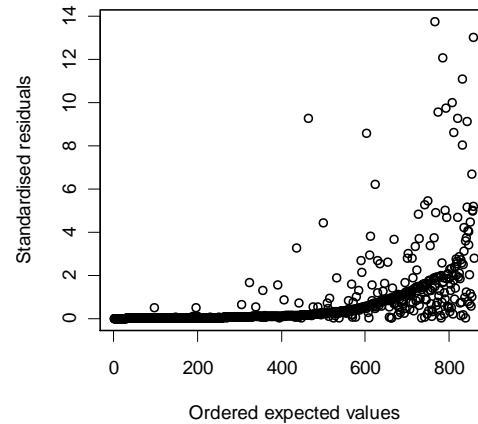


Fig. 4.5. Comparison of residuals of observer data when modelled using multi-component arrivals/departures model, and a GLM. (a). Residuals of best beta-binomial/negative binomial model over the ordered ranking of the expected values. (b). Residuals of expected values from GLM model of observer data from Chapter 3 over the ordered ranking of the expected values.

A number of environmental effects were identified as significant in their effect on the mean of the arrival and departure distributions. Birds were more likely to leave with increasing distance from the previous fishing location, with increasing latitude, and with increasing amounts of fish caught on the previous shot (Table 4.3b). They were more likely to arrive with increasing changes in bathymetry and with high or low sea surface altimetry (suggesting eddies).

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Table 4.3a. Two best models for binomial and Poisson model (Equation 3). Model 1 with slightly lower AICc.

	Model 1		Model 2	
Variable	Coefficient	s.d.	Coefficient	s.d.
Wind	0.2893	0.0280	0.2813	0.0282
Altimetry	0.0680	0.0129	0.0590	0.0131
ChangeInBathy			1.94×10^{-5}	3.31×10^{-5}
AICc	-65190		-65188	

Table 4.3b. Two best models, with variables and coefficients for beta-binomial and negative binomial model (Equation 5). Model 2 with lower AICc.

	Model 1		Model 2	
Variable	Coefficient	s.d.	Coefficient	s.d.
ChangeInBathy	1.02×10^{-4}	5.21×10^{-5}	2.86×10^{-4}	5.01×10^{-5}
Altimetry			22.76	2.39
Altimetry ²			7.79	40.23
Size	1.58×10^{-2}	9.67×10^{-4}	2.27×10^{-2}	1.56×10^{-3}
DistToPrev	89.25	8.62	87.92	23.04
Latitude	121.24	11.72	119.98	31.82
Fish	88.51	8.48	88.73	23.48
Shape 1	0.4234	0.4915	0.4233	0.4921
Shape 2	0.5627	0.4939	0.5619	0.4945
AICc	-3527		-3536	

Importantly, the departure distribution also includes an estimated second free parameter. This parameter controls the shape of the beta distribution in the beta-binomial, allowing the probability of the binomial to range from a symmetric uni-modal distribution through a skewed distribution to a bimodal distribution (Bolker 2008). Each shape parameter

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estimated in this model indicated a bimodal distribution, suggesting in this data there are excess zero counts, and excess large counts. This bi-modality cannot be represented in structurally less complex models. The areas where the largest deviations occurred were to the southwest of Lord Howe Island, and off the coast of Eastern Australia near 30°S (Fig 4.6).

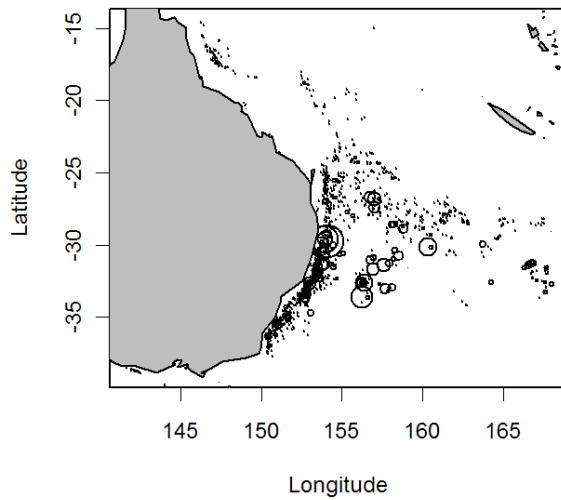


Fig 4.6. Distribution of standardized residuals (increasing size with increasing residuals).

DISCUSSION

A great deal of information about the distribution and abundance of seabirds is collected by fisheries observers during observations of fisheries operations. These are generally analysed at only the most basic level, indicating areas with increased numbers of birds around fishing vessels. These data have been regarded as a biased measure of seabird distribution and unable to be used for more complex analyses such as quantifying habitat associations (Camphuysen et al. 2004). Nevertheless Chapter 3 showed that if carefully chosen questions were asked, fisheries observer data could be used to usefully describe the habitat associations of the species. Taking account of the vessel's changing effect further improves this in terms of understanding relative abundance.

Many studies have shown that ecosystems operate over a range of scales (Wiens 1989, Schneider 2001). Foraging by seabirds is an example of a process operating at multiple scales in this fashion. At meso scales, breeding seabirds are constrained in how far they move from colonies due to the requirement to regularly feed their chicks, thereby determining the overall distribution of the birds. But within this larger scale, they will also respond to smaller scale features, for example when locating areas to forage. Areas in which they feed will be determined by local ecological processes such as up-wellings at the edges of eddies. While they may overall have a limited area in which to feed, they actually only use a subset of that and forage in suitable habitat. Therefore it is invaluable to consider a range of scales. Thus raw counts of seabirds behind fishing vessels can be used for looking at the distribution of interactions, but with relative counts it is possible we can look at habitat selection.

Animal survey data are often derived as a series of counts that are potentially autocorrelated. Autocorrelation may come from a number of sources, commonly in ecology it may derive from patchy distributions, however it may also be a result of successive counts along a spatial or temporal transect (Schneider 1990, 2001). A patchy distribution may result in an uneven spread of some feature of an area being studied, while spatial or temporal transects may be autocorrelated through the animal being

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studied following the studier from count to count. This is often dealt with by considering the variance structure, or not using some of the data (Bolker 2008). In this paper a multi-component arrivals/departures (AD) model was used to examine the second source of the autocorrelation. The study demonstrates that application of appropriate statistical methods applied to the complete data sets can provide new insights into the relationships between successive counts that otherwise would be treated as noise and discarded. This allows the study of the biology and oceanography of these successive counts to be captured.

The AD model accurately retrieved simulated data and gave a more accurate retrieval from simulated data than using a GLM. This is not unexpected, as the simulated data were generated using an arrivals/departures process that was more similar to the process used in the AD model. Evaluating the fit of the model to field data, residuals derived for the AD model were lower than those from a single component GLM when fitted to observer data. This is a useful validation of our model, as it is not a foregone conclusion that the AD model would provide a better fit. In addition to giving a better fit, the AD model is a more accurate representation of the hypothesized process that is occurring (*i.e.* birds are arriving and departing). While the model is still a simplification, it allows the introduction of such features as the bimodal shapes of departures. Simpler models, such as single component GLMs do not allow this. At some point adding further complexity in a model no longer adds greater fit. The bi-modal nature of the model here may suggest that there are two processes operating (such as a factor with two states), but which the model and data set do not have any information on that would allow the inclusion of an extra co-variate.

The model will work for counts that follow on from previous counts; however in its current form it cannot be used for the initial count during a cruise. This is because the initial count will relate to a somewhat different process. For the first count, birds will join the vessel from there being none present, and this relates to the water in between the port the vessel leaves from, until it gets to the site of the initial count, and will need to take into consideration all water masses that are crossed in between these positions. In

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addition, the first count will be a result of a cumulative process over a few days as vessels often steam for some time before fishing. Nevertheless, there will be times when the initial count could be fit into this model. Potentially this could be added by fitting the first count with a distribution such as a Poisson or negative binomial and parameters such as distance from port. It could then be fitted to the overall model with a joint likelihood. However, it is unclear whether this would lead to extracting more information on habitat associations, as this would be determined by the information content in the first counts versus the similarity of the underlying process to the other processes being modeled.

Most previous studies using data collected by fisheries observers have addressed broad scale, such as identifying the large scale distribution of seabirds (e.g. Otley et al. 2007; Chapter 3). However, by using single component models these investigations confound factors driving distributions at large and small scales. This study quantified the finer (coarse) scale environmental features of the distribution. The models indicated five influential factors.

Shearwaters were predicted to be more likely to leave the fishing boat with increasing distance between shots. This may be interpreted either as indicating the birds are less likely to stay with a vessel with increasing movements between fishing activities, which is akin to increasing distances between patches from an optimal foraging perspective (Charnov 1976). This is suggesting an energetic consideration for the shearwater. Alternatively, it may indicate that with increasing distance the vessel was more likely to have moved from an area the shearwater was feeding in to an area that the shearwater was less likely to feed in, suggesting a habitat-related cue.

Also important was increasing latitude, with shearwaters leaving as the vessel moved further north. This suggests that the vessel was moving into less suitable habitat the further north it travelled.

The magnitude of the catch on the previous shot was important, with shearwaters more likely to leave with greater catch, suggesting they had eaten sufficient food and hence left

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the vessel and returned to their colony, or alternatively, that the vessel had been operating in a productive area (hence the large catch) but that it had moved into areas that were less favourable to the shearwaters. Returning to the colony would be an energetic cue for the shearwater, while the alternative would suggest the vessel had left the suitable habitat.

Shearwaters arrived behind vessels more often with increasing (and an increasing change in) bathymetry. They were also more likely to arrive with the absolute depth being shallower, though the addition of this variable made the model worse. The shearwaters were therefore more likely to arrive behind vessels as the vessel moved into shallower water, such as if it moved onto a shelf or sea mount, but at the edge of the bathymetric feature. Shelf breaks have been demonstrated to be productive and attractive to seabirds (Haney 1986; Alderman et al. 2010).

Shearwaters were predicted to be more likely to arrive with high or low sea surface height. This suggests they were more likely to arrive when vessels are at eddies. Eddies generally have up-wellings and down-wellings, and so are particularly productive, and hence more likely to have food. Seabirds generally are thought to concentrate in these areas naturally (Haney 1986; Pinaud and Weimerskirch 2005), suggesting that the shearwaters are arriving behind the vessels because they are operating in areas that are good habitat.

Overall from the models, it is apparent that the shearwaters were more likely to attend vessels with increasingly productive areas (increased catch, eddies, shelf breaks) and with energetic considerations (departing with increasing distance from the previous shot). The oceanographic co-variables suggest that shearwaters were attending fishing vessels dependent on up-wellings or down-wellings, or the edges of bathymetric features, all of which are likely to be associated with eddy features. In the Baltic Sea, seabirds only attended fishing vessels which were operating in conditions with high productivity, but generally ignored vessels discharging fish when in unproductive waters (Skov and Durinck 2001). Elsewhere, in New Zealand Westland petrels *Procellaria westlandica* only foraged around fishing vessels that were operating in the areas that the petrels

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naturally feed (Freeman 1997). Attendance at fishing vessels by seabirds is therefore a local effect, though the size of this may differ depending on the mobility of the species. Attendance may only be initiated if the vessel is in a chosen foraging zone, but once one seabird has commenced attendance, it may act to attract many other seabirds from an area around due to flocking behaviour. The overdispersed residuals in the model may suggest flocking, which can be a useful method for foragers to pass information to each other in a patchy environment (Clark and Mangel 1984).

This study has demonstrated the utility of the AD modelling approach in analysing fisheries observer data of succeeding counts of seabirds, but can be applied more generally where there is a series of counts of populations but not of identifiable individuals. Commonly, there is autocorrelation due to the carrying over of individuals in time or space, such as for seedlings in forest quadrats or changes between locations of spotlight surveys of mammals (e.g. Harms et al. 2001; Caley and Morley 2002). The AD model may be particularly useful in situations where this carry over is thought to have some ecologically meaning information. For the seabirds the counts in sequential positions were related but changed due to the underlying oceanographic conditions. This may be equally relevant in spotlight surveys of mammals, though perhaps less so in seedling quadrats. Only a small amount of extra information is required due to the data being ill-determined. But it is relatively easy to get the data on the departures, and that sort of data is likely to be obtainable in other situations if a small amount of time is dedicated to it.

ACKNOWLEDGEMENTS

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5. The importance of recent experience and environment in determining large scale foraging patterns in a pelagic seabirds, the flesh-footed shearwater.

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ABSTRACT

We hypothesized that marine predators should take advantage of previous experience in locating foraging areas. Using experience of previous foraging areas is likely to increase foraging efficiency and increase the effectiveness of search methods such as area-restricted search or Lévy flights by locating the better areas initially, thereby reducing the subsequent search effort. At a coarse scale, for each visit to an area by a flesh-footed shearwater during the current trip, the odds of visiting the same area increased by between 5-531%, for each visit in the previous trip the odds of returning in the current trip increased by between 2-46% and for each visit in the second last trip, by between 4-25%. Using the length of time spent in an area as a proportion of previous trips as a proxy for quality of foraging in that area, we also identified a strong effect on the probability that birds chose to visit high quality locations on future trips. At the coarse scale, they were more likely to choose to visit an area with increasing Sea Surface Height Anomaly, while during incubation they chose to visit areas with increasing Sea Surface Temperature, but decreasing during chick-rearing. They were less likely to visit an area with increasing Chlorophyll-a. At the coarse scale, the use of experience was at least as important as any of the oceanographic variables tested.

Keywords: flesh-footed shearwater, Lord Howe Island, foraging, experience, memory, choice, Discrete Choice Model

INTRODUCTION

Pelagic marine predators live in an environment with patchily distributed resources, which presents challenges for them obtaining energy at sea (Weimerskirch 2007). Marine predators using the pelagic environment are characterised by foraging over large distances to encounter these dispersed resources (Jouventin and Weimerskirch 1990, Prince et al. 1992; Weimerskirch et al. 1999; Hindell et al. 2003; Phillips et al. 2006). This results in a relatively slow uptake of energy and leads to them having specialised breeding system such as low productivity and high investment in adult survival (Weimerskirch et al. 1987; Hindell 1991, Bradley et al. 2008). Many species, such as seabirds or seals, produce only a single young each year, and while survival of this offspring to breeding age is relatively low, once they reach breeding age, survival is high. In this context one would expect animals to adopt behaviours that maximize their encounter rate with ephemeral resource patches. Two possible mechanisms for achieving this end are utilization of efficient search methods and use of information from experience.

There is only limited information on the strategies they may employ to find these patchily distributed resources (Weimerskirch et al. 2005). Physical processes such as currents and their interactions with bathymetry are known to affect the distribution of plankton (Hunt et al. 1996). Seabirds, marine mammals and fish have all been shown to respond to such areas as fronts, shelf edges and up-wellings where productivity and prey are likely to be concentrated (Hunt et al. 1996; Young et al. 2001; Call et al. 2008). Several strategies could improve encounter rates with patchy resources; four are proposed here with increasingly complex use of information: i) use of search algorithms; ii) use of environmental cues; iii) previous experience of static features; and iv) previous experience of dynamic features.

Marine predators have been suggested to use efficient search methods for locating food resources, such as area restricted search, correlated random walks, Lévy flights and fractal patterns (Viswanathan et al. 1996; Fauchald and Tveraa 2003; Tremblay et al. 2007). While these methods decrease search times, they do not utilize information, and as

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such are unlikely to be employed in isolation of other sources of information. The use of environmental cues will provide better informed searches, but is only useful when the cue is present in real time. At meso- and sub-mesoscales (<10 km), seabirds find productive areas through smell or observing other predators (Au and Pitman 1986; Haney et al. 1992; Nevitt et al. 2008; Tew Kai et al. 2009).

Some predators return to approximately similar areas on consecutive foraging trips (Bradshaw et al. 2004; Weimerskirch et al. 2005). This provides qualitative evidence for the use of experience or inheriting, although it is static experience in the sense that once a pattern is learned it does not need to change (Weimerskirch 2007; Call et al. 2008). The most complex use of memory in foraging is dynamic memory, where areas of high quality habitat are remembered from past experience, but the interpretation of that information changes with time. One example would be discounting of information with time, such that the most recent experience is given the highest weight in predicting suitable areas in which to forage. Learning is useful if it enhances the long term fitness of an animal through behavioural changes, such as providing flexible search strategies when the environment shows temporal change (Eliassen et al. 2007, 2009). If variability is spatial, but does not vary over time, it is less important to be able to learn rapidly or forget the distant past (Mangel 1990; Eliassen et al. 2009). Learning is more useful with increasing life span (Eliassen et al. 2007).

Many marine predators are central place foragers, and thus their use of search tactics is constrained by the need to return to their breeding sites on a regular basis (Ashmole 1971). For seabirds there is a further restriction with differing behaviour during the breeding season due to whether they have eggs or chicks. When incubating eggs, the parents alternate at sea for relatively long trips. Since these foraging bouts have a fixed length, we hypothesize that the foragers will concentrate primarily on increasing their reserves by maximizing the net energy gain during their foraging bout. However, when they are on chicks (especially newly hatched) the condition of the chick declines the longer the foraging parent is away, thus we expect the forager to maximize the rate of energy uptake by the chick, instead of the net amount going to the forager. We expect

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that this difference will constrain the parent's ability to explore for new information during chick rearing, and leading birds to prefer reliable areas they have successfully foraged in previously. This preference would be expected to increase the importance of experience, and should be visible in their foraging patterns.

In this study we explore the importance of experience, and its impact relative to other environmental cues on foraging by flesh-footed shearwaters, *Puffinus carneipes*, nesting on Lord Howe Island. We address four questions in relation to the foraging of flesh-footed shearwaters: i) do they return to similar areas to those they have previously visited; ii) how does past success in the area affect this decision; iii) are they more likely to visit areas due to experience, or due to measured environmental variables; and iv) is the initial position after leaving the colony chosen differently from later positions.

METHODS

Study site and species

Flesh-footed shearwaters are a medium sized shearwater that breed on a number of islands, including Lord Howe Island in the Tasman Sea ($31^{\circ}30'S$ $159^{\circ}05'E$) (Marchant and Higgins 1990). They breed annually in the austral summer. They forage throughout the Tasman Sea in an area of temperate waters with complex bathymetry (shelf breaks off the east coast of Australia, and the Lord Howe Island Rise passing north/south through the Tasman Sea) and oceanography (East Australia Current, Tasman Front) and areas of varying productivity (Ridgway and Dunn 2003; Thalmann et al. 2009). The EAC is a western boundary current generating many large eddies which spin off past Lord Howe Island to form the Tasman Front (Ridgway and Dunn 2003).

Archival tag deployments

Light based geo-location data were obtained during the breeding season at Lord Howe Island during four summers (2004/5 ($n=23$), 2006/7 ($n=7$), 2007/8 ($n=13$) and 2008/9 ($n=2$)) (Table 5.1). Three 30 day deployments (early January-late January, late January-late February, and late February to mid April) were made during the summer of 2004/5. During the summers of 2006 and 2007, archival tags were attached in late October and retrieved during Chick-rearing (early February to mid April). Two archival tags deployed for the winter of 2008 were retrieved in March 2009, and so were used to provide locations for that summer. Two types of archival tags were used, LTD 2400 from Lotek (St Johns, Newfoundland) were used in the first three seasons, and Mk7 Global Location Sensing (GLS) loggers manufactured by the British Antarctic Survey (Cambridge) were used in the last two seasons. Archival tags were attached to the left leg of each shearwater using a 25 mm Velcro strip. Mk7 GLS loggers and their attachment weighed 5.1g, while the LTD 2400 and their attachment weighed 7.1g.

The LTD 2400 loggers recorded light levels, temperature and pressure (depth) every two seconds. The temperature sensor has a resolution of $0.05^{\circ}C$ and accuracy of $\pm 0.1^{\circ}C$.

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The Mk7 GLS loggers recorded light levels every minute and at the end of every ten minute period the maximum light level was recorded. Additionally, every three seconds the logger measured saltwater immersion. The number of these immersions was recorded every ten minutes (hence a range from 0 (fully dry) to 200 (fully wet)). The temperature sensor of these loggers takes ten minutes to stabilize, so temperatures were recorded after 20 minutes of continuous immersion. To conserve memory, another record was only taken after a subsequent dry event followed by a further 20 minutes of continuous immersion. Shearwaters rest on the water for a number of hours each night and hence most records of water temperature were taken in the hours of darkness. The sensor has a resolution of 0.625°C and an accuracy of $\pm 0.5^{\circ}\text{C}$.

Table 5.1. Summary of numbers of estimated positions for each year and month for four summers. During 2004, loggers were deployed and retrieved three times during the summer; in the other years, they were deployed early (October) and retrieved later during the year. Year is the first year of the season (i.e. 2004 = 2004/2005).

Year	2004	2006	2007	2008
Birds	23	7	13	2
Season				
Incubation	125	365	1026	307
Chick-rearing	248	8	425	47

The archival tags' record light levels at regular intervals, and this is used to estimate positions at each twilight (Sumner et al. 2009). Archival tags were turned on and exposed to the sky for 2-7 days before and after deployment. This serves to ground truth the loggers, as having known positions at the start and end of deployments assisted with the accuracy of positions estimated from the archival tags. Temperature recorded by each logger was calibrated by taking readings of known temperatures in a salt water bath.

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During 2007 and 2008 chicks of parents with archival tags, and chicks of parents without archival tags were weighed during mid-April; no differences were detected in weights (mean (g) (\pm standard error): with archival tags 706 ± 60 (n=15); without archival tags 695 ± 27 (n=74); $F_{1,67} = 0.0325$, $p = 0.86$).

Estimation of at-sea movements

At-sea movements were estimated using a Bayesian approach with a Markov Chain Monte Carlo method to approximate the posterior using the tripEstimation (version 0.0-24) package for the R statistical language (R Development Core Team 2009; Sumner et al. 2009). Initial positions were estimated from light intensities during twilight periods enabling two positions to be estimated each day (Sumner et al. 2009). The track developed this way can be considered as part of a state-space model, where there are incomplete observations of the system (here the positions recorded by the loggers), from which the “real” positions can be estimated by combining this initial position with other sources of information, including the presence or absence of land, sea surface temperature (SST) and knowledge of the shearwater’s distribution of likely speeds (Reid, unpublished data) to find a posterior track (Patterson et al. 2008; Sumner et al. 2009; Thiebot and Pinaud 2010). A burn-in period of 10,000 was used, followed by running a chain with 20,000 samples. An estimate of the position at each twilight was thus derived. Trips by a bird had to last for at least four days in order for a track to be derived. Hence, only trips of at least four days were used in analysis in this paper.

Sea surface temperature recorded at night by the logger was compared to weekly averaged 1x1 degree NCEP Reynolds Optimally Interpolated SST (Reynolds and Smith 1994). Locations were accepted when they were within the band between the maximum temperature recorded plus 2°C and the minimum temperature minus 2°C. Using a temperature band this wide meant that the derivation of positions was most heavily weighted from the light readings, but were restricted to a longitudinal band encompassing the Tasman Sea.

Data analysis

Kernel analysis

Two daily posterior positions were derived from tripEstimation, giving an even temporal spread to positions, and making them suited to Kernel density analysis. A two-dimensional binned kernel density estimate was used to identify areas of peak activity each breeding season (Eonfusion V2.0, Myriax 2009). This creates a grid with a matrix of density estimates. The kernel used a standard bi-variate normal density. In presenting the kernel plots, all records of flesh-footed shearwaters from a one-degree square around Lord Howe Island were excluded, as the high density of locations associated with departure and arrival at the colony obscured patterns of distribution elsewhere in the distributions.

Speed and distance from Lord Howe Island were calculated for each estimated position and summarised for each year and season. To test for seasonal or annual variation, these were tested using a linear mixed model using the package nlme (version 3.1-91) from the R statistical software (R Development Core Team 2009). Year and season were treated as fixed effects and bird and trip were treated as random effects. For both speed and distance it was necessary to perform a log-normal model to improve residuals.

Discrete Choice Models

Discrete choice models (DCM) describe a decision maker's choice among alternatives (Train 2003). Three attributes are required in a discrete choice framework; (i) the choices must be mutually exclusive, (ii) once one is chosen, it is implied that no others are made, and (iii) there is a finite number of alternative choices (Train 2003). In this framework, a causal perspective is taken, such that the decision maker's choice is determined, or caused, by a number of factors. Some of these factors are observed, and others are not. Because some factors are not observed, the model is not deterministic, and so there is a probability for any particular outcome (Train 2003).

Logit models, such as the multinomial logit model, are by far the most commonly used method in DCMs (Train 2003). This requires the choices to have independence of

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irrelevant alternatives, such that unobserved factors are uncorrelated over alternatives, and that they have the same variance over all alternatives, which while restrictive, can be interpreted as the outcome of a well-specified model (Train 2003). Under the assumption of independence, the error for one alternative supplies no information to the researcher about the error for another alternative (Train 2003). There is no clear reason to expect the spatial grids used in this study to be correlated other than in the ways applied in the model, and so a multinomial logit model is appropriate in this situation.

Using multiple decision makers (individual birds) adds complexity to the modelling, as each shearwater will have correlated errors (Pinheiro and Bates 2000; Bolker 2008). To combine this requirement with a multinomial logit model, a generalized linear mixed model is required (Bolker 2008).

A Discrete Choice Model was applied to the estimated tracks of the breeding flesh-footed shearwaters to identify factors that predict the areas in which they chose to forage. A grid of 1x1 degree blocks were drawn over the area of foraging. This grid size was used as a reasonable compromise between increasing the number of grid cells and hence the fineness of scale, and decreasing the potential for successive visits to a grid either by this or other shearwaters. It was hypothesized that a shearwater's decision to visit any block was influenced by a combination of oceanographic features and the shearwater's experience of locations where it had previously foraged.

Co-variates used in the model were chosen because they were considered either to relate to environmental cues (oceanographic or environmental co-variates), or because they related to the shearwaters previous experience (Table 5.2). Oceanographic and environmental co-variates were chosen that had been influential in previous models of the distribution of flesh-footed shearwaters (Chapter 3). The co-variates that were used in this paper are listed in Table 5.2. Environmental co-variate data were obtained from a number of sources using the SDODE interface (Table 5.3) (Hobday et al. 2006). Bathymetric data (*Bathy*) was obtained from 2-minute Gridded Global Relief Data from the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National

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Geophysical Data Center, 2006 (<http://www.ngdc.noaa.gov/mgg/fliers/06mgg01.html>).

Sea Surface Temperature (*SST*) was a CSIRO 6 day composite, with accuracy to

$0.036 \times 0.042^\circ$. Sea Surface Height anomaly (*SeaHeightAnom*) is a synTS CSIRO product

(<http://www.marine.csiro.au/dods-data/bluelink/synTS/>) produced and maintained by M.

Cahill. Chlorophyll A data (*ChlA*) was obtained every 7.7 days at $0.0833 \times 0.0833^\circ$ from

Seawifs (<http://seawifs.gsfc.nasa.gov/SEAWIFS>). Frontal density (*Front*) was obtained

every 7.94 days with $0.25 \times 0.25^\circ$ accuracy from CSIRO (J. Hartog and A. Hobday

unpublished). Distance (*Distance*) was calculated as the great circle distance of the centre of a block from Lord Howe Island.

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Table 5.2. Variables used in this study and hypothesized effect upon flesh-footed shearwater foraging, whether it relates to the food obtained during a trip, or the time spent away from the nest.

	Time	Food
Initial position	Memory -visit on previous trip -visit on second last trip -length of previous trip Environmental -distance from LHI	Memory -success on previous trip Environmental -bathymetry -Sea Height -SST -ChlA -Front
Rest of trip	Memory -visit on this trip/time spent -visit on previous trip -visit on second last trip -presence of other shearwaters -time away from LHI -length of previous trip Environmental -distance from LHI	Memory -success on previous trip Environmental -bathymetry -Sea Height -SST -ChlA -Front

A number of co-variates that related to the shearwaters and their foraging experience were also considered (Table 5.3). These were (i) whether a block had been visited previously by the shearwater, either in the current trip or in either of the previous two long trips, (ii) trip duration of the previous trip (relative to the maximum trip length in

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any month, hence the greater the value, the shorter the trip), (iii) the length of time the current trip had been going for, and (iv) whether other tracked shearwaters were in a square at the time. Only one interaction was deemed likely to be influential, that between how early the shearwater had returned on the previous trip and how long it spent in a square on that previous trip. The interpretation of this variable is that if a bird returns early, having visited a grid square, it is an indication that the bird was more successful at foraging in that grid square relative to other locations.

Table 5.3. Names and description of variables used for modelling.

Variable	Memory/Environment	
Visits	Experience	Number of visits to a location on current trip before the current time
Distance	Environment/Experience	Distance of centre of degree square from Lord Howe Island (100 km)
Previous1	Experience	Number of visits to a location on last long trip
TripDuration	Experience	Difference between length of the previous trip and the maximum length of trip in current month
Previous2	Experience	Number of visits to a location on second last long trip
GLS		Number of shearwaters with loggers in the current degree square
Time	Experience	Time away from Lord Howe Island.
ChlA	Environment	
SST	Environment	Sea Surface Temperature (°C).
SeaHeightAnom	Environment	Measure of sea height relative to the mean sea height.
Front	Environment	Frontal density
Bathymetry	Environment	m

Two random effects were included in the models, bird, relating to each individual bird, and trip, relating to each trip made by an individual bird (Pinheiro and Bates 2000).

During incubation, shearwaters made longer trips, whereas while attending chicks, shearwaters need to return to the colony regularly to feed the chick, and so made shorter trips (Table 5.4), hence separate models were developed for Incubation and Chick-rearing periods. Flesh-footed shearwater chicks hatch in late January (Priddel et al. 2006), and so 1 February was used as the time for defining two seasons, Incubation and Chick-rearing.

Table 5.4. Length (in days) of trips during each month through breeding season.

Trip length	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+	Total
Incubation	80	21	15	6	6	10	6	13	10	10	13	7	4	5	19	225
Chick-rearing	115	14	9	20	11	14	7	4	3	1	0	0	0	3	1	202
Total	195	35	24	26	17	24	13	17	13	11	13	7	4	8	20	

When departing from the colony, shearwaters were following different cues, and so the first observation on leaving was modelled separately from subsequent positions. The first position relates to how the shearwaters expend energy in order to move to the foraging region.

Modelling was performed using the MCMCglmm package (version 1.09) (Hadfield 2010) in the R statistical software (version 2.9.0; R Development Core Team 2009). Models were performed for each year and season due to computational memory limitations. No model selection methods were used to reduce the number of variables in models, instead less important variables will have distributions for their coefficients that are increasingly centred on zero (Bolker 2008)

RESULTS

During all four summers, flesh-footed shearwaters foraged predominantly to the west of Lord Howe Island, as far as the east coast of Australia, with most sightings between Fraser Island (25°15'S 153°10'E) and Sydney (33°53'S 151°10'E) (Fig. 5.1). Greatest densities were close to Lord Howe Island, with very few records over the Lord Howe Rise. One bird made two long trips north to near the Solomon Islands during Incubation 2006 (Fig 5.1a). In all summers concentrations were further north during Incubation than Chick-rearing (Fig 5.2). While birds were generally spread over deep water between the Lord Howe Ridge and the east coast of Australia (the Tasman Basin), there were concentrations along the western edge of the Lord Howe Rise where there are a number of seamounts and ridges such as the Dampier Ridge and the Lord Howe Sea Mount Chain (Fig 5.2) This is the general area that the Tasman Front would first strike the Lord Howe Rise. Birds would be expected to move to areas with potentially increased productivity in a patchy environment; the location of the Australian shelf break, the Lord Howe Rise and sea mounts will be predictable and may have increased productivity, while the Tasman Front striking the Lord Howe Rise is likely to cause up-wellings, though the Tasman Front will move north and south depending on such factors as the time of year. Eddies at the edges of fronts will be most productive, but least predictable.

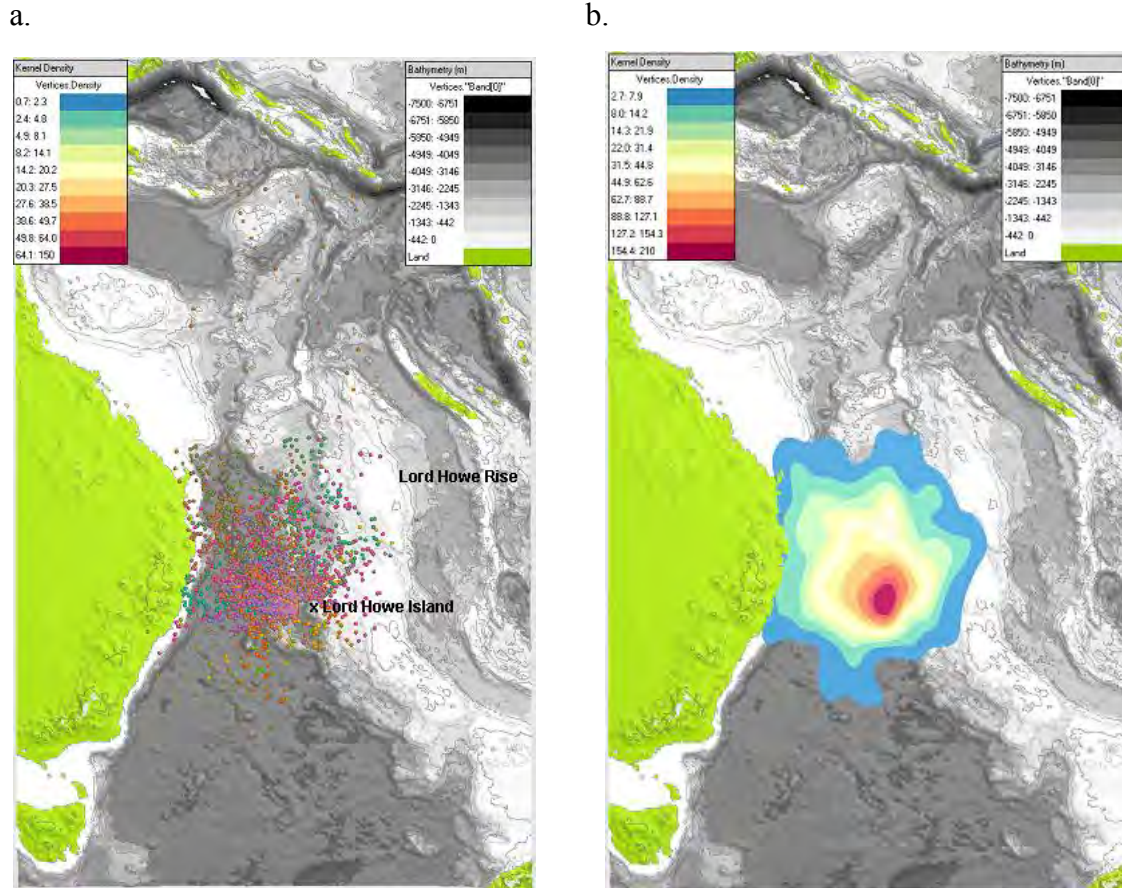
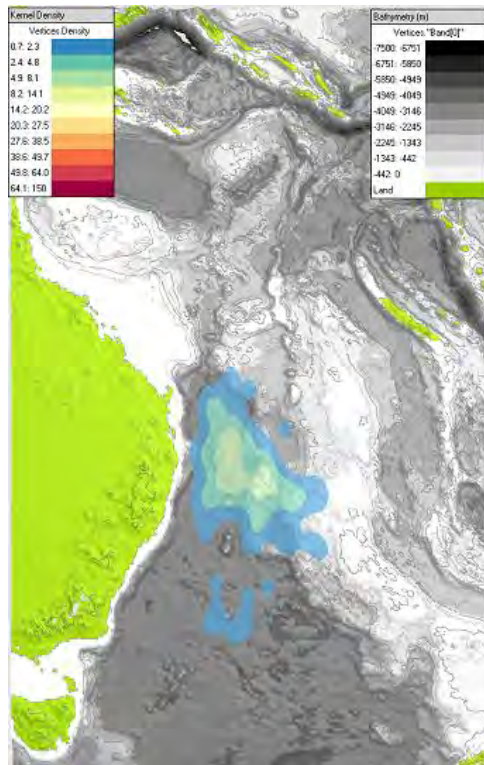


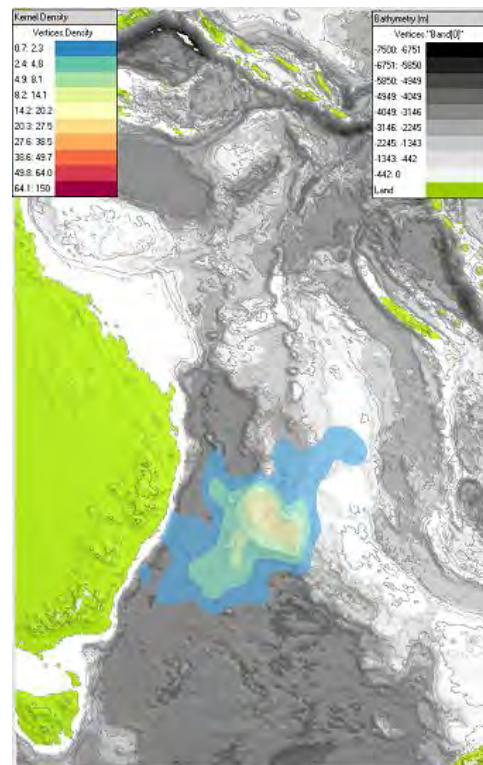
Fig 5.1 Distribution of all estimated positions of flesh-footed shearwaters during four breeding seasons (2004/5, 2006/7, 2007/8 and 2008/9) (a). Twilight positions of all archival tags in four summers. (b). Kernel density plot of all positions of flesh-footed shearwaters from all summers.

Mean travel speeds varied between years, but not between seasons (Fig. 5.3; Table 5.5). Mean distances that birds travelled from Lord Howe Island also varied within and between years, with birds travelling significantly further from the island during Incubation than during Chick-rearing period (Fig. 5.4; Table 5.6). Trips were also longer during the Incubation period than the Chick-rearing period, with most trips being less than seven days long (Table 5.4). The variance of trip lengths was also greater during the Incubation period (Table 5.4).

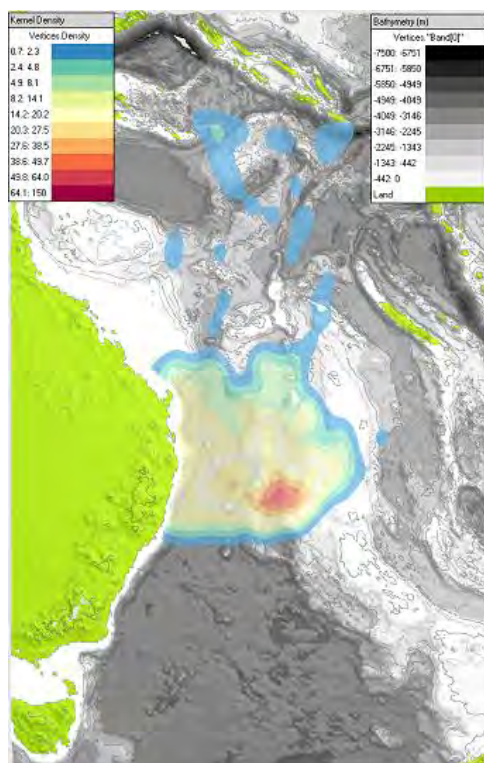
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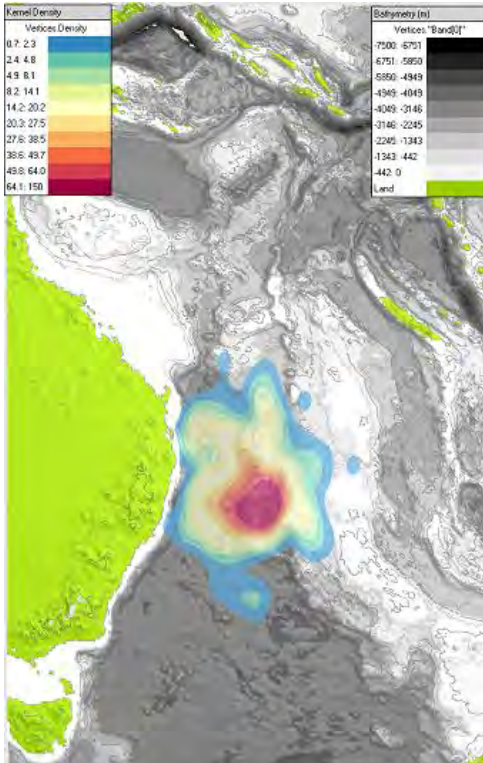
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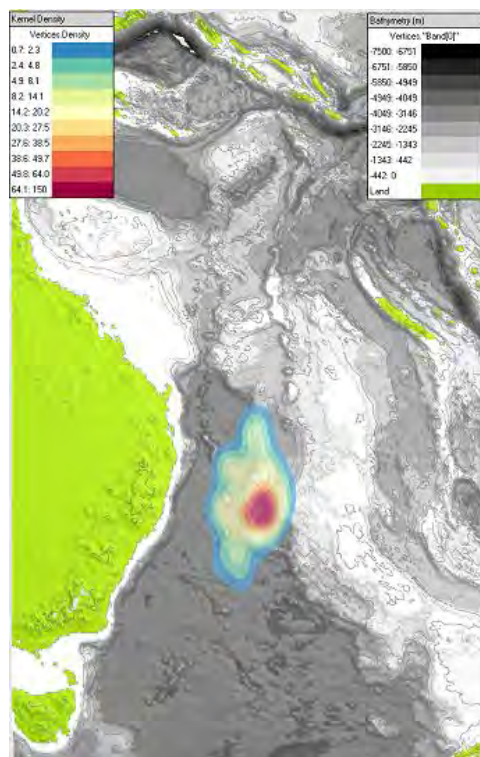


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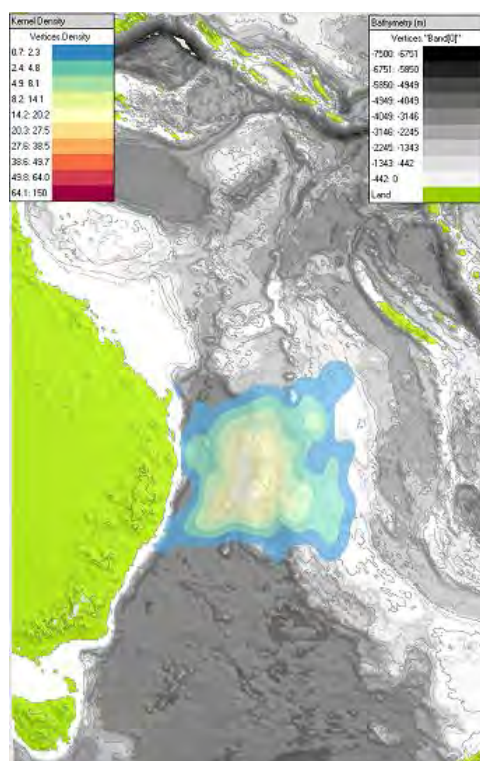


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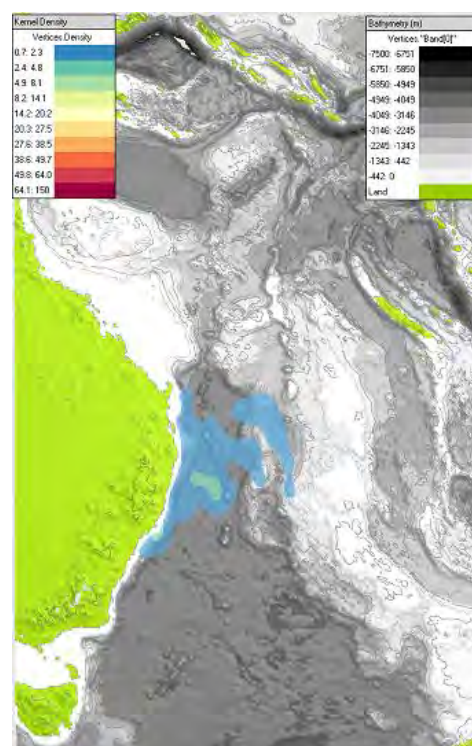
e.



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g.



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Fig 5.2. Kernel density plots of distributions of flesh-footed shearwaters during each year and season between 2004-2008. (Years aligned horizontally, seasons aligned vertically (Incubation then Chick-rearing). (a). Incubation 2004. (b). Chick-rearing 2004. (c). Incubation 2006. (d). Incubation 2007. (e). Chick-rearing 2007. (f). Incubation 2008. (g). Chick-rearing 2008.

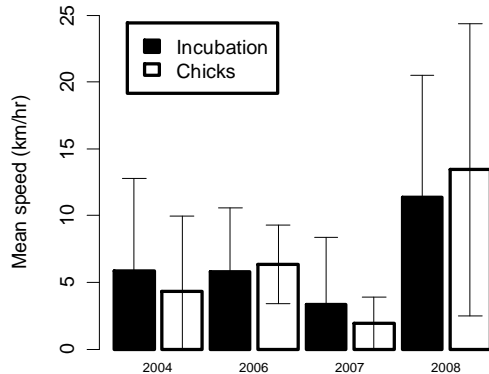


Fig 5.3. Mean (± 1 standard deviation) observed speed (km hr^{-1}) of flesh-footed shearwaters for each year and season for long trips (>4 days).

Table 5.5. Fixed terms for speed (km/hr with log transformation) for different years and two seasons (Intercept term for Chick-rearing in 2004). Random terms for model were bird and trip.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.46	0.10	2894	14.86	<0.01
Year 2006	0.19	0.18	38	1.08	0.29
Year 2007	-0.33	0.15	38	-2.18	0.04
Year 2008	0.79	0.29	38	2.70	0.01
Incubation	0.00	0.05	2894	-0.05	0.96

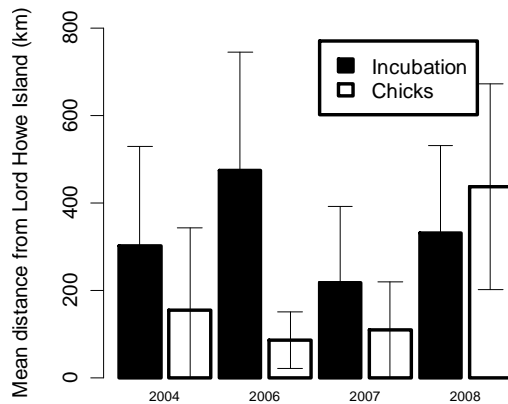


Fig 5.4. Mean (± 1 standard deviation) distance (km) of positions from Lord Howe Island during each year and season for long trips (>4 days).

Table 5.6. Fixed terms for distance from Lord Howe Island (km with log transformation) for different years and two seasons (Intercept term for Chick-rearing in 2004). Random terms for model were bird and trip.

	Value	Std.Error	DF	t-value	p-value
Intercept	2.18	0.25	2894	8.59	<0.01
Year 2006	1.20	0.34	38	3.53	<0.01
Year 2007	0.37	0.29	38	1.26	0.22
Year 2008	1.10	0.42	38	2.61	0.01
Incubation	1.21	0.21	2894	5.67	<0.01

Discrete Choice Models

First Position

The first position recorded after leaving Lord Howe Island was more likely to be close to Lord Howe Island (Table 5.7 and 5.8). Initial positions were also influenced by oceanographic variables (Tables 5.7 and 5.8) and were less likely to move initially to areas of high Chlorophyll-a concentration or Frontal Density, and moved to areas of deeper water. Past trips were not found to effect choice of location.

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Table 5.7. Model coefficients for first position after leaving Lord Howe Island for flesh-footed shearwaters during Incubation Period (before 1 February). Highlighted numbers are for those that were significant at a 95% level, as shown by the 2.5-97.5% MCMC confidence limits not including zero.

	2004				2006				2008			
	97.50				2.50 97.50				2.50 97.50			
Coefficients	Mean	SD	2.50%	%	Mean	SD	%	%	Mean	SD	%	%
Intercept	16.4				-				-			
Visits	20.30	3	-11.38	50.70	-0.30	5.13	10.26	9.80	-3.53	7.50	18.25	10.30
Distance	-2.55	0.90	-4.24	-0.86	-1.31	0.57	-2.52	-0.38	0.89	0.91	-0.84	2.73
Distance^2	0.15	0.09	-0.06	0.32	-0.08	0.09	-0.20	0.15	-0.48	0.12	-0.71	-0.28
Previous1	-0.48	3.71	-8.36	6.18	-0.39	0.45	-1.31	0.40	-2.13	1.50	-5.15	0.39
TripDuration	-0.35	0.30	-0.94	0.26	-0.02	0.05	-0.11	0.08	0.00	0.07	-0.13	0.14
Previous2					0.00	0.23	-0.49	0.41	0.55	0.38	-0.25	1.23
GLS	-1.51	1.52	-4.95	0.94	0.25	0.34	-0.48	0.84	33.25	2	68.29	-4.44
Time												
ChIA	90.84	3	0	-21.45	19.57	8	45.15	1.68	22.96	3	43.08	-3.17
SST	-0.52	0.61	-1.59	0.68	-0.03	0.20	-0.40	0.38	-0.10	0.32	-0.72	0.54
SeaHeightAnom	-3.74	3.51	-9.72	3.11	-3.23	2.55	-7.79	1.96	-3.45	3.62	10.09	3.31
Front	-6.30	2.89	-12.28	-1.32	-1.54	0.91	-3.76	-0.01	-1.64	0.90	-3.59	-0.27
Bathymetry(x100)	-0.09	0.00	-0.19	0.01	-0.09	0.02	-0.14	-0.05	-0.57	0.12	-0.81	-0.37
Previous1*TripDuration	-0.07	0.93	-2.32	1.60	0.04	0.03	-0.02	0.11	0.22	0.13	0.00	0.50

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Table 5.8. Model coefficients for first position after leaving Lord Howe Island for flesh-footed shearwaters during the Chick-rearing Period (after 1 February). Highlighted numbers are for those that were significant at a 95% level, as shown by the 2.5-97.5% MCMC confidence limits not including zero.

	2004				2007			
Coefficients	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
Intercept	1.99	14.78	-23.09	29.35	-34.39	21.86	-75.87	9.17
Visits								
Distance	-4.77	0.60	-6.04	-3.55	-9.88	2.35	-14.43	-5.57
Distance^2	0.35	0.10	0.15	0.51	0.82	0.37	0.14	1.50
Previous1	0.44	0.35	-0.18	1.19	0.03	0.22	-0.38	0.47
TripDuration	-0.02	0.16	-0.33	0.30	-0.23	0.17	-0.55	0.09
Previous2	-0.14	0.40	-0.93	0.60	-0.20	0.18	-0.56	0.15
GLS	0.11	0.27	-0.43	0.65	-0.18	0.31	-0.80	0.44
Time								
ChIA	-6.94	8.17	-23.11	8.04				
SST	-0.27	0.60	-1.37	0.74	1.03	0.90	-0.79	2.76
SeaHeightAnom	0.91	2.60	-4.41	5.39	-3.56	3.94	-11.33	3.88
Front	0.41	0.58	-0.83	1.44	-11.39	4.28	-19.53	-3.28
Bathymetry (x100)	-0.24	0.03	-0.30	-0.17	-0.57	0.12	-0.81	-0.37
Previous1*								
TripDuration	-0.06	0.10	-0.25	0.13	0.08	0.04	-0.01	0.16

Subsequent Positions

Shearwaters chose to visit areas they had previously visited on that trip (*Visits*) (odds ratio 105-531% for each extra visit), that they had visited during the previous trip (*Previous1*) (odds ratio 102-146% for each extra visit) and that they had visited two trips prior (*Previous2*) (odds ratio 104-125% for each extra visit) (Tables 5.9 and 5.10). The means of these co-efficients decreased, indicating decreasing importance of prior experience with time. They also chose to visit areas if they had visited an area on the previous trip and that trip had been short, though this was more apparent for the

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Incubation than the Chick-rearing period (*PreviousI*TripDuration*) (Tables 5.9 and 5.10). They were less likely to visit areas the further the area was from Lord Howe Island. They were less likely to visit any areas the longer the trip went, indicating there was some likely maximum to the length of trips. During one of four years in Incubation (Table 5.9) and two of three years in Chick-rearing the number of other shearwaters with loggers (*GLS*) showed a positive relationship with choosing to visit an area, though this included zero (Table 5.10), while in other years and seasons the relationship was centred on zero.

Flesh-footed shearwaters were more likely to visit an area with increasing Sea Height Anomaly (odds ratio 107-191% for each increase of 1 cm) (Tables 5.9 and 5.10). Sea Height Anomaly had a mean of 0.05 cm (s.d. 0.12). During incubation, they were more likely to visit an area with increasing Sea Surface Temperature (odds ratio 103-132% for each 1°C), but less likely to visit in the Chick-rearing period (odds ratio 6-97%). During Incubation they were less likely visit an area with increasing Chlorophyll-a (odds ratio <0.1-1%). Chlorophyll-a had a mean of 0.09 mg m⁻³ (s.d. 0.11). Frontal density showed little pattern.

Comparing the means of the coefficients of the experience and oceanographic variables (Table 9), during Incubation for Sea Height Anomaly, the increase in likelihood of visiting an area was approximately one third for each 1 cm of rise compared to each previous visit, it was also approximately one third for each 1°C rise in Sea Surface Temperature and was approximately 20 times for each fall of 1 mg m⁻³ of Chlorophyll-a. During Chick-rearing (Table 5.10), the increase in likelihood of visiting an area was similar for one visit, an increase of 1 cm of Sea Height Anomaly, a fall of 1°C in Sea Surface Temperature. The mean for Chlorophyll-a for a fall of 1 mg m⁻³ was approximately ten times that for a single visit.

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Table 5.9. Model coefficients for subsequent positions during Incubation Period (before 1 February). Highlighted numbers are for those that were significant at a 95% level, as shown by the 2.5-97.5% MCMC confidence limits not including zero.

	2004				2006				2007				2008			
Coefficients	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
Intercept	-13.47	3.58	-19.72	-5.90	-4.05	0.99	-6.01	-2.15	-7.33	0.73	-8.66	-5.83	-2.06	2.43	-4.88	1.15
Visits	0.98	0.13	0.72	1.23	0.55	0.03	0.50	0.60	0.47	0.02	0.44	0.51	0.66	0.07	0.51	0.81
Distance	-0.74	0.20	-1.13	-0.34	-0.76	0.07	-0.90	-0.62	-1.02	0.08	-1.16	-0.87	-0.21	0.11	-0.41	0.02
Distance^2	0.03	0.02	-0.01	0.07	0.04	0.01	0.03	0.06	0.05	0.01	0.03	0.07	-0.01	0.01	-0.04	0.01
Previous1	-1.34	0.92	-3.26	0.31	0.28	0.05	0.18	0.38	0.08	0.03	0.02	0.15	0.10	0.08	-0.05	0.24
TripDuration	-0.03	0.12	-0.28	0.19	0.01	0.01	-0.01	0.03	-0.01	0.01	-0.02	0.01	-0.01	0.01	-0.04	0.01
Previous2					0.15	0.03	0.09	0.21	0.08	0.02	0.04	0.12	0.11	0.08	-0.04	0.26
GLS	0.48	0.27	-0.05	0.99	-0.04	0.10	-0.23	0.15	0.03	0.06	-0.08	0.14	0.00	0.34	-0.66	0.60
Time	-0.05	0.03	-0.11	0.02	-0.02	0.01	-0.03	-0.01	-0.04	0.00	-0.05	-0.03	-0.02	0.01	-0.03	0.00
ChIA	-2.90	6.71	-16.44	9.70	-9.26	2.42	-13.67	-4.26					-13.88	2.38	-18.76	-8.46
SST	0.38	0.48	-0.55	1.36	0.14	0.06	0.03	0.26	0.17	0.05	0.07	0.28	-0.21	0.08	-0.37	-0.07
SeaHeightAnom	0.41	0.13	0.14	0.65	0.03	0.04	-0.04	0.11	0.13	0.03	0.07	0.19	-0.06	0.04	-0.14	0.03
Front	-0.58	1.01	-2.47	1.43	-2.28	0.53	-3.27	-1.15	2.20	0.30	1.63	2.81	-0.29	0.60	-1.45	0.84
Bathymetry (x100)	-0.03	0.01	-0.06	-0.01	-0.04	0.01	-0.05	-0.03	-0.06	0.00	-0.06	-0.05	-0.03	0.01	-0.04	-0.02
Previous1*																
TripDuration	0.46	0.21	0.05	0.92	-0.01	0.00	-0.02	0.00	0.00	0.00	0.00	0.01	0.04	0.02	0.01	0.06

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Table 5.10. Model coefficients for subsequent positions during Chick-rearing Period (before 1 February). Highlighted numbers are for those that were significant at a 95% level, as shown by the 2.5-97.5% MCMC confidence limits not including zero.

	2004				2007				2008			
Coefficients	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
Intercept	-12.62	3.70	-19.70	-4.85	-19.02	3.46	-26.15	-12.45	-18.83	11.60	-42.86	2.61
Visits	0.42	0.09	0.24	0.60	0.55	0.03	0.49	0.61	0.86	0.42	0.05	1.67
Distance	-2.21	0.18	-2.59	-1.88	-1.13	0.21	-1.56	-0.71	0.07	0.42	-0.74	0.89
Distance^2	0.16	0.02	0.11	0.21	-0.01	0.04	-0.09	0.05	-0.02	0.05	-0.11	0.07
Previous1	0.09	0.08	-0.07	0.26	0.00	0.05	-0.09	0.09	1.07	1.40	-2.08	3.46
TripDuration	-0.02	0.04	-0.10	0.08	-0.05	0.03	-0.10	0.01	0.00	0.16	-0.32	0.33
Previous2	-0.04	0.13	-0.31	0.21	0.15	0.04	0.08	0.22	-2.11	1.84	-5.80	0.59
GLS	0.16	0.11	-0.05	0.38	-0.02	0.07	-0.15	0.12	2.11	1.03	-0.17	3.98
Time	-0.07	0.03	-0.14	-0.01	-0.07	0.01	-0.10	-0.05	0.05	0.06	-0.06	0.17
ChIA	-4.52	2.63	-9.65	0.84					8.89	10.74	-12.51	29.43
SST	0.23	0.14	-0.09	0.46	-0.85	0.46	-1.93	-0.03	-1.18	0.64	-2.75	-0.22
SeaHeightAnom	0.40	0.15	0.09	0.67	0.66	0.14	0.38	0.96	0.53	0.47	-0.35	1.48
Front	0.84	0.60	-0.40	2.02	-0.52	0.56	-1.68	0.61	-0.50	1.51	-3.52	2.59
Bathymetry (x100)	-0.09	0.01	-0.11	-0.07	-0.06	0.01	-0.09	-0.03	0.03	0.04	-0.04	0.11
Previous1*												
TripDuration	-0.01	0.04	-0.08	0.06	0.04	0.01	0.02	0.05	-0.28	0.33	-0.93	0.42

DISCUSSION

We have shown that a central place foraging marine predator (the flesh-footed shearwater) chose to return to areas that they have previously been, suggesting that experience is influencing their choice of foraging area. Because their food resources are distributed patchily, choosing to forage somewhere that has already been used successfully offers clear advantages. However, this has only rarely been demonstrated. Black-legged kittiwakes *Rissa tridactyla* made an average of two trips per day to tidal fronts in Prince William Sound, Alaska (Irons 1998). Northern gannets (*Morus bassanus*) and red-footed boobies repeatedly departed their colonies in the same directions (Lewis et al. 2002; Weimerskirch et al. 2005). Northern fur-seals and southern elephant seals return to similar areas between foraging trips, from one year to the next (Bradshaw et al. 2004; Call et al. 2008).

The effect of experience was greater in the Incubation period than during the Chick-rearing period. They are less constrained in terms of time during Incubation, therefore they have more opportunity to find higher quality areas, which can be exploited on subsequent trips. In Chick-rearing, with less search time, the quality of the information may be less and therefore more readily discarded. Further, we have only considered longer trips. Thus in the Chick-rearing period, there may have been some short trips since the previous long trip. This may have diluted the memory of the previous long trip, either by increasing the time since the last long trip, or by creating memories of short trips in between.

At the scale used in this study, the experience variables were at least as important as oceanographic variables. Further, the oceanographic variables were not affecting choice in ways obviously corresponding to increased productivity. This may be scale related. In the Mozambique Channel, breeding great frigate-birds *Fregata minor* used sub-mesoscale surface mixing and transport structures (Lagrangian Coherent Structures) along the edges of eddies when foraging (Tew Kai et al. 2008). However, it was unknown how the frigate-birds located the areas, as they were up to 1,000 km from the breeding grounds (Tew Kai et al. 2008). These types of structures are also present in the East

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Australia Current and Tasman Front between Lord Howe Island and the east coast of Australia (Waugh et al. 2006), in areas to which the shearwaters were returning.

Learning increases foraging efficiency in bluegill sunfish *Lepomis macrochirus* and bumblebees *Bombus terrestris* (Werner et al. 1981; Peat and Goulson 2005). Although, these species forage over relatively short distances it would be similarly beneficial for a longer distance central place forager such as flesh-footed shearwaters. Search strategies such as correlated random walks have been hypothesized as the most efficient ways to find food in an environment with patchy resources (Viswanathan et al. 1996; Fauchald and Tveraa 2003; Tremblay et al. 2007) in the absence of other information, but if predators are able to reduce the area that needs to be searched through experience, this is going to greatly increase the efficiency of that predator. Minimising the time spent searching is advantageous by optimal foraging theory; by minimising the time spent searching the forager should also be able to minimise the time required to feed within a patch, or alternatively allow them to spend more time in a coarse scale patch to search for the areas of high productivity at the edges of eddies within this patch (Charnov 1976).

The shearwaters apparently use experience in a dynamic way, because the probability of visiting an area declined with the time since the last visit, suggesting the shearwaters discount the information they have gained with increasing time since they gained it. Bumblebee's memories of where they were foraging the previous day declines overnight, though not completely (Keaser et al. 1996). Alternatively, because the shearwaters were returning to productive areas on an ocean, the features are likely to be dynamic, and hence, they may have moved or degraded. Nevertheless, shearwaters with loggers foraged in approximately similar areas (to the west of Lord Howe Island) in different years, suggesting that experience at some scale still determines where the shearwaters go (Fig. 1). This indicates the effect of experience varies with the scale examined. At large scales, features such as the breeding site on Lord Howe Island and the Tasman Sea are highly predictable; but as scale declines, so does the predictability of features. While seamounts are also predictable, the currents that cause up-wellings around them shift in location and strength. At the smallest scale, that of eddies, features have lifetimes on the

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order of days to months, and thus could change substantially over the course of a few foraging trips.

The coarse scale used here for areas that the shearwaters were returning to have shown low levels of correspondence between spatial distribution of seabirds and zooplankton (Reid and Hindell 2000). Therefore, while they apparently use experience to get to areas they have previously visited and were more likely to have successfully foraged, once they are in the area, they must find food. Food is likely to be related to fine scale, dynamic features that are found within the coarse scale features that they are visiting using memory. Presumably this is when they adopt different means to find food, such as smell (Nevitt et al. 2008) or sighting other marine predators (Au and Pitman 1986; Haney et al. 1992). Scale is very important in analysing the distribution of foraging seabirds and their prey (Fauchald et al. 2000). Fauchald et al. (2000) hypothesised a hierarchical search pattern so that murrelets searched initially in a large-scale manner with long travel distances and low turning angles, and once within a large-scale patch they searched by using shorter travel distances and sharp turning angles. These larger scale searches could be analogous to the flesh-footed shearwaters using experience to find foraging areas. There may be two processes involved rather than one, with shearwaters choosing to go to an area, and then searching, rather than searching from the start.

The shearwaters were exhibiting a range of time scales for foraging. Most recent experience was also likely to be closest experience, so they used this at a large scale to determine where to go, but then at a fine scale as they are foraging to make decisions about whether to accept a new location or return to a location they visited earlier on the same trip. Experience of previous foraging areas is only useful if there is some chance of the feature they are returning to remaining where it was (or nearby). This is likely to vary depending on the feature. Ideally if a patch of food occurs permanently in some position, experience will be a very efficient manner to return to it. This would be a quite rare situation in the marine environment (though it may be approximated by tidal fronts (Irons 1998) or sea mounts). However, if food will intermittently occur in some general area, experience may assist the predator to find that general area, but other cues may be

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necessary to find the actual food at the time the predator is there. This is likely to be the situation with oceanographic features such as currents and eddies that occur within the Tasman Sea (Ridgeway and Dunn 2003). These features often generate areas of increased productivity, and patches of prey. However, the prey patches will not be permanent and so will move around in the general area that they have occurred. Further to this, over time, features such as these will degrade and move on to other areas. Therefore for this situation, it is useful for the information gained from experience to degrade also. At the opposite extreme to permanent features is totally (or near) random features, and for these experience of locations is useless.

Flesh-footed shearwaters were predominantly using experience, however, they were also choosing areas used by other tracked individuals. This may have been due to the shearwaters moving to similar areas due to other cues, or to their following congeners. Black-legged kittiwakes predominantly used experience to choose where to forage, apparently not using information from other birds (Irons 1998). The weakness of the relationship for the shearwaters may have indicated they only formed flocks for some of the time (perhaps in some years or seasons and not others), or that there were insufficient data (low number of tracked birds) to form a stronger pattern. This could be better tested using proximity loggers (Ji et al. 2005).

We used discrete choice models in an ecological context, because they allow the combination of environmental data and behavioural decisions, such as whether to return to an area, or which prey to hunt. Discrete choice models have been used in several other ecological situations: oceanographic preference of bluefin tuna (Teo et al. 2007), hunting decisions of cheetahs (Cooper et al. 2007), and resource selection by elk *Cervus elaphus* (Cooper and Millspaugh 1999).

CONCLUSIONS

At a coarse scale, flesh-footed shearwaters breeding on Lord Howe Island were using experience and the quality of the information they had to determine their choice of foraging area. They were more likely to visit an area the more often they had visited it

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during the current, or two previous trips; however the likelihood of returning became less the longer it was since a previous visit. This indicates that they were using previous experience, but that the birds discounted this information as it aged. We expect this to be an adaptive trait, given that the birds forage on ephemeral features such as the edges of eddies in oceanic fronts. Thus it is useful to „remember’ where a productive patch was in the immediate past, but the usefulness of this information decreases with time as the patches move and change. The use of experience by shearwaters is important in the understanding of how marine predators forage, as it should increase the foraging efficiency of the shearwaters, and allow them to utilize the other tools available to them, such as efficient search methods (*e.g.* area restricted search or Levy flights) or using environmental cues (smell or sight), in much smaller areas. Our results suggest that experience and memory may overwhelm the role of oceanographic variables in driving the foraging distribution of marine predators. The implication of this is that the search for predictive models of species distributions in marine systems based on remotely sensed data such as sea surface colour may never yield high quality predictive models.

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6. General Discussion and synthesis of results

The aim of this thesis was to investigate the continuing trends in the Lord Howe Island population of flesh-footed shearwaters, and how these trends were related to fisheries interactions and oceanography. Previously, the population had been shown to be declining, with habitat clearing and fisheries by-catch in the ETBF highlighted as likely contributing factors (Baker and Wise 2005; Priddel et al. 2006). The methods used for mitigating seabird by-catch were largely unsuccessful for this species (Baker and Wise 2005), most likely due to its manoeuvrability and deep diving ability (Brothers et al. 1999). This study has produced considerable new information on the status of the Lord Howe Island population of Lord Howe Island, and the threats it is facing, as well as suggesting means to mitigate fisheries by-catch, based on data on the at-sea distribution of the birds, and the factors that influence this. In spite of recent decreases in fisheries by-catch and land clearing, the population has continued to decline, with extra mortality noted on roads on the island (Chapter 2). Declining by-catch in the tuna fishery in the region can be explained by decreasing overlap between the fishery and the foraging shearwaters (Chapter 3); the shearwaters predominantly foraged in potentially rich areas (Chapter 4); and returned to similar areas over successive trips, indicating the use of experience to choose where to forage (Chapter 5). These results suggest the shearwaters are returning to approximately the same productive areas, indicating the use of closures of quite specific areas has the potential to be effective as a mitigation measure.

The results were interpreted in their own particular context at the end of each chapter, while this discussion will provide a synthesis of the findings, especially with regards the possibility of the results' use for mitigation of fisheries by-catch for species for which other more standard mitigation techniques have not worked.

Population trend

Chapter 2 demonstrated a posterior probability of 0.85 that the population is continuing to decline. Two sources implicated in the decline from 1978-2002 were breeding habitat

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loss on Lord Howe Island, and mortality in fisheries of the ETBF (Baker and Wise 2005; Priddel et al. 2006). However, the loss of breeding habitat had ceased over the 2002-2009 period, thus suggesting this was no longer the problem or that there is a time lagged effect of the loss. There was some evidence of lower breeding success in parts of colonies that were more disjointed. Further, there is now evidence to suggest that the rates of by-catch mortality have declined in the ETBF (Trebilco et al. 2010). Therefore other sources of mortality are apparently contributing to the decline.

During the summer of 2008/9 adult mortality of flesh-footed shearwaters on the roads on Lord Howe Island was 129-262 (an estimated annual adult mortality of 0.2-0.4%; Chapter 2). This is a similar magnitude to the current observed by-catch mortality rate within the ETBF (Trebilco et al. 2010; Baker pers. comm.). There is also evidence of plastics being consumed by the adults at sea and passed on to the chicks; though it remains unclear what effect this is having on the population (Hutton et al. 2008; Chapter 2).

Spatial overlap with fisheries

Flesh-footed shearwater by-catch in the ETBF has fallen in recent years, therefore, increasing our understanding of the spatial interactions with the fishery and how it may influence by-catch will potentially help with management of future changes of by-catch (Chapter 3). Counts of flesh-footed shearwaters behind vessels operating in the ETBF were used to model the areas of spatial overlap over the period from 2001-2006. This was done using a GLM approach. Overlap between the fishery and the flesh-footed shearwaters predominantly occurred to the west and south-west of Lord Howe Island. Using this model, in two of three years that the areas of interactions were predicted for (1998 and 2002), interactions were high as a significant proportion of the fishery was operating in the same area, targeting broadbill swordfish and yellowfin tuna. However, by 2006 most of the fishing effort was targeting albacore tuna, and operating well to the north of Lord Howe Island, and so the overlap between the fishery and the shearwaters was much reduced (Chapter 3). By-catch rates in the ETBF were much lower during this latter period (Trebilco et al. 2010). This makes sense, as by-catch rates were correlated to

the number of birds interacting with long-line vessels at the time of line setting (Trebilco et al. 2010).

Thus, the decline in the by-catch rate for flesh-footed shearwaters in the ETBF corresponds with the fishery shifting away from areas where the birds forage. The apparent decline in the by-catch rate is based on observer coverage of less than 5% of fishing effort (Trebilco et al. 2010). Hence there is much uncertainty in the estimated decline in by-catch rate, in particular the accuracy and representativeness of the estimates from such a small sample. A further issue is that the decline in by-catch rate has resulted from fishers changing target species and fishing area; there is some probability that at some time the fishers will change area and target species again and return to targeting those that resulted in spatial overlap and subsequent high by-catch rates.

Foraging choices of shearwaters

The models used in Chapter 3 to identify overlap between the fisheries and flesh-footed shearwaters are useful but limited. There are a number of limitations inherent in the assumptions behind them, such as they are unable to deal with the autocorrelation between successive counts in the data and they are linear in shape and so are unable to completely reflect underlying beliefs about the relationships being modelled.

Understanding the drivers for flesh-footed shearwater foraging, in particular the role of oceanographic conditions and experience, will improve knowledge of where shearwaters forage and how they use the environment, and this will further assist in fishery management. In order to do this, two novel statistical methods needed to be adapted.

In Chapter 4 a multi-component model was used to examine the abundance of flesh-footed shearwaters attending vessels, modelling abundance as a sum of arrivals and departures of individual birds at the vessel. This model was developed to reflect the underlying process driving the observations of birds attending vessels, and was estimated using maximum likelihood (Hilborn and Mangel 1997; Clark 2007; McCarthy 2007; Bolker 2008). This approach better reflects our understanding of the system, facilitating not only prediction but also learning. These more mechanistic statistical models are

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becoming more frequently used with the development of new ways to solve the mathematical issues in the models through increased computer power, and are at the cutting edge of analytical methods in ecology (McCarthy 2007).

By using an arrivals/departures models to analyse counts of flesh-footed shearwaters behind fishing vessels, it is possible to quantify the effect of smaller scale cues such as eddies or fish catch on attendance (Chapter 4). It is not possible to identify bird interactions at these scales using observer data and the models used in Chapter 3. At smaller scales, shearwaters were more likely to arrive behind fishing vessels when they were operating in areas of up-wellings and down-wellings at the edges of eddies in the Tasman Sea and along shelf-breaks. This suggested that the shearwaters were attending the vessels when they were operating in productive areas. Therefore, more birds may be attending the vessels due to there being more birds in the area, however they may only attend fishing vessels as one of a number of potential food sources while they are operating in the area the shearwaters had already chosen to forage. These patterns are supported by results from other seabirds attending fishing vessels. In the Baltic Sea seabirds were found to be much more responsive to changes in oceanographic conditions, such as up-wellings, or prey, rather than the quantity of food available from trawlers operating nearby (Skov and Durinck 2001). They found that the attraction of trawlers for seabirds was only a local process (< 10 km). Westland petrels off New Zealand were found to only attend fishing trawlers if they were operating in the areas the petrels naturally chose to forage (Freeman 1997).

In Chapter 5 a multinomial logit model was used to determine where individual flesh-footed shearwaters were foraging, and which factors were important in their choice. These so-called discrete choice models rely on an animal making a choice, where only one of a finite number of choices is possible at one time (Train 2003). In this context, the model allows the shearwater's choice of foraging area to be dependent on environmental and behavioural co-variates at the same time. Applications of this promising approach are rare in ecology, although there are some examples such as in studies of factors relating to hunting decisions by cheetahs (Cooper et al. 2007).

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During the breeding season, flesh-footed shearwaters generally foraged between the east coast of Australia and the Lord Howe Rise, a ridge running north-south through the Tasman Sea. Lord Howe Island is on the western edge of the ridge, and is in the region that the Tasman Front strikes the ridge (Ridgeway and Dunn 2003). Most interactions between fishing vessels in the ETBF and flesh-footed shearwaters also occurred to the west of the Lord Howe Rise (Chapter 3). The birds chose to visit areas that they had previously visited, including places that they had visited within the two previous trips. In addition, they were visiting areas that they were more likely to have foraged successfully in during the previous trip. The shearwaters were using previous experience to return to areas known to be profitable. Experience has been hypothesised as a means for animals to locate food, but only rarely demonstrated. Black-legged kittiwakes *Rissa tridactyla* returned to the same area at tidal fronts in Prince William Sound (Irons 1998), while northern fur-seals and southern elephant seals return to similar areas between foraging trips (Bradshaw et al. 2004; Call et al. 2008). Learning from experience is beneficial as it increases foraging efficiency (e.g. in bluegill sunfish *Lepomis macrochirus* and bumblebees *Bombus terrestris* (Werner et al. 1981; Peat and Goulson 2005)). Experience improved the foraging of a mobile crab, the blue crab *Calinectes sapidus*, but had no effect on a sedentary crab, the Atlantic mud crab *Panopeus herbsti* (Micheli 1997). The use of experience to locate patches can be thought of as fitting into optimal foraging theory through minimising the time spent between patches as well as accumulating information for future foraging success, especially for species with significant movements to patches (Charnov 1976; Clark and Mangel 1984). The effect of experience on the flesh-footed shearwaters decreased with passing time, indicating it was becoming less useful. The patches they were most likely returning to were likely to be dynamic, and hence it is useful to weight the usefulness of experience, with more recent experience being more useful than older experience. Bumblebees have been shown to partially forget experience overnight (Keaser et al. 1996). Learning is more useful for long lived foragers such as flesh-footed shearwaters (Eliassen et al. 2007). It is also more useful in temporally varied environments (Eliassen et al. 2009). This is likely to move closely match the Tasman Sea environment and fronts as encountered by shearwaters. Learning

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the locations of previously encountered prey patches allows birds to increase foraging efficiency, but forgetting allows for the use of a flexible foraging strategy (Eliassen et al. 2009).

Foraging scale

The results here (Chapters 4 and 5) suggest that flesh-footed shearwaters are foraging at a range of scales. During all four summers for which data were collected, they were foraging in approximately the same areas – predominantly between Lord Howe Island and the east coast of Australia. But at a coarse scale (~100 km) they were significantly likely to choose to remain in an area and return to that area on following trips. At smaller scales the shearwaters were apparently remaining in areas that were most productive. At sub-meso scales (<10 km), up-wellings of productive waters are formed at the edges of eddies; great frigate-birds were shown to forage in these in the Mozambique Channel (Tew Kai et al. 2008), while similar structures have been shown to occur in the same areas that the flesh-footed shearwaters are choosing to return to (Waugh et al. 2006). It can be hypothesised that the shearwaters are behaving in a similar way in the Tasman Sea to how the frigate-birds were behaving, and thus using similar structures in the edges of currents. Nevertheless, at coarse scales, the probability of choosing to return to an area declined over time, indicating that, at least at that scale, the shearwaters were „forgetting’ where they had been foraging. This is a useful characteristic due to the dynamic nature of the sub-meso scale features, so that the quality of the information would degrade.

Scale is an important means to look at aspects of the ecology of marine predators, and how they locate their food (Hunt and Schneider 1987). In the case of seabirds such as flesh-footed shearwaters, at a large scale they spend their time within the possible foraging range around Lord Howe Island. This could be viewed as a circle around Lord Howe Island encompassing how far they can potentially fly and return (though, this is too simplistic, as wind will also influence how far they can fly). However, within this, there are probably areas that are unsuitable (such as areas of ocean that are unproductive). Therefore, at coarse scales there are areas that have the potential to be productive (such as eddies and fronts at the edges of currents, shelf breaks or sea mounts), and others that are

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unsuitable. Over shorter time scales eddies and fronts at the edges of currents are relatively predictable as they move slowly enough such that they will remain in approximately similar areas on the time scale of a foraging trip, and so it is advantageous for foragers to return to them. Dynamic memory, which gives more weight to recent experience, allows foragers to return to these ephemeral areas, potentially greatly improving the efficiency of foraging effort. However, at smaller scales, productive areas are unevenly and unpredictably distributed (i.e. there are not up-wellings along the complete length of an eddy), therefore within coarse scale there is a need to locate the productive areas. At this scale, the use of efficient search patterns (such as correlated random walks) play an important role in predators foraging strategies.

A number of studies have used marine predators' movements to look at efficient search patterns (Viswanathan et al. 1996; Fauchald and Tveraa 2003; Tremblay et al. 2007). These studies have often used algorithms to look at animals moving a range of distances (especially using power laws such as Lévy flights). They have suggested it is efficient to be able to intermix longer and shorter movements (and changes of angle) in order to cover the environment efficiently in search of food patches (Viswanathan et al. 1996). However, these are using an essentially random process (hence the name correlated random walks) and require little information about the environment to be held by the forager. The use of experience has been shown to improve foraging efficiency in a number of species (Chapter 5). The results here for the flesh-footed shearwater suggests they use experience to return to similar areas, and so can greatly improve their foraging efficiency by eliminating (or at least reducing) the requirement to randomly move large distances, instead using past experience to limit their search to areas that are likely to have food. This would suggest foraging should be looked at as a two-state process, with two (or more) scales of searching, such as large scale and small scale searches (Fauchald et al. 2000).

Management

Management of conservation issues, such as a declining population, requires information on the nature and level of potential threats, their effects, and how to overcome them. The

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mortality on roads on Lord Howe Island is equal to that currently recorded in the ETBF, though an order of magnitude less than that recorded between 1998-2002 (Chapter 2; Baker and Wise 2005; Baker pers. comm.). Road mortality should be relatively easy to manage, requiring changes in behaviour of a relatively small number of people (island residents), and a somewhat straightforward solution, either slowing or eliminating vehicles on some roads on the island. Speed limits on roads have been implemented on Phillip Island in Victoria for the conservation of little penguins (Hancock 2002).

Fisheries by-catch is more difficult to manage for a number of reasons. One problem is that the observed and estimated by-catch are based on observer programs that often have less than 5% coverage, as is the case in the ETBF (Trebilco et al. 2010). Therefore, depending on the power within the data, the observed decrease in the mortality rate may not be accurately estimated. This may be stochastic, such that the observer coverage is low enough that periods of high mortality are missed. Alternatively, not all vessels operating in the ETBF may ever carry observers, due to issues of logistics or space. Thus it is possible that the observed vessels are not representative of the whole fleet; a vessel with a high by-catch rate is likely to be less co-operative in having observers on board to see their poor by-catch rate. One study has suggested that for common species, if the sample is unbiased, observer coverage of 20% is required to measure by-catch rates within 10% of the correct value, while 50% coverage is necessary for rarer species (Babcock and Pikitch 2003). The level of coverage required will depend on what precision is desired for any estimates derived from the data (Manly et al. 2002).

If the observer coverage is representative, and the decline in mortality is due to changing fishing tactics, the decline in the by-catch rate may be fortuitous, but it cannot be relied upon as a permanent solution. However, it does indicate that area closures can be useful in limiting by-catch. The use of area closures has only occasionally been used to manage by-catch by commercial long-liners. A long-line fishery in waters around Hawaii was closed for a period in the early 2000's due to capture of turtles (Curtis and Hicks 2000; Gilman et al. 2007), while the threat of area closures through severe catch limits were placed upon an Alaskan long-line fishery due to low levels of by-catch of short-tailed

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albatrosses (Gilman et al. 2006). Area closures are regarded as a measure of last resort, due to their severe economic impact upon the fishery (Curtis and Hicks 2000). For this to be used, other methods of mitigating the by-catch issue must be seen to have failed. There also needs to be some strong political imperative to act (in the case of the Hawaii turtles, there was a court ruling under U.S.A. threatened species regulations (Curtis and Hicks 2000)).

By-catch of seabirds in long-line fisheries in Australia is covered by national legislation via the Threat Abatement Plan (Australian Antarctic Division 2006). Under this plan, it is mandated that all fisheries must record seabird by-catch rates that do not exceed 0.05 birds per 1000 hooks in all seasons. Hence there is a political requirement in Australia to limit seabird by-catch in fisheries. This plan was aimed at threatened species, especially albatrosses, however the flesh-footed shearwater is classified as Vulnerable in New South Wales and as a Migratory and Marine species under National legislation in Australia (DEWHA 2010). It has been suggested that they should be listed under the Agreement on the Conservation of Albatrosses and petrels (ACAP) (Cooper and Baker 2008). In the ETBF, the observed by-catch rate of seabirds has fallen below the level prescribed by the Threat Abatement Plan in 2005 and 2006 after being much higher between 1998-2004 (Baker and Wise 2006; Trebilco et al. 2010). However this may be due to changed target species in the fishery, and so could increase again (Chapter 3). Therefore, it is useful to increase information and our understanding of the foraging movements of flesh-footed shearwaters for management of this eventuality.

Marine protected areas

Flesh-footed shearwaters from Lord Howe Island return to fairly specific areas that they have chosen from experience (Chapter 5). These overlap with the ETBF when the ETBF targets yellowfin tuna and broadbill swordfish (Chapter 3). In the absence of effective mitigation measures, the use of area closures may be considered. While there is the example of the Hawaii area closures for surface predators (Curtis and Hicks 2000), predominantly they have been used as a conservation measure in fisheries (Hilborn et al. 2004). Area closures can be made official by developing Marine Protected Areas. Marine

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Protected Area use or consideration was suggested in the Mediterranean Sea for the Balearic Shearwaters (Louzao et al. 2006), and for Cape gannets *Morus capensis* and African penguins *Spheniscus demersus* in the Benguela current (Pichegru et al. 2009).

Marine protected areas are a concept equivalent to terrestrial protected areas such as national parks. The International Union for Conservation of Nature (IUCN) has a series of levels that it uses to define marine protected areas, depending on the amount of protection they offer. Their size and location are ideally based on our understanding of environmental and ecological processes and how humans interact with these (Carr et al. 2003). However, there are marked differences with terrestrial reserves, in particular, marine areas are open due to the transport of nutrients through water movements (Carr et al. 2003). Some are effective at protecting ecosystems; *e.g.* in waters around Tasmania marine reserves on inshore rocky reefs have significantly larger fish and fish species richness, as well as abundance in some species (Barrett et al. 2007). In these situations, marine reserves act by giving a portion of the population a chance to grow larger and older, improve their breeding potential, and eventually through density pressure within the reserve some animals will move beyond the boundaries of the reserve and hence restock surrounding areas (Lauck et al. 1998; Wilder et al. 1999).

Combining a number of methods (from effort controls, catch quotas and area closures) may give the greatest buffer to uncertainty, with area closure combined with catch quotas giving the best results around Iceland (Stefansson and Rosenberg 2005). Many of the successful marine reserves have been small and for inshore ecosystems (Cole et al. 1990; Barrett et al. 2007). Nevertheless, the overall applicability of marine reserves is not unanimously accepted (Hilborn 2006). They may be most useful in the situation of sedentary, multi-species fisheries, but less for fisheries for highly mobile single species with little by-catch (Hilborn et al. 2004). They are thought to be effective for conservation, but it is unclear if they enhance fishery catch (Mangel and Levin 2005).

Marine protected areas and pelagic environments

Individuals of some species of marine animals have ranges that cannot be readily encompassed within the boundaries of a single marine protected area, and hence they are not well suited to a single protected area. For example flesh-footed shearwaters from Lord Howe Island disperse over 1,000 km during the breeding season foraging trips, and migrate to the northern Pacific Ocean in the Austral winter. Other wide-ranging animals include whales, seals or tuna. Marine protected areas therefore need to be considered at appropriate scales, and to consider the mobility of ecosystem components (Hyrenbach et al. 2000). However, even wide-ranging species can form predictable aggregations associated with oceanographic features (Hyrenbach et al. 2000). In order to implement pelagic protected areas, it is necessary to understand the dynamics of the physical mechanisms that influence the formation and persistence of these aggregations (Hyrenbach et al. 2000). To protect these features, the marine protected areas may need to be dynamic (Hyrenbach et al. 2000).

Some work has been conducted on the possibility of marine protected areas for larger species, mostly of the static form. The International Whaling Commission has declared a Southern Ocean Whale Sanctuary, which protects whales south of 40°S from commercial whaling. The use of Regional Fisheries Management Organisations for managing high seas fisheries and conservation has been suggested, but so far has met with little success (Sumaila et al. 2007). Closure of 20% of the high seas may lead to the loss of only 1.8% of current global reported marine fisheries catch and a decrease in profits to high seas fleets of US\$270 million per year (Sumaila et al. 2007).

Work has commenced upon identifying potential Marine Important Bird Areas (Birdlife International 2010a) in waters around Iberia (Birdlife International 2010b). Under this process, four criteria were identified: i) seaward extension to breeding colonies, ii) coastal congregations of non-breeding seabirds (predominantly sea-ducks), iii) migration bottlenecks, and iv) high seas sites (Birdlife International 2010a). In the western Mediterranean Sea, the foraging range of Balearic shearwaters was modelled from ship-board observations and oceanographic observations; this was used for identifying

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potential Marine Important Bird Areas under the context of the Birdlife International criteria, and more generally, marine protected areas (Louzao et al. 2006). The Balearic shearwaters predominantly foraged in a relatively small area where eddies were formed by currents along the continental shelf edge, and so a static area was identified under criterion iv as suitable as a Marine Protected Area (Louzao et al. 2006). In the Benguela up-welling the marine distribution of two species, the African penguin *Spheniscus demersus*, and the Cape gannet *Morus capensis* were examined in relation to fisheries and Marine Protected areas (Pichegru et al. 2009). African penguins foraged close to the breeding colonies, and so related to criteria i, and the Cape gannet, were more widespread, and so fitted criteria iv (Pichegru et al. 2009). Flesh-footed shearwater foraged up to 1,000 km from Lord Howe Island (Chapter 5), and hence would fit under criteria iv. However, while the Balearic shearwater foraged where eddies formed over a static bathymetric feature and so their distribution were somewhat consistent over a number of years, flesh-footed shearwaters were foraging at oceanographic features over more open ocean, and hence, more mobile features. Therefore, they foraged over a greater area, hence the use of static Marine Protected Areas in this case would require a great deal of ocean to be considered; however they were apparently foraging on eddies within this greater area, indicating only these edges need greater protection. Because these eddies move, dynamic area closures that move with those features may be more appropriate. Temporary (or dynamic) area closures would require the identification of oceanographic features that marine predators were aggregating at to be protected, and the protected area to move with the moving of the oceanographic feature. This therefore also requires the ability to track the dynamic feature. Dynamic area closures have been used in the management of right whale populations off the east coast of the United States (Sanchirico 2005).

Protecting a static protected area is easier from a management perspective, and more analogous to terrestrial protected areas. This may not be suitable for the pelagic environment, which is generally highly dynamic. Having temporary area closures has the advantage in the pelagic environment of protecting foraging concentrations, which may move about in a dynamic environment. While we have discussed them here in the context

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of protecting flesh-footed shearwater from long-line fishery by-catch, temporary area closures can be much more generalized, as the features of areas that are important for seabirds are likely to be similar for other wide-ranging marine predators such as large fish, turtles, whales and seals. Thus these areas, beyond being Important Bird Areas are likely to be ecologically important areas. While these dynamic protected areas would work in the marine environment, they may not work so readily in terrestrial environments, which are less spatially dynamic. To use temporary or dynamic area closures requires a great deal of knowledge of the habitat use by the marine predators being studied. This is only just becoming possible. Improving data collection will improve this, such as the use of increasingly accurate and smaller data devices attached to individuals, such as using GIS loggers for more accurate positions and acceleration loggers to identify behaviour, while standardising the collection of observation data will improve that data. Nevertheless, the use of more powerful statistical techniques that more closely match our understanding/hypotheses on the behaviour of marine predators allows the use of data collected in ways such as from fishing vessels and GLS loggers, as has been shown here (Chapters 4 and 5). Further, more powerful statistical techniques such as MCMC or maximum likelihood methods and increasing power in computers should also allow this to be applied. Thus state-space models applied to tracking data can give greater detail, but Discrete Choice Models as used in Chapter 5 can also answer many questions (e.g. Jonsen et al. 2006; Patterson et al. 2010). A further area that is only recently being developed for marine data is combining observation data collected from vessels (and hence relating to large numbers of individuals) and data collected from loggers attached to individuals (Louzao et al. 2009).

One issue encountered in terrestrial conservation networks may be an over-representation of higher vertebrates to lower plants. Charismatic organisms with large home ranges may not be appropriate surrogates for biodiversity (Aroujo 1999; Fjeldsa et al. 2004). While area closures may be useful in this situation for conserving a single species, species assemblages or communities are central to conserving biodiversity (Mangel and Levin 2005).

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The use of decision theory has been recommended in conservation planning (Colyvan et al. 2009). The central idea of this is that in any decision, the decision maker should aim for the best possible outcome with the resources that are available (Colyvan et al. 2009). There are problems with protecting endangered species which by definition have a high risk of extinction. It may be better to focus on species that are less likely to go extinct. Critically endangered species may well go extinct regardless of conservation efforts that may be made for them (Mangel and Tier 1994). Endangered or threatened species on the other hand may have more chance of recovery, and so it may be that there is better value, and a greater prospect of success, in concentrating on them (Colyvan et al. 2009). Either way there needs to be a clear goal to any conservation intervention and specific ways to measure success (Wilson et al. 2006; Colyvan et al. 2009).

As with other scientific disciplines, it is important to have clearly defined aims when developing conservation strategies so that effort does not go on indefinitely without ever conserving the initial problem. Reserves such as Marine Protected Areas can assist in this, though they are best used in conjunction with other methods.

In the case of flesh-footed shearwaters on Lord Howe Island, there is a reasonable sized population (albeit declining) and a number of identified threats, therefore conservation measures should have a good chance of success. Destruction of the breeding habitat on Lord Howe Island has previously been identified as a major issue, but this has largely ceased. Mortality on roads is currently a significant issue, but it is likely that reducing this should be manageable. By-catch in adjacent long-line fisheries has been a serious problem in the recent past and may become one again with changing fishing activities. It is likely that area closures in this fishery could assist in mitigating mortality, or alternatively areas identified in this way can be managed differently such that there are extra management requirements for fishers operating in these areas.

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