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Major changes in the red-billed gull (*Larus novaehollandiae scopulinus*) population at Kaikoura Peninsula, New Zealand; causes and consequences: a review

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Abstract We use previously published and new data from a long-term study of the red-billed gull (*Larus novaehollandiae scopulinus*) population at the Kaikoura Peninsula to review causes and consequences of population change. Currently the largest colony in New Zealand, the Kaikoura population, has undergone major changes over the past 52 years. In 1994 the population began to decline, and between 1983 and 2003 it dropped by 51%. Fledging success varied markedly between seasons. The major cause of reproductive failure was predation by introduced mammals, especially ferrets (*Mustela furo*) and feral cats (*Felis catus*). These predators became a problem when rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) increased in number, enhancing the predators' survival over-winter. Periodic failure in the availability of euphausiids, the main food of red-billed gulls, swamping of nests during high seas, and chilling of nestlings during long periods of bad weather also have been set backs to the population. However, in the absence of predation, these factors produced only a temporary impact to the population of long-lived gulls. The decline in both body size and survivorship of adults over the last 5 decades indicates that there are other factors at work, and indicate that the population has experienced some form of unfavorable environmental condition or stress over a long period.

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INTRODUCTION

The decline in seabird populations is a global problem. Data from 3,213 seabird population studies revealed that between 1950 and 2010, 70% have declined (Paleczny *et al*. 2015). The causes and consequences of many of these declines are not known because the studies have been of insufficient duration. Some of the declines have been linked to predation (Newton 1988), over exploitation of forage fish species (Anker-Nilssen *et al.* 1997; Newton 1998; Rindorf *et al.* 2000) and ocean climatic changes associated with influx of warm water (Anker-Nilssen 1997; Frederiksen *et al*. 2004). It has been established that dramatic changes

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in the composition and abundance of plankton is associated with climatic driven changes (Beaugrand 2004; Edwards & Richardson 2004; Frederiksen *et al*. 2006), indicating a bottom up control of the marine food web (Frederiksen *et al*. 2006). The same bottom up control occurs in the Kaikoura region (Mills *et al*. 2008).

Over the past 5 decades the red-billed gull (*Larus novaehollandiae scopulinus*) population breeding at the Kaikoura Peninsula, New Zealand (42°26′ S 173°42′ E), has undergone major changes (Mills *et al*. 2008). In the 1960's, a survey of the locations and status of colonies in New Zealand and its outlying islands (Gurr & Kinsky 1965) revealed that the Kaikoura population was the third largest in New Zealand. Since then, the 2 largest colonies (Three Kings Islands and Mokohinau Islands) have declined more than the Kaikoura colonies (Frost & Taylor 2018) and as a result the Kaikoura breeding population is now the largest in New Zealand, even though between 1993 and 2003 the Kaikoura population declined by 51% (Mills *et al*. 2008). Nationally the breeding population is believed to have declined by 33% since a 1965 survey (Frost & Taylor 2018), and the red-billed gull is now classified as 'At Risk - Declining' (Robertson *et al*. 2017) under the New Zealand Threat Classification System (Townsend *et al*. 2008).

This paper is a review, examining the changes in the Kaikoura red-billed gull population, the factors that have affected breeding success and the causes of the decline. Previously published results are combined with unpublished data covering the period 1964–2015. The source of all previously published information is cited.

MATERIALS AND METHODS

Study population

The red-billed gull population at Kaikoura has been banded for 58 years (1958–2015) and studied annually for 52 years (1964–2015). In all, over 70,000 nestlings have been banded, resulting in a large proportion of the population being of known age. A total of 5,052 adults have been individually colour-marked, of which 3,386 were of known age. Each season resighting of these colour-marked individuals was used to determine the proportion that bred and the fate of the nesting attempt. The Kaikoura population is an ideal subject for study because there is little emigration of breeding adults, and virtually all offspring of breeding age return to breed (Mills 1989; Mills *et al*. 2008).

Relatively few individually colour-marked gulls were missed during the breeding season. For example, of the 9,086 male and 12,792 female recoveries, or resightings, of individually colour-marked gulls at Kaikoura during seasons from 1975 to 2000, 84% of males and 86% of females were resighted in subsequent seasons (Mills *et al*. 2008). Among those that were resighted, 96% of males and 93% of females were seen the following season, and only 2% of individuals were not seen within 2 seasons of their last sighting (Mills *et al.* 2008). For calculation of lifespan of males and females, if a bird was missing from the environs of Kaikoura or the breeding grounds for 2 seasons, it was assumed to have died, and the death was considered to have occurred during the first year of its disappearance. To ensure that young individuals did not dominate the sample, the analysis of lifespan (the proportion of individuals that survived from 1 year to the next) was restricted to nestlings banded between 1958 and 1986, and followed until the 2015 breeding season. Adult red-billed gull survival was estimated using the MARK procedure (White & Burnham 1999) on recapture data of individually colour-marked gulls from 1975 to 2009.

Adults were sexed by a combination of 2 bill measurements, bill length and depth at gonys (Mills 1971), or molecular analysis (Given *et al*. 2002).

Occasionally white-fronted terns (*Sterna striata*) nested in areas adjacent to the red-billed gull colonies.

Annual census

From 1964 to 2015, an annual census of the number of pairs breeding in Kaikoura was made by nest counts at the end of November, coinciding with the period when most of the pairs of red-billed gulls were nesting. Between 1983 and 2003, estimates of the total adult gull population, including breeding and non-breeding individuals present at Kaikoura in the breeding season, were obtained using the Bailey Modified Lincoln Index (Bailey 1952; Parr *et al*. 1968). The procedure involved determining the total number of colour-marked individuals present in the breeding colonies, or in the environs of Kaikoura each breeding season, and randomly sampling the proportion of colour-marked to unmarked adults in the population (Mills *et al*. 2008).

Monitoring of annual breeding success

Nests containing eggs of colour-marked individuals were marked each breeding season between 1965 and 2015, with a total of 23,933 nests marked. The fates of eggs and chicks were checked at least every 2 to 3 days, and chicks in the marked nests were generally banded within 4 days of hatching. Chicks that survived to 35 days of age were considered to be fledged. Evidence of predation was confirmed either from the remains left at, or nearby, the nest, or from the disappearance of the nest contents. When possible, the predator responsible was determined by knowledge of the type of predator in the area from observations, scats, or dens, and the type of injury inflicted. However, in some cases it was not possible to identify the predator because eggs and chicks just disappeared from nests.

Determination of the diet of the mammalian predators

Over the 28 breeding seasons of the red-billed gull between 1964 and 1999 (September – January), a total of 1,455 prey items of stoats, 734 of ferrets and 273 of cats were identified adjacent to, or in, the dens. In the case of cats and ferrets, the list of items was incomplete because only 1 cat den and 3 dens of ferrets were located. On the Kaikoura Peninsula, these predators generally had dens in extensive, impenetrable flax (*Phormium tenax*) groves. In addition, some cats appeared to range over a large area, making it difficult to locate dens. The number of eggs listed in the diet of all predators refers only to the numbers found in dens or caches, and is therefore underestimated.

Predator control

For the first 11 years of the study (1964–74), the only mammalian predators present on the colonies were stoats, rats (*Rattus rattus*) and hedgehogs (*Erinaceus europaeus*) and there was no predator control. Thereafter Fenn traps (King & Edgar 1977) were set in artificially constructed tunnels in an attempt to control stoats. From 2005, more intensive predator control, involving trapping and shooting, was initiated by the Department of Conservation to protect endangered Hutton's shearwaters (*Puffinus huttoni*) which were transferred to the peninsula to establish an alternative population.

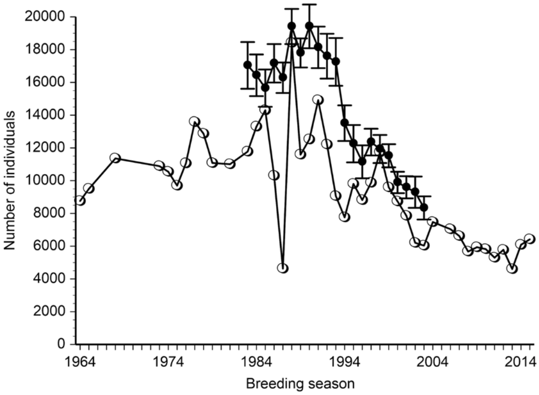

Fig.1. Estimates of the Kaikoura adult red-billed gull population (mean ± se) between 1983 and 2003 based on a modified Lincoln Index (Bailey 1952) (●) and the count of individuals breeding (number of nests x2) between 1964 and 2015 (○).

Availability of euphausiids

At Kaikoura, the red-billed gull is dependent on a regular and abundant supply of euphausiids, *Nyctiphanes australis* (krill) for successful breeding (Mills *et al.* 2008). An increase in the availability of euphausiids appears to increase the likelihood of breeding, especially in young individuals, encourage earlier laying, improve the condition of adults, increase egg volume, clutch size and fledging success, all of which are fitness components (Mills *et al*. 2008). *Nyctiphanes australis* is restricted in distribution to coastal continental shelves in south-east Australia and New Zealand, optimally in 12-18°C water (Sheard 1953; Mauchline & Fisher 1969; O'Brien 1988) and becomes available to the gull when it swarms at the surface.

The diet of the bird in the breeding season was determined from regurgitated food obtained from adults captured for banding or weighing. Changes in the types of food consumed relative to *N. australis*, and the number of birds that had no food to regurgitate, provided a reliable index of availability of euphausiids. The availability of the euphausiid to the gull has been estimated annually from 1975 to 2015. When euphausiids are abundant, adults complete a foraging trip in approximately 2 hours but when scarce the trips take as long as 5-6 hours (Mills *et al.* 2008). Birds captured within 60 minutes of returning from to the colonies readily regurgitated food. By capturing birds throughout the day, it was possible to assess the availability of euphausiids from the proportion of individuals that regurgitated this type of food. When euphausiids were abundant, a greater proportion of captured individuals would regurgitate euphausiids because there would be more frequent change-over of partners (Mills *et al.* 2008). So essentially it is an index of the ease with which the gull is able to obtain euphausiids and reflects availability. The causes of the variability of the availability of euphausiids are detailed in Mills *et al.* (2008).

RESULTS

Changes in the Kaikoura population size 1964–2015

The peak in the numbers of pairs nesting on the Kaikoura Peninsula, since counts began in 1964, occurred in 1988, when 9,212 pairs nested (Fig. 1). After 1991, the number of nests declined progressively until 2002. Thereafter the number of pairs nesting stabilized until 2015, fluctuating between 2,650 and 3,777 annually. Estimates of the total population present in the breeding season at

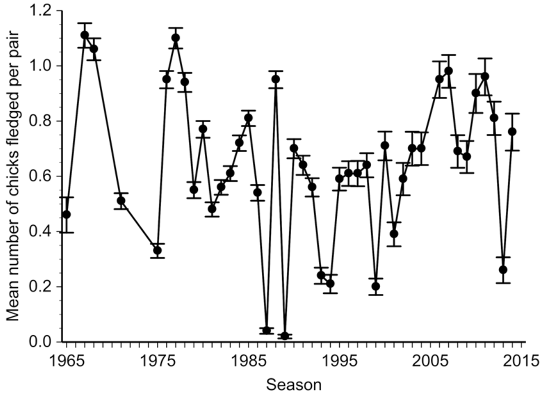

Fig. 2. Fluctuations in the number of chicks raised per pair (mean ± se) at Kaikoura from 1965 to 2014.

Kaikoura, based on a Lincoln Index (Bailey 1952; Parr *et al*. 1968), shows a similar pattern. This estimate included breeders and non-breeders. From 1983 to 1993, the adult population present remained relatively stable, at approximately 16,000–19,000 individuals, but after 1993 the population declined, and by 2003, numbers had decreased by 51% from the level in 1983 (Fig. 1) (Mills *et al*. 2008).

The difference between individuals that bred and the estimated population indicated a large non-breeding population (Fig. 1). The non-breeding element consisted of young individuals that had not yet bred, birds that had changed mates in previous seasons and had not yet obtained a new mate, and short and long-term non-breeders (Mills 1989; Mills *et al*.1996).

Fledging success

Between 1965 and 2014, 17,630 nests were monitored, and on average 0.64 ± se 0.006 chicks were fledged annually per pair. Over the period, there were marked fluctuations in the fledging success (Fig. 2). In 1987 and 1989, there were virtually no chicks fledged, and in 5 other seasons less than 0.33 chick per pair was produced.

Table 1. Mean lifespan (years ± sd) of known aged, individually colour-marked adult male and female red-billed gulls banded as chicks between 1958 and 1986 that survived to at least 2 years of age.

Sex	No. individuals	Mean lifespan
Female	1,211	15.74 ± 6.06
Male	1,204	12.87 ± 5.46

Average adult life span

An analysis of 2,415 colour-marked individuals that were known to have died, or were assumed to have died, shows that males that survived initially to at least 2 years of age, had a mean life span of 12.9 years. In contrast, females lived an average of 2.9 years longer (Table 1). Difference between female and male lifespan (t = 12.22, df = 2,413, P = 0.0001).

As a consequence of the higher survivorship of females, there is a surplus of females in the Kaikoura population. For example, between 1975 and 2008, 20,985 bird recoveries of known aged breeding and non-breeding individuals have been made. Overall the sex ratio was strongly biased towards females (55.1% females, $X^2_1 = 110.5$, $P < 0.001$) (Mills *unpub*.). On average, only 48% of the females in the population bred annually, compared to 70% of the males ($X^2_1 = 14517$, $P<0.001$) (Mills *et al.* (1996) and Mills *unpubl data.).* The shortage of males in the population restricts the number of breeding pairs.

Additional changes in the population

There have been 2 other important changes to the Kaikoura population over the course of the study. Firstly, the size of several morphological traits and body mass of both males and females has shown a statistically significant (P = 0.0001) decline over the last 5 decades (Teplitsky *et al*. 2008) (Fig. 3). An analysis of mean tarsus length at the phenotypic level has also decreased with time (estimate ± se: -0.376 ± 0.068, $F_{1,42} = 66$, $P< 0.001$) (Teplitsky *et al*. 2008). Secondly, the annual survivorship of both sexes has declined. Females declined from an annual average survival rate of 0.886 ± (se 0.052) in 1975 to 0.808 ± (se 0.079) in 2009, a decline in survival of 8.8% over 35 years. Similarly, males declined from 0.870 ± (se 0.50) in 1975 to 0.800 ± (se 0.072) in 2009 for a decline of 8.0% (Alho & Mills *unpub*.).

Predation

The major cause of reproductive failure in many of the seasons was predation (Fig. 4). Potential predators included ferrets, stoats and feral cats which prey on adults, chicks and eggs; black-backed gulls (*Larus dominicanus*) took small to medium sized chicks and some eggs; hedgehogs and rats took eggs and chicks, and some red-billed gulls specialized in egg-robbery, especially when euphausiid availability was low. It is not known how many eggs and chicks were taken by rats and hedgehogs, but it is not believed to be a large number. Over the years only 3 rat dens were located in the vicinity of the colonies, but no eggs or egg shell were located near the dens. Hedgehogs appeared to be passing through the area.

It was not until 1985 that feral cats and ferrets were observed on the colonies. Their appearance

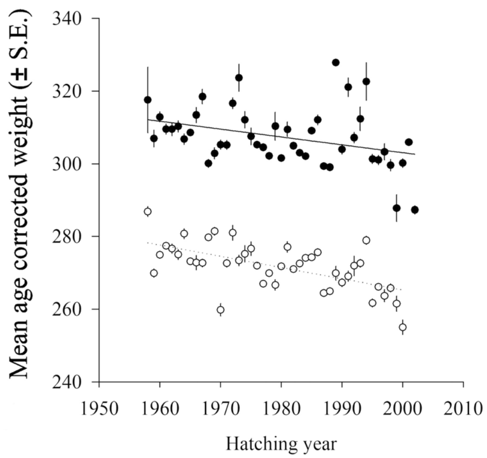

Fig. 3. Time trends in mean body mass for adult females (○) and males(●) as a function of hatching year between 1958-2002 (mean ± se). (From Teplitsky *et al.* 2008; "Bergmann's rule and climate change revisited Disentangling environmental and genetic responses in a wild bird population". Reproduced with permission of *Proceedings of the National Academy of Science USA* 105: 13492–13496. Copyright (2008) National Academy of Sciences, USA.)

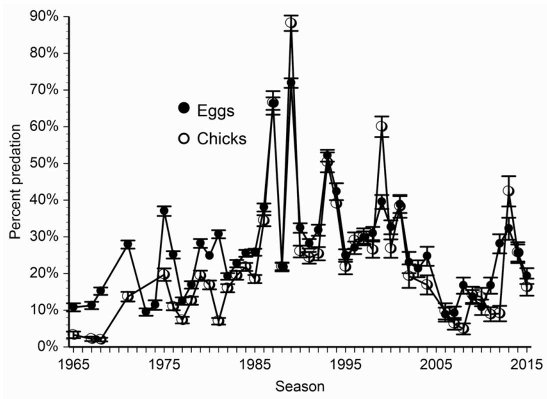

Fig. 4. The percentage of eggs (●) and chicks (○) lost to predation (mean ± se) at Kaikoura from 1965 to 2015.

coincided with an increase in rabbit (*Oryctolagus cuniculus*) and hare (*Lepus europaeus*) numbers. After 1987, rabbit and hare control by pest destruction agencies on the peninsula headland and adjacent farmland ceased, and the numbers of lagomorphs increased markedly. This increased the potential for cats and ferrets to survive over winter when the gulls had dispersed from Kaikoura.

Of the 23,933 nests monitored between 1964 and 2015, 44,759 eggs were laid in marked nests and 26.7% were lost to predation (Table 2). Of the 22,119 eggs that hatched, 22.0% of the chicks were taken by predators (Table 2). The extent of predation varied from season to season (Fig. 4). For all seasons, stoats, black-backed gulls and red-billed gulls preyed on the red-billed gull colonies. When cats and ferrets arrived on the Kaikoura colonies in 1985, predation on eggs and chicks increased dramatically. For the 26 seasons that stoats were the main predator, egg losses averaged 20% and chick losses 15% (Table 2). In comparison, for the 22 seasons when feral cats and ferrets were present for part or all of the red-billed gull breeding season, the loss of chicks (X^2_1 = 634, P = 0.0001) and eggs (X^2_1 = 1193, P = 0.0001) was on average 15% higher (Table 2). The reduction in cat and ferret numbers lessened chick and egg losses, but it was difficult to remove all cats and ferrets. When cats and ferrets were able to be eliminated prior to the start of the breeding season and there was no further immigration, such as occurred between 2006 and 2010, the proportion of chicks and eggs that were lost declined (Fig. 4). At the beginning of the gulls' breeding season in October, between 2005 and 2015, several cats were present in the vicinity of the colonies eating eggs. These cats were either missed by predator control prior to the season, or were newly arrived in the area. When their presence was discovered, they were shot, but not before 200-500 nests were

Table 2. Predation rates on red-billed gull nests, when either stoats, or cats and ferrets, were the main mammalian predators. Stoats were present in all seasons, but were only the main predator for 26 seasons (1964-1984, 2006-2012). Cats and ferrets were present for part, or all of, 24 red-billed gull breeding seasons (1985-2004, 2014-2015). The data includes renests after the earlier breeding attempt failed.

Main predator	No. seasons	No. nests	No. eggs laid	No eggs lost	% eggs lost	No. eggs hatched	No. chicks lost	% chicks lost
Stoats	26	13,261	24,592	4,965	20.2%	11,373	1,726	15.2%
Cats & ferrets	24	10,672	20,167	7,001	34.7%	10,746	3,139	29.2%
Total	50	23,933	44,759	11,966	26.7%	22,119	4,865	22.0%

Table 3. Known prey items of stoats, ferrets and cats recovered from dens between 1964 and 1999 at the Kaikoura Peninsula during the red-billed gull breeding season (September–January).

Prey		Stoats		Ferrets		Cats	
Red-billed gull	Adults	325	(22%)	198	(27%)	60	(22%)
	Chicks & juveniles	441	(30%)	316	(43%)	144	(53%)
	Eggs	419	(29%)	2	(<1%)	30	(11%)
White-fronted tern	Adults	183	(13%)	143	(19%)	10	(4%)
	Chicks & juveniles	51	(04%)	73	(10%)	25	(9%)
	Eggs	15	(<1%)				
Other bird species		18	(<1%)	2	(<1%)	1	(<1%)
Rabbits		3	(<1%)			2	(<1%)
Total		1,455		734		273	

destroyed. In 2013, not all of the cats could be destroyed, and consequently egg and chick losses increased (Fig. 4).

Breeding terns and gulls were less susceptible to predation than the nest contents. Over the 53 years, 624 adult red-billed gulls and 447 adult white-fronted terns were known to be killed by either cats, stoats or ferrets. This is considerably fewer than the 11,966 eggs and 4,865 chicks taken from marked red-billed gull nests (Table 2). During the day and on moonlight nights, the adults are able to avoid mammalian predators because an approaching predator would be detected and the nesting birds would flee. However, on dark nights when there is no moon, especially with rain, fog or drizzle, the protection breaks down because adult terns and gulls remain transfixed on the colony when the predators are present, since they are unable to orientate themselves as to where to escape (Mills *in prep*.).

For all mammalian predators, chicks and juveniles of red-billed gulls were the main prey items, making up 30% of the stoat diet, 43% for ferrets, and 53% for cats (Table 3). Adult red-billed gulls were also an important item for all predators, constituting similar amounts of the diet (22–27%). White-fronted terns did not breed in all of the seasons and therefore they did not constitute a higher proportion in the overall diet. Examination of the stomach contents of 6 adults and 18 juvenile stoats, most of which were captured in the 1975 season adjacent to the Kaikoura gull colonies, shows a slightly more varied diet than indicated from prey items collected from or near dens. Whilst bird bones made up 91% of the occurrence of the prey, and accounted for 84% of the composition by weight, mouse (*Mus musculus*), skink (*Leiolopisma* sp.) and arthropods collectively made up 16% of the frequency occurrence, and 7.2% composition by weight (Table 4) (Dr. C.M. King *pers. comm.*).

Predator control programme

The predator control programme was conducted throughout the year on the Kaikoura Peninsula (Table 5). The numbers of predators killed each year highlights the problem. Between 2005 and 2016, a total of 131 cats, 319 rats, 277 hedgehogs, 99 stoats, 14 ferrets, 39 weasels, 1005 rabbits and 12 hares were trapped, or shot, on the peninsula headland and adjacent farmland (Table 5). Particularly notable was the reduction in numbers of rabbits and hares because they are the staple food of stoats, ferrets and feral cats (Gibb & Flux 1973; Wodzicki 1950).

In spite of the large number of predators killed each year, there has been a steady recruitment of mammalian predators to the vicinity of the colonies. The reduction in cat and ferret numbers lessened

Table 4. Percentage frequency occurrence and percentage by weight of prey in guts of 6 adult and 18 juvenile stoats captured in dens adjacent to red-billed gull colonies. Most of the stoats were obtained in the 1975 season (Dr. C.M. King *pers comm*.).

	Percentage frequency occurrence of prey	Percent composition by weight
Bird bones	91	84.3
Bird eggs	3	8.4
Mouse	4	4.0
Skink	4	2.8
Arthropods	4	0.4

Table 5. The number of mammals that were shot or trapped on the Kaikoura Peninsula headland or adjacent farmland between 2005 and 2016. The 2016 data end in June. Of the total, 45 cats, 790 rabbits and 12 hares were shot by spot lighting at night and the rest were caught in 119 traps set from 2005 to 2014, 10 more traps were added in 2015 and another 36 in 2016. (nc denotes not counted).

Year	Cats	Ferrets	Stoats	Weasels	Rabbits	Hares	Rats	Hedgehogs	Mice
2005	7				nc	nc			
2006	13		8	8	60		44	44	
2007	11	1	1	10	65	1	14	30	
2008	11		14	1	142		21	21	
2009	6		4		89		15	15	
2010	9		18		246	2	17	17	
2011	2		16		86	4	28	11	
2012	10	4	5	7	196	5	57	44	
2013	19	5	3	5	93		43	24	7
2014	20	2	20	2	21		28	38	17
2015	19	2	10	6	7		52	33	
2016	4								
Total	131	14	99	39	1,005	12	319	277	24

chick and egg losses, but it was difficult to remove all cats and ferrets. Within 3.5 km of the colonies, there is a residual population of feral cats in the township and the local garbage dump, providing a source of cats to the headland of the peninsula where the gulls nest. Between 2008 and 2016, 111 feral cats were shot at the dump and a further 50 were destroyed in the nearby Kaikoura commercial area.

Availability of euphausiids

The relationship between euphausiid availability and the number of chicks fledged per pair over the years 1975 to 2014, (Fig. 5), is statistically significant (y =1.098x +0.3924, r =0.4630, P<0.01), even although other factors, such as predation, also had an effect on the number fledged per pair.

The importance that fluctuations in food availability and/or food abundance has on fledging success was demonstrated in an investigation of 14 seabirds, including the present red-billed gull study (Cury *et al*. 2011). Their analysis showed that for all 14 species examined there was a threshold, approximately one-third of the maximum prey biomass observed in the long-term studies, below which fledging success declined. The seabird populations do not consume one third of the biomass, but need that amount to be present in order to obtain sufficent food to sustain the population. Fig. 6 shows the 33% threshold of 0.145 in the euphausiid availability (Mills *et al.* 2008) which is needed to maintain the red-billed gull population. As can be seen, there are 12 seasons out of 37 seasons when availability of euphausiids was below the threshold. The poor seasons have generally been sporadic, rather than sequential. If the poor seasons become more frequent with few good seasons in between, the impact on the gull population would likely increase.

Factors affecting fluctuations in the availability of euphausiids

The causes of the variability in the availability of the euphausiids are detailed in Mills *et al.* (2008). In some seasons off the coast of Kaikoura, there were 2 main peaks in the abundance of adult *N. australis*, August-September and November-December (Bradford 1972). The peak in November-December is the second generation of euphausiids which become important to the breeding gulls. Consequently, there are 2 critical periods that impact the availability of euphausiids to the gulls during the gulls' breeding season from October to January.

The hydrography off the Kaikoura coast is extremely complex, and several factors have an impact on the productivity of *N. australis* populations (Mills *et al.* 2008). The critical period for the growth

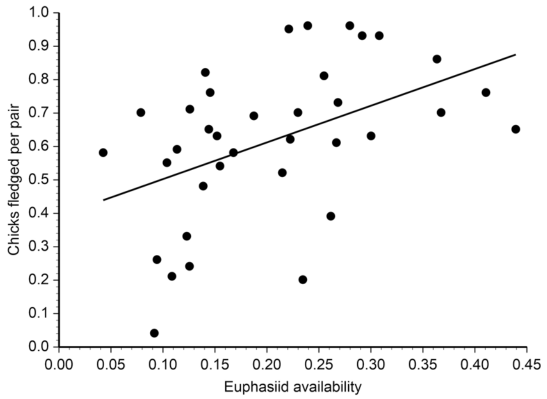

Fig. 5. The inter-annual variation in the mean number of chicks fledged per pair (1975 to 2014) in relation to euphausiid availability.

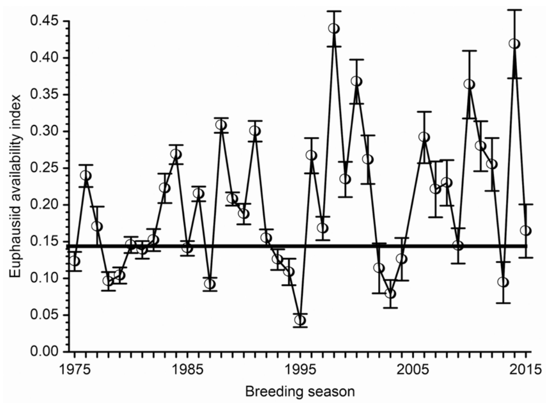

Fig. 6. Index of availability (Mills *et al.* 2008) of the euphausiid *Nyctiphanes australis* during the red-billed gull breeding season between 1975 and 2015. The 33% miminum threshold of 0.145 is indicated which is needed to maintain the population. Mean ± se.

and productivity of euphausiids occurs in winter at the peak of egg-laying of *N. australis* (O'Brien 1988). Thus, inflow of colder water from the south via the Southland Current in July and October and the availability of euphausiids to the gulls in the breeding season (Mills *et al.* 2008). The colder the inflow from the south, ultimately the higher the euphausiid availability to the gulls. The influx of the cold water impacted the chlorophyll-a content of the coastal water to the extent that approximately 61% of the variability in the availability of food for the gull in the breeding season was explained by the July variability of chlorophyll-a (Mills *et al.* 2008).

Additionally, during the gulls' breeding season from October to January, there were 2 different factors that also affected the availability of euphausiids at that time. Firstly, the quantity of euphausiids available in the breeding season was related to the frequency of north-east synoptic weather type (Mills *et al*. 2008). North-easterly wind conditions were connected with upwelling on the Kaikoura coast causing an offshore drift in the surface water at right angles to the wind stress, producing upwelling and more nutrients (Heath 1972; Chiswell & Schiel 2001). The resulting dissolved inorganic nutrient enrichment ensures an ongoing food supply for the next generation of euphausiids. Another factor influencing the availability, during October to December, of *N. australis* at Kaikoura is the wholesale influx of warm sub-tropical water from the north. If the influx is strong, it can displace the coastal water and its contained euphausiids (Bradford 1972). Less intensive intrusions of warm water into the Kaikoura region can result in warm water overlaying the colder water (Barnes 1985) and this may prevent the upward migration of euphausiids, making them unavailable to the gulls. In general, higher food availability occurs in La Niña conditions with more north-easterly wind flow, and the trend is for the availability to increase during positive phases of the Southern Oscillation (SOI) and decrease during negative phases (Mills *et al.* 2008). With the prospect of global climate change, westerly winds are expected to increase especially in winter and to a lesser extent in spring (Mullan *et al.* 2001). This could lead to a decrease in NE wind and a decrease in plankton availability and adverse consequences to the red-billed gull population.

Another factor that may affect the availability of euphausiids to surface feeding seabirds is the abundance of kahawai (*Arripis trutta*) which also feed on euphausiid swarms. At Kaikoura, the beginning of the decline in red-billed gull numbers coincided with increased fishing pressure on the kahawai population, as indicated by the commercial landing catches off the Kaikoura Coast in the management region KAH3, as defined in Hartill & Walsh (2005) (Fig 7a). To optimise the fishing effort, purse seign fishing boats used spotting planes to locate shoaling kahawai at euphausiid or small fish swarms. By 1995, the kawahai population was markedly reduced and a temporary moritorium was placed on futher exploitation. No further commercial catches have been taken since the mid to late 1990s off Kaikoura (Ministry of Primary Industries 2016). There was no way of knowing the standing crop prior to, or after, the increased exploitation of kahawai, but Dr. Bruce Hartill (*pers. comm.*) a fisheries scientist involved in

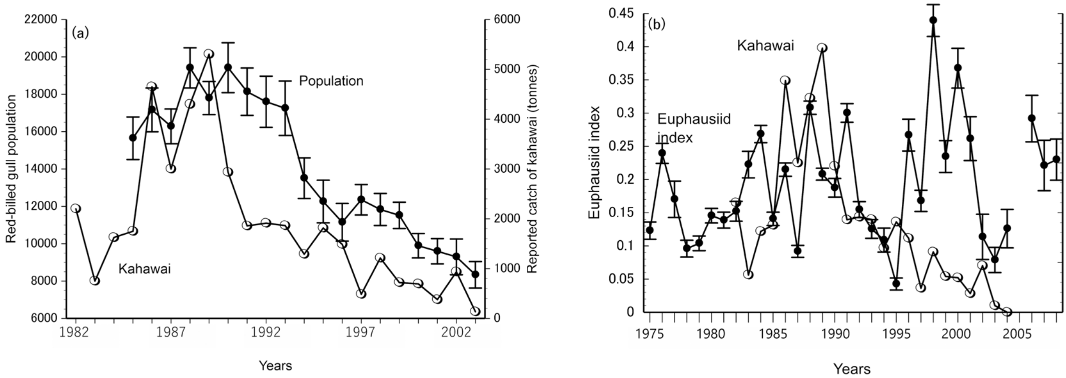

Fig.7. **(a)** The decline in red-billed gull population (●) at Kaikoura coincided with the commercial landing catch of kawahai off the Kaikoura coast (○) (mean ± se); **(b)** Comparison of the euphausiid availability index (●) with the commercial landing catch of kawahai off the Kaikoura coast (○) (mean ± se).

the assessment of the Kaikoura kahawai fishery, Hartill & Walsh (2005) considers that the biomass of kahawai would have been at an all time low during the early 1990's following a 5 year period of relatively intensive harvesting. Frost & Taylor (2018) suggest that the decline in shoaling fish stocks could be directly associated with the national decline in red-billed gull numbers because the predaceous fish may force the krill to the surface, where they become available to the surface feeding seabirds. They argue that the lowered fish stock may have had a detrimental effect by reducing the availability of euphausiids in the surface water. As well, it is possible that the disturbance in the surface water that occurs when the kawahai are feeding on euphausiid swarms can aid in attracting gulls to the site. These factors may play a role, but the availability of euphausiids to the gull at Kaikoura was high in some seasons after 1996, suggesting the impact was likely to have been minor (Fig. 7b). Further research is needed to establish whether, or how frequently, predators drive euphausiids to the surface and the possible impact on seabird populations

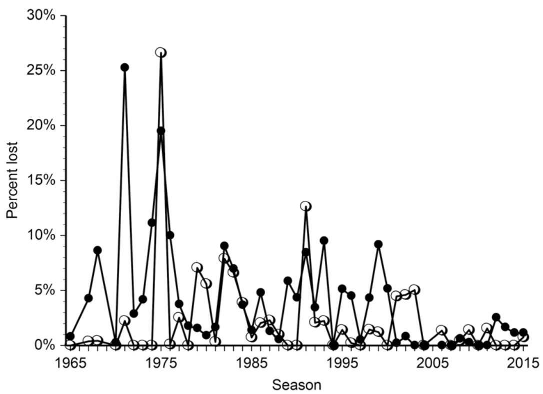

Fig. 8. The percentage of eggs (○) and chicks (●) lost to flooding of colonies by extreme high tides and or storm surges at Kaikoura from 1965 to 2015.

Swamping of nests and bad weather

Several of the colonies on the Kaikoura Peninsula are low lying and are subject to flooding during extreme high tides and or storm surges especially if they coincide. In 1971, 1975 and 1976, colonies were swamped and 25%, 11% and 19% respectively of the eggs laid were lost due to flooding. In another 4 seasons, over 9% of the eggs were lost by the same cause (Fig. 8).

Large chicks, are not able to be adequately brooded by a parent during prolonged periods of rain and tend to be susceptable to become chilled. Between 1965 and 2015, 4.1% of the 35,810 chicks from marked nests died from chilling. Chick deaths by chilling can be high in some seasons, amounting to 19% of chicks hatching in 1975, 20% in 1979, 13% in 1980 and 16% in 1983.

Ticks

Two tick species are present on the colonies at Kaikoura, *Ornithodoros capensis* and *Ixodes eudyptidis*. *Ornithodoros capensis* are rarely seen on chicks or adults because they tend to feed at night and fall off during the day. *Ixodes eudyptidis,* on the other hand, can remain on the bird for several weeks. It is not known what effect *O. capensis* has on survival of chicks and adults, but *I. eudyptidis* can cause the death of both chicks and adult red-billed gulls. Between 2000 and 2015, there were at least 131 deaths of adult red-billed gulls due to ticks. The birds had engorged ticks on the neck or face, and infected adults frequently developed a staggering gait. In advanced stages, the gulls were unable to stand or fly, and laid prostrate on the ground. However, the number dying from ticks could be much higher as seriously affected individuals might have died off the colony. For example, birds which have died with ticks have been found at fresh water areas away from the colonies where they congregated to drink or wash themselves. Red-billed gulls were able to minimise the effect of tick infected nesting areas, by deserting the area and relocating during the same season, or the next season. However, by relocating nest sites, they often spread the tick to new sites.

DISCUSSION

The results of this study over 52 years show that predation and fluctuations in the availability of euphausiids, the main food of the bird, are the most important influences on breeding success and population size.

For a species like the red-billed gull, which potentially lives to 32 years of age, with an average life span for adults of 12.9 years for males and 15.7 years for females, the occasional season when breeding success is low is not a serious problem. This applies to situations such as the periodic swamping of nests by extreme high tides and storms, and chilling of chicks during extended periods of bad weather and deaths from ticks, or even periodic drops in the food supply. Therefore, the bird could sustain periodic decreases in the availability of euphausiids in the absence of predation, but in the presence of high predation, fluctuations in the availability of food contribute to the decline. However, with the advent global climate change, it is envisaged that westerly winds over New Zealand will increase and this will affect the availability of euphausiids, and therefore the breeding success of the bird. If this occurs, it could affect the long-term viability of the Kaikoura red-billed gull population.

A major cause of the 51% decline of the red-billed gull population at the Kaikoura colonies is predation by introduced mammals. Feral cats have been the greatest problem. Between 1965 and 1984, predation was by stoats and black-backed gulls, and egg losses averaged 20%, and chick losses 15%. After cats and ferrets invaded the colonies, the predation rate on eggs and chicks increased by a further 15%. The constant high loss of the nest contents over an extended period has had a serious impact on the population. Worldwide, cats have been responsible for 26% of avian extinctions attributed to predators (King 1985, Newton 1998). If not for the intensive predator control programme at Kaikoura, especially the attempted eradication of rabbits and hares, which are an important food source especially in winter, the decline would have been substantially higher.

It has been difficult to remove all cats and ferrets from the area, and new arrivals occurred frequently. The eradication of cats on the mainland of New Zealand is extremely difficult proposition, especially near an urban setting such as at Kaikoura. The edge of the settlement is within 1.5 km, and the township is approximately 3.5 km away from the colonies. There is a residual population of feral cats in the township and the local garbage dump, which are potential sources of cats to the headland of the peninsula where the gulls nest. The continual arrival of cats and other mammalian predators means that predator control will need to be maintained. If it is relaxed in any way, it can be envisioned that the population of red-billed gulls will decline even further.

The Kaikoura population is a major source of red-billed gulls found along the eastern coast from Wellington to Timaru during autumn and winter. To maintain this traditional colony, it is imperative that more efficient control measures be developed to attract the predators to traps, or to poison predators, during and outside of the gulls' breeding season. To reduce the number cats arriving on the peninsula where the gulls and terns nest, there needs to be a community effort, which could involve spaying and neutering domestic cats, and an awareness programme to prevent residents from releasing cats when they are no longer wanted. It would also help if the Kaikoura District Council would require members of the community to register, microchip, and apply a collar, to their cats so they can be identified as pets.

Environmental stress

The findings that adult survivorship, body mass and morphological size have declined over the 52 years of the study suggest that the Kaikoura red-billed gull population has experienced some form of unfavorable environmental condition or stress over a long period of time. It has been shown that the decline in annual survivorship (Mills *unpubl. data*) and body size (Teplitsky *et al.* 2008) are not related to fluctuations in the availability of euphausiids in the breeding season. A number of mammalian and bird studies have demonstrated a decline in mean body size over time (Smith *et al.*, 1995; Yom-Tov 2001; Millien *et al.* 2006; Yom-Tov *et al.* 2006).

For some species, the decrease is thought to have resulted from increasing temperatures in relation to Bergmann's rule (Bergmann 1847). Bergmann's rule envisions that increasing mean body size with increases in latitude is an adaption to colder climates. The opposite occurs in warm climates. With a decrease in body size, the surface to volume ratio decreases, which facilitates the loss of excess heat. Millien *et al*. (2006) argue that a decrease in body size would be adaptive, and a genetically based response to global warming. However, most microevolutionary studies of climate change responses have overlooked or failed to elucidate evidence for genetic adaptation (Gienapp *et al*. 2008; Teplitsky *et al*. 2008). Although body mass in the red-billed gull is heritable (Teplitsky *et al.* 2008, 2009), an analysis of natural selection on body size showed no evidence for directional selection using lifetime production of recruits or fledglings as estimates of fitness (Teplitsky *et al.* 2008). Likewise, no evidence for directional selection through survival was observed (Teplitsky *et al*. 2008). These analyses question the likelihood that the decline in body size of the red-billed gull is an adaptation to climate warming; instead it can be interpreted as environmentally induced by some form of environmental stress (Teplitsky *et al*. 2008).

A possible explanation for the decline in body size could be related to a major change in the food availability outside of the breeding season. In the mid 1970's legislation was introduced that prevented the discharge of offal from fish and meat processing plants into the sea. Similarly, in the late 1980's, the authorities at garbage dumps began to cover rubbish as it was deposited. Discharge of waste from processing plants and garbage dumps provided food for large numbers of black-backed gulls and red-billed gulls. The birds that dominated at these sites tended to be large individuals, and small birds were often at a disadvantage as they found it difficult to compete. Conversely, when these sites were eliminated, big individuals were at a disadvantage feeding at sea because their bigger wing loading makes it more difficult to compete at euphausiid swarms, which require mobility and frequent, rapid changes in direction. However, the ultimate cause of the declines in size and survivorship requires further examination.

CONCLUSION

A central problem in studies of animal ecology is that important demographic processes controlling animal numbers occur over multiple years or decades (Clutton-Brock & Sheldon 2010). The present study has demonstrated the value of long-term research to the understanding of these complex systems in the Kaikoura red-billed gull population.

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LITERATURE CITED

Anker-Nilssen, T.; Barrett, R.T.; Krasnov, J.V. 1997. Long-term and short-term responses of seabirds in the Norwegian and Barents Seas to changes in stocks of prey fish. *Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems.* Fairbanks, University of Alaska.

Barnes, E.J. 1985. Eastern Cook Strait region circulation inferred from satellite derived, sea-surface, temperature data. *New Zealand Journal of Marine & Freshwater Research 19*: 405–411.

Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography 60:* 245-262.

Bergmann, C. 1847. Ueber die verhältnisse der wärmeökonomie der thiere zu iher grösse. *Gottinger Studien* 3: 595-708.

Bradford, J.M. 1972. *Systematics and ecology of New Zealand central east coast plankton sampled at Kaikoura*. Department of Scientific and Industrial Research Bulletin 207, New Zealand.

Bradford, J.M.; Lapennas, P.P.; Murtagh, R.A.; Chang, F.H.; Wilkinson, V. 1986. Factors controlling summer phytoplankton production in greater Cook Strait, New Zealand. *New Zealand Journal of Marine & Freshwater Research 20*: 253–279.

Chiswell, S.M.; Schiel, D.R. 2001. Influence of along-shore advection and upwelling on coastal temperatures at Kaikoura Peninsula, New Zealand. *New Zealand Journal of Marine & Freshwater Research 35*: 307–317.

Clutton-Brock, T.; Sheldon B.C. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology and Evolution 25:* 562–573.

Cury, P.M.; Boyd, I.L.; Bonhommeau, S.; Anker-Nilssen, T.; Crawford, R.J.M.; Furness, R.W.; Mills, J.A.;

Murphy, E.J.; Osterblom, H.; Paleczny, M.; Piatt, J.F.; Roux, J.-P.; Shannon, L.; Sydeman, W. 2011. Global seabird response to forage fish depletion – one third for the birds. *Science 334:* 1703–1706.

Edwards, M.; Richardson, A.J. 2004. Impact of climate change on marine pelagic phenology and tropic mismatch *Nature 430*: 881–884.

Frederiksen, M.; Wanless, S.; Harris, M.P.; Rothery, P.; Wilson, L.J. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. *Journal of Applied Ecology* 41: 1129–1139.

Frederiksen, M.; Edwards, M.; Richardson, A.J.; Halliday, N.C.; Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology 75*: 1259–1268.

Frost, P.G.H.; Taylor, G.A. 2018. The status of the red-billed gull (*Larus novaehollandiae scopulinus*) in New Zealand, 2014–2016 *Notornis 65*: 1–13.

Gibb, J.A.; Flux, J.E.C. 1973. Mammals. pp. 334–371 *In*: Williams, G.R. (*ed*.) *The natural history of New Zealand*. Wellington, A.H. & A.W. Reed.

Gienapp, P.; Teplitsky, C.; Alho, J.S.; Mills, J.A.; Merilä, J. 2008. Climate change and evolution; disentangling environmental and genetic responses. *Molecular Ecology 17*: 167–178.

Given, A.D.; Mills, J.A.; Baker, A.J. 2002. Isolation of polymorphic microsatellite loci from the red-billed gull (*Larus novaehollandiae scopulinus*) and amplification in related species. *Molecular Ecology Notes* 2: 416–418.

Gurr, L.; Kinsky, F.C. 1965. The distribution of breeding colonies and status of the red-billed gull in New Zealand and its outlying islands. *Notornis 12*: 223–240.

Hartwell, B.; Walsh, C. 2005. *Characterisation of the kahawai fisheries of New Zealand and review of biological knowledge*. Final research report for Ministry of Fisheries Research Project KAH 2004-01 Objective 1. Wellington, National Institute of Water and Atmospheric Research.

Heath, R.A. 1972. Oceanic upwelling produced by northerly winds on the North Canterbury coast, New Zealand. *New Zealand Journal of Marine & Freshwater Research* 6: 343–351.

King, W.B. 1985 Island birds: will the future repeat the past. *International Council for the Preservation of Birds Technical Publication 3*: 3-15.

King, C. M.; Edgar, R.L. 1977. Techniques for trapping and tracking stoats (*Mustela erminea):* a review, and a new system. *New Zealand Journal of Zoology 4*: 193–212.

Mauchline, J.; Fisher, L.R. 1969. The biology of euphausiids. pp. 1-454 *In*: Russell, F.S; Yonge, M. (*eds*.) *Advances in Marine Biology Vol 7.* London, Academic Press.

Millien, V.; Lyons, K.S.; Olson, L.; Smith, F.A.; Wilson, A.B.; Yom-Tov, Y. 2006. Ecotypic variation in the context of global climate change. Revisting the rules. *Ecology Letters 9*: 853–859.

Mills, J.A. 1971. Sexing red-billed gulls from standard measurements. *New Zealand Journal of Marine & Freshwater Research 5*: 326–328.

Mills, J.A. 1973. The influence of age and pair-bond on the breeding biology of the red-billed gull *Larus novaehollandiae scopulinus. Journal of Animal Ecology* 42: 147–162.

Mills, J.A. 1989. Red-billed gull. pp. 387–404 *In*: Newton I. (*ed*.) *Lifetime Reproduction in Birds.* London, Academic Press.

Mills. J.A.; Yarrall, J.W.; Mills, D.A. 1996. Causes and consequences of mate fidelity in red-billed gulls. pp 286–304 *In*: Black, J.M. (*ed.) Partnerships in birds: The study of monogamy*. London, Oxford University Press.

Mills, J.A.; Yarrall, J.W.; Bradford-Grieve, J.M.; Uddstrom, M.J.; Renwick, J.A.; Merilä, J. 2008. The impact of climate fluctuation on food availability and reproductive performance of the planktivorous red-billed gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology 77*: 1129–1142.

Ministry for Primary Industries 2016. *Fisheries Assessment Plenary, May 2016: stock assessments and stock status.* Compiled by the Fisheries Science Group. Wellington, Ministry for Primary Industries.

Mullan, A.B.; Wratt, D.S.; Renwick, J.A. 2001. Transient model scenarios of climate changes for New Zealand. *Weather & Climate 21*: 3–33.

Newton, I. 1998. *Population limitation in birds*. London, Academic Press.

O'Brien, D.P. 1988. Surface schooling behaviour of the coastal krill *Nyctiphanes australis* (Crustacea: Euphausiacea) off Tasmania, Australia. *Marine Ecology Progress Series 42*: 219–233.

Paleczny, M.; Hammill, E.; Karpouzi, V.; Pauly, D. 2015. Population trend of the world's monitored seabirds, 1950–2010. *PLOS one http:dx.doi.org/10.1371/journalpone.0129342*.

Parr, M.J., Gaskell, T.J.; George, B.J. 1968. Capture–recapture methods of estimating animal numbers. *Journal of Biological Education* 2: 95–117.

Robertson, H. A.; Baird, K.; Dowding, J.E.; Elliott, G.P.; Hitchmough, R.A.; Miskelly, C.M.; McArthur, N.; O'Donnell, C.F.J.; Sagar, P.M.; Scofield, P.R.; Taylor, G.A. 2017. Conservation status of New Zealand birds, 2016. *New Zealand Threat Classification Series 19.* Wellington, Department of Conservation.

Sheard, K. 1953. Taxonomy, distribution, and development of Euphausiacea (Crustacea). *Report of British Australian & New Zealand Antarctic Research Expedition Series B (Zoology and Botany) 8*: 1–72.

Smith, F.A.; Betancourt, L.; Brown, J.H. 1995. Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science 270*: 2012–2014.

Teplitsky, C.; Mills, J.A.; Alho, J.S.; Yarrall, J.W.; Merilä, J. 2008. Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Science USA 105*: 13492–13496.

Teplitsky, C.; Mills, J.A.; Yarrall, J.W.; Merilä, J. 2009. Heritability of fitness components in a wild bird population. *Evolution 63:* 716–726.

Townsend, A.J.; de Lange, PJ.; Duffy, C.A.J.; Miskelly, C.M.; Molloy, J.; Norton, D. 2008. *New Zealand Threat Manual*. Wellington, Department of Conservation.

White, G.C.; Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study 46* (Supplement): 120–139.

Wodzicki, K.A. 1950. *Introduced mammals of New Zealand. An ecological and economic survey*. Bulletin 98, New Zealand Department of Scientific and Industrial Research.

Yom-Tov, Y. 2001. Global warming and body mass decline in Israel passerine birds. *Proceedings Royal Society London Series B 268*: 947–952.

Yom-Tov, Y.; Yom-Tov, S.; Wright, J.; Thorne, C.J.R.; Du Feu, R. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos 112*: 91–101.