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# DEMOGRAPHIC CHARACTERISTICS OF THE ADÉLIE PENGUIN POPULATION ON BÉCHERVAISE ISLAND AFTER 12 YEARS OF STUDY

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Abstract

Demographic parameters (age-specific survival rates, fecundity levels and population numbers) were analysed for the Béchervaise Island Adélie penguin colony in eastern Antarctica after 12 years of monitoring under the CCAMLR Ecosystem Monitoring Program (CEMP). A life table was constructed, and predicted rates of population growth and breeding success calculated. The population model predicted an annual population growth rate of 0.3% compared to the 1.2–1.8% increase per annum indicated from field counts. Underestimation of adult survival rates was considered the most likely explanation for the discrepancy. As is the case for most long-lived seabird species, growth/decline rates of the Adélie penguin population at Béchervaise Island were found to be more sensitive to changes in annual survival rates, especially of young breeding adults, than to changes in fecundity parameters. Results are discussed in comparison with data from a declining Adélie penguin population in the Ross Sea studied during the 1960s and 1970s (Ainley et al., 1983), and in relation to other CEMP parameters, environmental factors and fishery regulations. The data collection and analysis methods outlined in this paper provide a basis for the development of data reporting formats for CEMP Standard Method A4.

Résumé

Les paramètres démographiques (taux de survie selon l'âge, fécondité et effectif de la population) de la colonie de manchots Adélie de l'île Béchervaise, dans l'est de l'Antarctique, font l'objet d'une analyse après 12 années de surveillance dans le cadre du Programme de contrôle de l'écosystème de la CCAMLR (CEMP). Une table de survie est dressée et les taux attendus de croissance de la population et la réussite de la reproduction sont calculés. Le modèle de population prévoit un taux de croissance annuel de la population de 0,3% contre une augmentation annuelle de 1.2–1.8% d'après les recensements sur le terrain. Il est considéré que cette différence résulte probablement d'une sous-estimation des taux de survie des adultes. Comme chez la plupart des espèces d'oiseaux à longue vie, il est constaté que les taux de croissance/déclin de la population de manchots Adélie à l'île Béchervaise sont plus sensibles aux changements des taux de survie annuels, notamment des jeunes adultes reproducteurs, qu'aux changements affectant les paramètres de fécondité. Les résultats sont comparés aux données d'une population de manchots Adélie en déclin dans la mer de Ross, ayant fait l'objet d'une étude dans les années 60 et 70 (Ainley et al., 1983), et examinés par rapport à d'autres paramètres du CEMP, aux facteurs environnementaux et aux règlements de pêche. Les méthodes de collecte et d'analyse des données décrites dans ce document pourront servir de base pour la création des fiches de déclaration des données de la méthode standard A4 du CEMP.

Резюме

Были проанализированы демографические параметры (повозрастная выживаемость, уровень плодовитости и численность популяции) для колонии пингвинов Адели о-ва Бешервэз в восточной Антарктике после 12 лет мониторинга в рамках программы АНТКОМа по мониторингу экосистемы (CEMP). Была составлена таблица выживания и рассчитаны прогнозные показатели роста популяции и репродуктивного успеха. Популяционная модель дала ежегодные темпы роста популяции 0.3%, но учет численности в колонии показал, что прирост составлял 1.2–1.8% в год. Это несоответствие скорее всего объясняется занижением выживаемости взрослых особей. Было обнаружено, что, как и в случае большинства долгоживущих видов морских птиц, темпы роста/сокращения популяции пингвинов Адели на о-ве Бешервэз более чувствительны к изменениям ежегодной выживаемости, особенно взрослых молодых размножающихся особей, чем к изменениям в параметрах плодовитости. Полученные результаты сравниваются с данными по сокращающейся популяции пингвинов Адели в море Росса, исследования которой проводились в 1960-е и 1970-е гг. (Ainley et al., 1983), и анализируются по отношению к другим параметрам СЕМР, экологическим факторам и правилам ведения рыбного промысла. Описанные в данной статье методы сбора и анализа данных дают основу для разработки форматов представления данных для стандартного метода СЕМР А4.

Resumen

Se analizaron los parámetros demográficos (tasas de supervivencia por edades, niveles de fecundidad y número de individuos) de la colonia de pingüinos adelia de isla Béchervaise en la Antártida oriental, luego de 12 años de seguimiento en el marco del programa de seguimiento del ecosistema de la CCRVMA (CEMP). Se elaboró una tabla de vida y se estimaron las tasas previstas de crecimiento y éxito reproductor de la población. El modelo demográfico predijo una tasa de crecimiento anual de la población de 0,3 %, comparado con el aumento anual de 1,2–1,8% indicado por los recuentos en terreno. Se atribuyó la subestimación de la tasa de supervivencia de las aves adultas como la causa más probable de esta discrepancia. Tal como ocurre para las especies de aves marinas más longevas, se encontró que las tasas de crecimiento/disminución de la población de pingüinos adelia en isla Béchervaise fueron más sensitivas a las variaciones en las tasas de supervivencia anual que a las variaciones en los parámetros de fecundidad, especialmente para las aves adultas más jóvenes en estado reproductor. Se analizaron los resultados en comparación con los datos de una población de pingüinos adelia en declinación en el mar de Ross estudiada durante las décadas de 1960 y 1970 (Ainley et al., 1983), y en relación con otros parámetros del CEMP, factores medioambientales y legislaciones pesqueras. Los métodos de recopilación y análisis de datos descritos en este trabajo proporcionan las bases para la elaboración de formularios de notificación de datos para el Método Estándar A4 del CEMP.

Keywords: Adélie penguin, CEMP, demography, survivorship, fecundity, life tables, population growth, CCAMLR

## INTRODUCTION

An Adélie penguin CCAMLR Ecosystem Monitoring Program (CEMP) site was established at Béchervaise Island in 1990 and CEMP data have been collected there according to Standard Methods A1 to A9 (CCAMLR, 2003) over the past 12 years. Demographic data (Standard Method A4) have not yet been reported to CCAMLR due to the need to build up a sufficiently long time series on known-age birds from which to determine useful estimates of survival, mortality, fecundity and rates of population change. Examination of data in relation to these parameters was commenced in 2001; this paper presents results of these analyses and extends the initial demographic results published in Clarke and Kerry (1998) and Clarke (1999). The use of demographic data in the development of survivorship curves and life history tables is illustrated in this manuscript. A life history table is constructed and used to calculate population growth rates and to compare these with results derived from population counts. Finally, the relative importance of the various demographic parameters as factors influencing variations in population size is discussed.

## METHODS

### General

Data were collected at Béchervaise Island (67°35′S 62°49′E) near Mawson station during each of the breeding seasons from 1990/91 to 2001/02. The Adélie penguin colony on this island consists of approximately 2 000 breeding pairs divided among 18 discrete sub-colonies (Kerry et al., 2000). All birds in four of these sub-colonies travel to and depart from their breeding sites through a narrow naturally occurring rocky gateway within which an Automated Penguin Monitoring System (APMS) has been installed. The APMS consists of a weighbridge, a tag detector, direction sensors and computer microprocessor (for more details see Kerry et al., 1993b; Clarke and Kerry, 1998). Each season since the APMS was first commissioned (1991/92), between 20 and 262 adult breeding penguins have been fitted with subcutaneously implanted identification transponders (referred to as ‘tags’ in this paper), and sexed by cloacal examination. Two hundred marked nests were observed annually to determine breeding success; attempts were made to ensure that all birds occupying these nests each season would carry tags so that long-term individual histories could be obtained. In addition, up to 300 fledgling chicks from the four study colonies have been implanted with tags annually in order to build up a known-age population from which to determine age-specific survivorship curves and data on age-specific fecundity. Tags were used in preference to flipper bands to avoid the deleterious effects associated with banding (Ainley et al., 1983; Culik et al., 1993; Jackson and Wilson, 2002). Potential ill effects due to tag implantation have been previously investigated (Clarke and Kerry, 1998) and were considered minimal.

### Population Size and Colony Breeding Success

Population size was estimated from annual whole-colony counts at two different stages of the breeding season: total penguins present at the end of the arrival period (CEMP parameter A9), and total nests with eggs during mid-incubation (CEMP parameter A3). Exponential equations were used to describe the rates of population growth/decline derived from colony counts to allow comparison with those derived from demographic parameters. Annual colony breeding success was calculated as the number of crèched chicks per nest with eggs (CEMP parameter A6, procedure C).

### Survival and Mortality

Survival rates of tagged adults and chicks were determined from resight information collected annually and stored in a comprehensive database. Resight data came from three sources: (i) detection by the APMS of tagged birds crossing the weighbridge; (ii) regular checks of breeding birds on the 200 marked nests; and (iii) nest checks of all 18 sub-colonies on the island at the times of peak male and peak female presence during the incubation period (Kerry et al., 1993a). A second APMS, situated at Verner Island, 5 km to the east of Béchervaise Island, was also used to detect tagged birds migrating between colonies. In addition, nest checks of colonies on Verner Island and also on Petersen and Welch Islands (a further 0.5 and 2 km east from Verner Island respectively) were carried out during incubation in 2000/01 and 2001/02. Thus individuals initially tagged at Béchervaise Island and later found breeding on other islands within an 8 km radius of their natal colony were able to be included in survivorship analyses. Detailed analysis of the movement of tagged birds between islands or amongst sub-colonies was not carried out; this is the subject of a current study into emigration patterns and effects of researcher disturbance on colony structure.

Survival rates were determined for adults and chicks separately to produce age-specific survivorship curves and to determine annual survival rates ($p_x$) for each age ($x$). Data from chicks were restricted to fledglings tagged between 1991 and 1998 to maximise probabilities of detection (>90% of penguins that survive to 6 years of age have been resighted by age 4 years). Mortality rates were calculated as $1 - p_x$, assuming minimal emigration beyond the local region within which resight data were collected. It was acknowledged that survival rates could be underestimated if emigration is a significant factor.

### Fecundity

#### Chicks per Breeding Female

Data on age-specific fecundity were limited because only a small number of penguins tagged as chicks have thus far entered the study population of 200 marked nests. These are the only nests currently monitored for individual breeding success by the program (in order that disturbance to other sub-colonies be minimised). Breeding in female Adélie penguins first occurs between 3 and 7 years of age and fecundity is known to increase with age up to 7 years (Ainley et al., 1983). The mean number of chicks crèched per breeding female aged 7 years and older within the study population of 200 nests was calculated on the basis of the assumption that established birds tagged as adults were at least 4 years of age when tagged. However, age-specific fecundity for younger birds was unable to be determined for use in the construction of life history tables. Instead, for ages 3 to 6 years, fecundity values derived by Ainley et al. (1983, Table 9.7) were used.

#### Proportion of Females Breeding

Breeding birds were defined as those having paired and produced at least one egg. The overall proportion of breeding females aged 7+ years was determined from study-nest data, i.e. the ratio of females in this age group laying eggs to the total number present on marked nests. Proportions of birds breeding in age groups 3 to 6 were determined using a combination of: (i) resight data to determine the proportions of those surviving to at least 6 years of age that were present at ages 3 to 6 years; (ii) APMS and nest observation data to determine the proportion of birds present at ages 3 to 6 years that were in the colony during the incubation period; and (iii) observations of known-age birds on unmarked nests during the incubation period of 1999/2000 to determine the proportion of those at ages 3 to 6 years actually breeding. The overall proportion of birds of ages 3 to 6 years which were breeding was equal to the product of the proportions in (i), (ii) and (iii) above for each age group. The sex of insufficient numbers of penguins tagged as chicks was known for the proportion breeding at ages 3 to 6 years to be able to be determined for each sex separately. Thus the data used in the life history table for these ages were for both sexes combined.

## RESULTS

### Population Size and Colony Breeding Success

The total numbers of Adélie penguins present on Béchervaise Island at the end of the arrival period (mid-November) were determined for each of the breeding seasons from 1990/91 to 2001/02. Counts of incubated nests were performed annually during mid-incubation (early December). Both sets of counts are presented in Table 1.

Exponential curves of the form $N_x = (N_0)e^{rx}$ were fitted to each set of counts to determine rates of population change over the 12 seasons, where $N$ is population size, $N_0$ is the population size at year 0, $x$ is years and $r$ is the annual rate of population increase (Figure 1). In terms of arrival counts, the population was growing at a rate of 1.2% per annum (SE = 0.007; $R^2 = 0.2564$). In terms of incubating nest counts, the population growth rate was 1.8% per annum (SE = 0.006; $R^2 = 0.4895$).

The numbers of chicks reaching crèche age in the colony were counted in early February each year (Table 1). Breeding success was calculated in terms of chicks per nest with eggs for each season (Figure 2). Average breeding success over all 12 seasons was 0.71 chicks crèched per nest with eggs (Table 1, Figure 2).

### Survival and Mortality

Numbers of chicks tagged in each season from 1991/92 to 1997/98 are shown in Table 2 along with the numbers and percentages surviving in subsequent years (Table 2a). The oldest tagged cohort was 10 years of age by 2001/02. Annual age-specific survival rates for all known-age Adélie penguins are shown in Table 2b. Overall pooled survivorship figures are provided in Table 2c. The mean annual survival rate for birds aged 3 to 9 years was 86.2%. There were no statistically significant differences between this mean value and those actually obtained ($z$-tests: $z$ ranging between 0.0774 and 1.503; $p$ ranging between 0.133 and 0.938).

Age-specific exponential survivorship curves were fitted to the survivorship data for penguins tagged as chicks (Figure 3). The predicted age to which 10% of an average cohort of Adélie penguin chicks could be expected to survive was 13 years. Data have been collected for insufficient numbers of years to determine whether survival rates decrease towards the end of the penguins' lifetime, as is the case for some long-lived seabird species (Bradley et al., 1989).

Annual survival rates by breeding season are shown in Table 2d for pooled known-age penguins of 3 to 9 years of age. Again the mean survival rate was 86.2%. Annual survival rates differed significantly from the mean value over the autumn–winter periods (hereafter referred to as 'winter') of 1998 and 2001. Penguin survival over the winter of 1998 was higher than the mean ($z = 3.182$, $p = 0.001$) and, over winter 2001, lower than the mean ($z = 3.031$, $p = 0.002$) (Figure 4).

Adult survivorship was analysed similarly to that of chicks, for males and females separately. Exact ages were unknown, although it was assumed that birds were at least 4 years of age when first tagged as adults (see next section). Thus 'age-specific' data were presented for groups whose minimum ages were 4 to 13 years (Tables 3 and 4). Mean annual survival rates were 86.1% for females and 84.0% for males. There were no significant differences between 'age classes'; however, annual survival rates by breeding season differed significantly from the mean pooled-sex value of 85.1% over the winters of 1992, 1995 and 1998. Over the winters of 1992 and 1995 adult survival was lower than the mean ($z = 2.038$, $p = 0.042$; $z = 2.669$, $p = 0.008$ respectively), and over the winter of 1998 survival was higher than the mean ($z = 2.233$, $p = 0.026$) as found for birds tagged as chicks (Figure 4).

### Fecundity

On average, 97% of females aged 7 years and over which were present in the colony laid eggs each season. The mean number of chicks produced by these females on marked study nests over the periods 1993/94 to 2001/02 was 0.89 chicks per female per year (Table 5). On the assumption that the ratio of male to female chicks raised to crèche age was 1:1, the mean annual fecundity of female Adélie penguins aged 7 years and over was 0.45 female chicks.

Resight data enabled determination of the ages at which birds that eventually returned to Béchervaise Island were first detected in the colony. Ninety-nine percent of all birds that returned had been resighted by 7 years of age. The proportions of penguins resighted by ages 3 to 6 years are shown in Table 6. The proportions of these present during the incubation period at each age are also shown. In the 1999/2000 season, the proportions of penguins of each age group present during incubation that were actually incubating eggs (i.e. breeding) were determined. These proportions are also provided in Table 6. For ages 3 to 6 years the overall proportions of each age group breeding were calculated (final column of Table 6).

### Life Tables

A life table for the Adélie penguin population at Béchervaise Island was constructed using the survivorship and fecundity data presented in Tables 2, 5 and 6 (Table 7). The mean annual survival rate of chicks aged 3 to 9 years from Table 2b (86.2%) was used for all birds aged 1 year and older. This mean value was employed to avoid the bias arising from sample size differences in the numbers of chicks monitored at different ages, and was considered valid on the basis that no significant differences in survival between age classes were evident (see earlier section). The survival rate for fledglings ($p_0$) was calculated on the basis that overall survivorship to age 3 years ($l_3$) was 51.4% (Table 2c) and on the assumption that the annual survival rates of 1 and 2 year olds ($p_1$ and $p_2$ respectively) were equal to the adult rate ($p_a$) (Reid, 1968). Alternatively it could have been assumed that $p_0 = p_1$ and $p_2 = p_a$ as per Ainley et al. (1983). Both options are equally valid given the present lack of knowledge of mortality rates during the pelagic non-breeding years of the Adélie penguin's life cycle. (Note that the calculations at the bottom of Table 7 are unaffected by the values of $p_0$, $p_1$ and $p_2$ providing that the product of these equals $l_3$.) Although the data from this study only cover penguins up to 13 years of age, the table was extended to include ages up to 19 years since Adélie penguins elsewhere have been shown to live up to 20 years of age (Reid, 1968; Ainley et al., 1983). A constant mortality rate throughout life was assumed on the grounds that even if survival rates are higher for the oldest birds, they comprise such a small percentage of the total population that the effect on the overall population model will be small. The numbers of fledglings produced by females aged 3 to 6 years were unknown parameters in our dataset; the values of Ainley et al. (1983), which are the only published age-specific fecundity figures available for Adélie penguins, were therefore used.

The lifetime expectation of female offspring produced per female penguin ($R_0$) can be calculated from the life history table according to the formula $R_0 = \Sigma l_x m_x$, where $l_x$ = probability of survival to age $x$, and $m_x$ = birth rate (female offspring) at age $x$ (Stearns, 1992). For the Béchervaise Island model, $R_0 = 1.03$ (Table 7). Generation time ($T$) is defined as the average age of the mothers of newborn offspring in a population of stable age structure and can be calculated as $T = (\Sigma\ x l_x m_x)\ R_0^{-1}$ (Stearns, 1992). For the Béchervaise Island model, $T = 9.55$ years of age (Table 1).

The *per capita* instantaneous rate of population increase ($r$) can be estimated as $r_{\text{est}} \approx ln(R_0)/T$ (Stearns, 1992). This estimate is usually within 10% of the true value (Stearns, 1992). The per-time-unit rate of multiplication of a population ($\lambda$) is defined as $\lambda = e^r$ (Stearns, 1992). According to the life history table (Table 7), $r_{\text{est}} \approx 0.003$ and therefore $\lambda_{\text{est}} \approx 1.003$. This suggests that the Béchervaise Island Adélie penguin population is increasing at a rate of approximately 0.3% per annum. It should be noted that this population model assumes stable age distribution and lack of density-dependent constraints.

Age structure for the Béchervaise Island population was calculated from the life history table and is shown in the final column of Table 7. An expected value for mean penguin breeding success over 20 years was also calculated. This value was 0.78 chicks per breeding female, which is slightly higher than the observed average colony breeding success over 12 seasons of 0.71 chicks crèched per nest with eggs.

## DISCUSSION

### Population Model

Field-based colony counts indicated somewhat larger population growth rates than those predicted by estimates from the life history tables. Using the latter, an expected annual population increase was calculated to be 0.3%. The field-based colony counts showed an average annual increase of 1.2% or 1.8% depending on whether counts of arriving birds or incubating nests were used. The most likely reason for the difference is an underestimation of adult survival rates in the life history table. When the values of adult survivorship in the table are increased by 1% over all ages > 3 years, the predicted population growth rate equals that derived from counts of arriving birds. Similarly, a 2% increase in adult survival results in a predicted population growth rate equivalent to that derived from counts of incubated nests. It is quite possible that these values of adult survival may be underestimated by this degree due to a combination of tag loss or failure, tag-associated mortality (believed to be low), and failure to successfully resight all surviving birds. Emigration is also an unknown factor, although it is likely to be low given the amount of bird movement so far detected between Béchervaise, Verner, Petersen and Welch Islands (~1% of birds have been found breeding somewhere other than their natal colony, Kerry et al., unpublished data). Immigration must also be taken into account when considering recruitment, especially as pools of potential recruits, if present, can buffer population size during periods of increased mortality of breeding birds (Porter and Coulson, 1987). In the Mawson region, rates of movement of tagged birds between Béchervaise and Verner Islands are approximately equal (unpublished data from APMS records).

Despite unknown levels of tag loss/failure, tag-associated mortality, resighting success and emigration, the life history table model predicted the observed rate of population increase and the mean colony breeding success reasonably well. It should be emphasised that this model assumes a stable rate of population growth, a stable age structure and no density-dependent constraints. For the Béchervaise Island colony the stability of age distribution is unknown. Density dependence (in terms of nest sites at least) is unlikely to be a constraining factor due to an abundance of available nesting material and snow-free ground in at least three sub-colonies on the island (personal observation). It should also be noted that the use of mean values of fecundity, survival rates and breeding success to formulate a life table or population model may not be valid if there are systematic changes occurring over time in these parameters (Cooch and Cooke, 1991). No such systematic trends have been identified in our data over the past 12 years of monitoring, nor have any changes in age at first breeding or proportion of birds breeding been detected over the duration of this study.

Few results of demographic studies on Adélie penguins are available in the literature to date. Of those published, the study carried out by Ainley et al. (1983) is the most comprehensive. Comparisons between demographic parameters measured in this study and those published by Reid (1968) and Ainley et al. (1983) are shown in Table 8. Various differences are apparent in terms of survival rates, breeding success and population growth. Most notable are the higher rates of juvenile survival measured in this study compared to the other two. Although the population studied by Ainley et al. (1983) had a higher rate of adult survival than the Béchervaise Island population, the high rate of juvenile survival at Béchervaise Island has more than compensated for the lower adult survival rate, as the latter population is growing while the former was declining. The various values in Table 8 provide examples of the degree of spatial and temporal variability between populations of the same species. They also serve to illustrate the degree of flexibility in demographic parameters available to Adélie penguins under differing environmental conditions.

## Demographic Parameters in relation to CEMP

Long-lived seabird species tend to have high adult survival and low recruitment rates. As a result their populations are more sensitive to changes in adult survival than to changes in breeding success or juvenile survival (Croxall and Rothery, 1991; Lebreton and Clobert, 1991; Perrins, 1991). Any decreases in adult survival of long-lived species must be compensated for by proportionally larger increases in juvenile survival, or even larger increases in breeding success. The latter requirement may easily go beyond that possible for the existing clutch size of the species. Initiation of breeding at an earlier age is another mechanism by which such species may increase their population size. However, delays in onset of breeding after the attainment of sexual maturity tend to be greatest for the longest-lived birds (Wooller et al., 1992). This implies the existence of a trade-off between survival and reproduction which limits the expression of such life history traits in free-living populations.

As is the case for other long-lived seabirds with low fecundity, the size of the Adélie penguin population at Béchervaise Island is more sensitive to changes in annual survivorship, especially of young breeding adults, than to changes in fecundity parameters (Table 7). Sensitivity analyses carried out by repeated modelling of the life history table indicate that $\lambda$ is most sensitive to changes in adult survival, particularly of birds aged 3 to 10 years. For the Béchervaise Island population, a 1% decrease in adult survival (age 3 years onwards) would require a 2% increase in juvenile survival (ages 0, 1 and 2 years) or a 6% increase in fecundity to effect an unchanged population growth rate.

Environmental conditions resulting in reduced summer or winter prey availability are likely to result in decreased population growth rates. In the case of harsh winters, effects will become apparent through decreased survival rates of adults or juveniles. In contrast, poor summer conditions are likely to reduce fecundity. According to our model, a 1% decrease in annual mortality for all birds aged 3 years and over will have the same effect on $\lambda$

as a 6% decrease in mean fecundity for the same population. This effect could be induced, for example, by doubling the present frequency of years in which all chicks starve to death (fecundity = 0) from 1 in 12 to 1 in 6, or by increasing the present frequency of harsh winters (in which adult survival rate = 0.76) from 2 in 10 to 3 in 10. Either of these scenarios, if persistent, would be sufficient to send the presently increasing Adélie penguin population into a state of decline. Introduction or expansion of a krill fishery in the region could potentially mimic or exacerbate the effects of such adverse environmental conditions.

Because population growth rate is strongly sensitive to adult survival and much less sensitive to fecundity for long-lived species, the detection of any sharp change in population growth rate for such species should lead one to first suspect a change in adult survival (Lebreton and Clobert, 1991). However, because of the low reproductive rates of seabirds, by the time significant adverse changes in breeding success, population size or adult survival have been detected, the factors underlying these changes are likely to have been operating for many years (Croxall and Rothery, 1991). Large sample sizes are required to detect significant changes in adult survival, and only a long time sequence of data prevents year-to-year variation from obscuring long-term trends on factors such as reproductive success, juvenile survival and adult mortality (Wooller et al., 1992).

For the reasons outlined above, adult survival may be the most important demographic parameter to measure accurately and to monitor regularly within the CEMP context. Sensitivity analyses need to be carried out to determine the numbers of adults and chicks that should be marked each year in order to detect significant differences in annual adult mortality and juvenile survival as well as to enable detection of correlations between these and other CEMP parameters. Likewise, data reporting formats must be developed for CEMP purposes. It would also be a valuable exercise to investigate whether other CEMP parameters (e.g. A1 – adult weight on arrival) are correlated with adult survival over the preceding winter. Adult weight prior to moulting may also be correlated with mortality over the following winter. Similarly, fledging mass (A7) may be correlated with juvenile survival. There are currently insufficient numbers of years of data to detect such correlations at a statistically significant level. Automated weighbridge systems such as the APMS may be of use in determining such associations over the long term (Kerry et al., 1993b; Clarke and Kerry, 1998; Clarke et al., 2002).

## CONCLUSIONS

The demographic parameters summarised within the life history table in this paper have enabled calculations to be performed showing that the size of the Adélie penguin population at Béchervaise Island is more sensitive to changes in annual survivorship than to changes in fecundity. Comparisons with data from the Ross Sea region illustrate the degree of flexibility in demographic parameters available to Adélie penguins under differing environmental conditions.

Adult survival is the most important demographic parameter to correlate with other CEMP parameters and must be measured accurately. Using this paper as a basis, data reports could include: numbers of adults and chicks tagged each season, updated return rates for these in following seasons, mean age of first sighting for each cohort, and mean age at first breeding for each cohort (the latter being highly labour-intensive).

Environmental conditions resulting in reduced summer or winter prey availability are likely to result in decreased population growth rates. Introduction or expansion of a krill fishery in the region could potentially mimic or exacerbate the effects of such adverse environmental conditions. Further thought needs to be directed towards determining exactly how demographic parameters might be used in fishery regulation, especially given the lag time between detection of changes and causal events. This latter question may eventually become redundant if changes in demographic parameters can be linked to changes in other CEMP parameters operating over shorter time scales, e.g. arrival weights (A1), foraging trip durations (A2 and A5) and fledging mass (A7).

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Table 1: Counts of Adélie penguins on Béchervaise Island at three stages over 12 breeding seasons. Breeding success in terms of chicks crèched per nest with eggs is shown in the final column.

| Season | Arrival Count (Penguins) | Mid-incubation Count (Nests) | Crèched Chicks | Breeding Success (Chicks/Nest) |
|---|---|---|---|---|
| 1990/91 | 3836 | 1791 | 1498 | 0.84 |
| 1991/92 | 3675 | 1829 | 1304 | 0.71 |
| 1992/93 | 3362 | 1485 | 1190 | 0.80 |
| 1993/94 | 3591 | 1711 | 1816 | 1.06 |
| 1994/95 | 3993 | 1736 | 34 | 0.02 |
| 1995/96 | 3575 | 1813 | 727 | 0.40 |
| 1996/97 | 3842 | 1873 | 1750 | 0.93 |
| 1997/98 | 4158 | 1933 | 1556 | 0.80 |
| 1998/99 | 4063 | 1880 | 720 | 0.38 |
| 1999/00 | 3731 | 1836 | 990 | 0.54 |
| 2000/01 | 3598 | 1939 | 1697 | 0.87 |
| 2001/02 | 4646 | 2207 | 2264 | 1.03 |
| Mean breeding success | | | | 0.71 |

Table 2: Age-specific survival rates of chicks at Béchervaise Island carrying implanted transponders. All chicks died of starvation in 1995. (a) Numbers and percentages of each cohort known to survive to minimum ages of 1 to 10 years. (Survival rates of 1 and 2 year olds are underestimates because the majority of birds are not first sighted until age 3.) (b) Annual age-specific survival rates for pooled cohorts of 3, 4, 5, 6, 7, 8 and 9 year olds. (c) Pooled age-specific survivorship to ages 3 to 10 years. (d) Annual survivorship by breeding season for all chicks 3 to 9 years of age pooled.

| | | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 |
|---|---|---|---|---|---|---|---|---|
| Number of chicks tagged | | 34 | 244 | 261 | 0 | 193 | 299 | 298 |
| (a) Number and % of chicks surviving to age | 1 years | 17 (50%) | 110 (45%) | 132 (51%) | | 110 (57%) | 171 (57%) | 170 (57%) |
| | 2 years | 17 (50%) | 110 (45%) | 132 (51%) | | 110 (57%) | 171 (57%) | 170 (57%) |
| | 3 years | 14 (41%) | 109 (45%) | 126 (48%) | | 108 (56%) | 162 (54%) | 164 (55%) |
| | 4 years | 12 (35%) | 96 (39%) | 115 (44%) | | 100 (52%) | 138 (46%) | 130 (44%) |
| | 5 years | 9 (26%) | 85 (35%) | 110 (42%) | | 85 (44%) | 113 (38%) | |
| | 6 years | 8 (24%) | 82 (34%) | 99 (38%) | | 62 (32%) | | |
| | 7 years | 7 (21%) | 76 (31%) | 88 (34%) | | | | |
| | 8 years | 3 (9%) | 63 (26%) | 70 (27%) | | | | |
| | 9 years | 2 (6%) | 51 (21%) | | | | | |
| | 10 years | 1 (3%) | | | | | | |

(continued)

Table 2 (continued)

| | | | | | |
|---|---|---|---|---|---|
| (b) Pooled age-specific annual survival ($p_x$) | age ($x$) | $N$ alive ($N_x$) | $N$ alive next season ($N_{x+1}$) | % survival ($p_x$) | $N$ cohorts pooled |
| | 3 | 683 | 591 | 86.5 | 6 |
| | 4 | 461 | 402 | 87.2 | 5 |
| | 5 | 289 | 251 | 86.9 | 4 |
| | 6 | 189 | 171 | 90.5 | 3 |
| | 7 | 171 | 136 | 79.5 | 3 |
| | 8 | 66 | 53 | 80.3 | 2 |
| | 9 | 2 | 1 | 50.0 | 1 |
| Mean annual survival for birds 3–9 years of age | | | | 86.2 | |
| (c) Chick survivorship ($l_x$) | | % survival ($l_x$) | $N$ cohorts pooled | | |
| Pooled age-specific survivorship ($l_x$) to age | 3 years | 51.4 | 6 | | |
| | 4 years | 44.5 | 6 | | |
| | 5 years | 39.0 | 5 | | |
| | 6 years | 34.3 | 4 | | |
| | 7 years | 31.7 | 3 | | |
| | 8 years | 25.2 | 3 | | |
| | 9 years | 19.1 | 2 | | |
| | 10 years | 2.9 | 1 | | |
| (d) Annual survival by season of birds tagged as chicks | Breeding season | $N$ alive | $N$ alive next season | % survival | $N$ cohorts pooled |
| | 1994/95 | 14 | 12 | 85.7 | 1 |
| | 1995/96 | 121 | 105 | 86.8 | 2 |
| | 1996/97 | 231 | 208 | 90.0 | 3 |
| | 1997/98 | 208 | 199 | 95.7 | 3 |
| | 1998/99 | 307 | 278 | 90.6 | 4 |
| | 1999/00 | 440 | 376 | 85.5 | 5 |
| | 2000/01 | 540 | 427 | 79.1 | 6 |
| Mean annual survival for birds 3 to 9 years of age | | | | 86.2 | |

Table 3: Survival rates of male adults at Béchervaise Island carrying implanted transponders. (a) Numbers and percentages of males tagged in one season surviving in subsequent years. Minimum age at tagging assumed to be 4 years. (b) Annual survival rates for aging groups of males: minimum ages of 4+, 5+, 6+, 7+, 8+, 9+, 10+, 11+, 12+ and 13+ years. (c) Pooled survivorship of aging groups to 13+ years of age. Calculations assume a 44% survival rate to 4 years of age based on chick survivorship data. (d) Annual survivorship by breeding season for all males pooled.

| | | 1991/92 | 1992/93 | 1993/94 | 1994/95 | 1995/96 | 1996/97 | 1997/98 | 1998/99 | 1999/00 | 2000/01 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of males tagged (minimum age 4 years) | | 76 | 54 | 59 | 30 | 20 | 28 | 10 | 25 | 17 | 30 |
| (a) Numbers and % of males surviving to minimum age | 5+ | 58 (76%) | 43 (80%) | 52 (88%) | 24 (80%) | 18 (90%) | 27 (96%) | 9 (90%) | 20 (80%) | 14 (82%) | 25 (83%) |
| | 6+ | 47 (62%) | 37 (69%) | 39 (66%) | 19 (63%) | 16 (80%) | 24 (86%) | 8 (80%) | 17 (68%) | 11 (65%) | |
| | 7+ | 35 (46%) | 29 (54%) | 35 (59%) | 18 (60%) | 15 (75%) | 22 (79%) | 7 (70%) | 17 (68%) | | |
| | 8+ | 27 (36%) | 25 (46%) | 32 (54%) | 17 (57%) | 12 (60%) | 16 (57%) | 6 (60%) | | | |
| | 9+ | 25 (33%) | 17 (31%) | 31 (53%) | 15 (50%) | 10 (50%) | 15 (54%) | | | | |
| | 10+ | 21 (28%) | 14 (26%) | 24 (41%) | 15 (50%) | 10 (50%) | | | | | |
| | 11+ | 19 (25%) | 12 (22%) | 20 (34%) | 14 (47%) | | | | | | |
| | 12+ | 12 (16%) | 9 (17%) | 18 (31%) | | | | | | | |
| | 13+ | 12 (16%) | 7 (13%) | | | | | | | | |
| | 14+ | 7 (9%) | | | | | | | | | |

| b) Pooled male age-specific annual survival ($p_x$) | age ($x$) | $N$ alive ($N_x$) | $N$ alive next season ($N_{x+1}$) | % survival ($p_x$) | $N$ groups pooled |
|---|---|---|---|---|---|
| | 4+ | 349 | 290 | 83.1 | 10 |
| | 5+ | 265 | 218 | 82.3 | 9 |
| | 6+ | 207 | 178 | 86.0 | 8 |
| | 7+ | 161 | 135 | 83.9 | 7 |
| | 8+ | 129 | 113 | 87.6 | 6 |
| | 9+ | 98 | 84 | 85.7 | 5 |
| | 10+ | 74 | 65 | 87.8 | 4 |
| | 11+ | 51 | 39 | 76.5 | 3 |
| | 12+ | 21 | 19 | 90.5 | 2 |
| | 13+ | 12 | 7 | 58.3 | 1 |
| Mean annual survival for males 4+ to 13+ years of age | | | | 84.0 | |

(continued)

Table 3 (continued)

| (c) Male survivorship ($l_x$) | | (Assuming 44% survival to age 4) | | (Assuming 100% survival to age 4) |
|---|---|---|---|---|
| | | % survival ($l_x$) | *N* groups pooled | % survival ($l_x$) |
| Pooled age-specific survivorship ($l_x$) to age | 5+ | 36.6% | 10 | 83.1 |
| | 6+ | 30.1% | 9 | 68.3 |
| | 7+ | 25.9% | 8 | 58.9 |
| | 8+ | 21.4% | 7 | 48.7 |
| | 9+ | 18.6% | 6 | 42.3 |
| | 10+ | 15.5% | 5 | 35.1 |
| | 11+ | 13.1% | 4 | 29.7 |
| | 12+ | 9.1% | 3 | 20.6 |
| | 13+ | 6.4% | 2 | 14.6 |
| | 14+ | 4.1% | 1 | 9.2 |

| (d) Annual survival by season of males 4+ to 13+ years of age | Breeding season | *N* alive | *N* alive next season | % survival | *N* groups pooled |
|---|---|---|---|---|---|
| | 1991/92 | 76 | 58 | 76.3 | 1 |
| | 1992/93 | 112 | 90 | 80.4 | 2 |
| | 1993/94 | 149 | 124 | 83.2 | 3 |
| | 1994/95 | 154 | 119 | 77.3 | 4 |
| | 1995/96 | 139 | 122 | 87.8 | 5 |
| | 1996/97 | 150 | 131 | 87.3 | 6 |
| | 1997/98 | 141 | 129 | 91.5 | 7 |
| | 1998/99 | 154 | 125 | 81.2 | 8 |
| | 1999/00 | 142 | 120 | 84.5 | 9 |
| | 2000/01 | 150 | 130 | 86.7 | 10 |
| Mean annual survival for males 4+to 13+ years of age | | | | 84.0 | |

Table 4: Survival rates of female adults at Béchervaise Island carrying implanted transponders. (a) Numbers and percentages of females tagged in one season surviving in subsequent years. Minimum age at tagging assumed to be 4 years. (b) Annual survival rates for aging groups of females: minimum ages of 4+, 5+, 6+, 7+, 8+, 9+, 10+, 11+, 12+ and 13+ years. (c) Pooled survivorship of aging groups to 13+ years of age. Calculations assume a 44% survival rate to 4 years of age based on chick survivorship data. (d) Annual survivorship by breeding season for all all females pooled.

| | | 1991/92 | 1992/93 | 1993/94 | 1994/95 | 1995/96 | 1996/97 | 1997/98 | 1998/99 | 1999/00 | 2000/01 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of females tagged (minimum age 4 years) | | 93 | 50 | 64 | 17 | 16 | 42 | 10 | 20 | 13 | 24 |
| (a) Numbers and % of females surviving to minimum age | 5+ | 70 (75%) | 44 (88%) | 52 (81%) | 11 (65%) | 14 (88%) | 41 (98%) | 8 (80%) | 18 (90%) | 12 (92%) | 18 (75%) |
| | 6+ | 61 (66%) | 40 (80%) | 39 (61%) | 10 (59%) | 11 (69%) | 36 (86%) | 8 (80%) | 16 (80%) | 11 (85%) | |
| | 7+ | 55 (59%) | 33 (66%) | 35 (55%) | 9 (53%) | 11 (69%) | 33 (79%) | 8 (80%) | 16 (80%) | | |
| | 8+ | 41 (44%) | 28 (56%) | 31 (48%) | 9 (53%) | 9 (56%) | 30 (71%) | 6 (60%) | | | |
| | 9+ | 37 (40%) | 27 (54%) | 26 (41%) | 7 (41%) | 9 (56%) | 29 (69%) | | | | |
| | 10+ | 29 (31%) | 26 (52%) | 20 (31%) | 6 (35%) | 9 (56%) | | | | | |
| | 11+ | 28 (30%) | 22 (44%) | 16 (25%) | 5 (29%) | | | | | | |
| | 12+ | 23 (25%) | 20 (40%) | 14 (22%) | | | | | | | |
| | 13+ | 20 (22%) | 15 (30%) | | | | | | | | |
| | 14+ | 19 (20%) | | | | | | | | | |

| b) Pooled female age-specific annual survival ($p_x$) | age ($x$) | $N$ alive ($N_x$) | $N$ alive next season ($N_{x+1}$) | % survival ($p_x$) | $N$ groups pooled |
|---|---|---|---|---|---|
| | 4+ | 349 | 288 | 82.5 | 10 |
| | 5+ | 270 | 232 | 85.9 | 9 |
| | 6+ | 221 | 200 | 90.5 | 8 |
| | 7+ | 184 | 154 | 83.7 | 7 |
| | 8+ | 148 | 135 | 91.2 | 6 |
| | 9+ | 106 | 90 | 84.9 | 5 |
| | 10+ | 81 | 71 | 87.7 | 4 |
| | 11+ | 66 | 57 | 86.4 | 3 |
| | 12+ | 43 | 35 | 81.4 | 2 |
| | 13+ | 20 | 19 | 95.0 | 1 |
| Mean annual survival for females 4+ to 13+ years of age | | | | 86.1 | |

(continued)

Table 4 (continued)

| (c) Female survivorship ($l_x$) | | (Assuming 44% survival to age 4) | | (Assuming 100% survival to age 4) |
|---|---|---|---|---|
| | | % survival ($l_x$) | *N* groups pooled | % survival ($l_x$) |
| Pooled age-specific survivorship ($l_x$) to age | 5+ | 36.3 | 10 | 82.5 |
| | 6+ | 31.4 | 9 | 71.4 |
| | 7+ | 28.2 | 8 | 64.1 |
| | 8+ | 23.2 | 7 | 52.7 |
| | 9+ | 21.1 | 6 | 47.9 |
| | 10+ | 16.5 | 5 | 37.5 |
| | 11+ | 13.9 | 4 | 31.7 |
| | 12+ | 12.1 | 3 | 27.5 |
| | 13+ | 10.8 | 2 | 24.5 |
| | 14+ | 9.0 | 1 | 20.4 |

| (d) Annual survival by season of females 4+ to 13+ years of age | Breeding season | *N* alive | *N* alive next season | % survival | *N* groups pooled |
|---|---|---|---|---|---|
| | 1991/92 | 93 | 70 | 75.3 | 1 |
| | 1992/93 | 120 | 105 | 87.5 | 2 |
| | 1993/94 | 169 | 147 | 87.0 | 3 |
| | 1994/95 | 164 | 124 | 75.6 | 4 |
| | 1995/96 | 140 | 124 | 88.6 | 5 |
| | 1996/97 | 166 | 148 | 89.2 | 6 |
| | 1997/98 | 158 | 144 | 91.1 | 7 |
| | 1998/99 | 164 | 140 | 85.4 | 8 |
| | 1999/00 | 153 | 137 | 89.5 | 9 |
| | 2000/01 | 161 | 142 | 88.2 | 10 |
| Mean annual survival for females 4+ to 13+ years of age | | | | 86.1 | |

Table 5: Mean breeding success (chicks crèched per nest with eggs) for female Adélie penguins aged 7 years and over.

| Season | Incubated Nests | Chicks Crèched | Chicks per Nest |
|---|---|---|---|
| 1993/94 | 42 | 62 | 1.48 |
| 1994/95 | 110 | 0 | 0.00 |
| 1995/96 | 134 | 80 | 0.60 |
| 1996/97 | 151 | 207 | 1.37 |
| 1997/98 | 97 | 119 | 1.23 |
| 1998/99 | 119 | 79 | 0.66 |
| 1999/00 | 108 | 80 | 0.74 |
| 2000/01 | 98 | 103 | 1.05 |
| 2001/02 | 128 | 151 | 1.18 |
| Mean chicks per nest | | | 0.89 |

Table 6: Proportions of Adélie penguins aged 1 to 6 years resighted at each age. Overall proportions breeding at each age were calculated by multiplying the first three columns.

| Age ($x$) | Proportion $x$-yr-olds Resighted by Age $x$ ($n$ = 235) | Proportion $x$-yr-olds Resighted at Age $x$ that were Present During Incubation ($n$ = 127) | Proportion $x$-yr-olds Present During Incubation Observed Breeding ($n$ = 115) | Overall Proportion Breeding |
|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 |
| 2 | 0.26 | 0 | 0 | 0 |
| 3 | 0.81 | 0.40 | 0.78 | 0.25 |
| 4 | 0.91 | 0.67 | 0.90 | 0.55 |
| 5 | 0.94 | 0.88 | 0.91 | 0.76 |
| 6 | 0.97 | 0.96 | 0.92 | 0.86 |

Table 7: Life history table for the Béchervaise Island Adélie penguin population based on the data in Tables 2, 5 and 6. Female fledglings per breeding female for ages 3 to 6 were taken from Ainley et al., 1983. The shaded rows are extrapolated using mean adult rates of survival and fecundity.

| Age Class ($x$) | Survival Rate ($p_x$) | Survival to Age $x$ ($l_x$) | Female Fledglings per Breeding Female | Proportion Females Breeding | Birth Rate (Female Offspring) ($m_x$) | $l_x m_x$ | $x l_x m_x$ | Age Structure ($c_0\, l_x\, \lambda^{-x}$) |
|---|---|---|---|---|---|---|---|---|
| 0 | 0.691 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.178 |
| 1 | 0.862 | 0.691 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.122 |
| 2 | 0.862 | 0.596 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.105 |
| 3 | 0.862 | 0.514 | 0.150 | 0.252 | 0.038 | 0.019 | 0.058 | 0.090 |
| 4 | 0.862 | 0.443 | 0.200 | 0.549 | 0.110 | 0.049 | 0.195 | 0.078 |
| 5 | 0.862 | 0.382 | 0.250 | 0.757 | 0.189 | 0.072 | 0.362 | 0.067 |
| 6 | 0.862 | 0.330 | 0.430 | 0.856 | 0.368 | 0.121 | 0.728 | 0.057 |
| 7 | 0.862 | 0.284 | 0.450 | 0.970 | 0.437 | 0.124 | 0.869 | 0.049 |
| 8 | 0.862 | 0.245 | 0.450 | 0.970 | 0.437 | 0.107 | 0.856 | 0.042 |
| 9 | 0.862 | 0.211 | 0.450 | 0.970 | 0.437 | 0.092 | 0.831 | 0.036 |
| 10 | 0.862 | 0.182 | 0.450 | 0.970 | 0.437 | 0.080 | 0.796 | 0.031 |
| 11 | 0.862 | 0.157 | 0.450 | 0.970 | 0.437 | 0.069 | 0.755 | 0.027 |
| 12 | 0.862 | 0.136 | 0.450 | 0.970 | 0.437 | 0.059 | 0.711 | 0.023 |
| 13 | 0.862 | 0.117 | 0.450 | 0.970 | 0.437 | 0.051 | 0.664 | 0.020 |
| 14 | 0.862 | 0.101 | 0.450 | 0.970 | 0.437 | 0.044 | 0.617 | 0.017 |
| 15 | 0.862 | 0.087 | 0.450 | 0.970 | 0.437 | 0.038 | 0.570 | 0.015 |
| 16 | 0.862 | 0.075 | 0.450 | 0.970 | 0.437 | 0.033 | 0.524 | 0.013 |
| 17 | 0.862 | 0.065 | 0.450 | 0.970 | 0.437 | 0.028 | 0.480 | 0.011 |
| 18 | 0.862 | 0.056 | 0.450 | 0.970 | 0.437 | 0.024 | 0.439 | 0.009 |
| 19 | 0.862 | 0.048 | 0.450 | 0.970 | 0.437 | 0.021 | 0.399 | 0.008 |

| | | |
|---|---|---|
| Lifetime expectation of female offspring | $R_0 =$ | 1.03 |
| Generation time | $T =$ | 9.55 |
| Instantaneous rate of increase | $r_{est} =$ | 0.003 |
| Per time rate of multiplication (annual) | $\lambda =$ | 1.003 |
| Mean breeding success (chicks/nest) | | 0.78 |

Table 8: Comparison between demographic parameters of Adélie penguins at Béchervaise Island (this study), Cape Crozier (Ainley et al., 1983) and Cape Hallett (Reid, 1968). The largest value for each row is shown in bold. $p_x$ denotes annual survival rate at age $x$.

| Parameter | | This Study | Ainley et al., 1983 | Reid, 1968 |
|---|---|---|---|---|
| Annual population growth/decline ($\lambda$) | | (growing) | (declining) | (stable) |
| from Leslie matrix | | **1.004** | 0.959 | |
| from life table | | **1.003** | 0.953 | |
| Adult survival (mean) | | 0.862 | **0.894** | 0.86 |
| Juvenile survival (mean) | | | | |
| assuming $p_{1+} = p_a$ | | **0.691** | 0.294 | 0.52 |
| assuming $p_0 = p_1$; $p_{2+} = p_a$ | | **0.772** | 0.513 | |
| Breeding success (chicks/breeding pair) | | | | |
| observed colony mean | | 0.71 | 0.80 | **1.15** |
| from life table | | 0.78 | **0.88** | |
| Lifetime expectation of female offspring ($R_0$) | | **1.03** | 0.62 | |
| Age structure (by proportion) | age 0 | 0.178 | **0.219** | |
| | 1 | **0.123** | 0.117 | |
| | 2 | **0.105** | 0.062 | |
| | 3 | **0.090** | 0.058 | |
| | 4 | **0.078** | 0.053 | |
| | 5 | **0.067** | 0.050 | |
| | 6 | **0.057** | 0.047 | |
| | 7 | **0.049** | 0.044 | |
| | 8 | **0.042** | 0.041 | |
| | 9 | 0.036 | **0.039** | |
| | 10 | 0.031 | **0.036** | |
| | 11 | 0.027 | **0.034** | |
| | 12 | 0.023 | **0.031** | |
| | 13 | 0.020 | **0.029** | |
| | 14 | 0.017 | **0.027** | |
| | 15 | 0.015 | **0.025** | |
| | 16 | 0.013 | **0.024** | |
| | 17 | 0.011 | **0.022** | |
| | 18 | 0.009 | **0.021** | |
| | 19 | 0.008 | **0.019** | |
| Proportion first seen | age 1 | 0.00 | 0.00 | |
| | 2 | 0.26 | **0.30** | |
| | 3 | **0.81** | 0.76 | |
| | 4 | 0.91 | **0.93** | |
| | 5 | 0.94 | **0.98** | |
| | 6 | 0.97 | **1.00** | |
| | 7 | 0.99 | **1.00** | |
| Proportion breeding | age 1 | 0.00 | 0.00 | |
| | 2 | 0.00 | 0.00 | |
| | 3 | **0.25** | 0.17 | |
| | 4 | **0.55** | 0.49 | |
| | 5 | **0.76** | 0.68 | |
| | 6 | **0.86** | 0.82 | |
| | 7+ | **0.97** | 0.90 | |

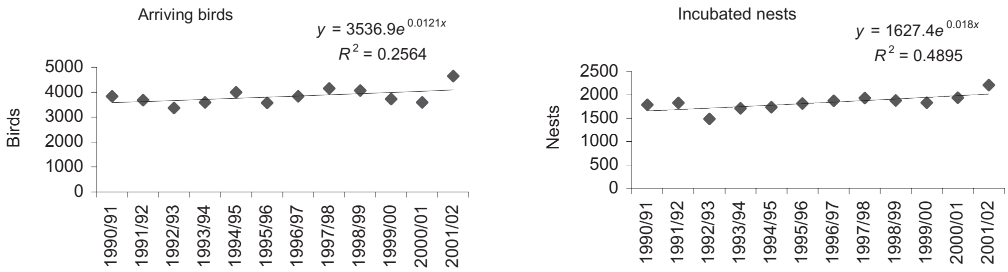


Figure 1: Exponential curves fitted to the population data in Table 1.

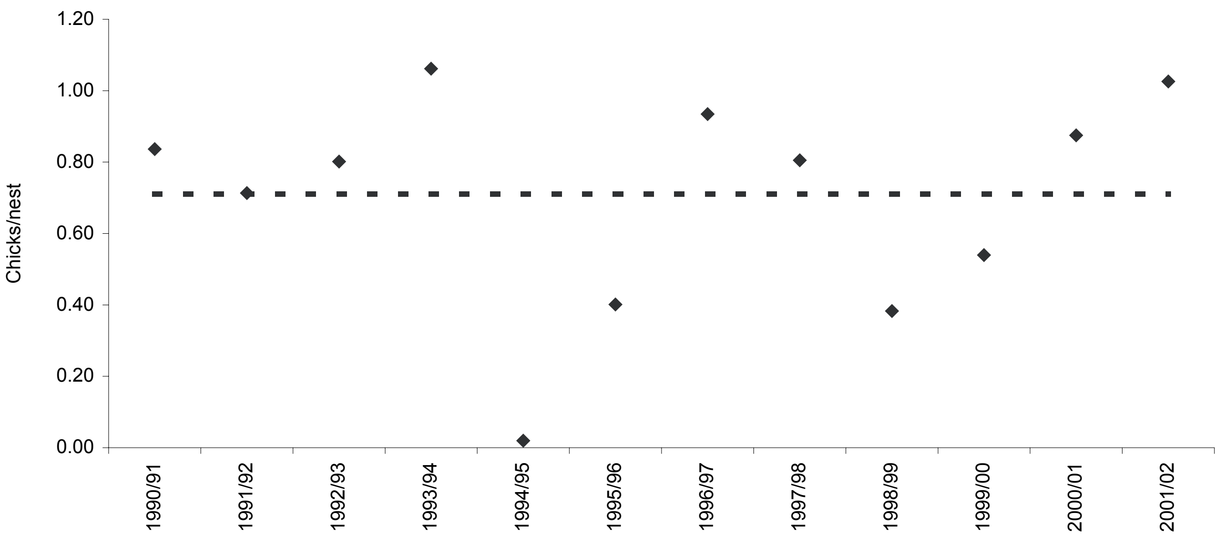


Figure 2: Annual breeding success for the Béchervaise Island Adélie penguin colony. The broken line indicates a mean breeding success, over 12 seasons, of 0.71 chicks/nest.

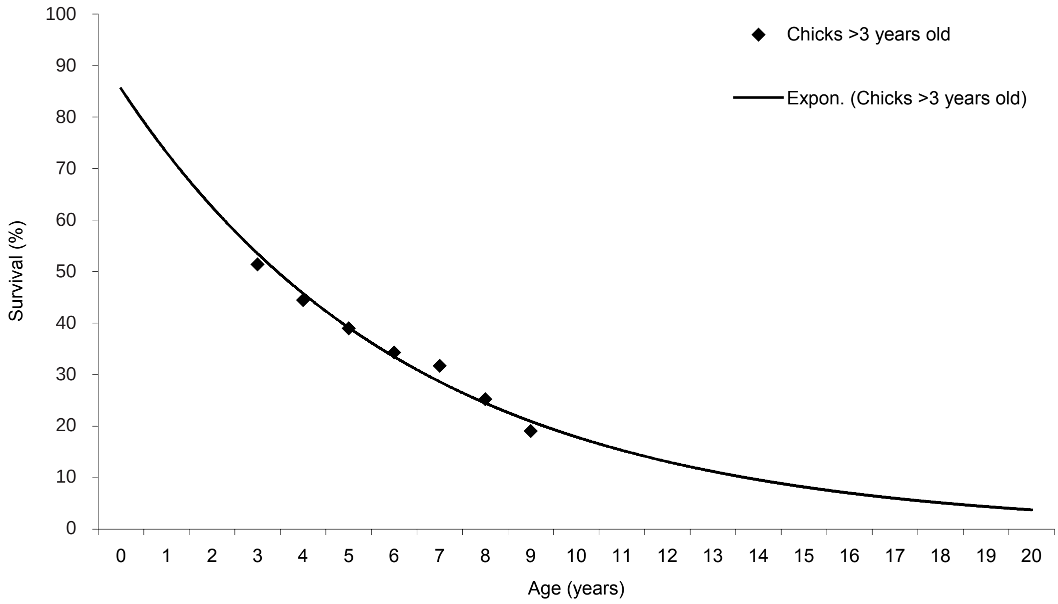


Figure 3: Age-specific survivorship for penguins tagged as chicks with exponential curve fitted to the data.

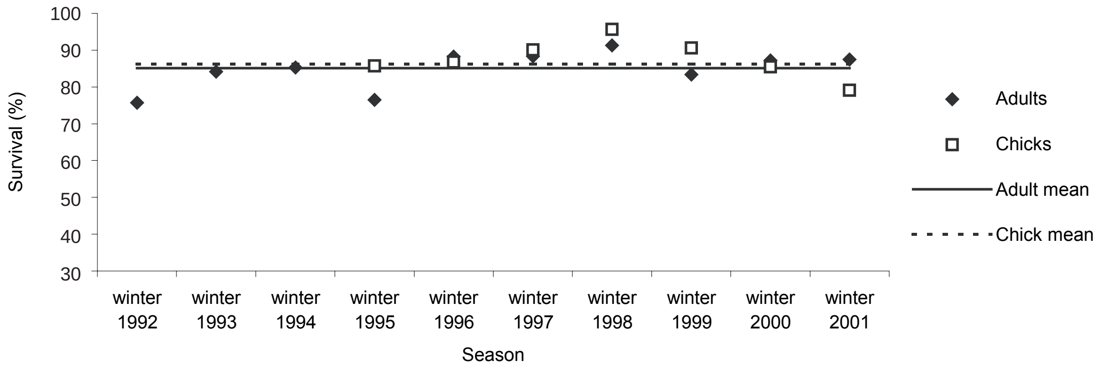


Figure 4: Annual survival, by season, for Adélie penguin adults and chicks relative to the mean values of 85.1% and 86.2% for adults and chicks respectively. The term 'winter' refers to the period between one breeding season and the next, and thus is not restricted purely to the winter months.

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