

Physical environmental influences on breeding performance of the
fairy prion (*Pachyptila turtur*)

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ABSTRACT

Breeding seabirds are affected by predation, food distribution, competition for food, nest site availability and environmental pressures (Ashmole 1971). Using 11 years of nest monitoring data and eight years of chick measurements of fairy prions (*Pachyptila turtur*) at a colony near Dunedin, New Zealand, I investigated the link between physical environmental factors, breeding success rates and chick fledging size. Data from the same colony were then used to analyse the relationship between chick fledging size, likelihood of natal-colony recapture and age at first recapture. The colony had remarkably steady breeding success rates and chick fledging mass throughout the study period, perhaps due to a consistent source of local food, the use of behavioural buffering mechanisms by fairy prion parents, or due to an overriding effect of nest-site limitation. Fledgling wing lengths were slightly different between years, and these differences could be predicted by late-winter values of the Southern Oscillation Index (SOI) and summer sea surface temperatures (SST). In years of high SOI and high SST, fairy prions fledged with longer wings. This could be a result of increased availability of *Nyctiphanes australis*, the main prey of fairy prions, in these conditions. River flows and rainfall were unrelated to any of the chick measurements, probably because the influence of freshwater on the marine system near Dunedin acts at smaller timescales than those studied here.

Investigation of fledging measurements, cohort and likelihood of recapture for the 2004 and 2005 fairy prion cohorts showed no evidence of a link between fledging size and likelihood of recapture, but there was a link between cohort and probability of recapture. The 2005 cohort had unusually low six-year recapture rates, and also shorter-than-average wing lengths. These findings suggest that fledging wing lengths are more sensitive to environmental influences than are breeding success or fledging weights; also, the combination of low sea temperatures and an El Niño event in 2005 may have led to a

reduction in *Nyctiphanes* availability, ultimately affecting post-fledging survival of the 2005 cohort.

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INTRODUCTION

Seabirds are generally long-lived and have low annual reproductive output, life-history traits that have been linked to the the stochastic nature of marine food resources (Lack 1968; Ricklefs 1990; Schreiber & Burger 2002). Seabird populations are regulated by environmental controls, predation pressure, availability of nest sites and competition for food (Ashmole 1971). In addition to large-scale population effects, the physical environment affects seabird breeding productivity on a more proximate scale as well, affecting the number of birds breeding in any given year, annual nest success, chick growth rates and adult survival (Schreiber 2002). One of the main mechanisms through which this occurs is an alteration in the distribution and availability of prey. Because seabirds forage at sea but breed on land, breeding birds are constrained by the energy requirements of locating appropriate food at sea and carrying it back to the colony; food availability and competition for food near breeding colonies can place pressure on breeding seabirds (Ashmole 1963). Individual breeding birds face a trade-off between current and future reproductive investment (Stearns 1992), so, when food availability is low, they should abandon a breeding attempt in favour of personal survival and the potential for future reproduction (Drent & Daan 1980).

Food availability affects the choice to breed in any given year (Warham 1990; Chastel, Weimerskirch, & Jouventin 1993; Mills *et al.* 2008), the timing of breeding (Wolf *et al.* 2009), the capacity of parents to successfully incubate an egg to hatching (Chastel, Weimerskirch, & Jouventin 1995; Gill, Hatch, & Lanctot 2002), the number of chicks fledged per pair (Frederiksen *et al.* 2006) and the provisioning rates for chicks (Croxall, Reid, & Prince 1999). Foraging ability of breeding birds can be diminished by water turbidity, strong winds and redistribution of prey (both vertically, within the water

column, and geographically) (Finney, Wanless, & Harris 1999; Baduini *et al.* 2001), which can affect their ability to successfully incubate eggs and feed nestlings (Chastel *et al.* 1995; Finney *et al.* 1999). For generalist species that are able to switch prey, it may not be the quantity, but the quality of food that is reduced in poor years (Finney *et al.* 1999; Wanless *et al.* 2005), leading to slower chick growth rates (Weimerskirch, Fradet, & Chere1 1999) and underweight fledglings (Wanless *et al.* 2005).

Beyond the nestling phase, young seabirds must survive at sea until they reach breeding age, and return to the colony to recruit into the breeding population. A number of studies have found a link between nestling condition and post-fledging survival in seabirds (Mougin *et al.* 2000; Weimerskirch, Barbraud, & Lys 2000). Chicks that are fed well during development, and that leave the nest in better condition, should have a greater chance of post-fledging survival, and may be able to recruit into the breeding population at an earlier age (Perrins, Harris, & Britton 1973; Coulson & Porter 1985). For species that end parental care before fledging, early survival of fledglings may be improved by increased ability to forage and avoid predators (Morrison *et al.* 2009). Fat stores of newly-fledged chicks may protect against starvation while they are learning to feed at sea (Merilä & Svensson 1997; Mougin *et al.* 2000; Weimerskirch *et al.* 2000), and long wings may improve foraging ability, predator avoidance and subsequent survival (Morrison *et al.* 2009). Fledging weights predict recruitment rates in ancient murrelets (*Synthliboramphus antiquus*) (see Gaston 2003), fledging wing length and fledging mass predict local juvenile survival in the tufted puffin (*Fratercula cirrhata*) (see Morrison *et al.* 2009), and fledging mass influences survival of the sooty shearwater (*Puffinus griseus*) (see Sagar & Horning 1998).

Hatching and fledging dates have also been implicated in post-fledging survival of some seabirds with precocial fledglings. Longer nestling periods are associated with greater survival and recruitment rates in black-legged kittiwakes (*Rissa tridactyla*) (see Cam, Monnat, & Hines 2003), and early-hatched common guillemot (*Uria aalge*) chicks have greater juvenile survival than those that hatch later, probably because higher-quality parents tend to lay eggs earlier (Harris, Frederiksen, & Wanless 2007). In some altricial species, e.g. Cory's shearwater (*Calonectris diomedea*), timing of fledging does not affect post-fledging survival (Mougin *et al.* 2000).

Environmental influences on marine ecology

Climate affects the dynamics and productivity of marine ecosystems through many processes. Solar radiation and wind influence ocean temperature and stratification, altering the availability of nutrients for phytoplankton (Behrenfeld *et al.* 2006) and affecting the abundance and distribution of plankton and fish (Harris *et al.* 1991). Winds can drop iron-rich dust from deserts to the adjacent ocean, adding trace minerals that stimulate phytoplankton blooms (Jickells *et al.* 2005). High river runoff can also alter the productivity of coastal marine systems, although the mechanisms involved are not well understood (Mann 1993). Physical processes impact biological systems in the marine environment.

Recent warming of the air and ocean has caused a wide range of effects in ecological systems throughout the world (Rosenzweig *et al.* 2007). Increased sea surface temperatures (SSTs) have reduced the density of the upper ocean layer in the California Current System, causing a reduction in upwelling of nutrient-rich water, thereby lowering primary productivity and the abundance of zooplankton and commercial fish

(McGowan, Cayan, & Dorman 1998). The recent increase in SST in the Gulf of Alaska (GOA), on the other hand, has been followed by increases in zooplankton abundance and catches of some commercial fish species (but decreases in populations of other fish species and some marine mammals and seabirds) (McGowan *et al.* 1998; Sherman *et al.* 2009; Sydeman *et al.* 2009). The surge in GOA productivity may be driven by an increase in currents transporting nutrients from the Alaskan gyre, or a shoaling of the mixed-layer depth, leading to increased light levels for the light-limited GOA phytoplankton (McGowan *et al.* 1998). Rising sea temperatures are causing latitudinal and biogeographic shifts of marine fish species (Perry *et al.* 2005), and may also be modifying development and behaviour of some species of plankton (Edwards & Richardson 2004), changing the availability and distribution of food for apex predators such as marine mammals and seabirds.

Environmental influences on breeding seabirds

A number of studies have found correlations between seabird breeding biology and sea surface temperatures. Above-average SSTs at Phillip Island have been linked with earlier breeding dates for little penguins (*Endiptyula minor*) (see Chambers 2004), and little penguin breeding success has been associated with both increased SST and decreased temperature gradients in Bass Strait (Mickelson, Dann, & Cullen 1992; Cullen *et al.* 2009). Frederiksen *et al.* (2007) found that breeding productivity of *Rissa tridactyla* was negatively correlated with SST in the UK, and Kitaysky & Golubova (2000) found a link between sea surface temperatures and breeding success of planktivorous and piscivorous alcids in the North Pacific.

The Procellariidae (albatrosses, petrels and prions) exhibit strong links between breeding success and SSTs in a variety of locations. Yellow-nosed albatross (*Thalassarche chlororhynchos*) breeding performance on Amsterdam Island is linked to sea surface temperature in the Indian Ocean (Weimerskirch, Zimmermann, & Prince 2001; Pinaud, Cherel, & Weimerskirch 2005). Warm sea surface temperatures in the Kerguelen Islands have been associated with decreased adult body condition, and hatching and fledging success of the blue petrel (*Halobaena carulea*) (see Guinet *et al.* 1998). Some aspects of thin-billed prion (*Pachyptila belcheri*) breeding success have been negatively correlated with SST in the Falkland Islands (Quillfeldt, Masello, & Strange 2003; Nevoux & Barbraud 2006; Quillfeldt, Strange, & Masello 2007). SSTs have also affected breeding success of eight species of Procellariiformes in the Kerguelen Islands, where warmer-than-average water temperatures increase breeding success of those species which forage north of the Polar Front, while depressing breeding success of species foraging south of the Front (Inchausti *et al.* 2003).

Rainfall alters the productivity of coastal marine systems by adding growth-stimulating nutrients from the atmosphere or from terrestrial runoff. Coastal systems are usually nitrogen-limited, and are therefore sensitive to any additional nitrogen inputs (Ryther & Dunstan 1971). Atmospheric nitrogen-loading (nitrogen-enriched precipitation) can increase phytoplankton production (Paerl, Rudek, & Mallin 1990), and nitrogen from terrestrial sources (discharged from rivers) can precipitate coastal algal blooms (Baek *et al.* 2009). Wind and river outflow drive coastal water circulation and mixing, thereby influencing nutrient availability for phytoplankton (Horner, Garrison, & Plumley 1997). Large-scale agricultural runoff in some estuarine and coastal systems increases available nitrogen and phosphorous, stimulating phytoplankton growth. Associated effects of the increase in nitrogen, increases in N:P and N:Si ratios, under certain conditions, have led

to silicon-limitation of diatoms, and subsequent increases in the abundance of non-siliceous phytoplankton (e.g. dinoflagellates) in these systems (Justic *et al.* 1995; Zhou, Shen, & Yu 2008).

The El Niño Southern Oscillation (ENSO) is a climate phenomenon that accounts for a large amount of the variability in air and water currents in the Pacific Ocean. When the atmospheric pressure in the southeast Pacific is much lower than that in Australia (El Niño phase), the Pacific trade winds weaken, resulting in an increase in sea temperature along the equator and the Peruvian coast; the opposite pressure gradient results in a La Niña event, which has the reverse effect. El Niño and La Niña events are generally characterised by departures from the long-term mean values for tropical Pacific sea temperature and atmospheric pressure gradients, persisting for at least 6 consecutive months. These events occur about 2 to 7 years apart, typically establishing around April - June and lasting for about a year or two thereafter. The ENSO can have wide-ranging effects on marine biology and fish stocks (Duffy 1990; Stenseth *et al.* 2002; Trathan, Forcada, & Murphy 2007)); massive die-offs of plankton, fish and seabirds have been associated with extreme El Niño events off the coast of Peru (Hobday 1992). The Southern Oscillation Index (SOI) is a measurement of the sea-level pressure difference between Darwin and Tahiti that describes the magnitude and direction of the ENSO at any given time. In New Zealand, the ENSO affects climate by altering wind, rainfall and temperature patterns (Mullan 1995; Salinger & Mullan 1999). The SOI has been positively correlated with reproductive performance of red-billed gulls (*Larus novaehollandiae scopulinus*) at the Kaikoura Peninsula, New Zealand, probably through increased upwelling driven by northeasterly winds (Mills *et al.* 2008).

The fairy prion

Fairy prions (*Pachyptila turtur*) are small (25 cm long, 56 cm wingspan) members of the order Procellariiformes (the petrels), distributed along the coasts of New Zealand, the Falkland Islands, South Georgia, south-east Australia and the Crozet Islands (Onley & Scofield 2007). They are the most abundant prion in New Zealand, where they breed in colonies on rat-free islands and rock stacks along the coastline of the South Island and on one site off the North Island (Marchant & Higgins 1990). Fairy prions are entirely nocturnal at their breeding colonies, arriving after dark and leaving before daylight to forage at sea (Harper 1976). Like most of the Procellariiformes, they are philopatric (Ovenden *et al.* 1991). Fairy prions are listed under the New Zealand Threat Classification System as “at risk, relict”; their breeding range was likely restricted by more than 90% following the introduction of predatory land mammals to New Zealand (Miskelly *et al.* 2008).

Fairy prions nest in burrows and rock crevices or caves, and breeding pairs lay a single egg per year, in mid-October to mid-November. Parents incubate the egg in shifts lasting between one and four days, through the total incubation period of about 46 days (Marchant & Higgins 1990). Incubating birds are visited by their partners on most nights, but they do not trade duties until the shift is complete. The incubating bird loses weight at the rate of approximately eight grams per day, so if relief does not come within five days, they must desert the egg for at least one day to feed. Absences of three days during the incubation period can affect hatching and survival rates of the young (Harper 1976). Eggs hatch in late November or December, and chicks are guarded by one parent for the first one to five days after hatching. Chicks are then fed nightly by at least one parent (often both) through the remainder of the nestling period, and fledge about 45

days later (Harper 1976). Since fairy prions return to the colony daily to feed young, they are dependent on local food availability during the breeding season, so breeding productivity should reflect local food abundance through this period, assuming there are no stronger controls acting on the population.

Prions are filter-feeders; they use special comb-like structures called lamellae at the sides of their bills to filter food particles from seawater (Morgan & Ritz 1982). The dimensions of these lamellae limit their diet to prey larger than about 0.9 mm, and preclude capture of smaller particles such as copepods (Prince & Morgan 1987). Fairy prions eat primarily euphausiids, and in New Zealand the bulk of their diet consists of *Nyctiphanes australis*, and, to a lesser extent, the amphipod *Parathemisto gracilipes* (see Harper 1976). They forage on the sea surface, using a combination of surface-seizing, surface-diving, pattering and dipping to collect their prey (Prince & Morgan 1987).

Fairy prions generally nest on predator-free islands, but there is a mainland colony of fairy prions near Dunedin, New Zealand, that is inaccessible to non-avian predators by virtue of its location on a steep sandstone cliff (Loh 2000). On Stephens Island, New Zealand, fairy prions share their burrows with tuatara (*Sphenodon punctatus*), which sometimes eat prion eggs and small chicks, however, the main factors regulating Stephens Island fairy prions are probably competition for burrows and mortality at sea following extreme weather events, not predation from tuatara (Walls 1978).

Environmental influences on *Nyctiphanes australis*

Nyctiphanes australis is the most abundant euphausiid in the waters off the Otago coast (Murdoch 1989), where *Nyctiphanes* form surface swarms in late summer and provide a

key food source for whales, seals, seabirds and fish. The optimal water temperature for survival of *Nyctiphanes australis* is 12 – 18°C; Sheard (1953) found that outside this range *Nyctiphanes* were plagued by an elliobiopsid parasite. The optimal salinity for *Nyctiphanes australis* is 34.05 – 34.72 parts per thousand (Mauchline & Fisher 1969; Haywood 2002). Otago *Nyctiphanes* are most abundant in the plumes of fresh water from the Clutha and Taieri rivers which are pushed along the shore of the Otago Peninsula by the Southland Current (O’Driscoll 1997; Haywood 2002); *Nyctiphanes* are also more numerous in a band of low salinity water which is present after periods of high flow from the Clutha river (O’Driscoll & McClatchie 1998). Lower sea surface temperatures have been linked to greater *Nyctiphanes* abundance near Otago (Haywood 2002), and decreases in numbers of *Nyctiphanes australis* have been observed in El Niño (low SOI) years in two locations off the eastern coast of the South Island of New Zealand: at the Otago Peninsula (Haywood 2002), and at the Kaikoura Peninsula (Mills *et al.* 2008).

Environmental effects on fairy prion breeding performance

Breeding adult fairy prions return nightly to the colony to feed chicks (Harper 1976), and are thus highly dependent on local populations of *Nyctiphanes australis* throughout the breeding season. Based on the described relationships between *Nyctiphanes australis*, sea surface temperatures, ENSO and river plumes, I expect fairy prion reproductive success to be linked with interannual variation in the Southern Oscillation Index, sea surface temperatures, Clutha river flows and rainfall near Dunedin.

Fledging size, recapture rates and age at first recapture

After fledging, chicks from the genus *Pachyptila* spend the first three to five years of life at sea, returning to their breeding colony after this time to search for a mate and a nest site (Warham 1990). Mortality of most seabirds is highest during these first years of life, presumably due to lack of experience in foraging and navigating (Warham 1996; Hamer, Schreiber, & Burger 2002). Richdale (1965) estimated the age at first breeding for fairy prions at four to five years and the average adult mortality rate at 84%, but to date there has been no detailed study of the age of first return of fairy prions to their natal colony. Based on the relationship between seabird nestling conditions and juvenile return rates described for sooty shearwaters (Sagar & Horning 1998) and tufted puffins (Morrison *et al.* 2009), I expect that fairy prion chicks that fledge with greater mass and longer wings should have a greater chance of survival and should return to the Dunedin colony at earlier ages than smaller chicks, and that these differences would be reflected in juvenile recapture rates.

Aims

The aims of this study were to use 11 years of monitoring to:

- I. Describe the relationship between fairy prion breeding success and physical environmental factors off the coast of Otago between 2000 and 2011

- II. Describe the relationship between physical environmental factors and fairy prion fledging size between 2004 and 2011

- III. Examine the effect of fledging size on local juvenile survival and age at first return at the Dunedin colony

Hypotheses

I hypothesised that:

- I. In years of lower sea surface temperatures, fairy prion breeding success would be greater and fledglings would be larger
- II. In years of higher flow rates from the Clutha river and higher monthly rainfall, fairy prion breeding success would be greater and fledglings would be larger
- III. In La Niña years, fairy prion breeding success would be greater and fledglings would be larger
- IV. Larger fledglings would have greater survival rates and would be recaptured at the colony at higher rates and at younger ages than would smaller fledglings

METHODS

1) Study site and colony history

The fairy prion breeding data were collected at a colony near Dunedin, New Zealand, on the sea cliffs between St Clair and Tunnel Beach (45.92° S, 170.47° E). The colony is located on a ledge, measuring approximately 52 m long and up to 8 m wide, protected from mammalian predators by a 24 m overhanging sandstone cliff (Loh 2000; Figure 1).

The colony has approximately 100 natural burrows dug into the sand, inhabited exclusively by fairy prions. Since 1994, Graeme Loh of the Ornithological Society of New Zealand has installed and maintained approximately 90 artificial burrows at the colony as well. The artificial burrows are of three types: holes dug into the base of the vertical sandstone wall and covered at the entrance by carpet curtains, wooden boxes with removable lids and enough space for one pair of prions, and larger wooden boxes with five separate compartments, most with their own short tunnel entrances.

From 2001 – 2011, all adult prions that attempted to breed in the artificial burrows were banded on the right leg, with a size D stainless steel band (issued by the Banding Office at the Department of Conservation). All prion chicks in these artificial burrows were banded in mid-January of each year, with a stainless band on the left leg.

G. Loh and other volunteers (including myself) monitored Parent ID and nesting success in the artificial burrows from 2001 – 2011. From 2004 – 2011, all chicks were also measured approximately every second day from banding through the end of the nestling period for weight and wing chord. G. Loh measured most wing lengths, I measured

some, and accuracy was ensured by repeated measurements of occasional individual birds. Throughout the study G. Loh and volunteers monitored colony attendance outside the breeding season by two nightly visits each month.

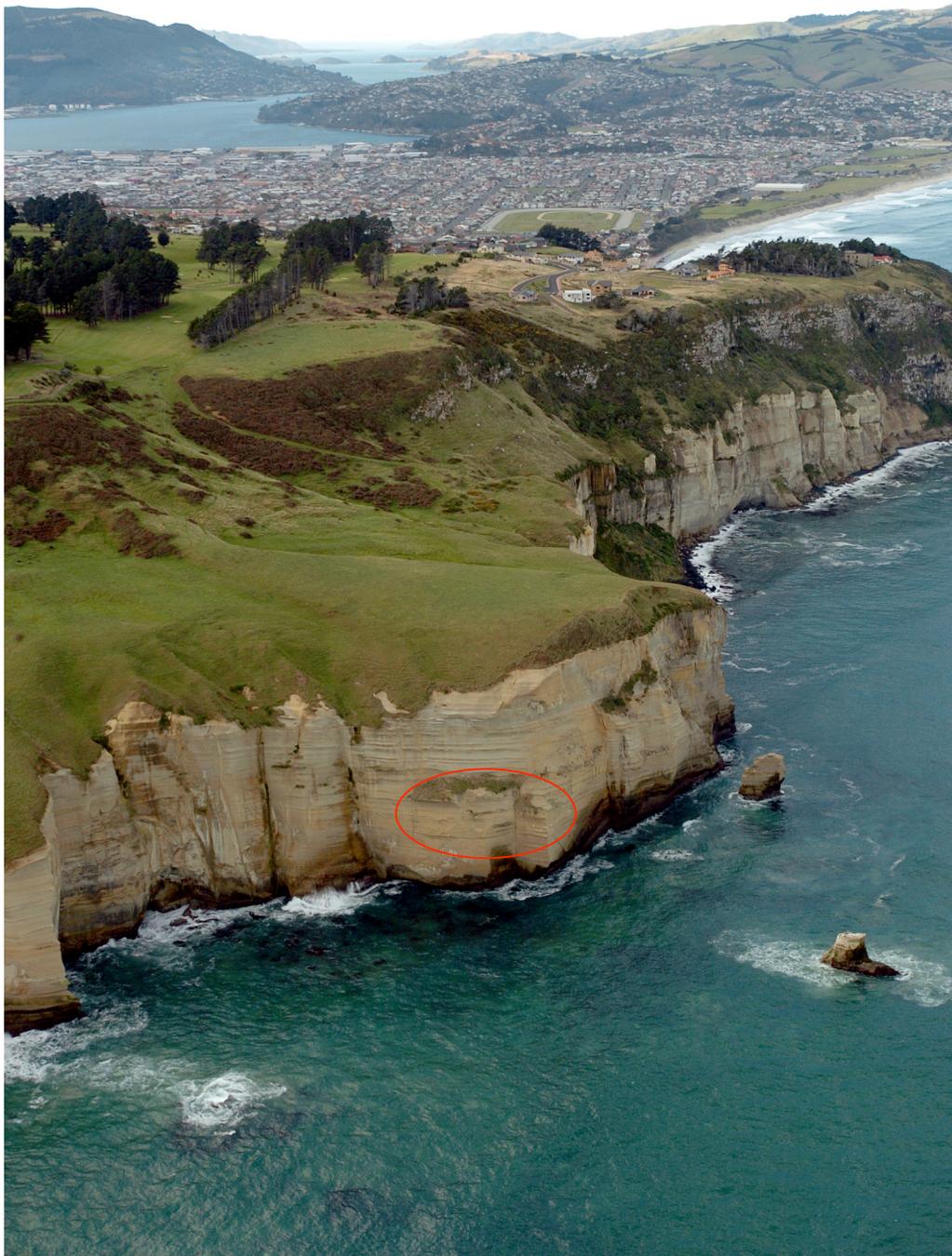


Figure 1. Photo of the study site. The fairy prion colony is circled in red; Dunedin city and the Otago Peninsula are visible in the background (source: Stephen Jacquierey, Otago Daily Times)

2) Environmental parameters

i) Sea surface temperature

Daily sea surface temperatures (SST) of ¼-degree resolution for February 2000 – January 2011 were extracted from the *SST Daily Optimum Interpolation, AVHRR Only, version 2* data set at the National Oceanic and Atmospheric Administration (NOAA) ERDDAP website (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg.html>). These *Optimum Interpolation* temperatures were obtained by combining satellite data with in-situ ship and buoy measurements (detailed in Reynolds *et al.*, 2007). For comparison with long-term mean temperatures, SST anomalies (temperatures in the area relative to the average over the base period of 1971 – 2000) were downloaded from the same website and plotted as well. The anomalies were not used for analyses; they just provided context for the current study.

The area of SST measurements was between 45.5°–46.25°S, and 170.25°–171.25° E (Figure 2). This area covers the neritic zone, from the coastline to the edge of the continental shelf and the Southland Front. Fairy prion foraging range during the breeding season is currently unknown, but, based on the homing experiment of Tickell (1962) on the closely-related Antarctic prion (*Pachyptila desolata*), Harper (1976) estimated a maximum range of 161 km for breeding fairy prions. The SST boundary used for the present study only extends 40 – 60 km from the Dunedin prion colony (Figure 2), but encompasses the mixing zone of subantarctic and subtropical water and the river plumes near the Otago Peninsula, the most important areas for the local population of *Nyctiphanes australis* (Jillett 1976; O’Driscoll 1997; Haywood 2002), the main prey item of fairy prions (Harper 1976). Daily SST values for each ¼-degree square were converted

to mean monthly SST values, which were then averaged over the entire area to obtain a mean temperature value for each month.

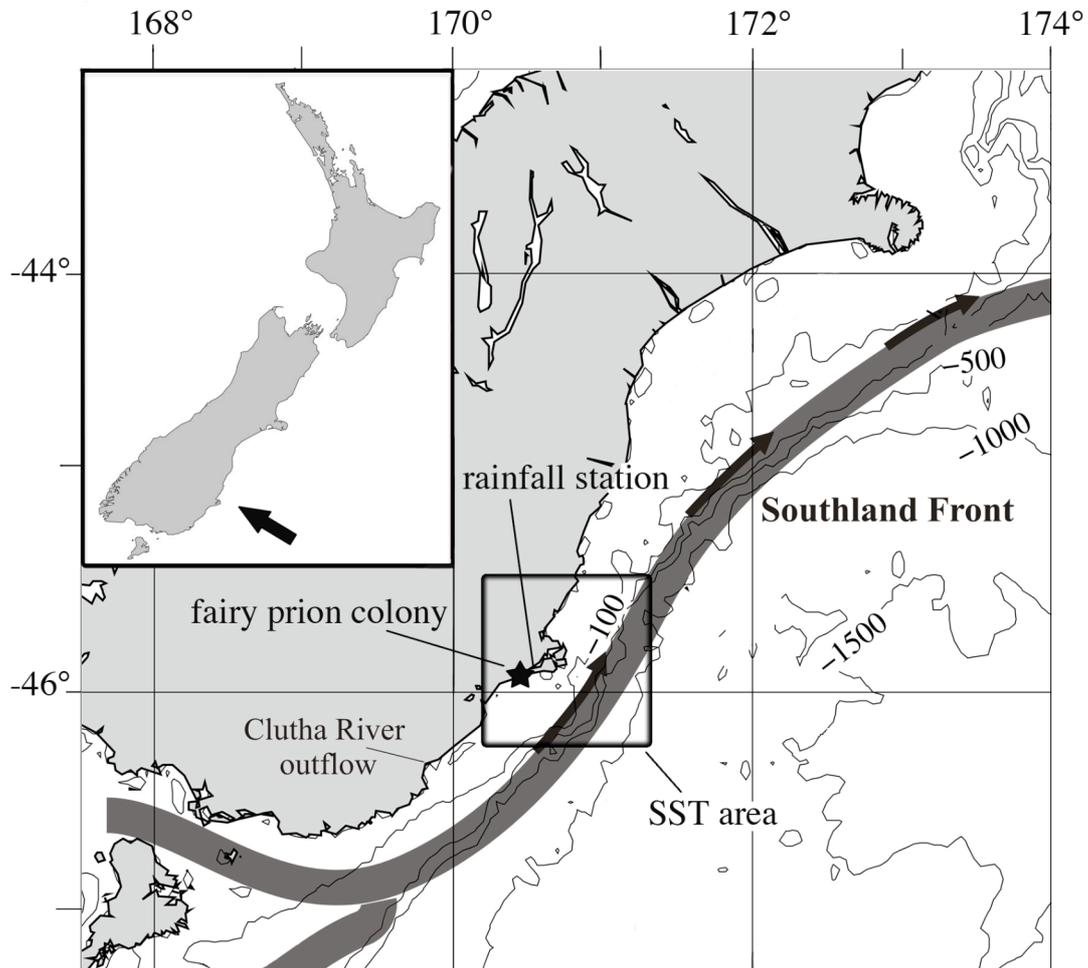


Figure 2. Location of Dunedin, New Zealand fairy prion colony at 45.92° S, 170.47° E, showing the area of sea surface temperature (SST) measurements, Musselburgh rainfall station, Clutha river outflow and the location of the Southland Front (adapted from Hopkins, Shaw, & Challenor, 2010).

ii) Clutha River flow

The Clutha River is the most important influence on surface salinity in the coastal waters near Dunedin (Jillett (1969); Figure 2). Mean monthly flow rates for the Clutha River at

Balclutha (the seaward-most flow monitoring station) were obtained from the Otago Regional Council.

iii) Rainfall

Total monthly rainfall measurements from the climate station at Musselburgh (on the Otago Peninsula; Figure 2) were downloaded from New Zealand's national climate database through the National Institute of Water and Atmosphere's Cliflo website (<http://cliflo.niwa.co.nz>).

iv) Southern Oscillation Index

Monthly Southern Oscillation Index (SOI) values (standardised Tahiti – standardised Darwin Sea Level Pressure) for 2001 – 2011 were downloaded from the NOAA Climate Prediction Center at: <http://www.cpc.ncep.noaa.gov/data/indices/soi>. A description of the SOI calculation can be found at: <http://www.cpc.ncep.noaa.gov/data/indices/Readme.index.shtml#SOICALC>.

3) Measures of reproductive performance

i) Colony breeding success

At the Dunedin colony, breeding pairs of fairy prions lay one egg in late October or early November, and the eggs hatch in mid-late December. Chicks grow to maturity through

early January and start to fledge around 20 January. Peak fledging occurs on about 26 January and most chicks have left the colony by 1 February.

For the purposes of this study, years were defined according to prion breeding seasons. Each breeding year started in February (after last year's chicks had fledged) and continued through the following January (when this year's chicks fledged).

Between 2001 and 2011, the artificial burrows were checked every fortnight through September and October, to establish the identities of the adults residing in each burrow. The burrows were checked once at the beginning of November and again a week later, to determine which pairs had laid eggs; another check in late December established hatch rates. Nests were left undisturbed through most of the incubation and hatching period to minimise investigator disturbance. If a burrow that had an egg in November was found empty in late December, the nest was assumed to have failed at the egg stage. For nests that failed post-hatching, in most cases a small chick carcass was found in the burrow. Presence of an eggshell only was taken to mean the egg had hatched, but the chick had died during hatching or shortly thereafter.

Colony breeding success was measured as the overall proportion of eggs laid at the colony that survived through hatching to fledge a chick. Hatching success was not estimated due to the infrequency of checks around hatching time.

ii) Chick measurements

From 2004, we measured wing chord and mass of fairy prion chicks in the artificial burrows every one to five days, during daylight hours, between 18 January and 6

February. Wing chord was the measure from the bend of the closed wing to the end of the longest primary, with the wing flattened and the feathers straightened. Wings were measured to the nearest millimetre on a 200-mm ruler. Chicks were weighed to the nearest gram using digital scales. No chicks regurgitated during measurement, but some defecated. The final measurements of each chick before the nest was found empty were taken as the fledging measurements. In order to increase precision in these data, I discarded chick measurements from boxes that went unchecked for more than three days near fledging. Chicks that fledged after the first week in February were also excluded from the analyses because nest checks were sporadic after this time.

4) Monitoring juvenile recaptures and age at first return

The fairy prions near Dunedin visit the colony year-round, except for the period immediately after breeding, when they leave to moult for two to three months, returning to the colony in late March or April (G. Loh, pers. comm). From 2004 – 2011, G. Loh and volunteers visited the Dunedin colony at least twice a month, near the new moon, to check for juvenile returns throughout the non-breeding season. These checks were carried out after dark, generally between the hours of 21:00 h and 02:00 h. On the first of the monthly visits, all boxes were checked for banded birds; on the second and subsequent visits, boxes that contained fewer than two birds on the first visit were re-checked. Band records of birds present outside the burrows were also collected opportunistically during the nighttime visits. In 2006, the boxes went unchecked for three months between June and August; this was the only substantial interruption in the monthly checks throughout the study.

Because of the reliance on volunteer effort, the steepness of the terrain and the delicate construction of the natural burrows, there was no way of checking the natural burrows or of recording every returning fledgling; I assume our chance of re-sighting any individual fledgling was equivalent to re-sighting any other fledgling present at the colony at any given time, so I do not think this is a source of bias.

Prion chicks that hatched at the colony were first recaptured when they were between two and six years old, so only fledglings from the 2004 and 2005 cohorts were included in the analyses to avoid biasing the data towards young birds.

5) Statistical analyses

i) Environmental influence on breeding success and chick morphometrics

ANOVA were used to test for differences in fledgling measurements (mass and wing length) between years; Tukey's Honest Significant Differences (HSD) were used for post-hoc analyses.

In order to determine which months of climate data were most relevant to breeding fairy prions, correlation analyses were performed between annual colony breeding success rates, annual mean chick mass, annual mean chick wing length and the environmental variables for each month of the breeding year, following the methodology of Cullen *et al.* (2009). Pearson's product-moment correlation (r) was used for the parametric statistics (wing length and mass) and Spearman's rank correlation (ρ) was used for the non-parametric analyses (breeding success). The data set for breeding success spanned all

years from 2001 – 2011; the mass and wing length data were only gathered from 2004 – 2011.

Because of the large number of statistical tests performed on the fairy prion data, there was a high probability of committing a Type I error. I did not use Bonferroni corrections, however, because of the increased chance of Type II error with this approach (Nakagawa 2004). The issue of multiple statistical testing is a contentious one; I decided to take the advice of Rosenthal (1978), described in Moran (2003):

“One significant test with a relatively large p-value (e.g. 0.025) in a large table would certainly be suspect. However, many significant results in a table indicate something important is occurring... several relatively high p-values are stronger evidence against a null hypothesis than one moderately low value”

I used caution when interpreting the uncorrected p -values, looking instead for multiple related significant results, examining effect sizes as well as significance values (looking for two or more consecutive months with ρ or $r > 0.7$) and discarding significant relationships that didn't logically follow from what I know about the system.

I used an information-theoretic approach to evaluate the relationships between the environmental data and the prion breeding data, adapting the methods of Cullen *et al.* (2009). All predictor variables were z-transformed (to a mean of 0 and standard deviation of 1) prior to modelling to make intercepts meaningful and allow comparisons between model coefficients (Schielzeth 2010; Grueber *et al.* 2011). Linear mixed models were fitted to all combinations of the relevant environmental predictors as well as null models, using the *lmer* function from the *lme4* package in R 2.14 (R Development Core Team 2011). Parental characteristics such as age, experience and quality have a strong effect on nest success and chick sizes in Procellariiformes (Wooller *et al.* 1990; Weimerskirch 1990; Mauck, Huntington, & Grubb Jr. 2004; Silva *et al.* 2007), so parent

ID was included as a random effect to control for the association of chicks from the same parents. All models were built using Maximum Likelihood, and Akaike's Information Criterion (AIC) was used to compare models. The top model set was comprised of all models with $\Delta AIC_c < 2$ (Burnham & Anderson 2002).

ii) Chick morphometrics and juvenile recapture rates

Colony attendance records from 2006 – 2011 were analysed to determine recapture rates and age at first return for the 2001 – 2005 cohorts. An information-theoretic approach was used to compare the effects of cohort, fledging wing length and fledging weight on: *a)* likelihood of recapture, and *b)* age at first recapture. All predictor variables were z-transformed, and generalised linear mixed models were fitted to the data using the *glmer* function from the *lme4* package in R. A logit-link function was added for the binomial data (recapture) and a log-link function was used for the count data (age). Parent ID was included in the models as a random effect, to account for association of offspring from the same parents. Models including all possible combinations of the predictor variables, as well as null models, were compared using AIC_c . The top model set was comprised of all models with $\Delta AIC_c < 2$ (Burnham & Anderson 2002). Differences between cohorts in fledging wing length, mass and age at first recapture were assessed with Mann-Whitney U-tests. All means are presented ± 1 SD (standard deviation).

RESULTS

1) Environmental parameters

i) Sea surface temperature

Annual low sea surface temperatures in the study area occurred in August, and measured between 8.8°C and 9.8°C; annual high temperatures occurred in February and ranged from 12.9°C – 14.6°C (Figure 3a). Within the breeding season (egg laying – chick fledging), the overall minimum temperature was 9.6°C (recorded in October 2005) and the overall maximum (in January 2006) was 14.3°C. The extreme low SST anomaly occurred in January 2005 and the extreme high anomaly occurred in September 2001 (Figure 3b).

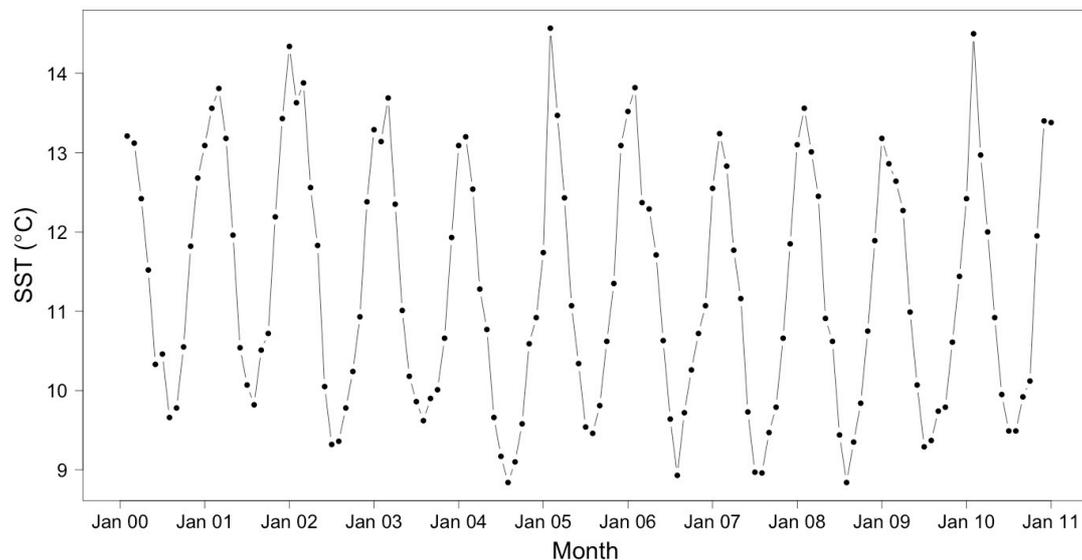


Figure 3a. Monthly mean sea surface temperatures (SST) off the coast of Dunedin, New Zealand (between 45.5°–46.25°S and 170.25°–171.25° E), from 2000 – 2011 (source: NOAA)

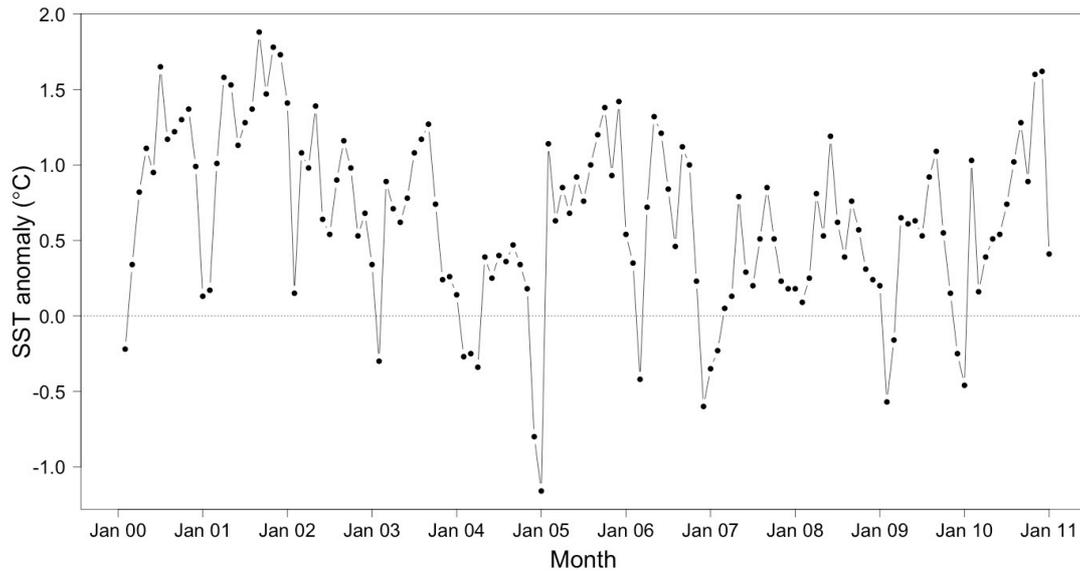


Figure 3b. Monthly mean sea surface temperature (SST) anomalies (computed relative to the base period of 1971 – 2000) off the coast of Dunedin, New Zealand (between 45.5°–46.25°S and 170.25°–171.25° E), from 2000 – 2011 (source: NOAA)

ii) Clutha River flow

Monthly river flows for the Clutha were less seasonal than the SST measurements; low values generally occurred between February and April, but annual highs occurred at any time of year (Figure 4). Overall, the minimum monthly flow rate of 281 cumecs was recorded in April 2003, and the maximum monthly flow rate of 1031 cumecs occurred in June 2000. The flow rate for January 2009 was unavailable.

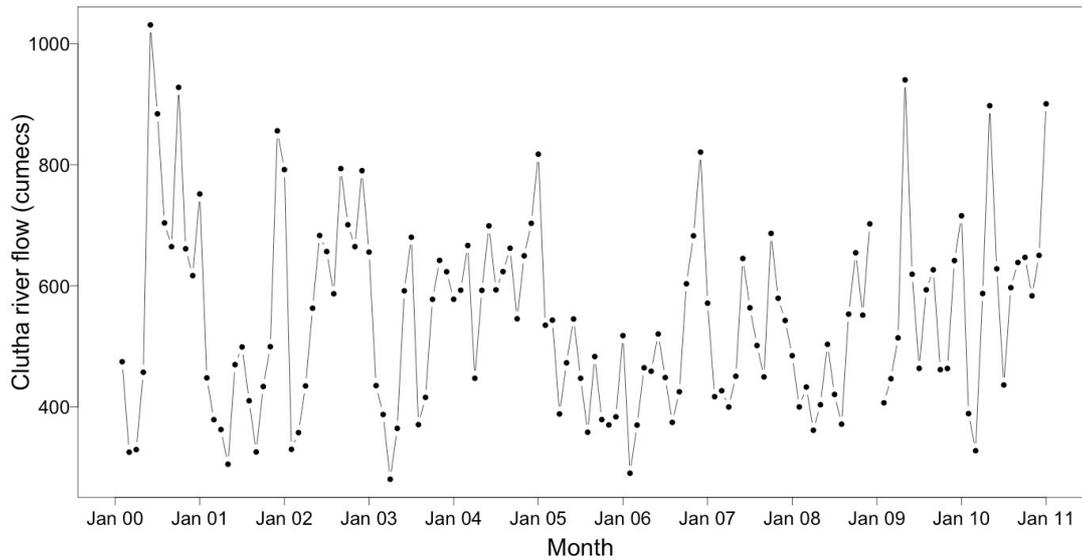


Figure 4. Monthly mean river flows (cumecs) recorded at the Balclutha flow station on the Clutha River, Otago, New Zealand from 2000 – 2011 (source: Otago Regional Council)

iii) Rainfall

Monthly rainfall extremes between 2000 and 2011 occurred at any time of year.

Minimum values ranged from 2 mm to 24 mm, and maximum values were between 61 mm and 168 mm (Figure 5). The overall minimum monthly rainfall occurred in March 2001 and the overall maximum occurred in May 2009. May 2000 measurements were unavailable.

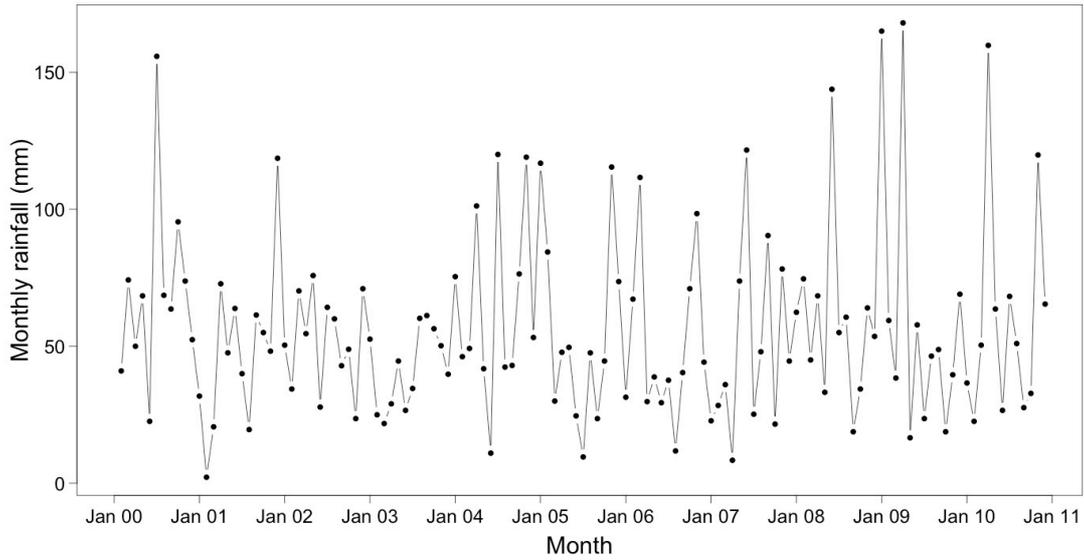


Figure 5. Total monthly rainfall recorded at the weather station in Musselburgh, Otago Peninsula, New Zealand from 2000 – 2011 (source: NIWA)

iv) Southern Oscillation Index

La Niña events occurred in 2000-01, 2007-08, and 2010-11; El Niño events occurred in 2002-03, 2004-05, 2006-07 and 2009-10 (Figure 6).

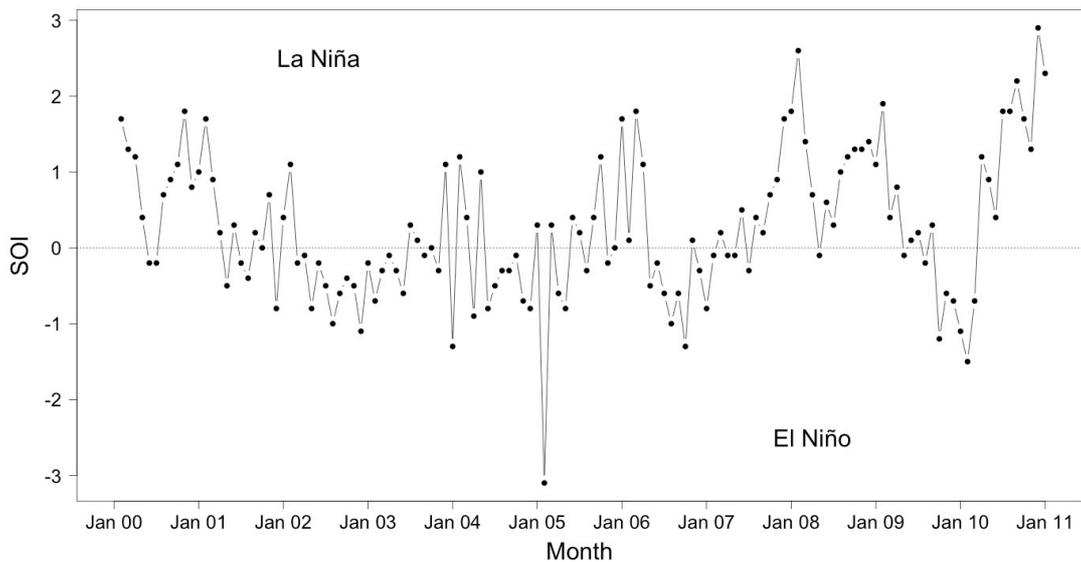


Figure 6. Monthly values for the Southern Oscillation Index (standardised Tahiti – standardised Darwin sea-level pressure) from 2000 – 2011 (source: NOAA)

2) Influence of environmental parameters on reproductive performance

i) Colony breeding success

All nest failure occurred in the egg stage or within the first week following hatch. The one exception was a chick in 2001 that remained at the colony after peak fledging and was found dead in its burrow in mid-February, after having dropped to a mass of 55 g. Annual nest success rates (number of chicks fledged ÷ number of eggs laid at the colony) were fairly consistent between 2001 and 2011, ranging between 0.73 and 0.88 chicks per pair (mean=0.80±0.05, $n=11$ years; Figure 7).

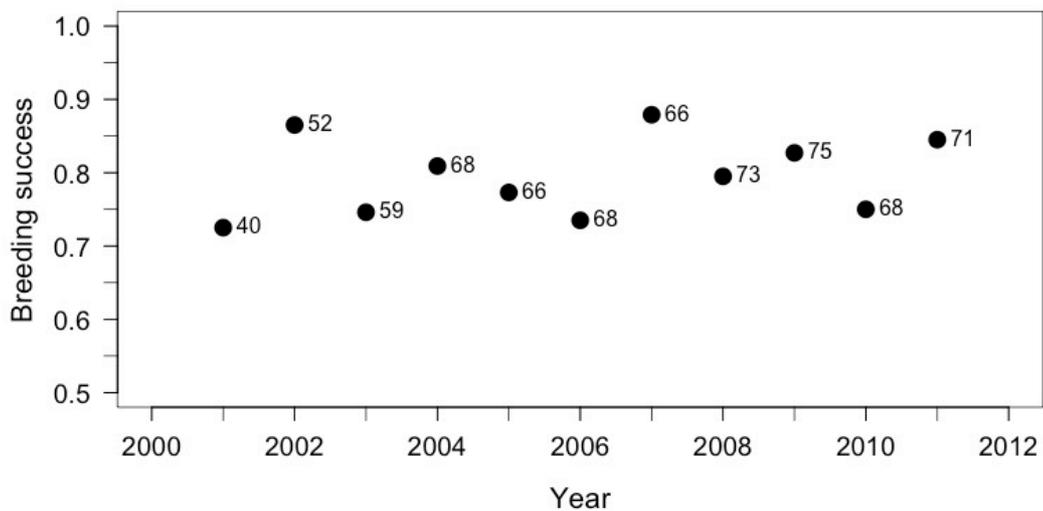


Figure 7. Annual colony breeding success (total no. chicks fledged ÷ total no. eggs laid in the artificial burrows) at the fairy prion colony near Dunedin, New Zealand, from 2001 – 2011 (number of eggs laid each year is indicated next to dots; 706 breeding attempts in total)

The only statistically significant relationship between fairy prion breeding success and the measured environmental parameters was a negative correlation with September flows in the Clutha River (Table 1). Because this was the lone significant ($p<0.05$) relationship in

the entire table, the result was discarded as a likely Type I error due to multiple statistical testing.

Table 1. Relationships between monthly environmental parameters and fairy prion breeding success (total no. chicks fledged ÷ total no. eggs laid) at the Dunedin colony from 2001 – 2011 (Spearman’s rank correlation coefficient; * $p < 0.05$). SST = monthly mean sea surface temperature near Dunedin, Clutha = mean monthly flow rates in the Clutha River, Rainfall = total monthly rainfall at Musselburgh, SOI = Southern Oscillation Index values ($n = 706$ nests)

	SST	Clutha	Rainfall	SOI
January	0.145	0.103	-0.182	-0.027
February	0.200	-0.464	-0.518	-0.014
March	-0.245	-0.136	-0.464	0.169
April	-0.036	0.200	0.009	0.267
May	0.036	-0.327	-0.030	0.000
June	0.327	-0.645	-0.364	0.170
July	0.127	-0.455	0.492	0.055
August	-0.118	-0.282	-0.027	-0.041
September	0.100	-0.627*	-0.427	-0.110
October	0.036	-0.173	-0.164	-0.068
November	0.100	0.082	-0.064	0.187
December	-0.036	0.600	0.145	0.196

ii) Chick measurements

(a) Fledging mass

Mean chick mass at fledging was 124 ± 12 g ($n=406$). Masses were significantly different between years (ANOVA, $F=3.25$, $p=0.002$, $df_{7,398}$; Figure 8). There were only three significant pairwise comparisons, though: 2006:2008 ($p=0.044$), 2006:2011 ($p=0.002$) and 2007:2011 ($p=0.043$) (Tukey’s HSD).

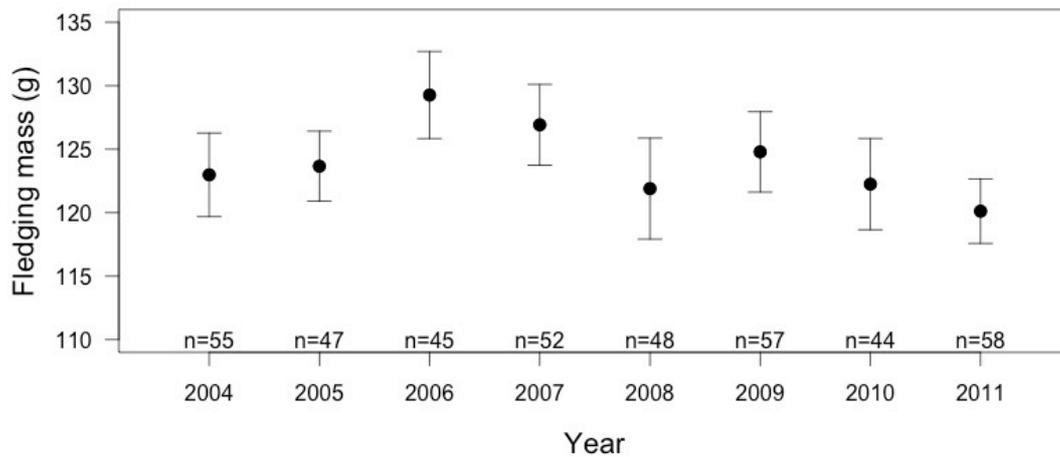


Figure 8. Annual mean fledgling mass (g) of chicks at the fairy prion colony near Dunedin, New Zealand, from 2004 – 2011; whiskers represent 95% confidence intervals ($n=406$ chicks total)

Correlation analyses of fledgling mass and environmental parameters resulted in only one statistically significant test (March rainfall) (Table 2); this result was likely a Type I error from repeated statistical testing.

Table 2. Relationships between environmental parameters and fairy prion fledgling mass at the Dunedin, New Zealand colony between 2004-2011 (Pearsons product-moment correlation coefficient; $*p<0.05$); $n=406$ chicks. See Table 1 for environmental parameter definitions

	SST	Clutha	Rainfall	SOI
January	0.101	-0.547	0.149	-0.068
February	0.375	0.151	0.207	-0.287
March	0.127	0.343	0.837*	0.578
April	0.407	-0.369	0.260	-0.294
May	0.425	-0.528	-0.474	-0.680
June	0.625	-0.623	-0.232	0.010
July	0.318	-0.273	-0.151	-0.470
August	-0.140	-0.689	-0.315	-0.620
September	-0.010	-0.424	-0.374	-0.428
October	0.646	-0.555	-0.411	-0.100
November	-0.101	-0.338	0.416	-0.297
December	-0.041	-0.233	0.250	-0.521

(b) *Fledging wing length*

Mean chick wing length at fledging was 174 ± 5 mm, $n=406$). Fledging wing lengths were significantly different between years (ANOVA, $F=3.12$, $p=0.0032$, $df_{7,398}$; Figure 9). The only years that were significantly different from each other at the 5% level were 2005:2009 ($p=0.025$) and 2005:2011 ($p=0.0037$) (Tukey's HSD).

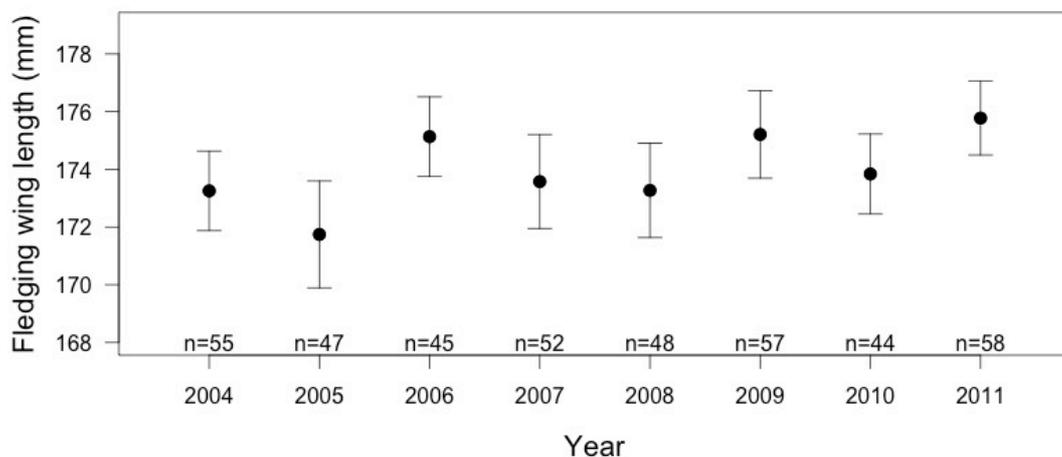


Figure 9. Annual mean fledging wing length (mm) of chicks at the fairy prion colony near Dunedin, New Zealand, from 2004 – 2011. The whiskers indicate 95% confidence limits ($n=406$ chicks total)

Fledging wing lengths were positively correlated with SSTs in multiple months throughout the summer, and with the SOI through late winter and spring (Table 3). Wing lengths were also negatively correlated with July Clutha River flows, but because this was a solitary significant result among many nonsignificant tests, the river correlation was discarded as a likely Type I error.

Table 3. Relationships between environmental parameters and fairy prion fledging wing lengths at the Dunedin, New Zealand colony between 2004-2011 (Pearsons product-moment correlation coefficient; * $p < 0.05$); $n = 406$ chicks. See Table 1 for environmental parameter definitions

	SST	Clutha	Rainfall	SOI
January	0.806*	0.097	0.541	0.524
February	0.705	-0.337	0.046	-0.318
March	0.341	-0.523	0.245	-0.101
April	0.640	0.247	-0.075	0.536
May	-0.021	0.217	0.249	-0.197
June	0.473	-0.563	0.108	0.786*
July	0.304	-0.724*	0.227	0.741*
August	0.368	-0.269	-0.392	0.601
September	0.531	0.046	0.273	0.804*
October	0.572	-0.009	-0.584	0.615
November	0.747*	-0.513	-0.518	0.640
December	0.808*	-0.279	0.090	0.569

The most significant correlations between SST and fledging wing length occurred between November and January; the greatest effect size of the Southern Oscillation Index on fledging wing length occurred between June and September (Table 3). Because of the number of significant tests in consecutive months with these variables, I decided to use the SST and SOI data for model selection.

The global model was of the form:

$$Y_i = (a + \beta_{\text{ParentID}_i})_{\text{(Intercept)}} + b_1 \text{SST}_{m1i} + b_2 \text{SST}_{m2i} + b_3 \text{SST}_{m3i} + b_1 \text{SOI}_{m1i} + b_2 \text{SOI}_{m2i} + b_3 \text{SOI}_{m3i} + b_4 \text{SOI}_{m4i} + \epsilon_{\text{resid}.i}$$

$$\beta_{\text{ParentID}_i} = N(0, \sigma_{\beta_0}^2)$$

$$\epsilon_{\text{resid}.i} = N(0, \sigma_{\epsilon}^2)$$

Where Y_i is the predicted fairy prion wing length in year i , $\beta_{\text{ParentID}_i}$ is the identity of the parents, SST_{m1i} is the mean monthly SST value in month $m1$ for year i , ..., SST_{m3i} is the mean monthly SST value in month $m3$ for year i , $b_1 \text{SOI}_{m1i}$ is the mean monthly SOI value

in month $m1$ for year i , ..., and $b_4\text{SOI}_{m4i}$ is the mean monthly SOI value in month $m4$ for year i . Given that the highest correlations between SST and wing length occurred in the summer and the highest correlations for SOI occurred in late winter, for the SST variables, $m1 = \text{November}$, $m2 = \text{December}$ and $m3 = \text{January}$, and for the SOI variables, $m1 = \text{June}$, $m2 = \text{July}$, $m3 = \text{August}$ and $m4 = \text{September}$. Upon examination of the model set, I realised that the models including more than one SST or SOI variable would violate one of the assumptions of regression analysis (linear independence of predictor variables). All models including more than one predictor variable were thus eliminated from the model set, to avoid the issue of multicollinearity. The linear mixed effects models for predicting fledging wing length are presented in Table 4.

Table 4. Support for linear mixed models predicting fairy prion fledging wing length in relation to late winter measurements of the Southern Oscillation Index (SOI) and summer Sea Surface Temperatures (SST). Predictor variables were standardised using z-transformation and ParentID was included as a Random Effect in each model. K is the number of parameters in the model, $\log(L)$ is the log likelihood, AIC_c is Akaike's information criterion and ΔAIC_c is the difference between the AIC of each model and that of the top model ($n=406$ chicks).

Model	K	$\log(L)$	AIC_c	ΔAIC_c
SeptSOI+(1 ParentID)	4	-1250.69	2509.47	0.00
JuneSOI+(1 ParentID)	4	-1252.19	2512.47	3.00
DecSST+(1 ParentID)	4	-1252.68	2513.46	3.99
JulySOI+(1 ParentID)	4	-1252.93	2513.96	4.48
JanSST+(1 ParentID)	4	-1253.21	2514.53	5.06
NovSST+(1 ParentID)	4	-1253.29	2514.69	5.22
AugSOI+(1 ParentID)	4	-1254.76	2517.62	8.15
1+(1 ParentID)	3	-1260.74	2527.54	18.07

The top model for predicting fledging wing length included September SOI as a predictor variable. No other models had ΔAIC_c values of less than two (Table 4).

3) Influence of fledging size on recapture rates and age at first recapture

i) Recapture rates and age at first recapture

Two hundred twenty-seven chicks were banded at the Dunedin colony between 2001 and 2005. Of these, 97 (43%) were recaptured at the colony by the end of 2011.

Ninety-four of the 97 birds (97%) were first recaptured between the ages of one and six years; the remaining three birds were recaptured at seven and nine years old (Figure 10).

Based on these recapture rates and considering that we did not collect chick measurements prior to 2004, I decided to use the six-year recapture rates of the 2004 and 2005 cohorts for the modelling.

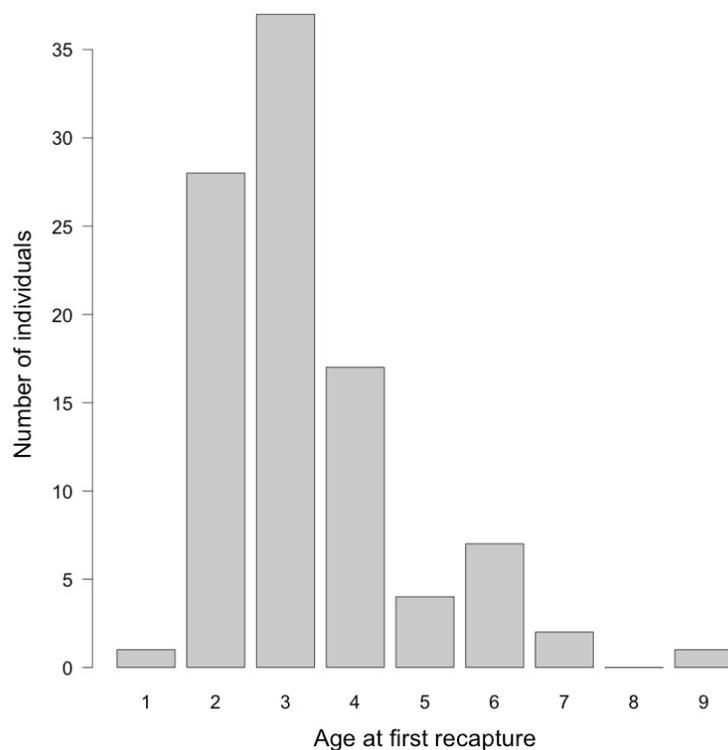


Figure 10. Number of individuals of each age class from the 2001-2005 cohorts of fairy prions first recaptured at their natal colony near Dunedin, New Zealand, between 2002 and 2011 ($n=97$ birds)

Fairy prion fledging mass was similar in both 2004 and 2005 (Mann-Whitney U test; $U=1206$, $\xi=0.581$, $p=0.564$, $r=-0.058$); wing length at fledging was also similar between years (Mann-Whitney U test; $U=1473$, $\xi=1.214$, $p=0.226$, $r=0.120$). Wing length and mass were positively correlated (Spearman's rank correlation, $\rho = 0.197$, $p = 0.047$; Figure 11), so any models incorporating both of these measurements together were removed from the model set.

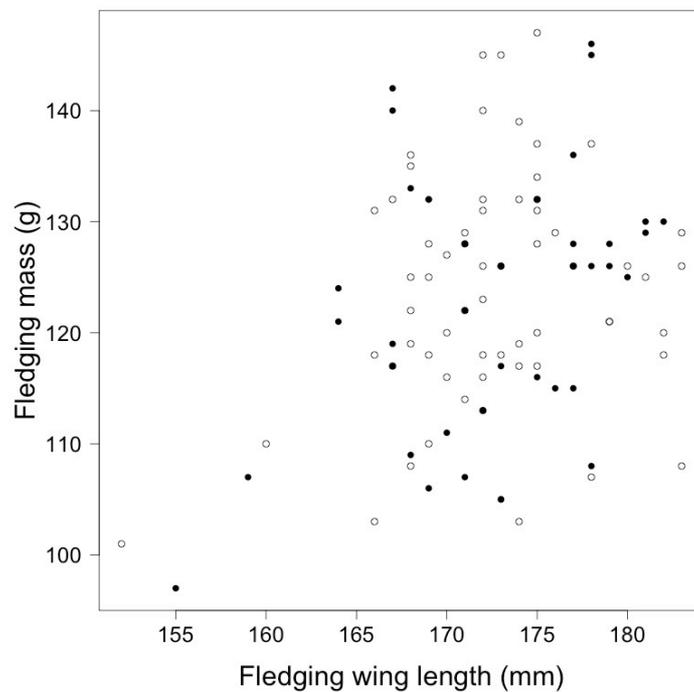


Figure 11. Relationship between wing length (mm) and mass (g) of the 2004 and 2005 cohorts of fairy prion fledglings at the Dunedin, New Zealand colony. Solid circles represent birds that were recaptured at the colony within six years; empty circles represent birds that were not seen again within six years

a) *Fledging size and recapture rates*

Five fledglings from the 2005 cohort were removed from the regression analyses because measurements were missing from these birds. The top model for predicting likelihood of recapture of a juvenile from the 2004 and 2005 cohorts included a single predictor variable, Year (cohort); other models with $\Delta AIC_c < 2.1$ were the null model, the model including fledging mass and cohort, and the model incorporating wing length and cohort (Table 5). The top model reflects the different recovery rates from the two cohorts: twenty-six out of the 55 fledglings of the 2004 cohort (47%) were recaptured at the colony within the following six years (2005 – 2010), but only 14 of 47 fledglings (30%) of the 2005 cohort were recaptured between 2006 and 2011. There was no significant difference in fledging mass between the birds that were recaptured and those that were not (Mann-Whitney U test; $U=1314.5$, $\hat{\alpha}=0.511$, $p=0.612$, $r=0.051$), nor was there a significant difference in fledging wing lengths between the two groups (Mann-Whitney U test; $U=1215.5$, $\hat{\alpha}=-0.168$, $p=0.868$, $r=-0.017$) (Figure 11).

Table 5. Support for generalised linear mixed models predicting likelihood of recapture of the 2004 and 2005 cohorts of Dunedin, New Zealand fairy prions, in relation to cohort (Year), fledging mass (Weight), and fledging wing length (Wing), including ParentID as a random effect; ‘1’ is the null model. K is the number of parameters in the model, $\log(L)$ is the log likelihood, AIC_c is Akaike’s information criterion and ΔAIC_c is the difference between the AIC of each model and that of the top model. ($n=102$ fledglings)

Model	K	$\log(L)$	AIC_c	ΔAIC_c
Year + (1 ParentID)	3	-66.62	139.48	0.00
1 + (1 ParentID)	2	-68.30	140.72	1.24
Weight + Year + (1 ParentID)	4	-66.46	141.33	1.85
Wing + Year + (1 ParentID)	4	-66.58	141.57	2.09
Weight + (1 ParentID)	3	-68.12	142.48	3.01
Wing + (1 ParentID)	3	-68.30	142.84	3.36

The six-year recovery rate for the 2005 cohort was unusually low. Before removal of the birds with missing measurements, six-year recapture rates were between 40% and 50% (mean=45±3%) for the 2001 – 2004 cohorts, but only 27% of birds from the 2005 cohort were recaptured by 2011 (Figure 12). Fledging wing lengths from this 2005 cohort were also significantly shorter than the average over all other years from 2004 – 2011 (2005 wings: 172±6 mm, other years: 174±5 mm; Mann-Whitney U test; $U=10569$, $\chi=2.824$, $p=0.005$, $r=0.140$).

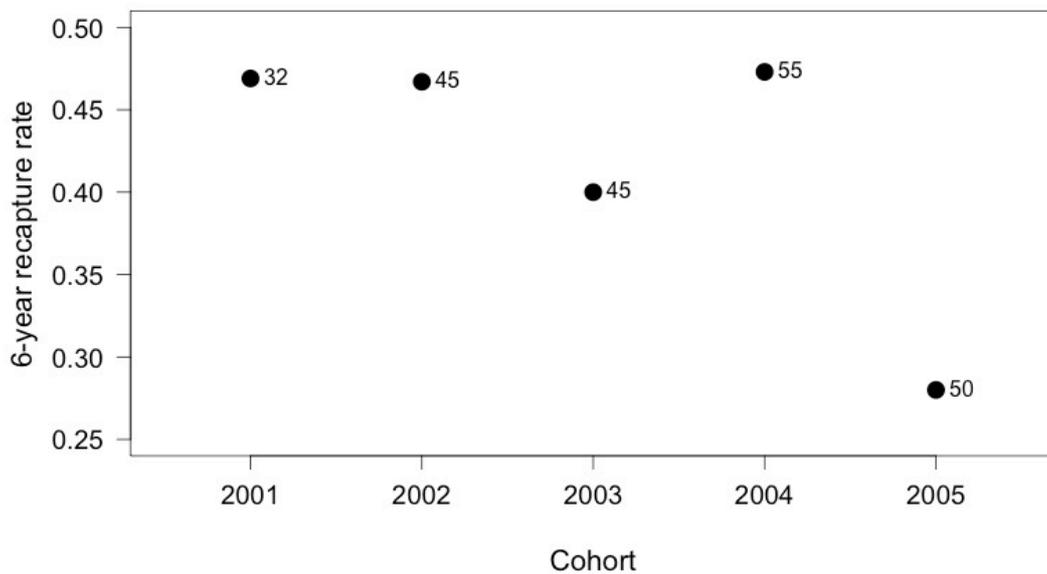


Figure 12. Six-year recapture rates for the 2001 – 2005 cohorts of fairy prions at the Dunedin, New Zealand colony. Total numbers of chicks fledged from the colony in each year are indicated next to the dots

b) Fledging size and age at first recapture

The age at first recapture of the 40 resighted individuals from the 2004 and 2005 cohorts ranged from two to six years: 28% of recaptured birds were first caught when two years old, 45% were three years old, 18% were four years old, and the remaining 10% were five

or six years old. The median age at first recapture was not significantly different between the two cohorts (Mann-Whitney U test, $U=219.5$, $z=1.132$, $p=0.265$, $r=0.179$)

The top model for predicting age at first recapture was the null model; the wing length and the weight models were also part of the top model set ($\Delta AIC_c < 2$; Table 6). Because the lowest AIC value actually belonged to the null model, there is little evidence that either of the fledging measurements had much influence on age at first recapture.

Table 6. Support for generalised linear mixed models predicting age at first recapture of the 2004 and 2005 cohorts of fairy prions at Dunedin, New Zealand, in relation to cohort (Year), fledging mass (Weight) and fledging wing length (Wing). K is the number of parameters in the model, $\log(L)$ is the log likelihood, AIC_c is Akaike's information criterion and ΔAIC_c is the difference between the AIC of each model and that of the top model ($n=40$ resighted individuals)

Model	K	$\log(L)$	AIC_c	ΔAIC_c
1 + (1 ParentID)	2	-6.97	18.25	0.00
Wing + (1 ParentID)	3	-6.06	18.78	0.52
Weight + (1 ParentID)	3	-6.77	20.22	1.96
Year + (1 ParentID)	3	-6.93	20.52	2.27
Wing + Year + (1 ParentID)	4	-6.01	21.17	2.92
Weight + Year + (1 ParentID)	4	-6.73	22.60	4.35

DISCUSSION

The fairy prion breeding parameters measured in this study were remarkably consistent between 2001 and 2011. Colony breeding success rates (no. of young fledged \div no. of eggs laid) were steady at around 80% throughout the duration of this study, and these breeding success rates were unrelated to fluctuations in Clutha River flows, rainfall measurements, sea temperatures or SOI values. Most of the differences in annual breeding success at the fairy prion colony were due to mortality at the egg stage, or shortly after hatching, which is consistent with the pattern for other Procellariiformes (Warham 1990). Fairy prion chick fledging masses were also similar from year to year, with very few interannual differences and only a few significant relationships between fledging mass and any of the environmental parameters. Many seabirds can maintain constant levels of parental care and breeding productivity over a wide range of food abundance by adjusting their foraging effort, prey species and nestling periods, thus “buffering” the effects of prey fluctuations (Cairns 1988; Burger & Piatt 1990; Bryant, Jones, & Hipfner 1999; Piatt 2007; Quillfeldt *et al.* 2007). The range of food abundance near Dunedin may be such that fairy prions are able to maintain consistent reproductive output using these behavioural buffering mechanisms.

Other *Pachyptila* species show limited sensitivity to environmental variability and krill abundance in terms of their breeding biology. Thin-billed prion breeding success was steady over a period of severely diminished food availability at the Falkland Islands, but feeding rates and chick masses were depressed in poor years (Quillfeldt *et al.* 2007).

Liddle (1994) found that Antarctic prions (*Pachyptila desolata*) had remarkably steady chick growth and survival rates through fluctuating abundance of Antarctic krill (*Euphausia superba*) at Bird Island, South Georgia, and postulated that this was because

Antarctic prions have palatal lamellae, which allow them to sieve out smaller prey like copepods, when krill are unavailable. Fairy prions lack palatal lamellae, so they are unable to feed on small particles (Morgan & Ritz 1982), but they do eat prey other than *Nyctiphanes australis* (see Croxall & Prince 1980), and it is plausible that they may switch to other food such as *Parathemisto gracilipes* or small fish or squid when *Nyctiphanes* are unavailable.

Walls (1978) proposed that the demographics of fairy prions on Stephens Island, New Zealand were mainly limited by nest site availability and mass mortality events. Mass mortality events (prion “wrecks”) occur frequently in New Zealand, and are associated with extended periods of severe weather, which lead to death of birds through starvation and fatigue (Powlesland 1989; Warham 1990). In other New Zealand colonies, competition for suitable burrows is fierce; early in the season fairy prion colonies contain a large number of non-breeding birds (the “unemployed population”) each year in addition to the breeding population, and these unemployed birds are evicted from nest cavities when established breeders return (Richdale 1965; Harper 1976; Walls 1978). This nest site limitation is probably also in effect at the colony in Dunedin, where new nest boxes are inhabited often within a week of installation (G. Loh, pers. comm.). Some birds may move to nearby colonies when the main ledge is overcrowded, but the availability of suitable burrows in predator-free areas on the sea cliffs near Dunedin is limited. If the Dunedin fairy prions are more limited by nest site availability than they are by food availability, we may not observe much variation in breeding parameters between years.

Environmental influence on fledging wing length

Fairy prion fledging wing lengths were significantly different between years, but these differences were slight; the mean fledging wing lengths of chicks differed by less than 5 mm in most years, and there were only two significantly different inter-year comparisons (2005:2009 and 2005:2011). The biological significance of this variation is unclear, but a similar scale of wing length variability has been linked to variability in juvenile survival of the tufted puffin, probably through early flight capability for foraging and avoidance of predators (Morrison *et al.* 2009). Summer water temperatures throughout the egg and chick phases were linked with fledging wing lengths, but the direction of the correlation was not as predicted (I expected prion wing lengths to be longer in years of lower SST, but the reverse was true). This could be due to the fact that summer water temperatures near Dunedin ranged between 9.6°C and 14.3°C, often falling below *Nyctiphanes* optimal temperature range of 12°C – 18°C (Sheard 1953), which may mean that *Nyctiphanes* are never heat-stressed in Dunedin waters during the summer months, but that they may be limited by cold waters in winter. If higher summer water temperatures were associated with greater prey availability throughout the fairy prion breeding season, feeding rates of adults and growth of chicks would be positively correlated with SSTs throughout the entire summer. The breeding success and fledging masses do not follow this pattern, but the fledging wing lengths do.

In a survey of *Nyctiphanes australis* near Dunedin, Haywood (2002) found that they were more abundant in the La Niña year of 1996-97, a relatively cold year (13-14°C along the survey transect) compared to the following El Niño year of 1997-98 (14-15°C). The fledging wing lengths measured in the present study agree with the La Niña trend, but are inconsistent with the SST trend. A plausible explanation involves the scale of

observation. Haywood (2002) measured temperature over one transect across the Southland Front and at intervals a month or more apart; for the present study, the remotely-sensed SST measurements were computed daily and combined into monthly averages over a much larger area. Haywood (2002) also measured elevated sea surface temperature in El Niño years, but during the present study El Niño was associated with colder sea temperatures, implying that the temperature effect of the SOI may also be scale-dependent.

Late-winter (particularly September) Southern Oscillation Index (SOI) values were positively correlated with fairy prion fledgling wing lengths at the Dunedin colony; in years where the SOI was positive (La Niña years), chicks fledged with longer wings and in negative SOI (El Niño) years, fledglings' wings were shorter. The 1988 La Niña was associated with warm waters and lower *Nyctiphanes* numbers on the Tasmanian shelf, but in that year the shelf waters passed above 18°C (Harris *et al.* 1991), too hot for *Nyctiphanes australis* (see Sheard 1953). Since the waters near Dunedin never reached 18°C, La Niña might have a different effect on the euphausiids in this system. Wind-driven mixing of waters is extremely important to phytoplankton production and *Nyctiphanes* abundance over the Tasmanian Shelf (Harris *et al.* 1991). La Niña conditions have been associated with greater availability of euphausiids off the Kaikoura coast, possibly due to increased northeasterly winds (Mullan 1995) and subsequent increases in upwelling and food availability to euphausiids (Mills *et al.* 2008). A similar process could be occurring near Dunedin, leading to greater availability of *Nyctiphanes australis* and an increase in fairy prion fledgling growth in La Niña years.

Knowledge of the relationship between the El Niño Southern Oscillation and the Southland Front is important to understanding the productivity fluctuations in the waters

near Dunedin (Hopkins *et al.* 2010). La Niña events are associated with warmer water temperatures at the Southland Front (Hopkins *et al.* 2010), which may improve conditions for *Nyctiphanes australis*, as the water temperatures near Dunedin are often below *Nyctiphanes*' optimal range. Another potential mechanism for increased prey availability near Dunedin in La Niña years involves the gradient across the Southland Front. During the summer months of a La Niña year, the temperature gradient across the Southland Front weakens (Hopkins *et al.* 2010). A strong temperature gradient across the Front can inhibit movement of nutrients and prey species (Jackson, Shaw, & Lalas 2000; Hopkins *et al.* 2010), so a weakening of the gradient may increase productivity.

There were no significant relationships between the fairy prion breeding parameters and the monthly Clutha River flow rates. The issue here is again likely one of scale. Surface salinity decreased between zero and two days after rainfall and nitrogen peaked two to five days after heavy rainfall in Sagami Bay, Japan, but salinity increased again two to three days later (Baek *et al.* 2009). *Nyctiphanes* abundance increases near Dunedin in an area of low-salinity water that is created after high flow from the Clutha River (O'Driscoll & McClatchie 1998), but this low-salinity band disappears in a matter of days if the river flow drops (O'Driscoll 1997). Any increase in *Nyctiphanes* abundance associated with Clutha River flows would improve prey availability for the fairy prions for a period of time, but because Clutha River outflows are highly variable over a timescale of hours due to the effects of hydro schemes on the river and flow interactions with tidal cycles, the monthly mean flows used in this study may be too coarse to detect this variability.

Monthly mean rainfall measurements were also unrelated to any of the fairy prion breeding parameters; this was probably due to the fact that the major freshwater input into the coastal system near Dunedin is the Clutha River (Jillett 1969), not direct runoff from the Otago Peninsula. If rainfall has an effect on the fairy prions breeding near Dunedin, it is probably more of a physical connection involving the breeding colony itself. Heavy rain can flood, or even damage or destroy burrows (Warham 1990), so we might expect to find a negative relationship between breeding success and heavy rainfall events, but such an investigation was beyond the scope of this study.

Wind mixing may have a greater influence on surface salinity than either rainfall or river inputs in the neritic zone near Dunedin. One of the most influential environmental parameters measured in this study was the Southern Oscillation Index, which influences wind patterns in the area, but the wind inputs to coastal waters may enhance productivity by mixing water masses and nutrients at the same time as dispersing low-salinity water, complicating the impact on *Nyctiphanes australis* distribution.

Influence of fledging size and cohort on juvenile recapture rates and age at first recapture

Contrary to the findings of Perrins *et al.* (1973) for Manx shearwaters (*Puffinus puffinus*), Mougín *et al.* (2000) for Cory's shearwaters and Morrison *et al.* (2009) for tufted puffins, there were no clear links between fledging size and likelihood of recapture or age at first recapture at the Dunedin fairy prion colony. Cohort was the only reliable predictor of recapture rate in the present study: 2004 chicks were recaptured at the colony at a much higher rate over the six-year postfledging period than were 2005 chicks. This could be a consequence of greater survival rates of the 2004 chicks, or it could simply reflect a trend towards later returns in the 2005 cohort. Most (97%) of recaptured fairy prion juveniles

were first recaptured by the age of six, but two birds were recaptured at seven years, and one bird was undetected at the colony until it was nine years old. If this study were to carry on over a few more years, it is possible we would continue to detect more individuals from the 2005 cohort and that might alter the recapture trends. Such extremely late returns from the 2005 cohort would be unlikely, though, considering the recapture records from earlier years.

The 2005 cohort not only had a diminished chance of six-year recapture (as compared with all cohorts from 2001 – 2004); birds from the 2005 cohort also left the colony with significantly shorter wings than the combined mean of fledglings from all other years (2004 – 2011). 2005 was an unusually cold year and summer water temperatures were 1°C colder on average than through the same period in 2004. 2005 was an El Niño year, but El Niño conditions were also present in 2003, and the recapture rate for the 2003 cohort was much higher (40%) than that for the 2005 cohort (27%) (although the 2003 recapture rate was the second-lowest overall). We did not collect wing lengths in 2003, so we do not know whether the birds from that cohort also had short wings. Sea temperature and ENSO effects, and possibly other aspects of climate or prey availability likely combined to make 2005 an especially poor year for the fairy prions at Dunedin.

Juvenile survival of fairy prions may be linked to other aspects of the nestling phase that were not measured in this study. Manx shearwaters and Cory's shearwaters that are heavier at fledging have higher survival rates (Perrins *et al.* 1973; Mougín *et al.* 2000), but because these are migratory species, the fat reserves might be more important for them than they are for fledging fairy prions. Larger eggs generally produce larger chicks (Amundsen, Lorentsen, & Tveraa 1996), and there is evidence from other procellariids that egg size, rather than fledging size, influences post-fledging survival (Meathrel &

Carey 2007), but we did not measure eggs at the Dunedin colony through the current study. Also, in some seabird species, return rates to the natal colony are sex-biased (e.g. western gulls (*Larus occidentalis*): (Spear, Pyle, & Nur 1998); Cory's shearwater: (Mougin *et al.* 2000). We had no information on chick sex at the Dunedin colony, so this could be confounding the results.

The recapture rates measured in this study are only partly representative of the overall return rates of chicks. Most procellariids are highly philopatric (Warham 1990), and there is evidence of this in fairy prions as well, although the level of philopatry may differ between colonies (Ovenden *et al.* 1991). There were likely many more juveniles returning to the Dunedin colony than we were able to detect through the course of this study, and some of the fledglings would have migrated to nearby colonies as well. However, a 2008 survey of half the birds (at least 1500 individuals) at the large prion colony at Green Island, located 6 km from the Dunedin prion cliff, detected no birds from the Dunedin colony (G. Loh, pers. comm.). Assuming there were no differences in philopatry rates from year-to-year, the different recapture rates between cohorts were probably indicative of underlying differences in juvenile survival rates.

Limitations of this study

There may be annual variability in other breeding parameters at the Dunedin fairy prion colony. There is evidence from thick-billed murre (*Uria lomvia*), short-tailed shearwaters (*Puffinus tenuirostris*) and thin-billed prions that chick growth and pre- and post-fledging survival are strongly influenced by egg size, which would suggest that these characteristics are determined well before the nesting period (Hipfner & Gaston 1999; Meathrel & Carey 2007; Silva *et al.* 2007). The condition of fairy prion adults leading up

to the breeding season is probably important in determining egg size, overall breeding success and chick sizes, but the foraging range of birds outside the breeding season is much greater, and these birds are able to exploit a much larger area of sea in the search for food. This study of local sea temperatures would not necessarily reflect the prions foraging area through this time, but the SOI, which incorporates larger-scale oceanographic and climactic patterns, might.

There could be inter-year and inter-individual variability in other chick morphometrics that were not measured in this study. Procellariiform seabirds have a characteristic growth curve that consists of an increase up to a peak mass, followed by a period of mass loss before fledging (Warham 1990; Miskelly & Gummer 2004; Miskelly *et al.* 2009). Fledging chicks may be constrained to a certain weight because of physical limits imposed by wing-loading. Fairy prion chicks at the Dunedin colony reach a maximum mass about two weeks before fledging that is about 50 – 75 g heavier than their mass at fledging (Graeme Loh, pers. comm.). The early fat reserves may play an important role in the chicks' growth and brain development (Kitaysky *et al.* 2006). There is some evidence that chicks of black-legged kittiwakes and fairy prions reach higher peak mass with increased food availability, but chicks fledge at similar weights regardless of food differences (see Gill *et al.* 2002; Miskelly & Gummer 2004). For the wandering albatross (*Diomedea exulans*), peak chick mass might be more important to survival to adulthood than fledging mass (Weimerskirch *et al.* 2000); the parameters measured in the present study (fledging wing and mass) may not be very sensitive to changes in provisioning rates, if there are any. Seabird chicks may also preferentially allocate food resources to maintain plumage growth to maximise early flight capability (Lack 1968), and there is evidence from some seabirds that diet effects on wing growth are less pronounced than effects on structural (bone and bill) growth (Lyons & Roby 2011).

In the wandering albatross, survival of male chicks was more closely linked to fledging mass than to peak mass, but female survival was dependent on peak mass, not mass at fledging (Weimerskirch *et al.* 2000). Fairy prions are not sexually dimorphic as adults, but fairy prion chicks may have sexually-dependent chick growth or survival or philopatry patterns which could have confused the results of the present study. Another potentially confounding issue in the present study was the lack of a standardised time for chick measurement. We know that fairy prion chicks lose 10 – 20 g of mass throughout the day as they are converting food energy into feather growth (Harper 1976). During the study of fairy prions near Dunedin, chick measurements were taken opportunistically during daylight hours through the nestling period, which was anywhere between 07:00 h and 21:00 h, potentially adding enough noise to the data set to miss any meaningful trends.

The length of the nestling period was not measured through this study, but considering the growth curve for a fairy prion nestling (Harper 1976), chicks that remain at the colony longer would probably weigh less than chicks that fledge earlier, which could confound the use of fledging weights as a proxy for fitness. Also, some seabird species coordinate their breeding to take advantage of local peaks in food availability (Mills *et al.* 2008). Fairy prion laying is synchronised (Mauchline & Fisher 1969), and all chicks at the Dunedin colony hatch within two weeks in the latter half of December, but chicks that hatch a week earlier may have better access to food if local prey abundance declines near the end of the breeding season. Hatching dates have been implicated in the survival rates of other procellariid chicks as well (Mougin *et al.* 2000), but an examination of survival in relation to hatching dates and nestling periods was beyond the scope of the current study.

If availability of *Nyctiphanes australis* is diminished in some years, and Dunedin fairy prions switch to other types of prey in those years, the food quality differences might not necessarily be reflected in chick fledging weights, but could manifest in other ways. Red-legged kittiwake (*Rissa brevirostris*) chicks fed a lipid-poor diet showed reduced cognitive abilities that could reduce fitness by decreasing foraging ability (Kitaysky *et al.* 2006). If chicks had a dietary restriction early in the nestling period, their fledging weights would not necessarily be affected, but the early effects of a low-lipid diet could still cause diminished brain function, which can affect survival (Kitaysky *et al.* 2006).

Conclusions

The consistency of fairy prion breeding success and chick fledging masses suggests one of two things about the Dunedin colony: either that the prey fluctuations in the area are low enough that the prions can use behavioural buffering to maintain consistent reproductive output, or that breeding success and chick masses are insensitive to the variability in the system due to the overriding effect of nest-site limitation on their breeding biology. The introduction of predatory land mammals has seriously diminished the availability of appropriate nesting habitat for fairy prions in New Zealand; as a result, nest-site limitation may be more of a control on fairy prion populations than food availability. Fledging wing lengths were more variable and were linked with in-season SOI and SST measurements, which may indicate that wing growth is more sensitive to summer food availability than either nest success or fledging mass are. Fledging weight and wing length were unrelated to likelihood of recapture on the individual scale, but there was a cohort effect on the recapture rate of the 2004 and 2005 birds; the 2005 birds returned to the colony at a lower rate than the 2004 birds. The 2005 cohort also fledged with unusually short wings, and the sea temperatures recorded in 2005 were abnormally

low. The combined effects of El Niño and an especially cold sea on euphausiid abundance and distribution may have led to the poor performance of the 2005 cohort.

Recommendations for future study

The nestling period of fairy prions may change from year to year, depending on food availability (with chicks extending their stay at the colony in good years to allow for more weight loss before fledging (see Miskelly & Gummer 2004)); colony visits should be extended to detect chick hatching dates as well as fledging dates, in order to examine this connection. Fairy prion fledging mass is remarkably steady between individuals and across years. In order to detect a difference in provisioning between years, we should start to collect information on peak nestling weights instead of fledging weights. The weights of nestlings could be collected in early-mid January instead of mid-late January, in order to capture this element of nestling growth. Automated scales for the collection of adult arrival and departure weights would remove some of the uncertainty regarding meal sizes and provide a more accurate measure of provisioning rates. Fledging wing lengths should continue to be measured, as these show the most promise as an indicator of food availability and survival rates.

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